

## RESEARCH ARTICLE

# Jumping mechanisms in dictyopharid planthoppers (Hemiptera, Dictyopharidae)

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**ABSTRACT**

The jumping performance of four species of hemipterans belonging to the family Dictyopharidae, from Europe, South Africa and Australia, were analysed from high-speed images. The body shape in all was characterised by an elongated and tapering head that gave a streamlined appearance. The body size ranged from 6 to 9 mm in length and from 6 to 23 mg in mass. The hind legs were 80–90% of body length and 30–50% longer than the front legs, except in one species in which the front legs were particularly large so that all legs were of similar length. Jumping was propelled by rapid and simultaneous depression of the trochanters of both hind legs, powered by large muscles in the thorax, and was accompanied by extension of the tibiae. In the best jumps, defined as those with the fastest take-off velocity, *Engela minuta* accelerated in 1.2 ms to a take-off velocity of 5.8 m s<sup>-1</sup>, which is the fastest achieved by any insect described to date. During such a jump, *E. minuta* experienced an acceleration of 4830 m s<sup>-2</sup> or 490 g, while other species in the same family experienced 225–375 g. The best jumps in all species required an energy expenditure of 76–225 μJ, a power output of 12–80 mW and exerted a force of 12–29 mN. The required power output per mass of jumping muscle ranged from 28,000 to 140,200 W kg<sup>-1</sup> muscle and thus greatly exceeded the maximum active contractile limit of normal muscle. To achieve such a jumping performance, these insects must be using a power amplification mechanism in a catapult-like action. It is suggested that their streamlined body shape improves jumping performance by reducing drag, which, for a small insect, can substantially affect forward momentum.

**KEY WORDS:** Kinematics, Biomechanics, Resilin, Auchenorrhyncha

**INTRODUCTION**

Many species of insects include jumping in their locomotory repertoire to enable fast movement or rapid escape from predators, or to launch into flight. To generate such rapid and powerful movements requires particular motor patterns that coordinate the legs in a different way from those used for walking, and specialisations of the muscles, skeleton and limb joints. One order of insects that contains the most able jumpers is Hemiptera. The sub-order Auchenorrhyncha, which is unlikely to be monophyletic, contains three groups that each have members that are able jumpers: the Membracoidea (leafhoppers and treehoppers), the Cercopoidea (froghoppers) and Fulgoroidea (planthoppers). All are characterised by the use of the same large trochanteral depressor muscles in the thorax to propel rapid movement of the two hind

legs in the same plane underneath the body. A catapult-like mechanism is used in which the trochanteral depressor muscles contract slowly, energy is stored and is then released suddenly (Burrows, 2006a; Burrows, 2007b; Burrows, 2009). Despite these important common features, each group has particular specialisations of its own that define its jumping abilities. These include differences in body shape, in the length of the hind legs and in the anatomy of the coxae.

Most leafhoppers have hind legs that are two to three times longer than the other legs and are 90% of the body length (Burrows, 2007b). By contrast, froghoppers and planthoppers have hind legs that are only 40–50% longer than the other legs and approximately 50–70% of body length (Burrows, 2006a; Burrows, 2009). The length of the hind legs does not, however, affect the take-off velocity when a catapult mechanism is used because the release of energy stored in elastic cuticular structures is nearly independent of strain rate (Alexander, 1995; Bennet-Clark, 1990). Longer legs, however, take longer to accelerate so that ground reaction forces are lower than those applied by shorter legs (Burrows and Sutton, 2008). Longer legs should therefore reduce energy loss when jumping from more compliant surfaces and therefore enable take-off from flexible leaves, the speciality of leafhoppers.

Planthoppers, like froghoppers but unlike leafhoppers, have large internal skeletal structures in the metathorax, called pleural arches, that are a composite of hard cuticle and the rubber-like protein resilin (Andersen and Weis-Fogh, 1964), and which are bent like archery bows when the large trochanteral depressor muscles contract in preparation for a jump (Burrows et al., 2008). They store the energy of these prolonged muscle contractions and then unfurl rapidly to release the stored energy and propel the depression of the hind legs (Burrows, 2010).

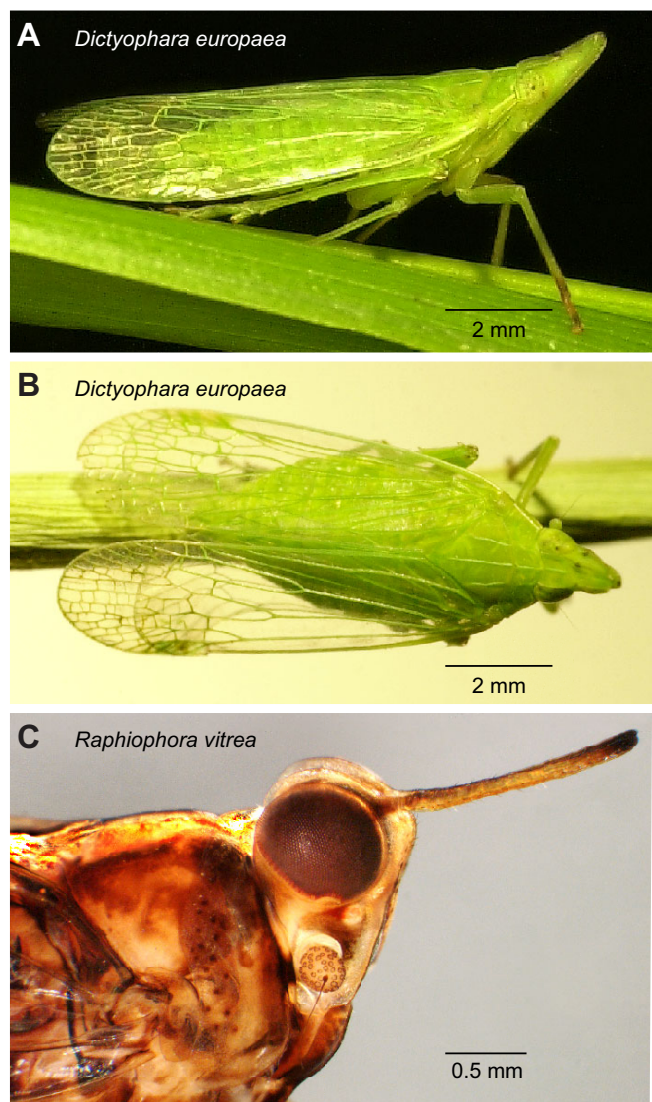
The three groups of hopper also differ in the mechanical engagement between the coxae and femur when the hind legs are levated in preparation for a jump. Froghoppers have prominent coxal and femoral protrusions that are both covered in microtrichia and must disengage before depression of the hind legs can occur (Burrows, 2006b). By contrast, in leafhoppers the protrusions are absent. In the planthoppers *Issus coleoptratus*, the coxal protrusion is prominent but it engages with a flat, slightly raised area on the femur that bears no microtrichia. *Issus coleoptratus* also have a mechanical interaction between the left and right trochanters that is lacking in froghoppers, and that ensures synchrony of movement between the two hind legs when jumping (Burrows, 2009).

There are 20 families of planthoppers, but only one (Issidae) has so far been analysed to determine jumping mechanisms. The other families show a great diversity in the size and shape of the body so that the range of overall appearance differs markedly. The aim of this paper is to determine whether the characters so far discovered for one family extend across other families of the planthopper group and to assess whether the elongated body of the family Dictyopharidae affects jumping performance. It is shown

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**Fig. 1. Body structure in dictyopharids illustrated by two of the four species studied.** (A,B) Photographs of *Dictyophara europaea* viewed from the side (A) and from dorsal (B). (C) Photograph of the head of *Raphiophora vitrea* to show the anterior protrusion from the head.

that four species from three continents all use a catapult mechanism to accelerate in 1–2 ms to remarkable take-off velocities of 4–5.8 m s<sup>-1</sup> that rank with the highest values recorded for any insect.

