

Jumping behaviour in a Gondwanan relict insect (Hemiptera: Coleorrhyncha: Peloridiidae)

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Summary

Jumping by a relict insect, *Hackeriella veitchi* (Hacker 1932), belonging to the ancient Coleorrhynchan line that diverged from other Hemiptera in the late Permian, was analysed from high-speed images captured at rates of 2000 s⁻¹ and from its anatomy. This 3 mm long, flightless insect weighs up to 1.4 mg and can jump by rapid movements of the hind legs that accelerate the body in 1.5 ms to a take-off velocity of 1.5 m s⁻¹. This performance requires an energy expenditure of 1.1 µJ and a power output 0.74 mW, and exerts a force of 1.24 mN. It achieves this with a body design that shows few specialisations for jumping compared with those of other groups of Hemipterans such as the froghoppers or leafhoppers. The hind legs are only 10% longer than the front and middle legs by virtue of longer tibiae and tarsi, and are only 65% the length of the body. The main thrust for a jump is

provided by the rapid rotation of the fused trochanter and femur about the coxa of a hind leg, in a movement that forces the hind tarsus against the ground and raises the body to take off. In some jumps the two hind legs move together, but in others the movements may not be closely synchronised, thereby imparting a rotation on the body that is maintained once airborne. When the time difference is larger, the rapid movement of just one hind leg results in the insect falling from its perch in an adaptive escape response.

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Introduction

Jumping is a widely used form of locomotion that enables an animal to escape imminent predation by moving rapidly from one place to another, to escape from unfavourable conditions, to leap from one food source to another, to circumvent obstacles in a difficult terrain and to launch into flight. This form of locomotion places particular demands on the limbs, skeleton and muscles. Amongst the vertebrates, kangaroos, bush babies, hares and frogs have all evolved long hind legs, which give better leverage for jumping (Alexander, 1995). The smaller size of insects means that the legs can only provide limited leverage even though bush crickets in particular have exploited this feature (Burrows and Morris, 2003). To jump with short legs has led to the evolution of storage mechanisms in which muscle force is developed slowly and energy stored in deformations of the skeleton before being released suddenly in a catapult action. This mechanism has been exploited by the best-known jumping insects such as grasshoppers (Bennet-Clark, 1975), fleas (Bennet-Clark and Lucey, 1967; Rothschild et al., 1972) and flea beetles (Brackenbury and Wang, 1995; Furth, 1988; Furth et al., 1983; Maulik, 1929).

A diverse group of prodigious jumping insects that have been less well studied are the Hemipteran bugs. Amongst these are the froghoppers, or spittle bugs (Cercopidae), which outperform all

other insects in their jumping abilities by using a catapult mechanism (Burrows, 2003; Burrows, 2006a). The Hemiptera also contains many other closely related families of bugs, such as tree and leafhoppers in the probably paraphyletic sub-order 'Auchenorrhyncha', and bugs such as jumping plant lice (Psyllidae) in the sub-order Sternorrhyncha. All have evolved differing designs for jumping. Some members of an ancient sub-order, the Coleorrhyncha, also jump. This group split from the evolutionary lineage of other Hemipterans in the late Permian (Popov and Shcherbakov, 1996). The present distribution of this group is restricted to the southern hemisphere (Australia, New Zealand, New Caledonia and the southern tip of South America), suggesting that it must have been in existence before the break up of Gondwana (Evans, 1981). The extant Coleorrhyncha consist of just 25 species belonging to 13 genera in a single family, the Peloridiidae, all but one of which are flightless. The close resemblance of living species to those of Mesozoic fossils, (Popov and Shcherbakov, 1996) and the key position of Coleorrhyncha within the Hemiptera (Bourgoin and Cambell, 2002; Schlee, 1969) suggests that they may give clues about the evolution of jumping and about the jumping mechanisms that may have been present in the basal ancestral groups.

In this paper, we describe the jumping performance and the associated leg movements as captured with high-speed imaging

of a small coleorrhynchan, *Hackeriella veitchi*, from Australia. We show that it accelerates its body in 1.5 ms by rapid movements of both hind legs to a take-off velocity of 1.5 m s^{-1} , experiencing a force of 100 times gravity. The short hind legs, which provide the main propulsive force for the jump, show few specialisations for jumping compared with those of modern Auchenorrhyncha.

Materials and methods

Adult *Hackeriella veitchi* (Hacker 1932) were collected from Springbrook National Park, Queensland, Australia by G. Monteith (Queensland Museum, Brisbane). They were transferred with their original host moss plant to Germany where they were kept in small groups in 70 mm diameter plastic dishes together with the moss *Brachythecium rutabulum*. *Hackeriella veitchi* belongs to the order Hemiptera, suborder Coleorrhyncha, and to the family Peloridiidae. The systematic position of the Coleorrhyncha within the Hemiptera is shown in Fig. 1A.

