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Early development of the gill and implications for feeding in *Pecten maximus* (Bivalvia: Pectinidae)

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Abstract Despite the importance of understanding feeding in the early stages of bivalve development, little information is available concerning the organogenesis of the bivalve gill. The present study used histological and scanning electron microscopical techniques to present a detailed account of gill development in the early stages of the scallop *Pecten maximus* L. (Bivalvia: Pectinidae). Live specimens from larval cultures were observed daily using light microscopy, while five scallops were sampled for electron and light microscopy every 2 to 3 d from Day 18 to 35, then weekly to Day 56, with a final sampling on Day 58. Although development was continuous, four distinct stages were identified (1-primordia, 2-homorhabdic unreflected, 3-homorhabdic reflected, 4-heterorhabdic), partially recapitulating the presumed phylogenetic evolution of this character in the Pectinidae. The absence of a ventral groove in all stages suggests that the particle transport mechanism of pectinids evolved independently of such a structure, which is found in other bivalve families. Similarly, the absence of latero-frontal cilia in all specimens up to the largest observed (4 mm) indicates that the single row found in adults is a later development, rather than a vestige of a more abundant ciliation in ancestral forms. The anatomical data, together with in vivo observations of feeding in postlarvae, suggest that the developmental stages of the *P. maximus* gill correspond to critical changes in gill function. The early life of *P. maximus* may thus be characterized by distinct functional changes in feeding.

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Introduction

Renewed interest in the mechanisms of particle capture and transport in adult bivalves has led to vigorous research in this field (see Jørgensen 1990; Beninger et al. 1992; Ward et al. 1993 for review and references). Studies of the structure and ultrastructure of the adult scallop gill (Beninger et al. 1988; Le Pennec et al. 1988 a) provided the basis for understanding direct endoscopic observations of feeding processes (Beninger et al. 1992). To date, little attention has been paid to the structure of the gill in earlier life stages, and none at all to the functioning of this developing organ. Lacaze-Duthiers (1856), Jackson (1890) and Ridewood (1903) provided rudimentary descriptions of gill morphogenesis in several bivalve families; however, information was somewhat limited by the observational techniques available at that time. Subsequent studies extended these observations to various species (Yonge 1926; Cole 1937; Quayle 1952; Creek 1960; Ansell 1962; Sastry 1965; Caddy 1969; Hickman and Gruffydd 1971; Hodgson and Burke 1988; Bower and Meyer 1990). A detailed study by Waller (1981) described the development of *Ostrea edulis*, but data on gill morphogenesis concentrated on the posterior gill bridge and very early stages of the gill buds or primordia, as was also the case for *Crassostrea virginica* (Elston 1980). A short textual summary of gill organogenesis in the pectinid *Patinopecten yessoensis* was provided by Reid et al. (1992); however, no complete, detailed description with supporting photomicrographs is yet available. This lack of information underscores the need to understand feeding in larval and postlarval bivalves, particularly in the context of hatchery culture, where mass mortalities often occur in these stages (ÓFoighil et al. 1990). The present study therefore examines gill organogenesis in the scallop *Pecten maximus* L. and relates this to functional correlates of feeding by in vivo observation and by comparison with the adult gill system.

Materials and methods

Larval rearing

Larvae were obtained from thermo-mechanically induced spawning and cross-fertilization (Gruffydd and Beaumont 1970) of adult *Pecten maximus* at both the Tinduff and Argenton hatcheries (Finistère, France). After 48 h, stage D larvae were recovered on a 45-µm screen, counted and measured using a Nikon Profile microscope. The larvae were then reared in containers washed with aqueous sodium hypochlorite. The culture medium consisted of 450 litres of 1-µm filtered seawater containing 8 mg l^{-1} chloramphenicol. The medium was changed and the containers washed thrice weekly, at which times the larvae were counted and measured. A 5-litre mixture of 60 cells μl^{-1} of the unicellular algae *Pavlova lutheri*, *Isochrysis galbana* (Tahitian strain, T-Iso), and *Skeletonema costatum* was provided daily. Dead or slow-growing larvae were eliminated.

When 50 to 70% of the larvae retained on a 150-µm screen were double-barred (Gérard et al. 1989), they were transferred to the Tinduff nursery for metamorphosis and post-larval rearing. Spat settlement was favoured by feeding daily as above in still water. Any non-settled larvae were eliminated after 5 d. The spat were then fed using non-filtered ambient seawater, supplemented with the mixture of cultured algae provided by a self-regulating pump.

