

# Morphology and action of the hind leg joints controlling jumping in froghopper insects

Malcolm Burrows

*Department of Zoology, University of Cambridge, Cambridge CB2 3EJ, UK*

e-mail: mb135@hermes.cam.ac.uk

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## Summary

The morphology and movements of key joints of the hind legs that generate the rapid jumping of froghoppers were analysed. The movements of an individual hind leg during a jump occur in three phases. First, the trochanter is slowly levated about the coxa so that the femur moves anteriorly and engages with a lateral protrusion on the coxa. Second, both hind legs are held in this fully levated (cocked) position without moving for a few seconds. Third, both hind legs depress and extend completely in less than 1 ms. The critical, power-generating movement underlying a jump is the rapid and simultaneous depression of the trochanters about the coxae.

The lever arm of the hind trochanteral depressor muscle is smallest at the cocked position, but does not appear to go over the centre of the pivot. It then increases to a maximum after some 80° of depression movement. By contrast, the lever arm of the trochanteral levator tendon is similar over the range of joint movements and is exceeded by that of the depressor only after 40° of depression. Three prominent arrays of hairs on the trochantin, coxa and trochanter are appropriately positioned to act as proprioceptors signalling key movements in jumping.

In the fully levated position, a protrusion on the dorsal, proximal surface of a hind femur engages with a protrusion from the ventral and lateral part of a coxa. These structures are not present on the front and middle legs. Both protrusions are covered with a dense array of small projections (microtrichia) that both increase the surface area and may interlock with each other. To depress rapidly in a jump these protrusions must disengage. If the hind leg of a dead froghopper is forcibly levated, it will lock in its cocked position, from which it can depress rapidly by movement of the coxo-trochanteral joint and disengagement of the femoral and coxal protrusions. A prominent click sound occurs at the start of a jump that results either from the initial movements of the coxo-trochanteral joint, or from the disengagement of the microtrichia on the coxa and femur. Larval *Philaenus*, which do not jump, lack a femoral protrusion and have no microtrichia in equivalent positions on either the coxa or femur.

Key words: locomotion, tendon, muscle, Auchenorrhyncha.

## Introduction

Froghopper insects (Hemiptera, Cercopoidea) can launch themselves into a jump in less than 1 ms, achieving take-off velocities of 4.7 m s<sup>-1</sup> and experiencing an acceleration of more than 550 g (Burrows, 2006) that propels them to a height of about 115 times their body length (Burrows, 2003). The key movements of the hind legs in generating these movements are the rapid depression of the trochanters about the coxae, accompanied by extension of the tibiae about the femora. The hind legs are, however, only about half the length of the body, indicating that the mechanical advantages to be gained by using long levers (Alexander, 1995) are not exploited by froghoppers in jumping. The force requirement for a jump is much greater than could be provided by direct muscle contractions in the brief time (less than 1 ms) that the acceleration is applied. Short

hind legs coupled with the intrinsic limitations of muscle suggest that a catapult mechanism must be used. This, in turn, implies that there must be anatomical specialisations of the hind legs to allow force to be generated slowly, whilst they remain stationary, and then to be delivered suddenly to produce a rapid and powerful movement.

Many insects that jump have accompanying specialisations of their limbs, joints, muscles and motor patterns that allow rapid movements to be generated. These specialisations are most marked in the hind legs that generate the propulsive force. Fleas power their jumps by contracting the enlarged trochanteral depressor muscles and storing energy in resilin (Bennet-Clark and Lucey, 1967; Rothschild and Schlein, 1975; Rothschild et al., 1972). The stored force is released apparently by the contraction of a small muscle that changes the point of

action of the depressor muscle so that the short hind legs can be depressed rapidly. Flea beetles have enlarged hind femora each containing a spring formed by the curling and chitinisation of the extensor tibiae tendon (Furth, 1988; Maulik, 1929). The tibia is probably locked into the flexed position when a small triangular plate at the femoro-tibial joint is moved by contraction of the flexor muscle and is released in a jump by changes in the flexor force and as the spring snaps back to its original shape.

Grasshoppers have hind legs that are both long and robust with femurs that are 10 times the mass of those of the other legs. The contractions of the large extensor tibiae muscle within the femur distort the femoral cuticle and bend highly sclerotised semi-lunar processes at the femoro-tibial joint, so storing energy to provide the propulsive force for a jump (Bennet-Clark, 1975; Burrows and Morris, 2001). The tendon of the small flexor tibiae muscle has a pouch that engages with a femoral lump that changes the line of action of the tendon as the tibia flexes (Heitler, 1974). These specialisations restrain movements of the tibiae while the large extensor muscles contract slowly before a jump. False stick insects (Orthoptera, Proscopiidae) have long hind legs with curved tibiae, but still require energy to be stored before a jump. The semi-lunar processes on the femora are much reduced and are not bent before a jump, but the tibiae themselves do bend (Burrows and Wolf, 2002). Again, complex arrangements of the lever arms ensure that the small flexor tibiae muscle can restrain the contractions of the larger extensor before the tibia is rapidly extended to power a jump. Both of these insects combine an ability to store energy in advance of a jump and then release it suddenly, with the beneficial effects of long legs as levers. Bush crickets, however, seem to rely more heavily on the leverage from their exceptionally long hind legs so that some jumps are powered by direct muscle contractions acting on long levers (Burrows and Morris, 2003).

This paper examines the specialisations of froghopper hind legs that make possible their extraordinary jumping ability. It focuses on the structure and actions of the coxo-trochanteral joint of a hind leg, the rotation of which is the key action in generating rapid jumping movements (Burrows, 2006). It describes the structure and articulation of this joint, possible proprioceptors that monitor its movements and the lever arms of its depressor and levator muscles. It demonstrates how a novel locking mechanism between the femur and the coxa might enable the trochanteral depressor muscle to contract slowly without moving the leg and then suddenly release the rapid jumping movement.

### Materials and methods

Froghoppers *Aphrophora alni* (Fallén 1805), *Philaenus spumarius* (Linnaeus 1758) and *Cercopis vulnerata* Illiger were collected around Cambridge, UK. *Lepyronia coleoptrata* (Linnaeus 1758) were collected in the region of Nanus and near Ljubljana in Slovenia. All belong to the order Hemiptera, sub-order Auchenorrhyncha and to the superfamily Cercopoidea.

*Cercopis* belongs to the family Cercopidae, the others to the family Aphrophoridae.

The anatomy of the hind legs and metathorax was examined in live insects, in insects preserved in 50% glycerol, in 70% alcohol, after fixation in 5% buffered formaldehyde and subsequent storage in 70% alcohol, and when cleared by boiling in 5% potassium hydroxide. Drawings of the legs, joints and muscles were made with the aid of a drawing tube attached to a Leica MZ8 or MZ16 stereomicroscope. Photographs from these microscopes were made with Nikon D1 or Nikon DXM1200 digital cameras. Dried specimens were also mounted on specimen holders, sputter coated with gold and then examined in a Philips XL-30 Scanning Electron Microscope.

Sequential images of the movements of hind legs that underlie jumping, or imposed movements of the hind legs, were captured at rates of 500, 1000 or 2000 s<sup>-1</sup> with a high speed camera (Redlake Imaging, San Diego, CA, USA) and associated computer. Movements of a hind leg of a restrained *Aphrophora* or *Cercopis* were also recorded by gluing a small disc of reflective tape to a hind femur close to the femoro-tibial joint. A modified single lens reflex camera with a concentric light around the lens was focussed on the disc and the light reflected from it was captured by a photocell in the film plane of the camera (Hedwig, 2000).

## Results

### General structure of hind legs

The hind legs of different species of froghopper are 1.4–1.6 times longer than the front and middle legs but only 52–66% the length of the body (Burrows, 2006). They have a mass that is only 2% of the total body mass, largely because the main muscles powering a jump and controlling the movements of the trochantera are in the thorax (Burrows, 2007). The tibia of a hind leg is longer than the femur (Fig. 1). For example, in *Philaenus* it is 1.8±0.07 mm (mean ± s.e.m., *N*=34) and thus 64% longer than the femur (1.1±0.03 mm). In larger froghoppers this difference is accentuated so that in *Cercopis* a tibia is 81% longer than a femur and in *Aphrophora* it is 92% longer. A hind tibia in all species has two outwardly pointing spines and two semi-circular rows of smaller spines on its ventral surface close to the articulation with the tarsus. The two most proximal tarsal joints also have a ventral, semi-circular row of spines. These spines should increase traction as thrust is applied through the tibia and tarsus to the ground at take-off in a jump. The front and middle pairs of legs have no spines and have usually lost contact with the ground before take-off in a jump.

Further prominent differences between the hind and the other legs are in the structure of the coxa and the femur (Fig. 1). A hind, but not a front or middle coxa, has a prominent lateral extension, the lateral and anterior corner of which provides one of its two pivot points with the thorax. A ventral, ovoid protrusion also arises from this lateral region of the hind coxa and is visible from a ventral view when the trochanter is

depressed but covered by the femur when the leg is fully levated (Fig. 1). It is not present on the front or middle legs. The medial surfaces of the left and right hind coxae, but not those of the front and middle legs, are closely apposed and at these points of contact each has a field of microtrichia [a dense array of small protuberances (Gorb, 2004)] that engage with those of the other coxa.

