



Pergamon

Journal of Insect Physiology 46 (2000) 1517–1527

Journal  
of  
Insect  
Physiology

www.elsevier.com/locate/jinsphys

# Locomotory modes in the larva and pupa of *Chironomus plumosus* (Diptera, Chironomidae)

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Received 2 October 1999; received in revised form 6 April 2000; accepted 6 April 2000

## Abstract

The locomotory kinematics of *Chironomus plumosus* larvae and pupae were investigated in order to determine how different locomotory techniques may be related to (a) possible underlying patterns of muscle activation and (b) the particular lifestyles and behaviours of these juvenile stages. Larvae display three independent modes of motile activity: swimming, crawling and whole-body respiratory undulation. Swimming and respiratory undulation involve the use of metachronal waves of body bending which travel in a head-to-tail direction. Whereas swimming is produced by side-to-side flexures of the whole body, respiratory undulation employs a sinusoidal wave. Crawling appears to result from an independent programme of muscle activation. Instead of a longitudinally transmitting metachronal wave of body flexure, a simultaneous arching of the body, combined with the alternating use of the abdominal and prothoracic pseudopods as anchorage points, produces a form of locomotion analogous to caterpillar-looping. Larval swimming has a set speed and rhythm and is an 'all-or-nothing' locomotory manoeuvre, but the neural programme controlling larval crawling is adaptable; switching from a less to a more slippery substrate resulted in a shorter, faster stepping pattern. The pupa displays two swimming modes, somersaulting and eel-like whole-body undulation, the former being principally a brief, escape manoeuvre, the latter being a faster form of locomotion employed to deliver the pupa to the surface prior to adult emergence. Comparison with the pupa of the culicid *Culex pipiens* shows that this insect also uses the somersault mechanism but at a higher cycle frequency which produces a faster swimming speed. This appears to be related to differences in lifestyle; the surface-living culicid pupa is exposed to greater predator threat than the bottom-dwelling chironomid pupa, and consequently needs a faster escape. © 2000 Elsevier Science Ltd. All rights reserved.

**Keywords:** Kinematics; Swimming; Crawling; Somersaulting; Respiratory undulation; Muscle activation sequences; Locomotory control; Ecology

## 1. Introduction

Free-living invertebrates with elongated, worm-like bodies display two characteristic forms of motile activity: whole-body sinusoidal undulations, as practised by aquatic nemertine, nematode and annelid worms (Gray, 1968; Trueman, 1975; Full, 1997), and telescopic peristalsis, found in earthworms (Gray and Lissmann, 1938), caterpillars (Barth, 1937; Hughes, 1974; Casey, 1991; Brackenbury, 1999a) and the wood-burrowing larvae of longhorn beetles (personal observation). Both kinds of activity involve serial recruitment of the locomotory musculature, in the form of a metachronal wave which travels either tailwards, as in worms and centipedes (Manton, 1977; Anderson et al., 1995), or headwards (caterpillars, Barth, 1937; saw-fly larvae, personal observation). Being of extremely ancient lineage, met-

achronism is still recognisable in the walking patterns of modern-limbed hexapods (Hoyle, 1976).

Kinematic studies on animal locomotion can serve a dual purpose, providing not only a description of mechanical events but also rudimentary evidence on the way in which the locomotory control system may be organised. In view of the paucity of direct information on locomotory control in simple, soft-bodied invertebrates compared with existing knowledge on the control of walking patterns in limbed arthropods (Huber, 1974; Hoyle, 1976; Delcomyn, 1981; Eaton, 1985), indirect studies of this nature can be particularly useful. As a group, the juvenile stages of Diptera lend themselves to such an approach since they share a common body plan (limbless, segmented, elongate) but occupy a variety of niches and have evolved a corresponding diversity of locomotory styles. The latter range from telescopic crawling (terrestrial maggots, Berrigan and Lighton,

1993; Berrigan and Pepin, 1995), sinusoidal undulation (aquatic ceratopogonids, Nachtigall, 1961) and side-to-side flexure (chironomid, culicid and corethrid larvae and/or pupae, Nachtigall 1961, 1962). Dixid larvae swim like chironomid larvae (lateral flexure) and also modify the same technique to skate on the water surface (Brackenbury, 1999b). The larvae of certain cecidomyiids and the Mediterranean fruit-fly *Ceratitis capitata* (Maitland, 1992) show the most intriguing locomotion of all—jumping using elastic energy stored in the integument.

It could justifiably be said that juvenile Diptera, as an assemblage, have exploited the design capabilities of the simple, segmented elongated body to their maximum potential. Between-species comparisons of locomotory techniques show the degree to which specific designs can be adapted to different physical environmental circumstances. But an additional dimension can be gained by examining individual species which display not one but several locomotory patterns, since they may provide information on the organisation and versatility of the locomotory control system. The present study began from field observations by the author that the aquatic stages of *Chironomus plumosus* display between them at least five distinct patterns of motile activity. Further patterns of motor behaviour, for instance tube-building by the larvae, may exist independently of the motile systems, but they are not considered here. The objectives of the study were (a) to identify, from kinematic analysis, any evidence of the employment of similar patterns of body flexure to generate different types of locomotion, and (b) to relate the various types of locomotion identified in the larvae and pupae to their respective lifestyles.

## 2. Materials and methods

*Chironomus plumosus* larvae (final stage) and pupae were collected from local rain-pools in early summer and kept in tanks in the laboratory in daylight conditions at ambient temperatures of 20–22°C, which were in general only one or two degrees above outside temperatures for the time of year. The pupae are exclusively bottom-dwellers, only attempting brief swimming sorties when disturbed or during the final ascent to the surface in anticipation of adult emergence. Once brought into the laboratory, the larvae readily constructed tunnels in the detritus at the bottom of the container and showed normal behaviour including whole-body respiratory undulation, crawling and open-water swimming. Videography of larval and pupal movements was performed with a NAC 400 high-speed video system (NAC Inc., Japan) with synchronised stroboscopic illumination generating 200 or 400 frames  $s^{-1}$ . Additional high-resolution pictures were obtained using a Panasonic video camera with

a normal frame rate of 25  $s^{-1}$ . By using a stroboscope (Drelloscop 1018, Drelloscop, Germany) at 50 Hz, it was possible to double the imaging rate to 50 fields  $s^{-1}$ , two separate images being obtained for each binary field normally making up a single frame. Data were recorded on a video cassette player equipped with a single field advance facility for detailed image measurement. Body profiles and swimming trajectories were traced by hand directly from the video screen. The mechanics of larval crawling underwater was investigated in two experimental conditions, the substrate at the bottom of the container being provided either by glass or sand (particle size <0.8 mm). Crawling and swimming appear to be kinematically distinct kinds of locomotion but in order to determine whether or not there may be gradations between them observations were made on larvae swimming in water in which the viscosity had been artificially increased by the addition of small amounts of gelatine. The viscosity of the resulting media was not quantified but at its maximum was sufficient to halt forward motion, without stopping locomotory movements of the body. Experimental values are quoted as means  $\pm 1$  standard error. Paired values were compared for significant differences using the 't'-test at a significance level of 5%. In total, approximately 50 larvae and 20 pupae were examined with an average of 3–4 measurements per parameter per animal, although it was not practical to obtain data for all locomotory techniques in every individual.