Sampling and observation

Larvae and postlarvae were sampled daily for in vivo observation of general condition with light microscopy. Five specimens were sampled for determination of developmental stage and shell length (using a calibrated ocular micrometer) every 2 to 3 d from Day 18 to 35, then weekly to Day 56, with a final sampling on Day 58 (total $N = 60$). At each sampling, two of these specimens were processed for scanning electron microscopy (SEM), two for light microscopy using resin sections, and one for histology using paraffin sections. As these techniques are both tedious and complementary, the number of observations was deemed to be adequate for descriptive purposes. Light microscopic observations on living postlarvae included the addition of the mixture of unicellular algae to visually assess gill functioning. For electron microscopy, the following cold fixation technique was used to avoid valve closure: glass tubes containing larvae were placed in a refrigerator at 8 °C for 10 to 15 min before adding one drop of fixative (2% glutaraldehyde in 0.4 *M* sodium cacodylate buffer). After 5 to 10 min, a volume of fixative equal to that of seawater in the tube was added. The fixed larvae/postlarvae were recovered on an appropriately sized screen and rinsed with a 1 : 1 mixture of 0.4 *M* sodium cacodylate buffer and 5.2% NaCl.

Specimens were prepared for SEM by dehydration in an ascending ethanol gradient, critical-point dried for 4 h and mounted on stubs using double-sided adhesive tape. A fine needle was used to remove one valve (to allow observation of internal organs), and the specimens were sputter-coated with gold.

Specimens were prepared for semi-thin resin sections by post-fixation in 4% osmium tetroxide-cacodylate buffer, followed by decalcification for 12 to 24 h in an aqueous solution of 1% ascorbic acid and 8.77% NaCl. After rinsing twice in cacodylate-NaCl buffer, the larvae were dehydrated in an ascending ethanol series and embedded in Spurr resin. Semi-thin (1-µm) sections were stained with toluidine blue and observed using light microscopy.

Results

For the sake of coherence and consistency, the following nomenclature was adopted to designate the various developmental stages – premetamorphic larva : veliger and pediveliger stages; veliger : pelagic stage, up to approximately 220–230 µm (measured as maximum shell length parallel to the hinge line; pediveliger : alternately pelagic and reptant stage, from approximately 230 up to 240 µm; postlarva : postmetamorphic larva : bysally-fixed stage, up to approximately 4–5 mm. Since morphogenesis of several organ systems continues well beyond settlement (Dwiono 1992), "metamorphosis" is here defined as the period during which the velum and anterior adductor muscle are resorbed (these being characteristic larval organs).

Table 1 *Pecten maximus*. Mean shell lengths and standard deviations (SD) corresponding to age of larvae at sampling

Age (d)	Mean shell length (µm)	SD
18	237.7	14.6
21	242.2	9.8
23	255.2	10.5
25	282.4	11.6
28	291.3	44.8
30	347.5	69.0
32	443.5	110.1
35	560.5	160.1
42	983.6	210.8
50	1787.8	383.6
56	2436.4	675.5
58	3162.2	948.6

The mean shell lengths and standard deviations for each sampling are reported in Table 1.

Gill morphogenesis

The gill anlagen differentiated from the general external epithelium in the second week of the pelagic veliger phase. These cells were symmetrically positioned to the left and right of the base of the foot, and soon formed distinct buds, or primordia (Fig. 1 A, B). These gill buds lengthened and organized into a row of straight gill filaments as other buds formed and lengthened in a postero-anterior sequence. In recently-metamorphosed 260-µm postlarvae, the first gill filament was ca. 20 µm long, and the fourth gill bud had formed. In 270 to 500-µm postlarvae there were five filaments and three gill buds on each side of the foot (Fig. 1 C). Histological data showed that the filaments were composed of a single tubular layer of ciliated epithelial cells (Fig. 2 D). Estimates from histological sections showed that lateral cilia were up to 20 µm long, while the smaller frontal cilia measured up to 10 µm in length. No laterofrontal cilia were observed. In vivo observations using light microscopy showed that the filaments of the right and left inner demibranchs moved slightly and continually at this stage.

