

RESEARCH ARTICLE

Surface roughness effects on attachment ability of the spider *Philodromus dispar* (Araneae, Philodromidae)

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SUMMARY

The morphology of the tarsal attachment system of the running spider *Philodromus dispar* Walckenaer 1826 (Araneae, Philodromidae) was studied using scanning electron microscopy and its performance was experimentally tested in traction force measurements. Each pretarsus bears a hierarchically built hairy adhesive pad that consists of a dense array of flattened setae covered with numerous microtrichia on the substrate-facing side. Microtrichia carry spatulate end tips that allow close contact with the substrate. Forces were estimated on tethered living specimens on rough epoxy resin surfaces (asperity size 0.3, 1, 3, 9 and 12 μm) and on a smooth surface as a control. A strong reduction in adhesion was observed for substrates with an asperity size of 0.3 and 1 μm . Comparison of the present data with previous results of different organisms demonstrates that the difference in force reduction on rough substrata depends on the dimensions of terminal contact elements (spatulae).

Key words: attachment, adhesion, friction, biomechanics, cuticle, microstructure, Arthropoda.

INTRODUCTION

Specialized tarsal setae with an attachment function have evolved independently several times among arthropods (Gorb and Beutel, 2001). They enable effective, dynamic attachment to various surfaces during locomotion. In hairy adhesive pads, the adhesive performance is enhanced by multiple contact sites (Jagota and Bennison, 2002), a high compliance of setae (Persson, 2003) and terminal contact elements (Persson and Gorb, 2003), and a hierarchical organization (Kim and Bushan, 2007; Gasparetto et al., 2009). Adhesion enhancement due to multiple contacts can be explained by the involvement of various effects, such as crack propagation prevention (Chung and Chaudhury, 2005) and surface roughness compatibility (Peressadko and Gorb, 2004a; Bhushan et al., 2006).

Under natural conditions, animals attach to unpredictable surfaces of very different roughness, which normally reduces adhesion even in the hairy attachment devices of geckos and insects. In previous work, it has been shown that there is a critical roughness causing a strong decrease in attachment ability depending on the size and shape of end plates that contact the substrate (Persson and Gorb, 2003). In experiments on the fly *Musca domestica* (Peressadko and Gorb, 2004b), the beetles *Leptinotarsa decemlineata* (Voigt et al., 2008) and *Gastrophysa viridula* (Bullock and Federle, 2011), and the lizard *Gekko gekko* (Huber et al., 2007), the critical roughness was revealed for substrates with an asperity size ranging from 0.3 to 1 μm .

Attachment devices of spiders (scopulae) occur only in wandering spiders that do not build orb webs for hunting their prey, such as members of the Salticidae, Philodromidae, Clubionidae, Sparassidae, Ctenidae and Zoridae families. Beyond Araneae, adhesive scopulae have also been reported from opilionids (Rambla, 1990). Scopulae located at the praetarsus are called claw tufts. Additionally, there are often tarsal and metatarsal scopulae located on the ventral and lateral sides of corresponding leg segments. The scopula has

previously been reported as a dry adhesive system that is not supplemented by fluid secretions (Roscoe and Walker, 1991). This feature, together with hierarchical organization, makes it more similar to the gecko adhesive system than to the hairy attachment devices of insects, such as flies and beetles. However, recently it was shown, with the help of interference reflection microscopy, that spiders can secrete a fluid in the contacts of their attachment pads (Peattie et al., 2011). But, in contrast to insects, spiders can adhere without the help of the fluid as it is apparent only occasionally. It remains unknown under what circumstances secretion occurs and how it contributes to adhesion.

In spiders, the terminal contact elements (spatulae) are larger (0.7 μm width) (Hill, 1977) than in geckos (0.2 μm) (Ruibal and Ernst, 1965), but smaller than in flies (1.8 μm) (Peressadko and Gorb, 2004b) and beetles (6 μm) (Voigt et al., 2008), whereas the density of the subcontacts is lower than in geckos but higher than in insects (Arzt et al., 2003; Peattie and Full, 2007). It has previously been shown that the spider scopula generates strong adhesion (Kesel et al., 2003) and friction (Niederegger and Gorb, 2006) on smooth substrates, but its attachment ability on rough surfaces remains unknown. Kesel and colleagues (Kesel et al., 2003) showed that spider adhesive pads have a huge safety factor (160 on a smooth surface). We have hypothesized that this is a compensation for strong limitations in the adhesive performance on micro-rough surfaces.

