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Flow through mantle cavities revisited: Was sanitation the key to fissurellid evolution?

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Abstract. Traditional scenarios of gastropod evolution suggest that the apical openings and marginal slits of keyhole limpets and other fissurellids play a key role in maintaining mantle cavity sanitation by facilitating separation of clean incurrent and waste-laden excurrent flow. The occurrence of animals that never develop excurrent openings or in which the opening is blocked by fouling organisms, however, indicates that this may not be the case. We examined the mantle cavity morphology and characterized the respiratory flow of individuals of *Diodora aspera* in which the apical opening was naturally or experimentally blocked. We found no evidence of damage to the mantle cavity or associated organs. Water entered ventro-posteriorly to the gill tips, which were extended beyond the mantle margin, and exited over the head. Thus the apical opening is not necessary for the effective removal of wastes. The opening *is* necessary, however, to induce passive flow through the mantle cavity. We suggest that this function of the apical opening may have been as significant as its role in sanitation for the evolution of fissurellid gastropods.

Additional key words: prosobranch, gastropod, mollusc, keyhole limpet, *Diodora*

The evolutionary changes in the gill-cavity are somewhat complicated morphologically, but physiologically can be summed up in a single word, sanitation.

Walter Garstang

The molluscan mantle cavity functions to protect and enclose sites of metabolic exchange between the animal and its environment. It is bounded on one side by the body wall and on the other by a thin lining of mantle tissue. The gills or ctenidia project into the mantle cavity, and the anus, renal pores, and gonoducts may also empty directly into the mantle cavity. Cilia located primarily on the gills create currents that convey oxygenated water to the gills and carry feces, urine, and gametes away.

Garstang (1928) was the first to postulate what has become the conventional scenario describing the evolution of gills and currents within the mantle cavity of prosobranch gastropods. As a result of torsion the gastropod mantle cavity is situated above the head. According to Garstang (1928) and as elaborated by

Yonge (1947), the ancestral gastropod condition consisted of two bilaterally symmetrical gills located on either side of the excretory pores. Water was drawn into the mantle cavity laterally behind the tentacles, passed through the gills, and exited the mantle cavity mid-dorsally over the head. Garstang and Yonge suggested that this ventilation pattern would create sanitation problems because feces and urine would be released directly over the head.

Modern gastropods are thought to have modified this putative ancestral flow pattern to prevent the excretory products from contaminating the incurrent flow (see Voltzow 1994 for review). In modern caenogastropods and trochoideans, only the left gill is retained. Water enters the mantle cavity on the left side; passes through the gill; then passes the anus, renal pores, and gonoducts; and finally exits the mantle cavity on the right, effectively carrying waste products away from the head and gills. In the archaeogastropod (*sensu* Hickman 1988) superfamilies Fissurelloidea and Pleurotomarioidea, a unidirectional current is usually produced with the aid of one or several openings in the shell and mantle. In the keyhole limpet *Diodora aspera* (RATHKE 1833), the incurrent flow enters the mantle cavity ventrally, immediately posterior to the

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cephalic tentacles and exits the mantle cavity through the "keyhole," an opening at the shell apex (e.g., Murdock & Vogel 1978). Experiments performed in a recirculating flow tank with the abalone *Haliotis kamtschatkana* JONAS 1845 have demonstrated that water enters passively either posterior to the left cephalic tentacle or through one of the anterior holes in the shell, or tremata, and leaves the mantle cavity via the more posterior tremata (Voltzow 1983). Because of the posterior location of the anus and gonopores in these genera, water passes through the gills before it collects the excretory products.

The flow patterns observed in *D. aspera* and *H. kamtschatkana* may provide additional advantages to these animals. In moving water the apical location of the excurrent opening of *D. aspera* helps create an induced flow through the mantle cavity, increasing the efficiency of the respiratory current independent of the direction of ambient flow (Murdock & Vogel 1978). Shell sculpture and the height of tremata in three species of *Haliotis* have also been shown to increase the passive component of the animal's respiratory flow (Tissot 1992). Individuals of *H. rufescens* SWAINSON 1822 and *H. kamtschatkana*, which have moderately elevated tremata and moderate shell sculpture, show a significant increase in passive flow through the mantle cavity at low external flow velocities (less than 10 cm/s). Individuals of *H. cracherodii* LEACH 1814, which have smooth shells and flush tremata, show little increase in induced flow at low external velocities but have a significant increase in internal current with external velocities above 30 cm/s.

