Jumping performance of planthoppers (Hemiptera, Issidae)

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SUMMARY

The structure of the hind limbs and the kinematics of their movements that propel jumping in planthopper insects (Hemiptera, Auchenorrhyncha, Fulgoroidea, Issidae) were analysed. The propulsion for a jump was delivered by rapid movements of the hind legs that both move in the same plane beneath the body and parallel to its longitudinal axis, as revealed in high-speed sequences of images captured at rates up to 7500 images s^{-1}. The first and key movement was the depression of both trochantera about their coxae, powered by large depressor muscles in the thorax, accompanied by rapid extension of the tibiae about their femora. The initial movements of the two trochantera of the hind legs were synchronised to within 0.03 ms. The hind legs are only 20% longer than the front and middle legs, represent 65% of the body length, and have a ratio of 1.8 relative to the cube root of the body mass. The two hind coxae have a different structure to those in frog- and leafhoppers. They are fused at the mid-line, covered ventrally by transparent cuticle, and each is fixed laterally to a part of the internal skeleton called the pleural arch that extends to the articulation of a hind wing. A small and pointed, ventral coxal protrusion covered in microtrichia engages with a raised, smooth, white patch on a dorsal femur when a hind leg is levated (cocked) in preparation for a jump. In the best jumps by a male Issus, the body was accelerated in 0.8 ms to a take-off velocity of 5.5 m s^{-1}, was subjected to a force of 719 g and was displaced a horizontal distance of 1.1 m. This performance required an energy output of 303 μJ, a power output of 388 mW and exerted a force of 141 mN, or more than 700 times its body mass. This performance implies that a catapult mechanism must be used, and that Issus ranks alongside the froghopper Philaenus as one of the best insect jumpers.

INTRODUCTION

Animals jump to escape from predators both large and small, to launch into flight, or to move rapidly and efficiently from one place to another within a complex habitat. In insects, the ability to jump has arisen many times amongst members of different orders, and has been adopted by insects that range in size from tiny springtails (Brackenbury and Hunt, 1993) and fleas weighing less than 1 mg to grasshoppers (Bennet-Clark, 1975; Brown, 1967) that weigh several grams and which are among the largest extant insects. The mechanisms used for jumping also differ widely.

Insects use various parts of their body for jumping. For example, the larvae of the fruit fly *Ceratitis capitata* when ready to pupate jump to avoid predators by anchoring mouth hooks at the rear of the body to roll up the body and then unfurling it rapidly by elastic recoil (Maitland, 1992). Springtails rapidly extend an abdominal appendage (Brackenbury and Hunt, 1993; Christian, 1978) and click beetles jack-knife their body at the junction between the pro- and mesothorax (Evans, 1972; Evans, 1973; Kaschek, 1984). The ant *Gigantiops destructor* jumps by rapidly extending both the middle and hind pairs of legs while moving part of the abdomen forwards and holding it there during a jump (Baroni et al., 1994; Tautz et al., 1994). The Thailand winged stick insect *Sipyloidea* sp. jumps by flicking its abdomen forwards and then backwards while extending the tibiae and depressing the femora of the hind and middle legs (Burrows and Morris, 2002).

The majority of insects, however, use their legs to propel jumping, but even here there are two distinct mechanisms. First, where energy requirements are low, direct muscle contractions can propel a jump. Bush crickets (Orthoptera, Ensifera, Tettigoniidae) that have particularly long hind legs power their jumps by direct action of the muscles acting on these long levers (Burrows and Morris, 2003). Small insects such as *Drosophila* which jump by movements of their middle legs to launch into flight may also be able to generate enough force by the direct action of the muscles (Zumstein et al., 2004). Where energy requirements are higher and the legs are short so that acceleration times are restricted, catapult mechanisms are used. These allow prolonged contractions of the muscles to build up and store the necessary energy, which can then be released rapidly. Fleas (Bennet-Clark and Lucey, 1967; Rothschild et al., 1975; Rothschild et al., 1972) and locusts (Bennet-Clark, 1975) both use such catapult mechanisms.

An insect order containing a large number of prodigious jumpers is the Hemiptera, with examples found in all four of its major sub-orders. First, in the basal Coleorrhyncha at least one extant species jumps (Burrows et al., 2007). The second sub-order, the Heteroptera, contains a wide diversity of bugs, but only two families have species that are reported to jump and only one, the Saldidae or shore bugs has been analysed (Burrows, 2009). In the third sub-order, the Sternorrhyncha, one family, the Psyllids or jumping plant lice, are, as their colloquial name implies, well known for their jumping but their performance is only currently being investigated (M.B., manuscript in preparation).

The ability of these Hemipteran insects to jump reaches its zenith, however, in the Auchenorrhyncha, a fourth sub-order of diverse plant sucking bugs, which is probably not monophyletic and is either considered as two sub-orders, the Cicadomorpha and the

Fulgoromorpha (Bourgoin and Cambell, 2002) or as three superfamilies. The Cercopoidea or froghoppers (spittle bugs) have the best jumping performance of any insect described so far, accelerating their bodies in less than 1 ms to a take-off velocity of 4.7 m s^{-1}, experiencing a force of approximately 550 g (Burrows, 2003; Burrows, 2006a). This outstanding performance is achieved by using a catapult mechanism in which force is developed by the slow contraction of huge thoracic muscles restrained by mechanical locks, and the force stored in the internal skeleton (Burrows et al., 2008) is then released rapidly (Burrows, 2007c). The second superfamily, Cicadelloidea, or leafhoppers, are also accomplished jumpers (Burrows, 2007a; Burrows, 2007b) with one group having long hind legs and another short hind legs although both achieve comparable take-off velocities (Burrows and Sutton, 2008). The third superfamily, Fulgoroidea or planthoppers and in particular, species of one its 19 families, the Issidae, form the subject of this paper. How does the mechanism of jumping and the resulting jumping performance in these insects compare with that of the other families within the Auchenorrhyncha and across insects more generally? It is shown that the structure of the proximal joints of the hind legs of Issids is substantially different from froghoppers and leafhoppers, but high speed imaging of their jumping performance shows that it either matches in some features, or outstrips in others, the performance of froghoppers.

MATERIALS AND METHODS

Adult planthoppers *Issus coleoptratus* (Fabricius 1781) of either sex were collected on ivy (*Hedera* sp.) during August and September in Aachen, Germany. *Latissus dilatatus* (Fourcry 1785) were collected in July from oak (*Quercus* sp.) saplings in the Nanus region near Ljubljana, Slovenia. Both species belong to the order Hemiptera, sub-order Auchenorrhyncha, superfamily Fulgoroidea and family Issidae.

The anatomy of the hind legs and metathorax was examined in intact insects and those preserved in the following ways: fixed in 5% buffered formaldehyde and stored in 70% alcohol; fixed and stored in 70% alcohol; preserved in 50% glycerol; cleared by boiling in 5% potassium hydroxide. Drawings were made with the aid of a drawing tube attached to a Leica MZ16 stereo microscope (Wetzlar, Germany). Individual colour photographs of both live and preserved specimens 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 an XL-30 FEG scanning electron microscope (Philips, Eindhoven, The Netherlands).

