

WATER SKATING IN THE LARVAE OF *DIXELLA AESTIVALIS* (DIPTERA) AND *HYDROBIUS FUSCIPES* (COLEOPTERA)

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Summary

The kinematics of locomotion was investigated in the aquatic larvae of *Dixella aestivalis* and *Hydrobius fuscipes* with the aid of high-speed video recordings. Both insects are able to skate on the surface of the water using the dorso-apical tracheal gill as an adhesive organ or 'foot'. Progress relies on the variable adhesion of the foot between 'slide' and 'hold' periods of the locomotory cycle. The flexural body movements underlying skating in *D. aestivalis* can be derived directly from the figure-of-eight swimming

mechanism used in underwater swimming. The latter is shown to be similar to figure-of-eight swimming in chironomid larvae. This study shows how the deployment of a 'foot' enables simple side-to-side flexural movements of the body to be converted into effective locomotion at the air–water interface.

Key words: water skating, kinematics, locomotion, air–water interface, *Dixella aestivalis*, *Hydrobius fuscipes*.

Introduction

The limbless, wormlike planform is widespread throughout the animal kingdom from vertebrates such as eels, snakes and amphibia to invertebrates such as nematode, nemertine and annelid worms and various insect larvae (Gray, 1968; Trueman, 1975). As opposed to pedestrian locomotion (for reviews of invertebrate pedestrian locomotion, see Herreid, 1981; Full, 1994), propelling a limbless body on land requires serpentine or concertina movements, as seen in snakes (Jayne, 1986; Jayne and Davis, 1991; Secor et al., 1992), or telescoping of the body segments, characteristic of earthworms (Gray and Lissman, 1938), caterpillars (Barth, 1937; Casey, 1991; Brackenbury, 1997) and terrestrial fly (Berrigan and Lighton, 1993; Berrigan and Pepin, 1995) and beetle (Crowson, 1981) larvae. Special forms of limbless jumping in tephritid (Maitland, 1992) and cecidomyiid (Imms, 1964) fly larvae have also been described. Telescopic locomotion is only effective when the insect is crawling across or tunnelling within a solid or semi-solid medium, and limbless aquatic insect larvae, particularly dipterous, employ a variety of lashing movements of the whole body to achieve propulsion through frictional drag. Whereas ceratopogonid and chironomid larvae rely entirely on undulations of the body itself to achieve locomotion (Nachtigall, 1961), culicid larvae and pupae increase the efficiency of swimming using paddles at the end of the abdomen (Nachtigall, 1962a, 1963, 1974).

In this study, I show that the simple side-to-side flexural movements of the body responsible for swimming in aquatic insect larvae can be adapted, through the intervention of a tracheal gill modified to serve as a variable-resistance 'foot',

to produce a novel kind of limbless skating at the air–water interface.

Materials and methods

The insects studied were freshwater larvae of *Dixella aestivalis* (Diptera, Dixidae) and *Hydrobius fuscipes* (Coleoptera, Hydrophilidae). Comparative observations were also carried out on *Chironomus plumosus* (Diptera, Chironomidae). The insects were collected between May and September 1998 from local ponds in Cambridgeshire and kept in a container measuring 20 cm×30 cm wide and 20 cm deep. Observations were carried out only on final-instar larvae measuring approximately 0.5–0.6 cm in length, usually on the day of collection. Both main species spend most of their time moving about and resting within the surface film: *D. aestivalis* is a filter-feeder, whilst *H. fuscipes* is carnivorous, feeding on small invertebrates and carrion found amongst the floating detritus. Water temperature was 18–22 °C, and illumination for filming was *via* daylight coming in through the laboratory window. More than 30 individuals of each species were filmed, although mean values are based on 20 individuals in each case. Locomotion was recorded using a NAC 400 high-speed video camera (NAC Incorporated, Japan) with inbuilt stroboscopic illumination giving 200 and 400 frames s⁻¹ and a Panasonic KS 152 video camera (Matsushita Communication Industrial Co. Ltd, Japan) giving 50 half-fields s⁻¹ and illuminated by a Drelloscop 1018 stroboscope (Drelloscop, Germany). Data were recorded on video cassette recorders equipped with a frame-by-frame playback facility for detailed image analysis.

Results are expressed as mean values ± 1 standard deviation (S.D.).

Results

Locomotion of Dixella aestivalis larvae

Although *D. aestivalis* larvae are often reported as resting upon the water surface supported by the surface tension film, the body in fact floats horizontally just below the surface attached only by the water-repellent tracheal gill situated dorso-apically on the abdomen (Fig. 1A). The larvae are metapneustic, the two main tracheal trunks terminating in a plexus of fine branches in the neighbourhood of the spiracles (Imms, 1964). In addition to functioning as the organ of gas exchange and flotation, the gill can serve as a 'foot' to propel the body across the surface in a form of 'skating'. Movement is powered by rhythmical side-to-side flexures of the body performed at a frequency of 3 Hz. Fig. 2 illustrates the kinematics of locomotion. Starting arbitrarily with the body fully flexed to the left (stage 1), the larva extends forward against the foot which, at this stage, remains anchored to the surface tension film (stage 2). Next, flexure to the right draws the foot forwards and simultaneously pulls the head backwards through half a body length (stage 3). With the foot fixed for a second time, the body again extends (stage 4), but at an angle of approximately 45° ($46.4 \pm 9.5^\circ$, $N=19$) to its previously extended position. Finally, flexure to the left completes the cycle, drawing the foot forwards through a further half body length. Geometric considerations show that, with a divergence angle of 45° between left and right extensions, in what could loosely be described as the 'stance' phase of the foot (Fig. 2B), the resultant stride length per cycle of locomotion should be

Table 1. Kinematic variables for *Dixella aestivalis* and *Hydrobius fuscipes* moving at the air-water interface

	<i>D. aestivalis</i>		<i>H. fuscipes</i>
	Skating ($N=20$)	Swimming ($N=20$)	Skating
Body length (cm)	0.55 ± 0.15	0.47 ± 0.07	0.58 ± 0.14 ($N=6$)
Stroke frequency (s^{-1})	3.0 ± 0.5	2.8 ± 0.5	1.0 ± 0.1 ($N=12$)
Distance per stroke (cm)	0.53 ± 0.08	0.39 ± 0.12	0.54 ± 0.08 ($N=28$)
Speed ($cm\ s^{-1}$)	1.6 ± 0.3	1.1 ± 0.3	0.54*
Relative speed (body lengths s^{-1})	2.9*	2.3*	0.93*

Values are means \pm S.E.M.
*Calculated values.

