Jumping mechanisms in jumping plant lice (Hemiptera, Sternorrhyncha, Psyllidae)

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With 9 Figures

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Summary

3 Jumping mechanisms and performance were analysed in three species of psyllids (Hemiptera,
4 Sternorrhyncha) that ranged from 2 to 4 mm in body length and from 0.7 to 2.8 mg in weight.
5 Jumping was propelled by rapid movements of the short hind legs that were only 10-20%
6 longer than the other legs and 61-77% of body length. Power was provided by large thoracic
7 muscles that depressed the trochantera so that the two hind legs moved in parallel planes on
8 either side of the body. These movements accelerated the body to take-off in 0.9 ms in the
9 smallest psyllid and 1.7 ms in the largest, but in all species imparted a rapid forward rotation
10 so that at take-off the head pointed downwards, subtending angles of about -60 degrees
11 relative to the ground. The front legs thus supported the body just before take-off and either
12 lost contact with the ground at the same time as, or even after the hind legs. In the best jumps
13 from the horizontal, take-off velocity reached 2.7 m s^{-1} and the trajectory was steep at 62 - 80
14 degrees. Once airborne the body spun rapidly at rates up to 336 Hz in the pitch plane. In
15 many jumps the wings did not open to provide stabilisation, but some jumps led directly to
16 sustained flight. In their best jumps the smallest species experienced a force of 637 *g*. The
17 largest species had an energy requirement of 13 µJ, a power output of 13 mW and exerted a
18 force of nearly 10 mN. In a rare jumping strategy seen in only 2 of 211 jumps analysed, the
19 femoro-tibial joints extended further and resulted in the head pointing upwards at take-off
20 and the spin rate being greatly reduced.

21

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Introduction

24

25 Jumping as a fast means of locomotion or escape is widespread amongst the four sub-orders
26 of Hemipteran insects, most of which move their hind legs in the same plane beneath the
27 body, while others including the subjects of this paper, the psyllids, move them along the
28 sides of the body. Jumping performance reaches its peak in the Auchenorrhyncha; the
29 froghopper (spittle bug) *Philaenus spumarius* and the planthopper *Issus coleoptratus* have the
30 best jumping performance of any insect described so far. They accelerate their bodies in less
31 than 1 ms to a take-off velocity of 4.7 and 5.5 m s^{-1}, experiencing a force of 550 and 720 *g*
32 respectively (Burrows, 2003; Burrows, 2006; Burrows, 2009a). This exceptional performance
33 is accomplished by a catapult mechanism. Large forces are developed by the slow contraction
34 of enormous thoracic muscles that store energy by bending paired bow-shaped elements of
35 the internal skeleton. These energy stores are built of a composite of hard cuticle and the soft
36 elastic protein resilin (Burrows et al., 2008). Sudden release of the stored energy then powers
37 the rapid and simultaneous depression of the hind legs (Burrows, 2007b).

38

39 In a second hemipteran sub-order, the basal Coleorrhyncha, at least one wingless species
40 jumps, but it shows few specialisations for jumping (Burrows et al., 2007). Its hind legs are
41 only 10% longer than the other legs and their rapid movements accelerate it in 1.5 ms to a
42 take-off velocity of 1.5 m s^{-1}. This insect experiences a force of 100 *g*, and once airborne
43 rotates about any of the three body axes.

44

45 A third sub-order, the Heteroptera, contains a wide diversity of bugs, but only two families
46 have species that are reported to jump, and only one of these, the Saldidae or shore bugs has
47 been investigated in detail (Burrows, 2009b). The hind legs of these bugs are 80% longer

1 than the other legs and in a quarter of all jumps are used as the sole means of accelerating the
2 body in 4 ms to a take-off velocity of 1.2 m s^{-1}. The majority of its jumps are, however,
3 accompanied by movements of the wings and achieve similar take-off velocities and similar
4 jumping performance.
5
6 Jumping abilities of members of a fourth sub-order, the Sternorrhyncha which includes
7 aphids, coccids and whiteflies, have not been analysed although one group, the Psylloidea or
8 jumping plant lice, are, as their colloquial name implies, renowned for their jumping. The
9 group is widespread throughout many parts of the world although individual species
10 generally feed on the phloem of a particular species of usually dicotyledonous plants. On
11 many crop species as diverse as carrot, olive, pear and apple they can become a pest, but can
12 also be beneficial in controlling some alien invasive plants such as broom and mesquite. The
13 anatomy of the thorax and hind legs of this group has been well described (Crawford, 1914;
14 Weber, 1929). This paper shows that jumps by three species of psyllids are propelled by the
15 hind legs, under the control of large trochanteral muscles in the thorax. The jumps are
16 characterised by an unusual take-off posture in which the head points downwards and the
17 front tarsi provide support for the body in movement that resembles a human hand stand.
18 Once airborne the body spins at high rates in the pitch plane. Energy is thus lost to rotation
19 but the body is nevertheless accelerated rapidly to a take-off velocity of 2.7 m s^{-1}. A rarely
20 used strategy involving more extensive movements of the femoro-tibial joints of the hind
21 legs, enables take-off with the head up and with a greatly reduced rate of body spin.
22
23

Materials and Methods

25 Three species of psyllids were caught on their host trees in Girton, Cambridge, U.K., in
26 Ljubljana, Slovenia, and in Aachen, Germany: 1. *Cacopsylla peregrina* (Foerster), from
27 hawthorn (*Crataegus monogyna*), 2. *Psyllopsis fraxini* (L.) from ash (*Fraxinus excelsior*), 3.
28 *Psylla alni* (L.) from alder (*Alnus glutinosa*). They all belong to the order Hemiptera, sub-
29 order Sternorrhyncha and to the family Psyllidae.
30
31 Sequential images of jumps were captured at 5000 frames s^{-1} and with an exposure time of
32 0.05 ms with a single Photron Fastcam 1024PCI high speed camera (Photron (Europe) Ltd,
33 West Wycombe, Bucks., UK), fitted with a 60 mm Nikon lens. The images were fed directly
34 to a laptop computer. The jumps either occurred spontaneously or after the psyllids had been
35 manoeuvred with a fine paint brush toward the middle of a glass chamber which measured 80
36 mm wide, 40 mm tall, and 10 mm deep at floor level, widening to 25 mm at the top. The floor
37 was of high density foam. Some jumps were also captured from vertically placed pieces of
38 the same foam. The camera pointed at the centre of this chamber. A psyllid was able to jump
39 in any direction. Detailed measurements of changes in joint angles and distances moved were
40 made from jumps that were parallel to the image plane of the camera, or as close as possible
41 to this plane. Jumps that deviated to either side of the image plane of the camera by up to
42 $\pm\,30^{\circ}$ would result in a maximum error of 10% in the measurements of leg joint, or body
43 angles. Sequences of images were analysed with Motionscope camera software (Redlake
44 Imaging, Tucson, AZ, USA), or with Canvas 12 (ACD Systems of America, Miami, FL,
45 USA). The time at which the legs lost contact with the ground and the psyllid became
46 airborne was designated as t = 0 ms, thus allowing different jumps by the same or different
47 psyllids to be compared. The time at which the hind legs started to move and propel the jump
48 was also labelled and the time between these two events defined the period over which the