We used *D. aspera* to assess the consequences of enclosing bilaterally symmetrical gills in a shell that lacks excurrent openings. We traced the patterns of water flow through the mantle cavities of different individuals, comparing an animal in which the apical opening was naturally occluded with normal animals and with animals in which the openings were artificially occluded. The mantle cavities were also examined to determine if elimination of feces and urine over the head had damaged the mantle, gills, or head.

Methods

Organisms

A keyhole limpet, *Diodora aspera* (RATHKE 1833), whose apical opening was completely overgrown by the coralline red alga *Lithothamnion phymatodeum* FOSLIE 1902 was found on the west side of San Juan Island, Washington, USA in June 1994. Another individual dredged from San Juan Channel from about 70 m in April 1994 had an empty barnacle shell, *Balanus balanus* (LINNAEUS 1758), encircling the excur-

rent opening. The barnacle must have blocked the apex in life, but had died, and the remaining barnacle shell formed a chimney above the keyhole. Normal individuals of *D. aspera* collected from Edward's Reef on the west side of San Juan Island were used to test experimentally the short-term effects of obstructing the excurrent opening.

Experimental manipulation and morphological assessment

The apical openings of six normal limpets and the one whose apex had been covered by the barnacle were covered with modeling clay. Six controls had clay applied to the dorsal surface of the shell just anterior to the apical opening. Six additional controls had no clay. The shells ranged from 3.8 to 5.4 cm in aperture length. All limpets were placed in a tank with running seawater at the University of Washington's Friday Harbor Laboratories on San Juan Island, where they grazed on glassware that had been overgrown with a mat of algae, diatoms, and associated microorganisms.

The mantle cavity and associated organs were observed periodically to assess any possible damage caused by occluding the excurrent opening. Two weeks after applying the clay, we relaxed half of the limpets in each treatment by slowly adding 7.5% MgCl₂·6H₂O until they no longer retracted their tentacles when touched. The gills and mantle were examined with the naked eye and with a dissecting microscope, and the limpets were allowed to recover. After four weeks all animals were relaxed and examined in the same way. Several of the animals from each treatment were removed from their shells by cutting the attachment of the columellar muscle to the shell with a scalpel. After examining the dorsal surface of the mantle we deflected it to examine the ctenidia and rectum. In some cases the mantle was cut open with scissors to permit closer examination of the mantle cavity and its organs.

Flow visualization

To visualize the flow of water through the mantle cavity, a fine stream of fluorescein dye in seawater or of milk (commercial Half-and-Half composed of equal parts of cream and homogenized milk) was released along the anterior edge of the foot and shell. Observations were made on animals in still or moving water in a recirculating flow tank (Vogel & LaBarbera 1978) with a trough 10 cm wide at flow rates of 3–5 cm/s.

The day after adding clay and one week later we examined the flow through the mantle cavity of half of the experimentally plugged animals and the con-