A hind femur has a protrusion on its dorsal surface that is not present on the front or middle legs (Fig. 2A). As the trochanter levates fully, this protrusion rides over the coxal protrusion and engages with it so that in this cocked position (shown on the right in Fig. 1), the proximal femur is closely apposed to the coxa. The more distal parts of a hind leg, including the femoro-tibial joint, then lie between the thorax and a middle leg.

#### *Angular movements of the leg joints*

The coxae of the two hind legs are closely apposed at their medial surfaces, in contrast to those of the front and middle legs that are widely separated, so that the mouthparts are interposed between them. A hind coxa can move about its articulation with the sternal region of the metathorax by some  $25^\circ$  in a plane that allows the whole hind leg to be rotated forwards and downwards, or backwards and upwards, in a plane nearly parallel to the long axis of the body (Fig. 2A). When viewed ventrally (see drawing in Fig. 1, Fig. 3 and scanning electron micrographs in Figs 7–9), one pivot of this thoraco-coxal joint is seen to be at the anterior, ventral edge of the lateral coxa and the second at the anterior, medial edge of the coxa. Movements of the trochantin, a sclerite embedded in the flexible cuticle

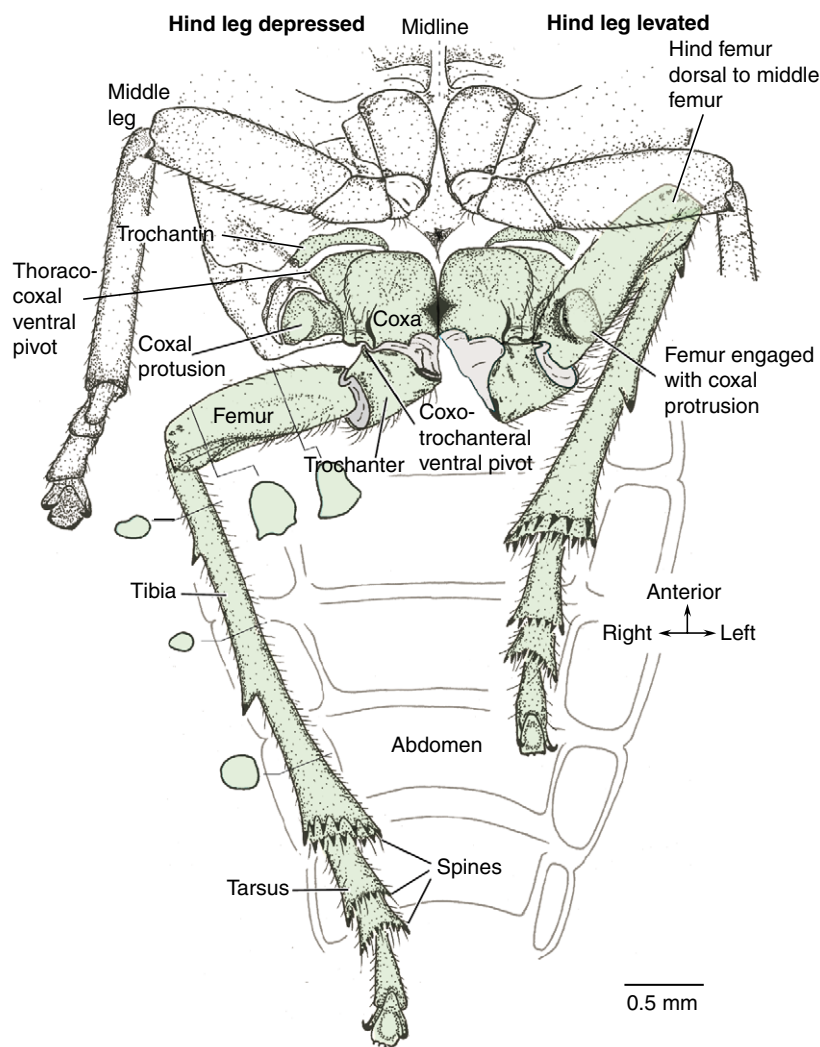


Fig. 1. Drawing of a ventral view of *Aphrophora* to show the specialisations of the hind legs (green). The left hind leg is shown with the trochanter fully levated (cocked) about the coxa so that the femur is engaged with the coxal protrusion and the femoro-tibial joint is dorsal to the left middle leg but ventral to the thorax. The right leg is shown with the trochanter partly depressed about the coxa so that the coxal protrusion is exposed. Cross sections through the right femur and tibia show the profiles at five levels. The medial surfaces of both hind coxae are closely apposed. The tibia of a hind but not a middle leg has two ventral rows of spines at its joint with the tarsus and the two proximal segments of a hind tarsus have a single row of spines at their articulation with the next segment.

linking the coxa anteriorly with the thorax (Fig. 1) have not been analysed.

The pivots of the coxo-trochanteral joint are, by contrast, dorsal and ventral so that the trochanter is depressed or levated in a horizontal plane through angles of 75–100° (Fig. 2C). The ventral pivot is at the lateral edge of the main part of the coxa

and close to the lateral edge of the trochanter, whilst the dorsal pivot is more medial.

The femur is not fused to the trochanter and can rotate about it through some 30° (Fig. 2B). The dorsal and ventral pivots are both lateral so that the plane of movement is similar to that of the trochanter. The tibia can flex or extend through some

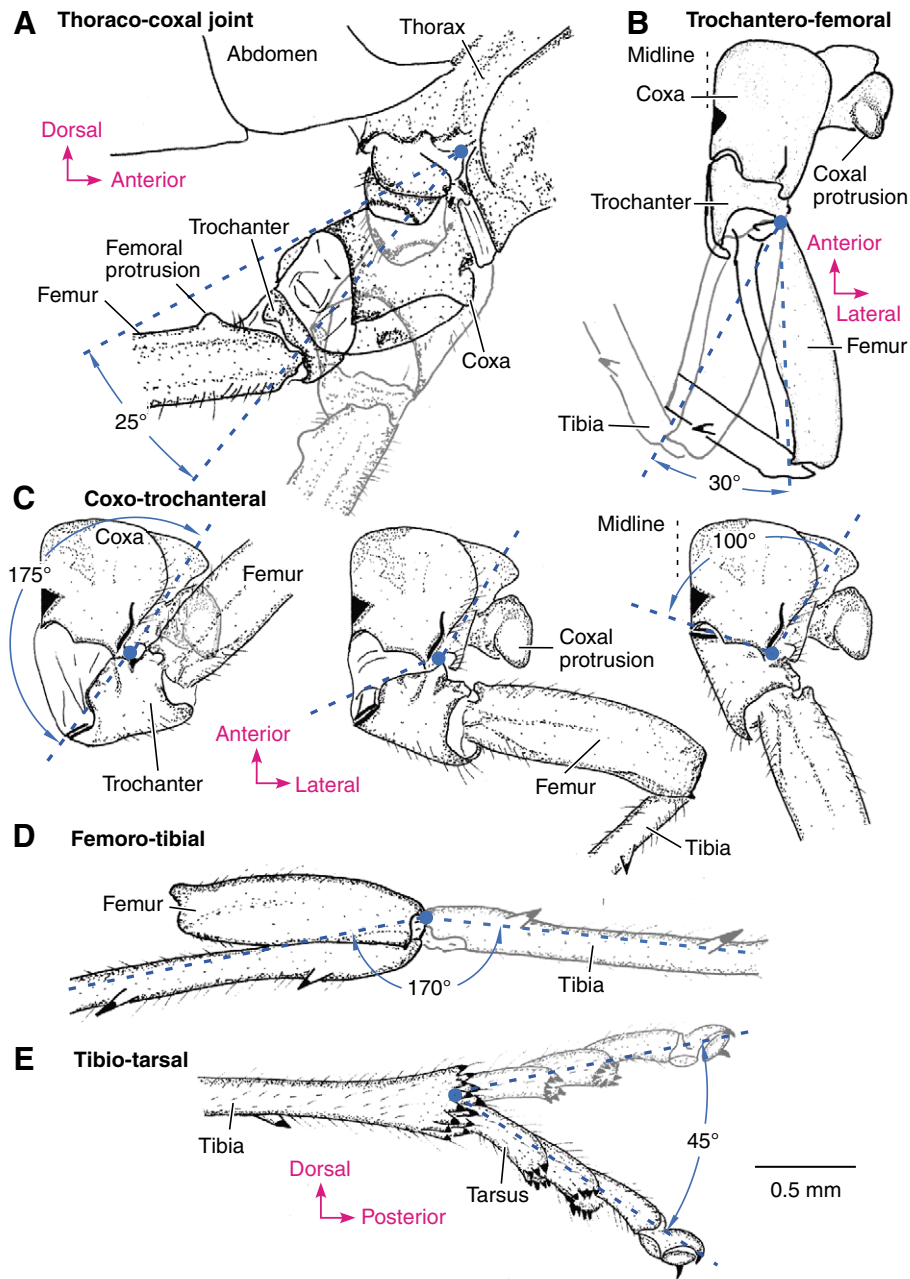


Fig. 2. Angular movements possible at the five joints of a hind leg in *Aphrophora*. The pivot of each joint is indicated by a blue dot, and the broken lines indicate the positions of same parts of the joints in their different positions. In A,B,D,E one extreme position is shown in grey, the other in black. (A) The thoraco-coxal joint viewed laterally. The coxa can rotate by some 25° about the thorax. In this diagram the femur has also moved about the trochanter. (B–E) Ventral views. (B) The femur can rotate by some 30° about the trochanter. (C) Three positions of the coxo-trochanteral joint: almost fully levated, mid position, and almost fully depressed. The trochanter can levate and depress by some 75–100° about the coxa. (D) The tibia can flex and extend by some 170° about the femur. (E) The tarsus can levate and depress by some 45° about the tibia.

