GILL MOVEMENTS OF NYMPHAL *EPHEMERA DANICA* (EPHEMEROPTERA) AND THE WATER CURRENTS CAUSED BY THEM

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(With Eight Text-figures)

The nymphs of *Ephemera danica* living in burrows in the sandy mud of flowing waters present a problem of current production in the water, quite different from those so far investigated (Eastham, 1932, 1934, 1936, 1937). Percival & Whitehead (1926) collected data indicating that this species is found most commonly in water, flowing over a sandy floor, which contains about 65% coarse sand, 2% fine sand and about 1% each of silt, fine silt and clay. Their observations also showed that from this type of environment there was little or no migration to neighbouring places where the sand was present in smaller amount and the silt and clay predominated. Experiments showed that the animals always displayed a preference for the soft surface into which burrowing could be effected, but no adequate explanation of the relationship between nymphs and sand was forthcoming. Questions regarding the unsuitability of silt or clay, in any but small quantities, remain unanswered.

The burrowing habit of *E. danica* is so well known that no special references need be made to it. Suffice it to say that a curved burrow, concave side uppermost, is made, through which water is passed from in front over the back of the animal and so out over the caudal filaments to the open water of the stream. The manner of making this burrow, a process in which head, mouthparts and prothoracic legs share, does not concern us, but the fact of its existence would appear to be related to the form of the gills, to the manner in which they oscillate to produce currents of water to aerate those same gills, as well as to the nature of the substratum in which the burrows are made.

METHODS OF OBSERVATION

By means of the stroboscope (Gray, 1930), gill movements were observed on gills as single units, as pairs, in conjunction with others of the same side adjacent to them, and when working together as a complete system. The rate of oscillation was such as to make stroboscopic observation possible without interference from flicker phenomena. The usual precautions were taken to avoid stroboscopic re-

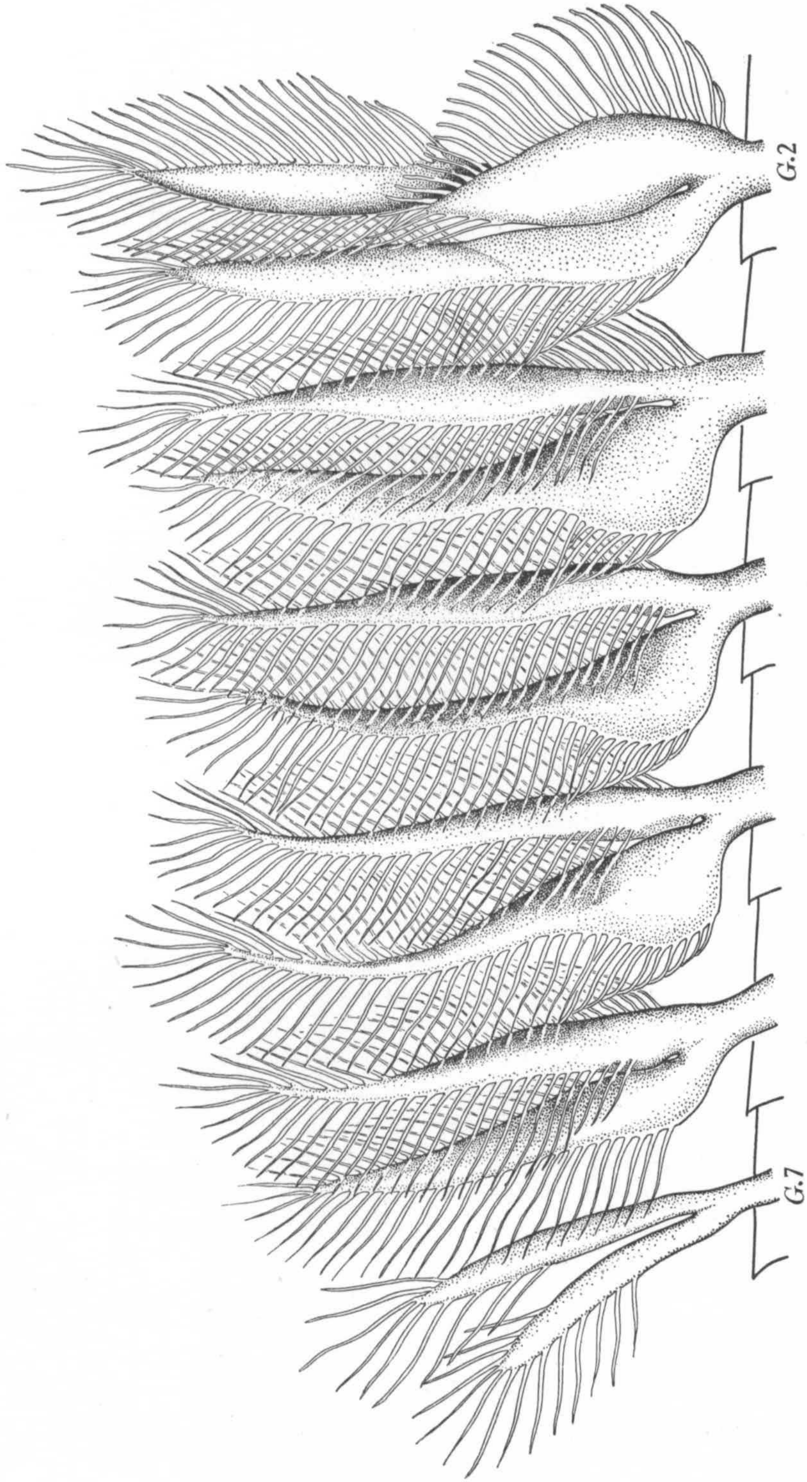

Fig. 1. The gills of the left side seen from the middle line of the body. *G.* 2 second gill, G. 7 seventh gill. The fringing filaments are shown in reduced condition to indicate the manner of overlapping of the gills in series.

versal. Currents were observed by introducing fine suspensions such as lamp black into the water. Normal suspensions of the environmental waters were often sufficient to demonstrate the main currents.

