Ciliary Currents in the Mantle Cavity of the Atlantidae.

By

C. M. Yonge, D.Sc.

(University of Bristol.)

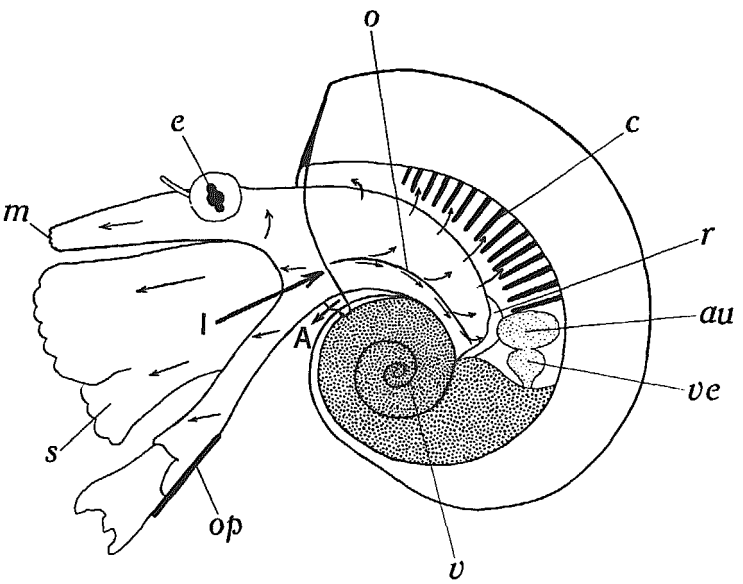
With 2 Text-figures.

Introduction.

It has previously been claimed (Yonge, 1938) that the ciliary currents concerned with the rejection of sediment from the mantle cavity of pectinibranch Prosobranchia may be divided into three groups. These are, (*A*) currents which reject by way of the inhalant aperture heavy particles which sink to the floor of the mantle cavity almost immediately after entry, (*B*) currents which carry medium particles across the floor of the mantle cavity, and (*C*) currents which, in association with the purely respiratory current, convey fine particles, largely in suspension, over and between the gill filaments which project downwards from the roof of the mantle cavity. These particles are later consolidated in mucus secreted by the hypobranchial gland the function of which is thus to prevent fouling of the respiratory chamber. Material in currents *B* and *C* is rejected by way of the exhalant opening on the right side.

These conclusions were based largely on the study of the ciliary currents in the mantle cavity of Buccinum undatum. But to do this the mantle cavity had to be opened and conditions as they exist in the intact animal deduced. Really satisfactory results could clearly only be obtained from the examination of some small Prosobranch with a transparent shell. Such examination would also have the advantage of revealing whether the inhalant current does directly impinge on the osphradium. It had been suggested (Yonge, 1938) that this is the case, and that the osphradium represents the line of separation of currents *B* and *C*. The theory had previously been advanced (Hulbert and

Yonge, 1937) that the osphradium is not a chemoreceptor, as it has usually been considered, but instead a tactile organ concerned with the estimation of the amount of sediment brought into the mantle cavity by the inhalant current created by the lateral cilia on the filaments of the ctenidia.



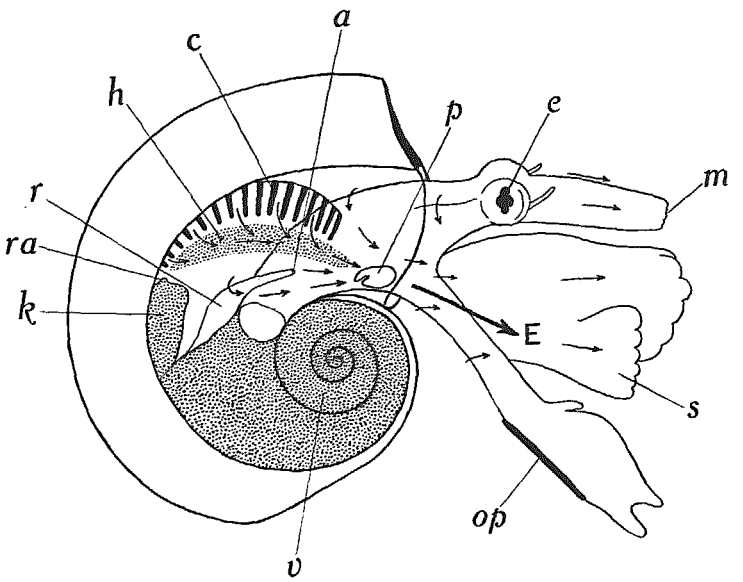
TEXT-FIG. 1.