1   body was accelerated in a jump. A one frame error in estimating both the first movement of
2   the hind legs and the take-off time would result in a 10 % error in measuring acceleration
3   time. Peak velocity was calculated as the distance moved in a rolling 3 point average of
4   successive frames captured at 0.2 ms intervals before take-off. The point on the body
5   measured was close to the centre of mass just behind the hind legs. Movies 1 and 2 of jumps
6   are included as supplementary material.
7
8   The anatomy of the hind legs and metathorax was examined in intact psyllids and in those
9   preserved in 70% alcohol, or in 50% glycerol. Drawings of the legs, joints and muscles were
10 made with the aid of a drawing tube attached to a Leica MZ16 stereo microscope (Wetzlar,
11 Germany). Individual colour photographs were taken with a Nikon DXM1200 digital camera
12 attached to the same microscope. Dried specimens were also mounted on specimen holders,
13 sputter coated with gold and then examined in a Philips XL-30 scanning electron microscope
14 (Philips, Eindhoven, The Netherlands). Lengths of the parts of the legs of fixed specimens
15 were measured to an accuracy of 0.1 mm on images captured with a digital camera attached
16 to a Leica MZ16 microscope and projected onto a 24" monitor. Body weights were
17 determined to an accuracy of 0.1 mg with a Mettler Toledo AB104 balance (Beaumont Leys,
18 Leicester, UK).
19
20 A total of 211 jumps by 41 psyllids were captured and analysed; 113 jumps by 17 hawthorn
21 psyllids (*Cacopsylla*), 32 jumps by 5 ash psyllids (*Psyllopsis*) and 66 jumps by 19 alder
22 psyllids (*Psylla*). Measurements of body weight were made on these psyllids and on other
23 members of the same species whose jumps were not recorded. Measurements are given as
24 means ± standard error of the mean (s.e.m.). Temperatures in all experiments ranged from 23-
25 26º C.
26
27   **Results**

28 **Body shape**
29 All three species of psyllids analysed had a similar body shape with large translucent front
30 wings held to form a roof covering the thorax and abdomen and extending beyond the tip of
31 the abdomen (Fig. 1A,B). The body was slung low to the ground and supported by legs
32 placed on the ground to either side of the body. *Cacopsylla* was the smallest, with a body
33 length of 1.9 ± 0.1 mm (mean ± s.e.m, N = 13) and a body weight of 0.7 ± 0.03 mg (N = 35).
34 *Psylla* was the largest, with a body of twice the length of the other two species, at 4.0 ± 0.3
35 mm (N = 7) and of almost 4 times greater weight at 2.8 ± 0.1 mg (N = 29) than *Cacopsylla*
36 (Table 1). *Psyllopsis* had a body only 10% longer than *Cacopsylla,* at 2.2 ± 0.1 mm (N = 7),
37 but a body weight 62% greater at 1.2 ± 0.1 mg (N = 19).

38 **Structure of the hind legs**
39 In *Cacopsylla* the hind legs were only 10% longer than the front and middle legs, giving a
40 ratio of leg lengths of 1 front: 1 middle: 1.1 hind (Table 1). In *Psylla* and *Psyllopsis* the hind
41 legs were 20% longer than the front and middle legs, giving a ratio of leg lengths of 1: 1: 1.2.
42 In *Cacopsylla* the hind tibia was the same length as the hind femur, but in *Psylla* it was 25%
43 longer and in *Psyllopsis* it was 50% longer. Relative to the length of the body, the hind legs
44 were also short, ranging from 61% of body length in *Psylla*, 66% in *Cacopsylla*, and to 76%
45 in *Psyllopsis*. Relative to the cube root of body weight the ratio of the hind leg lengths had a
46 similar ratio ranging from 1.5 – 1.7.
47

1　The two large hind coxae were closely apposed at the midline and did not move visibly
2　relative to the metathorax during jumping (Figs 2,3). By contrast, the small trochanter rotated
3　through some 220 degrees about the coxa and swung the hind leg from its fully levated
4　position before a jump (Fig. 2A) to its fully depressed position after take-off (Figs 2B,C, 3B).
5　In its fully levated position, the hind femur fitted into a groove in the coxa at the side of the
6　body and abutted anteriorly with a the trochantin (Figs 1A, 3). At its fully depressed position,
7　the hind tibia and tarsus projected anteriorly in front of the head. A pointed protrusion, the
8　meracanthus (Figs 2A, B-D, 3) projected posteriorly and ventrally from the coxa, but did not
9　appear to engage with any part of the hind leg during these movements. The femur rotated
10　through a small angle about the trochanter; the tibia through some110 degrees about the
11　femur, and the tarsus through some 70 degrees about the tibia. Ventrally-pointing spines were
12　present on the distal tibia at the tibio-tarsal joint that could increase traction with the surface
13　from which a psyllid jumps.
14
15　Depression of the trochanter was powered by large muscles located in the metathorax (Fig.
16　2D). The muscles arise from the dorsal and anterior walls of the metathorax and insert within
17　the thorax on a large, stiff tendon that runs through the coxa to insert on the medial, ventral
18　rim of the trochanter (Fig. 2D).

19　A number of hair fields are placed such that they could provide proprioceptive information
20　about the movement or position of a hind leg (Fig. 3). On the ventral surface of the hind
21　coxae were two symmetrically-placed fields which would be contacted by a hind femur when
22　it was levated (Fig. 3A). Each field consisted of numerous articulated hairs 25-50 µm in
23　length and thus much shorter than the sparse 500 µm trichoid sensillum located nearby on the
24　femur (inset in Fig. 3A). These fields were exposed when the hind legs were depressed (Fig.
25　3B) revealing the gradation in length of their constituent hairs. When levated, a hind leg also
26　engaged with a hair field on the lateral surface of the coxa that again consisted of a large
27　number of short hairs (Fig, 3 B, C). On the ventral and posterior part of the trochantin was
28　another hair field which would be contacted by the hind femur in advance of the jump (Fig.
29　3A, C). Together these hair fields should be able to signal the initial levated position of a hind
30　leg before a jump and its depressed position once a jump has been propelled.