At a size range of 500 to 800 µm, a total of seven filaments and three to four gill buds were visible (Figs. 1 D, 2 E, F). The distal extremity of each filament was distinctly bulbous, and presented several tufts of cilia. The abfrontal cells were characterized by a wedge-shaped, non-ciliated apex (Fig. 2 E, F, G). Microscopic observations of living scallops showed that particle capture was very ineffi-

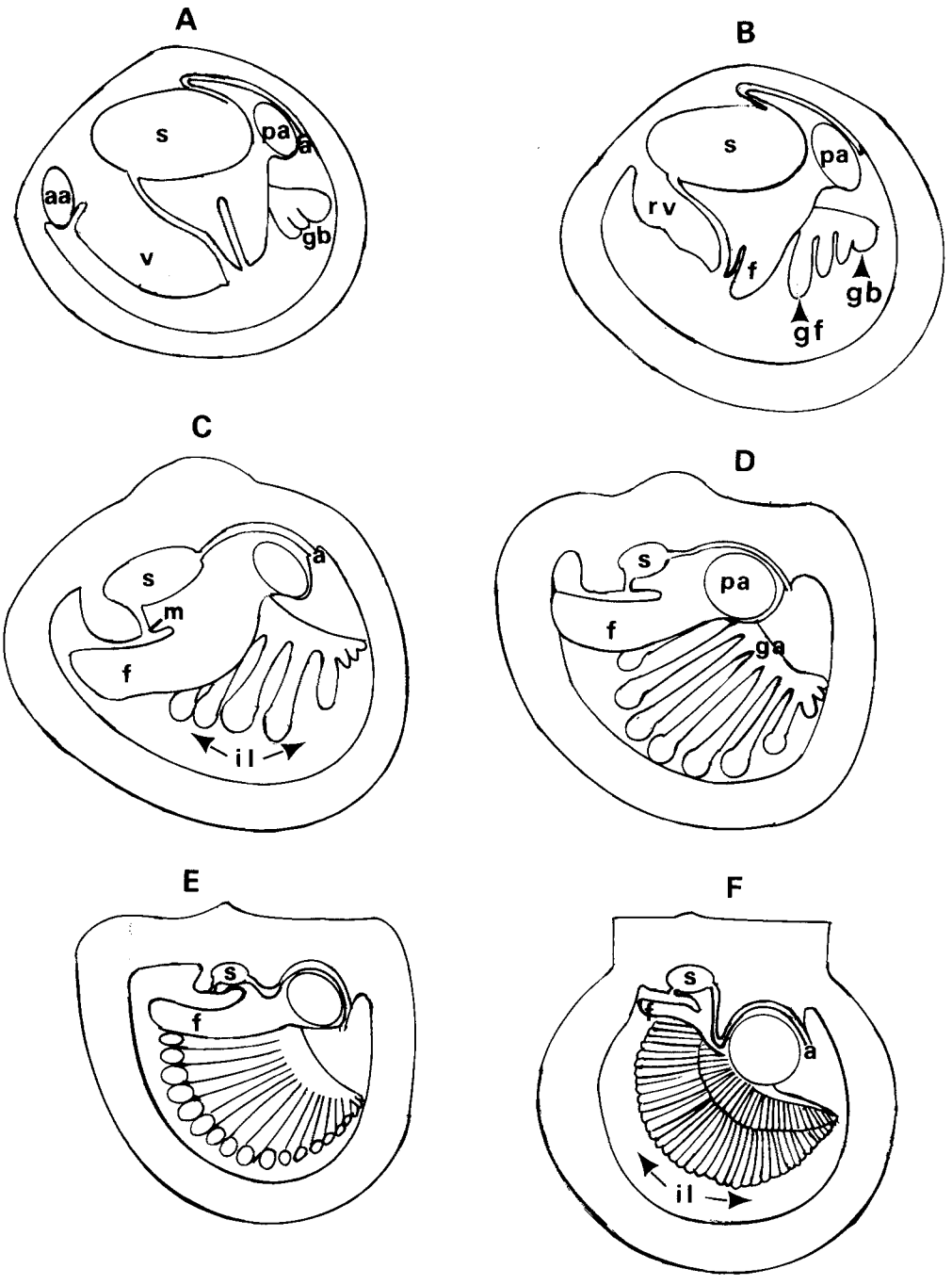

Fig. 1 *Pecten maximus.* Schematic diagram showing development of the gill and other organs. (A) 240-µm pediveliger. (B) 260-µm postlarva immediately after metamorphosis. (C) 300-µm postlarva. (D) 500-µm postlarva. (E) 1-mm postlarva. (F) 3-mm postlarva. a: anus; aa: anterior adductor muscle; f: foot; ga: gill axis; gb: gill buds; gf: gill filaments; il: inner lamella; m: mouth; pa: posterior adductor muscle; s: stomach; rv: resorbing velum; v: velum

cient at this stage (most particles bounced off the gill filaments and escaped into the excurrent flow).

