

THE ABDOMINAL MUSCULATURE OF NYMPHAL *CHLOEON*
DIPTERUM L. (INSECTA: EPHEMEROPTERA) IN RELATION TO
GILL MOVEMENT AND SWIMMING

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(With 7 figures in the text)

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INTRODUCTION

Chloeon dipterum L. as a nymph, inhabits stagnant waters and is probably in many regions the commonest ephemeropteran of ponds. It may be found in all parts of the water body—on the substratum at some depth as well as among water weeds near the surface. It moves with rapidity, propelling itself by means of lateral rhythmical movements of its abdomen which behaves in this respect much as does the tail of a fish in swimming and this in spite of the fact that the fringed caudal filaments lie in the horizontal plane and appear to be more likely to bring about progression in the manner of a whale.

It is thus a pelagic creature and presents a different type of environmental adaptation from those previously dealt with by me, viz. *Leptophlebia*, *Ephemera*, *Caenis* and *Ecdyonurus* (Eastham, 1932; 1934; 1936; 1937 and 1938).

The purpose of this paper is to describe the gills, the currents set up by them over the body and the muscular mechanisms which make these and swimming possible.

The techniques employed are similar to those previously employed except that cinematography has been resorted to to amplify observations made by means of the stroboscope.

The features described here are specific to *Chloeon dipterum* L.

THE GILLS

Figs. 1 and 2.

On each of the first seven segments of the abdomen is a pair of gills borne on the posterior-lateral angles of the segments. Those of the first segment

consist each of a circular plate articulated to the body by a short stalk and carrying on its anterior face a lanceolate lamella. This lies over the middle part of the circular lamella with which it makes slight contact at its distal extremity. The gills of the seventh segment are similar in form to this except that they possess no anterior lamella.

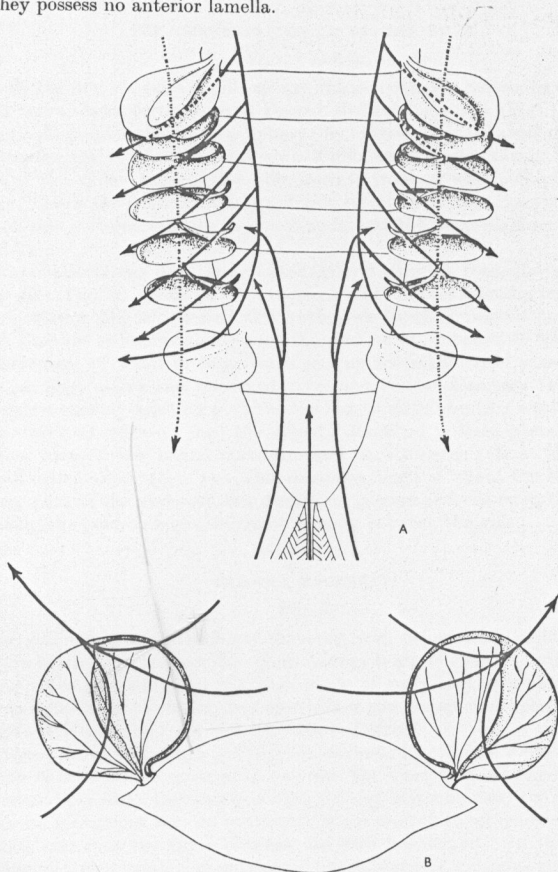


Fig. 1.—A. Dorsal view of the abdomen of *Chloeon* to show the main water currents.
B. Transverse sectional view of a gill bearing segment as seen from in front.

Each gill on segments 2 to 6 is circular in form and concave anteriorly. Its anterior lamella is semicircular coinciding with the median half of the

posterior circular lamella over which it lies (Fig. 1). Each such anterior lamella is also concave in front with its median border turned forwards for all its length and its lower lateral border also turned forwards so as nearly to meet the posterior surface of the gill next in front. For the remainder of its length the lateral edge of the anterior lamella is flat. In motion it will later be shown that the anterior lamella of a gill applies itself to the surface of the gill in front of it thus enclosing a space between them which is open to the environment dorso-laterally where this flattened border occurs.

