# Evolutionary trajectories of a redundant feature: lessons from bivalve gill abfrontal cilia and mucocyte distributions

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**Abstract:** Recent data on the distributions of cilia and mucocytes on the bivalve gill abfrontal surface are analysed with respect to evolutionary relationships of the principal autobranch gill types. From the primitive function as a mucociliary cleaning surface in the protobranchs, two evolutionary trajectories are evident: (1) progressive reduction of both cilia and mucocytes with resultant loss of surface function, seen in the homorhabdic filibranchs studied; (2) reduction of cilia but retention or increase in acid mucopolysaccharide-secreting (AMPS) mucocyte density in the eulamellibranchs, corresponding to the assumption of a new function, probably in the reduction of frictional resistance to flow in the water canals. Heterorhabdic gill abfrontal surfaces present a mixture of these characteristics: reduction of cilia and mucocytes on the ordinary filaments, and retention of both on the principal filaments. The retention of AMPS mucocytes on the abfrontal surface of the pseudolamellibranchs may be related to the degree of interlamellar fusion, reducing frictional resistance to water flow as in the eulamellibranchs. The gill abfrontal surface thus constitutes an excellent candidate for the study of the different evolutionary options and trajectories of a redundant feature.

Compared to the intensive anatomical and functional studies of the frontal surface of bivalve gills [see Winter (1978), Jørgensen (1990) and Beninger & St-Jean (1997) for reviews and references], the abfrontal surface has been virtually ignored, with only very cursory descriptions of surface and histological characteristics. This lack of interest is perhaps understandable from a functional point of view, since the immense majority of bivalves are suspension feeders and the frontal surface of the gill plays a key role in particle processing (Atkins 1938; Nelson 1960; Beninger & St-Jean 1997; Beninger *et al.* 1993, 1997*a*; Nielsen *et al.* 1993; Riisgård *et al.* 1996; Silverman *et al.* 1996; Ward *et al.* 1998). In contrast, the abfrontal surface is not involved in any stage of particle processing and, indeed, if any particles were available to it, there would be no route to the digestive tract. However, this surface presents a very interesting peculiarity in that its presumed original protobranch cleaning function has been obviated by the separation of the pallial cavity into more or less modified infra- and suprabranchial chambers (Yonge 1941; Morton 1996; Waller 1998), such that the risk of fouling is virtually absent in contemporary autobranchs (*sensu* Autobranchia, non-protobranch bivalves; Morton 1996; Salvini-Plawen & Steiner 1996). It therefore constitutes an excellent opportunity to study the evolution of a redundant feature throughout the Bivalvia. Two main evolutionary trajectories are available to such a structure: (1) retention or augmentation of the original functional characteristics, in response to either neutral or positive selection for a new function to which the original features were pre-adapted; (2) reduction or loss of the original functional characteristics in response to negative selection, i.e. the metabolic cost of maintaining these features.

The chief functional characteristics of the primitive bivalve gill abfrontal surface are cilia and mucocytes, present in the protobranch condition and variously reported in the autobranchs (Ridewood 1903; Atkins 1936, 1938; Nelson 1960; Jones *et al.* 1990; Richard *et al.* 1991; Beninger *et al.* 1997*a*; Dufour & Beninger in press) . The types and abundances of these two characteristics may thus serve as markers to trace the evolutionary trajectories of the abfrontal surfaces within the major bivalve taxa. Here such a study is presented,

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based largely on a recent detailed account of cilia and mucocyte densities on the abfrontal surfaces of eight bivalve species representing the four principal autobranch gill types, including primitive and advanced conditions (Dufour & Beninger in press). The elucidation of such heretofore poorly studied characteristics may also reinforce the significance of gill structure in taxonomy and phylogeny (Salvini-Plawen 1980; Salvini-Plawen & Steiner 1996).

## Database

To date, reports on the distribution of bivalve abfrontal cilia and mucocytes have been confined to indications of their presence or absence, sometimes with subjective comments on their abundance (e.g. Atkins 1938; Nelson 1960; Eble & Scro 1996), and no systematic investigation of the entire abfrontal surface appears to have been carried out for any species. The data for the present work is therefore drawn from a systematic investigation of the types and distribution of cilia and mucocytes of the abfrontal surfaces of eight bivalve species, representing seven families and the four major autobranch gill types (Dufour & Beninger in press). Briefly, this study showed the following. (1) In the homorhabdic filibranchs, varying degrees of reduction of the abfrontal cilia and mucocytes were observed; *Mytilus edulis* presented the greatest density of cilia and mucocytes, and the most mucocyte secretion types; *Modiolus modiolus* presented a much smaller density of both cilia and mucocytes, and fewer mucocyte secretion types; *Arca zebra* displayed the greatest degree of reduction, with few cilia and low densities of mucocytes, and only one mucocyte secretion type. (2) In the homorhabdic eulamellibranchs, reduction of cilia was extreme and only one mucocyte secretion type was present – acid mucopolysaccharides (AMPS). However, the density of mucocytes was high, with an extraordinarily high density of *Spisula solidissima*. (3) In the heterorhabdic species, ciliation of the abfrontal surface of the ordinary filaments (OF) was greatly reduced, while that of the principal filaments (PF) was dense. The density of mucocytes was also greater on PF cf. OF, with a mixture of mucopolysaccharide types in the heterorhabdic filibranch *Placopecten magellanicus* and AMPS only in the pseudolamellibranch *Crassostrea virginica*. The observations of cilia and mucocyte densities may be summarized graphically, using scaleless axes in which each quadrant embodies a different functional outcome (Fig. 1). The relative positions of the gill types studied may thus be interpreted from a functional and evolutionary standpoint.