Although the gill filaments were heretofore unreflected, they were curved inward, forming a "gill basket" within the pallial cavity (Fig. 2C, D, E). The distal extremities of each filament interdigitated with their counterparts from the opposite gill (Fig. 2C).

To this point, all of the developing filaments belonged to the future inner demibranch. Three major changes occurred at a size of 900 to 1000 µm (Figs. 1E, 3A, B, C): (1) the inner demibranch filaments (now numbering approximately 20) moved much closer together; (2) these filaments began to fold dorsally and medially, later assuming the V-shape of the juvenile and adult; (3) the formation of a row of gill buds parallel and exterior to the inner demibranch filaments; these buds developed directly and rapidly into reflected filaments to form the future outer demibranch. The developing outer demibranch was readily visible by transparence under light microscopy in postlarvae measuring 1.1 mm (Fig. 3E). Histological sections show the same features as described above (Fig. 3D). At 3 mm, the inner demibranch was composed of a row of complete V-shaped filaments which all resembled the ordinary filaments of the adult, while the outer demibranch presented the same characteristics with fewer and smaller filaments (Fig. 1F). At approximately 4 mm, several fila-

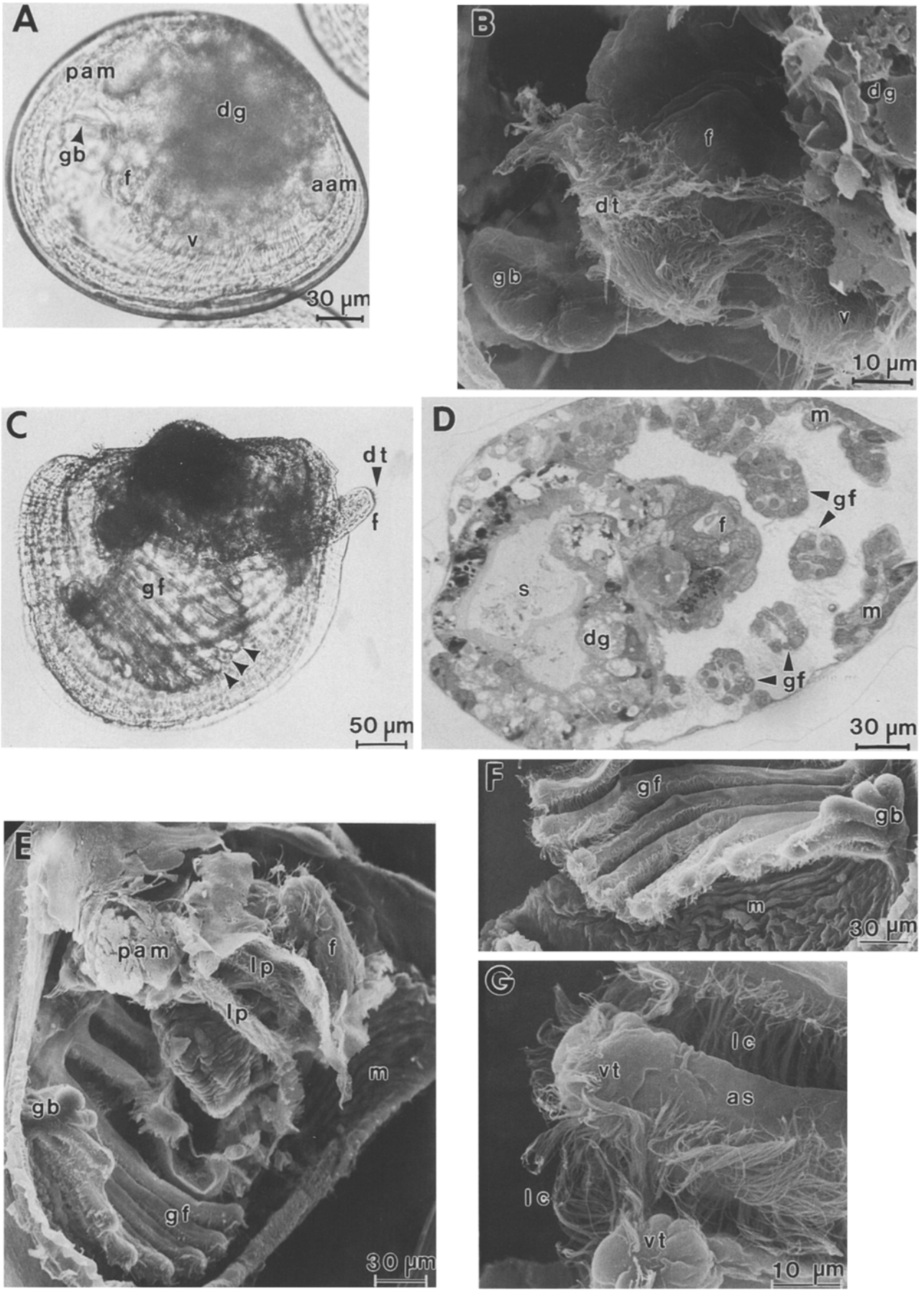
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Table 2 *Pecten maximus.* Stages of gill organogenesis. Sizes are approximately. See Table 1 for size variability

