The mechanism of movement of the gill-filaments in Teleostei

Our knowledge of the structure of the gills and of the way, in which the gill-elements function in Teleostei, is mostly of older date and has not yet been adapted to the results of the recent physiological investigations of the respiration of these fishes.

It is a well-known fact, that every gill-bar bears a double row of filaments (gill-plates of the first order), the two hemibranchiae. The filaments of both hemibranchiae of a gill alternate with each other. Every filament is supported by a piece of skeleton, the gill-rod, which is connected with the visceral arch. The filaments are movable through the action of small muscles in the sense of an adduction of the filament-tips of the two hemibranchiae of a gill and the anterior one of its immediate successor in the schemes (fig. 1 a). As early as 1932 WOSKOBOINIKOFF concluded that in living Teleostei the filaments of two successive branchial arches shut off the slits between these arches. Only in this way there is a maximum of contact between the respiratory water and the blood in the lamellae; the respiratory water is now forced to pass only through the small slits between the lamellae (fig. 1 b). If there

even speaks of fanning movements (fächelnde Bewegungen) of the gill-filaments in the Gobiiformes, to which the action of these adductor muscles should contribute. According to RIESS the blood of the arteria branchialis should be pushed by the heart-power only as far as the branches of the filaments. By a successive contraction and relaxation of the adductor muscles the afferent vessels for the filaments should be closed and opened alternately, which would cause the current of the blood through the filaments. It is evident, that these authors start from the supposition, that the adductor muscles have a rhythmical action, in which contraction and relaxation follow each other continuously.

When we have a look at the figures of a horizontal section of the branchial region in a Teleost in the different textbooks of zoology and comparative anatomy (GEGENBAUR, p. 226; BOAS, p. 511; HERTWIG, p. 526; CLAUS-GROBBEN-KÜHN, p. 919; NEAL and RAND, p. 247; PARKER and HASWELL, p. 86) we always see a wide aperture between the filament-tips of the posterior hemibranchia of one gill and the anterior one of its immediate successor in the schemes (fig. 1 a). It is remarkable that in the first years of control the number of losses of females is far higher than that of males. This observation coincides with the ascertained fact that the reported number of females found dead is nearly double the corresponding number of males.

(4) According to the notifications of dead animals found during quiet respiration (after BOAS, 1922), b Correct reproduction of the position of the filaments during quiet respiration. a, gill-arch. f, filament with lamellae. i. c. inspiratory cavity. i. e. expiratory cavity.

should be a wide aperture between the filament-tips, the greater part of the respiratory water would flow away without having passed the lamellae. Under these conditions the difference in quantity of oxygen of the water before and after passing the gills (the utilization of the oxygen) should be low. On the contrary van DAM asserts

1. The greatest age of Myotis myotis hitherto ascertained by means of the marking method, is 12 years.

2. The annual loss, observed with striking regularity, amounts to 40%.

3. It is remarkable that in the first years of control the number of losses of females is far higher than that of males. This observation coincides with the ascertained fact that the reported number of females found dead is nearly double the corresponding number of males.

4. According to the notifications of dead animals found during quiet respiration (after BOAS, 1922), b Correct reproduction of the position of the filaments during quiet respiration. a, gill-arch. f, filament with lamellae. i. c. inspiratory cavity. i. e. expiratory cavity.

5. It is a well-known fact, that every gill-bar bears a double row of filaments (gill-plates of the first order), the two hemibranchiae. The filaments of both hemibranchiae of a gill alternate with each other. Every filament is supported by a piece of skeleton, the gill-rod, which is connected with the visceral arch. The filaments are movable through the action of small muscles in the sense of an adduction of the filament-tips of the two hemibranchiae of a gill, which belong to one gill. The exchange of carbonic acid and of oxygen takes place in the blood-lacunae of the thin lamellae (gill-plates of the second order), which are placed on both sides of the filaments, nearly perpendicular to the surface.

