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# *Metachronal Rhythms and Gill Movements of the Nymph of* Caenis horaria (*Ephemeroptera*) *in Relation to Water Flow.*

By L. E. S. Eastham, M.A., M.Sc., The Department of Zoology, the University of Sheffield.

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## *Introduction.*

The gills of some Ephemerid nymphs are always motionless, *e.g.*, many Bætine forms of English streams. In many others, however, the gills move rapidly in metachronal rhythm, by virtue of which currents are created in the water. These currents are peculiar to the species and probably have an adaptational significance. In many forms already under investigation, *e.g.*, *Chloen dipterum*, *Siphlurus* sp. *Ecdyonurus venosus*, *Ephemerella* sp. *Leptophlebia marginata* and *Ephemera vulgata*, a common feature is noticeable. This is that in their rhythmical movements both members of each pair of gills beat together, *i.e.*, and their movements are co-phasedly synchronized. Since, therefore, the effect of the gills on one side of the body is exactly duplicated on the other, whatever may be the precise mechanism for the production of currents, the latter are symmetrical with the longitudinal axis of the body (Eastham, 1932).

An interesting exception is the nymph of *Caenis horaria*. In this animal the currents pass over the body from one side to the other. The gills beat in metachronal rhythm down each side of the body, but though the rhythms are synchronous there is a time phase difference between them. In other words, members of a pair are not co-phasedly synchronized in movement. We have thus in *Caenis horaria* a bi-laterally symmetrical animal producing movements in the surrounding medium which are not of the nature of an axial flow. It is with this phenomenon that this paper deals.

## *Methods.*

The currents produced in water by the movement of the gills are easily determined by observing fine particles in suspension. Suspensions of fine mud serve quite well for this purpose as also do cultures of Ciliate Protozoa. The latter have an advantage over non-living suspensions since they do not come to rest. Ordinary microscopic methods served for observing currents. Metachronal movements of the gills in relation to the latter were examined by means of a stroboscope. This instrument, fashioned on the lines described by Gray (1930), consists of a perforated disc rotated by an electric motor the speed of which is regulated by a variable resistance. An electric light is mounted behind the disc and the whole is enclosed in a wooden box firmly screwed to the bench.

The gills lie flat over the back of the animal so making observation in dorsal view by transmitted light almost impossible. Direct illumination from the stroboscope in a dark room gave better results, though still more satisfactory views were obtained by observing the animals in side view by transmitted light. For this purpose the nymphs were fixed on their sides between small glass plates. Fine entomological pins, inserted through the wing covers and bent at appropriate angles served well for holding the nymphs under observation in different attitudes. In this way a clear picture was obtained of all aspects of the gills in slow motion. The gills are easily detached from the body and thus various combinations of gills in action could be observed after removal of the others. Comparison was then possible with the effects produced by the complete set of gills. To avoid the possible ill-effects associated with mutilation a fine needle was also employed to hold certain gills motionless while observations were made on the remainder which were free to move.

The frequency of gill oscillation was measured by means of a speedometer fixed to the motor spindle. The speed of the stroboscope disc (the frequency of illumination) was then adjusted until the gills appeared to be motionless, frequency of oscillation and of illumination being then identical.

To observe the gills in slow motion the motor was speeded up to a rate beyond that of the oscillating gills. It was then gradually slowed down until the gills appeared to be perfectly still. A further slight reduction in the frequency of illumination then gave a clear slow-motion picture of the gills, their apparent direction of motion under these conditions being the same as their actual motion.

With the stroboscope operating under these conditions it often happens that the frequency of oscillation falls below the light frequency. The gills then appear to be rising when they are actually falling and *vice versa*. Unless this is recognized the observer runs the risk of jumping to strange conclusions as to the mechanism involved in current production. Every care was taken in this work to avoid the pitfalls coincident with the phenomenon of stroboscopic reversal (Gray, 1930).

*The Gills.*

The nymph of *Caenis* possesses six pairs of gills on the first six segments of the abdomen. The first pair are slender, immobile, tactile processes attached to the postero-lateral angles of the first segment. The second pair similarly attached to the next segment have the form of sub-quadrangular plates resembling the elytra of certain adult insects. I shall refer to these as the

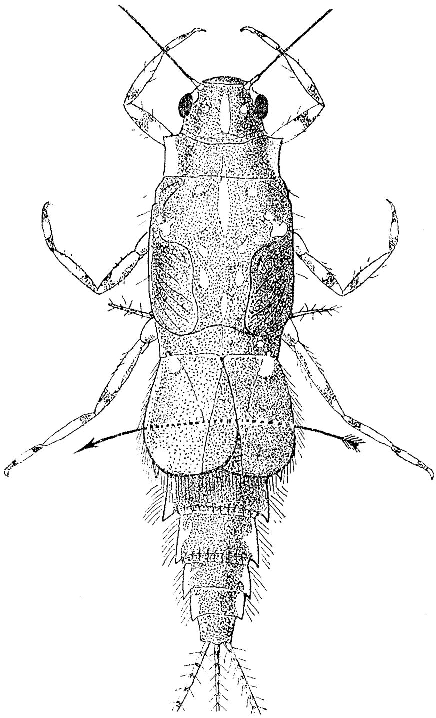


Fig. 1.—The nymph of *Caenis horaria* to show the current passing under the pseudo-elytra from one side of the body to the other. The first pair of gills are represented as a setose process projecting at each side.

pseudo-elytra. When at rest they overlap slightly in the middle line of the body and extend posteriorly so as to cover the gills of the next succeeding four abdominal segments. They can be raised to a stationary position at an angle of about 30° to 40° with the body surface while the remaining four pairs of gills oscillate beneath them. The pseudo-elytra never oscillate, and doubtless their main function is protective and to a lesser extent respiratory.

