

## LABIAL EXTENSION IN THE DRAGONFLY LARVA *ANAX IMPERATOR*

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The extension mechanism of the larval dragonfly's labium has been under discussion since Snodgrass (1954) drew attention to the absence of muscles at the head/postmentum joint (p-h, Fig. 1A) and proposed that it was extended by blood pressure, due to the abdominal muscles which also cause jet propulsion. This proposition is supported by evidence that the anus closes (Pritchard, 1965), and the abdominal muscles contract (Caillère, 1972; Olesen, 1972) during labial extension; and by reports of an increase in abdominal pressure of 5000 Pa (Olesen, 1979) and 4000–12 000 Pa (Tanaka & Hisada, 1980). From high-speed film of *Aeschna nigroflava*, Tanaka & Hisada (1980) calculate a maximum torque of  $40 \mu\text{N}\cdot\text{m}$  (neglecting water resistance) and state that this would require a joint pressure of 6000 Pa. They also claim that the labium extends normally when a pressure of 8000 Pa is applied to a dead animal under water, thus indicating the relatively small effect of water resistance. However, these conclusions raise a number of questions. In deriving the pressure of 6000 Pa, they appear to have used the torque/pressure characteristic of the postmentum/prementum joint (p-p, Fig. 1A). Had they used the p-h joint characteristic (their Fig. 6) a required pressure of 24 000 Pa would have been obtained. And the statement that 8000 Pa, applied to a head preparation under water,

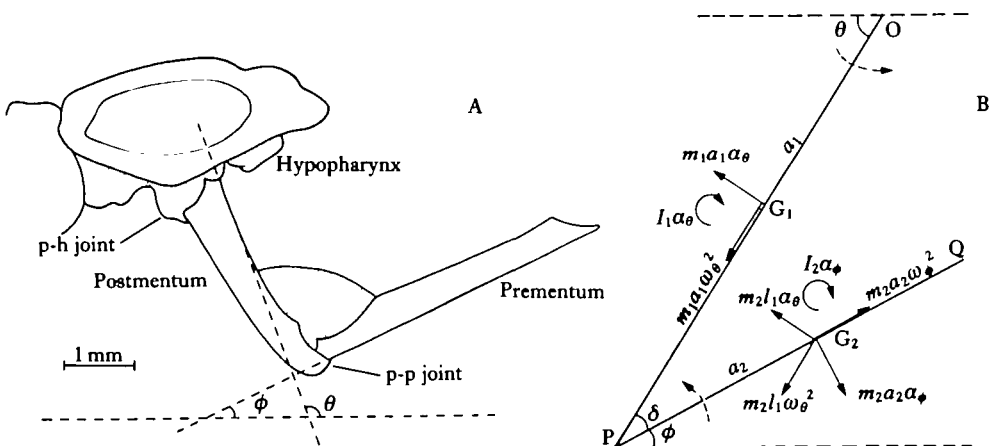


Fig. 1. (A) *Anax imperator*. Head showing partially extended labium with angles  $\theta$  and  $\phi$ , measured with reference to the animal's 'perch'. (B) Inertial forces and torques acting on a jointed rod OPQ rotating about O and P.  $G_1$  and  $G_2$  are the centres of mass of OP and PQ.

Key words: Dragonfly larva, labial mechanism, hydraulic joint.

produces normal extension, is not borne out by a comparison of their Figs 5 and 8, which again only relates to the p-p joint. Confusion between the p-h and p-p joint may be due to the erroneous view that the torques at the two joints must, for mechanical reasons, be equal. Their data on labial movement is subject to large standard error and no estimate is made of the error caused by the use of a simplified model, which assumes that the mass of the prementum is concentrated at the end of the postmentum.

I have used fresh data, from *Anax imperator* (Leach), and a less approximate model, to recalculate the p-h joint torque and estimate the effect of water resistance; and have also briefly considered the p-p joint extensor mechanism. Second-year larvae were filmed at 500 frames  $s^{-1}$  and 15–20 °C while attacking living *Calliphora* grubs (Fig. 2). From a number of trials, three successful sequences were obtained involving two specimens of different size. From plots of the angles  $\theta$  and  $\phi$  (Figs 1A and 3), angular velocities ( $\omega$ ) and accelerations ( $\alpha$ ) were calculated over 4-ms intervals.

