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LETTERS

Meniscus-climbing insects

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Water-walking insects and spiders rely on surface tension for static weight support[1,2] and use a variety of means to propel themselves along the surface[3–8]. To pass from the water surface to land, they must contend with the slippery slopes of the menisci that border the water's edge. The ability to climb menisci is a skill exploited by water-walking insects as they seek land in order to lay eggs or avoid predators[4]; moreover, it was a necessary adaptation for their ancestors as they evolved from terrestrials to live exclusively on the water surface[3]. Many millimetre-scale water-walking insects are unable to climb menisci using their traditional means of propulsion[2,3,9]. Through a combined experimental and theoretical study, here we investigate the meniscus-climbing technique that such insects use. By assuming a fixed body posture, they deform the water surface in order to generate capillary forces[10–13]: they thus propel themselves laterally without moving their appendages. We develop a theoretical model for this novel mode of propulsion and use it to rationalize the climbers' characteristic body postures and predict climbing trajectories consistent with those reported here and elsewhere[3].

Although the surfaces of standing bodies of water such as ponds are flat on human scales, there is significant topography on the scale of millimetre-scale water-walking insects. To water-walking insects small relative to the capillary length ($l_c = (\sigma/\rho g)^{1/2} = 0.27$ cm, where $\sigma = 70\,\mathrm{dynes\,cm^{-1}}$ is the surface tension, $\rho = 1\,\mathrm{g\,cm^{-3}}$ the water density, and $g = 980\,\mathrm{cm\,s^{-2}}$ the gravitational acceleration), the menisci adjoining land and emergent vegetation appear as frictionless mountains. Some water-walking arthropods, such as the adult water strider[3] and fisher spider[14], are capable of leaping over menisci. Some insects cannot do this, but have developed an ingenious means of ascent. By locking into a fixed posture in which they deform the free surface, they generate a tangential force that draws them up the slope (Fig. 1). Meniscus climbing has been reported and described qualitatively by previous investigators[2,3,9]; however, the precise physical mechanism was not elucidated and no theoretical model was proposed.

Fluid mechanicians[10–12,15] have long known that lateral capillary forces exist between small floating objects, an effect responsible for the formation of bubble rafts in champagne and the clumping of breakfast cereal in a bowl of milk[16]. Recently, such capillary forces have been recognized as a means by which to promote self-assembly of microstructures at a free surface[13,17–19]. Here we describe the use of analogous capillary effects in the ascent of menisci by semiaquatic insects.

We collected water-walking insects *Mesovelia* and *Microvelia* and beetle larvae *Pyrrhalta* from local freshwater ponds and maintained them in aquaria. The insects were filmed using a high-speed video camera (500 frames $\mathrm{s^{-1}}$) and the images digitized and analysed using Midas motion analysis software.

An insect approaching an object long relative to the capillary length, such as a shoreline or floating log, must first ascend an effectively two-dimensional meniscus whose shape, $z = \eta(x)$, is prescribed by the Young–Laplace equation[20], $\rho g \eta = \sigma \nabla \cdot \mathbf{n}$ (where $\mathbf{n}$ is the unit outward normal; see Fig. 1c), that expresses the balance between hydrostatic and curvature pressures at the interface. Provided the interfacial slope is everywhere sufficiently small, $\eta_x \ll 1$, this equation may be solved to yield a meniscus shape of $\eta(x) = l_c \cot\theta\ e^{-x/l_c}$ where θ is the contact angle[10]. Consider a small massless body that deforms the surface by applying a vertical force $T\hat{z}$ at a horizontal distance x_0 from the wall. Provided the body is small relative to the capillary length, the applied force may be treated as a point force and the lateral force on the body may be written exactly[11] as

$$\mathbf{F}(x_0) = -T\cot\theta\ e^{-x_0/l_c}\hat{x} \qquad (1)$$

A small buoyant object ($T > 0$) floating in the presence of a larger meniscus is thus drawn up the slope[12]; conversely, a negatively buoyant body ($T < 0$) is driven downwards.

