

# Froghoppers jump from smooth plant surfaces by piercing them with sharp spines

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**Attachment mechanisms used by climbing animals facilitate their interactions with complex 3D environments and have inspired novel types of synthetic adhesives. Here we investigate one of the most dynamic forms of attachment, used by jumping insects living on plants. Froghopper insects can perform explosive jumps with some of the highest accelerations known among animals. As many plant surfaces are smooth, we studied whether *Philaenus spumarius* froghoppers are able to take off from such substrates. When attempting to jump from smooth glass, the insects' hind legs slipped, resulting in weak, uncontrolled jumps with a rapid forward spin. By contrast, on smooth ivy leaves and smooth epoxy surfaces *Philaenus* froghoppers performed strong jumps without any slipping. We discovered that the insects produced traction during the acceleration phase by piercing these substrates with sharp spines of their tibia and tarsus. High-speed microscopy recordings of hind legs during the acceleration phase of jumps revealed that the spine tips indented and plastically deformed the substrate. On ivy leaves, the spines of jumping froghoppers perforated the cuticle and epidermal cell walls, and wounds could be visualized after the jumps by methylene blue staining and scanning electron microscopy. Improving attachment performance by indenting or piercing plant surfaces with sharp spines may represent a widespread but previously unrecognized strategy utilized by plant-living insects. This novel attachment mechanism may also provide inspiration for the design of robotic grippers.**

biomechanics | biomaterials | indentation | attachment | Auchenorrhyncha

## Introduction

Attachment devices used by climbing animals such as geckos, spiders and insects have outstanding properties that make them excellent models for biomimetics. The adhesives they use for locomotion are rapidly controllable, re-usable, and self-cleaning (1-6), and have therefore inspired new types of synthetic adhesives (7-10). However, many natural attachment systems are still unexplored.

Strong grip and highly dynamic surface attachment are particularly important for animals which jump to escape from predators or rapidly move through complex environments, and the action of jumping brings unique biomechanical challenges. Consequently, studying jumping animals may reveal novel solutions to biomechanical problems (11), and can also provide new insights into attachment mechanisms (12).

In this study we show that jumping froghoppers produce traction on plant surfaces by piercing them with sharp spines on their hind legs. The use of claws and spines for attachment is widespread in animals, and has inspired the foot design for walking and climbing robots (13-15). Previous studies have focused on the interlocking of spines with rough surfaces (16-18). However, little is still known about attachment by penetration of surfaces in robotic and natural systems, both in terms of the underlying mechanisms and the biological adaptations involved (but see 15, 19).

Most jumping insects live on plants, which can have smooth surfaces. Accelerating forward from such surfaces without slipping requires high friction forces. To allow forward jumps with

a take-off angle  $<45^\circ$  relative to the surface, the friction forces have to be larger than the normal load, implying that the friction coefficient between legs and the substrate must be very large ( $>1$ ). How do jumping insects avoid slipping during take-off?

Some of the fastest and most powerful jumps are performed by plant-sap sucking bugs of the order Hemiptera, which includes froghoppers, leafhoppers and planthoppers. *Philaenus spumarius* froghoppers use a catapult mechanism to reach extreme accelerations of 550 g and take-off velocities of up to 4.7 m s<sup>-1</sup> (20-22). In these jumps, the acceleration can last less than 1 millisecond. In a previous study, we showed that *Aphrodes bicinctus/makarovi* leafhoppers were able to jump from smooth glass substrates by briefly bringing some soft tarsal pads (platellae) on their hind legs into surface contact during the acceleration phase of the jump (12). In contrast, froghoppers such as *P. spumarius* lack soft platellae on their hind legs; they slipped when attempting to jump from glass, resulting in uncontrolled upward jumps with a rapid forward spin (12, 23). How, therefore, do froghoppers jump successfully from the plants on which they live? Smooth plant surfaces differ from glass in that they are more hydrophobic and softer (24, 25). In this study, we investigated how *P. spumarius* froghoppers are able to jump from smooth plant surfaces and hydrophobic polymer substrates, and the interaction between their hind feet and the substrate during the acceleration phase.

## Results

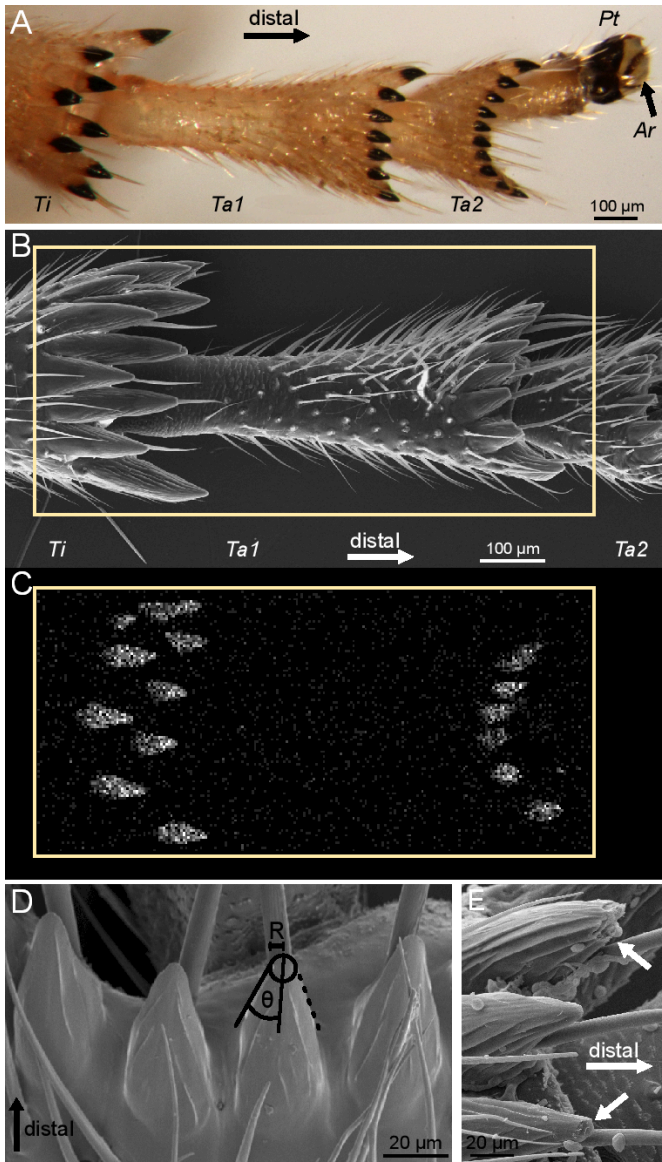
The feet of *Philaenus spumarius* froghoppers consist of three tarsal segments (tarsomeres) and a pretarsus with a pair of claws and an arolium between the claws (Fig. 1). The hind legs (but