Jumping performance was analysed on the day the insects were caught, or after a few days in the laboratory where they were maintained on their host plants. Sequential images of jumps were captured by a Photron Fastcam 1024PCI high speed camera [Photron (Europe), Marlow, Buckinghamshire, UK] at rates of 4000 frames s^{-1}, 5000 frames s^{-1} or 7500 frames s^{-1} and with exposure times of 0.03–0.05 ms. The images were fed directly to a laptop computer. The camera pointed at the middle of a glass chamber 80 mm wide, 80 mm tall, and 10 mm deep at floor level, widening to 25 mm at the top. The floor was horizontal, or a few degrees from horizontal, and was made of high density foam. The insects were free to jump in any direction but the shape of the chamber constrained most jumps to the image plane of the camera. Jumps that deviated by ±30 deg. to either side of this plane would result only in a maximum error of 10% in the measurements of joint or body angles. 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. Details of proximal joint movements were evaluated most easily when a jump was viewed from underneath and from a glass surface. Sequences of images were analysed for changes in joint and body positions with Motionscope camera software (Redlake Imaging, Tucson, AZ, USA), and for changes in angles with Canvas X (ACD Systems of America, Miami, FL, USA). A point on the body that could be recognized in successive frames and was close to the centre of mass, as determined by balancing the insect on a pin, was selected for measurements of the velocity and trajectory of the body. The time at which the hind legs lost contact with the ground and the insect became airborne was designated as t=0 ms so that different jumps could be aligned and compared. The time at which the hind legs started to move and propel the jump was also labelled so that the time between these two events defined the period over which the body was accelerated in a jump – the take-off time, or acceleration time. Peak velocity was calculated as the distance moved in a rolling three point average of successive frames. Movies of two jumps by *Issus* are included as supplementary material (supplementary material Movies 1 and 2).

The results are based on an analysis of 30 *Issus* and six *Latissus*. Eighty-seven jumps by 15 *Issus* (10 male and five female) were analysed to determine their jumping performance at 25–30°C. Measurements are given as means ±standard error of the mean (s.e.m.).

RESULTS
Body shape

Adult female *Issus* body mass was 32.2±2.01 mg (mean ± s.e.m., N=5, range 29–40 mg) whereas the body mass of males was significantly less, 21.5±0.56 mg (mean ± s.e.m., N=10, range 20–25 mg; t-test, $t_{53.2}$=18.2, P<0.001; Table 1). The body length of females was 8.1±0.14 mm (N=16, range 7.5–9.4 mm), which was significantly longer (t-test, t_{30}=8.93, P<0.001) than that of males, which was 6.7±0.07 mm (N=16, range 6.2–7.3 mm). At its broadest point in the thorax, the body was 4.4±0.11 mm wide (N=16, males and females pooled) as measured from the lateral edges of the front wings when folded (Fig. 1B). The body mass of *Latissus* was 18.1±0.28 mg (N=6, males and females pooled) and the body length 5.8±0.31 mm (N=6).

Structure of hind legs

The hind legs were held beneath the body and moved in a plane that was almost parallel to the long axis of the body. On average the hind legs of *Issus* were 5.3 mm long and only about 20% longer than the front and middle legs, which were 4.3 mm, so that the ratio of leg lengths was 1:1:1.2 (front:middle:hind; Table 1). In the shorter and lighter *Latissus* the ratio of leg lengths was similar at 1:1:1.3. In both species the slightly greater length of the hind legs resulted from longer tibiae; in *Issus* the hind tibiae were 46% longer than the middle and 51% longer than the front tibiae. The hind legs represented 65% of the body length in *Issus* and 79% in *Latissus*. Relative to the cube root of the body mass, a relationship taken to normalise against body mass in insects of different shapes and lengths, the ratio was 1.8 in *Issus* and 1.7 in *Latissus*.

Coxa

The coxae of the hind legs are opposed to each other at the ventral midline and appear to be firmly fixed to each other at a small, raised circular region (Fig. 1A). Laterally they are fused to the thorax where a paired element of the internal thoracic skeleton called a pleural arch curves ventrally from its dorsal articulation with a hind wing (Fig. 1A, Fig. 2A,B). A single coxa can therefore not move independently of the other coxa, and similarly the two coxae cannot

Table 1. Body form in *Latissus* and male and female *Issus* compared with the froghopper (*Philaenus*) and from short- (*Ulopa*) and long-legged (*Aphrodes*) leafhoppers

Insect	Body mass (mg)	Body length (mm)	Hind leg tibia (mm)	Hind leg femur (mm)	Ratio of leg lengths			Hind leg length as % of body length	Normalized hind leg length (mm)/ mass (mg)$^{0.33}$
					Front	Middle	Hind		
Latissus	18.1±0.28 (*N*=6)	5.8±0.31 (*N*=6)	2.2±0.14	1.4±0.07	1	1	1.3	79.4±2.6	1.7
Issus male	21.5±0.56 (*N*=10)	6.7±0.07 (*N*=16)							
Male and female *Issus* female	32.2±2.01 (*N*=5)	8.1±0.14 (*N*=16)	2.6±0.08	1.7±0.05	1	1	1.2	65.4±1.8	1.8
Philaenus (froghopper)*	12.3±0.74 (*N*=34)	6.1±0.08	1.8±0.07	1.1±0.03	1	1	1.5	66	1.7
Ulopa (short-legged leafhopper)†	2.1±0.12 (*N*=7)	3.1±0.1	0.9±0.05	0.5±0.03	1	1.1	1.4	58	1.1
Aphrodes (long-legged leafhopper)‡	18.4±1.3 (*N*=8)	8.5±0.22	3.8±0.06	2.2±0.03	1	1.2	2.2	84	2.3

*Data from Burrows, 2006a.
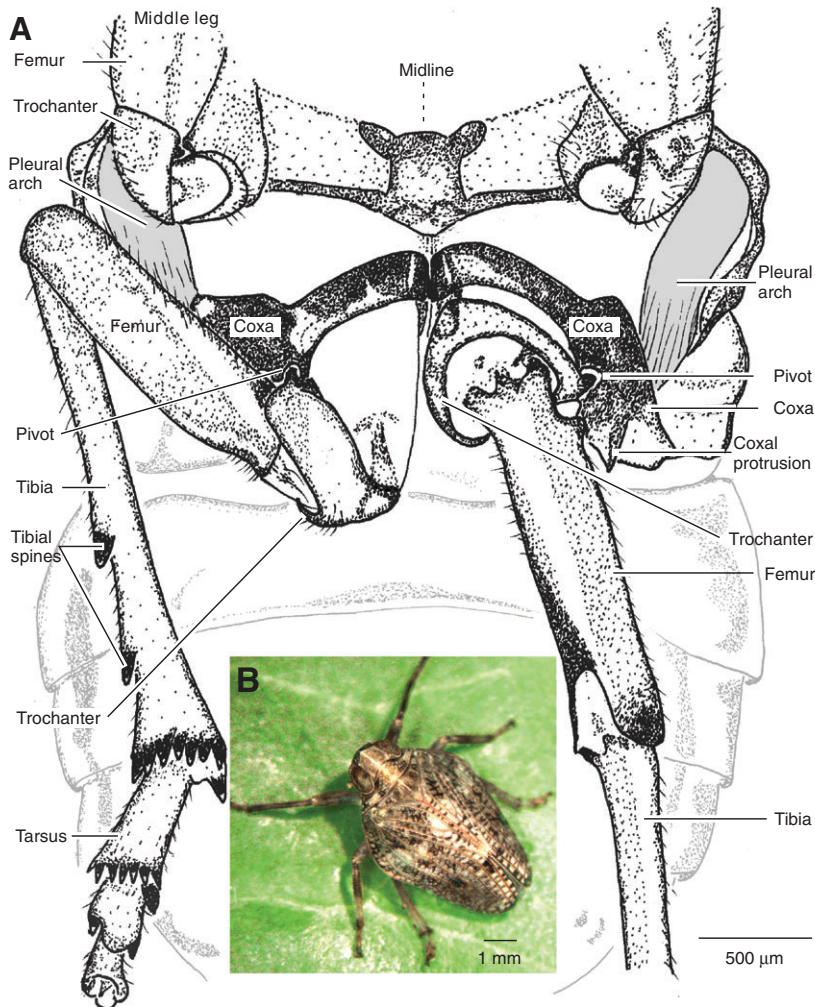†Data from Burrows and Sutton, 2008.
‡Data from Burrows, 2007b.