Water-walking insects are generally covered with a mat of dense hair that renders them effectively non-wetting[4,21], but some have developed specialized feet with retractable hydrophilic claws or 'ungues' that allow them to raise the free surface[2,4], an adaptation critical for meniscus-climbing. Water-walking insects such as *Mesovelia* (Fig. 1) ascend menisci by assuming a static posture in which they pull up on the free surface with the wetting tips of their front and rear tarsi and push down with their middle tarsi.

A simple theoretical model allows us to rationalize this body configuration. Consider an insect of mass M with its centre of mass a horizontal distance x_0 from a vertical wall (Fig. 1c). Each of its front and rear tarsi pull up with forces F_1 and F_3 at horizontal positions $x_0 - L_1$ and $x_0 + L_3$, respectively; the middle tarsi push down with force F_2 at the position $x_0 + L_2$. According to equation (1), the front and rear legs are attracted to the background meniscus while the middle pair are repelled. The insect may adjust L_i subject to the geometrical constraints imposed by its size, and F_i subject to the constraint that the force per unit length applied on any of its limbs cannot exceed 2σ, lest its legs pass through the free surface.

The local slope of the interface is assumed to be small and the forces F_i applied normal to the meniscus. The normal force balance on the insect and torque balance about the middle legs are written in the Methods section as equations (2) and (3), respectively. The acceleration of the insect is determined by the tangential force balance in equation (4). We note that if the insect is too heavy, it will be unable to climb owing to the combined influence of its weight and the repulsive capillary force generated by its middle legs. Because the capillary force decays exponentially with distance from the wall, the insect generates the majority of its thrust with its front legs. It should thus extend its front legs and pull up as hard as possible, while maximizing the extension of its back legs and pulling up with the force sufficient to balance torques, as prescribed by equation (3). Because the range of capillary forces corresponds to the capillary length, insects must scramble onto the meniscus to initiate their ascent.

We have thus far assumed for the sake of simplicity that the meniscus climber assumes a laterally symmetric leg configuration.

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Andersen[3] and Miyamoto[9] note that several climbers, such as *Hydrometra*, tilt their bodies during ascent (see inset B in Fig. 3). Presumably, such tilted postures are assumed in order to maximize the capillary thrust. Theoretical modelling of the tilted postures requires consideration of additional torque balances that are immediately satisfied in the symmetric posture, specifically, those that prevent the insect's angular acceleration about a vertical axis (yaw) and about an axis aligned with the mean direction of motion (roll).

Miyamoto[9] reported that a number of terrestrial insects have also developed the ability to ascend menisci, an adaptation exploited as they seek land having fallen onto water, often from overhanging vegetation. Unlike water-walking insects whose hairy legs render them effectively non-wetting[3,20,21], terrestrial insects must deform the surface with their wetting body perimeters. For example, the larva of the waterlily leaf beetle is circumscribed by a contact line, and deforms the free surface by arching its back (Fig. 2). The beetle larva will be drawn up the meniscus if the anomalous surface energy generated by arching its back exceeds the gain in the system's gravitational potential energy associated with its ascent. By arching its back to match the curvature of the meniscus, the beetle larva may generate a lateral force that drives it up the meniscus. We note that for a randomly oriented beetle larva, the forces (in equation (1)) produced by its arched posture generate a torque about the vertical axis that serves to align the beetle larva perpendicular to the meniscus; the beetle thus abuts the wall tail first.

Figure 3 shows the observed trajectories of a *Mesovelia* individual of length 2 mm and weight 0.2 dynes. Accompanying theoretical trajectories were obtained by numerically integrating equation (4). The insect's position and leg configuration were recorded by high-speed video; the insect's weight and the meniscus contact angle on plexiglass (40°) were measured using a scale and a still camera, respectively. Given the leg position and meniscus contact angle, there is a single unknown in the model, F_1. For *Mesovelia*, F_1 was inferred from the trajectory to be 2–4 dynes, values comparable to $\sigma\pi w$, the maximum force the front leg tip of diameter $w \approx 60\,\mu$m can apply to