### Significance

**Attachment mechanisms of climbing animals provide inspiration for biomimetics but many natural adaptations are still unexplored. Animals are known to grip by interlocking claws with rough surfaces, or engaging adhesive pads on smooth substrates. Here we report that insects can use a third, fundamentally different attachment mechanism on plant surfaces. When accelerating for jumps, froghoppers produce traction by piercing plant surfaces with sharp metal-enriched spines on their hind legs, deforming the cuticle plastically and leaving behind microscopic holes, like a biological nanoindenter. This mechanism depends on the substrate's hardness, and requires special adaptations of the cuticle at the spine tips. Piercing may represent a widespread attachment strategy among plant-living insects, promising inspiration for novel robotic grippers and climbers.**

### Reserved for Publication Footnotes

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**Fig. 1.** Hind leg morphology of *Philaenus spumarius* froghoppers. (A) ventral view of distal tibia and tarsus. The dark brown colour of the spines indicates strong sclerotization. (B) Scanning electron micrograph of hind leg (ventral view). (C) Energy-dispersive X-ray spectroscopy (EDX) scan of the same leg as in B, showing the location of zinc ( $K_{\alpha}$  X-ray emission) in the tips of the spines. Rectangle in B shows the area sampled in C. (D) Conical spines on the distal end of the first tarsal segment. (E) Broken spine tips on the first tarsal segment (arrows, ventral view). Ar: arolium, Pt: pretarsus, R: tip radius, Ta1: tarsomere 1, Ta2: tarsomere 2, Ti: tibia.

not the two other leg pairs) are equipped with arc-shaped rows of distally-oriented, strongly sclerotized spines, located ventrally on the distal margins of the tibia and first two tarsomeres. A single, long hair ("acutella"; 26) protrudes from the dorsal side of each spine. The spines are approximately conical (half opening angle  $18.5 \pm 3.2^\circ$ , 137 spines of 11 animals, Fig. 1D) and have sharp tips (tip radius of curvature  $3.6 \pm 1.0 \mu\text{m}$ , 115 spines without signs of wear of 11 animals). The tips of the spines are dark brown and more sclerotized than the lighter surrounding cuticle. Energy-dispersive X-ray spectroscopy analysis revealed that zinc is incorporated in the tips of the spines; zinc could be detected in the distal 50-85  $\mu\text{m}$  of each spine (Fig. 1C). One out of three froghoppers directly collected from the field and prepared for SEM had several spines with fractured tips, indicating that high

stresses are acting on them under natural conditions. In animals that were not immediately euthanized after capture, more spines were fractured and fractures were larger (Fig. 1E).

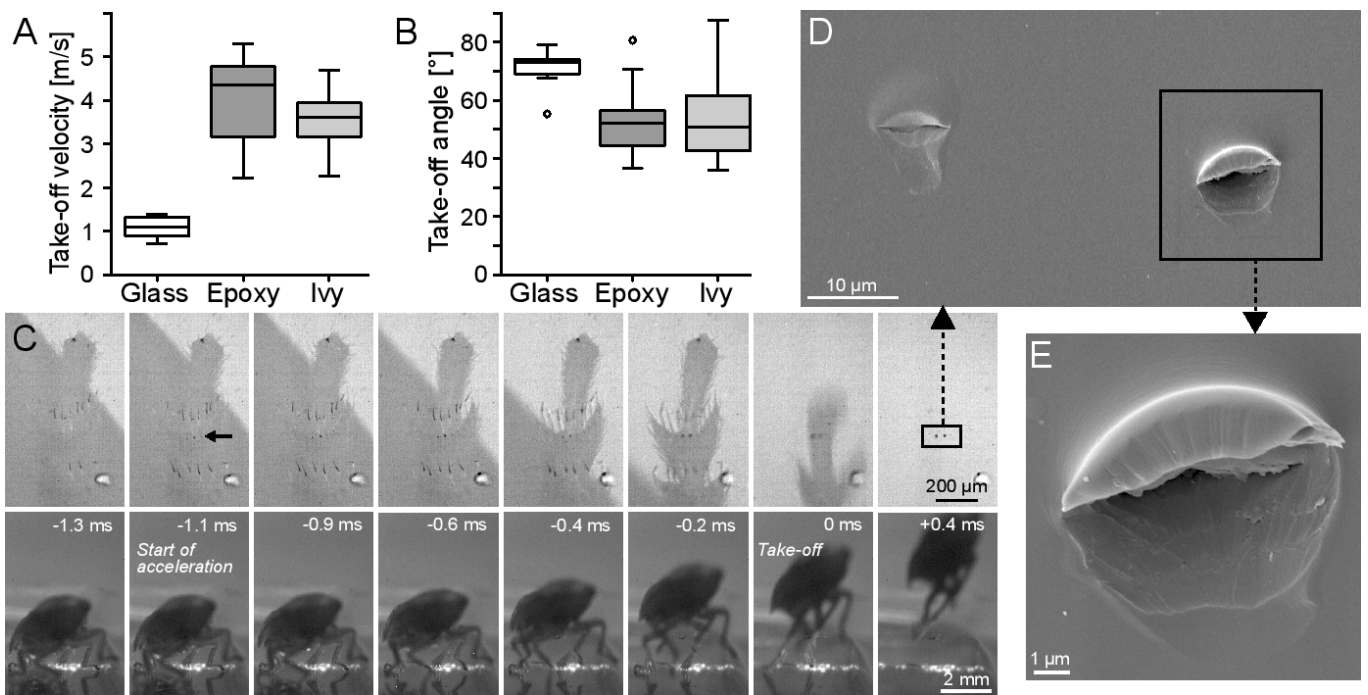
When *P. spumarius* froghoppers jumped from smooth glass surfaces, their hind legs always slipped, resulting in steep jumps with a rapid forward spin and a low take-off velocity (12). By contrast, *P. spumarius* froghoppers never slipped when jumping from smooth epoxy, resulting in fast jumps with a low take-off angle. Take-off velocity on epoxy ranged from 2.2 to 5.3  $\text{m s}^{-1}$  (mean:  $3.9 \pm 1.1 \text{ m s}^{-1}$ ; 11 jumps), much higher than for jumps from glass ( $1.1 \pm 0.2 \text{ m s}^{-1}$ ; Welch's t-test:  $t_{10,98} = 8.46$ ,  $p < 0.001$ ; Fig. 2A; data for glass from (12)); take-off angles ranged from  $36.6$  to  $80.7^\circ$  (mean:  $53.2 \pm 13.1^\circ$ , significantly lower than for jumps from glass ( $71.3 \pm 6.5^\circ$ ;  $t_{14,88} = 4.07$ ,  $p = 0.001$ ; Fig. 2B). The froghoppers avoided slipping on epoxy surfaces by plastically indenting the surface with the sharp zinc-enriched spines on their hind legs during the acceleration phase. Before the acceleration phase of the jump, the pretarsal arolium (in 6 out of 7 jumps) and acutellae on the first and second tarsomere (in 4 out of 7 jumps) contacted the surface. At the start of the acceleration (defined here as the first frame with a visible leg movement), 4 to 7 spines (per leg) on the first and second tarsomere indented the epoxy substrate (7 jumps by 5 froghoppers, Fig. 2C). The spines plastically deformed the epoxy so that the indentation marks remained visible in the substrate after take-off (Fig. 2D-E).