The four pairs of gills behind them, which in this paper will be referred to as Nos. 1, 2, 3, and 4, are similar to each other except in size, fig. 2. Each consists of a somewhat semicircular plate slightly concave below and convex above, and articulated to the posterior angle of its segment by a narrow stalk. The gill, fig. 3, when at rest lies nearly flat on the body with its straighter border towards the front. Each overlaps the next one behind it. Passing through the gill-plate is a rich system of branching tracheæ, the fine ends of which pass into numerous fine filaments with which the gill is fringed. The distal marginal filaments on the gill are longest. The proximal ones are short and a small part of the proximal anterior border is fringeless. Except for the shortest proximal ones the marginal filaments are branched—the longer the

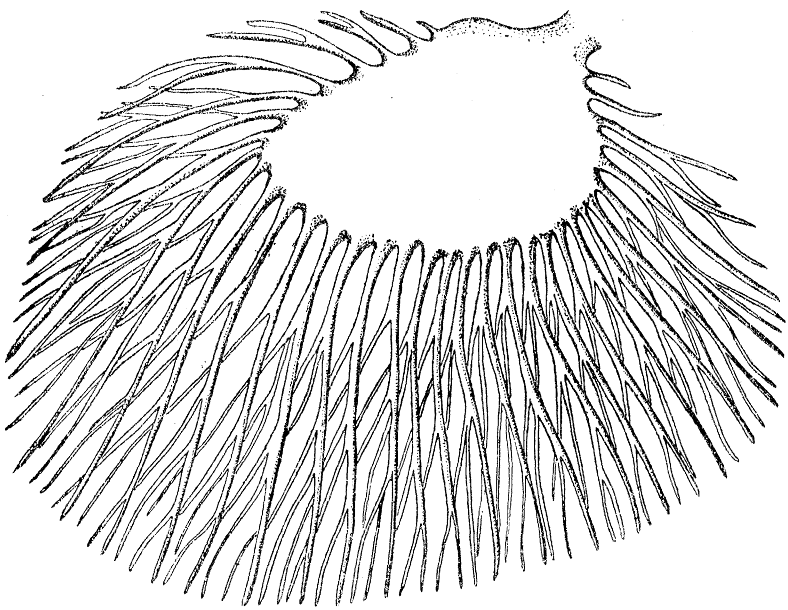


Fig. 2.—Dorsal view of the 1st oscillating gill (morphological 3rd) of the right side. Note the branches of the marginal filaments.

filament the more branched is it. Such branches invariably pass ventrally to neighbouring main filaments in regular arrangement as shown in fig. 2.

The members of any pair of gills are normally equal in size, but any gill is greater than the one next behind it. This difference of size is of such an order that the posterior marginal filaments of one gill extend nearly as far back as do those of the one next behind it. In the resting position the distal borders of a pair of gills nearly meet in the middle line, the marginal fringe of one overlapping that of the other. Each gill of the right side overlaps its fellow of the other at a particular moment. At other times the reverse condition applies. An individual can and does change the arrangement of its gills in this respect.

*Water Currents caused by the Gills.*

The main current is observed to enter the space beneath the pseudo-elytra at one side and pass out at the other, fig. 1. The direction of this lateral flow may be from either side to the other. If the pseudo-elytra be removed no appreciable difference in the current is observed, either in direction or strength. Small eddies from the sides of the thorax pass backwards and join the main transverse flow. A current, so weak as at most times to escape detection, passes from before backwards along the distal edges of the gills. This probably occurs when the pseudo-elytra are present, but owing to the opacity of these organs this cannot be determined. It may, I think, be safely assumed that the pseudo-elytra are not concerned with any directional effect on the current.

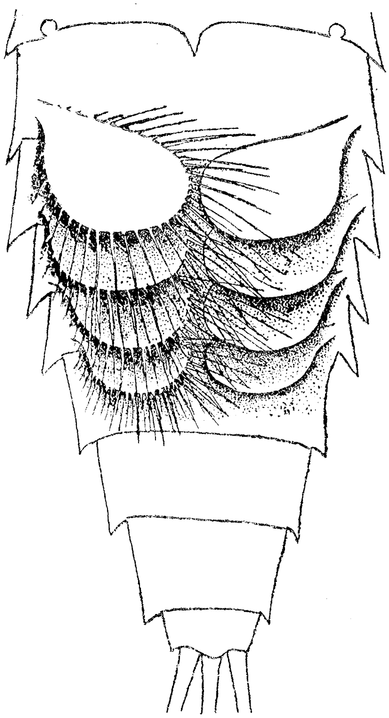


Fig. 3.—View of four pairs of gills at rest after removal of the pseudo-elytra. The filaments of those of the left side only are shown in very simplified form.

The flow of water is not continuous but pulsating, the pulsations coinciding with the gill oscillations. In this pulsating flow each thrust in the main direction is preceded by a shorter and less pronounced movement in the opposite direction. An individual can reverse its current. Reversal of flow is always preceded by a momentary stoppage during which the gills are rearranged in a manner to which I shall refer later.

From time to time the nymphs of *Caenis* swim by means of slow undulations of the abdomen. During progress the gills are commonly in motion. The effect of the oscillating gills on the water is the same as when the animal is stationary. Instead, however, of moving the water over its body the body is made to roll over sideways in a direction opposite to that in which the water is made to move. Thus in addition to the forward propulsion of the animal produced by abdominal undulations there is a body spin imparted by the oscillating gills. That this is due to the gills can be readily shown by their removal, when the animal swims dorsal side up. The spin imparted to the body described above is of some advantage to the animal. As *Caenis* swims upwards it finds itself with its feet uppermost and within reach of the surface film. To the latter it clings with its claws and hanging therefrom, it proceeds for some time to pass the clear surface water over its gills. Thus by means of a strange acrobatic feat the animal can at any time and for an indefinite period explore the more oxygenated water of its environment.

