CHAPTER

3

Scallop Structure and Function

Peter G. Beninger and Marcel Le Pennec

INTRODUCTION

Efforts to collate and provide syntheses of the vast literature pertaining to bivalve structure and function may be said to have begun in the 1990s, with the publication of the first edition of this volume (Beninger and Le Pennec in Shumway, 1991), followed by *The Eastern Oyster: Crassostrea virginica* (Kennedy et al., 1996), *Biology of the Hard Clam* (Kraeuter and Castagna, 2001), and volume 6A of the *Microscopic Anatomy of Invertebrates* series (Morse and Zardus, 1997). In addition to the constitution of very important information resources, each of these works has considerably raised the profile of bivalve anatomy and function, while at the same time rendering the field accessible and comprehensible to non-specialists. As in all fields of science, new information and ideas continue to enrich our knowledge of structure and function in bivalves, and particularly so in scallops.

The common term 'scallop' may be used to designate members of the superfamily Pectinoidea, which includes the extant families Pectinidae, Entoliidae, Spondylidae, and Propeamussiidae (Waller, 1991). As the other families of this group either have alternate common names (the Spondylidae are also called 'thorny oysters') or are poorly known to non-specialists (the Propeamussiidae are small, very poorly known deep-water species, while the Entoliidae are represented today by only one known species, described as 'very rare, cryptic, and surviving only in disjunct populations in the Caribbean and central and Western Pacific ocean') (Waller, 1991), we will herein restrict the term 'scallop' to members of the family Pectinidae, which are the subject of this chapter. Although the *Bathypecten* genus will be excluded (because *Bathypecten vulcani* has been shown to be a propeamussiid; Dufour et al., 2006), we include the genus *Minnivola*, reported to possess a heterorhabdic gill structure and yet greatly reduced ascending lamellae, suggesting a contemporary representative of a Pectinidae–Propeamussiidae transitional form (Morton, 1996).

AN OVERVIEW OF THE SCALLOP BODY

The family Pectinidae displays one of the greatest degrees of anatomical differentiation within the Bivalvia. Organs are quite distinct and easily located; although this facilitates the anatomical study of scallops, one is quickly impressed with the complexity of the body systems themselves.

Until the 1980s, much of the state of our knowledge concerning scallop anatomy had been derived from meticulous studies performed in the late nineteenth and early twentieth centuries, when observational techniques were still quite limited. Although a prodigious body of knowledge was built up by the work of Kellogg (1892, 1915), Drew (1906), and Dakin (1909, 1910a,b), it is appropriate to integrate more recent observations of scallop anatomy and function using the techniques now available. Accordingly, much of the emphasis in this chapter will be placed upon the results of more recent studies of scallop structure and function.

One of the earliest detailed descriptions of scallop general anatomy was that of Drew (1906). Other general descriptions of overall anatomy in various scallop species may be found in Kellogg (1892), Gutsell (1931), Pierce (1950), Yonge (1951), Bourne (1964), and Mottet (1979). As the structure of the shell, the adductor muscle and the larva have been treated elsewhere in this work (Chapters 1, 2, and 4), only the postlarval soft body parts with the exception of

Scallops: Biology, Ecology, Aquaculture, and Fisheries.
S.E. Shumway and G.J. Parsons (Editors).

the adductor muscle will be presented here (Figure 3.1). Despite some inter-taxon anatomical variation, the following general overview of the scallop body may be considered representative.

The Pectinidae and other monomyarians are characterised by several important modifications of the more primitive isomyarian body form. The region corresponding to the isomyarian 'anterior' is greatly reduced, such that the anterior adductor muscle is completely absent. Similarly, the isomyarian 'ventral' region is shifted anteriorly, the foot being quite close to the mouth. The inadequacy of such conventional terms as anterior and ventral when describing scallop anatomy has been pointed out by Yonge (1951); Stasek (1963) has recommended that such terms not be used to refer to orientation, but rather to the relation of body parts with one another. While

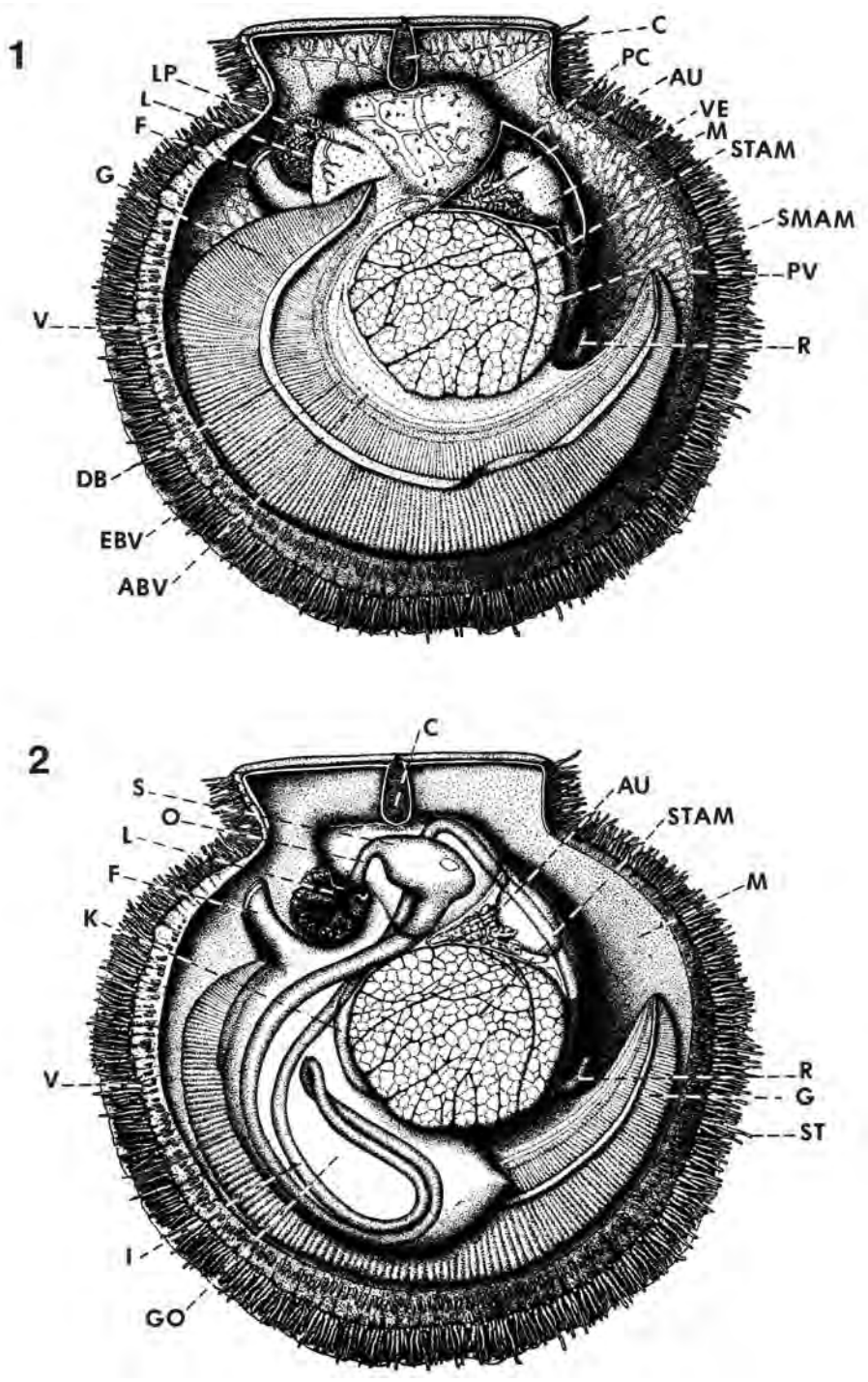


FIGURE 3.1 General anatomy of a large pectinid, *Placopecten magellanicus*. Figure 3.1.1: Left shell and mantle removed. Figure 3.1.2: Left shell, mantle, and gill removed. ABV, afferent branchial vessel; AU, auricle; C, chondrophore; DB, dorsal bend of gill filaments; EBV, efferent branchial vessel; F, foot; G, gill; GO, gonad; I, intestine; K, kidney; L, lips; LP, labial palp; M, mantle; O, oesophagus; PC, pericardium; PV, pallial vessels; R, rectum; S, stomach; ST, sensory tentacle; SMAM, smooth adductor muscle; STAM, striated adductor muscle; V, velum. *After Drew (1906)*.

such an approach is technically justified, it would render the present text confusing to those less familiar with bivalve anatomy. For the sake of simplicity, the term 'dorsal' will be considered to indicate those structures closest to the hinge line, while the term 'anterior' will be used to designate those structures closest to the extreme point of the shell margin on the side where the mouth is located. The terms 'ventral' and 'posterior' will of course refer to the opposite directions, respectively, of the preceding. The large posterior adductor muscle, situated near the centre of the shell, serves as a convenient reference point for the other body parts.

The internal shell faces are covered by a very thin, transparent mantle, which thickens and divides into distinct folds at the shell margin. The most evident of these folds is the mantle curtain, or velum, which modulates the exit of water from between the valves during valve adductions, such as the rejection of pseudofaeces and the swimming response. The margin of the mantle carries a large and variable number of sensory tentacles and eyes.

The heart is contained within a thin, transparent pericardium immediately dorsal, and slightly posterior to the adductor muscle. It is composed of two auricles and a single, large ventricle from which an anterior aorta extends antero-dorsally, while a posterior aorta arises from the ventricle and curves around the ventral margin of the adductor muscle. These two vessels then ramify to form the peripheral arterial system. The venous system is chiefly composed of a number of sinuses from which the blood flows through the kidneys to the gills. Blood from the gills enters the corresponding right or left auricle via an efferent branchial vessel.

The paired kidneys are attached directly to the anterior margin of the adductor muscle. The kidneys open internally into the anterior region of the pericardial cavity, and externally into the common uro-genital pore at their ventral extremity.

The gonad of sexually mature scallops is also directly attached to the anterior margin of the adductor muscle, covering the kidneys. It curves around the ventral margin of the adductor muscle, where it is unattached. In some species, such as *Hinnites multirugosus* and *Placopecten magellanicus*, gonadal tissue may extend dorsally into the labial palps, digestive gland, or mantle from its anterior end (Yonge, 1951; P.G. Beninger, unpublished personal observations). The foot and its associated byssal complex arise from the antero-dorsal extremity of the gonad, being attached to the left valve by a single pedal retractor muscle, which is variably developed in different species.

Ventral to the gonad are the two large gills, which are attached to the adductor muscle via suspensory membranes on the right and left insertions of the muscle to the shell. The relaxed gill follows the curvature of the shell margin, from the postero-dorsal level of the adductor muscle to a point just ventral to the anterior hinge margin. Each anterior gill extremity is enveloped on the right and left sides by the paired labial palps, which themselves become greatly folded to form the dorsal and ventral lip-apparatus, covering the mouth.

The oesophagus leads directly to the stomach, which is situated within the digestive gland, just ventral to the chondrophore. The intestine describes several loops in the digestive gland, which it exits posteriorly, descends ventrally, and enters the gonad at its most antero-dorsal extremity. After a single elongated loop in the gonad, the intestine curves around the dorsal portion of the adductor muscle and up towards the hinge line, descends ventrally, and traverses the pericardium and ventricle. The distal portion of the intestine is attached to the posterior side of the adductor muscle, becoming free in the region of the rectum and anus.

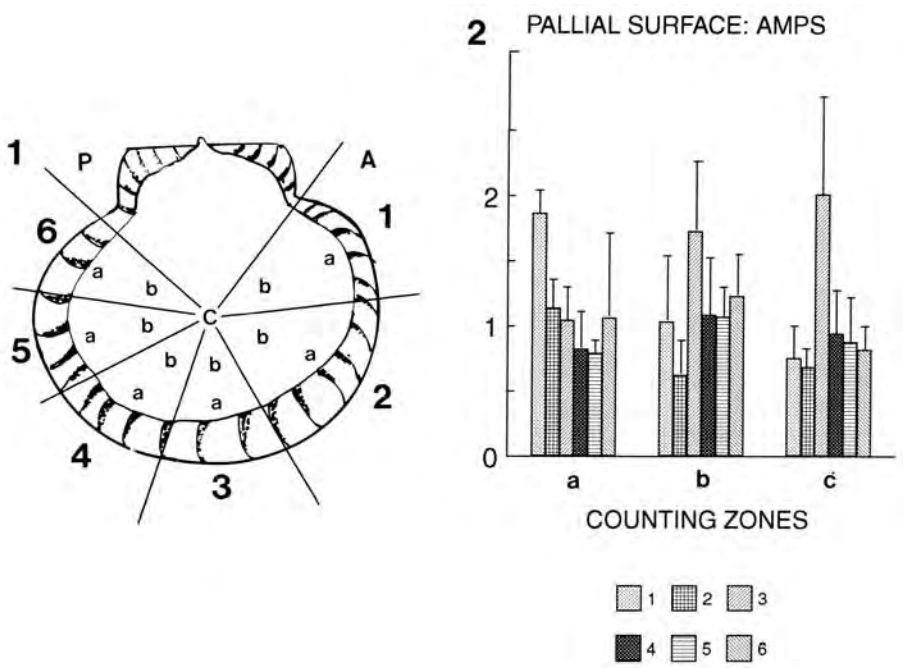
Although transparent and therefore somewhat difficult to see, the most conspicuous parts of the scallop nervous system are the two ganglionic concentrations. The parietovisceral ganglion is located on the antero-ventral surface of the adductor muscle. It innervates the adductor muscle, ventral mantle region, gills, and some viscera. The fused pedal and cerebral ganglia are slightly ventral to the mouth, and are linked to the parietovisceral ganglion by a pair of cerebro-visceral connectives. These ganglia and connectives innervate the rest of the scallop body.

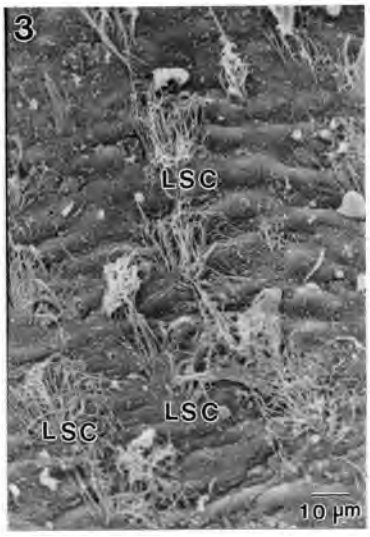
THE MANTLE AND ITS DERIVATIVES

The scallop mantle is a two-faced epithelial membrane, which intervenes in several key functions, such as secretion of the shell and ligament, sensory perception, and swimming response via the velum. Its role in pallial water circulation is probably minor, given its patchy cilia distribution (see below).

Gross Functional Anatomy

The mantle is composed of a sparsely ciliated (Figures 3.2.3 and 3.2.4) right and left lobe, which are fused dorsally along the cardinal plate and closely connected to the adductor muscle, digestive gland, and pericardium.





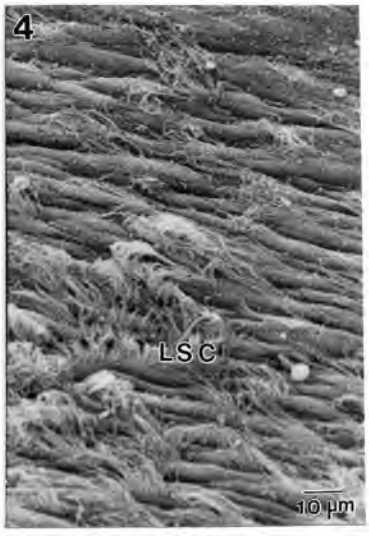


FIGURE 3.2 Mucocytes and cilia on the pallial surface of *Placopecten magellanicus*. Figures 3.2.1. and 3.2.2: Left mantle lobe divided into six regions within which semi-quantitative mucocyte counts were effected centripetally (a→c). 1 – Few mucocytes; 2 – mucocytes easily distinguished but distinct; 3 – mucocyte abundance makes individual mucocytes barely distinguishable; 4 – mucocyte abundance makes individual cells indistinguishable. Only acid mucopolysaccharide-secreting (AMPS) mucocytes were observed, and no distinct pattern (and therefore no distinct rejection pathway) was reported (Beninger and Saint-Jean, 1997b). Figures 3.2.3 and 3.2.4: Sparse, randomly located tufts of long simple cilia (LSC) on the posterior (Figure 3.2.3) and anterior (Figure 3.2.4) pallial surface of the right mantle lobe, indicating lack of distinct rejection pathway (Beninger et al., 1999).

The two thin lobes separate from the visceral mass at the base of the gills, enclosing the large ventral pallial cavity. They are connected to the right and left shell valves by strands of connective tissue terminating in specialised tendon cells (Bubel, 1984). At the mantle margin are found the various folds and grooves, including the numerous eyes and tentacles.

Although in the Pectinidae there are no specialised fused mantle regions to form siphons, the inhalant and exhalent currents follow definite trajectories due to the directed beating of the gill cilia. Thus, in *Pecten maximus* and *Chlamys (= Aequipecten) opercularis*, inhalant currents are created around the entire mantle, with the exception of a narrow postero-dorsal region where an exhalent current is evident (Dakin, 1909; Ghiretti, 1966). Similar observations have been made by Kellogg (1915) on *Placopecten magellanicus* and *Argopecten irradians*.

The free edges of the mantle lobes are well-developed and divided into three folds and two grooves. The terminology for these structures in the Pectinidae is derived from the studies of Drew (1906), Dakin (1909), Gutsell (1931) and summarised for bivalves in general by Petit (1978). The recent interest in bivalve functional anatomy has resulted in excellent presentations of the mantle lobes and periostracal formation in non-pectinid

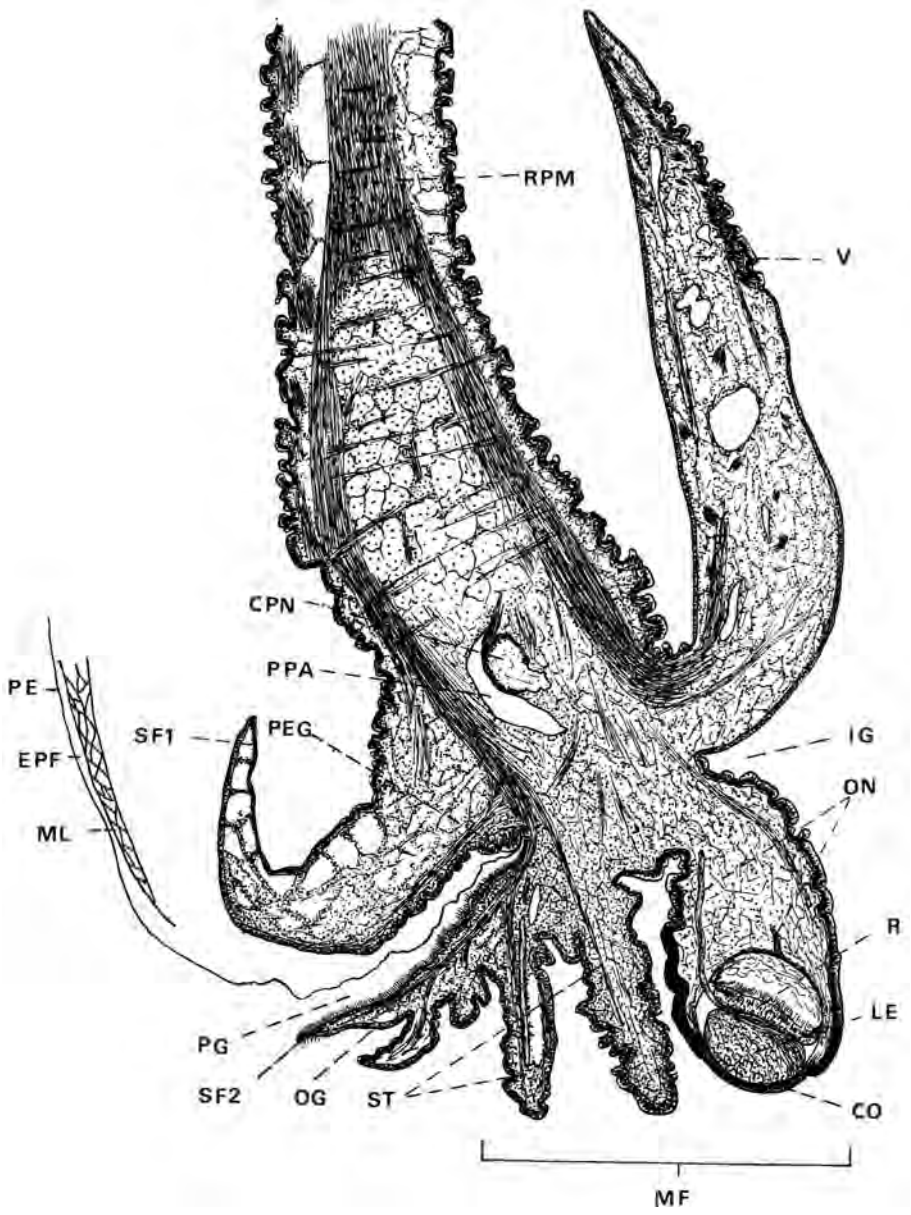


FIGURE 3.3 Diagram of a section through the mantle margin of *Placopecten magellanicus*, showing the secretion of the periostracum. CO, cornea; CPN, circumpallial nerve; EPF, extrapallial fluid; IG, inner groove; LE, lens; MF, middle fold; ML, mineral layer; ON, optic nerves; OG, outer groove; PE, periostracum; PEG, periostracal groove; PPA, posterior pallial artery; R, retina; RPM, radial pallial muscles; SF1, primary shell fold; SF2, secondary shell fold; ST, sensory tentacles; V, velar fold. *Modified after Drew (1906).*

species (Morse and Zardus, 1997; Kraeuter and Castagna, 2001). Beginning with the most external formation, it is possible to identify the following (Figure 3.3):

- an external or shell fold, subdivided into a primary shell fold, a periostracal groove, and a secondary shell fold;
- an external groove;
- a middle or sensory fold;
- an internal groove;
- an internal or velar fold.

The small shell fold contains the periostracal groove, which constitutes the glandular system responsible for secretion of the periostracum. Although Dakin (1909) stated that this fold bears long, extensible tentacles in both *Pecten maximus* and *Chlamys (= Aequipecten) opercularis*, none are reported for either *Argopecten irradians* (Gutsell, 1931), *Placopecten magellanicus* (Drew, 1906; P.G. Beninger, personal observations), or *Minnivola pyxidatus* (Morton, 1996). The shell fold of *P. magellanicus* does, however, bear numerous short tentacles (Moir, 1977a), which respond to tactile stimulation (P.G. Beninger, unpublished observations), while long, extensible sensory tentacles are situated slightly medially to the eyes at the lateral margin of the more well-developed middle mantle fold

(also called the ophthalmic or sensory fold). The eyes are considered in detail in Chapter 5 and the sensory tentacles in the 'Epithelial Sensory Cells and Tentacles' section of this chapter.

The internal fold (also called the velum, velar fold, or mantle curtain) is the most conspicuous fold, consisting of a flap of tissue extending towards the pallial cavity at right angles to the shell in an undisturbed animal. In the dorsal-most anterior and posterior regions, this fold is progressively less developed towards its point of fusion at the hinge line. A row of guard tentacles is present on the inner-most margin of the velum in *Argopecten irradians* (Gutsell, 1931) and in *Placopecten magellanicus* (Bourne, 1964; Moir, 1977a); however, Morton (1996) distinguishes primary and secondary velar tentacles in *Minnivola pyxidatus*. The muscular velar fold plays an important role in water movement within the pallial cavity, notably during the swimming response, when it partially seals the pallial cavity, thereby directing jets of water which provide thrust. As the two valves close, the vela fold inward under the control of the parietovisceral ganglion and the radial pallial nerves, thus avoiding damage to the sensory structures of the mantle edge (Stephens, 1978).

In the median dorsal region, the mantle is inserted into the ligament cartilage. There is no cardinal pallial crest (Ranson, 1939) or pallial isthmus (Owen et al., 1953; Le Pennec, 1978), and the hinge is almost totally reduced to the ligament; however, the cardinal region does show several long protuberances, which are in fact cardinal teeth or crura. The formation of the ligament and cardinal teeth is detailed in Chapters 1 and 2.

The ligament is composed of two parts: the very prominent median internal cartilage, or resilium, resting upon a specialised shell formation called the resilifer, and a very fine external layer extending along the exterior dorsal shell margin. These two components of the ligament oppose an antagonistic force to that of the adductor muscle, so that in a relaxed state the two valves gape slightly, facilitating the circulation of water within the pallial cavity. Whereas in other bivalves the ligament is composed of calcium carbonate and a hydrated protein, in pectinids it is not calcified (Marsh et al., 1976). The rubbery consistency of the scallop ligament is more mechanically efficient than that of other bivalves, allowing the animal to swim and clear debris from the pallial cavity with a minimal energy cost (Trueman, 1953). The ligament cartilage may be used to determine the age of individual scallops, as it often bears growth checks, which are more distinct than those of the shell (Mottet, 1979).

Microanatomy and Functions

Along the cardinal plate and in the regions where it adheres to the adductor muscle, digestive gland, and pericardium, the mantle is simply composed of an internal epithelium and a thin subjacent conjunctive layer. In all other regions, the mantle is composed of three well-defined layers consisting of an internal and external epithelium separated by a thin layer of lacunar connective tissue. This middle layer is traversed by the pallial blood vessels, nerves, and muscles, which are particularly well-developed near the mantle margin.

Both the internal and the external epithelia rest upon a basal lamina composed of collagen fibres. The internal epithelium is composed of three cell types: columnar, microvilli-bearing cells, irregularly distributed columnar cells bearing long ciliary tufts, and mucocytes (Figure 3.2.3). The secretions contained within the mucocytes are acid (high-viscosity) mucopolysaccharides (MPSs). In contrast to those bivalves equipped with siphons and gill ventral particle grooves, neither the ciliary nor the mucocyte distributions present any pattern; this has been linked to the valve-clapping mode of pseudofaeces evacuation from the pallial cavity (Beninger and Saint-Jean, 1997a,b; Beninger et al., 1999). It is likely that the radially ventral particle transport previously depicted for the mantle surface of *Pecten maximus* (Orton, 1912) is actually the result of the ventralward beat of the frontal cilia of the gill ordinary filaments (OFs) as viewed in a half-shell preparation, since the patchy distribution of mantle cilia would not be effective in particle transport. The high viscosity of the mucocyte secretions, in the absence of other mucociliary transport adaptations, suggests that they facilitate the passage of water over the mantle surface, as has been suggested for other pallial surfaces in bivalves (Beninger et al., 1997a; Beninger and Saint-Jean, 1997a,b; Beninger and Dufour, 2000; Dufour and Beninger, 2001). The mantle cilia of *Placopecten magellanicus* probably do not contribute much to the flow of water in the pallial cavity, due to their sparse distribution (Beninger et al., 1999). Additional studies on other pectinid species would be most welcome.

The large pallial surface area of the mantle is greatly multiplied by the apical microvilli; together with the finely branched blood vessels of the connective layer, this indicates that the mantle may be an important site for the exchange of gases and other dissolved molecules. Wandering amoebocytes and mantle epidermal cells are capable of absorbing particulate matter from the pallial cavity of several non-pectinid bivalves, and the ultrastructural characteristics of these cells indicate that they are capable of digesting such material (Bevelander and Nakahara, 1966; Nakahara and Bevelander, 1967; Machin, 1977). As for the other surfaces of the pallial cavity,

it is likely that direct exchange with the external medium may at least supplement the metabolic needs of the numerous epithelial cells.

We are unaware of data concerning the cell types of the external (shell-side) epithelium in pectinids. In other bivalves, tall columnar cells presenting ultrastructural characteristics typical of translocation (e.g. apical microvilli and thick, convoluted basal lamina) have been observed (Neff, 1972), and up to seven different cell types have been reported. Caecal cells extend mitochondria-rich processes into the shell itself, terminating on the outer shell surface (Reindl and Haszprunar, 1996). This is clearly a very complex surface, which merits much further investigation.

Shell formation in bivalves generally follows two major steps: the cellular processes of ion transport and secretion of the organic matrix proteins; and the physico-chemical processes whereby calcium carbonate crystals are nucleated, oriented, and assembled due to the presence of the organic matrix (for details, see Wilbur and Saleuddin, 1983). The carbon incorporated into calcium carbonate is entirely derived from dissolved carbon in the external medium, and the newly incorporated shell carbonate is in isotopic equilibrium with the external medium, making it a good candidate for the reconstruction of high-resolution records of both contemporary and palaeotemperature and palaeoproductivity cycles (Hickson et al., 1999; Owen et al., 2002; Chute et al., 2012), and even habitat provenance (Broadaway and Hannigan, 2012).

The detailed process of shell formation and ontogenetic changes in shell microstructure and minerology have been intensively studied by a number of workers in selected bivalve species (see reviews by Wilbur, 1972, 1985; Crenshaw, 1980; Wilbur and Saleuddin, 1983; Watabe, 1984), and for pectinids in particular (see Chapter 1 for review and references).

The shell is covered externally by a thin, fibrous organic layer called the periostracum, which may vary in thickness depending on the amount of mechanical abrasion and/or damage due to epizoonts. The periostracum serves as a matrix for the deposition of the calcium carbonate crystals of the shell (Taylor and Kennedy, 1969; Saleuddin and Petit, 1983). The formation of the periostracum has been studied in detail in the freshwater bivalve *Amblema plicata perplicata* (Petit, 1978) as well as in several marine species (Neff, 1972; Saleuddin and Petit, 1983; Petit et al., 1988). Glandular cells located at the base of the periostracal groove secrete the periostracal components, including quinone-tanned protein fibres (Petit, 1978), polysaccharides, and lipids (Brown, 1952). The nascent periostracum, or periostracal lamina, is secreted by the basal cells of the periostracal groove (Richardson et al., 1981). It maintains contact with the shell edge and is composed of two layers: an outer layer which forms the periostracum over the shell and an inner layer which thickens the shell itself (Paillard and Le Pennec, 1993).

The outer edge of the shell fold contains numerous depressions, such that an extrapallial fluid is contained between the shell fold and the newly formed periostracum (Figure 3.2.2), creating an enclosed environment for supersaturation, the precursor to crystallization. Calcification is initiated at the small spicules of periostracum within this fluid-filled space, presumably by the mitochondrion-rich lateral cells (Richardson et al., 1981) and progressively thickens (Wilbur and Saleuddin, 1983). Extrapallial fluid may also be found in sub-periostracal depressions distributed within the shell. Five cell types have been reported in the outer epithelium of the outer shell fold (Neff, 1972), which secretes a calcifying matrix composed of proteins, glycoproteins, proteoglycans, polysaccharides, and chitin, which interact with the mineral ions to form crystallites (Marin and Luquet, 2004). Mantle enzyme secretion has been studied in a number of bivalve species (Brown, 1952; Waite and Wilbur, 1976; Waite and Andersen, 1978, 1980). Among the enzymes discovered, acid phosphatase and phenoloxidase are of particular interest. Acid phosphatase intervenes in the structural modification of the inner face of the periostracal layer (Chan and Saleuddin, 1974), while phenoloxidase is involved in the tanning of the periostracal proteins (Bubel, 1973a,b).

Between the outer (shell-side) and inner (pallial-side) epithelia, several cell types have been reported in non-pectinid bivalves: amoebocytes, porocytes/rhogocytes, nerve cells, haemocytes, gliointerstitial cells, as well as musculo-connective tissues (Reindl and Haszprunar, 1996). Despite its deceptively simple gross appearance, the mantle is one of the most complex, multi-tasked organs in the Bivalvia.

PALLIAL ORGANS AND PARTICLE PROCESSING

The pectinid pallial organs are comprised of the mantle, gill, labial palps, and lips. Studies to date have shown that, in pectinids, all of these structures save the mantle are involved in particle processing (Figure 3.4), as outlined below. It is impossible to understand the mechanisms of particle processing without a good grasp of the underlying anatomy and micro-anatomy.

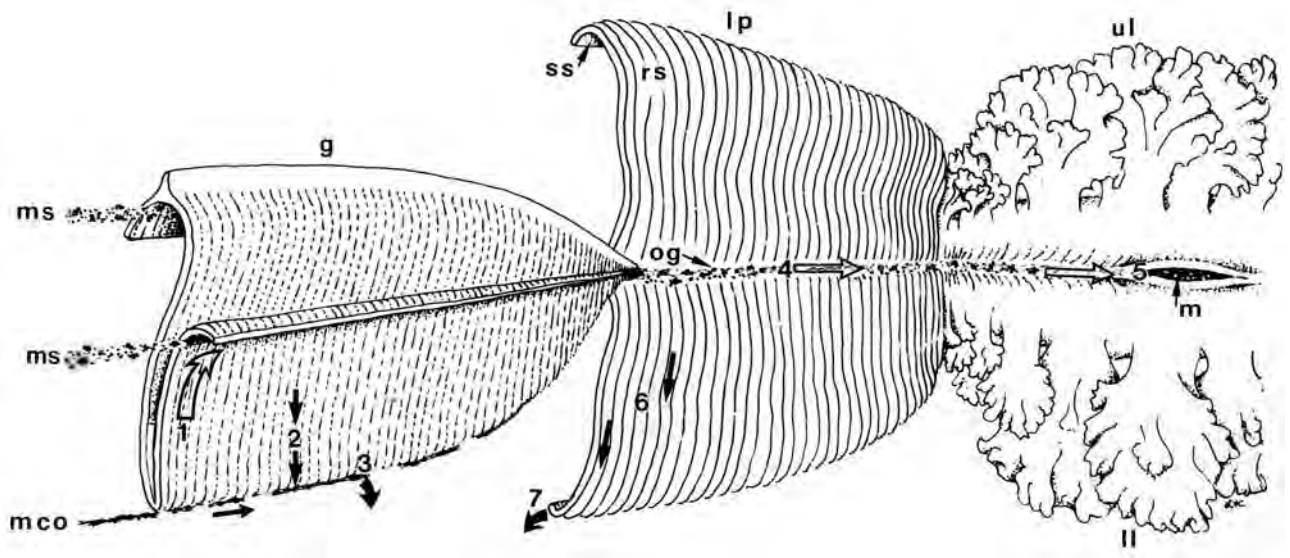


FIGURE 3.4 General organisation and function of the pallial organs involved in particle processing: gill (g), smooth (ss) or aboral surface, and ridged or oral surface of labial palps (lp), and upper (ul) and lower (ll) lips. Retained particles destined for further processing on the peribuccal organs are directed dorsally in the principal filament troughs (1), where they are incorporated into the anteriorward flow of mucus-particle slurry (ms) in the ciliated tracts of the gill arch and dorsal bend. Particles destined for rejection are directed ventrally in a viscous mucus on the ordinary filament plicae (2), where they are incorporated into mucus cords and masses of various length (mco), which are periodically expelled from the gill and pallial cavity (3) by valve adductions. Particles arriving from the dorsal ciliated tracts onto the labial palps (4) may continue along the oral groove (og), in a reduced-viscosity mucus, for ingestion (5) by the mouth (m). Particles rejected on the labial palps travel laterally in a viscous mucus within the troughs to the ventral margin (6), where they join pseudofaeces moving posteriorly and are finally expelled from the postero-ventral tip (7). *Modified from Beninger et al. (1990a).*

Gills

Much of the groundwork for bivalve gill anatomy was laid by Kellogg (1892, 1915), Janssens (1893), Ridewood (1903), Drew (1906), Setna (1930), and Atkins (1936, 1937a,b,c, 1938a,b,c, 1943). More recent studies on scallop gills in particular include the work of Owen and McCrae (1976), Morse et al. (1982), Reed-Miller and Greenberg (1982), Ciocco (1985), Beninger et al. (1988), Le Pennec et al. (1988), Beninger and Dufour (2000), and Dufour and Beninger (2001). Prior to the 1990s, function was largely inferred either from the possibilities afforded by the gill anatomy, by indirect means such as particle retention and clearance studies, or by observation of particle movement on opened animals. The resulting state of knowledge concerning particle processing mechanisms was eminently conjectural, and even an attempt to indicate the sizeable gaps and paradoxes concerning this subject in scallops was itself, in hindsight, somewhat naïve (although some of the conjectures were later borne out; Beninger, 1991). From this point forward, an intense research effort was brought to bear on the problem, supplementing the existing techniques with tools specifically developed or adapted for the purpose: video endoscopy, mucocyte and cilia mapping, and confocal laser microscopy. The relevant studies concerning pectinids are, to date as follows: Ward et al. (1991, 1993); Beninger et al. (1992, 1993, 1999); Beninger and Saint-Jean (1997a,b); Beninger and Dufour (2000); Dufour and Beninger (2001); Beninger et al. (2004). The following account of gill structure and function incorporates the information from all of these sources.

Adult scallops possess a heterorhabdic plicate gill, which means that the W-shaped left and right gills are composed of a series of two different types of filaments, suspended from the gill axis in a corrugated or plicate fashion. The principal filaments (PFs) are situated in the troughs of the plicae, separated from each other by a variable number (11–20) of OFs. The ascending branches of the filaments are usually approximately two-thirds the length of the descending branches (Figures 3.5 and 3.6.1), although the ascending branches are greatly reduced in *Minnivola pyxidatus* (Morton, 1996).

The single reported exception to the heterorhabdic condition was the pectinid *Hemipecten forbesianus*, which was said to possess a homorhabdic gill (Yonge, 1981); however, re-examination of the specimens studied by Yonge show unequivocally that the gill is heterorhabdic (Beninger and Decottignies, 2008). There is thus no known exception to the rule of heterorhabdy in the pectinids; this may prove to be a diagnostic taxonomic character for the family.

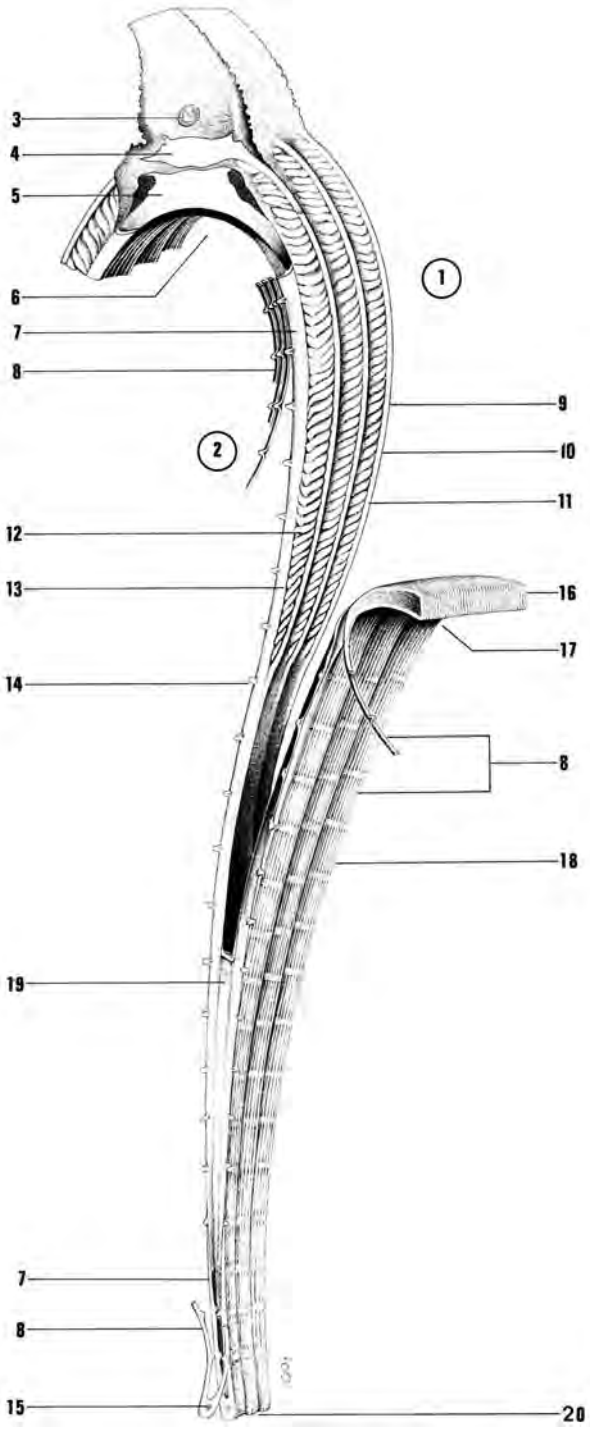


FIGURE 3.5 General organisation and macro-anatomy of the gill; 1 – suprabranchial chamber, 2 – infrabranchial chamber, 3 – branchial nerve, 4 – afferent branchial vessel, 5 – efferent branchial vessel, 6 – gill arch, 7 – lateral wall of principal filament, 8 – ordinary filaments, 9 – descending branch of principal filament, 10 – dorsal expansion, 11 – afferent vessel, 12 – interconnecting vessel, 13 – efferent vessel in principal filament, 14 – ciliated spur (cilifer), 15 – ciliated disc, 16 – dorsal bend, 17 – ciliated tract, 18 – ascending filaments, 19 – interlamellar junction, 20 – ventral bend.

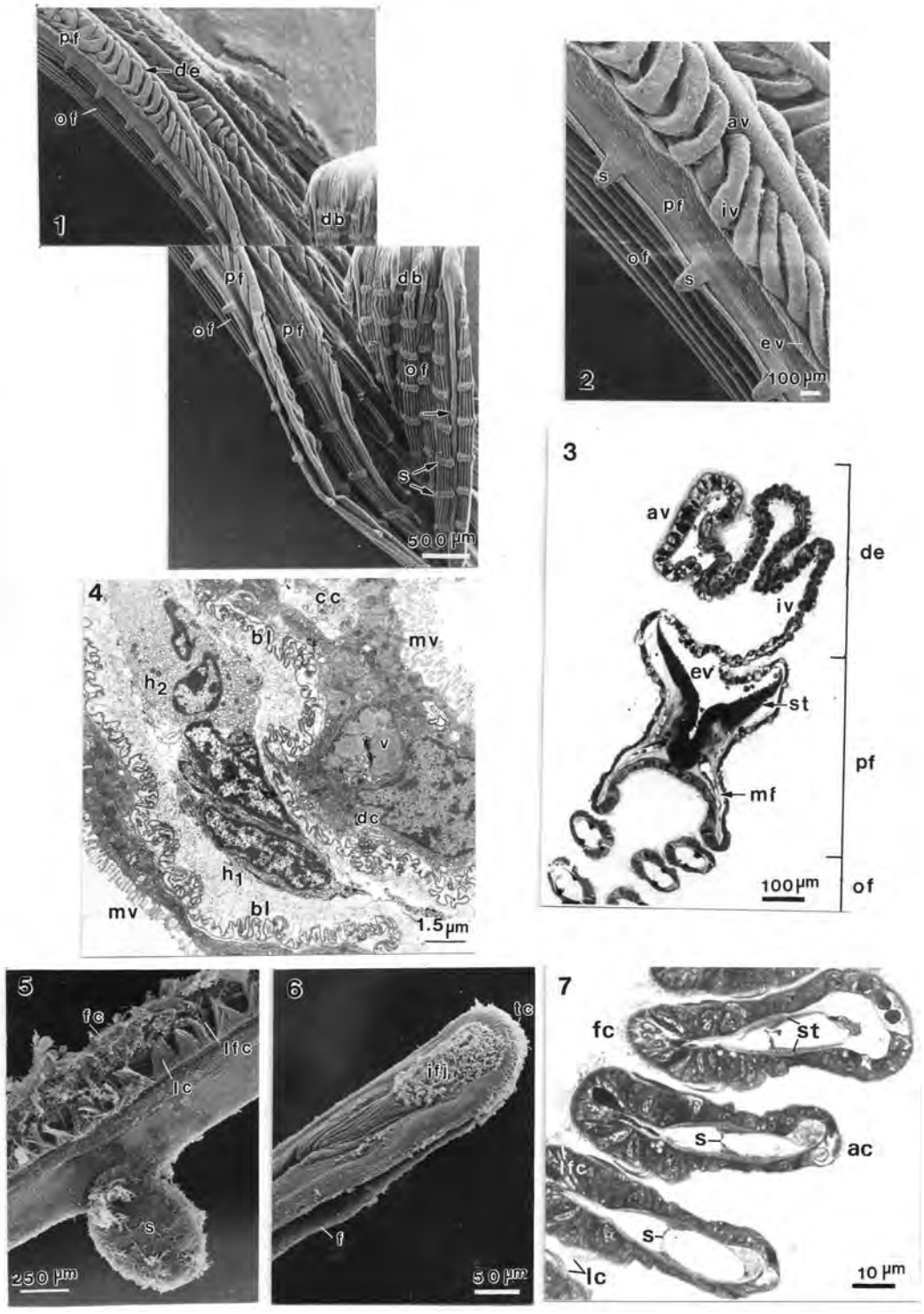


FIGURE 3.6 General organisation and micro-anatomy of the gills of *Placopecten magellanicus.* Figure 3.6.1: Low-power scanning electron micrograph showing general organisation of principal (pf) and ordinary (of) filaments. Note rows of ciliated spurs (s) on abfrontal surface of ordinary filaments, responsible for structural integrity of plicae. de, dorsal expansion; db, dorsal bend. Arrow indicates abfrontal surface of ascending branch of principal filament. Ascending principal filaments are in contracted state. Figure 3.6.2: Scanning electron micrograph detail of dorsal expansion of principal filament (pf). av, afferent vessel; ev, efferent vessel; iv, interconnecting vessels; of, ordinary filaments; s, ciliated spurs. Figure 3.6.3: Thin section light micrograph of a principal filament (pf) and dorsal expansion (de). av, afferent vessel; ev, efferent vessel; iv, interconnecting vessel; of, ordinary filaments; st, supporting structures; mf, muscle fibres. Figure 3.6.4:Transmission electron micrograph of a longitudinal section of the dorsal expansion interconnecting vessels. Cells with dark nuclei and cytoplasm (dc), capable of containing large vacuoles (v). Cells with clear nuclei and cytoplasm (cc). Both haemocyte types I (h_1) and II (h_2) are present in the narrow lumen (see 'Haemocytes' section). Note the apical microvilli (mv) and greatly indented basal lamina (bl). Figure 3.6.5: Scanning electron micrograph detail of an ordinary filament. lc, lateral cilia; lfc, latero-frontal cilia; fc, frontal cilia; s, ciliated spur. Figure 3.6.6: Scanning electron micrograph of the interfilamentar junction (ifj) at ventral bend of an ordinary filament. Another ordinary filament (f) is attached behind. Note ciliated disc of interfilamentar junction, terminal cilia (tc) at ventral extremity, and absence of a particle groove. Figure 3.6.7: Thin section light micrograph of ordinary filaments. Rare abfrontal cilia (ac), lateral cilia (lc), latero-frontal (lfc) and frontal cilia (fc); supporting structures (st) and septum (s). *Modified after Beninger et al. (1988) and Le Pennec et al. (1988).*

Gill Axis and Arch

A thin suspensory membrane joins the gill axis to the adductor muscle. Within the gill axis is situated, in a dorso-ventrally aligned sequence, the branchial nerve, the afferent branchial vessel, and the efferent branchial vessel (Figure 3.5). On either side of the gill axis is situated the eversible osphradial ridge (see 'Osphradia' section). Relatively abundant, but distinct ciliary tufts are found from the dorsal extremity of the gill axis to the osphradial ridge; below this feature, the axis is abundantly covered with simple cilia.

The gill arch comprises the fused and staggered proximal extremities of the PF and OF. Here the afferent and efferent blood vessels of the PFs join with their counterparts in the gill axis and arch (Figures 3.5, 3.6.2, and 3.6.3). The ventral surface of the arch forms a ciliated groove, which collects and transports particles arriving in a mucus slurry from the PFs (Figure 3.5); the arch itself contains very few mucocytes (Beninger et al., 1992, 1993).

PFs and Dorsal Expansion

PFs differentiate well after metamorphosis, at a size of about 4 mm in *Pecten maximus*, and 3.3–5.0 mm in *Placopecten magellanicus* (Veniot et al., 2003). This represents a change in both gill structure and function, and therefore in particle processing mechanisms. It may thus be a critical stage, and potential indirect cause of mortality, in the early life of pectinids (Beninger et al., 1994).

