Liquid secretion and setal compliance: the beetle's winning combination for a robust and reversible adhesion

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Abstract

This paper is a brief review and discussion of the recent literature on the hairy adhesive pads of beetles, with the focus on two features of these pads, (i) compliant setal tips and (ii) a liquid secretion, that together guarantee robust cycles of attachment / detachment on smooth and rough substrates. The compliance is required to ensure sufficient contact between the setal tips and the substrate with a minimum of elastically stored energy at the contact interface. The secretion fills potential gaps between both surfaces, generates capillary adhesive forces, and enhances self-cleaning of these microstructures. Furthermore, the secretion might prevent setal dehydration and subsequently maintain setal tip compliancy. The paper also pinpoints a series of open questions on the physical mechanisms at play to passively regulate the contact forces developed by these hairy pads during locomotion.

Keywords: Hairy adhesive pads, setal, elastocapillarity, biomimetic adhesion, slender microstructures

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Highlights

- Robust adhesion results from combination of setal tip compliance and secretory fluid.
- Chemical composition of the fluid provides good wettability of diverse substrates.
- Adhesion could result from a balance of elastic, capillary and van der Waals forces.

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- The secretory fluid additionally prevents dehydration and enhances self-cleaning.

Introduction

In their evolution, insects have developed two distinctly different mechanisms to attach themselves to a variety of substrates: smooth pads (e.g. Blattodea, Phasmatodea, Orhtoptera, Thysanoptera, Hymenoptera) and setose (hairy) surfaces (e.g. Coleoptera, Dermaptera, Heteroptera, Diptera). These highly specialised structures are not restricted to one particular area of the leg. The hairy pads comprise slanted, fine and long cuticle outgrowths (setae) terminated by thin plate-like tips (spatulae) [1] (Fig. 1a-b). They may be located on different parts, including the claws, derivatives of the pretarsus, the tarsal apex, tarsomeres, or tibia. Phylogenetic analysis of the pad characters, processed together with characters of other organ systems, has aided in resolving the question of pad evolution and showed that these structures have evolved independently several times [2].

In this manuscript, we review two complementary features of coleopteran pads (taken as a model system) that are key to robust and reversible adhesion, namely the compliance of the setal tips and the production of a liquid secretion. After having presented the relevant physical properties of both setae and secretion, we consider the different contributions to the force that these pads generate. Finally, we briefly discuss the self-cleaning ability of the pads.

Compliant hairy pads

To generate sufficient adhesion on a surface, the adhesive pads need to establish an intimate contact with a minimum of stored elastic deformation energy at the interface [3]. On natural surfaces usually having roughness on different length scales, from the macroscopic (e.g. the size of an insect tarsus) to the macromolecular scale, this is rather difficult to achieve. However, the hairy adhesive pads seem to have evolved to overcome this difficulty [3, 4, 5]. The compliance (low bending stiffness) of individual setae allows to conform to large-scale roughness (i.e. larger than the size of spatulae) at minimal load (Fig. 1c), whereas the thin spatulae, which actually form the adhesive contact, are intended to adapt to the small-scale roughness (Fig. 1d).

However, there are inherent design constraints for a fibrillar structure that limit its mechanical stability. Depending on their density, aspect ratio, and materials flexibility, fibrils can collapse and form clusters with neighboring structures [4, 6, 7, 8, 9]. As a result, the ability of contact formation and thus adhesion can be reduced in subsequent adhesion cycles [10, 11]. Nevertheless, insects seem to be less susceptible to this problem, despite the significant density (one per cell, i.e. one every 100 μm^2) [12] and high aspect ratios of setae (up to 80 in the black earwig *Chelisoches morio* [13]). A possible explanation relies on the presence of material gradients along individual setae (Fig. 1e). The setal tips are soft and mainly composed of resilin-rich rubber-like protein material, whereas the central and basal parts mainly consist of the more rigid sclerotized cuticle material [14]. For setae of the seven-spotted ladybird beetle *Coccinella septempunctata*, such material gradient correlates with a gradient in Young's modulus E, from about $E \sim 1$ MPa at setal tip to about $E \sim 7$ GPa at setal basis [14]. Interestingly, similar gradients were also shown to occur in other hairy pads, e.g. flies [15] and stink bugs [16], suggesting a convergent evolution of this feature in various insect lineages [17]. For the further analysis, we restrict our discussion of insect adhesion to the hairy attachment system of beetles.