Fig. 1. Body form of *Issus*. (A) Drawing of the ventral surface to show the structure of the hind legs and the posterior part of the thorax. The right hind leg is shown in the fully levated position and the left hind leg depressed. Only the proximal joints of the two middle legs are shown. (B) Photograph of a dorsal view of *Issus*.

rotate about the thorax. By contrast, the front and middle coxae pivot laterally with the thorax, so that they can rotate independently. The front coxae are 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 anterior edges of the two hind coxae are separated ventrally from the boundary between the meso- and metathorax by flexible and transparent membrane through which can be seen the large trochanteral depressor muscles of the hind legs and their large tendons. The coxae extend laterally beyond their articulation with the trochantera and their cuticle is heavily sclerotised particularly as it wraps around the side of the body (Fig. 2B). Ventrally, each coxa has a posteriorly directed protrusion that measures 300–400 μm at its base narrowing along its 150 μm length to a point (Fig. 3A,C). The whole protrusion is covered with microtrichia which are most dense toward the centre where each is 6–7 μm long, 3.5–4 μm wide and 1.5 μm thick and with flattened ends (Fig. 3C–E). Adjacent microtrichia almost touch and are packed in rows separated by about 4 μm. Away from the centre, both the density of the microtrichia and their size gradually diminishes, and they become more pointed.

Trochanter

A hind trochanter rotates about a coxa though about 100 deg. from its fully levated position when the hind legs are cocked in readiness for jumping, to its fully depressed position after take-off in a jump. The joint consists of two pivots, one ventral and lateral (Fig. 1A), and one dorsal and more medial (Fig. 4A). Each pivot is formed by a sclerotised cuticular horn of the trochanter engaging with a socket in the coxa. The ventral horn of the trochanter has a small group of stout, laterally projecting hairs that are deflected as the trochanteral horn progressively engages with its coxal socket when the trochanter is fully levated about the coxa (Fig. 3A,B). These hairs could act as a proprioceptor signalling that the joint is fully levated.

Femur

The femora of the hind legs are 6% shorter than the middle and 7% shorter than the front femora. A further characteristic of a hind femur is a patch of smooth, white cuticle on its proximal dorsal surface (Fig. 4A). The coxal protrusion engages with this patch of the femur when a hind leg is fully levated in preparation for a jump. This patch is slightly raised from the surrounding dark cuticle of the dorsal femur and measures approximately 175 by 120 μm (Fig. 4A–C). The proximal edge of this patch has a row of six prominent hairs, spaced evenly every 10 μm and ranging in length from 70 μm laterally to 15 μm medially (Fig. 4C). On both the medial and lateral edges are hairs that are less regularly arranged but of a higher density than those along the more distal edges of the femur. The trochantero–femoral joint of a hind leg has a semi-circle of flexible membrane that permits rotation at this joint (Fig. 1A, Fig. 2A, Fig. 3A). This arrangement contrasts with the trochantera of the front and middle legs which appear to be fused to the femora of their legs, so that there is little if any rotation at their trochantero-femoral joints.

Tibia and tarsus

The tibiae are the longest segments of a hind leg. They are light and cylindrical in shape, widening at the joint with the tarsus, and have two prominent spines toward the distal end that point posteriorly and laterally (Fig. 1A, Fig. 2A). At a tibio–tarsal joint a semi-circular row of smaller, sclerotised spines on the ventral surface of the tibia point ventrally. A similar semi-circular row of spines is present on the proximal segment of the tarsus, and on the second
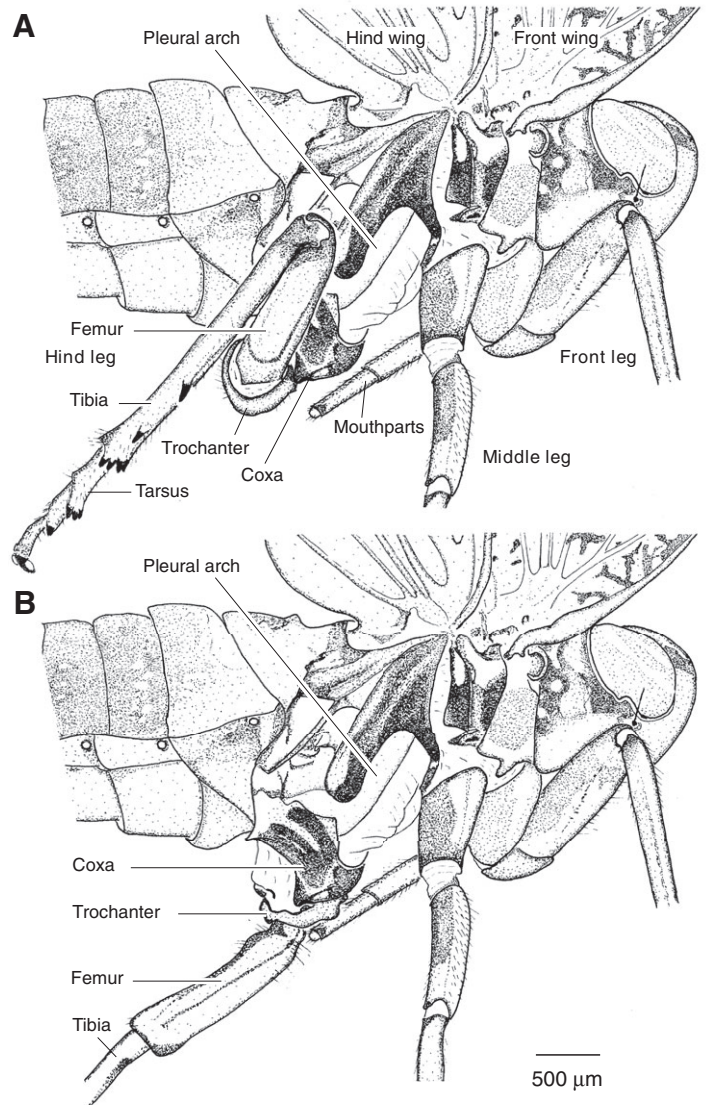

Fig. 2. Drawing of *Issus* from the right side with the right hind leg fully levated (A) and depressed (B). Only the proximal segments of the right front and middle legs, and the proximal parts of the front and hind wings are shown. The shape of the hind coxa is different from the front and middle coxae and is highly sclerotised, as are the metathoracic pleura. A pleural arch of more translucent cuticle links the right hind wing with the right coxa.

tarsal joint there are two spines. These arrays of spines all point ventrally and could increase traction as the tibia is thrust downwards and the tarsus is pressed against the ground during take-off for a jump.