## 3. Results

### 3.1. Larval movements

In open water the larva uses the familiar 'figure-of-eight' style of swimming, produced by side-to-side flexion of the body (Fig. 1A). The hydrodynamics of chironomid larval locomotion has previously been analysed by Nachtigall (1961) and the present study concentrates on evidence that the kinematics of swimming may reveal about underlying patterns of muscle recruitment. Viewing the larva from its dorsal aspect it can be seen that successive half-strokes rotate the longitudinal axis of the body back and forth through 180° (Fig. 1A). As a result, the head and abdominal tip trace out double cycloidal paths through the water, on alternate sides of the mean forward swimming line (Fig. 1B). Throughout the cycle, axial length remains constant, indicating the absence of any telescoping of body segments (Fig. 1C).

Plotting successive body profiles during the half-stroke in head-fixed co-ordinates allows the changes in body shape and the resultant motion of the abdominal tip relative to the head to be examined (Fig. 2A). The transition in body shape from a condition of maximum flexure on one side to maximum flexure on the contralat-

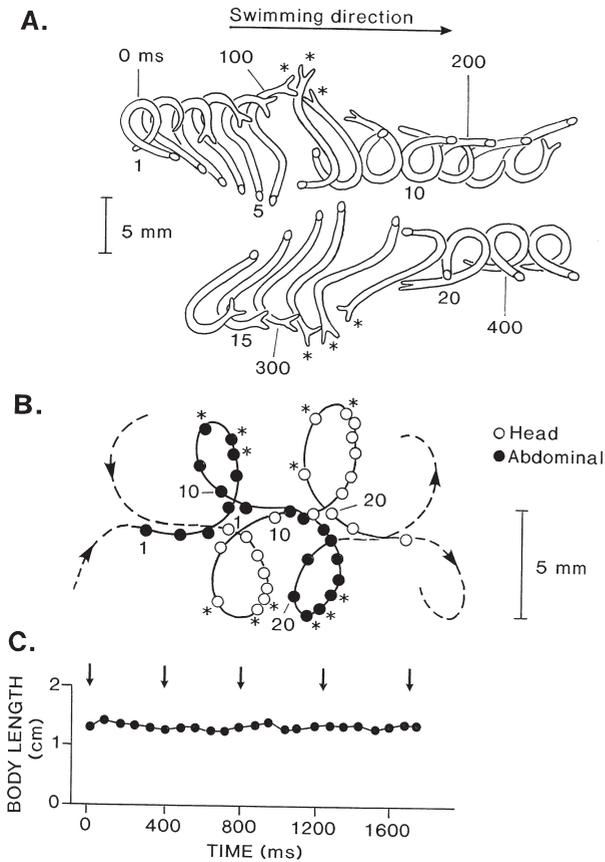


Fig. 1. (A) Successive profiles of the body of *C. plumosus* larva during a complete swimming cycle. The insect is viewed from the dorsal surface and moves in the horizontal plane of the body. A complete swimming cycle involves a contraction of the whole body to the right (phases 0–200 ms) then the left (phases 220–400 ms). For ease of viewing the horizontal axis has been expanded approximately three times compared with normal. (B) Paths traced out by the head and abdominal tip during successive 20-ms intervals. (C) Axial length of the body during four successive swimming cycles (marked by arrows). Asterisks in A and B signify phases when the head and abdominal tip are moving backwards with respect to the mean swimming direction.

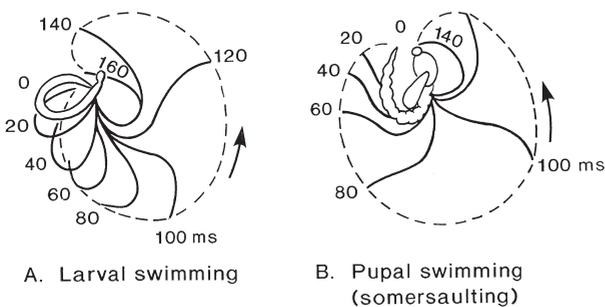


Fig. 2. (A) Profiles of the body of swimming *C. plumosus* larva during successive 20-ms intervals of contraction of the body. The insect is viewed from the dorsal surface and the head is assumed to be stationary. The dotted line plots the motion of the abdominal tip relative to the head. (B) Corresponding profiles during the upstroke of a somersaulting *C. plumosus* pupa.

eral side is produced by a contractile wave of bending running in a head-to-tail direction. In the initial uncoiling phase (0–80 ms in Fig. 2A), a node of maximal curvature can be seen moving progressively tailwards, as in the unfolding of a whip. This is followed by a rapid phase of straightening and flexure to the other side (100–140 ms), during which the angular velocity of the tip of the abdomen relative to the head is of the order of  $4 \times 10^3 \text{ deg s}^{-1}$ . Comparing Figs 1A and 2A shows that the second phase coincides with the stage in the swimming cycle when the two ends of the body are moving backwards most rapidly relative to the water (marked by asterisks in the figures). It is noteworthy that the pair of pseudopods on the abdominal tip are maximally abducted during this stage (Fig. 1A) in contrast to the adducted state assumed during the ensuing stages as the body progressively flexes to the contralateral side. These rhythmical movements of the pseudopods appear to be directed towards maximising the drag on the end of the abdomen during the thrust-generating phase and ‘feathering’ the tip of the abdomen during its phase of forward movement relative to the water.