### *Gill Movement.*

When the pseudo-elytra are raised, the four pairs of gills behind and beneath them begin to oscillate. There is some slight variation in the speed of movement. Readings taken on a number of individuals gave an average of 8·5 oscillations per second. At times the rate falls to about 7 per second and in individuals becoming exhausted through removal of some of their gills it may fall so low as to make stroboscopic vision impossible (Gray, 1930). Removal of the pseudo-elytra is necessary before the gill movement can be properly seen. From the resting position each gill is raised on its stalk to an angle of about 45° with the body surface. In rising, the marginal filaments lag behind the gill plate so increasing the concavity of the undersurface. At the same time the branches of the longer filaments lag behind the latter so as to lie directly beneath and in line with them, fig. 4. On the return stroke a distinct thrust is noticeable. The flexed filaments straighten out and their branches return to their normal position, *i.e.*, so as to cross obliquely under the main filaments adjacent to them, fig. 4.

In addition to the rise and fall in periodic motion as here described, each gill pivots on its stalk in both up and down movements. The pivoting causes (i) the gill to face to one side in the upstroke and to the other in the downstroke ; (ii) the gill to traverse an elliptical path in its upward and downward movement, figs. 6 and 9.

Thus with flow from right to left the underside of each gill turns to the right in its upward beat and to the left in its downward beat. With such a current each gill passes upwards to the right-hand side of its vertical axis of motion and downwards to the left-hand side of it, fig. 6A.

With a current in the opposite direction the underside of the gill faces left on its upward and right on its downward beat. On rising, each gill moves in a half ellipse to the left of its vertical axis of motion and in falling completes its elliptical path by passing to the right of this axis, figs. 5 and 6B. That these phenomena have an important effect in determining the direction of flow will easily be realized.

Metachronal rhythm in the movement of the gills is evident as soon as the pseudo-elytra are removed. Only by means of the stroboscope, however, can such details as the phase difference between adjacent gills be determined. Since the gills overlap each other from before backwards, a view from the side or from the middle line of the body is most convenient for seeing the rhythm

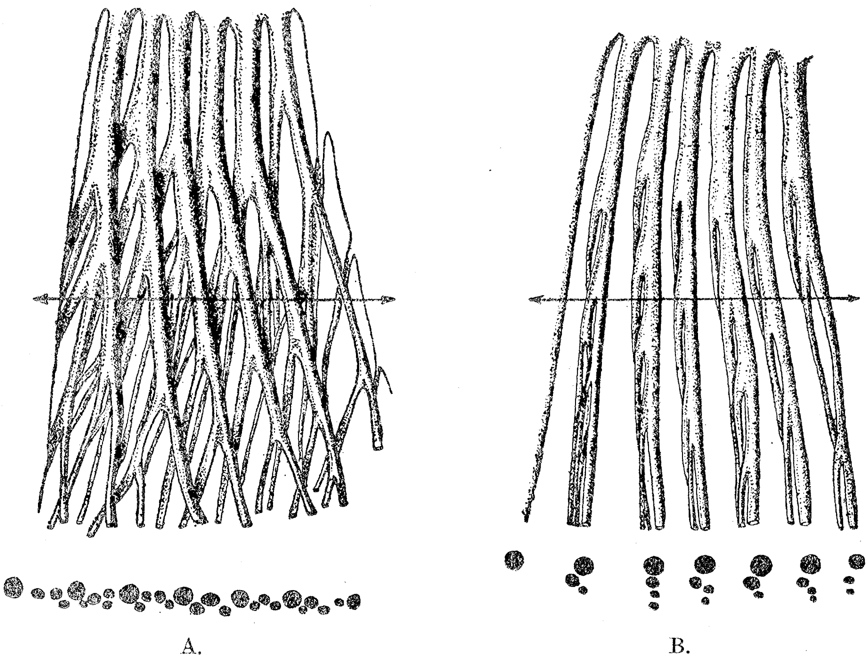



Fig. 4.—Dorsal view of a portion of the marginal fringe of gill shown in fig. 1. A, in the position assumed during the effective downstroke; B, in the upstroke attitude. Beneath each figure is shown the arrangement of filaments as seen in transverse section across the fringe along the line drawn across.

along a longitudinal series of gills. The phase difference between two adjacent gills is then seen to be one-third of a complete oscillation. Further, any gill has a leading phase relation to the one next behind it. Thus the first gill performs one-third of a complete oscillation, *i.e.*, passes through two-thirds of its upward stroke before the second gill of its own side begins its upward stroke. It follows from this that the rhythm is from before backwards and that the first and fourth gills of the same side are in the same phase of movement. The latter fact can be easily verified by watching the first and fourth gills after Nos. 2 and 3 have been removed. The above order of phase difference between the gills in motion is not absolute. Certain individuals had a rhythm in which the phase difference between gills in motion was such as to put the first and fourth out of phase with each other. Such variations are, however, of little moment. No form was found to have any but an antero-posterior rhythm. It is worthy of note that in all Arthropods examined by Cannon (1928), the rhythm of their limb movement was in the opposite direction.