0.92 body lengths, practically the same as the measured value (Table 1).

Kinematically, the foot tacks from side-to-side along a zig-zag path consisting of a series of hold points, where its forward velocity is approximately zero (Figs 2C, 3), linked by sections of sliding where its forward velocity is equal and opposite to that of the head. Mechanically, the body behaves like a pair of compass arms hinged at the centre, the posterior half resisting the backwards drag force on the anterior part during the opening (extension) phase, then being drawn forward by the anterior half during the closing (flexion) phase. The foot and

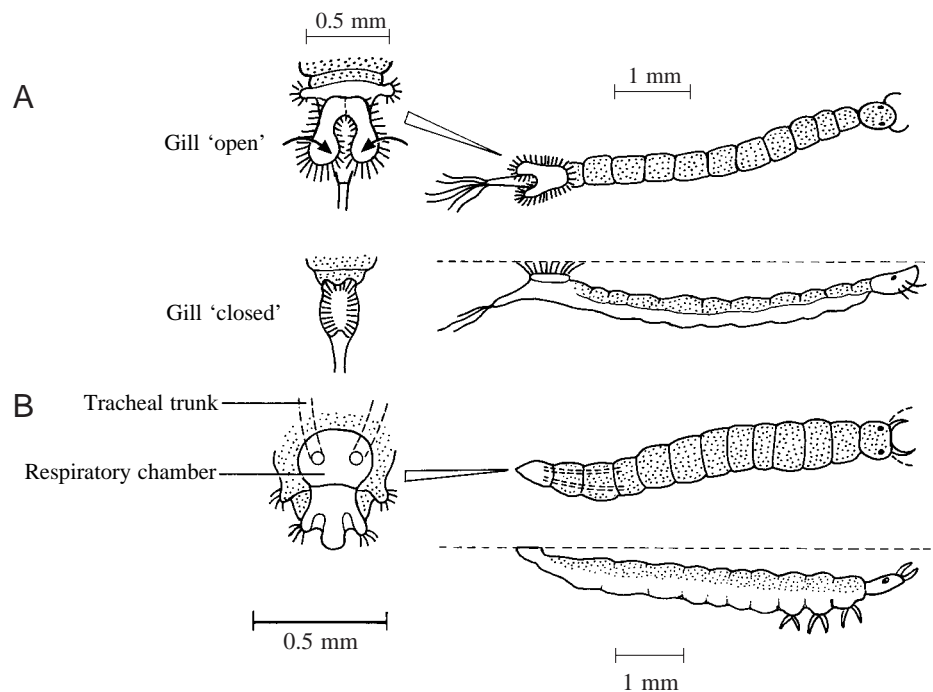


Fig. 1. Dorsal (upper drawing) and lateral (lower drawing) views of *Dixella aestivalis* (A) and *Hydrobius fuscipes* (B) larvae floating at the surface of the water. Enlarged drawings on the left show details of the tracheal gills. Arrows in A indicate the direction of the infolding of the lobes of the tracheal gill of *D. aestivalis* during submergence.

