Respiration in Mollusca

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Mechanism of respiration

Most molluscs have true gills, or ctenidia. However, many have lost the ctenidia and either rely on secondarily derived “gills” or on gas exchange across the mantle or general body surface. The presumed **primitive gill condition**, seen in several living groups, like many of the primitive gastropods (archaeogastropods) and primitive bivalves (protobranchs), can serve to explain how molluscan gills work. In these cases, the gill, or ctenidium, is built around a long, flattened axis projecting from the wall of the mantle cavity. To each side of the axis are attached triangular or wedge-shaped filaments that alternate in position with filaments on the opposite side of the axis. This arrangement, in which filaments project on both sides of the central axis, is called the **bipectinate** (or **aspidobranch**) **condition**. There is one gill on each side of the mantle cavity, held in position by membranes that divide the mantle cavity into upper and lower chambers (Figure 1A, B). Cilia covering the gill surface draw water into the **inhalant** (**ventral**) **chamber**, from which it passes upward between the gill filaments to the **exhalant** (**dorsal**) **chamber** and then out of the mantle cavity (Figure 2). Two vessels run through each gill axis. The afferent vessel carries oxygen-depleted hemolymph into the gill, and the efferent vessel drains freshly oxygenated hemolymph from the gill to the atria of the heart, as noted above. Hemolymph flows through the filaments from the afferent to the efferent vessel. Ctenidial cilia carry water over the gill filaments in a direction opposite to that of the flow of the underlying hemolymph in the ctenidial vessels. This countercurrent phenomenon enhances gas exchange between the hemolymph and water by maximizing the diffusion gradients of O_2 and CO_2 (Figure 2).

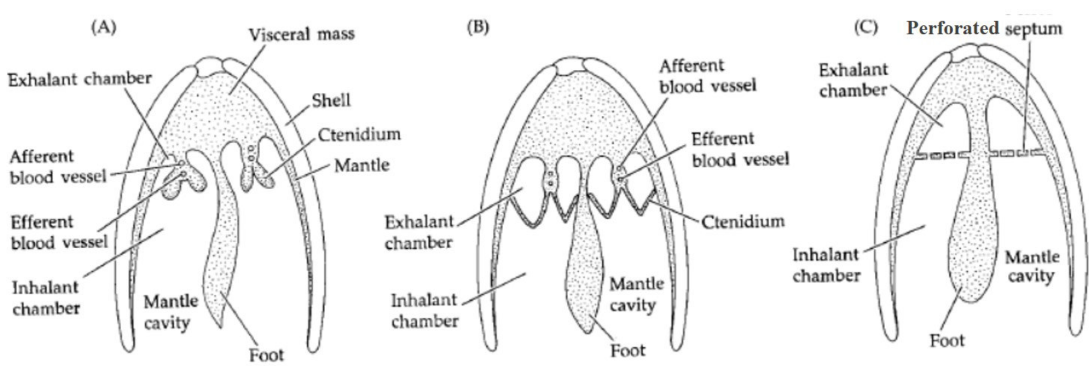

Figure 1: Arrangement of ctenidia in some bivalves (transverse sections). (A) Protobranch. (B) Lamellibranch. (C) Septibranchiate anomalodesmatan.

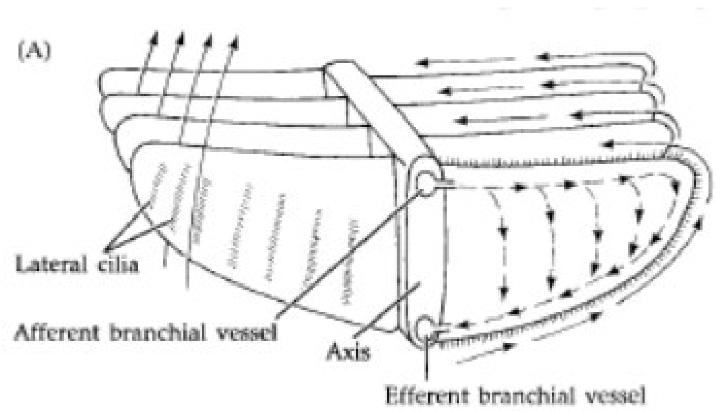

Figure 2: Ctenidial structure in bivalve molluscs. In all drawings, solid arrows indicate the direction of water flow (from inhalant space, between ctenidial filaments, to exhalant space). (A) Section through the gill axis in a protobranch, with four alternating filaments (leaflets) on each side. Dashed arrows indicate direction of hemolymph flow in the filament.

Gaseous exchange in different Mollusca

In the **aplacophorans**, gills are usually absent or, if present, form a ciliated, lamellar pouch arising directly off the posterior region of the pericardial chamber. Caudofoveatans have a similar posterior gill.

Monoplacophoran gills are similar to those of gastropods, but they occur as three to six pairs, aligned bilaterally within the pallial groove, reminiscent of chitons. Well developed lamellae occur only on one side of the monoplacophoran gill axis, similar to the monopectinate condition of advanced gastropods.

In the **polyplacophorans (chitons),** the mantle cavity forms a **pallial groove** extending along the body margin and encircling the foot. A large number of simple gills lie laterally in this groove. The mantle is held tight against the substratum, largely enclosing this pallial chamber. However, the mantle is raised on either side at the anterior end to form incurrent channels, and is raised in one or two places at the posterior end to form excurrent areas. Water enters the inhalant region of the pallial chamber lateral to the gills, then passes medially between the gills into the exhalant region along the sides of the foot. Moving posteriorly, the current passes over the gonopores, nephridiopores, and anus before exiting.

