

Adhesion measurements on the attachment devices of the jumping spider *Evarcha arcuata*

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Summary

The feet of the jumping spider *Evarcha arcuata* attach to rough substrates using tarsal claws. On smooth surfaces, however, attachment is achieved by means of a claw tuft, the scopula. All eight feet bear a tarsal scopula, which is equipped with setae, these again being covered by numerous setules. In *E. arcuata*, an estimated 624 000 setules, with a mean contact area of $1.7 \times 10^5 \text{ nm}^2$, are present. The spider's entire contact area thus totals $1.06 \times 10^{11} \text{ nm}^2$. Adhesion to the substrate does not depend on the secretion of an adhesive fluid. Analysis *via* atomic

force microscopy (AFM) shows that a single setule can produce an adhesive force (F_a) of 38.12 nN perpendicular to a surface. Consequently, at a total F_a of $2.38 \times 10^{-2} \text{ N}$ and a mean body mass of 15.1 mg, a safety factor (SF; F_a/F_m , where F_m is weight) of 160 is achieved. Tenacity (τ_n ; F_a/A , where A is area of contact) amounts to $2.24 \times 10^5 \text{ N m}^{-2}$.

Key words: dry adhesion, ultrastructure, scopula, claw tuft, seta, setule, safety factor, atomic force microscopy, scanning electron microscopy, spider, *Evarcha arcuata*.

Introduction

Feet are one of the primary points of contact between an animal and its environment. Consequently, they feature morphological adaptations required for survival of an animal in its natural habitat. Larger animals often minimise friction between the feet and the substratum during locomotion with hard-walled hooves and claws. In comparison, smaller animals maximise friction, and a variety of attachment devices has evolved accordingly. A broad diversity of coupling and clamp-like structures that ensure attachment to rough surfaces can be found (e.g. Nachtigall, 1974; Stork, 1980a; Gorb, 2001; Scherge and Gorb, 2001); other devices enable attachment to comparably smooth surfaces. These latter systems usually involve small-scale structural modifications and can be categorised into wet adhesion and dry adhesion systems. The former is present in frogs (e.g. Emerson and Diehl, 1980; Green, 1981; Hanna and Barnes, 1991) and many insects. Flies, for example, make use of an adhesive fluid that is secreted from specialised glands and pores (e.g. Hasenfuss, 1977; Bauchhenß, 1979; Walker et al., 1985; Gorb, 1998). Dry adhesion, on the other hand, is used by geckoes (e.g. *Gecko gecko*). The great adhesive capacity of these reptiles relies on ultrastructural specialisations of their foot pads (e.g. Ruibal and Ernst, 1965; Hiller, 1968; Williams and Peterson, 1982; Stork, 1983; Autumn et al., 2000).

An analogous ultrastructure is found in spiders. In addition to the tarsal claws, which are present on the tarsus of all spiders, adhesive hairs can be distinguished in many species. These adhesive hairs are either distributed over the entire tarsus, as for example in Lycosid spiders (Rovner, 1978), or concentrated on the pretarsus as a tuft (scopula) lying ventral

to the claws (Hill, 1977), as also found in the jumping spider *Evarcha arcuata* (Salticidae), where a scopula is found on each pretarsus. So far, the effectiveness of these attachment structures has not been analysed. In the present study, the adhesive force (F_a) of the cuticular scopula was analysed *via* atomic force microscopy. This method permits highly localised measurements of mechanical surface parameters (Binning et al., 1986; Radmacher et al., 1994) and, thus, for the first time, the determination of the adhesive characteristics of the tiny terminal ends (setules) that supply the initial contact area with the substrate (Fig. 1).

Materials and methods

Animals

Spiders of the species *Evarcha arcuata* Clerck (Salticidae) were collected near Saarbrücken (south-western Germany), weighed and kept frozen until scanning electron microscopy (SEM) preparation. Atomic force microscopy (AFM) analyses were carried out on recently captured, untreated individuals.