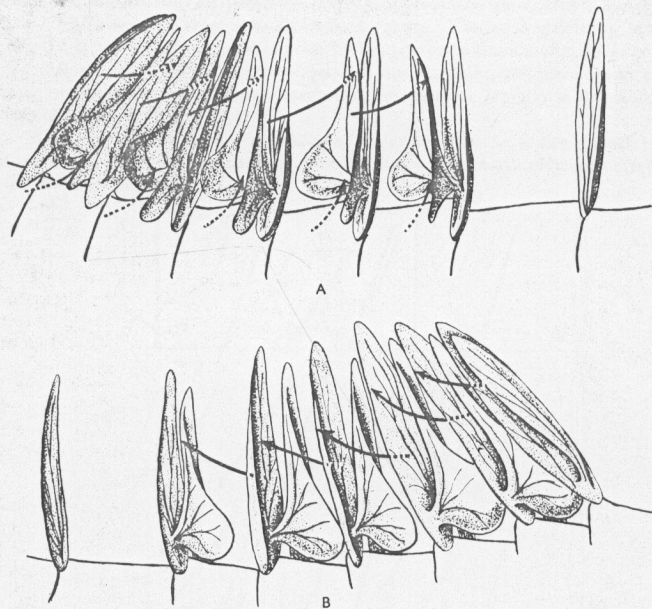


Fig. 2.—A. The gills of the right side as seen from the middle line of the body.

B. The gills of the right side as seen from the outer side of body. Note the gaps between posterior and anterior lamellae of adjacent gills through which water escapes to the side.

The gills are disposed in such a way that their surfaces, held more or less erect, are roughly at right angles to the longitudinal axis of the body. Those of the last gill bearing segment are perpendicular, those in front of it tilting backwards towards them. The more anterior the gill the more is the gill tilted backwards at an angle with the perpendicular, (Fig. 2), thus producing a crowding effect of the anterior gills of a side.

This disposition of gills bringing them into close contact with each other in each lateral series is important in bringing about precise water currents when the gills are put in motion.

THE CURRENTS SET UP BY THE GILLS

Figs. 1 and 2

Only the first six pairs of gills move—the seventh pair remaining stationary at all times, held vertically and turned slightly outwards (Figs. 1 and 2). Movement occurs in short bursts followed by longer periods of absolute rigidity.

Between the two longitudinal rows of gills water passes slowly backwards entering the valley between the gills from in front at each side of the wing cases. This is the median antero-posterior current and from it water is drawn to each side between the gills in a postero-lateral and upwards direction (Figs. 1 and 2).

Water also passes into these postero-lateral currents from above the level of the gills (Fig. 1). Such parts of these currents as pass laterally between the more posterior gills is deflected well to the side by the immobile posterior gill which thus act as buffers giving a pronounced lateral direction to the water.

Movement of water in these ways sets up several induced currents. For instance from above the upcurved cerci and caudal filaments there passes forwards a current reaching as far as the last three gill-bearing segments there to be deflected sideways into the already described postero-lateral currents. Another induced low lateral current passes back at each side at the level of the gill articulations (Fig. 1). This dissipates itself at about the level of the last segment of the abdomen but during its passage it feeds from the sides of the body the postero-lateral currents passing between the gills.

THE GILL MOVEMENTS

Fig. 3.

The gills move in metachronal rhythms from before backwards, members of pairs beating synchronously. This rhythm being of such an order that the second gill is found to be in the same phase of movement as is the sixth. It follows from this that phases of suction and of compression between neighbouring gills in series follow one another with regularity.

