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Interacting gears synchronise propulsive leg movements in a jumping insect

by

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With 2 Figures and 3 supplementary movies

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1 **Structures that look like intermeshing gears are found rarely in animals and have never**

2 **been reported to engage and rotate functionally like a set of mechanical gears. We now**

3 **demonstrate the action of functional gears in the ballistic jumping movements of the**

4 **flightless planthopper insect, *Issus*. Synchronous movements of the propulsive hind legs are**

5 **essential both to propel and to control the direction of a jump. The nymphs, but not adults,**

6 **have a row of cuticular gear (cog) teeth around the curved medial surfaces of their two**

7 **hind trochantera. High speed images showed that during both the preparatory cocking and**

8 **the propulsive phases of jumping, the gear teeth on one trochanter engaged with and**

9 **sequentially moved past those on the other trochanter. The spacing between the gear teeth**

10 **and the close registration between the two gears ensured that both hind legs moved at the**

11 **same angular velocity, ensuring that the body was propelled forwards without yaw**

12 **rotation. At the final moult to adulthood, this synchronisation mechanism is jettisoned.**

13 ~~**These gear teeth and their actions therefore represent the first description of an animal**~~

14 ~~**using a set of mechanical gears to regulate locomotion.**~~

15

16 Adults and nymphs (Figure 1A) of the planthopper *Issus coleoptratus* (Hemiptera: Fulgoroidea:

17 Issidae) live together on the same host plants and in both, rapid and synchronous movements of *[Results should not be presented in the intro]*

18 the two hind legs propel high-speed ballistic jumps ~~to escape predators~~. The most rapid

19 acceleration to take-off by nymphs occurred in just 2 ms (mean 2.01 ± 0.1 ms (s.e.m.) for 8

20 nymphs) (supplementary material, Movie 1) leading to take-off velocities of 3.9 m s^{-1} in their

21 fastest jumps (mean 2.2 ± 0.56 m s^{-1}, N=8). The two propulsive hind legs started moving within

22 30 µs of each other. Such high degree of synchrony would be difficult to achieve by neural

23 control in which each spike signal is 30 times longer. The synchrony is essential since if the hind

24 legs move at different times the insect spins rapidly in the yaw plane, dissipating much energy in

25 rotation (*1-2*). This problem is a consequence of the hind legs moving counter-rotationally in

26 approximately the same near-horizontal plane beneath the body during a jump. The coxae of the

27 hind legs are opposed to each other at the ventral midline and appear to adhere to each other so

28 that they provide a stable base about which the trochantera can be rotated to generate the

29 propulsive thrust for jumping. Each hind trochanter of nymphs of all instars is characterised by

30 the presence of a curved strip of gear teeth (Figure 1B), a feature that extends to other nymphal

31 Fulgoroidea (*3-4*). The gear on one trochanter interdigitated with a corresponding gear on the

[Instead of jumping directly into result & descriptions here, it would be better to give a short paragraph of background on jump propulsion in insects more generally. After that, present a brief description of your methods, then present the results and description of the gears. Finally, conclude w/ comparison to other natural gear-like structures and your final conclusions.]
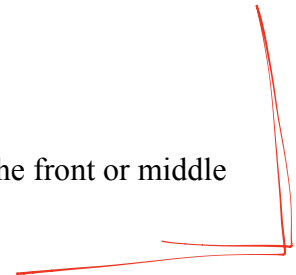
1   other trochanter (Figure 1C,D). No structures resembling these are present on the front or middle

2   legs nor are they present on the hind legs of adults.

3

4   Each strip of gears was 350 - 400 µm long, contained 10-12 teeth wrapped around the medial

5   surface of the hind trochanter with a radius of curvature (ρ) of about 200 µm (Figure 1E,F). The

6   numbers of gear teeth on the left and right hind trochantera were the same, resulting in a gearing

7   ratio of 1:1. One tooth occurred for every $8.5 \pm 1.0^{\circ}$ (N = 9 nymphs) of rotation of the coxo-

8   trochanteral joint. As measured in final instar nymphs, the width of an individual tooth was 80

9   µm at the anterior end of the curved strip tapering to 30 µm at the posterior end (Figure 1B).