**Table 1. Body form of dictyopharids**

Species	Body mass (mg)	Body length (mm)	Hind leg, femur (mm)	Hind leg, tibia (mm)	Ratio of leg lengths			Hind leg length	
					Front	Middle	Hind	% of body length	Length (mm)/body mass <sup>1/3</sup> (mg)
<i>Engela minuta</i> (N=1)	5.7	6.6	1.9	2.9	1	1	1.3	89	3.4
<i>Thanatodictya praeferata</i> (N=3)	8.1	8.3	0.8	1.4	1	1	1.5	82	1.7
<i>Raphiophora vitrea</i> (N=7)	19.6±1.0	8.9±0.2	2±0.1	4.1±0.1	1	0.8	1	82	3.3
<i>Dictyophara europaea</i> (N=7)	22.9±0.7	8.8±0.3	2.2±0.1	4.2±0.2	1	1.1	1.5	91	2.8

Body length and mass, and lengths of the hind femora and tibiae in the four species of dictyopharids analysed. *N* indicates the number of individuals from which the measurements were taken. Data are means ± s.e.m. The ratio of leg lengths is given relative to the front legs.

## RESULTS

### Body shape

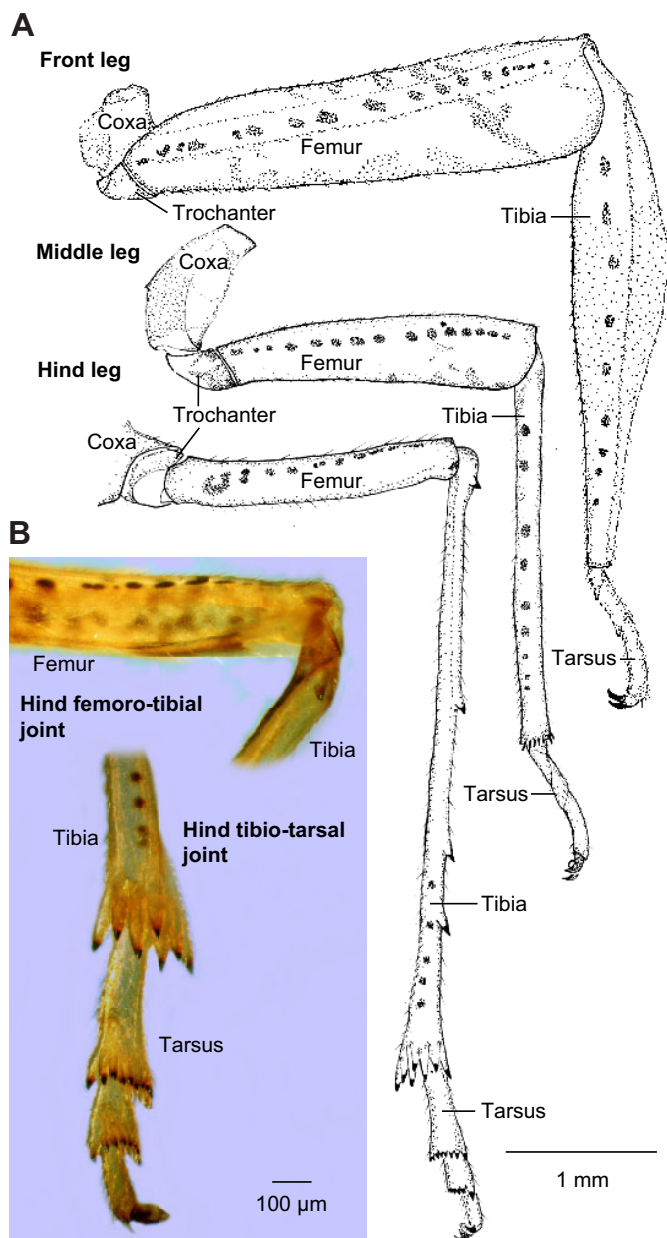
The body shape of the four species analysed was characterised by a prominent forward projection of the frons so that the compound eyes were set back from the front of the head by 1 to 2 mm. In three of the species analysed here, *Dictyophara europaea* (Fig. 1A,B), *Engela minuta* and *Thanatodictya praeferata*, the head tapered gradually, giving the body a pointed and seemingly streamlined appearance. In the fourth species, *Raphiophora vitrea*, the frons was 1.4 mm long but only 100 µm in diameter, so that the transition with the rest of the head was more abrupt (Fig. 1C). In all species the antennae were short and were set ventral to the compound eyes on the side of the head. Both pairs of wings were membranous and in all but *E. minuta* extended beyond the tip of the abdomen. The length of the body ranged from 6.6 mm in *E. minuta* to a third longer at 8.9±0.2 mm (*N*=7) in *R. vitrea* (Table 1). Body mass was lowest at 5.7 mg in *E. minuta* but four times higher at 22.9±0.7 mg in *D. europaea*.

### Structure of the hind legs

The hind legs provided the main propulsive force for jumping in each of the four species analysed. They were held beneath the body and both moved in the same plane as each other, almost parallel with the under surface of the body. They were longer than the other two pairs of legs in three of the four species analysed. In *E. minuta*, the hind legs were 30% longer than the front and middle legs so that the ratio relative to the front legs was 1 front:1 middle:1.3 hind (Table 1). In *T. praeferata* and *D. europaea*, the hind legs were 50% longer than the front legs, with ratios of 1:1:1.5 in the former and 1:1.1:1.5 in the latter. By contrast, in *R. vitrea*, the hind legs were the same length as the front legs but both were longer than the middle legs, so that the ratio was 1:0.8:1. This is due to the front femora, which were 50% longer than both the middle and hind femora, and to the front tibia, which were 30% longer than the middle tibiae and only 13% shorter than the hind tibiae (Fig. 2). The front legs also appeared to be more substantial than the other legs because both the femur and tibia were flattened and wider, suggesting that they might be used in grasping or searching. In all species, the hind legs represented between 82 and 91% of body length. The length of the hind legs expressed as a ratio relative to the cube root of the body mass ranged from 1.7 in *T. praeferata* to 3.5 in *R. vitrea* (Table 1). The following description of the structure of the hind legs relevant to jumping applies to all four species studied.

### Coxa

The ventral region of the metathorax between the boundary with the mesothorax and the anterior edges of the two hind coxae was



**Fig. 2. Anatomy of the legs of *Raphiophora vitrea*.** (A) Drawings of a front, middle and hind leg. The front leg has a wide femur and tibia; the hind tibia is long and thin; the middle leg is shortest. (B) Photographs of the hind femoro-tibial joint viewed laterally and the hind tibio-tarsal joints viewed ventrally.

covered by transparent and flexible membrane through which could be seen the large trochanteral depressor muscles of the hind legs (Fig. 3A). The fibres of these muscles inserted on an anterior circular expansion of the large tendon, which then tapered to a strap-like structure that ran through the coxa to its insertion on the anterior rim of the trochanter. These tendons could be seen to move anteriorly and posteriorly within the thorax as the hind legs were levated and depressed.

The coxae of the hind legs were closely opposed to each other at the ventral midline and laterally they were fused to the thorax at the posterior and ventral extremes of the pleural arches (Fig. 3, Fig. 4A). The black cuticle of the hind coxae extended laterally and wrapped around each side of the body and could be seen to pivot with the

lateral wall of the thorax, allowing a forward and backward rotation of some 20 deg. A hind coxa did not appear to move independently of the other coxa. By contrast, the front coxae were separated from each other at the midline by the posterior part of the head, and the middle coxae by the mouthparts containing the stylets. The coxae of both the front and middle legs pivoted independently with the thorax.

The pleural arches of the internal thoracic skeleton [also called Ugsprungsplatte (Heilig and Sander, 1986; Sander, 1957)] curve anteriorly from the coxae toward their dorsal articulations with the hind wings. When the metathorax was cleared of soft tissue and then illuminated with ultraviolet (UV) light, the pleural arches fluoresced bright blue, clearly delineating them from other thoracic structures, which did not show any fluorescence (Fig. 3B). The blue fluorescence is indicative of the presence of resilin. These structures were bent during preparation for a jump when the trochanteral depressor muscles contracted without moving the hind legs from their fully levated and cocked positions.

