# THE RHYTHMICAL MOVEMENTS OF THE GILLS OF NYMPHAL *LEPTOPHLEBIA MARGINATA* (EPHEMEROPTERA) AND THE CURRENTS PRODUCED BY THEM IN WATER

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(With Three Text-figures)

Reference has been made to the general problem of gill movements of ephemerid nymphs (Eastham, 1932), and the special features presented by *Caenis horaria* have already been described (Eastham, 1934). The following is an account of gill movement in *Leptophlebia marginata.*

*Methods.* Examination of the currents produced was made by introducing suspensions of lamp black into the water, and the gill movements with reference to such currents were analysed by the stroboscope (Gray, 1930). In the slowly moving waters in which the nymphs live, as also in still water, gill movements are rather slow. Their rate of oscillation in these conditions is too high to make direct observation possible and too low to avoid the phenomenon of "flicker" when observed by the stroboscope. Movements of the gills, however, are conditioned by the oxygen tension of the water, and it was found possible to stimulate gill activity by lowering this oxygen tension. Thus by using previously boiled water or by mounting the nymph in a cavity slide under a cover-slip and so producing a condition of asphyxiation, sufficiently rapid movements of the gills could be induced to make stroboscopic observation possible. The normal rate of gill oscillation was not measured, but it may be assumed to be somewhere below 6·5 per second, as this appears to be the limit below which the flicker effect with the stroboscope is produced (Gray, 1930). Under conditions of asphyxiation the gills oscillated at 7·5 per second. Precautions were taken to avoid the phenomenon of stroboscopic reversal.

*The gills.* There are seven pairs of gills which are more or less similar. They are bilamellate, the anterior lamella of each lying flat against its posterior counterpart but slightly towards the outer side of it when at rest (Fig. 1 B). Each lamella is lanceolate and tapers to a point in which runs the terminal part of a trachea which passes through the centre of the lamella and supports it. The gills are borne on narrow pedicels at the postero-lateral angles of the gill-bearing segments 1–7 of the abdomen. Of these gills, numbers 1 and 7 are much narrower than the others and do not join the others in rhythmical movement. Contrary to the descriptions given for members of this genus by Rousseau (1921), the gills when at rest are held from the body at different angles from each other (Fig. 1 B, C). This is important, since the angles at which the gills operate with respect to the body determine the level of water that each gill explores relative to that body. The first pair of gills is held approximately vertically. The second gills are held above the body in line with its longitudinal axis but deflected backwards at an angle of about 45°. The third gills are similarly disposed except that they project laterally so as to make an angle of about 30° with the lateral border of the body. The fourth gills are still more deflected laterally and are held less erect than are the third members, while the fifth gills are held laterally almost at right angles to the body in the horizontal plane. The sixth project downwards and backwards and occupy a position relative to the ventral body surface similar to that of the second gills with reference to the dorsal surface. Projecting from beneath the body from segment seven are found the narrow seventh pair of gills directed backwards so as to make an angle of about 40° with the ventral surface of the body. Within certain limits the angles and attitudes mentioned here are subject to some variation in different individuals, but the phenomenon of difference of attitude shown by the gills in