Sequential images of 10 jumps by 11 adults of either sex were captured at rates of 2000 s^{-1} and an exposure time of 0.1 ms with a Photron Fastcam 512PCI camera [Photron (Europe) Ltd, Marlow, Bucks., UK] that fed images directly to a computer. A high-speed video of a jump captured with these parameters is included as Movie 1 in supplementary material. Spontaneous jumps, and jumps encouraged by delicate mechanical stimulation with a fine paintbrush, were performed from a platform of thin card 80 mm long and 10 mm wide. Selected image files were analysed with Motionscope camera software (Redlake Imaging, San Diego, CA, USA) or Canvas X (ACD

Systems of America, USA). The time at which the hind legs lost contact with the ground and the insect therefore took off and became airborne was designated as time $t=0$ ms, so that different jumps could be aligned and compared.

The anatomy of the hind legs and metathorax was examined in intact insects and in insects preserved in 96% alcohol. Measurements of body and leg length were taken from live insects and from others preserved in 96% ethanol. For scanning electron microscopy, *Hackeriella* were cleared by boiling in 10% potassium hydroxide and subsequently lightly rubbed with a fine paintbrush and a needle to remove the surface film covering the cuticle. They were dehydrated in increasing concentrations (96–100%) of ethanol, critical-point dried, mounted on aluminium specimen stubs with adhesive pads, and coated with gold–palladium. They were examined in a LEO 1450VP Scanning Electron Microscope at 10 kV. Images were stored digitally and subsequently processed with Adobe Photoshop.

Measurements are given as means \pm standard error of the mean (s.e.m.). Temperatures in all experiments ranged from 24–26°C.

Results

The jumping behaviour of *Hackeriella veitchi* was first observed by Geoff Monteith in his laboratory shortly after the insects had been brought in from their natural habitat. He describes jumps that reached 50 mm in height and a horizontal distance of 150 mm (G. Monteith, personal communication). We have also observed jumps of similar heights and distances.

Body form

Hackeriella has a dorso-ventrally flattened body with compound eyes on lateral protrusions of the head (Fig. 1B). The adults are flightless; tegmina are present, but the hind wings are absent. Females are heavier and larger than the males. They have a mass of $1.39 \pm 0.03 \text{ mg}$ ($N=10$), which is significantly heavier (T -test, $T_{1,18}=9.655$, $P<0.0019$) than the males at $1.05 \pm 0.03 \text{ mg}$ ($N=10$). Similarly, they have a body length of $3.04 \pm 0.02 \text{ mm}$ ($N=10$) that is significantly longer ($T_{1,8}=3.374$, $P=0.010$) than that of males at $2.83 \pm 0.06 \text{ mm}$ ($N=10$).

Jumping movements

Hackeriella jumped infrequently from surfaces of any orientation. The jumps occurred spontaneously or could be induced by mechanical or vibrational stimuli from a fine paintbrush. In 17 h of recording, 11 jumps were captured with high-speed imaging. The descriptions that follow are of jumps from a flat, horizontal surface.

In preparation for a jump, the angle of the body relative to the ground was first set by movements of the front and middle legs. Once this posture had been adopted, the first movements that initiated jumping were the rapid depression and extension movements of both hind legs (Fig. 2). When viewed from the side, the femora were depressed downwards and backwards and the tibiae extended about the femora. The restricted movement of the coxa about the thorax and the fusion of the trochanter with the femur (see below) implies that the femoral movements resulted from a depression movement of the coxo-trochanteral joint. These movements initially pushed the tarsi of both hind

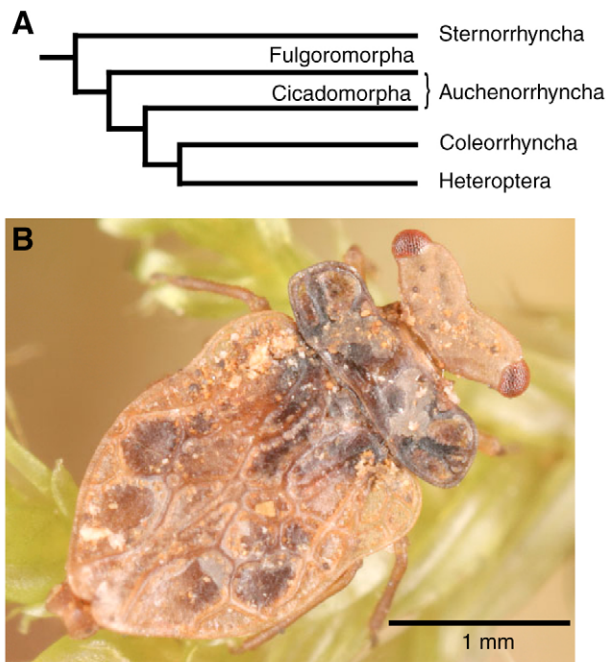


Fig. 1. (A) The phylogenetic relationships of the Coleorrhyncha (based on Bourgoin and Cambell, 2002), showing some of the modern Hemipteran families. The Peloridiidae represent the only modern family of Coleorrhyncha. (B) Photograph (by J. Deckert) of a male of *Hackeriella veitchi*, viewed dorsally, on its host plant.