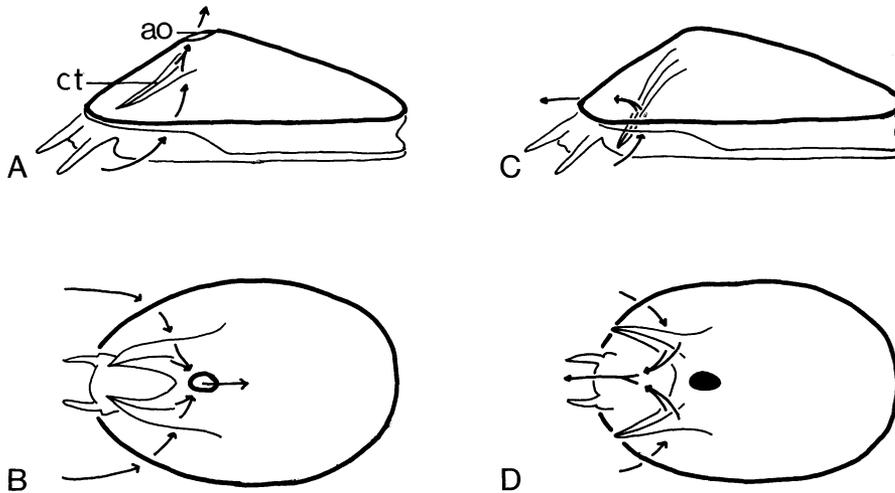


Fig. 1. Diagrams of flow through the mantle cavity in *Diodora aspera*. **A,B.** Normal limpet. **C,D.** Occluded limpet. **A,C** are lateral views; **B,D** are dorsal views. Shell and mantle drawn as if transparent. Anterior is left. Arrows indicate the paths of water flow. Apical opening of shell (ao); ctenidium (ct).

trols. At the end of four weeks the movement of water through the mantle cavity was observed in the controls and in the naturally and artificially plugged animals before and after removing the plugs.

Results

Mantle cavity damage

Three of the controls that had no clay on their shells showed slight abnormalities or asymmetries of the tips of the gills. The gills and mantles of the experimental animals showed no sign of damage or deterioration. There was no evidence of accumulation of feces at the posterior region of the mantle cavity. In the limpet whose apex had been blocked by a barnacle the mantle tissue lining the apical opening was slightly longer than in normal individuals.

Flow visualization

Two distinct patterns of flow were observed (Fig. 1). All control animals and the animal whose excurrent opening had been blocked by a barnacle had ventilation patterns typical of keyhole limpets as diagrammed by Hickman (1985) (Fig. 1A,B). Dye and milk released along the anterior edge of the shell were taken up at either side of the head and were released as a steady plume through the excurrent opening (Fig. 2). Feces and gametes exited through the apical opening as well.

Three individuals were observed to spawn in mid-April and early June in the laboratory. The eggs from one female exited primarily through the apical opening and fell to the bottom of the dish containing her. A second female spawned exclusively through the apical opening; some of these eggs remained suspended in the surrounding water (M. G. Hadfield, pers. comm.).

Sperm from the male that spawned exited through the apical opening.

The individual whose shell was covered by a coralline alga showed a distinctive behavioral adaptation. It extended its gills so that the tips were exposed beyond the edge of its mantle and foot (Figs. 3, 4). Dye and milk were taken up slightly ventro-posterior to the gill tips on either side and exited the mantle cavity anterior to the gills or directly over the head (Figs. 1C,D, 4). Feces also left the mantle cavity over the head.

Normal animals that had been plugged for one week showed no distinct respiratory currents, either in still or moving water. Dye or milk released along the lateral and anterior edges of the mantle cavity entered posterior to the cephalic tentacles. We observed no discrete excurrent stream.

Within four weeks of having their excurrent openings plugged with clay, the experimental animals showed a pattern of mantle cavity ventilation similar to that of the animal plugged with the coralline alga. One or both gills extended so that the tips were visible; water entered ventro-posterior to the tips and exited between the gill and tentacle on the same side, directly over the head, or over the opposite tentacle. The animal whose excurrent opening had been covered by the barnacle exhibited this behavior within one day of being plugged with clay. Fecal pellets exited the mantle cavity between the gill and tentacle or over the head.

Immediately after the coralline alga or clay plugs were removed, all animals reverted to the normal ventilation pattern observed in the controls (Fig. 5).

Discussion

Although proposed phylogenies of archaeogastropods are poorly resolved, these animals are generally