The proximal third of the abfrontal surface of the PF presents a rather complex structure historically termed the 'dorsal respiratory expansion' (Setna, 1930). No studies have yet been performed to evaluate its contribution to gas exchange, or any other role. Here it will simply be referred to as the *dorsal expansion*. The dorsal expansion consists of an abfrontal afferent vessel, an efferent vessel contained within the wall of the PF, and a number of variously shaped interconnecting vessels (Figures 3.6.1–3.6.3). The afferent vessel is covered with patchy but abundant simple cilia, whereas the efferent and interconnecting vessels bear only tufts of simple long cilia (Beninger et al., 1988; Dufour and Beninger, 2001). The convoluted basal lamina of the shallow, one-cell-thick layer of the interconnecting vessels together with their extensive, ramified apical microvilli (Figure 3.6.4) indicate a specialised role in translocation of dissolved substances between the external medium and the gill (Le Pennec et al., 1988). In addition to evaluating the extent of gas exchange, future studies should also examine dissolved organic substances, which are actively taken up by the mussel gill (Manahan et al., 1982; Wright et al., 1984; Wright, 1987).

The PF displays a dynamic anatomical organisation, due to the periodic contractions of portions of its lateral walls – the 'concertina' response (Kellogg, 1915; Setna, 1930; Owen and McCrae, 1976; Beninger et al., 1988, 1992). In the resting state, the filament comprises a ciliated frontal surface within a trough formed by the lateral walls (Figure 3.6.3). The margins of the lateral walls bear ciliated spurs or cilifers (Kellogg, 1892; Reed-Miller and Greenberg, 1982), which are directed out and away from the PF (Figures 3.6.1–3.6.3). The inner surface of the cilifer is ciliated, and interlocks with the cilia of similar spurs situated on the abfrontal surfaces of the OFs. The spurs of the OFs are ciliated on both sides, allowing adjacent filaments to adhere to each other at intervals along their lengths, thus preserving the structural integrity of the gill (Figure 3.6.1). It appears that the orientation of the PF cilifers, which are ciliated on their inner side only, is responsible for the normal plicate arrangement of the gill filaments (Beninger et al., 1988). Contractions of the PF lateral walls modify the orientation of the cilifers, producing the concertina response, and are one of the mechanisms used to clear the gill and thus reduce ingestion volume when the stomach is full (Beninger et al., 1992, and see 'Particle Processing on the Gill' section).

On the frontal surface of *Placopecten magellanicus*, the PF mucocytes contain a mixture of acid and neutral MPS secretions (Figure 3.7), which would produce a mucus of medium-to-low viscosity, typical of enclosed or semi-enclosed transporting surfaces, which lead directly to other such surfaces, in bivalves (Beninger et al., 1993; Beninger and Saint-Jean, 1997b).

Ordinary Filament

The OFs have no dorsal expansions or lateral walls, and possess frontal, latero-frontal and lateral ciliary tracts on their frontal surfaces (Figures 3.6.5–3.6.7). Contrary to many other bivalves, which possess a row of compound latero-frontal cilia, the pectinid latero-frontal tract consists of only a single row of simple cilia, which have been termed the pro-laterofrontal cilia (Owen and McCrae, l976). Rare cilia on the abfrontal surfaces are considered vestigial (Beninger et al., 1988; Beninger and Dufour, 2000) (Figure 3.6.7), and it is interesting to contrast this with the dense abfrontal ciliation of the PFs. The presence of abundant cilia and mucocytes on the PF abfrontal surface has been related to the tardy evolutionary and ontological development of the PFs compared

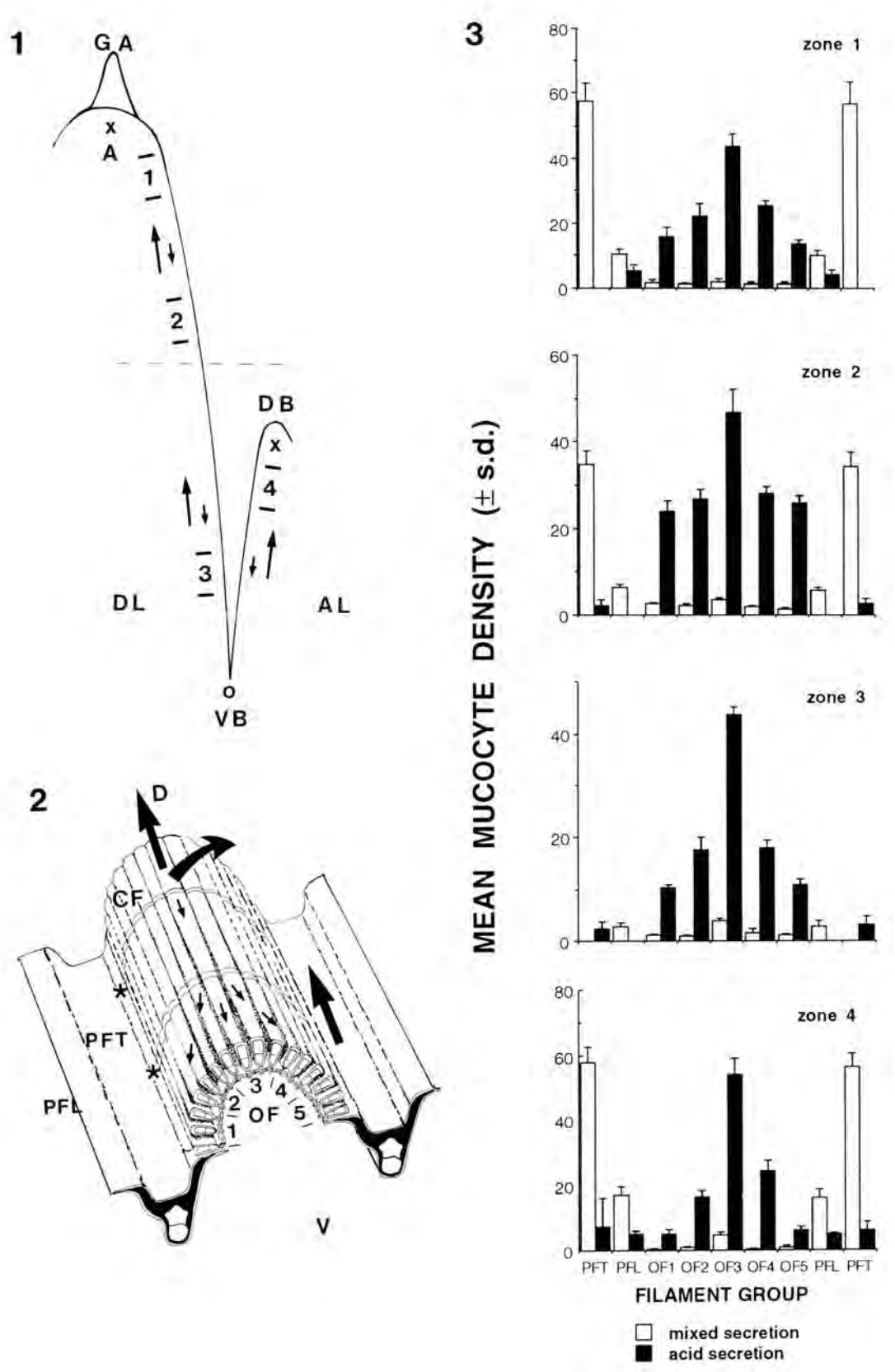


FIGURE 3.7 *Placopecten magellanicus* gill. Relationship between particle trajectories, filament types, dorsal (acceptance) and ventral (rejection) tracts, and mucocyte types and distributions. Figure 3.7.1: Schematic drawing of gill viewed along antero-posterior axis. Numbers designate mucocyte counting zones of Figure 3.7.3, large arrows show particle movement on principal filaments (acceptance), small arrows

to the OFs; it has also been suggested that the mucocytes may play a role in preserving the structural integrity of the gill during valve adductions (Beninger and Dufour, 2000).

The ordinary and PFs are organically joined only in the region of the dorsal bend (Morse et al., 1982; Le Pennec et al., 1988), which itself adheres to the mantle by means of interlocking cilia (Beninger et al., 1988). The ciliary connection to the mantle is easily broken when the gill retracts prior to valve adduction, or during a shunt response.

The ventral bend of each ordinary and PF bears a terminal ciliary tuft; the ventral bends are aligned via ciliary interfilamental junctions, forming a ciliated tract at the ventral bend, although there is no specialised trough (Figure 3.6.6). In addition, the ventral bends are imperfectly aligned along the dorso-ventral axis, such that this ciliated tract is in fact staggered (Beninger et al., 1988), probably aiding in the detachment of mucus-particle masses destined for rejection at this extremity (Figure 3.8.3).

The gill filaments gradually decrease in length towards the anterior and posterior extremities. In the anterior-most region of the gill, this shortening of the filaments results in the convergence of the dorsal feeding tracts with the oral groove at the base of each pair of labial palps (Figure 3.4).

Haemolymph Circulation in the Gill

The gill filaments are essentially hollow tubes within which the haemolymph circulates. The internal walls of the filaments are strengthened by collagenous (*not* chitinous, an error often repeated in the literature) supporting structures (Figures 3.6.3 and 3.6.7), which appear to be more numerous in the region of the ventral bend (Le Pennec et al., 1988). Blood enters the afferent vessel of the dorsal expansion, flows down the PF lumen, and enters the organic junction between filaments in the dorsal bend. It then flows down the ordinary and PF lumina and rises dorsally to join the efferent vessel of the PF, which empties into the efferent branchial vessel (Morse et al., 1982). The lack of a distinct anatomical separation between afferent and efferent blood in the lumina of the filaments indicates that mixing of haemolymph probably occurs.

Particle Processing on the Gill

Owen (1978) originally proposed a non-'filter'-feeding mode of particle capture for several bivalve families, including the Pectinidae. In these species, the plical arrangement of the relaxed gill results in particle-laden water currents being directed towards the densely ciliated troughs of the PFs and thence dorsally. Detailed *in vivo* endoscopic observations of the gills of *Placopecten magellanicus* and *Pecten maximus* support this proposed mechanism (Beninger et al., 1992, 2004), but the microscopic events are not yet known. It is clear that the PFs send particles destined for secondary processing by the peribuccal organs dorsally to the gill arch and dorsal bend. A reduced-viscosity mucus accompanies these particles (Beninger et al., 1992) (Figure 3.4).

The OF plicae possess ventralward-beating frontal cilia, which direct mucus-particle masses to the ventral bend; this is probably accomplished by the phylogenetically ubiquitous mechanism of mucociliary transport, as has been recently documented *in vitro* for *Mytilus edulis* (Beninger et al., 1997b). These masses are characterised by a high-viscosity mucus, in keeping with the exposed surface and predominantly counter-current water flow (Beninger et al., 1992, 1993; Beninger and Saint-Jean, 1997b). Most of these masses are rejected from the ventral bend and exit the pallial cavity via valve adductions (Kellogg, 1915; Owen and McCrae, 1976; Beninger et al., 1992, 1999) (Figure 3.8.3).

◀ show particle movement on ordinary filament plicae (rejection), and dashed line represents plane of section for Figure 3.7.2. A, gill arch (ciliated tract); AL, ascending lamella; DB, dorsal bend (ciliated tract); DL, descending lamella; GA, gill axis; VB, ventral bend (ciliated tract); x, anteriorward direction of particles in dorsal ciliated tracts (A + DB = acceptance) perpendicular to plane of drawing; o, anteriorward direction of particles at ventral ciliated tract (VB; rejection) perpendicular to plane of drawing. The particle-mucus masses at the ventral bend are periodically dislodged by valve-clap movements. Figure 3.7.2: Schematic stereodiagram of descending lamella, showing filament groups of Figure 3.7.3 used for counting mucocytes. Large arrows indicate dominant currents and trajectories of particles destined for further processing on the labial palps (acceptance), small arrows indicate movement of particles destined for rejection beneath the dominant currents. Asterisks show dorso-ventral boundaries for a given count, corresponding to rows of cilifers (CF) visible through ordinary filaments. D, dorsal; OF 1–5, ordinary filament groups constituting a plica; PFL, principal filament lateral wall; PFT, principal filament trough; V, ventral. Figure 3.7.3: Mean mucocyte densities (± standard deviation) for each of the counting zones illustrated in Figure 3.7.1 and each of the filament groups illustrated in Figure 3.7.2. OF 1–5, ordinary filament groups 1–5; PFL, principal filament lateral wall; PFT, principal filament trough. Note association of acid mucopolysaccharide-secreting mucocytes with rejection function of ordinary filaments, mixed mucopolysaccharide-secreting mucocytes associated with transport of particles in semi-enclosed acceptance tracts of principal filaments. *From Beninger et al. (1993).*

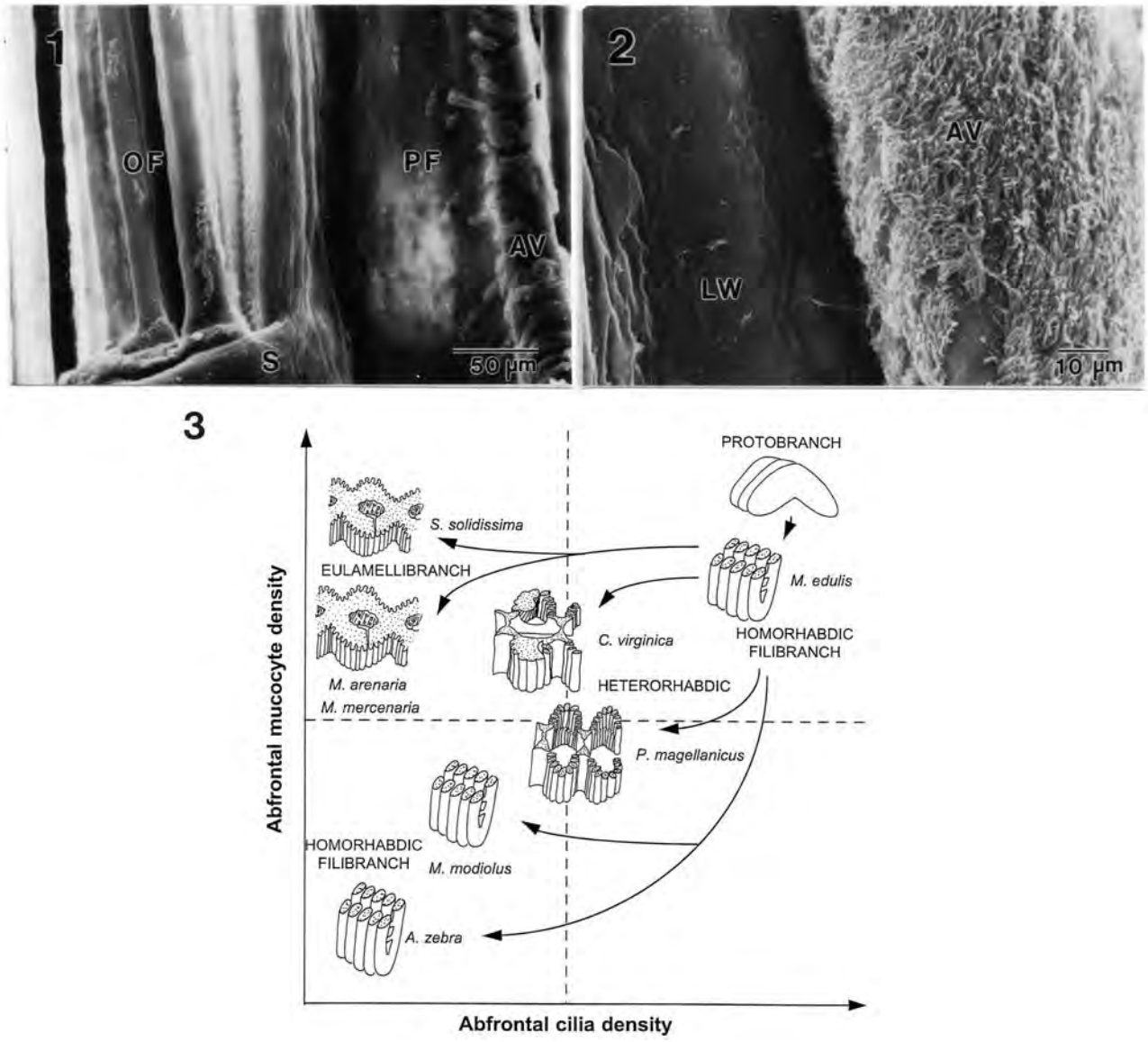


FIGURE 3.8 Cilia and mucocyte distributions on abfrontal surface of *Placopecten magellanicus* gill. Figure 3.8.1: SEM of abfrontal surface, showing extremely sparse ciliation of ordinary filaments (OF), much greater ciliation of principal filament (PF) afferent vessel (AV). S, ciliated spur (=cilifer). Figure 3.8.2: SEM detail of abfrontal surface of PF. Note dense ciliation of afferent vessel (AV), extremely sparse ciliation of lateral wall (LW). Figure 3.8.3: Relative position of *P. magellanicus* gill compared to other major gill types with respect to abfrontal cilia and mucocyte density. Note general tendency towards reduction of cilia on all ordinary filaments in more recent gill types. *From Beninger and Dufour (2000) and Dufour and Beninger (2001).*

Particle Selection at the Gill

As explained above, particles sent dorsally in the PF tracts are more likely to be ingested, whereas those sent ventrally are more likely to be rejected. It is tempting to invoke a selective process for such a system, as has been suggested/demonstrated for the heterorhabdic gill in general (Atkins, 1937a; Beninger and Saint-Jean, 1997a), and the pseudolamellibranch oyster gill in particular (Ward et al., 1998; Cognie et al., 2003). This question was definitively settled for the pectinids by presenting known mixtures of intact and empty diatoms (*Coscinodiscus perforatus*) and *in vivo* sampling of the dorsal and ventral gill tracts, as well as palp pseudofaeces, combined with microscopic determinations of particle proportions at each sampling site (Beninger et al., 2004). Qualitative particle selection was indeed demonstrated on the gill, and a second level of particle selection was also found at the labial palps. This was, in fact, the first unequivocal localisation of qualitative particle selection sites for any

bivalve species. The organic casing and associated organic molecules of this diatom appear to constitute a key quality cue for this scallop (Beninger and Decottignies, 2005).

In contrast to the oyster gill, the width of the scallop PF trough (approx. 200 μm in *Placopecten magellanicus* and *Pecten maximus*), as well as its relative plasticity, allows the admission of most suspended particles (no doubt accounting for the presence of some very large particles in the stomachs of scallops) (Mikulich and Tsikhon-Lukanina, 1981; Shumway et al., 1987). The upper size constraint on the qualitative selection of particles at the scallop gill is thus much larger than that of the other major heterorhabdic gill type, the pseudolamellibranch gill of the oyster (Cognie et al., 2003). At this point, however, the detectors, effectors and microscopic sequence of events involved in qualitative selection are poorly known; it has been suggested that such processes may involve lectin-type recognition mechanisms (Pales Espinosa et al., 2009, 2010a,b,c).

Particle Retention Lower Size Limit

The lower size limit for the efficient retention of natural particles in scallops is approximately 5 μm (Møhlenberg and Riisgard, 1978; Riisgard, 1988). Clearance studies indicate that pectinids, which possess only a single row of simple latero-frontal cilia, have a low retention efficiency for particles less than 5–7 μm in diameter, in contrast to the majority of bivalves studied, which possess well-developed, compound latero-frontal cilia called *cirri* (Møhlenberg and Riisgard, 1978; Riisgard, 1988). It is difficult to make direct comparisons, however, as the vast majority of bivalves possessing cirri also have a homorhabdic gill. The oyster (Fam. Ostreidae) is an interesting oddity in the bivalve world. Kellogg (1892) called it a 'very degenerate form', which however, possesses the most complex of gill types, with both latero-frontal cirri (albeit reduced in size) on its OFs, a heterorhabdic gill and a ventral particle groove. Much is still to be learned concerning gill function in this peculiar group.

Ingestion Volume Regulation on the Gill

Five different mechanisms of ingestion volume regulation have been identified in the functioning scallop gill (Beninger et al., 1992): rejection of particles from the PF troughs onto the OF plicae, arrest of the anteriorward dorsal feeding currents, reduction of input from the PFs to the dorsal tracts, detachment of the dorsal bends from the mantle, allowing a flow-through shunt (Figures 3.8.1 and 3.8.2), and the concertina response described above. The variety of such mechanisms indicate that this is an important process in scallops, particularly under the typically high seston concentrations encountered on soft-sediment habitats, and also that the scallop is probably able to fine-tune ingestion volume using a combination of these mechanisms.

Labial Palps and Lips

In addition to the paired labial palps found in all bivalves, pectinids possess a complex, ramified pair of lips covering the mouth. While considerable progress has been made in the understanding of their roles in particle processing, the extreme sensitivity of the scallop peribuccal structures to any local mechanical disturbances has rendered direct observation of particle processing impossible to date.

Labial Palps

The labial palps of scallops are similar to those of the majority of bivalves, consisting of a right and left pair of tissue flaps, into which the anterior ends of the gills are inserted (Figure 3.4). The detailed structure and ultrastructure of scallop labial palps has been reported for only two species, *Placopecten magellanicus* and *Chlamys varia* (Beninger et al., 1990a). The two surfaces facing the gill consist of a ciliated epithelium organised into a series of troughs and ridges oriented at right angles to the gill axis (Figures 3.11.1 and 3.11.2). Each ridge consists of an anterior fold, a crest, and a posterior fold (Figures 3.10.2 and 3.10.3). At the base of the folded inner surfaces is a ciliated oral groove leading anteriorly to the mouth (Figures 3.4 and 3.11). The 'smooth' outer or aboral surfaces of the palps possess tufts of cilia, which appear too sparse to be involved in mucociliary transport. The aboral surface is rich in mucocytes, however, probably facilitating the passage of pallial currents (Figure 3.10.1). Between the inner and outer epithelia is a haemolymph sinus, within which numerous haemocytes may be observed, traversed by lacunar muscular–connective tissue (Figures 3.10.1 and 3.10.2). The outer edges of the palps are fused to the visceral mass and mantle, forming a 'hood' in some species which live in particularly turbid habitats, and it is proposed that this allows greater efficiency in pseudofaeces rejection (Morton, 1996).

The basal lamina of the labial palp oral surface is thick, complex, folded, and presents numerous indentations (Figure 3.10.4). Together with the highly branched microvilli and the observation of lysosomes in the apical

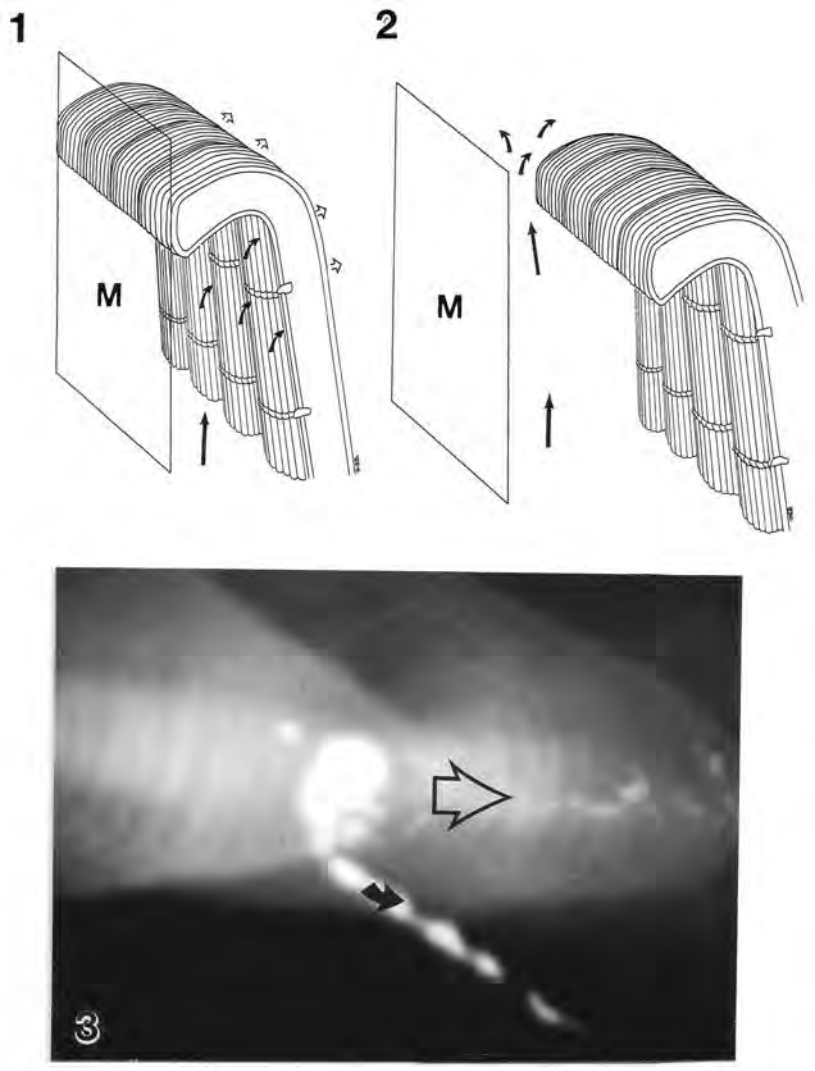


FIGURE 3.9 Ingestion volume regulation and pseudofaeces formation on the *P. magellanicus* gill. Figure 3.9.1: Diagram showing dorsal bend in normal feeding position applied to the mantle surface (M). Solid arrows show direction of particle-laden water currents in infrabranchial cavity, open arrows show passage of particle-depleted water through the interfilamentar spaces. Figure 3.9.2: Dorsal bend detached from mantle surface, allowing particle-laden water to exit directly into the suprabranchial cavity. Figure 3.9.3: Video endoscopic micrograph showing mucus-particle mass detaching from ventral bend (solid arrow). Open arrow indicates anteriorward direction of pseudofaeces movement along the ventral bend. *From Beninger et al. (1992).*

region, these observations suggest that the palp oral surface is involved in absorption, although this requires much further study (Beninger et al., 1990a).

Particle Processing on the Labial Palps

Pseudofaeces are voided from both the labial palps and gill in the same manner, that is by valve adduction; it is thus difficult to determine the exact origin of the various pseudofaeces masses once they have been expelled from the mantle cavity. It may be recalled that particle-mucus masses on the gill ventral ciliated tracts may or may not ultimately be destined for rejection as pseudofaeces, so *in vivo* sampling here (as in Beninger et al., 2004) cannot ascertain the ultimate fate of the sampled material. *In vivo* sampling allows at least the sampling of pseudofaeces observed to be rejected by the postero-ventral palp extremity (see below), so it is possible to affirm that the palps constitute a second site of qualitative particle selection. It is not yet known what the relative contributions of the gills and labial palps are to ingestion volume regulation and qualitative selection, and this is likely to be a very complex matter of investigation. Both of these processes involve rejection and acceptance, however, and mucocyte mapping data shed some light on the underlying mechanisms of each (Figures 3.7 and 3.11).

Particles destined for ingestion are accompanied in the oral groove by a medium-viscosity MPS, in keeping with the semi-enclosed nature of the transporting surfaces (Beninger and Saint-Jean, 1997a,b) (Figure 3.11.1). Particles entering the palp troughs of several non-pectinid species have been observed via endoscopy to be destined for rejection, and this agrees with observations performed on dissected, live specimens of *Placopecten magellanicus* (Beninger and Saint-Jean, 1997a; Beninger et al., 1997a). Particles destined for rejection are accompanied

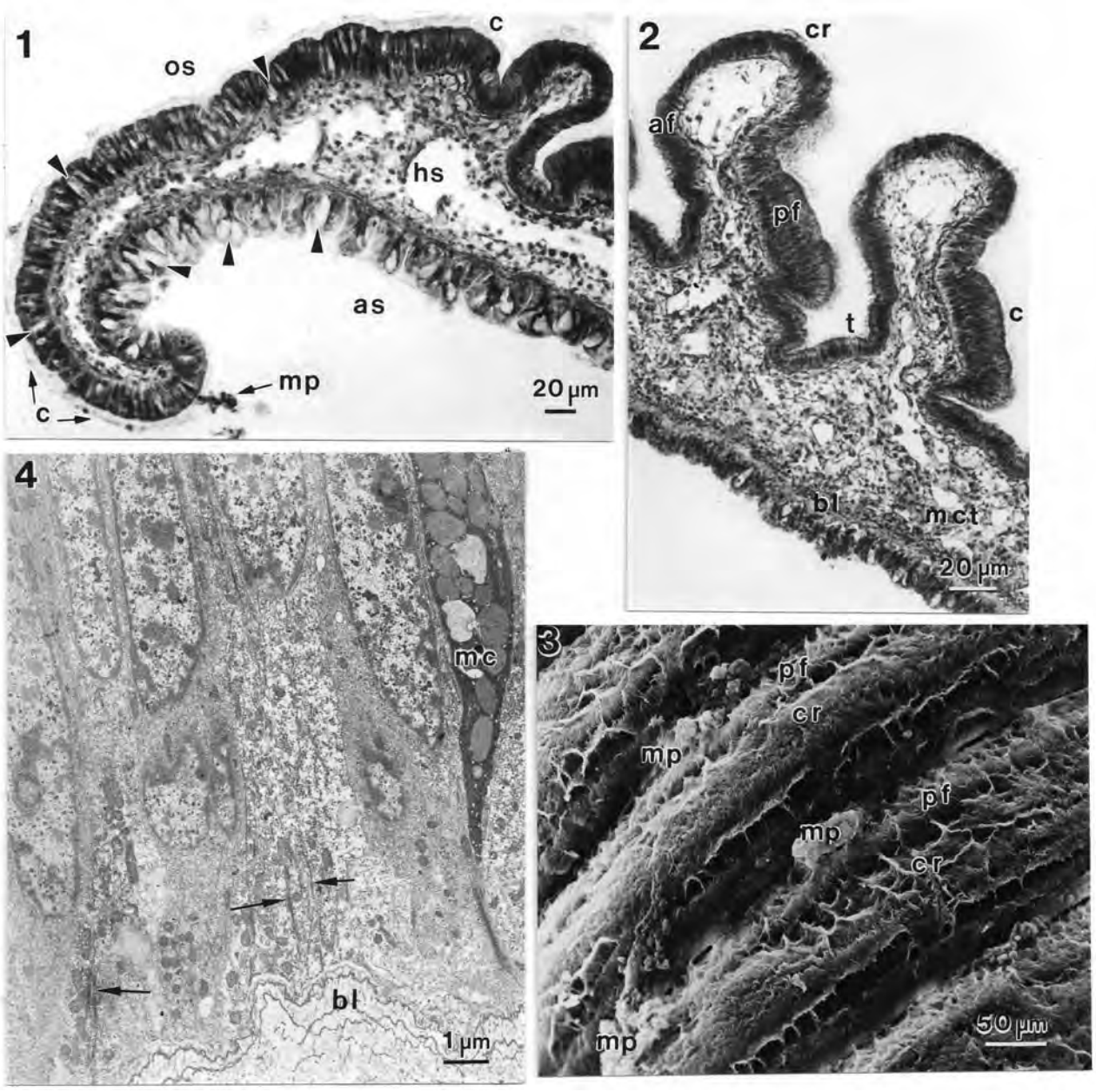


FIGURE 3.10 Labial palps of *Placopecten magellanicus* Figure 3.10.1: Transverse histological section of palp margin. Note flattening of crests at the approach to the VENTRAL margin, and mucus-particle mass of pseudofaeces (mp) at margin edge. Arrowheads indicate numerous narrow mucocytes on oral surface (os), goblet-cell type mucocytes on aboral surface (as). c, cilia; hs, haemolymphatic sinus. Modified Masson trichrome. Figure 3.10.2: Transverse histological section in mid-region of palp, showing structure of ridges and troughs. af, anterior fold; bl: basal lamina; c: cilia; cr, crest; mct, lacunar muscular-connective tissue; pf, posterior fold; t, trough (rejection tract). Modified Masson trichrome. Figure 3.10.3: SEM of densely ciliated palp oral surface, mid-region. cr, crest; mp, mucus-particle masses; pf, posterior fold. Figure 3.10.4: TEM detail of basal region of oral surface epithelium, 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 lamina (bl). *From Beninger et al. (1990a).*

by acid (viscous) MPS in the palp troughs, to the lateral (ventral) margins which are also rich in acid MPS (Beninger and Saint-Jean, 1997a) (Figure 3.11), conforming to the rule of mucociliary transport on surfaces which are themselves exposed and subjected to a counter-current water flow, or on surfaces which lead directly to same (Beninger and Saint-Jean, 1997b). At the posteriormost tip of the palp ventral margin, the mucocyte viscosity again decreases; this probably assists in the release of the pseudofaeces (Figure 3.11.2), following which they are expelled from the pallial cavity by valve adduction (Beninger et al., 1999).

Lips

Despite their strategic position and visibly complex anatomy, the lips of pectinids have received very little attention. Drew (1906) described them briefly as ramifications of the labial palps, while Dakin (1909) also gave a summary account of these structures, suggesting that the ramified margins allow the lips to form a hood over the oral groove. Some observations of the lips of *Pecten maximus* were made by Gilmour (1964, 1974), although photomicrographs of these observations were largely lacking. Detailed structural and ultrastructural observations are only available for *Placopecten magellanicus* and *Chlamys varia* (Beninger et al., 1990b).

The lips arise as ramifications of the anterior margins of the paired labial palps (Figure 3.4). Their dendritic configuration completely covers the mouth; upon separation they may be seen to comprise an upper and a lower lip (Figures 3.4 and 3.12.1). Similar to the labial palps, the cauliflower-like branches possess two distinct surfaces: a ciliated oral epithelium and a non-ciliated aboral epithelium (Figures 3.12.2–3.12.4). Both of these epithelia terminate in a covering of apical microvilli. Whereas the mucus secretion of the aboral surface probably facilitates

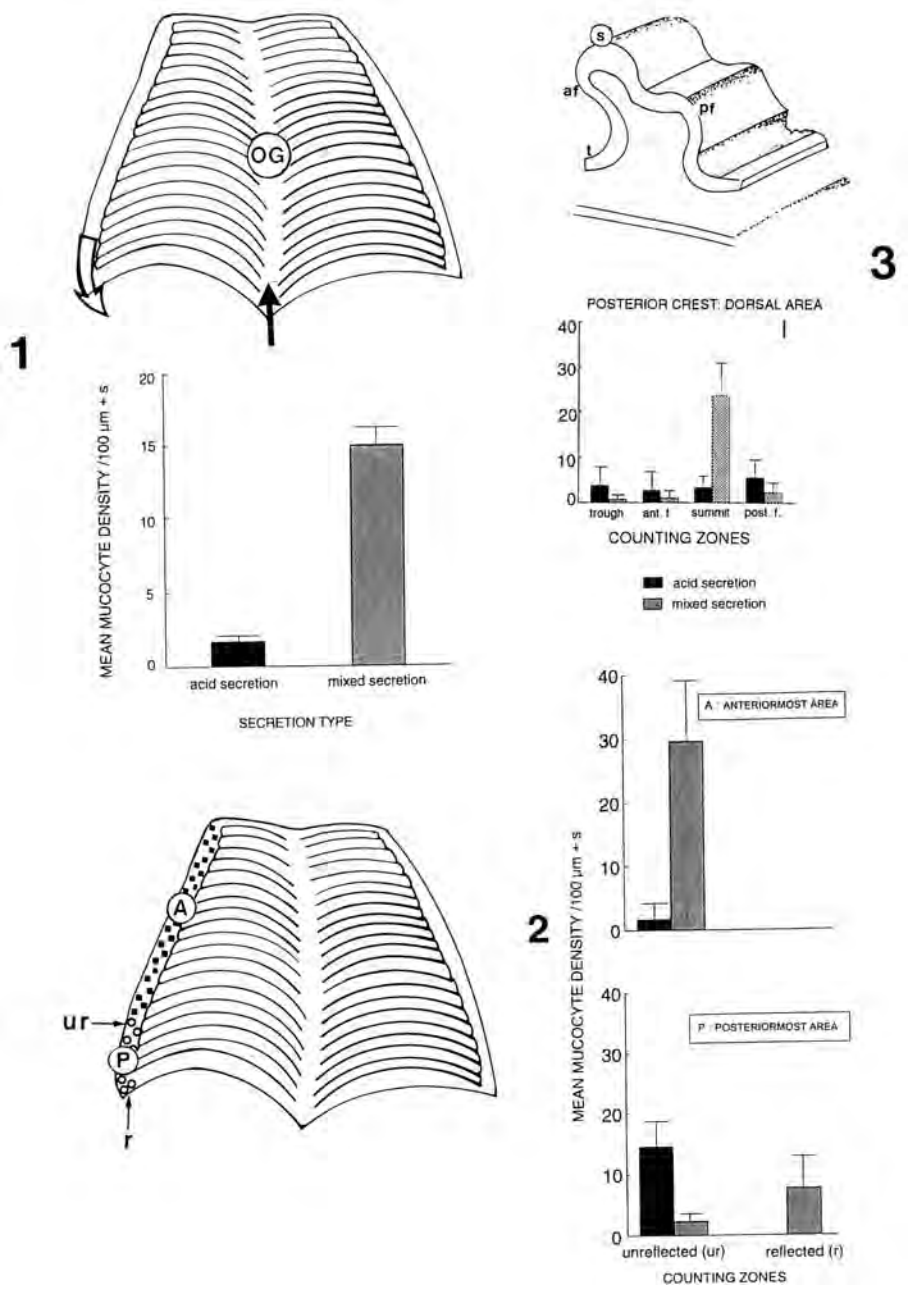


FIGURE 3.11 Mucocyte types and distribution on labial palps of *Placopecten magellanicus*. Figure 3.11.1: Labial palp mucocyte types and density throughout the oral groove (OG, means ± standard deviations). Note dominance of lower-viscosity mixed secretions in this semi-enclosed surface. Bold arrow denotes arrival of mucus slurry from gill arch, hollow arrow shows rejection pathway from ventral margin. Figure 3.11.2: Labial palp mucocyte types and densities (means ± standard deviations) on anterior (A) and posterior (P) ventral margin, on unreflected surface (UR) and reflected surface (R). Note the absence of acid mucopolysaccharide-secreting mucocytes on reflected surface, facilitating discharge of pseudofaeces. Figure 3.11.3: Mucocyte types and densities (means ± standard deviations) on representative crest of palp oral surface (postero-dorsal region). Note the dominance of acid mucopolysaccharides in trough (t), which is a semi-enclosed surface leading directly to the exposed surface of the palp ventral margin. Note also the dominance of reduced-viscosity mucopolysaccharide-secreting mucocytes on crest summit (s), allowing extraction of particles from mucus for sorting. af, anterior fold; pf, posterior fold. *From Beninger and Saint-Jean (1997a).*

the passage of pallial currents over this complex surface, the types and distribution of mucocytes on the oral surface presents a very definite gradient (Figure 3.12.1), with a large number of acid-dominant MPS-secreting mucocytes close to the mouth, and a smaller number of acid and acid-dominant MPS-secreting mucocytes in the mid-region of the lips. It has been suggested that these characteristics function to prevent the removal of food particles destined for ingestion when the scallop initiates its frequent valve adductions for pseudofaeces clearance (Beninger and Saint-Jean, 1997b).

The internal structure of the lips consists of a haemolymphatic sinus containing numerous haemocytes, traversed by a lacunar muscular-connective tissue. Muscle fibres attached to the basal lamina are responsible for the rapid contraction observed in response to the slightest mechanical disturbance in the vicinity of the lips (Figure 3.13.2).

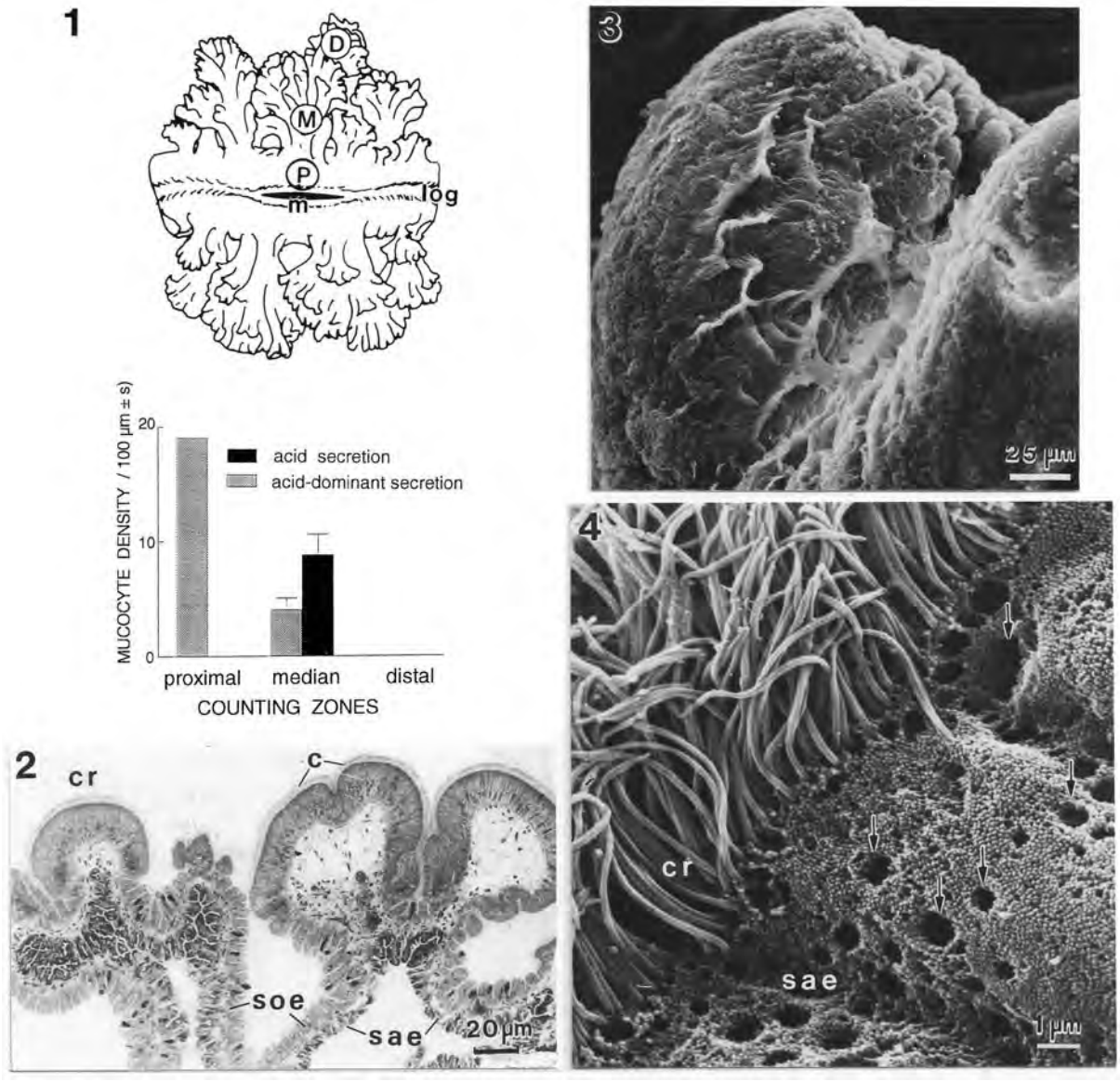


FIGURE 3.12 Lips of *Placopecten magellanicus*. Figure 3.12.1: Mucocyte types and distribution on the lips of *Placopecten magellanicus*. Mean counts + standard deviation for epithelial mucocytes in three counting zones: D, distal; M, median; P, proximal to mouth (m). Note the dominance of acid and acid-dominant mucopolysaccharide-secreting mucocytes in median region, facilitating trapping of particles dislodged from oral groove (see text). Standard deviation for proximal zone negligible. log, left oral groove. Figure 3.12.2: Semi-thin section of lips, showing ciliated (c) crests (cr) and intermediate sparsely ciliated epithelium of oral surface (soe), and sparsely ciliated aboral epithelium (sae). Figure 3.12.3: SEM of ciliated crest, showing dense ciliation and wave beat pattern. Figure 3.12.4: SEM of transition from ciliated epithelium of crest (cr, oral surface) to sparsely ciliated epithelium of aboral surface (sae). Arrows indicate surface openings of mucocytes. *From Beninger et al. (1990a) and Beninger and Saint-Jean (1997b).*

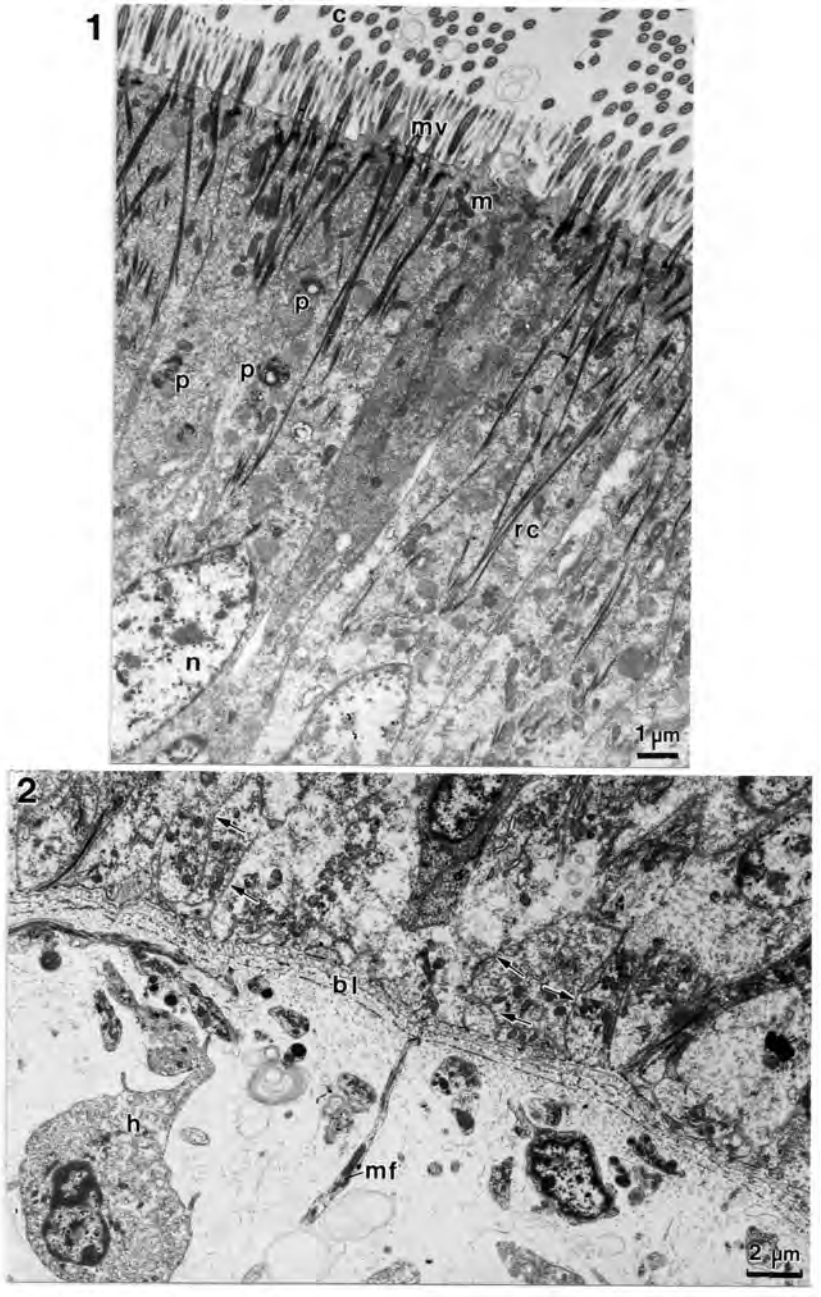


FIGURE 3.13 TEM details of *Placopecten magellanicus* lip, ciliated crest of oral surface. Figure 3.13.1: Apical region of epithelium. Note branched microvilli (mv) and phagosomes (p), indicating absorption of material from the epithelial surface. Ciliary roots (rc) extend beyond apical mitochondria (m) to the region of the nucleus (n). c, cilia. Figure 3.13.2: Basal region of epithelium. Note thick, multi-layered basal lamina (bl), with long indentations (arrows), indicative of transport to the underlying haemolymphatic sinus. h, haemocyte; mf, muscle fibre responsible for lip contraction. *From Beninger et al. (1990b).*

It may be presumed that the extension of the lips is accomplished via a forced flow of haemolymph into the lacunar connective tissue.