*P. spumarius* froghoppers were also able to jump from smooth plant surfaces (Movie S1). When jumping from ivy leaves, *P. spumarius* froghoppers never slipped and reached take-off velocities of  $3.6 \pm 0.6 \text{ m s}^{-1}$  in forward jumps, with take-off angles ranging from  $35.9$  to  $87.4^\circ$  (mean:  $53.6 \pm 14.1^\circ$ ; 2 jumps each by 12 froghoppers), both results similar to epoxy but significantly different from glass (take-off velocity: epoxy:  $t_{12,88} = 1.03$ ,  $p = 0.32$ ; glass:  $t_{31,93} = 17.40$ ,  $p < 0.001$ ; take-off angle: epoxy:  $t_{20,91} = 0.08$ ,  $p = 0.94$ ; glass:  $t_{31,56} = 5.01$ ,  $p < 0.001$ , Fig. 2A-B). After the froghoppers had jumped from the ivy leaves, subsequent staining with methylene blue always revealed 1 or 2 blue spots at the position of the first two tarsal segments of the hind legs during the acceleration phase, indicating that the surface had been perforated by the spines (41 jumps by 9 froghoppers from 10 leaves, Fig. 3A-C). Some smaller blue spots were also visible in other areas of the leaf, but these were also present in leaves where no froghoppers had jumped (Fig. 3C). The tracks left in the leaves by the froghoppers were also visible by scanning electron microscopy (Fig. 3D-F). Jumping froghoppers left between 3 and 9 indents per leg, which were arranged in the same way as the froghopper spines in 1 or 2 transverse, curved rows. Both the spacing between spines in each row and the distance between rows matched the dimensions of the spines on the first two tarsal segments of the froghoppers' hind legs as measured by SEM (spacing between spines on tarsomere 1, ivy tracks:  $57.2 \pm 14.6 \mu\text{m}$  ( $N = 4$  tarsomeres), hind tarsi:  $51.0 \pm 8.4 \mu\text{m}$  ( $N = 8$ ); spacing between spines on tarsomere 2: ivy tracks:  $39.3 \pm 9.2 \mu\text{m}$  ( $N = 4$ ), hind tarsi:  $38.2 \pm 6.9 \mu\text{m}$  ( $N = 8$ ); distance between tarsomere rows, ivy tracks:  $217.6 \pm 26.6 \mu\text{m}$  ( $N = 4$ ), hind tarsi:  $201.4 \pm 10.7 \mu\text{m}$  ( $N = 12$ ); see Fig. 3C-D). In 29 out of 34 indents from 9 jumps, the spines appeared to have penetrated the outer cell wall of the epidermis (see Fig. 3F).

**Discussion**

Insects employ a combination of different attachment mechanisms allowing them to live on plant surfaces. They use claws and spines to interlock with asperities on rough surfaces, and soft adhesive pads to cling to smooth substrates (27). Many insects also possess special "heel" pads on the tarsus that produce high friction when pressed against the substrate (12, 28-30). Our study shows that insects can use a fundamentally different mechanism to grip on smooth plant surfaces.

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**Fig. 2.** Take-off performance and foot-substrate interaction of *P. spumarius* whilst jumping. (A) Take-off velocity and (B) Take-off angle for jumps from smooth glass, smooth epoxy, and ivy leaves. (C) Images of a *P. spumarius* jumping from epoxy in side view, captured at 4700-frames- $s^{-1}$  (below), and ventral view using coaxial illumination (above). Before the jump, only acutellae and arolium were visible in surface contact. At the start of the acceleration phase, spines started to pierce into the surface and indentations remained visible even after the insect's take-off (arrow marks first visible indentation). Take-off was defined as the first frame in which the animal was airborne (time set to 0 ms), and start of acceleration as the frame with the first visible hind leg movements. (D, E) Scanning electron micrographs of the plastic deformation caused by the tarsal spines.

*Philaenus* froghoppers were able to perform powerful jumps with take-off angles as low as  $36^\circ$  from ivy leaves and smooth epoxy surfaces, but they slipped on glass (Fig 2 B). When accelerating for a jump, the sharp backward-pointing spines on the tibia and tarsus of their hind legs pierced the epoxy substrate and the ivy leaves, but not the glass surface.

Piercing involves plastic deformation or fracture of the substrate and depends mainly on the substrate's material properties rather than its topography (roughness) or wettability.

To investigate the substrate properties required for this interaction, we estimated the forces acting on a single spine during the acceleration phase of a jump. The force  $F_{body}$  in the direction of the jump can be calculated from the take-off velocity  $v$ , the acceleration time  $t$ , and the froghopper's mass  $m$  as  $F_{body} = mv/t$  (assuming constant acceleration). Assuming that both hind legs engaged the same number of spines and that all spines carried the same load, the four jumps where we simultaneously recorded both take-off angle/velocity and the number of spines in contact produced forces  $F_{spines}$  of 4.2 to 7.9 mN per spine.