Jumping movements

In preparation for a jump, both hind legs were levated by rotation about the coxo–trochanteral joints so that the dorsal surface of the femur came to lie closely apposed to the ventral surface of the lateral region of the hind coxa (Fig. 5). In this position the protrusion from the lateral coxa engaged with the white patch of cuticle on the dorsal proximal femur. The tibiae were also flexed about the femur so that their femoro–tibial joints came to lie between the femora of the middle legs and the ventral surface of the thorax. The movements of the coxo–trochanteral and femoro–tibial joints resulted in the tarsi
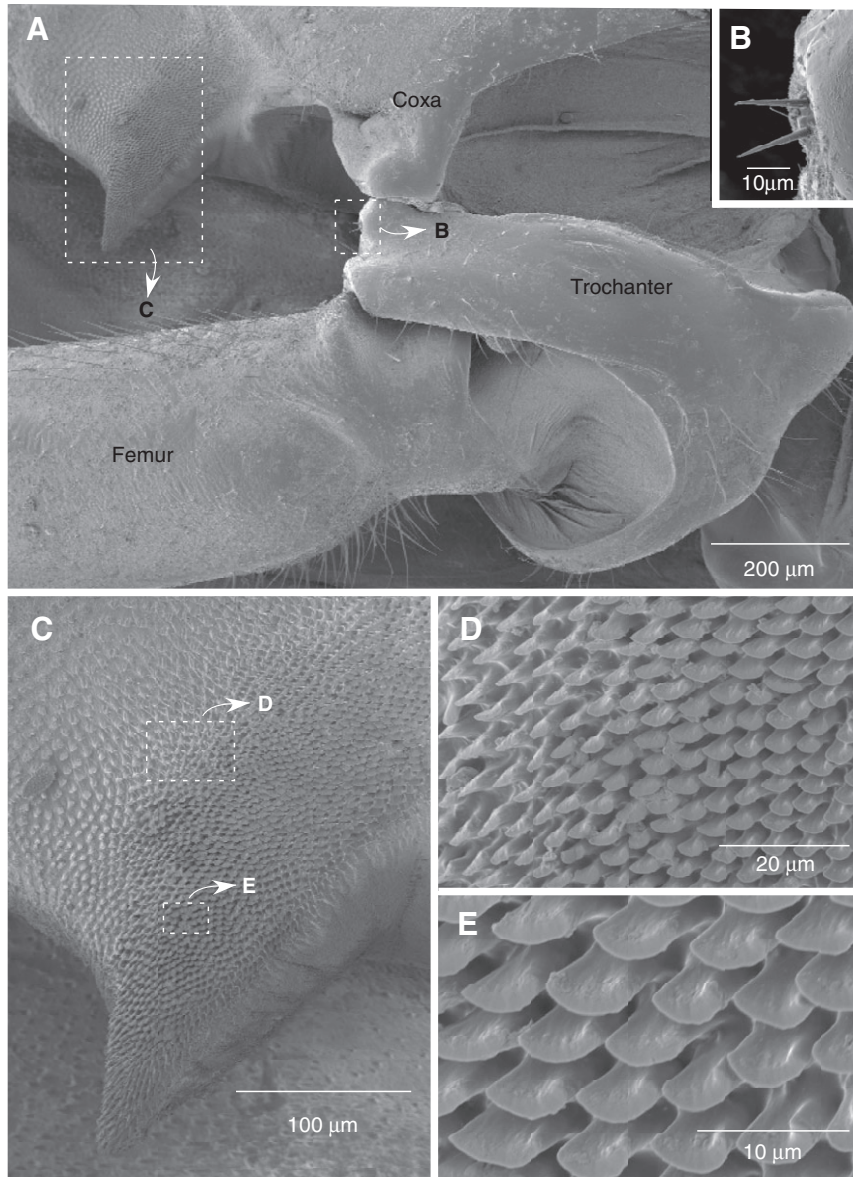
Fig. 3. Scanning electron micrographs to show the structure of the coxa and trochanter of *Latissus*. (A) The ventral articulation of the trochanter with the coxa and of the femur with the trochanter. The two regions outlined with white dashed lines are shown in more detail in B and C. The right hind leg is viewed ventrally. (B) Prominent stiff hairs on the horn of the trochanter that engages ventrally with the coxa. (C) The coxal protrusion at higher magnification reveals that it is covered in small but densely packed microtrichia. (D,E) The microtrichia from the coxal protrusion at progressively higher magnifications.

of each hind leg being placed on the ground beneath the body at the midline, but so that they did not touch each other. This first phase of jumping lasted a few hundred milliseconds.

The second phase of the jumping sequence was characterised by the hind legs remaining in this cocked position for a few seconds with only the tips of the tarsi in contact with the ground. Distortions of the metathorax also occurred that caused both coxae, and hence the more distal segments of both hind legs, to move together anteriorly. Movements of the front and middle legs could raise or lower the front of the body and thus adjust its angle relative to the ground. These adjustments set the elevation of a jump and always preceded the propulsive movements of the hind legs in the third phase.

The start of the third and final phase of the jump was signalled by a sudden and rapid depression of both hind trochantera about the coxae, most easily seen when viewed from underneath (Fig. 5, yellow lines). The femora also moved together with the trochantera and were accompanied by extension of both tibiae. The movements of these joints continued until both depression of the trochantera and extension of the tibiae were complete and the insect had been

propelled from the substrate. During this period the trochanter progressively depressed about the coxa at average rotational rates of about $66,000\,\mathrm{deg.\,s^{-1}}$ and the tibia was rotated at a similar rate about the femur (Fig. 5, cyan lines).

When a jump was viewed from the side (Fig. 6), the first apparent movement of the hind leg was a downwards movement of the femur that forced the tibia backwards and pressed the tarsus fully onto the ground. These movements of the hind leg were, however, powered by the depression of the trochanter about the coxa. The progressive movements of both hind legs propelled the body forwards and upwards so that the middle and front legs lost contact with the ground while the hind legs continued to apply force to the ground. In the example shown in Fig. 6, the middle legs lost contact with the ground $0.8\,\mathrm{ms}$ before take-off and the front legs a further $0.4\,\mathrm{ms}$ later and before the loss of contact of the hind legs signalled take-off and that the insect was airborne. This sequence of lift-off by the front and middle legs resulted from the low angle of the body relative to the ground; in jumps where the take-off angle was greater, the front legs were the first to lose contact. In jumps where the angle of the body relative to the ground was large, the front and to a lesser extent
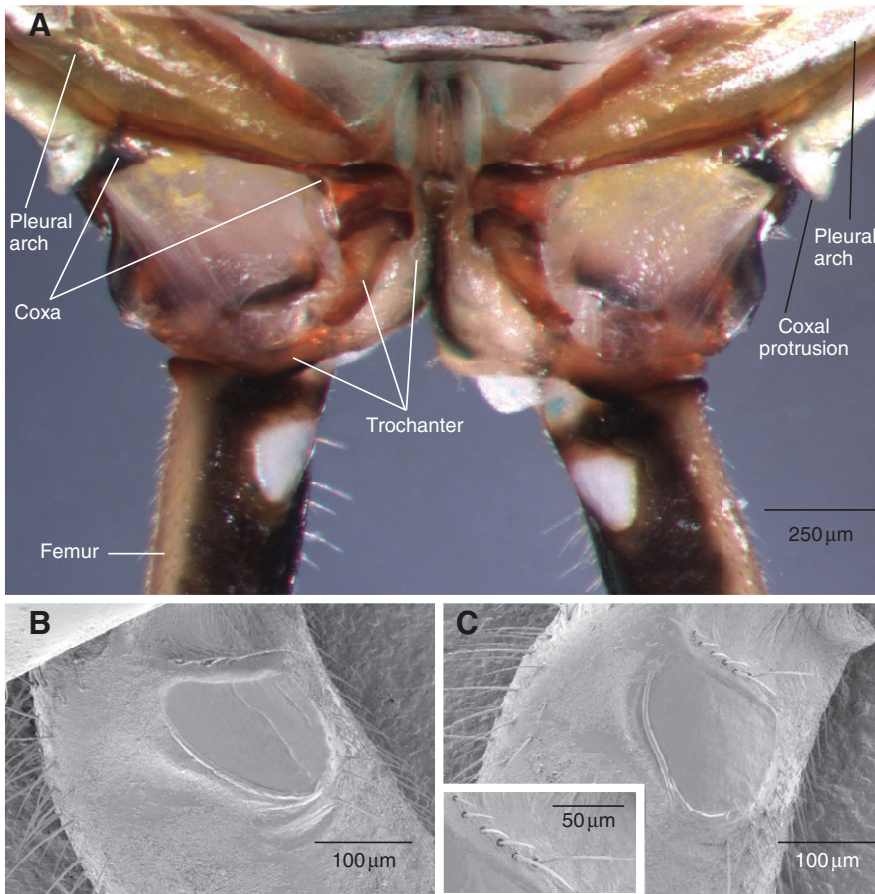
Fig. 4. Dorsal view of the proximal joints of the hind legs of *Issus*. (A) Photograph with both hind legs depressed and extended, after removal of the abdomen. Two white patches are present on the dorsal, proximal surface of the femora. (B,C) Scanning electron micrographs of these patches reveal that they are smooth, though sometimes wrinkled during preparation. A row of hairs is aligned with the proximal edge of the patch (inset in C shows an enlargement).

the middle legs were already fully extended and could therefore make little contribution to forces applied at take-off. Sometimes, the front legs were off the ground before any movement of the hind legs occurred and thus could not contribute thrust to the jump.