170° about the femur, again in much the same plane, and the tarsus can levate and depress through some 45° about the tibia (Fig. 2D,E). Thus the segments distal to the coxa move in the same plane that is determined by the rotation of the coxa about the thorax. Thrust applied by depression of the trochanter will

thus be applied in the same plane through all of the more distal joints of a hind leg.

#### *Movements of the joints during a jump*

To resolve the detailed movements of the proximal joints of

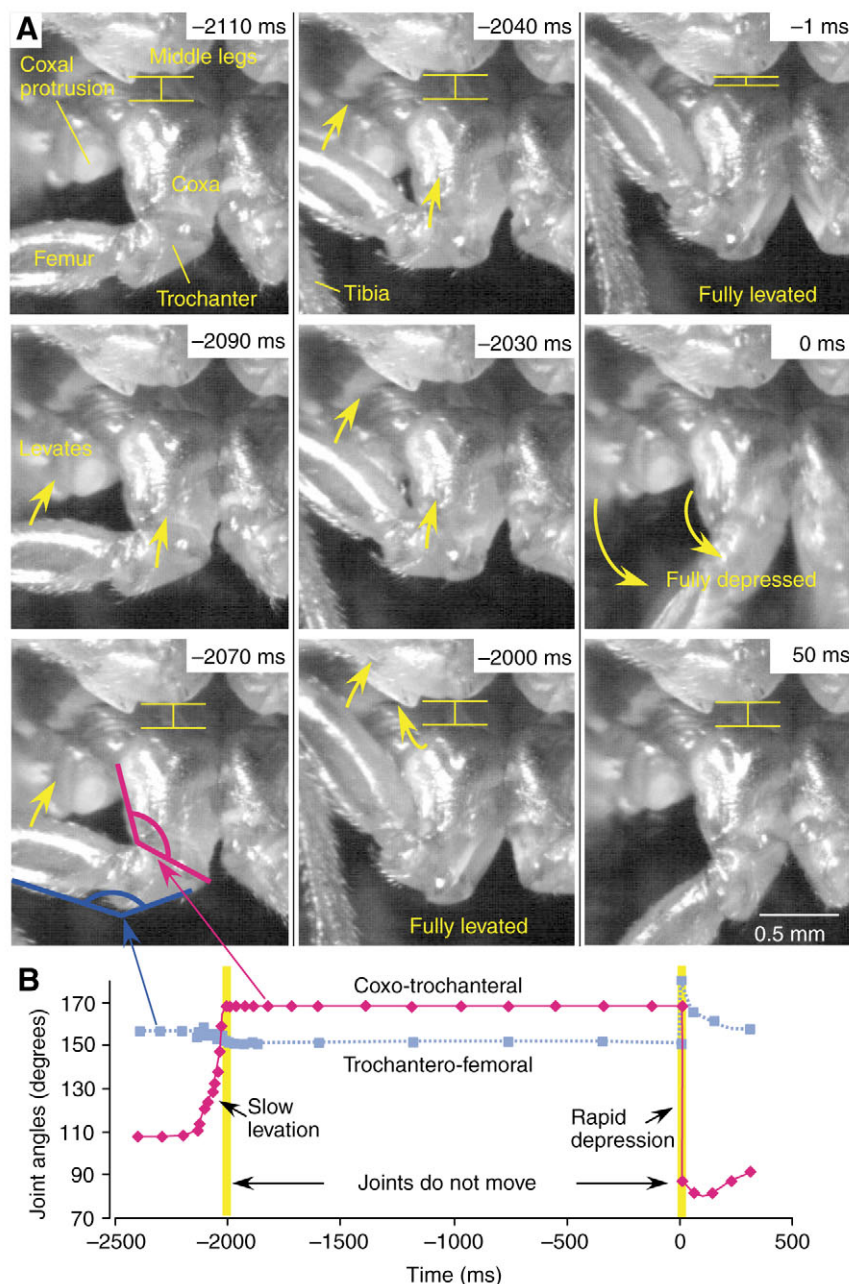


Fig. 3. Attempted jump by a restrained *Aphrophora* viewed ventrally. All the legs are free to move but make no contact with any substrate. (A) Images captured at 1000 s<sup>-1</sup> and with an exposure time of 0.5 ms, are arranged in three columns. Between frames -2110 and -2000 ms, the right hind leg is gradually swung anteriorly by a levation of the trochanter about the coxa. The femur now obscures the lateral protrusion of the coxa. The leg remains in this levated and cocked position for 2 s with no changes in the angles of coxo-trochanteral joint or other more distal joints. Toward the end of this period (between frames -2000 and -1 ms), the coxa moves forward about the thorax, indicated by the reduction in distance between its anterior edge and the posterior edge of the coxa of a middle leg (yellow horizontal lines). The joint between the trochanter and the coxa then depresses rapidly so that within 1 ms the whole leg has been extended (frames -1 ms and 0 ms). (B) Plot of the angular changes of the coxo-trochanteral and trochantero-femoral joints of the hind leg during the whole sequence. The vertical yellow bars indicate when the hind legs achieved their fully cocked position (left) and when the jump occurred (right).

the hind legs during jumping, *Aphrophora* were fixed ventral surface uppermost in Plasticene™ in such a way that all the legs were free to move. Very rapid and simultaneous movements of both hind legs occasionally occurred spontaneously or could be evoked by gentle tickling hairs on the abdomen with a fine paintbrush. No differences in the form, sequence, or timing of the movements of the two hind legs could be discerned in images of these sequences compared with those in free jumping (Burrows, 2006; Burrows, 2007). The sequence of movements of an individual hind leg could be resolved into the following sequence of actions (Fig. 3).

First, there was a slow levation of the trochanter about the coxa and a smaller decrease in the angle of the femur about the trochanter, accompanied by a flexion of the tibia about the femur. These changes moved the femur anteriorly so that it passed ventral to a lateral protrusion on the coxa, with which it then engaged, and medially so that it was pressed against the lateral edge of the coxa (Fig. 3A,B). This cocking movement of a hind leg lasted some 110 ms in the example shown, but in different attempted jumps by *Aphrophora*, the

mean time taken was  $187.3 \pm 8.9$  ms, range 88–353 ms, median 183 ms,  $N=45$  (Burrows, 2007).

Second, the hind legs remained in this cocked position without moving for a period of 2 s in this example, though again this period was variable in different attempted jumps by *Aphrophora* (mean  $2.9 \pm 0.16$  s,  $N=160$ ) (Burrows, 2007). Compression of the ventral thorax during this period meant that the hind legs moved anteriorly and thus closer to the middle legs, thereby pressing the trochantin against the flexible membrane of the metathorax and against the middle legs (see pairs of horizontal lines in Fig. 3A).

Third, after this long period with no visible movements of the leg joints, both hind legs depressed and extended completely in 1 ms (Fig. 3A,B). The main movement of each hind leg was a rapid depression of the trochanter about the stable coxa, accompanied by a small increase in the trochantero-femoral angle that may have resulted from the centrifugal forces generated by the rapid depression of the coxo-trochanteral joint. The structure of this joint was therefore examined in detail.

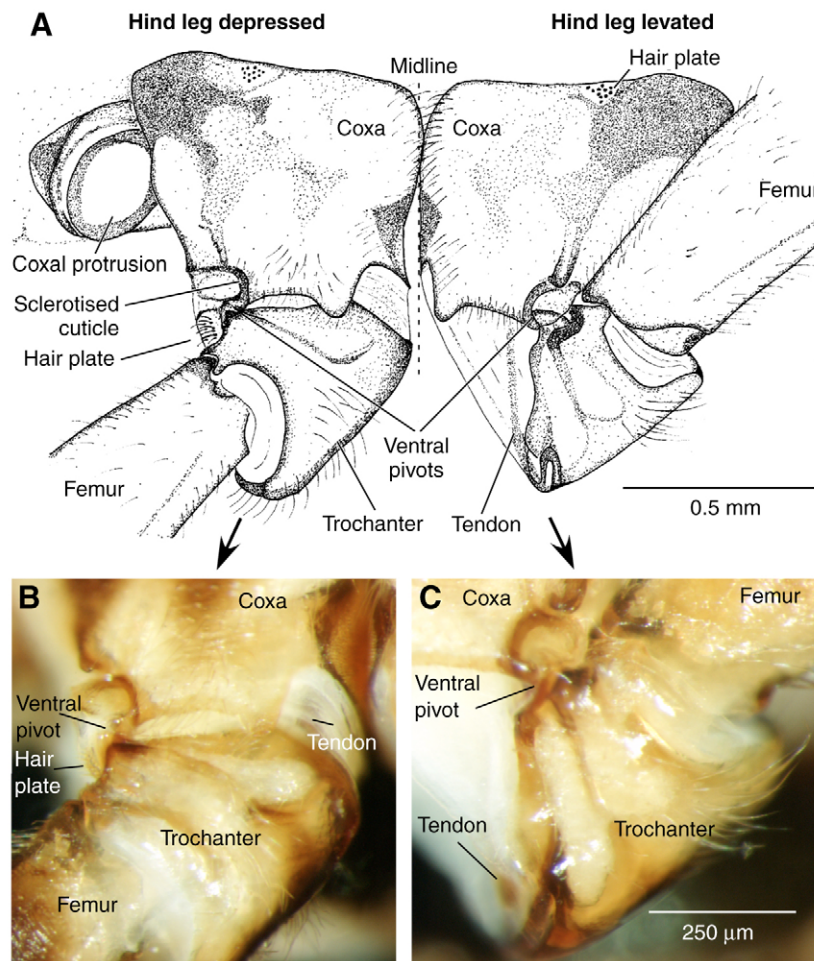


Fig. 4. Drawings and photographs of the structure and articulation of the trochanter and coxa of *Lepyrionia* viewed ventrally. (A) Drawing showing the left trochanter fully levated and the right trochanter almost fully depressed. (B,C) Photographs with the joints in the same positions as in the drawings.