Scanning electron microscopy

Prior to SEM studies, individuals were dehydrated in ascending acetone concentrations (70%, 80%, 90%, 100%), cleaned with ultrasound, critical-point-dried (CPD 030 Critical Point Dryer; Bal-Tec, Witten/Ruhr, Germany) and sputter-coated with gold (SCD 005 Sputter Coater; Bal-Tec). Specimens were examined in high vacuum using a Zeiss DSM 940A electron microscope at 10–15 kV.

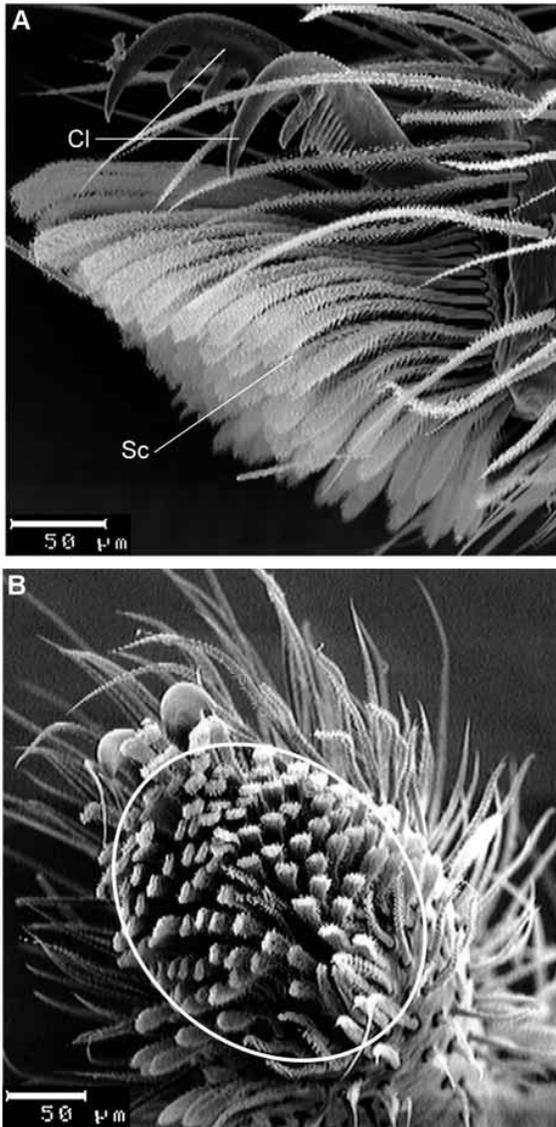


Fig. 1. (A) Lateral view of the tarsal adhesive apparatus of *E. arcuata*, showing both claws (Cl) and the scopula (Sc). (B) Ventral view of the scopula; the differentiation into single setae is clearly visible. The plotted oval is used to estimate the scopula area (here: $3.2 \times 10^4 \mu\text{m}^2$; mean: $3.7 \times 10^4 \mu\text{m}^2$).

Atomic force microscopy

In order to carry out adhesion measurements with AFM, untreated individuals captured shortly before use were supinely embedded in 5-min epoxide resin (R&G GmbH, Waldenbuch, Germany). Scopula hairs were kept free of the embedding medium. To ensure that the mechanical properties of the setules were not altered by a covering layer of epoxide, capillary rise of the fluid resin between the setules was avoided by a short waiting period prior to embedding of specimens (resin curing time approximately 1.5 min). Further preparations were not necessary for this measuring technique. Measurements were accomplished under ambient conditions (23°C; 45% air humidity).

A commercial AFM (Topometrix® Explorer; controller software SPMLab 4.01; Santa Clara, CA, USA) was used to measure the adhesive force of the terminal setule contact area. Pointspectroscopy was performed in order to obtain data. In doing so, a highly local contact between certain defined points on the sample and the instrument's probe was established. According to Hartmann (1991), this application of ATM is especially suitable for determining van der Waals forces of samples. In this case, the probe was an ultrathin silicon–nitride cone, mounted on a cantilever. Prior to the actual probing of the setule surface, the cantilever was lowered towards a glass surface and tapped onto the latter. Due to this dynamic contact, the cone-shaped probe tip was flattened, which allowed us to assume a two-dimensional, flat contact area for the probe tip when interacting with the setules. Probe tip area ($3.6 \times 10^5 \text{ nm}^2$) was determined using SEM, as was the successful flattening of the probe tip. The cantilever had a spring constant of 5.95 N m^{-1} .