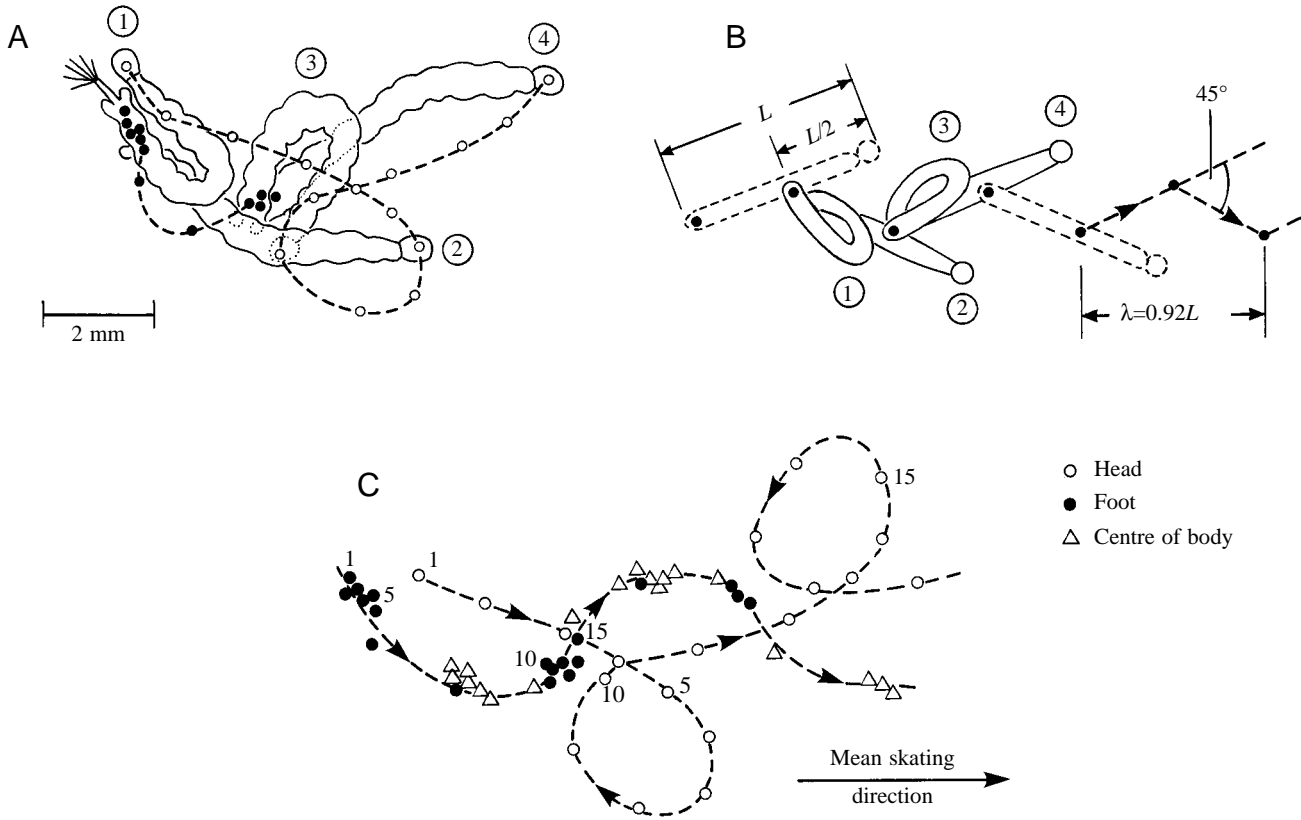


Fig. 2. (A). Diagram showing the movements of the body of a larva of *Dixella aestivalis* during surface skating. Open and filled circles indicate the path of the head and abdominal tip, respectively, at 20 ms intervals. (B) Schematic interpretation of the locomotory cycle. Numerals refer to corresponding body positions in A. Hold positions of the 'foot' are signified by single filled circles. Assuming that the foot is drawn forward by 0.5 body length ($L/2$) with each flexion (stages 1, 3, etc.) and that consecutive extensions (stages 2, 4, etc.) occur at 45° to one another, the stride length λ is equal to $0.92L$. (C) Paths traced out by the head, foot and centre of the body during consecutive 20 ms intervals during the skating cycle. Numerals indicate frame numbers.

the centre of the body follow the same path through the water (Fig. 2C), indicating that the posterior 'arm' of the body moves in a direction approximately parallel to its own longitudinal axis and therefore incurs relatively little frictional drag. In contrast, the anterior 'arm' weaves a cycloidal path from side to side about the mean locomotory path (Fig. 2C). Forward propulsion is given to the body during the closing phase when the anterior 'arm' is moving backwards (Fig. 3); Fig. 3 also shows that the centre of the body only accelerates forwards during the flexion phase.

Technically, skating in *D. aestivalis* larvae can be regarded as a hybrid of walking and swimming because, although progress depends on the variable adhesion of a 'foot' during the 'stance' (extension) and 'swing' (flexion) phases of

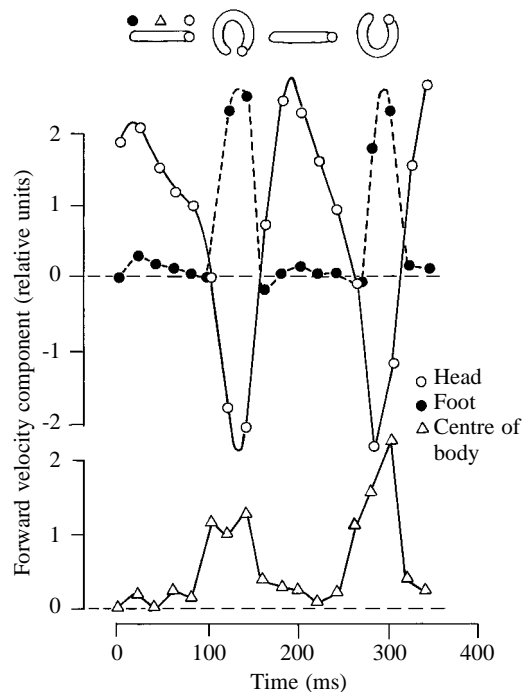


Fig. 3. Forward velocity components of the motion of the head, foot and centre of the body during the skating cycle of a *Dixella aestivalis* larva. Note how the head oscillates back and forth during flexion and extension, whereas the foot is motionless during the extension phase (phases are shown by cartoons above the graph). The stationary foot resists the backward force produced by viscous drag on the head during the extension phase. Velocity is given in arbitrary units. The mean forward velocity of the centre of gravity is 1.6 cm s^{-1} (Table 1).