The addition of a liquid secretion

Beetles produce a liquid secretion that may fill roughness voids in the contact zone. Footprints of this secretion have been found for all insect groups studied to date [18]. It suggests that there is one capillary bridge between each setal tip (of surface area $S \sim 25\mu\mathrm{m}^2$ [19, 20]) and the substrate (Fig. 1b). Pads manually pressed to a substrate leave tiny droplets after pull off of the order of 1 fL per seta [19, 21, 22]. Assuming that each droplet results from the symmetrical rupture of a capillary bridge, the thickness H of this bridge would be $H \sim 80$ nm. However, a freely walking insect often leaves marginal footprints, so the liquid volume might be overestimated. The secretion complements the setal tip compliance in many different ways, that are discussed in the forthcoming sections. Hairy pad species for which the secretion is lacking had to come up with alternative strategies to generate significant contact on rough substrates. For example, the dry setae of geckos are hierarchical structures that subdivide several times into branches of smaller structures, down to the nanoscale at which intermolecular attraction forces can be significant [23].

Beetle footprints are mostly composed of n-alkanes, methyl-branched alkanes and alkenes [24, 25], possibly produced in dedicated glands at the setal basis [24]. It is unknown if the secretion is of identical composition, or if it contains additional compounds, e.g. a dispersed aqueous phase forming an emulsion. Moreover, the transportation of the secretion towards the capillary bridge is still unresolved, both in terms of transportation system (through setal lumen, through pore canals of the exo- and epicuticle, or through cuticle perforations associated to dermal glands [24]) and associated flow rate regulation [26]. The secretion exhibits a small contact angle on most substrates (e.g. less than 10^o on mica [27]) since its compounds are mostly non-polar. Moreover, these latter are similar to the cuticular lipids, which ensures an even stronger affinity for the pad cuticle (full wetting) and therefore reduces the risk that the secretion gets entirely soaked by a rough substrate [28].

The detected hydrocarbons are in the C25-C33 range [25], so they are mostly non-volatile. Consequently, they can form a barrier film that prevents dehydration within setal tips [29] and thus maintains their compliance [14]. The proportion of each hydrocarbon influences the dynamic viscosity μ of the secretion [22], which increases along with chain length, and decreases in presence of unsaturations (C=C double bonds) and methyl branches [30]. Estimations through