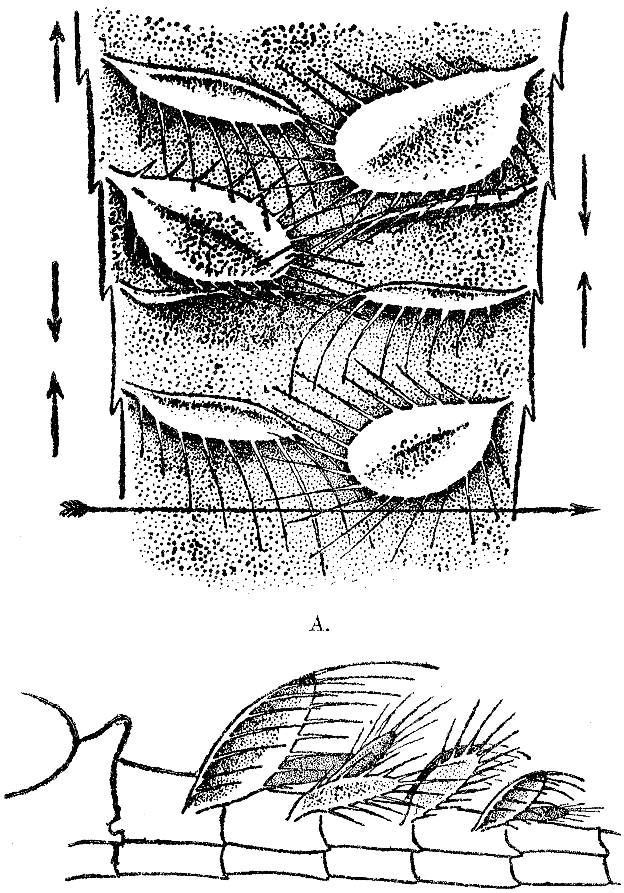
The above facts were obtained first by using animals with all the gills intact, and later they were verified on animals from which the gills of one side had been removed. By this means a single row of gills could be observed from both lateral and median aspects of the body.

Though the gill movements are synchronous throughout, there is clearly a time phase difference between the rhythms passing along the two lateral rows of gills. The members of pairs are not co-phasedly synchronized in movement. Between members of pairs the phase difference is one-third of a complete oscillation, *i.e.*, a difference of the same order as that which exists between adjacent gills in a longitudinal series, fig. 5.

In addition, therefore, to the metachronal rhythm along the gills down each side of the body there is a second rhythm passing transversely over each of the four gill-bearing segments involving in each segment two elements, the members of a pair.

The transverse rhythm is reversible. At one time the left gill of each pair may have a leading phase relation to its fellow of the opposite side. In such animals it is found that each left gill underlies by its filaments the right gill of its own segment in the middle line of the body. Such an arrangement is invariably accompanied by a flow from the left side of the body to the right, fig. 5. At another time the right gill of each pair underlies, and has a leading phase relation to, its fellow of the left side. With this arrangement the current produced passes from right to left. It has been observed that the gills come to rest momentarily at intervals of from 30 to 60 seconds and a change in direction of flow often follows. Reversal in the transverse rhythm as described above does not involve a change in the axial rhythms themselves. The relation of one axial rhythm to the other alone is changed.

Since it is easy with the stroboscope to obtain an impression of *apparent* reversal of rhythm which is not *real*, it ought to be pointed out that every precaution was taken to avoid this error. When a view of the gills " in reverse " is obtained one sees a gill appearing to move down while in the attitude actually assumed by the gill in its upstroke. It has been pointed out that on the actual upstroke the filaments lag behind the gill plate whereas on the downstroke they straighten out. If through a too high frequency of illumination the phenomenon of stroboscopic reversal is obtained, the gills will continue to rise and fall in periodic motion. On the *apparent* upstroke, however, the



A.

B.

FIG. 5.—A, simplified diagram of the gills in motion as seen from above when producing a current from left to right. The arrows at the sides indicate the particular movements being performed by the gills next to them. Note that right and left series are out of phase with each other and that each right-hand gill overlaps its fellow of the left side by means of its filaments. B, diagram of a lateral view of the gills shown in fig. A. In producing the flow from left to right each gill turns its lower surface to the left in rising (see left gills 1 and 4) and to the right in falling (see left gill 3).

filaments will be outstretched and on the *apparent* downstroke they will be flexed downwards. Also under such conditions, since the gills appear to be moving up when they are actually moving down the phase relations between adjacent gills will *appear* to be reversed. Gill movement is under nervous control and the rate of oscillation may change while observations are being made. Thus if the frequency of illumination has been fixed to give a slow motion picture of actual movement, a slight lowering in the rate of gill oscillation may produce a picture of the gills in stroboscopically reversed movement and with reversed rhythm. A lower frequency of illumination will remedy this, provided that the effect of "flicker" does not necessitate too great a reduction in the intensity of light (Gray, 1930).

### *The Form of the Gill in Relation to Flow.*

Before considering the phenomena of metachronal rhythm in relation to flow let us first discuss the possible mechanism whereby the gills cause their local flow.

An important characteristic of the gill is its marginal fringe. This I consider forms a bounding surface liable to prevent wasteful eddies. It is well known that a wall, topped with stiff grass, will, to a person sitting behind it, afford more shelter than one without such a fringe. This is because the grass can sway with the stream line of the wind, and the eddies which would otherwise be set up on the leeward side of the wall are largely diminished. The gill fringe will act similarly in preventing eddies round the gill border. That it does so may be inferred from the weakness of the axial current which passes backwards along the gill edges (p. 34).