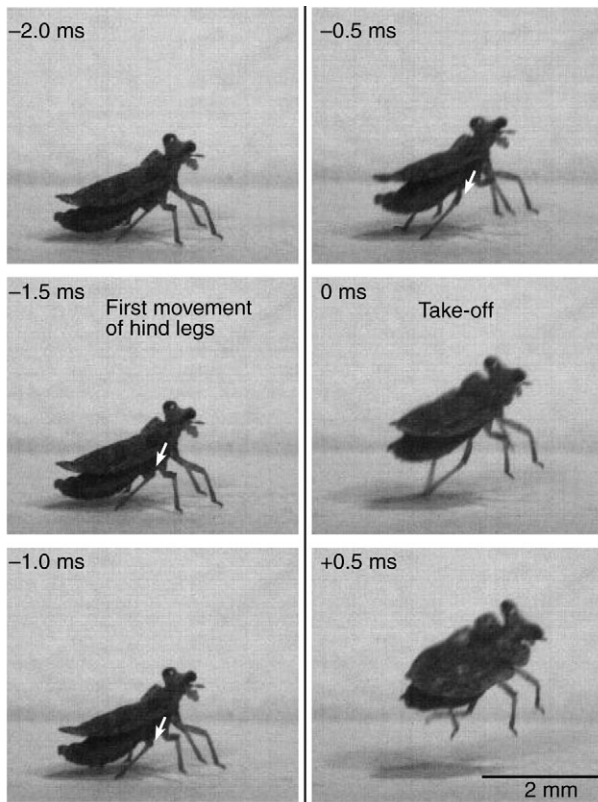


Fig. 2. Images of a jump from left to right with the long axis of the body parallel to the camera, captured at 2000 images s^{-1} . Selected images at the times indicated are arranged vertically in two columns. The first movement of a hind leg occurred 1.5 ms (frame -1.5) before take-off (0 ms) and can be seen as a downwards and backwards movement of the femur (white arrow). The two hind tarsi were positioned separately beneath the body. At take-off they moved closer together and then once clear of the ground, the tibiae of the two hind legs crossed beneath the body.

legs firmly against the ground beneath the body but positioned separately from each other. The thrust thereby applied to the ground raised the body and lifted the front and middle legs from the ground (Fig. 2, Fig. 3A,B). In all jumps recorded, the front and middle legs were lifted off the ground before take-off and sometimes the front legs were off the ground before the hind legs even started to move. At take-off, when the weight of the body was no longer supported by the hind legs, each moved medially so that both tarsi were apposed to each other beneath the body. After take-off, the residual thrust of the hind legs moved them further medially so that the tibiae now crossed.

In the best jumps, the time from the first movements of the hind legs until the insect was launched into the air at take-off took just 1.5 ms (average 2 ms in 10 jumps) (Figs 2, 3). This very short time therefore represents the period during which the body can be accelerated to its take-off velocity.

The trajectory of the jump was variable for different jumps by the same animal and was related to the starting angle of the body relative to the ground. The trajectory was also influenced by the spin of the body after take-off (Fig. 4). In the example shown, the body started to rotate about the long axis of the body