Stage	Approximate shell length (μm)	Salient feature	Characters
1	240	3–5 Primordial buds	Filaments not yet formed Non-functional
2	250–900	Homorhabdic unreflected filaments	Development of inner demibranch only Gill basket formed by curved filaments Cannot function as any known adult gill
3	900–4000	Homorhabdic reflected filaments	Development of inner and outer demibranchs Increased efficiency due to presence and reflection of both demibranchs Homologous to homorhabdic condition; cannot function as adult heterorhabdic gill
4	>4000	Heterorhabdic	Differentiation of ordinary (OF) and principal (PF) filaments begins PF responsible for particle transport for ingestion, OF for rejection

ments of the inner demibranch began to differentiate into principal filaments (development of the dorsal respiratory expansion on the abfrontal surface), between which were interspersed eight to ten ordinary filaments; this signalled the onset of the heterorhabdic condition. The outer demibranch followed the same pattern, with a variable lag time.

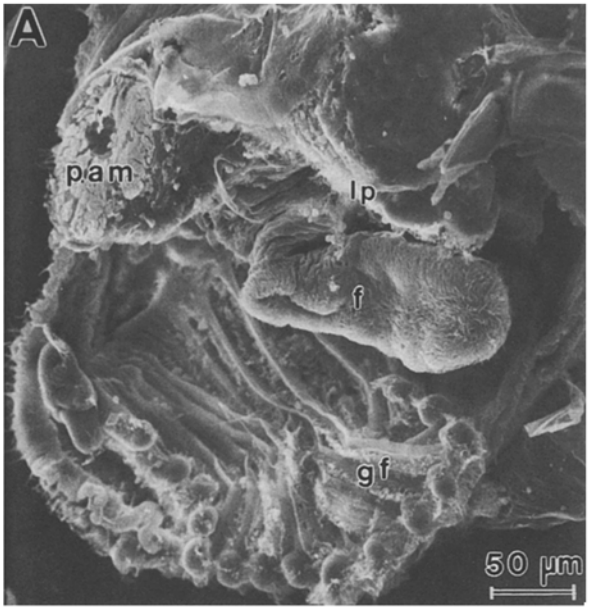
Discussion

Although gill development is continuous in *Pecten maximus*, four anatomically and functionally distinct stages can be identified (Table 2). The primordial bud stage (stage 1) occurs prior to metamorphosis, while the velum is still the principal feeding organ. The unreflected homorhabdic stage (stage 2), which appears at metamorphosis, gives rise to a gill basket which bears no resemblance to any known adult bivalve gill system, and which must function in a similarly unique manner. The homorhabdic reflected stage (stage 3) is homologous to the adult filibranch gill type. The incipient differentiation of ordinary and principal filaments (stage 4) heralds the final adult heterorhabdic condition of the Pectinidae. Further filament addition is accomplished by elongation of the anterior extremity of the gill, as body growth proceeds. The aquisition of a homorhabdic filibranch gill prior to the development of a heterorhabdic gill would thus seem to partially recapitulate the phylogenetic development of this pectinid character (Allen 1985). Further confirmation of the ontogenetic recapitulation of pectinid gill phylogeny comes from the hydrothermal vent "living fossil" *Bathypecten vulcani* (Le Pennec et al. 1988b) which lacks principal filaments (and is thus homorhabdic) and latero-frontal cilia, as in the postlarvae of *Pecten maximus*.