A second function may be attributed to the gill fringe—a function depending on the difference in its behaviour in up and downstrokes. The marginal fringe is so thick and the spaces between them so small as to offer considerable resistance to water flow between them. When the filament branches lie across their neighbours a close meshwork is formed round the gill plate which is probably for all ordinary purposes impervious to water. It is when the gill is in this position, fig. 4A, that it makes its effective beat downwards, thrusting the water from the inter-gill space between the falling gill and the one next behind it. On the upstroke, however, the filaments become flexed and their branches lagging behind, take up a position beneath and in line with the main filaments to which they belong, fig. 4B. Thus in the upstroke when the inter-gill space (between the rising gill and the one next behind it) is filling with water, there may be expected an inflow between the filaments from above. Fig. 4 represents diagrammatically surface and sectional views of the filamentar region in up and downstrokes, Each gill therefore has a form which, like the feathers on a bird's wing, makes an impervious vane on the effective beat and a pervious vane on recovery. The different resistance of water offered to the gill in the two halves of a complete oscillation is accentuated by the curvature of the gill plate itself. In rising the upper convex surface will allow water to slide over it easily as air does over the bird's wing in its upstroke. On falling, however, the concave surface meets the water and the maximum resistance is encountered. This is the effective stroke thrusting the water away.

In connection with the above, the following measurements are of some interest. The distances between neighbouring filaments of a gill under the conditions of upward and downward movement were measured. The spaces between adjacent filaments during the upstroke vary from 0·013 mm. proximally to 0·03 mm. distally. The distance apart of the filament branches forming the meshwork during the downstroke is about 0·007 mm.

### *Gill Movement in Relation to Flow.*

Since both axial and transverse rhythms exist the effects of both should be apparent, yet the transverse flow predominates. Even when the gills of one side only are present the flow is still to the side. We are justified, therefore, in concluding that whatever be the causes of transverse flow, the transverse rhythm is not the only factor. An analysis of the action of a single gill is obviously called for.

It was at first thought that the clue to the situation lay in the fact that the gill possessed a fringe of filaments of varying length along its border. The parts where the fringe is longest might be regarded as places where the viscous resistance to water flow is greater than the places where the fringe is shorter. On this theory a flow with a unidirectional component from the middle line of the body (longest fringe region) to the side (short fringe region) might be expected. To test this idea the delicate operation of cutting away the fringe from all the gills was performed and no difference in direction of flow was noticed. The flow was, of course, weaker, the effective area of each gill having been reduced by the operation. It follows from this that the fringe is not responsible in any marked fashion for the side flow in the manner suggested.

I have already referred to the fact that in addition to periodic up and down motion the gill executes a pivoting movement. Let us consider the gill as a flat plate oscillating in the manner described, and in relation to a lateral flow caused thereby. In fig. 6 the line XY represents the axis of water flow in the direction of the arrows, and the dotted ellipse, the path traversed by the gill. The attitudes of the gill in different parts of its path are indicated by the firm lines.

It is clear that the gill is moving at an angle with its own path of motion. Further, this angle varies as the gill performs a complete oscillation. $\theta$ is the angle between the gill surface and the vertical axis of motion, this being at right angles to the axis of flow. This angle is least when the gill is crossing the axis of flow and greatest when it is farthest away from it.

Such a set of circumstances are comparable with those described in the movements of fish by Gray (1933, *a*, *b*, and *c*). The gill of *Caenis* is related in its vertical movement to the axis of flow (across the body) in the same way as the tail of a fish is related to its own longitudinal axis of motion. Gray has shown that the net effect of moving a segment of the fish's body through the water at an angle to its own direction of motion is to impress on the body two forces, tangential and normal, the resultant of which represents the net propulsive thrust which drives the body against the resistance of the water.

With *Caenis* the animal is stationary and the forces generated are expended in producing a flow of water across the body. According to Gray, as the angle $\theta$ decreases, the thrust effected on the water increases and *vice versa.* In other words, the greatest thrust is effected when the body segment of the fish crosses its longitudinal axis of motion. The greater efficiency of propulsion at this point also depends on the greater velocity of the body at the time when the longitudinal axis is being crossed. That the velocity of the gill varies in a similar manner I have observed, though only the employment of cinematographic methods would enable me to analyse it quantitatively. We thus have an interesting parallel in the forces involved in fish body movement and in insect gill movement. Both are operating on the " screw " principle (Gray, 1933, *a*, *b*, *c*) the fish performing a figure of eight, the gill an ellipse in each oscillation.

In the simplified system just described the gill would be expected to thrust water to the side equally in both up and downstrokes. That it does not do so will at once be understood when it is remembered that (i) the upper surface of the gill is convex and the lower, concave ; (ii) the marginal filaments are flexed during the upstroke ; (iii) the filament branches behave in the upstroke in such a way as to allow water to pass between them.

These facts introduce a feature of additional interest in that the principle of the oar in rowing is involved as well as that of the screw.

We may suppose that the description given here applies to any single gill of the left side and concerned with producing a flow from right to left, fig. 6A.

Its fellow of the right side would perform exactly the same movements. It would turn its undersurface to the right on the upward stroke and to the left on the downward beat. Also it would traverse an elliptical path in its vertical movement passing to the right of its median vertical axis of movement as it rises and to the left of this axis as it falls. Since one gill of a pair, however, is out of phase with its fellow, one gill would be in advance of the other in its action. Thus the effect of a gill, say, the right in a flow from right to left, is reinforced by the effect of the left gill, the latter being one-third of a complete oscillation behind the former.