In this study, the performance of the attachment system of the running spider *Philodromus dispar* (Araneae, Philodromidae) was experimentally studied on substrates of varying roughness, in order to compare generated forces with those previously obtained from insects and geckos. Because of the branched organization of spider setae and lower dimensions of spatulae, a smaller reduction of attachment forces on surfaces with fine roughness was expected than found in insects. As the spider spatula size is larger than that in geckos, a correspondingly greater force reduction was expected.

MATERIALS AND METHODS

Animals

Philodromus dispar Walckenaer 1826 (Araneae, Philodromidae) is a widespread European spider that can easily be recognized by its sexual dimorphism, which is not typical of its family (Roberts, 1996). Body length ranges from 4 mm (males) to 5 mm (females). *Philodromus dispar* is a diurnal, ambushing hunter that can also rapidly run along plant surfaces. It has a well-developed claw scopula. Both sexes were collected from the vegetation at the New Botanical Garden, Christian Albrechts University of Kiel (Northern Germany) during May and June. Collected specimens were anaesthetized with carbon dioxide and spinnerets were sealed with a droplet of wax to prevent spinning silk that might potentially contaminate the scopulae. The animals were then weighed on an AG 204 Delta Range scale (Mettler Toledo GmbH, Greifensee, Switzerland). Females were more than twice the mass of males (25.3 ± 7.7 and 11.0 ± 0.8 mg, respectively; means \pm s.e.m.). The spiders were kept in plastic tubes at 22–24°C and a relative humidity of 40–50%, and fed with juvenile house crickets (*Acheta domesticus*), obtained from a local pet shop.

Substrate preparation

To exclude the influence of differences in the chemical properties of different substrates used in experiments, epoxy resin casts of a clean glass surface and polishing papers with defined asperity sizes (0.3, 1, 3, 9 and 12 μ m) were made using a two-step moulding method (Gorb, 2007). The finished substrate plates had a diameter of 9 cm and were stored in plastic containers under laboratory conditions. The roughness of these substrates has previously been characterized using three different methods: white light interferometry, atomic force microscopy and profilometry (Table 1) (Peressadko and Gorb, 2004b).

Traction force experiments

Specimens of *P. dispar* were anaesthetized with carbon dioxide. One end of a 15–20 cm long human hair was fixed with a droplet of molten wax on the prosoma. The other end of the hair was fixed onto a force sensor that was connected to a FORT-10 transducer (10 g capacity; World Precision Instruments Inc., Sarasota, FL, USA). Data were recorded using AcqKnowledge 3.7.0 software (Biopac Systems Ltd, Goleta, CA, USA). After recovering for 15 min, the animals were animated, with a slight push, to run in a direction perpendicular to the force sensor. When the spider started to pull on the hair, time–force curves were recorded. The generated traction force should depend on both the strength of the animal and adhesion to the substrate. As spiders did not pull continuously, only the three highest peaks of time–force curves generated during 5 min of the experiment were taken into account. The specimens tended to tire very quickly, after just a few pulls, and then rested with a

residual force of 0.6 mN. If the spider did not pull in the right direction, it was loosened and put back in its plastic tube to recover. More females ($N=11$) than males ($N=3$) were analysed because the males tended to change direction when running forward was prevented by tightening of the hair. The experiment was performed during the day at 24°C and 45% relative humidity. Substrates were presented in a random order. Data were tested with Kruskal–Wallis one-way ANOVA on ranks using Sigma Stat Software (Systat Software Inc., San José, CA, USA).

Scanning electron microscopy

The eight walking legs of two freshly killed spiders (one female and one male) were removed with a scalpel and air dried for 48 h. The samples were sputter-coated with 15 nm gold–palladium and viewed from ventral and lateral sides using a Hitachi S-4800 scanning electron microscope (SEM; Hitachi High-Technologies Corp., Tokyo, Japan) at 2.0–5.0 kV. Images were taken at magnifications of 400–35,000. The dimension of structures was measured with DatInf[®] Measure 2.1 software (DatInf GmbH, Tübingen, Germany).