## Discussion

The basic premise of this work is that functionally coupled organs key to the success of an organism respond more strongly to their respective selective pressures than other organs whose functioning is not significantly affected by those pressures. In the case of the Bivalvia, the ready availability of planktonic particles doubtless conferred a significant advantage to those individuals which presented gill modifications from the primitive protobranch type, enabling increasingly efficient capture and processing. Hence, the bivalve gill underwent rapid evolution within each of the major taxa, while other organs, such as the heart, retained their form, as witnessed in the uniformity of this organ throughout the class (Beninger & Le Pennec 1991; Eble 1996). It is thus possible to use the data on gill abfrontal ciliation to trace the evolutionary changes of this surface in the gill itself, and to relate these to changes in the overall form and function of the gill, independent of the larger phylogenetic trajectories.

There is little doubt that the filibranch condition evolved from the protobranch gill type (Yonge 1941; Morton 1979; Salvini-Plawen 1980; Morton 1996; Waller 1998). The gill of the family Nuculidae, which best represents the primitive protobranch condition (Yonge 1941), is characterized by a uniform, dense abfrontal ciliation which participates in particle transport, principally in cleaning (Orton 1912). Although no study of the mucocyte distribution on the nuculid gill has been made, particle transport, and especially cleaning a ciliated surface, involves mucociliary transport (see Beninger *et al.* 1997*b*), and thus a dense array of mucocytes. The abfrontal surface of the contemporary autobranch gill is most probably a vestigial mucociliary epithelium (Dufour & Beninger in press), whose original protobranch cleaning function was lost with the reflection of the gill filaments to form the homorhabdic filibranch gill, separating the pallial cavity into infra- and suprabranchial chambers. Indeed, the assumption of the filibranch condition may have been the most important factor in the diversification and proliferation of the Bivalves from the early Ordovician (Cope 1996). This is, however, the most primitive contemporary autobranch gill type, present in only 7% of extant families. Given the large species numbers and extensive habitats of the eulamellibranch heterodonts, the proportion of homorhabdic filibranch species is probably even smaller [data from Newell (1965)]. Within the taxa presenting this gill type, the data suggest an evolutionary gradation of the abfrontal surface. *Mytilus edulis* presents the most abundantly ciliated abfrontal epithelium, followed by *Modiolus*

