THE GILL MOVEMENTS OF NYMPHAL *ECDYONURUS VENOSUS* (EPHEMEROPTERA) AND THE CURRENTS PRODUCED BY THEM IN WATER

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(With Four Text-figures)

WITH further reference to the phenomena of mayfly gill movement (Eastham, 1932, 1934, 1936), an examination of the gills of *Ecdyonurus venosus* has been made.

The methods adopted for analysing gill movement and for observing the currents were similar to those employed for *Caenis* and *Leptophlebia* (Eastham, 1934, 1936) and need not be described here. It is perhaps sufficient to remark that the gills may be induced to oscillate at the rate of about seven per second thus making observation by means of the stroboscope possible (Gray, 1930).

THE GILLS

The nymph of *Ecdyonurus* is well-known as occupying the water of fast-flowing streams with stony bottom. The nymphs cling to the undersurface of stones, feeding on the algae which grow thereon. They commonly rest with head pointing upstream and their stream-lined form, to which reference will be made later, is one which admirably adapts these animals to their environment. The paired gills are borne on the first seven abdominal segments, each being attached by a narrow stalk to the postero-lateral angle of its own segment. A typical gill (Fig. 1) from any of the segments 2–6 is a bilamellate organ, in which the anterior lamella is developed as a broad plate while the posterior lamella is reduced to a small palmate structure the border of which is surmounted with branching filaments so as to resemble on a less elaborate scale the filamental gill of *Caenis* (Eastham, 1934). The broad anterior lamella, which I will call the gill plate, possesses a narrow pedicel and is articulated to its body segment in such a way as to project downwards and backwards when in an attitude of rest so as to make an angle of about 45° with the body in the vertical plane and about 75° with the longitudinal axis of the body in the horizontal plane. Its anterior surface thus faces outwards and forwards. This gill surface is concave, the opposite surface which of course faces backwards and inwards to the sides of the body, is correspondingly convex. The anterior concavity is shallow and trough shaped, the bottom of the trough being marked by a median longitudinal trachea which passes through the gill plate. The anterior border of the gill plate for about two-thirds of its length is stiffened proximally by a thickening of chitin so providing an efficient cutting edge to the gill as it moves through the water in appropriate attitudes. For about its proximal half the upper posterior border is similarly stiffened. Distally the gill plate becomes thinner and its concavo-convex shape almost flattens out. Attached to the posterior aspect of the pedicel of the gill plate and occupying the angle between the latter and the body is found the filamental lamella. This, which I will call the gill tuft, consists of a much reduced gill plate. Its fringing filaments, of which there are about 20, branch laterally in a stagshorn manner as described for *Caenis* (Eastham, 1934), and project above the level of the gill plate in whose axis they lie (*vide* Rousseau (1921) for *Ecdyonurus fluminum*). The richly developed tracheal system which passes through the basal part of the lamella, branching so as to end in the filamental fringe, leaves no doubt as

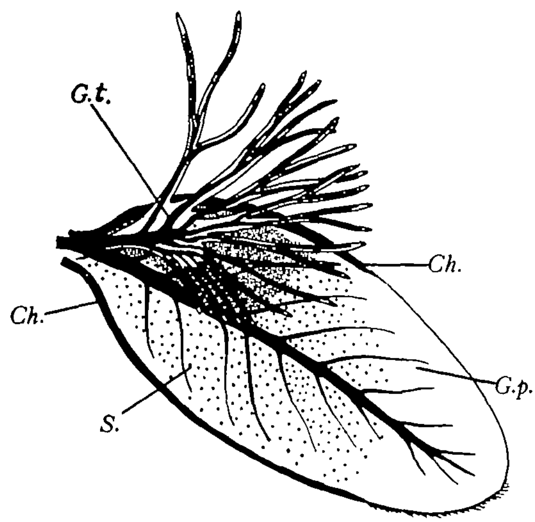

Fig. 1. Posterior surface of second gill of right side showing *Ch.*, chitinous stiffenings to the gill borders, *G.p.* gill plate, *G.t.* gill tuft, *S.* sensillae.

to the importance of this organ in respiration. On the other hand the more sparsely distributed tracheae of the gill plate suggests this latter as of less importance in this respect. We shall see that the gill plate performs the function of a paddle which continually bathes its respiratory gill tuft with water.