Increasing the viscosity of the medium by adding powdered gelatine affected the path pursued through the water but not the underlying dynamics of body shape changes. In the most viscous conditions, normal swimming efforts were executed at a stroke rate of  $2.6 \pm 0.4 \text{ Hz}$  ( $N=6$ ), not significantly different from the stroke rate in normal water,  $2.7 \pm 0.3 \text{ Hz}$  ( $N=33$ ). The ends of the body oscillated backwards and forwards relative to the water but there was no nett forward movement nor any inversion of the body between half-strokes (Fig. 3A,B).

The method of crawling underwater on a solid substrate is kinematically distinct from that of swimming in open water and involves a totally different pattern of muscle recruitment. During forward crawling the substrate is gripped alternately by the prothoracic and abdominal pseudopods. With each ‘cycle’ the body is first pulled forwards towards the affixed prothoracic pseudopod by the upward arching of the anterior segments of the body, then driven forwards by extension against the affixed abdominal pseudopod (Fig. 4A). The method resembles the ‘looping’ of geometric caterpillars, the chironomid pseudopods playing similar roles to those of the thoracic and abdominal pro-legs of the caterpillar. However, chironomid crawling differs from caterpillar crawling in that it is non-hydraulic and does not make use of peristalsis; an analysis in 10 individuals showed no significant change in axial length from the extended ( $1.4 \pm 0.09 \text{ cm}$ ) to the flexed ( $1.4 \pm 0.08 \text{ cm}$ ) states. The degree of adhesion between the pseudopods and the substrate directly affected crawling kinematics; the pseudopods tended to slip backwards on glass and the pattern of locomotion was faster and shorter than on the firmer surface provided by sand (Table 1). Backward crawling was also possible, by reversing the roles of the

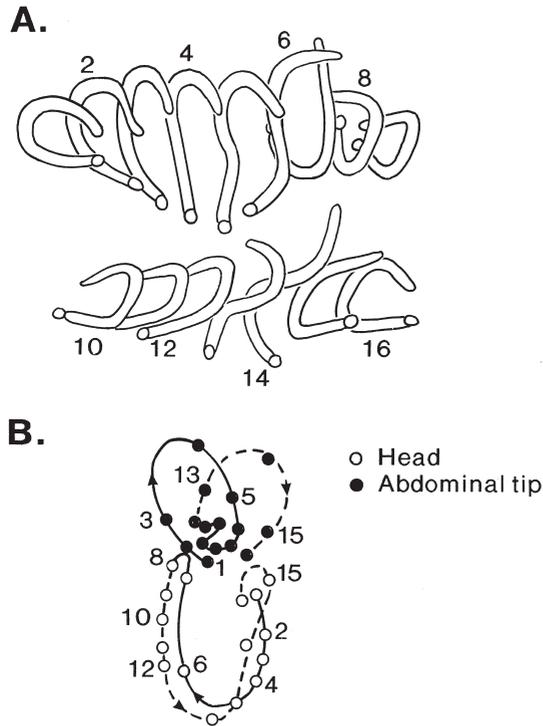


Fig. 3. (A) Profiles of the body of a *C. plumosus* larva during successive 40-ms intervals of a complete swimming cycle in a highly viscous medium. The insect is viewed from the dorsal surface. It undergoes no nett translation although, as a comparison with Fig. 1A demonstrates, normal swimming movements are performed by the body. (B) Paths traced through the medium by the head and abdominal tip. Note that the head and tip simply oscillate backwards and forwards, with no inversion of the body between half-strokes.

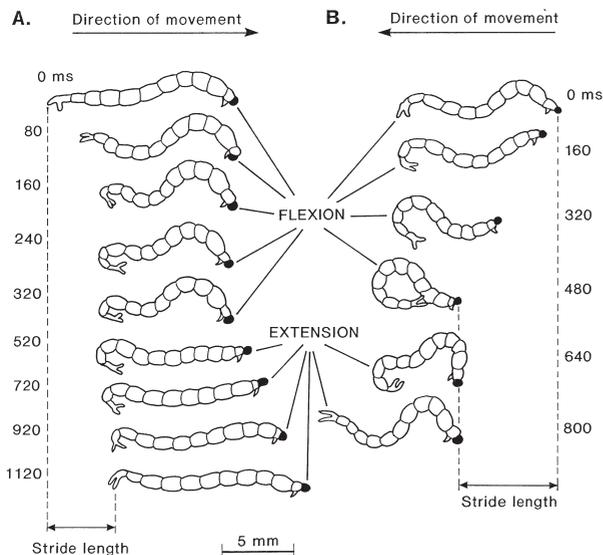


Fig. 4. Profiles of *C. plumosus* larva during a cycle of forward (A) and backward (B) crawling on sand. Time (in ms) indicated beside each profile. Drawings from original video recordings. Note the time interval change halfway through the forward crawling cycle, due to a brief pause in movement.

pseudopods (Fig. 4B), but it was not performed with sufficient regularity for quantitative data to be obtained.

The third distinctive kind of larval motion to be identified was associated with respiration and took the form of eel-like undulation of the body in the dorsoventral plane, produced by a sinusoidal wave of bending travelling from the head to the tail (Fig. 5A). The wavelength of the metachronal wave was the same as the body length. Respiratory undulation appears to be contingent upon the body being attached to a solid substrate either by its anterior or posterior pseudopods. Normally it occurs when the larva is attached inside its burrow at the bottom of the water, via the abdominal pseudopods, but it may also be performed in open water provided the larva can hold on to a vertical surface by either its prothoracic (Fig. 5A) or abdominal pseudopods. Rhythmic respiratory movements have the same frequency as swimming movements (Table 1) but occur in the sagittal as opposed to the horizontal plane of the body. Flow lines traced out by small (<0.1 mm) particles of detritus in the water in the vicinity of the body showed a current being driven in a head-to-tail direction towards the abdominal gills (Fig. 5B). Although an exhaustive study was not undertaken, the evidence suggests the presence of a ring vortex around the mid-region of the body, together with a smaller vortex generated by the sweeping motion of the abdominal pseudopods.

### 3.2. Pupal locomotion

The pupa is largely sedentary, resting inside or in the later stages just outside the larval tube at the bottom of the water. In the latter case it rests on its side adopting a characteristic U-shape with the abdomen curled beneath the head/thorax. In the early stages the body is denser than water and if released into open water sinks with a free-fall velocity of  $2.01 \pm 0.35$  body lengths  $s^{-1}$  ( $N=20$ ) but in the period leading up to adult emergence, increased buoyancy of the head/thorax raises the pupa off its side so that it rests in a head-up attitude with the outside of the U-bend of the abdomen touching the bottom. The gradual increase in buoyancy appears to facilitate the final journey to the surface which can only be achieved by active swimming and, as propulsion is provided by the abdomen, the head-up orientation of the body automatically favours upward movement.