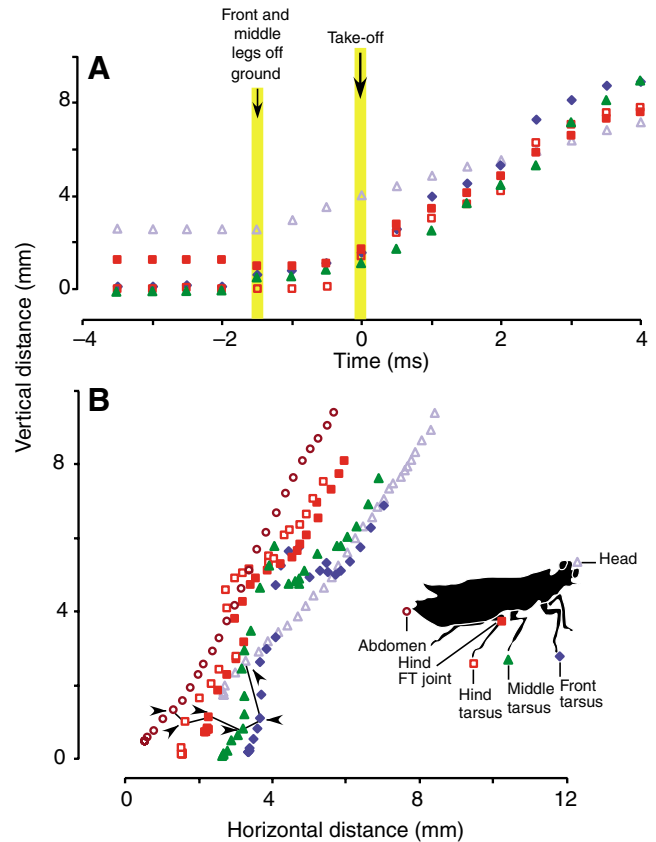


Fig. 3. Leg and body movements during the jump shown in Fig. 2. (A) The position of the head, the femoro-tibial (FT) joint of the right hind leg, and the tarsi of the three right legs (see cartoon inset in B) are plotted against time. The first movement of a hind leg occurred 1.5 ms before take-off (left arrow and yellow bar) and caused the tarsi of the front and middle legs to lose contact with the ground. Take-off at time 0 ms is indicated by the right arrow and the right, vertical yellow bar. (B) Sequential movements of the six points on the body during a jump. The black arrowheads and the linking black lines show the position of these six points at take-off (0 ms). The corresponding positions of these points at different times during the jump can be read point by point from these positions at take-off, with each point representing the distance moved in 0.5 ms.

at take-off and rotated with an initial periodicity of about 10 ms whilst the insect remained within the view of the camera. In some jumps, the body spun about the transverse axis of the body so that the abdomen periodically reversed positions with the head to be in the lead. In other jumps, the body spun about both axes.

Lack of synchrony between movements of the hind legs

The spin of the body about its longitudinal axis often appeared to be imparted by a lack of synchrony between the rapid movements of the two hind legs (Fig. 5). In the example shown, the right hind leg moved first (at -2.0 ms) so that its tarsus was pushed firmly onto the ground, whilst the tarsus of the left hind leg was held motionless and off the ground. The continuing depression of the right hind leg tilted the front of the body in a clockwise direction (when viewing the body from in

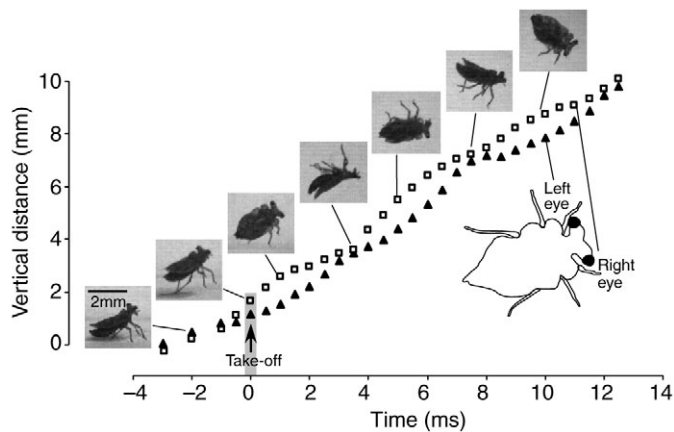


Fig. 4. Trajectory of a jump. The position of the left and right eyes (see cartoon inset) in the vertical plane are plotted against time. Selected frames to show the orientation of the body are shown at the times indicated. Once airborne the body spins about the longitudinal axis of the body with each rotation lasting about 4 ms, as indicated by the periodic convergence of the two sets of points at these intervals. Images were captured at 2000 s^{-1} .

front) so that the left side of the head moved closer to the ground. One millisecond later the left hind leg moved (at -1.0 ms) and its subsequent depression reversed the body tilt in an anti-clockwise direction so that the right side of the head was now closer to the ground than the left side. After take-off the right side of the body continued to rotate in this anti-clockwise direction about the long axis of the body. The spinning continued as the insect gained height in the jump.

The asynchrony in the movements of the hind legs could also result in the insect falling from its perching position (Fig. 6). In the example shown, the insect was standing on the edge of the platform with the tarsus of the right hind leg held off the ground. This hind leg then moved suddenly so that its tarsus was pushed against the ground and the subsequent further depression of its femur progressively raised the right side of the body. While this rapid movement was happening the left hind leg did not move. Eventually the tilting of the body was so great that the insect overbalanced and fell from the platform. On different occasions, either the left or the right hind leg could depress by itself so that the fall occurred to one side or the other.

Jumping performance

Jumping performance was calculated from the high-speed images of the movements and from measurements of the body mass (Table 1). The peak take-off velocity averaged over seven jumps was $1.2 \pm 0.08 \text{ m s}^{-1}$, with the best jump by one individual achieving 1.5 m s^{-1} . The applied acceleration during the period when the hind legs were moving but still in contact with the ground was almost 1000 m s^{-2} so that at take-off the insect experienced the equivalent of almost 100 g . The energy required to achieve this performance was $1.1 \mu\text{J}$ because the mass of the body is small, the power output was 0.74 mW and the force exerted was 1.24 mN .