The Gills (Fig. 1)

Ephemera danica has seven pairs of bilamellate gills borne on the first seven segments of the abdomen, each gill being articulated to the postero-lateral angle of its appropriate segment in a dorsal position. Each gill of the first pair (not figured) is a small bifid structure held in an erect attitude in the angle between the metathoracic leg and the side of the body. These gills do not move. The remainder are larger and exhibit considerable powers of movement.

In gill 2 (Fig. 2), the anterior lamella is lanceolate and tapers to a point distally. It is twisted in such a way that the surface which faces outwards to the sides proximally, faces forwards at about the middle of its length and inwards towards the middle line of the body in its upper distal region. Both its borders are freely fringed with tracheate filaments, the curvature of which conforms to the general form of the lamella at their own level. The posterior lamella has a similar shape. It is less twisted than the anterior lamella and presents a deeply concave surface postero-laterally, the fringing filaments, as in the case of the anterior lamella, conforming to the curvature of the gill surface at all levels.

Except for the proximal region of the anterior lamella, where an open concave surface is presented laterally, the rich filamentous fringe on the gill's outer side is brush-like. On the inner or median surface, however, the posterior filaments of the anterior lamella overlap the posterior lamella and its filaments—this regular antero-posterior overlap thus producing an even surface on the side of the gill which faces the middle line of the body.

In gill 3 (Fig. 3), anterior and posterior lamellae in the erect position are arranged as are the tiles on a roof and, as seen in cross-section, are turned so that one border of each is directed in a postero-median and the other in an antero-lateral direction. Thus each has an anterior face directed inwards and a posterior face directed outwards. By means of the fringing filaments, with which both borders of each lamella are provided, the lamellae overlap each other considerably: from before backwards on the median surface and from behind forwards on the outer.

Mesially, this overlapping occurs so that the gill presents an even surface as in the case of gill 2. On the outer side, however, such an even surface is broken in a variety of ways. Thus, in the proximal (lower) region of the anterior lamella, the otherwise anterior surface faces outwards owing to the twisted nature of the gill, and so the anterior fringe faces outwards. Further, the antero-lateral filaments of this lamella form a thick brush, many parts of which project laterally as do also the corresponding filaments of the posterior lamella. (This brush arrangement is not figured.) In the lower third of the posterior lamella, anterior and posterior fringing filaments are recurved on to the outer lamellar face so as to meet for a short distance in the middle line.

Only in insignificant and inconstant details do the gills of segments 4, 5 and 6 differ from the one just described. The twisted character of the anterior lamella diminishes in these gills as we pass posteriorly, so that the sixth gill is a simple

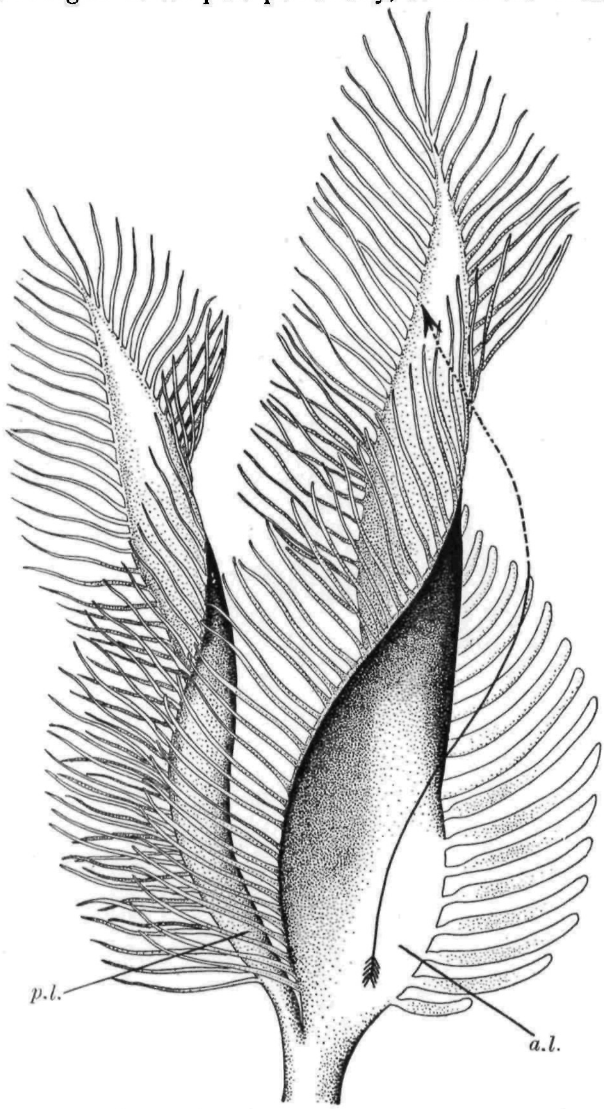

Fig. 2. Second gill of right side seen from the outer side with filamentous fringe much simplified, *a.l.* and *p.l.* anterior and posterior lamella respectively. The arrow indicates the nature of water flow during outward movement to the erect position, see text.

bilamellate organ with a smooth alignment of its filament on the mesial surface but brush-like arrangement on the outer side.