RESULTS

Scanning electron microscopy

The claw tuft is oval shaped with a length of $123 \pm 18 \mu$ m ($N=13$) and a width of $88 \pm 15 \mu$ m (means \pm s.d.; $N=12$) in the resting position (Fig. 1a,b). The claw tuft is divided down the middle into two halves. The adhesive sides of the setae are orientated in a proximal direction in the distal parts of the claw tuft, but slightly rotated to the midline of the tuft in the proximal part. The scopula area increases from anterior to posterior legs while seta density decreases slightly. Female claw tufts had 32 ± 5 setae ($N=8$) covering an area of $8.5 (\pm 1.3) \times 10^3 \mu$ m² ($N=7$). Males are normally smaller, and bear 27 ± 3 setae ($N=5$) in a scopula area of $7.0 (\pm 1.3) \times 10^3 \mu$ m² ($N=5$). A seta emerges from a shaft with a diameter of about 5 μ m that is embedded at its base in an elliptic socket providing some freedom for deflection in a preferred direction. Setae are broader and longer in the distal part of the claw tuft. Proximal setae are $12.5 \pm 1.5 \mu$ m ($N=98$) broad and 35–70 μ m long, whereas distal ones are $19.2 \pm 2.6 \mu$ m ($N=110$) broad and 80–100 μ m long. The apically rounded and broadened part of a seta carries the setules, ~4 μ m long ventrally curved cuticle protuberances located at the ventral side of each seta. Distal setae bear 1037 ± 200 ($N=14$) setules; proximal setae have 631 ± 174 ($N=14$). The base of a single setula is about 0.3 μ m thick, which corresponds to the thickness of the tip of the seta. Close to its terminal plate (the spatula), each setula is about 0.17 μ m thick. Setules are more densely distributed in setae located in the proximal part of the claw tuft ($1.47 \pm 0.31 \mu$ m⁻²; $N=8$) than in those from its distal part ($1.19 \pm 0.17 \mu$ m⁻²; $N=8$). The spatulate end plate of each setula has a width of $0.82 \pm 0.08 \mu$ m ($N=165$) at its distal end and an

Table 1. Surface profile characteristics of the substrates

Nominal surface asperity diameter (mm)	R_a (nm)	r.m.s. (nm)	R_z (nm)
0 (smooth)	29.5 ± 3.5	36.2 ± 4.1	135.9 ± 24.3
0.3	74.0 ± 2.1	90.0 ± 2.7	450.1 ± 14.6
1.0	198.0 ± 4.7	238.4 ± 6.0	1071.3 ± 43.1
3.0	953.0 ± 105.7	1156.7 ± 133.1	5415.7 ± 590.2
9.0	2025.0 ± 63.7	2453.7 ± 87.2	11350.7 ± 446.6
12.0	2520.3 ± 136.5	3060.3 ± 207.7	14339.7 ± 1114.2

Data were obtained by scanning white light interferometry (Peressadko and Gorb, 2004b) and are presented as means \pm s.d., $N=9$.

R_a , roughness average (absolute value of the surface height averaged over the surface); r.m.s., root mean square or quadratic mean (a statistical measure of the magnitude of a varying quantity); R_z , determined roughness (average of N individual roughness depths over a specified length).