The small muscles, which move the filaments, are described as adductor muscles. They really act as adducting powers for the filament-tips of the two hemibranchiae of a gill. Several authors (RIESS, WOSKOBOINIKOFF, ELFRIEDE SCHOTTLE) ascribe to these adduction movements of the filament-rows of a gill a significance for the renewal of the water during breathing and for the propulsion of the blood through the vessels of the gill-filaments. ELFRIEDE SCHOTTLE (1932, p.10)

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7. CLAUS-GROBBEN-KÜHN, Lehrbuch der Zoologie, 10. Auflage, 1932.
11. L. v. DAM, On the utilisation of oxygen and regulation of breathing in some aquatic animals. Diss., Groningen 1938.
found in the eel and the trout a utilization of 80%; and according to HAZELHOFF\textsuperscript{1} this value amounts to an average of 62% in some other Teleostei. Without knowing WOSKOBONIKOFF'S publication, VAN DAM\textsuperscript{2} concluded in the same way from the value of the utilization of the oxygen, that the wall separating the inspiratory and the expiratory cavity must be a wall without big slits.

In perfect agreement with these conclusions are the results of experiments on \textit{Tinca tinca}, carried out by Mrs HOFDIJK-ENKLAAR (Zoological Laboratory of the University of Groningen; not published). By looking under the gill-cover in the phase of expiration it is possible to watch the position of the filament-tips. Mrs HOFDIJK-ENKLAAR could observe that in this phase of the respiration the filament-tips of one hemibranchia and those of the successive one of a following branchial arch lean against each other. As in the inspiratory phase the gill-cover lies close to the body, it is not possible to observe the filaments during this phase of breathing. It was necessary to make a small circular opening in the gill-cover in order to observe the filament-tips during both phases of breathing. A bit of transparent celluloid was inserted in the little circular hole to prevent, that the pressure relations in the expiratory cavity should change. Mrs HOFDIJK-ENKLAAR could prevent, that the pressure relations in the expiratory arch lean against each other. As in the inspiratory phase the gill-cover lies close to the body, it is not possible to watch the position of the filament-tips. Mrs HOFDIJK-ENKLAAR found, that in this phase of the respiration the filament-tips of one hemibranchia and those of the successive one of the next gill touch each other during inspiration as well as during expiration.

It was also noticed, that in apparently clean water a normally breathing fish opens the gill-clefts at regular intervals, e.g. 8 times to 50 breathing movements. It makes so-called coughing movements. If small fragments of defilement (small filaments of filtering paper, a large quantity of detritus, etc.) are added to the water, these coughing movements become more frequent. In his investigations concerning the respiration of the Teleostei KUIPER\textsuperscript{3} observed these abnormal respiratory movements which he rightly interpreted as coughing movements. In his detailed study (1907) he accurately describes the sequence of opening and closing of mouth and gill-cover during the coughing movements.

Mrs HOFDIJK-ENKLAAR could observe through the celluloid window of the gill-cover, that during the coughing movements the gill-clefts open for a moment by the adduction of the filament-tips of one hemibranchia and those of the successive one of a gill. In his detailed study (1907) he accurately describes the sequence of opening and closing of mouth and gill-cover during the coughing movements. Mrs HOFDIJK-ENKLAAR found two types of adductor muscles (fig. 3 and 4). The muscles of the two types act in a different way. A muscle of the first type, as it is found e.g. in \textit{Esox lucius} moves the hole filament. The filament pivots in the syndesmosis between gill-rod and gill-bar (fig. 3).

\begin{figure}[h]
\centering
\includegraphics[width=0.8\textwidth]{fig2.png}
\caption{Schematic diagram of the position of the filaments and the lamellae in the living animal showing the blood-circulation in the filament.}
\end{figure}

\begin{figure}[h]
\centering
\includegraphics[width=0.8\textwidth]{fig3.png}
\caption{Schematic diagram of a section through two successive gills with adductor muscles of the first type: \textit{a} during quiet respiration; \textit{b} during the coughing movements.}
\end{figure}

As we study the coughing movements in the above mentioned way, it appears, that the opening of the gill-clefts during these movements occurs actively, that is to say by the action of the adductor muscles. We found two types of adductor muscles (fig. 3 and 4). The muscles of the two types act in a different way. A muscle of the first type, as it is found e.g. in \textit{Tinca tinca} moves the hole filament. The filament pivots in the syndesmosis between gill-rod and gill-bar (fig. 3).