The seventh gills are much simpler in form than the foregoing, the lamellae being narrower and the fringing filaments only sparsely distributed along the distal halves of the lamellar borders.

For each of these gills there is an overlapping of anterior and posterior filaments on the lamellar borders. A similar overlapping arrangement occurs between adjacent gills of a side, each gill overlapping the next one behind it when viewed from the middle line of the body (Fig. 1).

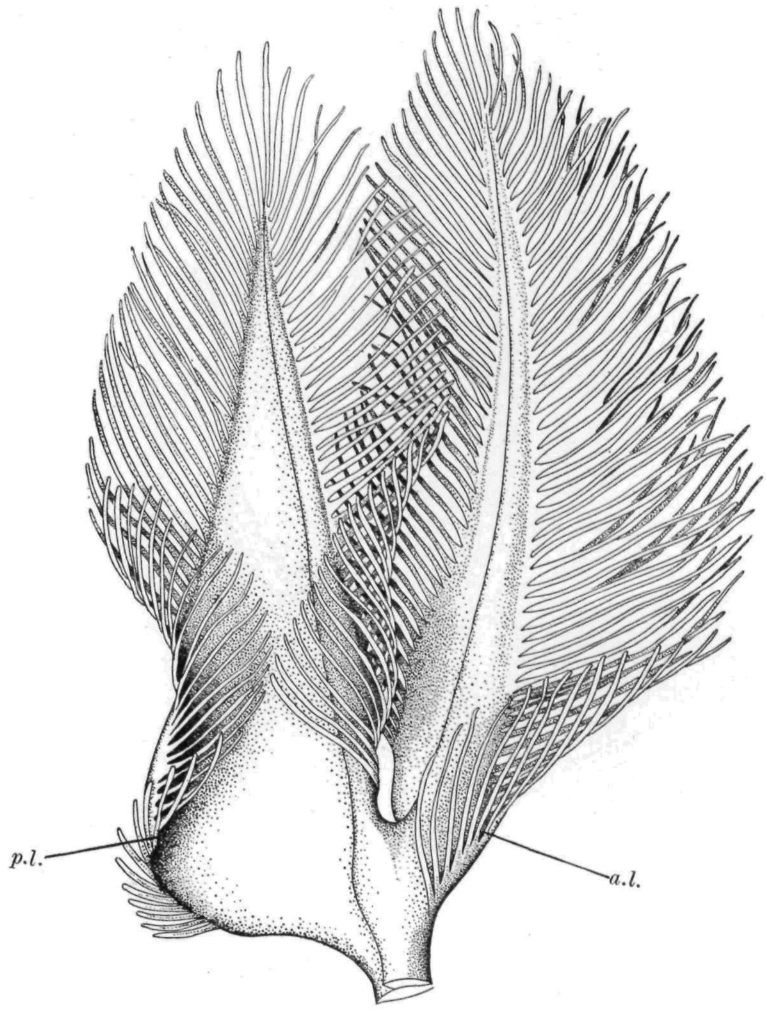

Fig. 3. Third gill of right side seen from the outer side, with filamentous fringe much reduced. *a.l.* and *p.l.* anterior and posterior lamella respectively.

We can thus regard the two longitudinal series of gills as forming two barriers separating the water which lies on their outer or lateral sides from the water lying on their median sides, i.e. over the middle line of the body. As far as the gills themselves are concerned these barriers are incomplete at the gill bases where no fringing filaments occur (Fig. 1). These gaps are filled by tufts of long setae on the body wall, which arise on those pleural regions lying opposite to the intergill spaces.

Currents in the water (Fig. 4)

As indicated by the movements of suspended particles, the water passes backwards from under the metathoracic legs and upwards to the middle line of the body over the vestigial first pair of gills; thence it races backwards over the dorsal side

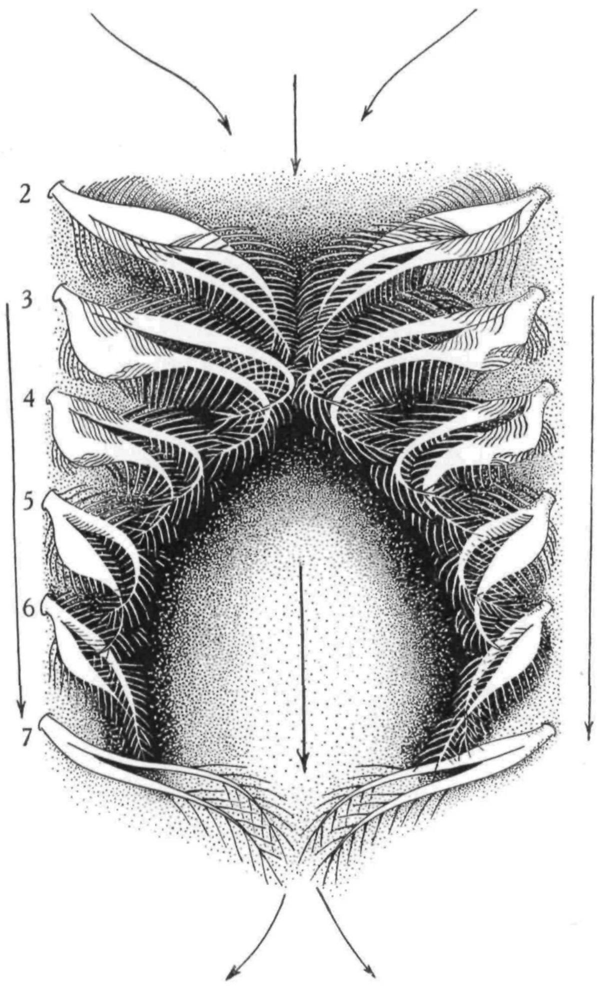

Fig. 4. Semidiagrammatic view of the gills in motion as seen from above. Arrows indicate the direction of principal currents. Numbers refer to gills.