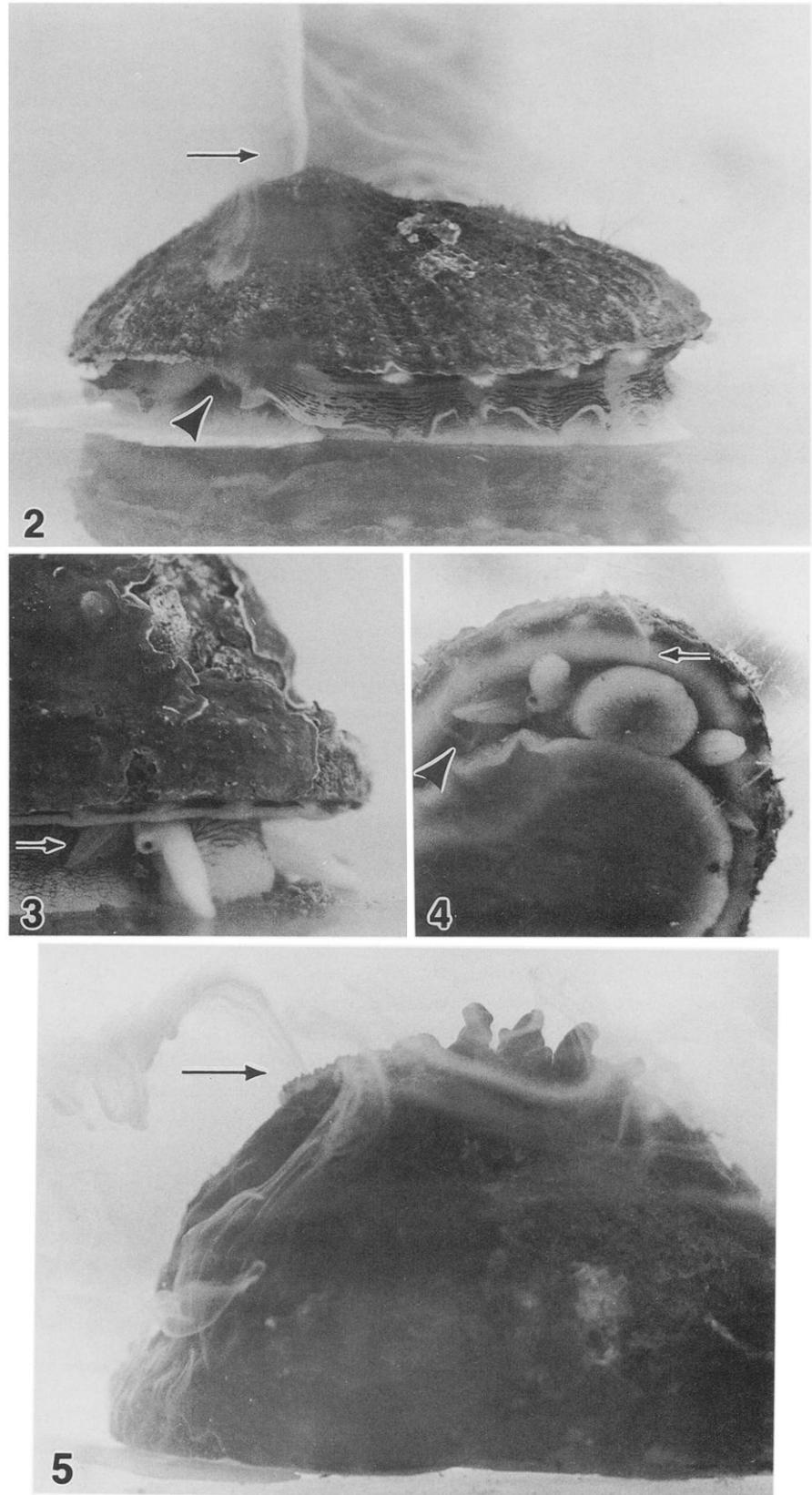


Fig. 2. Path of water flow through the mantle cavity of a normal keyhole limpet in standing water. Water labelled with milk entered the mantle cavity at a point where the mantle was raised (arrowhead) and exited at the apical opening (arrow).

Fig. 3. Right side of the keyhole limpet whose apical opening was occluded by the coralline alga *Lithothamnion phymatodeum*. Note the exposed tip of the right ctenidium (arrowhead).

Fig. 4. Ventral view through plexiglass of the keyhole limpet whose apical opening was occluded by the coralline alga *Lithothamnion phymatodeum*. Fluorescein dye released near the ventral edge of the shell on the right side entered the mantle cavity just posterior to the tip of the ctenidium (arrowhead) and exited in a stream over the head (arrow).