At a constant velocity (0.5 m s^{-1}), the probe was slowly brought into contact with the sample and then retracted, passing through a predetermined traverse path (l ; 200–400 nm; maximum error, $\pm 4 \text{ nm}$). Contact was made perpendicular to the ventral surface of the scopula. The traverse path l was registered by a linearised scanner (EX 179807) via strain gauge. Due to the probe's low driving velocity, load application was taken as quasi-static (Burnham and Kulik, 1999).

During probe–sample contact, the cantilever was deflected, in turn leading to the deflection of a laser beam that was projected on the upper surface of the cantilever. Laser deflection was measured by the change in current of a photodetector. This change in current served as a measurement signal directly related to the traverse path and was recorded by an internal data processor. The current changes were converted to force values based on a previous calibration of the instrument. The calibration of the experimental set-up was accomplished by applying known masses to the cantilever and recording the occurring current alterations. A calculated regression equation obtained in this process served as a calibration curve. The internal AFM measurement error for the registered forces accounted for a maximum of 10%. No further data processing was performed. Data were plotted as a force–distance curve in which the readings of the ‘pull-off’ forces during spontaneous detachment of probe and sample represented the adhesive force F_a between the two (Fig. 4; Radmacher et al., 1994). Control measurements were conducted on glass as well as with the epoxide used (resin curing time approximately 1 h under ambient conditions).

Results

Scanning electron microscopy

In *E. arcuata*, no additional claws or coupling structures other than the above-mentioned tarsal claws were found on any of the feet. As was to be expected, however, all eight feet were equipped with a tuft-like scopula ventral to the claws (Fig. 1).

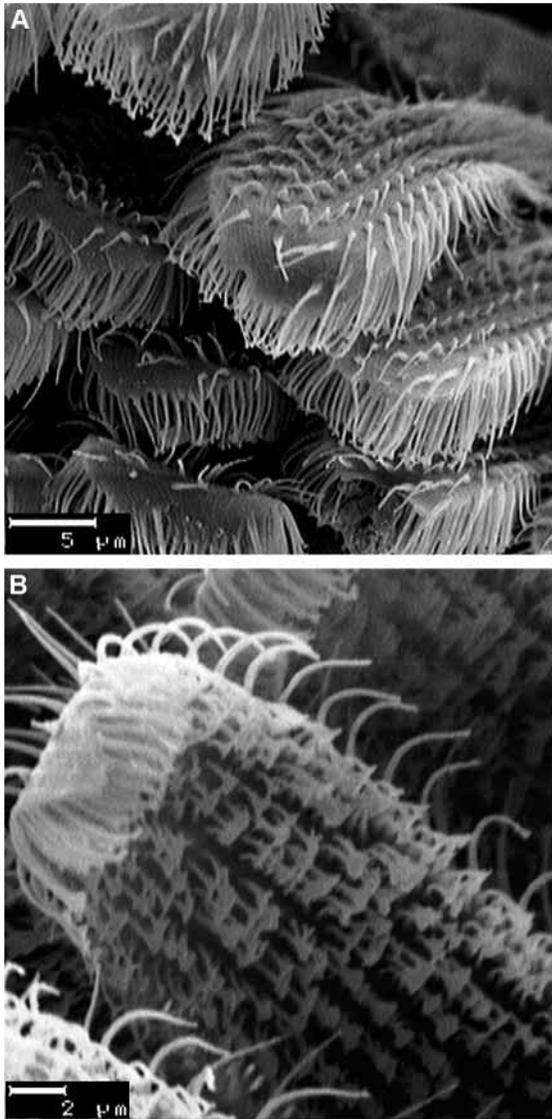


Fig. 2. (A) Each seta is covered by numerous setules, which are tapered on the seta's dorsal side. (B) On the seta's ventral side, the setule density is noticeably higher. Here, setules are broadened towards their ends, forming a sail-like shape.