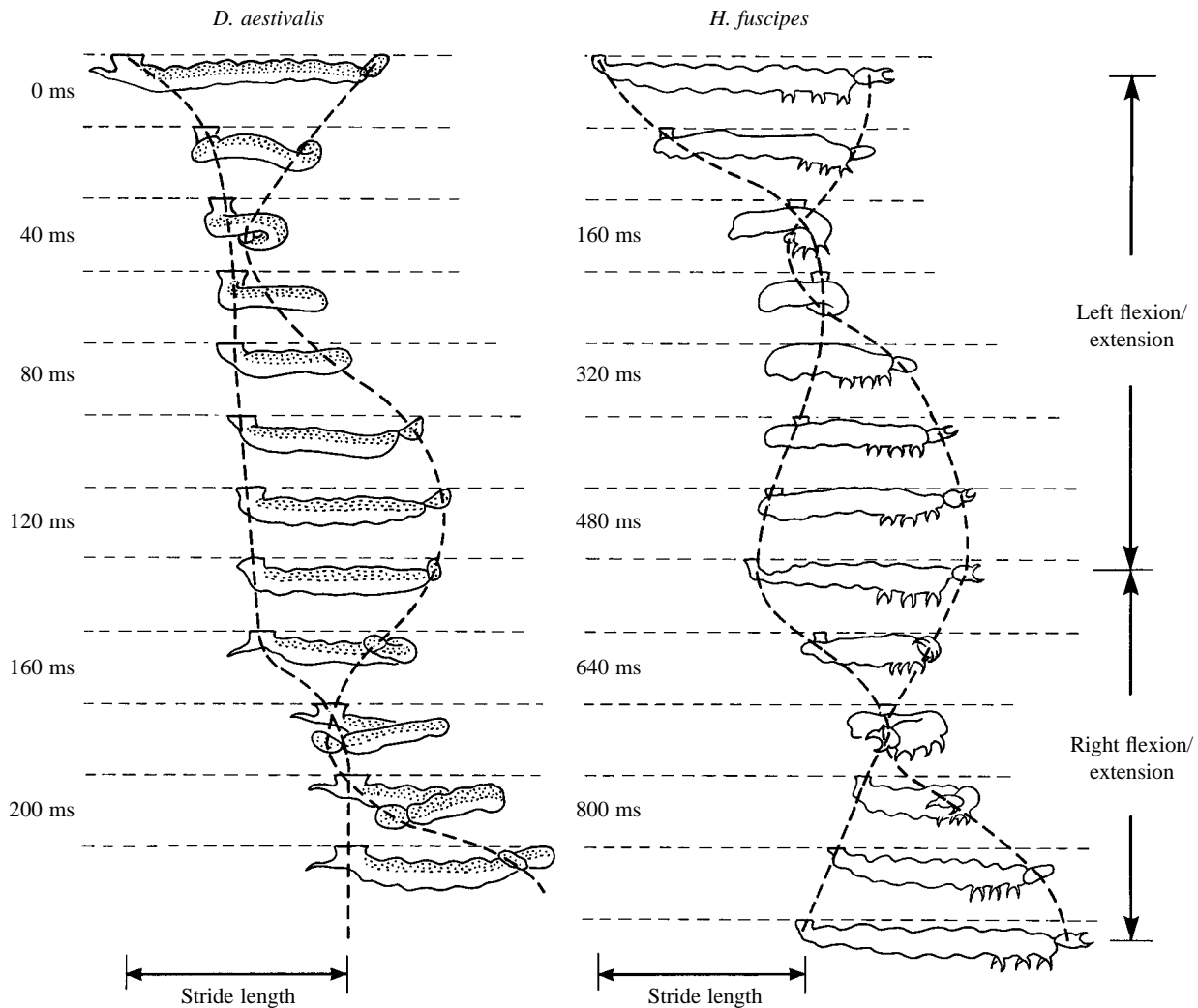


Fig. 4. Lateral views of *Dixella aestivalis* and *Hydrobius fuscipes* larvae during a complete skating cycle. Bold broken lines trace the forward/backward movement of the head and foot. Note how in *D. aestivalis* the foot is drawn forward during flexion and remains anchored during the ensuing extension, whilst in *H. fuscipes* the foot is drawn forward during flexion but slips partly backwards during the next extension. The horizontal dashed line indicates the water surface.

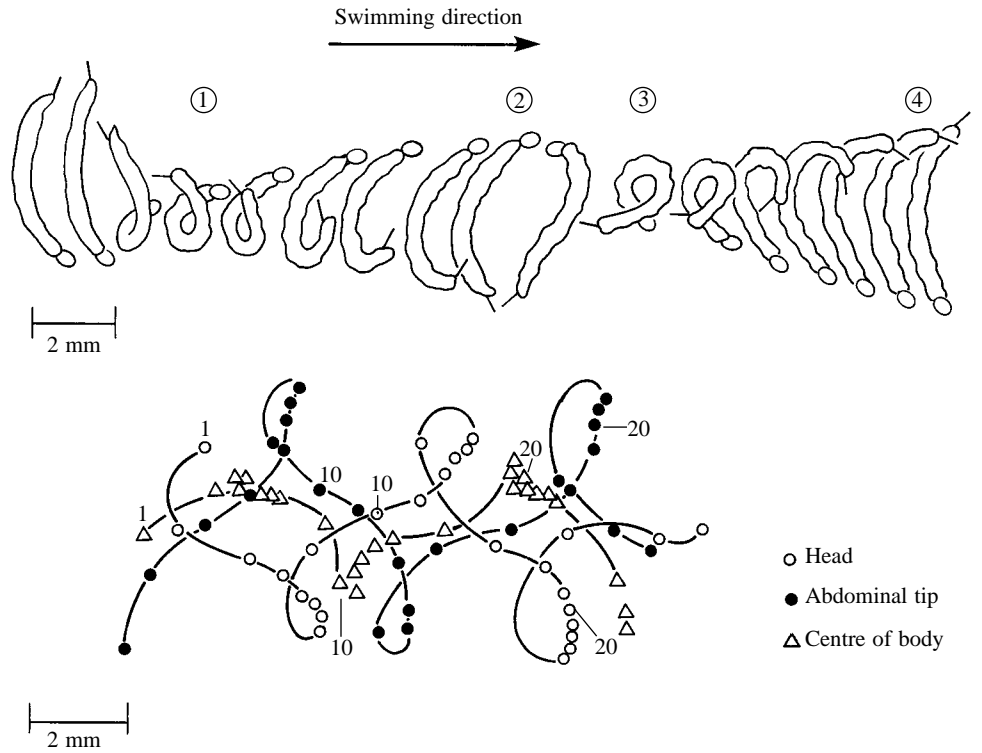
movement, the forces experienced by the body are hydrodynamic in nature. Videographs taken from obliquely below the water-line show that the foot does not lose contact with the surface film at any point during the cycle (Fig. 4). Its ability to hold firm during extension and to slide freely during flexion presumably depends on phase-to-phase variations in the contact angle between the water surface and the hydrophobic surface of the hair-fringed gill (see Fig. 1A), leading to corresponding changes in local surface tension.

In a completely immersed *D. aestivalis* larva, the lobes of the tracheal gill become automatically drawn closely together around a residual air bubble, therefore effectively stowing away the 'foot' (Fig. 1A). Side-to-side flexural movements of the body, with the same frequency as those employed during skating, now result in a form of a swimming in which the body progresses forward in an alternating series of clockwise and anti-clockwise half-turn rolls (Fig. 5A), each rotation

corresponding to a single left or right flexion/extension cycle. The absence of the constraint imposed on the motion of the body by the surface-active foot during skating can now be seen; both head and foot are free to undergo cycloidal movements about the mean swimming pathway (Fig. 5B). The forward and lateral components of the velocity of the anterior and posterior arms of the body are roughly equal in magnitude (Fig. 6) and, as during skating, forward thrust is delivered to the centre of the body during the flexion phase of the locomotory cycle.