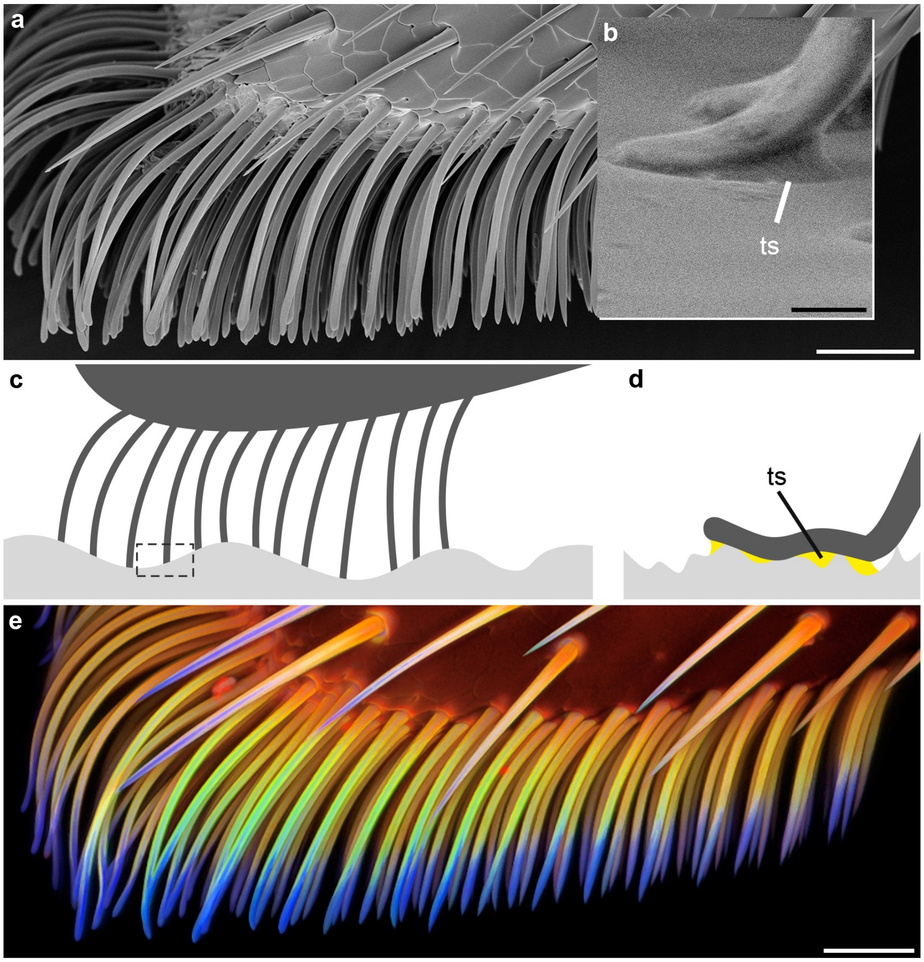
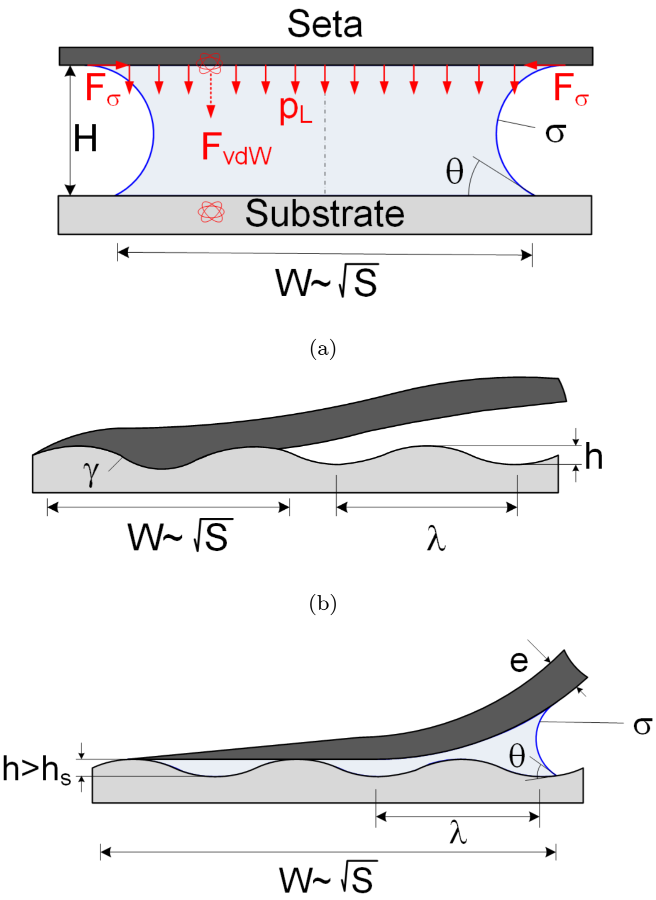


Figure 1: (a) Scanning electron micrograph of the ventral part of the second adhesive pad of a foreleg of a female *Coccinella septempunctata*, lateral view. (b) Cryo-SEM micrograph of an individual spatula-shaped seta in contact with smooth substrate. (c) Schematic illustration of how the hairy adhesive pad can conform a large-scale surface roughness. (d) Magnified view (see dashed rectangle in (c)) of an individual spatula-seta in contact with a surface exhibiting small-scale roughness. Yellow regions indicate tarsal secretion (ts). (e) Maximum intensity projection of a visualisation by Confocal Laser Scanning Microscopy, showing an overlay of four different autofluorescences, and indicating the presence of a material gradient along individual setae. The scale bars are 25 µm in (a,e) and 2 µm in (b). Images (a) and (e) are adapted from [14].

Brownian motion of submicron particles added to the secretion [31, 32] suggest that $\mu \sim 22$ mPa.s. However, the measured viscosity increases along with processing time, which betrays some evaporation of the most volatile hydrocarbons in the footprints [21]. So far, no viscoelastic behavior could be inferred from this observed Brownian motion [31, 32].

Adhesive forces



(a)

(b)

(c)

Figure 2: Hypothetic configurations of setal tips: (a) Flat and parallel to a smooth substrate, with an intervening liquid bridge. (b) Elastically deformed to match some sinusoidal roughness, (c) With a liquid bridge that fills the gaps.