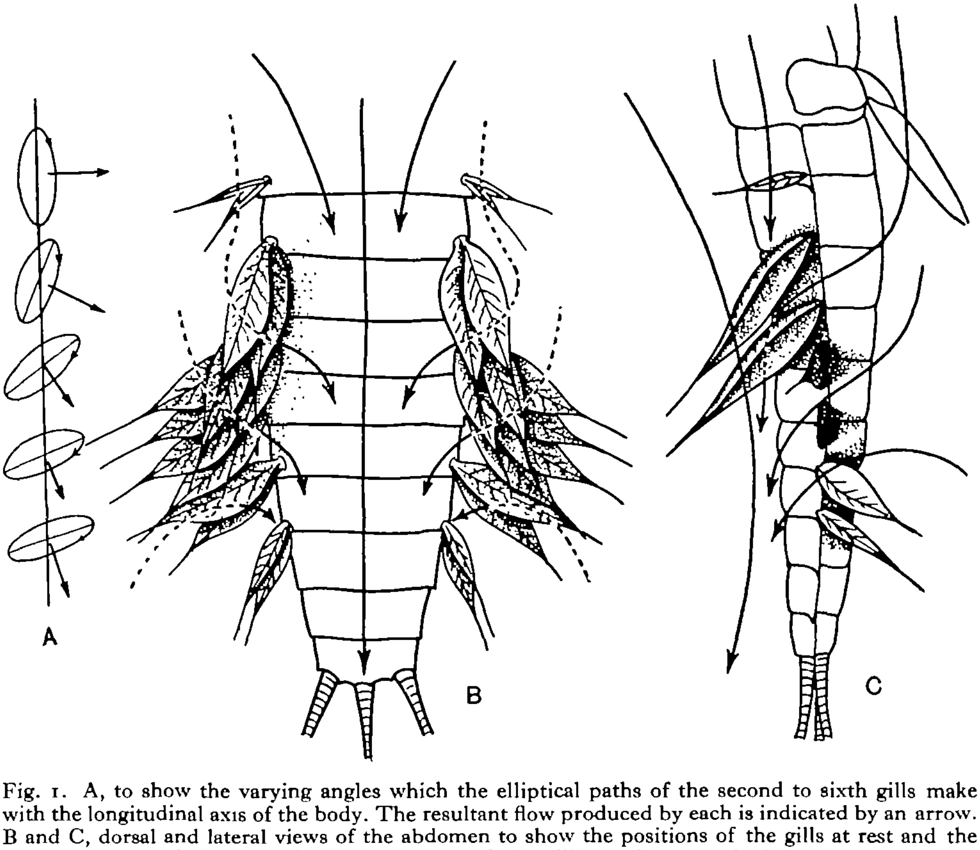

Fig. 1. A, to show the varying angles which the elliptical paths of the second to sixth gills make with the longitudinal axis of the body. The resultant flow produced by each is indicated by an arrow. B and C, dorsal and lateral views of the abdomen to show the positions of the gills at rest and the currents produced by them when in motion. In C the gills are shown as single lamellae.

series is found in all (Fig. 1), the result being that as one passes along the gills from before backwards the gills project into successively lower levels of water.

*Currents.* Reference to Fig. 1 will obviate a lengthy description of the currents produced in the water. The main currents indicated there are symmetrical with the body axis, the water passing from before backwards. Further, it is seen that water from above, from the sides and from below the animal is passed over the gills.

*Gill movements.* With the exception of the first and seventh pairs which take no part in the concerted movements of the others and for the most part remain stationary, the gills behave alike. The antero-posterior metachronal rhythm exhibited by the moving gills is generally of such an order that any one gill is about one-sixth of a complete oscillation in advance of the next behind it (cf. *Caenis*, Eastham, 1934).

Taking the second pair of gills as an example and considering only the anterior lamella of each we find that each of these starting from a position of rest traverses an elliptical path rotating outwards and forwards, backwards and inwards. It reaches the vertical position at the end of the forward movement, and at the end of the backward beat it rests flat on the body. In the forward movement the outer edge of each lamella is turned in the direction of motion so as to cut the water, the terminal filament of each being flexed backwards by the water through which the movement is executed (Fig. 2). On reaching the anterior limit of the stroke each lamella rotates on the basal pedicel sufficiently to bring that surface which was outer in the forward stroke into a leading position during backward movement (Fig. 3). Thus effective and recovery parts of a complete oscillation are clearly defined, the effective beat being executed during backward, the recovery during forward motion. During the effective stroke the leading surface of the lamella is also inclined towards the middle line of the body. Owing to this and to the fact that the path of motion is elliptical it will be seen that as the lamella moves backwards it makes an angle with its own path of motion. This angle varies as the various phases of the oscillation are passed through (Fig. 3). As was shown by Gray (1933 *a*, *b* and *c*) in the case of fish movement, such a moving surface will be subjected to forces

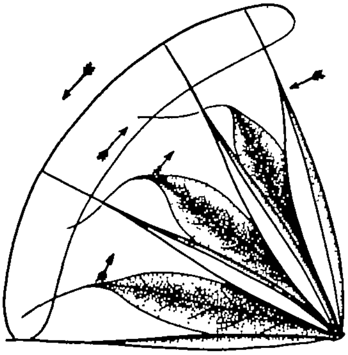

Fig. 2. Diagram to show successive phases in a complete oscillation of the second left gill as seen from the middle line of the body, one lamella only being shown.

normal and tangential to it. The resultant of these in the case under consideration represents the net propulsive thrust made by the gill against the water, and the animal being stationary its effect will be shown in currents produced in the water. Such resultant thrust is for either member of the pair directed both medially and posteriorly, *i.e.* in the direction in which the currents are actually observed to flow over that region of the body. An interesting parallel therefore is found between the principles governing the mechanics of fish movement (Gray, 1933 *a*, *b* and *c*), and those concerned with movements of water by the gills of Ephemerid nymphs, *e.g.* *Caenis* (Eastham, 1934) and in *Leptophlebia* as here described.