The inability of the developing postlarval gill to function in the adult mode was recognized by Yonge (1947). Assuming that an adult gill structure was necessary for particle capture in postlarvae led to the conclusion that gill reflection must be the result of filament elongation with both extremities attached (visceral mass and mantle), as described for *Venus striatula* (Ansell 1962) and in contrast to the observations of Lacaze-Duthiers (1856), Rice (1908), and Caddy (1969). The results of the present study clearly demonstrate that in *Pecten maximus* elongation precedes reflection in the first demibranch to develop (inner), while the two occur simultaneously in the outer demibranch. In neither case is the distal extremity attached during elongation or reflection. Postlarval gill function is thus de facto different from that of the adult.

The developmental stages described above correspond to critical changes in gill function. While the gill is nonfunctional in the primordial bud stage (stage 1) of the pediveliger, it is presumably at least partially functional in the homorhabdic unreflected stage (stage 2). In vivo observations showed that in stage 2 larvae, the gill established the dominant ventro-dorsal and postero-anterior currents in the gill cavity, and was capable of intercepting some suspended particles (although many others simply bounced off the gill basket and exited the pallial cavity).

Fig. 2 *Pecten maximus.* Pediveliger and postlarva. (A) light micrograph of whole 240-μm pediveliger, right valve uppermost. Several organs visible through the shell: anterior (aam) and posterior adductor muscles (pam), digestive gland (dg), foot (f), gill buds (gb), and velum (v). (B) Scanning electron micrograph (SEM) detail of posterior region of a 240-μm pediveliger. Note ciliary tuft (dt) on distal extremity of foot. (C) Light micrograph of whole 305-μm postlarva. The