When jumps were viewed from directly in front or behind, it was apparent that the two tarsi, which had been placed at different positions on the ground while thrust was being applied to accelerate the body, moved medially once the insect was airborne so that they became apposed to each other, or even crossed. In the first few milliseconds of the jump, the hind legs trailed behind, fully depressed at their coxo–trochanteral joints, almost fully extended at their femoro–tibial joints and with the tarsi touching each other. As the airborne phase of the jump continued, they were drawn forwards by levation of the coxo–trochanteral joints and by flexion of the femoro–tibial joints.

Synchrony of hind leg movements

In none of the 87 natural jumps that were captured by high speed imaging was there a detectable difference in the timing of the movements of the two hind legs in the final propulsive movements of the hind legs. By contrast, the two hind legs could move independently and at different times into their cocked positions, although the most common action was for them to move together. The frame rates used to capture natural jumping gave a best time resolution of 0.13 ms. To determine more precisely how closely synchronised the hind legs moved in the jumping phase, *Issus* was restrained on its back and the abdomen tickled to induce rapid movements of both hind legs that had the same characteristics as those just described during natural jumping. Eighteen jumps by four

Issus were captured at 30,000 frames s^{-1} to give a time resolution of 0.03 ms. In 16 (89%) of these jumps the initial movements of the two coxae occurred in the same frame and were thus synchronised to a resolution of better than 0.03 ms. In one jump the left trochanter moved one frame (0.03 ms) before the right, and in a second jump the reverse occurred.

The need for such close synchrony between the movements of the hind legs and the balancing of forces applied to the ground, was exemplified by the jumping performance an *Issus* that had lost its right hind leg distal to its coxo–trochanteral joint (Fig. 7). When the left hind leg was rapidly depressed at the coxo–trochanteral joint, the body was lifted a little from the ground and then started to rotate in the horizontal plane so that it turned toward the camera. As the depression and extension of the left hind leg continued, the body was further raised, particularly toward the rear so that the head pointed downwards while horizontal rotation continued. The spin eventually led to the *Issus* hitting the front wall of the chamber.

Jumping performance
Acceleration time

The time from the first detectable movements of the hind legs that powered a jump and the loss of contact of the hind legs with the ground defined the time over which the body was accelerated – the acceleration time, or take-off time. Females had an acceleration time of 1.6±0.034 ms (*N*=34, range 1.25–2.2 ms), which was significantly longer than the 1.49±0.037 ms (*N*=47, range 0.78–1.95 ms) taken by males to accelerate their bodies in a jump (*t*-test, t_{79}=2.4, *P*=0.018; Table 2). The acceleration achieved during these short periods was 2261±176.2 m s^{-2} in males and 1403±105.5 m s^{-2} in females
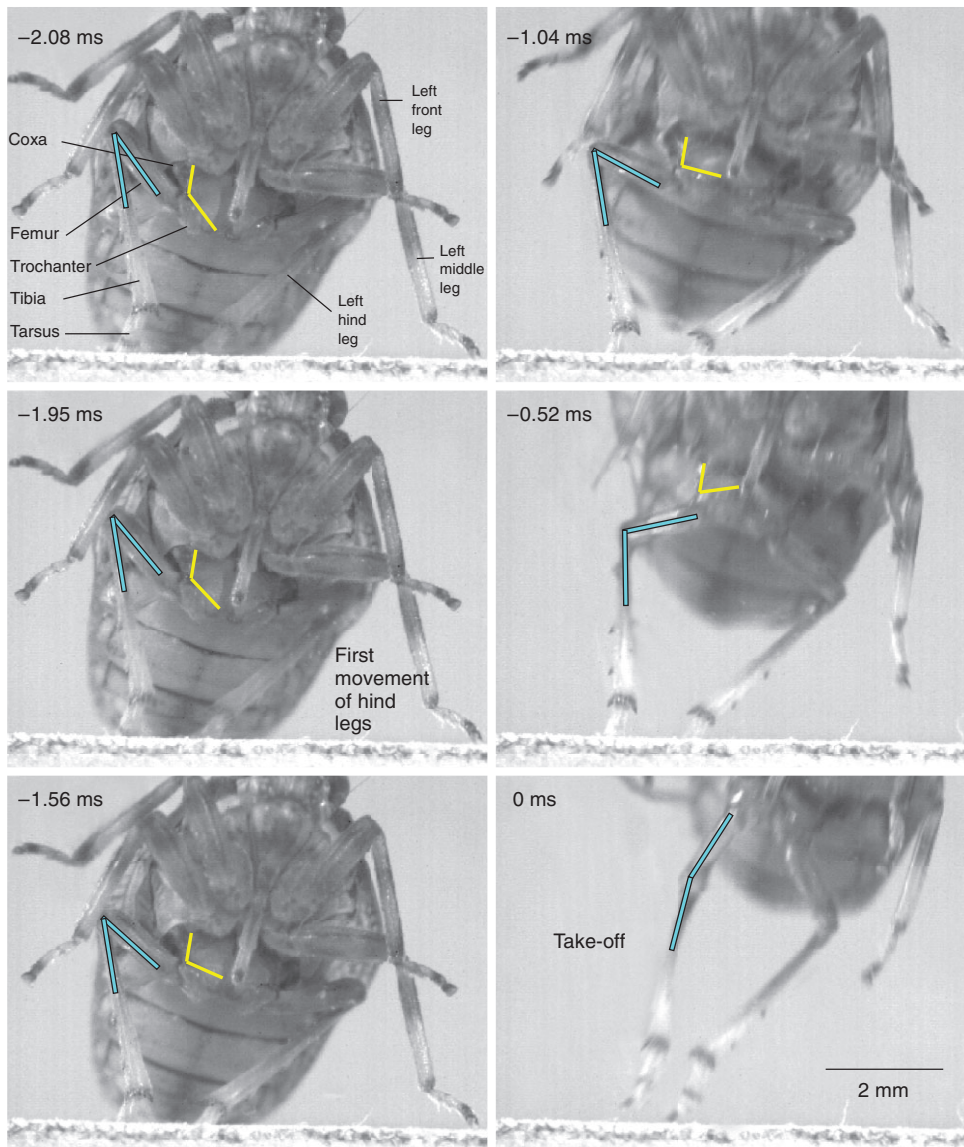
Fig. 5. Jump by *Issus* viewed from underneath as it jumped from the front wall of the chamber. Images were captured at a rate of 7500 frames s^{-1} and with an exposure time of 0.05 ms and are arranged in two columns with the bottom left hand corner of each frame providing a constant reference point. The times indicate the sequence of the selected frames relative to take-off at time 0 ms. The yellow lines show the progressive depression of the trochanter about the coxa, and the cyan lines the extension of the tibia about the femur of the right hind leg.

(averages of peak accelerations in 31 jumps by 10 males, and 27 jumps by five females). In their best jumps males accelerated at an astonishing 7051 m s^{-2} and thus experienced a force of 719 g.

Take-off velocity

Take-off velocity was measured as a rolling three point average during the period just before (the acceleration time) and for a few milliseconds after take-off when the insect remained in the frame of the camera. Velocity peaked just before take-off and then declined once airborne (Fig. 8A). Males had a higher peak take-off velocity with a mean in 31 jumps of 3.2±0.21 m s^{-1}, compared with a mean in 27 jumps by females of 2.2±0.14 m s^{-1} (*t*-test, t_{56}=−3.631, P=0.001).

Males also achieved the fastest take-off velocities with one reaching 5.5 m s^{-1} compared with the best jump by a female of 3.8 m s^{-1}. The energy required to achieve these performances in males (mean and best) was 121±14.9 and 303 μJ, the power output was 89±11.6 and 388 mW and the force exerted was 49±3.9 and 141 mN (Table 2).

Take-off velocity depended strongly on acceleration time, ANCOVA ($F_{1,54}$=12.49, P=0.001) and less strongly on gender,

ANCOVA ($F_{1,54}$=6.66, P=0.013). Mass by itself was without effect, ANCOVA ($F_{1,54}$=2.7, P=0.106). The faster the body was accelerated (shorter acceleration time) the higher was the take-off velocity for both males (R^2=0.183) and females (R^2=0.226; Fig. 8B).

