ON THE MECHANISM OF VENTILATION
IN APHRODITE ACULEATA

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(With Six Text-figures)

APHRODITE ACULEATA L., the sea mouse, is generally dredged from muddy bottoms, where it burrows head-first into the mud. Usually only the anal extremity, which is very mobile and often held in an upturned position, remains uncovered.

In dorsal view the parapodia are hidden by a beautiful fringe of setae which project from the sides of the body. The true dorsal surface is concealed by a felt formed by long matted threads, which arise from the parapodia. In the cavity enclosed by the felt and dorsal body wall lie the elytra (Fig. 1). These leaf-like structures issue in a double row from the dorsum, which they completely conceal. They are epidermal expansions arising from the dorsal wall of pouches called elytrophores (Fig. 5).

As was described by Fordham (1925, p. 29) the elytra serve to ensure the circulation of water over the dorsum, which is, therefore, considered to be the true respiratory surface. At intervals they are depressed. The depression begins with the anterior pair and passes rapidly backwards. This flattening of the elytra on to the dorsum forces a jet of water out through the exhalent aperture, which is situated at the dorsal side of the anal extremity.

As soon as expiration is completed the exhalent aperture is closed. Immediately afterwards inspiration begins: the elytra are again elevated.

From this point Fordham’s description runs as follows (1925, p. 39): “Whilst the water beneath the felt is being rhythmically pumped out by way of the ejection apparatus, a fresh supply is continually percolating in through the felt” (my italics).

Hazelhoff (1938, p. 312), however, when

Fig. 1. Diagram of Aphrodite in dorsal view. In the felt an opening has been made so that ten elytra are visible. The elytra overlap one another from before backwards and individually from left to right and right to left, alternately. Six body segments are indicated. It is seen that the elytra, by means of their elytrophores (dotted areas), issue from alternate segments. a-b, section represented in Fig. 5; c-d, section represented in Fig. 4. Somewhat reduced.
working on the utilization of oxygen in *Aphrodite*, observed a marked current of water going in near the animal’s tail. This discrepancy led me to reinvestigate the mechanism of ventilation. The present paper deals with the results obtained.

**EXPERIMENTS**

The animals used were obtained from the marine Zoological Station at Den Helder. They were apparently healthy; when turned over on their backs they soon righted themselves.

The respiratory currents were made visible by adding, to the ingoing water, a small amount of a Chinese ink suspension prepared by rubbing solid Chinese ink with sea water in a mortar. The fluid thus obtained is very suitable for demonstrating respiratory currents, for it contains no extraneous chemicals and therefore has no irritating effect.

First, a specimen was placed in a normal position in a Petri dish filled with sea water. Its head was placed against the wall of the dish, so that it was prevented from moving forward. After some 5–10 min., when the locomotory efforts of the animal had ceased, ink was administered near its tail. In accordance with Hazelhoff’s observations, every twenty or thirty seconds a current of water was seen to enter the space under the upturned anal extremity. At the same time another current escaped from the exhalent aperture.

In order to follow the current disappearing under the animal and to approach more closely to natural conditions, I covered a specimen with a layer of sand, about 1 or 2 cm. thick (cf. Fig. 2). The animal soon curved its tail upwards through the surface of the sand. By doing so it gains free access to the water, and is therefore able

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**Fig. 2.** Diagram of a transverse section of *Aphrodite* passing through a right and left parapodium. The *animal* is placed in a Petri-dish filled with water and is covered with sand. There is no sand under the animal. The dish is placed on a glass plate, so that the animal’s ventral side can be observed with the aid of a mirror. Small dots: elytra. Heavy dots: sand. Matted lines: felt. Somewhat reduced.
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to maintain respiration. Care was taken that there was no sand between the ventral side of the animal and the glass bottom of the Petri dish. The dish was then placed on a glass plate and the animal's ventral side illuminated with a lamp. In this way the ingoing current could easily be followed with the aid of a mirror. It was found that during each expiration (i.e. the ejection of water from the exhalent aperture) the animal's ventral side is lifted up from the substratum—as shown in Fig. 4—and water flows into the space thus formed. The chief paths along which the water flows are shown in Fig. 3.1