Fig. 1B shows the inertial forces and torques acting on the labium, treated as a jointed rod OPQ. By d'Alembert's Principle, the sum of the moments about O and the hydraulic torque at O ( $T_O$ ) must be zero, and we have:

$$T_O = [I_1\alpha_\theta + m_1a_1^2\alpha_\theta] + [m_2l_1\alpha_\theta(l_1 - a_2 \cos \delta) + m_2l_1\omega_\theta^2(a_2 \sin \delta)] + [I_2\alpha_\phi - m_2a_2\alpha_\phi(l_1 \cos \delta - a_2) - m_2a_2\omega_\phi^2(l_1 \sin \delta)]$$

where the terms in square brackets relate to the rotation of OP about O, PQ about O and PQ about P, respectively. I express the labium's mechanical characteristics in terms of the conveniently measured prementum length  $l_2$  (see Table 1) which largely removes the effect of specimen size. Substituting mean values:

$$T_O/l_2^5 = [2.7\alpha_\theta] + [11.8\alpha_\theta + 9.2(\omega_\theta^2 \sin \delta - \alpha_\theta \cos \delta)] + [9.0\alpha_\phi - 9.2(\omega_\phi^2 \sin \delta + \alpha_\phi \cos \delta)] \text{ N.m/m}^5.$$

If, instead, as assumed by Tanaka & Hisada (1980), the mass of PQ is concentrated at P, this expression reduces to:  $T_O^*/l_2^5 = 14.5 \alpha_\theta \text{ N.m/m}^5$ . Neglecting water

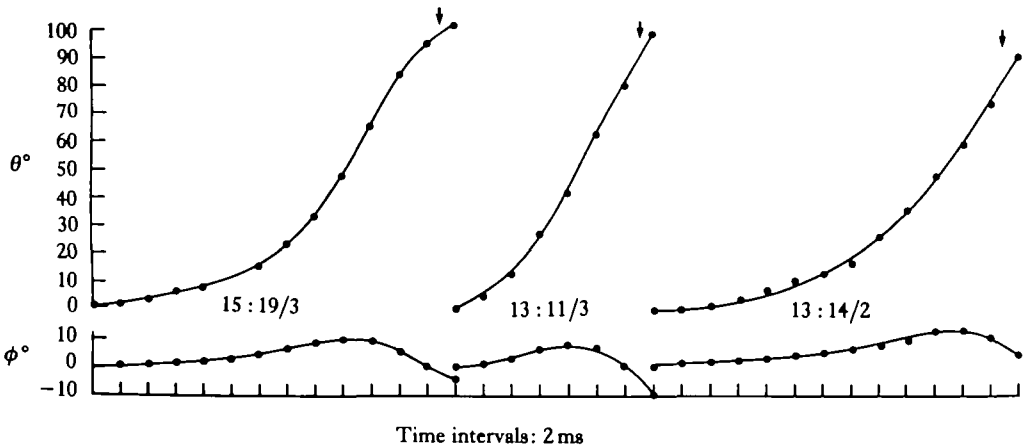


Fig. 3. Change of  $\theta$  and  $\phi$  with time (time intervals: 2 ms) for three labial extensions: specimen 13, sequences 11/3 and 14/2; specimen 15, sequence 19/3. Arrows indicate moment of contact with prey. Each angle was measured four times from 18 cm  $\times$  12 cm prints, giving s.d. mostly  $< \pm 1^\circ$ .