The first gill is essentially of the same nature as that just described, but while possessing a gill tuft of normal proportions its gill plate is greatly reduced in size and occupies the narrow space in the angle between the basal joints of the metathoracic legs and the body. This projects upwards as a narrow spatulate structure, concave in front and convex behind. The seventh gill consists of a normally proportioned gill plate projecting more posteriorly than do the others. Its gill tuft is absent. Fig. 2 shows the arrangement of the gills in the position of rest. Features to notice are the perfect alignment of the gills 2–7 in series down each side of the body; their overlapping from before backwards and the fact that they occupy on each side of the body the triangular space between the large metafemur and the abdomen.

CURRENTS

All currents are produced by movements of the gill plates of gills 2–6. They are, as shown in Fig. 2, symmetrical with the body axis. A main stream passes backwards along the middle line of the body dorsally and is fed by water which is passed to it from the sides and from beneath the thorax and the abdomen. We may define as direct those currents passing between the gills from below and the sides to the dorsal surface of the body. Others, caused secondarily by the latter, may be termed indirect or induced. Falling in the latter category are the longitudinal dorsal current and the mid-ventral thoracic currents.

GILL MOVEMENTS

As in *Leptophlebia* (Eastham, 1932, 1936) members of pairs beat simultaneously and synchronously and to this fact must be ascribed the symmetrical nature of the flow since the movement of any gill is the mirror image of that of its fellow of the opposite side. With the exception of the first pair, which on occasion remain motionless, and the seventh, which never move, the gills perform regular oscillations in the water, there being a metachronal rhythm from before backwards.

The main principle in water movement is that depending on the metachronal rhythmical movements of gills in alignment with each other. Under these conditions suction and compression phases follow each other in orderly succession and cause a continuous flow of water, the direction which this water takes depending on the attitudes adopted by each gill in all phases of its movement. Let us consider therefore a single gill in movement. To observe clearly the path traversed by a single gill it is advisable to remove the two gills adjacent to it. The single gill can then be seen at all phases of its movement without interference from its neighbours. It is then observed that the path traversed by a gill is elliptical, a point best illustrated by reference to Fig. 3.

The position of a gill at rest, Figs. 2 and 3, is that in which the distal extremity touches the substratum. The long axis of the gill projects backwards, making an angle of about 75° with the longitudinal axis of the body, and the anterior concave surface makes an angle of about 45° with the vertical. This position for each gill represents the anterior limit of an oscillation and from this point the gill moves backwards to lie in line with the body axis, being pressed in this position against the gill next behind it, its originally tilted anterior surface now vertical. The tip of the gill in this movement has passed backwards and upwards along one of the long sides of an ellipse which is inclined upwards, backwards and at the same time inwards towards the body (Fig. 3 A). In this movement, the effective beat of the gill plate, the posterior surface is in the leading position, and this surface increases its angle of incidence with the water through which it is passing from the original 45° to 90°, an almost completely broadside position.

Here again, as was shown in the case of *Caenis* and *Leptophlebia* (Eastham, 1934, 1936), the same principle as that significant in fish movement (Gray, 1933), is operative, viz. that of a moving surface making a continuously increasing angle with its own path of motion, the water being moved along a line which represents the resultant R of forces normal N and tangential T to the moving surface (Fig. 3 B.) The elliptical path being inclined upwards as well as towards the body in the