31　**Kinematics of the jump**
32　The following description is of jumping by *Psylla*, the largest of the psyllids studied (Figs 4,
33　6) with further characteristics illustrated by the other two species (Figs 5, 7). The key feature
34　of the jump was that the propulsive movements of the hind legs rotated the head downwards
35　so that the front legs were often the final means of support. This posture at take-off resulted
36　in high rates of spin in the pitch plane once airborne (Figs 4-6. Movie 1, supplementary
37　material). Before a jump, both hind legs were fully levated so that the anterior edge of each
38　femur is pressed against the associated trochantin. The body was held at an angle of about
39　+20 degrees relative to the horizontal so that the tip of the abdomen was close to the ground
40　and the head was raised by the front and middle legs (Fig. 4; see diagram on first frame). The
41　first observable movement of a hind leg was depression of the trochanter about the coxa
42　which resulted in the progressive downward movement of the femur (Movie 2,
43　supplementary material). Initially the angle between the femur and the tibia did not change,
44　but as the rotation of the trochanter continued, then from 0.4 ms before take-off, the tibia did
45　begin to extend. At take-off the tibia was almost fully extended about the femur and the angle
46　of the body relative to the horizontal was -76 ± 6 degrees (Table 2, Fig. 4; see diagram on
47　frame 0 ms) with the head pointing downwards. During the 2.4 ms acceleration period in this
48　jump the angular rotation of the body was therefore 40,000 degrees s^{-1}. The middle legs were
49　the first to lose contact with the ground between 0.6 and 0.4 ms before take-off. The forward

1   pitch of the body was so great that the front legs supported the body until take-off. The
2   angular movements of the joints of the front legs indicated that they were providing balance
3   rather than thrust to the jump. Take-off was marked by the front and hind legs losing contact
4   with the ground at about the same time. After take-off, rapid rotation of the body continued in
5   the pitch plane.
6
7   Three jumps by the same psyllid *Cacopsylla* viewed from the side (Fig. 5A), from in front as
8   it jumped toward the camera (Fig. 5B), and from underneath as it jumped from the vertical
9   glass wall of the chamber (Fig. 5C) illustrate further features of the sequence of leg
10   movements. Before the jump, the tarsi of the hind legs were placed lateral to the body and
11   remained in that position as they transmitted the force generated by the trochanteral muscles
12   in the thorax to the ground. The rotation of the trochantera resulted in the femoro-tibial joints
13   of the two hind legs moving medially and thus closer to each other so that they came to lie
14   underneath the body (Fig. 5C). The body was pitched forwards at even higher angular
15   rotation rates of 145,000 degrees s^{-1} during the much shorter (0.6 ms long) acceleration
16   period. Take-off was again marked by the front and hind legs losing contact with the ground
17   at about the same time. In all species the body always pointed downwards at take-off with the
18   head close to the ground and the abdomen raised in the air. Body angles at take-off were
19   similar in all species ranging from -58 ± 3 degrees in *Psyllopsis* (mean of means of 19 jumps
20   by 5 psyllids), -61 ± 5 degrees in *Cacopsylla* (mean of means of 40 jumps by 8 psyllids), to -
21   66 ± 3 degrees in *Psylla* (mean of means of 32 jumps by 7 psyllids) (Table 2). The numbers
22   of jumps and animals given here also apply to subsequent data.
23
24   The time taken to accelerate to take-off was related to the body weight of a particular species
25   of psyllid. In the lightest species, *Cacopsylla*, the acceleration time was shortest with a mean
26   of 0.9 ± 0.3 ms and with a fastest acceleration of only 0.4 ms in the best jump recorded. In
27   *Psyllopsis* the time rose to 1.2 ± 0.2 ms (fastest 0.8 ms) and in the heaviest species, *Psylla,*
28   acceleration took almost twice as long as in *Cacopsylla* at 1.7 ± 0.2 ms (fastest 1.0 ms) (Table
29   2). By contrast, the velocity at take-off did not correlate with body weight; both the lightest
30   and the heaviest had the same take-off velocities (*Cacopsylla* 1.7 ± 0.2 m s^{-1} (fastest 2.5
31   m s^{-1}), *Psylla* 1.7 ± 0.2 m s^{-1} (fastest 2.7 m s^{-1})), with *Psyllopsis*, of intermediate weight,
32   having the lowest take-off velocity of 1.1 ± 0.1 m s^{-1} (fastest 1.9 m s^{-1}) (Table 2).
33
34   In the experimental chamber, psyllids jumped from the horizontal floor or from a vertical
35   surface (Fig. 6A,B), but in their natural habitat they often jumped from the under surface of
36   leaves. No matter what the starting position, the thrust and spin that was imparted by
37   movements of the hind legs translated into two characteristic features of the jump trajectory.
38
39   First, the angle of the trajectory was steep. Take-off elevation was controlled by the posture
40   of the front and middle legs which set the initial position of the body in advance of the
41   acceleration phase of the jump. In *Cacopsylla* , the take-off angle was 80 ± 1 degrees and in
42   the largest species, *Psylla* it was not significantly different at 76 ± 6 degrees, but in *Psyllopsis*
43   the angle was shallower at 62 ± 7 degrees (Table 2). These figures indicate that take-off angle
44   is not a function of body size and weight.
45
46   Second, the rate of spin in the pitch plane was high. In *Psylla* and *Psyllopsis* the mean
47   rotation rates in the first 80 ms after take-off were 211 ± 11 Hz and 199 ± 17 Hz respectively,
48   but the smaller *Cacopsylla* had a higher rate of 336 ± 14 Hz. As for take-off angles, similar
49   rates of body spins were seen when jumping from surfaces of different orientations. Once

1   airborne, wind resistance gradually slowed the rate of rotation in all species. The wings did
2   not immediately open upon take-off to stabilise the body against these pitch rotations. The
3   earliest the wings were seen to open was after some 5 cycles of rotation (Fig. 6), but in many
4   jumps the wings remained closed throughout the jump so that continuing rotation of the body
5   resulted in landings that were not controlled. Opening of the wings was sometimes followed
6   by flapping movements which re-oriented the body and resulted in stable forward flight.