unreflected parallel descending gill filaments form the gill basket; arrows indicate interdigitating filament ventral extremities. The active foot (f) extends through the byssal notch. Note the densely ciliated distal tuft (dt). (D) Longitudinal histological section of the same postlarva showing the position of the gill filaments (gf) in the pallial cavity. dg: digestive gland; f: foot; m: mantle; s: stomach. Scale bar = 30 μm. (E) SEM of 740-μm postlarva. gb: gill buds; gf: gill filaments; f: foot; pam: posterior adductor muscle; lp: labial palps; m: mantle. (F) Detail of gill buds (gb) and filaments (gf) of a 740-μm postlarva. m: mantle. (G) Detail of distal extremities of the same postlarva (740 μm), showing ventral ciliary tufts (vt) from which frontal (not visible) and lateral cilia (lc) derive. Cilia absent on the abfrontal surface (as)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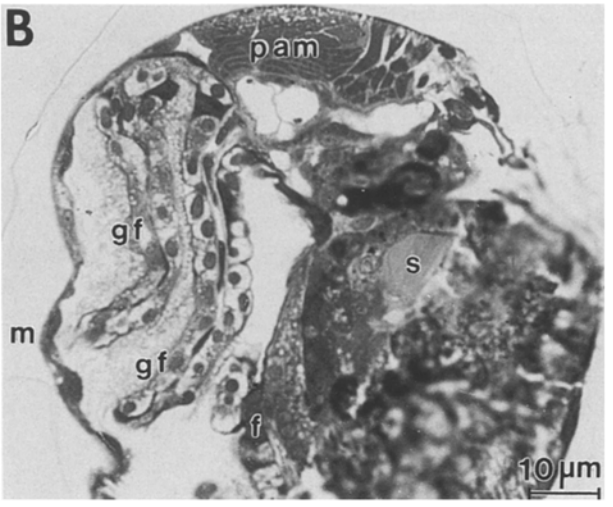
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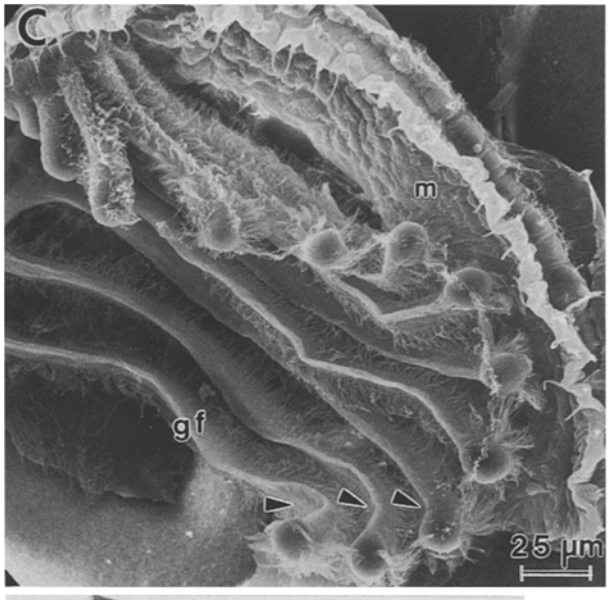
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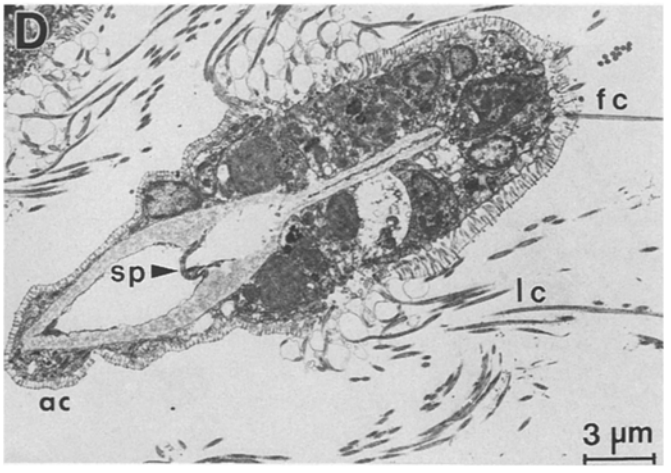
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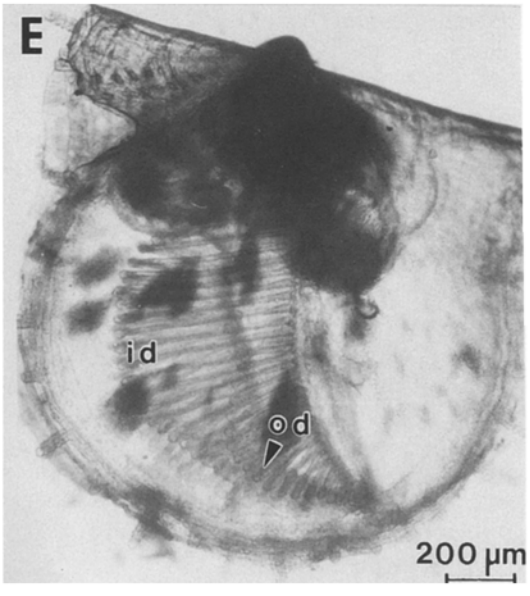
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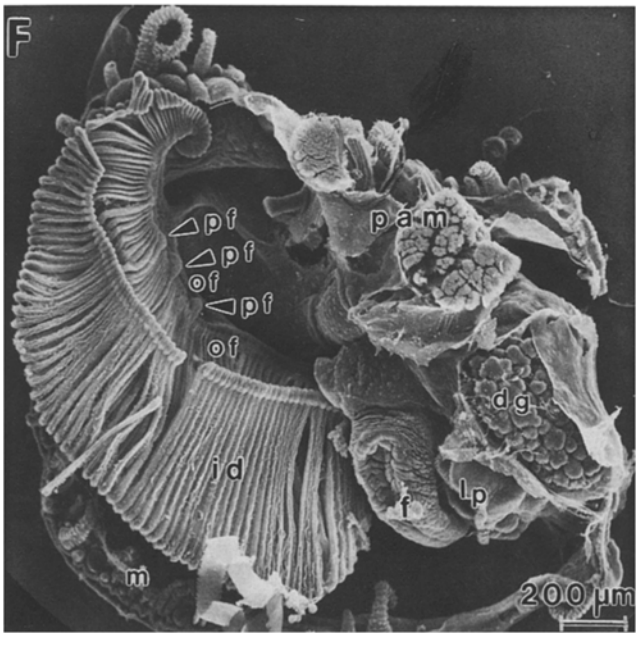
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The homorhabdic reflected gill of stage 3 postlarvae represents a filibranch organisation, with the notable absence of the ventral groove found in adult filibranchs. The stage 3 gill would thus be unable to function in either the typical filibranch or heterorhabdic modes; further research will be required to elucidate the exact mode of function. The transformation to the heterorhabdic gill organization occurs in stage 4, at which time the mechanism of particle capture and transport changes to that of the adult (Beninger et al. 1992).