As was observed for the scallop labial palps, the lip oral epithelium presents highly branched apical microvilli, phagosomes, and a thick, greatly indented basal lamina (Figures 3.13.1 and 3.13.2), suggestive of absorption and transport of dissolved or colloidal substances to the underlying haemolymphatic sinuses.

DIGESTIVE SYSTEM AND DIGESTION

The scallop digestive system consists of the mouth, oesophagus, stomach, crystalline style, digestive gland, intestine, rectum, and anus. Its anatomy and function are similar to that of other bivalves (see Purchon, 1977 and Morton, 1983 for review), with several primitive features which are outlined below.

Mouth and Oesophagus

Particles and associated mucus enter the mouth from the oral groove at the base of the labial palps. The mouth is a simple ciliated opening to the narrow, ciliated oesophagus. The oesophageal epithelium is plicate, allowing accommodation, which may account for the presence of comparatively large food particles in the stomach (Mikulich and Tsikhon-Lukanina, 1981; Shumway et al., 1987). Both the buccal and oesophageal epithelia are mucociliary, with a dominance of acid MPS-bearing mucocytes in the peribuccal region, and a mixture of acid and neutral MPS mucocytes in the oesophagus, as is the rule for exposed and enclosed mucociliary surfaces, respectively, in bivalves (Beninger et al., 1991; Beninger and Saint-Jean, 1997b). The beating cilia of the mouth and oesophagus assist in transporting the relatively low-viscosity mucus-particle masses towards the stomach (Beninger and Saint-Jean, 1997b). Apart from the epithelial mucocytes, no glands are present in the scallop oesophagus (in contrast to the 'salivary glands' found in other molluscs, including *Mytilus edulis*; Beninger and Le Pennec, 1993).

The pectinid alimentary canal is characterised by a pseudostratified, microvillous-bearing epithelium with a dominance of tall, narrow, ciliated cells, interspersed with acid, and neutral MPS-containing mucocytes (Figures 3.14 and 3.18), as well as non-ciliated absorptive cells. The epithelium rests upon a thick basal lamina,

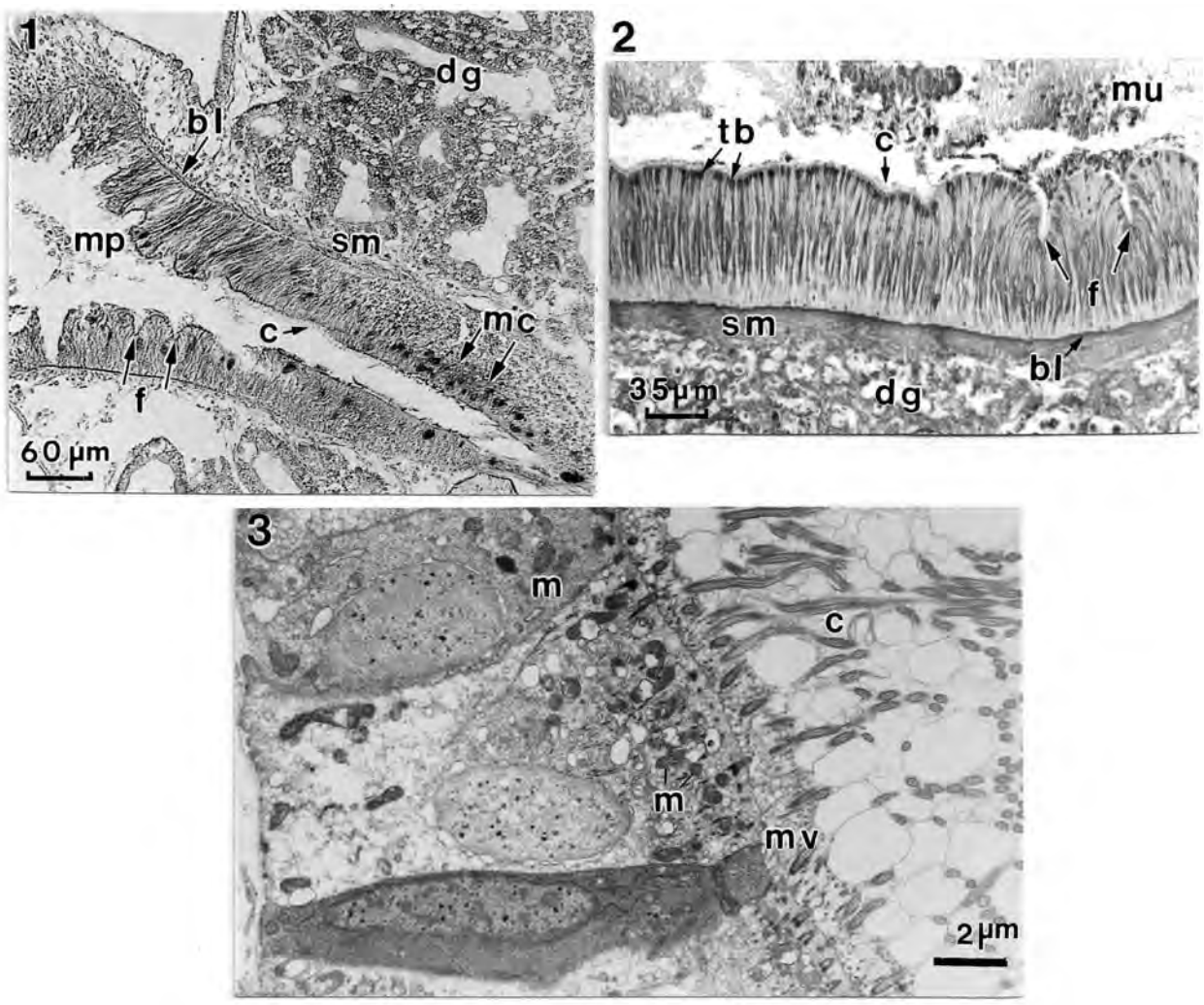


FIGURE 3.14 Structure and ultrastructure of the oesophagus in *Pecten maximus* and *Placopecten magellanicus*. Figure 3.14.1: Histological section of *Pecten maximus* oesophagus. Cilia (c) of ciliated pseudostratified epithelium, containing mucocytes (mc), beneath which are found a basal lamina (l), a smooth muscle layer (sm), and the digestive gland (dg). Note mucus-particle masses (mp) at the entry to the oesophagus, and folds (f) which allow ingestion of particles larger than the oesophageal diameter. PAS-alcian blue stain. Figure 3.14.2: Histological section of *Placopecten magellanicus* oesophagus. General structure as in Figure 13.14.1, but note terminal bulbs (tb) of mucocytes, characteristic of this species. Abundant mucus (mu) is visible in the oesophagus, histochemically similar to that contained in the mucocytes. PAS-alcian blue stain. Figure 3.14.3: Transmission electron micrograph of the ciliated epithelium of the *Pecten maximus* oesophagus. Note the numerous mitochondria (m) at the bases of the cilia (c). The apical surface is covered with microvilli (mv). *Figure 3.14.2: From Beninger et al. (1991).*

surrounded by a thick layer of muscular-connective tissue (Beninger et al., 1991; Le Pennec et al., 1991b) (Figures 3.14.2 and 3.18.4).

Stomach, Crystalline Style, and Gastric Shield

A detailed description of the pectinid stomach may be found in Purchon (1957). According to his system of classification, scallops possess a type IV stomach with the following salient features:

The oesophagus enters the stomach anteriorly and somewhat dorsally. The stomach is roughly oval in shape, with irregular folds and depressions delimiting different regions. A crystalline style projects across the stomach and into a well-developed dorsal hood, which is situated just above the gastric shield. The style originates in the style sac, which is conjoined to the intestine in the Pectinidae. Depending on its degree of development, the style may occupy most of the lumen of the descending loop of the intestine. The historic term 'crystalline style' is a misleading one, as the style is not crystalline, and it may only be presumed that the adjective refers to its translucent, pale coloration.

The exact composition of the crystalline style is not yet known, although it must be a stabilised MPS-type structure. Using very rudimentary methods, Dakin (l909) detected unspecified proteinaceous substances in the style of *Pecten* sp. In a more modern study of the styles of 12 bivalve species, including *Pecten novaezelandae*, Judd (1987) concluded that the crystalline style is probably composed of mucin-type glycoproteins rather than glycosaminoglycans. The viscosity of these glycoproteins, or acid MPSs, varies considerably among individuals and conditions, probably as a result of varying gut pH (Mathers and Colins 1979); in any event, the crystalline style can appear to be quite well-defined (but very easily broken or sectioned), or very poorly defined (rather syrupy). It is presumably secreted by the walls of the style sac (Dakin, 1909; Mathers, 1976).

The gastric shield is situated at the head of the crystalline style. It covers the stomach epithelium and is easily visualised in histological sections with either Fast Green or Alcian Blue. Shaw and Battle (1958) presented strong evidence that the oyster gastric shield may be composed of chitin (*N*-acetyl-D-glucosamine), and this has henceforth been supposed to be the case for bivalves in general (Morse and Zardus, 1997). Apart from the shell secretion epithelium of the mantle outer shell fold, chitin does not seem to be present anywhere else in the Bivalvia, so its presence in the gastric shield is intriguing. Obviously, the mechanical properties of chitin make it suitable for the grinding function it appears to perform (see below), and it may be that no other non-mineralised substance could perform such a task effectively. Although it contains other digestive enzymes (see below), the crystalline style does not appear to contain chitinases (Wojtowicz, 1972); this is understandable, given the chitin composition of the gastric shield (Shaw and Battle, 1958).

Although it was long assumed that one of the functions of the crystalline style was to drag mucus-particle 'strings' into the stomach (e.g. Purchon, 1977), mucociliary transport via the ciliated epithelium of the oesophagus seems a much more plausible mechanism. Moreover, as described above, particles appear to be ingested in a reduced-viscosity mucus, which would not lend itself to a 'capestan' model; however, the style rotation, effected by the co-ordinated ciliary beat of the stomach and intestinal epithelia, accomplishes two important functions: (i) it triturates the particles against the gastric shield, situated at the head of the style, and (ii) it stirs the stomach contents, placing them in contact with plicate ciliary sorting areas located on the inner wall of the stomach (Purchon, 1977). The crystalline style also undergoes periodic partial dissolution, liberating enzymes, which participate in extracellular digestion. In a study of *Placopecten magellanicus*, Wojtowicz (1972) identified relatively high α-amylase and laminarinase activity from the crystalline style. These enzymes originate in the style sac; they are incorporated into the style as it is secreted.

A cycle of dissolution-reconstitution of the crystalline style has been observed in both *Pecten maximus* and *Chlamys varia* subjected to diurnal changes in current flow (Figure 3.15); this cycle has been attributed to variations in the pH of the style sac resulting from rhythmic activity in the digestive gland. This rhythmic activity in *P. maximus* and other nearshore bivalves appears to correspond to distinct feeding cycles as a function of the tides (Langton and Gabbott, 1974; Mathers, 1976; Mathers and Colins, 1979).

The discovery of bacteriolytic activity in bacteria associated with the crystalline style of *Mytilus edulis* (Seiderer et al., 1987) raises the possibility that some extracellular digestion of bacteria occurs in the stomachs of bivalves. Such studies should be extended to the Pectinidae.

The Digestive Gland

The terminology of the architecture of the digestive gland has been largely based on reconstructions of histological sections. Principal ducts from the gland open laterally into the plicated sorting regions of the stomach

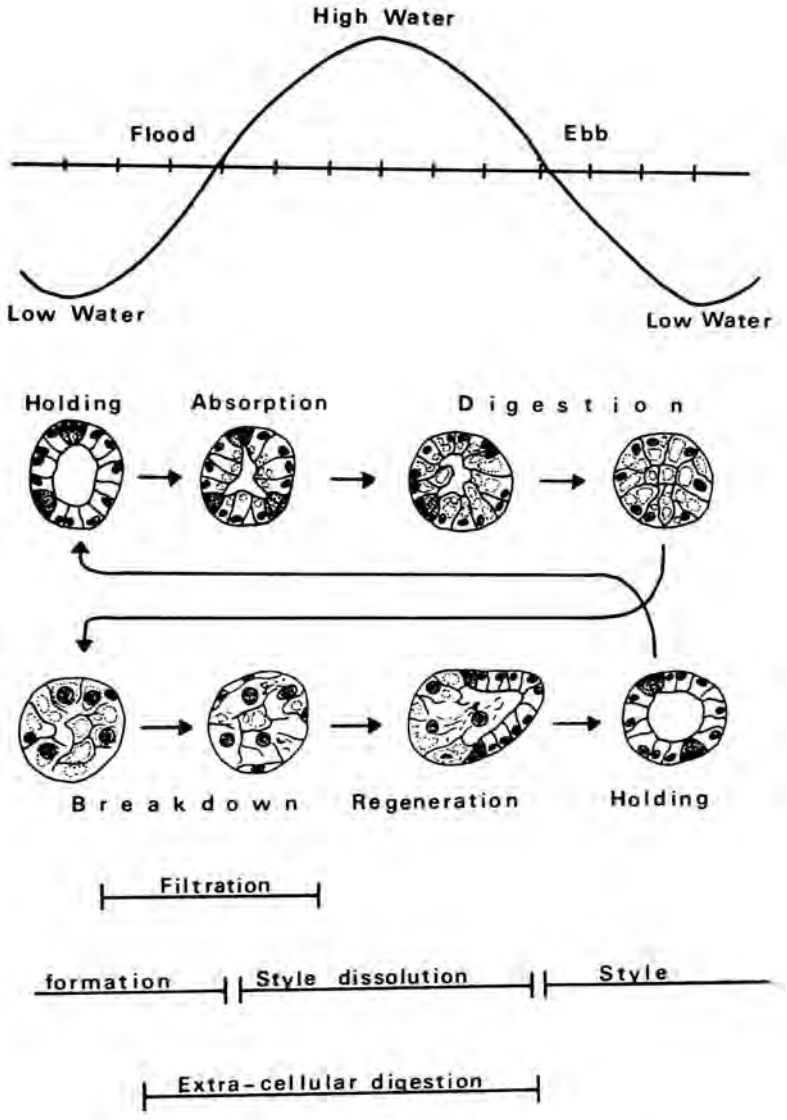


FIGURE 3.15 Diagrammatic illustration indicating the correlation of tidal cycle over a 12-h period with the cycles of feeding, extracellular digestion, and diphasic intracellular digestion in the tubules of a single individual of *Pecten maximus*. *From Mathers (1976).*

(two ducts in *Chlamys (= Aequipecten) opercularis* and four in *Pecten maximus*; Purchon, 1957). The principal ducts branch into secondary ducts, and finally into blind digestive 'tubules'. Recent studies using injected resin moulds, however, show that the secondary ducts of *P. maximus* terminate in a short tubular region, followed by an acinus rather than a tubule (Le Pennec, 2000) (Figures 3.16.1 and 3.16.2).

The probable mechanism of particle entry into the ducts and acini has been described by Owen (1955, 1966). Although the stomach and principal duct cilia create currents directed away from the principal ducts, a compensating current is created due to the distribution of cilia on only one side of the principal ducts (such a current was later demonstrated in *Ostrea edulis* by Mathers, 1972). The movement of fluids into the non-ciliated secondary ducts and the acini is accomplished by aspiration, replacing the fluids absorbed by the digestive cells of the tubules. The weak current allows only the finest suspended particles to reach the acini (Owen, 1955); larger particles are presumably digested in the stomach and intestine (see below).

The exact nature and number of different cell types in the bivalve digestive acini has been the object of considerable debate (see review by Morton, 1983 and Weinstein, 1995 for references). Although immature digestive cells are usually reported to be present in depressions or 'crypts' of the acini (e.g. Henry et al., 1991), such crypts do not appear to be a constant feature in *Pecten maximus* (Henry et al., 1991; Le Pennec et al., 2001). Whether found in crypts or between and below the acinal cells, the immature cells are probably undifferentiated precursors for all of the other cell types observed in the tubule. The immature cells pass through a transient flagellated stage

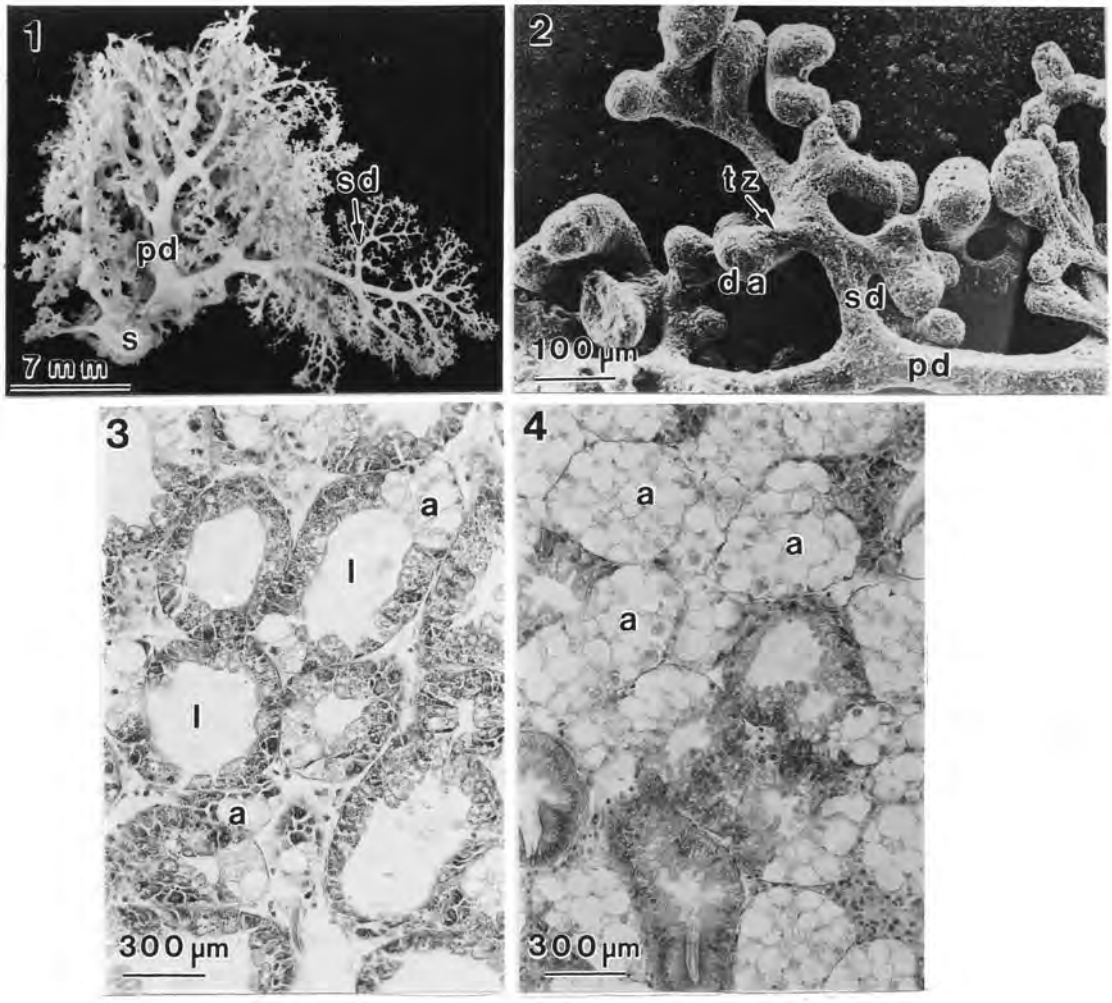


FIGURE 3.16 Topology and histology of the digestive gland in *Pecten maximus*. Figure 3.16.1: Internal mould of digestive gland, showing three-dimensional structure and anatomical relationships of point of attachment to stomach (s), principal duct (pd), and secondary duct (sd). Figure 3.16.2: Detail of internal mould, showing ramification of secondary duct (sd) from principal duct (pd), the short tubular zone (tz), terminating in the digestive acinus (da). Figure 3.16.3: Histological section of tubular and acinal regions in the Bay of Brest in April. Note large lumen (l), and few adipocyte-like digestive cells (a). Figure 3.16.4: Same type of section as in Figure 16.3, but from a specimen sampled in the Bay of Brest in December. Note the virtual absence of lumina and abundance of adipocyte-like digestive cells (a) in the digestive acini. *Micrographs courtesy of G. Le Pennec, Université de Bretagne Sud.*

(Figure 3.17.3), after which they differentiate either into absorptive (digestive) cells or secretory cells. The mature absorptive cells pinocytose particulate matter, which is digested within vacuoles called digestive spherules (Figure 3.17.5). In *P. maximus*, the end product of this digestion appears as 'residual bodies' (Mathers, 1976) (Figure 3.17.6). The absorptive cells eventually rupture, entraining the degeneration of the acinus (Mathers, 1976; Mathers and Colins, 1979), and the wastes are swept towards the stomach and ultimately the intestine. Acini are regenerated by immature cells.

The mature secretory cells possess an electron-dense cytoplasm rich in rough endoplasmic reticulum and Golgi bodies (Figures 3.17.2 and 3.17.4). These structures probably secrete digestive enzymes. Precise localisation of the enzymes is difficult, because cell type cannot be readily deduced from histochemical preparations. Whereas secretory cells would primarily secrete enzymes into the acinal lumen for extracellular digestion, intracellular digestion would be continued using the enzymatic equipment within the absorptive cells. A wide range of enzymes has been identified within the digestive gland (both the acini and the digestive ducts) of *Placopecten magellanicus* (Wojtowicz, 1972), *Argopecten irradians* (Brock et al., 1986) and *Pecten maximus* (Henry et al., 1991), notably those involved in carbohydrate and peptide digestion. The absence of proteases (Henry et al., 1991) suggests that initial protein digestion occurs in the stomach.

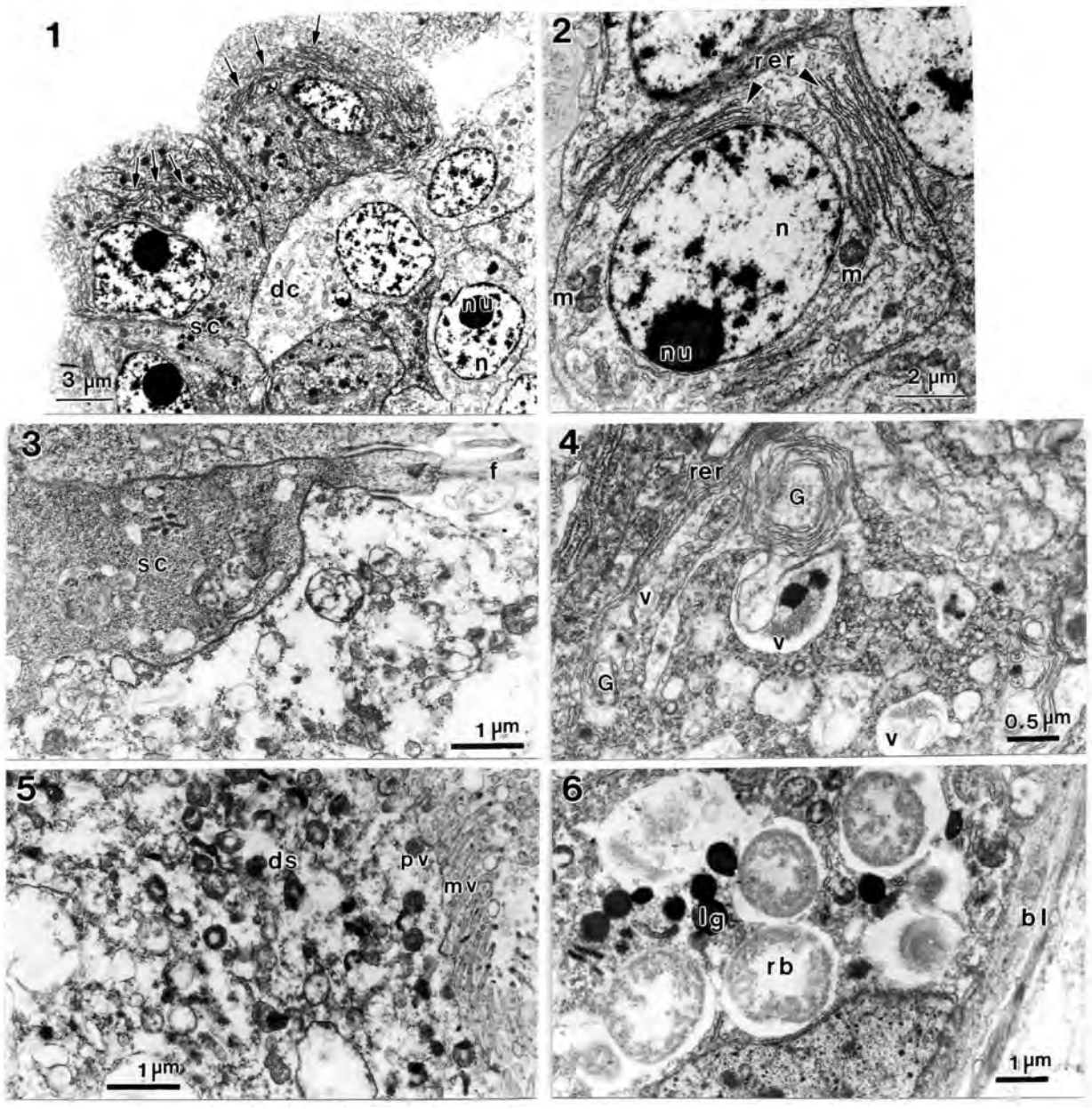


FIGURE 3.17 Transmission electron micrographs of digestive gland ultrastructure in *Pecten maximus*. Figure 3.17.1: Low-power micrograph showing general aspect of digestive (dc) and secretory (sc) cells. ⟶ indicate rough endoplasmic reticulum in secretory cells. n, nucleus; nu, nucleolus. Figure 3.17.2: Detail of secretory cell, showing mitochondria (m) and rough endoplasmic reticulum (rer). Figure 3.17.3: Transmission electron micrograph of the apical region of a young secretory cell (sc) in the digestive gland. Note the presence of flagella (f). Figure 3.17.4: Transmission electron micrograph of the basal region of a mature secretory cell. Note the numerous vacuoles (v), extensive rough endoplasmic reticulum (rer), and the characteristic annular Golgi apparatus (G). Figure 3.17.5: Transmission electron micrograph of the apical region of a mature digestive cell, showing extensive microvilli (mv). Pinocytotic vesicles (pv) become digestive spherules (ds). Figure 3.17.6: Transmission electron micrograph of the basal region of an absorptive cell. Numerous residual bodies (rb) and lipid granules (lg) are present. Note the thick basal lamina (bl). *Micrographs courtesy of A. Donval and G. Le Pennec, Université de Bretagne Occidentale, Brest, France.*

Chitinase (*N*-acetylglucosaminase) is abundant in the digestive gland of *Pecten maximus* (Henry et al., 1991); this probably enables scallops to utilise the energy-rich chitin contained in some diatom frustules (McLachlan et al., 1965; Jeuniaux, 1982), as well as in the pieces of crustacean exoskeletons which may be abundant in bivalve stomachs, including those of pectinids (Shumway et al., 1987; Davenport and Lehane, 2000; Lehane and Davenport, 2002). Restriction of chitinases to the digestive gland (and intestine, see 'Stomach, Crystalline Style and Gastric Shield' and 'Intestine, Rectum and Anus' sections) may be sufficient to protect the gastric shield.

Distinct digestive phases have been identified in the digestive glands of several bivalve species (Morton, 1977; Robinson and Langton, 1980; Robinson et al., 1981), including *Pecten maximus* and *Aequipecten opercularis* (Mathers, 1976, Mathers and Colins, 1979). These phases are cyclic and linked to environmental factors such as the tidal cycle (Figure 3.15), and may be somewhat complex, as in the case of *A. opercularis*, which displays co-dominant diphasic cycles as a function of tidal rhythm.

In addition to cyclicity on short time scales such as the tidal cycle, recent investigations have shown that ultrastructural characteristics of the digestive gland cells in *Pecten maximus* present long-term changes over the course of a year, notably with respect to the amount of lipid present in digestive cells within the acinus, which may resemble adipocytes at certain periods of the year (Le Pennec et al., 2001). The digestive cells of the tubular region store smaller lipid droplets, and these two types of lipid reserves are used differentially; it has been proposed that the lipid droplets of the tubular digestive cells are used for maintenance energy reserves, whereas those of the acinus are used for acute demand states such as gametogenesis (Le Pennec et al., 2001) (Figures 3.16.3 and 3.16.4). Long-term variations in digestive gland lipid contents have also been observed in *P. maximus* using biochemical analyses (Strohmeier et al., 2000).

The pronounced endocytotic character of the digestive gland may account for the prevalence of prokaryotic infections of this organ by *Chlamydia*-like organisms (Morrison and Shum, 1982).

Intestine, Rectum, and Anus

The remainder of the pectinid alimentary canal may be divided into three regions of similar length: the descending and ascending portions of the intestine, and the rectum. The descending portion of the intestine leaves the stomach mid-ventrally, passes through the digestive gland and into the gonad. In *Pecten maximus* and *Placopecten magellanicus*, the intestine continues almost to the distal extremity of the gonad before looping back, whereas in *Chlamys* (= *Aequipecten*) *opercularis*, the intestine curves back at about the level of the junction between the ovarian and seminal portions of the gonad. The ascending limb then returns through the digestive gland to follow the course previously described (see 'An Overview of the Scallop Body' section).

The cell types which form the intestine are similar to those described for the alimentary canal in general. In the portion which is exposed to the pallial cavity, a thin outer epithelium surrounds and protects the intestinal epithelium (Figure 3.18.2). Although several studies of the anatomy and histology of the intestine have been performed on non-pectinid bivalves (see Morton, 1983 for review), we are only aware of scattered information for a scallop species (*Pecten maximus*; Le Pennec et al., 1991a,b; Beninger et al., 2003). The intestinal epithelium consists of cells with apical microvilli and cilia, resting on a thick basal lamina (Figures 3.18.1 and 3.18.4). The underlying tissue is muscular-connective (Figures 3.18.1 and 3.18.4). Numerous mitochondria are present, and (presumably desquamated) decomposing dead cells are frequently observed (Figures 3.18.3 and 3.18.4). The intestinal cells themselves contain numerous enzymes: non-specific esterases, alkaline and acid phosphatases, chitinase, and leucine aminopeptidase (Le Pennec et al., 1991a).

The cellular structure of the rectum has been studied in *Patinopecten (= Mizuhopecten) yessoensis*. This region consists mainly of ciliated cells, with few mucus cells. Some solitary cells of apparently neuroendocrine origin have also been observed, but their function has not been determined (Usheva, 1983); the production of endocrines, especially serotonin, appears to be a widespread feature of the metazoan intestine (Costedio et al., 2007; Manocha and Khan, 2012).

The scallop digestive system terminates in an anus, which is curved dorsally and away from the adductor muscle, such that the faeces are voided in the excurrent water flow (Drew, 1906). The anus is surmounted by a prominent lip (Dakin, 1909), which in *Placopecten magellanicus* may function as a sphincter (P.G. Beninger, personal observations).

Digestive Sites and Post-Ingestive Selection

The digestive gland is not the only site of extra- and intracellular digestion in bivalves. The intestine is also active in both types of digestion (Zacks, 1955; Mathers, 1973a,b; Stewart and Bamford, 1976; Le Pennec et al., 1991a,b; Beninger et al., 2003; Figure 3.18.1) and cannot simply be considered as a conduit for wastes and particles 'rejected' from the stomach and digestive gland (Brilliant and MacDonald, 2000). Indeed, as detailed in 'Cardio-vascular System' section, transfer of material from the intestine to developing oocytes suggests that in scallops the gonad intestinal loop may be an important site of both digestion and metabolite transfer to the gonad. As the majority of the intestine passes through the gonad and digestive gland, it is thus not possible to conclude that material therein is necessarily indigestible or that it has been 'rejected' following ingestion.

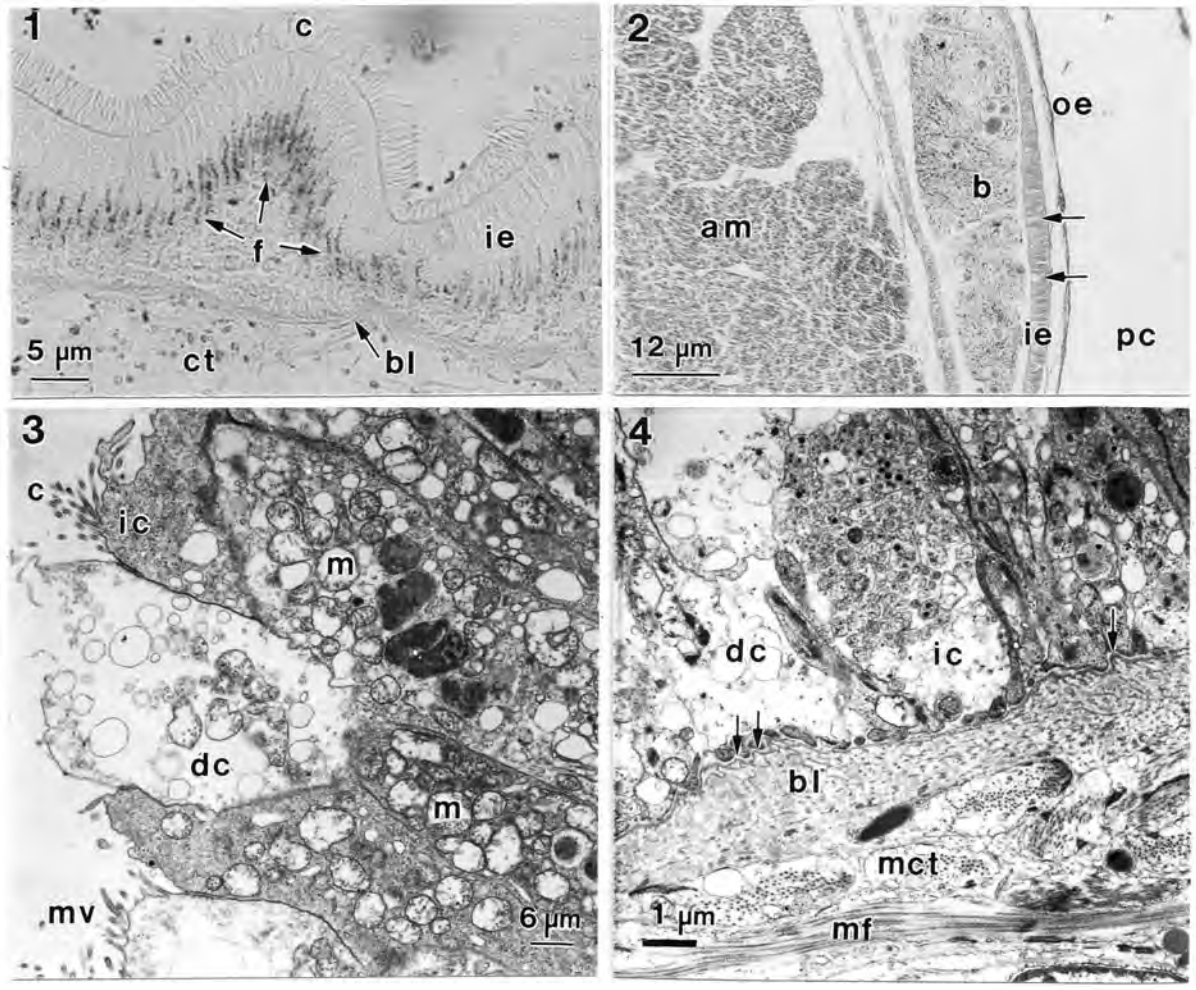


FIGURE 3.18 Histology, ultrastructure, and assimilation in the intestine of *Pecten maximus*. Figure 3.18.1: Portion of intestine passing through gonad. The intestinal epithelium (ie) is composed of tall, thin, pseudostratified, mainly ciliated (c) cells, resting on a thick basal lamina (bl), and surrounded by connective tissue (ct). Ferritin (f) injected into the intestinal lumen has been readily assimilated by the cells. The alimentary tract was allowed to purge for 48 h prior to injection. Prussian blue–nuclear red stain. Figure 3.18.2: Portion of intestine exposed to the pallial cavity (pc). Note thin outer epithelium (oe) surrounding intestinal epithelium (ie). Clear spaces (arrows) indicate acid mucopolysaccharide-secreting mucocytes. am, adductor muscle; b, bolus. Masson trichrome stain. Figure 3.18.3: Transmission electron micrograph of the apical region of intestinal epithelium cells. The intestinal cells (ic) bear cilia (c) and microvilli (mv). The numerous mitochondria (m) are dilated due to hypotonic fixation. Dead cells (dc) are frequently observed. Figure 3.18.4: Transmission electron micrograph of the basal region of the intestinal cells (ic). Note the thick basal lamina (bl) and the muscle fibres (mf) in the muscular-connective tissue (mct). Dead cells (dc) are again present. *Micrographs courtesy of A. Donval, Université de Bretagne Occidentale, Brest, France.*

While it is not evident what physiological significance may be attributed to the difference in location of digestion, it is clear that the presence of a given particle or fragment in the intestine does not signify that it will not be or has not been at least partially assimilated. Whereas the routing of particles to the digestive gland or to the intestine for eventual digestion indicates a difference in treatment, and hence a form of post-ingestive sorting, it is not known if this reflects a difference in the percentage of each particle type assimilated by the digestive system. Rather, significantly different gut retention times may simply indicate that less nutritious particles spend less time in the digestive system (Brilliant and MacDonald, 2003).

CARDIO-VASCULAR SYSTEM

As in all bivalves, the pectinid circulatory system is said to be open, as venous haemolymph is collected chiefly in a number of well-developed sinuses. These sinuses also function as reservoirs for structures which rely

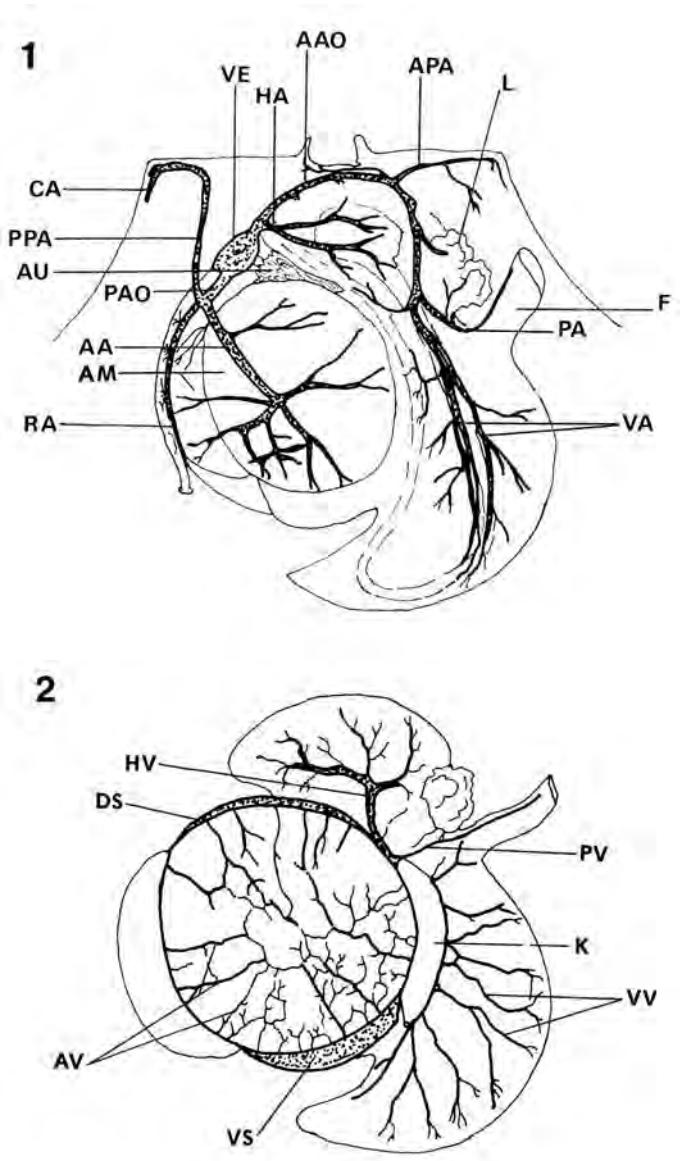


FIGURE 3.19 Schematic illustration of the arterial and venous systems in *Pecten maximus*. Figure 3.19.1: Arterial system. AA, adductor muscle artery; AAO, anterior aorta; AM, adductor muscle; APA, anterior pallial artery; AU, auricle; CA, circumpallial artery; F, foot; HA, hepatic artery; L, lips; PA, pedal artery; PAO, posterior aorta; PPA, posterior pallial artery; RA, rectal artery; VA, visceral arteries; VE, ventricle. Figure 3.19.2: Venous system. AV, adductor muscle veins; DS, dorsal sinus; HV, hepatic vein; K, kidney; PV, pedal vein; VS, ventral sinus; VV, visceral veins. *After Gutsell (1931)*.

upon haemolymph for extension (pallial organs, tentacles, etc.); however, as Jones (1983) has pointed out, the term 'open' should not be taken to mean that capillary vessels are absent. In fact, capillaries are visible in injected preparations (Drew, 1906; Dakin, 1909), and little is actually known concerning the microcirculation of bivalves (Figure 3.19).

General Circulation

The general circulation has been described in *Placopecten magellanicus* (=*Pecten tenuicostatus*) by Drew (1906), in *Pecten maximus* by Dakin (1909) and in *Argopecten irradians* by Gutsell (1931); this knowledge base has not since been significantly expanded. The following description is, therefore, based essentially on these sources. The general circulation may be divided into an arterial and a venous system (Figure 3.19).

The Arterial System

Two main vessels constitute the central elements of the arterial system: the anterior and posterior aortas.

Anterior Aorta

The anterior aorta supplies most of the visceral mass and is thus, the more complex of the two vessel systems. It arises from the dorsal-most margin of the ventricle and curves dorsally around the digestive gland. Almost immediately after leaving the ventricle, it gives off a left and a right branch, which supply blood to the digestive gland; these are visible at the surface of the gland as they begin to ramify and enter the gland itself.

The main branch of the aorta passes over the right side and into the anterior region of the digestive gland, producing ramifications, which pass through the gland to the left side and the left mantle lobe. Just before entering into the digestive gland, a branch separates from the aorta and continues dorsally and anteriorly. This is the anterior pallial artery; it bifurcates to form the left and right circumpallial arteries, which follow the margins of the left and right mantle lobes, branching off small connections to the mantle and becoming progressively smaller in diameter until they meet with the corresponding posterior circumpallial arteries. Drew (1906) states that in *Placopecten magellanicus* (=*Pecten tenuicostatus*), the posterior pallial vessel also arises from the anterior aorta, whereas Dakin (1909) affirms that in *Argopecten irradians* it arises from the posterior aorta.

From within the digestive gland, the aorta gives off a branch, which passes anteriorly to supply the dorsal lip and the outer labial palps. As the aorta continues ventrally within the gland, it gives rise to another branch, which proceeds ventro-anteriorly and then curves dorsally into the foot. This is the pedal artery, and at its point of inflection it bifurcates, sending a vessel which supplies the lower lip and inner labial palps.

The aorta continues ventrally, giving rise to another branch running posteriorly to the digestive gland, then dividing into three vessels from within the gonad, supplying both the gonad and the convoluted intestine.

Posterior Aorta

The posterior aorta chiefly supplies the rectum, the adductor muscle and the two mantle lobes. It leaves the ventral-most margin of the ventricle and proceeds ventrally along the rectum for a short distance before dividing into three branches. One of these continues along the rectum, supplying it with small branches to its extremity. A second curves dorsally to the fused mantle margin, where it bifurcates to become the right and left posterior circumpallial arteries. These vessels follow the mantle margin to meet with the anterior circumpallial arteries. The third branch of the posterior aorta constitutes the adductor artery. It runs antero-ventrally to the adductor muscle, ramifying most extensively from a point near the centre of the striated portion of the muscle.

The Venous System

In addition to haemolymphatic vessels, the venous system comprises a number of sinuses, which collect haemolymph from the various body parts. These sinuses are all located along the margin of the adductor muscle.

A large hepatic vein runs ventrally to join the pedal vein in a dorsal sinus, located between the pericardium and the adductor muscle. Venous haemolymph from the muscle also flows into this sinus, which communicates with the dorsal extremities of the right and left kidneys. Two ventral sinuses situated on the antero-ventral margin of the adductor muscle extend antero-dorsally to enter the dorsal extremities of the respective right and left kidneys.

Most of the haemolymph from the intestine and visceral mass flows through distinctly visible veins at the surface of the gonad to the external sides of the kidneys, where the veins communicate with the small kidney vessels. In summary, therefore, all returning haemolymph thus far described passes into the kidneys. From there, the haemolymph flows towards the right and left afferent branchial vessels in the right and left gill axes. After circulating in the gills (as described in 'Pallial Organs and Particle Processing' section), the haemolymph joins the right and left efferent branchial vessels within the right and left gill axes. These vessels continue dorsally between the digestive gland and the adductor muscle, opening into the apices of the auricles. The right and left pallial veins join the corresponding efferent branchial vessels just prior to their entry into the right and left auricles; they drain haemolymph from the very fine vessels and lacunae of the right and left mantle lobes.

The Heart

Scallops possess a typical bivalve heart composed of two auricles and one ventricle. In addition to its contractile role, the heart is also involved in excretion, as outlined below.

The Ventricle

The ventricle is a smooth-walled chamber with a rather complex morphology (Dakin, 1909). The rectum passes through the central portion of the ventricle, which is sac-shaped, while on either side joining the corresponding auricles are two pouches, thus creating a chamber with three very incompletely separated compartments. Both Drew (1906) and Dakin (1909) mentioned the existence of muscular sphincters or valves between the auricles and the ventricle; these structures may be seen in the histological section of Figure 3.20.1. The valves presumably ensure a one-way flow of haemolymph from the auricles to the ventricle.

The chamber of the ventricle is traversed by numerous muscle fibres (trabeculae), giving a distinct spongy appearance in section. This arrangement, also found in the auricles, is responsible for the great degree of contraction of the heart (Figures 3.20.1–3.20.3).

The Auricles and Their Excretory Structures

The internal structure of the auricles resembles that of the ventricle, with criss-crossing muscle fibres and numerous lacunae (Figures 3.20.1–3.20.3). The walls of the auricles are not smooth, as is the case for the ventricles, due to the presence of lateral, papillose outgrowths, which constitute the pericardial gland. This gland was observed by Dakin (1909) to be a site of nitrogenous waste uptake in *Pecten* spp. Although some differences of opinion exist, most recent studies on this system tend to confirm that haemolymph is ultrafiltered via numerous podocytes in this gland from the auricles to the pericardial cavity (see Jones, 1983 for review). More recently, Morse and Zardus (1997) have confirmed this function in the pectinids *Chlamys hastata*, *Placopecten magellanicus*, and *Patinopecten caurinus*. In these pectinids, the ultrafiltrate passes to the kidneys via pedicels at the bases of the podocytes (Morse and Zardus, 1997).

A second type of excretory cell, the pore cell, is found beneath the podocyte-containing outer epithelium of the pericardial gland, within the underlying muscular-connective tissue. These cells are capable of taking up large organic molecules (Morse and Zardus, 1997), functioning to pre-filter the haemolymph prior to ultrafiltration by the podocytes. They are naturally brown in colour, giving this region a brownish colour in living specimens. The pericardial cavity thus participates in at least two important physiological processes: refilling the heart (as mentioned in 'Refilling' section), and excretion (in which it acts as a reservoir for the auricular ultrafiltrate). More will be said of the excretory functions of this structure in 'Pericardial and Auricular Glands' section.

A band of myocardial tissue situated on the ventral part of the pericardium connects the two auricles.