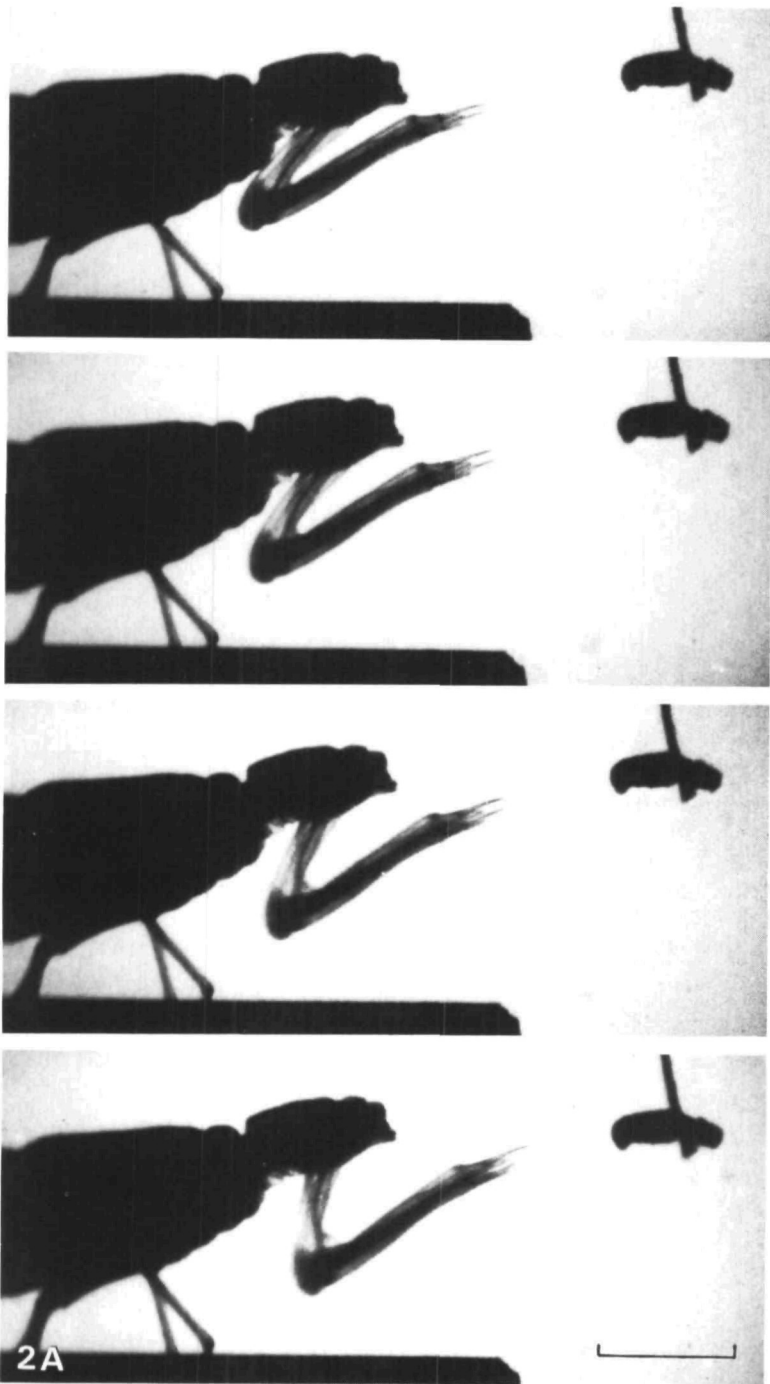


Fig. 2. *Anax imperator*. Labial extension filmed at 500 pictures per second (2 ms between frames). The beginning of the extension has been omitted. Scale bar = 5 mm.