A posteriorly directed protrusion emerged from the lateral and ventral region of each coxa that measured 80 µm at its base, narrowing along its 170 µm length to a point (Fig. 3, Fig. 4A,B). The whole protrusion and the adjacent, anterior of the coxa were covered with microtrichia arranged in overlapping rows (Fig. 4B,C). At the base of the protrusion, each of the microtrichia protruded some 6 µm from the surface of the cuticle and was 5 µm wide but progressively changed in shape along the protrusion itself, with their tips becoming more pointed. These microtrichia increase the surface area and thus friction with a particular area of the dorsal femur with which the coxa comes into contact when the hind leg is levated fully in preparation for a jump.

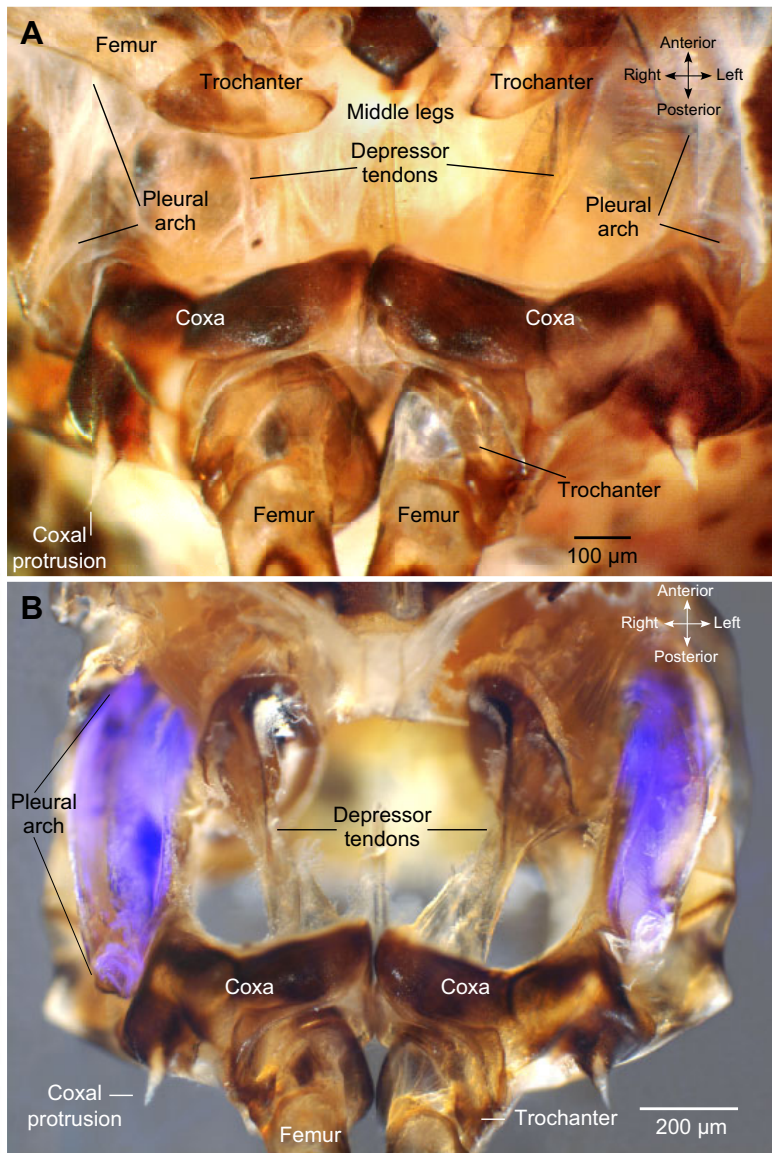
#### Trochanter

A hind trochanter could rotate about a coxa through some 130 deg from its fully levated position when the hind legs were cocked in readiness for jumping, to its fully depressed position that was achieved at take-off. The joint consisted of two pivots, one ventral and lateral (Fig. 3A), and one dorsal and more medial. Each pivot was formed by a black cuticular horn of the trochanter that engaged with the coxa.

#### Distal segments

The joint between the trochanter and the femur allowed a small angular excursion of the distal part of the leg. The femoro-tibial joint consisted of two pivots that allowed extension and flexion through some 170 deg (Fig. 2B). The femur had a patch of five to seven campaniform sensilla on its proximal ventral surface (Fig. 4A) that might give information about strains at the nearby trochantero-femoral joint. On the proximal dorsal surface of the femur was a small, raised but flat and smooth area of cuticle with a number of long hairs at its perimeter. This patch is in the same location where froghoppers have a femoral protrusion that engages with the coxal protrusion during preparation for jumping (Burrows, 2006b).

The hind tibia was the longest segment of any of the legs, but was thin, tubular and light. It had a series of four outwardly pointing spines along its length and an array of ventrally pointing spines at its articulation with the tarsus (Fig. 2A,B). The tarsus itself had three segments with arrays of short ventrally pointing spines at the proximal two joints. These spines were pressed against the ground during a jump and their orientation should increase traction and thus prevent the hind legs from slipping. At the tip of the distal tarsal segment was a pair of hooks.



**Fig. 3. Photographs of the thorax of *Raphiophora vitrea* to show the structure of the proximal joints of the hind legs.**

(A) Ventral view with the trochantera of both hind legs fully depressed about the coxae. The pleural arches linking the lateral and ventral part of a coxa to the hinge of a hind wing dorsally are both visible at the lateral edges of the thorax. The large tendons of the trochanteral depressor muscles can be seen through the transparent soft cuticle of the metathorax. (B) Superimposed images of the dissected thorax, from which the trochanteral depressor muscles were removed, viewed ventrally under UV and then brightfield illumination. The pleural arches on both sides fluoresce bright blue under UV illumination.

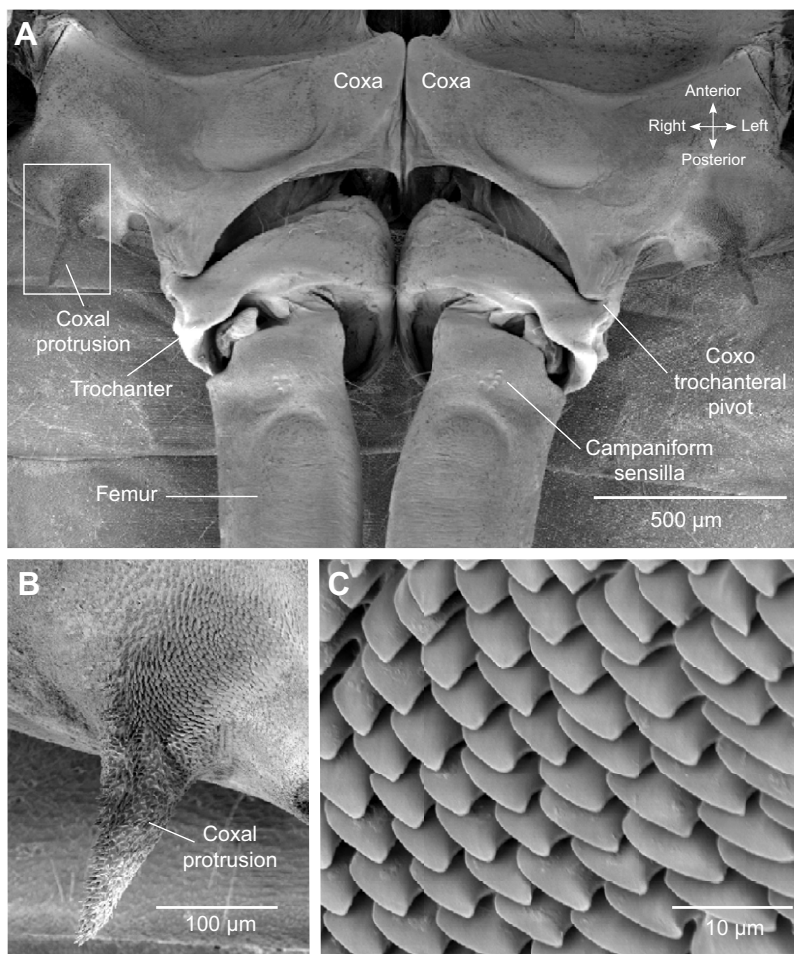
### Kinematics of the jump

Jumping movements were analysed from high-speed videos taken from different orientations; side and ventral views are illustrated for *T. praeferata* (Figs 5, 6; see supplementary material Movies 1, 2). Side views as this dictyopharid jumped from the horizontal floor provided detailed information about the timing of movements by the different legs and enabled the body angle at take-off, as well as the jump trajectories, to be determined (Fig. 5, Table 2). Furthermore, the acceleration time for a jump could be measured from the first detectable movements of the hind legs to the time at which they lost contact with the ground and the insect became airborne. Views of an insect from underneath as a jump was propelled from the front surface of the glass chamber gave detailed information about the sequence of movements of individual joints and of the co-ordination between the two hind legs (Figs 6, 7). Jumps by two further species, *E. minuta* and *R. vitrea*, are illustrated in Figs 8 and 9, respectively. Jumps by all species analysed showed the following features.