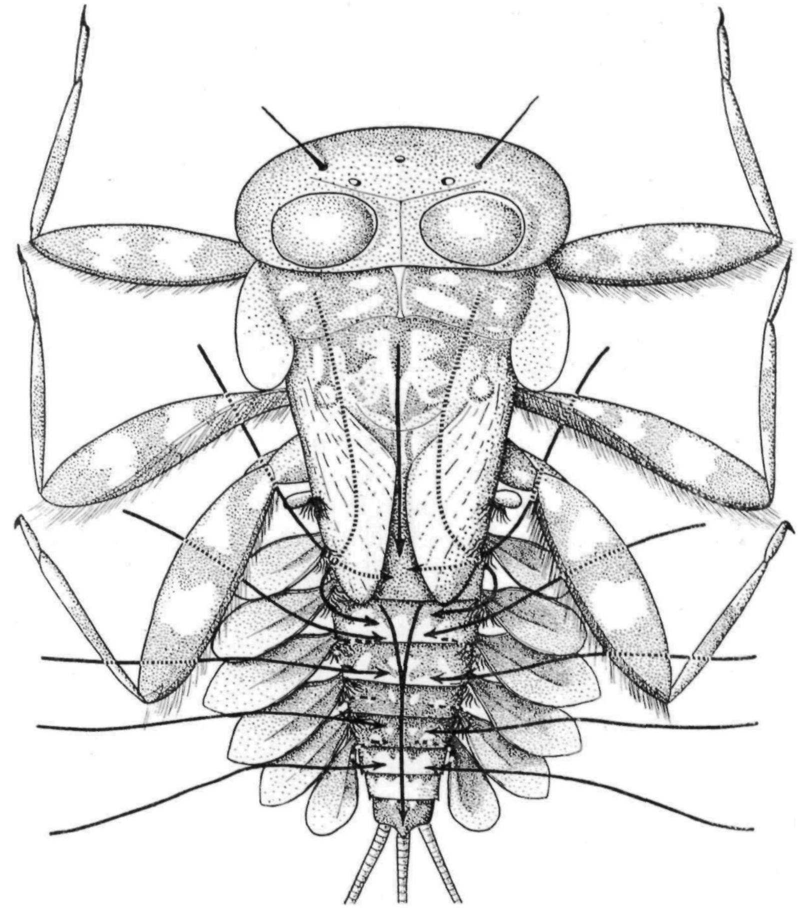

Fig. 2 A. Dorsal view of the nymph of *Ecdyonurus* in the attitude of rest, facing upstream.

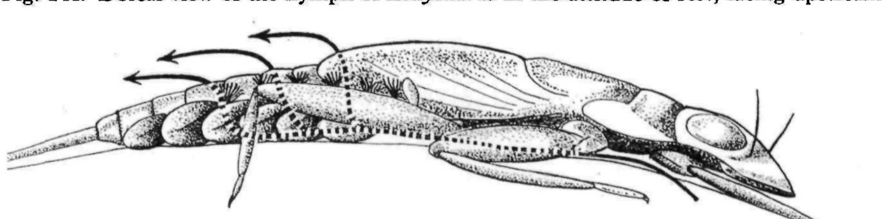

Fig. 2 B. Side view of same. The arrows indicate the currents produced by the gills in motion.

manner described, it follows that the resultant (Fig. 3 B) must be along a line directed upwards, backwards and inwards towards the body.

At the upper limit of this oscillation the gill pivots rapidly so as to bring the anterior concave surface into the leading position. So completely, however, is this pivoting effected that the lower anterior gill border is given the lead and this cuts through the water, the gill plate making little or no angle with its path of motion. In other words this, the recovery part of the oscillation, is performed as is the

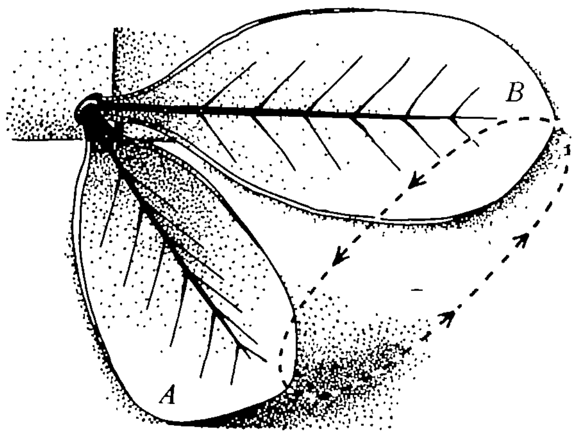

Fig. 3 A. A gill of the left side in the attitudes assumed at the extreme points of an oscillation as seen from the left side. *A*, the anterior limit; *B*, the posterior limit of the beat.