As soon as expiration is completed, i.e. after the exhalent aperture has been closed, the animal's ventral surface begins to flatten again. During this process of flattening, the water under the animal, together with some water from under its tail, is seen to pass between the parapodia. Apparently it is sucked up into the dorsal respiratory cavity. That this is actually the case is proved by the fact that during the next expiration a stream of ink-coloured water escapes from the exhalent aperture.

It thus appears that during expiration the scales become more and more depressed. Consequently the water contained in C (Fig. 4a) is forced out through the ejection apparatus. At the same time the ventral body wall is elevated, so that water from under the tail is drawn into the space formed under the body.

During inspiration the scales are again elevated and at the same time the ventral body wall is depressed. In consequence, water from under the animal passes between the parapodia and then flows via the intersegmental openings in the felt (see Fig. 4a) into the dorsal respiratory cavity C.

The same analysis holds good for an animal which is not covered with sand. A specimen was laid on the surface of the sand, either in a normal position or on its back. In both cases the ink, administered between some of the parapodia, was readily sucked up at the next inspiration. At the next expiration it re-appeared in the outgoing current.

On the other hand, when some ink was pipetted on to the dorsal felt, no suction through the latter could be observed through a binocular microscope.

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1 The ventral body surface, between the segments, shows more or less well-defined grooves. It is particularly in these grooves that the water is seen to flow in a lateral direction.

2 In an animal covered with sand, the dorsal felt follows the movements of the scales very closely.

3 In specimens lying free on the substratum the felt seems to move to a smaller extent.

4 The felt is formed by threads which issue from the parapodia, and exhibits small lateral intersegmental openings.
Fig. 4. Diagrams of transverse sections through Aphrodite showing the respiratory movements of dorsum, scales, etc. The degree of movement was somewhat roughly estimated. Each section passes on the left side through a parapodium, on the right side between two parapodia (c–d, Fig. 1). × 2½.
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From the above, it is clear that Fordham's view must be rejected. The inhalent current does not percolate continuously through the felt, but passes, during inspiration only, through the intersegmental openings in the felt into the dorsal respiratory cavity.1

The lateral apertures in the felt open both into the space between felt and elytra (D, Fig. 4) and into that between elytra and dorsum (C, Fig. 4). Therefore the water might flow directly into C or first enter D, then pass between the scales and thus flow into C. To decide between these alternatives the following experiments were carried out.

An opening was made in the felt, thus exposing one or two pairs of elytra. This opening was covered with a piece of transparent cellophane. The animal was then entirely covered with sand, except over the centre of the cellophane window. Thereupon, ink was added to the ingoing current, either under the tail or between those parapodia which were situated at the left or right side of the window; in the latter case, of course, these parapodia were not covered with sand. In this experiment, no ink was seen to stream over the upper side of the elytra, i.e. between elytra and cellophane, although the exhalent current was distinctly black. Apparently the respiratory current flows directly into the space under the scales.

The following experiments with methylene blue confirm the above conclusions. A specimen was covered with sand, and with the aid of a pipette a strong solution of methylene blue was added to the ingoing current for some 30 minutes. After removal of the felt, all parts of the body surface and elytra were found to have been stained blue, except (1) the upper sides of the elytra and (2) those parts of their lower sides which were covered by a part of the adjacent elytra (cf. Fig. 5).

A specimen, not covered with sand, was left for some 45 min. in a strong solution of methylene blue. The felt was then removed. Again, only the exposed lower sides of the elytra had been coloured. If an animal was left for a longer time in this solution, the inner side of the felt and the upper sides of the elytra were also found to be stained, but at first only at those places where the felt was rather thin. Apparently, in this case, some dye had permeated through the felt. It seems quite clear that the respiratory current does not enter the space between felt and elytra, but flows directly into that under the scales.