When, for instance (i) a gill is in its backward path it is a little ahead of the gill next behind it so tending to close the space between them. On the other hand (ii) when the hinder of these two gills has reached the limit of its backward movement the one in front of it has started to return to its forward position and thus the space between the gills is enlarged. In this example the first is a compression phase during which water is squeezed out from the inter-gill space, the second a suction phase in which water is drawn in to fill that same inter-gill space. The direction from which the water is drawn (suction) and in which it is subsequently forced (compression) depends on the precise form of the gill and the turning movements performed during its oscillations.

The effective space between serially adjacent gills appears to be that between an anterior lamella of a gill and the posterior lamella of the gill next in front of it. This is disclosed by both the stroboscope and by cinematograph films. The spaces between anterior and posterior lamella of gills themselves is fairly constant and little affected by the metachronal movements. It would appear then that the anterior lamella is a device to bridge the gap between neighbouring gills of a series; this gap being determined by the length of the body segments (Fig. 2).

Let us consider the gills of one side of segments 4 and 5. As gill 4 begins to move backwards, its posterior lamella approaches the anterior lamella of gill 5 which now also starts to move backwards. The lagging anterior lamella of gill 5 is now closely pressed against by the posterior lamella of gill 4 so enclosing a space from which water is squeezed out laterally and upwards at those very points where the lateral border of the anterior lamella is flat and not forward-curved (Fig. 2).

Posterior and anterior lamellae of adjacent gills in series therefore fit together to form something like pipette bulbs with asymmetrical outlets to the sides and upwards.

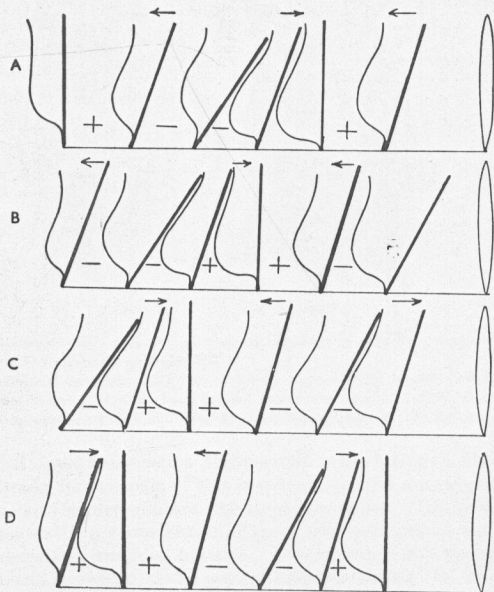


Fig. 3.—A, B, C, D. Four phases of gill movements of a series of one side to show the nature of the metachronal rhythm and the pressures set up between the gills when in motion. For further explanation see text.

A lateral impetus is thus given to the water between these lamella. When next the gills begin to separate from each other as for instance when gill 4 begins its forward movement, water is drawn in from above the middle line of the body. This is made possible by the greater forward curvature of the lateral border of the anterior lamella which tends to maintain contact with the posterior lamella in front of it for a longer time than does its median (less curved) border.

Fig. 2, A and B is an attempt to depict the gills of a series as seen from both median (A) and lateral (B) aspects and there is shown the close packing of the gills brought about partly by the leaning of the gills towards those next behind in the series and the effective filling up of the space between the gills by the strongly curved anterior lamella.

The movements of individual gills—all but one having been removed—were observed and these were seen to be of such an order as to direct water from above the middle line of the body to the side. Each gill in its backward movement rotates on its stalk of attachment so as to turn the anterior face upwards and outwards to the side of the body. In this action not only is water behind the gill pressed backwards but such water as lay on the anterior surface at the beginning of the beat is baled sideways. Such an action clearly reinforces the currents set up by the metachronal movements of the gills in series, but is regarded as playing a relatively insignificant part in current creation.

Fig. 3 is a diagram taken from cinematograph films of the gills in movement and shows in series four phases of gill activity, the rhythm being such that a gill is in the same phase of movement as is the one five segments next behind it. In each of the four phases the stationary erect posterior gill is to the right of the diagram. The direction of movement of the gills is shown by arrows and the pressures set up between neighbouring gills, by + and - signs.