A minimum estimate of the pressure at the tip of the spine is obtained by assuming that the tip is loaded uniformly; this pressure  $P_{mean} = F_{spines}/R^2\pi$  (where  $R = 3.6 \mu m$  is the spine tip radius) ranges from 103.2 to 194.0 MPa, significantly exceeding the compressive strength of epoxy (40 MPa) but not that of borosilicate glass (yield strength  $\sim 264$ – $384$  MPa; see 31)<sup>1</sup>.

This implies that the tip of the spine will plastically deform the substrate and sink in on epoxy but not on glass. Therefore, each froghopper spine acts like a conical nanoindenter that can determine the hardness of a material.

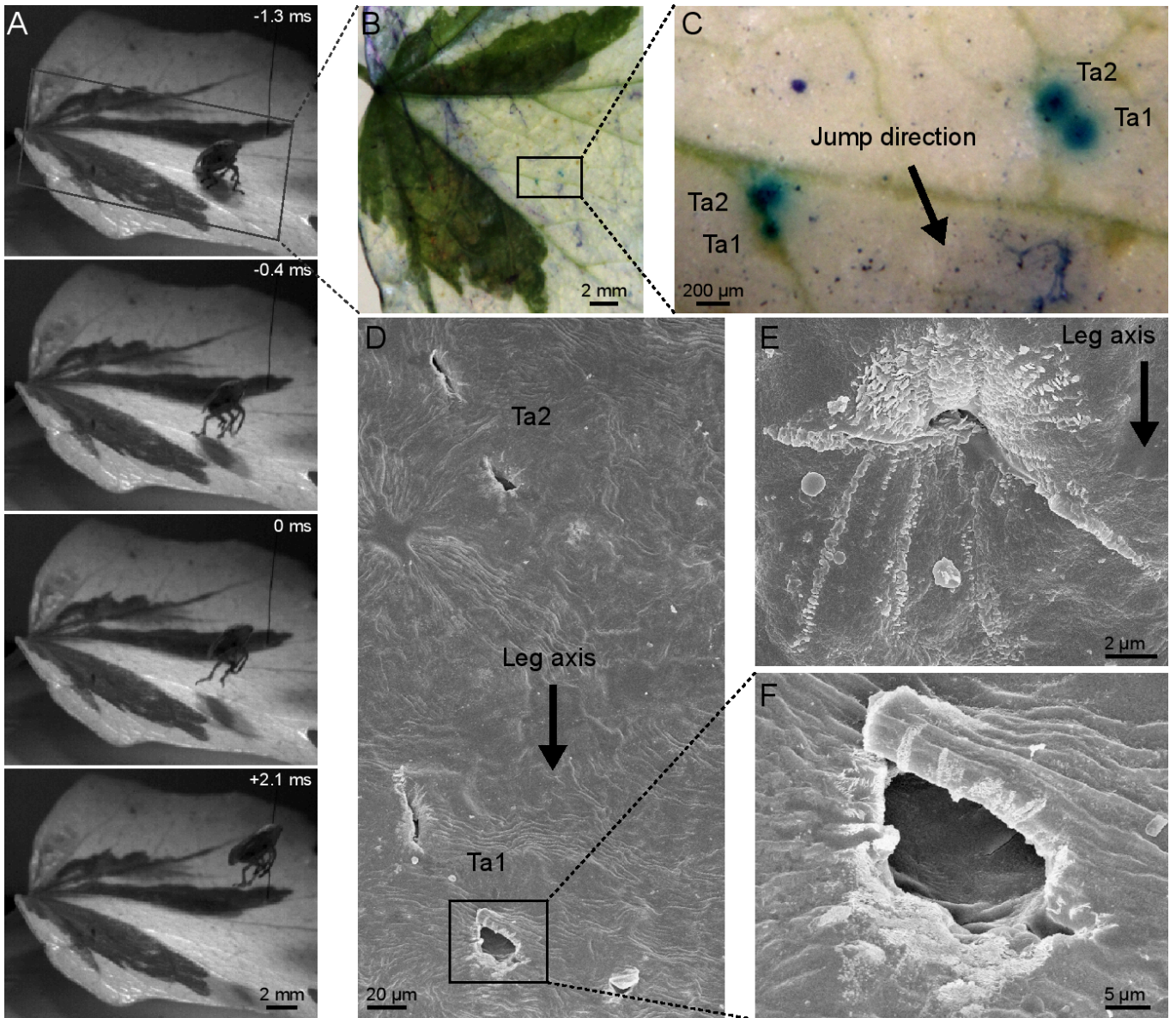
The stresses at the tips of froghopper spines also clearly exceed those needed to plastically deform and pierce natural plant surfaces. The strength of plant leaves measured by punch or tear tests ranged from 0.69 to 11.2 MPa (35). More localized nanoindentation measurements of leaf surfaces yielded higher

strengths (3–127 MPa; 36, 37), but these values were obtained from dried specimens and likely overestimate the strength of hydrated epidermis. In plants, compressive strengths exceeding the pressures produced by froghopper spines have only been reported from nanoindentation studies on specialized silica cells in rice leaves and bamboo stems (as high as 900 MPa; 37, 38), suggesting that only exceptionally hard plant surfaces could cause any difficulties for froghoppers.

The estimated pressure  $P_{mean}$  may also come close to the yield strength of sclerotized insect cuticle (ca 100–500 MPa; 39, 40). As the yield strength of epoxy and plant tissue is lower, however, these substrates will yield first and higher stresses may not be reached.

During attempted jumps from glass, however, the pressure at the spine tips may reach the level estimated above, and the contact pressure in the centre of the spine tip, calculated using the Hertz theory, is even higher (2.6 to 3.3 GPa; see equ. S6, Supporting Information). These high contact pressures therefore suggest that during a jump from glass, the tips of the spines should become plastically deformed or fractured.