The scopulae were composed of single setae, which were covered by numerous tiny cuticular processes (setules; Fig. 2). Setule tips on the ventral side of the setae were broadened towards their distal end, forming a flattened triangular surface with a mean area of $1.7 \times 10^5 \pm 0.34 \times 10^5 \text{ nm}^2$ ($N=7$; Fig. 3). These tips represent the direct points of contact with the substrate. Setule density is clearly lower on the dorsal side of the setae, and single setules are not broadened at their distal end but taper down to a point.

With a mean setule density of $2.1 \pm 1.0 \text{ setules } \mu\text{m}^{-2}$ ($N=48$) or $2.1 \times 10^6 \text{ setules mm}^{-2}$ on the setae's ventral side and an estimated scopula area of $0.037 \pm 0.008 \text{ mm}^2$ ($N=4$) per scopula, a single foot is provided with roughly 78 000 setules. This gives a total of more than 624 000 possible contact points with a substratum for all eight feet.

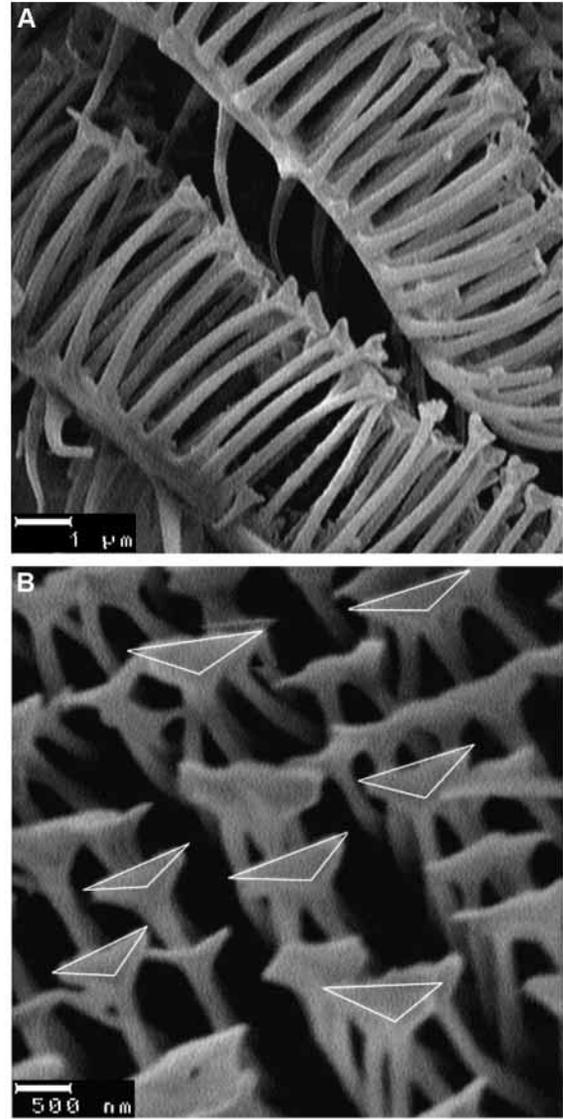


Fig. 3. (A) The terminal setule broadening represents the contact point between the spider and the substrate. (B) A setule density of $1.5 \text{ setules } \mu\text{m}^{-2}$ (mean setule density: $2.1 \pm 1.0 \text{ setules } \mu\text{m}^{-2}$; $N=48$) as well as a mean setule area of $1 \times 10^5 \text{ nm}^2$ ($\pm 0.34 \times 10^5 \text{ nm}^2$; $N=7$) can be calculated from the above figure.

Atomic force microscopy

Using the recorded data from pointspectroscopy (Table 1), as well as estimates of areas obtained from the SEM micrographs, the total force of adhesion, F_a , was calculated as follows.