*Structure of the coxo-trochanteral joint*

The cuticle of the coxa and the trochanter close to their pivots is heavily sclerotised and appears black (Fig. 4A–C). A strip of ventral coxal cuticle extending anteriorly from the ventral pivot is also strengthened and sclerotised (Fig. 4A,C). In the dorsal coxa, two struts run medially and laterally from the dorsal pivot to form a V-shaped internal scaffold (Fig. 5B–E). The ventral and dorsal pivots each consist of a

curved medially pointing horn of cuticle extending anteriorly from the trochanter that each engage in an indentation of the coxa (Fig. 4A,C; Fig. 5B–D). As the trochanter depresses about these pivots, its ventral anterior edge moves dorsal to a posterior projection of the coxa until at full depression the medial and anterior edge of the trochanter abuts against the medial and posterior edges of the coxa (Fig. 4A,B; Fig. 5A,C). The tendon of the trochanteral depressor muscle inserts on the

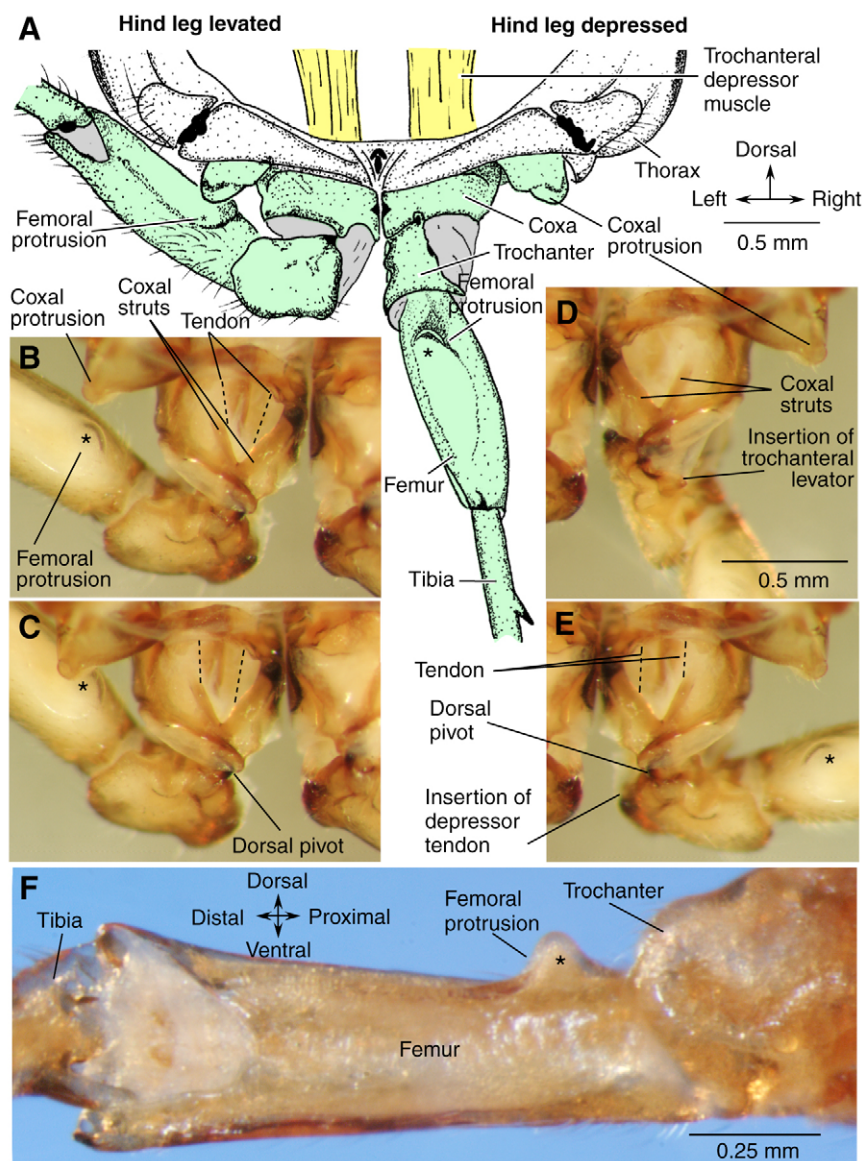


Fig. 5. The articulation of the trochanter and coxa in *Aphrophora* viewed dorsally and posteriorly. (A) Drawing to show the trochanter of the right leg fully depressed and that of the left leg fully levated. A protrusion on the dorsal surface of the femur (asterisk) engages with the lateral protrusion of the coxa when the leg is fully levated. The trochanteral depressor muscle within the thorax is shown. Cuticular parts of the hind leg are coloured green. (B) Photograph to show the trochanter almost fully levated. The tendon of the trochanteral depressor muscle can be seen where the dorsal cuticle of the coxa has been removed; the broken lines show its full width. (C) The trochanter is fully levated so that the femoral protrusion is engaged with the coxal protrusion. (D) The trochanter is fully depressed about the coxa. (E) The trochanter is approximately in the middle of its range of movements. These photographs also show the insertion of a trochanteral levator muscle on a lateral cuticular protrusion of the trochanter and the insertion of the trochanteral depressor on heavily sclerotised medial cuticle of the trochanter. Cuticular reinforcing struts in the coxa extend anteriorly from the coxo-trochanteral pivot. Between these struts the tendon of the trochanteral depressor muscle is visible. (F) Photograph from a medial aspect to show the prominent femoral protrusion at the proximal end of the femur.

thickened and sclerotised medial rim of the trochanter, with the area of sclerotisation wrapping around both the ventral and dorsal surfaces of the trochanter (Fig. 4A–C). In contrast to the extensive area of insertion of the depressor tendon, the trochanteral levator muscles insert on two small lateral protrusions of the trochanter, one dorsal (Fig. 5D) and the other ventral, which are again both sclerotised.

#### Lever ratios

The lever ratios of the trochanteral depressor and levator muscles were determined from individual frames captured at rates of  $1000\text{ s}^{-1}$  as a hind leg moved naturally, or when forcibly moved over its entire angular range. When viewed ventrally (Figs 1, 4) the line of action of the depressor tendon always appears to have a positive mechanical advantage, even when the joint was in its most levated position. It does not appear to go over the centre of the pivot in this cocked position, and because the pivot is so lateral there would be little room for it to move into such a position within the coxa. Images of the joint movement were also captured from a posterior perspective, enabling both pivots to be seen at the same time (Fig. 6A–C). In the most levated (cocked) position, the insertion of the depressor tendon is medial to the pivot and the line of action of the tendon positive. As the coxo–trochanteral joint depressed the distance between the insertion of the tendon and the line of the pivot increased. Plotting the lever arm of the depressor muscle showed that it was smallest at the most

levated position (Fig. 6D). For the first  $10^\circ$  of depression movement the lever arm remained the same, but then increased rapidly to a maximum after some  $80^\circ$  of movement and remained at this value during further depression of the joint. By contrast, the lever arm of the levator tendon was similar over the full range of joint movement. The lever arm of the depressor exceeded that of the levator after  $40^\circ$  of depression.

#### Proprioceptors

Scanning electron micrographs of the trochantin, coxa and trochanter revealed three prominent arrays of hairs that would appear to act as proprioceptors signalling the movements of one segment of a hind leg relative to another (Fig. 7). The movements that all three are likely to signal are those that occur in preparation for jumping. Other leg movements that have been observed would not be likely to stimulate them.

First, a hair row on the trochantin consists of some 15 hairs (trichoid sensilla),  $15\text{--}50\text{ }\mu\text{m}$  long, which are stouter than those distributed more widely over the legs and body (Fig. 7A,B). They would be stimulated when the trochantin either touches the flexible membrane linking it to the mesothorax, or the middle legs. Such a movement occurs during the compression of the thorax when the hind legs are held in their cocked positions in preparation for a jump.