THE ABDOMINAL AND GILL MUSCULATURE

The muscles of the abdomen in gill bearing segments are modifications of the normal longitudinal and dorso-ventral muscles which occur in insects in general.

They serve two functions, viz. to move the abdomen in such a way as to propel the animal through the water and to oscillate the gills so as to create water currents over the body.

Longitudinal muscles Figs. 4, 5 and 6.

On each side of the middle line both ventrally and dorsally strong longitudinal muscles pass between the anterior borders of tergites of successive segments and similarly between the anterior borders of sternites.

Each such longitudinal muscle, whether dorsal or ventral, has a disposition which is peculiar to these animals. Thus taking those of one side dorsally as an example, we find that the main muscle mass of a segment is divided into two bands which cross each other in each segment to produce a cruciform effect (Fig. 4). This is effected in such a way that half the muscle passes from a more median origin on the tergite's anterior border to a more lateral insertion on the anterior border of the tergite next behind it. The other half passes

under this in precisely the opposite direction, namely from a more lateral origin on the tergite's anterior border to a more median insertion on the anterior border of the tergite next behind.

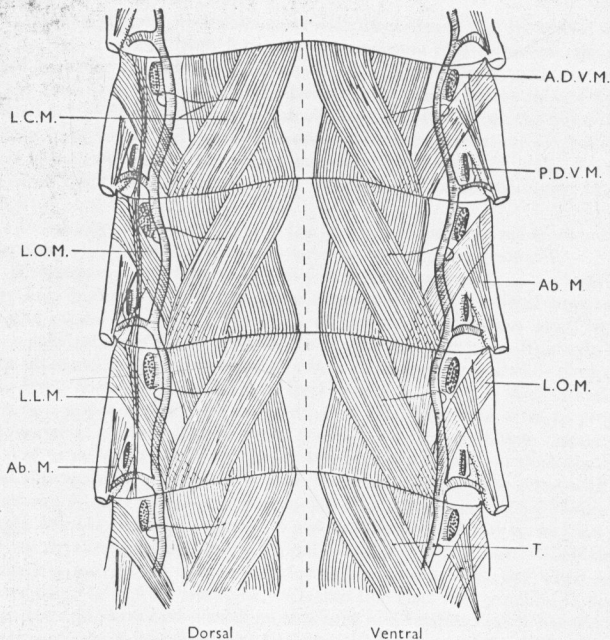


Fig. 4.—The muscles of three adjacent gill bearing segments as seen by transparency dorsally on the left and ventrally on the right.
 Ab.M. Abductor muscle; A.D.V.M. Anterior dorso-ventral muscle; L.L.M. Lateral longitudinal muscle; L.C.M. Longitudinal cruciform muscle; L.O.M. Lateral oblique longitudinal muscle; P.D.V.M. Posterior dorso-ventral muscle; T. Trachea.

The plaited appearance which the muscles present is well illustrated in Figs. 4 and 5. A further part of this same longitudinal muscle mass has its anterior origin on the pleuro-lateral border of the tergite. This passes mesiad to its insertion on the anterior border of the tergite next behind but lateral to the already described cruciform muscles. This lateral muscle passes between the anterior and posterior dorso-ventral muscles shortly to be described (Figs. 4 and 5). I will call this the *lateral oblique longitudinal* muscle. Laterally a narrow muscle strand passes dorsally between one segment and the next behind it, in a direction more or less parallel to the longitudinal body axis.

This muscle which I will call the *lateral longitudinal muscle* also passes in its course between the anterior and posterior dorso-ventral muscles (Fig. 4).

The ventral longitudinal muscles have a similar disposition except that there appears to be no counterpart to the slender lateral longitudinal muscle of the dorsal series described above (Fig. 4). Reference to Figs. 4 and 5 obviates any further description of these.