10   Each tooth was 9 µm thick from front to back, was separated from the next tooth by 30 µm and

11   projected from the surface of a trochanter by 15 - 30 µm, again tapering from the anterior to the

12   posterior end of the strip. The stiffness and dark colouration of the teeth contrasted with the

13   lighter surface of the underlying cuticle and suggests that these structures are heavily sclerotised

14   (Figure 1B).

15

16   The teeth of the gears had only some of the features that characterise man-made gears. A feature

17   in common was the presence of a curved fillet at the base (Figure 1E), which in man-made gears

18   is designed to reduce the likelihood of shearing. In *Issus,* however, the sides of each tooth were

19   hooked (Figure 1D-F), whereas those of man-made gears have two curvatures, called an

20   involute, that enable contact to remain constant throughout their engagement (*5*). The involute,

21   however, is a solution for two perfectly circular gears each rotating about their respective

22   centres; the trochanteral gears, by contrast are neither perfectly circular, nor are they rotating

23   about their centres.

24

25   To determine the action of the gears in jumping, high speed images were captured of a nymph

26   restrained on its back but with its hind legs free to move. Rapid and synchronous movements of

27   both hind legs in movements that have all the characteristics of natural jumps (*6*) could then be

28   readily induced in some animals by touching the abdomen with a fine paintbrush. These

29   experiments showed that the gears of one trochanter clearly engaged with those on the other

30   trochanter during both the preparatory movements for a jump and during the rapid depression

31   movements that propel a jump itself (Figure 2A-C). In preparation for a jump, the hind legs were

1   levated at their coxo-trochanteral joints so that both hind legs were rotated forwards (*7*) (Figure

2   2A,B and supplementary material, Movie 2). In the propulsive jumping movements both hind

3   legs were depressed at the coxo-trochanteral joints that rotated with angular velocities as high as

4   200,000 $^{\circ}$ s^{-1} (Figure 2C and supplementary material, Movie 3). With one tooth every 4.3 $^{\circ}$, the

5   left and right trochantera were mechanically constrained to depress within 21 µs of each other.

6

7   In some cocking and jumping movements the gears would disengage at the end of a movement.

8   For example, during the cocking part of a jump the two hind legs would sometimes be levated

9   beyond the last engagement point of the most anterior tooth, or the hind legs would be pulled

10   apart laterally so that a gap opened up medially between the two strips of teeth. Movements of

11   the trochantera then led to re-engagement of the teeth before the start of the next propulsive

12   movement of a jump. Similarly, at the end of a jump the depression would sometimes go beyond

13   the last engagement point of the most posterior tooth. Re-engagement was then restored during

14   the first part of a subsequent levation movement. On other rarer occasions, the gears failed to

15   engage immediately at the start of the propulsive phase of a jump and one hind leg then

16   depressed fractionally in advance of the other so that some teeth span past each other. After these

17   few misses, one tooth made contact with and engaged with a tooth on the other hind leg which

18   then began its rapid depression, delayed only by a few microseconds relative to the first hind leg.

19   This emphasises that it was critical for the gear on the hind leg moving first to engage with the

20   gear on the other leg so as to nudge it to start its movement and thus maintain close synchrony.

21

22   The torque generated in a jump was calculated to be about 0.7 mN mm from the measured body

23   mass and from the ground reaction force determined from the kinematics of natural jumping.

24   Each hind leg and hence each gear is controlled by separate sets of trochanteral levator and

25   depressor muscles so that not all the torque goes through each tooth. If, however, one leg moves

26   first at the start of a jump, its gear teeth will engage with and transmit power to the other

27   stationary leg inducing it to move. The power producing muscles of the two legs are innervated

28   by different sets of two motor neurons each, but all four motor neurons carry highly

29   synchronised spike patterns that should help to ensure that the same amount of force is generated

30   in both legs (*7*). This neural mechanism assists with the synchrony of the leg movements, but one

31   which is unable to deliver the level of synchrony measured during jumping. Thus the primary

role fulfilled by the gears is to ensure the hind legs move synchronously within microseconds of each other. Smaller nymphs have shorter hind legs and hence will have a correspondingly briefer time to accelerate a jump. This will in turn result in a greater need to ensure that the legs move synchronously if body spin is to be avoided. This mechanically coupled movement means that azimuth direction cannot be controlled by altering the timing of movement by the two hind legs, and modelling has independently shown that this would not be effective at maintaining a controlled trajectory (*2*). The required azimuth angle of a jump is instead controlled by varying the angles of the two hind femoro-tibial joints.