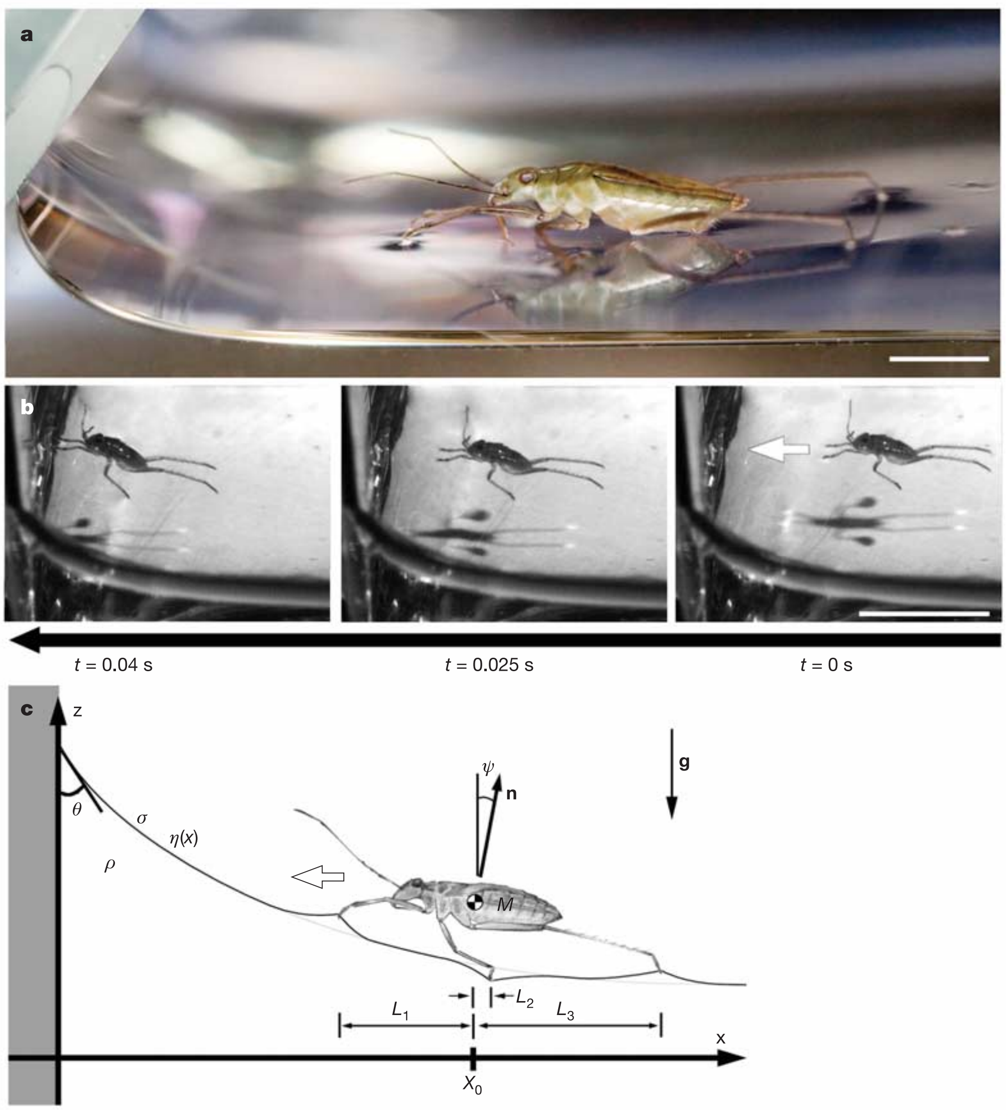

Figure 1 | Meniscus climbing by the water treader *Mesovelia*. **a**, *Mesovelia* approaches a meniscus, from right to left. The deformation of the free surface is evident near its front and hind tarsi. **b**, High-speed video images of an ascent. Lighting from above reveals the surface deformation produced. In pulling up, the insect generates a meniscus that focuses the light into a bright spot; in pushing down, it generates a meniscus through which light is diffused, casting a dark spot. Characteristic speeds are 1–10 cm s^{-1}. Scale bars, 3 mm. See Supplementary Information for the accompanying video sequence. **c**, Schematic illustration of the meniscus-climbing *Mesovelia*: it pulls up with its wetting front and hind claws, and pushes down with its middle legs. **n** denotes the normal to the undeformed meniscus, and x_0 the lateral position of the insect's centre of mass.