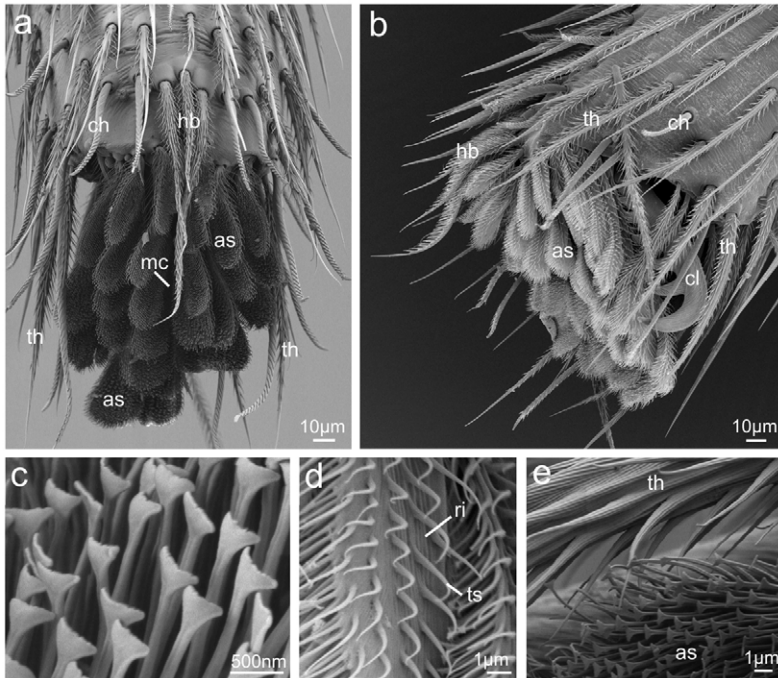


Fig. 1. Scanning electron microscope (SEM) micrographs of the pretarsus of *Philodromus dispar* (female). (a) Pretarsus of an anterior leg, ventral view. (b) Pretarsus of a posterior leg, lateral view. (c) Spatulae of an adhesive seta. (d) Back (non-adhesive dorsal side) of an adhesive seta. The surface is sculptured by microripples and covered by bent, tapered microtrichia. (e) Detail of a tactile hair and an adhesive seta. as, adhesive seta; ch, chemosensitive hair; cl, tarsal claw; hb, bunch of non-adhesive hairs; mc, median divide of the claw tuft; ri, longitudinal grooves; th, tactile hair; ts, tapered, bent microtrichia.

area of $0.18 \pm 0.05 \mu\text{m}^2$ ($N=50$). The size of the spatula is inversely correlated to the density. The $\sim 30\text{--}40\text{ nm}$ thick spatula is stabilized by slightly thickened lateral edges. Traces of abrasion in the form of minute notches were observed at the front edge of some spatulae.

The backing of the seta (dorsal side) is relatively smooth, but appears rippled at higher magnification (Fig. 1d). Additionally, there are rows of tapered microtrichia that are bent to the lateral sides of the seta.

When compared with other animals with hairy attachment devices, adhesive setae of *P. dispar* have rather similar geometrical parameters to those previously described for salticids *Phidippus audax* (Hill, 1977), *Portia fimbriata* (Foelix et al., 1984), *Salticus scenicus* (Roscoe and Walker, 1991), *Evarcha arcuata* (Kesel et al., 2003) and *Plexippus setipes* (Moon and Park, 2009), theraphosid *Aphonopelma seemanni* and ctenid *Cupiennius salei* (Niederegger and Gorb, 2006), although seta size and density differ slightly.

Traction force experiments

Measured force varied among the specimens; however, we could not normalize force data to animal weight because of the different amounts of food taken and the varying egg load in females. For this reason forces measured on various substrata were compared with forces generated by individual animals on the smooth substrate. As no structural differences were detected between attachment structures of females and males, data from the two sexes were pooled for data analysis.

The highest traction forces (10–14 mN) were achieved on the smooth substrate (Fig. 2). Adhesion was significantly reduced on all rough surfaces tested (Tukey's test with $P < 0.05$). A strong reduction in the observed traction forces occurred on substrates with an asperity size of 0.3, 1 and $3 \mu\text{m}$. On these surfaces, especially the substrate with an asperity size of $1 \mu\text{m}$, the tarsi often began to slide when the spider pulled itself forward, and the contact had to be renewed several times. On the substrates with an asperity size of 9 and $12 \mu\text{m}$, forces were lower than on the smooth surface, but significantly higher than on the $0.3\text{--}3 \mu\text{m}$ asperity size substrates.

DISCUSSION

Spatula dimensions and force reduction

The adhesion of a seta depends on the real contact area between two surfaces. Close contact is necessary for the action of intermolecular forces (Persson, 2003; Glassmaker et al., 2004). The spider cuticle consists of relatively stiff materials (chitin, arthropodin) (Barth, 1969; Barth, 1970; Barth, 1973). It can be assumed that these provide sufficient stability to spatulae and prevent collapsing of the spatula under load. However, spatulae are flexible enough because of their low thickness (about 30 nm). Such a geometry has a very low bending stiffness and therefore can adapt well to most surface profiles (Persson and Gorb, 2003; Varenberg et al., 2010) and thus generate strong contact forces (friction, adhesion). This prediction is well supported for spiders by the present experiment.

At higher grades of roughness (9 and $12 \mu\text{m}$ asperity size), the substrate profile on a scale of spatula size ($0.9 \mu\text{m}$) is similar to that of the flat substrate. However, the real contact area and the resulting adhesion force are lower than on the smooth substrate because the seta can adapt to the surface profile only to some extent (Fig. 3C). On surfaces with asperity sizes comparable to ($1 \mu\text{m}$) or smaller than ($0.3 \mu\text{m}$) the spatula dimension, such intimate contact cannot be achieved (Fig. 3B), which results in a loss of attachment ability.