7   **Controlling jump trajectory**
8   In the vast majority (209 of 211) of jumps by all three species, the head pointed downwards
9   at take-off and the body rotated rapidly forwards in the pitch plane once airborne. Two jumps
10   using a different strategy were performed by the same *Psyllopsis* (Fig. 7A). In these jumps,
11   the head was raised progressively during the acceleration period so that at take-off it pointed
12   upwards and the angle of the body relative to the horizontal was +12 degrees (Fig. 7B). By
13   contrast, in a preceding jump by the same *Psyllopsis* the most common strategy was used so
14   that the head pointed downwards, and the body angle at take-off was some -40 degrees (Fig.
15   7C). At take-off, the trochanter had been rotated about the coxa by about the same amount in
16   both jumping strategies. The difference in body orientation between the two strategies thus
17   resulted from different movements of the femoro-tibial joints of the hind legs (Fig. 7D); in a
18   jump with head up, the femoro-tibial joint was fully extended (180 degrees) compared to
19   achieving an angle of only half this value in jumps with the head down. Despite the similar
20   acceleration times, jumps with the head up had a lower take-off velocity than those with the
21   head down (Fig. 7E) and trajectories were shallower (Fig. 7F). The direction and rate of
22   rotation once airborne were also different. When the head pointed upwards, the body spun
23   backwards and when downwards the body spun forwards. The pitch rate was 1,360 degrees s$^-$
24   ^{1} when the head pointed up compared to 22,270 degrees s^{-1} when it pointed down.

25   **Synchrony of hind leg movements**
26   The two hind legs moved in parallel planes on either side of the body and their only point of
27   contact was between the medial edges of the coxae, which did not appear to rotate about the
28   thorax. To propel a jump, both hind legs normally started to move together or within 0.2 ms
29   (1 frame of the video) of each other. In some jumps, however, the movements of the hind legs
30   were less closely synchronised. Four examples of the types and times courses of asynchrony
31   in jumping by *Psylla* are illustrated (Figs 8,9). In the first (Fig. 8A), both hind legs began in
32   contact with the ground, but at -1.6 ms before take-off , the left hind leg began to move
33   although the right hind leg did not. The trochanteral depression of the left, but not the right,
34   hind leg is shown in frame -1.0 ms before take-off (Fig. 8A). This resulted in the left hind leg
35   progressively raising the body from the ground, so that the right hind leg also lost contact
36   with it, although it had not moved actively. Then at 0.8 ms before the jump, the right hind leg
37   was suddenly and rapidly depressed so that its tarsus regained contact with the ground. In the
38   last 0.2 ms before take-off, the insect was therefore propelled by both hind legs which
39   reached the same angles of trochanteral depression and femoro-tibial extension at take-off. In
40   the second example (Fig. 8B), the left hind leg again moved first and raised the body so that
41   the right hind leg was lifted from the ground. This time, when the right hind leg began to
42   move at -0.8 ms, it immediately depressed and extended almost fully and thus only the left
43   hind leg contributed thrust during the last 0.2 ms before take-off. In the third example (Fig.
44   8C), the left hind leg was the first to move at -1.8 ms and it then depressed the trochanter and
45   extended the tibia fully in 0.4 ms. Only then did the right hind leg begin to depress and it
46   movements for the next 1.4 ms alone provided the thrust for the jump. In the fourth and final
47   example (Fig.9A,B), both hind legs started to depress at the same time, but while the left hind
48   continued to depress and extend fully, further depression of the right hind leg was delayed for

1   0.6 ms. For the last 0.8 ms of the acceleration period, this jump was propelled by the action of
2   a single hind leg.
3
4   In jumps such as these with such asynchronous movements of the hind legs, there were no
5   significant differences in the take-off angles of the body or the rate of pitch rotation
6   compared to jumps with more synchronous movements. Moreover, there was no rotation in
7   the yaw plane and rotation in the roll plane was not apparent. These results therefore indicate
8   that jumping performance of *Psylla* is resilient to asynchronies of 0.4 – 1.0 ms or 24 to 59%
9   of the acceleration period.

10 **Jumping performance**
11 Further features of the jumping performance were calculated from the data obtained from the
12 high-speed images (Table 2). The average acceleration over the whole of the take-off period
13 in an average jump was not significantly different in *Psylla* at 1060 m s^{-2} and 910 m s^{-2} in
14 *Psyllopsis,* but was almost twice as large at 2405 m s^{-2} in the smaller *Cacopsylla*, which also
15 had the shortest acceleration time. In their best jumps, *Psylla* and *Psyllopsis* experienced 275
16 ***g*** and 204 ***g*** respectively, but *Cacopsylla* experienced more than twice as much at 637 ***g***. The
17 energy required to achieve these performances was on average 4.6 µJ in *Psylla* rising to 13.1
18 µJ in its best jumps, and 0.8 - 1.1 µJ (2.6 -3.1 µJ in their best jumps) in the other two species.
19 The power output in an average jump by *Psylla* was 2.7 mW rising to 13 mW in its best
20 jumps. In *Psyllopsis* the comparable figures were 0.6 and 3.3 mW and in *Cacopsylla* 1.2 and
21 7.8 mW. The force exerted by *Psylla* in an average jump was 3 mN rising to 9.7 mN in its
22 best jumps; in *Psyllopsis* the comparable values were 1.1 and 3.5 mW, and in *Cacopsylla* 1.4
23 and 6.3 mW.
24
25 It was hard to get reliable measurements of the height and distance jumped by psyllids
26 because their small size and tumbling motion made it difficult to distinguish jumps in which
27 the wings were not moved from those that were eventually assisted by flapping movements of
28 the wings.
29
30

31 # Discussion

32 Jumping in psyllids is propelled by rapid movements of the hind legs that are less than three
33 quarters the length of the body and only 10-20% longer than the other legs. They are moved
34 in parallel planes on either side of the body by large trochanteral depressor muscles located in
35 the metathorax. Most frequently, both hind legs are moved within 0.2 ms of each other, but
36 jumping performance is not greatly affected when there is delay of 1 ms between the two.
37 These movements accelerate the body to take-off in 0.9 ms to 1.7 ms depending on the body
38 weight of the particular species. In the best jumps from the horizontal, take-off velocity
39 reached 2.7 m s^{-1} and the trajectory was steep. Once airborne the body spun rapidly forwards
40 in the pitch plane at rates of 200 -300 Hz, depending on the species. The wings did not
41 usually open to provide stabilisation during the early part of the trajectory, but some jumps
42 eventually led directly to sustained flight. In their best jumps, a psyllid could experience a
43 force of 637 g. The largest species had an energy requirement of 13 µJ, a power output of 13
44 mW and exerted a ground reaction force of nearly 10 mN. The short acceleration time and the
45 energy required for jumping indicate that direct muscle contractions could not generate these
46 jumps (Askew and Marsh, 2002; Ellington, 1985; Josephson, 1993; Weis-Fogh and
47 Alexander, 1977). Instead a catapult mechanism must be used, as in many other jumping

1 insects such as fleas (Bennet-Clark and Lucey, 1967; Sutton and Burrows, 2011), locusts
2 (Bennet-Clark, 1975; Heitler and Burrows, 1977), froghoppers (Burrows, 2006), leafhoppers
3 (Burrows, 2007a), and planthoppers (Burrows, 2009a).