of the body between the two rows of gills. The current diverges to right and left as it passes under and between the seventh gills. The above-mentioned currents over the first gills are also supplied by water passing round the front of each second gill from the side. Lateral currents, parallel to the main dorsal flow and running in the same direction, occur on each side of the two rows of gills. These lateral currents appear to be completely distinct from the median one, no water having been observed to pass between them by way of the intergill spaces. Small currents pass upwards from the distal extremities of the gills as members of pairs approach each other in downward movement. These are probably leakage currents, the result of eddies round the gill tips.

Gill movements

The average rate of movement of the gills is, under normal circumstances, between 6 and 7 complete oscillations per second. This was determined by adjusting the frequency of light of the stroboscope so that the gills appeared stationary, the light frequency being then timed by a stop-watch. This was checked by timing the rate of rotation of the stroboscope spindle with an attached mechanical counter.

The gills move in metachronal rhythm from before backwards as in other ephemerids already examined (Eastham, *loc. cit.*). Though the time-phase difference between the gills in motion shows some variation in different individuals, it has generally been found to be such that when gill 2 is at one end of an oscillation, gill number 6 is at the other. In this rhythm, as in all species so far examined except *Caenis* (Eastham, 1934), members of a pair beat simultaneously and synchronously, each gill performing a movement which is the mirror image of that of its fellow of the opposite side (Fig. 4).

At the outermost limit of an oscillation the gills are erect at their bases with their distal extremities pointing backwards. At the inner limit of the stroke the main body of a gill is placed horizontally across the body with its pointed tip reflected upwards and applied against the corresponding part of the gill opposite to it. In this way a pair of gills alternately expose and cover the dorsal surface of the body between them. When covering the body in this latter case the two members of a pair form a closed archway over the water on the back which, moving downwards, squeezes the water from beneath it. At any one segment, therefore, conditions of increased and reduced pressure alternate with one another with perfect regularity (Fig. 8).

In order to understand clearly the movements performed by a single gill it is desirable to free it from contact with those adjacent to it. Removal of the latter is an easy matter, and the movements of those remaining seem in no way to be impaired by this operation.

It will be convenient to consider the gill first as a simple lamella, not complicated by its filamentous fringe. The path traversed by the gill is elliptical, and the effective and recovery strokes of an oscillation are not clearly defined by differences in the angle offered by the gill to the water through which it passes. We will term the movement towards the middle line of the body the "effective", and the return to the lateral erect position, the "recovery" stroke. In the effective stroke the leading surface is that which in the erect position faces inwards and slightly forwards. During recovery, the reverse side is in the leading position. In both phases of movement the gill makes an appreciable angle with its own path of motion, and the same forces as those described for other nymphal gills are involved (Eastham, 1934, 1936, 1937). The similarity of these forces to those concerned in fish propulsion (Gray, 1933) has already been commented on with reference to *Caenis*, *Leptophlebia* and *Ecdyonurus*. Assuming here that in effective and recovery strokes there is no difference in angle of the gill surface, reference to Fig. 5 B shows that