The gear teeth are present through all nymphal stages but are abandoned at the final moult into adulthood. Adults are, nevertheless, even better jumpers than the nymphs; they reach take-off velocities of more than 5 m s^{-1} (adult males fastest velocity 5.5 m s^{-1} ; mean 3.2 ± 0.2 m s^{-1} for 10 males) in less than 1 ms (best time to take-off 0.8 ms, mean 1.5 ± 0.04 ms), and experience forces of 700 *g* (*8*). They now ensure synchronous movements of the two hind legs through frictional contact between the more proximal coxae (*1*). Their improved performance may be due to many factors rather than a consequence of abandoning the gear mechanism. An inherent limitation of gears in general and for their particular role in *Issus* is that if one tooth breaks, their synchronising function is lost. In nymphs that live for only a short time before moulting, a possible breakage can perhaps be tolerated because a repair can be effected shortly at the next moult. For the longer lifespan of the adults during which repair is not possible, the risk of losing directional control in jumping must be too great. Alternatively, the larger size of the adult body may mean that friction between stiffer body parts is a more effective synchronisation mechanism.

Gears occur rarely in the animal kingdom and none have been described to act like those analysed here, or those in many man-made machines. The cog wheel turtle *Heosemys spinosa* is named after the spines arranged around the edge of its shell. Similarly, the wheel bug *Arilus cristatus* (Hemiptera, Reduviidae) has tooth-like protrusions from the edges of its pronotum, but again these appear to act as ornaments and are not used as mechanical gears. The hearts of crocodilians have a cog wheel valve (*9-11*) that closes during each heart beat and can increase the resistance in the pulmonary outflow (*12*). In some insects and some crustaceans, rows of

1   regularly spaced protrusions are found (*13*) that have a similar appearance to the rows of teeth in

2   *Issus*. They are, however, used in sound production when each protrusion is struck in turn by

3   another structure; they do not interdigitate to assist a movement. The clear actions during

4   jumping of the gears analysed here, emphasise the role played by the mechanics of the skeleton

5   in generating rapid and powerful movements and their importance for the survival of the animal.

6   The gears in *Issus*, like the screw in the femora of beetles (*14*) demonstrate that mechanisms

7   previously thought only to be used in man-made machines have evolved in nature. Nymphal

8   planthoppers possess the only known example of gears that have evolved to play an essential

9   functional role in a natural behaviour.

10

11

Figure Legends

Figure 1

Structure of the gears on the hind trochantera of nymphs of *Issus*. (A) A nymph viewed from the side. (B) The gears on the left and right hind trochantera viewed posteriorly. (C) Scanning electron micrograph of the articulation between the hind trochantera and coxae, and the engagement of the gears on the two sides as viewed ventrally. The trochantera of both hind legs are partially levated about the coxae. (D) Higher magnification to show the interdigitation of the gears. (E). Diagram to show the radius of curvature of the surface (ρ_{gear}), the angular placement of the gear teeth, and how the teeth of the two gears enmesh. (F) Drawing of the profile of a gear tooth in *Issus* (left) compared with a man-made involute gear tooth (right). The radius of curvature of the fillet (ρ_{fillet}) is indicated.

Figure 2

Engagement of the two gears during jumping movements of the hind legs. (A) Levation of the hind legs into their cocked position in preparation for a jump. Three images, at the times indicated, and captured at a rate of 5000 s^{-1} of the hind trochantera and proximal femora (see Movie 2 in Supplementary Material for the full sequence). The first movement of a trochanter starts at time 0 ms and cocking is completed 80 ms later. (B) Drawings of the progressive movements of the gears and joints during cocking. The horizontal black arrows indicate the correspondence between the frames in (A) and the drawings here. (C) Rapid and synchronised depression of the two hind legs that power a jump (see Movie 3 in Supplementary material for the full sequence). Four images starting from the first detectable depression movement of the hind trochantera (time 0 ms). Full depression was completed 1.8 ms later. The curved, black arrows show the direction of movement of each hind leg, and the curved, open arrows the direction of rotation of the two gears.