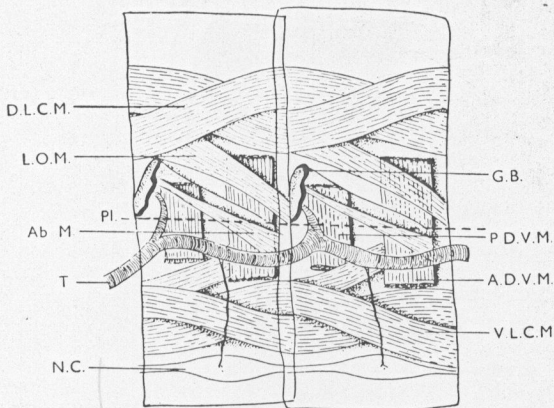


Fig. 5.—The muscles of two neighbouring gill bearing segments seen by transparency from the right side, tergal (above) and sternal (below) regions shown as if flattened out in one plane.

Ab.M. Abductor muscle; A.D.V.M. Anterior dorso-ventral muscle; D.L.C.M. Dorsal longitudinal cruciform muscle; G.B. Gill base; N.C. Nerve cord; P.D.V.M. Posterior dorso-ventral muscle; T. Trachea; V.L.C.M. Ventral longitudinal cruciform muscle; Pl. Tergo-sternal junction. (*Lateral longitudinal muscle not shown*).

The Dorso-ventral muscles

The dorso-ventral muscles—those passing between tergite and sternite have similarly become divided into separate units.

The first is an anterior dorso-ventral muscle, lateral to the main longitudinal muscles as well as to the longitudinal trachea of the body. It lies in the angle between the cruciform muscles and the lateral oblique longitudinal muscle (Fig. 4).

The second is a posterior muscle passing from its origin on the sternite of a segment, upwards vertically to the raised part of the body wall on which the gill is inserted. This muscle is shorter and weaker than its anterior counterpart.

The third muscle of this series passes, from its origin on the sternite anterolaterally, to its insertion on the tergite above on the outer wall of the gill base. It passes upwards and backwards in its course (Fig. 5). Because this muscle passes between sternite and tergite—however obliquely—it would appear

clearly to be a modification of the normal dorso-ventral muscle group. I will call it the abductor muscle since from its attachment to the gill base (Fig. 5) it causes the gill to turn outwards. Much of the movement of the abdomen as a whole and the gills in particular can be inferred from the disposition of the muscles.

The nymph holds itself stationary with its abdomen slightly curved upwards at its tip. It flicks itself forwards by increasing this curvature, raising and then lowering its widely spread out caudal filament in a sudden movement. Thus the thrust comes from the horizontally placed setose caudal filaments which in this first movement are moved up and down as are the tail flukes of a whale. As far as can be ascertained by direct observation or photography this is the only time when such a method of propulsion is used. Dorsal and ventral longitudinal muscles of the last segments of the abdomen bring this about.

In subsequent swimming, once the first thrust has been made, the abdomen together with its caudal filaments behaves in the piscine manner.

C. dipterum swims by rhythmical side to side movements of the body. This rhythm, produced by the cruciform muscles already described, imparts itself to the caudal filaments. The track of such movements can often be traced on a substratum of silt over which the caudal filaments move from side to side. The filaments are now held relatively close to each other and while photography has given no very clear picture of their precise attitudes in their lateral movements it appears that they are rotated on their long axis so as to present to the water at the side against which they are moving an oblique surface. This is due to an outer leading filament being at a higher level than the median and this again at a higher level than the remaining one, the setae with which they are fringed forming a semblance of a membrane. The filaments are freely flexible and it is difficult to see how they could fail to respond to the lateral rhythm imposed by the abdominal segments in front. They thus are caused to move from side to side turning as does a single oar when used for propelling a boat from the stern. We thus find that the nymph of *C. dipterum* uses both cetacean and piscine mechanisms and further that it has the ability to convert the former into the latter method of locomotion. The cruciform disposition of both dorsal and ventral muscles of the longitudinal series can easily account for the piscine method of locomotion, i.e. by rhythmical lateral waves of movement about a vertical axis passing down the body. It seems reasonable to regard the cruciform longitudinal muscles as the result of a modification of normal uncrossed segmental muscles. By the separation of these into muscles orientated in opposite directions in each segment, opposing or antagonistic muscles have been brought into being. Thus as explained diagrammatically in Fig. 7 a muscle passing medianwards from before backwards can on contraction on a fixed anterior origin move the posterior boundary of its segment to the left side. In so doing it puts its crossing antagonistic member (this passing lateralwards from before backwards) into a state of tension, stimulating this in turn to contract. The result of this is to swing the posterior boundary of the segment in the direction opposite to that already undergone i.e. from left to right. Successive segments from before backwards,