Similar effects have previously been demonstrated in other hairy attachment devices of flies (Peressadko and Gorb, 2004b), beetles (Peressadko and Gorb, 2004b; Voigt et al., 2008; Hosoda and Gorb, 2011; Bullock and Federle, 2011) and geckos (Huber et al., 2007). All these studies have revealed the presence of a so-called critical roughness, where contact forces were strongly reduced. If we compare force reduction on the substrate with the smallest asperity size ($0.3 \mu\text{m}$) relative to the smooth surface for different animals, we clearly see that the degree of the force reduction tends to depend on the dimensions of the terminal elements: the larger the spatulae, the stronger the force reduction (Fig. 4). Assuming similar mechanical properties of the arthropod cuticle (Vincent and Wegst, 2004) and gecko keratin (Huber et al., 2008; Puthoff et al., 2010), one of the reasons for such an effect is that not only are the length

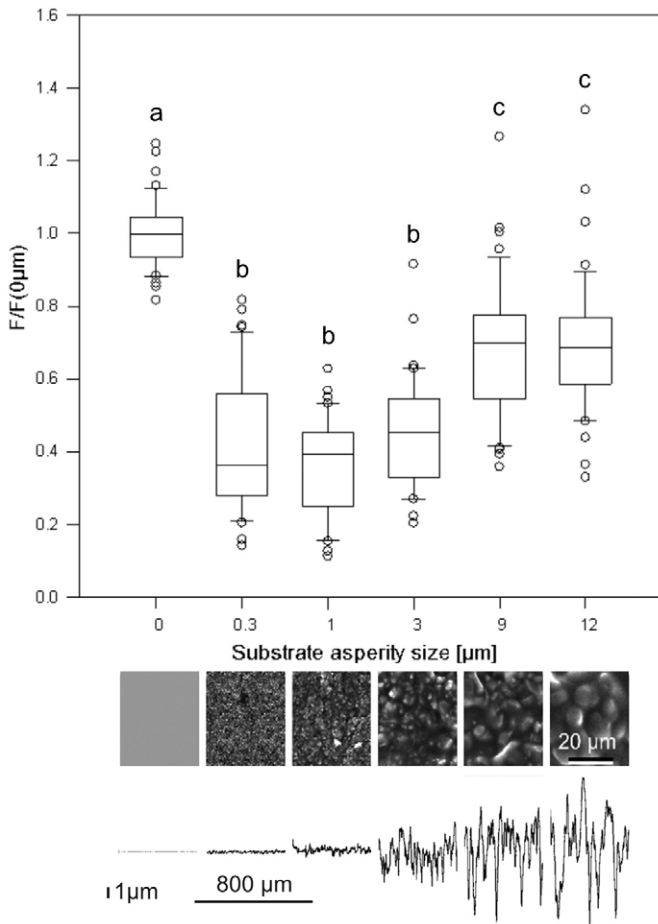


Fig. 2. Maximal traction force achieved by *P. dispar* on epoxy resin surfaces with different asperity sizes. Data are normalized to the individual average of traction force maxima obtained on the smooth surface. Box endings describe the 25th and 75th percentiles; the line within shows the median; error bars define the 10th and 90th percentiles; rest values are marked by single circles. Significant differences (Tukey's test with $P < 0.05$) are marked by different letters. Insets show SEM images and profiles of tested substrates (for details, see Table 1).

and width of the plate larger in insects than in geckos and spiders but also the thickness is greater, which is crucial for contact formation with rough substrata [beetle 400 nm (Eimüller et al., 2008), fly 180 nm (Bauchhens 1979; Gorb, 1998); spider 30–40 nm (estimated from this study); gecko 20 nm (Persson and Gorb, 2003; Huber et al., 2005)].

Are hairy attachment devices 'overbuilt'?