The take-off angle was similar in both sexes; in males it was 42.7±1.8 deg. (N=31 jumps) and in females was 44.7±1.7 deg. (N=26 jumps, *t*-test, t_{55}=0.81, P=0.42). The orientation of the body relative to the ground was, however, different; males at take-off had a lower body angle of 17.1±2.4 deg. (N=28 jumps) compared with 26.5±1.5 deg. in females (N=27 jumps, *t*-test, t_{45}=3.2, P=0.002). The longest distance jumped was 1.1 m by a male with a mass of 20.5 mg.

Trajectory

The initial trajectory followed a linear path to take-off and for the first few milliseconds once airborne (Fig. 9A). The initial elevation angle of the trajectory was influenced by the angle of the body relative to the ground at take-off because the thrust applied by the rapid movements of the hind legs was always in the same direction relative to the body. In 68 jumps analysed, only 20 (29%) showed any rotation of the body in the first few milliseconds when airborne. Of these, 13 (65%) pitched head-down about the transverse body
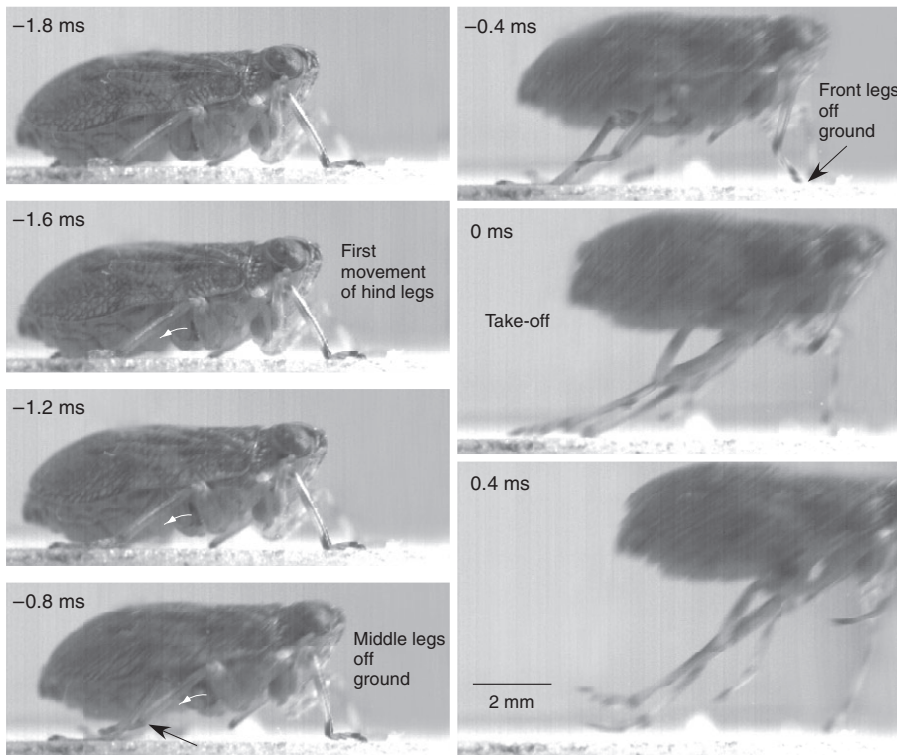
−1.8 ms

−1.6 ms
First movement of hind legs

−1.2 ms

−0.8 ms
Middle legs off ground

2 mm

−0.4 ms
Front legs off ground

0 ms
Take-off

0.4 ms

Fig. 6. Jump by *Issus* viewed from the side. Images were captured at a rate of 5000 frames s^{-1} and with an exposure time of 0.05 ms. Selected frames at the times indicated are shown arranged in two columns. The curved white arrows indicate the progressive downward movement of the right hind femur. The middle and front legs (black arrows) left the ground at 0.8 and 0.4 ms, respectively, before take-off.

axis, 2 (10%) pitched head-up (Fig. 9B), and 5 (25%) rolled about the longitudinal body axis. The average rotation rate in the pitch axis was 43±6.1 Hz (range 22-69, *N*=7) and in roll axis the two jumps that could be measured accurately the rate was 83 and 42 Hz respectively. In none of the jumps recorded were the wings opened either before or just after take-off. The jumps are therefore neither assisted or stabilised by wings being opened or flapped. No jumps were seen to be a launch into flapping flight.

DISCUSSION

In their best jumps male *Issus* accelerated their bodies in less than 0.8 ms to take-off velocities of 5.5 m s^{-1} experiencing forces of 719 *g*

−1.5 ms
Right hind leg missing
-1.6

−1.25 ms
First movement of left hind leg
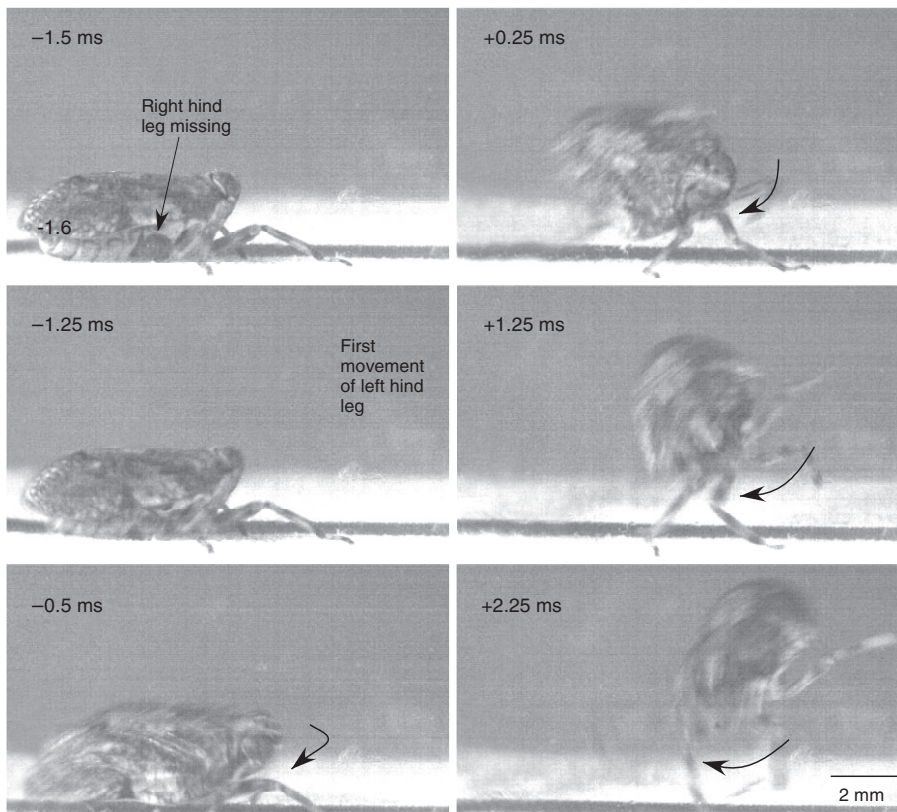
−0.5 ms

+0.25 ms

+1.25 ms

+2.25 ms

2 mm

Fig. 7. A jump by an *Issus* that had lost the distal segments of its right hind leg. The propulsion from the left hind leg caused the body to spin (curved arrows) around the long axis of the body without gaining height or forward momentum. Images were captured at 4000 frames s^{-1} and with an exposure of 0.25 ms.

and propelling themselves a distance of 1.1 m at a take-off angle close to 45 deg. *Issus* propelled its jumping by rapid and tightly synchronised movements of its two hind legs, powered by muscles located in the thorax that depressed the trochantera. The jump movement was divisible into three distinct phases. First, the two hind legs were cocked slowly by a levation of the trochantera about the coxae. Second, there was a prolonged period in which the hind legs remained in their cocked position although the angle of the body relative to the ground could be adjusted by movements of the front and middle legs. Third, the hind legs were rapidly depressed and extended to propel the insect into the air. The initial movements of the trochantera of the hind legs that power a jump were synchronised to within 0.03 ms; when only one hind leg was present the body spun rapidly in the yaw plane. The wings did not open so the jump was powered solely by the hind legs and was not observed to lead directly to flight. Jumping in these insects would thus appear to be an escape response, or a means of improving the speed of locomotion between the vegetation in their habitat. This extraordinary performance ranks planthoppers alongside froghoppers as the best insect jumpers. The same principles of jumping are used as in froghoppers and leafhoppers, but the differences in the mechanisms used are substantial.