Structure and Ultrastructure of Heart Cells

Scallop and other bivalve myocardial cells present some marked differences from vertebrate cardiac muscle cells. Sarcolemmic and T-tubules are absent in scallop myocardial cells, while the sarcoplasmic reticulum forms a network of tubules extending throughout the cell. This contrasts with adductor muscle cells, in which the sarcoplasmic reticulum is situated only under the sarcolemma. Stimulus for calcium release in scallop myocardial cells is presumably initiated at the sarcolemma and propagated along the sarcoplasmic reticulum to the interior of the cell (Sanger, 1979).

Electron microscopic observations reveal the existence of numerous mitochondria, as well as both thin and thick filaments in the myocardial cells (Sanger, 1979; Huang et al., 2010). The diameter of the thin filaments (6 nm) corresponds to that of actin, while the rather large diameter of the thick filaments (40 nm) led Sanger (1979) to suggest that they were composed of both myosin and paramyosin. Although Dakin (1909) believed that the myocardial muscle fibres of *Pecten maximus* were not striated, it is now known that scallop heart muscle fibres are striated, presenting distinct solid Z-bands (Sanger, 1979).

Both intercalated discs and gap junctions are observed in scallop myocardial cells (Sanger, 1979), as is true for oyster and mussel heart cells (Irisawa et al., 1973); hence, these cells are both mechanically and electrically coupled, in contrast to scallop adductor muscle cells which present intercalated discs only and are thus mechanically but not electrically coupled (Sanger, 1979). The scallop heart, like that of all other bivalves, therefore constitutes a functional syncytium.

The fine innervation of the bivalve myocardium has not been extensively studied. Nerve endings with at least two different vesicle types are closely associated with the myocardium; these two vesicle types may correspond to different neurotransmitters (Sanger, 1979).

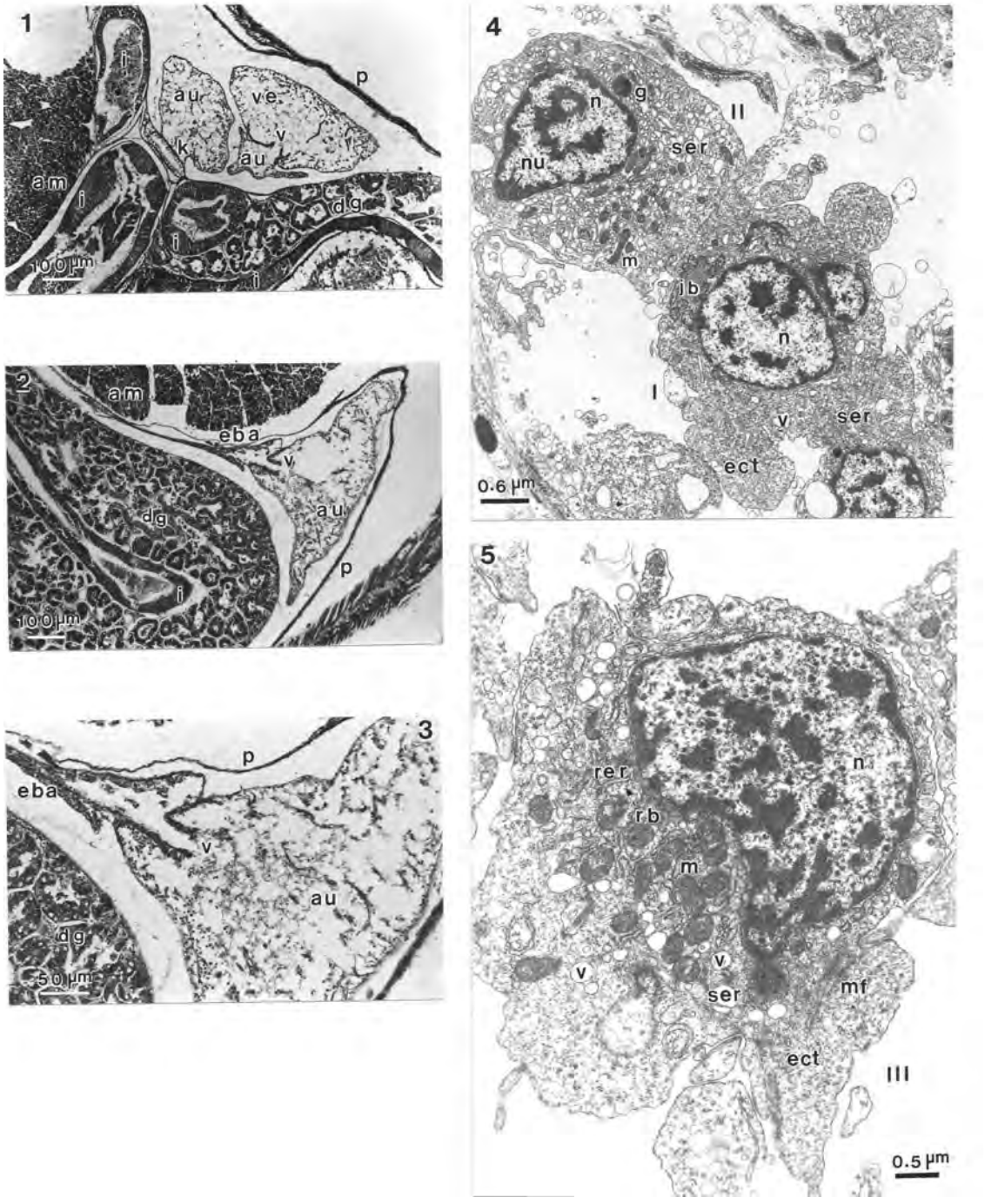


FIGURE 3.20 Structure of the pectinid heart and haemocytes. Figure 3.20.1: Histological section of a juvenile specimen of *Pecten maximus*, showing the anatomical relationships of the heart to surrounding structures. Note the sponge-like appearance of the heart due to the abundant criss-crossing muscle fibres. am, adductor muscle; au, auricle; dg, digestive gland; i, intestine; k, kidney; p, pericardium; v, valve-like structure between the auricle and ventricle (ve). Figure 3.20.2: Histological section through the auricle (au), efferent branchial artery (eba) and valve (v) of a juvenile specimen of *P. maximus*. Other abbreviations as in Figure 3.20.1. Figure 3.20.3. Detail of Figure 3.20.2 showing the auricular insertion of the efferent branchial artery and associated valve. Abbreviations as in Figure 3.20.2. Figure 3.20.4: Transmission electron micrograph of haemocyte types I and II in *Mimachlamys varia*. Haemocyte type I: lobed nucleus (n) with associated juxtanuclear body (jb), around which are found numerous round mitochondria. The smooth endoplasmic reticulum (ser) is extremely well-developed and dilated, forming abundant saccules. The ectoplasm (ect) presents pseudopodial-type elongations, and vacuoles (v) of apparently endocytotic origin are visible. Haemocyte type II: the irregular nucleus (n) contains a small nucleolus (nu) close to the nuclear envelope. Numerous elongated mitochondria (m) are dispersed throughout the cytoplasm, which is chiefly occupied by dilated smooth endoplasmic reticulum (ser). A large, electron-dense granule (g) is present. Figure 3.20.5: Transmission electron micrograph of a type III haemocyte. Note the irregular nucleus (n), with its characteristic indentation near the cell centre. Numerous mitochondria (m) are grouped near this indentation. Rough endoplasmic reticulum (rer) and free ribosomes (rb) are abundant, while smooth endoplasmic reticulum (ser), showing dilated vesicles, is less common. Microfilaments (mf) are present at the boundary between the organite-rich endoplasm and the ectoplasm (ect). Vacuoles (v) are relatively abundant. *Micrographs courtesy of P. Beninger, Université de Nantes, and M. Auffret, Université de Bretagne Occidentale.*

Heartbeat

The scallop heartbeat involves several related phenomena: refilling, coordination of the alternate auricular-ventricular beat, pacemaker mechanism, and regulation of the pacemaker mechanism.

Refilling

The passage of venous blood through large sinuses would intuitively result in low venous haemolymph pressure, especially in light of the initially low systolic ventricular pressures of bivalve hearts, including those of scallops (see Jones, 1983 for review). Ramsay (1952) proposed a mechanism of refilling in the hearts of invertebrates possessing a pericardial cavity. This mechanism was developed by Krijgsman and Divaris (1955) to explain the refilling of the bivalve heart; it has come to be known as the 'constant volume' or 'volume-compensating' mechanism. These authors concluded that contraction of the ventricle decreases the hydrostatic pressure in the pericardial cavity, thus forcing the auricle walls to expand; hence ventricular contraction automatically results in auricular expansion. This may be readily verified by cutting or piercing the pericardium at any point – the auricles and ventricle then fail to expand to any appreciable extent. The one-way valves at both extremities of the auricles ensure that auricular contraction will also automatically result in ventricular expansion.

The pericardium has a consistently lower pressure than either the auricles or the ventricles at all stages of the beat cycle of the bivalve heart; consequently it will promote the expansion of whichever chamber is in diastole (Jones, 1983). Although there are some objections to this model, it is the most parsimonious explanation for the refilling of the bivalve heart (Jones and Peggs, 1983; and see Jones, 1983 for review).

Coordination of Alternate AV Beat

The volume-compensating mechanism provides an obligate mechanical link between the auricular and ventricular contractions, thereby ensuring a certain coordination of their respective beats. The actual coordinating stimulus is also purely mechanical, being mediated by alternate stretching of the auricular and ventricular myocardia. There appears to be no direct electrical interaction between the auricles and ventricle (Uesaka et al., 1987).

Pacemaker Mechanism

The case for a diffuse myogenic pacemaker in the bivalve heart was put forward by Krijgsman and Divaris (1955); this has since become conventional wisdom (Brand and Roberts, 1973; Jones, 1983). Supporting evidence for the myogenic nature of the pacemaker comes from the electrocardiogram of the bivalve heart, which resembles a true myogram, with no trace of nervous impulses (Krijgsman and Divaris, 1955). The pacemaker action potential is thus probably initiated by relatively unmodified myocardial cells.

Evidence for the diffuse nature of the myogenic pacemaker is much more equivocal. While denervated heart preparations amply demonstrate the existence of the pacemaker within the heart itself, contradictory results have accumulated which variously indicate a truly diffuse pacemaker, a relatively local pacemaker, and a 'wandering' pacemaker in bivalve hearts (Jones, 1983). We are unaware of any studies on the location of the pacemaker in pectinids.

Although no accounts of scallop heart action potential have been published to date, other bivalve species exhibit one of three different types of action potential: fast, slow, and spike-plateau. It has been suggested that these differences may be related to phylogeny (Jones, 1983).

Regulation of Pacemaker

The bivalve heart receives nerves from the cerebro-visceral connectives; hence, cardiac nerves enter both the right and left auricle (Jones, 1983). These nerves originate in the parieto-visceral ganglion (Krijgsman and Divaris, 1955), and they contain both inhibitory and excitatory fibres (Jones, 1983). As mentioned previously, the two different types of vesicles found in the nerve endings may correspond to different neurotransmitters; however, it should be noted that the neurochemistry of the bivalve heart is an evolving field and it is difficult to present a coherent synopsis at this point (see Jones, 1983 for review).

The pacemaker frequency may be modified by environmental or endogenous physiological factors, and these have been intensively investigated in many bivalve species, including pectinids (e.g. Greenberg, 1965, 1970; Wilkens and Greenberg, 1973; Elliott, 1980; Ono et al., 1992; Ferreira and Salomao, 2000). Brand and Roberts (1973) observed hypoxia-induced bradycardia followed by an overshoot when preparations of *Pecten maximus* were restored to normoxic conditions. Thompson et al. (1980) demonstrated a regulation of heartbeat during

work in *Placopecten magellanicus*. The cardiac rhythm of this species was shown to increase two- to threefold during the rapid contractions of the adductor muscle valve–snap response. It is important, however, not to generalise too hastily between taxa. For example, ouabain had no effect on heterodont hearts, whereas it elicited positive tonotropic responses from most pteriomorph hearts, including that of *Argopecten irradians* (Deaton and Greenberg, 1980). Similarly, pectinid hearts respond differently to serotonin and acetylcholine than many other taxons, which also differ greatly among themselves (Greenberg, 1965).

Reported values for resting heartbeats in scallops maintained in well-oxygenated seawater, measured via electrodes passing through holes in the shell, are as follows: 15–20 beats min^{-1} in *Pecten maximus* at 12 °C (Brand and Roberts, 1973), 5–10 beats min^{-1} in *Placopecten magellanicus* at 5 °C (Thompson et al., 1980). Earlier values of 25–30 beats min^{-1} reported for *P. magellanicus* (Drew, 1906) should not be retained, as the conditions of observation and measurement were not provided.

Cardiac output has been determined to be 64 mL h^{-1} in the previously described preparations of *Placopecten magellanicus* (Thompson et al., 1980). More studies are required to determine such values in other species.

Haemolymph

The haemolymph of bivalves participates in a variety of physiological functions, including gas exchange, osmoregulation, nutrient distribution, elimination of wastes, and internal defence. It also serves as a hydrostatic skeleton, such as during movements of the labial apparatus, tentacles, foot and mantle edges.

Most bivalves lack circulating respiratory pigments (Booth and Mangum, 1978; Barnes, 1987), and there are no reports of such pigments in any scallop species. Certainly, the low oxygen uptake efficiency of the haemolymph of *Placopecten magellanicus* (42%; Thompson et al., 1980) tends to confirm the lack of haemolymph respiratory pigments in this species. The essentially sedentary life habit, the enormous exposed body surface area, and the epibenthic habitat of scallops probably obviate the need for circulating respiratory pigments.

Plasma

Studies concerning the chemical composition of marine bivalve plasma have been reviewed by Burton (1983). The steady-state osmotic concentration of the plasma is equal to or marginally greater than that of the surrounding seawater. A slight hyperosmolarity may be necessary to the maintenance of urinal flow and mucus secretion. In any event, the metabolic cost of maintaining a significant long-term plasma-seawater osmotic gradient would be prohibitive in organisms such as bivalves, which have vast surface areas exposed to the external medium (Burton, 1983).

Many pectinid species are marine, some inhabit reduced-salinity waters, and none are adapted to freshwater (the current accepted common name for *Placopecten magellanicus* – 'sea scallop' – is rather inappropriate, as there are no freshwater scallops). The ionic composition of the haemolymph in *Chlamys (= Aequipecten) opercularis* has been studied by Shumway (1977); concentrations of Na^+, Mg^{2+}, and Ca^{2+}, as well as overall osmotic concentration, followed that of the external medium in short-term fluctuating salinity regimes. The plasma K^+ concentration of bivalves is greater than that of seawater by a factor of one to two (Burton, 1983); this probably reflects the normal intracellular–extracellular K^+ gradient (Natochin et al., 1979; Hochachka and Somero, 1984).

Bivalve plasma contains numerous dissolved organic molecules. Little information is available on this subject for scallops, with the notable exception of *Placopecten magellanicus* (Thompson, 1977). Plasma determinations performed immediately after field sampling yielded the following values (means and standard deviations): protein 153 ± 28, ammonia – N 0.24 ± 0.12, total carbohydrate 5.2 ± 1.2, lipid 13.7 ± 2.4 mg 100 mL^{-1}. The major pectinid plasma protein has been partially characterised as the metal-binding histidine-rich glycoprotein, common to several other bivalve taxa (Abebe et al., 2007). It should be noted that plasma metabolite concentrations are influenced by physiological events such as short-term osmoregulation (see Pierce, 1982) or the reproductive cycle (Thompson, 1977).

Haemocytes

Although there are many descriptions of bivalve haemocytes in the literature, the lack of a universal classification scheme has greatly hindered attempts to draw together existing knowledge (Auffret, 1988). Indeed, for a single bivalve species, a table of reported haemocyte types and names spans two full pages (Cheng, 1996). In an extensive review paper, Cheng (1981) proposed a classification based on three categories of cell populations: hyalinocytes, granulocytes, and serous cells. While this scheme may apply to most bivalves, neither Auffret (1985)

nor Estrada et al. (2013) observed any typical granulocytes in *Pecten maximus*, *Chlamys* (=*Mimachlamys*) *varia*, or *Nodipecten subnodosus*. The 'serous cells' were not considered to be true haemocytes by Auffret (1985) and not reported at all by Estrada et al. (2013). As these appear to represent the only recent studies of pectinid haemocytes, the cell types will be summarised here, with special reference to *M. varia*.

Haemocyte Types

Type I haemocytes contain central, lobed nuclei with abundant chromatin, partially condensed into small clots and a peripheral chromatin shell. Many round mitochondria are situated close to the nucleus; in *Mimachlamys varia*, these form a typical juxtanuclear body. The endoplasmic reticulum (ER) is smooth and often dilated to form numerous saccules. Electron-dense granules are rare (in contrast to the granulocytes of other bivalves), but there are numerous cytoplasmic inclusions and some glycogen particles, as well as vacuoles of apparently endocytotic origin. Electron-lucent domains may fill large portions of the cytoplasm (Figure 3.20.4). These cells correspond to the 'blast cells' of Estrada et al. (2013).

Type II haemocytes have non-lobed, eccentric nuclei containing abundant chromatin, either uncondensed or condensed in large masses of heterochromatin; a peripheral chromatin shell and nucleolus are also present. The numerous mitochondria are elongated and distributed throughout the cytoplasm. The smooth ER resembles that of the type I haemocytes except that it is even more vesiculated, filling most of the cytoplasm. Large electron-dense granulations are sometimes present (Figure 3.20.4).

Type III haemocytes were observed in *Chlamys varia* but not in *Pecten maximus*, therefore inter-specific differences in haemocyte types may exist within the Pectinidae. Type III haemocytes have very irregular shapes, and a polymorphic nucleus indented near the cell centre, containing numerous clots of heterochromatin and a peripheral chromatin shell. The endoplasm is very dense, with many elongated mitochondria near the nuclear indentation at the cell centre; rough ER is well developed while smooth ER is not; many free ribosomes are present. The ectoplasm is less dense than the endoplasm, containing large, possibly endocytotic vacuoles and microfilaments at the bases of the cell prolongations (Figure 3.20.5).

The search for the site(s) of haematopoesis has been a fruitless endeavour for several decades. The close association of blast-like haemocytes with the pluripotent muscular-connective tissue (Hine, 1999; Estrada et al., 2013) found throughout bivalve tissues may indicate that haematopoesis is, in fact, a delocalised process.

Functions of Haemocytes

Circulating haemocytes participate in five classes of physiological function in bivalves: wound repair, shell repair, nutrient digestion and transport, excretion, and internal defence. Details concerning the roles of haemocytes in these functions may be found in the review by Cheng (1981). Briefly, haemocytes intervene in wound repair by successive infiltration, clumping, and plugging of the wound (without a fibrinogen-thrombin-fibrin system), followed by wound repair and phagocytosis of necrotic elements. Their known role in shell repair is that of calcium and organic matrix transfer from the digestive gland to the repair site. Haemocytes are present not only in the vascular system but are also found wandering through tissues (an 'open' circulatory system characteristic). They may thus absorb nutrients from the alimentary tract and pass them directly to other tissues, or to developing oocytes (see 'Vitellogenesis and Metabolite Transport to the Oocyte' section). Thompson (1977) observed seasonal variations in the glycogen content of haemocytes of *Placopecten magellanicus*, with greater levels in summer than in winter.

Haemocytes may participate directly in excretion by absorbing wastes, passing directly across the epithelium of the nephridial tubules into the kidney lumen and thence to the exterior.

Most recent attention has been directed towards the roles of haemocytes in internal defence (Cheng, 1981; Rodrick and Ulrich, 1984). Although it is difficult to summarise the often contradictory observations, the following general points may be mentioned. Bivalve leucocytes are capable of phagocytosing foreign materials and degrading them via the lysosomes. The glycogen granules frequently found in bivalve haemocytes (including pectinids; Auffret, 1985) may originate from digested bacteria (Rodrick and Ulrich, 1984). In this respect, internal defence and nutrition are somewhat interrelated, and this dimension is nowhere more spectacular than in the symbiotic associations found in bivalves inhabiting reducing habitats. Haemocytes also intervene in the extracellular lysis of bacteria through the production of circulating lysozymes (Cheng, 1975).

EXCRETORY SYSTEM

The excretory system of bivalves comprises a number of diverse sites of excretory function (see review by Andrews, 1988). The principal excretory organs are the auricular and pericardial glands, and the paired kidneys, also called nephridia or (historically) organs of Bojanus, who mentioned them first in 1819. The anatomical relationships of these structures to each other and to the gonad are illustrated in Figure 3.21. Ubiquitous cells specialised in metal ion transport may also participate in excretory function.

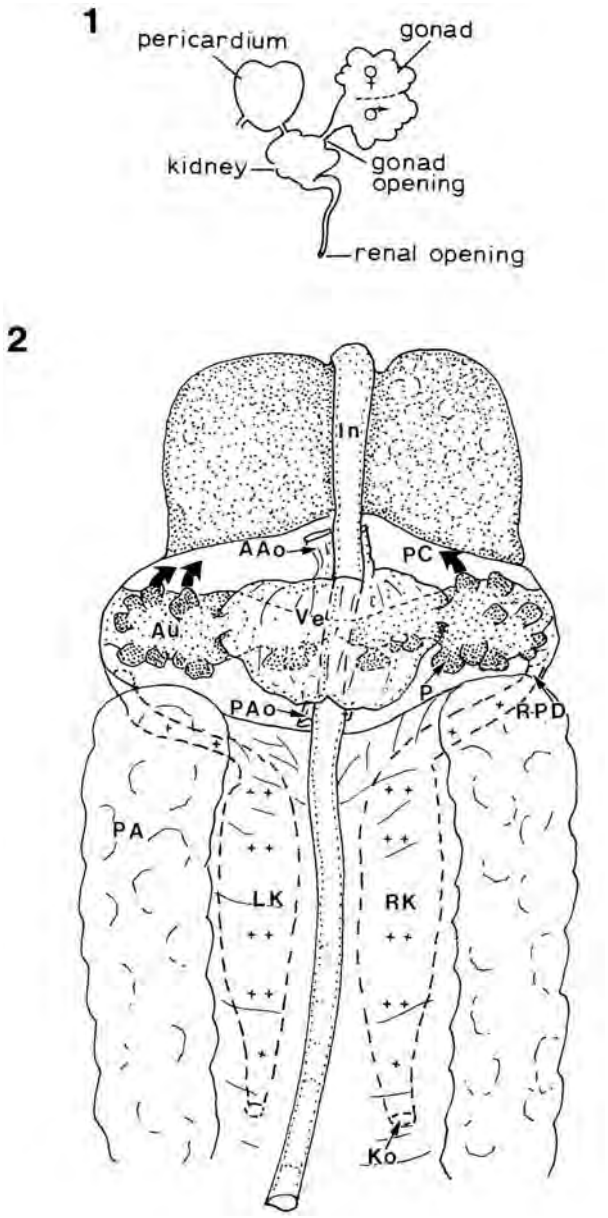


FIGURE 3.21 Schematic representation of the anatomical relationships between the pericardium, kidney, and gonad in pectinids. Figure 3.21.1: The gonad opening to the kidney. Figure 3.21.2: Dorsal view of the heart–pericardial cavity–kidney complex in *Chlamys hastata*. Primary urine formation occurs via ultrafiltration of haemolymph across podocytes (P) of auricular gland (curved arrows) into pericardial cavity (PC). Aao, anterior aorta; Au, auricle; In, intestine; Ko, kidney opening or nephrostome; LK, left kidney; PA, posterior adductor muscle; Pao, posterior aorta; RK, right kidney; RPD, right reno-pericardial duct. *Figure 3.21.1: Modified after Mackie (1984), Figure 3.21.2: Modified from Morse and Zardus (1997).*

Pericardial and Auricular Glands

Gröbben (1888) was apparently the first to suggest an excretory function for the glands located in the auricular and pericardial walls of bivalves; however, it was not until 1942 that White demonstrated their excretory function and showed that their products were collected in the pericardial cavity, from whence they presumably exited via the reno-pericardial canal and kidney. This has since been confirmed for *Mytilus edulis* (Pirie and George, 1979). Ultrastructural data show that these glands, also (historically) known as Keber's organs, appear to be the site of primary urine formation (i.e. ultrafiltration) in bivalves (Meyhöfer et al., 1985; Andrews and Jennings, 1993; Morse and Zardus, 1997).

There is some understandable confusion in the designation of auricular and pericardial glands. Glands, which originate in the outer auricle wall and project into the pericardial cavity, have been termed both 'auricular' and 'pericardial' glands. We will follow the terminology of Andrews and Jennings (1993): glands originating on the auricular wall are auricular glands, while those originating on the inner pericardial wall and projecting into the pericardial cavity are pericardial glands.

Auricular excretory glands appear to be the primitive condition in bivalves; their position in the auricle wall appears to impose a size constraint on the glands themselves, because an excessive development here would compromise auricular contraction. Most Pectinidae have auricular glands, but some species such as *Chlamys* (=*Azumapecten*) *ruschenbergerii* have both auricular and pericardial glands (White, 1942). The following description covers the general case (auricular glands); a good description of pericardial glands may be found in Eble (2001).

The auricular glands of *Pecten maximus* and *Chlamys* (= *Aequipecten*) *opercularis* were first described by Dakin (1909). More recent histological and ultrastructural studies of pectinid auricular glands include those of Meyhöfer et al. (1985), Andrews and Jennings (1993) and Morse and Zardus (1997). The general anatomical relationships of the scallop auricular glands are shown in Figure 3.21.2. The ultrafiltration barrier is the greatly folded basal lamina of the podocytes which cover the auricular glands (the cytoplasmic folds at the base of the podocytes are called pedicels, which serve to greatly increase the surface area of ultrafiltration). Within the underlying connective tissue are distinctive cells termed pore cells or brown cells (Morse and Zardus, 1997), which do not appear to participate in ultrafiltration; more will be said of these below. Almost the entire cell volume is filled with secretory products; their numbers in the auricular wall give this structure a slightly brownish colour. Haszprunar (1996) proposed the name rhogocyte (=Leydig's cell), based on the diagnostic feature of slits formed by the parallel pedicels rather than pores. Although quite dense in the auricular glands, as mentioned above, these cells are ubiquitous in the bivalve body and can be found as solitary wandering cells in the haemolymph, and so may also be considered as a type of haemocyte. Although a partial homology to podocytes has been suggested (Haszprunar, 1996), substantial ultrastructural differences exist (Morse and Zardus, 1997). Pore cells appear to function in metal ion transport, and may have a role in metal detoxification, complementing that of the kidney (see below) and supporting the suggestion of a homology with nephrocytes (Haszprunar, 1996).

Ultrafiltered haemolymph flows from the pericardial cavity to the kidneys via the reno-pericardial ducts or canals (Drew, 1906; Pelseneer, 1906; Dakin, 1909; Potts, 1967) (Figure 3.21.2), where it is further processed as described below.

Kidney

The kidneys of scallops appear as brownish, flattened sacs attached to the ventral face of the adductor muscle, partially occluded by the gonad. Figures 3.21.2 and 3.22.1 show each kidney consists of a straight tube, surrounded by glandular tissue (as opposed to the U-shaped tube found in many other bivalves). The tube has classically been divided into a proximal or pericardial section, and a distal section or posterior sinus. The proximal sections of the right and left kidney tubules are connected by a transverse branch on their outer surfaces (Dakin, 1909). The distal sections terminate in the renal or kidney openings (nephrostomes) to the pallial cavity (Figure 3.6.1). Given their dual function of evacuating kidney fluid and gametes, these openings are also called the reno-genital apertures.

Although historically considered to reflect separate secretory and excretory functions (Franc, 1960), the division of the kidney tubule into proximal and distal sections is quite arbitrary, as it is lined by a single type of epithelial cell (Jennings, 1984, cited by Andrews, 1988). There exists a close anatomical relationship between the kidney and the parietovisceral ganglion (Figure 3.22.1), and neurosecretory cells have been shown to penetrate the kidney tissue (Le Roux et al., 1987). The kidneys and the pericardial glands usually display a brownish coloration, due to the presence of granular concretions within their cells (Dakin, 1909).

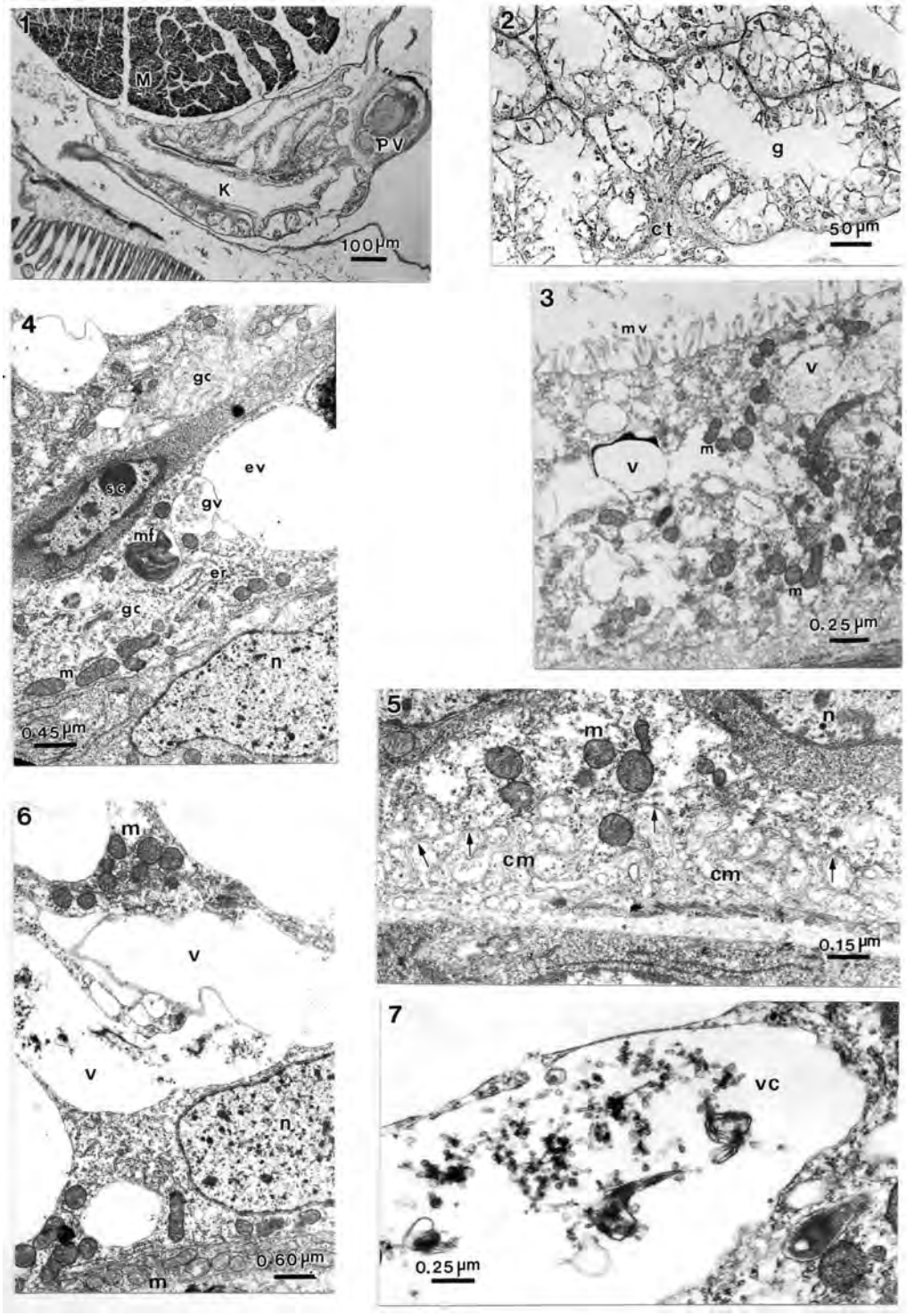


FIGURE 3.22 Tissue and cellular details of the kidney in *Pecten maximus*. Figure 3.22.1: Histological section of *P. maximus*, showing relationships between adductor muscle (M), kidney (K), and the parietovisceral ganglion (PV). Figure 3.22.2: Histological section of the kidney tubules, showing greatly vacuolated gland (g) cells. ct, connective tissue. Figure 3.22.3: Transmission electron micrograph of apical pole of a glandular kidney cell. Note the numerous mitochondria (m), the apical microvilli (mv), and the variously sized vacuoles (v). Figure 3.22.4: Transmission electron micrograph showing two glandular cells (gc) separated by a supporting cell (sc). An empty vacuole (ev), a granular vacuole (gv), and a myelin figure-containing vacuole (mf) are visible in one gland cell. er, endoplasmic reticulum; m, mitochondria; n, nucleus. Figure 3.22.5: Transmission electron micrograph of the basal poles of two glandular cells. Note the greatly indented cell membrane (cm, arrows). m, mitochondria; n, nucleus. Figure 3.22.6: Transmission electron micrograph of a greatly vacuolated glandular cell. The vacuoles (v) contain variously sized particles. m, mitochondria; n, nucleus. Figure 3.22.7. Transmission electron micrograph showing detail of diverse vacuolar contents (vc). *Micrographs courtesy of A. Donval and P. Beninger, Université de Bretagne Occidentale, Brest, France.*

The kidney tubules open into numerous glandular ducts, giving the kidney tissue a spongy appearance (Turchini, 1923; Andrews, 1988), as in Figure 3.22.2. The columnar external epithelium of the kidney rests upon a lacunar muscular-connective tissue (Figure 3.22.2). The nephrocytes lining the kidney tubules of *Pecten maximus* have a basal nucleus with dispersed chromatin and few organelles, with the exception of numerous mitochondria (Figures 3.22.3–3.22.6). These cells contain many variously sized vacuoles, which may fill most of the cell volume (Figures 3.22.2, 3.22.3, 3.22.6, and 3.22.7). Some vacuoles appear empty, while others contain variably electron-dense granules (Figure 3.22.7) or myelin figures (=membrane whorls, indicative of cellular degradation; Figure 3.22.4). The apical vacuole is a site of heavy metal concretion, as is the basal lamina (Nigro et al., 1992). The cell membrane of the basal pole of the glandular cells presents numerous deep indentations (Figure 3.22.5), while the apical pole is covered with microvilli (Figure 3.22.3). These two characteristics indicate that these cells are sites of considerable exchanges with the renal fluid. Supporting cells are interspersed among the glandular cells of the kidney tubules (Figure 3.22.4).

Summary: Pathway of Excretion

Given the complexity of even the main excretory pathway, it is useful to summarise the sequence and sites involved. Haemolymph passes into the heart auricles, where some of it, under the pressure of auricular contraction, filters across the basal lamina of the slits formed by the pedicels at the basal region of the podocytes lining the auricular glands. The filtrate then passes through the gaps between the podocyte bodies into the urinary space and diffuses into the pericardial cavity. This ultrafiltered fluid then flows through the reno-pericardial canal to the proximal portion of the kidney, towards the distal portion, and finally out through the nephrostome to the exhalent current of the pallial cavity, where it is voided in the excurrent flow.

Functions of the Kidney and Pericardial Glands

Numerous authors have attempted to identify the composition of the urinary fluid of bivalves and elucidate the functions of their excretory system (see Franc, 1960; Lucas and Hignette, 1983; Martin, 1983; Andrews, 1988). Dakin (1909) states that uric acid is not found in bivalve kidneys, and that hippuric acid is eliminated by the pericardial glands of scallops; however, with the exception of Brunel's (1938) studies, which mention the existence of an allantoicase, a urease, an allantoinase and a uricase, little is known concerning the processes of organic nitrogen catabolism (Franc, 1960).

The site of primary urine formation is now known to be the auricular or pericardial glands (Meyhöfer et al., 1985; Andrews and Jennings, 1993). Further processing occurs within the kidney nephrocytes and auricular gland pore cells, where various substances, notably metal ions, are accumulated, and which may combine with each other to form intracellular concretions or granules (Figure 3.22.7). These concretions may be excreted either as solids, re-dissolved and eliminated as solutes, or grow until the intracellular fluid pressure ruptures the glandular cell, liberating the concretions (Franc, 1960). Histochemical and ultrastructural studies in various bivalves suggest an apocrine-type secretion of renal concretions as residual bodies via the lysosomal-vacuolar system (Lowe and Moore, 1979; Pirie and George, 1979; George et al., 1980; Sullivan et al., 1988). In mussels, the concretions observed in the renal cells and in the pericardial gland pore cells are extruded to the renal tubules and excreted with the urine, which thus contains much particulate matter (Pirie and George, 1979).

Mineral concretions were discovered very early in the kidneys of a variety of scallops, including *Argopecten irradians* (Kellogg, 1892), *Placopecten magellanicus* (Drew, 1906), *Pecten maximus*, and *Chlamys* (= *Aequipecten*) *opercularis* (Dakin, 1909). Several of these authors also gave a qualitative chemical analysis of the concretions, showing the predominance of calcium phosphate, the nearly universal absence of urates, and traces of metals such as magnesium and iron (Lucas and Hignette, 1983). The accumulation of these metals was considered to represent either a long-term storage, or a means of detoxification–excretion of toxic elements (Simkiss, 1976; Coombs and George, 1977; Nigro et al., 1992).

Using diverse techniques (differential centrifugation, X-ray diffraction, atomic absorption spectrophotometry, and microanalysis), the quantitative composition of metals within the concretions has been determined, notably for *Pecten maximus* (George et al., 1980) and *Argopecten irradians* (Doyle et al., 1978; Carmichael et al., 1979). The concretions are chiefly composed of amorphous metal phosphates, which appear to be more closely related to the brushite–monetite series of phosphorites than to apatite (George et al., 1980). In *P. maximus*, for example, the elements Ca, Zn, Mn, and P comprise 50% of concretion dry weight, while organic material constitutes approximately 21–26% of concretion dry weight (George et al., 1980). In the Antarctic scallop *Adamussium colbecki*, the dominant metals in the nephrocytes

were Fe, Zn and Cu, and in the amoebocytes, Ag, Se, Fe, and Cu (Nigro et al., 1992). The organic substances identified are proteins (6–9%) and oxalate (7%; Overnell, 1981). In addition to these static observations, studies of the seasonal variations in composition of the concretions have been performed, as well as studies of the dynamics of their formation (Bryan, 1973; Lucas and Hignette, 1983; Yevich and Yevich, 1985).

Through their accumulation of various trace metals in concretions (especially kidney granules), bivalves may act as biological concentrators (Martoja et al., 1975). The analysis of these metals or of their radioactive isotopes may thus be a means of monitoring environmental pollution (Chipman and Thommeret, 1970; Masson and Ancellin, 1976). The *in vitro* bioaccumulation of cadmium has been demonstrated in this way in the kidneys of *Argopecten irradians* (Carmichael and Fowler, 1981); however, extreme care must be exercised in the interpretation of data from environmental monitoring studies, as the natural variation of granule elemental composition may be very large (George et al., 1980).

Excretion and Osmoregulation

Throughout the Metazoa, excretion, and osmoregulation are closely connected functions. In bivalves, osmoregulation has been studied either by determining osmotic element fluctuations in whole tissue and/or in the haemolymph and pallial fluid (Shumway, 1977a; Shumway et al., 1977; Shumway and Youngson, 1979; Pierce, 1982; Somero and Bowlus, 1983; Beninger, 1985; Kube, et al., 2006), such that virtually nothing is known about the exact anatomical sites of the various osmotic responses observed. This is a field of research waiting to be explored.

REPRODUCTIVE SYSTEM

A sound knowledge of the structure and function of the scallop reproductive system is obviously necessary for the understanding of their ecology, aquaculture, and fisheries. For these reasons, the scallop reproductive system merits detailed consideration.

Sexuality: Gonochory, Hermaphroditism, and Their Variants

Bivalves have long been considered gonochoric (sexes separate and invariable) in their overwhelming majority (De Lacaze-Duthiers, 1854; Pelseneer, 1894; Coe, 1943b, 1945; Sastry, 1979). The presence of a few hermaphroditic individuals in normally gonochoric species led Coe (1945) to conclude that primary germ cells (stem cells) are potentially ambisexual, cellular differentiation being based on an inhibition of one or the other potentiality. An incomplete inhibition would thus produce animals with varying degrees of hermaphroditism.

Contrary to most bivalve families, the Pectinidae are predominantly hermaphroditic, with many specific and individual variations, and a general tendency towards protandry (producing first male and later female gametes; Coe, 1945). Environmental factors may influence sex determination. In *Argopecten irradians*, low food and temperature levels result in male gametogenesis, whereas oogenesis is suppressed if food is absent (Sastry, 1968).

Scallops cited as being predominantly gonochoric are *Chlamys tigerina*, *Chlamys* (=*Palliolum*) *striata*, *Chlamys furtiva* (=*Palliolum incomparabile*) (Reddiah, 1962), *Placopecten magellanicus* (Drew, 1906; Posgay, 1950; Naidu, 1970), *Patinopecten* (=*Mizuhopecten*) *yessoensis* (Yamamoto, 1943), and *Chlamys islandica* (Sundet and Lee, 1984). Even in strictly gonochoric species, a low frequency of hermaphrodites may be found (Merrill and Burch, 1960; Wakui and Obara, 1967; Naidu, 1970; Ozanai, 1975), while gonochoric features may be found in some normally hermaphroditic species (Mason, 1958).

Most simultaneous hermaphroditic scallop species (male and female gametes developing at the same time) have gonads with distinct male and female portions, the male portion of the gonad being proximal and the female portion distal; however, a general tendency towards protandry precludes self-fertilisation in most cases (Sastry, 1963; Fretter and Graham, 1964). Although self-fertilised eggs are considered inferior to cross-fertilised ones in *Argopecten irradians concentricus* (Sastry, 1965), self-fertilisation may be a natural phenomenon in *Pecten maximus* (Wilkins, 1978).

Origin and Formation of the Gonad

In the post-larval scallop, the gonad differentiates after most of the other organs; the organogenesis of this structure will therefore be described here. Primordial germ cells first appear in juvenile *Chlamys* (=*Mimachlamys*) *varia*

in the region bounded dorsally by the pericardium, anteriorly by the developing kidney and postero-ventrally by the margin of the adductor muscle. They arise from a group of mesodermal cells (Raven, 1966; Wada, 1968), and may be observed in *M. varia* in animals as young as 6 months, measuring only 2–3 mm (Lucas, 1965). In most pectinids, however, the gonad reaches its first maturity after 1 year (Reddiah, 1962; Ozanai, 1975).

Development of the gonad begins with the ventral extension of primordial germ cells in the form of tubules accompanied by loose connective tissue (Coe, 1943a, 1945; Lucas, 1965). The tubules then become folded, assuming the acinal-type structure of the gonad. The evacuating ducts differentiate as the germ cells multiply along the walls of the acini. This ontogenetic sequence suggests that a tubular gonad organisation is a primitive gonad feature, which may be found, however, in both the Protobranchia (*Acharax aline*; Beninger and Le Pennec, 1997) and the more recent Veneroidea (*Tapes philippinarum*; Beninger, personal observations). Only the acinal type organization has been reported in adult pectinids.

Anatomy, Histology, and Ultrastructure of the Adult Gonad

Since the first published anatomical description of a pectinid gonad *Chlamys* (=*Mimachlamys) varia* by De Lacaze-Duthiers (1854), numerous authors have used basic histological techniques to study the dynamic anatomy of this organ in various scallop species. Sastry (1979) provides a list of 15 pectinid species whose spawning periods have been determined, usually by microscopic examination of the gonad. Surprisingly, few ultrastructural studies of gonad structure and gametogenesis have been performed in bivalves, notably those of Pipe (1987a,b; *Mytilus edulis*), Eckelbarger and Davis (1996a,b; *Crassostrea virginica*), Beninger and Le Pennec (1997; *Acharax alinae*), and Eckelbarger and Young (1999; *Bathymodiolus childressi*). Fortunately, similar studies have also been performed in some detail for various pectinid species (Dorange and Le Pennec, 1989a,b; Dorange et al., 1989a,b). The following account is based on this body of work, supported by micrographs.

In summary description, the gametogenic gonad contains a large number of acini, whose walls are composed of tightly interwoven, fibrous connective tissue cells, from which the stem cells (primary germ cells) differentiate. The lumen of the acinus is more or less filled with sex cells in varying stages of gametogenesis (Figure 3.23.2), depending on the reproductive state of the gonad. The acini empty into a network of ramified evacuating tubules, which consolidate as they approach the kidney (Figure 3.23.3). The gametes are shed into the pallial cavity via the reno-genital openings of the right and left kidneys (Figure 3.21). In some species and latitudes, the acinal organisation disappears over the winter months, leaving only loose connective tissue, which re-forms acini in the spring (Naidu, 1970). The intestine and part of the crystalline style also occupy some of the gonad (see 'Digestive System and Digestion' section). Between these structures is a lacunar connective tissue, and the gonad is bounded by a thick outer epithelium (Figures 3.23.1 and 3.26).

Although in many species, the male gonad (or portion in simultaneous hermaphrodites) is yellowish-white and the female gonad (or portion) is variably reddish-orange, sexing cannot be accomplished on the basis of gonad colour in all scallop species (Lucas, 1965; Mottet, 1979).

Outer Epithelium

Apart from the brief descriptions of Mason (1958, 1963) for *Pecten maximus* and Lucas (1965) for *Chlamys* (=*Mimachlamys*) *varia*, most of our knowledge concerning the outer epithelium is derived from the electron microscopic studies of Dorange et al. (1989a) for *P. maximus*. The following description is based on the observations of the latter study.

The outer epithelium is generally cuboidal, although some regions containing non-differentiated cells may show a pseudostratified appearance. Three cell types dominate in the epithelium: microvillous cells, ciliated cells, and mucocytes. Ultrastructural details for each cell type may be found in Dorange et al. (1989a). These cells rest upon a thick, often deeply folded basal lamina, indicative of translocation (Figures 3.23.4–3.23.6).

Perigonadal Connective Tissue

The perigonadal connective tissue contains various cell types, as well as abundant collagen fibres. Smooth muscle cells are frequently observed (Figures 3.23.1 and 3.23.4); hence the designation 'muscular-connective tissue' is in fact more appropriate. Mason (1958, 1963) suggests that this muscular-connective tissue may, through localised contractions, assist in the evacuation of gametes. The myocytes may also aid in the circulation of haemolymph within the gonad (Mason, 1958, 1963).