However, the tips of the tibial and tarsal spines in *Philaenus* are adapted to minimise plastic deformation and fracture by the high zinc content of their tips (Fig. 1 C). Sclerotized insect cuticle with incorporated metals such as zinc and manganese has been found to exhibit increased hardness, corresponding to yield strengths as high as 500 MPa (39, 41, 42). Moreover, when *Philaenus* froghoppers slip on glass, most of the energy of the jump is dissipated by the rapid slipping and kicking of the hind legs. The body's kinetic energy is more than 9-fold reduced (12), and the 4-fold smaller take-off velocity may result in a proportional reduction in the pressure at the centre of the spines (ca. 0.6 to 0.8 GPa). Thus, the tips of the spines may still escape plastic deformation when they slip on glass substrates. Nevertheless, jumps from rough and hard substrates such as rocks



**Fig. 3.** Jumps of *P. spumarius* from ivy leaves and tracks left in the leaf surface. (A) Image sequence of *P. spumarius* jumping from variegated ivy leaf. (B, C) Same leaf stained with methylene blue after the jump in A, showing blue marks at the position of both hind feet during the jump. (D-F) Scanning electron micrographs of damage to leaf tissue left by frog hopper spines. Arrows point in the proximal direction of the leg, corresponding approximately to the jump direction. Ta1 and Ta2: indentations by spines on hind left tarsomeres 1 and 2.

would probably cause deformation, wear or fracture of the spine tips. As frog hoppers spend most of their life on plants, they will only rarely perform jumps from such substrates under natural conditions.

#### Ploughing friction model for spines on smooth substrates.

What friction forces can frog hopper spines achieve? When the spines sink into the substrate, their friction coefficient can be estimated using a simple theory proposed by Bowden and Tabor (43; and Supplementary Information) that considers a rigid conical spine with opening half-angle  $\theta$  in contact with a smooth surface of a softer, purely plastic material (Fig. S1)

$$\mu = \frac{\tau}{\sigma_y} + \frac{2}{\pi} \cot \theta \quad (1)$$

where  $\tau$  is the shear stress of the spine-substrate interface.

Estimating  $\tau \approx 0.1 \text{ MPa}$  for the shear stress of cuticle on epoxy (44, 45),  $\sigma_y \approx 40 \text{ MPa}$  and  $\theta \approx 18.5^\circ$ , it can be seen that the inter-

facial shear term is negligible compared to the ploughing term:  $\mu \approx 0.0025 + 1.9028 \approx 1.9053$ . With such a high friction coefficient, frog hoppers should be able to jump forward with take-off angles as low as  $\tan^{-1}(1/1.9053) \approx 27.7^\circ$ , consistent with the observation that *Philaenus* frog hoppers never slipped on epoxy.

The above estimate of the friction coefficient is a simplification for several reasons. First, the model considers a perpendicularly oriented conical spine, whereas frog hopper spines during the acceleration phase may be tilted by some angle. Second, the model considers a fully plastic substrate material (thereby potentially overestimating ploughing friction; 46) and ignores the shear resistance arising from material piling up ahead of the sliding cone (thereby potentially underestimating ploughing friction). These factors are considered in more complex models of ploughing friction (47) but difficult to quantify, and their opposite effects on friction may approximately cancel out.

545 Why do frog hopper spines slip on glass? The Hertzian esti- 613  
546 mate for the contact area of the spines (see equ. S7, Supplemen- 614  
547 tary Information) gives maximally  $3.6 \mu\text{m}^2$  on glass. Assuming  $45^\circ$  615  
548 jumps, producing the required forward thrust of 3.0 to 5.6 mN 616  
549 would involve shear stresses of 833 to 1555 MPa. These values 617  
550 exceed shear stresses measured for adhesive cuticle by at least two 618  
551 orders of magnitude (44, 45), confirming that the elastic increase 619  
552 in contact area alone is insufficient to produce the required 620  
553 friction forces. Only when stresses exceed the yield strength of the 621  
554 substrate can the spines plastically deform the substrate, thereby 622  
555 allowing high friction and jumps without slipping. 623

556 **Wider implications – biology and robotics.** All jumping in- 624  
557 sects living on plants face the challenge that they have to take 625  
558 off from surfaces which can be microscopically smooth (48, 49). 626  
559 To achieve large jump distances, take-off angles of  $45^\circ$  or slightly 627  
560 less are optimal (50), but such jumps require high forces parallel 628  
561 to the ground. For take-off angles  $<45^\circ$ , these shear forces have 629  
562 to exceed the normal force, which is only possible for friction 630  
563 coefficients ( $F_{\text{shear}}/F_{\text{normal}}$ ) greater than 1. However, friction co- 631  
564 efficients for rigid, dry surfaces are usually less than 1 (51), 632  
565 indicating that insects have to develop special adaptations to solve 633  
566 this biomechanical problem. 634

567 We recently showed that leafhoppers (*Aphrodes bicinctus/makarovi*, 635  
568 Cicadellidae) possess several soft, pad-like structures (platellae) on 636  
569 their hind tarsi, which contact the surface briefly during the accelera- 637  
570 tion phase of the jump, thereby producing the high friction forces 638  
571 required for a jump (12). Platellae are absent in frog hoppers, which explains why *Aphrodes* but not 639  
572 *Philaenus* were able to jump from smooth glass surfaces without 640  
573 slipping (12). On natural plant surfaces, however, *Philaenus* can 641  
574 jump successfully by piercing the surface with sharp spines. 642

575 Why have two lineages of the Hemiptera evolved such differ- 643  
576 ent solutions to the same problem? A key biomechanical differ- 644  
577 ence between *Philaenus* frog hoppers and *Aphrodes* leafhoppers 645  
578 is that *Philaenus* have hind legs 1.8 times shorter than *Aphrodes*, 646  
579 and that they accelerate with a 2.6 times higher force acting on 647  
580 the feet (21, 52). 648

581 Therefore, using soft, pad-like structures for jumping may not 649  
582 work for frog hoppers, as producing higher friction forces over 650  
583 a shorter acceleration time with adhesive pads would require 651  
584 these to have much larger contact areas, and to attach and 652  
585 detach extremely rapidly, thereby exposing these soft structures 653  
586 to significant damage and wear. 654

587 For *Aphrodes* leafhoppers, on the other hand, using spines 655  
588 to pierce plant surfaces may not be feasible as high forces and 656  
589 stresses are required to use this strategy efficiently. Moreover, 657  
590 *Aphrodes* possess very short spines at the same locations as those 658  
591 of *Philaenus*, and we did not detect any zinc in them, both 659  
592 factors making them even less suitable for piercing plant sur- 660  
593 faces. The tibial spines of *Aphrodes* leafhoppers are also flexibly 661  
594 articulated with the tibia whereas the spines are not hinged in 662  
595 *Philaenus* frog hoppers (12). It is likely that the compliant link- 663  
596 age in *Aphrodes* will help distribute the load between different 664  
597 spines and thereby reduce peak stresses, which will be beneficial 665  
598 for gripping on rough surfaces (a principle recently explored in 666  
599 climbing robots; 18). By contrast, the stiff, non-articulated spines 667  
600 in *Philaenus* may serve to concentrate stresses on a small number 668  
601 of spines, helpful for penetrating plant tissue. 669