Normally, both in the wild and in the laboratory, the pupa shows little sign of locomotory activity until the immediate pre-emergence period, although it will respond to tactile stimuli by brief periods of swimming. The first of these, somersaulting, is vigorous and jerky and is best viewed as an escape behaviour. The body is driven forwards by large-amplitude up-and-down strokes of the abdomen about its extremely mobile connection to the head/thorax. Each half-stroke of the abdomen drives the body forwards and simultaneously counter-

Table 1  
Kinematic parameters of larval and pupal locomotion of *C. plumosus*<sup>a</sup>

Stage	Type of movement	Contraction frequency (cycles s <sup>-1</sup> )	Stride length (prop. of body length)	Speed (body lengths s <sup>-1</sup> )	Velocity (cm s <sup>-1</sup> )
Larva	Crawling on glass	1.44±0.27 (25)	0.10*	0.15±0.05 (18)	0.20*
	Crawling on sand	0.44±0.13 (18)	0.29±0.07 (27)	0.13*	0.18*
	Swimming	2.66±0.25 (33)	0.84±0.16 (33)	2.23*	3.04*
	Respiratory undulation	2.50±0.50 (15)	—	—	—
Pupa	Sinusoidal swimming	11.3±0.8 (20)	0.32*	3.6±0.7 (20)	4.07*
	Somersaulting	2.45±0.80 (17)	0.96*	2.34±0.68 (15)	2.64*

<sup>a</sup> Measurements are given as mean values±1 standard deviation, with number of observations in brackets. Asterisked figures were estimated from other measured parameters. Larval and pupal body lengths were 1.36±0.07 (10) cm and 1.13±0.08 (10) cm respectively.

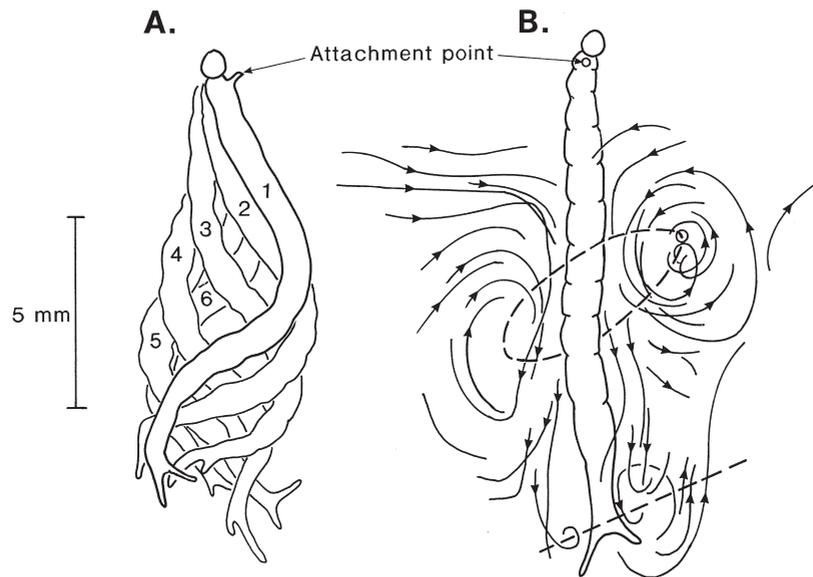


Fig. 5. (A) Profiles at 60-ms intervals of *C. plumosus* larva during a cycle of respiratory undulation. Drawings from original recordings. The larva was attached to a vertical surface by means of its prothoracic pseudopod and is viewed from the right side. (B) Streamlines in the vicinity of a larva attached by its prothoracic pseudopod and performing undulatory movements. The dashed lines indicate the core of a putative ring vortex around the middle of the body and a smaller vortex generated by the sweeping motion of the abdominal pseudopods.

rotates it through nearly a full circle (Fig. 6). Viewed from its right-hand side, the pupa pitches backwards during the upstroke (0–200 ms) and forwards during the downstroke (200–360 ms) through an angle of  $301\pm38^\circ$  ( $N=33$ ).

The tip of the abdomen is equipped with a pair of tail-plates which, if they are presumed to behave like the corresponding structures found in culicid pupae (Nachtigall, 1963), generate most of the hydrodynamic force. The abdominal tip traces out a cycloidal path through the water (Fig. 7A), similar to that traced out by the abdomen of the larva (Fig. 1B) except that it is asymmetrical about the mean swimming line, the dorsal cycloid being larger and more elongated in the direction of swimming than the ventral cycloid. In contrast, the path traced out through the water by the centre of the head/thorax shows little departure from the mean swimming line throughout the cycle. Consequently, any part

played by the head/thorax in generating forward propulsion must be small. An examination of tail-plate velocity relative to the water at different stages of the stroke as illustrated in Fig. 7A makes it clear that a backward velocity component is present during a very limited period at the start of each half-stroke (Fig. 8). This period corresponds with the point in the cycle of change in body shape when the abdomen is rapidly extending and beginning to flex to the contralateral side (Fig. 2B).

A crude estimate of the relative thrust generated by the tail-plates in the fore–aft direction can be gained from their instantaneous velocity  $V$  and angle of attack  $\alpha$  relative to the water (Fig. 9A) together with certain assumptions about the nature of the flow regime, as reflected in the Reynold's number. With a mean forward velocity of  $\sim 2.5$  cm s<sup>-1</sup> and a mean body length of  $\sim 1$  cm (Table 1), the Reynold's number of the somersaulting pupa is of the order of 300. Assuming that iner-