Primitive archaeogastropods, with two bipectinate ctenidia, circulate water in across the gills, then past the anus and nephridiopore, and away from the body via slits or holes in the shell. This circulation pattern is used by the slit shells, abalones, and volcano limpets. Most other gastropods have lost the right ctenidium and with it the right atrium; they circulate water in from the left side of the head and then straight out the right side, where the anus and nephridiopore open (Figure 3). Other gastropods have lost both ctenidia and utilize secondary respiratory regions, either the mantle surface itself or secondarily derived gills of one kind or another.

In more advanced gastropods, such as the mesogastropods and neogastropods, one ctenidium is almost always missing, as are the dorsal and ventral suspensory membranes of the remaining gill, which attaches directly to the mantle wall by the gill axis. The gill filaments on the attached side have been lost, while those of the opposite side project freely into the mantle cavity. This advanced arrangement of filaments on only one side of the central axis is referred to as the **monopectinate** (or **pectinobranch**) **condition**. The dorsal attachment of the monopectinate ctenidium in some species helps prevent fouling in soft sediments. Some advanced mesogastropods and neogastropods have also evolved **inhalant siphons** by extension and rolling of the mantle margin (Figure 3). In these cases, the margin of the shell may be notched, or drawn out as a canal to house the siphon. The siphon provides access to surface water in burrowing species, and may also function as a mobile, directional sense organ.

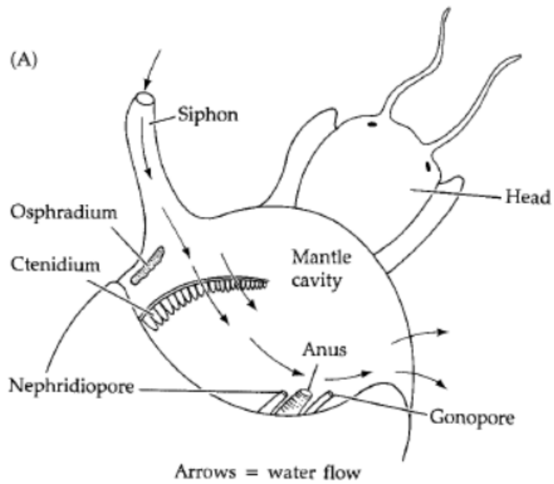

Figure 3: A neogastropod with a fleshy siphon, depicted with the shell removed. The animal has lost the posttorsional right ctenidium (and atrium and nephridium). Water flows into the mantle cavity through the siphon from the left, passes over the osphradium and ctenidium and then over the excretory pore and anus before leaving the mantle cavity to the right.

Opisthobranch gastropods are largely detorted. In some, the one remaining gill is **plicate**, or folded, rather than filamentous, and in fact may not be homologous with the prosobranch ctenidium. Trends toward detorsion, loss of the shell and ctenidia, and reduction of the mantle cavity occur in many opisthobranchs, and the process has apparently occurred several times within this group. Some nudibranchs have evolved secondary dorsal gas exchange structures called **cerata**. Many also have a circlet of postdorsal gills around the anus that may or may not be homologous to the true ctenidia.

Wholly terrestrial gastropods generally lack gills, and exchange gases directly across a vascularized region of the mantle, usually within the mantle cavity. The whole arrangement is often referred to as a **lung**. In terrestrial pulmonates, the edges of the mantle cavity have become sealed to the back of the animal except for a small opening on the right side called a **pneumostome**. Instead of having gills, the roof of the mantle cavity is highly vascularized. By arching and flattening the mantle cavity floor, air is moved into and out of the lung.

In bivalves the capacious mantle cavity allows the ctenidia to develop a greatly enlarged surface area, serving in most species for both gas exchange and feeding. In addition to the folded, W-shaped ctenidial filaments seen in many bivalves (Figure 1B), some forms (e.g., oysters) bear **plicate ctenidia**. A plicate ctenidium is thrown into vertical ridges or folds, each ridge consisting of several ctenidial filaments. The grooves between these ridges of ordinary filaments bear so-called **principal filaments**, whose cilia are important in sorting sediments from the ventilation and feeding currents. The plicate condition gives the ctenidium a corrugated appearance and further increases the surface area for gas exchange. In septibranchs, which have reduced gills, the mantle surface is the principal area of gas exchange. Most bivalves appear to lack respiratory pigments in the hemolymph, although globins occur in a few species and hemocyanin is found in protobranchs.

Scaphopods have lost the ctenidia, heart, and virtually all vessels. The circulatory system is reduced to simple hemolymph sinuses, and gas exchange takes place mainly across the mantle and body surface.

In most cephalopods, the gills are folded, increasing their surface area for greater gas exchange associated with a high metabolic rate. The circulatory system that is effectively closed, with many discrete vessels, secondary pumping structures, and even capillaries. The vessels leading into the ctenidia are enlarged into powerful accessory **branchial hearts**, which boost the low venous pressure as the hemolymph enters the gills.

References

Brusca R.C. and Brusca G.J. (2003). Invertebrates. 2nd Edition. Sinauer Associates Inc. Publishers, USA.

Ganguly B.B., Sinha A. and Adhikari S. (1977). Biology of Animals, Vol. I. 3rd Edition. New Central Book Agency (P) Ltd., Culcutta.

Kotpal R.L. (2013). Modern Text Book of Zoology: Invertebrates. Tenth revised edition. Rastogi Publication, Meerut.

Parker T.J. and Haswell W.A. (1972). Textbook of Zoology, Vol. I: Invertebrates. Seventh Edition. The Macmillan Publishers Limited, London.

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