Second, on the anterior, ventral surface of the coxa is an approximately circular hair plate, the coxo–trochantinal hair plate, consisting of some 13 hairs (trichoid sensilla), ranging

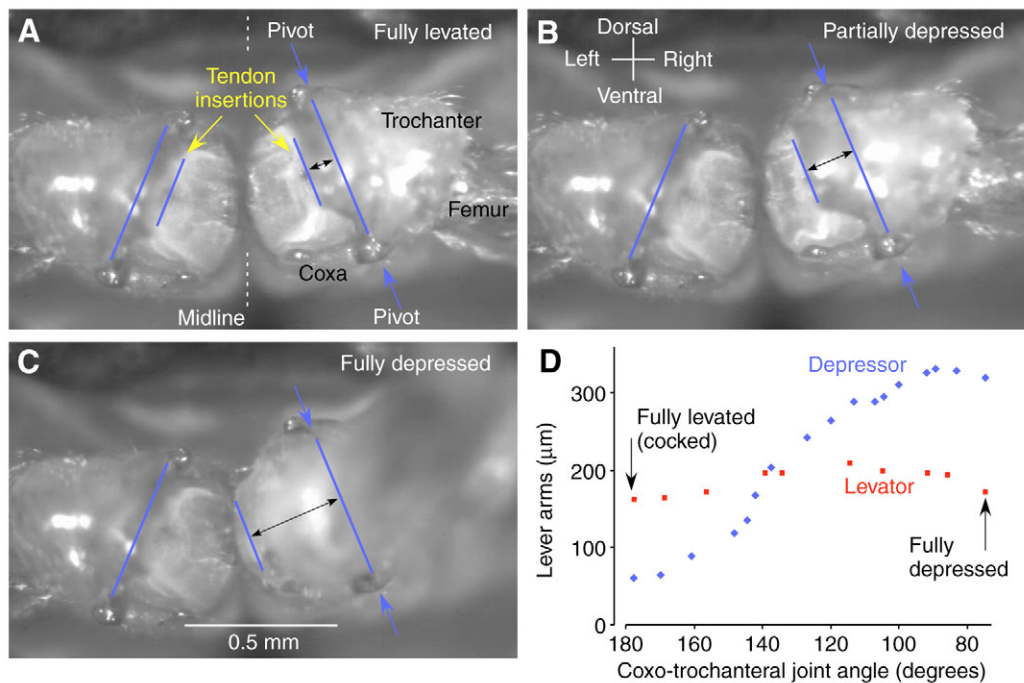


Fig. 6. Movements of the hind coxo-trochanteral joints of *Aphrophora* viewed posteriorly. The joint was moved from the fully levated position (A) through a partially depressed position (B) to the fully depressed position (C). Both the ventral and dorsal pivots of the joint are indicated by the blue arrows and are joined by the blue lines. The shorter blue lines indicate the insertions of the trochanteral depressor muscles. (D) Plot of the effective lever arms of the trochanteral levator and depressor muscles expressed as perpendicular distances between their insertion points and the axis of the pivot of the coxo-trochanteral joint over the full angular range of coxo-trochanteral joint movements.

from 8–15  $\mu\text{m}$  in length (Fig. 7A,C). These hairs could signal contact of the coxa with the trochantin during movements that precede the sudden depression of the trochanter in a jump.

Third, on the lateral edge of the trochanter is a hair plate consisting of two rows of regularly spaced hairs, ranging in length from 5–10  $\mu\text{m}$  (Fig. 7D). This hair plate could signal the initial contact of the trochanter with the lateral, distal edge of the coxa when it is levated into its fully cocked position, and the continuing contact while it is held cocked before a jump.

#### *Cocking of the hind legs*

In the fully levated position, the femur of a hind leg moves ventral to the lateral, ventral protrusion of the coxa so that it is closely engaged with it (Figs 1, 3). The detailed structure of this region of engagement was therefore examined in the scanning electron microscope from a ventral perspective for the coxa (Fig. 8A–D) and from a dorsal perspective for the femur (Fig. 9A–D).

#### *Coxal protrusion*

Micrographs show clearly that the oval, domed-shaped

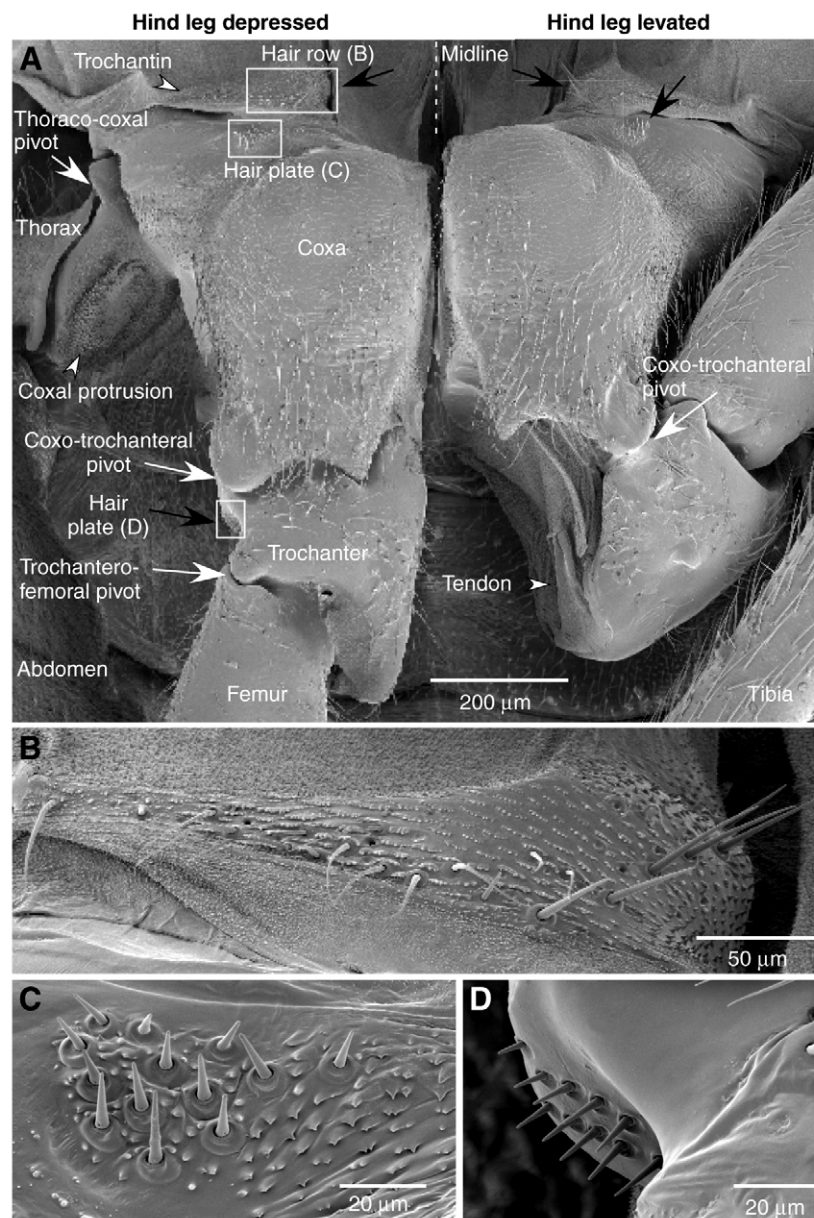


Fig. 7. Scanning electron micrographs of the proximal hind leg joints of *Philaenus* viewed ventrally. (A) The trochanter of the left hind leg is almost fully levated about the coxa and the right trochanter is fully depressed. The large white arrows indicate the pivot points of the proximal leg joints and the black arrows three prominent arrays of proprioceptive hairs. (B) Hair row on the right trochantin; midline is to the right. (C) The right coxo-trochanteral hair plate. (D) The right trochanteral hair plate.

lateral protrusion is part of the coxa, and that in contrast to the surrounding cuticle of the coxa, it is covered in a dense array of small protrusions called microtrichia (Fig. 8B–D). They are similar in appearance to those on the apposed, medial surfaces of the coxae (Gorb, 2004). Over most of a coxal protrusion the microtrichia are 5–8  $\mu\text{m}$  high, 3–6  $\mu\text{m}$  wide and are separated by intervals of 1–2  $\mu\text{m}$ . The size decreases with distance from the peak of the protrusion and the spacing between them increases so that they taper into the smooth cuticle of the rest of the coxa. The microtrichia on the dome of the protrusion point anteriorly. In many coxae examined in fixed insects, the dome of the protrusion was dimpled and the microtrichia there appeared flattened (Fig. 8C). In live insects, the cuticle on the dome is soft and can easily be dimpled by slight external pressure, indicating that its appearance in the micrographs most

likely results from the collapse of the underlying, flexible membrane.