Oxygyrus keraudreni, male, viewed from left side, drawn from life. ×15. *A*, rejection current; *au*, auricle; *c*, ctenidium; *e*, eye; *I*, inhalant current; *m*, mouth; *o*, osphradium; *op*, operculum; *r*, rectum; *s*, sucker; *v*, visceral mass; *ve*, ventricle. Arrows indicate the direction of ciliary currents.

The only Prosobranchia with transparent shells are the Heteropoda. Of the three families which compose this group, the Carinariidae and the Pterotracheidae are highly specialized. But in the Atlantidae the mantle cavity and its contained organs are in all essentials typical of those of the pectinibranch Prosobranchia.

Advantage was taken of a visit to the Stazione Zoologica, Naples, during Easter 1938, to examine a living male specimen

of Oxygyrus keraudreni Les. Drawings were made of both sides of the animal when fully expanded to show the ciliary currents. Subsequently the mantle cavity was opened to permit more detailed examination of the organs. No further specimens were available, but sections were later cut of specimens of the



TEXT-FIG. 2.

Oxygyrus keraudreni, viewed from right side. ×15. *a*, anus; *h*, hypobranchial gland; *E*, exhalant current; *k*, kidney; *p*, penis; *ra*, renal aperture. Other lettering as before. Arrows indicate the direction of ciliary currents.

closely allied Atlanta peronii Les. which had been collected and fixed in Bouin's fluid at the then Station Zoologique Russe, Villefranche-sur-Mer, in 1926. Acknowledgements are due to the Directors of these two laboratories.

CURRENTS IN THE MANTLE CAVITY OF OXYGYRUS KERAUDRENI.

Oxygyrus lives well in captivity and expands readily. The addition of a little carmine to the water enabled the currents in the mantle cavity and on the head and foot to be followed with

ease by the aid of a low power binocular microscope. The powerful inhalant current (Text-fig. 1, *I*) enters on the left side somewhat below the middle line. The heaviest particles could be seen to fall out of suspension almost immediately and to be rejected by way of currents which lead to the base of the inhalant opening (Text-fig. 1, *A*). But the great bulk of the suspended matter was observed to be carried fully into the mantle cavity and to impinge on the line of the osphradium (*o*.).

The osphradium, which is a broad, pectinate structure in many Prosobranchia, is elongated in the Atlantidae. Associated with it is a ridge of epithelium consisting of tall cells bearing conspicuously long cilia. Sections of Atlanta peronii reveal that in this species they attain a length of 30μ. These cilia, which can be detected even through the shell in the intact animal, beat rather slowly, and they throw fine particles dorsally so that they remain in the respiratory current and are carried on to and between the ctenidial filaments. Larger particles or masses tend to accumulate along the line of the osphradium ventral to this conspicuously ciliated ridge and to be carried slowly back. Beneath the epithelium, under the line of their accumulation, runs the osphradial nerve. If, as previously suggested (Hulbert and Yonge, 1937), the sensory cells which are present in the epithelium overlying this nerve are tactile in function, they would be admirably placed for estimating the amount of sediment brought into the mantle cavity.

After being carried back to the posterior regions of the mantle cavity, these larger particles are conveyed across the floor of the mantle cavity into the exhalant region on the right side. The ciliated tracts which conduct them constitute current *B*. Some material is also carried across the floor of the mantle cavity in more anterior regions (see Text-fig. 1).

The particles which are thrown upwards by the line of long cilia pass into the exhalant cavity by way of the roof of the mantle cavity, i.e. in current *C*. Cilia on the ctenidial filaments are primarily responsible for this. The ctenidium (Text-figs. 1 and 2, *c*) consists of relatively few but large filaments which hang down from the roof of the mantle cavity. The ctenidium is here mid-dorsal in position and not on the left side. Each

filament is in form an isosceles triangle, the base being somewhat shorter than the other two sides. Each possesses frontal, abfrontal, and lateral cilia. All are extremely active. The lateral cilia apparently extend across the entire width of each filament instead of being restricted to a narrow tract as in Buccinum and other Prosobranchs examined (Yonge, 1938). They are responsible for the very powerful respiratory current. Both frontals and abfrontals beat, as usual, to the free tips of filaments, but in life the great bulk of the suspended particles are carried in the respiratory current between the relatively widely separated filaments.