Beetles must generate adhesive forces normal to the substrate, e.g. to balance their weight when they walk upside down. The measured adhesive force of a single setal tip is in the range of 0.5 μN [33, 34]. Adhesive van der Waals forces F_{vdW} between two parallel surfaces (Fig. 2a) scale as

$$F_{\mathrm{vdW}} \simeq \frac{AS}{6H^3} \quad , \tag{1}$$

where $A \sim 10^{-19}$J is the Hamaker constant associated to the interaction of the tip cuticle with the substrate, and H is the gap between both surfaces. In order to reach $F_{\mathrm{vdW}} \sim 0.5$μN, H must be smaller than about 10 nm, which would require that the setal tip matches the substrate roughness and that the secretion has sufficient time to be squeezed out from the contact zone.

The bridge formed by the secretion between the tip and the substrate yields capillary forces that can also be adhesive. If the bridge is assumed of constant thickness $H \ll \sqrt{S}$ [35, 36] and fully wetting the setal tip (Fig. 2a), the capillary force in the direction normal to the substrate results from the Laplace pressure associated to the interface curvature:

$$F_L = p_{\mathrm{Laplace}} S \simeq \frac{\sigma S(1+\cos\theta)}{H} \quad , \tag{2}$$

where $\sigma \sim 0.02$N/m is the surface tension of the secretion (first order approximation for hydrocarbons) and θ is the contact angle with the substrate. For the beetle setal tip, a thickness H as large as 2 μm could explain the measured force. It also rationalizes the observation that underwater adhesion is increased on immersed hydrophobic substrates (θ small), and decreased on immersed hydrophilic substrates (θ large) [37].

However, parallel plate models of adhesion are not very realistic, precisely because the setal tips are compliant. As their measured bending stiffness is about 0.5 N/m [33], they may experience a displacement of the order of 1 μm, comparable to their length, in response to adhesive forces. Consequently, setal tips are not initially parallel to the substrate, but are forced to bend and comply with it [19]. This induces a repulsive reaction force from the substrate that almost balances the Laplace pressure. The resulting force may nevertheless be adhesive, but it is rather of the order of $\sigma W \sim 1$ μN, where $W \sim \sqrt{S}$ is the setal width [19]. This order of magnitude is similar to the capillary force F_σ exerted at the contact line (Fig. 2a), as well as to the Kendall model for the stretching-dominated peeling of a dry tape (surface tension σ is then replaced by the work of solid-solid adhesion per unit surface γ) [38].

The liquid secretion may also serve to fill the gaps left in between the compliant setal tips and a rough substrate (Fig. 1b), thereby maintaining high adhesion forces. Without the secretion, the setal tip may comply to a substrate with 1-D periodic roughness [39] of profile $z = h\sin^2(\pi x/\lambda)$ if the corresponding elastic energy is less than the solid-solid adhesion energy γS (Fig. 2b). For a setal tip cross-section assumed homogenous and of average thickness $e \sim 500$ nm [40], the required bending energy U_b (proportional to the squared curvature of the deformed tip) would scale as $\pi^4 E e^3 h^2 S/(12\lambda^4)$ and the stretching energy U_s would scale as $\pi^4 E e h^4 S/(16\lambda^4)$. The latter is less than the former as soon as

$h < e$. Solid-solid adhesion is then possible if $U_b < \gamma S$, which yields

$$h < h_S = \frac{\lambda^2}{\pi^2}\sqrt{\frac{12\gamma}{Ee^3}} \tag{3}$$

On the other hand, a volume V of the secretion may fill the gaps up to a thickness $h_L \simeq 2V/S \simeq 160$ nm. Therefore, the liquid would be needed to mediate the contact as soon as $h_S < h < h_L$, which may occur for $\lambda < 1\mu\text{m}$ (Fig. 2c). The wax crystals on dock leafs *Rumex obtusifolius* would be in such configuration ($\lambda \sim 500$ nm, $h \sim 50$ nm, $h_S \sim 35$ nm) [41]. This scaling analysis may also explain the decreased maximum traction forces measured on wrinkled surfaces with $\lambda \simeq 900$ nm and $h \simeq 250$ nm [42]. In the extreme case where the substrate is porous and oleophilic, the secretion can be completely absorbed and the adhesion force is then diminished [43].