Structure of the hind legs

In both males and females there is a significant but small

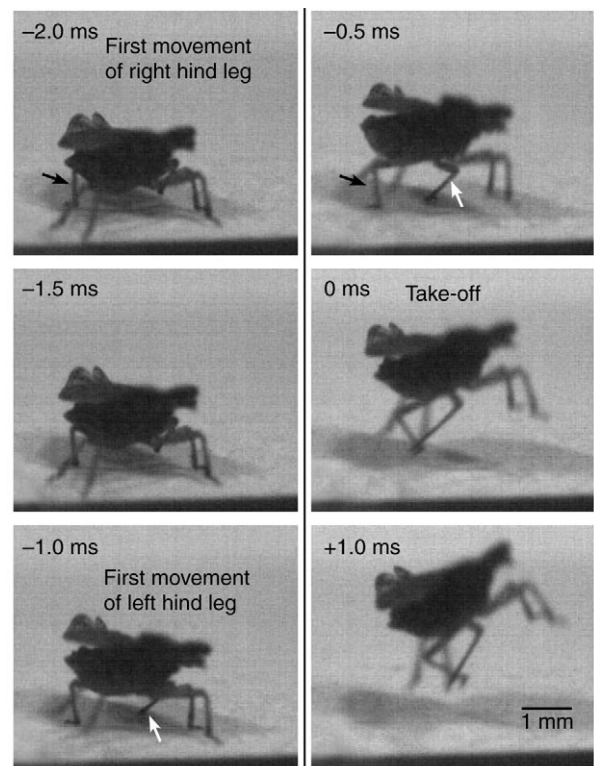


Fig. 5. Asynchrony in the movements of the two hind legs leads to a rotation of the body at take-off. The right hind leg (black arrow) was first depressed at frame -2.0 ms so that its tarsus was placed fully on the ground. The tarsus of the left hind leg is off the ground. The effect was to rotate the body so that the left side moved closer to the ground. At -1.0 ms the left hind leg was depressed (white arrow) so that its tarsus now contacted the ground. The contribution of this leg now rotated the body in the opposite direction and this rotation dominated at take-off and when airborne.

difference in leg length between the hind legs and the front and middle legs (MANOVA – multivariate analysis of variance – $F_{2,7}=1081.715$, $P<0.0001$). A *post-hoc* analysis of leg lengths (Bonferroni-corrected least significant difference) showed that the hind legs were significantly longer by some 10% than the front and middle legs, which did not differ significantly from each other. The ratio of lengths for the front:middle:hind legs is therefore 1:1:1.1. The hind legs are 67% of the length of the body in the shorter males and 63% in the longer females. The increased length of the hind legs in both sexes resulted from the longer lengths of the tibiae with a contribution from the longer tarsi. The hind tibiae are significantly longer (MANOVA, $F_{2,7}=41.959$, $P<0.0001$) than those of the front and middle legs. Similarly, a hind tarsus is longer than a middle tarsus (MANOVA, $F_{2,7}=36.003$, $P<0.0001$), which in turn is longer than a front tarsus (*post-hoc* test). The other leg segments are of similar lengths in all three pairs of legs. The coxae and trochantera of the three pairs of legs are similar in general structure but they differ in their orientation.

The coxae of the front legs pivot at an angle of about 55° to the longitudinal body axis, the middle coxae at 72° and the hind coxae at right angles (Fig. 7A). The hind coxae are $250 \mu\text{m}$ wide and are thus larger than the $200 \mu\text{m}$ wide front and middle

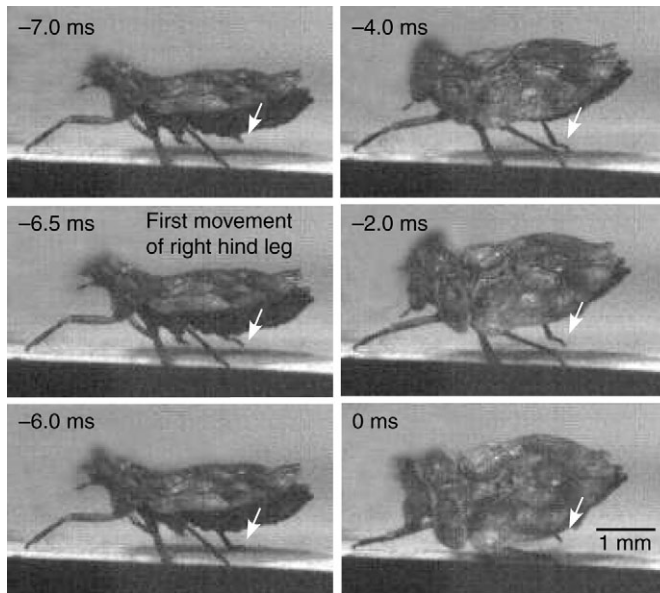


Fig. 6. Falling movement caused by a rapid movement of one hind leg. In the first frame (–7.0 ms) the right hind leg (white arrow) was off the ground and the left hind leg was on the ground. A rapid depression of the right hind leg, without a movement by the left hind leg, pushed its tarsus to the ground (–6.0 ms). The applied force progressively tilted the body so that the left side moved downwards and the insect fell from the platform.

coxae. They are not fused to thorax so that they are able to rotate through some 70° about the thorax.