It has often been reported from measurements on single setae or spatulae that hairy adhesive systems must have an extremely high safety factor, which means that a small part of the attachment system would be sufficient to carry the body weight of the animal. For example, the lizard *G. gecko* can theoretically adhere to a glass ceiling by using only 0.03% of its setae (Autumn and Peattie, 2002), which means that the forces generated by all the setae together must be 30,000 times stronger than the body weight (safety factor). For the jumping spider *E. arcuata*, a safety factor of 160 has been found (Kesel et al., 2003). However, these numbers have never been demonstrated in experiments using the entire animal. One reason for this is that spatulae and setae can be partially damaged. Another reason is that all natural surfaces normally have different length

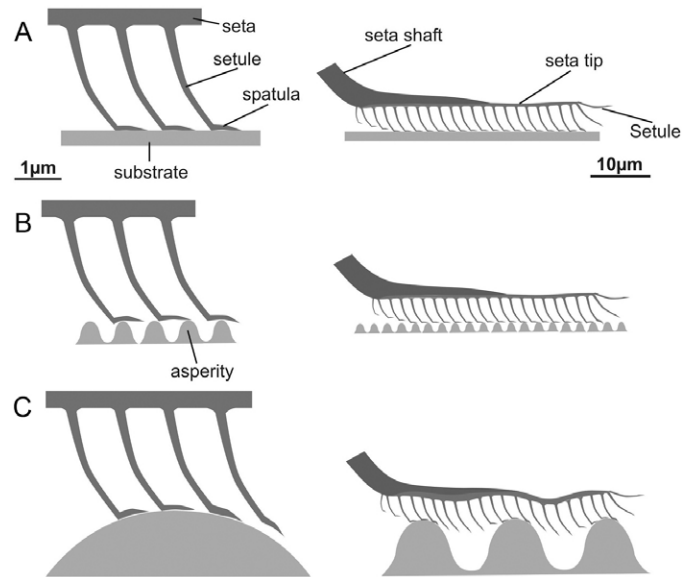


Fig. 3. Diagram explaining the reduction of the traction force on rough surfaces. Close contact between spider attachment devices and the substrate leads to force enhancement. This is only provided by flat structures, which, because of their low bending stiffness, can adapt to the surface profile (A,C). At an asperity size comparable with the size of the spatula, spatulae are not able to follow the substrate profile. Hypothetical contact geometry were viewed at the level of the spatula (left) or seta (right). (A) Smooth surface (no asperities). (B) Surface with an asperity size of 0.3 µm. (C) Surface with an asperity size of 9 µm.

scales of roughness. This means that the full adhesion force of a hairy attachment pad can never be achieved under natural conditions. Thus, hairy attachment systems are so strongly 'overbuilt', because during locomotion only a portion of the entire spatulae set comes into contact with the substrate and this has to generate sufficient adhesion to hold the body mass on an incline, wall or ceiling. The reason for the occurrence of scaling effects (larger number of subcontacts per unit area in attachment devices of heavier animal groups) (Artz et al., 2003) might be to compensate for the reduction of adhesion forces on small scale roughness. This is due to the increase of the real contact area at the level of single contacts and the increase of the overall crack length between the attachment pad and substrate (Varenberg et al., 2010). *Philodromus dispar* spiders can support their body weight and are capable of walking on rough walls and ceilings, although their attachment forces, as shown by the present study, are strongly reduced on these substrata.

Substrata with critical roughness naturally occur in some plants, preventing adhesion of insects with hairy attachment devices, for protection (Gorb et al., 2008; Gorb and Gorb, 2002), predation (Gaume et al., 2004; Gorb et al., 2005) or pollination (Oelschlägel et al., 2009). However, the mechanism of adhesion reduction is not only based on the roughness itself but also may include some contamination effects (Gorb and Gorb, 2006; Hosoda and Gorb, 2011) and adsorption of adhesive fluids (Gorb and Gorb, 2002; Bauer and Federle, 2009; Gorb et al., 2010).

Possible mechanism of prevention of self-sticking between setae

Small scale roughness might also play a role within the attachment system itself. Our SEM micrographs show that pretarsal microstructures, such as tactile hairs (Fig. 1e), claws and the back