602 *Aphrodes* could theoretically compensate for their lower 670  
603 jumping forces by developing sharper spines (with a  $\sqrt{2.6} \approx 1.6$  671  
604 times smaller tip radius, assuming that they have to achieve 672  
605 similar spine stress levels as *Philaenus*). However, such sharp 673  
606 structures might be at a high risk of fracture or wear during other 674  
607 types of locomotion. 675

608 The importance of tip strength is highlighted by the fact 676  
609 that some spine tips in *Philaenus* were broken (Fig. 1 E). The 677  
610 large number of spines on the tibia and the first two tarsomeres 678  
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612

613 provide some redundancy so that slipping is still prevented if a 614  
615 few individual spines have become blunt or have broken off. 616

617 The spines of frog hoppers may not only be adapted for high 618  
619 sharpness and strength, but also for preventing excessive pene- 620  
621 tration, in order to allow easy detachment. Sinking too deep into 622  
623 soft tissue may be avoided by the spines being relatively short and 624  
625 by the hairs protruding from their dorsal side (Fig. 1 A-B), which 626  
627 might act as penetration arresters. 628

629 Piercing of plant tissue by insects is common among plant 630  
631 sap-sucking insects and insects ovipositing in plant tissue. The 632  
633 mouthparts and ovipositors that pierce and cut into plant tissue 634  
635 also possess sharp tooth-like structures enriched with zinc and 636  
637 manganese, but the sensory, chemical and biomechanical adapta- 638  
639 tions are much more complex as they include mechanisms for 640  
641 continued cutting and targeted steering through plant tissue, pre- 642  
643 ventation of buckling, egg transport and deposition, fluid injection 644  
645 and drinking, and inhibition of plant defences (53-58). 646

647 Piercing of plant surfaces by sharp spines may represent a 648  
649 widespread attachment strategy but has been little documented. 649  
650 We are aware of only one report of a similar interaction in 651  
652 crawling caterpillars, where sharp claw-like crochets on the ab- 652  
653 dominal prolegs cut visible footprints into leaf tissue (59, 60), 653  
654 and it is still unclear under which biomechanical conditions these 654  
655 footprints are produced. Unlike the situation in hind legs during 655  
656 a jump, climbing insects can produce high forces against the 656  
657 substrate independent of their body acceleration by pulling to- 657  
658 gether opposite legs (adduction), potentially allowing their claws 658  
659 to grip by piercing. Future work should explore the distribution of 659  
660 this attachment mechanism among plant-living insects, and what 660  
661 adaptations insects and plants have evolved for it. 661

662 Our findings may provide biological inspiration for robotic 662  
663 grippers. Insect-inspired spines have been used to enhance sur- 663  
664 face attachment in wall-climbing robots (14); moreover, the im- 664  
665 proved traction mediated by spines of jumping locusts and crick- 665  
666 ets has inspired new foot designs for jumping robots (15, 19). 666  
667 Such robots can navigate large obstacles and could be used for 667  
668 search and rescue missions in disaster areas (61, 62). Generally, 668  
669 gripping smooth and plastic materials is an engineering challenge 669  
670 with many potential applications. Needle-grippers have been used 670  
671 for handling soft foodstuff such as meat and cakes (63), but could 671  
672 also be adapted for handling of plastic and cardboard packaging. 672  
673 Studying the detailed biomechanics of penetration-based grip 673  
674 in natural systems and the relevant adaptations in plants and 674  
675 insects may provide information for the design of new biomimetic 675  
676 grippers. 676

## 677 Materials and methods

678 **Animals.** A total of 57 adult *Philaenus spumarius* (Linnaeus, 1758) frog hop- 678  
679 pers were collected in and around Cambridge (UK) between late May and 679  
680 November (body mass:  $12.0 \pm 2.6$  mg; data given as mean  $\pm$  standard 680  
681 deviation unless stated otherwise). *P. spumarius* can be found on diverse 681  
682 plant species but were mostly collected from thistle (*Cirsium arvense*) and 682  
683 occasionally ivy (*Hedera helix*). Ivy leaves possess a smooth cuticle membrane 683  
684 (64, 65) with an elastic modulus of  $\approx 0.3$  GPa (64). To produce epoxy 684  
685 substrates for microscopy, glass coverslips were coated with low-viscosity 685  
686 epoxy (PX672H/NC, Robnor Resins, Swindon, UK; elastic modulus  $\approx 1.8$  GPa 686  
687 (66); compressive strength: 40 MPa, from technical data sheet). 687

688 **Morphology.** Hind legs of *P. spumarius* were investigated using light 688  
689 microscopy (Leica MZ 16, Leica Microsystems GmbH, Wetzlar, Germany) and 689  
690 scanning electron microscopy (SEM, see SI Materials and Methods). The 690  
691 presence of metals in tibial and tarsal spines was studied using energy- 691  
692 dispersive X-ray spectroscopy (EDX, see SI Materials and Methods). 691

692 **High-speed recordings of jumps.** Jumps were recorded with two syn- 692  
693 chronized Phantom V7.1 high-speed cameras (Vision Research, Wayne, USA) 693  
694 at 4700 frames per second. Frog hoppers jumped voluntarily or were gently 694  
695 stimulated to jump with a single human hair. To film jumps from transparent 695  
696 glass or epoxy substrates (glass coverslips coated with low-viscosity epoxy 695  
697 PX672H/NC; Robnor Resins, Swindon, UK; elastic modulus  $\approx 1.8$  GPa (66); 696  
698 compressive strength: 40 MPa, from technical data sheet), one camera 697  
699 recorded a side view while the other was attached to a Leica DMIRE2 698  
700 inverted microscope (Leica Microsystems GmbH, Wetzlar, Germany) to record 698  
701 the surface contact and movements of hind feet from below with high 699  
702 magnification and epi-illumination (5x lens; field of view: 3.6 mm x 2.7 mm). 700

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To film jumps from ivy leaves, the cameras were both oriented horizontally at an angle of 90° to each other to record side views of the jumps.