The rostrum of the sucking mouthparts protrudes between and therefore separates the left and right coxae of all three pairs of legs (Fig. 7A). The hind coxae are, however, set more closely together and may touch each other toward their most dorsal medial edges where some tubercles (microtrichia) are present. They are not, however, tightly linked together by attachment devices in contrast to those of froghoppers (Burrows, 2006b) or leafhoppers (Burrows, 2007a). The antero-lateral edge of a coxa has a broad depression, which is surrounded by tubercles (Fig. 7C). Internally the depression projects as an apodeme-like structure, which is not present in a front and middle coxae. A hind coxa has no protrusion on its ventral, lateral surface (Fig. 7B) as is present in some Auchenorrhyncha such as froghoppers (Burrows, 2006b). Similarly the dorsal surface of the proximal femur has no protrusion (Fig. 7C). The hind legs therefore lack an external locking device that could engage the femur with the coxa and prevent the depression movements of

jumping until sufficient muscular force has been developed to propel take-off. A hair plate consisting of a group of 4–6 short (6–8 µm) and stout hairs on the anterior edge of a coxa could monitor the movements of the coxa relative to the thorax (Fig. 7B).

The angle of rotation of the trochanter about the coxa relative to the midline is also different for each pair of legs; the angle of the front coxo-trochanteral joint is 140°, the middle leg joint is 18° and the hind leg joint is 40° (Fig. 7A). A hind trochanter can be levated and depressed about a coxa through an angle of some 110°. The articulation of a trochanter with a coxa consists of a ventral and a dorsal horn of the trochanter, which articulate in curved indentations of the coxa allowing a movement in one plane. A small hair plate with up to 5 hairs some 6–8 µm in length on the lateral edge of a trochanteral horn at its ventral pivot with the coxa could signal movements of this joint when it is close to full levation (Fig. 7B). The tendon of the trochanteral depressor muscle was traced from its insertion on the trochanter, through the coxa and into the thorax where, in cercopid (Burrows, 2006b) and fulgorid (Sander, 1957) bugs, as in other insects, the main part of this muscle lies.

The demarcation between the hind trochanter and hind femur is marked by a clear suture line that indicates fusion between the two. No movement between them occurred during jumping so that a movement of the trochanter was always accompanied by a movement of the femur. The femur of a hind leg is of similar size to that of the other legs, indicating that the extensor tibiae muscle is not enormously enlarged as in locusts and is thus not a major contributor to the generation of force in jumping. Furthermore, a hind femoro-tibial joint shows no obvious specialisations over those of the middle and front legs.

The hind tibia pivots with the femur in such a way that it can move through an angle of some 155° in the same plane as the movements of the trochanter about the coxa. The movements of this joint are similar to those of the other two pairs of legs. The hind tibia has a semi-circular row of spines on its ventral surface close to its joint with the tarsus (Fig. 7D), which would contact the ground at the same time as the tarsus. They are likely to improve traction with the ground particularly during jumping.

The hind tarsus also moves about the tibia in the same plane as the more proximal joints. It has unguis claws (Fig. 7D) and tarsal pads that should again increase traction with the ground during jumping.

Discussion

Coleorrhynchans represent an ancient line of the Hemiptera which diverged in the late Permian before the break up of Gondwana. Their morphological similarity to Mesozoic

Table 1. *Jumping performance of Hackeriella veitchi*

	Time to take-off (ms)	Take-off velocity* (m s ⁻¹)	Mass (mg)	Body length (mm)	Acceleration† (m s ⁻²)	Force (×g)	Energy (µJ)	Power (mW)	Force (mN)
Average	2	1.2	1.28		575	59	0.85	0.42	0.74
Best	1.5	1.5			966	99	1.1	0.74	1.24
Female			1.39	1.05					
Male			3.04	2.83					

*Peak value; †average value.