Specialisations of the hind legs for jumping

The overall design of the hind legs of *Issus* is similar to that of froghoppers in their proportions relative to the length of the other pairs of legs, to body length and body mass (Table 1). The similarity also holds for short-legged leafhoppers (cicadellids) but is in marked contrast to long-legged cicadellids in which the long tibiae mean that the hind legs are twice as long as the front and middle legs and nearly the length of the body. Nevertheless, the jumping performance of short- and long-legged cicadellids is similar and implies that the length of the hind legs has little to do with jumping performance when a catapult mechanism is used (Burrows and Sutton, 2008). In all these species the hind legs are held under the body and moved in the same plane as each other parallel to the long axis of the body. They are powered by muscles in the thorax that move the trochantera, thus allowing legs themselves to be light and thus easier to accelerate. This contrasts strongly with grasshoppers where the hind legs are much longer than the other legs and move in different planes to each other at the side of the body. They are also powered by muscles that move the tibiae.

The distal segments of the hind legs of frog-, leaf- and planthoppers all have arrays of ventrally pointing spines at the tibio–tarsal, and tarsal joints that would aid traction when leaping from the ground or a plant. The tibiae of froghoppers and planthoppers have just two spines whereas the long-legged cicadellids have rows of shorter spines. The femoro–tibial joints of all are similar and show no specialisations that could be attributed to jumping.

It is in the proximal joints that the biggest differences occur. The coxae in leafhoppers are solid, large and occupy most of the ventral part of the metathorax. In adults (Emeljanov, 1987; Gorb, 2001), but not in the freely moving and jumping nymphs, they are joined at the midline by a protrusion of one coxa that fits snugly into a socket on the other – a sort of press-stud or popper arrangement – augmented by arrays of microtrichia (Burrows, 2007a). In froghoppers the closely apposed medial surfaces of the coxae have microtrichia that interdigitate but allow some independent action, but in planthoppers the coxae are firmly apposed to each other and were not observed to move independently. The coxae of planthoppers are also less rigid with their ventral surface covered

Table 2. Jumping performance of *Issus* compared with froghoppers and leafhoppers

Units	Body mass mg	Body length mm	Time to take off ms	Take-off velocity m s⁻¹	Take-off angle deg.	Body angle at take-off deg.	Acceleration m s⁻²	*g* force *g*	Energy μJ	Power mW	Force mN	Power/muscle mass⁻¹ W kg⁻¹
Formula	m			v			$f = v/t$	$g = f/9.86$	$e = 0.5\,m\,v^2$	$=e/t$	$=m\,f$	$p/(11 \times m)$
Planthoppers												
Issus, male												
Mean (N=31)	21.5±0.56	6.7±0.07	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
Issus, female												
Mean (N=27)	32.2±2.01	8.1±0.14	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
Froghoppers												
Philaenus*(N=34)												
Mean	12.3±0.74	6.1±0.08	1	2.8±0.1	46.8±2.0	28±1.9	2800	286	48	48	34	35,500
Best			0.875	4.7			5400	550	155	155	66	114,500
Leafhoppers												
Aphrodes†(N=43)												
Mean	18.4±1.3	8.5±0.22	4.4±0.18	2.5±0.09	37.1±4.4	36.7±5.0	568	58	58	13	11	6500
Best			2.75	2.9			1055	108	77	28	19	14,000

The body mass for the best jump by a male or female *Issus* is for the individual that gave this performance.
**Philaenus spumarius* (Linnaeus 1758). Data from Burrows, 2006a.
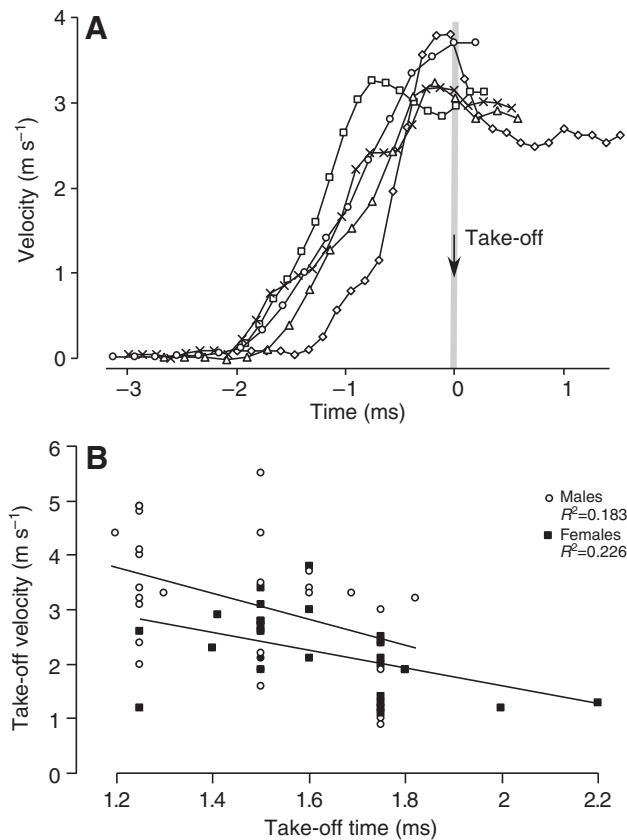†*Aphrodes* of the *makarovi* Zachvatkin, 1948/*bicinctus* (Schrank) group. Data from Burrows, 2007b.

Fig. 8. (A) Velocities measured as a rolling three point average of five jumps by the same *Issus* when jumping to the right and parallel to the image plane of the camera. Images of the jumps were captured at either 5000 and 7500 frames s^{-1}. (B) Graph of the relationship between take-off time and the resulting take-off velocity. In both male (open circles) and female (filled squares) *Issus*, shorter take-off times resulted in faster take-off velocities.
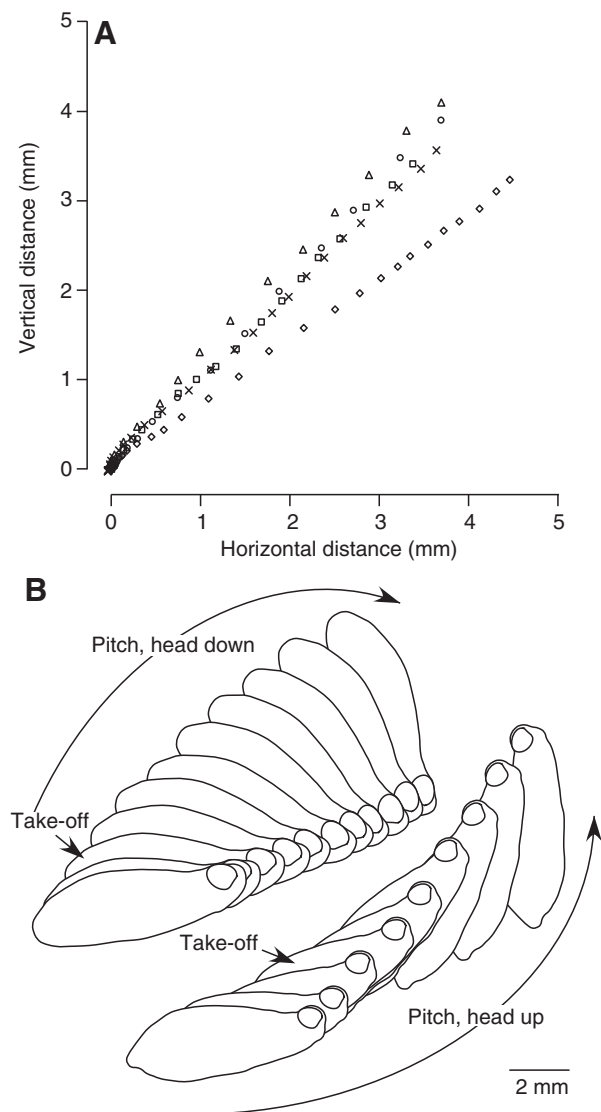

Fig. 9. (A) Trajectories of the same five jumps shown in Fig. 8A. (B) Rotations in the pitch plane. Tracings of the body outline from alternate images in two jumps to the right and parallel to the image plane of the camera and captured at 4000 frames s^{-1}. Each drawing is therefore separated in time by 0.5 ms from the next in the sequence. In the jump at the top, the head pitched downwards (curved arrow), and in the jump on the bottom it pitched upwards.

in transparent flexible cuticle rather than hard chitinous cuticle as in the other two families. The dominant feature of each design is a solution to the problem of providing a rigid foundation for the rapid depression movements of the trochantera about the coxae powered by large depressor muscles in the thorax, the tendons of which run through the coxae to insert on the trochantera.