#### *Femoral protrusion*

On the dorsal surface of a femur at its proximal end is a prominent protrusion with its highest point at the anterior edge (Fig. 5A,B,F; Fig. 9A,B). It protrudes by 130  $\mu\text{m}$  from the dorsal surface of the femur at a point where the dorso-ventral depth of the femur is 220  $\mu\text{m}$  (Fig. 5F). It tapers steeply on its distal side but more gradually toward the proximal end of the femur. This protrusion is again covered in an array of microtrichia which are somewhat shorter at 4–6  $\mu\text{m}$  high, and broader at 5–7  $\mu\text{m}$  wide and more widely spaced at 2–3  $\mu\text{m}$  than those on the coxal protrusion. The size of the microtrichia decreases and their spacing increases with distance from the

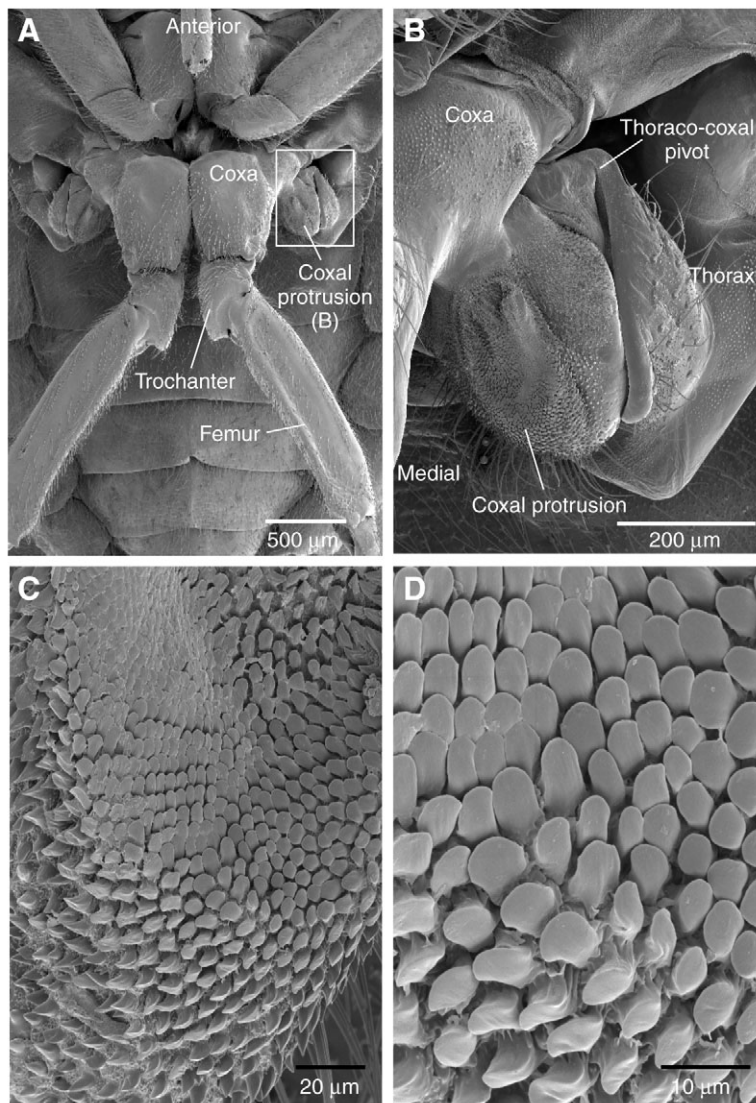


Fig. 8. Scanning electron micrographs of the lateral protrusions on the hind leg coxae viewed ventrally. (A) The trochanters of both hind legs are fully depressed to reveal the coxae. (B) Higher magnification to show the articulation of the coxa with the thorax and the coxal protrusion (boxed area in A) arising laterally. (C) The coxal protrusion is covered in swirls of microtrichia. (D) Higher power view of the microtrichia.

slope of the protrusion so that they taper into the smooth cuticle of the surrounding femur. On the protrusion, the microtrichia are oriented posteriorly and somewhat medially.

For a hind leg to move into its most levated (cocked) position, the protrusion on the dorsal femur must ride over the coxal protrusion and engage in front of it. This will bring the two surfaces bearing microtrichia into direct contact with each other and the orientation of the microtrichia on these two surfaces should ensure that many will interlock. Furthermore, the flexible dome on the coxal protrusion should allow it to fit snugly into the shape of the femoral protrusion so that the two sets of microtrichia are fully apposed or engaged. The increased surface area provided by the microtrichia, the interlocking between them and the engagement of the femoral protrusion in front of the coxal protrusion together provide an impediment,

or an increased area of friction, to the depression of the leg. To allow the femur to be extended in a jump, these two surfaces must disengage and the femoral protrusion must ride over the coxal protrusion. The hind leg could be held in its cocked position by this mechanism and allowed to move suddenly only when sufficient depression force was generated.

#### Larvae

The larvae, which live in the protected environment afforded by their secretion of a froth or 'cuckoo spit', have a small coxal protrusion that is smooth and entirely devoid of microtrichia (Fig. 10A). The dorsal surface of the proximal part of a hind femur has no protrusion and no microtrichia (Fig. 10B). The larvae do not jump and if they do emerge from their froth, they walk to another feeding site. The femoral and coxal

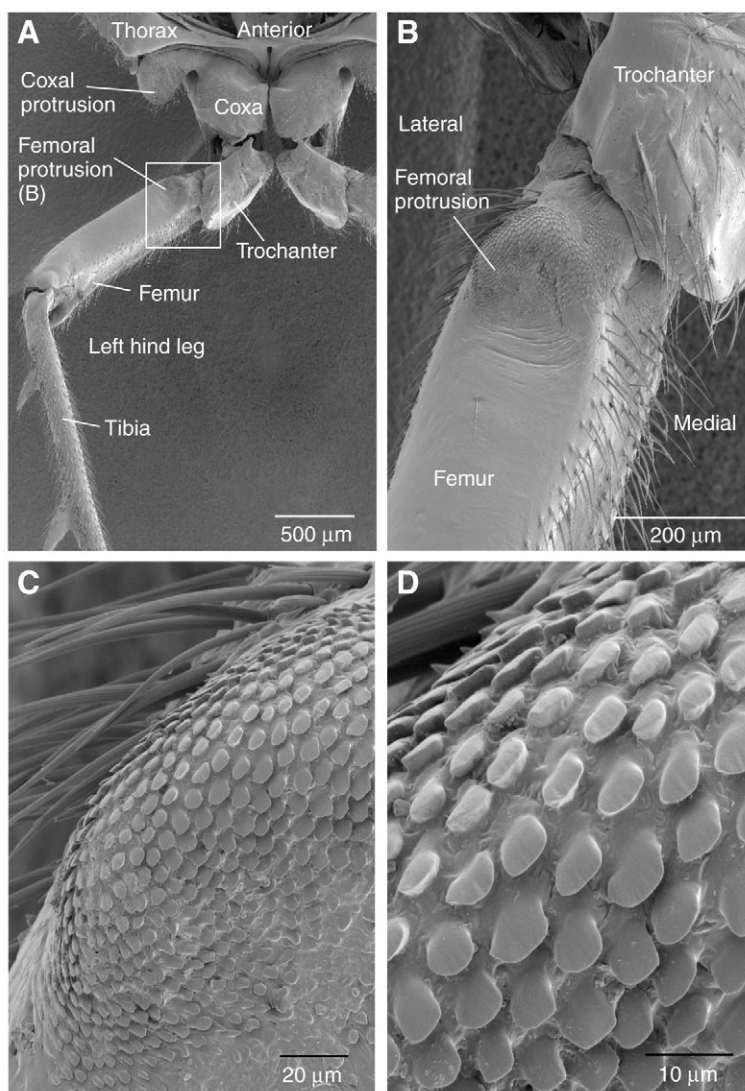


Fig. 9. Scanning electron micrographs of the femoral protrusion of a left hind leg viewed dorsally. The different parts of this figure are shown at the same magnification as comparable parts of Fig. 8. (A) The trochanters of both hind legs are partially depressed and reveal the femoral protrusion and the coxal protrusion on the left hind leg. (B) Higher magnification of the femoral protrusion (boxed in A) shows that it is covered in microtrichia whereas the surrounding cuticle is smooth. (C) Microtrichia cover the femoral protrusion and closely spaced hairs are present anteriorly. (D) Higher power view of the microtrichia on the femoral protrusion.

protrusions, and their associated microtrichia, appear only after the final moult. Within a few minutes of emergence from its froth, an adult is able to jump.

#### *Depression movements in two stages*

The stages in the movement of a hind leg that allow its release from its fully levated position was analysed in froghoppers that had recently died (Fig. 11). In such insects, a hind leg can be forcibly rotated forwards so that the trochanter is fully levated about the coxa and the femur engaged with the coxal protrusion. The leg will then lock into and remain in its cocked position solely because of the mechanical construction of the leg and in the absence of any active muscular contraction. Sometimes the leg will then spontaneously and rapidly depress, or can be induced to do so by applying a backwards force to the femur or the tibia. During a spontaneous movement from the cocked position, the coxo-trochanteral joint depressed and the femur moved backwards to expose the coxal protrusion to view (Fig. 11A). The movement of the hind leg was rapid and was completed in 2 ms even though it was not powered by any muscular contraction. When powered by muscular contractions, the jump movement in equivalent circumstances (when not bearing the weight of the body) is complete in 0.3 ms (see Fig. 12C) (Burrows, 2006a). The rapidity of the movement in a dead insect, suggests that the forced levation stretched tendons and muscle fibres and elastic force was stored in these structures, or in associated deformations of the cuticle, which was then released suddenly to provide the propulsive power.

In a movement triggered by the application of external force to the distal end of the femur, the unlocking of the leg that must occur before a rapid jump movement could be resolved into two steps (Fig. 11B). The first movement was a small depression of the coxo-trochanteral joint that was then followed by the femoral protrusion disengaging from the coxal protrusion. Only then were the femur and the more distal segments of the leg able to move, demonstrating the contribution of the engagement between the femur and the coxa

to the cocking of the hind leg, and its subsequent disengagement to the rapid jumping movement.