The contact area of the probe tip ($3.6 \times 10^5 \text{ nm}^2$) was clearly larger than the surface area of the setule tips ($1.7 \times 10^5 \text{ nm}^2$; see Fig. 3). Thus, the possibility arises that the probe tip comes into contact with more than one setule at a time. Such multiple events are easily identified by their 'stepped' pull-off character, and curves that contained such multiple pull-off events were not taken into consideration for the further calculation of adhesive forces. Therefore, we assume that the terminal setule

Table 1. Adhesive forces taken from force–distance curves

	Force of adhesion	
	Mean \pm s.d. (nN)	<i>N</i>
Glass	1315.50 \pm 23.3	20
Epoxide	443.72 \pm 145.2	19
Setula	38.12 \pm 14.6	45

tip represents the relevant adhesive contact area. A mean F_a of 38.12 \pm 14.6 nN ($N=45$; Fig. 4) was obtained from the force–distance curves of the AFM measurements. Thus, the mean adhesion was 38.12 nN per setule.

Given an estimated 78 000 setules or contact points per scopula, a single foot is calculated to produce an adhesive force of 2.97×10^{-3} N when contact to the substrate is maximal. Providing that all eight feet or, respectively, all eight scopulae are in full contact with the underlying surface, adhesion perpendicular to the substrate would measure 2.38×10^{-2} N, and the tenacity [τ_n ; the ratio of F_a to contact area (A)] would then be 2.24×10^5 N m $^{-2}$.

E. arcuata has a mean body mass of 15.1 \pm 1.96 mg ($N=8$), which corresponds to a weight (F_m) of 1.48×10^{-4} N. Consequently, the adhesive force of *E. arcuata* is 160 times its weight when maximum contact with a surface is achieved.

Discussion

SEM analysis – design and material

As a typical representative of the Dionycha, only two main claws are present on the pretarsus of *E. arcuata*. A smaller middle hook as well as other claws or hairs with analogous functions to those described in Araneids (Foelix, 1992) are absent. The comparatively simple design of the tarsal claw apparatus can be interpreted as an adaptation to a roaming and hunting lifestyle. Jumping spiders do not build webs and hence do not require specialisations for handling silk threads. Therefore, no bristled hairs or accessory claws have developed.

However, an attachment system with such an organisation of setae and setules possesses an enormous adaptability to any given substrate and results in the largest possible contact area between the two. In particular, the setose elements, with setal lengths ranging between 100 μ m and 280 μ m, setule lengths of 3–4 μ m, a setule stem diameter of 0.2 μ m and the setule tip surface area of approximately 0.17 μ m 2 provide the geometrical features required for this high adaptability.

Fine-scale specialisation of tarsal elements to such a high degree is not uncommon in arthropods, yet in *E. arcuata* it reaches a level that is far more differentiated than so far described in other arthropods, e.g. insects. Setal length in marmelade hoverfly *Episyrphus balteatus* (Syrphidae), for example, measures merely 34 μ m, with a stem diameter of approximately 0.5 μ m (Gorb, 1998), and setal branching is usually totally absent. Thus, *E. arcuata*, with 624 000 contact points, ranges clearly higher than the data documented for insects. When the latter possess setose structures beside their