Defining features of jumping

5 The characteristic features of jumping in psyllids are that the head points downwards at take-
6 off and that once airborne the body rotates rapidly forwards in the pitch plane. Both features
7 indicate that the force applied by the rapid depression of the hind trochantera is not passing
8 directly through the centre of mass of the psyllid. Moreover, the angle of the take-off
9 trajectory was consistently much higher than the 45 degree optimum for achieving the
10 greatest translational distance of the body in a jump. The forward rotation of the body began
11 during the acceleration period of the jump, and resulted in the abdomen being raised from the
12 ground but the head tilting closer towards it. This in turn meant that the weight of the body
13 was being moved onto the front legs and that their support was an integral part of the
14 propulsive mechanism for jumping. By contrast, insects as diverse as locusts and froghoppers
15 may lift their front legs from the ground before the propulsion from the hind legs has been
16 completed. In psyllids the front legs lose contact with the ground at the same time as, or even
17 after the hind legs. They therefore play a key role in supporting the body while thrust is
18 applied by the hind legs. The posture adopted by psyllids as they are about to jump is
19 strikingly similar to that of a human performing a hand stand. A head down posture is also
20 adopted by psyllids when feeding naturally with their piercing mouthparts, which emerge
21 ventrally between the front and middle legs (see Fig. 2A), pressed against its host plant and
22 into its phloem. From this posture, the common head down, jumping strategy would provide
23 the most rapid escape.
24
25 The initial rate of rotation once airborne is remarkable, ranging from 200 Hz in the larger
26 species to more than 300 Hz in the smallest species. The rotation was limited to the pitch
27 plane and results from application of force by the hind legs behind the centre of mass. The
28 only insects known to exceed these rotation rates during a jump are springtails which propel
29 themselves by extending the forked furca at the end of their abdomen, and thus well behind
30 their centre of mass, with resulting spin rates of 480 Hz (Christian, 1979). In pygmy mole
31 crickets the spin rate is above 100 Hz, but in these insects the pitch rotation is backwards
32 (Burrows and Picker, 2010), and in flea beetles the forward spin rates range from 21 - 187 Hz
33 in different species (Brackenbury and Wang, 1995). In froghoppers and leafhoppers, the spin
34 rates are much lower and do not exceed 10 Hz (Brackenbury, 1996). Spinning at high rates
35 will consume much energy that could otherwise have contributed to the forward momentum,
36 and hence displacement of the body. Wings were not opened or flapped in the initial stages of
37 any jumps and could not therefore contribute to stabilisation. Some jumps do, however, lead
38 directly to stable flight later in a trajectory.
39
40 What evolutionary advantage could spinning add to jumping, or is it just a consequence of
41 body shape? In springtails, which use an appendage at the rear end of the body in jumping,
42 there seems little scope in adjusting the point of force application relative to the centre of the
43 body mass. With the use of hind legs that move at the side of the body, as in psyllids, scope
44 for adjustment is limited by the length of the metathoracic segment relative to the centre of
45 mass. A mechanism for varying the spin rate is, however, available to psyllids but it appears
46 to be used rarely. In only 2 of 211 jumps analysed, the movements of the femoro-tibial joints
47 were more extensive and resulted in the head pointing upwards at take-off and the resulting
48 spin rate was greatly reduced. The mechanics of how this is achieved await determining the
49 natural circumstances under which psyllids will more readily use this jumping strategy.

Given that psyllids can generate jumps with little spin, why do they so frequently jump in a way that generates high spin rates? First, spinning will add to the unpredictability of the trajectory of a jump and the subsequent landing. A predator seeking to catch an airborne psyllid will find it harder to predict its position from its starting position. Second, if the spin rate can be varied, then predators will not be able to predict accurately the landing site. Such advantages as these must outweigh those where all the energy is put into achieving the highest velocity of a jump, and argue in favour of psyllid jumping being a mechanism of escape from predators rather than a fast way of moving from one place to another. Potential predators are numerous and include lacewings, wasps and ladybirds. If detected in time, a rapid jump should displace psyllids from the grasp of such predators.

Jumping performance

The jumping performance of psyllids places them firmly amongst the most accomplished of jumping insects. The acceleration time of a jump is much shorter than that of larger locusts (Bennet-Clark, 1975), and is similar to froghoppers (Burrows, 2006), planthoppers (Burrows, 2009a) and fleas (Sutton and Burrows, 2011). Their take-off velocities, however, fall well short of those of the first two groups, but match that of leafhoppers (Burrows, 2007a), and exceed that of fleas (Sutton and Burrows, 2011). It has not been possible to compare jumping distances because spinning psyllids are hard to distinguish from ones flapping their wings. All of the insects mentioned here use catapult mechanisms. This implies that the power-producing muscles must contract slowly before a jump, energy must then be stored in structures within the body and then released suddenly. The energy storage mechanisms are only know for a few insects and they are varied: flea beetles are suggested to use a spring in the hind femur (Furth, 1988; Furth et al., 1983): locusts use several sites including active bending of semi-lunar springs in the femur (Bennet-Clark, 1975; Burrows and Morris, 2001; Cofer et al., 2010): froghoppers and planthoppers actively bend the metathoracic pleural arches by prolonged contractions of trochanteral depressor muscles and then unfurl them before a jump (Burrows, 2010; Burrows et al., 2008). These arches are made of a composite of the soft, elastic protein resilin and hard cuticle (Burrows et al., 2008). The next task in psyllids must be to identify the structures that store the energy generated by the trochanteral depressor muscles and to analyse whether they are made of a composite of resilin and hard cuticle.

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1 # Figure Legends

2 **Fig. 1**
3 Photographs of *Psylla alni*. A. Side view. B. Ventral view. Scale bar 0.5 mm.

4 **Fig. 2**
5 Drawings of *Psyllopsis fraxini*. A. View of the right side with the right hind leg fully levated
6 and ready to propel a jump. The femur locates in a hollowed and membranous area of the side
7 wall of the metathorax bounded anteriorly by the trochantin. B. The same view with the right
8 hind leg fully depressed, as it would be at the end of a jump. The large coxa of the right hind
9 leg is now visible. The tibiae and tarsi of the front and middle legs are omitted. C. Ventral
10 view with the hind legs fully depressed and pointing forwards. D. The left half of the
11 metathorax viewed from inside, to show the large trochanteral depressor muscle of a hind leg
12 and its tendon.