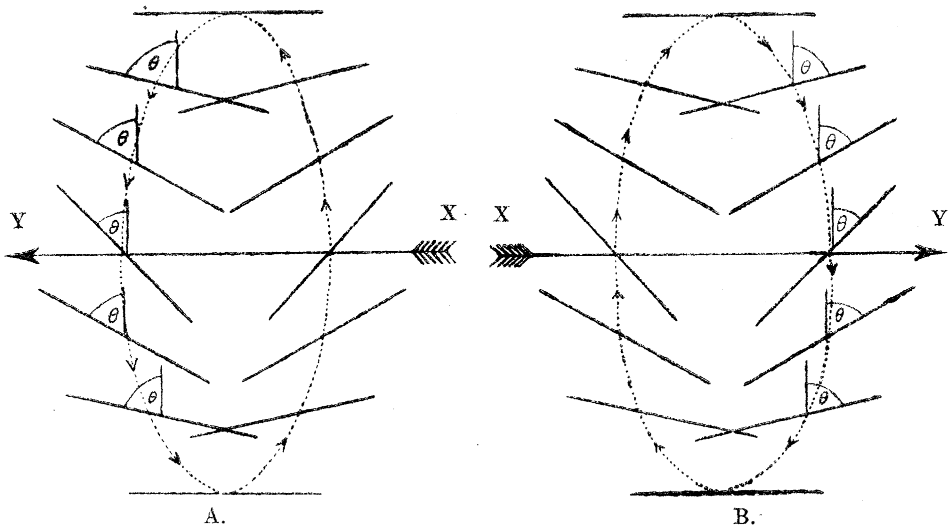



FIG. 6.—Diagram to show the elliptical path traversed by a gill in periodic up and down motion and the changing angle of the gill to its own path of motion. The arrows on the dotted ellipse indicate the actual path of motion ; in A, of any gill concerned with a flow from right to left ; in B, of any gill concerned with a flow from left to right. θ is the angle between the gill and a line at right angles to the main axis of flow indicated by the large arrow.

Considering further an animal with only the first pair of gills intact : if one of these gills is held still by means of a fine needle, the current for reasons given above still flows to the side. The same flow persists if the fixed gill be allowed to oscillate and the other one is held still. Now if this same pair of gills changes the direction of the current in the water, we find again that either gill is capable of producing a lateral flow in the new direction. Thus a single gill can produce a flow in either direction.

Proceeding then from our description of a single gill producing a flow from right to left ; if this flow is reversed the path traversed is the reverse of that already described, fig. 6B; and the pivoting movements will take place in the opposite manner. Should both members of a pair be present we would again find one gill, viz., the right, reinforcing the effect produced by the left which precedes it in its oscillation.

Let us now consider the gills in one linear series. If from a complete individual producing, for example, a current from right to left, the gills of the right side be removed, the current usually continues to flow from right to left. The

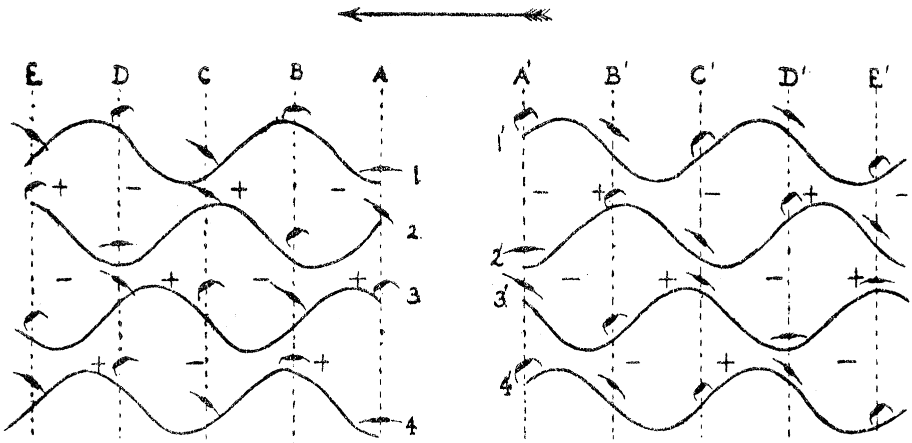



FIG. 7.—Sine curves 1, 2, 3, 4 (for the left) and 1′, 2′, 3′, 4′ (for the right) showing oscillatory movements of all the gills in producing a flow from right to left. The curves are drawn to read from the middle line, those for the left gills towards the left, those for the right towards the right side. The period of time involved in the movements indicated has been divided into four equal intervals ending at the dotted lines B, C, D, E, respectively for the left gills and at B¹, C¹, D¹, E¹, respectively for the right gills. Between adjacent gills periods of compression are marked by the sign +, and of suction by the sign —. The attitudes of the gills are given in the small figures above each curve. In falling the lower surface of each is turned to the *left* and the filaments are outstretched; in rising the lower side of each faces *right* and the filaments are flexed (see figures over curve I under B′ and A′ respectively). Positions of gills of one side correspond with those of the other under the same letter, A with A′, B with B′, C with C′, and so on.

gills producing this flow move in metachronal rhythm from before backwards. They all exhibit the same type of pivoting movement, therefore the effect of any gill is reinforced by that of the gill behind it. But because of the rhythm. forces of suction and compression are exerted on the water in the inter-gill spaces. In fig. 7 by means of sine curves the oscillatory movements of the gills in this rhythm are shown on the left of the middle line. Reference to this figure indicates that a phase when gills 1 and 2 move apart (suction), is followed by a phase when they approach each other (compression). When gills 1 and 2 are beginning a suction phase, Nos. 2 and 3 are in compression, and gills 3 and 4 are coming to the end of a suction phase. Periods of suction and compression alternate with each other down the series on the principle expounded by Cannon (1928), for the Crustacean *Chirocephalus*. That the forces invoked in these phenomena are significant in moving water is patent. We must conclude, however, from the capacity of a single gill to cause a side flow, that the effects that might be expected from rhythmical alternations of suction and compression between non-pivoting plates, are changed when the pivoting factor is introduced, the result being a side flow.