A key element in the preparatory movements that preceded the launch of a jump was levation of the coxo-trochanteral joints of both hind legs. The result was that both hind legs were rotated forwards so that the femora were pressed against the ventral surfaces of the

coxae and the metathorax. The coxal protrusions then contacted the small protrusions from the dorsal surface of the femora of both hind legs. The tibiae were also partially flexed about the femora so that the tarsi were placed on the ground close to the lateral edges of the posterior segments of the abdomen (Figs 5, 6). These positions were held for a minimum of a few hundred milliseconds, but this period was variable and could extend to seconds. During this time, the pleural arches that link the lateral articulation of the coxa with the dorsal articulation of the hind wing were seen to bend. Adjustments of the front legs during this period set the elevation angle of the body relative to the ground. At take-off, the body angle varied only over a narrow range in the different species: from a mean angle of 41 deg in *T. praeferata* to a mean angle of 53 deg in *E. minuta* (Table 2).

This initial, preparatory period was followed by a rapid and simultaneous depression and extension of both hind legs and a forward propulsion of the body to take-off in a jump. The first propulsive movement of the hind legs was a simultaneous depression of both trochantera about the coxae, most clearly seen in views from underneath (Figs 6, 7). This movement of the two hind legs occurred at the same time within the resolution limit of 0.2 ms



**Fig. 4. Scanning electron micrographs to show the structure of the proximal joints of the hind legs of *Dictyophara europaea*.** (A) Ventral view of the ventral coxo-trochanteral and trochanteral-femoral articulations. A group of campaniform sensilla is visible on each proximal femur. (B) An enlarged view of the right coxal protrusion shows it to be covered in microtrichia, which spread anteriorly over the coxa. (C) A region of the microtrichia at higher power.

set by the frame rate of  $5000\text{ s}^{-1}$  used to capture the jumps. In fewer than 1% of the jumps, one trochanter was seen to move 1 frame (0.2 ms) before the other, but no greater asynchronies were seen. Unfurling of the bent pleural arches accompanied these rapid movements of the hind legs.

In side views (Figs 5, 8, 9), where the trochanter was largely obscured, this first propulsive movement was visible as a downward and backwards movement of the femur that in turn resulted in the closer application of the proximal tarsus to the substrate. The continuing depression of a hind trochanter caused a further downward movement of the femur and an extension of the tibia (Figs 5, 8, 9). These movements propelled the body forwards and raised it from the ground so that the middle legs were the first to lose contact with the ground. In *R. vitrea* this happened at  $-1.4\text{ ms}$ , in *T. praeferrata* and *D. europaea* at  $-0.8\text{ ms}$  and *E. minuta* at  $-0.6\text{ ms}$  before take-off. The front legs lost contact between 0.2 and 0.4 ms later, so that during the last part of the acceleration phase of the jump only the hind legs were in contact with the ground and could provide propulsion. In *R. vitrea*, however, the length of the front legs sometimes meant that the hind legs had completed their depression and extension movements before the front legs lost contact with ground. In these circumstances, therefore, take-off was only completed when the front legs left the ground. The posture of the front legs and the lack of observable changes in the angles of their coxo-trochanteral or femoro-tibial joints suggested that their contact with the ground did not provide substantive thrust to such jumps in the later stages of the acceleration phase. This conclusion is supported by other jumps in which the front legs were stretched out

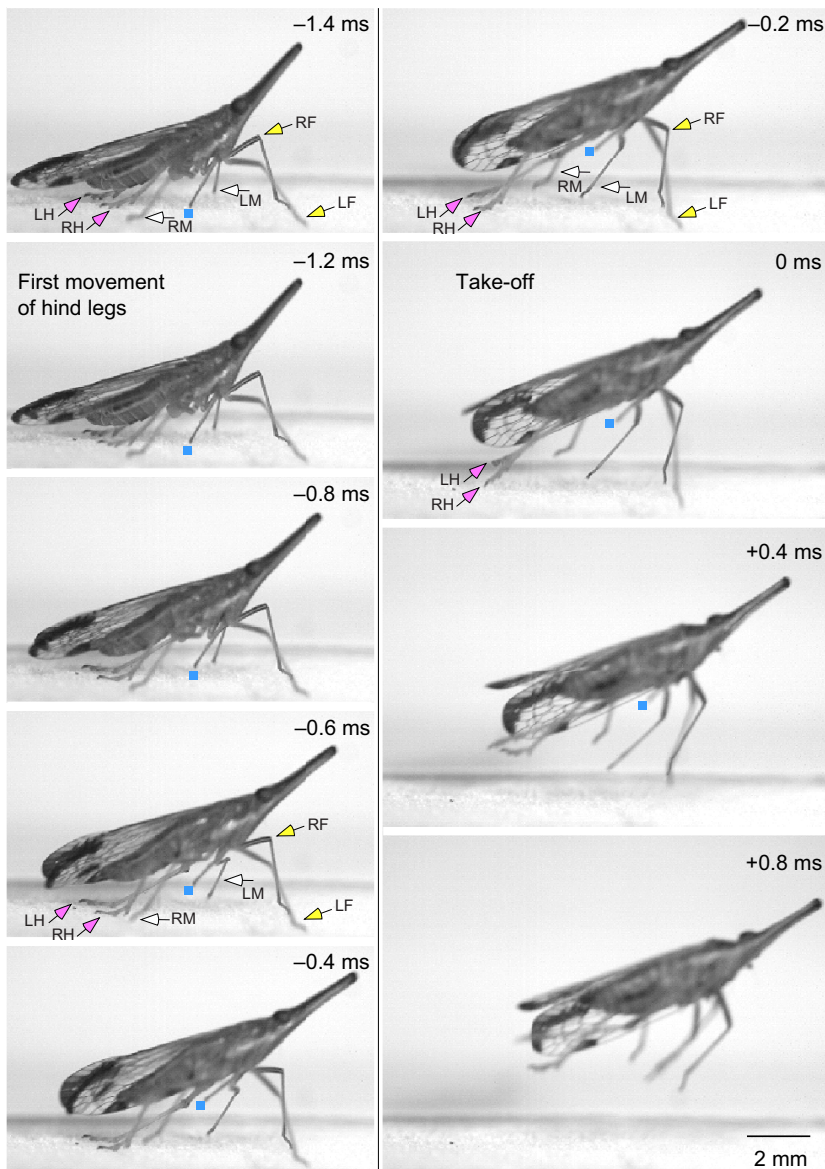
in front of the body and were not in contact with the ground during the entire acceleration phase. The take-off velocity of such jumps was no different from those in which the front legs were initially on the ground.

Throughout this acceleration phase of a jump, the forward velocity of the body continued to rise and reached a peak just before take-off, only to decline once all legs had lost contact with the ground and the insect was airborne (Fig. 5A). At take-off, both the coxo-trochanteral and femoro-tibial joints reached the full extent of their depression and extension movements, respectively (Figs 5–7). After take-off, the hind legs either remained in this state alongside the abdomen, or the tibiae could partially flex again (Fig. 7). Both hind tarsi also came together at the midline of the body and in some jumps then crossed.