being brought in sequence under the corresponding muscle action, must therefore oscillate about a vertical axis and so with the help of the setose caudal filaments bring about forward propulsion through the water in much the same way as happens in fishes.

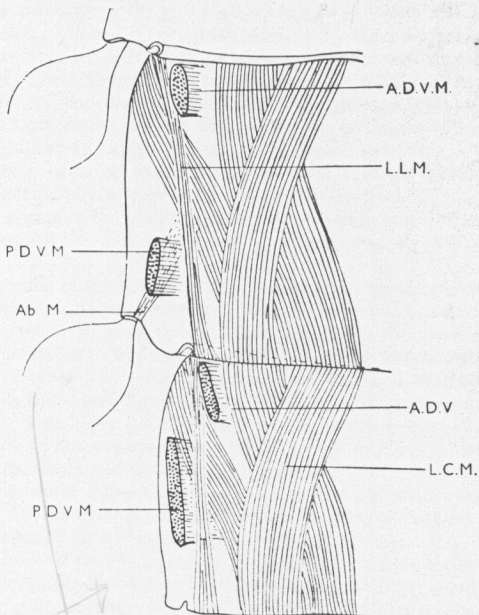


Fig. 6.—Muscles of the last gill bearing segment and the segment next behind it as seen dorsally. Ab.M. Abductor muscle; A.D.V.M. Anterior dorso-ventral muscle; L.L.M. Lateral longitudinal muscle; L.C.M. Longitudinal cruciform muscle; P.D.V.M. Posterior dorso-ventral muscle.

The majority of swimming insects propel themselves by their legs. Those that move by abdominal movements e.g. *Ephemera danica* do so by rather clumsy up and down movements about a horizontal transverse axis. Examination of the longitudinal muscles in such a case, shows no cruciform disposition.

All the other muscles would appear to have functions related to gill rather than body movement.

The insertion of each gill on its base is by way of a flexible arthroial membrane and therefore any muscle attached to the base is able only indirectly to cause gill movements. I nevertheless propose to regard these muscles now under consideration as the direct muscles of the gills. The posterior dorso-ventral muscles depress the gill base and hence must elevate the gill. The

abductor muscle pulls on the outer border of the gill base and thus causes the gill to rotate outwards on its insertion.

The lateral oblique muscles of the longitudinal series would appear to pull indirectly on the gill base of the segment next in front (Fig. 4) and thus further assist the posterior dorso-ventral muscle to this end.

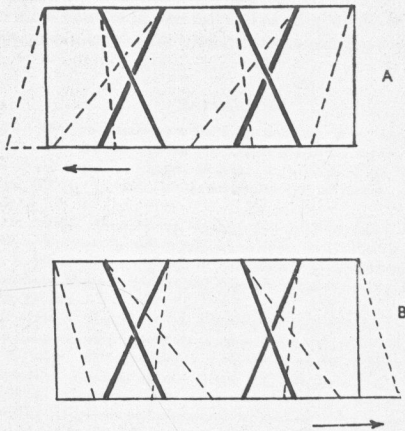


Fig. 7.—Diagram of the cruciform muscles of a segment and the effect on that segment of the contraction of one element of the cruciform series in bringing the posterior boundary of the segment A, to the left, assuming the anterior segmental border to be fixed, and B, to the right.