13 **Fig. 3**
14 Scanning electron micrographs of the right hind leg of *Psylla alni*. A. Ventral view of the
15 right trochanter and femur which lies in a groove in the side wall of the thorax bounded
16 anteriorly by the trochantin. A pointed meracanthus projects posteriorly from the coxa. The
17 inset shows the dorsal surface of the femur touching the edge of a hair field on the coxa. B.
18 Ventral view of the right hind trochanter which is fully depressed so that the hind leg points
19 anteriorly and reveals the articulation of the trochanter with the coxa. The insertion of the
20 tendon of the large trochanteral depressor muscle is visible. C. Lateral view of the right hind
21 leg of *Psylla alni*. The hind leg is depressed fully so that it projects forwards to reveal the
22 articulation between the right trochanter and the coxa and the groove between the coxa and
23 trochantin. Two hair fields are visible; the larger with more densely packed sensilla on the
24 coxa, and a smaller one on the trochantin.

25 **Fig. 4**
26 Images of a jump by *Psylla alni* viewed from the side and captured at 5000 s^{-1}, each with an
27 exposure time of 0.05 ms. The images are arranged in two columns, with the bottom left-hand
28 corner of each image providing a constant reference point in this and in Figs 5, 7-9. The hind
29 legs started to move at -2.4 ms and the continuing depression of the hind trochantera raised
30 the rear of the body so that the middle legs lost contact with the ground and the head pitched
31 forwards. Once airborne, the body rotated rapidly in the pitch plane. The cartoons show how
32 the angle of the body relative to the ground was measured when the head was pointing
33 upwards (frame -2.4ms) and then downwards (frame 0 ms).

34 **Fig. 5**
35 Images of three jumps by the same *Cacopsylla peregrina* viewed from different orientations
36 to show the sequence of movements of the hind legs. Images were captured at 5000 s^{-1}, each
37 with an exposure time of 0.05 ms. A. Jump viewed from the side. B. Jump toward and to the
38 right of the camera. C. Jump from the front, glass wall of the chamber and viewed from
39 underneath.

40 **Fig. 6**
41 Body rotations in the pitch plane after take-off from jumps by *Psylla alni* plotted as vertical
42 displacement against horizontal displacement; the open symbols show the position of the
43 front of the head every 0.4 ms and the black symbols give a time scale of every 2 ms. The

cartoons show the orientation of the body at the points indicated and the curved arrows with
white heads indicate the direction of rotation. A. Four jumps in which three *Psylla* jumped
from a vertical wall (vertical, gray bar) in the chamber. In all jumps the body rotated and in
two jumps the wings were opened at the points indicated by the black arrows and began to
flap. B. Four jumps, all by the same *Psylla*, from the floor of the chamber (horizontal, gray
bar). In one jump, the wings were opened (black arrow) and began to flap.

Fig. 7
Two distinct jumping strategies used sequentially by the same *Psyllopsis fraxini*. A. Jump
powered by movements of the coxo-trochanteral joints of the hind legs in which the head
pointed downwards at take-off (open symbols in graphs C-F). B. Jump powered by
movements of the femoro-tibial joints in which the head pointed upwards at take-off (closed
symbols in graphs C-F). C. Graph of body angle relative to ground in a jump. In the
commonly used strategy (A) the head pointed downwards at take-off and the body angles
were negative; in a rarely used strategy (B) the head pointed upwards at take-off and the body
angles were positive. D. Graphs of the changes in the femoro-tibial and thoraco-femoral
angles. The inset frames show the different positions of the hind leg joints at take-off in the
two jumping strategies. E. Take-off velocities in both jumping strategies. F. The trajectory of
the take-off was steeper using the strategy in A compared with the strategy in B.

Fig. 8
Asynchrony of hind leg movements during jumping. Selected frames from three jumps by
Psylla alni are arranged in columns A-C. A diagram on each frame shows the angles of the
trochanter relative to the body, the femoro-tibial angle and the tibio-tarsal angle for each hind
leg (right in black, left in magenta). The pink line indicates the angle of the body relative to
the horizontal. The movements of the left hind leg, which are partially obscured by the body
in the initial frames in this and the next figure, were determined from the position of the hind
tarsus, the length of the hind tibia which was visible, and from knowledge of the position of
the trochantero-coxal joint visible in later frames. In A, B, the ground is indicated by the
horizontal white bar; in C take-off was from the front wall of the glass chamber.

Fig. 9
Jump by *Psylla alni* powered predominantly by one hind leg. A. Selected frames from the
jump with diagrams (as in Fig. 8) showing the progressive changes in the joint angles of the
two hind legs (right filled symbols, left open symbols) and the orientation of the body (pink
triangles). B. Graphs of the changes in joint angles (as indicated in the cartoons on the right)
of the right and left hind leg.

Supplementary Material

Movie 1
A jump by *Psylla alni* captured at 5000 frames s^{-1} and replayed at 30 frames s^{-1}. The insect is
viewed from the side as it jumps and is then propelled through the air spinning forwards in
the pitch plane. After two complete cycles of rotation the wings are opened and then begin to
flap.

1   **Movie 2**
2   A close-up view from the side of a jump by *Psylla alni* captured at 5000 frames s^{-1} and
3   replayed at 10 frames s^{-1}. The rapid extension of the hind legs lifts the abdomen and lowers
4   the head so that the front legs are the last to lose contact with the ground at take-off.
5

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Table 1. Body form in Psyllids

Insect	Body length, mm	Body weight, mg	Hind leg Tibia, mm	Hind leg Femur, mm	Ratio of leg lengths			Hind leg length as % of body length	Hind leg length (mm)/ body weight ^ 1/3 (mg)
					Front	Middle	Hind		
Cacopsylla peregrina (Hawthorn psyllid)	1.9±0.1 (N=13)	0.7±0.03 (N=35)	0.5±0.02 (N=13)	0.5±0.02 (N=13)	1	1	1.1	66	1.5
Psyllopsis fraxini (Ash psyllid)	2.2±0.1 (N=7)	1.2±0.1 (N=19)	0.9±0.02 (N=7)	0.6±0.01 (N=7)	1	1	1.2	76	1.6
Psylla alni (Alder psyllid)	4.0±0.3 (N=7)	2.8±0.1 (N=29)	1.0±0.1 (N=7)	0.8±0.02 (N=7)	1	1	1.2	61	1.7

Body length and weight, and lengths of the hind femora and tibiae in three species of psyllids; N indicates the number of individuals from which the measurements were taken. The ratio of leg lengths is given relative to the front legs.