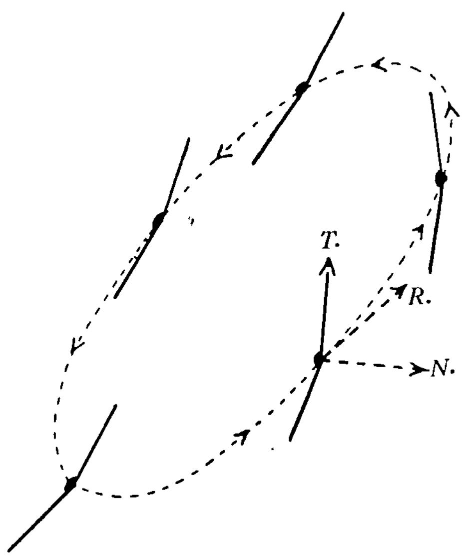

Fig. 3 B. The elliptical path of a gill of the left side as seen from behind. In the upward movement of the gill the posterior surface makes an increasing angle with its own path of motion. In the downward and outward movement the anterior gill border is in the leading position, so that the gill plate presents little or no obstacle to the water through which it is passing. *T*, *N*, *R*, forces tangential, normal and resultant respectively to the gill surface.

movement of an oar in feathering and offers no resistance to the water. That these facts explain the determination of recovery from effective parts of an oscillation is shown by the greater length of time which the latter takes by comparison with the former. The relation which these facts have to the actual direction of flow will now be clear. We have seen that the flow of water is from the sides and in front of the body towards the dorsal surface and to some extent backwards, and a consideration of the moving gill in its effective stroke has supplied us with an explanation for this directional flow.

A consideration of the gill on morphological grounds alone might lead to erroneous conclusions. Thus it is concave in front and convex behind. It might therefore be expected to oscillate in such a way as to scoop water in front of it by means of this concave surface. Along each border of the gill is a strengthening ridge of chitin which disappears in the distal third. This might be expected to cause a differentiation of the gill into proximal stiff and distal flexible regions. Indeed it is a simple matter to make a model of a gill in paper which illustrates the well-known principle of the ability of a concavo-convex membrane to bend more easily to the obverse concave than to the reverse convex surface. Such a model will serve well for paddling through water, for in meeting the water with the concave surface it will remain rigid, whereas when the convex surface meets the water it will bend against the resisting water. Thus effective and recovery strokes will be defined. If we were to rely on the application of mechanical principles to models such as these in order to explain the working of the gill we might conclude that the concave surface of the gill would have a leading position in the effective part of a stroke and the convex in recovery. But if the path of motion is as described above, the result of such an effective concave surface would be to drive water in a direction exactly the reverse of that which occurs. These points are deemed worthy of mention to show the serious error into which an investigator would fall were he to arrive at his conclusions as the result of the application of simple mechanical principles to the study of form alone.

Though the water-moving power of a single gill out of contact with its neighbours is appreciable, a much more powerful effect is obtained from the concerted action of two or more adjacent gills. This increase in efficiency, indicated by the more violent movements of particles in the water, is due not only to the fact that more gills are working, but because there is now operating the main principle of metachronal rhythm of gill plates in alignment with resulting alternation of suction and compression phases between them.

The metachronal rhythm in the gill movement of this species is characterized by the small time-phase difference between adjacent gills. So small is this difference that the gills appear to operate like the oars of an *almost* perfectly timed crew of oarsmen. But though the gills in series *appear* to work in phase with each other their out-of-phaseness is real and significant. Any gill commences its backward beat in advance of the one next behind it. The rotation of the anterior of these two brings the lower border of the anterior gill against the surface of the hinder one (Fig. 4), the two plates making an angle between them which is open above. Both these gills now are swinging round backwards to approach the body and as they do so the angle between them steadily decreases until the two plates lie flat against the body and against each other. Such water therefore as lay in the intergill space becomes first cut off from below then steadily squeezed out in an upward direction and inwards towards the body as the gills oscillate backwards. In the ensuing suction phase the anterior of two adjacent gills moves forwards first, so enlarging the intergill space. This, by the rotation of the forward moving gill plate, becomes widely open below and so suction is expressed as a flow into the intergill space from below. It is probably at this stage that water passes from the subabdominal region as well as from the more lateral regions towards the gills. It might be pointed out that compression coincides with the effective beat and suction with the recovery beat of each gill, a coincidence made possible by the small time-phase difference between gills in motion.