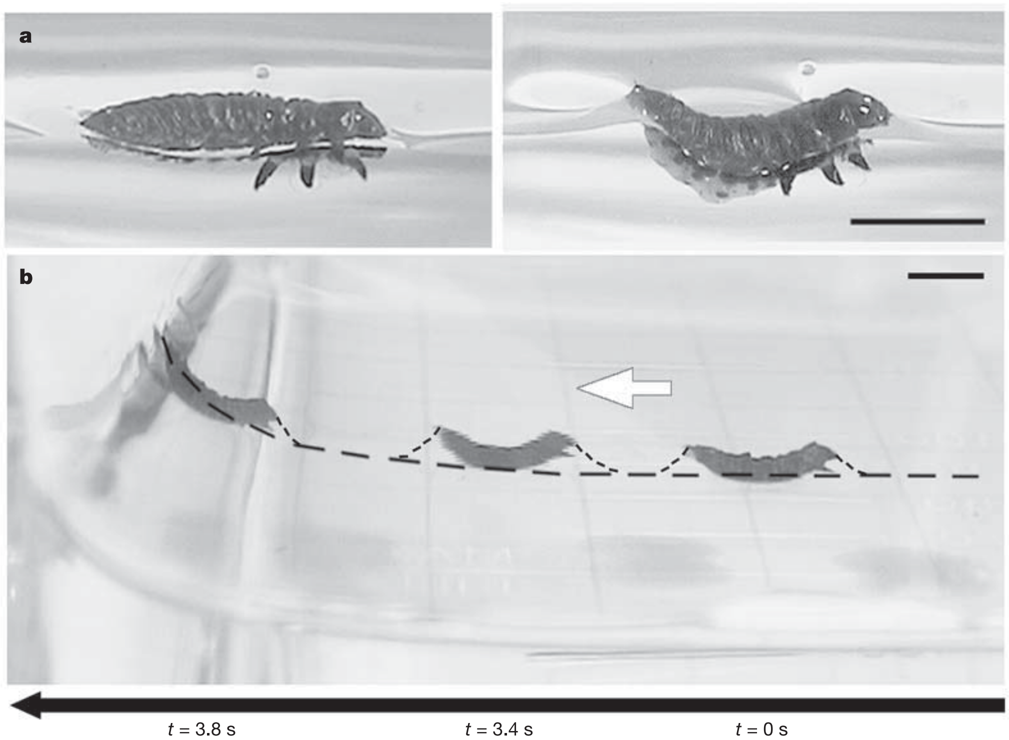

Figure 2 | **Meniscus climbing by the larva of the waterlily leaf beetle.** The beetle larva is a terrestrial insect unsuited to walking on water but it is nevertheless able to ascend the meniscus, from right to left. **a**, It is partially wetting and so circumscribed by a contact line. It deforms the free surface by arching its back, thus generating the desired capillary thrust. **b**, The beetle larva's ascent is marked by peak speeds in excess of $10\,\mathrm{cm\,s^{-1}}$. Scale bars, 3 mm. See Supplementary Information for the accompanying video sequence.