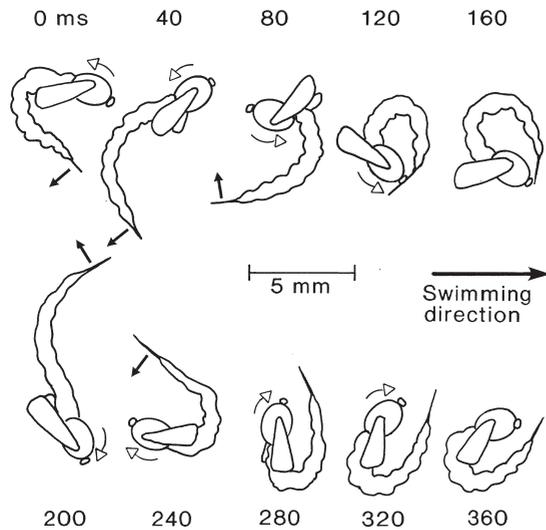


Fig. 6. (A) Successive profiles of the body of a *C. plumosus* pupa during a complete cycle of somersaulting. The insect is viewed from the right side and is swimming from left to right. During the upstroke of the abdomen (stages 0–120 ms) the body rotates approximately 300° counter-clockwise, and during the downstroke (stages 160–360 ms) it rotates approximately 300° clockwise. Filled and open arrows indicate directions of movement of the abdominal tip relative to the base of the abdomen and the head/thorax around its centre, respectively. Time (in ms) beside each profile. For ease of viewing the horizontal axis has been expanded by approximately 10 times compared with normal.

tial effects of the water and the mass of the body outweigh those due to viscous drag, the instantaneous force generated by the tail-plate movement in the fore–aft direction can be expressed as:

$$F \propto V^2 \sin \alpha \cos \theta \quad (1)$$

where it is assumed for simplicity that the coefficient of drag is proportional to  $\sin \alpha$ .  $\theta$  is the angle between the mean swimming direction and the instantaneous direction of motion of the tip of the abdomen (Fig. 9A). The results of such calculation (Fig. 9B) show that most of the forward thrust is generated in the form of a brief pulse at the start of the downstroke with very little hydrodynamic work being performed during the upstroke. This inequality reflects the asymmetry in the path of the tail-plates through the water shown in Fig. 7A. This simplified analysis assumes that the thrust is generated by drag and ignores any possible contribution by lift. An indication of the part that lift might play can be gained by sketching the orientation of the lift vectors perpendicular to the incident flow. When such a procedure is performed on Fig. 9A the lift vector has a forward-directed (in the overall swimming direction) component that could contribute to thrust at two points in each cycle, namely, just after the reversal points of the motion of the abdominal tip through the water (e.g. frame numbers 6, 7 and 12–15).

The angular motion of the abdominal tip about its basal pivot and simultaneously of the head/thorax about

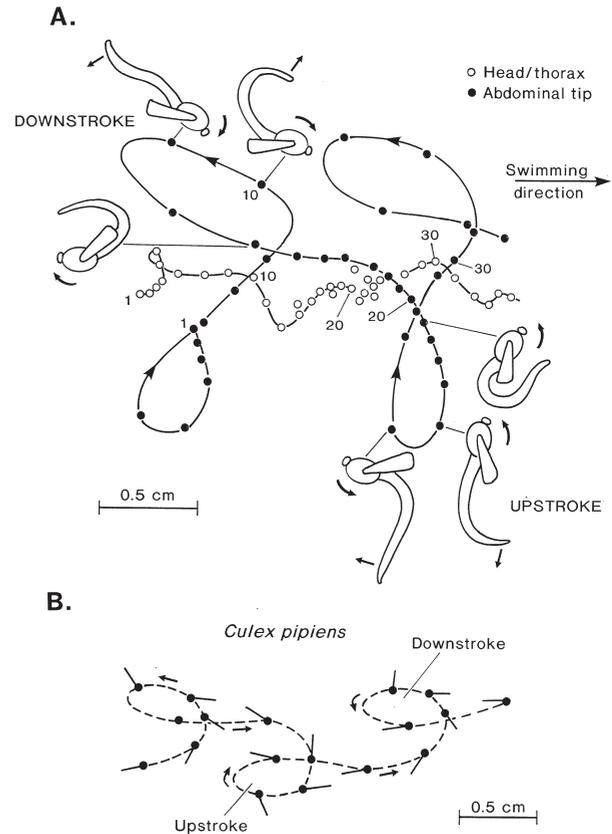


Fig. 7. (A) Paths traced out by the abdominal tip and the centre of the head/thorax during the upstroke/downstroke cycle of somersaulting in *C. plumosus* pupa. Points are indicated at 20-ms intervals and numerals correspond to frame numbers. Cartoons show approximate configurations of the body at the start of the upstroke and downstroke. Straight arrows indicate motion of abdominal tip about the base of the abdomen. Curved arrows indicate rotation of the head/thorax. (B) Path traced out at 10-ms intervals by the abdominal tip of a somersaulting *Culex pipiens* pupa. Bars indicate orientation of tail-plates.

its own geometric centre are illustrated in Fig. 10. The active up- and downstrokes are of approximately equal duration but the interstroke pauses during which the abdomen is inactive are different. During the very brief (30–40 ms) end-upstroke pause the tail-plates lie in close contact with the head so that the whole body forms a closed circle (120, 160 ms in Fig. 6). In contrast, the end-downstroke pause lasts about 150–200 ms and furthermore a gap remains between the stationary tail-plates and the head (280–360 ms in Fig. 6). In both cases the body continues to rotate under its own momentum until the starting point for the next half-stroke has been reached, but the rate of ‘free-spin’ is slower during the downstroke pause and consequently more time is required to complete the full 301° of rotation. Slower spinning during the downstroke pause may be related to the greater profile drag imposed on the body in the ‘open’ as opposed to the ‘closed’ loop configuration.

Chironomid pupae also display an alternative method of locomotion in which the abdomen undulates in the

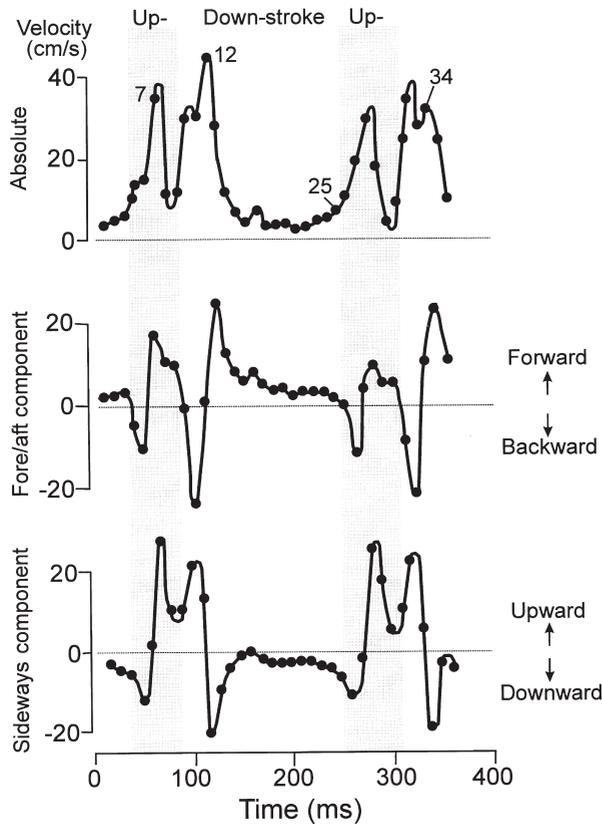


Fig. 8. Absolute velocity relative to the water and fore–aft and sideways velocity components of the motion of the abdominal tip during the somersaulting of *C. plumosus* pupa shown in Fig. 7A.