Friction forces

Beetles must generate friction forces parallel to the substrate, e.g. to balance their weight on a vertical wall. In controlled pad kinematics, maximum friction forces can be one order of magnitude higher than maximum adhesive forces [44]. A few tens of setae already generate enough friction to stop the proximal leg motion during attachment [20]. Moreover, in upside-down free walk, setae in contact do not often slide significantly [20]. It suggests that the tips experience large static friction (positive intercept of about 75 kPa in the relation between shear stress and shear rate) that cannot be explained by the hydrodynamic lubrication of a newtonian fluid [45, 18]. Contact angle hysteresis may give rise to a force tangent to the substrate, but it would only result in an equivalent shear stress of the order of $\sigma/W \sim 4$ kPa at most. An emulsion (with a dispersed phase, either aqueous or lipid-like) could behave as a non-newtonian Bingham fluid when confined [46], and so exhibit non-zero static friction [47]. Although there is currently no direct evidence of such emulsion for the beetle pads, the corresponding friction forces depend on humidity, which suggests that water could nevertheless be present in the contact zone [27]. The only other formulated hypothesis to explain static friction is the transition from the classical elasto-hydrodynamic lubrication regime (where there is a continuous liquid film separating the cuticle from the substrate) to the boundary / mixed lubrication regime (where there is local formation of dry rubber-like contacts between the cuticle and the substrate) [35, 48]. It is unknown in which lubrication regime the setal tips work, and it would certainly depend on both the volume of liquid in the bridge and the substrate roughness. The few setal tips that sometimes slide during the proximal pull at attachment may smear an excess of fluid on the substrate until the film transitions to this mixed lubrication regime [49, 20]. However, until now there is no experimental evidence for the occurrence of dewetting or direct contacts between the cuticle and the substrate [35], though it would be optically challenging to observe. Dry contacts might also induce abrasive damage of the cuticle, so the secretion could prevent premature wear

[14]. The wear repair is low in old insects, which results in a stiffer cuticle and a decrease of locomotion abilities [50].

Attachment and detachment kinematics

The adhesion of hairy pads is reversible. Indeed, contact forces must switch direction at every step. The control mechanism of the adhesion level is again not fully understood. It seems to result mostly from an appropriate kinematics of the pads, including peeling and twisting motions [20]. These motions induce a geometrical reconfiguration of the setal tips and a subsequent shift of their elastocapillary equilibrium, resulting in a possible modulation of the corresponding adhesion force [19]. Surprisingly, the kinematics is not time-reversible, as detachment is observed to occur on a timescale 10 times shorter than attachment (resp. 10 ms and 100 ms) [20]. Fast detachment, combined to some observed elastic loading induced during attachment, is correlated to a decreased amount of liquid left in footprints, which suggests that the kinematics might also be optimized for saving secretion from one step to the next [20].

Switching adhesion requires a timely drainage of the secretion in and out the intervening space. The associated timescale results from the balance of the driving force F (adhesion, pull-off) and viscous forces from the sheared fluid. Changing the gap $H(t)$ between parallel plates gives rise to a Stefan viscous force

$$F_S \sim \frac{\mu S^2}{H^3}\frac{dH}{dt}. \tag{4}$$

The timescale τ required for H to change significantly then scales as

$$\tau \sim \frac{H}{dH/dt} \sim \frac{\mu S^2}{H_0^2 F} \tag{5}$$

where H_0 is the initial gap thickness. The measured adhesion force per tip $F \sim 0.5\mu\text{N}$ yields a timescale $\tau \sim 4$ ms at $H_0 = 80$ nm (based on footprint volume), and $\tau \sim 275$ ms at $H_0 = 10$ nm (based on van der Waals forces). The former is in agreement with the detachment time observed for *G. viridula* [20], while the latter is prohibitively long compared to the walking pace. However, the parallel plate model is again a non-realistic representation of the setal tip, and a lubrication theory coupled to the elastocapillary model would yield a better estimation of the drainage timescale. In any case, this latter would increase with viscosity. Consequently, the size of hydrocarbon chains probably results from a compromise between low volatility and low viscosity.

Self-cleaning

Beetle's hairy pads are particularly efficient at self-cleaning, more than the smooth pads of other insects [51], and much more than gecko's dry hairy pads [52]. In a few steps, possibly with sliding [53], the wet hairy pads can be completely depleted from most contaminant particles. Only those of the order of 10 µm (i.e. the spacing between setae) tend to lodge in between the stalks. The exact way in which the secretion helps self-cleaning is not yet known, but many particles are found in footprint droplets [51]. The secretion could certainly behave as a lubricant that would favor the sliding of particles to the sides of the bridge [53]. On the other hand, viscous hydrodynamic forces would hardly be sufficient to detach a particle of size $R \lesssim H$ already in contact with the cuticle. Indeed, the ratio of viscous drag to JKR theory (Johnson, Kendall and Roberts) friction forces would scale as $(\mu U R)/(\gamma H) \ll 1$, U being the sliding velocity. In that case, a transition to the mixed lubrication regime would be necessary to remove these particles.