It might be expected that in its rotation, the gill should set up vortical currents passing inwards towards the point of attachment of the gill as was shown to be the case in *Hemimysis* by Cannon and Manton (1927). That these are either absent or so insignificant as to be ignored in *Leptophlebia* is probably due to the elliptical path of motion as compared with the more circular movements executed by the limbs of *Hemimysis*. So far we have only been considering the first gill as consisting of a single lamella, and the foregoing remarks apply strictly to the anterior lamella of the two. The posterior lamella executes a more passive movement lagging behind the anterior. It never reaches so far forwards during oscillation as does the anterior, and there thus develops a gradually increasing space between the lamellae of a gill which attains its maximum at the end of the forward movement (Fig. 3). Since each lamella cuts the water as it progresses forwards it is only after the commencement of the backward beat that this interlamellar space becomes significant. When the anterior lamella begins its backward journey it meets its posterior counterpart at

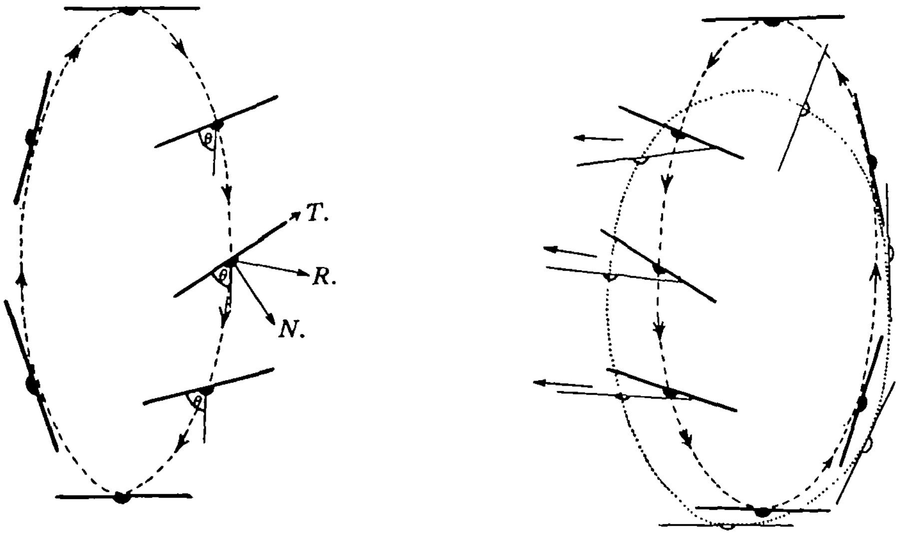

Fig. 3. To show the attitudes of the second pair of gills in one complete oscillation. On the left the left gill is depicted as a single lamella. The varying angle which the gill makes with its own path of motion is indicated at $\theta$. *N.* and *T.* indicate respectively the normal and tangential forces to which the moving gill is subjected; *R.*, the resultant of these. The relation of posterior to anterior lamella of the right gill during movement is shown on the right, anterior and posterior lamellae being indicated by thick and thin lines respectively.

an angle. This angle is open towards the middle line of the body and at the same time directed backwards (Fig. 3)[1]. As the backward movement proceeds, the two lamellae become more closely applied to each other, the angle between them being gradually diminished until at the end of this phase of oscillation the two lamellae rest flat against each other and against the body surface. From between them therefore water is squeezed out and directed towards the middle line of the body. Since the posterior lamella in the latter phase of movement is in the leading position its own leading surface will naturally perform those functions in water movement which have already been described in our consideration of the gill as consisting of a single lamella. The tendency is then for each gill of the second pair to drive water from the sides towards the middle line of the animal.