dorsoventral plane (Fig. 11). Undulatory swimming often follows as the sequel to a brief bout of somersaulting, and it is also the swimming mode selected to perform the final journey to the surface of the water prior to adult emergence. As stated earlier, upwards swimming during this terminal phase of pupal existence appears to be facilitated by an increase in buoyancy of the head/thorax. Once the pupa has made contact with the surface, further effort is no longer needed since the prothoracic tracheal gills become held automatically by surface tension. The undulations of the abdomen are produced by a metachronal wave of bending at a frequency of  $\sim 11$  Hz (Table 1) and with a wavelength equivalent to one body length. The angular motion of the tail-plates relative to the abdominal base is much less than during somersaulting:  $106.0 \pm 10.2^\circ$  ( $N=17$ ) as opposed to approximately  $300^\circ$  in the latter case. The counter-rotation of the long axis of the head/thorax is also much less:  $50.3 \pm 10.2^\circ$  ( $N=17$ ) compared with  $301^\circ$ . Although the distance covered by the body per stroke is only one-third of that during somersaulting (Table 1) the forward velocity is 50% higher due to the greater stroke rate. At  $2.6 \text{ cm s}^{-1}$  the swimming velocity achieved during somersaulting is only fractionally greater than the free-fall velocity of the pupa, whereas the more effective

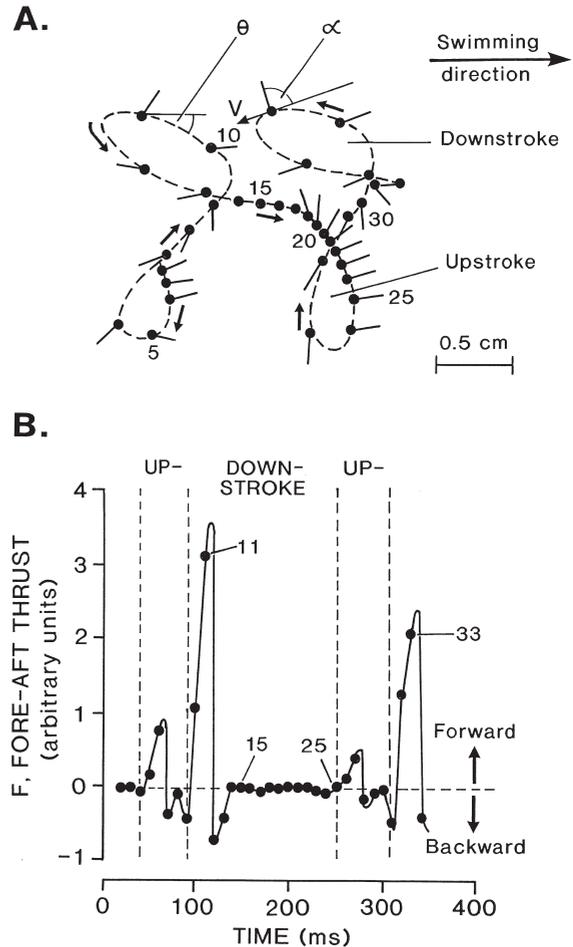


Fig. 9. (A) Path traced out by the abdominal tip during two upstroke/downstroke cycles of somersaulting in *C. plumosus* pupa, redrawn from Fig. 7A. Bars on each point indicate the orientation of the tail plates.  $V$ , instantaneous velocity of the tail-plates relative to the water;  $\alpha$ , angle of attack of tail-plates relative to the water;  $\theta$ , angle between mean swimming direction and direction of instantaneous motion of abdominal tip. (B) Thrust in the fore–aft direction, relative to the mean swimming line, calculated from  $V$ ,  $\alpha$  and  $\theta$  as explained in the text. Frame numbers in A and B correspond with those in Fig. 7A.

sinusoidal swimming generates a velocity of twice the free-fall velocity.

## 4. Discussion

### 4.1. Larval locomotion

The main aim of this study was to relate the methods of locomotion identified in the insects concerned to the dynamic changes in body shape which underlie them and to consider these findings in the light of available knowledge on locomotion in other soft-bodied insects, particularly terrestrial dipteran larvae and caterpillars. None of the three distinct styles of body movement displayed by larval chironomids, i.e. swimming, crawling and res-

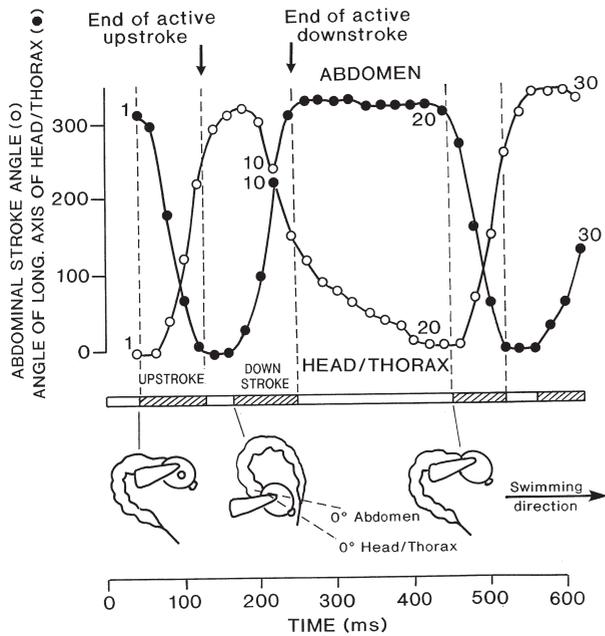


Fig. 10. Angular rotation of the tip of the abdomen about its base, and of the longitudinal axis of the head/thorax about its centre, during the upstroke/downstroke cycle of somersaulting in *C. plumosus* pupa. Angles are measured relative to their positions at the start of the downstroke, as shown in the cartoon below. Dashed lines indicate the points in the cycle at which active motion of the abdomen has ceased; note how the head/thorax continues to rotate under its own circular momentum after these points. Numerals on graphs correspond to stages shown in Fig. 7A.