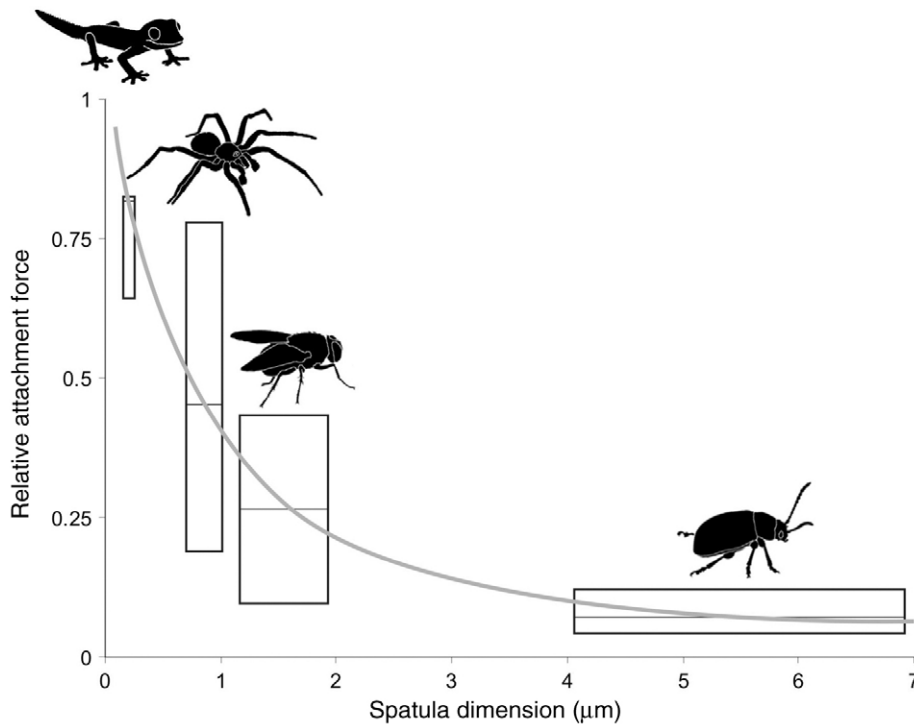


Fig. 4. Comparison of force reduction in hairy attachment devices of lizards *Gekko gekko* (Huber et al., 2007), spiders *P. dispar* (this study), flies *Musca domestica* (Peressadko and Gorb, 2004b) and beetles *Leptinotarsa decemlineata* (Voigt et al., 2008). Attachment forces on similar substrates with 0.3 µm asperity size are normalized to the forces measured on smooth surface. Force reduction increases with the size of the contact-forming element.

of adhesive setae (Fig. 1d) have a rippled surface with an approximate wavelength of 0.25 µm, which is in the range of the critical roughness for the adhesion system of *P. dispar*. The backs of the setae additionally bear short, bent, tapered microtrichia arranged in regular rows. It can be assumed that these microtrichia are non-adhesive as they lack spatulate tips and because of this they reduce the area in contact with spatulate tips of the neighbouring seta. Presumably, both described microstructures present an adaptation against self-mating (condensation, conglutination) of setae (Jagota and Bennison, 2002; Spolenak et al., 2005), which would reduce the effectiveness of the attachment device. Similar adaptations have previously been described for hairy attachment devices of Dermaptera (Haas and Gorb, 2004), beetles (Stork, 1980b; Federle, 2006) and reduviid bugs (Weihrach, 2007).

The role of claws on rough surfaces

The pretarsus of *P. dispar* bears two claws that provide a safe grip on rough surfaces. Experiments with beetles on rough surfaces showed that pretarsal claws can significantly increase friction, when asperity sizes are much bigger than the claw tip (Dai et al., 2002; Bullock and Federle, 2011). This can be explained by the interlocking of the claw tip with asperities as the claw is a relatively hard, inflexible structure (Dai et al., 2002). As the tip of the distal claw hook in *P. dispar* is 1.79±0.13 µm (N=4; obtained from the SEM micrographs), these may have had an influence on the traction force experiment at substrates with 3, 9 and 12 µm asperity sizes. This could be eliminated by the removal of claws, but that could easily damage the claw tuft, as claws are located close to the seta array. Furthermore, claws are connected with the pretarsal plate that bears the seta sockets and can be moved by the pretarsal levator and depressor (Hill, 1977). Claw amputation might destroy parts of this mechanism. For this reason such an ablation experiment was not carried out here. However, the results obtained on smooth surfaces and those with asperity sizes of 0.3 and 1 µm should hardly be affected, as no interlocking can be expected (Dai et al., 2002; Bullock and Federle, 2011).

CONCLUSIONS

Similar to previous studies on other organisms with hairy attachment systems (geckos, flies, beetles) the present study shows the existence of a critical roughness (0.3 µm, 1.0 µm). Comparison of the present data with previous results demonstrates that the force reduction of different organisms on rough substrata depends on the dimensions of terminal contact elements (spatulae). Both the microtrichia and longitudinal grooves at a dimension of 0.25 µm, observed on the back of each seta, are interpreted as the mechanism for the prevention of self-sticking between setae.

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