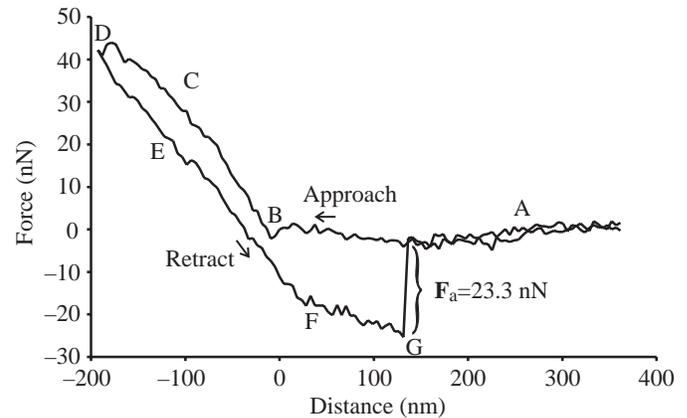


Fig. 4. Original registration of a force–distance curve recorded on a single setule. Points labelled in the diagram are as follows: (A) Probe not in contact with sample. (B) Contact between probe and sample is established. (C) The sample is indented by the probe with a defined force, F . (D) Turning point (F =maximum), retraction begins. (E) During retraction, the force between the probe and the sample decreases. (F) Due to adhesive forces, the probe remains in contact with the sample during retraction. (G) Contact abruptly breaks off ('pull-off' event); the registered force value during this sudden cantilever instability represents the adhesive force F_a [here: 23.3 nN; mean (\pm s.d.) for all measurements: 38.12 \pm 14.6 nN; $N=45$].

tarsal claws and not just adhesive pads, as in, for example, the Aphidae, Hymenoptera and Orthoptera, 5000–42 000 contact points were found in *E. balteatus* and the blowfly *Calliphora vomitoria*, respectively (Gorb, 1998; Walker et al., 1985). Only tortoise beetle *Hemisphaerota cyanea*, with its 120 000 points of contact, reaches a comparable order of magnitude (Attygalle et al., 2000; Eisner and Aneshansley, 2000).

The number of contact points to the substrate in *E. arcuata* even seems above average for Araneae. In zebra spider *Salticus scenicus* (Salticidae), which is comparable in size and body mass, whole animals are reported to have only 211 000 setules, with a terminal setule surface area of only approximately 0.048 μ m 2 (Roscoe and Walker, 1991). Consequently, the total adhesive area in *S. scenicus* is only about 10% of that in *E. arcuata*.

Besides a high number of contact points, a soft material is required to conform to the substrate surface texture. Furthermore, in terms of material behaviour, viscose as well as elastic properties are demanded in order to attain an adequate number of attachment–detachment cycles. To date, few analyses of the mechanical properties of arthropod cuticle are available, in particular as far as material hardness is concerned. The few documented figures lie between 200 MPa and 400 MPa (Hillerton et al., 1982; Kreuz et al., 2000). The far better analysed material elasticity is distinguished by a high degree of variability. Values between 10^3 Pa (Vincent and Pentrice, 1973) and 10^{10} Pa (Jensen and Weis-Fogh, 1962) are stated for the Young's modulus of *Locusta* cuticle. Even less data are available for chelicerates. Recently, the rates of elasticity were determined for the alloscutum of the tick *Ixodes ricinus*, with

values ranging between 0.17 GPa and 1.5 GPa (Seidl, 2002). By integrating the rubber-like protein resilin in defined locations, further functionally adequate, high elasticities can be obtained in *I. ricinus* (Dillinger and Kesel, in press). Providing that the cuticular material of the attachment system possesses similar characteristics, it is supplied not only with the structural elements but also with the material properties required for a detailed reproduction of the substrate.