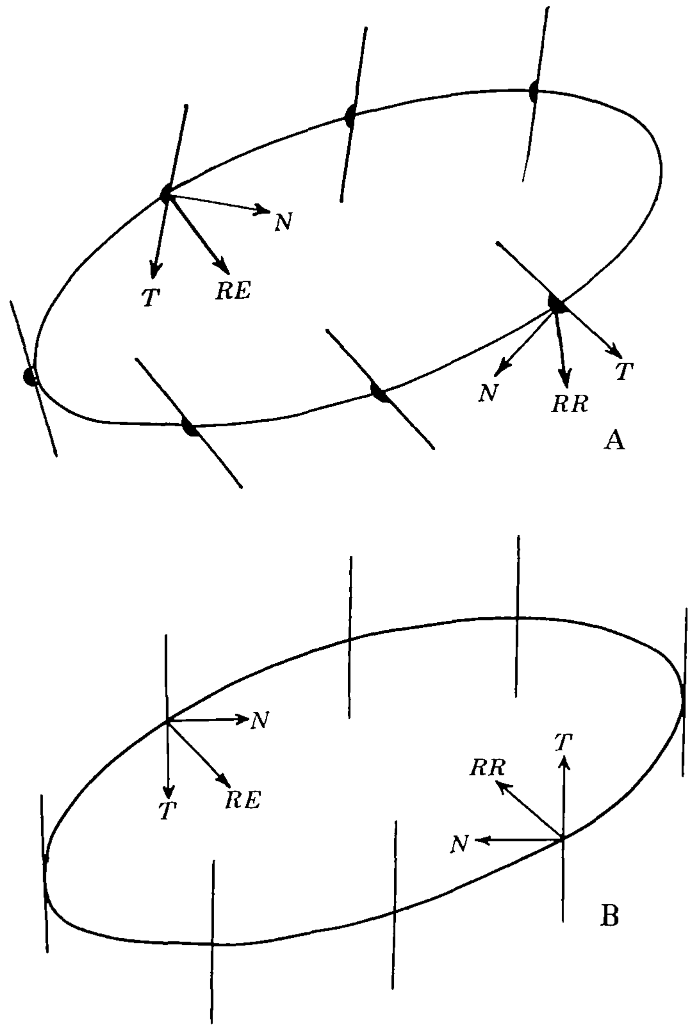

Fig. 5. Elliptical path of a gill; A in which the angle of incidence between the gill and the path of motion varies in effective and recovery beats; B, in which no difference of angle in effective and recovery beat exists. *N* and *T*, force components normal and tangential to the gill respectively. *RE*, resultant force during the effective beat. *RR*, resultant force during the recovery beat. The outer limit of the oscillation is at the left for each figure.

the forces set up in both parts of an oscillation cancel each other out. Thus in the effective beat the resultant (*RE*) of normal (*N*) and tangential (*T*) forces will point inwards and backwards. During the recovery stroke, however, the resultant (*RR*) will point outwards and forwards. Should, however, effective and recovery strokes differ in angle as indicated in Fig. 5 A, resultants of effective and recovery strokes should combine to set up a backward flow. The close similarity in the angle made by the gill's leading surface in effective and recovery strokes to its own path of motion suggests that the state indicated in Fig. 5 B exists.

A condition then for a single gill resembles that described by Harris (1937) for the pectoral fin movements of certain teleost fishes. But for each gill other forces come into play. As the gill moves inwards and downwards from its erect position an undulatory wave passes from its base to its tip. The effect of this will be to set up a flow in the direction of the wave (Fig. 6 A). A condition is in fact set up which is similar in effect to that of a flagellum of a protozoan with the flagellum serving as a propeller, where the flagellar wave proceeding from base to tip causes movement of the animal in the opposite direction (Gray, 1928). The gill, attached in this case to a stationary animal, should set up a flow along its surface in the direction of the

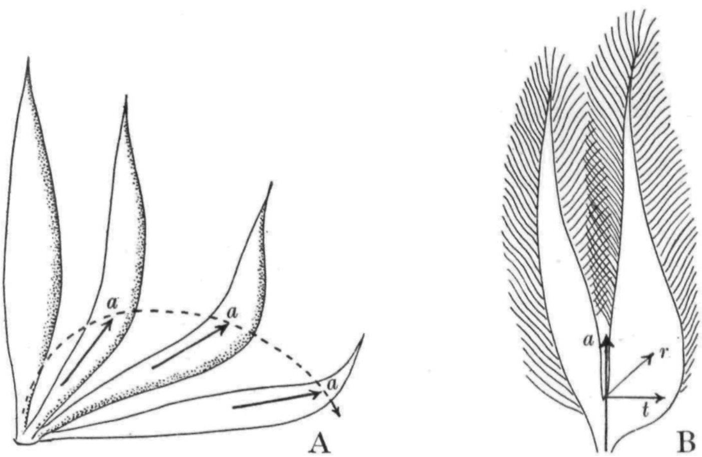

Fig. 6. Force components involved in the undulatory movements of a gill; A, to show the axial component of a gill arising from an axial undulation; B, to show the lateral aspect of a gill of the left side and the force components resulting from axial and transverse undulations. *a*, *t* and *r*, axial transverse and resultant forces.

undulation. For each gill, therefore, a force component longitudinal with the gill axis exists. We will call this force component A. In addition to this axial undulation each gill experiences a wave form across its breadth. This undulation passes from before backwards across the gill surface and is in line with the general metachronal rhythm which characterizes gill movement as a whole. A force component T will thereby result, tending to drive water across the gill surface transversely and in line with the longitudinal axis of the body (Fig. 6 B). A particle, free to move under the influence of the force component A, and starting at the gill base, would pass along the gill surface reaching the apex of the latter when it is lying over the middle line of the body (Fig. 6 A). The resultant R of these two components should therefore lie diagonally across the body and be directed backwards. A single gill can be shown to produce a current in this direction. Small upward eddies are seen to pass away from the tip of an isolated gill in motion, and these may be due to the axial component exerting its own influence in setting up a flow to the gill tip during those phases of movement which occur between the erect and prone positions. If so, a condition similar to that analysed by Harris (1937) for the median fins of teleost fishes might exist in which the resultant of the two force components involved, lay in an upward direction and not absolutely in line with the fish axis.

When two gills of a pair are in motion, we have seen that they form a falling archway from beneath which the water is squeezed (Fig. 4). The water is squeezed not only downwards but also backwards, since at the moment that the two gills are in contact they are moving backwards along the median parts of their respective elliptical paths (Fig. 5). If this analysis is correct it would appear that each gill sets up a current diagonally backwards. Meeting in the middle line these currents take a common path backwards and at the same time receive an additional backward thrust by the falling archway made by the gills over the body.

So far the gill has been described as a flexible membrane capable of movement along an elliptical path and with undulations passing in two directions over its surface. In view of the known bilamellate form of the gill, the question now arises whether each lamella behaves separately in the manner described or whether the two lamellae of a gill act as one compound flexible plane. From my observations, for each gill of segments 3–6, it appears that the two lamellae act as one, maintaining contact with each other at all times.