Among the other cell types observed in the perigonadal connective tissue are macrophage-like cells, fibroblasts, and large vacuolar cells. The macrophage-like cells appear to correspond to 'quiescent' type II haemocytes,

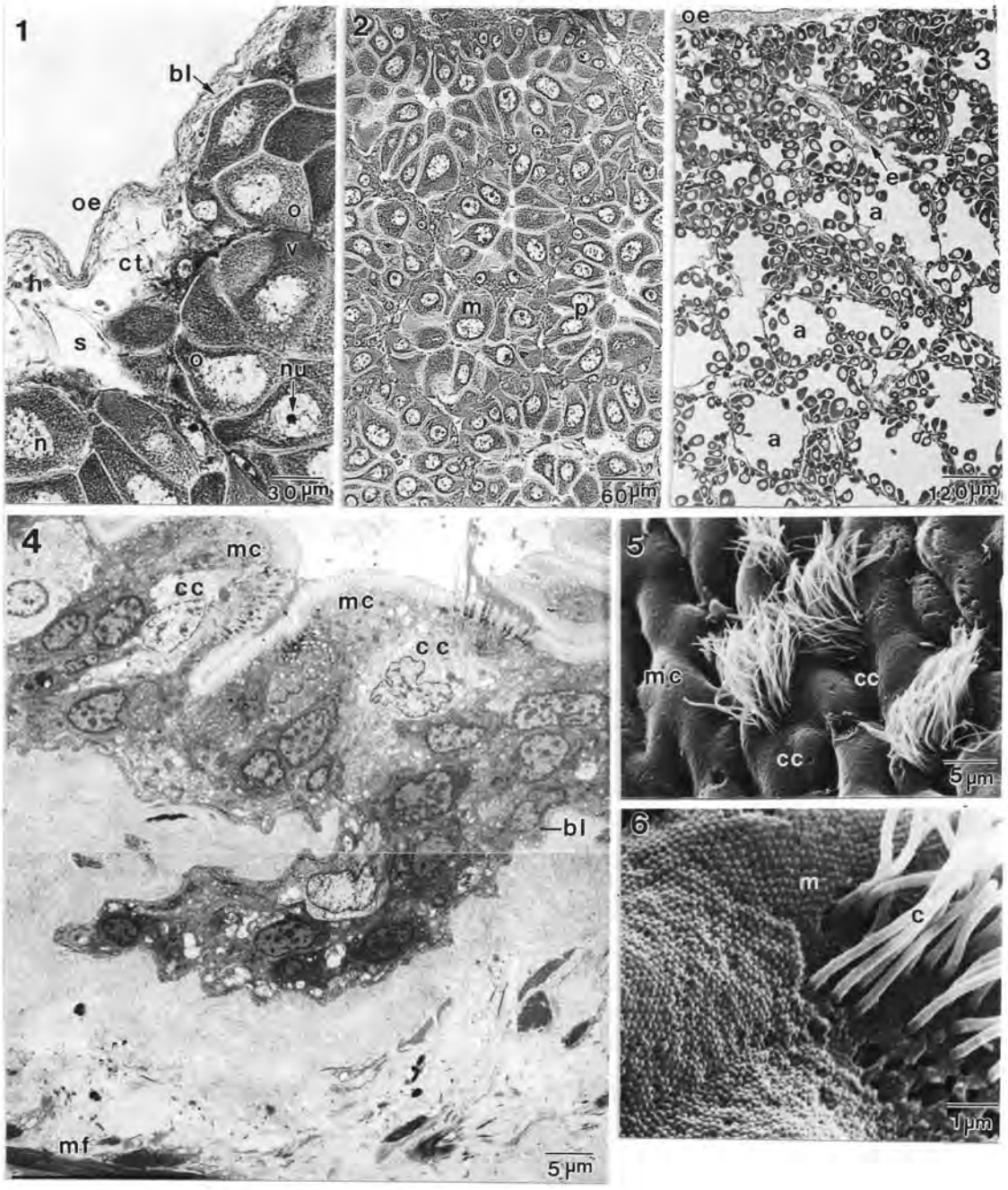


FIGURE 3.23 Structure of the female gonad in *Pecten maximus*. Figure 3.23.1: Histological section of the outer portion of a mature female gonad. bl, basal lamina; ct, perigonadal connective tissue; h, haemocytes; n, nucleus containing dispersed heterochromatin; nu, nucleolus; o, oocyte; oe, outer epithelium; s, haemolymph sinus; v, vitellus. Masson trichrome stain. Figure 3.23.2: Histological section of the interior of a mature female gonad, showing mature (m) and pedunculated (p) oocytes. Masson trichrome stain. Figure 3.23.3: Histological section of a partially spawned female gonad. Most remaining oocytes are pedunculated. a, acinus; e, evacuating duct opening into acinus; oe, outer epithelium. Masson trichrome stain. Figure 3.23.4: Transmission electron micrograph of the gonad outer epithelium. bl, basal lamina; cc, ciliated cells; mc, non-ciliated microvillous cells; mf, muscle fibres. Figure 3.23.5: Low-power scanning electron micrograph of the gonad outer epithelium. cc, ciliated cell; mc, non-cilated microvillous cell. Figure 3.23.6: Scanning electron micrograph detail of the gonad outer epithelium. m, microvilli; c, cilia. *Micrographs courtesy of G. Dorange, Université de Bretagne Occidentale, France.*

which are not involved in internal defence, but rather in the assimilation and transport of the products of gamete lysis following atresia (Poder, 1980; Dorange et al., 1989b). This topic will be dealt with in detail in the 'Gametogenesis' section.

Inter-acinal Connective Tissue

As the gametes are produced in acini and not follicles, the name inter-acinal connective tissue is now widely used to describe the lacunar tissue found between the acini. It is structurally similar to the perigonadal connective tissue (Figures 3.23.1 and 3.23.4). The amount of this tissue varies throughout the reproductive cycle, and it probably serves as an energy reserve for the developing gametes (Coe, 1943a; Beninger, 1987; Eckelbarger and Davis, 1996a).

Haemolymph Sinuses

These sinuses are present beneath the perigonadal connective tissue (Figure 3.23.1) and are particularly abundant in the inter-acinal connective tissue and at the peripheries of the evacuating ducts; the intestinal loop is surrounded by a large sinus (Figure 3.26). They are frequently associated with the infoldings of the outer epithelia, which increase the amount of surface area for exchange. Numerous haemocytes may be observed in these sinuses (see 'Cardio-vascular System' section), and macrophagous type II haemocytes are also present in the acini among the debris of oocyte lysis after spawning, during sexual resting periods, and in the later stages of atresia (see 'Gametogenesis' section).

Acini

The acini are irregularly bulb-shaped structures composed of an outer layer of tightly woven connective tissue, from which arise the inner layer of primordial germ (=stem) cells; the gametes produced by these cells are eventually shed via the evacuating ducts. The developing gametes are readily visible along the inner margins of the acini, variably filling the lumina depending on the stage of gametogenesis (Figures 3.23.1–3.23.3, 3.25.1, 3.26.1, 3.28.1, 3.28.2 and see 'Gametogenesis' section).

Evacuating Ducts

The ciliated columnar epithelium of the evacuating ducts (Figure 3.28.1) rests upon a basal lamina, which is irregular at the junction of the gonoduct and acinus. The evacuating ducts coalesce to a single gonoduct leading to the kidney; in the simultaneous hermaphroditic species *Minnivola pyxidatus*, a visible reproductive papilla may be seen on the gonad at the junction of the male and female gonoducts (Morton, 1996).

Gametogenesis

Gametogenesis and spawning are controlled by both endogenous and exogenous factors, among which the most important are temperature and food (Sastry, 1966, 1968; Taylor and Capuzzo, 1983), although in the field, depth is also important (Iglesias et al., 2012). The process of gametogenesis in bivalves has been detailed in several works, such as those by Raven (1961), Sastry (1979), Dohmen (1983), Pipe (1987), Eckelbarger and Davis (1996a,b), and Morse and Zardus (1997). For the Pectinidae, the principal histological studies are those of Coe (1945), Mason (1958, 1963), Lubet (1959), Reddiah (1962), Sastry (1963, 1966), Lucas (1965), Naidu (1970), and Allarakh (1979). Ultrastructural studies have been performed on the gonads of *Pecten maximus* (Dorange and Le Pennec, 1989a,b; Dorange et al., 1989a,b), allowing a better understanding of the events involved in the reproductive cycle. The following description is based largely on these ultrastructural studies.

Oogenesis

In pectinids, as in all other molluscs (and most other animals as well), complete meiosis of the female gametes is delayed until after spawning and fertilisation (see Longo, 1983 for review). The mature scallop oocyte is blocked in either prophase I or metaphase I of meiosis; the remaining meiotic stages are rapidly accomplished after fertilisation. This is readily observed *in vitro* by the appearance of polar bodies after fertilisation (Desilets et al., 1995).

Oogenesis may be divided into three distinct stages: pre-meiotic, pre-vitellogenic, and vitellogenic; these are schematically summarised in Figure 3.24.

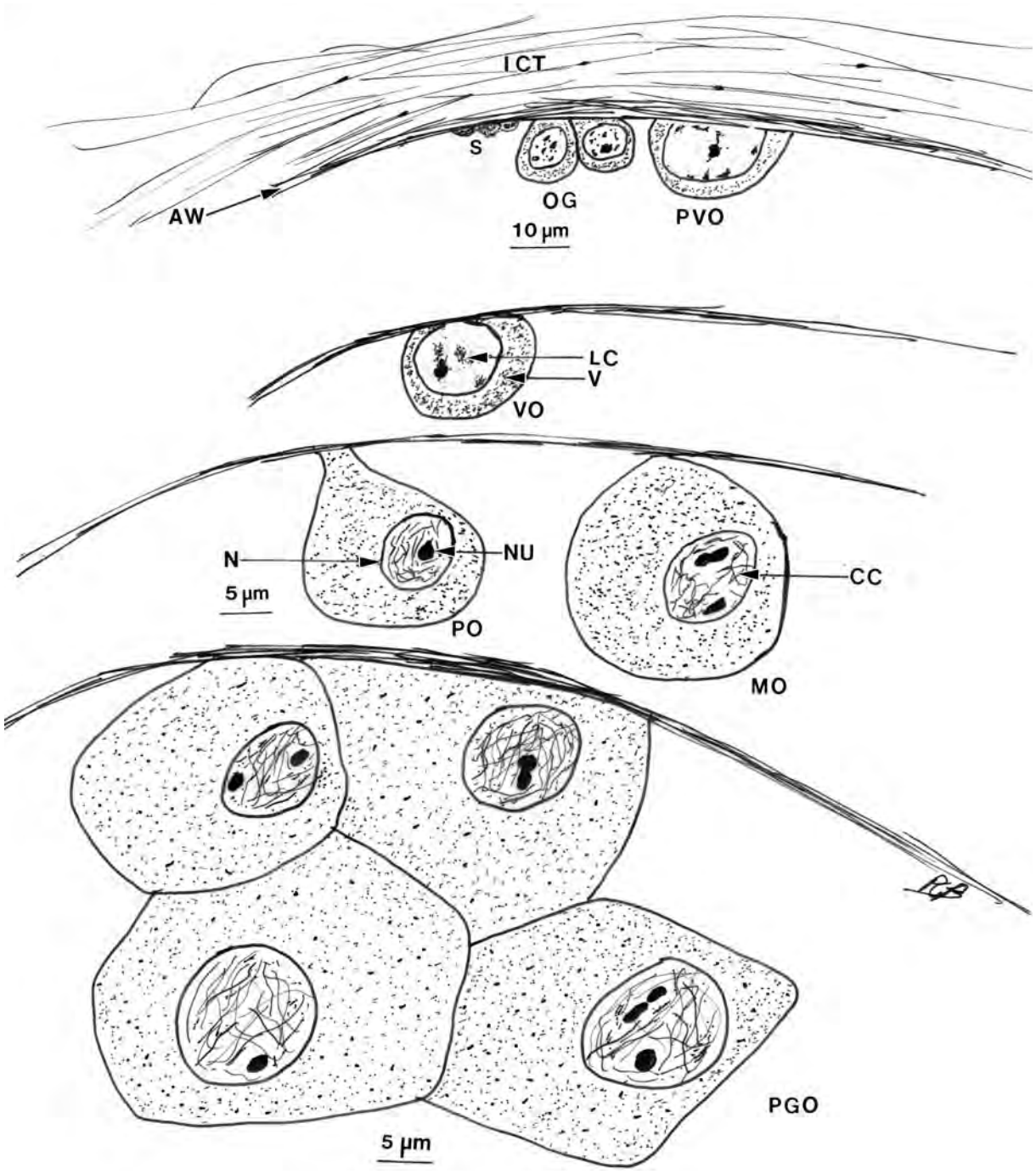


FIGURE 3.24 Schematic overview of oogenesis in *Pecten maximus*. Stem cells (S) arise from the connective tissue of the acinus wall, itself derived from the inter-acinal connective tissue (ICT). The stem cells become oogonia (OG), which, after several divisions, become pre-vitellogenic oocytes (PVO), with a visible nucleolus and clumped chromatin within the nucleus. These become vitellogenic oocytes (VO), with characteristic lampbrush chromosomes (LC) sometimes visible in light micrographs (zygotene-pachytene and diplotene of meiotic prophase 1), indicative of active transcription of many genes. As the vitelline reserves (V) are built up, the oocyte grows towards the acinal lumen, remaining attached by a thinner peduncle (pedunculated oocyte, PO). Condensed chromatin is visible as thin fibres in the nucleus, and several variously shaped nucleoli (NU) may be present, indicating active ribosome synthesis and assembly, important for the protein synthesis necessary for vitteline constitution. Mature oocytes (MO) detach from the acinal wall and fill the acinal lumen, where they become tightly packed and hence assume a slightly polygonal shape in section (polygonal oocyte, PGO).

Pre-meiotic Stage

The stem cells, which arise from the connective tissue forming the walls of the acini, differentiate to primary oogonia (8–10 μm), characterised by a high nuclear-cytoplasmic ratio. The nucleus contains clumped chromatin and occasionally a single, 3–4 μm nucleolus. Some mitochondria and endoplasmic reticulum (ER) cisternae are present in the cytoplasm. These cells divide mitotically to produce secondary oogonia. This stage is termed pre-meiotic because all divisions are purely mitotic.

Pre-vitellogenic Stage

The secondary oogonia enter into the first prophase of meiosis to yield pre-vitellogenic oocytes (Raven, 1961). During the pre-vitellogenic stage, the nucleus and cytoplasm of the oocyte increase in volume. The ultrastructural characteristics of the nucleus reveal young oocytes in leptotene, zygotene–pachytene, and diplotene stages of prophase (Figure 3.25.2). In leptotene, the chromosomes become visible, whereas the nucleolus disappears. In zygotene–pachytene, the round or ovoid cells are easily identified due to the presence of the synaptonemal complex and the familiar lampbrush chromosomes.

As they enter diplotene, the oocytes elongate (Figure 3.25.2). With the reappearance of the nucleus, dense aggregates (probably nuclear extrusions rich in ribonucleotides) accumulate in the cytoplasm. At this stage, auxiliary cells (Coe, 1943a; Mason, 1958, 1963; Raven, 1966; Dorange and Le Pennec, 1989a) migrate from the periphery of the acinus, establishing an intimate contact with the developing oocytes (Figures 3.25.2 and 3.25.4). The auxiliary cells are rarely distinguishable histologically. The ultrastructural characteristics of the auxiliary cells in *Pecten maximus* are similar to those described for *Mytilus edulis* (Pipe, 1987) and *Crassostrea gigas* (Eckelbarger and Davis, 1996a). These cells participate in oocyte maturation as described below.

Vitellogenesis and Metabolite Transport to the Oocyte

Knowledge of the exact pathways and mechanisms of metabolite transfer to the developing gametes is rather limited. A summary of known and proposed pathways may be found in Le Pennec et al. (1991), including a proposed pathway from the gonad intestinal loop. Experimental support for this pathway has been provided using ferritin histochemistry (Beninger et al., 2003). Ferritin molecules are absorbed by the intestinal epithelial cells, transferred to the basal lamina, incorporated into vacuolated haemocytes, which migrate along connective tissue fibres to the acini (Figure 3.26). The haemocytes are able to penetrate the acinal basal lamina and transfer the ferritin to developing oocytes. It is quite possible that similar haemocytes arrive in the acinus from the digestive gland. The relationship between these migrating haemocytes and auxiliary cells (see below) is not yet clear; the former may serve as intermediaries between the intestine and the acinus.

Developing oocytes enter into vitellogenesis in the diplotene stage (Dorange et al., 1989b). Their size increases and they progressively become pedunculated (Figures 3.24, 3.25.1, and 3.25.4). Various nuclear, cytoplasmic, and membranal modifications occur before the oocyte detaches from the acinus wall.

Cortical glycoprotein granules become progressively denser in the cytoplasm while the oocyte is still largely attached to the underlying connective tissue. At this stage, the ER is abundant. As the oocyte develops, the cortical granules and Golgi apparatus multiply. There is an intense production of vesicular and lamellar ER, as well as of various vitelline inclusions (Figures 3.25.1, 3.25.3, and 3.25.4). Three or four dictyosomes also appear at this point.

Throughout oogenesis, the attached auxiliary cells also present cytological modifications as their cytoplasmic volume increases. The granular ER multiplies, indicating intense protein synthesis. Mitochondria, smooth ER vesicles, α-glycogen vesicles, and lipid-like globules appear in the cytoplasm. Similar ultrastructural changes have been observed in the auxiliary cells of *Mytilus edulis* (Pipe, 1987) and *Crassostrea gigas* (Eckelbarger and Davis, 1996a). Endocytotic figures may be seen between the developing oocyte and the auxiliary cell, indicating a transfer of nutrients.

The plasma membrane changes as the oocyte becomes peduncular. At the apical pole, microvilli appear and a fibrillar glycocalyx develops, forming the vitelline envelope. This envelope initially appears close to the auxiliary cell and progressively surrounds the oocyte (Figure 3.25.3). Close contact is maintained with the auxiliary cell via zonula adherens type junctions. Near the adherance zone, fibril-containing vacuoles are visible in the cytoplasm of the auxiliary cells.

The auxiliary cells detach from the oocytes at the end of the peduncular or late-vitellogenic stage. The cytoplasm of the auxiliary cells then becomes vacuolated and myelin figures appear, indicative of membrane breakdown (Figure 3.25.2).

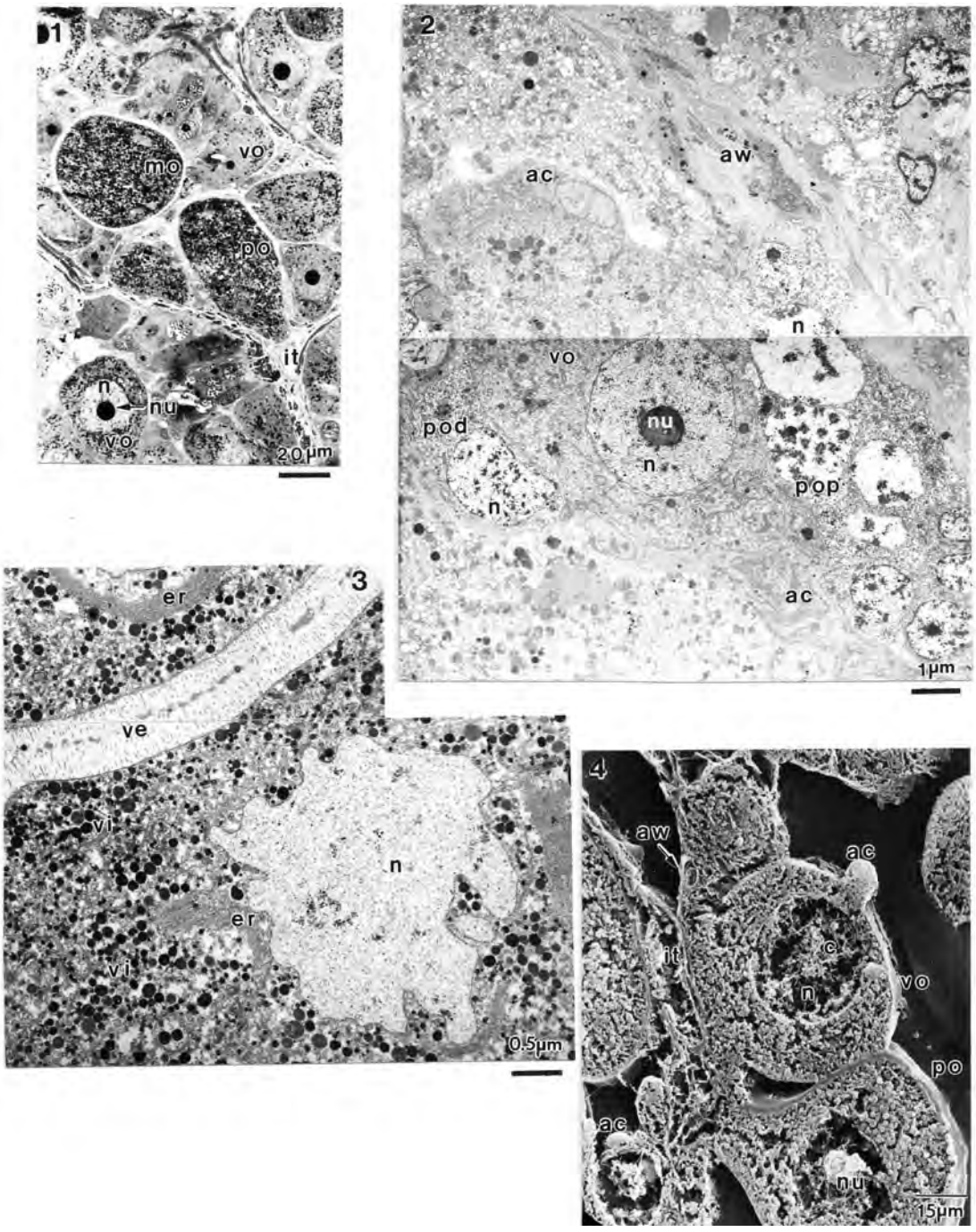


FIGURE 3.25 Cellular details of oogenesis in *Pecten maximus.* Figure 3.25.1: Semi-thin resin section of oocytes in various stages of development. it, inter-acinal connective tissue; mo, mature oocyte; n, nucleus; nu, nucleolus; po, pedunculated oocyte; vo, oocyte at beginning of vitellogenesis. Figure 3.25.2: Transmission electron micrograph of oocytes in various stages of development. Note the auxiliary cells (ac) adhering to the vitelline envelope. aw, acinus wall; it, inter-acinal connective tissue, n, nucleus; nu, nucleolus; pod, pre-vitellogenic oocyte in diplotene stage of first meiotic prophase; pop, pre-vitellogenic oocyte in pachytene stage of first meiotic prophase; vo, vitellogenic oocyte. Figure 3.25.3: Transmission electron micrograph of part of vitellogenic oocyte. Note abundant endoplasmic reticulum(er), interspersed among the vitelline inclusions (vi) which they secrete. n, nucleus; ve, vitelline envelope. Figure 3.25.4: Scanning electron micrograph of oocytes in various stages of development. ac, auxiliary cell; aw, acinus wall; c, chromatin within nucleus (n); it, inter-acinal connective tissue; nu, nucleolus; po, pedunculated oocyte surrounded by vitelline envelope; vo, vitellogenic oocyte. *Micrographs courtesy of G. Dorange, Université de Bretagne Occidentale.*

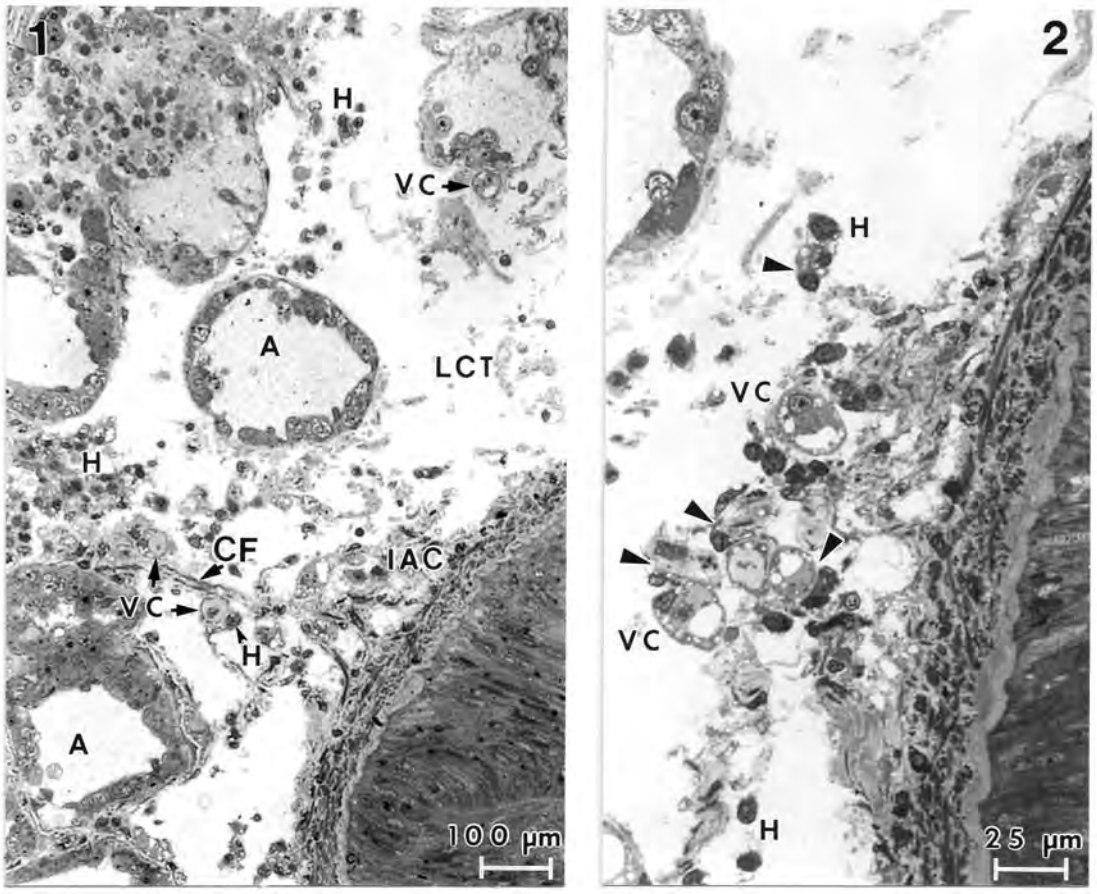


FIGURE 3.26 Anatomy of the intestinal loop pathway of metabolite transfer to developing oocytes in *Pecten maximus*. Semi-thin sections of the epithelium of the gonad intestinal loop. Toluidine blue stain. Figure 3.26.1: Low-power micrograph showing proposed anatomical pathway for transfer of metabolites from intestine to haemocyte (H)-vesicular cell (VC) couples, and thence to acini (A) via intestine–acinus transfer complex (IAC), and connective fibres, (CF), within loose connective tissue (LCT). Figure 3.26.2: Detail of an intestinal-acinus transfer complex, showing greatly vacuolated vesicular cells (VC) along pathway to acinus. Smaller haemocytes (H), with extensive filamentous cytoplasmic projections, can be seen in close contact with the vacuolated vesicular cells (arrows). Parts of another pathway may be observed in the upper right quadrant of the micrograph. *From Le Pennec et al. (1991).*

At the end of vitellogenesis, the thick vitelline envelope is slightly separated from the cytoplasmic membrane by a vitelline space, while vitelline reserves are abundant in the cytoplasm. β-glycogen particles are present, along with typical ringed lamellae whose function is not known. Cortical granules are numerous at the periphery of the oocyte.

The mature oocytes of scallops measure 15–120 μm in diameter, depending on the species (Table 3.1). In a mature gonad, they often assume a polyhedral (polygonal in section) shape due to crowding in the acini, but resume a rounded shape when spawned.

Oocyte Atresia

In the medical literature, the term 'ovarian follicular atresia' refers to the degeneration and resorption of several follicles and their ovules (a form of apoptosis) prior to the maturation and release of one ovule from a healthy follicle. This term has been carried over to the context of oocytes in any animal system. Although accounts of oocyte atresia are very widespread in the vertebrate literature, the phenomenon has been very poorly studied in bivalves. Degenerating residual gametes (after spawning) are often mentioned, but few studies have reported atresia prior to spawning (Lubet et al., 1987), and fewer still have reported the ultrastuctural events involved (see Albertini, 1985; Lubet et al., 1986; Pipe, 1987 for *Mytilus edulis*; and Vaschenko et al., 2013 for *Crassostrea angulata*). One of the first observations of bivalve oocyte atresia was that of Tang (1941) in

TABLE 3.1 Dimensions (μm) of Mature Gametes in Various Pectinids

Species	Oocytes	Spermatozoa		References
		Head	Flagellum	
Aequipecten opercularis	50–70			Amirthalingam (1928)
Mimachlamys varia	50–70	1.5–2		Reddiah (1962)
	45–50	2	45	Lucas (1965)
	65			Le Pennec (1978)
Chlamys distorta (=*Talochlamys pusio*)	58	2		Lucas (1965)
	60–70			Le Pennec (1978)
Chlamys tehuelcha	15–45			Christiansen and Olivier (1971)
Equichlamys bifrons	119.6			Dix (1976)
Argopecten irradians	63			Sastry (1968)
Argopecten gibbus	60			Costello et al. (1973)
Placopecten magellanicus	80–90	1.5		Naidu (1970); Culliney (1974); MacDonald and Thompson (1986); Langton et al. (1987)
Pecten meridionalis (=*fumatus*)	71.1			Dix and Jardin (1975)
Pecten maximus	70–80			Tang (1941)
	80–90			Mason (1958)
	70			Le Pennec (1978)
	75			Lubet et al. (1987)
	65–70			Paulet et al. (1988)
Argopecten ventricosus		1.7	45	Dorange (pers. comm.)
		1.69		Maldonado-Amparo and Ibarra (2002)

Dimensions are for histologically or electron-microscopically processed material.

Pecten maximus. This phenomenon was later observed in *Chlamys tehuelcha* (Christiansen and Olivier, 1971), and *Patinopecten* (=*Mizuhopecten*) *yessoensis* (Ozanai, 1975); the only ultrastructural studies of oocyte atresia in pectinids are those of Dorange and Le Pennec (1989a) and Dorange et al. (1989b) for *Pecten maximus*. Pre-spawning oocyte atresia is usually observed at the end of vitellogenesis, but even pre-vitellogenic oocytes may be affected due to the presence of lytic enzymes, which spread throughout the acinus when other oocytes lyse.

The histological appearance of atresic oocytes is characterised by a modification of their staining affinities, beginning with the nucleus, which loses its basophilic properties. The peripheral cytoplasm then becomes clear, and the oocytes take on a much-deformed 'jigsaw puzzle' appearance (Figure 3.27.2). Finally, the cell membranes rupture, discharging the nuclear and cytoplasmic contents, including lytic enzymes. In this terminal stage, the oocytes appear as empty, deformed sacs piled against each other (Figure 3.27.3).

In *Pecten maximus*, the first noticeable ultrastructural modification is the appearance of one or two nodules within the ER, consisting of concentric masses of cisternae. The rough and smooth ER then dilates, accompanied by a vacuolar degeneration of the cell. The mitochondria lose their cristae and become clear and deformed. The nuclear envelope expands into the cytoplasm, and the nucleus becomes multilobed prior to bursting (Figure 3.27.5). A peripheral cytoplasmic necrosis then develops. Granules (probably cortical granules released following rupture of the cell membrane) appear between the vitelline envelope and the plasma membrane. The perivitelline space increases, the microvilli detach, and the plasma membrane ruptures. Glycogen granules accumulate in the lysed zones and in the vitelline envelope, which finally bursts, discharging the oocyte contents into the acinus (Figure 3.27.4). Lytic debris spreads among the intact oocytes, while macrophage cells converge in the acinus (Dorange and Le Pennec, 1989a).

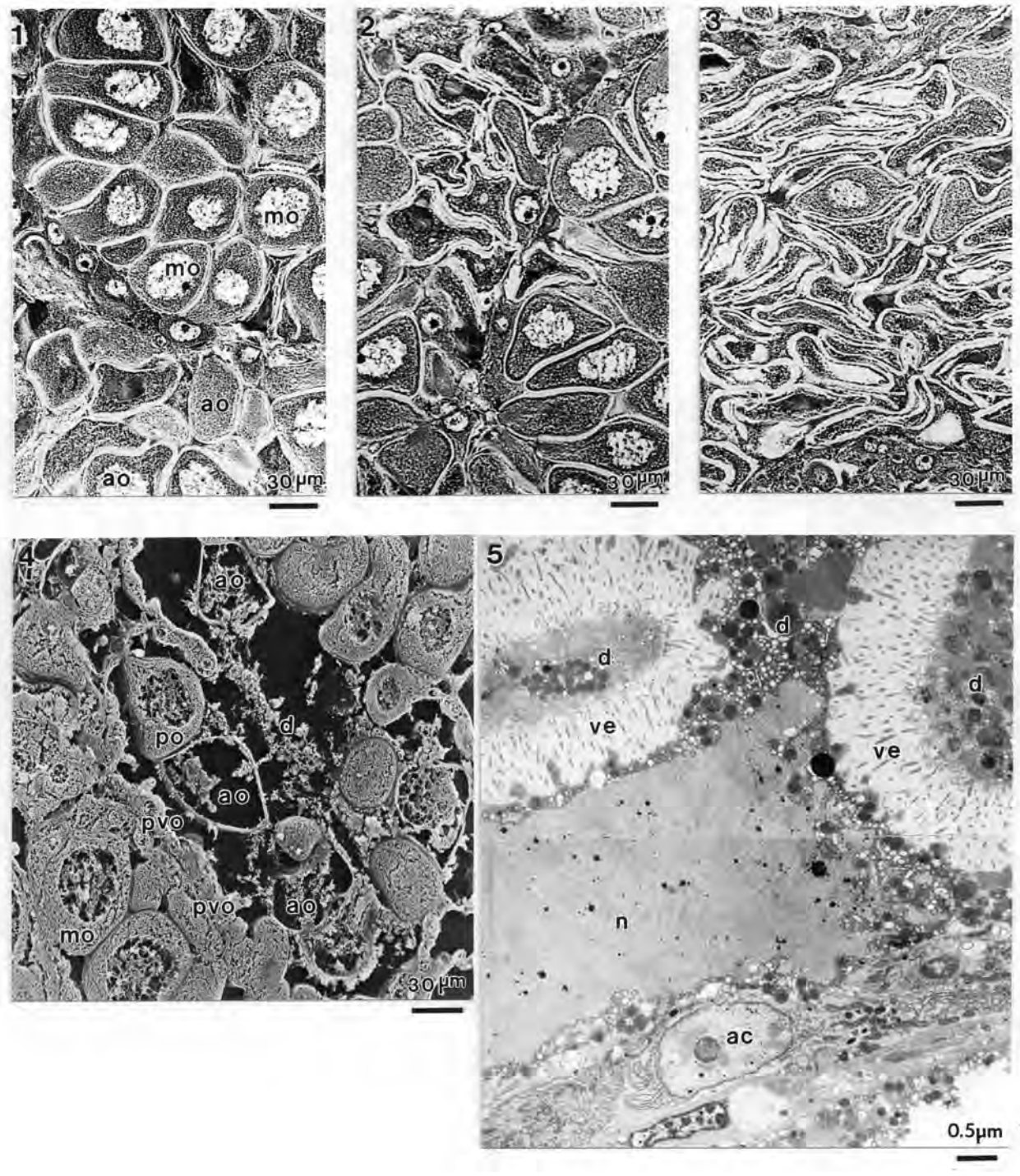


FIGURE 3.27 Oocyte atresia in *Pecten maximus*. Figure 3.27.1: Histological section of acini containing mature oocytes (mo) and atresic oocytes beginning lysis (ao). Figure 3.27.2: Histological section of gonad showing characteristic 'jigsaw puzzle' shape of oocytes in mid-atresia. Figure 3.27.3: Histological section showing advanced atresia. All oocytes are lysed. Masson Trichrome stain for Figures 3.27.1–3.27.3. Figure 3.27.4: Scanning electron micrograph of atresic oocytes (ao), healthy mature oocytes (mo), pedunculated oocytes (po), and pre-vitellogenic oocytes (pvo). Note lytic debris (d) releases from atresic oocytes. Figure 3.27.5: Transmission electron micrograph of an atresic oocyte in which the nucleus (n), bereft of recognisable chromatin, has lysed, and is now in contact with lytic debris from the cytoplasm (d). Parts of two other atresic oocytes are visible, with vitelline envelopes (ve) surrounding lytic debria (d). ac, auxiliary cell. *Micrographs courtesy of G. Dorange and YM Paulet, Université de Bretagne Occidentale, France.*

Although the regulating mechanism of oocyte atresia is not well known, Lubet et al. (1986) demonstrated a neuroendocrine control *in vitro* for *Mytilus edulis*; it is probable that a similar mechanism exists in scallops. Environmental stimuli such as temperature may act as cues. In *Pecten maximus* from St.-Brieuc Bay (France), spawning only takes place if the water temperature reaches 15.5–16.0 °C; if not, pronounced atresia occurs in the mature gonads (Paulet et al., 1988). As adductor muscle reserves are at their lowest at this time, it is possible that the lysed oocytes are recycled as maintenance substrates for the animal (Le Pennec et al., 1991b). Macrophagous type II haemocytes play an important role in the resorption of lytic debris and the redistribution of nutrients to the germ cells, which often begin to develop under favourable environmental conditions even as the last debris is cleared from the acini.

Spermatogenesis, Spermatozoon Ultrastructure, and Taxonomy

Contrary to the female gametes, the pectinid male gametes complete both meiotic divisions prior to spawning. Spermatogenesis in scallops has been studied by several authors, notably Lubet (1951, 1959), Mason (1958), Sastry (1963, 1966, 1979), Lucas (1965), and Naidu (1970), using light microscopy; and by Dorange and Le Pennec (1989b) and Maldonado-Amparo and Ibarra (2002), using both light and electron microscopy. The following description is based on these studies. Dimensions are for histologically or electron mocroscopically processed material.

The developing gametes are grouped in acini (Figures 3.28.1 and 3.28.2). Two cell types are visible in the acinus wall: stem cells, easily recognised by their finely granular nucleus and oval nucleolus, and spermatogonia, which are derived from these cells after several mitotic divisions (Figure 3.28.3).

The primary spermatogonia are approximately 12 μm long and 7 μm wide. Their oval nucleus is about 5 μm in diameter, containing dispersed clumps of chromatin and one or two nucleoli. Numerous mitochondria are present in the cytoplasm. Primary spermatogonia divide mitotically to produce secondary spermatogonia, from which they are not easily distinguished under the light microscope.

The secondary spermatogonia are numerous at the start of sexual maturity. They measure approximately 7 μm long and 5 μm wide, with a rounded nucleus containing one nucleolus. The chromatin clumps are denser and the cytoplasm is reduced in comparison to primary spermatozoa. During sexual maturation, polynuclear spermatogonia are frequently observed in *Pecten maximus* (Dorange et al., 1989b). The secondary spermatogonia become spermatocytes, which detach from the acinus wall (Figures 3.28.3–3.28.5). They are slightly smaller than the secondary spermatogonia. Primary spermatocytes present the various stages of the first meiotic division (Figure 3.28.3). The first meiotic division products are the secondary spermatocytes, which are rarely observed because the second meiotic division occurs almost immediately. Their nucleus contains a dense network of chromatin (Lucas, 1965).

The meiotic division of the secondary spermatocytes produces young spermatids, which differentiate to form older spermatids (Figure 3.28.4) which are small (approximately 3 μm in diameter), containing a dense, round nucleus (approximately 1.8–2.4 μm). Their most characteristic feature is the three to five mitochondrial spheres, which form a collar at the base of the nucleus (Figure 3.28.4). Several structural changes transform the spermatid into a mature spermatozoon (spermiogenesis). An annular Golgi structure, consisting of two concentric sacs, forms the acrosome, which elongates, invaginates, and becomes comma-shaped. The sacs then appear to fuse, giving rise to the definitive acrosome. The centriolar system migrates to the base of the nucleus and the distal-most centriole modifies to give rise to the flagellum. Throughout these latter stages of spermatogenesis, there is a progressive reduction of the cytoplasm.

The ultrastructure of bivalve spermatozoa has been intensively studied, due to their usefulness in elucidating phylogenetic and taxonomic relationships (e.g. Popham, 1979; Hodgson and Bernard, 1986; Healy, 1995, 1996; Eckelbarger and Davis, 1996b; Garrido and Gallardo, 1996; Le Pennec and Beninger, 1996; Beninger and Le Pennec, 1997; Morse and Zardus, 1997; Kafanov and Drozdov, 1998; Healy et al., 2000; Bieler et al., 2014). As underscored by Healy et al. (2000), specific data for pectinids are scarce; however, the ultrastructural features of *Pecten maximus* have been detailed in Dorange and Le Pennec (1989b) and in the previous editions of this volume (Beninger and Le Pennec, 1991, 2006). To date, the only comparative study of pectinid spermatozoon morphology and ultrastructure deals with 10 species of confirmed pectinids (Le Pennec et al., 2002). The following description is based upon these works.

Two general categories of pectinid spermatozoon have been defined: the more primitive Category 1, characterised by a rounded shape, and the more advanced, elongated Category 2 spermatozoon (Le Pennec et al., 2002).

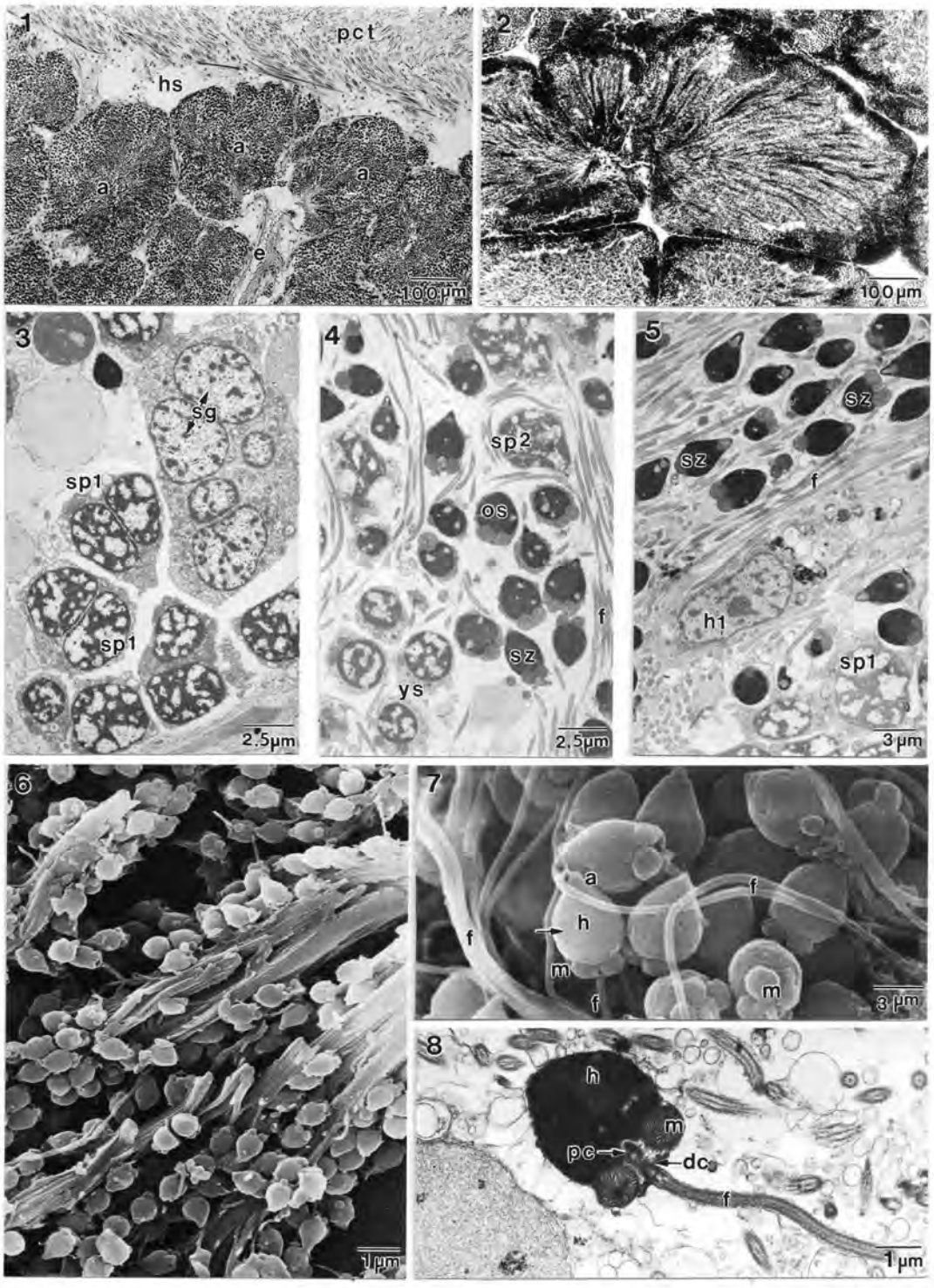


FIGURE 3.28 Spermatogenesis in scallops. Figure 3.28.1: Histological section of *Pecten maximus* gonad showing general organisation of acini (a) filled with developing gametes near perigonadal connective tissue (pct). An evacuating duct (e) drains two acini. A haemolymph sinus (hs) is visible. Figure 3.28.2: Histological section of a mature acinus in *Placopecten magellanicus*. Showing characteristic 'flow' pattern of mature spermatozoa towards the acinus lumen. Figure 3.28.3: Transmission electron micrograph of spermatogenesis in *P. maximus*. sg, spermatogonia dividing mitotically; sp1, primary spermatocytes near the end of the first meiotic division. Each sister cell will become a secondary spermatocyte. Figure 3.28.4: Transmission electron micrograph showing the development of the spermatids. f, flagellae; os, older spermatid; sp2, secondary spermatocyte, sz, spermatozoon; ys, young spermatid. Figure 3.28.5: Transmission electron micrograph of a relatively mature acinus in *P. maximus*. f, flagellae; h1, nucleus of macrophagous type I haemocyte; sp1, primary spermatocyte; sz, spermatozoa. Figure 3.28.6: Scanning electron micrograph showing orientation of mature spermatozoa within an acinus of *P. maximus*. Figure 3.28.7: Scanning electron micrograph of mature spermatozoa from *Mimachlamys varia*. The arrowed spermatozoon presents its acrosome (a), head (h), mitochondrial spheres (m), and flagellum (f). Figure 3.28.8: Transmission electron micrograph of a mature spermatozoan from *P. maximus*. f, flagellum; h, head; m, mitochondrial sphere; dc, distal centriole which has formed the flagellum; pc, proximal centriole. *Micrographs courtesy of G. Dorange, Université de Bretagne Occidentale, and P Beninger, Université de Nantes, France.*

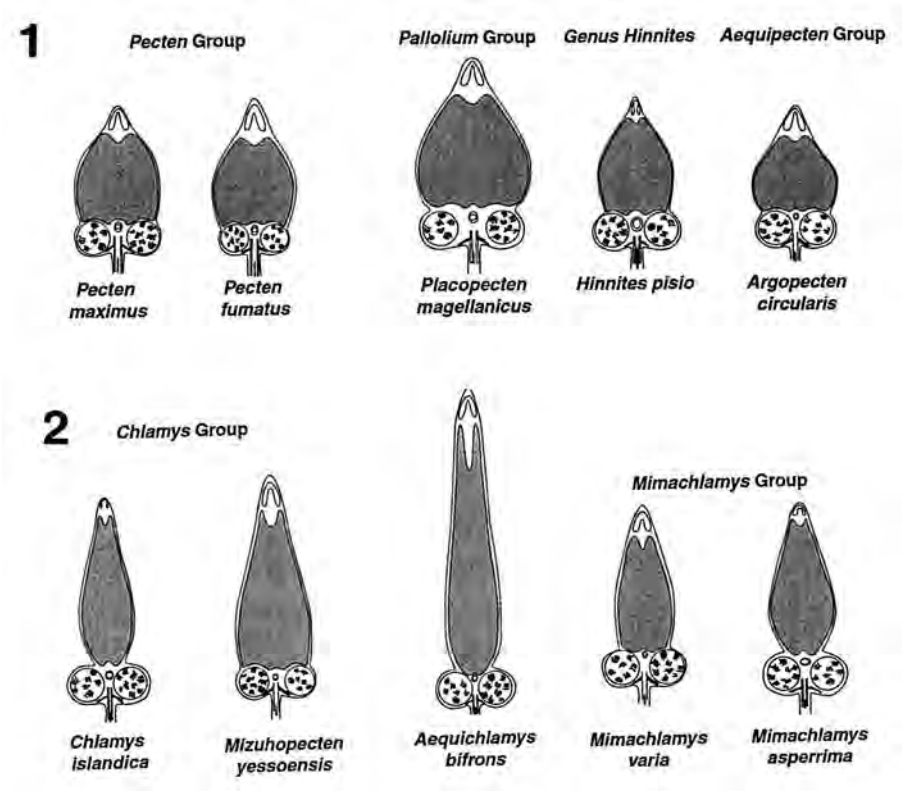


FIGURE 3.29 Schematic representations of pectinid spermatozoa, assembled into Categories 1 and 2, and into Groups (Waller 1991) corresponding to taxonomic affiliations (Le Pennec et al., 2002). For scale, *Pecten maximus* width = 1.6 μm.

Within these two categories are several groups, based on ultrastructural characteristics, which correspond well with the taxonomic affinities of Waller (1991): the *Pecten* group, the *Palliolium* group, the genus *Hinnites*, the *Aequipecten* group, the *Chlamys* group, and the *Mimachlamys* group (Figure 3.29). The ultrastructural distinctions are based on the shape of the nucleus and the acrosomal depressions.