Before contraction : muscles and segmental boundaries in full line.

After contraction : muscles and segmental boundaries in broken line.

The disposition then of the muscles can explain much of gill movement, always having regard to the important factor of elasticity of the cuticle in the concerned regions which must account for part of the movement at the end of a muscle's contraction.

It is interesting to note that the musculature of the last gill-bearing segment (Fig. 6), differs in no appreciable manner from that of the segments immediately in front, and this in spite of the fact that these gills are immobile. On segment 8 of the abdomen (Fig. 6), there is no abductor muscle, a feature that might well be expected since no gill is present there. The posterior dorso-ventral muscle, which in gill-bearing segments is short and small, is here widely extended in its insertion and origin and is more anteriorly placed than in gill-bearing segments thus presumably concerned with normal segmental activity from which perhaps gill musculature and movement has evolved.

DISCUSSION

That the currents set up by gill movements in *Chloeon* are probably of importance only when the water is deficient in oxygen is shown by the increased activity of the gills under the latter conditions. This has also been proved by the findings of Wingfield (1939). But that they have a function to perform in irrigating the gills themselves and the body surface would seem clear from the precision of the currents set up by the gills in motion. This is further substantiated by the means whereby it is ensured that fresh water, as distinct from that already used and presumably robbed of some oxygen, is explored by gill movement. Thus the most posterior gills serve to deflect used water away from the body and prevent the setting up of vortical currents which would merely exploit the same water time after time.

That water from all surrounding regions is explored by the currents set up seems adequately to reflect the pelagic habit of the animal. For though most of it passes over the animal from above and in front of the body, other currents supply the gills from below the body level at each side and from behind.

The question of the homology of gills with other structures depends largely on musculature. Börner (1908) regards gills as homologous with true limbs since they appear to arise embryologically in much the same way as do the legs. The embryonic buds on the abdomen which are serially homologous with those destined to form appendages on the head and thorax, become converted in Ephemeroptera into gills. Arguing from this point Börner (1908) proceeds to homologise the dorso-ventral gill muscle (elevator) with the subcoxal muscle of the thoracic limb and the direct rotatory (abductor) muscles with the coxotergal and coxo-subcoxal muscles.

Börner however refuses to homologise tracheal gills with wings as does also Dürken (1907) on grounds of musculature though he disagrees with Dürken in that the latter author regards gills as of tergal origin.

On grounds of pure morphology as distinct from development, the gills of *Chloeon* do appear to be tergal structures and without going so far as to homologise gills with wings as was suggested by Gegenbaur (1878) and Heymons (1896), there would seem to be good grounds for regarding the musculature of the lateral regions of the gill-bearing abdominal segments as evolutions of the longitudinal and dorso-ventral muscles of an unmodified body segment, analogous to the muscle changes which have occurred in wing-bearing segments of the thorax.

The cruciform arrangement of the longitudinal muscles of the abdomen is peculiar and would appear to be a caenogenetic adaptation subserving the purpose of locomotion in an animal which has become an expert swimmer using its abdomen rather than its limbs as is more usual in aquatic insects.

SUMMARY

1. The nymph of *Chloeon dipterum* is a pelagic animal living in ponds. Its plate-like bilamellate gills are described.
2. By means of metachronal rhythmical movements of the gills, in which members of pairs beat synchronously, currents of water are set up over the

body. These currents which are on the whole axial to the body explore water from all regions surrounding the body.

3. The gill and abdominal musculature is described and it is shown that a modification of normal musculature has occurred to provide direct muscles to the gill bases and also to make possible the habit of swimming by rhythmical movements of the abdomen rather than by limbs. These movements are lateral and are made about a vertical axis. Swimming is always preceded by a vigorous up and down movement of the caudal filaments. This movement about a transverse axis as in the tail flukes of a whale is then abandoned as the side to side movements of the abdomen take charge, when the animal swims as does a fish.

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