**Study of tracks left on leaf surfaces.** After froghoppers had jumped from ivy, the leaves were stained with 0.1% methylene blue to reveal possible foot marks and imaged using SEM (see SI Materials and Methods).

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Footnotes <sup>1</sup> In order to discuss the material's resistance to plastic deformation, we are using available literature values for compressive strength or yield strength, the latter being linearly related to the more commonly measured hardness:  $\sigma_y \approx H / 3$  (32-34).

1. Autumn K (2007) Gecko adhesion: structure, function, and applications. *MRS Bull* 32: 473-478.
2. Peattie A (2009) Functional demands of dynamic biological adhesion: an integrative approach. *J Comp Physiol B* 179: 231-239.
3. Federle W (2006) Why are so many adhesive pads hairy? *J Exp Biol* 209: 2611-2621.
4. Autumn K, Dittmore A, Santos D, Spenko M, Cutkosky M (2006) Frictional adhesion: a new angle on gecko attachment. *J Exp Biol* 209: 3569-3579.
5. Labonte D, Federle W (2016) Biomechanics of shear-sensitive adhesion in climbing animals: peeling, pre-tension and sliding-induced changes in interface strength. *J R Soc Interface* 13: 20160373.
6. Hansen WR, Autumn K (2005) Evidence for self-cleaning in gecko setae. *Proc Natl Acad Sci USA* 102: 385-389.
7. Bogue R (2008) Biomimetic adhesives: a review of recent developments. *Assembly Autom* 28: 282-288.
8. Hancock MJ, Sekeroglu K, Demirel MC (2012) Bioinspired directional surfaces for adhesion, wetting, and transport. *Adv Funct Mater* 22: 2223-2234.
9. Xue L, Steinhart M, Gorb SN (2013) Biological and bioinspired micro- and nanostructured adhesives. *Biomaterials Surface Science*, eds. Taubert A, Mano JF, Rodríguez-Cabello JC (Wiley-VCH, Weinheim, Germany), pp. 409-439.
10. Kamperman M, Kroner E, del Campo A, McMeeking RM, Arzt E (2010) Functional adhesive surfaces with "gecko" effect: the concept of contact splitting. *Adv Engin Mater* 12: 335-348.
11. Burrows M, Sutton G (2013) Interacting gears synchronize propulsive leg movements in a jumping insect. *Science* 341: 1254-1256.
12. Clemente CJ, Goetzke HH, Bullock JMR, Sutton GP, Burrows M, Federle W (2017) Jumping without slipping: leafhoppers (Hemiptera: Cicadellidae) possess special tarsal structures for jumping from smooth surfaces. *J R Soc Interface* 14: 20170022.
13. Spagna JC, Goldman DI, Lin P, Koditschek DE, Full RJ (2007) Distributed mechanical feedback in arthropods and robots simplifies control of rapid running on challenging terrain. *Bioinspir Biomim* 2: 9-18.
14. Provancher WR, Clark JE, Geisler B, Cutkosky MR (2005) Towards penetration-based clawed climbing. *Climbing and Walking Robots Proceedings of the 7th International Conference CLAWAR 2004*, eds. Armada M, González de Santos P (Springer Berlin Heidelberg), pp. 961-970.
15. Woodward MA, Sitti M (2018) Morphological intelligence counters foot slipping in the desert locust and dynamic robots. *Proc Natl Acad Sci USA* 115: E8358-E8367.
16. Dai Z, Gorb SN, Schwarz U (2002) Roughness-dependent friction force of the tarsal claw system in the beetle *Pachnoda marginata* (Coleoptera, Scarabaeidae). *J Exp Biol* 205: 2479-2488.
17. Patrick JG, Labonte D, Federle W (2018) Scaling of claw sharpness: mechanical constraints reduce attachment performance in walking insects. *J Exp Biol* 221: jeb188391.
18. Asbeck AT, Kim S, Cutkosky MR, Provancher WR, Lanzetta M (2006) Scaling hard vertical surfaces with compliant microspine arrays. *Int J Rob Res* 25: 1165-1179.
19. Lee JS (2018) in *Mechanical Engineering* (University of California, Berkeley, Berkeley).
20. Burrows M (2003) Froghopper insects leap to new heights. *Nature* 424: 509.
21. Burrows M (2006) Jumping performance of froghopper insects. *J Exp Biol* 209: 4607-4621.
22. Burrows M (2006) Morphology and action of the hind leg joints controlling jumping in froghopper insects. *J Exp Biol* 209: 4622-4637.
23. Sutton GP, Burrows M (2010) The mechanics of azimuth control in jumping by froghopper insects. *J Exp Biol* 213: 1406-1416.
24. Barthlott W, Neinhuis C, Cutler D, Ditsch F, Meusel I, Theisen I, Wilhelm H (1998) Classification and terminology of plant epicuticular waxes. *Bot J Linn Soc* 126: 237-260.
25. Lucas PW, Turner IM, Dominy NJ, Yamashita N (2000) Mechanical defenses to herbivory. *Ann Bot* 86: 913-920.
26. Emeljanov AF (1982) Structure and evolution of the tarsus in the Dictyopharidae (Homoptera). *Entomol Rev* 61: 44-59.
27. Gorb S (2001) *Attachment devices of insect cuticle*. (Kluwer Academic Publishers, Dordrecht, Boston).
28. Clemente CJ, Federle W (2008) Pushing versus pulling: division of labour between tarsal attachment pads in cockroaches. *Proc R Soc B* 275: 1329-1336.
29. Endlein T, Federle W (2015) On heels and toes: how ants climb with adhesive pads and tarsal friction hair arrays. *PLoS ONE* 10: e0141269.
30. Labonte D, Federle W (2013) Functionally different pads on the same foot allow control of attachment: stick insects have load-sensitive "heel" pads for friction and shear-sensitive "toe" pads for adhesion *PLoS ONE* 8: e81943.
31. Ashby MF, Shercliff H, Cebon D (2013) *Materials: engineering, science, processing and design*. (Butterworth-Heinemann, Oxford, UK).
32. Dugdale DS (1958) Vickers hardness and compressive strength. *J Mech Phys Solids* 6: 85-91.