The figure-of-eight contortions of the body of *D. aestivalis* during swimming recall those of chironomid larvae, the swimming mechanism of which was described by Nachtigall (1961). A comparison between Figs 7 and 5 confirms the essential similarity between the kinetics of swimming in *C. plumosus* and *D. aestivalis* larvae. Fig. 8 shows that the period of backward motion of the anterior and posterior parts of the

Fig. 5. (A) Profiles of the body of a *Dixella aestivalis* larva during consecutive 20ms intervals of the swimming cycle. Swimming occurs from left to right with the body rotating clockwise through 180° (up to stage 2) then anti-clockwise through 180° (between stages 2 and 4) in the vertical plane. Numerals refer to corresponding stages of the locomotory cycle during skating in Fig. 2A. For convenience, the horizontal axis has been expanded by approximately six times compared with normal swimming. (B) Paths traced out by the head, abdominal tip and centre of the body during successive 20ms intervals during the swimming cycle. Numerals indicate frame numbers.



body, where forward propulsion can be generated from viscous drag, is relatively brief compared with the period when the ends of the body are moving forwards and incurring a backwardly directed force. The force on a section of body, however, is governed not only by its instantaneous velocity through the water but also by its angle of attack θ . The value of $\sin\theta$ reaches a maximum at the start of the flexion phase of the locomotory cycle as both the anterior and posterior ends of the body are accelerating backwards (Fig. 8).

Locomotion of Hydrobius fuscipes larvae

Like *Dixella aestivalis*, the larva of the aquatic beetle *Hydrobius fuscipes* also attaches to the surface film via a dorso-apical tracheal gill, consisting of a respiratory chamber receiving the two main tracheal trunks (Fig. 1B). The method of locomotion is similar to that of *D. aestivalis*, and corresponding stages in the skating cycle are illustrated in Fig. 9A. The foot remains attached to the surface throughout the cycle (Fig. 4), and the main difference from *D. aestivalis* is that the foot is unable entirely to resist the backwardly directed forces on the body during extension and therefore slips backwards during this phase, although this loss of ground is partly compensated by the fact that the foot is brought forwards during the flexion phase at a greater velocity, and therefore

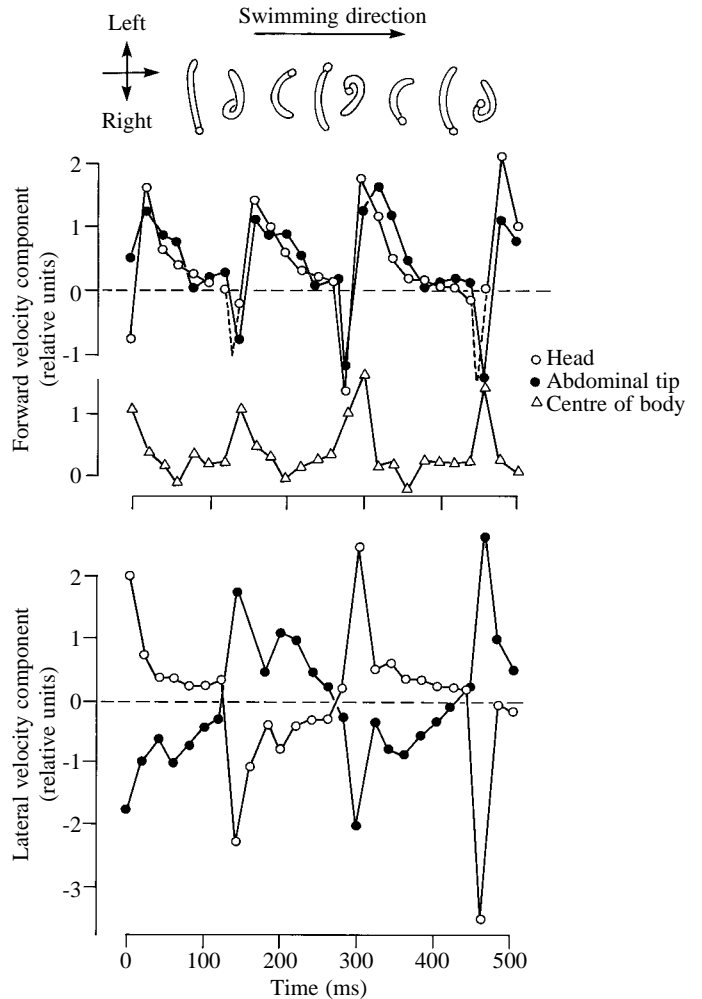
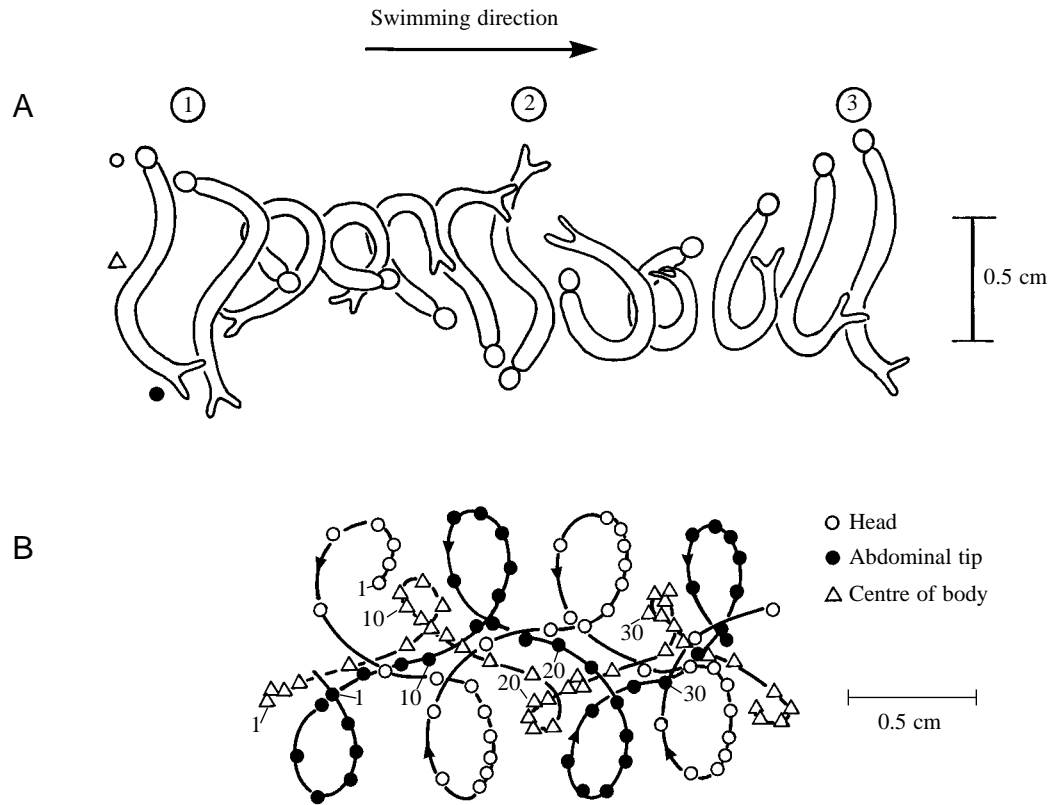