Since the gill tufts lie proximally in the intergill spaces, such water, the movements of which have been described, will irrigate them in a manner which is

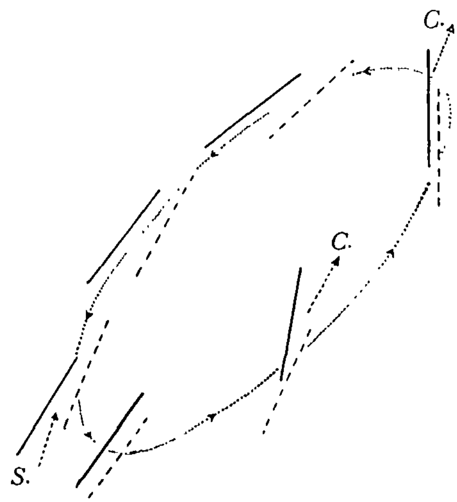

Fig. 4. The attitudes of two adjacent gills of the left side as viewed from behind through one complete oscillation. The anterior gill is indicated by plain, the posterior by dotted lines. Arrows indicate the elliptical path of motion and at *S*, the entrance of water to the intergill space during suction, at *C*, the exit of water from this space during compression.

obvious without further comment. The seventh gill of each side remains stationary at all times and forms a buffer against which the sixth gill can operate. When the sixth gill plate presses against it, water is passed over the sixth gill tuft. Perhaps the stationary habit and the absence of gill tuft for this gill are related to each other, there being no means for irrigating the gill tuft were it present.

It is convenient at this stage to compare the principles involved in the gill movements of *Ecdyonurus* with those already described in *Caenis* and *Leptophlebia* (Eastham, 1934, 1936).

Caenis seems to stand apart as a form producing a flow transverse to the body axis. The out-of-phase oscillations of members of a pair of gills are partly responsible for producing a transverse metachronal rhythm across each body segment. For purposes of the present paper the most important thing is the mechanism for determining the difference between effective and recovery strokes. In *Caenis* this mechanism depends on the elaborate fringe of branching filaments with which each moving gill is provided. The resemblance to the feather movements of a bird's wing in flight has been pointed out (Eastham, 1934). Longitudinal metachronal rhythm in gill movement was shown to be significant in assisting water flow by allowing of suction and compression phases alternately between the gills.

In *Leptophlebia*, because the gills operate at different angles with the body, metachronal rhythm plays no part in establishing suction and compression phases between the gills. Only between the two lamellae of individual gills does this principle appear to be of value. Each gill acts as a paddle for its own region and the necessity for properly defined recovery and effective beats is provided for by the rotation of the gill.

In *Ecdyonurus* a compromise may be said to have been made in so far as the perfect alignment of the gills in series enables the rapid antero-posterior rhythm to be effective in allowing of suction and compression between the gills, the turning movements of each gill at the same time causing it to behave as a paddle or oar in rowing. Recovery and effective parts of a complete oscillation are determined by the rotation of each gill. The flexibility of the distal third of each gill plate has not been observed to play any conspicuous part in determining the difference between recovery and effective parts of a beat.

Ecdyonurus inhabits the waters of rapidly flowing streams and that it presents features illustrative of the streamline principle was pointed out by Steinmann (1907, 1908), and though his account is in some details inaccurate the shape and attitude of body, as shown in Fig. 2, would indicate the correctness of his main thesis.

In its natural environment *Ecdyonurus* clings to the stones by means of strong claws on its widely straddled legs. Its head and cerci are held close to the substratum. The body is dorso-ventrally flattened and is broad and flat in front and narrow behind. Its head and prothorax are laterally extended into flat flanges which on occasion only leave the narrowest space between the body and the substratum and the inclination of the head is such as to direct the environmental current above the body rather than below it. The angles at which the legs are held are such as to enable the animal to keep close to the substratum and thus to present little obstacle to the water which flows over it. Each femur is as a broad flat blade, its posterior border fringed with long hairs and tilted upwards and backwards. Such a fringe of hair may be expected to sway with the water current passing over it and so afford considerable protection to the region behind it in the same way that tall grass growing at the top of a wall will bend with the wind streamline and set up a region of quiet, free from eddies on the lee side. The tibia and tarsal joints are, however, slender and non-setose and being in line with the stream flow offer no resistance to it. The gills lie in the angle between the body and the metafemora and are thus protected from the full force of the environmental current.