In all 64 jumps analysed in the four species, the wings remained closed and were neither opened nor flapped as the body was accelerated to take-off by the movements of the hind legs. In only one jump by *D. europaea* did the wings start to open some 2 ms after the insect became airborne, so that there was a smooth transition from jumping to flying.

#### Trajectories

The take-off angle, defined as the angle subtended by the path of the body relative to the ground during the last 1 ms of the acceleration period and in the first 4 ms when airborne, was  $40\pm 5.4\text{ deg}$  in *E. minuta*. In the other three species, the value was higher but similar in all, ranging only from 61 to 69 deg (Table 2). The trajectories during the first 4 ms after take-off were highly stable with no



**Fig. 5. Side view of a jump by *Thanatodictya praeferrata* from a horizontal surface.** Images were captured at rate of 5000 images  $s^{-1}$  with an exposure time of 0.05 ms. In this and Figs 6, 8 and 9, the following conventions are used: the left (L) and right (R) hind (H) legs are indicated by arrows with pink heads, the middle legs (LM, RM) by arrows with white heads, and the front legs (LF, RF) by arrows with yellow heads. The tip of the piercing mouthparts is labelled with a blue square. Selected images are arranged in two columns at the times indicated, with take-off designated as  $t=0$  ms; the bottom left-hand corner of each image represents a constant point of reference.

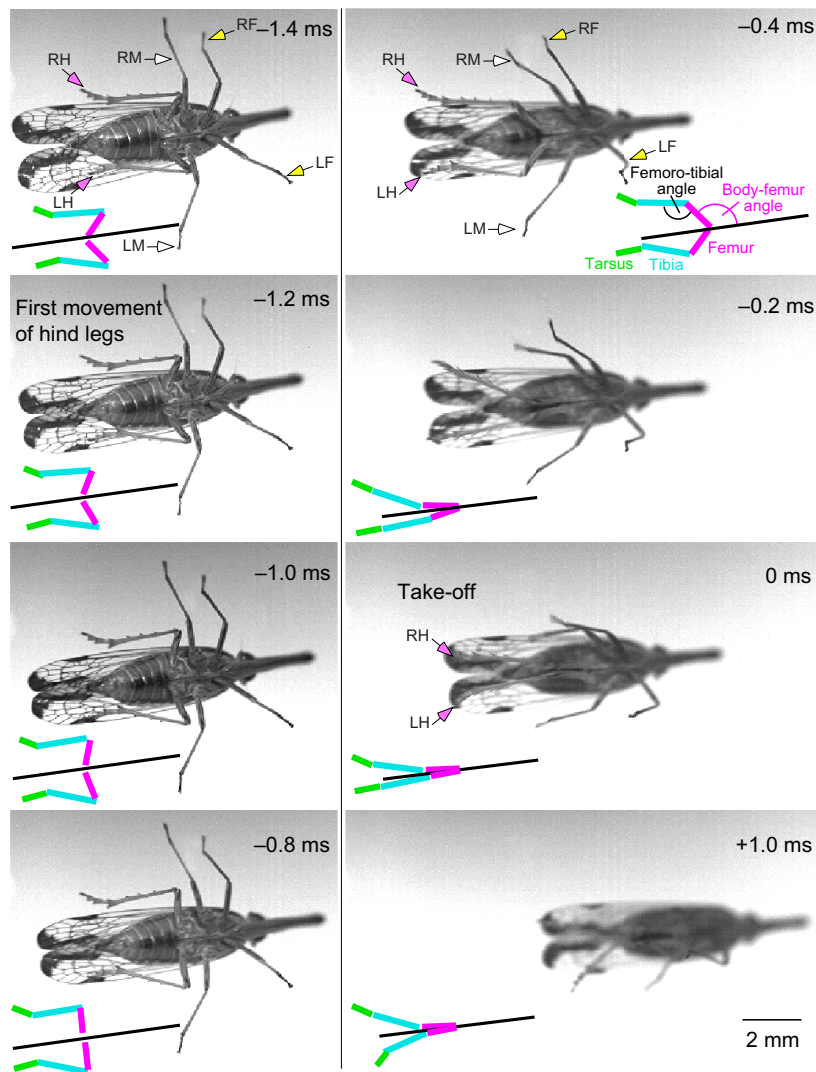
measurable rotations in the pitch and yaw planes. Rotation in the roll plane was limited to a low rate (see supplementary material Movie 2). The wings did not move during this period so the trajectory was purely the result of the propulsive forces generated mostly by the hind legs.

### Jumping performance

These kinematic analyses allowed the jumping performance to be defined in the following terms. Mean acceleration times were the same at  $1.40 \pm 0.03$  ms in *E. minuta* and *T. praeferrata*, the two lightest species; they were slightly longer at  $1.55 \pm 0.05$  ms in *R. vitrea*, but significantly longer at  $2.44 \pm 0.08$  ms in the heaviest species, *D. europaea*. The first three species achieved fastest take-off times of 1.2 ms, but *D. europaea* only achieved 2.0 ms. Take-off velocity was measured as a rolling three-point average from successive frames, and therefore at 0.2 ms intervals, just before take-off. The mean of means velocities for all the individuals of a particular species ranged from  $3.1 \pm 0.2$   $m s^{-1}$  in *R. vitrea* to  $4.8 \pm 0.5$   $m s^{-1}$  in *E. minuta* (Table 2). In their fastest jumps, individuals of all species had take-off velocities above  $4$   $m s^{-1}$ , with

*E. minuta* achieving the remarkable value of  $5.8$   $m s^{-1}$ . The applied accelerations in these jumps ranged from  $2200$   $m s^{-2}$  in *D. europaea* to more than twice this at  $4830$   $m s^{-2}$  in *E. minuta*. At take-off, all species experienced forces in excess of  $200$  g in their fastest jumps, with *E. minuta* experiencing  $490$  g. The energy required to achieve these performances ranged from  $76$   $\mu J$  in *T. praeferrata* to  $254$   $\mu J$  in the heavier *D. europaea*. The power output ranged from  $63$  mW in *T. praeferrata* to  $127$  and  $129$  mW in *D. europaea* and *R. vitrea*, respectively. The force exerted was at its lowest at  $28$ – $29$  mN in *E. minuta* and *T. praeferrata*, and highest at  $58$  and  $64$  mN in the heaviest species *D. europaea* and *R. vitrea*. The trochanteral depressor muscles of the hind legs constitute approximately 10% of the body mass, as in the planthopper *I. coleopratus* (Burrows, 2009), so that a power per muscle mass of  $48,400$ – $140,200$   $W kg^{-1}$  would be required in the fastest jumps by the different species (Table 2).

The speed of these jumps and small numbers of available specimens of some species made it difficult to measure the distances and heights achieved in natural jumping. Therefore, to estimate the distance jumped ( $s$ ) and the maximum height reached ( $h$ ), it was



**Fig. 6.** Selected images, at the times indicated, of a jump by *Thanatodictya praeferata* from the vertical, front surface of the glass chamber and viewed from underneath. Images were captured at a rate of 5000 images  $s^{-1}$  and with an exposure time of 0.05 ms. The stick diagrams show the propulsive movements of the hind legs during a jump, with the femora in pink, the tibiae in cyan, the tarsi in green, and the longitudinal axis of the body in black. The angles plotted in Fig. 7 are indicated.

assumed that the body acted like a small projectile as described by the equations below:

$$s = v \cos \Theta (2v \sin \Theta / 9.81), \quad (1)$$

$$h = (v \sin \Theta)^2 / (2 \times 9.81), \quad (2)$$

where  $v$  is the velocity at take-off and  $\Theta$  is the take-off angle. Calculations based on the motion of such an inert body (Alexander, 1968) were then made and are shown in Table 3.

The distances and heights predicted for the best jumps are remarkable. For example, *E. minuta*, the smallest of the dictyopharids analysed, is predicted to jump forwards for 3 m or more than 550 times its body length. Even a longer and heavier species such as *R. vitrea* is predicted to jump almost 1.5 m, more than 100 times its body length.