Froghoppers have complex protrusions on the ventral surface of a coxa and on the proximal dorsal surface of a femur, both of which are covered with microtrichia (Burrows, 2006b). These protrusions engage with each other only when a hind leg is fully levated and cocked ready for a jump. The microtrichia may interdigitate on the two opposed surfaces so increasing the adhesion. During the prolonged contraction of the trochanteral depressor muscles which stores energy by bending the pleural arches, the two protrusions remain engaged and prevent the leg from unfurling (Burrows, 2006b; Burrows, 2007c). If the leg is to depress, then the increased friction provided by the apposition of the microtrichia, the forces resulting from their inter-digitation, and the physical barrier of the protrusions themselves must all be overcome. When sufficient force has been developed by the trochanteral depressor muscles, the protrusions suddenly disengage and the hind legs then rapidly depress and extend to power the jump.

Leafhoppers do not have protrusions on either the ventral coxa or on the dorsal proximal femur. Correlated with this, the acceleration time is four to six times longer and the take-off off

velocity is less than half that of a froghopper (Burrows, 2006a; Burrows, 2007b). Nevertheless, one species of cicadellid, *Aphrodes*, despite having an acceleration time that is 4.4 times longer than that of a froghopper achieves a take-off velocity that is only a little lower (comparing the average performance by the different insects) (Burrows, 2007b).

Planthoppers have a protrusion on a coxa that is covered in microtrichia, but the dorsal femur lacks a prominent protrusion. Instead there is a patch of white cuticle which contrasts with the darker surroundings of the femoral cuticle. It is also smooth and lacks microtrichia. Proximally it has a row of stout hairs which will be stimulated when the hind legs are fully levated in preparation for a jump and it engages with the coxal protrusion white patch on the femur. These hairs could therefore provide information about

the cocked position of a hind leg. It is unclear whether there are adhesive forces between the coxal microtrichia and the femoral patch that would allow these structures to work in the same way as in a froghopper.

Jumping performance relative to other insects

Where does the jumping performance place *Issus* among other Hemipterans and amongst other insects that power jumping by movements of the legs? Froghoppers are the champion insect jumpers, in terms of the force exerted relative to body mass. Despite its greater mass, but similar body length, the planthopper *Issus* matches the performance of the froghopper *Philaenus* in terms of the time taken to accelerate its body to take-off and with some males having faster take-off velocities. Its heavier body and short acceleration time also means that the acceleration experienced by a male *Issus* at take-off is 30% higher than a froghopper experiences in its best jumps (Burrows, 2006a). The forces experienced by *Issus* at take-off are on average similar to those of froghoppers [231g (males) or 310g (females) compared with 286g], but in the best jumps can be considerably higher: 719g compared with 550g in froghoppers (Table 2).

The other Hemipteran jumping insects so far examined have a jumping performance that is substantially less than the frog- or planthoppers but is still impressive. Amongst the cicadellids, *Aphrodes* can achieve take-off velocities of 2.9 m s^{-1} but the long legs mean that acceleration times are longer (Burrows, 2007b). Other long-legged cicadellids, the short-legged cicadellids (Burrows and Sutton, 2008) and shore bugs (Hemiptera, Heteroptera, *Saldidae*) have take-off velocities that range from 1.6 to 1.85 m s^{-1} (Burrows, 2009). *Hackeriella* (Coleorrhyncha, a sister sub-order to the Heteroptera) has a mean acceleration time of 2 ms and a best take-off velocity of 1.5 m s^{-1} (Burrows et al., 2007).

The jumping performance of *Issus* also exceeds that of both smaller or larger insects from other orders. Fleas (Siphonaptera) accelerate their body in 1 ms to a take-off velocity of 1 m s^{-1} (Bennet-Clark and Lucey, 1967; Rothschild et al., 1975; Rothschild et al., 1972) but different species of fleas may have higher take-off velocities (Bossard, 2002). The performance of *Issus* is also better than that of flea beetles (Coleoptera, Alticinae) (Brackenbury and Wang, 1995). The heavier Orthopteran insects all fall well short of the performance of *Issus*. For example, locusts (Orthoptera, Caelifera, Acrididae) with a mass of 1–2 g take 20–30 ms to extend their long hind legs (Brown, 1967) and accelerate their body to a take-off velocity of 3 m s^{-1} (Bennet-Clark, 1975), while the false stick insect *Prosarthria teretrirostris* (Orthoptera, Caelifera, Proscopiidae) with a mass of 280 mg takes 30 ms of acceleration to achieve a take-off velocity of 2.5 m s^{-1} (Burrows and Wolf, 2002). The bush cricket *Pholidoptera* (Orthoptera, Ensifera, Tettigoniidae) weighing 600 mg extend its hind legs fully within 30 ms achieve a take-off velocity of 2.1 m s^{-1} (Burrows and Morris, 2003). In all of these insects the forces experienced at take-off are much less than those experienced by either froghoppers or planthoppers.

How do the muscles act and store energy?

The high energy and power requirements of the jump raise three questions about how they can be met by the neural, muscular and skeletal machinery of a planthopper.

First, the power output per mass of muscle can exceed 160,000 W kg^{-1} in the best jumps, assuming that, as in froghoppers (Burrows, 2007c), the mass of the trochanteral depressor muscles, which generate the propulsive movements of the hind legs, represents about 11% of body mass. This far exceeds the maximum active contractile limit, which ranges between 250 and 500 W kg^{-1} of energy that can be produced by the direct contraction of muscle (Askew and Marsh, 2002; Ellington, 1985; Josephson, 1993; Weis-Fogh and Alexander, 1977). If the assumption about the proportions of the jumping muscles is too low and it is instead assumed that the body mass is made up almost entirely of the jumping muscle, then the power achieved by a jumping *Issus* would still exceed that achieved by the best muscle. This clearly indicates that power amplification must be used in jumping and that contractions of the power-producing trochanteral depressor muscles must begin well in advance of the jump. Energy must be stored during these prolonged muscular contractions and then released suddenly to effect the rapid movements of the hind legs. The power must therefore be produced by a catapult-like mechanism rather than by direct contractions of the muscles. How do the muscles act to generate the necessary force, and how are movements of the hind legs constrained while the catapult is loaded?

Second, the energy generated by a slow contraction of the power-producing muscles will need to be stored. In froghoppers this is achieved by bending the paired, bow-shaped pleural arches that link each coxa to the articulation with a hind wing on the same side of the body (Burrows et al., 2008). The internal skeletal elements are composite structures of stiff cuticle and the rubber-like resilin. The stiff cuticle means that the muscles do not have to bend the bows far and the resilin ensures that the stiff cuticle does not fracture and that the pleural arches return to their original shape after a jump, thus restoring the natural body shape in readiness for further jumping. Are similar structures used to store energy in froghoppers?

Third, the initial movements of both hind legs are synchronised to within 0.03 ms. Achieving such tight synchronisation would require extreme precision in neural control that would perhaps challenge the computational capacity of the nervous system. Alternatively, is there a simpler mechanism involving a mechanical linkage between the two hind legs of *Issus*?

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