The postmetamorphic life of *Pecten maximus* is thus characterized by a succession of major changes in feeding structures and mechanisms. It is likely that the transformations to each successive stage are moments of increased risk of mortality. Biochemical studies on the rock scallop *Crassodoma gigantea* have recently shown that early postmetamorphic larvae process food at a rate insufficient to support shell deposition and growth (Whyte et al. 1992).

The potential problems associated with periodic transformations and rearrangements of the early postlarval gill may be compensated by other feeding mechanisms. The utilisation of stored reserves is considered important (Holland and Spencer 1973; Gabbott 1975; Whyte et al. 1992). Another trophic source is the direct absorption of dissolved organic matter, which has been demonstrated on the vela of bivalve larvae and in the developing gill buds of *Crassostrea gigas* and *Pecten maximus* (Manahan and Crisp 1982, 1983; Marshall and Lee 1991). An additional possibility is feeding using more developed structures. The ventral aspect of the developing foot is densely ciliated (Reid et al. 1992; present study), with an apical tuft which may be used to forage for food in the substratum (e.g. benthic diatoms, bacteria, etc.). Such pedal probe-feeding has been shown to be important in all bivalve postlarvae examined (Reid et al. 1992), and probably contributes to the nutrition of *P. maximus* at this critical stage. The lack of a suitable substrate for pedal probe-feeding may partially explain the considerable postlarval mortalities occasionally experienced in commercial hatcheries.

Fig. 3 *Pecten maximus*. Postlarval gill development. (A) Scanning electron micrograph (SEM) of 900-µm postlarva, left gill lamella removed. Note densely-ciliated ventral surface of the foot (f), located between the gill filaments (gf) and the labial palps (lp). pam: posterior adductor muscle. (B) Transverse section, slightly oblique, of the median region of a 900-µm postlarva. Gill filaments (gf) of the inner demibranch have not yet begun reflection. f: foot; m: mantle; pam: posterior adductor muscle; s: stomach. (C) SEM of another 900-µm postlarva, showing the beginning of reflection (arrow heads) in the inner demibranch. gf: gill filaments; m: mantle. Scale bar = 25 µm. (D) Semi-thin section of a gill filament from a 900-µm postlarva. ac: abfrontal cells; fc: frontal cilia; lc: lateral cilia; sp: septum. (E) Light micrograph of a 1100-µm postlarva. The inner demibranch (id) is formed and new filaments are being formed to constitute the outer demibranch (od). (F) SEM of a 4000-µm juvenile. Several gill filaments are differentiating to become principal filaments (pf) on the left inner demibranch (id, appearance of dorsal respiratory expansions); ordinary filaments (of) are interspersed between the principal filaments, and the demibranch is still non-plicate. dg: digestive gland; f: foot; lp: labial palps; m: mantle; pam: posterior adductor muscle

The absence of a ventral groove in all stages of the gills of *Pecten maximus* suggests that such a structure has either never been present or has long been lost in the Pectinidae. Contrary to many other bivalve gill types (e.g. those of *Mytilus edulis*, *Mya arenaria*, and *Ostrea edulis*), in which this groove plays an important role in particle transport (Ward et al. 1993), the pectinid gill appears to have evolved a transport mechanism independent of the ventral groove (Beninger et al. 1992). Similarly, the lack of latero-frontal cilia even in specimens up to 4 mm indicates that the single row of latero-frontals in adults is a later development rather than a vestige of a more abundant latero-frontal ciliation in ancestral forms of Microciliobranchia. This, in turn, may merit more detailed consideration in the study of bivalve phylogeny (see Allen 1985 for review).

From the foregoing it is evident that gill organogenesis is an important aspect of the biology of the early life stages of *Pecten maximus*; future studies should investigate the functioning of the stage 2 gill basket and the stage 3 homorhabdic reflected gill, as well as the relationship between gill organogenesis and such parameters as energy budget, mortality, and growth of representative bivalve species.

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