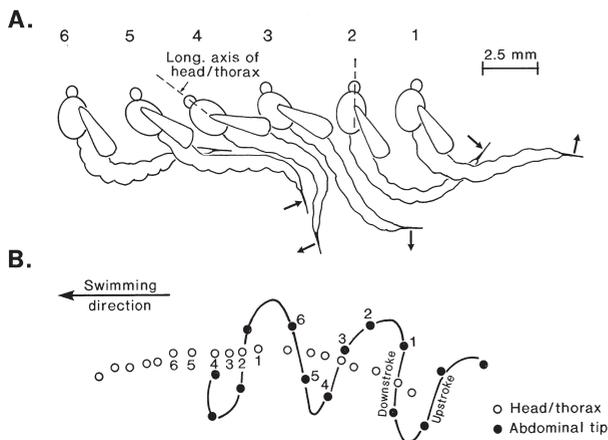


Fig. 11. (A) Successive profiles at 20-ms intervals of the body of a *C. plumosus* pupa during a cycle of undulatory swimming. The long axis of the head/thorax counter-rotates through approximately  $50^\circ$  during each half-stroke. (B) Paths traced out at 20-ms intervals of the centre of the head/thorax and the tip of the abdomen during undulatory swimming. Numerals correspond with stages profiled in A.

piratory undulation, is based on the peristaltic mode of segmental contraction and dilatation which characterises terrestrial maggot and caterpillar locomotion. Peristalsis involves the transmission of a metachronal wave of bilateral muscle activation from one end of the body to the

other. Berrigan and Pepin (1995) described caterpillar-like waves of vertical displacement travelling forwards along the bodies of crawling *Protophormia terraenovae* and *Sarcophaga bullata* maggots. With each 'stride' the head hooked down to provide anchorage although the body often slipped backwards even on rough surfaces. The use by caterpillars of the thoracic and more particularly the highly adhesive abdominal pro-legs to increase the foothold makes telescopic crawling more reliable. Looping geometrid caterpillars dispense with the intermediate abdominal pro-legs and the undulatory wave, and instead use a novel form of locomotion involving arching the body by a local simultaneous contraction of the ventroflexors in the mid-abdominal segments (Brackenbury, 1999a). The loss of the metachronal wave in these specialised caterpillars also appears to be correlated with an inability to telescope the body segments; instead of coiling tightly in response to threat, they adopt a rigid crypsis.

The different muscle deployment patterns in looping as opposed to the more conventional shuffling caterpillar styles of locomotion provide a model for comparing chironomid and terrestrial maggot crawling. Chironomid and geometrid looping both rely on the use of anterior and posterior pro-legs in co-ordination with non-metachronal, non-telescopic, bilateral activation of the segmental muscles. In contrast, the locomotion of maggots and the majority of caterpillars is based on serial and bilateral activation of segmental muscles. Whether the parallel between chironomid crawling and geometrid looping reflects a deeper, homologous convergence of muscle activation patterns in the two groups begs further questions relating to the neural control of locomotion which go beyond the immediate scope of this study. However, in view of the scarcity of information on this subject in limbless, soft-bodied invertebrates, as opposed to the much fuller understanding of the control of walking patterns in limbed hexapods (Huber, 1974; Hoyle, 1976; Delcomyn, 1981; Eaton, 1985), the circumstantial evidence of the present study is worth considering in this context. Chironomid larval crawling, unlike the mechanisms used in larval and pupal swimming, is not simply 'all-or-nothing', but contains the basis for adaptation. Loss of traction on glass, leading to the adoption of a faster, shorter stepping pattern (Table 1), is similar in principle to two- and four-legged vertebrates taking shorter steps on ice. In both cases stresses detected at the periphery complete a feedback loop designed to modify output to the locomotory muscles. In limbed insects, adaptation of walking gaits is based on sensory hairs located near joints (see references above). The precise location of putative mechanoreceptors in the integument of larval chironomids is unknown, but intersegmental membranes and the abdominal and prothoracic pseudopods would seem to be good candidates. Again, a comparison with the nearest 'functional homologue', i.e.

caterpillars, may be instructive. It has been shown that the ambulatory gaits of some species of caterpillar can adapt to behavioural stimuli; in response to threat, for instance, the metachronal wave can be reversed and its transmission speed adjusted to engineer a variety of escape manoeuvres (Brackenbury, 1999a). Caterpillar locomotion is co-ordinated by the central nervous system acting in tandem with local reflexes initiated by integumentary stretch receptors (Weevers, 1966; Hughes, 1974). Evidently such a system is flexible enough to enable escape behaviour in caterpillars to be matched to the perceived intensity of threat, and it forms part of a suite of behavioural responses which is far from simple. Similarly, crawling in chironomids may be only the most obviously identifiable manifestation of a locomotory system that can also be used to perform other manoeuvres such as borrowing and tube-construction.

Despite apparent differences in underlying muscle activation patterns, crawling chironomids, terrestrial maggots and caterpillars produce similar stride lengths. As a fraction of body length, the stride lengths of the caterpillars *Malacosoma americanum* (0.25, Joos, 1992), *Lymantria dispar* (0.20, Casey 1991) and *Pleurotya ruralis* (0.25, Brackenbury, 1999a) are similar to those of the maggots of *Drosophila melanogaster*, *Musca domestica* and *Sarcophaga bullata* (all ~0.25, Berrigan and Pepin, 1995). It is also relevant to point out that these values are similar to the advance ratio (distance covered per wave of contraction) of the swimming ceratopogonid larva (0.25, Nachtigall, 1961) although the locomotory technique which it uses is very different.

The present study has shown that chironomid larval crawling and swimming are kinematically distinct forms of movement which may be independently programmed within the locomotory control system. As long as it is surrounded by a fluid medium, regardless of its viscosity, the larva will attempt to 'swim': no attempt is made to 'crawl' through a treacle-like medium. The initiation of a crawling reflex appears to depend on specific contact being made between the pseudopods and a solid surface, such as the bottom of the pond. Such contact, however, is not a sufficient condition to release crawling behaviour; in hypoxic conditions, for example, attachment via the pseudopods is the necessary prelude to the initiation of respiratory undulation (Fig. 5). If homologous patterns of muscle activation really do exist in this relatively simple insect, they are more likely to be found between swimming and respiratory movements, as discussed in the following section, than between swimming and crawling movements.