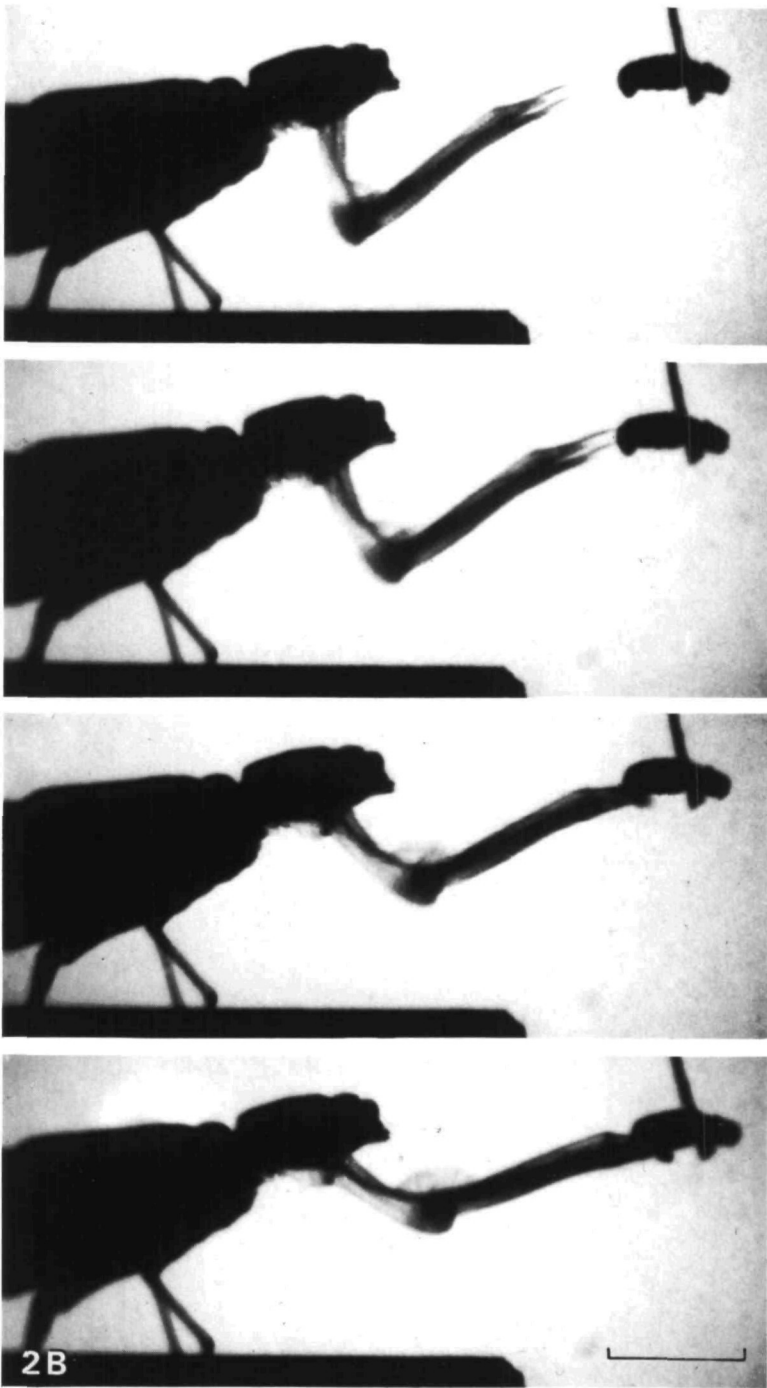


Table 1. Mechanical characteristics of labium of *Anax imperator*

	Absolute values			Values in terms of prementum length $l_2$		
	*Specimen 13	†Specimen 15	†Specimen 15	Specimen 13	Specimen 15	Mean
<b>Postmentum</b>						
Mass $m_1$	13.5 mg	3.5 mg		$16.78l_2^3 \text{ kg m}^{-3}$	$16.20l_2^3 \text{ kg m}^{-3}$	$16.49l_2^3 \text{ kg m}^{-3}$
Length $l_1$	6.4 mm	4.2 mm		$0.69l_2$	$0.70l_2$	$0.69l_2$
†Centre of mass $a_1$	3.3 mm	2.1 mm		$0.35l_2$	$0.35l_2$	$0.35l_2$
†Radius of gyration $k_1$	1.8 mm	1.2 mm		$0.19l_2$	$0.20l_2$	$0.20l_2$
M.I. $I_1 = k_1^2 m_1$	$43.74 \times 10^{-12} \text{ kg m}^2$	$5.04 \times 10^{-12} \text{ kg m}^2$		$0.63l_2^5 \text{ kg m}^{-3}$	$0.65l_2^5 \text{ kg m}^{-3}$	$0.64l_2^5 \text{ kg m}^{-3}$
<b>Prementum</b>						
Mass $m_2$	20.4 mg	5.2 mg		$25.36l_2^3 \text{ kg m}^{-3}$	$24.07l_2^3 \text{ kg m}^{-3}$	$24.72l_2^3 \text{ kg m}^{-3}$
Length $l_2$	9.3 mm	6.0 mm		—	—	—
†Centre of mass $a_2$	5.0 mm	3.2 mm		$0.54l_2$	$0.53l_2$	$0.54l_2$
†Radius of gyration $k_2$	2.4 mm	1.7 mm		$0.26l_2$	$0.28l_2$	$0.27l_2$
M.I. $I_2 = k_2^2 m_2$	$117.50 \times 10^{-12} \text{ kg m}^2$	$15.03 \times 10^{-12} \text{ kg m}^2$		$1.69l_2^5 \text{ kg m}^{-3}$	$1.93l_2^5 \text{ kg m}^{-3}$	$1.81l_2^5 \text{ kg m}^{-3}$

\* Mass: 777 mg; length: 39 mm.

† Mass: 259 mg; length: 25 mm.