#### *Sound association with rapid leg movements*

When froghoppers performed an unrestrained jump, a consistent click could be heard and recorded by a microphone placed at the point of take-off (Fig. 12A). The sound occurred during take-off. When a froghopper was restrained on its back in Plasticene and encouraged by gentle tickling to produce the rapid, simultaneous movements of its hind legs that underlie jumping, they were again accompanied by a click sound (Fig. 12B). In this experimental arrangement, the hind legs made no contact with the substrate or with any other object, so that the sound must have resulted from the rapid movements of the hind legs themselves. When images of the movement were captured at  $1000\text{ s}^{-1}$ , the sound could be correlated to the 1 ms period when the legs moved from their cocked to their fully depressed position. To provide greater time resolution, a disc of reflective tape was fixed to the distal femur enabling changes in the angle between the coxa and femur to be detected (Fig. 12C). Allowing for the conduction of the sound to a microphone 5 mm away, the sound must have occurred just 0.035 ms after the movement started and full depression of the hind leg was completed in 0.3 ms. The sound must therefore result from events at the very start of the rapid depression movement, such as the initial movement of the coxo-trochanteral joint, or the disengagement of microtrichia on the coxal and femoral protrusions.

### Discussion

#### *Movements of the hind legs in jumping*

Rapid and simultaneous movements of the hind legs propel jumping in froghoppers. High speed images of the jumping movements (Burrows, 2006) and the detailed anatomy presented here suggest that the following sequence of movements underlie jumping. First, the hind legs are levated slowly into their cocked positions and the femoral protrusions

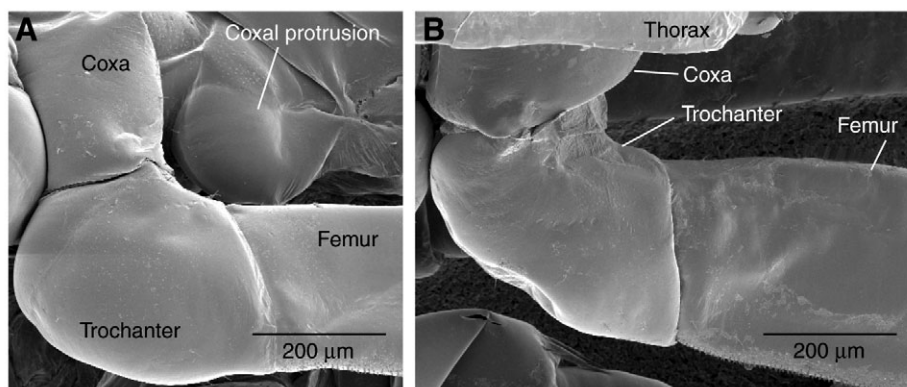


Fig. 10. Larval *Philaenus* lack microtrichia on the coxal protrusions and proximal femora of their hind legs. (A) The cuticle of the left coxal protrusion is smooth and has no microtrichia as viewed ventrally. (B) The right femur viewed dorsally has no protrusion at its proximal end and microtrichia are absent.

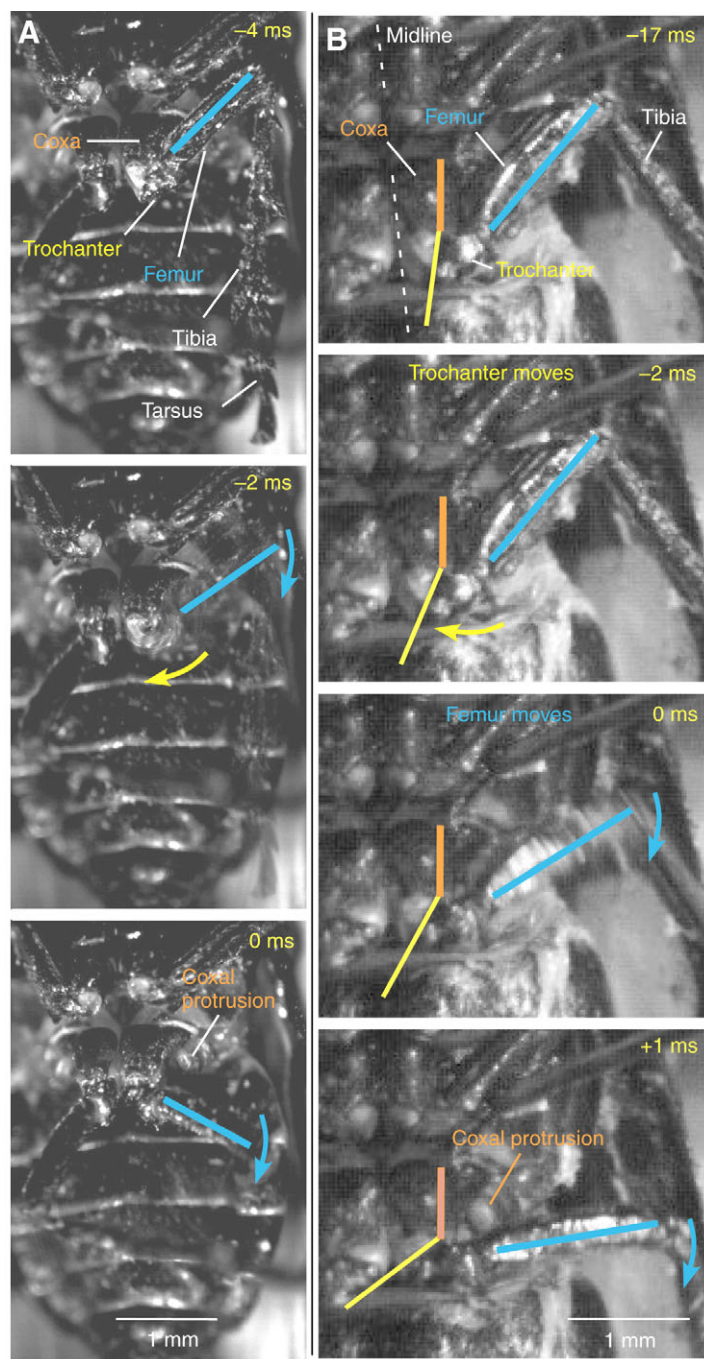


Fig. 11. Depression movements of a hind leg in dead *Cercopis*. (A) Ventral view in which the left hind was forcibly moved into the cocked position so that the coxo-trochanteral joint was fully levated and the femoral protrusion engaged with the coxal protrusion. The leg then spontaneously depressed with the whole movement being completed in 2 ms. Note the rotation of the trochanter about the femur (yellow arrow) and the movement of the femur (blue line and arrow). (B) Two stage depression of the left hind leg in a second *Cercopis*. Ventral view. The first image (–17 ms) shows the leg in the fully levated position. The tibia was pushed posteriorly and the coxo-trochanteral joint depressed partially (image –2 ms) while the femur stayed in the same position. At 0 ms the femur moved and was accompanied by a further depression of the coxo-trochanteral joint. In the final image (+1 ms) the continuing movement of the femur exposed the coxal protrusion. Images were captured at  $500\text{ s}^{-1}$  in A and at  $1000\text{ s}^{-1}$  in B.

engage with their respective coxal protrusions. Second, the hind legs remain stationary for seconds in their cocked position, but the thoracic cuticle is deformed and may act as an energy store (Rothschild et al., 1975; Sander, 1957). Third, both hind legs move rapidly by a depression of their coxo-trochanteral joints at angular velocities of  $75\text{--}500\text{ deg. s}^{-1}$  and an extension of their tibiae about the femora. These movements are completed in less than 1 ms or 100 times faster than the initial cocking movements, while accelerating the load of the body. For a hind leg to move rapidly from its cocked position, the coxal and femoral protrusions must disengage. A prominent click sound is generated by the early events associated with the rapid depression and extension movements.

#### *Design of the hind legs for jumping*

The differences in the design of the hind legs of froghoppers and their other two pairs of legs appear to relate to this key role in jumping. The hind legs, however, are short relative to the body, ranging from only 52–66% of body length, and relative to the other legs they are only 1.4–1.6 times longer due entirely to a longer tibia (Burrows, 2006). This contrasts with the hind legs of locusts and bush crickets, which are much longer relative to body length. The hind legs of froghoppers are also light, with their mass representing only a small (2%) proportion of body mass, contrasting again with locusts where the proportion is 14% (Bennet-Clark, 1975). In froghoppers, the low mass of the hind legs results from the location of the main power producing muscles (the trochanteral depressors) in the thorax. This is the same as in fleas (Bennet-Clark and Lucey, 1967; Rothschild and Schlein, 1975), but contrasts with locusts where the power-producing extensor tibiae muscles are in the femur.

The specialisations of the hind legs critical for jumping lie in the detailed structure of particular joints, the improved traction provided by the tibio-tarsal and tarsal joints, strategically placed proprioceptors to monitor the large forces, the presence of a mechanism for locking the femur against the coxa when the leg is cocked in readiness for jumping, and in the lever arrangements of the muscles in the thorax that move the trochanter. All of these features are unique to the hind legs and most are not present in the larvae that have restricted lives underground, or above ground in a protective froth.

#### *Mechanisms for increasing traction*

The sudden and powerful application of thrust by the hind legs requires good traction if the force is to be applied effectively to the ground. If both legs slip then only a very weak jump occurs and if one leg slips the body skews to one side at take-off. Traction is improved by arrays of small spines at the ventral surface of the articulation of the tibia with the tarsus and at the proximal two tarsal joints. The first movement of a hind leg before take-off results in the tarsus being pushed flat to the ground so that the spines

engage with the substrate (Burrows, 2006). These arrays of spines are not present on the front and middle legs, and nymphs of *Philaenus* that do not jump lack prominent arrays of spines on the hind tarsi.