Table 2. Jumping Performance of Psyllids

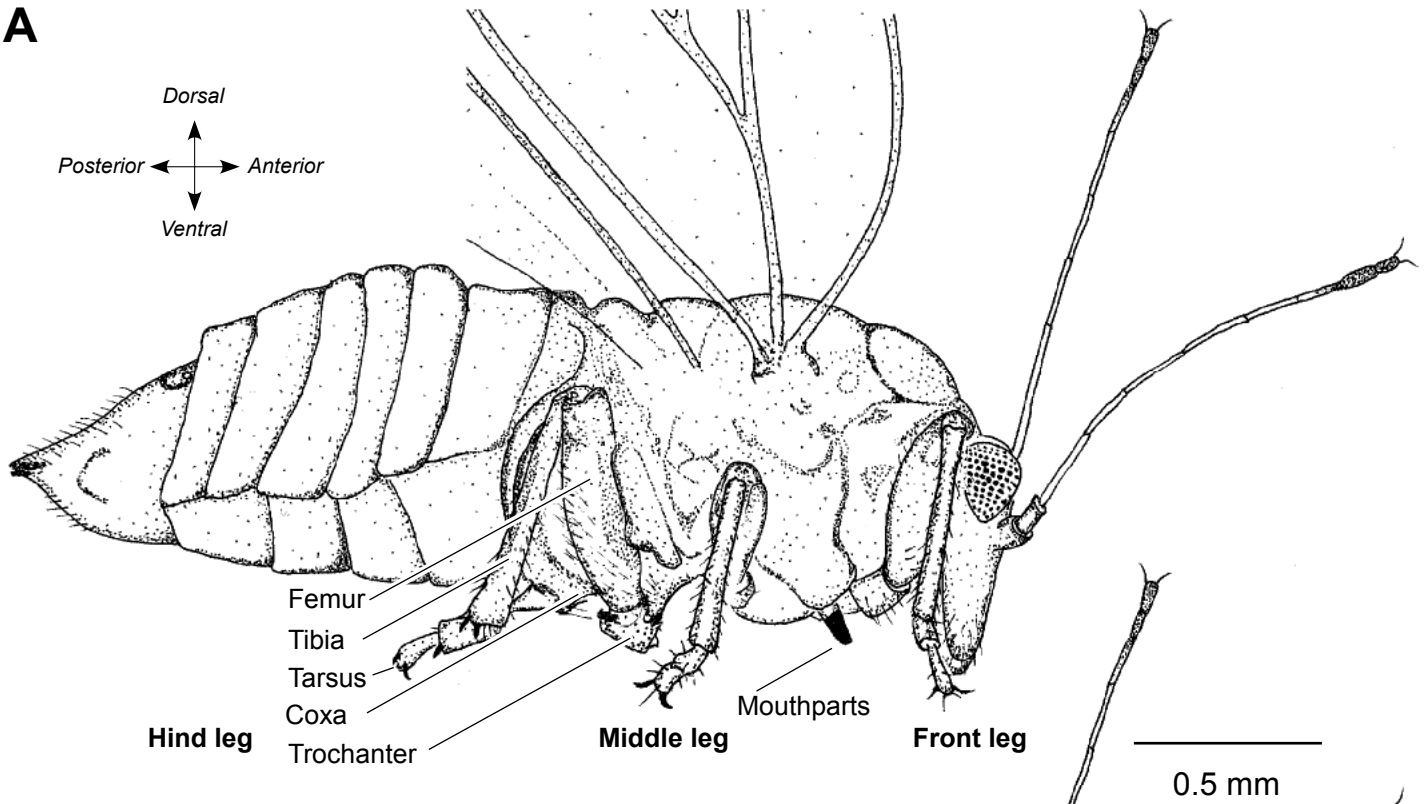|	Body weight (m)	Time to take off (t)	Take-off velocity (v)	Take-off angle	Body angle at take-off	Acceleration (f)	g force	Energy (e)	Power (p)	Force	Rotation
Formula						$f= v/t$	$g= f/9.86$	$e=0.5*m.v^2$	$= e/t$	$= m\,f$	
Units	mg (10^{-6}kg)	ms (10^{-3}s)	m s^{-1}	degrees	degrees	m s^{-2}	g	µJ (10^{-6}J)	mW (10^{-3} W)	mN (10^{-3} N)	Hz
Cacopsylla peregrina											
average	0.7±0.1	0.9±0.3	1.7±0.2	80±1	-61±5	1910	195	1.1	1.2	1.4	336±14
best	1	0.4	2.5			6250	637	3.1	7.8	6.3	
Psyllopsis fraxini											
average	1.2±0.1	1.2±0.2	1.1±0.1	62±7	-58±3	910	93	0.8	0.6	1.1	199±17
best	1.5	0.8	1.9			2340	240	2.6	3.3	3.5	
Psylla alni											
average	2.8±0.1	1.7±0.2	1.7±0.2	76±6	-66±3	1060	108	4.6	2.7	3.0	221±11
best	3.6	1.0	2.7			2700	275	13.1	13.0	9.7	