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2 Cambridge colleagues for their many helpful suggestions during the course of this work and for

3 their comments on the manuscript.

4

Supplementary Material

Material and Methods

7 *Issus coleoptratus* (Fabricius 1781) was found living on ivy (*Hedera helix*) in Aachen Germany

8 and Cambridge, England. It has some 5 nymphal instars that progressively increase in size and

9 all live freely in the same habitat as the adults. *Issus* belongs to the order Hemiptera, sub-order

10 Auchenorrhyncha, super-family Fulgoroidea and family Issidae. The nymphs analysed in this

11 study were of different instars as indicated by: 1. differences in the number of circular pit sense

12 organs on the notum of the mesothorax; 2. body mass, which ranged from 3.4 to 10 mg (average

13 6.6 ± 0.76 mg, N=9); 3. body length which ranged from 2.8 to 5.1 mm (average 4.1 ± 0.25 mm,

14 N=9). The hind legs were $35 \pm 0.2\%$ (7 nymphs) longer than the front legs so that the ratio of the

15 lengths of the front, middle and hind legs was 1:1:1.35. The hind legs of nymphs were 81.1 ± 4.5

16 % (7 nymphs) of the body length.

17

18 Sequential images of natural jumps by nymphs were captured at a rate of 5 000 s^{-1} and an

19 exposure time of 0.03 ms, with a single Photron Fastcam 512PCI camera (Photron (Europe) Ltd,

20 West Wycombe, Bucks., UK). Jumps occurred within a chamber made of optical quality glass

21 (width 80 mm, height 80 mm, depth 10 mm at floor level expanding to 25 mm at the ceiling).

22 The floor was made of high density foam (Plastazote) that gave good purchase for the tarsi.

23 Images of restrained jumps to analyse the movements of the gears were made with nymphs held

24 in Plasticene under a Leica MZ16 microscope (Wetzlar, Germany) to which the high speed

25 Photron camera was attached through a trinocular head. Frame rates of 30 000 s^{-1} were used to

26 determine the synchrony of the leg movements and 5 000 s^{-1} to reveal the movements of the

27 gears. Temperatures ranged from 24-30º C.

28

The anatomy of the hind legs and metathorax was examined in intact insects and in those preserved in 70% alcohol. Dried specimens were also mounted on specimen holders, sputter coated with gold and then examined in a Philips XL-30 Scanning Electron Microscope (Eindhoven, The Netherlands). Body masses were determined to an accuracy of 0.1 mg with a Mettler Toledo AB104 balance (Beaumont Leys, Leicester, UK).

Movie 1

Spontaneous jump of a nymph viewed from the side. The images were captured at a rate of 5 000 images s^{-1} and with an exposure time of 0.03 ms and are replayed at 30 frames s^{-1}.

Movie 2

Movements of the gears during cocking of the hind legs in preparation for a jump by a nymph restrained on its back in Plasticene. Images were captured at a rate of 5 000 images s^{-1} and with an exposure time of 0.03 ms and are replayed at 30 frames s^{-1}.

Movie 3

Movements of the gears during a restrained jump by a nymph fixed on its back in Plasticene. Images were captured at a rate of 5 000 images s^{-1} and with an exposure time of 0.03 ms and are replayed at 30 frames s^{-1}. The hind legs pushed against the flexible hairs of a small brush that slowed the velocity of their propulsive movements.