## DISCUSSION

This paper has shown that dictyopharids accelerated their bodies to a jump in only 1.2 to 2 ms, depending on the body mass of the particular species, and achieved fast take-off velocities. Indeed, the smallest species achieved a take-off velocity of  $5.8 \text{ m s}^{-1}$ , which is the highest recorded for any insect to date. Even the larger species studied that have more than three times the mass had take-off velocities of  $4 \text{ m s}^{-1}$  or higher. These jumps were all propelled by

hind legs that are only 30–50% longer than the other legs, and shorter than the overall body length. All were powered by large trochanteral depressor muscles in the thorax. No jumps were accompanied by movements of the wings and none showed marked body spin in any plane, perhaps reflecting a stabilising influence of the elongated body shape, which is also suggested to improve performance by reducing drag.

## Power output for jumping

Calculations from the kinematics indicate that jumping requires high power outputs from the muscles. In many jumping bugs, such as froghoppers (Burrows, 2006a) and planthoppers (Table 2) (Burrows, 2009), the large trochanteral muscles that provide the power comprise approximately 10% of body mass. On this basis, the power requirements for the best jumps of dictyopharids analysed ranged from 28,000 to  $140,200 \text{ W kg}^{-1}$  in the different species. Such outputs are far beyond the maximum active contractile limit of normal muscle; direct contraction of the muscles would only produce power outputs from 250 to  $500 \text{ W kg}^{-1}$  (Askew and Marsh, 2002; Ellington, 1985; Josephson, 1993; Weis-Fogh and Alexander, 1977). Jumping in dictyopharids must therefore also involve a power amplification mechanism such as that provided by a catapult, as in fleas (Bennet-Clark and Lucey, 1967), locusts (Bennet-Clark, 1975) and hemipterans. Recordings from the jumping muscles of hemipterans

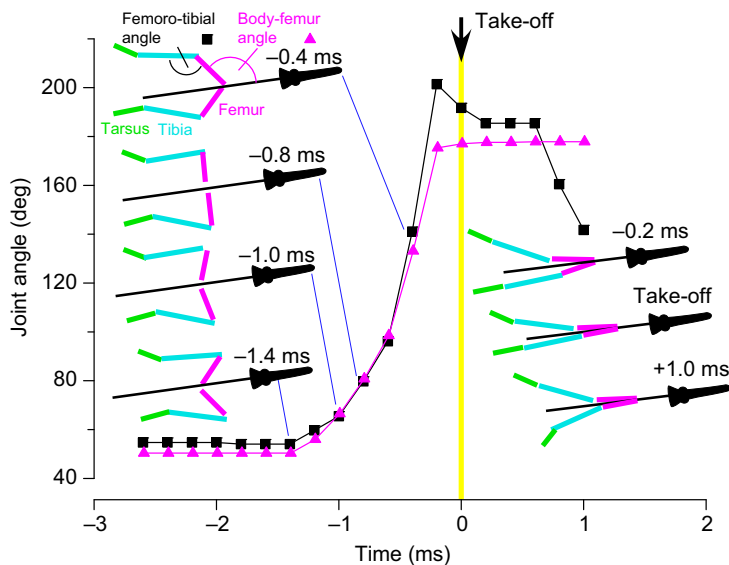
**Table 2. Jumping performance of dictyopharids**

Formula	Body mass (m)	Time to take-off (t)	Take-off velocity (v)	Take-off angle (elevation)	Body angle at take-off	Acceleration ( <i>a</i> )	<i>g</i> force	Energy (E)	Power (p)	Force (F)	Power/muscle mass
Units	mg	ms	m s <sup>-1</sup>	deg	deg	m s <sup>-2</sup>	$g = f/9.81$ <b>g</b>	$E = 0.5m v^2$ μJ	$p = E/t$ mW	$F = mf$ mN	$p/(0.1m)$ W kg <sup>-1</sup>
<i>Ergela minuta</i> (N=1, n=9)											
Mean	5.7	1.4±0.1	4.8 ± 0.5	40±5	53±9	3430	350	66	47	20	82,300
Best	5.7	1.2	5.8	35	35	4830	490	96	80	28	140,200
<i>Thanatodictya praeferata</i> (N=3, n=18)											
Mean	8.1	1.4±0.1	3.7±0.2	69±3	41±5	2570	260	53	38	21	46,300
Best	7.8	1.2	4.4	68	35	3670	375	76	63	29	80,700
<i>Raphiophora vitrea</i> (N=4, n=20)											
Mean	19.6 ± 1.0	1.6±0.1	3.1±0.2	65±4	45±2	1930	200	82	55	38	28,000
Best	19.3	1.2	4.0	57	33	3330	340	154	129	64	66,700
<i>Dictyophara europaea</i> (N=4, n=16)											
Mean	22.9 ± 0.7	2.4±0.1	3.9±0.1	61±3	51±3	1630	170	174	73	37	31,700
Best	26.2	2.0	4.4	75	60	2290	225	254	127	58	48,400
<sup>a</sup> <i>Issus coleoptratus</i> , male											
Mean (N=31)	21.5±0.56	1.49±0.04	3.2±0.21	42.7±1.8	17.1±2.4	2261±176.2	231±17.9	121±14.9	89±11.6	49±3.9	37,600
Best	22	0.78	5.5	56	10	7051	719	303	388	141	160,300
<sup>a</sup> <i>Issus coleoptratus</i> , female											
Mean (N=27)	32.2±2.01	1.6±0.03	2.2±0.14	44.7±1.7	26.5±1.5	1403±105.5	143±10.8	85±10.4	55±7.0	44±3.5	15,500
Best	30	1.25	3.8	52	34	3040	310	195	156	82	47,000

The jumping performance of the four species of dictyopharids analysed. Data in the five columns on the left are the means ± s.e.m. (*E. minuta*), or the mean of means for the performance of each individual insect of the other three species of dictyopharids; the best performance of a particular individual is also given. A best jump is defined by the highest take-off velocity achieved by an individual of the named species. The calculated values in the five columns on the right for acceleration are derived from these measured data. *N* indicates the number of animals, *n* the total number of jumps analysed for that species.

<sup>a</sup>Data from Burrows (Burrows, 2009).





**Fig. 7. Graphs of the angular changes at joints of the hind legs during the jump by *Thanatodictya praeferata* shown in Fig. 6.** The angles between the body and the femur (pink triangles) and of the femoro-tibial joint (black squares) are plotted. The stick diagrams show the positions of the femora (pink), tibiae (cyan) and tarsi (green) of the left and right hind legs at the times indicated. The yellow vertical bar shows the time of take-off (0 ms).

such as froghoppers (Burrows, 2007c), leafhoppers (Burrows, 2007a) and planthoppers [*I. coleoptratus* (Burrows and Bräunig, 2010)] show that they contract well in advance of the rapid jumping movements of the hind legs. What then prevents these slow contractions from extending the hind legs until all the energy required for a jump has been stored? In froghoppers, the engagement of their prominent and coxal and femoral protrusions provides a mechanical restraint to depression that is overcome only when sufficient force has been generated (Burrows, 2006b). These protrusions are covered in microtrichia that increase the surface area of contact and may interdigitate. They are found more generally where body parts of insects need to engage and even lock together (Gorb, 2001). In planthoppers, such as the ones analysed here, the coxal protrusion is present and is covered in microtrichia, but the femoral protrusion is represented only by a slight raising of the dorsal surface. This flat patch bears no microtrichia but does contact the coxal protrusion when a hind leg is levated into its cocked position in preparation for a jump. It seems unlikely that this engagement could act as a mechanical restraint, so its role remains enigmatic. The other possibility lies in control of the line of action of the trochanteral depressor muscle, perhaps by a separate but small part of the depressor muscle located in the coxa (Burrows and Bräunig, 2010).