‡ Determined graphically from a photographic outline of the dorsal surface.

resistance, maximum values for  $T_0/l_2^5$ , and the corresponding torques  $T_0$ , for the three sequences analysed, were:

Specimen	Sequence	$T_0/l_2^5$ (N.m/m <sup>5</sup> )	$T_0$ ( $\mu$ N.m)	$T_0^*$ ( $\mu$ N.m)	Pressure (Pa)
13 ( $l_2 = 9.3$ mm)	11/3	108 000	7.5	10.7	4100
	14/2	132 000	9.2	7.2	5000
15 ( $l_2 = 6.0$ mm)	19/3	168 000	1.3	1.8	2600
[ <i>A. nigroflava</i> ( $l_2 = 9.0$ mm)]		677 000	–	40.0	23 900]

Tanaka & Hisada (1980, Fig. 6) obtain a torque/pressure ratio equivalent to  $0.0023 l_2^3$  N.m/Pa for the p-h joint of *A. nigroflava*. Now torque/pressure  $\propto \Delta V/\Delta\theta$  where  $V$  and  $\theta$  are joint volume and angle (Parry & Brown, 1959) and as the anatomy of the joints in this species and in *A. imperator* are similar, I have applied the same ratio to the latter, giving the pressures shown above. These pressures are well within the maximum values recorded. The much greater torque and corresponding pressure in *A. nigroflava* is mainly due to its much more massive prementum ( $m_2 = 60.4 l_2^3$  kg m<sup>-3</sup> c.f.  $24.7 l_2^3$  kg m<sup>-3</sup> in *A. imperator*). Note that concentrating the mass of the prementum at the end of the postmentum may over- or underestimate the maximum torque depending on the exact configuration of the extending labium.

The inertial effect of the surrounding water can be estimated by calculating the additional torque due to the mass of water accelerated by the transverse components of labial movement. We can take its effective mass ( $m_w$ ) to be  $\frac{1}{4}\pi s^2 l \rho$  where  $s$  and  $l$  are the width and length of the labial segment, and  $\rho$  is the density of water (Lighthill, 1975, p. 74); and assume that its centre of mass and radius of gyration coincide with that of the corresponding labial segment. We find that  $m_w/l_2^3 = 26.1$  and  $121.1$  kg m<sup>-3</sup> for the postmentum and prementum respectively, and:

$$T_{O(w)}/l_2^5 = [4.3\alpha_\theta] + [(58.2 \cos \delta - 45.3)(\alpha_\theta \cos \delta - \omega_\theta^2 \sin \delta)] + [\alpha_\phi(44.1 - 45.3 \cos \delta)] \text{ N.m/m}^5.$$

Maximum values of  $T_0/l_2^5$  and  $T_{O(w)}/l_2^5$  do not coincide and their combined values, in the three sequences analysed, do not exceed twice the value of  $T_0/l_2^5$  alone. Thus the required pressure still lies within the maximum values reported.

Proceeding as above, I have calculated the maximum torques at the p-p joint and find that, if it were to operate hydraulically, the required pressure would be similar to that at the p-h joint – the more favourable torque/pressure relation (Tanaka & Hisada, 1980, Fig. 6) being offset by the greater inertial water resistance. But this method of extension cannot be assumed without taking into account the pressure gradient in the postmentum, due to blood flowing into the p-p joint. By Pousieulle's equation,

$$p = \frac{v}{t} \cdot \frac{8l\eta}{\pi r^4}$$

where  $v$  = joint volume ( $= 0.008 l_2^3$ , determined by cannulating the head with a bubble-containing capillary);  $t$  = time for joint to open ( $= 20$  ms);  $l$  = postmentum

length ( $= 0.69 l_2$ );  $r$  = equivalent radius of postmentum ( $= 0.08 l_2 f$  where  $f$  = equivalent radius/external radius); and  $\eta$  = blood viscosity (taken as  $0.0017 \text{ Pa s}^1$  – Frew, 1929). This gives a pressure drop of  $30/f^4 \text{ Pa}$ . Now the postmentum contains two pairs of muscles and a large trachea, so  $f$  is unlikely to be more than  $1/3$ – $1/4$ , giving a pressure drop of the same order of magnitude as the p–h joint pressure. So we may conclude that the p–p joint is unlikely to operate by blood pressure despite its favourable configuration (for which the need to fold back on itself offers an alternative explanation). This is in accordance with the presence of extensor (and flexor) muscles at this joint.

Tanaka & Hisada (1980) attach importance to a click mechanism at the p–p joint of *Aeschna nigroflava* – viz. paired knobs on the postmentum that slide along grooves in the prementum ‘as if the engaged position is the real pivot of the p–p joint’ (which would be inconsistent with a firm joint articulation). In *Anax imperator* no such structure has been found and the joint may be observed to rotate smoothly about its articulation.

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