AFM analysis – adhesion and tenacity

As expected, the elaborate attachment system of *E. arcuata* results in a high adhesive force (2.4×10^5 N), with absolute values similar to those documented for larger and heavier animals such as the cockroach *Periplaneta americana* (Pell, cited in Walker, 1993). Thus, the body mass-related safety factor (SF; F_a/F_m) of 160 appears surprisingly high. Insects achieve factors of between 1.5 (*P. americana*; Pell, cited in Walker, 1993) and 50 (knotgrass leaf beetle *Chrysolina polita*; Stork, 1980b), although a safety factor of 146 has been reported (cocktail ants *Crematogaster spec*; Federle et al., 2000). In fact, the safety factor of *E. arcuata* is only exceeded by that of the beetle *Hemisphaerota cyanea*, which is temporarily able to adhere with a force 200 times its body mass (Attygale et al., 2000). The adhesive tenacity (τ) produced by insects is reportedly between 2×10^3 N m⁻² (great green bush cricket *Tettigonia viridissima*; Jiao et al., 2000) and 8×10^4 N m⁻² (*H. cyanea*; estimated from Attygale et al., 2000). Significantly higher values have been obtained when adhesive tenacity is measured parallel to (τ_p) rather than normal (τ_n) to the contact surface. Under these circumstances, additional friction forces contribute considerably to adhesion. With an adequate experimental set-up, Walker (1993) registered a τ_p of 28.6×10^4 N m⁻² for *C. vomitoria*, which was ten times larger than τ_n (2.9×10^4 N m⁻²). Thus, the τ_n (2.24×10^5 N m⁻²) for *E. arcuata*, gained by adhesion measurements perpendicular to a contact surface in the present study, lies approximately one order of magnitude above that described for insects. Comparably large adhesive capacities have, until now, only been documented for geckoes. The gecko's attachment system is remarkably similar to that of *E. arcuata*. Gecko adhesion is also made possible by a highly structured attachment system of comparable dimensions, and the keratin contact elements, the so-called spatulae, are also reported to be free of adhesive secretions (Ruibal and Ernst, 1965; Hiller, 1968; Stork, 1983). Although adhesive forces are not documented for single spatulae, they are for single setae and, with a τ of 5.76×10^5 N m⁻², these range within the same order of magnitude as measured here for *E. arcuata* (Autumn et al., 2002). Analogous to the findings in *Calliphora* (Walker et al., 1985; Walker, 1993) and Syrphids (Gorb et al., 2001), it was shown that a perpendicular preloading and subsequent pulling of the attachment system parallel to the substrate surface dramatically enhances the adhesive force in geckoes (Autumn et al., 2000). It can thus be concluded that friction forces dominate over all other possible adhesive forces in any attachment system. Nevertheless, dry adhesive mechanisms

seem superior to wet adhesive mechanisms with regard to the adhesive force perpendicular to surfaces.

The physical principle forming the basis for wet adhesion is surface tension of an adhesive secretion between the attachment device and substrate (Bauchhenß, 1979; Walker et al., 1985; Dixon et al., 1990; Walker, 1993). By contrast, van der Waals forces have recently been discussed for the dry adhesive system in geckoes (Autumn et al., 2000, 2002). These short-ranged forces are relatively independent of the materials in contact but demand close proximity (only a few nanometres) of the contacting areas. The ultrastructural design of the spider scopula shown here could allow such a close approach. As previously mentioned, pointspectroscopy, as carried out in this study, is a valid method for determining van der Waals forces (Hartmann, 1991). Thus, the measured 38.12 nN were interpreted as the mean van der Waals force of a single, isolated setule contact area. Admittedly, evidence still has to be provided as to whether adhesion to a substrate results from van der Waals forces in the living system.

In addition, it should be pointed out that the extremely high SF of 160 can only be attained if all 624 000 setules are in full contact with the substrate. This represents the upper limit. The same situation was observed in geckoes, for which the high total adhesive force was calculated from single seta measurements (Autumn et al., 2000, 2002). Experiments on live animals provided significantly reduced figures, with a tenacity of only 8.7×10^4 N m⁻² (Irschick et al., 1996). Analogous reductions can be expected for *E. arcuata*. Furthermore, the hunting lifestyle, especially the associated dynamics, substrate contamination, wear of the cuticular attachment devices and numerous other factors should result in a drastic decrease in adhesion. Nonetheless, even a significantly reduced SF should be sufficient to guarantee a secure grip on smooth plant surfaces as well as successful prey capture. As behavioural studies of salticids have shown, prey capture is even possible when hanging in an upside-down position with some of the feet holding on to the substrate while the other feet firmly cling to the prey.

The remarkable adhesive capacities presented for *E. arcuata* raise a final and important question: how does the spider detach its feet from a substrate? Although it is known that the animals do detach their front legs before jumping, a detailed study of the actual detachment process at the level of the scopula has yet to be performed. Further experiments are planned to address this issue.

List of symbols

A	contact area
F_a	adhesive force (N)
F_m	weight (N)
l	distance of AFM cantilever to sample (nm)
N	number of measurements
SF	safety factor
τ	tenacity (N m ⁻²)

τ_n tenacity normal to surface ($N\ m^{-2}$)
 τ_p tenacity parallel to surface ($N\ m^{-2}$)

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