In some text-books, it is stated that the respiratory current flows "between dorsum and felt" (Buddenbrock, 1928, p. 309) or flows "beneath the felt" (Hempelmann, 1934, p. 127). It is clear that these statements are incorrect, for beneath the

1 Nierstrasz & Hirsch (1922, p. 41) described an anterior, inspiratory opening in the felt. This is erroneous; such an opening is only present in damaged specimens.
felt, i.e. between felt and elytra, no respiratory current is found. For the same reason the statement of Nierstrasz & Hirsch (1922, p. 41) that the felt covers the respiratory cavity, is incorrect.

In *Hermione*, the dorsal felt is absent. In this genus the inspiratory openings are also situated laterally between the body and the scales (Claparède, quoted by Pagenstecher, 1875). Therefore, the mechanism of ventilation in *Aphrodite* and *Hermione* may be assumed to be of essentially the same nature.

We may now consider how the animal, during expiration, prevents water from flowing back through the inspiratory openings in the felt.

To solve this question, I made an opening in the felt and removed parts of the scales, thus exposing some elytrophores and non-elytrous pouches. By lifting up these scales somewhat and looking under them in a lateral direction it is possible to observe the true inhalent apertures (cf. Fig. 4a). The lateral walls of these openings are formed by the dorsal side of an elytrous and a non-elytrous pouch respectively, whilst the roof is formed by an elytron.

During expiration, as already shown, the ventral body wall is drawn concavely inwards. Moreover, elytrous and non-elytrous pouches are pressed against one another so that the narrow channels between these (cf. Fig. 5) are closed. At the same time both dorsum and non-elytrous pouches are elevated (cf. Fig. 4) and the scales depressed. In other words: during expiration elytra and dorsum move towards one another. During the first stage of expiration, the inspiratory openings are closed; at a later stage elytron and non-elytrous pouch are pressed against one another over a considerable area (cf. Fig. 4b). In this way, water in the respiratory cavity is prevented from flowing back through the inspiratory openings; it does not escape between the elytra, since these structures overlap one another over a considerable length (cf. Figs. 1, 4, 5).

Fordham (1925, p. 39) believes that two flexures of the body play an important part in elevating the scales: "One is an antero-posterior flexure of the trunk...with its concavity ventralwards. The other flexure is at right angles to this; its concavity is also ventralward, by it the right and left margins of the body are drawn slightly together below." Such flexures may be observed, especially those of the latter type. As far as I could see, they are less marked than is indicated in Fordham’s drawing (1925, p. 40) and occur during expiration only, i.e. during the depression of the scales. In my opinion, depression of the scales is caused by a muscular contraction of the elytrophores, whereas the elevation is brought about mechanically by the pressure of the coelomic fluid. The cavity in the elytrophores is in open communication with the coelomic cavity.

Fordham’s drawing (1925, Fig. 7b, p. 40), is incorrect in two points. First,
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because it indicates that the right and left margins of the body, i.e. the tips of the parapodia, which lie on the substratum, display vertical movements. Secondly, because in a transverse section of the animal passing through an elytrophore, the scales in reality do not show a free lateral area (cf. my Figs. 4 and 6); for this reason Fordham's Fig. 38, Pl. V, is also incorrect.

SUMMARY

In Aphrodite aculeata the floor of the respiratory cavity is formed by the dorsal body wall, the roof is formed by the elytra. Ventilation is effected by pumping movements both of the dorsum and of the elytra.

During inspiration water is sucked into the respiratory cavity via lateral inspiratory openings in the felt.

During expiration the inspiratory openings are closed, and dorsum and elytra move towards each other. Consequently, the water in the respiratory cavity is forced out through the exhalent aperture, situated at the tip of the anal extremity.

When burrowing, the animal holds its tail in an upturned position above the sand. It has free access to the water via the space formed, during expiration, between ventral body surface and sand.

REFERENCES