The movements of the bilamellate gill are further complicated by its bordering fringes of tracheal filaments. It acts as a single lamellar unit capable of changing its width by the separation and approach of its two lamellar components in different parts of an oscillation. During the inward effective stroke the posterior lamella lags behind the anterior, while on the return outward stroke they are close together. This separation of the lamellae during the effective stroke, however, does not open the water space between them owing to the overlap of the filaments belonging to adjacent borders (Fig. 1).

Lamellar filaments of a gill overlap from before backwards when viewed from the middle line. During the inward stroke therefore (Fig. 7 A) (while pressure of water against the gill surface tends to bend the fringing filaments back), the posterior filaments of the anterior lamella are held against the posterior lamella and its anterior fringe. A filamentous curtain between the two lamellae is thus maintained. The absence of any visible flow between the lamellae suggests that the interlamellar curtain forms a meshwork of such fine dimensions that it is impermeable to flow. The two lamellae in the effective stroke may therefore act as one wide surface effectively moving the water against which it is pressing. When a gill is working as an isolated unit with no neighbouring gills to interfere with it, its anterior and posterior bordering filaments must bend with the streamline and allow water to pass round their edges. The flow round the edges, expected under these circumstances, does indeed occur (Fig. 7 A).

When the gill moves in the opposite direction, in recovery to the erect position, closure between the lamellae is still maintained. But in this case the anterior filaments of the posterior lamella are held against the anterior lamella, thus forming a similar filamentous curtain to that made in the effective stroke and which again offers a decided resistance to the flow of water. Anterior filaments (of the anterior lamella) and posterior filaments (of the posterior lamella) bend as before with the stream line and allow water to pass round them (Fig. 7 B).

When two adjacent gills are working together, there is no flow between them, and the two gills work as a continuous membrane just as did the two lamellae of a single gill. The absence of leakage currents between adjacent gills is determined by two factors. In the first place, a thick tuft or erect setae arises from the pleuron of each gill-bearing segment and effectively closes the gap between the gill stalks where lamellar extensions and filaments are lacking. Secondly, between each gill and its neighbour of the same side, a close curtain formed by the overlapping filaments of the adjacent borders of these same gills occurs. The above-mentioned setae and these latter filaments form, in each case, a barrier preventing any observable flow of water across it. Fig. 1 shows the intergill arrangement somewhat

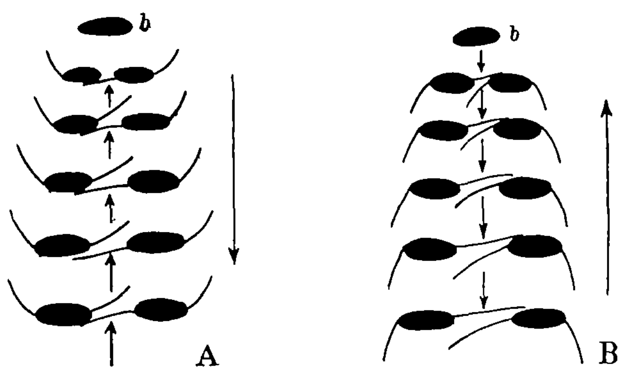

Fig. 7. Diagrams of transverse sections of a gill at different levels, A, during inward, and B, during outward movement. The interlamellar filaments close the interlamellar space in both movements. Long arrows indicate direction of movement of a gill from base level *b*. Short arrows indicate the direction of water pressure.

diagrammatically, the gills being figured as possessing a much sparser filamentous apparatus than actually occurs. A similar filamentous membrane, impervious to flow in certain phases of gill movement, has been recorded in the case of *Caenis* (Eastham, 1934).

If now we consider two adjacent gills in motion we see that contact is maintained between them during all phases of movement. Reference to Fig. 1 shows that the filaments of gill 3, for instance, must retain contact with those of gill 4, when both are undergoing inward-forward movement. When gills 3 and 4 are moving in opposite directions as when gill 3 moves outwards and number 4 inwards, the intergill space is clearly seen to close. Any tendency for the posterior filaments of gill 3 to lag in this movement and so open the intergill space is counteracted by the anterior filaments of gill 4 lying athwart gill 3, thus efficiently closing the gill space. Even during the phase of movement, when gill 3 moves inwards away from gill 4, the lag of the posterior filaments of the former gill is prevented by falling against the gill next behind, viz. the 4th.

Overlapping of gills and filaments is thus arranged so as to prevent filamentous lag during motion, and the intergill space is closed to the passage of water. The description of the two adjacent gills 3 and 4 applies equally well to the others; gills 3, 4, 5 and 6 behaving alike in this respect. Down each side of the body they make a continuous membrane, by virtue of the fineness of the mesh formed by the filamentous fringes of the gills.

This gill "membrane", owing to the metachronal rhythm of its component gills, undulates from before backwards, and at a succession of its parts will impart a backward thrust on the water through which it moves, each part setting up forces and resultant flows in the manner already described for a single gill. Since a pair of gills, by meeting over the body, effect a downward and backward thrust on the water and squeeze it from beneath them, the two gill membranes will meet at a series of points as they undulate synchronously. The backward and downward thrust of any one part, as represented by one pair of gills, must always be reinforced by that produced by the next succeeding part.