### Energy storage

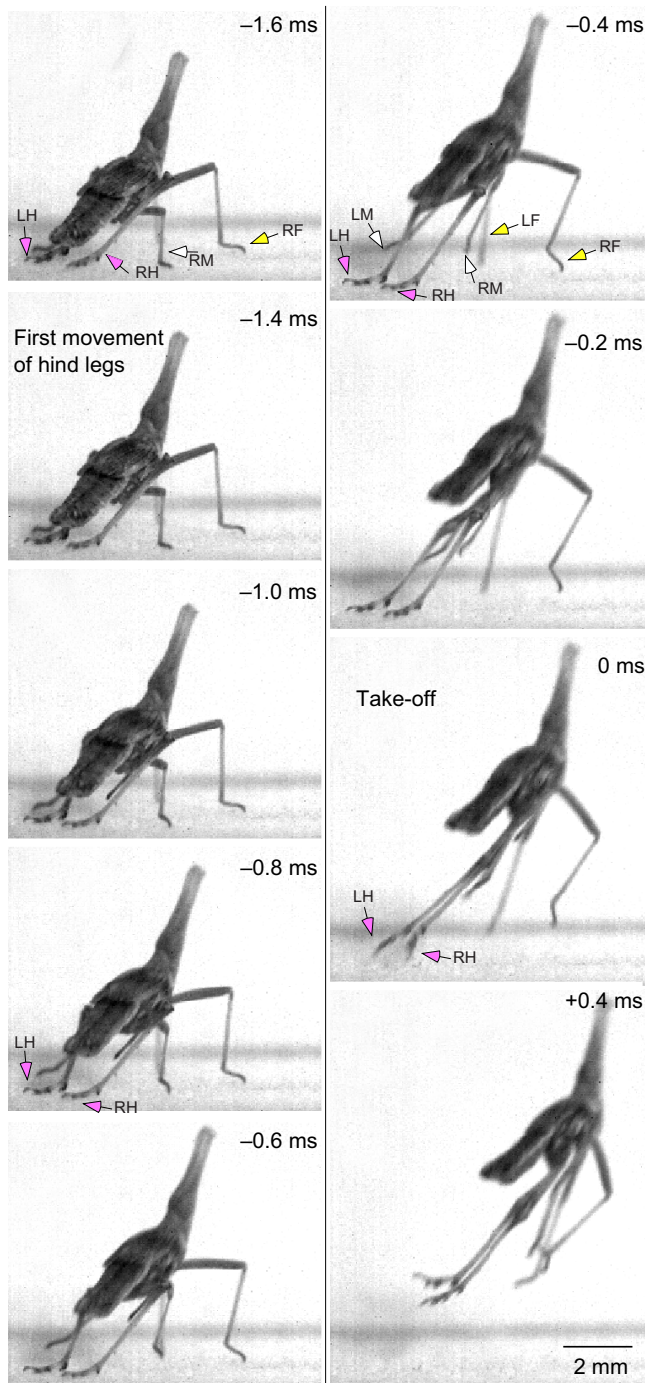
Power amplification requires energy storage. In froghoppers and the planthopper *Issus coleoptratus*, the slow contractions of the muscles bend internal skeletal structures (the pleural arches) that are built of a composite of hard cuticle and the rubber-like protein resilin (Burrows et al., 2008). Energy is stored in bending these structures, which is then released suddenly to propel a jump. In dictyopharids, the pleural arches of the hind legs have been observed here to bend in preparation for a jump and then to unfurl as the hind legs rapidly extend. They therefore act like the pleural arches in froghoppers and in the planthopper *Issus coleoptratus* (Burrows, 2009; Burrows et al., 2008). In the dictyopharids analysed here, these structures also fluoresce bright blue under specific wavelengths of UV light. The properties of this fluorescence are the same as that emitted by the pleural arches of froghoppers, which have been analysed in detail (Burrows et al., 2008). Two key signatures of resilin are met by the specificity of the emissions and by their dependence on the pH of a bathing solution (Neff et al., 2000). Furthermore, in a species of the

planthopper genus *Delphacodes* (Hemiptera, family Delphacidae) and in froghoppers (Hemiptera, family Cercopidae), the fluorescence in the pleural arches precisely matches (Burrows et al., 2011) the staining with an antibody raised against gene CG15920 in *Drosophila melanogaster* (Elvin et al., 2005). The first exon of this gene has been cloned in *Escherichia coli*, in which it expressed a soluble protein, and which when cross-linked formed a resilient, rubbery hydrogel called Rec-1 resilin. The antibody also stains resilin in three other insect orders (Lyons et al., 2011). Three criteria therefore indicate that the pleural arches contain resilin in planthoppers. In froghoppers, the resilin forms a composite with hard cuticle that can withstand bending strains without fracturing, store the requisite energy for a jump, unfurl to deliver the stored energy for a jump and then finally return the body to its original shape (Burrows et al., 2008).

### Jumping performance

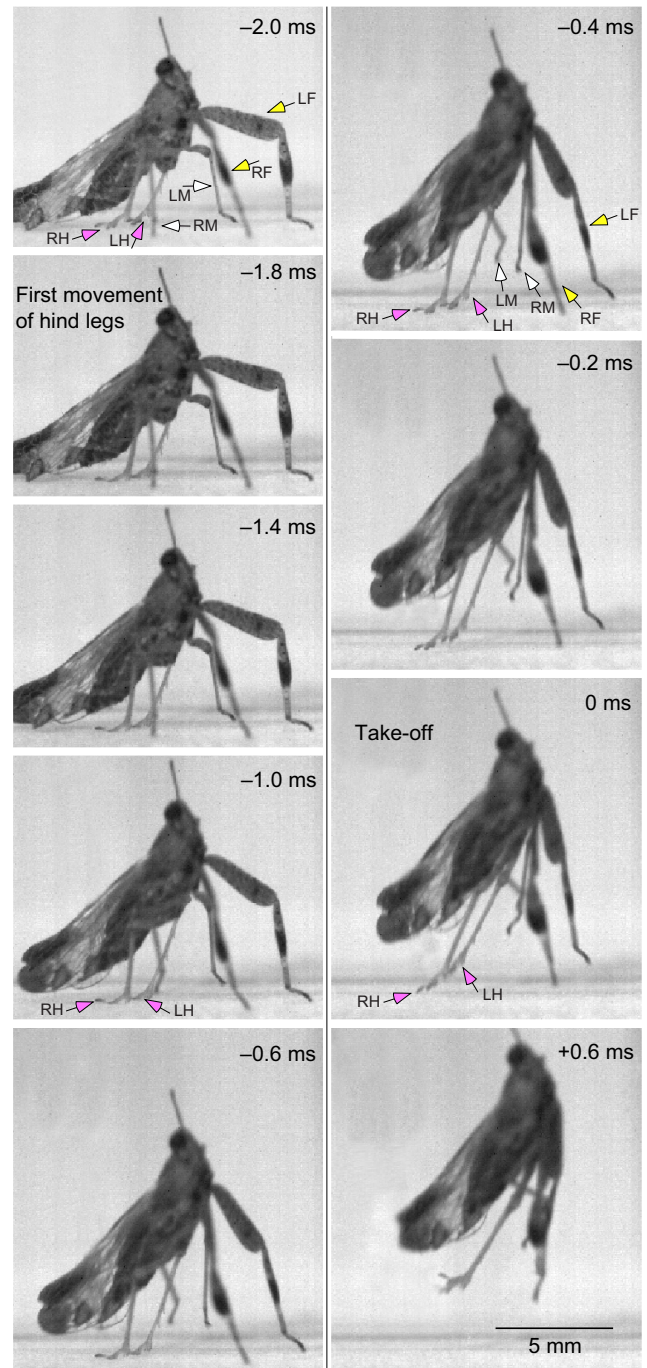
The rapid acceleration of the body and the power developed by the jumping muscle results in the insects experiencing  $g$  forces ranging from 225 to 490 in the best jumps by the different species. The angle of the longitudinal axis of the body relative to the ground at take-off was similar for the four species analysed, with means of 41 to 53 deg. By contrast, the angle of elevation for the initial part of the jump trajectory ranged more widely, with means of 40 to 69 deg for the four species.