It has generally been found that an animal from which the gills of one side have been removed will continue for some time to deliver water to that side which retains its gills. This was so commonly noticed that it was at first wrongly thought to be the rule. A current in the reverse direction can, however, occur. If such an animal with a current flowing away to the side on which the gills are retained be fixed on its mutilated side, and a thick suspension of fine mud particles be introduced towards this latter side the current often reverses and flows against the proffered mud suspension. This reversal is accompanied by a reversal in the nature of the pivoting movement. No change of rhythm occurs.

Therefore, with one linear series of gills several principles are involved in current production (i) that which depends on the behaviour of the gill fringe in up and down movement—the bird's wing principle; (ii) the principle of the "screw"; (iii) the capacity of the gill to reverse this screw action by reversal of pivoting; (iv) that which concerns the alternation of suction and compression between the gills, caused by the metachronal rhythm.

The remarks made on the gills in one linear series apply equally to the gills in the linear series of the other side, see fig. 8 on the right.

There remains to consider the metachronal rhythms and gill movements when the gills of both sides are present. We have already seen, in considering the gill action in relation to the screw principle, that the effect of any gill is to reinforce the effect of its fellow—the result being a flow to one side. It may be that this is the only principle involved. There appears, however, to be the possibility of an additional factor.

Let us consider a single pair of gills, say the first, producing a flow from right to left. A point of some importance is the fact that the right gill, by means of its filaments, underlies the left in this case. Also, the phase difference between them in movement is such that the right has a leading phase relation to the left, of one-third of a complete oscillation. Since the right gill moves in advance of the left and underlies it by its filaments it is perhaps not unduly simplifying the case to think of the gills of a pair as being applied to each other so as to form a continuous membrane. This almost continuous unit may then be said to undergo a peristaltic wave from right to left. An initial suction phase on the right is followed by a suction phase on the left, a compression phase on the right having meanwhile come into existence. Thus on account

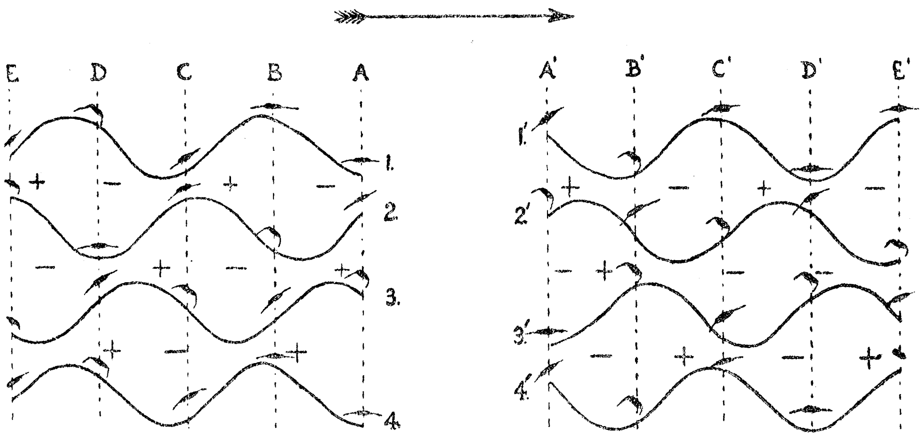



FIG. 8.—Sine curves 1, 2, 3, 4 (for the left) and 1′, 2′, 3′, 4′ (for the right) showing the oscillatory movements of all the gills in producing a flow from left to right. The curves are drawn to read from the middle line, those for the left gills towards the left, those for the right towards the right side. The period of time involved in the movements indicated has been divided into four equal intervals ending at the dotted lines B, C, D, E, respectively for the left gills, and at B′, C′, D′, E′, respectively for the right gills. Between adjacent gills periods of compression are marked by a + sign, and of suction by a — sign. The attitudes of the gills are given in the small figures above each curve. In falling the lower surface of each is turned to the *right* and the filaments are outstretched; in rising the lower side of each faces *left* and the filaments are flexed (see figures over curve 1 under A′ and B′ respectively). Positions of gills of one side correspond with those of the other under the same letter, A with A′, B with B′, and so on.

of the nature of the rhythm across a pair of gills, suction and compression alternate across the two members of a pair so as to cause a current in line with the rhythm, *i.e.*, across the body segment. If the gills rose and fell in simple periodic motion in such a rhythm without pivoting, a peristalsis of this kind would cause a cross flow. We have already seen, however, that for a flow from right to left, both gills of a pair turn to the right in the upstroke and to the left on the downstroke, a movement which of itself can account for lateral flow. It would appear, therefore, that with a single pair of gills in action, peristalsis and pivoting are complementary factors in the production of a flow of water across the body. The fact that the water enters a sub-gill space by passing between the gill filaments during the upstroke of the gill introduces a factor which does not seem seriously to affect the principles described above. When a single pair of gills with a current from right to left effects a reversal of flow, the gills come to rest momentarily. The originally underlying right gill now assumes an overlying position with regard to its fellow and at the same time the left gill assumes a leading phase relation to the right one. Further, the pivoting action which under the conditions of the first current was directed