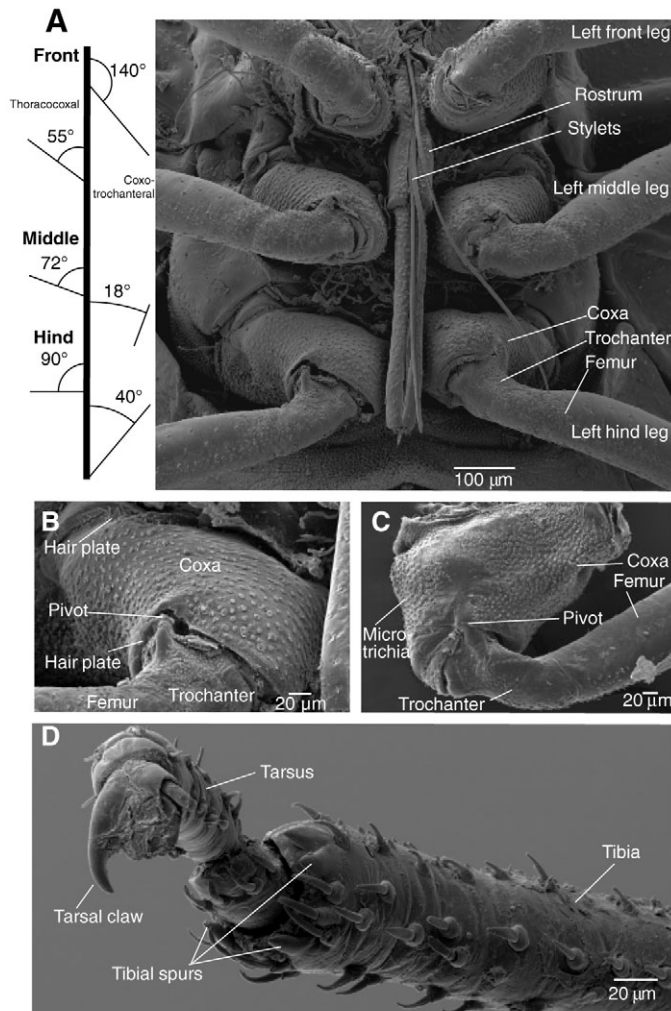


Fig. 7. Scanning electron microscope images of the legs. (A) All three pairs of legs have proximal segments of similar shape but different orientations. One stylet has come out of the sheathing rostrum. The diagram at the left shows the thoraco-coxal and coxo-trochanteral angles of the legs. (B) Ventral view of the coxo-trochanteral joint. A hair plate is present on the anterior edge of the coxa and on the lateral edge of the ventral horn of the trochanter but there is no protrusion from the lateral coxa. (C) Dorsal view of the proximal joints of the right hind leg to show the microtrichia on the medial surface of the coxa, the fusion of the trochanter with the femur and the absence of a protrusion on the dorsal, proximal femur. (D) The tarsus and distal tibia to show the ventral, semi-circular ring of tibial spines at the tibio-tarsal joint.

Karabasiidae (Popov and Shcherbakov, 1996) suggests that the few extant species in restricted parts of the Southern Hemisphere have changed little in the intervening period. Nevertheless, this is the first report that they are accomplished but reluctant jumpers, although previous reports have indicated that they do not jump (Popov and Shcherbakov, 1996), indicating that this form of locomotion is ancient within the Hemiptera. In its best jumps, *Hackeriella* accelerates its small, light body at 1000 m s^{-2} in 1.5 ms to a take-off velocity of 1.5 m s^{-1} , expending $1.1 \mu\text{J}$ of energy, developing a power output 0.74 mW and exerting a force of 1.24 mN . It achieves

this with a body design that shows few specialisations for jumping compared with those of other Hemipterans such as the froghoppers (Burrows, 2003; Burrows, 2006a) belonging to the Auchenorrhyncha.

Design for jumping

The body shape does not immediately suggest a design suited for jumping. The head is broad with laterally placed eyes with the dorsal surface of the body is covered by a rigid ribbed tegmina. The hind wings are absent so that there are no wings that could assist take-off or generate forward propulsion when airborne.

Propulsion for jumping is delivered by rapid movements of the hind legs, with the front and middle legs typically losing contact with the ground well before take-off and showing no movements that could add greatly to the thrust. The key movements of the hind legs are depression movements of the coxo-trochanteral joints produced by trochanteral depressor muscles located in the thorax. Placing the main power-producing muscles in the thorax minimises the mass of the legs and thus enables them to be accelerated rapidly. The hind legs are, however, short relative to both the body and to the other legs, so that the leverage (Alexander, 1995) they can provide in jumping is limited. Structurally, there is little that sets the hind legs apart from the middle or front legs, or which obviously proclaims their role in providing the main propulsive force for jumping. For example, neither the ventral coxae nor dorsal femora have protrusions, or arrays of microtrichia that could engage with each other and restrain the movements of the legs in preparation for jumping. This contrasts with froghoppers, which have an elaboration arrangement of protrusions and microtrichia that may act as a mechanical lock that allows force to develop slowly and then be rapidly released in a jump (Burrows, 2006b).

How are the rapid movements of the hind legs generated?

Evidence from the high speed images of jumping and from the external anatomy of the legs suggests that the following sequence of events takes place.

The hind legs are first fully levated at their coxo-trochanteral joints. This results in a forward and medial movement of the legs so that only the distal tips of the tarsi touch the ground. The jump movement itself begins with a depression of the coxo-trochanteral joint that moves the fused trochanter and femur downwards and backwards and results in the whole ventral surface of the tarsus being placed firmly on the ground. As a consequence of the give in the tarsi, there is no upward displacement of the body in this initial movement. Further depression of the coxo-trochanteral joint then occurs and this now begins to raise the body. This movement continues and is accompanied by extension of the femoro-tibial joint until both joints reach their maxima, at which point the body has been lifted so that the hind tarsi are the last to leave the ground and the insect becomes airborne. It is unlikely that a direct contraction of the trochanteral depressor muscles could power such a rapid movement with such short hind legs as levers. Instead, a mechanism is implicated in which a slow contraction of the muscle generates force, which is stored in elastic structures in the hind leg or metathorax and is then released

suddenly to power the movement. Such a catapult mechanism is proposed for jumping in fleas (Bennet-Clark and Lucey, 1967) locusts (Bennet-Clark, 1975) and froghoppers (Burrows, 2003). This requires structures in which energy can be stored and which either restrain movements of the legs until sufficient force has been generated, or give mechanical advantage to the trochanteral depressor or levator muscle at different angles of the coxo-trochanteral joint. These structures have been identified in the insects cited but remain to be discovered in *Hackeriella*. Furthermore, this strategy requires a distinct motor pattern to control all of the muscles involved, particularly in coordinating the movements of the two hind legs.