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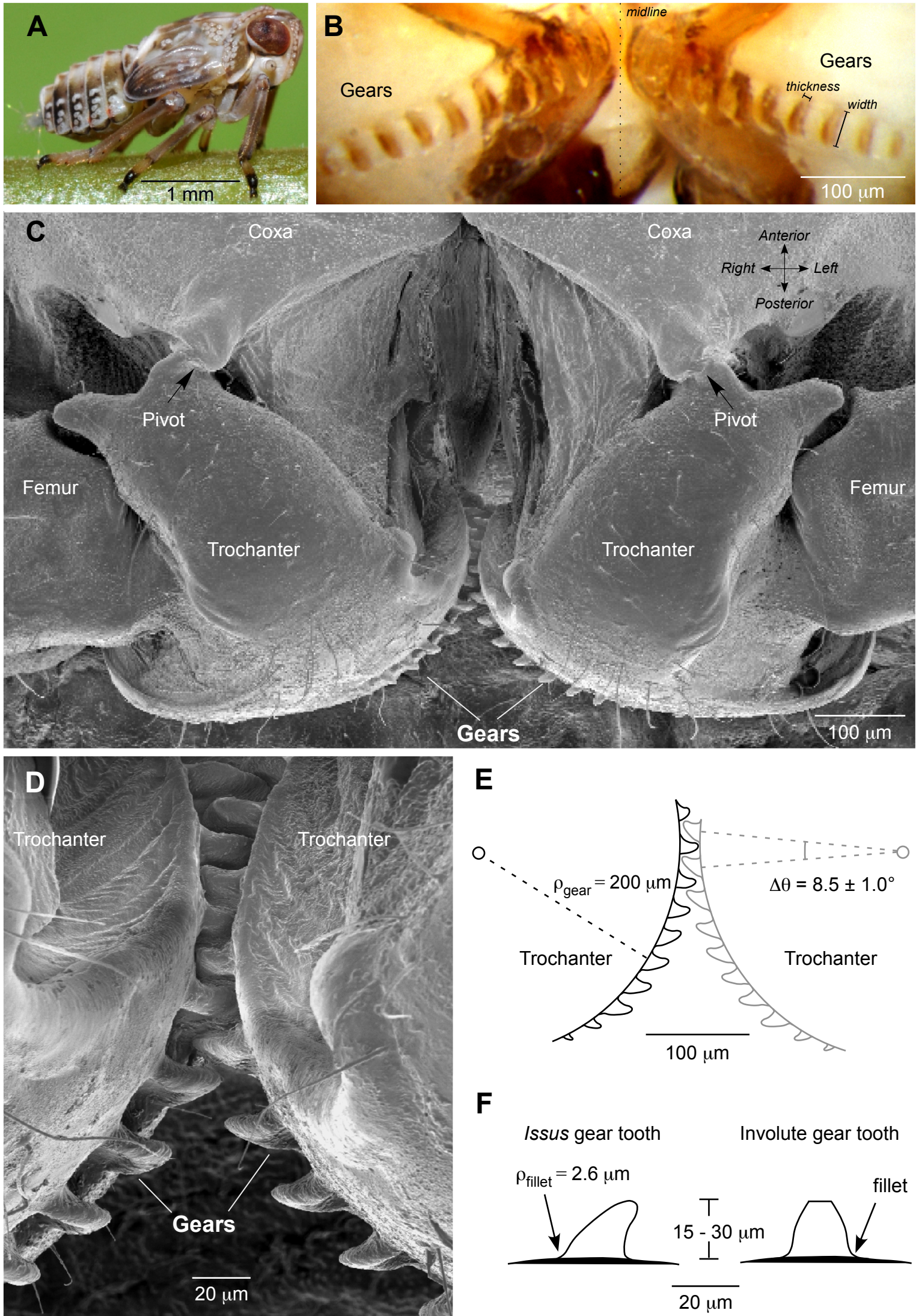
Figure 1

A 1 mm

B midline / Gears / Gears / thickness / width / 100 μm

C Coxa / Coxa / Anterior / Right / Left / Posterior / Pivot / Pivot / Femur / Femur / Trochanter / Trochanter / **Gears** / 100 μm

D Trochanter / Trochanter / **Gears** / 20 μm

E $\rho_{gear} = 200\ \mu m$ / $\Delta\theta = 8.5 \pm 1.0°$ / Trochanter / Trochanter / 100 μm

F *Issus* gear tooth / Involute gear tooth / $\rho_{fillet} = 2.6\ \mu m$ / fillet / 15 - 30 μm / 20 μm

Figure 2

A Cocking
- Coxa, Coxa
- Trochanter, Trochanter
- Femur, Femur
- 0 ms
- 38.4 ms
- 78.4 ms
- 200 μm

B Cocking
- Trochanter
- Trochanter
- Femur
- Femur
- 0 ms
- 15.6 ms
- 38.4 ms
- 54.6 ms
- 78.4 ms
- 200 μm