### Proprioceptors

Three external proprioceptors would appear to signal critical aspects in the preparation for a jump and the consequences of the very large forces that are generated. It is likely that more internal proprioceptors and campaniform sensilla exist. First, the prominent hair row on a trochantin is

likely to signal movements of a coxa and trochantin as they move forwards due to the contractions of the trochanteral depressor muscle. Second, the hair plate on the medial edge of the coxa could provide additional information about the contraction of the trochanteral depressor muscle by signalling contact with the trochantin during preparation for a jump. Third, the hair plate on the lateral trochanter consists of two rows of stout hairs that are stimulated as the trochanter is levated about the coxa. They could therefore signal the levation movement to the fully cocked position, and the maintenance of the trochanter in this position during

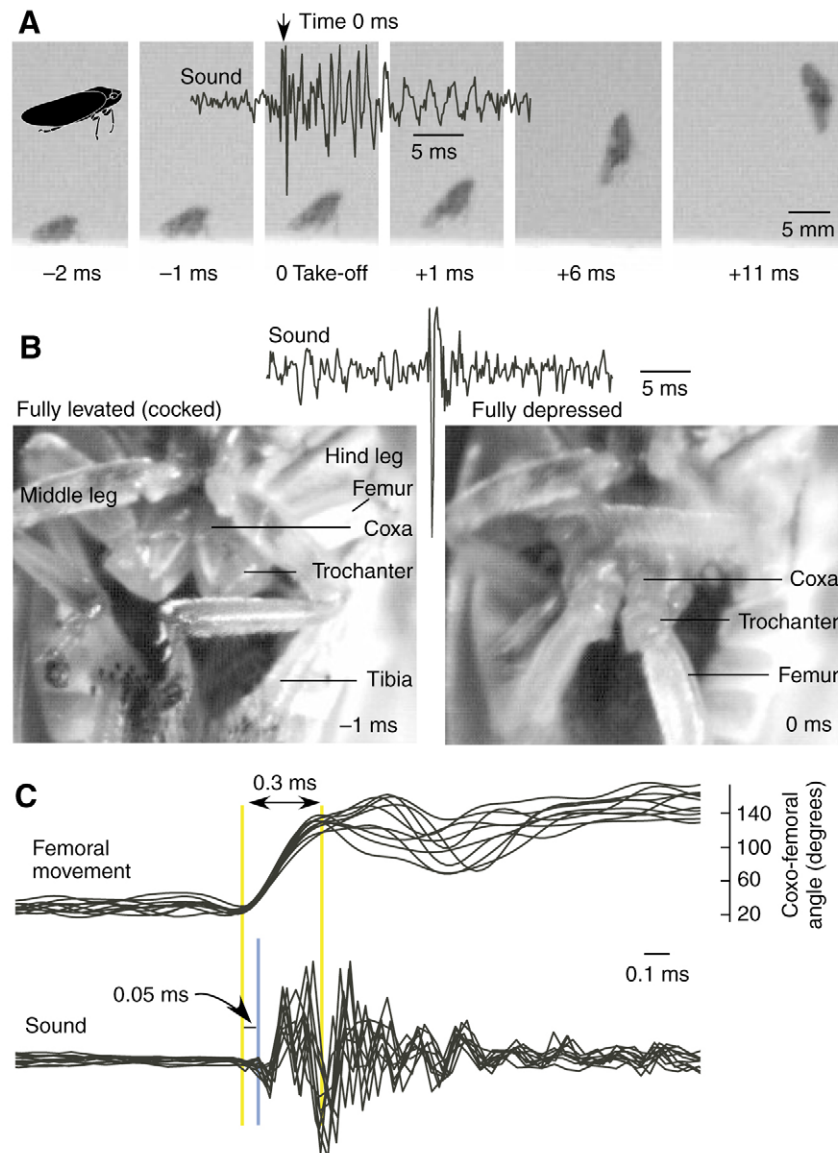


Fig. 12. An audible click occurs when froghoppers jump. (A) During a free jump, a click occurred at the time of take-off. Images were captured at  $1000\text{ s}^{-1}$ . A cartoon of a froghopper is shown in the first frame to clarify the images. (B) *Aphrophora* was fixed ventral surface uppermost in Plasticene<sup>TM</sup> and with a microphone 5 mm from the right hind leg. Movements of the hind legs were captured at  $1000\text{ s}^{-1}$ . The rapid simultaneous movement of both hind legs was accompanied by a click even though the hind legs did not contact anything during their movement. The left image of a ventral view shows the hind legs fully cocked and tucked between the overlying middle legs and the thorax. The right image shows both hind legs fully depressed 1 ms later. (C) Movements of a hind leg were recorded opto-electronically together with the sound, and 10 jump movements by one *Aphrophora* were superimposed. The first sound occurred only 0.05 ms after the start of the movement.

preparation for jumping. The movements that would stimulate the first two proprioceptors only occur when the leg is fully levated and the trochanteral depressor muscles are contracting without being able to move the leg from its cocked position. Their likely action is therefore limited to jumping. A full levation of the trochanter that stimulates the third proprioceptor is again only likely to occur if the legs are being cocked in readiness for jumping.

#### *Lever arms*

In preparation for a jump, the hind legs are moved into their most levated (cocked) position and remain in that position for seconds before they are rapidly depressed and extended in the movement that powers a jump. In this cocked position, the lever arm of a trochanteral depressor muscle is smallest and is exceeded by the lever arm of the levator. The tendon of a trochanteral depressor muscle inserts on the strengthened medial edge of the trochanter some 500  $\mu\text{m}$  from the joint pivot that is toward the lateral edge of the coxa. This arrangement means that even in the cocked position the trochanteral depressor tendon has a positive mechanical advantage and does not go over-centre. During depression, the lever arm of the depressor muscle increases rapidly to reach a maximum after some 80° of movement. After only 40° of movement, it exceeds the lever arm of the levator that changes little throughout the whole range of joint movement.

#### *Locking mechanisms*

To move into the cocked position, a sloping protrusion on the dorsal surface of a hind femur must ride over and engage with a lateral and ventral protrusion of a coxa. Once the femoral protrusion is anterior to the coxal protrusion, the hind leg is effectively cocked and poised to extend by a rapid depression of the trochanter and extension of the tibia. The effectiveness of this passive locking device has been demonstrated experimentally in dead froghoppers. Pushing a hind leg into its cocked position results in it locking under the passive forces of the engagement between the coxal and femoral protrusions, and a possible involvement of the coxo-trochanteral joint. If a force is now applied to a hind leg in the same direction as a depression movement, then resistance is encountered. When the applied force is sufficient to overcome this resistance, a hind leg will suddenly and rapidly extend in about 2 ms, indicating that the cocking movement had stored energy either by stretching muscles and tendons or distorting cuticular elements. Images captured at high speed indicate that the rapid movement occurs only when the femoral and coxal protrusions have disengaged.

The coxal and femoral protrusions are both covered by dense arrays of microtrichia. These increase the friction between two apposed surfaces, or those on one surface may interlock with those of the other, much in the manner of 'Velcro' fasteners. Microtrichia are often found in insects wherever two apposed surfaces must lock together under particular circumstances. For example, they are found at the articulation of the head with the prothorax in dragonflies and damselflies where they stabilise

the head particularly in flight; in some beetles they occur in patches on the thorax and on the wings to lock the wings to the thorax when not flying; in some Lepidoptera on the front and hind wings to ensure that they are locked together during flight (Gorb, 2001). In froghoppers, microtrichia also occur on the medial surfaces of the hind coxa where they have been interpreted to synchronise the coxae in jumping (Gorb, 2001; Gorb, 2004). I have shown that the critical synchrony in movements of the hind leg during jumping is between the rapid movements of the trochantera. The microtrichia on the two coxae are thus more likely to provide a stable base for these rapid movements than to contribute to the synchrony of the propulsive leg movements.

This elaborate locking mechanism between the femur and coxa is not found in other insects that jump by a rapid propulsive extension of their hind legs, but other locks do occur. No similar structure is described in fleas (Bennet-Clark and Lucey, 1967; Rothschild and Schlein, 1975), which jump by depression of the hind trochantera about the coxae, and in locusts, bush crickets and false stick insects, the propulsion comes from an extension of the tibiae about the femora. In froghoppers, a key role for these structures in jumping is emphasised by their occurrence only on the hind legs of adults. They are not present on the middle and front legs of adults, and in nymphs that do not jump they are also absent on the hind legs. A meracantha on the hind coxa engaging with a yellow spot on the proximal femur has been described on a hind leg of some Homopterans including froghoppers (Emeljanov, 1987) and a protrusion from the coxa has also been described on the hind legs of Lantern Flies (Homoptera, Fulgoridae) (Sander, 1957). Emeljanov suggests that these structures could act as a possible proprioceptor but provides no evidence. The meracantha may be the structure to which I have applied the purely descriptive term of coxal protrusion. I have not seen a yellow spot on the femur but perhaps it corresponds to the structure I have called the femoral protrusion. My experiments described here show that these structures provide a locking mechanism, but their engagement could also stimulate nearby hairs or other as yet undescribed sensory structures that could provide further proprioceptive information.

Further understanding of the mechanisms underlying the movements of the hind legs in jumping, requires that timings and sequences of the muscle actions be determined. This will be the subject of my next paper (Burrows, 2007).

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