Notwithstanding the differences noted above, the mature scallop spermatozoan contains a dense, granular nucleus with two acrosomal depressions (Figures 3.28.4–3.28.8 and 3.29). The mid-piece presents four to five mitochondrial spheres (diameter 0.7–0.8 μm) (Figures 3.28.7 and 3.28.8), which surround the centriolar system and possess long crests. Together these sections measure approximately 3–6 μm, whereas the flagellum, of 9+2 structure, is approximately 45 μm long (Table 3.1 and Figure 3.28.8), and 0.2–0.3 μm in diameter; these dimensions are typical of littoral bivalve species (Beninger and Le Pennec, 1997). The spermatozoa develop in a centripetal manner, with their flagella towards the lumen of the acinus (Figure 3.28.2).

Fertilisation

The events of fertilisation have been studied in detail in *Placopecten magellanicus*. Although similar to the accounts for other bivalve species, some differences were observed, notably the absence of a zygote nucleus (the male and female chromosomes align immediately on the mitotic spindle of the first meiotic division). There does not seem to be a general rule for the stage of blockage of the first meiotic division in mature pectinid oocytes, as some species are blocked in prophase and others in metaphase (Desilets et al., 1995).

NERVOUS AND SENSORY SYSTEMS

The anatomical modifications of scallops (reduction of the anterior region, circumpallial mantle eyes, and tentacles, central position of posterior organs such as the adductor muscle) are reflected in the general organisation of the nervous system (Figure 3.30). Accordingly, the cerebral ganglia are reduced and closely related to the pedal ganglia, while the visceral ganglia are fused and complex, forming the distinctive pectinid parietovisceral ganglion. This structure innervates the majority of the scallop body (Figure 3.30).

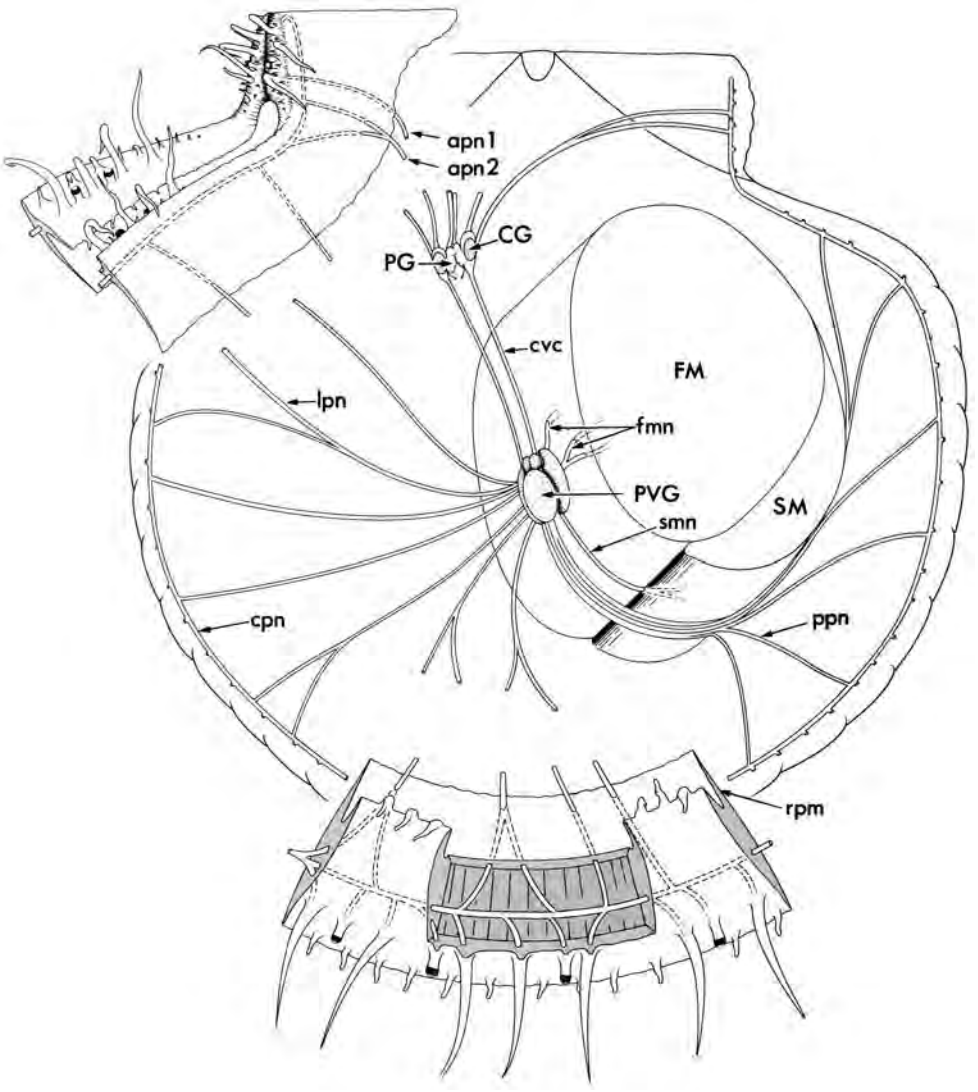


FIGURE 3.30 Diagram of the principal ganglia and their nerves in relation to body structure in *Pecten ziczac*. The upper left and lower insets illustrate the innervation of the mantle in the dorsal and ventral regions. apn, anterior pallial nerve; CG, cerebral ganglion; cpn, circumpallial nerve; cvc, cerebro-visceral connective; FM, fast striated muscle groups; fmn, fast motor nerve; lpn, lateral pallial nerve; PG, pedal ganglion; ppn, posterior pallial nerve; PVG, parietovisceral ganglion; rpm, radial pallial musculature; SM, smooth muscle groups; smn, slow motor nerve. *From Wilkens (1981).*

General Organisation of the Nervous System and Functional Anatomy of Principal Ganglia

The scallop nervous system consists of two main ganglionic concentrations and their nerves: the cerebral and pedal ganglia and the parietovisceral ganglion (Figures 3.30 and 3.31).

Cerebral and Pedal Ganglia

The paired cerebral and pedal ganglia are located quite close together beneath the integument, between the ventral lip and the foot. Wilkens (l981) shows them as contiguous structures in *Pecten* (=*Euvola*) *ziczac*, and this agrees with our own histological observations in *Placopecten magellanicus* (Figures 3.30 and 3.33.1); however, Drew (1906) and Dakin (1909, 1928a) show these two paired structures as being somewhat more distinct in *Pecten maximus*, *Chlamys* (= *Mimachlamys*) *varia*, and *P. magellanicus*. They are linked to each other by a pair of cerebropedal connectives. The individual cerebral ganglia themselves are joined dorsally by a circumoesophageal cerebral commissure immediately posterior to the mouth (Figure 3.31).

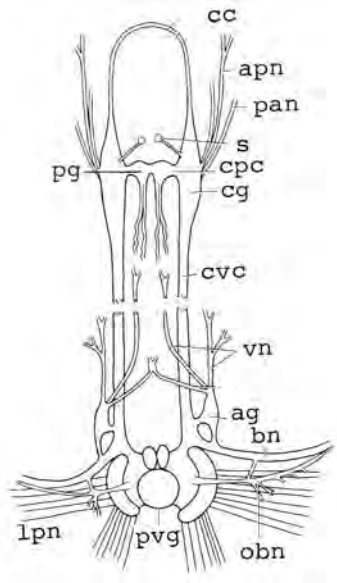


FIGURE 3.31 Diagram of the central nervous system of *Argopecten irradians* (rotated ventral view; see Figure 3.30 for actual orientation). ag, accessory ganglion; apn, anterior pallial nerve; bn, branchial nerve; cc, cerebral commissure; cg, cerebral ganglion; cpc, cerebro-pedal connective; cvc, cerebro-visceral connective; lpn, lateral pallial nerve; obn, osphradio-branchial nerve; pan, palp nerve; pg, pedal ganglion; pvg, parietovisceral ganglion; s, statocyst, and nerve; vn, nerves to viscera. *From Bullock and Horridge (1965), after Gutsell (1931).*

Also arising from the antero-dorsal portion of the cerebral ganglia are the right and left anterior pallial nerves, which run towards the oesophagus and through the digestive gland to enter the mantle above the dorsal lip. Here they split into several branches which join the circumpallial nerve (Figures 3.30 and 3.31).

Three smaller nerves also originate from the antero-dorsal region of the left and right cerebral ganglia (Figure 3.31): the anterior pallial nerve, the palp nerve, and the statocystic nerve (the otocystic nerve of Drew, 1906 and Dakin, 1909).

The pedal ganglia are almost fused due to the massive pedal commissure. A large pedal nerve arises from each ganglion, ramifying and innervating the foot muscles (Figures 3.31 and 3.33.1).

The Parietovisceral Ganglion and Its Nerves

The paired visceral ganglia characteristic of other bivalve families have become greatly modified in the Pectinidae, being completely fused to form one large, complex parietovisceral ganglion composed of several distinct lobes (Figure 3.32.1). This is the largest and most intricate ganglion found in the Bivalvia (Bullock and Horridge, 1965) and as such it merits special attention. The external anatomy of this structure has been described in *Pecten maximus* and *Chlamys* (=*Aequipecten*) *opercularis* by Dakin (1910b, 1928a), in *Argopecten irradians* by Spagnolia and Wilkens (1983), and in *Patinopecten* (=*Mizuhopecten*) *yessoensis* by Matsutani and Nomura (1984). It consists of a large ventro-central (=posterior) lobe, flanked by two crescent-shaped lateral lobes. Its external anterior surface is surmounted by two bulbous dorso-central (=anterior) lobes (Figures 3.32.1 and 3.33.2). Near the point of insertion of the cerebro-visceral connectives are two spherical structures called accessory lobes (=accessory ganglia), which are considered to be part of the parietovisceral ganglion by Spagnolia and Wilkens (1983), but not by Matsutani and Nomura (1986).

The parietovisceral ganglion is situated slightly postero-ventrally to the excretory pore of the right kidney, and is in close anatomical relation with this organ. It gives rise to most of the nerves of the viscera, adductor muscle and mantle (along with its specialised sensory structures). Two cerebro-visceral connectives link the ventral parts of the cerebral ganglia to the parietovisceral ganglion (Figures 3.30 and 3.31). Close to the junction with the cerebro-visceral connectives are the large branchial nerves, which innervate the gills. Joining the ganglion on the right and left sides are the pallial nerves, adductor muscle nerves, osphradial nerves, and osphradio-branchial nerves. Ventrally on either side of the ganglion, large posterior pallial nerve tracts arise which curve around the adductor muscle, joining the circumpallial nerve by several branches, and ramifying to innervate most of the mantle. The circumpallial nerve innervates the mantle margin and its associated sensory structures

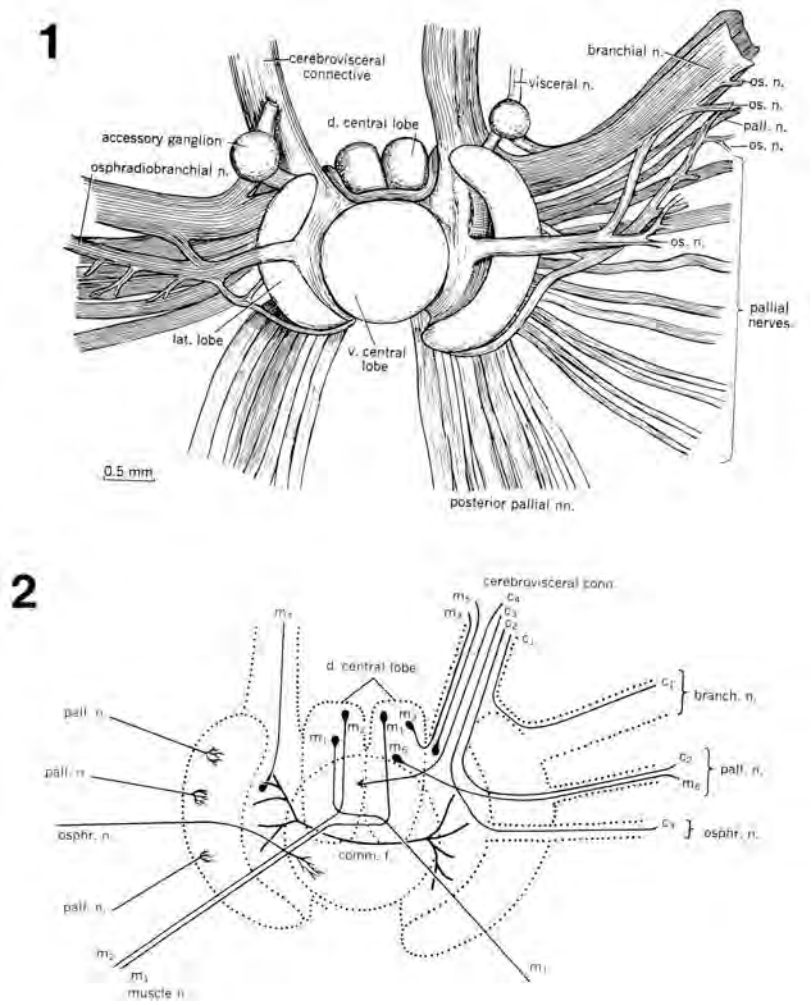


FIGURE 3.32 Anatomy and principal nerve tracts of the parietovisceral ganglion in *Pecten maximus* and *Mimachlamys varia*. Figure 3.32.1: Rotated ventral view of the ganglion. d., dorsal; lat., lateral; n., nerve; nn., nerves; os. or osph., osphradial; pall., pallial; v, ventral. Figure 3.32.2: Principal nerve tracts based on the observations of Dakin (1910). Afferent pathways are shown on the right, and efferent pathways on the left. branch. n., branchial nerve; C 1–4, nerve fibres from cerebral ganglion; comm. f., commissural fibres; m 1–6, motor neurons; other abbreviations as in Figure 3.32.1. *Figures 3.32.1 and 3.32.2 are from Bullock and Horridge (1965) after Dakin (1910b).*

(e.g. tentacles and eyes via the tentacle and optic nerves, respectively), as well as some of the pallial muscles (Figures 3.30, 3.31, 3.34.1, and 3.34.6).

An interesting aspect of the external anatomy of the parietovisceral ganglion is the relative sizes of the two lateral lobes. The left lateral lobe is larger than the right one in *Pecten maximus*; this has been related to the greater number of eyes on the left mantle margin in this species (Dakin, 1910b). In *Argopecten irradians*, however, the two lateral lobes are symmetric, corresponding to an equal number of eyes on each side (Spagnolia and Wilkens, 1983). The role of the lateral lobes in vision is dealt with in detail in Chapter 5.

Histology and Neurosecretions of the Ganglia

The cerebral and pedal ganglia show similar histological organisation, with a cortex of ganglionic cells from which nerve fibres extend to the core or neuropile region (Figure 3.33.1). The parietovisceral ganglion presents a more complex internal anatomy. While the ventro-central lobe is composed of a fibrillar neuropile and a peripheral ganglionic cortex, the two dorso-central lobes are almost entirely made up of the largest ganglion cells (Figures 3.33.2 and 3.33.3), whose nerve fibres ramify throughout other regions of the ganglion (Stephens, 1978). Most of the pear-shaped ganglion cells are unipolar, but bipolar and multipolar cells also occur. Neuroglia cells and their fibres envelop the ganglion cells and are also present in the neuropile and in the nerves. There are very few blind endings of nerve fibres in the neuropile (Dakin, 1910b).

Much of our knowledge of the nerve tracts of the parietovisceral ganglion is based on the fragmentary observations of Dakin (1910b), presented by Bullock and Horridge (1965) and shown in Figure 3.31. The routes of the radial pallial nerves were traced within the parietovisceral ganglion of *Argopecten irradians* by Stephens (1978). The internal

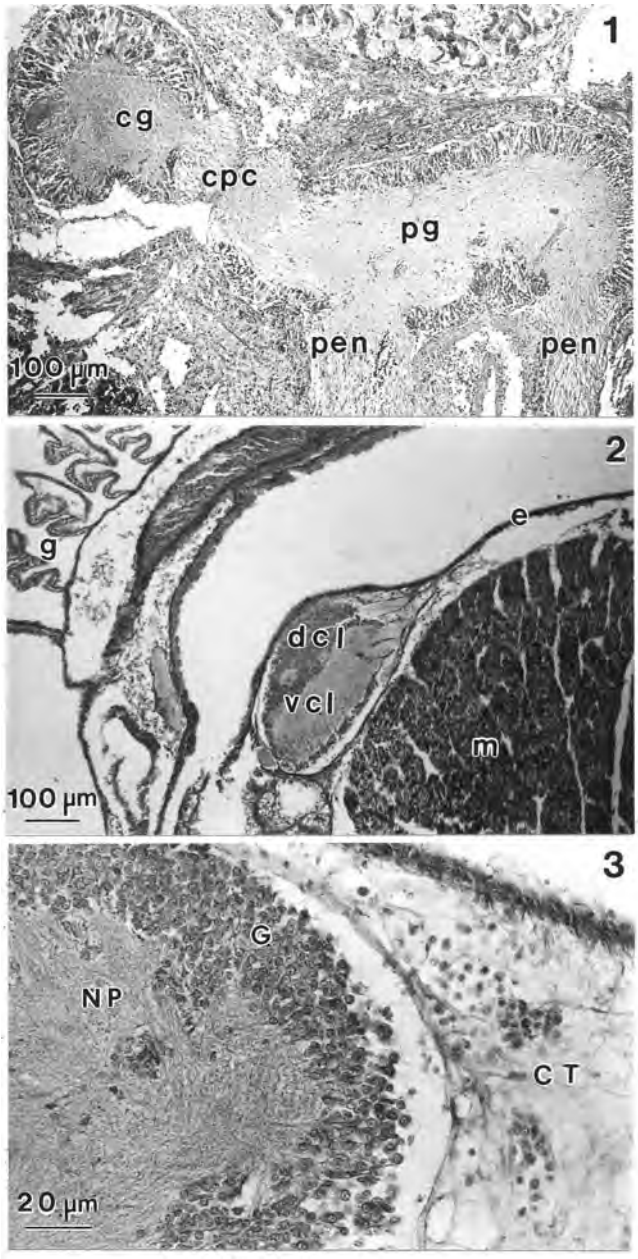


FIGURE 3.33 Structure and histology of the principal ganglia in *Placopecten magellanicus* and *Pecten maximus*. Masson trichrome stain. Figure 3.33.1: Histological section of *Placopecten magellanicus* showing the anatomical relationship between one cerebral ganglion (cg), the fused pedal ganglia (pg), the cerebro-pedal connective (cpc), and the two pedal nerves (pen). Figure 3.33.2: Histological section of the parietovisceral ganglion in a juvenile specimen of *Pecten maximus*. dcl, dorsocentral lobe; g, gill filaments arising from suspensory membrane; e, limiting epithelium; m, adductor muscle; vcl, vertrocentral lobe. Figure 3.33.3: Histological section of the ventrocentral lobe of the parietovisceral ganglion in a juvenile specimen of *Pecten maximus*. CT, connective tissue; G, ganglion cells; NP, neuropile region. *Micrographs courtesy of A. Donval, Université de Bretagne Occidentale, and P. Beninger, Université de Nantes.*

structure and nerve tracts of the lateral lobes have been studied in detail by Spagnolia and Wilkens (1983), and are presented in Chapter 5.

Details of the synaptic structure in bivalve ganglia are rather scant, with the notable exceptions of the study by Cobb and Mullins (1973) on the visceral ganglion of *Spisula solidissima*, and the work of Vitellaro-Zuccarello and DeBiasi (1990) on *Mytilus edulis*. In both species, most axons were shown to be varicose, containing several types of vesicles, while specialised synaptic contacts were rare or absent. These authors proposed that the varicose axon type may function in a similar manner as the unspecialised varicose terminals of the vertebrate autonomic

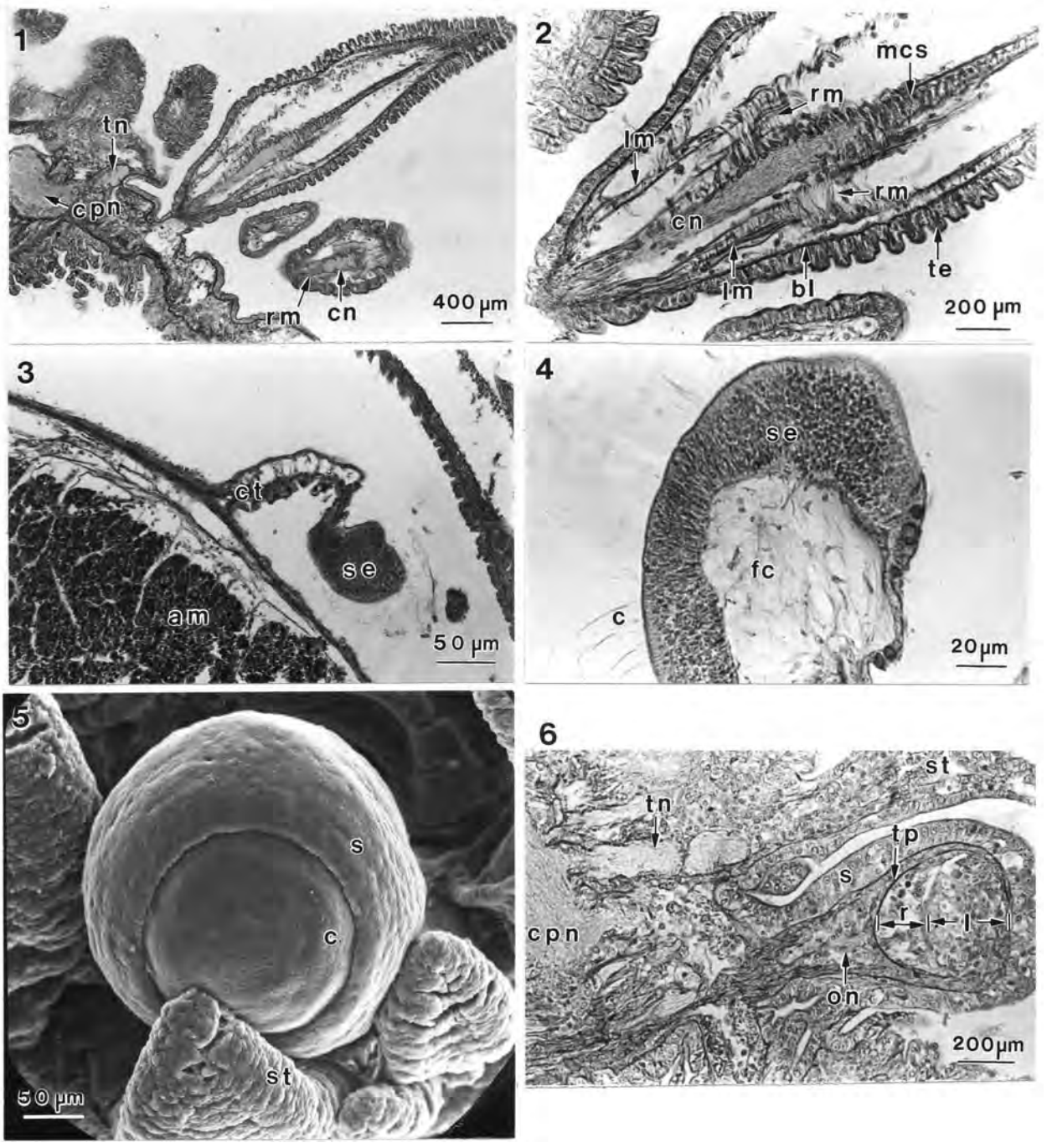


FIGURE 3.34 Structure and histology of various sensory organs in *Pecten maximus* and *Mimachlamys varia*. Masson trichrome except for Figure 3.34.5. Figure 3.34.1: Longitudinal and cross-sections of a long tentacle (retracted) on the middle fold of the mantle of a juvenile *Pecten maximus*. cn, central tentacle nerve; cpn, circumpallial nerve; rm, radial muscles; tn, tentacle nerve. Figure 3.34.2: Detail of basal region of long sensory tentacle. bl, basal lamina; cn, central tenticle nerve; lm, longitudinal retractor muscle; mcs, musculo-connective sheath; rm, radial muscles; te, tentacle epithelium. Figure 3.34.3: Anatomical relationships of the abdominal sense organ in a juvenile *Pecten maximus*. am, adductor muscle; ct, connective tissue fold; se, sensory epithelium. Figure 3.34.4: Detail of the abdominal sense organ of a juvenile *Pecten maximus*. c, cilia; fc, fibrillar core; se, sensory epithelium. Figure 3.34.5: Scanning electron micrograph of an eye and sensory tentacles in *Mimachlamys varia*. c, cornea; s, eyestalk; st, sensory tentacle (retracted). Figure 3.34.6: Longitudinal section of the eye in a juvenile *Pecten maximus*, also showing the tentacle nerve (tn) in an adjacent tentacle, emanating from the circumpallial nerve (cpn). l, lens; on, optic nerve; r, retina; st, sensory tentacle; tp, tapetum. *Micrographs courtesy of A. Donval, Université de Bretagne Occidentale, and P. Beninger, Université de Nantes.*

neurons, with non-synaptic neurotransmitter vesicle release. Such studies should be extended to the more complex visceroparietal ganglion of the Pectinidae.

Several studies have localised serotonin-like monoamines in the scallop ganglia (e.g. Chang et al., 1984; Matsutani and Nomura, 1986; Paulet et al., 1993). The relation between serotonin and spawning is well known in many bivalve species, and it is not surprising that serotonin receptors are also situated in the walls of the gonad acini (Matsutani and Nomura, 1986). This relation is explored further in 'Osphradia' and 'Neurotransmitters and Neurohormones' sections.

A polyamine neuropeptide, FMRFamide (Phe-Met-Arg-Phe-NH_2) was found to be most concentrated in the cerebral, pedal and parietovisceral ganglia of *Placopecten magellanicus*, especially in the cortical cell bodies and the fibres projecting into the neuropile region (Too and Croll, 1995). Many other hormones have been localised in the three pectinid ganglia, underscoring their role as a production and storage centre for neurohormones, particularly those involved in the key processes of reproduction and somatic growth (Yuan et al., 2012; Nagasawa et al., 2015).

The Circumpallial Nerve

The circumpallial nerve is located just interior to the circumpallial artery. It is innervated by both the anterior and posterior pallial nerves, which originate in the cerebral and parietovisceral ganglia, respectively. The circumpallial nerves of the two mantle lobes are fused anteriorly and posteriorly at the hinge line. Both Drew (1906) and Dakin (1909) state that this nerve is physiologically a ganglion, as it is well supplied with ganglion cells and contains abundant nerve cells; however, integrative properties do not appear to exist in relation to visual stimuli (see Chapter 5).

Sensory Structures

Knowledge concerning the various sensory structures of scallops is quite unequal. While the visual system has been the object of continued study for over a century, the remaining structures have received much less attention and are still largely enigmatic.

Visual System

The eyes are a conspicuous feature of scallops, which have been the subject of some study from time to time in the literature (e.g. Dakin, 1910a, 1928b; Land, 1965, 1968; Morton, 2000, 2008; Speiser and Johnsen, 2008a). The eyes are distributed around the margin of the middle (sensory) fold of the mantle, and originate at the base of the tentacles (Butcher, 1930; Figures 3.34.5 and 3.34.6). The eye itself consists of a cornea, lens, double retina, and tapetum (Figure 3.34.6). Light is reflected off the tapetum to the inverted retina. Not only are both types of photoreceptor present in the pectinids, but they may also be present in the same individual and in the same eye (Hiesinger and Meinertzhagen, 2009). The optic nerve from each eye joins the circumpallial nerve (Figure 3.34.6), which is innervated by tracts from the lateral (optic) lobes of the parietovisceral ganglion. A detailed description of visual physiology is presented in Chapter 5.

Although pectinid pallial eyes are conventionally assumed to function in predator detection, they may also function in directional swimming during the escape response (von Buddenbrock and Moller-Racke, 1953), in detection of favourable habitats (Hamilton and Koch, 1996), and they even appear to mediate behavioural responses to small moving particles, and thus may also function in the detection of environmental particle load conditions (Speiser and Johnsen, 2008b).

Epithelial Sensory Cells and Tentacles

Epithelial sensory cells are probably scattered over the scallop epidermis, but correlative ultrastructural and electrophysiological studies are lacking. Sensory cells are concentrated on papillae in the distal third of the long tentacles, situated at the margin of the middle mantle lobe (see 'The Mantle and Its Derivatives' section). The haemocoel of the tentacle contains a central tentacular nerve, surrounded by a protective musculo-connective sheath, and flanked by two longitudinal retractor muscles (Figures 3.34.1 and 3.34.2). Extension of the tentacle is affected by hydrostatic pressure from the haemolymph, which fills the haemocoel; contraction of the longitudinal tentacle muscles causes the tentacles to retract to approximately one-tenth of the extended length (Figure 3.34.1). The central tentacular nerve is an extension of the tentacular nerve that radiates from the circumpallial nerve (Figures 3.34.1, 3.34.2, and 3.34.6).

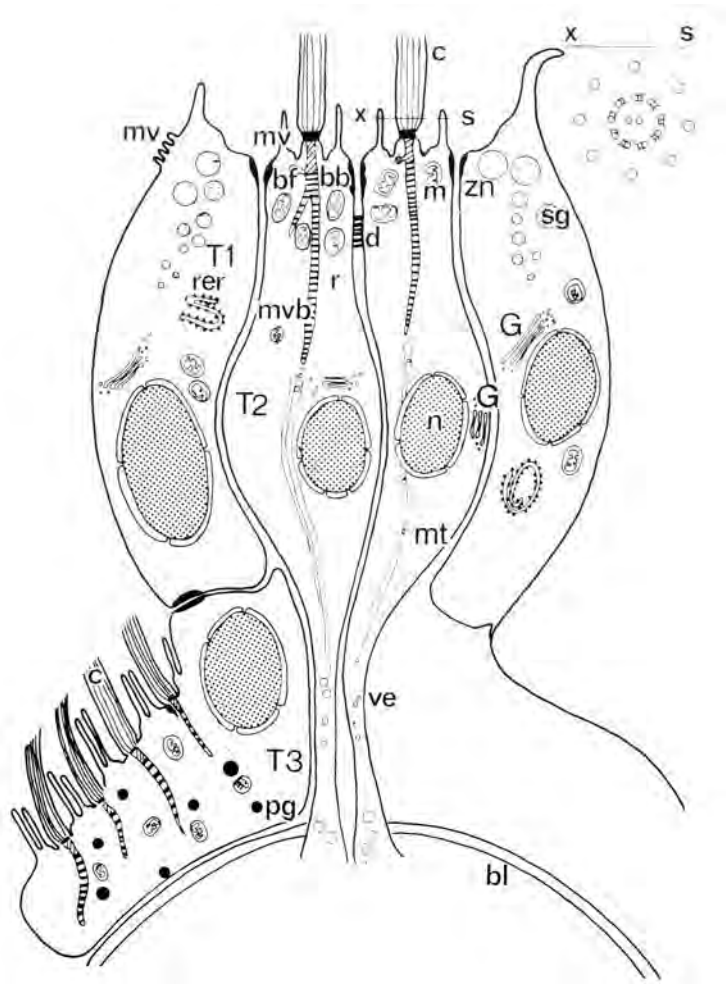


FIGURE 3.35 Composite diagram of a ciliated papilla on the distal third of a sensory tentacle in *Placopecten magellanicus*. bb, basal body; bf, basal foot of basal body; bl, basal lamina; c, cilia; d, septate desmosomes; G, Golgi apparatus; m, mitochondria; mt, microtubules; mv, microvilli; mvb, multivesicular bodies; n, nucleus; pg, pigment granules; r, ciliary root; rer, rough endoplasmic reticulum; sg, secretory granules; T1, type I cell, (non-ciliated supporting cell); T2, type II cell (ciliated sensory cell); T3, type III cell (macrocilia-bearing cell); X-S, plane of cross-section shown in inset; zn, zonula adherentes. *From Moir (1977a).*

Although histologically similar to ordinary epithelial cells, the tentacle sensory cells are often much narrower and bear cilia much longer than those of the other epithelial cells. The base of the sensory cell is joined to nerve fibres running to the central tentacular nerve (Dakin, 1909). The structure and ultrastructure of the ciliated receptor cells on the papillae of the long tentacles of *Placopecten magellanicus* have been studied in detail by Moir (1977a). Each papilla bears three specialised cell types: a supporting cell associated with the putative sensory cell which carries up to five cilia, a third cell type at the base of the papilla possessing many cilia and the macrocilia (Figure 3.35). The sensory cells are known to respond to mechanical stimulation.

Abdominal Sense Organ

The abdominal sense organ was first described in pectinids by Dakin (1909). It is visible as a small, yellowish fold of tissue situated on the adductor muscle near the anus (Figure 3.34.3). Since Dakin's work this enigmatic organ was virtually ignored, until the detailed structural and ultrastructural study by Moir (1977b), and the electrophysiological studies of Zhadan and Semen'kov (l984), Zhadan and Doroshenko (1985), and Zhadan (2005). Ciocco (1985) and Morton (1996) also described the histology of this structure. The following is a summary of these authors' work as well as our own histological data presented here.

The sensory epithelium consists of two basic cell types: sensory cells and mucocytes. Zhadan and Semen'kov (1984) described two categories of sensory cells – those with single, long cilia, and those with multiple, short cilia. These two distinct cell categories are innervated by different nerve fibres, which descend towards the fibrillar inner core (Figure 3.34.4). A third group of nerve fibres innervates the base of the organ. All three groups of nerve fibres respond to mechanical stimulation of the sensory cells and are connected to the parietovisceral ganglion via one of the posterior pallial nerves. Each group of fibres exhibits different response characteristics.

Although the structural evidence would indicate a chemosensory role for the abdominal sense organ (Dakin, 1909; Moir, 1977b), it has also been suggested that it functions in mechanoreception (Charles, 1966; Moir, 1977b; Morton, 1996). Zhadan and Semen'kov (1984) and Zhadan and Doroshenko (1985) demonstrated the electrophysiological responses of this organ to mechanical stimulation and suggested that cAMP and cAMP-dependent phosphorylation may be involved in mechanoreception. Specifically, it may compensate for the relative paucity of other sensory structures in the hinge region, thus aiding in predator detection from this side of the animal (Zhadan, 2005). Summarising, the abdominal sense organ, being situated directly in the path of exhalent water flow within the pallial cavity, may function in the regulation of water flow and, thus, in the regulation of feeding (Charles, 1966; Moir, 1977b), and/or in the detection of predator-induced vibrations on the hinge (dorsal) side of the scallop (Zhadan, 2005).

Osphradia

Sensory structures called osphradia are well known in gastropods (see Garton et al., 1984 for references), and zoologists have long supposed that similar structures exist in bivalves. Most authors agree that the osphradia of bivalves are small and difficult to detect (Drew, 1906; Bullock and Horridge, 1965; Charles, 1966). Indeed, Gutsell (1931) was unable to observe osphradia at all in *Argopecten irradians*. To date, anatomical evidence indicates that in all probability the osphradia of gastropods and bivalves are not homologous (Kraemer, 1979; Lindberg and Sigwart, 2015).

The early work of Dakin (1909) described putative osphradial ganglia in *Pecten maximus*, but did not pinpoint their location. Setna (1930) stated that in several scallop species, the osphradia are paired sensory structures situated along the most lateral margins of the gill axis as raised ridges of tissue, which are only visible in fresh specimens or in histological section. The osphradia are innervated by branches of the branchial nerve and contain both ciliated sensory cells and bipolar neurons. Haszprunar (1985a,b, 1987a,b, 1992) did extensive electron microscopic investigations on the osphradia of various molluscan groups, but not the Pectinidae. Such a study was later performed in *Placopecten magellanicus* and *Pecten maximus* (Beninger et al., 1995a). The structure consists of an eversible ridge with subjacent muscle fibres (Figure 3.36.2) and a dorsal tuft cilia region. The eversible character of the ridge may account for the confusion concerning the location of the osphradium in species in which it is not pigmented (see below). The ridge epithelium contains many secretory cells, which appear to produce neurosecretions which are transported along microtubules to the bases of the cells, where axons join the osphradial nerve (Figures 3.36.3–3.36.5). In *Pecten maximus*, pigment granules are also secreted by these cells, giving the osphradium a distinct orange pigmentation (and hence a sure way of locating the structure!). The tuft epithelium appears sensory in structure, with both free nerve fibres and ciliated cells (Figure 3.36.6) similar to those described by Haszprunar (1987a). No specialised cilia form is observed, and it is probable that the 'paddle cilia' previously reported as diagnostic features of the osphradium (e.g. Haszprunar, 1985a,b) are artefacts of hypotonic fixation (Beninger et al., 1995b).

Numerous functions have been proposed for the bivalve osphradium, reviewed by Haszprunar (1987a). This author concluded that the most probable function is that of chemoreception of a gamete release signal. The histological and ultrastructural data for *Placopecten magellanicus* and *Pecten maximus*, together with data on the innervation of the osphradium and the location of monoamines in *Pecten maximus*, led Beninger et al. (1995a) to support this view, proposing a dual function of both stimulus reception (for the sensory cells), and of serotonin production (for the secretory cells of the osphradial ridge), which is then axonally transported (Figure 3.36.5) and stored in the accessory lobe of the parietovisceral ganglion (Figure 3.37). The rate of serotonin production and storage could depend on approximate timing cues, such as cyclic temperature changes or even more proximate changes due to downwelling events (Bonardelli et al., 1996). Release of the stored serotonin would induce gamete release in the nearby gonad, allowing vitally precise synchronisation, enhancing the probability of fertilisation within a population. The nature of the stimulus is not yet known but is presumed to be a substance contained in male ejaculate.

Statoreceptors

Much of the remarkable early work concerning pectinid statoreceptors (Drew, 1906; Buddenbrock, 1915) was confirmed and extended in Barber and Dilly (1969) and Morton (1994, 1996). The terminology used by the earlier authors is rather more complex; they distinguish statocysts, or closed statoreceptor sacs, and statocrypts, or statoreceptors, which communicate with the external medium. In addition, they distinguish statoliths, or single endogenously formed crystals, and statoconia, or multiple small crystals. Statoconia of exogenous origin (in the case of statocrypts) are termed pseudostatoconia. The statoreceptors of scallops have been termed both statocrypts and statocysts by these authors. Regardless of semantics, the statoreceptors of most scallops show a marked asymmetry, the left one being more developed than the right one (although not so in *Minnivola pyxidatus*; Morton, 1996).

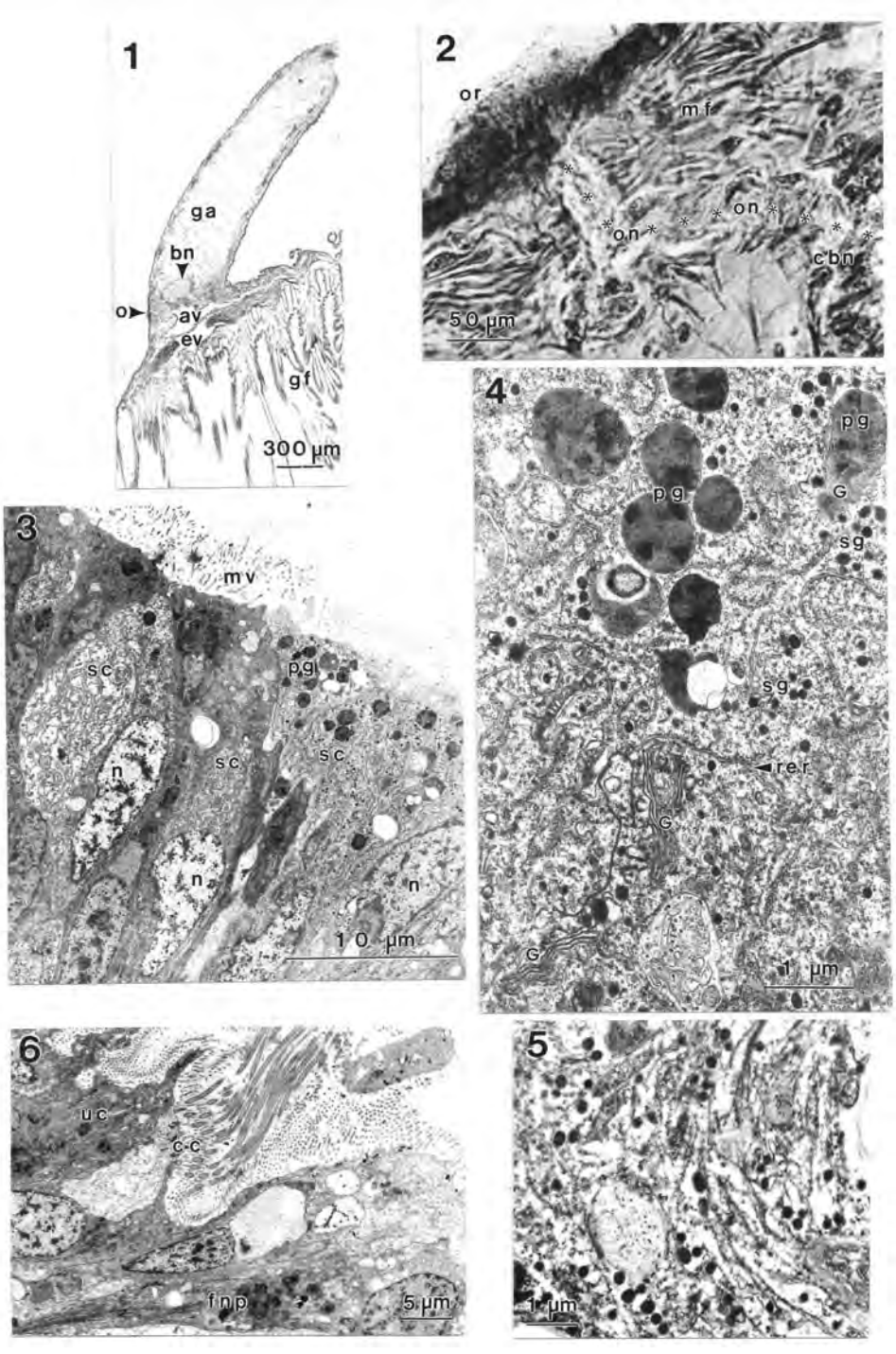


FIGURE 3.36 The osphradium in *Pecten maximus* and *Placopecten magellanicus*. Figure 3.36.1: Histological section showing general anatomical relationships: gill axis (ga), branchial nerve (bn), afferent vessel (av), efferent vessel (ev), osphradium (o), and gill filaments (gf). Figure 3.36.2: Histological section showing detail of osphradial ridge (or), an osphradial nerve (on), cortex of branchial nerve (cbn), and muscle fibres (mf) beneath osphradial epithelium. Figure 3.36.3: TEM showing secretory cells of osphradial ridge (sc), with large basal nuclei (n), and apical pigment granules (pg). mv, microvilli. Figure 3.36.4: TEM detail of apical region of a secretory cell in *Pecten maximus*. G, Golgi complexes; pg, pigment granules; rer, rough endoplasmic reticulum; sg, secretion granules. Figure 3.36.5: TEM detail of the basal region of a secretory cell, showing secretory granules aligned along microtubules, indicative of axonal transport. Figure 3.36.6: TEM detail of tuft cilia region, showing tuft cilia arising from ciliated cell (cc), adjacent free nerve process (fnp), and undifferentiated (supporting) cell (uc). *From Beninger et al. (1995).*

Each statoreceptor consists of a sac-shaped sensory epithelium, and a fluid-filled lumen containing one or several crystals. The sensory cells are inappropriately called hair cells, due to the sensory cilia at their apical extremities. The left statoreceptor sensory cells present up to 30 9+2 type cilia each, with striated roots penetrating deeply into the cell body, whereas the right statoreceptor sensory cells only have about 10 such cilia. Each hair cell produces an axon at its basal extremity (Figure 3.38). Both statoliths and statoconia have been reported in scallops (Drew, 1906; Buddenbrock, 1915; Barber and Dilly, 1969), the latter being sometimes arranged into a compact, hollow sphere (Morton, 1996). Buddenbrock (1915) believed the statoconia of *Pecten inflexus* to be exogenous, being predominantly formed of sponge spicules (which presumably enter via the statocystic canals) and cemented by mucus

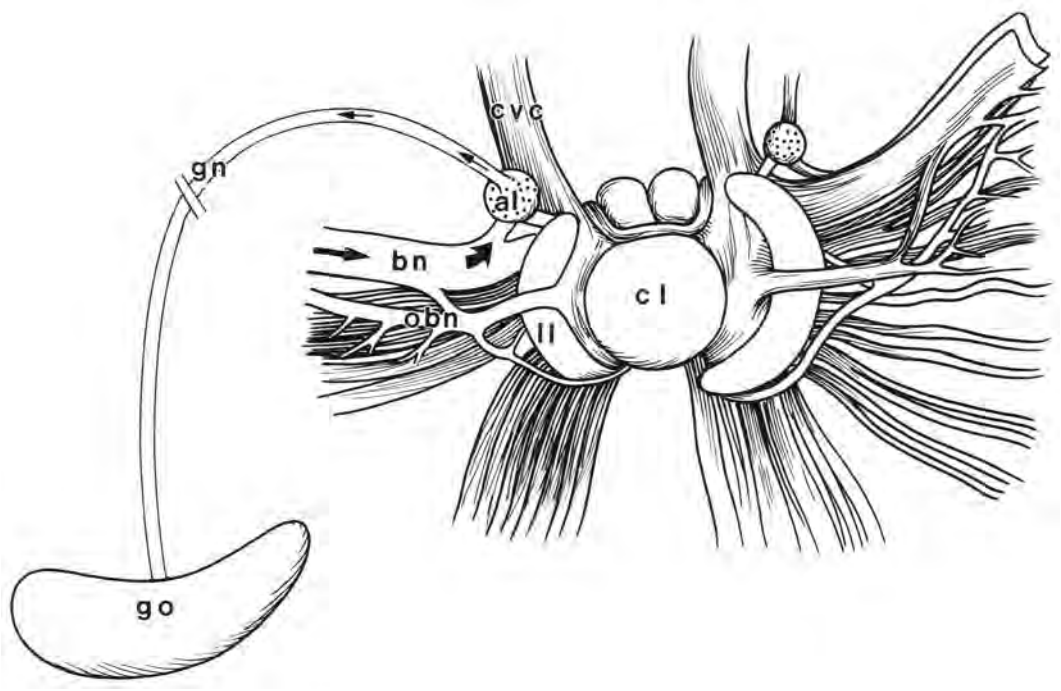


FIGURE 3.37 The proposed pathway for axonal transport of neurosecretions produced in the secretory cells of the pectinid osphradium (arrows). The dotted regions indicate sites of monoamine storage. *Modified after Beninger et al. (1995a).*

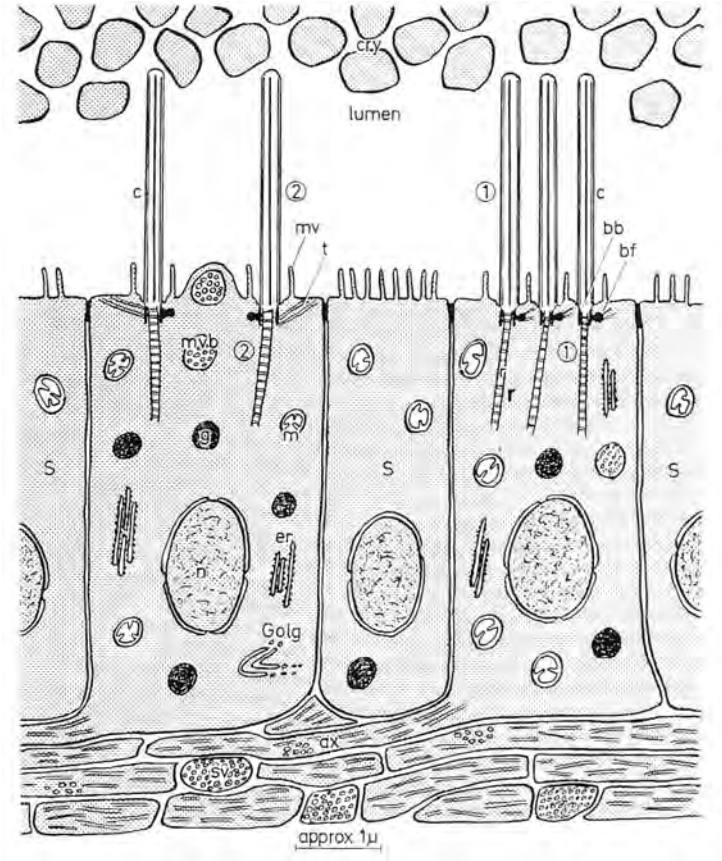


FIGURE 3.38 Diagram of the statoreceptor wall in *Pecten* sp. ax, sensory cell axons; bb, basal bodies (cinetosomes); bf, basal feet (in type 1 ciliary arrangement); c, cilia (putatively sensory); cry, statoreceptor crystals; er, endoplasmic reticulum; g, membrane-bound granules; Golg, Golgi bodies; m, mitochondria; mv, microvilli; mvb, multivesicular bodies; n, nuclei; r, ciliary roots; s, supporting cells; sv, synaptic vesicles; t, microtubular attachments (in type 2 ciliary arrangement). *Reprinted from Barber and Dilly (1969).*

into a compact mass, whereas he reported other scallop species such as *Mimachlamys varia* to have true endogenous statoliths, the canal to the exterior being blind and vestigial (Buddenbrock, 1915). The statoreceptor axons group to form the statocystic nerves leading to the cerebral ganglion, as mentioned previously.