A further point is also worthy of note. As the "membranes" approach the middle line of the body, the water is subjected to a rapidly increasing pressure from above. This region of high pressure moves steadily backwards with the metachronal rhythm and is followed immediately by a corresponding region of reduced pressure as the parts of the gill membranes separate from each other (Fig. 8). Cannon (1928) described such movements of pressure systems in *Cheirocephalus*.

Returning to a consideration of the metachronal rhythm of the gills in relation to water flow, it has been ascertained that the rhythm is of such an order that when gill 2 is at one end of its elliptical path, the sixth is at the other. The time-phase difference necessary for this is fairly constant.

Since each gill is in a more forward position at the inner limit of a beat than when at the outer, it follows that, when gill 3 is at its most forward (inward) position, gill 6 must be in its most posterior (outer) position, the other gills falling in a regular series of intermediate places. As Fig. 8 shows, the gills being in contact along their whole length, at this time the "membrane", formed by the gills of either side between segments 3 and 6, is at its maximum length. Let each gill now move from the point stated, through half a complete oscillation. Gill 3 will now be at its most backward (outer), and gill 6 at its most forward (inner) position, with again the other gills in appropriate intermediate places. A line joining the gills in this phase, as shown in Fig. 8*b*, *b'*, represents the gill membrane at its minimum length. Each series of gills may then be said to form an undulating membrane, capable of change in length by the sliding over each other of the individual gills which compose it. Columns of water of different length and width lie between the gill "membranes" as the phases of the latter change; and as the gills form the membranes at maximum extension (Fig. 8*a*, *a'*) they may be said to be reaching forwards for water, later to press it back. This feature in itself must contribute to the characteristic backward flow. It must also be an important factor in determining the flow from in front towards the first segments of the abdomen from which point the gills are fed with water. The described flow would appear to depend, therefore, on the ability of the gills to form continuous membranes which, by their composition, allow of changes in length, without the inconvenient foldings which would appear on membranes not so made up of separate units.

The gills of segments 3–6 are formed, as we have seen, on the same general plan and operate alike. The others differ from these in various features. In the majority

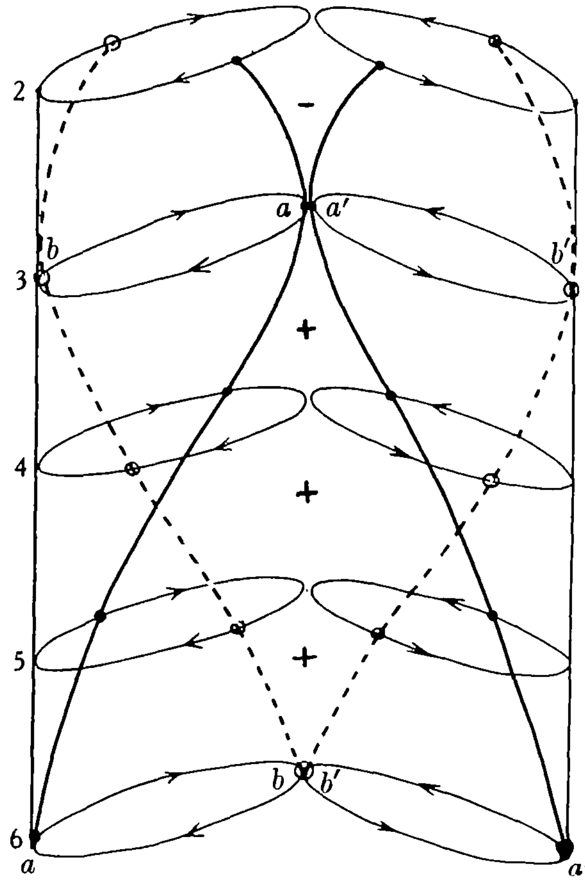

Fig. 8. Diagram of the elliptical paths of gills 2 to 6. Numbers refer to paths of gills in order from in front. Complete lines *a'a'* and *aa* represent the positions of gills 3 to 6 when the gill 'membrane' is at its maximum length. Broken lines *bb* and *b'b'*, the positions of these same gills when the 'membrane' is shortest. High and low pressure conditions between gills of series *aa* and *a'a'* are shown by + and − signs.

of ephemerid nymphs the first gills are small vestigial structures and are little more than miniature replicas of those which follow. In *Ephemera* they are reduced to minute bifid stationary organs which play no part in current production. There is a clear channel on the body surface of segment 1, leading from below the body and from behind the posterior legs, upwards to the middle region of the body between the second pair of gills. Few or no pleural setae occur in this region, and it seems as if the reduced condition of the first gills is concerned with the maintenance of a clear channel for water on each side of the dorsally arched nymphal wing cases. It is along these lateral channels that the water comes before entering the stream between the moving gills.

The second gills are large and differ prominently from those which follow by virtue of the spiral twist of their anterior lamellae and the smooth contour presented by the anterior and outer surfaces of the latter. The water movements in this region have been described and, consisting of currents converging from beneath the legs and from the sides of the body to meet over the back of the animal, differ markedly from the steady backward flow past the remaining gills.

Since the oscillations of the second gills differ in no marked way from those of the gills behind them, the difference between the currents past them must be attributable to the peculiar form of these second gills. Their twisted form is shown in Fig. 2 and the following explanation attempts to relate this form and the gill's method of oscillation to the type of current which has been observed.

Just as a wave, propagated along the flagellum of a stationary protozoan, sets up a water current in its own direction, so also is a spiral current created when the wave passes both along and round the flagellum (Gray, 1928). In the latter case tangential and normal force components, at any one point, result in pressure being applied to the water in a particular direction. The tangential component is the same at all points along the flagellum, but the normal component varies with the spiral movement of the flagellum, as does, of course, the resultant from these two components. The spiral flow is the result.