These values are calculated to propel these insects to extraordinary distances: *E. minuta* to more than 3 m, *T. praeferata* and *R. vitrea* to almost 1.5 m and the heaviest *D. europaea* to approximately 1 m. All are more than 100 times their body lengths, with *E. minuta* predicted to reach almost 500 times its body length. The heights predicted are equally impressive; both *T. praeferata* and *D. europaea* are predicted to reach a height of almost 1 m or approximately 100 times their body lengths. None of the calculations consider the considerable drag that will be exerted on the body (Bennet-Clark and Alder, 1979; Vogel, 2005). Vogel has estimated that the froghoppers *Philaenus spumarius* [which has a mean mass of 12 mg and a mean length of 6.1 mm (Burrows, 2006a)] would lose some 25% of its jumping range because of drag, a smaller flea beetle would lose 40% and an even smaller flea would lose 80% (Vogel, 2005). *Engela minuta*, which has a body mass and length similar to that of *Philaenus spumarius*, might therefore be expected to lose a quarter of its range to drag and the larger species



**Fig. 8.** Side view of a jump by *Engela minuta* from a horizontal surface. Image was captured at rate of 5000 images  $s^{-1}$  with an exposure time of 0.03 ms. Take-off occurred at time 0 ms.

somewhat less. Is this where the elongated and tapered shape of the head, that seemingly equates with streamlining, starts to have an effect on jumping performance? The rapid acceleration, the take-off velocity and the expected distances jumped both upwards and forwards elevate these insects to a rank alongside the best of insect jumpers such as *Philaenus spumarius* (Burrows, 2003; Burrows, 2006a). The streamlined shape of dictyopharids contrasts with the squat and blunt body shape of *I. coleoptratus* (Burrows, 2009), which some species can outperform (Table 2).



**Fig. 9.** Selected images, at the times indicated, of a jump by *Raphiophora vitrea* from a horizontal surface. The insect is viewed from the side, and the image was captured at 5000 images  $s^{-1}$  with an exposure time of 0.05 ms. Take-off occurred at time 0 ms.

## MATERIALS AND METHODS

Adult *Dictyophara europaea* (Linnaeus 1767) were caught around Ljubljana, Slovenia, *Engela minuta* Distant 1906 at Silvermine Nature Reserve, Table Mountain, South Africa (34°04'30"S, 18°23'55"E, 450 m altitude), *Raphiophora vitrea* (Schaum 1850) on *Strychnos* trees at Lapalala, Waterberg Biosphere Reserve, Mpumalanga, South Africa (23°54'0.70"S, 28°19'23.67"E), and *Thanatodictya praeferrata* (Distant 1892) on Govetts track near Blackheath in the Blue Mountains, NSW, Australia (−33°37'28.9632"S, 150°18'39.9456"E). All species belong to the order Hemiptera, suborder Auchenorrhyncha, superfamily Fulgoroidea, family Dictyopharidae.

**Table 3. Jumping distances and heights**

Species	Take-off velocity (m s <sup>-1</sup> )	Take-off angle (deg)	Body length (mm)	Horizontal distance (mm)	Horizontal distance (body lengths)	Vertical height (mm)	Vertical height (body lengths)
<i>Engela minuta</i>	5.8	35	6.6	3222	488	564	85
<i>Thanodictya praeferrata</i>	4.4	68	8.3	1371	165	848	102
<i>Raphiophora vitrea</i>	4	57	8.9	1490	167	573	64
<i>Dictyophara europaea</i>	4.4	75	8.8	987	112	920	105

Calculated distances and heights of the best jumps by individuals of the four species of dictyopharid insects analysed. The calculations assume the properties of a projectile with no influence of wind resistance.

Sequential images of jumps were captured with a single Photron Fastcam 512PCI camera (Photron Europe, West Wycombe, Bucks, UK) at a rate of 4000 s<sup>-1</sup> and an exposure time of 0.25 ms for *D. europaea*, and at 5000 s<sup>-1</sup> and an exposure time of 0.03 or 0.05 ms for the other three species. The images were recorded directly to a computer for later analysis. Sixteen jumps by four *D. europaea*, nine jumps by one *E. minuta*, 20 jumps by four *R. vitrea* and 16 jumps by four *T. praeferrata* were captured. Jumps occurred spontaneously, or were elicited by fine mechanical stimulation with a small paintbrush, in a chamber made of optical quality glass (width 80 mm, height 80 mm, depth 10 mm at floor level expanding to 25 mm at the ceiling). The floor was made of high-density foam (Plastazote, Watkins and Doncaster, Cranbrook, Kent, UK) so that the tarsi did not slip when jumping. The camera, fitted with a 60 mm Micro Nikkor lens or a 100 mm micro Tokina lens, pointed directly at the middle of this chamber, the shape of which constrained most jumps to the image plane of the camera (see supplementary material Movies 1 and 2 for jumps viewed from the side and the ventral surface of the insect, respectively). Measurements of distances moved were made from jumps that were parallel to the image plane of the camera, or as close as possible to this plane. Changes in joint angles were measured from these images and from those captured from underneath as a dictyopharid jumped from the front glass surface of the chamber. Jumps that deviated from the image plane of the camera by  $\pm 30$  deg were calculated to result in a maximum error of 10% in the measurements of joint or body angles. Peak velocity was calculated as the distance moved in a rolling three-point average of successive images and the values given are for the final millisecond before take-off. The centre of mass was determined by balancing an insect on a pin post mortem. A fixed point on the body just behind the hind legs and close to the centre of mass was followed in each image. The body angle was defined as the angle subtended by its longitudinal axis relative to the horizontal both when standing and during a jump. Selected image files were analysed with Motionscope camera software (Redlake Imaging, Tucson, AZ, USA). The time at which the hind legs lost contact with the ground and the insect therefore became airborne was designated as the take-off time ( $t=0$  ms) so that different jumps could be aligned and compared. The period from the first detectable movement of the hind legs until take-off defined the acceleration time of a jump. A one-frame error in estimating both the first movement of the hind legs and the take-off time would result in a 10% error in measuring acceleration time. Data were not sorted according to sex of the insect because the differences between individuals were not marked and because the number of individuals of each species that could be obtained was small (see Tables 1, 2). Measurements are given as means  $\pm$  s.e.m. Temperatures ranged from 24 to 30°C.

The anatomy of the hind legs and metathorax was examined in intact insects and in those preserved in the following ways: fixation in 5% buffered formaldehyde and subsequent storage in 70% alcohol; fixation and storage in 70% alcohol or 50% glycerol; and cleared by boiling in 10% potassium hydroxide. Drawings of the legs, joints and muscles were made with the aid of a drawing tube attached to a Leica MZ16 stereo microscope (Wetzlar, Germany). Individual colour photographs were taken with a Nikon DXM1200 digital camera attached to the same microscope. Dried specimens were also mounted on specimen holders, sputter coated with gold and then examined in a Philips XL-30 Scanning Electron Microscope (Eindhoven, The Netherlands). Lengths of the legs of fixed specimens (see Table 1 for numbers of individuals from each species) were measured against a ruler to an accuracy of 0.1 mm from images captured with a digital camera attached to a Leica MZ16 microscope and projected onto a 24 inch monitor. Body

masses were determined to an accuracy of 0.1 mg with a Mettler Toledo AB104 balance (Beaumont Leys, Leicester, UK).

To search for the possible presence of resilin, dissected dictyopharids were viewed through Olympus MPlan  $\times 5/0.1$  NA and Olympus MPlan  $\times 10/0.25$  NA objective lenses, under ultraviolet (UV) or white epi-illumination on an Olympus BX51WI compound microscope (Olympus UK, London, UK). UV light from an X-cite series 120 metal halide light source (EXFO, Chandlers Ford, Hants, UK) was conditioned by a Semrock DAPI-5060B Brightline series UV filter set (Semrock, Rochester, NY, USA) with a sharp-edged (1% transmission limits) band from 350 to 407 nm. The resulting blue fluorescence emission was collected at wavelengths from 413 to 483 nm through a dichroic beam splitter. Images captured under UV and white light were superimposed in Canvas 14 (ACD Systems International, Seattle, WA, USA).

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#### Supplementary material

Supplementary material available online at <http://jeb.biologists.org/lookup/suppl/doi:10.1242/jeb.093476/-DC1>

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