The pronounced asymmetry of scallop statoreceptors may correspond to its sedentary life habit, with the animal always resting on the same valve (usually the right one); however, it should be noted that ablation of the statoreceptors in the scallop species studied by Buddenbrock (1915) did not affect the righting reflex. Furthermore, the vertical steering component of the swimming reflex is affected by removal of the left statoreceptor, though unaffected by removal of the right one (Buddenbrock, 1915). The left statoreceptor may thus be an essential element in the control of the swimming reflex. Swimming is covered in detail in Chapters 11 and 12.

Neurotransmitters and Neurohormones

Several different neurotransmitters have been partially identified in the scallop nervous system. The distribution of acetylcholinesterase and monoamine oxidase in the central nervous system of *Patinopecten* (= *Mizuhopecten*) *yessoensis* indicates the presence of acetylcholine and a serotonin-like monoamine, respectively (Chang et al., 1984). A serotonin-like monoamine was also detected by Paulet et al. (1993) in the parietovisceral ganglion. Subsequent histochemical work revealed the presence of FMRFamide (Phe-Met-Arg-Phe-NH_2)-like molecules in all of the ganglia of *Placopecten magellanicus* (Too and Croll, 1995). It was suggested that FMRFamide plays an important role in neuron−neuron interactions, and its distribution in many peripheral structures indicated that it may participate in the regulation of a wide range of physiological and sensory processes.

Using HPLC, Pani and Croll (1995) detected the presence of the catecholamines 3,4 dihydroxyphenylalanine, dopamine, norepinephrine, epinephrine, and the indoleamine 5-hydroxytryptamine (serotonin), in the ganglia, as well as in most organs of *Placopecten magellanicus*. From the foregoing, it is clear that we are presently detecting the types of putative neurotransmitters found in gross anatomical structures; precise mapping to the level of precision now available for the human nervous system is a seemingly distant goal.

The rudimentary knowledge base acquired to date indicates that our understanding of pectinid and indeed bivalve neurophysiology is quite embryonic at this stage. The roles of the various bivalve neurotransmitters are even less well known. Serotonin has been implicated in the regulation of sodium transport (Dietz et al., 1984), gamete release (see Ram et al., 1997 for review), ciliary beat (e.g. Jørgensen, 1976; Silverman et al., 1999), with cAMP mediation (Stommel and Stephens, 1985), cardiac function (Welsh and Moorhead, 1960), and probably also in the extremely ubiquitous and polyvalent function of mucus secretion (Lent, 1974).

While all of the molecules mentioned above may function as neurotransmitters, it is equally likely that they also have roles as neurohormones. The existence of neurosecretory cells was demonstrated in all of the ganglionic concentrations of several bivalve species by Gabe (1955). Lubet (1955) showed the relationship between the secretory activity of these cells and the reproductive cycle of *Chlamys* (= *Mimachlamys*) *varia* and *Mytilus edulis*. In *Mytilus edulis*, the greatest concentration of such cells appears to be in the cerebral ganglia (Lubet and Mathieu, 1982), from which a gonial mitosis stimulating factor has been isolated (Mathieu et al., 1988). Studies using organ cultures have shown that gametogenesis in *M. edulis* is influenced by non-species-specific neurosecretions of the cerebral ganglia (Lubet and Mathieu, 1982). In addition, the gametogenesis of cultured *Chlamys* (= *Aequipecten*) *opercularis* tissue may be triggered by *M. edulis* ganglia secretions (Allarakh, 1979, cited by Toullec et al., 1988).

Since the experiments of Matsutani and Nomura (1982), it is known that serotonin stimulates the actual spawning in *Patinopecten (= Mizuhopecten) yessoensis*. The same effect has also been obtained for a variety of other bivalves, including *Argopecten irradians* (Gibbons and Castagna, 1984). Perikarya of serotonin-like monoamine-secreting neurons have been observed in the cerebral, pedal, and accessory lobes of the parietovisceral ganglia of *Patinopecten* (=*Mizuhopecten*) *yessoensis*, while serotonin-like, monoamine-secreting fibres derived mostly from the cerebro-visceral connective terminate in the acinal walls and collecting tubules of the pectinid gonad (Matsutani and Nomura, 1984, 1986; Croll et al., 1995). Beninger et al. (1995a) proposed that secretions formed in the scallop osphradium were monoamines axonally transported and stored in the accessory lobes of the parietovisceral ganglion (which are the only parts of this ganglion rich in serotonin; Croll et al., 1995); release to the gonad via the gonadal nerve would provoke gamete emission (Figure 3.37). Fine-tuning of gametogenesis also appears to depend upon neurohormones produced in the ganglia (Yuan et al., 2012; Nagasawa et al., 2015).

In addition to neurosecretions involved in reproduction, the bivalve nervous system includes secretory neurons that regulate somatic growth. A non-species-specific growth factor isolated from the cerebral ganglia of *Mytilus edulis* is active with *Pecten maximus* tissue, indicating that a similar secretion exists in pectinids (Toullec

et al., 1988). A somatostatin-like substance has also been isolated from peripheral cells of the parietovisceral ganglion of *Pecten maximus* (Le Roux et al., 1987). Somatostatin-like receptor cells have been identified in the kidney (see 'Pericardial (Auricular) Glands' section) and in the digestive gland (Le Roux et al., 1987). Clearly, much further study needs to be done concerning the nature and roles of both neurotransmitters and neurohormones in bivalves, and notably in pectinids.

FOOT–BYSSAL COMPLEX

In contrast to mytilids (see Morse and Zardus, 1997; Frank and Belfort, 2002 for references), relatively few studies have been performed on the foot and byssal complex of the Pectinidae. This is probably due to the fact that are much more accessible, produce much more byssus, and usually live in high-energy habitats, making the study of mytilid byssus of great interest in materials science research (Hagenaua et al., 2011; Suhre et al., 2014). Nevertheless, a good account of the structure and function of this system in pectinids may be derived from the work of Mahéo (1968, 1969), Gruffydd (1978), and Gruffydd et al. (1979).

External Morphology and Development of the Foot–Byssal Complex

The pectinid foot arises out of the antero-dorsal surface of the gonad and is roughly cylindrical in shape, terminating in a sucker-like formation called the sole (Drew, 1906; Gruffydd, 1978), or, more appropriately, the cornet (Pelseneer, 1906; Mahéo, 1969). The cornet is wedge-shaped in longitudinal section, the dorsal surface being more prominent than the ventral surface. The pedal groove, which runs along the mid-ventral portion of the foot, is enclosed except for a small portion, which is visible as a slight depression just behind the cornet (Figure 3.39).

The pectinid foot is small compared to that of the Mytilidae; furthermore, it may be more or less developed depending on the adult life habit and the importance of byssal attachment in different species. Most scallops begin their postlarval life as byssally attached juveniles; some species retain this capability while others grow into free-living adults. In byssally fixed species such as *Chlamys (= Mimachlamys) varia*, the very active foot can be extended out through the byssal notch between the valves. In species in which the adult is motile, such as *Pecten maximus*, the adult foot is a degenerate structure, which plays no role in locomotion or in fixation. Other species in which the foot–byssal complex regresses in the juvenile stage include *Pecten jacobeus*, *Chlamys islandica*,

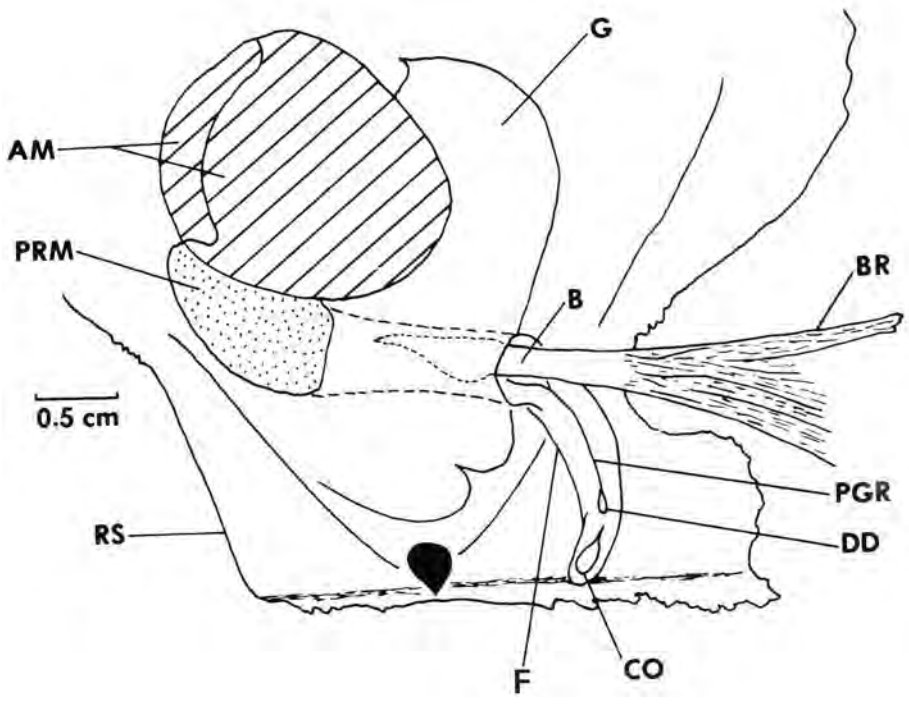


FIGURE 3.39 Schematic illustration of the anatomical relationships of the foot and byssal gland of *Mimachlamys varia*. AM, adductor muscle; B, byssus; BR, byssal ribbon; CO, cornet; DD, distal depression; F, foot; G, gonad; PGR, pedal groove; PRM, pedal retractor muscle; RS, right shell. *After Mahéo (1969).*

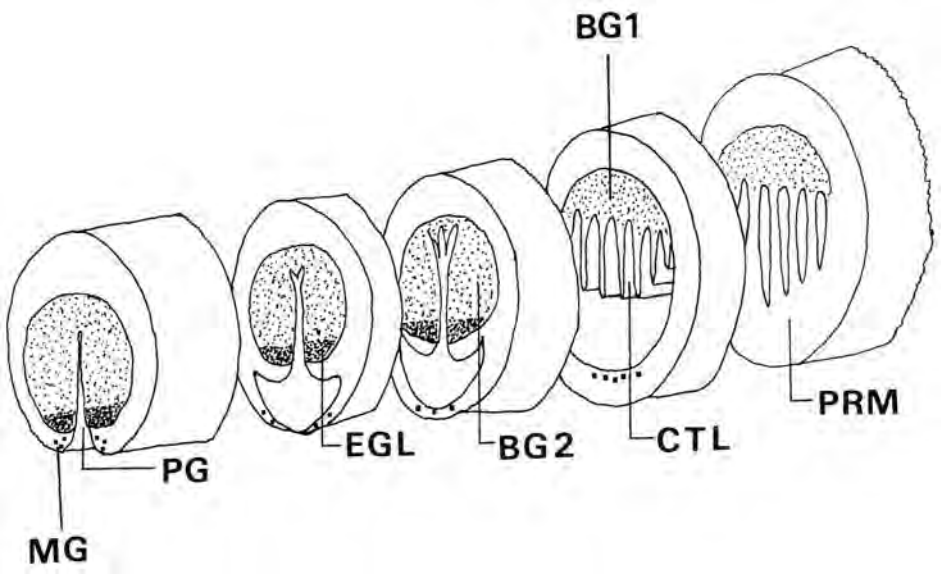


FIGURE 3.40 Schematic illustration of the glandular systems of the foot–byssal complex of *Chlamys varia*. BG1, primary byssus gland; BG2, secondary byssus gland; CTL, connective tissue lamellae; EGL, enzyme gland; MG, mucous gland; PG, pedal groove; PRM, pedal retractor muscle. *Modified after Mahéo (1969)*.

Laevichlamys squamosa, and *Similipecten greenlandicus*. In *Placopecten magellanicus* and other non-attached scallop species, Drew (1906) suggests that the foot may be used to clean the labial palps and the anterior part of the gills, as observed in pearl oysters (*Pinctata* spp.). This interesting hypothesis merits verification.

Anatomy and Histology of the Foot–Byssal Gland Complex

In most bivalves, the foot is connected to the shell via an anterior and a posterior pair of pedal retractor muscles. In monomyarians, however, the anterior pedal retractor muscles are generally absent, and in the Pectinidae only the left posterior pedal retractor remains, being inserted on the left shell close to the dorsal margin of the adductor muscle (Figure 3.39). The degree of development of this muscle varies among species according to the degree of development of the foot, being rather well-developed in *Chlamys (= Aequipecten) opercularis* and rudimentary in *Pecten maximus*.

The external covering of the foot consists of a typical pseudostratified ciliated epithelium (Mahéo, 1969). Beneath this layer are found the glandular systems, nerve fibres from the pedal nerves, circular and longitudinal muscle fibres, and lacunar connective tissue filled with haemolymph (Figure 3.41). The glandular systems, occupying nearly half the volume of the foot, consist of a protein gland, an enzyme gland, and a mucous gland (Figures 3.40 and 3.41).

The Protein Gland

The protein gland is the most voluminous gland of the foot–byssal complex. It is situated on both sides and above the pedal groove, and also extends into the proximal dorsal portion of the foot. In this region, the dorsal surface of the pedal groove becomes progressively folded, assuming an accordion-like appearance (Figures 3.40 and 3.41). The folds consist of connective tissue, and are simply called connective tissue folds or lamellae. The large (10–15 μm) glandular cells secrete a proteinaceous substance either directly into the pedal groove (distal portion) or across the connective tissue lamellae in the proximal portion of the foot. In this region, the secretions traverse the lamellae at their ciliated crypts and are then swept into the pedal groove by the ciliary action of the epithelial cells lining the groove. Each crypt or trough of the lamellae secretes its own individual ribbon (Gruffydd et al., 1979). Gruffydd (1978) divided the protein gland into two components: the primary (lamellar) byssal gland and the secondary (distal) byssal gland running along the pedal groove (Figure 3.40).

The Enzyme Gland

The enzyme gland consists of a thin layer of tissue situated below the protein gland, on either side of the pedal groove (Figures 3.40 and 3.41). It does not extend into the proximal portion of the foot. The secretions of this gland include a polyphenoloxidase (Mahéo, 1969; Gruffydd, 1978).

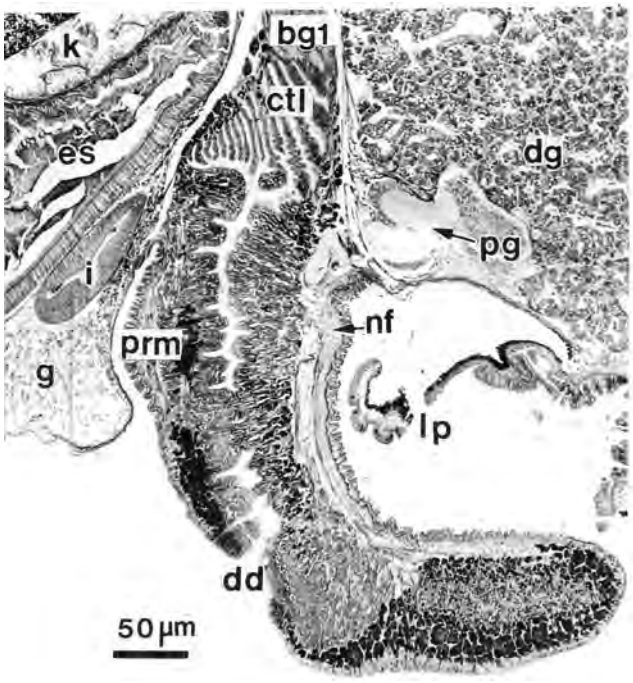


FIGURE 3.41 Oblique saggital section of the foot and surrounding structures of a juvenile *Pecten maximus*. bg1, primary byssus gland; cs, crystalline style within the descending loop of the intestine; ctl, connective tissue lamellae; dd, distal depression; dg, digestive gland; es, oesophagus; g, developing gonad; i, ascending loop of the intestine; k, kidney; lp, sectioned labial palp; nf, nerve fibres; pg, pedal ganglion; prm, pedal retractor muscle. The Masson trichrome l stain does not allow the other glandular systems to be distinguished. *Micrograph courtesy of A. Donval, Université de Bretagne Occidentale, and P. Beninger, Université de Nantes.*

The Byssus

The byssus is formed of a root from which extend several relatively thick ribbons, in contrast to the many thin threads of the Mytilidae (Mahéo, 1969; Gruffydd, 1978; Gruffydd et al., 1979). It is composed of complex proteinaceous molecules (Bubel, 1984). The root is formed of 30–50 fibrous ribbons formed from secretions of the primary byssus gland (Gruffydd, 1978; Gruffydd et al., 1979). These fibres are covered by a thin matrix of amorphous material at their proximal extremities. The proximal portions are thick and unstructured, whereas the distal portions are finely folded and the matrix covering becomes progressively thinner (Gruffydd et al., 1979). The ribbons are bound together by a fibrous sheath, secreted by the secondary byssus gland (Gruffydd et al., 1979).

Functioning of the Foot–Byssal Complex

Prior to fixation, the foot extends out from the byssal notch in the shell and actively explores the surrounding substrates. The cornet then presses against a substrate, and several minutes later (4–10 min in *Chlamys varia*) the foot retracts, leaving a filament which fixes the animal to the substrate (Mahéo, 1969). Throughout the period of extension, protein granules are secreted by the primary and secondary byssus gland and are swept into the pedal groove. The secretions are presumably tanned by the products of the enzyme gland, although it is not yet known exactly how the proteinaceous secretions are formed into distinct ribbons bounded by a sheath. The ciliary beating of the pedal groove epithelial cells probably acts to mix the aromatic proteins and the polyphenoloxidase, promoting tanning. Gruffydd et al. (1979) propose that incompletely tanned ribbons are stored in a special pouch of the primary byssus gland, being moved into the pedal groove and stretched outward by ciliary action.

Once the ribbon is tanned and anchored to the substratum, the sides of the pedal groove curl outward along the short non-enclosed length, leaving a ribbon, which extends into the primary byssus gland. A new thread may then be put in place, more or less fused with the previous one by incomplete tanning. In the proximal region of the foot, the accumulation of untanned and partially tanned ribbons forms the byssal root. The root is held in place by the continuous contraction of numerous muscle fibres. Prior to the swimming response, these muscles relax, separating the untanned portions of the ribbons from the primary byssus gland. The byssus then detaches and the animal is freed of its connection to the substrate (Mahéo, 1969).

Acknowledgements

I thank Drs. Sandra Shumway and Jay Parsons for their patience and editing efforts in this and the previous editions of this chapter. Funding during the preparation of the third edition of this chapter was provided by the Syndicat Mixte pour le Développement de la Pêche et de l'Aquaculture aux Pays de la Loire, although not for this project.

References

Abebe, A.T., Devoid, S.J., Sugumaran, M., Etter, R., Robinson, W.E., 2007. Identification and quantification of histidine-rich glycoprotein (HRG) in the blood plasma of six marine bivalves. Comp. Biochem. Physiol. B 147, 74–81.

Albertini, C., 1985. Recherches cytologiques et expérimentales sur l'ovogénèse chez la moule (*Mytilus edulis* L., Mollusque Bivalve). Thèse 3e cycle, Université de Caen, Caen, France. 117 p.

Allarakh, C., 1979. Recherches histologiques et expérimentales de la différenciation sexuelle et du cycle de reproduction de *Chlamys opercularis* L. (Mollusque Lamellibranche). Thèse 3e cycle, Université de Caen, Caen, France. 148 p.

Amirthalingam, C., 1928. On lunar periodicity in reproduction of *Pecten opercularis* near Plymouth in 1927–28. J. Mar. Biol. Assoc. U.K. 15, 605–641.

Andrews, E.B., 1988. Excretory systems of molluscs. In: Trueman, E.R., Clarke, M.R. (Eds.), Form and Function. The Mollusca, vol. 11. Academic Press, San Diego, CA, pp. 381–448.

Andrews, E.B., Jennings, K.H., 1993. The anatomical and ultrastructural basis of primary urine formation in bivalve molluscs. J. Molluscan Stud. 59, 223–257.

Atkins, D., 1936. On the ciliary mechanisms and interrelationships of lamellibranchs. Part I: new observations on sorting mechanisms. Q. J. Microsc. Sci. 79, 181–308.

Atkins, D., 1937a. On the ciliary mechanisms and interrelationships of lamellibranchs. Part II: sorting devices on the gills. Q. J. Microsc. Sci. 79, 339–373.

Atkins, D., 1937b. On the ciliary mechanisms and interrelationships of lamellibranchs. Part III: types of lamellibranch gills and their food currents. Q. J. Microsc. Sci. 79, 375–421.

Atkins, D., 1937c. On the ciliary mechanisms and interrelationships of lamellibranchs. Part IV: cuticular fusion. Q. J. Microsc. Sci. 79, 423–445.

Atkins, D., 1938a. On the ciliary mechanisms and interrelationships of lamellibranchs. Part V: note on gills of *Amussium pleuronectes* L. Q. J. Microsc. Sci. 80, 321–329.

Atkins, D., 1938b. On the ciliary mechanisms and interrelationships of lamellibranchs. Part VI: pattern of the lateral ciliated cells of the gill filaments. Q. J. Microsc. Sci. 80, 331–344.

Atkins, D., 1938c. On the ciliary mechanisms and interrelationships of lamellibranchs. Part VII: latero-frontal cilia of the gill filaments and their phylogenic value. Q. J. Microsc. Sci. 80, 345–436.

Atkins, D., 1943. On the ciliary mechanisms and interrelationships of lamellibranchs. Part VIII: notes on gill musculature in the microciliobranchia. Q. J. Microsc. Sci. 84, 187–256.

Auffret, M., 1985. Morphologie comparative des types hémocytaires chez quelques Mollusques Bivalves d'intérêt commercial (Thèse de doctorat de spécialité). Université de Bretagne Occidentale, Brest, France, 155 p.

Auffret, M., 1988. Bivalve hemocyte morphology. In: Pal, S.G. (Ed.), Disease Processes in Marine Bivalve Molluscs. American Fisheries Society, Bethesda, MD, pp. 169–177. , Special Publication Series 18.

Barber, V.C., Dilly, P.N., 1969. Some aspects of the fine structure of the statocysts of the molluscs *Pecten* and *Pterotrachea*. Z. Zellforsch. Microsk. Anat. 94, 462–478.

Barnes, R.D., 1987. Invertebrate Zoology. Saunders College Publishing, Philadelphia, PA, 893 p.

Beninger, P., 1987. A qualitative and quantitative study of the reproductive cycle of the giant scallop *Placopecten magellanicus*, in the Bay of Fundy (New Brunswick, Canada). Can. J. Zool. 65, 495–498.

Beninger, P.G., 1985. Long-term variations in cation content of two populations of adult marine clam (*Tapes decussatus* L. and *T. philippinarum*) reared in a common habitat. Comp. Biochem. Physiol. 82A, 945–949.

Beninger, P.G., 1991. Structures and mechanisms of feeding in scallops: paradigms and paradoxes. In: Shumway, S.E., Sandifer, P.A. (Eds.), An International Compendium of Scallop Biology and Culture. World Aquaculture Workshops, vol. 1. World Aquaculture Society, Baton Rouge, LA, pp. 331–340.

Beninger, P.G., Decottignies, P., 2005. What makes diatoms attractive to suspensivores? The organic casing and associated organic molecules of *Coscinodiscus perforatus* are quality cues for the bivalve *Pecten maximus*. J. Plankton Biol. 27, 11–17.

Beninger, P.G., Decottignies, P., 2008. Worth a second look: gill structure in *Hemipecten forbesianus* Adams & Reeve, and taxonomic implications for the Pectinidae. J. Mollusc. Stud. 74, 137–142.

Beninger, P.G., Dufour, S.C., 2000. Evolutionary trajectories of a redundant feature: lessons from bivalve gill abfrontal cilia and mucocyte distributions. In: Harper, E.M., Taylor, J.D., Crame, J.A. (Eds.), The Evolutionary Biology of the Bivalvia. Geological Society, London, pp. 273–278. , Special Publications 177.

Beninger, P.G., Le Pennec, M., 1991. Functional anatomy of scallops. In: Shumway, S.S.E. (Ed.), Scallops: Their Biology, Ecology and Aquaculture. Elsevier Science Publishers, Amsterdam, pp. 133–223.

Beninger, P.G., Le Pennec, M., 1993. Histochemistry of the bucco-oesophageal glands of *Mytilus edulis*: the importance of mucus in ingestion. J. Mar. Biol. Assoc. U.K. 73, 237–240.

Beninger, P.G., Le Pennec, M., 1997. Reproductive characteristics of a primitive bivalve from a deep-sea reducing environment: giant gametes and their significance in *Acharax alinae* (Cryptodonta: Solemyidae). Mar. Ecol. Prog. Ser. 157, 195–206.

Beninger, P.G., Le Pennec, M., 2006. Structure and function in scallops. In: Shumway, S.S.E., Parsons, G.J. (Eds.), Scallops: Their Biology, Ecology and Aquaculture, second ed. Elsevier Science Publishers, Amsterdam, pp. 123–227.

Beninger, P.G., Saint-Jean, S., 1997a. Particle processing on the labial palps of *Mytilus edulis* and *Placopecten magellanicus* (Mollusca, Bivalvia). Mar. Ecol. Prog. Ser. 147, 117–127.
Beninger, P.G., Saint-Jean, S., 1997b. The role of mucus in particle processing by suspension-feeding marine bivalves: unifying principles. Mar. Biol. 129, 389–397.
Beninger, P.G., Le Pennec, M., Salaün, M., 1988. New observations of the gills of *Placopecten magellanicus* (Mollusca: Bivalvia), and implications for nutrition. Mar. Biol. 98, 61–70.
Beninger, P.G., Auffret, M., Le Pennec, M., 1990a. The peribuccal organs of *Placopecten magellanicus* and *Chlamys varia* (Mollusca: Bivalvia): structure, ultrastructure and implications for feeding. I. The labial palps. Mar. Biol. 107, 215–223.
Beninger, P.G., Le Pennec, M., Auffret, M., 1990b. The peribuccal organs of *Placopecten magellanicus* and *Chlamys varia* (Mollusca: Bivalvia): structure, ultrastructure, and implications for feeding. II. The lips. Mar. Biol. 107, 225–233.
Beninger, P.G., Le Pennec, M., Donval, A., 1991. Mode of particle ingestion in five species of bivalve molluscs. Mar. Biol. 108, 255–261.
Beninger, P.G., Ward, J.E., MacDonald, B.A., Thompson, R.J., 1992. Feeding processes of the gill in *Placopecten magellanicus* (Gmelin) (Mollusca: Bivalvia) as revealed using video endoscopy. Mar. Biol. 114, 281–288.
Beninger, P.G., St-Jean, S., Poussart, Y., Ward, E., 1993. Gill function and mucocyte distribution in *Placopecten magellanicus* and *Mytilus edulis* (Mollusca: Bivalvia): the role of mucus in particle transport. Mar. Ecol. Prog. Ser. 98, 275–282.
Beninger, P.G., Dwiono, S., Le Pennec, M., 1994. Early development of the gill and implications for feeding in *Pecten maximus* (Bivalvia: Pectinidae). Mar. Biol. 119, 405–412.
Beninger, P.G., Donval, A., Le Pennec, M., 1995a. The osphradium in *Placopecten magellanicus* and *Pecten maximus* (Bivalvia, Pectinidae): histology, ultrastructure and implications for spawning synchronisation. Mar. Biol. 123, 121–129.
Beninger, P.G., Potter, T.M., St-Jean, S.D., 1995b. Paddle cilia fixation artefacts in pallial organs of adult *Mytilus edulis* and *Placopecten magellanicus*. Can. J. Zool. 73, 610–614.
Beninger, P.G., Dufour, S., Bourque, J., 1997a. Particle processing mechanisms on the pallial organs of the eulamellibranchs *Spisula solidissima* and *Mya arenaria*. Mar Ecol. Prog. Ser. 150, 157–169.
Beninger, P.G., Lynn, J.W., Dietz, T.H., Silverman, H., 1997b. Mucociliary transport in living tissue: the two-layer model confirmed in the mussel *Mytilus edulis* L. Biol. Bull. 193, 4–7.
Beninger, P.G., Veniot, A., Poussart, Y., 1999. Principles of pseudofeces rejection on the bivalve mantle: integration in particle processing. Mar. Ecol. Prog. Ser. 178, 259–269.
Beninger, P.G., Le Pennec, G., Le Pennec, M., 2003. Demonstration of nutrient pathway from the digestive system to oocytes in the gonad intestinal loop of the scallop *Pecten maximus* L.: the intestinal loop pathway. Biol. Bull. 205, 83–92.
Beninger, P.G., Decottignies, P., Rincé, Y., 2004. Localization of qualitative particle selection sites in the heterorhabdic filibranch *Pecten maximus* (Bivalvia: Pectinidae). Mar. Ecol. Prog. Ser. 275, 163–173.
Bevelander, G., Nakahara, H., 1966. Correlation of lysosomal activity and ingestion by the mantle epithelium. Biol. Bull. 131, 76–82.
Bieler, R., Mikkelsen, P.M., Collins, T.M., Glover, E.A., González, V.L., Graf, D.L., et al., 2014. Investigating the Bivalve Tree of Life – an exemplar-based approach combining molecular and novel morphological characters. Invert. Syst. 28, 32–115.
Bojanus, L.H., 1819. Mémoire sur les organes respiratoires et circulatoires des coquillages bivalves en général, et spécialement sur ceux de l'Anodonte des Cygnes (*Anodon cygneum*). J. Physiol. 89, 108–134.
Bonardelli, J.C., Himmelman, J.H., Drinkwater, K., 1996. Relation of spawning of the giant scallop, *Placopecten magellanicus*, to temperature fluctuations during downwelling events. Mar. Biol. 124, 637–649.
Booth, C.E., Mangum, C.P., 1978. Oxygen uptake and transport in the lamellibranch mollusc *Modiolus demissus*. Physiol. Zool. 51, 17–32.
Bourne, N., 1964. Scallops and the offshore fishery of the Maritimes. Bull. Fish. Res. Board Can. 145, 60.
Brand, A.R., Roberts, D., 1973. The cardiac responses of the scallop *Pecten maximus* (L.) to respiratory stress. J. Exp. Mar. Biol. Ecol. 13, 29–43.
Brilliant, M.G.S., MacDonald, B.A., 2000. Postingestive selection in the sea scallop, *Placopecten magellanicus* (Gmelin): the role of particle size and density. J. Exp. Mar. Biol. Ecol. 253, 211–227.
Brilliant, M.G.S., MacDonald, B.A., 2003. Postingestive sorting of living and heat-killed *Chlorella* within the sea scallop, *Placopecten magellanicus* (Gmelin). J. Exp. Mar. Biol. Ecol. 290, 81–91.
Broadaway, B.J., Hannigan, R.E., 2012. Elemental fingerprints used to identify essential habitats: Nantucket Bay Scallop. J. Shellfish Res. 31, 671–676.
Brock, V., Kennedy, V.S., Brock, A., 1986. Temperature dependency of carbohydrate activity in the hepatopancreas of thirteen estuarine and coastal bivalve species from the North American east coast. J. Exp. Mar. Biol. Ecol. 103, 87–101.
Brown, C.H., 1952. Some structural proteins of *Mytilus edulis*. Q. J. Microsc. Sci. 4, 487–502.
Brunel, A., 1938. Sur la dégradation des substances d'origine purique chez les Mollusques Lamellibranches. C. R. Acad. Sci. Paris Ser. III 206, 858–860.
Bryan, G.W., 1973. The occurrence and seasonal variation of trace metals in the Scallops *Pecten maximus* (L.) and *Chlamys opercularis* (L.). J. Mar. Biol. Assoc. U.K. 53, 154–166.
Bubel, A., 1973a. An electron microscopic study of the periostracum formation in some marine bivalves. I. The origin of the periostracum. Mar. Biol. 20, 213–221.
Bubel, A., 1973b. An electron microscopic study of the periostracum formation in some marine bivalves. II. The cell lining in the periostracal groove. Mar. Biol. 20, 222–234.
Bubel, A., 1984. Mollusca. In: Bereiter-Hahn, J., Matoltsy, A.G., Sylvia Richards, K.S. (Eds.), Biology of the Integument. I. Invertebrates. Springer-Verlag, Berlin, pp. 421–447.
Buddenbrock, W.V., 1915. Die Statocyste von *Pecten*, ihre histologie und physiologie. Zool. Jahrb. Abt. Allg. Zool. Physiol. Tiere 35, 301–356.
Bullock, T.H., Horridge, G.A., 1965. Mollusca: pelecypoda. In: Bullock, T.H., Horridge, G.A. (Eds.), Structure and Function in the Nervous Systems of Invertebrates, vol. 2. W.H. Freeman and Company, San Francisco, CA, pp. 1390–1431.
Burton, R.F., 1983. Ionic regulation and water balance. In: Saleuddin, A.S.M., Wilbur, K.M. (Eds.), The Mollusca, Volume 5, Physiology, Part 2. Academic Press, New York, NY, pp. 291–347.

Butcher, E.O., 1930. The formation, regeneration, and transplantation of eyes in *Pecten* (*Gibbus borealis*). Biol. Bull. Mar. Biol. Lab. Woods Hole 59, 154–164.
Carmichael, N.G., Fowler, B.A., 1981. Cadmium accumulation and toxicity in the kidney of the bay scallop *Argopecten irradians*. Mar. Biol. 65, 35–43.
Carmichael, N.G., Squibb, K.S., Fowler, B.A., 1979. Metals in the molluscan kidney: a comparison of two closely related bivalve species (*Argopecten*), using X-ray microanalysis and atomic absorption spectroscopy. J. Fish. Res. Board. Can. 36, 1149–1155.
Chan, J.F.Y., Saleuddin, A.S.M., 1974. Acid phosphatase in the mantle edge of the shell-regenerating snail. Top. Curr. Chem. 64, 1–112.
Chang, Y.G., Matsutani, T., Mori, K., Nomura, T., 1984. Enzyme histochemical localization of monoamine oxydase and acetylcholinesterase in the central nervous system of the scallop, *Patinopecten yessoensis*. Mar. Biol. Lett. 5, 335–345.
Charles, G.H., 1966. Sense organs (less cephalopods). In: Wilbur, K.M., Yonge, C.M. (Eds.), Physiology of Mollusca, vol. 2. Academic Press, New York, NY, pp. 465–521.
Cheng, T.C., 1975. Lysosomal and other enzymes in the hemolymph of *Crassostrea virginica* and *Mercenaria mercenaria*. Comp. Biochem. Physiol. 52B, 443–447.
Cheng, T.C., 1981. Bivalves. In: Ratcliffe, N.A., Rowley, A.F. (Eds.), Invertebrate Blood Cells, vol. 1. Academic Press, London, pp. 223–300.
Cheng, T.C., 1996. Hemocytes: forms and functions. In: Kennedy, V.S., Newell, R.I.E., Eble, A.F. (Eds.), The Eastern Oyster, *Crassostrea virginica*. Maryland Sea Grant Books, College Park, MD, pp. 299–333.
Chipman, W., Thommeret, J., 1970. Manganese content and the occurrence of the fallout of ^{54}Mn in some marine benthos of the Mediterranean. Bull. Inst. Oceanogr. Monaco 69 (1402), 15.
Christiansen, H.R., Olivier, S.R., 1971. Sobre el hermaproditismo de *Chlamys tehuelcha* D'orb. 1846. (Pelecypoda, Filibranchia, Pectinidae). An. Soc. Cient. Argent. 3, 115–127.
Chute, A.S., Wainright, S.C., Hart, D.R., 2012. Timing of shell ring formation and patterns of shell growth in the sea scallop *Placopecten magellanicus* based on stable oxygen isotopes. J. Shellfish Res. 31, 649–662.
Ciocco, N.F., 1985. Biologia y ecologia de *Chlamys tehuelcha* d'Orbigny en el Golfo san José (Provincia del Chubut, Republica Argentina) Pelecypoda, Pectinidae (Ph.D. thesis). Universidad Nacional de La Plata, Argentina.
Cobb, J.L.S., Mullins, P.A., 1973. Synaptic structure in the visceral ganglion of the lamellibranch mollusc, *Spisula solidissima*. Z. Zellforsch. 138, 75–83.
Coe, W.R., 1943a. Development of the primary gonads and differentiation of sexuality in *Teredo navalis* and other pelecypod mollusks. Biol. Bull. 84, 178–187.
Coe, W.R., 1943b. Sexual differentiation in molluscs. I. Pelecypods. Q. Rev. Biol. 18, 154–164.
Coe, W.R., 1945. Development of the reproductive system and variations in sexuality in *Pecten* and other pelecypod mollusks. Trans. Conn. Acad. Arts Sci. 36, 673–700.
Cognie, B., Barillé, L., Massé, G., Beninger, P.G., 2003. Selection and processing of large suspended algae in the oyster *Crassostrea gigas*. Mar. Ecol. Prog. Ser. 250, 145–152.
Coombs, T.L., George, S.G., 1977. Mechanisms of immobilization and detoxication of metals in marine organisms. In: McLusky, D.S., Berry, A. J. (Eds.), Physiology and Behavior of Marine Organisms. Proceedings of the 12th European Marine Biology Symposium. Pergamon Press, Oxford, pp. 179–187.
Costedio, M.M., Hyman, N., Mawe, G.M., 2007. Serotonin and its role in colonic function and in gastrointestinal disorders. Dis. Colon. Rectum. 50, 376–388.
Costello, T.J., Hudson, M.J., Dupuy, J.L., Rivkin, S., 1973. Larval culture of the calico scallop *Argopecten gibbus*. Proc. Natl. Shellfish. Assoc. 63, 72–76.
Crenshaw, M.A., 1980. Mechanisms of shell formation and dissolution. In: Rhoads, D.C., Lutz, R.A. (Eds.), Skeletal Growth of Aquatic Organisms. Plenum, New York, NY, pp. 67–86.
Croll, R.P., Too, C.K.L., Pani, A.K., Nason, J., 1995. Distribution of serotonin in the sea scallop *Placopecten magellanicus*. Invertebr. Reprod. Dev. 28, 125–135.
Culliney, J.L., 1974. Larval development of the giant scallop *Placopecten magellanicus*. Biol. Bull. 147, 321–332.
Dakin, W.J., 1909. *Pecten*. Liverpool Marine Biology Committee Memoirs No. 17. 146 p.
Dakin, W.J., 1910a. The eye of *Pecten*. Q. J. Microsc. Sci. 55, 49–112 + 2 pl.
Dakin, W.J., 1910b. The visceral ganglion of *Pecten*, with some notes on the physiology of the nervous system, and an inquiry into the innervation of the osphradium in Lamellibranchia. Mitt. Zool. Statz. Neapel 20, 1–40 + 2 pl.
Dakin, W.J., 1928a. The anatomy and phylogeny of *Spondylus*, with a particular reference to the lamellibranch nervous system. Proc. R. Soc. Lond. B Biol. Sci. 103, 337–354.
Dakin, W.J., 1928b. The eyes of *Pecten, Spondylus, Amussium*, and allied lamellibranchs, with a short discussion on their evolution. Proc. R. Soc. (B) 103, 355–365.
Davenport, J., Lehane, C., 2000. Mussels *Mytilus edulis*: significant consumers and destroyers of mesozooplankton. Mar. Ecol. Prog. Ser. 198, 131–137.
De Lacaze-Duthiers, H., 1854. Recherches sur les organes génitaux des acéphales lamellibranches. Ann. Sc. Nat. Paris, 4e sér. Zool. 3, 155–248, Pl. 5–9.
Deaton, L.E., Greenberg, M.J., 1980. The ionic dependence of the cardiac action potential in bivalve molluscs: systematic distribution. Comp. Biochem. Physiol. 67A, 155–161.
Desilets, J., Gicquaud, C., Dubé, F., 1995. An ultrastructural analysis of early fertilization events in the giant scallop, *Placopecten magellanicus* (Mollusca, Pelecypoda). Invertebr. Reprod. Dev. 27, 115–129.
Dietz, T.H., Steffens, W.L., Kays, W.T., Silverman, H., 1984. Serotonin localization in the gills of the freshwater mussel, *Ligumia subrostrata*. Can. J. Zool. 63, 1237–1243.
Dix, T.G., 1976. Larval development of the Queen scallop *Equichlamys bifrons*. Aust. J. Mar. Freshwater Res. 27, 399–403.
Dix, T.G., Jardin, S., 1975. Larvae of the commercial scallop, *Pecten meridionalis* from Tasmania, Australia. Aust. J. Mar. Freshwater Res. 26, 109–112.

Dohmen, M.R., 1983. Gametogenesis. In: Verdonk, N.H., van den Biggelaar, J.A.M., Tompa, A.S. (Eds.), Development. The Mollusca, vol. 3. Academic Press, London, pp. 1–48.
Dorange, G., Le Pennec, M., 1989a. Ultrastructural study of oogenesis and oocytic degeneration in *Pecten maximus* from the Bay of St. Brieuc. Mar. Biol. 103, 339–348.
Dorange, G., Le Pennec, M., 1989b. Ultrastructural characteristics of spermatogenesis in *Pecten maximus* (Mollusca, Bivalvia). Invertebr. Reprod. Dev. 15, 109–117.
Dorange, G., Paulet, Y.M., Le Pennec, M., 1989a. Etude cytologique de la partie femelle de la gonade de *Pecten maximus* récolté en baie de St Brieuc. I. Caractéristiques ultrastructurales des tissus somatiques. Haliotis 19, 287–297.
Dorange, G., Paulet, Y.M., Le Pennec, M., 1989b. Etude cytologique de la partie femelle de la gonade de *Pecten maximus* récolté en baie de St. Brieuc. II. Ovogénèse et lyse ovocytaire. Haliotis 19, 299–314.
Doyle, L.J., Blake, N.J., Woo, C.C., Yevich, P., 1978. Recent biogenic phosphorite: concretions in mollusk kidneys. Science 199, 1431–1433.
Drew, G.A., 1906. The habits, anatomy, and embryology of the giant scallop (*Pecten tenuicostatus*, Mighels). Univ. Maine Studies Series, No. 6, Orono. 89 p.
Dufour, S.C., Beninger, P.G., 2001. A functional interpretation of cilia and mucocyte distributions on the abfrontal surface of bivalve gills. Mar. Biol. 138, 295–309.
Dufour, S.C., Steiner, G., Beninger, P.G., 2006. Phylogenetic analysis of the peri-hydrothermal vent bivalve *Bathypecten vulcani*, based on 18S rRNA and anatomical characters. Malacologia 48, 35–42.
Eble, A.F., 2001. Anatomy and histology of *Mercenaria mercenaria*. In: Kraeuter, J.N., Castagna, M. (Eds.), Developments in Aquaculture and Fisheries Science. Biology of the Hard Clam, vol. 31. Elsevier, Amsterdam, pp. 117–220.
Eckelbarger, K.J., Davis, C.V., 1996a. Ultrastructure of the gonad and gametogenesis in the eastern oyster, *Crassostrea virginica*. I. Ovary and oogenesis. Mar. Biol. 127, 79–87.
Eckelbarger, K.J., Davis, C.V., 1996b. Ultrastructure of the gonad and gametogenesis in the eastern oyster, *Crassostrea virginica*. II. Testis and spermatogenesis. Mar. Biol. 127, 89–96.
Eckelbarger, K.J., Young, C.M., 1999. Ultrastructure of gametogenesis in a chemosynthetic mytilid bivalve (*Bathymodiolus childressi*) from a bathyal, methane seep environment (Northern Gulf of Mexico). Mar. Biol. 135, 635–646.
Elliott, E., 1980. Three types of acetylcholine response in bivalve heart muscle cells. J. Physiol. 300, 283–302.
Estrada, N., Velázquez, E., Rodríguez-Jaramillo, C., Ascencio, F., 2013. Morphofunctional study of hemocytes from lions-paw scallop *Nodipecten subnodosus*. Immunobiology 218, 1093–1103.
Ferreira, R.P., Salomao, L., 2000. The ionic basis of cardiac activity in the bivalve mollusc *Perna perna*. J. Exp. Mar. Biol. Ecol. 249, 1–12.
Franc, A., 1960. Classe des bivalves. In: Grassé, P.P. (Ed.), Traité de Zoologie, Tome 5, Fascicule 2. Librairie Masson, Paris, pp. 845–2133.
Frank, B.P., Belfort, G., 2002. Adhesion of *Mytilus edulis* foot protein 1 on silica: ionic effects on biofouling. Biotechnol. Prog. 18, 580–586.
Fretter, V., Graham, A., 1964. Reproduction. In: Wilbur, K.M., Yonge, C.M. (Eds.), Physiology of Mollusca, vol. 1. Academic Press, New York, NY, pp. 127–164.
Gabe, M., 1955. Particularités histologiques des cellules neurosécrétrices chez quelques Lamellibranches. C.R. Acad. Sci. Paris 240, 1810–1812.
Garrido, O., Gallardo, C.S., 1996. Ultrastructure of sperms in bivalve molluscs of the Mytilidae family. Invertebr. Reprod. Dev. 29, 95–102.
Garton, D.W., Roller, R.A., Caprio, J., 1984. Fine structure and vital staining of osphradium of the southern oyster drill, *Thais laemastoma canaliculata* (Gray) (Prosobranchia: Muricidae). Biol. Bull. 167, 310–321.
George, S.G., Pirie, B.J.S., Coombs, T.L., 1980. Isolation and elemental analysis of metal-rich granules from the kidney of the scallop *Pecten maximus* (L.). J. Exp. Mar. Biol. Ecol. 42, 143–156.
Ghiretti, F., 1966. Respiration. In: Wilbur, K.W., Yonge, C.M. (Eds.), Physiology of Mollusca, vol. II. Academic Press, New York, NY, pp. 209–231.
Gibbons, M.C., Castagna, M., 1984. Serotonin as an inducer of spawning in six bivalve species. Aquaculture 40, 189–191.
Gilmour, T.H.J., 1964. The structure, ciliation and function of the lip-apparatus of *Lima* and *Pecten* (Lamellibranchia). J. Mar. Biol. Assoc. U.K. 44, 485–498.
Gilmour, T.H.J., 1974. The structure, ciliation and function of the lips of some bivalve molluscs. Can. J. Zool. 52, 335–343.
Greenberg, M.J., 1965. A compendium of responses of bivalve hearts to acetylcholine. Comp. Biochem. Physiol. 14, 513–539.
Greenberg, M.J., 1970. A comparison of acetylcholine structure—activity relations on the hearts of bivalve molluscs. Comp. Biochem. Physiol. 33, 259–294.
Grobben, K., 1888. Die Pericardialdrüse der lamellibranchiaten. Arb. Zool. Inst. Univ. Wien 7, 355–444.
Gruffydd, Ll.D., 1978. The byssus and byssus glands in *Chlamys islandica* and other scallops (Lamellibranchia). Zool. Scr. 7, 277–285.
Gruffydd, Ll.D., Budiman, A., Nott, J.A., 1979. The ultrastructure of the byssus and the byssus glands in *Chlamys varia* L. (Lamellibranchia). J. Mar. Biol. Assoc. U.K. 59, 597–603.
Gutsell, J.S., 1931. Natural history of the bay scallop. Bull. U.S. Bur. Fish. 46, 569–632.
Hagenaua, A., Periklis Papadopoulos, P., Kremer, F., Scheibel, T., 2011. Mussel collagen molecules with silk-like domains as load-bearing elements in distal byssal threads. J. Struct. Biol. 175, 339–347.
Hamilton, P.V., Koch, K.M., 1996. Orientation toward natural and artificial grassbeds by swimming bay scallops, *Argopecten irradians* (Lamarck, 1819). J. Exp. Mar. Biol. Ecol. 199, 79–88.
Haszprunar, G., 1985a. The fine morphology of the osphradial sense organs of the mollusca. I. Gastropoda, Prosobranchia. Philos. Trans. R. Soc. Lond. B 307, 63–73.
Haszprunar, G., 1985b. The fine morphology of the osphradial sense organs of the mollusca. II. Allogastropoda (Architectonicidae, Pyramidellidae). Philos. Trans. R. Soc. Lond. B 307, 497–505.
Haszprunar, G., 1987a. The fine morphology of the osphradial sense organs of the mollusca. IV. Caudofoveata and Solenogastres. Philos. Trans. R. Soc. Lond. B 315, 63–73.
Haszprunar, G., 1987b. The fine morphology of the osphradial sense organs of the mollusca. III. Placophora and Bivalvia. Philos. Trans. R. Soc. Lond. B 315, 37–61.