The jumping performance of three species of psyllids. The data are the mean of means for the performance of individuals; 40 jumps by 8 *Cacopsylla*, 19 jumps by 5 *Psyllopsis* and 32 jumps by 7 *Psylla*, with a minimum of 3 jumps by each psyllid. The best performance of a particular individual for each species is also given.
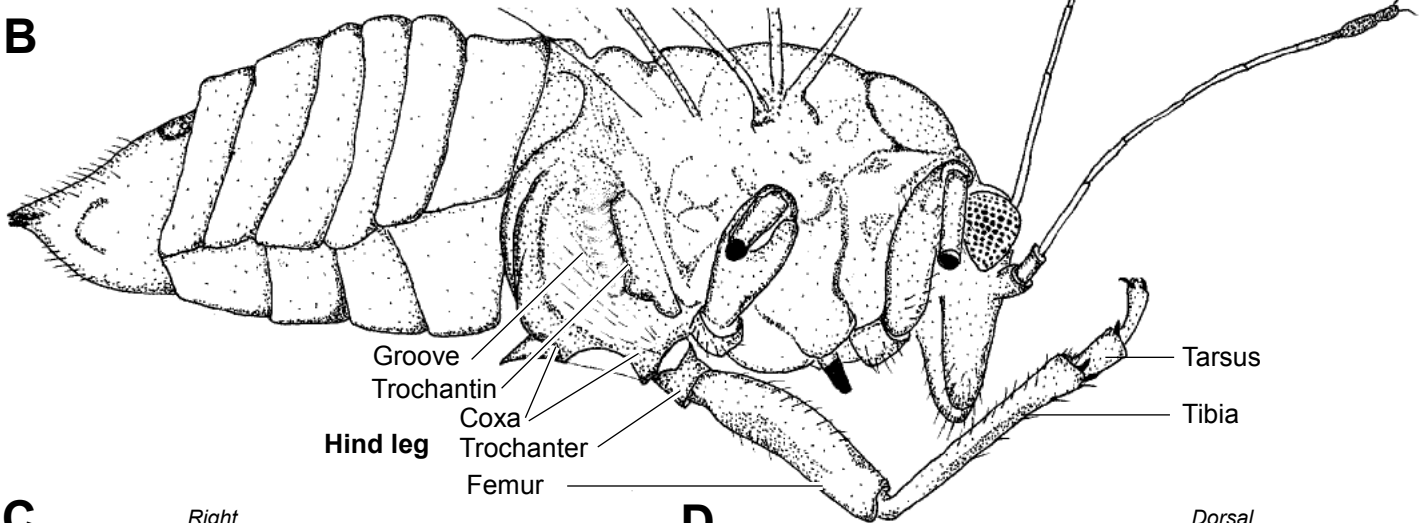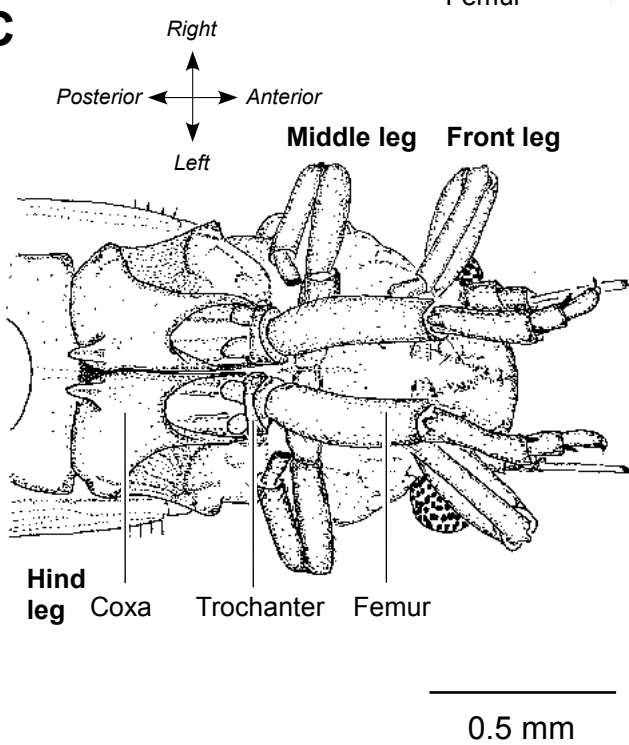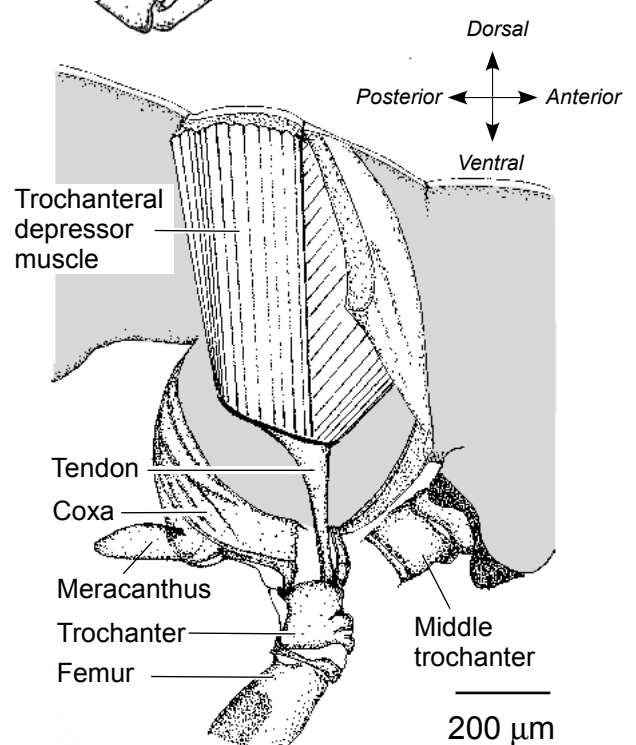
Figure 1

Figure 2

A

Dorsal

Posterior ← → Anterior

Ventral

Femur
Tibia
Tarsus
Coxa
Hind leg
Trochanter

Mouthparts

Middle leg

Front leg

0.5 mm

B

Groove
Trochantin
Coxa
Hind leg
Trochanter
Femur

Tarsus

Tibia

C

Right

Posterior ← → Anterior

Left

Middle leg   **Front leg**

Hind leg   Coxa   Trochanter   Femur

0.5 mm

D

Dorsal

Posterior ← → Anterior

Ventral

Trochanteral
depressor
muscle

Tendon
Coxa
Meracanthus
Trochanter
Femur

Middle
trochanter

200 μm

Figure 3

Figure 4

Psylla

-2.4 ms

First movement of hind legs

-1.6

-1.2

-0.8

-0.4

0 ms

Take-off

Rotation rate 40,000 degrees s^{-1}

+0.4

2 mm

Figure 5

A *Cacopsylla*

-0.6 ms

side view

-0.4

-0.2

0 ms   Take-off

Rotation
rate
145,000
degrees s^{-1}

+0.4

B

facing camera

C

underneath

1 mm

Figure 6

Figure 7

A *Psyllopsis*

Take-off

2 mm

B -2.2 ms

-1.2

-0.8

0 ms

+1

+2

+4

+6

C Take-off

Body angle (degrees)

Time (ms)

D Hind leg joint angles (degrees)

1 mm

Femoro-tibial

Thorax/femur

Time (ms)

E Velocity (m s⁻¹)

Time (ms)

F Vertical distance (mm)

Horizontal distance (mm)

Figure 8

Figure 9

A

Right — 125° · Left — 61° · -2.0 ms · *Psylla*

178° · 79° · -1.2

180° · 86° · -0.8

167° · 122° · -0.4

Take-off · 160° · 126° · 0 ms

2 mm

B

Angle (degrees)

200 · 100 · 0 · -100

Take-off

Right
Femoro-tibial
Left

Thorax/femur

Body

Time (ms)

-2 · -1.5 · -1 · -0.5 · 0

Femoro-tibial

Thorax/femur

Body/ground