Fig. 6. Forward and lateral velocity components of the motion of the head, abdominal tip and centre of the body (forward component only shown) during the swimming cycle of a *Dixella aestivalis* larva (phases are shown by cartoons above the graph). Note how the centre of the body is accelerated forwards during the flexion phases of the cycle. Velocity is given in arbitrary units. The mean forward velocity of the centre of gravity is 1.1 cm s⁻¹ (Table 1).

Fig. 7. (A) Profiles of the body of a *Chironomus plumosus* larva during consecutive 40 ms intervals of the swimming cycle. The motion consists of flexion to the left followed by extension (stages 1–2), then flexion to the right followed by extension (stages 2–3). For convenience, the horizontal axis has been expanded approximately $\times 6$ compared with normal swimming. (B) Paths traced out by the head, abdominal tip and centre of the body during successive 20 ms intervals of the locomotory cycle. Numerals indicate frame numbers. The insect is moving from left to right.



through a greater distance, than the corresponding backwards movement of the head: these features can be seen from the velocity recordings in Fig. 10. As a consequence, the foot is

drawn forward between consecutive extension phases through a distance of 0.6 body lengths (Fig. 9B), which is significantly greater than the value of 0.5 body lengths calculated for the larva of *D. aestivalis* (see Fig. 2B). The divergence angle between consecutive extensions is 61° ($60.8 \pm 8.4^\circ$, $N=28$), compared with 45° in *D. aestivalis*, and the resultant stride length per complete left/right cycle is the same: 0.93 body lengths (Table 1). As in the swimming and skating *D. aestivalis* larva, the centre of the body of the *H. fuscipes* larva is accelerated forwards during the flexion phase of the cycle (Fig. 10). The greater motility of the foot of *H. fuscipes* means that it shadows the motion of the head much more closely than is the case in *D. aestivalis*: both extremities pursue a cycloidal path alternately to the left and right of the mean path followed by the centre of the body (Fig. 9C), although the amplitude of lateral excursion of the foot is less than that of the head.

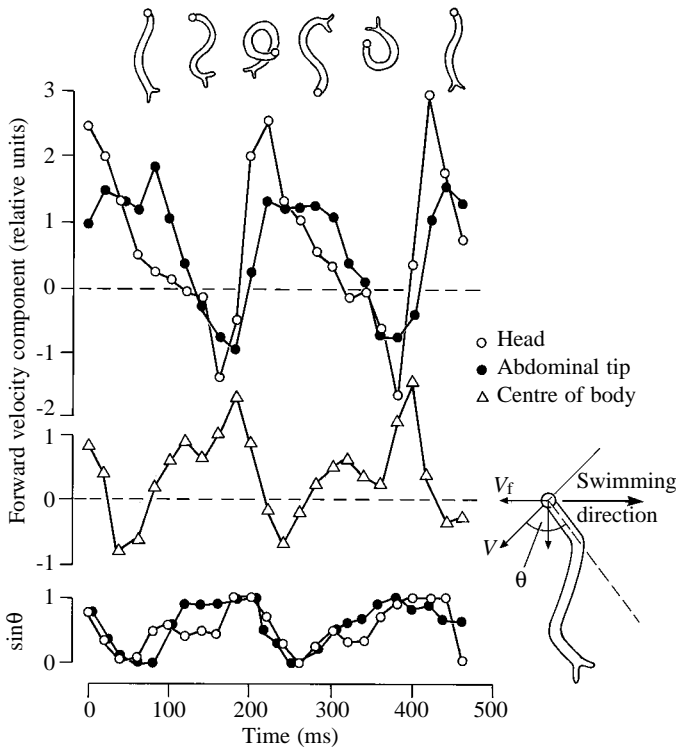


Fig. 8. Forward velocity components of the movement of the head, the abdominal tip and the centre of the body during the swimming cycle of a *Chironomus plumosus* larva. The lowermost graph plots $\sin\theta$, where θ is the angle between the longitudinal axis of the anterior (or posterior) third of the body and the instantaneous direction of movement of the head (or tail). Note how the centre of the body accelerates forward during the flexion phases of the cycle (phases are shown by cartoons above the graph) when the anterior and posterior thirds of the body are moving backwards and present the greatest angle of attack to the line of motion. V , instantaneous velocity of head (or tail). V_f , forward component of instantaneous velocity.