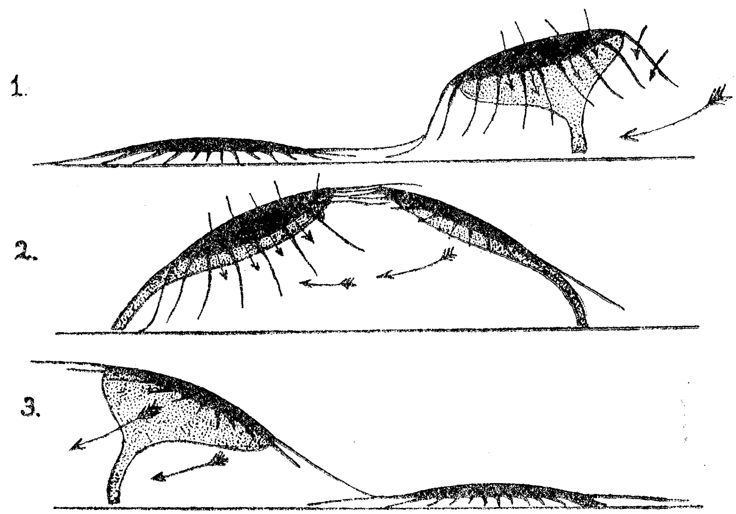



FIG. 9.—Diagram of a posterior view of a pair of gills in three successive phases of movement, 1, 2, and 3, producing a flow from right to left. The arrows indicate the direction of flow. In 1, the right and in 2, the left gill is rising. In 2, the right and in 3, the left gill is falling. It should be noted that the left gill overlaps the right, that the right gill is one-third of complete oscillation in advance of the left and that the pivoting movements of right and left gills are practically identical.

to the left side of the body is now reversed and directed to the right. Fig. 9 indicates diagrammatically the possible effect of peristalsis across a pair of gills where three successive phases of movement are shown.

Let us now consider the first pair of gills in relation to those behind them. Since the axial rhythm is from before backwards the transverse rhythm across any segment must occur, in point of time, a little before that over the segment behind it. This being so, the flow over the body across a segment is reinforced by that over the one behind it. An examination of fig. 7, where oscillatory movements of the gills are shown by sine curves and the pivoting movements by the small sketches appended above each curve, will dispense with any lengthy explanation. In a flow from right to left the compression phase between gills 1 and 2 of the right side occurs during the suction phase of the left. In other words, the space between gills 1 and 2 of the left side is widening to receive water which can be forced into it by the compression phase between the right-hand gills. Add to this the fact that the gills are pivoting so as to assist this directional flow and the transverse flow where two adjacent pairs of gills are involved will be understood.

What applies to the first inter-gill space will apply equally well to the inter-gill spaces between gills 2 and 3 and gills 3 and 4.

The same principles will also hold for a current passing in the opposite direction; transverse rhythm, overlapping relations between members of pairs, and pivoting being of the opposite order to those described above, fig. 8. Actual reversal is always accompanied by changes in rhythm, overlapping and pivoting.

I have pleasure in thanking Dr. J. Gray, F.R.S., for the loan of a stroboscope during the early part of the work and for much helpful advice on its use. To Mr. K. G. Blair I am indebted for identifying the adult insects on emergence, and to Dr. C. G. Lamb for helpful discussion during the progress of the work.

*Summary.*

(1) The nymph of *Caenis*, by means of the oscillatory movements of four pairs of gills, produces a flow of water across the body from one side to the other. The current so produced is reversible.

(2) The gills rise and fall in periodic motion traversing an elliptical path, and make, by a pivoting action, an angle with their own path of motion. The metachronal rhythm in the movements of gills along each side of the body is from before backwards, but the gills of one side when in motion are always out of phase with those of the other. A transverse rhythm therefore exists across each pair of gills, this rhythm being in the direction of the water flow across the body. The transverse rhythm is reversed when the direction of the water current is reversed.

(3) The following factors are significant in determining transverse flow :—

(*a*) The filamentar fringe along the edge of each gill behaves differently in the upward and downward parts of each oscillation. Water passes between the filaments to the sub-gill space during each upstroke. In each downstroke

the filaments, by lying across each other, form a close mesh which by virtue of the smallness of its pores may be regarded as a membrane impervious to water. The gill is thereby rendered more efficient for moving water in the downward part of an oscillation than in the upward beat.

(*b*) Each gill turns its undersurface against the direction of flow in the upstroke and with the direction of flow in its downstroke. The principle of the screw involved, by virtue of the fact that the gill is inclined at an angle to its own direction of motion, is sufficient in itself to account for a flow across the body. A single gill can and does produce such a flow, and by its capacity to reverse the nature of its pivoting movements is able to cause a flow from right to left or from left to right.

(*c*) Since the gills act as plates moving in metachronal rhythm from before backwards, the alternating periods of suction and compression passing along any series of gills are significant in causing water movement.

(*d*) Any pair of gills by means of their filaments overlap, the one over the other in the middle line of the body. Upward movement of the underlying one begins first, and the transverse rhythm passing over them acts as a peristaltic wave driving water across. The effect of such a peristaltic wave over any segment is reinforced by that over the segment next behind it because of the metachronal rhythm which passes over the longitudinal series of gills from before backwards.

(4) Reversal of flow is associated with changes in (i) the method of pivoting of the gills ; (ii) their manner of overlapping as members of pairs ; and (iii) the direction of the transverse rhythm over the gills.

The axial rhythms never change individually, but the relation of the axial rhythm of one side changes with respect to the axial rhythm of the other thus causing a reversal of the transverse rhythms involving gills forming segmental pairs.

## REFERENCES.


Cannon, H. G. (1928). 'Trans. Roy. Soc. Edin.,' vol. 55, p. 807.

Eastham, L. E. S. (1932). 'Nature,' vol. 130, p. 58.

Gray, J. (1930). 'Proc. Roy. Soc.,' B, vol. 107, p. 313.

—— (1933, *a*). 'Not. Proc. Roy. Inst.,' vol. 26, p. 849.

—— (1933, *b*). 'J. Exp. Biol.,' vol. 10, p. 88.

—— (1933, *c*). 'J. Exp. Biol.,' vol. 10, p. 391.