There is only a limited water space beneath the thorax, but in the abdominal region the sternum is raised to accommodate the downward projecting gills which, as already described, touch the substratum with their tips when at rest. Under the abdomen therefore there exists a substantial subabdominal water space. Contact between the sternum and the substratum as claimed by Steinmann never occurs.

It is suggested that such a region for reasons already given is one of comparative quiet, and it is from this and from the protected areas behind the hindlegs that the gills draw their water. At times the animal will be seen to raise its body from the substratum, its head and cerci being lifted. This attitude of standing "on its toes" is invariably a preliminary to swimming. In rapid gliding over stones, only the head and cerci are raised, the rest of the body remaining in close approximation to the substratum. Popovici-Baznosanu (1928), on the basis of faulty observations, such as that the cerci are raised at all times, and that the gills never touch the substratum, doubts the significance of the streamline principle here, but his inaccuracies tend to render his criticisms invalid. As pointed out by Hora (1929) the form of *Ecdyonurus* very properly adapts this animal to life in running water, and here is additional evidence in the same direction in that the gills work in a region which is protected from the brusque flow in which the animal lives, and in doing so are able to draw water from an area of comparative quiet. It seems possible also that the pivoting of the gill is thereby facilitated.

On the gills of *Caenis* have recently been described a large number of sense organs both campaniform and trichoid, which it is suggested are functionally related to the animal's ability to detect certain densities of suspended particles in water (Eastham, 1936). Sensillae of a similar kind are also found on the gill plates of *Ecdyonurus*. Both surfaces of each gill plate are provided with many campaniform sensillae, and while at the moment their structure has not been examined, enough can be made out from surface view to justify the assumption that they are like those on the gills of *Caenis*. One can only guess their significance and in the absence of experimental evidence, which is desirable, the suggestion is put forward that just as the sensillae of *Caenis* might enable the animal to detect changes in its surroundings as far as suspended particles are concerned, so *Ecdyonurus* may be enabled to detect disturbances in the water resulting in changes in rate of flow or in the amount of matter passing in suspension over the animal's body. It would appear from this that the bilamellate gill of *Ecdyonurus* shows a specialization of one lamella for mechanical and nervous purposes, the other being concerned entirely with respiratory exchange. In *Leptophlebia* both lamellae are alike and serve mechanical and respiratory purposes equally, while in *Caenis* all functions, mechanical, respiratory and nervous are combined in a single structure.

SUMMARY

1. The gills of the nymph of *Ecdyonurus* consist each of a gill plate and a proximal gill tuft. The gill plate of the first gill is reduced in size while the seventh gill possesses no gill tuft.

2. By movements of the gills, currents are set up in the water which are symmetrical with the body axis, and which pass from the sides of the body upwards to the mid-dorsal line and backwards.

Members of pairs beat synchronously and in phase with each other.

3. Each gill pivots on its pedicel and moving backwards and upwards, increases its angle of incidence with the water through which it passes. This phase is the

effective part of an oscillation and is brought about with the posterior gill surface in the leading position. The recovery beat is effected by the gill turning so as to place the anterior border in a leading position. The direction of flow is largely determined by these gill movements.

4. The gills beat in metachronal rhythm from before backwards, the time phase difference between adjacent gills being so small as to make the gills appear to work together and without rhythm. The rhythm, however, is important in setting up suction and compression phases, the compression phase occurring during backward effective movement, the suction during forward recovery movement. Compression expresses itself as a flow from between the gills upwards and backwards, suction as a flow into the intergill space from the sides and below.

5. The principles of gill movement in relation to water flow in *Caenis*, *Leptophlebia* and *Ecdyonurus* are compared.

6. The currents and gill movements in adaptation to environment are briefly discussed.

7. Campaniform sense organs occur on both surfaces of the gill plates and it is suggested that these are concerned with informing the animal of changes in the environmental flow of water.

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