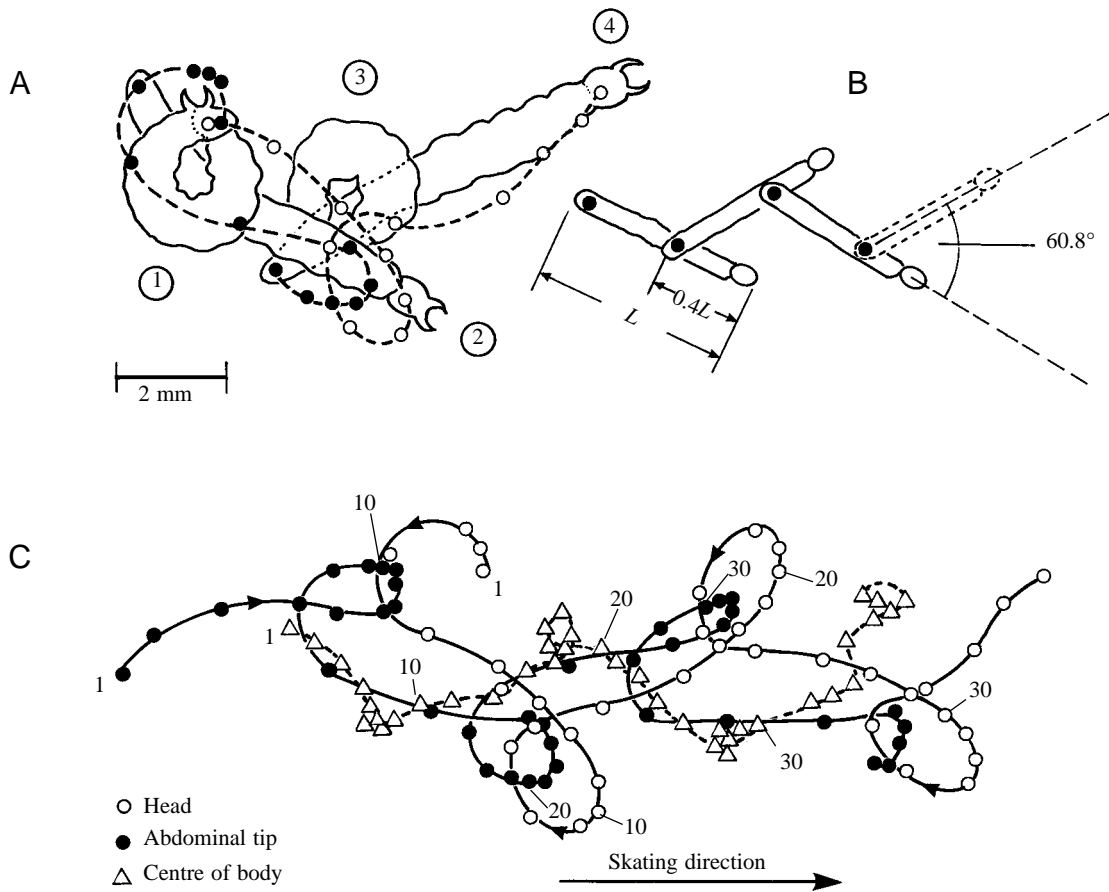
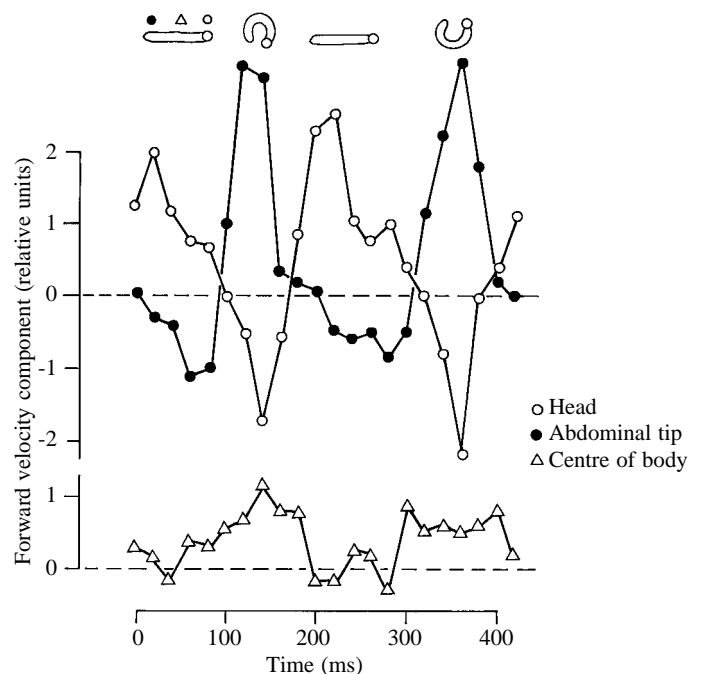


Fig. 9. (A) Diagram showing movements of the body of *Hydrobius fuscipes* larva during skating. Open and filled circles indicate paths of the head and abdominal tip, respectively, at 60 ms intervals. Numerals indicate corresponding positions to those in a skating *Dixella aestivalis* larva in Fig. 2A. (B) Schematic interpretation of the locomotory cycle: during successive extensions, the body elongates at an angle of 61° to its previous orientation, with the foot becoming located 60% of a body length diagonally forward of its previous position. (C) Paths traced out by the head, the tip of the abdomen and the centre of the body during consecutive 60 ms intervals of the skating cycle. Numerals indicate frame numbers.

Discussion

Many arthropods are supported by and move about within the air-water interface, including pondskaters (Gerridae, Veliidae), water-measurers (Hydrometridae), water spiders (*Argyroneta*, *Dolomedes*), gyrenid beetles, backswimmers (Notonectidae) and poduran springtails. These all use limbs to row or walk upon the water, and the limbless method of skating displayed by *D. aestivalis* and *H. fuscipes* larvae appears to be unique. There is some evidence that the method used by *D. aestivalis* larvae is derivative, being a modification of the normal underwater swimming motion. For example, the contractile frequencies are the same during skating and swimming, suggesting, although not proving, that the contractile rhythm is governed by the same pattern generator.

Fig. 10. Forward velocity components of the motion of the head, the tip of the abdomen and the centre of the body during the skating cycle of *Hydrobius fuscipes*. Locomotory phases are shown by cartoons above the graph. Note how the tip of the abdomen accelerates forward during flexion then loses ground during extension. Velocity is given in arbitrary units. The mean forward velocity of the centre of the body is 0.54 cm s^{-1} (Table 1).