33. Gilman JJ (1975) Relationship between impact yield stress and indentation hardness. *J Appl Phys* 46: 1435-1436.
34. Zhang P, Li SX, Zhang ZF (2011) General relationship between strength and hardness. *Mat Sci Eng A Struct* 529: 62-73.
35. Read J, Sanson GD (2003) Characterizing sclerophylly: the mechanical properties of a diverse range of leaf types. *New Phytol* 160: 81-99.
36. Wang S, Ren L, Liu Y, Han Z, Yang Y (2010) Mechanical characteristics of typical plant leaves. *J Bionic Eng* 7: 294-300.
37. Sato K, Ozaki N, Nakanishi K, Sugahara Y, Oaki Y, Salinas C, Herrera S, Kisailus D, Imai H (2017) Effects of nanostructured biosilica on rice plant mechanics. *RSC Advances* 7: 13065-13071.
38. Yu Z, Jiang Z, Zhang X, Yu Y (2016) Mechanical properties of silica cells in bamboo measured using in situ imaging nanoindentation. *Wood Fiber Sci* 48: 1-6.
39. Cribb BW, Lin CL, Rintoul L, Rasch R, Hasenpusch J, Huang H (2010) Hardness in arthropod exoskeletons in the absence of transition metals. *Acta Biomater* 6: 3152-3156.
40. Wegst UGK, Ashby MF (2004) The mechanical efficiency of natural materials. *Philos Mag* 84: 2167-2186.
41. Edwards AJ, Fawke JD, McClements JG, Smith SA, Wyeth P (1993) Correlation of zinc distribution and enhanced hardness in the mandibular cuticle of the leaf-cutting ant *Atta sexdens rubropilosa*. *Cell Biol Int* 17: 697-698.
42. Schofield RMS, Nesson MH, Richardson KA (2002) Tooth hardness increases with zinc-content in mandibles of young adult leaf-cutter ants. *Naturwiss* 89: 579-583.
43. Bowden FP, Tabor D (1950) *The friction and lubrication of solids*. (Oxford University Press, Oxford).
44. Federle W, Baumgartner W, Hölldobler B (2004) Biomechanics of ant adhesive pads: frictional forces are rate- and temperature-dependent. *J Exp Biol* 207: 67-74.
45. Drechsler P, Federle W (2006) Biomechanics of smooth adhesive pads in insects: Influence of tarsal secretion on attachment performance. *J Comp Physiol A* 192: 1213-1222.
46. Lafaye S, Gauthier C, Schirrer R (2006) The ploughing friction: analytical model with elastic recovery for a conical tip with a blunted spherical extremity. *Tribol Lett* 21: 95-99.
47. Mishra M, Egberts P, Bennewitz R, Szulafarska I (2012) Friction model for single-asperity elastic-plastic contacts. *Phys Rev B* 86: 045452.
48. Barthlott W, Mail M, Bhushan B, Koch K (2017) Plant surfaces: structures and functions for biomimetic innovations. *Nano-Micro Lett* 9: 23.
49. Riederer M, Müller C (2006) *Biology of the plant cuticle*. (Blackwell Publishing, Oxford UK).
50. Vogel S (2005) Living in a physical world II. The bio-ballistics of small projectiles. *J Biosci* 30: 167-175.
51. Rabinowicz E (1995) *Friction and wear of materials*. (Wiley, New York).
52. Burrows M (2007) Kinematics of jumping in leafhopper insects (Hemiptera, Auchenorrhyncha, Cicadellidae). *J Exp Biol* 210: 3579-3589.
53. Kundanati L, Gundiah N (2014) Biomechanics of substrate boring by fig wasps. *J Exp Biol* 217: 1946-1954.
54. Cerkenik U, van de Straat B, Gussekloo SWS, van Leeuwen JL (2017) Mechanisms of ovipositor insertion and steering of a parasitic wasp. *Proc Natl Acad Sci USA* 114: E7822-E7831.
55. Leopold RA, Freeman TP, Buckner JS, Nelson DR (2003) Mouthpart morphology and stylet penetration of host plants by the glassy-winged sharpshooter, *Homalodisca coagulata*, (Homoptera: Cicadellidae). *Arthropod Struct Dev* 32: 189-199.
56. Polidori C, García AJ, Nieves-Aldrey JL (2013) Breaking up the wall: metal-enrichment in ovipositors, but not in mandibles, co-varies with substrate hardness in gall-wasps and their associates. *PLoS ONE* 8: e70529.
57. Pollard DG (1973) Plant penetration by feeding aphids (Hemiptera, Aphidoidea): a review. *Bull Entomol Res* 62: 631-714.
58. Quicke DLJ, Wyeth P, Fawke JD, Basibuyuk HH, Vincent JFV (1998) Manganese and zinc in the ovipositors and mandibles of hymenopterous insects. *Zool J Linn Soc* 124: 387-396.
59. Bown AW, Hall DE, MacGregor KB (2002) Insect footsteps on leaves stimulate the accumulation of 4-Aminobutyrate and can be visualized through increased chlorophyll fluorescence and superoxide production. *Plant Physiol* 129: 1430-1434.
60. Hall D, MacGregor K, Nijse J, Bown A (2004) Footsteps from insect larvae damage leaf surfaces and initiate rapid responses. *Eur J Plant Pathol* 110: 441-447.
61. Lee JS, Plecnik M, Yang J-h, Fearing RS (2018) Self-engaging spined gripper with dynamic penetration and release for steep jumps. *IEEE International Conference on Robotics and Automation*
62. Kovač M, Schlegel M, Zufferey J-C, Floreano D (2010) Steerable miniature jumping robot. *Auton Robot* 28: 295-306.
63. Lien TK (2013) Gripper technologies for food industry robots. *Robotics and Automation in the Food Industry*, ed. Caldwell DG (Woodhead Publishing, Cambridge UK), pp. 143-170.
64. Wiedemann P, Neinhuis C (1998) Biomechanics of isolated plant cuticles. *Bot Acta* 111: 28-34.
65. Ensikat HJ, Boese M, Mader W, Barthlott W, Koch K (2006) Crystallinity of plant epicuticular waxes: electron and X-ray diffraction studies. *Chem Phys Lipids* 144: 45-59.
66. Zhou Y, Robinson A, Steiner U, Federle W (2014) Insect adhesion on rough surfaces: analysis of adhesive contact of smooth and hairy pads on transparent micro-structured substrates. *J R Soc Interface* 11: 20140499.