Haszprunar, G., 1992. Ultrastructure of the osphradium of the tertiary relict snail, *Campanile symbolium* Iredale (Mollusca, Streptoneura). Philos. Trans. R. Soc. Lond. B 337, 457–469.
Haszprunar, G., 1996. The molluscan rhogocyte (pore cell, blasenzelle, cellule nucale), and its significance for ideas on nephridial evolution. J. Molluscan Stud. 62, 185–211.
Healy, J.M. 1995. Comparative spermatozoal ultrastructure and its taxonomic and phylogenetic significance in the bivalve order Veneroida. In: Jamieson, B.G.M., Ausio, J., Justine, J.-L. (Eds.). Advances in Spermatozoal Phylogeny and Taxonomy. Mem. Mus. Hist. Nat., vol. 166. pp. 155–166.
Healy, J.M., 1996. Molluscan sperm ultrastructure: correlation with taxonomic units within the Gastropoda, Cephalopoda, and Bivalvia. In: Taylor, J. (Ed.), Origin and Evolutionary Radiation of the Mollusca. Oxford University Press, Oxford, pp. 99–113.
Healy, J.M., Keys, J.L., Daddow, L.Y.M., 2000. Comparative sperm ultrastructure in pteriomorphan bivalves with special reference to phylogenetic and taxonomic implications. In: Harper, E.M., Taylor, J.D., Crame, J.A. (Eds.), The Evolutionary Biology of the Bivalvia. Geological Society, London, pp. 169–190. , Special Publications 177.
Henry, M., Boucaud-Camou, E., Lefort, Y., 1991. Functional micro-anatomy of the digestive gland of the scallop *Pecten maximus* (L.). Aquat. Living Res. 4, 191–202.
Hickson, J.A., Johnson, A.L.A., Heaton, T.H.E., Balson, P.S., 1999. The shell of the Queen Scallop *Aequipecten opercularis* (L.) as a promising tool for palaeoenvironmental reconstruction: evidence and reasons for equilibrium stable-isotope incorporation. Palaeogeogr. Palaeoclimatol. Palaeoecol. 154, 325–337.
Hiesinger, P.R., Meinertzhagen, I.A., 2009. Visual system development: invertebrates. In: Squire, L.R. (Ed.), Encyclopedia of Neuroscience, vol. 10. Academic Press, Oxford, pp. 313–322.
Hine, P.M., 1999. The inter-relationships of bivalve haemocytes. Fish Shellfish Immunol. 9, 367–385.
Hochachka, P.W., Somero, G.N., 1984. Biochemical adaptation. Water Solute Adaptations: The Evolution and Regulation of Biological Solutions. Princeton University Press, Princeton, NJ, pp. 304–354. (Chapter 10).
Hodgson, A.N., Bernard, R.T.F., 1986. Ultrastructure of the sperm and spermatogenesis of three species of Mytilidae (Mollusca, Bivalvia). Gamete Res. 15, 123–135.
Huang, Q.Y., Fang, C.W., Huang, H.Q., 2010. Alteration of heart tissue protein profiles in acute cadmium-treated scallops *Patinopecten yessoensis*. Arch. Environ. Contam. Toxicol. 60, 90–98.
Iglesias, P., Louro, Á., Román, G., 2012. The effect of depth on the reproductive and reserve storage cycles of the pectinids *Aequipecten opercularis* (l., 1758) and *Chlamys varia* (l., 1758) in Galicia, northwest Spain. J. Shellfish Res. 31, 677–684.
Irisawa, H., Irisawa, I., Shigeto, N., 1973. Physiological and morphological correlation of the functional syncytium in the bivalve myocardium. Comp. Biochem. Physiol. 44A, 207–219.
Janssens, F., 1893. Les branchies des acéphales. La cellule 9, 6–90.
Jennings, K.H., 1984. The organization, fine structure and function of the excretory systems of the estuarine bivalve, *Scrobicularia plana* (da Costa) and the freshwater bivalve *Anodonta cygnea* (Linné) and other selected species (Ph.D. thesis). University of London, England, Cited by E.B. Andrews (1988).
Jeuniaux, C., 1982. La chitine dans le règne animal. Bull. Soc. Zool. Fr. 107, 363–386.
Jones, H.D., 1983. The circulatory systems of gastropods and bivalves. In: Saleuddin, A.S.M., Wilbur, K.M. (Eds.), Physiology, Part 2. The Mollusca, vol. 5. Academic Press, New York, NY, pp. 189–238.
Jones, H.D., Peggs, D., 1983. Hydrostatic and osmotic pressures in the heart and pericardium of *Mya arenaria* and *Anodonta cygnea*. Comp. Biochem. Physiol. 76A, 381–385.
Judd, W., 1987. Crystalline style proteins from bivalve molluscs. Comp. Biochem. Physiol. 88B, 333–339.
Jørgensen, C.B., 1976. Comparative studies on the function of gills in suspension-feeding bivalves, with special reference to effects of serotonin. Biol. Bull. 151, 331–343.
Kafanov, A.I., Drozdov, A.L., 1998. Comparative sperm morphology and phylogenetic classification of recent Mytiloidea (Bivalvia). Malacologia 39, 129–139.
Kellogg, J.L., 1892. A contribution to our knowledge of the morphology of the lamellibranchiate molluscs. Bull. U.S. Fish Comm. 10, 389–434 + Pl. 79–94.
Kellogg, J.L., 1915. Ciliary mechanisms of lamellibranchs with descriptions of anatomy. J. Morph. 26, 625–701.
Kennedy, V.S., Newell, R.I.E., Eble, A.F. (Eds.), 1996. The Eastern Oyster, *Crassostrea virginica*. Maryland Sea Grant Books, College Park, MD, 734 p.
Kraemer, L.R., 1979. Suprabranchial and branchial shelves of bivalved molluscs: structural/functional context of visceral ganglion, osphradium and branchial nerves. Am. Zool. 19, 959.
Kraeuter, J.N., Castagna, M., 2001. Biology of the Hard Clam. Developments in Aquaculture and Fisheries Science, vol. 31. Elsevier, Amsterdam, 751 p.
Krijgsman, B.J., Divaris, G.A., 1955. Contractile and pacemaker mechanisms of the heart of molluscs. Biol. Rev. Camb. Philos. Soc. 30, 1–39.
Kube, S., Gerber, A., Jansen, J.M., Schiedek, D., 2006. Patterns of organic osmolytes in two marine bivalves, *Macoma balthica*, and *Mytilus* spp., along their European distribution. Mar. Biol. 149, 1387–1396.
Land, M.F., 1965. Image formation by a concave reflector in the eye of the scallop, *Pecten Maximus*. J. Physiol. 179, 138–153 + 1 pl.
Land, M.F., 1968. Functional aspects of the optical and retinal organization of the mollusc eye. Symp. Zool. Soc. Lond. 23, 75–96.
Langton, R.W., Gabbott, P.A., 1974. The tidal rhythm of extracellular digestion and the response to feeding in *Ostrea edulis*. J. Mar. Biol. Assoc. U.K. 24, 181–187.
Langton, R.W., Robinson, W.E., Schick, D., 1987. Fecundity and reproductive effort of sea scallop *Placopecten magellanicus* from the Gulf of Maine. Mar. Ecol. Prog. Ser. 37, 19–25.
Le Pennec, G., 2000. La glande digestive de la coquille Saint Jacques *Pecten maximus*. Caractérisation fonctionnelle et mise en place d'un nouveau modèle *in vitro* (Doctoral thesis). Université de Bretagne Occidentale, 219 p.
Le Pennec, M., 1978. Genèse de la coquille larvaire et postlarvaire chez divers Bivalves marins (Thèse de Doctorat d'état). Université de Bretagne Occidentale, Brest, France, 216 p., 108 pl.

Le Pennec, M., Beninger, P.G., 1996. Ultrastructural characteristics of spermatogenesis in three species of deep-sea hydrothermal vent mytilids. Can. J. Zool. 75, 308–316.
Le Pennec, M., Beninger, P.G., Herry, A., 1988. New observations of the gill of *Placopecten magellanicus* (Mollusca: Bivalvia), and implications for nutrition. II. Internal anatomy and microanatomy. Mar. Biol. 98, 229–238.
Le Pennec, M., Dorange, G., Beninger, P.G., Donval, A., Widowati, I., 1991a. Les relations anse intestinale- gonade chez *Pecten maximus* (Mollusque, Bivalve). Haliotis 21, 57–69.
Le Pennec, M., Beninger, P.G., Dorange, G., Paulet, Y.-M., 1991b. Trophic sources and pathways to the developing gametes of *Pecten maximus* (Bivalvia: Pectinidae). J. Mar. Biol. Assoc. U.K. 71, 451–463.
Le Pennec, G., Le Pennec, M., Beninger, P.G., 2001. Seasonal digestive gland dynamics of the scallop *Pecten maximus* L in the Bay of Brest (France). J. Mar. Biol. Assoc. U.K. 81, 663–671.
Le Pennec, G., Le Pennec, M., Beninger, P.G., Dufour, S., 2002. Spermatogenesis in the archaic hydrothermal vent bivalve, *Bathypecten vulcani*, and comparison of spermatozoon ultrastructure with littoral pectinids. Invertebr. Reprod. Dev. 41, 13–19.
Le Roux, S., Bellon-Humbert, C., Lucas, A., 1987. Mise en évidence par immunocytochimie d'une substance apparentée à la somatostatine dans le système nerveux, le rein, et la glande digestive de juvéniles de *Pecten maximus* (Mollusque Bivalve). C. R. Acad. Sci. Paris Ser. III 304, 115–118.
Lehane, C., Davenport, J., 2002. Ingestion of mesozooplankton by three species of bivalve: *Mytilus edulis*, *Cerastoderma edule*, and *Aequipecten opercularis*. J. Mar. Bio. Assoc. U.K. 82, 615–619.
Lent, C.M., 1974. Neuronal control of mucus secretion by leeches: toward a general theory for serotonin. Am. Zool. 14, 931–942.
Lindberg, D.R., Sigwart, J.D., 2015. What is the molluscan osphradium? A reconsideration of homology. Zoologischer Anzeiger. 256, 14–21.
Longo, F.J., 1983. Meiotic maturation and fertilization. In: Verdonk, N.H., van den Bigelaar, J.A.M., Tompa, A.S. (Eds.), Development. The Mollusca, vol, 3. Academic Press, New York, NY, pp. 49–89.
Lowe, D.M., Moore, M.N., 1979. The cytochemical distribution of zinc (Zn II) and iron (Fe III) in the common mussel *Mytilus edulis* and their relationship with lysosomes. J. Mar. Biol. Assoc. U.K. 59, 854–858.
Lubet, P., 1951. Sur l'émission des gamètes chez *Chlamys varia* L. (Moll. Lamellibr. C. R. Hebd. Seances Acad. Sci. 233, 1680–1681.
Lubet, P., 1955. Cycle neurosécrétoire de *Chlamys varia* (L.) et de *Mytilus edulis* L. C. R. Acad. Sci. Paris 241, 119–121.
Lubet, P., 1959. Recherches sur le cycle sexuel et l'émission des gamètes chez les Mytilidés et les Pectinidés. Rev. Trav. Inst. Pêches Marit. 23, 395–548.
Lubet, P., Mathieu, M., 1982. The action of internal factors on gametogenesis in pelecypod molluscs. Malacologia 22, 131–136.
Lubet, P., Albertini, L., Robbins, I., 1986. Recherches expérimentales au cours des cycles annuels sur l'action gonadotrope exercée par les ganglions cérébroïdes sur la gamétogenèse femelle chez la moule *Mytilus edulis* L. (mollusque bivalve). C. R. Acad. Sci. Paris, Ser. III 303, 575–580.
Lubet, P., Besnard, J.-Y., Faveris, R., Robbins, I., 1987. Physiologie de la reproduction de la coquille Saint-Jacques (*Pecten maximus* L.). Océanis 13, 265–290.
Lucas, A., 1965. Recherches sur la sexualité des Mollusques Bivalves. Bull. Biol. Fr. Belg. 99, 115–247.
Lucas, A., Hignette, M., 1983. Les concrétions rénales chez les bivalves marins: etudes anciennes et récentes. Haliotis 13, 99–113.
MacDonald, B.A., Thompson, R.J., 1986. Production, dynamics and energy partitioning in two populations of the giant scallop *Placopecten magellanicus* (Gmelin). J. Exp. Mar. Biol. Ecol. 101, 285–299.
Machin, J., 1977. Role of integument in molluscs. In: Gupta, B.L., Moreton, R.B., Oschman, J.L., Wall, B.J. (Eds.), Transport of Ions and Water in Animals. Academic Press, London, pp. 735–762.
Mackie, G.L., 1984. Bivalves. In: Tompa, A.S., Verdonk, N.H., Van Den Biggelaar, J.A.M. (Eds.), Reproduction. The Mollusca, vol. 7. Academic Press, San Diego, CA, pp. 351–403.
Mahéo, R., 1968. Observations sur l'anatomie et le fonctionnement de l'appareil byssogène de *Chlamys varia* L. Cah. Biol. Mar. 9, 373–379.
Mahéo, R., 1969. Contribution à l'étude de l'anatomie et du fonctionnement du complexe byssogène de quelques Bivalves (Thèse de 3e cycle). Contribution à l'étude de l'anatomie et du fonctionnement du complexe byssogène de quelques Bivalves (Thèse de 3e cycle). Université de Rennes, France, 91 p. + 12 pl.
Maldonado-Amparo, R., Ibarra, A.M., 2002. Ultrastructural characteristics of spermatogenesis in diploid and triploid Catarina scallop (*Argopecten ventricosus* Sowerby II, 1842). J. Shellfish. Res. 21, 93–101.
Manahan, D.T., Wright, S.H., Stevens, G.C., Rice, M.A., 1982. Transport of dissolved amino acids by the mussel, *Mytilus edulis*: demonstration of net uptake from natural seawater. Science 215, 1253–1255.
Manocha, M., Khan, W.I., 2012. Serotonin and GI disorders: an update on clinical and experimental studies. Clin. Transl. Gastroenterol. 3, e13. Available from: http://dx.doi.org/10.1038/ctg.2012.8.
Marin, F., Luquet, G., 2004. Molluscan shell proteins. C. R. Palevol. 3, 469–492.
Martin, A.W., 1983. Excretion. In: Saleuddin, A.S.M., Wilbur, K.M. (Eds.), Physiology, Part 2. The Mollusca, vol. 5. Academic Press, San Diego, CA, pp. 353–405.
Marsh, H., Hopkins, G., Fisher, F., Saas, R.L., 1976. Structure of the molluscan bivalve hinge ligament, a unique calcified elastic tissue. J. Ultrastruct. Res. 54, 445–450.
Martoja, R., Alibert, J., Ballan-Dufrancais, C., Jeantet, A.Y., Lhonore, D., Truchet, M., 1975. Microanalyse et écologie. J. Microsc. Biol. Cell 22, 441–448.
Mason, J., 1958. The breeding of the scallop *Pecten maximus* L., in Manx waters. J. Mar. Biol. Assoc. U.K. 37, 653–671.
Mason, J., 1963. Queen Scallop Fisheries in the British Isles. Fishing News Book, Farnham, 144 p.
Masson, M., Ancellin, J., 1976. Aspects physiologiques et écologiques des contaminations des mollusques pélécypodes par les radionucléides et autres éléments à l'état de traces. Haliotis 7, 123–130.
Mathers, N.F., 1972. The tracing of natural algal food labelled with a carbon 14 isotope through the digestive tract of *Ostrea edulis* L. Proc. Malac. Soc. Lond. 40, 115–124.

Mathers, N.F., 1973a. A comparative histochemical survey of enzymes associated with the process of digestion in *Ostrea edulis* and *Crassostrea angulata* (Mollusca: Bivalvia). J. Zool. 169, 169–179.
Mathers, N.F., 1973b. Carbohydrate digestion in *Ostrea edulis* L. Proc. Malacol. Soc. Lond. 40, 359–367.
Mathers, N.F., 1976. The effects of tidal currents on the rhythm of feeding and digestion in *Pecten maximus* L. J. Exp. Mar. Biol. Ecol. 24, 271–283.
Mathers, N.F., Colins, N., 1979. Monophasic and diphasic digestive cycles in *Venerupis decussata* and *Chlamys varia*. J. Molluscan Stud. 45, 68–81.
Mathieu, M., Lenoir, F., Robbins, I., 1988. A gonial mitosis-stimulating factor in cerebral ganglia and haemolymph of the marine mussel *Mytilus edulis* L. Gen. Comp. Endocrinol. 72, 257–263.
Matsutani, T., Nomura, T., 1982. Induction of spawning by serotonin in the scallop, *Patinopecten yessoensis* (Jay). Mar. Biol. Lett. 3, 353–358.
Matsutani, T., Nomura, T., 1984. Localization of monoamines in the central nervous system and gonad of the scallop *Patinopecten yessoensis*. Bull. Jap. Soc. Sci. Fish. 52, 425–430.
Matsutani, T., Nomura, T., 1986. Serotonin-like immuno-reactivity in the central nervous system and gonad of the scallop, *Patinopecten yessoensis*. Cell Tissue Res. 244, 515–517.
McLachlan, J., McInnes, A.G., Allen, J.A., 1965. Studies on the chitan (chitin: poly-*n*-acetylglucosamine) fibers of the diatom *Thalassiosira fluviatilis* Hustedt. Can. J. Bot. 43, 707–713.
Merrill, A.S., Burch, J.B., 1960. Hermaphroditism in the sea scallop, *Placopecten magellanicus* (Gmelin). Biol. Bull. 119, 197–201.
Meyhöfer, E., Morse, M.P., Robinson, W.E., 1985. Podocytes in bivalve molluscs: morphological evidence for ultrafiltration. J. Comp. Physiol. B 156, 151–161.
Mikulich, L.V., Tsikhon-Lukanina, Ye.A., 1981. Food of the scallop. Oceanology 21, 633–635.
Moir, A.J.G., 1977a. Ultrastructural studies on the ciliated receptors of the long tentacles of the giant scallop, *Placopecten magellanicus* (Gmelin). Cell Tissue Res. 184, 367–380.
Moir, A.J.G., 1977b. On the ultrastructure of the abdominal sense organ of the giant scallop, *Placopecten magellanicus* (Gmelin). Cell Tissue Res. 184, 359–366.
Morrison, C., Shum, G., 1982. Chlamydia-like organisms in the digestive diverticula of the bay scallop, *Argopecten irradians* (Link). J. Fish Dis. 5, 173–184.
Morse, M.P., Zardus, J.D., 1997. Bivalvia. In: Harrison, F.W., Kohn, A.J. (Eds.), Microscopic Anatomy of Invertebrates. Mollusca II, vol. 6A. Wiley-Liss, New York, NY, pp. 7–118.
Morse, M.P., Robinson, W.E., Wehling, W.E., 1982. Effects of sublethal concentrations of the drilling mud components attapulgite and Q-broxin on the structure and function of the gill of the scallop, *Placopecten magellanicus* (Gmelin). In: Vernberg, W.B., Calabrese, A., Thurberg, F.P., Vernberg, F.J. (Eds.), Physiological Mechanisms of Marine Pollutant Toxicity. Academic Press, New York, NY, pp. 235–259.
Morton, B., 1977. The tidal rhythm of feeding and digestion in the Pacific oyster, *Crassostrea gigas* (Thunberg). J. Exp. Mar. Biol. Ecol. 26, 135–151.
Morton, B., 1983. Feeding and digestion in bivalvia. In: Saleuddin, A.S.M., Wilbur, K.M. (Eds.), Physiology, Part 2. The Mollusca, vol. 5. Academic Press, New York, NY, pp. 65–147.
Morton, B., 1994. The biology and functional morphology of *Leptopecten latiauratus* (Conrad, 1837): an 'opportunistic' scallop. Veliger 37, 5–22.
Morton, B., 1996. The biology and functional morphology of *Minnivola pyxidatus* (Bivalvia: Pectinoidea). J. Zool., Lond. 240, 735–760.
Morton, B., 2000. The function of pallial eyes within the Pectinidae, with a description of those present in *Patinopecten yessoensis*. In: Harper, E. M., Taylor, J.D., Crame, J.A. (Eds.), Evolutionary Biology of the Bivalvia. Geological Society Publishing House, Bath, UK, pp. 247–255. , Geological Society Special Publication 177.
Morton, B., 2008. The evolution of eyes in the bivalvia: new insights. Am. Malacol. Bull. 26, 35–45.
Mottet, M.G., 1979. A Review of the Fishery Biology and Culture of Scallops. State of Washington Department of Fisheries Technical Report No. 39, 99 p.
Møhlenberg, F., Riisgard, H.V., 1978. Efficiency of particle retention in 13 species of suspension feeding bivalves. Ophelia 17 (2), 239–246.
Nagasawa, K., Osugi, T., Suzuki, I., Itoh, N., Takahashi, K.G., Satake, H., et al., 2015. Characterization of GnRH-like peptides from the nerve ganglia of Yesso scallop, *Patinopecten yessoensis*. Peptides 71, 202–210.
Naidu, K.S., 1970. Reproduction and breeding cycle of the giant scallop *Placopecten magellanicus* (Gmelin) in Port au Port Bay, Newfoundland. Can. J. Zool. 48, 1003–1012.
Nakahara, H., Bevelander, G., 1967. Ingestion of particulate matter by the outer surface cells of the mollusc mantle. J. Morphol. 122, 139–146.
Natochin, Yu.V., Berger, V.Ya, Khlebovich, V.V., Lavrova, E.A., Michailova, O.Yu, 1979. The participation of electrolytes in adaptation mechanisms of intertidal molluscs' cells to altered salinity. Comp. Biochem. Physiol. 63A, 115–119.
Neff, J.M., 1972. Ultrastructure of the outer epithelium of the mantle in the clam *Mercenaria mercenaria* in relation to calcification of the shell. Tissue Cell 4, 591–600.
Nigro, M., Orlando, E., Regoli, F., 1992. Ultrastructural localization of metal binding sites in the kidney of the Antarctic scallop *Adamussium colbecki*. Mar. Biol. 113, 637–643.
Ono, J.K., Hampton, D.R., Koch, R.A., 1992. Immunohistochemical localization and radioenzymatic measurements of serotonin (5-hydroxytryptamine) in hearts of *Aplysia* and several bivalve molluscs. Cell Tissue Res. 269, 421–430.
Orton, J.H., 1912. The mode of feeding of *Crepidula*, with an account of the current-producing mechanism in the mantle cavity, and some remarks on the mode of feeding in Gastropods and Lamellibranchs. J. Mar. Biol. Assoc. U.K. 9, 444–478.
Overnell, J., 1981. Protein and oxalate in mineral granules from the kidney of *Pecten maximus* (L.). J. Exp. Mar. Biol. Ecol. 52, 173–183.
Owen, G., 1955. Observations on the stomach and digestive diverticula of the Lamellibranchia. I. The Anisomyaria and Eulamellibranchia. Q. J. Microsc. Sci. 96, 517–537.
Owen, G., 1966. Digestion. In: Wilbur, K.M., Yonge, C.M. (Eds.), Physiology of Mollusca, vol. 2. Academic Press, New York, NY, pp. 53–96.
Owen, G., 1978. Classification and the bivalve gill. Philos. Trans. R. Soc. Lond. B 284, 377–385.
Owen, G., McCrae, J.M., 1976. Further studies on the latero-frontal tracts of bivalves. Proc. R. Soc. Lond. B 194, 527–544.

Owen, R., Kennedy, H., Richardson, C., 2002. Experimental investigation into partitioning of stable isotopes between scallop (*Pecten maximus*) shell calcite and sea water. Palaeogeogr. Palaeoclimatol. Palaeoecol. 185, 163–174.
Owen, G., Trueman, E.R., Yonge, C.M., 1953. The ligament in the Lamellibranchia. Nature 171, 73–75.
Ozanai, K., 1975. Seasonal gonad development and sex alteration in the scallop, *Patinopecten yessoensis*. Bull. Mar. Biol. Stn. Asamushi 15, 81–88.
Paillard, C., Le Pennec, M., 1993. Ultrastructural studies of the mantle and the periostracal lamina in the Manila clam, *Ruditapes philippinarum*. Tissue Cell. 25, 183–194.
Pales Espinosa, E., Perrigault, M., Ward, J.E., Shumway, S.E., Allam, B., 2009. Lectins associated with the feeding organs of the oyster *Crassostrea virginica* can mediate particle selection. Biol. Bull. 217, 130–141.
Pales Espinosa, E., Perrigault, M., Ward, J.E., Shumway, S.E., Allam, B., 2010a. Microalgal cell surface carbohydrates as recognition sites for particle sorting in suspension-feeding bivalves. Biol. Bull. 218, 75–86.
Pales Espinosa, E., Hassan, D., Ward, J.E., Shumway, S.E., Allam, B., 2010b. Role of epicellular molecules in the selection of particles by the blue mussel, *Mytilus edulis*. Biol. Bull. 219, 50–60.
Pales Espinosa, E., Perrigault, M., Allam, B., 2010c. Identification and molecular characterization of a mucosal lectin (MeML) from the blue mussel *Mytilus edulis* and its potential role in particle capture. Comp. Biochem. Physiol. A 156, 495–501.
Pani, A.M., Croll, R.P., 1995. Distribution of catecholamines, indoleamines, and their precursors and metabolites in the scallop, *Placopecten magellanicus* (Bivalvia, Pectinidae). Cell. Mol. Neurobiol. 15, 371–385.
Paulet, Y.M., Lucas, A., Gerard, A., 1988. Reproduction and larval development in two *Pecten maximus* L. populations from Brittany. J. Exp. Mar. Biol. Ecol. 119, 145–156.
Paulet, Y.M., Donval, A., Bekhadra, F., 1993. Monoamines and reproduction in *Pecten maximus*, a preliminary approach. Invertebr. Reprod. Devel. 23, 89–94.
Pelseneer, M.J., 1894. Hermaphroditism in mollusca. Q. J. Microsc. Sci. 37, 19–46.
Pelseneer, P., 1906. Mollusca. A Treatise on Zoology. Part V. Ray Lankester Ltd, London, 355 p.
Petit, H., 1978. Recherches sur des séquences d'évènements périostracaux lors de l'élaboration de la coquille d'*Amblema plicata perplicata* Conrad 1834. Thèse de doctorat d'Etat. Université de Bretagne Occidentale, Brest, France, 185 p.
Petit, H., Le Pennec, M., Martin, J., 1988. Ultrastructure du sillon periostracal du Mytilidae des sources hydrothermales profondes du Pacifique oriental. Oceanol. Acta, Spec. Publ. Number 8, 191–194.
Pierce, M.E., 1950. Pecten irradians. In: Brown, F.A. (Ed.), Selected Invertebrate Types. John Wiley and Sons Inc., New York, NY, pp. 321–324.
Pierce, S.K., 1982. Invertebrate cell volume control mechanisms: a co-ordinated use of intracellular amino acids and inorganic ions as osmotic solute. Biol. Bull. 163, 405–419.
Pipe, R.K., 1987. Oogenesis in the marine mussel *Mytilus edulis*: an ultrastructural study. Mar. Biol. 95, 405–414.
Pirie, B.J.S., George, S.G., 1979. Ultrastructure of the heart and excretory system of *Mytilus edulis* (L.). J. Mar. Biol. Assoc. U.K. 59, 819–829.
Poder, M., 1980. Les réactions hémocytaires inflammatoires et tumorales chez *Ostrea edulis* (L.). Essai de classification des hémocytes des Mollusques Bivalves (Thèse de doctorat de 3^{e} cycle). Université de Bretagne Occidentale, Brest, France, 95 p.
Popham, J.D., 1979. Comparative spermatozoan morphology and bivalve phylogeny. Malacol. Rev. 12, 1–20.
Posgay, J.A., 1950. Investigations of the Sea Scallop, Pecten grandis. Third Report on Investigations of Methods of Improving the Shellfish Resources of Massachusetts. Massachusetts Dept. Nat. Resources, Div. Mar. Fish., pp. 24–30.
Potts, W.T.W., 1967. Excretion in the molluscs. Biol. Rev. Camb. Philos. Soc. 42, 1–41.
Purchon, R.D., 1957. The stomach in the Filibranchia and Pseudolamellibranchia. Proc. Zool. Soc. Lond. 129, 27–60.
Purchon, R.D., 1977. The Biology of the Mollusca, 2nd ed Pergammon Press, Oxford, pp. 225–243.
Ram, G.L., Ram, M.L., Smith, S.S., Croll, R.P., 1997. Peptinergic and serotinergic mechanisms regulating spawning and egg-laying behavior in gastropods and bivalves. Malacol. Rev. 30, 1–23.
Ramsay, J.A., 1952. A Physiological Approach to the Lower Animals. University Press, Cambridge, MA, pp. 18–36.
Ranson, G., 1939. Le provinculum de la prodissoconque de quelques Ostréidés. Bull. Mus. Nat. Hist. Nat. (Paris) 2, 318–332.
Raven, C., 1961. Oogenesis: The Storage of Development Information. Pergamon Press, New York, NY, 274 p.
Raven, C.P., 1966. Morphogenesis. The Analysis of Molluscan Development, 2nd ed. Pergamon Press, New York, NY.
Reddiah, K., 1962. The sexuality and spawning of manx Pectinids. J. Mar. Biol. Assoc. U.K. 42, 683–703.
Reed-Miller, C., Greenberg, M.J., 1982. The ciliary junctions of scallop gills: the effects of cytochalasins and concanavalin A. Biol. Bull. (Woods Hole) 163, 225–239.
Reindl, S., Haszprunar, G., 1996. Fine structure of caeca and mantle of arcoid and limopsoid bivalves (Mollusca: Pteriomorpha). Veliger 39, 101–116.
Richardson, C.A., Runham, N.W., Crisp, D.J., 1981. A histological and ultrastructural study of the cells of the mantle edge of a marine bivalve, *Cerastoderma edule*. Tissue Cell 13, 715–730.
Ridewood, W.G., 1903. On the structure of the gills of the Lamellibranchia. Philos. Trans. R. Soc. Lond. B 195, 147–284.
Riisgard, H.U., 1988. Efficiency of particle retention and filtration rate in 6 species of Northeast American bivalves. Mar. Ecol. Prog. Ser. 45, 217–223.
Robinson, W.E., Langton, R.W., 1980. Digestion in a subtidal population of *Mercenaria mercenaria* (Bivalvia). Mar. Biol. 58, 173–179.
Robinson, W.E., Penington, M.R., Langton, R.W., 1981. Variability of tubule types within the digestive glands of *Mercenaria mercenaria* (L.), *Ostrea edulis* L. and *Mytilus edulis* L. J. Exp. Mar. Biol. Ecol. 54, 265–276.
Rodrick, G.E., Ulrich, S.A., 1984. Microscopical studies on the hemocytes of bivalves and their phagocytic interaction with selected bacteria. Helgol. Wiss. Meeresunters. 37, 167–176.
Saleuddin, A.S.M., Petit, H., 1983. The mode of formation and the structure of the periostracum. In: Saleuddin, A.S.M., Wilbur, K.M. (Eds.), Physiology, Part 1. The Mollusca, vol, 4. Academic Press, New York, NY, pp. 199–234.
Sanger, J.W., 1979. Cardiac structure in selected arthropods and molluscs. Am. Zool. 19, 9–27.
Sastry, A.N., 1963. Reproduction of the bay scallop, *Aequipecten irradians* Lamark. Influence of temperature on maturation and spawning. Biol. Bull. 125, 146–153.

Sastry, A.N., 1965. The development and external morphology of pelagic larval and post-larval stages of the bay scallop, *Aequipecten irradians concentricus* Say, reared in the laboratory. Bull. Marine Sci. 15, 417–435.
Sastry, A.N., 1966. Temperature effects in reproduction of the bay scallops, *Aequipecten irradians* Lamarck. J. Mar. Biol. Assoc. U.K. 130, 118–134.
Sastry, A.N., 1968. Relationships among food, temperature and gonad development of the bay scallop, *Aequipecten irradians concentricus* Say, reared in the laboratory. Bull. Mar. Sci. 15, 417–435.
Sastry, A.N., 1979. Pelecypoda (excluding Ostreidae). In: Giese, A.C., Pearse, J.S. (Eds.), Molluscs: Pelecypods and Lesser Classes. Reproduction of Marine Invertebrates, vol. V. Academic Press, New York, NY, pp. 113–292.
Seiderer, L.J., Newell, R.C., Schultes, K., Robb, F.T., Turley, C.M., 1987. Novel bacteriolytic activity associated with the style microflora of the mussel *Mytilus edulis* (L.). J. Exp. Mar. Biol. Ecol. 110, 213–224.
Setna, S.B., 1930. Neuro-muscular mechanism of the gill of *Pecten*. Q. J. Microsc. Sci. 73, 365–391.
Shaw, B.L., Battle, H.I., 1958. The chemical composition of the gastric shield of the oyster *Crassostrea virginica* (Gmelin). Can. J. Zool. 37, 214–215.
Shumway, S.E., 1977. Effect of salinity fluctuation on the osmotic pressure and Na^{+}, Ca^{2+} and Mg^{2+} ion concentrations in the hemolymph of bivalve molluscs. Mar. Biol. 41, 153–177.
Shumway, S.E. (Ed.), 1991. Scallops: Biology, Ecology, and Aquaculture. Developments in Aquaculture and Fisheries Science, vol. 21. Elsevier, Amsterdam.
Shumway, S.E., Youngson, A., 1979. The effects of fluctuating salinity on the physiology of *Modiolus demissus* (Dillwyn). J. Exp. Mar. Biol. Ecol. 40, 167–181.
Shumway, S.E., Selvin, R., Schick, D.F., 1987. Food resources related to habitat in the scallop *Placopecten magellanicus* (Gmelin, 1791): a qualitative study. J. Shellfish Res. 6, 89–95.
Shumway, S.E., Gabbott, P.A., Youngson, A., 1977. The effect of fluctuating salinity on the concentrations of free amino acids and ninhydrin-positive substances in the adductor muscles of eight species of bivalve molluscs. J. Exp. Mar. Biol. Ecol. 29, 131–150.
Simkiss, K., 1976. Intracellular and extracellular routes in biomineralisation. In: Duncan, J.C. (Ed.), Calcium in Biological Systems. Cambridge University Press, Cambridge, MA, pp. 423–444.
Silverman, H.S., Lynn, J.W., Beninger, P.G., Dietz, T.H., 1999. The role of latero-frontal cirri in particle capture by the gills of *Mytilus edulis*. Biol. Bull. 197, 368–376.
Somero, G.N., Bowlus, R.D., 1983. Osmolytes and metabolic end products of molluscs: the design of compatible solute systems. In: Hochachka, P.W. (Ed.), The Mollusca Vol. 2: Environmental Biochemistry and Physiology. Academic Press, New York, NY, pp. 77–100.
Spagnolia, T., Wilkens, L.A., 1983. Neurobiology of the scallop. II. Structure of the parietovisceral ganglion lateral lobes in relation to afferent projections from the mantle eyes. Mar. Behav. Physiol. 10, 23–55.
Speiser, D.I., Johnsen, S., 2008a. Comparative morphology of the concave mirror eyes of scallops (Pectinoidea). Amer. Malacol. Bull. 26, 27–34.
Speiser, D.I., Johnsen, S., 2008b. Scallops visually respond to the size and speed of virtual particles. J. Exp. Biol. 211, 2066–2070.
Stasek, C.R., 1963. Orientation and form in the bivalved Mollusca. J. Morphol. 112, 195–214.
Stephens, P.J., 1978. The sensitivity and control of the scallop mantle edge. J. Exp. Biol. 75, 203–221.
Stewart, M.G., Bamford, D.R., 1976. Absorption of soluble nutrients by the mid gut of the bivalve *Mya arenaria*. J. Molluscan Stud. 42, 63–73.
Stommel, E.W., Stephens, R.E., 1985. Cyclic AMP and calcium in the differential control of *Mytilus* gill cilia. J. Comp. Physiol. A 157, 451–459.
Strohmeier, T., Duinker, A., Lie, Ø., 2000. Seasonal variations in chemical composition of the female gonad and storage organs in *Pecten maximus* (L.) suggesting that somatic and reproductive growth are separated in time. J. Shellfish Res. 19, 741–747.
Suhre, M.H., Gertz, M., Steegborn, C., Scheibel, T., 2014. Structural and functional features of a collagen-binding matrix protein from the mussel byssus. Nat. Commun. 5, 3392.
Sullivan, P.A., Robinson, W.E., Morse, M.P., 1988. Isolation and characterization of granules from the kidney of the bivalve *Mercenaria mercenaria*. Mar. Biol. 99, 359–368.
Sundet, J.H., Lee, J.B., 1984. Seasonal variations in gamete development in the Iceland scallop, *Chlamys islandica*. J. Mar. Biol. Assoc. U.K. 64, 411–416.
Tang, S.F., 1941. The breeding of the scallop (*Pecten maximus* L.) with a note on the growth rate. Proc. Liverpool Biol. Soc. 54, 9–28.
Taylor, J.D., Kennedy, W.J., 1969. The influence of the periostracum on the shell structure of bivalve molluscs. Calcif. Tissue Res. 3, 274–283.
Taylor, R., Capuzzo, J., 1983. The reproductive cycle of the bay scallop *Argopecten irradians irradians* (Lamarck), in a small coastal embayment on Cape Cod, Massachusetts. Estuaries 6, 431–435.
Thompson, R.J., 1977. Blood chemistry, biochemical composition, and the annual reproductive cycle in the giant scallop, *Placopecten magellanicus*, from Southeast Newfoundland. J. Fish. Res. Board Can. 34, 2104–2116.
Thompson, R.J., Livingstone, D.R., de Zwaan, A., 1980. Physiological and biochemical aspects of the valve snap and valve closure responses in the giant scallop *Placopecten magellanicus*. I. Physiology. J. Comp. Physiol. 137, 97–104.
Too, C.K.L., Croll, R.P., 1995. Detection of FMRFamide-like immunoreactivities in the sea scallop *Placopecten magellanicus* by immunohistochemistry and Western Blot analysis. Cell Tissue Res. 281, 295–304.
Toullec, J.Y., Lenoir, F., Van Wormhoudt, A., Mathieu, M., 1988. Nonspecies-specific growth factor from cerebral ganglia of *Mytilus edulis*. J. Exp. Mar. Biol. Ecol. 119, 111–117.
Trueman, E.R., 1953. The ligament of *Pecten*. Q. J. Microsc. Sci. 94, 193–202.
Turchini, J., 1923. Contribution à l'étude de l'histologie comparée de la cellule rénale. L'excrétion rénale chez les mollusques. Arch. Morph. Gén. Exp. 18, 7–253.
Uesaka, H., Yamagishi, H., Ebara, A., 1987. Stretch-mediated interaction between the auricle and ventricle in an oyster *Crassostrea gigas*. Comp. Biochem. Physiol. 88A, 221–227.
Usheva, L.N., 1983. Cell histomorphology and proliferation of the posterior intestine epithelium in the Yezo scallop *Patinopecten yessoensis*. Biol. Morya 3, 17–24.
Vaschenko, M.A., Hsieh, H.L., Radashevsky, V.I., 2013. Gonadal state of the oyster *Crassostrea angulata* cultivated in Taiwan. J. Shellfish Res. 32, 471–482.

Veniot, A., Bricelj, V.M., Beninger, P.G., 2003. Ontogenetic changes in gill morphology and potential significance for food acquisition in the scallop *Placopecten magellanicus*. Mar. Biol. 142, 123–131.
Vitellaro-Zuccarello, L., DeBiasi, S., 1990. Ultrastructure of the ganglia and submicroscopical localization of putative neurotransmitters. In: Stefano, G.B. (Ed.), Neurobiology of *Mytilus edulis*. Manchester University Press, Manchester, pp. 57–73.
von Buddenbrock, W., Moller-Racke, I., 1953. Über den Lichtsinn von *Pecten*. Pubbl. Stn. Zool. Napoli 24, 217–245.
Wada, S.K., 1968. Mollusca. 1. Amphineura, Gastropoda, Scaphopoda, Pelycypoda. In: Kume, M., Dan, K. (Eds.), Invertebrate Embryology. Nolit Publishing House, Belgrade, pp. 485–525.
Waite, J.H., Andersen, S.O., 1978. 3,4-Dihydroxyphenylalanine in an insoluble shell protein of *Mytilus edulis*. Biochim. Biophys. Acta 541, 107–114.
Waite, J.H., Andersen, S.O., 1980. 3,4-Dihydroxyphenylalaline and sclerotization of the periostracum in *Mytilus edulis*. Biol. Bull. 158, 164–173.
Waite, J.H., Wilbur, K.M., 1976. Phenoloxidase in the periostracum of the marine bivalve *Modiolus demissus* Dillwyn. J. Exp. Zool. 195, 358–368.
Wakui, T., Obara, A., 1967. On the seasonal change of the gonads of scallop, *Patinopecten yessoensis* (Jay), in lake Saroma, Hokkaido. Bull. Hokkaido Reg. Fish. Res. Lab. 32, 15–32.
Waller, T.R., 1991. Evolutionary relationships among commercial scallops (Mollusca: Bivalvia: Pectinidae). In: Shumway, S.E. (Ed.), Scallops: Biology, Ecology, and Aquaculture. Developments in Aquaculture and Fisheries Science, vol. 21. Elsevier, Amsterdam.
Ward, J.E., Beninger, P.G., MacDonald, B.A., Thompson, R.J., 1991. Direct observations of feeding structures and mechanisms in Bivalve molluscs using endoscopic examination and video image analysis. Mar. Biol. 111, 287–291.
Ward, J.E., MacDonald, B.A., Thompson, R.J., Beninger, P.G., 1993. Mechanisms of suspension-feeding in Bivalves: resolution of current controversies using endoscopy. Limnol. Oceanogr. 30, 265–272.
Ward, J.E., Levinton, J.S., Shumway, S.E., Cucci, T., 1998. Particle sorting in bivalves: *in vivo* determination of the pallial organs of selection. Mar. Biol. 131, 283–292.
Watabe, N., 1984. Shell. In: Bereiter-Hahn, J., Matoltsy, A.G., Richards, K.S. (Eds.), Biology of the Integument. I. The Invertebrates. Springer-Verlag, Berlin, pp. 448–485.
Weinstein, J.E., 1995. Fine structure of the digestive tubule of the Eastern oyster, *Crasssotrea virginica* (Gmelin, 1791). J. Shellfish Res. 14, 97–103.
Welsh, J.H., Moorhead, M., 1960. The quantitative distribution of 5-hydroxytryptamine in the invertebrates, especially in their nervous systems. J. Neurochem. 6, 146–169.
White, K.M., 1942. The pericardial cavity and the pericardial gland of the Lamellibranchia. Proc. Malacol. Soc. Lond 25, 37–88.
Wilbur, K.M., 1972. Shell formation in molluscs. In: Florkin, M., Scheer, B.T. (Eds.), Mollusca. Chemical Zoology, vol. VII. Academic Press, New York, NY, pp. 243–282.
Wilbur, K.M., 1985. Topics in molluscan mineralization: present status, future directions. Am. Malacol. Union Bull., Special Edition 1, 51–58.
Wilbur, K.M., Saleuddin, A.S.M., 1983. Shell formation. In: Saleuddin, A.S.M., Wilbur, K.M. (Eds.), Physiology, Part 1. The Mollusca, vol. 4. Academic Press, New York, NY, pp. 235–287.
Wilkens, L.A., 1981. Neurobiology of the scallop. I. Starfish-mediated escape behaviors. Proc. R. Soc. Lond. B Biol. Sci. 211, 241–372.
Wilkens, L.A., Greenberg, M.J., 1973. Effects of acetylcholine and 5-hydroxytryptamine and their ionic mechanisms of action on the electrical and mechanical activity of molluscan heart smooth muscle. Comp. Biochem. Physiol. 45A, 637–651.
Wilkins, N.P., 1978. Length correlated changes in heterozygosity at an enzyme locus in the scallop (*Pecten maximus* L.). Anim. Blood Groups Biochem. Genet. 9, 69–77.
Wojtowicz, M.B., 1972. Carbohydrases of the digestive gland and the crystalline style of the Atlantic deep-sea scallop (*Placopecten magellanicus*, Gmelin). Comp. Biochem. Physiol. 43A, 131–141.
Wright, S.H., 1987. Alanine and taurine transport by the gill epithelium of a marine bivalve: effect of sodium on influx. J. Membr. Biol. 95, 37–46.
Wright, S.H., Southwell, K.M., Stevens, G.C., 1984. Autoradiographic analysis of amino-acid uptake by the gill of *Mytilus californianus*. J. Comp. Physiol. 154, 249–256.
Yamamoto, G., 1943. Gametogenesis and the breeding season of the Japanese common scallop *Pecten (Patinopecten) yessoensis* Jay. Bull. Jap. Soc. Sci. Fish 12, 21–26.
Yevich, C.A., Yevich, P.P., 1985. Histopathological effects of cadmium and copper on the sea scallop *Placopecten magellanicus*. In: Vernberg, F.J., Thurberg, F.P., Calabrese, A., Vernberg, W. (Eds.), Marine Pollution and Physiology: Recent Advances, University of South Carolina Press, Columbia, SC, pp. 187–198.
Yonge, C.M., 1951. Studies on Pacific coast mollusks. III. Observations on *Hinnites multirugosus* (Gale). Univ. Calif. Publ. Zool. 56, 409–420.
Yonge, C.M., 1981. On adaptive radiation in the Pectinacea, with a description of *Hemipecten forbesianus*. Malacologia 21, 23–34.
Yuan, Y., Tanabe, T., Maekawa, F., Inaba, K., Maeda, Y., Itoh, N., et al., 2012. Isolation and functional characterization for oocyte maturation and sperm motility of the oocyte maturation arresting factor from the Japanese scallop, *Patinopecten yessoensis*. Gen. Comp. Endocrinol. 179, 350–357.
Zacks, S.I., 1955. The cytochemistry of the amoebocytes and intestinal epithelium of *Venus mercenaria* (Lamellibranchiata), with remarks on a pigment resembling ceroid. Q. J. Microsc. Sci. 96, 57–71.
Zhadan, P.M., 2005. Directional sensitivity of the Japanese scallop *Mizuhopecten yessoensis* and Swift scallop *Chlamys swifti* to water-borne vibrations. Russ. J. Mar. Biol. 31, 28–35.
Zhadan, P.M., Doroshenko, P.A., 1985. Cyclic AMP-dependent processes and mechanosensitivity of the abdominal sense organ of the scallop *Patinopecten yessoensis* (Jay). Biol. Membr. 2, 285–291.
Zhadan, P.M., Semen'kov, P.G., 1984. An electrophysiological study of the mechanoreceptory function of the abdominal sense organ of the scallop *Patinopecten yessoensis* (Jay). Comp. Biochem. Physiol. 78A, 865–870.

This page intentionally left blank