Although kinematically distinct, swimming and skating are equally effective forms of locomotion, achieving comparable forward speeds and stride lengths (Table 1). This is perhaps not surprising since, in both cases, the forward motion of the centre of the body is produced during the flexion phase of the locomotory cycle (Figs 3, 6), i.e. the phase when the foot has least effect on skating and the hydrodynamic behaviour of the body is therefore comparable in both forms of locomotion. The overall effect of the presence of the foot during skating is to rotate the mean propulsive force vector through 90° . This can be deduced from a comparison of Figs 2 and 5, where it can be seen that the mean skating path is parallel to the longitudinal axis of the body in the extended state, whereas the mean swimming path is at right angles to the longitudinal axis of the body in the extended state. Put more simply, the larva of *D. aestivalis* skates forward (i.e. head first), but swims sideways. The difference springs from the effects of the foot on the gross movements of the skating and swimming insect. In the former, the foot constrains the motion of the rear half of the body to an angle of $\pm 23^\circ$ away from the mean skating pathway (Fig. 2B), whereas in the swimming larvae, the whole longitudinal axis of the body is rotated through 180° (Fig. 5A).

The swimming technique used by *D. aestivalis* larvae appears to be almost identical to that described in chironomid larvae by Nachtigall (1961). For analytical purposes, Nachtigall (1961) divided the chironomid larval body into thirds, finding that propulsion was provided by the backward motion of the two ends of the body, the central third having no locomotory function. Although the larval body of *D. aestivalis* behaves geometrically more like independent halves than thirds, the dynamics of swimming appears to be essentially the same as in *C. plumosus*. According to Nachtigall (1961, 1962a, 1963, 1974), chironomid swimming is extremely inefficient compared with that of dipteran larvae and pupae that employ abdominal paddles such as *Aedes* spp. and *Chaoborus plumicornis*. With only 3% of the available mechanical energy converted into forward motion, the swimming performance of *C. plumosus* larvae is twenty times poorer than that of aquatic beetles, although it is comparable with that of ceratopogonid larvae which, like chironomid larvae, rely exclusively on whole-body undulations, rather than paddles, to provide thrust. In contrast, swimming dipteran larvae, including *Ceratopogon* spp., *C. plumosus* and *D. aestivalis*, out-perform their terrestrial counterparts in both speed and stride length. For example, 4 mm long *Drosophila melanogaster* larvae crawl at only 0.1 cm s^{-1} and achieve a stride length of only 0.25 body lengths per locomotory cycle (Berrigan and Pepin, 1995). The fastest maggot studied by these authors, *Sarcophagus bullata*, crawled at 0.6 cm s^{-1} but still only achieved a stride length of 0.25 body lengths. In both cases, the crawling speed was equivalent to approximately $0.25 \text{ body lengths s}^{-1}$. By comparison, the distance covered by swimming *D. aestivalis* larvae per contraction cycle was 0.85 body lengths and the speed was $2.3 \text{ body lengths s}^{-1}$ (Table 1). So even the least effective of dipteran larval swimming techniques is several times better than those based on telescopic contractions of the

body segments. Although relative speeds may simply be a consequence of different styles of locomotion in water as opposed to on land, it seems likely that faster swimming would bestow an advantage in terms of escape from predators such as fish and carnivorous water beetles. *D. aestivalis* larval skating is also much faster than telescopic crawling, and in some ways this provides a more meaningful comparison since skating and telescopic crawling are both assisted by anchorage provided by the tip of the abdomen (as well as the head in crawling dipterans). The greater stride length (0.92 body lengths) of *D. aestivalis* compared with that of crawling Diptera is due directly to the drawing forward of the foot during the flexion phase, a feat rendered relatively simple by the synchronized contraction of unilateral longitudinal intersegmental muscles, but one that is well beyond the capabilities of a system based on peristaltic contraction. In this sense, the increased stride length of the *D. aestivalis* larva can be compared with the corresponding increase achieved by geometric caterpillars, whose looping style breaks free of the constraints imposed by normal caterpillar crawling, which is also based on peristaltic contraction of the longitudinal muscles (Casey, 1991; Brackenbury, 1996, 1997).

Such a comparison is valid, since skating *D. aestivalis* larvae and looping caterpillars both make progress by drawing the two ends of the 'loop' together during the flexion phase. Caterpillar looping, in common with the similar locomotory style used by leeches, involves successive application of the head and tail as fixed points, the tail 'pushing' and the head 'pulling' the body forwards. This method achieves a stride length per contractile cycle of 1 body length. A single contractile cycle of a looping caterpillar is equivalent to one left or right flexion/extension phase of *D. aestivalis* or *H. fuscipes* larval skating, which produces only 50% of this ideal, i.e. approximately 0.5 body length. This is due to 'loss of ground' by the backward slipping of the head during the flexion phase, which is responsible for the 'cycloidal' component of the path followed by the head in *D. aestivalis* (Fig. 2C) and *H. fuscipes* (Fig. 9C). The larva of *H. fuscipes* also suffers backwards slip of the foot during the extension phase, resulting in a cycloidal component in the path of the abdominal tip (Fig. 9C). The greater efficiency of the *D. aestivalis* larval foot in resisting forward extension of the body, compared with the *H. fuscipes* larval foot, may be related to its much greater relative size offering an increased perimeter of contact with the surface tension film.

Whereas the skating of the *D. aestivalis* larva is clearly related to and probably derived from swimming, no such pedigree is visible in *H. fuscipes*. Apart from the use of the thoracic legs for normal walking, the only other locomotory techniques displayed by *H. fuscipes* larvae are feeble telescopic and dorsoventral undulations of the abdomen. I have not observed any form of underwater swimming. The most common method of swimming in aquatic beetle larvae is paddling with the thoracic legs, which are often hair-fringed to increase their effectiveness, sometimes supplemented by abdominal lashing in the vertical plane (Nachtigall, 1962b;

Crowson, 1981). The similarity between the skating techniques used by these two completely unrelated insects must be seen as an unusual case of convergent evolution.

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