In his analysis of the hydrodynamics of chironomid larval swimming, Nachtigall (1961) divided the body into three segments. Propulsion was generated by the backwards motion of the anterior and posterior segments, the middle segment having little dynamic role. The present study shows how the pattern of muscle acti-

vation and the resulting changes in body configuration are matched to the different phases of the locomotory cycle. The gradual unfolding of the body coincides with the phase in the swimming cycle when the head and abdominal tip are moving forwards relative to the water and are therefore incurring an energy penalty. The rapid extension phase coincides with the period in the stroke when the extremes of the body are moving backwards and generating useful thrust. Nachtigall (1961) described the chironomid style of swimming as 'luxurious' because it was so energetically wasteful, only 3% of the mechanical energy generated being converted to forward motion. Nachtigall was comparing chironomids with other aquatic dipteran larvae and pupae which are equipped with tail-plates which increase the efficiency of swimming by acting like oars. But there are also other ways of defining efficiency: measured in terms of the distance travelled by the body per muscle contraction cycle, equivalent to the stride length of walking and crawling insects, chironomid swimming is very effective, each 'stride' being equivalent to 84% of the body length (Table 1), almost three times the value found in crawling maggots and caterpillars.

The curious figure-of-eight swimming style of chironomid larvae is also shared by dixid larvae (Brackenbury, 1999b). In this case also, the distance travelled per stroke was 83% of the body length. *Dixella aestivalis* uses the same body movements employed in swimming to execute a novel kind of surface skating. The corresponding stride length in this case is 0.96 body lengths. This was shown to be approximately one-half the theoretical value achievable in ideal circumstances in which a cylindrical animal moves forward by flexing from side to side, using its head and tail as alternating fixation points, and experiences no backwards slip. In *Dixella*, swimming and skating are homologous locomotory styles, presumably driven by the same basic motor programmes although in the present paper no attempt is made to define whether the hypothetical programme generator is located centrally or peripherally. According to Nachtigall (1961), chironomid larval swimming is derived from pendular respiratory movements, an evolutionary development which allowed the normally sessile larva to venture occasionally into open water. Whilst the muscles of swimming and respiration are indeed driven at the same frequency (Table 1), the latter is a sinusoidal movement, whereas the former is a side-to-side flexure. Sinusoidal swimming is characteristic of very small aquatic worms (Gray, 1968) but it is uncommon in aquatic dipteran larvae and pupae, ceratopogonid larvae (Nachtigall, 1961) being a notable exception.

#### 4.2. Pupal locomotion

Sinusoidal swimming in chironomid pupae, with a distance covered per stroke of 0.32 body lengths (Table

1), appears to be rather more effective than in ceratopogonid larvae, which have an advance ratio of 0.2 (Nachtigall, 1961). The head of a swimming ceratopogonid larva oscillates from side to side with an amplitude of 60% of that of the tail oscillation, twice as much as in the eel, and this reduces the hydrodynamic efficiency of the sinusoidal wave (Nachtigall, 1961). In contrast, the anterior end of the sinusoidally swimming chironomid pupa maintains a relatively unswerving course (Fig. 11B) allowing a more effective transfer of forwardly directed thrust to the body. However, probably more important than these considerations is the presence of the tail-plates which increase the efficiency of swimming by acting like the caudal fin of a fish. Compared with somersaulting, the greater forward speed of sinusoidal swimming, combined with its better directional control, makes it a more suitable method for overcoming the inherent body density and delivering the pupa to the surface of the water for final emergence.

In considering the kinematics and dynamics of somersaulting, it is relevant to compare the lifestyles and kinematics of the chironomid studied here with those of the culicid previously studied by the author (Brackenbury, 1999c). Unlike the chironomid pupa, its culicid counterpart is buoyant throughout its entire life, and in order to escape potential aggressors it is forced to swim downwards from the surface against its own buoyancy. By contrast, the somersaulting chironomid pupa tends to move upwards off the bottom. In both cases, somersaulting can be seen as an energetic form of escape behaviour but the different lifestyles of the two pupae affects the degree to which the behaviour is developed. The *C. pipiens* pupa is continuously exposed at the surface, for several days, to potential enemies such as fish, diving beetles and notonectid bugs, whereas the *C. plumosus* pupa tends to be found in temporary rain-pools with a much lower incidence of natural predators and in addition it is more effectively camouflaged amongst the detritus at the bottom of the water. It could be argued that *C. pipiens* has refined the somersault technique to its maximum degree in response to such predation pressures. The forward speed of a somersaulting *C. pipiens* pupa, 13–14 cm s<sup>-1</sup>, is equivalent to that of the fastest carnivorous diving beetles of the same size (Nachtigall, 1977) and in terms of body lengths s<sup>-1</sup> this is approximately nine times the speed of the somersaulting *C. plumosus* pupa. This relative increase is partly due to a fourfold increase in stroke rate, but more importantly to a doubling of the stride length. The main difference in kinematics between these two species is a virtual absence in *C. pipiens* of the end-downstroke pause that is characteristic of chironomid pupal somersaulting (Fig. 10). The pause represents a ‘dead-spot’ in the locomotory cycle, when thrust is no longer being generated since the abdomen is motionless, and the pupa is simply ‘waiting’ for the body to re-orientate to its starting position.

By cutting out the waiting period, and establishing a symmetric stroke pattern (Fig. 7C), the *C. pipiens* pupa gains in power and efficiency. Furthermore, the profile drag on the rotating body is reduced to a minimum by holding the tail-plates in contact with head during the end-downstroke as well as the end-upstroke phases of the locomotory cycle.

Part of the refinement of the somersault technique in *C. pipiens* is the possession of an integumentary click-mechanism which regulates the timing of the stroke but there is no morphological evidence of such a mechanism in the *C. plumosus* pupa. The evolutionary design of the swimming technique in *C. pipiens* seems to have been directed towards achieving higher speeds so that ipso facto inertial forces of the water and the body could be more effectively exploited. This is reflected in the relatively high Reynold’s number of ~1100, four times its value in somersaulting *C. plumosus*.

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