Most jumps of *Hackeriella* result from synchronised movements of the two hind legs with the body set by the front and middle legs to such an angle that a forward trajectory is achieved. Close synchronisation of the hind legs is needed because of the very short time in which the body is accelerated. In some jumps the hind legs move with a time difference of 1 ms and this then results in the body first being tilted to one side and then to another. The result is that the body spins once airborne. The extreme of this asynchrony is reached when only one hind leg extends rapidly while the other does not move. These asynchronous movements of the hind legs may then provide a mechanism by which the insect can fall rapidly from its perch with the potential to avoid a predator approaching from the front and into whose path a forward jump would propel it.

Comparison with other jumping Hemipterans

How does the jumping performance of *Hackeriella* compare with that of other Hemipteran insects? Most of our knowledge of Hemipteran jumping comes from the Auchenorrhyncha and the Cercopidae (froghoppers) in particular (Burrows, 2003; Gorb, 2004). Froghoppers accelerate their body in 0.8 ms to a take-off velocity of 4.7 m s^{-1} , experiencing 550 g and exerting a force of 66 mN or more than 400 times their body mass (Burrows, 2006a). *Hackeriella* does not achieve this performance, but it does match the take-off velocity of the flea (Bennet-Clark and Lucey, 1967; Rothschild et al., 1972), some leafhoppers (Brackenbury, 1996) and some flea-beetles (Brackenbury and Wang, 1995). Where *Hackeriella* differs from froghoppers is in its lack of directional control over a jump, which in turn results from the lack of a tight synchrony of movements by the two hind legs. Closely coordinated movements are necessary to produce a directed jump with hind legs that move in the same plane beneath the body. In *Hackeriella* the hind legs can move at the same time, independently, or with different timing differences between their rapid actions. The inability to generate a directed jump may, however, be more than offset by the adaptive use each hind leg with some independence that can result in a rapid escape by falling from their perch on a plant.

What do the jumping mechanisms in *Hackeriella* suggest about the evolution of jumping mechanisms and strategies in other Hemipterans? The common and perhaps therefore ancestral features that we report are the following:

(1) The use of thoracic muscles to power a rapid rotational movement of the hind trochantera about their respective coxae. A consequence of this is that the mass of the hind legs is reduced.

(2) The orientation of the hind legs means that when they are extended about the coxo-trochanteral joints, both move in the same plane beneath the body. This strategy thus differs substantially from a mechanical perspective from that used by many grasshoppers, the hind legs of which move in separate planes on either side of the body (G. P. Sutton and M. Burrows, manuscript submitted for publication).

(3) The hind legs are short relative to the other legs and to the length of the body, and are used in both jumping and walking. These light legs can therefore be accelerated rapidly but their short length provides little leverage.

Modern auchenorrhynchans have elaborated on this basic plan and have specific mechanisms for the production of faster and more powerful movements:

(1) Froghoppers have an elaborate mechanical catch between the hind femur and coxa that enables a hind leg to be restrained in its fully cocked position while the trochanteral depressor muscle slowly generates force in preparation for a jump. The elaboration of these mechanisms has resulted in the hind legs being held in a cocked position ready to propel a jump and not contributing thrust to horizontal walking.

(2) There are a variety of mechanisms in auchenorrhynchans that link the coxae of the two hind legs, presumably to provide a stable base for the explosive movements of the distal parts of the legs. Froghoppers have fields of microtrichia on the medial surface of the two hind coxae that engage with each other (Gorb, 2004). Leafhoppers have a press-stud (popper) arrangement between the hind coxae in which a protrusion of one engages in a socket of the other (Burrows, 2007a). In Issids, the left and right hind coxae are fused at the midline. Larval Fulgoromorpha [except for the Tettigometridae (Asche, 1988)] also have projections on the medial surface of a trochanter that can engage with similar projections from the other trochanter rather in the manner of a cogwheel (Sander, 1957).

(3) Froghoppers have neural mechanisms that ensure synchrony of motor spikes in the left and right trochanteral depressor muscles that generate the force for jumping (Burrows, 2007b), presumably to improve the probability of synchronous movements of the two hind legs.

Many other families in the Auchenorrhyncha also jump (e.g. Heilig and Sander, 1986), as do some Sternorrhyncha (Rietschel, 1952; Weber, 1930) and some Heteropterans (e.g. Parsons, 1960; Parsons, 1963). Analyses of jumping currently underway of the many different Hemipteran families should shed light on the evolutionary process and the functional role of particular mechanisms as related to jumping performance.

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