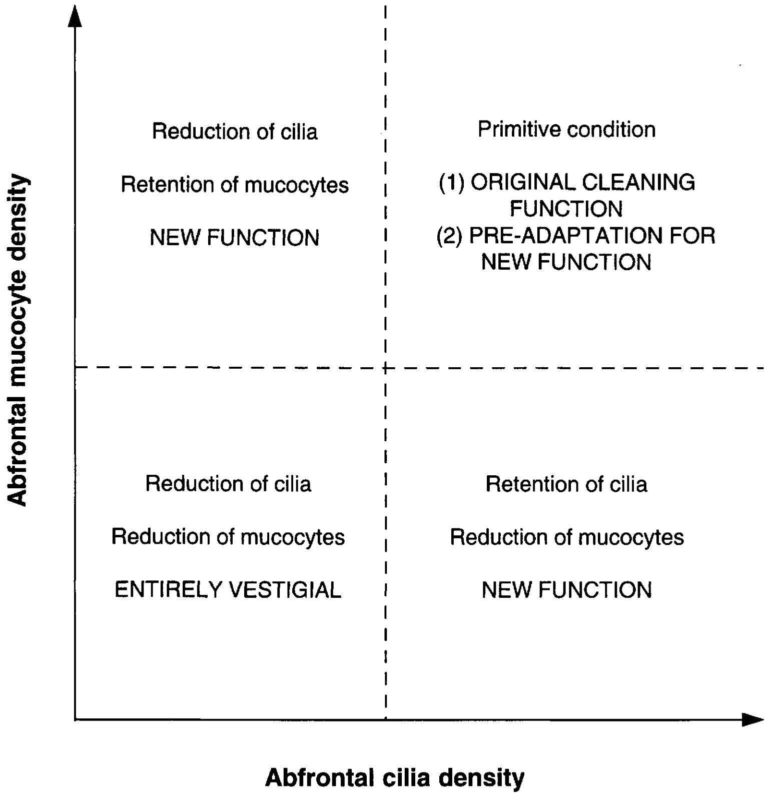


**Fig. 1.** Scaleless graph of relative abfrontal mucocyte and ciliary densities showing functional significance of positions within each of the quadrants. In the upper right quadrant, the original (protobranch) condition of high mucocyte and ciliary densities is situated, as well as eventual pre-adaptations of this condition for new functions. In the upper left quadrant, high mucocyte densities and low ciliary densities indicate the loss of the original cleaning function, with the assumption of a new function for this surface – possibly in reduction of drag and thus increase in efficiency of water flow. In the lower left quadrant, low mucocyte and ciliary densities indicate a loss of the original cleaning function, with no new surface function. Finally, in the lower right quadrant, low mucocyte densities and high ciliary densities indicate loss of the original cleaning function, and assumption of a new function accomplished by cilia alone (e.g. water pumping).

*modiolus*, with *Arca zebra* presenting only very sparse cilia (Fig. 2).

It is not known whether the more primitive *Mytilus edulis* homorhabdic filibranch gill has retained the original abfrontal cleaning function, but since this surface is normally exposed to moving, 1 μm filtered seawater (Møhlenberg & Riisgård 1978), any cleaning would be restricted to occasional removal of faeces or gametes not voided in the excurrent flow. Two more probable interpretations may be made: (1) the abfrontal cilia may be vestigial and largely non-functional in the primitive homorhabdic filibranch gill of *Mytilus edulis* [other vestigial mucociliary surfaces are known in this species, see Beninger *et al.* (1995)]; or (2) the dense abfrontal ciliation in *M. edulis* might assist in water pumping (Orton 1912; Jones *et al.* 1990, 1992; Jones & Richards 1993). It is currently impossible to visualize simple cilia *in vivo*, even using endoscopy (Beninger 2000), so this interesting hypothesis cannot be unequivocally confirmed. In this scenario, the abfrontal ciliation would be a pre-adaptation for more efficient water pumping, perhaps partly responsible for the numerical success of the Mytilidae. However, the abfrontal mucocytes would still be non-functional and vestigial.

The sparse ciliation and the few small mucocytes in *Modiolus modiolus* render cleaning or pumping functions impossible, as do the near-bare abfrontal surface and rare mucocytes of *Arca zebra* (Fig. 2). These three species thus present increasing degrees of reduction of the abfrontal mucociliary surface of the homorhabdic filibranch gill, from *Mytilus*

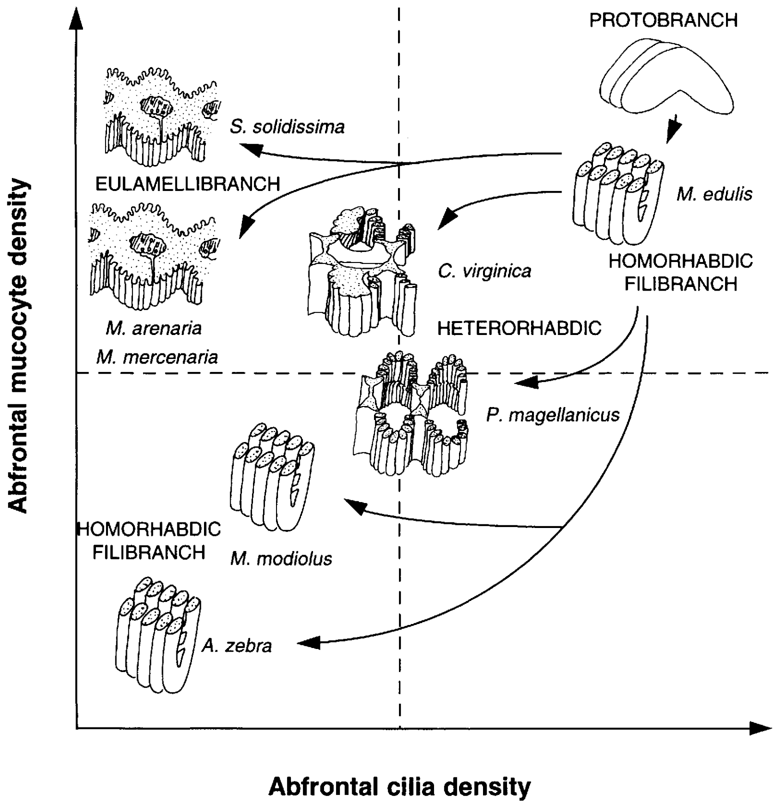


**Fig 2.** Relative positions of the gill types examined with respect to abfrontal mucocyte and cilia density. Note new function assumed by the abfrontal surface of eulamellibranch gills, loss of surface function in the advanced homorhabdic filibranchs *Modiolus modiolus* and *Arca zebra*. None of the representatives of the four principal gill types presents reduction of mucocytes with retention of cilia (lower right quadrant).