Fig. 5. Keyhole limpet that had been covered with coralline alga immediately after the alga was removed from the apical opening. Seawater labeled with milk exited the mantle cavity through the apical opening (arrow).

thought to represent a grade in the evolution of the gills, respiratory current, and mantle cavity (Voltzow 1994). Most fissurelloideans possess a bilaterally symmetrical mantle cavity, paired symmetrical gills, and an excurrent opening at or near the shell apex or a short slit at the anterior margin of the shell. Pleurotomarioideans have paired gills and either a longer slit at the anterior margin of the shell or a series of tremata on the dorsal surface of the shell. Garstang (1928) and Yonge (1947) proposed evolutionary scenarios in which these openings and slits represent an adaptation to allow the respiratory current to flow through the gills before picking up feces and urine and exiting the mantle cavity through the excurrent slit or openings. Because most other prosobranch gastropods have a single asymmetrical gill with an asymmetrical current through the mantle cavity, they were thought not to need an excurrent opening.

Based on several lines of evidence, including the observations reported in this paper, we question the basic assumptions of this traditional scenario (see Voltzow 1994 for review). We found that individuals of *Diodora aspera* with blocked excurrent openings were able to maintain adequate respiratory currents. Water entered the mantle cavity laterally, posterior to the cephalic tentacles, and was expelled either to the sides of the cephalic tentacles or directly over the head. Entrainment of water was probably aided by extending the gills beyond the edge of the mantle. Feces exited the mantle cavity with the water current. We observed no deterioration of the gills or mantle cavity in animals experimentally occluded for one month. The barnacle that had grown over the excurrent opening of one animal was large enough to be between four months to one year in age (R. R. Strathmann, pers. comm.). Although some of its early growth may not have affected the excurrent flow of its host, it eventually must have completely blocked the apical opening. The coralline alga encrusting the other naturally occluded limpet was thick enough at the shell apex to have been in that position for about a year (Dethier 1994 and pers. comm.) Neither of these animals showed any deterioration of the mantle cavity or gills. This suggests that blockage of the excurrent opening does not cause long- or short-term damage to the mantle cavity or pallial organs.

Our results show that these animals have a behavioral plasticity that enables them to reposition their ctenidia to maintain a functional flow of water through the mantle cavity even when the apical opening is occluded for long (at least several months) periods. This alternate behavior is reversible, as demonstrated by the return of the limpet with the coralline alga to the typical flow pattern as soon as the apex was reopened.

That the individual with the barnacle chimney was quicker to assume the alternate behavior than were the other clay-plugged animals implies some form of memory, since presumably this animal spent several months with its gills extended while its apex was occluded with the living barnacle. The mechanism underlying this behavioral change and the alternate flow pattern it produces is not clear and merits further investigation.

Evidence from other taxa also indicates that an excurrent opening is not necessary for functional respiratory currents. The superfamily Fissurelloidea includes genera having well-developed apical excurrent openings (for example, *Diodora* and *Fissurella*), smaller subapical openings (*Puncturella*), marginal slits (*Emarginula*), or no slit or opening at all (*Scutus*, *Hemitoma*) (Abbott & Dance 1986). Fissurelloideans that lack special excurrent openings very likely have flow patterns similar to that observed in individuals of *D. aspera* with blocked excurrent openings.

Although relatively rare, individual haliotids that lack excurrent openings have been reported. Specimens of *Haliotis cracherodii* lacking tremata were previously placed in distinct subspecies (Abbott 1974). Leighton (1960) also described individuals of *H. rufescens* in which tremata failed to develop.

Clearly the excurrent opening is not necessary for respiratory function in animals with fissurellid pallial morphology. However, it may enhance respiratory exchange by permitting an induced passive flow through the mantle cavity. Induced flow has been demonstrated in *D. aspera* and in species of *Haliotis* (Murdock & Vogel 1978; Voltzow 1983; Tissot 1992). Induced flow may contribute to the respiratory efficiency and breadth of environmental tolerance of these animals. Elevated excurrent openings may also contribute directly to an animal's reproductive success. Individuals of *D. aspera* and *Haliotis* spp. release gametes via their outgoing respiratory current. This could facilitate the transport of gametes into the water column and reduce the risk that they will be trapped in the boundary layer near the foot. Thus the excurrent openings of these animals may be advantageous for creating induced flow or enhancing dispersal of gametes as well as maintaining good sanitation in the mantle cavity.

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