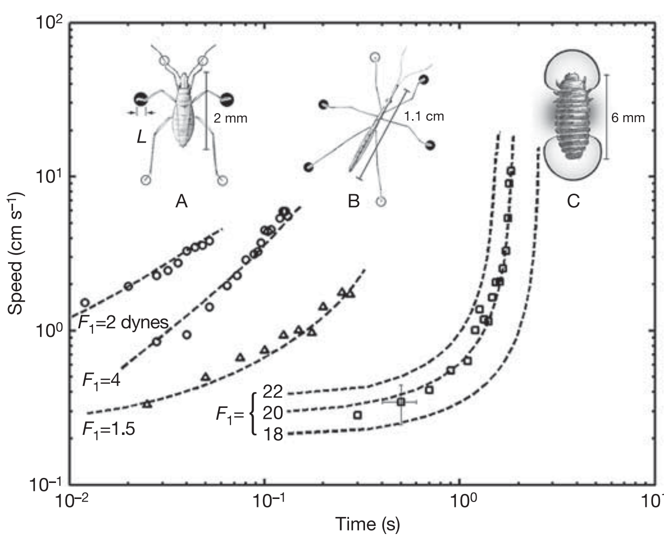

Figure 3 | **Observed evolution of insect speed during the ascent of menisci.** Insects are *Mesovelia* (A, circles), *Hydrometra*[3] (B, triangles) and the beetle larva (C, squares). Circles around the insects' feet indicate the sense of the surface deflection: white upwards and black downwards. Theoretical predictions based on equation (4) are presented as dashed lines. Inferred forces F_1 applied by the frontmost appendage are given in dynes. The sensitivity of the theoretical trajectories to F_1 are indicated for the beetle larva trajectory. For the *Hydrometra* data[3], the best-fit trajectory yielded the net capillary force, from which the individual F_i values were calculated. We assumed the meniscus contact angle to be 40°, comparable to the contact angle of water on plexiglass, and then inferred the net capillary force by optimally fitting the observed trajectory. The individual forces F_i applied by the insect were then calculated by consideration of the four governing equations (the normal force balance and three torque balances) and the upper bounds on the forces applied by each leg. The error bars (shown for one point but applicable to every data point) reflect the uncertainty associated with measuring the body position.

the free surface without breaking through. The corresponding force F_2 is comparable to the maximum force, $2\sigma L$, the insect leg can apply without breaking through with the tarsal segment of length L of its middle leg (see inset A in Fig. 3). The trajectory of the beetle larva, of length 6 mm and weight 150 dynes, was similarly computed using equation (4), by setting $F_2 = 0$. Again, the single unknown in modelling the beetle larva's ascent is F_1, which is equal to F_3 by symmetry; the best fit is obtained with a force of 20 dynes that corresponds to the maximum surface tension force it can generate with its frontal perimeter of 3 mm. Figure 3 also shows the climbing trajectory for the tilting climber *Hydrometra*, a water-walker of length 1.1 cm and weight 1.8 dynes, reported by Andersen[3]. An accompanying theoretical trajectory was computed from the reported leg positions and inferred values of θ and the net capillary force.

Meniscus climbing is an unusual means of propulsion in that the insect propels itself in a quasi-static configuration, without moving its appendages. Biolocomotion is generally characterized by the transfer of muscular strain energy to the kinetic and gravitational potential energy of the creature, and the kinetic energy of the suspending fluid[22–25]. In contrast, meniscus climbing has a different energy pathway: by deforming the free surface, the insect converts muscular strain to the surface energy that powers its ascent.

METHODS

The following equations were considered in computing the trajectories of the meniscus-climbing insects. Normal and tangential directions refer to orientation with respect to the meniscus at the point x_0. We assume that the meniscus slope does not vary appreciably over the length of the insect. Terms are defined in Fig. 1c. The normal force balance on the insect is

$$2F_2 = 2F_1 + 2F_3 + Mg\cos\psi(x_0) \tag{2}$$

The torque balance about the insect's middle legs is

$$2F_3L_3 = 2F_1L_1 - MgL_2\cos\psi(x_0) \tag{3}$$

The tangential force balance on the insect is

$$M\frac{d^2x_0}{dt^2} = -2B(F_i, L_i)\cot\theta\cos\psi(x_0)e^{-x_0/l_c} + Mg\sin\psi(x_0) \quad (4)$$

where the first term on the right-hand side represents the net capillary force and

$$B(F_i, L_i) = F_1e^{L_1/l_c} - F_2e^{-L_2/l_c} + F_3e^{-L_3/l_c} \quad (5)$$

As a caveat, we note that the validity of equation (1) and therefore of equation (4) is expected to break down when the slope of the meniscus becomes large.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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