When a gill of the second pair oscillates, it is observed that its spiral or screw form is maintained throughout movement. When it oscillates, therefore, it must affect the water through which it moves as does a screw. Let us consider the second gill of the right side in that phase of oscillation in which it is raised from the prone to the erect position (Fig. 2). Applying the principles invoked for the spiral flow caused by a flagellum with a spiral wave movement, we can relate the nature of the flow to the force components, which come into being at the gill surface, during movement. Tangential and normal force components occur at all points on its surface. The tangential component (axial for the gill) is the same at all points along the surface, but the normal component varies with the gill curvature. Consequently the resultant of these two components at any selected point differs from that at all other points on the surface of the same gill. Because of the spiral curvature, the summation of all the resultants at a series of points on the outer surface of the gill from base to tip must be expressed as a spiral flow over the gill surface, as shown in Fig. 2. The effect of such a flow is to carry water which first lies on the outer side of the gill proximally, round the anterior surface, ultimately to transfer it to the gill's median surface. This is in agreement with the *general* observations made on the currents. It must, however, be pointed out that the *details* of the spiral flow over the gill surface have not been observed with precision, owing to the small dimensions involved. To this extent the explanation that the second gill operates as a screw directing water from the sides to the middorsal line of the body is inferential.

The seventh gills are reduced in size. Although they oscillate, the amplitude of their beat is so small and their filamentous fringe so poorly developed as to render them of little moment. It is only in the rapid swimming movements of the nymphs that these gills move with any vigour. As soon as the nymph swims, all the gills, including the seventh pair, are moved vigorously to the sides and held there in an erect attitude for as long as the animal remains in motion. In recapitulation, we may note a number of factors contributing to water movement, in the analysis of which the system appears to be in no way simple. There is the force resulting from the axial and transverse force components set up on a single gill: that resulting from the gills of one side acting as a continuous undulating membrane: the force resulting from the meeting of right and left gill membranes above the body; the movement of pressure systems from before backwards and lastly the feeding of the gill system with water by virtue of the power of the gill membranes to increase their length and by the spiral flow caused by the oscillations of the twisted first lamellae of the second pair of gills.

Adaptation of the gill mechanism to environment

The existence of *Ephemera* nymphs in burrows of sand with some small fraction of mud and silt to assist in binding materials together, suggests that the simple type of current only would suit the conditions. The nymphs avoid the light and, given a choice of hard surfaces and sand, always burrow into the latter (Percival & Whitehead, 1926). If placed in a vessel containing small plates of stone and detritus their first response is to hide under these to avoid the light. In a burrow of the shifting materials which characterize the environment of these forms the gills commence to work, creating the antero-posterior flow over the body. Such a simple current disturbs the minimum amount of materials forming the burrow walls. In view of the delicate nature of the gill filaments one might suppose that any serious disturbance of the sand, etc., would be detrimental to their proper function. Accidental or intentional upset of the burrow induces the nymph to escape and so crawl out to the light which it had spontaneously avoided in the first place. Were the current which passes over the back of the animal supplemented by lateral inflows between the gills as in the case of *Leptophlebia* (Eastham, 1936), such inflow would disturb the walls of the burrow. The avoidance of this event must then be an important matter in the maintenance of the animal in a burrow, away from light, where food is available and where the optimum respiratory currents of clear water can be exploited.

It may be mentioned that the freedom of gill filaments from adherent detritus is evidently of importance to the animal; when the gills become entangled in any form of debris they are combed out by the tibial setae combs of the last pair of legs. The precision with which this operation is carried out gill by gill is remarkable. In view of these facts it may well be that the preference of *Ephemera* for a substratum containing the proportions of sand, clay and silt quoted by Percival & Whitehead (1926), is determined by the need for a burrow of some permanence, easy to make and from which it can easily escape and still one through which water can pass with the minimum disturbance to its walls. In the absence of direct evidence it is suggested that the proportions of the above ingredients allow of these possibilities with no serious clogging of the gill filaments by the stickier clay and silt particles.

SUMMARY

1. The six pairs of gills in *Ephemera danica* causing currents in the water are bilamellate and feather-like.

2. The gills move in metachronal rhythm from before backwards, and set up currents which are symmetrical with the body axis. Members of pairs of gills beat synchronously and in phase with each other. The difference of phase between two adjacent gills of the same side is about one-eighth of a complete oscillation.

3. For a single gill there is little or no difference in the angle presented by the gill to its own path of motion, in the two halves of an oscillation. This factor (angle of incidence) is not of great importance in directing water backwards. Forces of importance in moving water in the direction taken are (i) the resultant of axial and transverse force components for single gills, (ii) the pressure effected on the water over the animal's back by the two members of a pair of gills falling, (iii) the movement backwards of alternating pressure regions over the back, (iv) the undulations of the second screw-like gills which feed the main current from in front and from the sides.

4. The fringing filaments of adjacent gills overlap each other from before backwards (as seen from the middle line of the body), and thus each row of gills forms a "membrane" composed of separate gill units. The latter appear never to lose contact with each other during movement, and since no sideways flow is observed between the gills it is assumed that the overlapping filaments between the gills form a membrane impermeable to flow.

5. The adaptation of *Ephemera* to its sandy environment is shortly discussed.

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