C Rapid depression
- Trochanter, Trochanter
- 0 ms
- 1.2 ms
- 1.6 ms
- 1.8 ms
- 200 μm
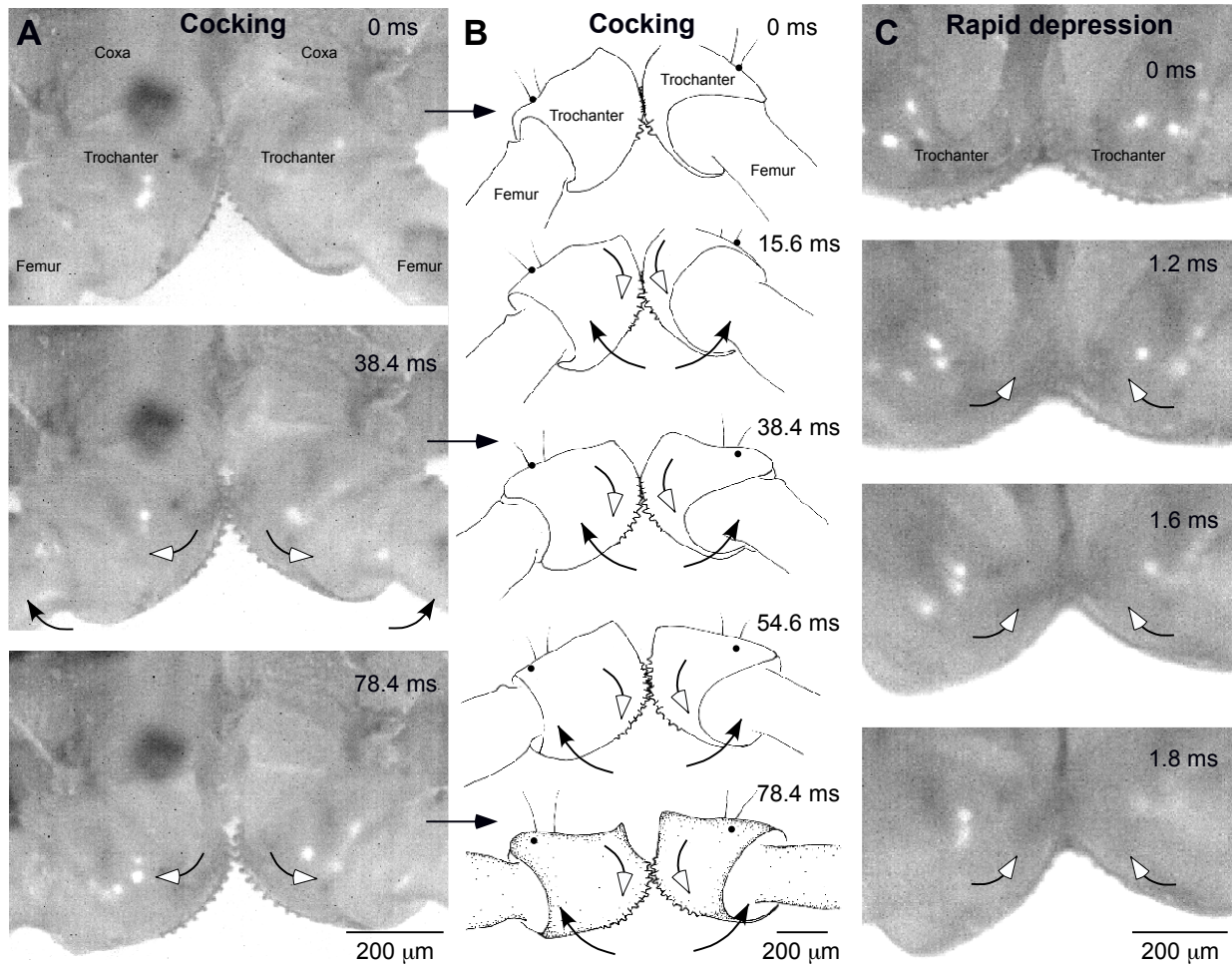
Additional material

We wish to submit three short movies as additional material. The website will not allow upload of these files. We are therefore following your instructions to submit a CD containing these files.