Members of pairs of gills beat synchronously, the phenomena described for *Caenis* (Eastham, 1934), where each member of a pair was out of phase with its fellow, and so associated with a transverse flow across the body, are never shown. Since the right and left gills of the second pair beat so as to direct water towards the middle line and backwards the meeting of the two opposing flows in the middle line might be supposed to impart to the moving water an impetus in the posterior direction. If this factor is significant in producing the posterior flow the removal of the gills of one side should result in the production by the remaining gills of the other side of a flow across the body with the minimum posterior component. Such a transverse current is not observed under these conditions, and it would appear unnecessary to invoke forces other than those already mentioned to account for the currents over this segment of the body.

Each of the succeeding gills performs movements similar to those described for the second pair. But since the gills lie at different angles with the body a series of water masses of gradually increasing depth is explored by the gills from before backwards. Not only is the water explored at increasing depths by the gills, but the elliptical paths traversed by the gills in series from before backwards vary with reference to the body axis. Thus the second pair of gills perform an elliptical movement as described more or less parallel with the longitudinal axis of the body. The elliptical path traversed by the third pair of gills is inclined at an angle with the body such as to give a more posteriorly directional flow. Those which follow describe ellipses placed at angles to the body which are progressively increasing, thus rendering more pronounced the posterior direction of flow. Reference to Fig. 1A will make this clear if the resting position of each gill is taken as lying along the axis of the ellipse of each. In Fig. 1A the elliptical paths of gills 2–6 are indicated to show their reference to the longitudinal axis of the body: their different levels to the body are not shown. Assuming that the effect of each gill is to produce a flow approximately at right angles to the ellipse described, it is clear that the flow produced becomes directed more posteriorly as we pass from before backwards. That this is so can be proved by observing the current produced by each gill after removal of the others.

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[1] The extent to which this angle is directed posteriorly increases as we pass along the gills from before backwards.

The angles at which the various gills are held to the body are determined by the morphological peculiarities of gill articulation, and these angles in turn determine the position of the volume of water through which each gill rotates. It also determines the nature of the elliptical path passed through by each gill in its movement.

Because of these differences of gill attitude, alternate suction and compression phases between adjacent gills during metachronal rhythm do not occur. This common principle in water movement, employed by serially arranged appendages in alignment with each other, seems here to be provided for only in the bilamellate structure of each gill. The net result arising from the arrangement described would be that the animal is enabled to explore water from all sides of its body, *i.e.* from above, from the sides, and from below, and to produce a flow from before backwards in general alignment with the body axis.

It has been observed in many Arthropoda that limbs which move normally in a particular rhythm are able to accommodate themselves to changes introduced into the rhythm by amputation of odd limbs. This accommodation expresses itself in a change of rhythm in the remaining limbs, so that limbs hitherto moving synchronously may alternate in movement and *vice versa* (Von Holst, 1935). These phenomena appear to have no place in the movement of mayfly nymphal gills. For instance, to examine in greater detail the movements of a single gill all but that gill may be removed from that side, those of the other side of the body remaining intact. Or, the better to analyse the difference of phase between adjacent gills in series, alternate gills may be removed from one side, all those on the other side again remaining intact. In these cases and many others of a similar nature no alteration from the original rhythm or from the original manner of movement was observed.

Von Holst's review tells us that the factors concerned in co-ordination of arthropod limb movement are the stimulation of proprioceptors of the limbs themselves, and the way in which the nervous impulses entering the central cord disintegrate in their passage to other segments or from one side of the body to the other. While there is as yet no agreement as to the physiological mechanism involved in co-ordination in the Arthropoda, the apparent absence of any power of this mayfly nymph to accommodate the rhythmical movements of its gills to conditions of amputation would suggest that the factors governing co-ordination are different from those applying to arthropod legs. It may be mentioned in passing that the nymphs of *Caenis* showed a similar inability to alter the original rhythm after amputations.

## SUMMARY

1. The currents produced in water by the gills of the nymph of *Leptophlebia* are symmetrical with the body axis. The gills which lie at different angles with the body explore water above, at the sides and below the animal.

2. Each gill in movement shows a backward effective beat sharply defined from a forward recovery beat. In the latter the gill meets the water, edge forwards. In the former (effective) the gill moves through the water with its leading surface

making an angle with its own path of motion. The forces involved are similar to those invoked for fish motion.

3. Each gill is a bilamellate structure, and a significant thing in water movement is the compression of water from between anterior and posterior lamellae during effective parts of an oscillation.

4. The symmetry of the current is related to the synchronous movements of members of pairs of gills.

5. After amputation of certain of the gills there appears to be no modification in the rhythmical movements of the remainder.

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