*edulis* to *Arca zebra*, paralleling the reduction and disappearance of the original cleaning function.

The great degree of reduction of the abfrontal cilia in the eulamellibranch gills studied clearly demonstrates the extension of the trend to reduction and loss of the primitive mucociliary function in the homorhabdic gill type (Fig. 2). However, the retention of a relatively high density of abfrontal mucocytes indicates that, in this gill type, there has either been neutral selection for this trait or that the mucocytes have been retained and redirected toward a new function by positive selection. The presence of only AMPS (i.e. viscous)-secreting mucocytes on the eulamellibranch abfrontal surface, and their extremely dense distribution in *Spisula solidissima*, argues strongly for the latter interpretation. The most probable new function of the mucocytes of the abfrontal surface in this gill type is the reduction of frictional resistance to water flow (Faillard & Schauer 1972; Hoyt 1975; Daniel 1981) across the epithelia of the suprabranchial chamber, which is highly modified to form water tubes. This would increase the efficiency of water flow in these species and parallels the pronounced morphological modifications of the gills, allowing enhanced flow as well as a consequently smaller gill:pallial cavity volume ratio.

The eulamellibranch gill is widely believed to be derived from the ancestral homorhabdic filibranch condition (Orton 1912; Yonge 1941; Morton 1979; Salvini-Plawen 1980; Allen 1985; Waller 1998). The modifications to the abfrontal surface described in the present study indicate that this gill type not only continues the trend to reduction or loss of the original cleaning function, but that this surface has assumed a new function commensurate with the increased efficiency of water flow in this gill type.

In the two heterorhabdic gill types studied, the total absence of cilia on the abfrontal surface of the OF plicae clearly demonstrates the loss of the primitive mucociliary cleaning function in these species. The presence of abundant ciliation and high densities of mucocytes on the PF may be related to the tardy evolutionary development of PF cf. OF. It is likely that PF are formed from modified OF, and both phylogenetic and ontogenetic studies show that PF arise well after OF (Le Pennec *et al.* 1988; Beninger *et al.* 1994). The developmental sequence of the PF may thus be quite different from that of the OF, with the notable retention of the primitive mucociliary characters. In *Placopecten magellanicus*, it has been suggested that the PF abfrontal mucocytes may provide the lubrication necessary for the retraction of the gill during rapid valve adduction, such as the swimming escape response common in juveniles or sudden valve closure in adults (Beninger *et al.* 1988). However, only about two-thirds of the abfrontal surface would actually be in contact with the apposing mantle surface under such conditions (the remaining third being the frontal surface of the ascending branch of the PF outer demibranch). The abfrontal secretions may also reduce friction between apposed lamellae following collapse of the ascending lamellae from the ciliary attachment to the mantle prior to retraction, assisting in the preservation of structural integrity during the clap response. In the Ostreidae, the relatively high degree of interlamellar and interfilamentar fusion has resulted in a suprabranchial cavity akin to the water canals in eulamellibranchs; the retention of AMPS mucocytes only on the PF may indicate that they play a similar role in the reduction of frictional resistance to water flow. In any event, the unique context of the evolutionary and developmental history of the heterorhabdic gill has resulted in a mixed condition (Fig. 2), with the phylogenetically older OF presenting a degree of reduction similar to the advanced homorhabdic filibranch or eulamellibranch condition, whereas the phylogenetically recent PF have retained the original mucociliary characters of the abfrontal surface.

It is noteworthy that no gill types appear in the lower right quadrant of Fig. 2. The abfrontal surface of a gill type in this region would present reduced mucocyte numbers and a high ciliary density; the fact that a high ciliary density is always accompanied by a moderate to high density of mucocytes reinforces the conclusion that this surface was originally mucociliary. The only conceivable new function for the abfrontal surface in this quadrant would be the propulsion of water; none of the gills examined appears to have derived from lines which selectively reduced mucocytes while retaining cilia for such a function.

While the present study proposes an evolutionary paradigm for the distribution of cilia and mucocytes on the abfrontal surface of bivalve gills, it clearly requires additional data from all gill types in order to evaluate the universality of this scheme. In particular, observations of the abfrontal surface of early developmental stages will be important in validating the evolutionary sequences proposed herein for the bivalve gill.

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