Conclusions and open questions

The adhesive pads of beetles are remarkable, not only because they can sustain several times the beetle's weight, but also because they are capable of a virtually infinite number of short attachment/detachment cycles, efficient on most surfaces. Different insect species have evolved independently towards a similar solution to manage terrestrial locomotion [2]. A key functional principle of these adhesive pads is the combination of the tuned compliance of fibrillar structures and the secretion of a liquid to mediate proper contact. In this short review, we discussed the advantages of this combination to maintain a robust adhesion on substrates with roughness at any length scale. We also pinpointed several open questions that require further physical characterization of the biological system, e.g. (1) the secretion rheology and the corresponding lubrication regime in the contact zone, (2) the secretion transportation (pathway and regulation), and (3) the control of adhesive forces. Finally, adhesive pads have been studied on an extremely small fraction of the estimated 300 000 beetle species, and it is unknown yet to which extend the adhesion strategy discussed herein varies across Coleoptera. However, all beetle species with adhesive pads studied so far contain hairy structures with specific terminal elements, material gradients and adhesive fluid. Therefore, the effects discussed here, might apply to the rest of Coleoptera.

Beyond reusable adhesives [54], beetle's pads could provide a solution to the challenge of downscaling robotics, including pick-and-place [55]. A biomimetic approach is appropriate, given the similar requirements of both natural and industrial systems. There have already been many attempts to mimic various aspects of hairy insect adhesive pads. Most studies focused on (1) dry fibrillar adhesives usually with micrometer-sized mushroom-shaped surface structures ([56] and refs. therein), (2) fabrication of functionally graded fibrillar adhesives [57], (3) mimicking the secretion itself [48], (4) mimicking the secretion process [58, 59], and (5) dry fibrillar adhesives under flooded conditions [60]. However, a thorough implementation of a controlled secretion supply in combination with compliant thin plate-like fibrillar tips has not yet been realized.

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Competing interests

We declare that we have no competing interest.

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Reference annotations

14 (Peisker *et al.*, 2013): Using Confocal Laser Scanning Microscopy and Atomic Force Microscopy nanoindentation, this study provides the first evidence of a material composition gradient and subsequent Young's modulus gradient in the longitudinal direction of the setae. The setal tips are sufficiently compliant to adapt to rough substrates, while the setal stalks are sufficiently rigid to prevent clustering.

19 (Gernay *et al.*, 2016): This paper investigates the bending of setal tips during contact in the presence of a secretory fluid, and provides a first elastocapillary model that rationalizes the observed adhesion levels.

20 (Gernay *et al.*, 2017): This paper provides a detailed kinematic analysis of the adhesion cycles of a walking beetle, from the scale of the legs to the scale of individual setal tips.

27 (Heepe *et al.*, 2016): This paper shows that friction forces are dependent on ambient humidity. It suggests that a dispersed aqueous phase in the wet contact zone, either secreted or simply adsorbed from the environment, may significantly affect the attachment dynamics.

33 (Bullock and Federle, 2011): This paper provides direct measurements of adhesion force and stiffness for individual setae in a leaf beetle. It highlights differences between spatulate, discoidal and pointed setal tips.

35 (Dirks, 2014): This paper is a review of the possible roles played by the liquid secretion. Among others, it sheds light on the unexplained static friction of the setal tips and suggests several potential rationales.

48 (Betz *et al.*, 2017): This paper investigates the tribometry of the secretion of smooth adhesive pads and its influence on attachment forces. The effect of natural secretion is compared to that of artificial fluids.

53 (Amador *et al.*, 2017): This paper quantifies the self-cleaning ability of wet hairy adhesive pads. It shows that in a free walk, beetles with soiled pads perform sliding movements to efficiently clean them.

56 (Heepe and Gorb, 2014): This paper reviews several biological attachment systems and their biomimetic counterparts, with a focus on mushroom-shaped micropillars. This geometry is particularly adapted to long-term reversible attachment. Adhesion and friction forces developed by these structures in various environmental conditions are discussed.

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