After passing through or over the ctenidium, particles in current *C* are carried on to the surface of the hypobranchial gland (Text-fig. 2, *h*). This consists of an elongated area of large mucus-secreting cells and lies on the right side of the roof of the mantle cavity. Here the particles are consolidated into masses with mucus, and are conveyed by ciliary currents anteriorly towards the exhalant aperture. At the anterior end of the gland they unite with material from current *B* which, as shown in Text-fig. 2, has been carried along the floor of the mantle cavity. Material from both sources, together with faeces discharged from the anus (Text-fig. 2, *a*), is then ejected in the very powerful exhalant current (Text-fig. 2, *E*). Excrement from the renal aperture (Text-fig. 2, *ra*) is also passed out in this current.

Currents on the Head and Foot.

As indicated by the arrows in Text-figs. 1 and 2, the head and complex foot are everywhere ciliated and particles are carried anteriorly over their surfaces. Only at the base of the head, posteriorly to the eyes (*e*), is material carried first to the right side. The ciliation in this latter region therefore resembles that on the floor of the mantle cavity.

Discussion.

These observations on a living representative of the Atlantidae have enabled conclusions to be reached on two points: (1) the course taken by suspended matter within the intact mantle

cavity of a Prosobranch, and (2) the nature of such specializations as occur within the mantle cavity of these Heteropoda.

The existence of currents *A*, *B*, and *C* has been demonstrated clearly. The previous opinion that particles carried in suspension by the inhalant current impinge on the surface of the osphradium has been confirmed, also that this organ represents the line of separation of currents *B* and *C*. The accumulation of material along the line of the osphradium also gives greater force to the argument that this is a tactile receptor.

Some evidence of specialization for pelagic life was found. The great power of the respiratory current created by the lateral cilia on the ctenidial filaments may well be attributed to the greater metabolism associated with the swimming habit. Currents concerned with rejection of sediment are equally powerful. Withdrawal into the shell did not occur even when heavy concentration of suspended matter entered the mantle cavity. The particles were rapidly disposed of without disturbing the normal swimming movements. Oxygyrus certainly remains expanded in water the sediment content of which would cause bottom-living Prosobranchia to withdraw into the shell. The unusually widespread and active ciliation on the head and foot is presumably also correlated with the need for rapid removal of sediment.

The structure of the ctenidium reflects these specializations. It is instructive to compare it with that of the sedentary Vermetus gigas (Yonge and Iles, 1939); the metabolic needs are correspondingly less than those of the average Prosobranch. In Oxygyrus the ctenidium is mid-dorsal in position, permitting the greater development of the filaments and thus the maintenance of a greater respiratory current. In Vermetus it remains on the left side. In Oxygyrus the filaments are relatively very large but few in number and so well spaced. This permits the presence of a wide zone of lateral cilia which create the powerful respiratory current, and also enables the finer particles drawn in with this current to pass between the filaments. In Vermetus the filaments are numerous and closely applied but are extremely small, while the lateral cilia are confined to a narrow tract and create a weak respiratory current.

The entrance of even small amounts of sediment causes the animal to withdraw into its tube so that there is no need for the filaments to be spaced out.

The currents in the mantle cavity of the Atlantidae, though normal in origin and direction, are thus specialized to permit the rapid removal of sediment brought in with the powerful respiratory current. This specialization represents part of the adaptations necessary for the assumption of a pelagic life by these animals.

Summary.

The ciliary currents in the mantle cavity of the Heteropod, Oxygyrus, were examined in the intact animal. The presence of three sets of currents concerned with the rejection of sediment, already postulated from examination, after dissection, of the mantle cavity in other Prosobranchs, was confirmed. The great majority of the sediment brought in with the respiratory current impinges on the line of the osphradium. This favours the conclusion that this organ is tactile in function and not a chemoreceptor. The extent to which the organs and currents in the mantle cavity are modified as a result of pelagic life is discussed.

References.

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