Adhesion of Individual Attachment Setae of the Spider Cupiennius salei to Substrates With Different Roughness and Surface Energy

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Dynamic adhesion is a key ability for animals to climb smooth surfaces. Spiders evolved, convergent to geckos, a dry adhesive system made of setae branching into smaller microtrichia ending as spatulae. Several previous studies concentrated either on the whole adhesive claw tuft on the spider’s foot that consists of attachment setae or on the single adhesive contact elements, the microtrichia with spatula-shaped tips. Here, the adhesion of single setae of the spider Cupiennius salei was examined and the morphology of the pretarsus and the fine structure of the setae were studied in further detail. Using individual setae fixed to force sensing cantilevers, their adhesion at different contact angles with a glass substrate was measured as well as their adhesive performance on substrates with different roughness and on smooth surfaces with different surface energies. The results show an individual variability of the adhesive forces corresponding to the seta morphology and especially to the seta tip shape. The tip shapes of the setae vary largely even in neighboring setae of the pretarsal claw tuft that comprises approximately 2,400 setae. Regarding surface energy of the substrate, the adhesion force on hydrophobic polytetrafluoroethylene was 30% of that on a hydrophilic glass substrate, which points to the importance of both van der Waals interactions and hydrogen bonds in spider adhesion.

Keywords: adhesion, claw tuft, locomotion, pretarsus, scopula, spider hair, surface properties

INTRODUCTION

The ability to climb almost every surface is a big advantage for animals. Therefore, many species convergently evolved different types of adhesive footpads to perform locomotion even on smooth vertical surfaces. One of these types is a soft bubble based smooth adhesive system that has been discovered for example in Orthoptera, Hymenoptera, Solifugae and Scincidae. The second type are fibrillary/hairy, seta based adhesive pads found for example in Dipterans, Coleopterans, Araneae, Gekkonidae and Anolinae (Gorb and Heepe, 2017). Among the animal groups using fibrillar pads, the geckos (Gekkonidae) and spiders (Araneae) developed an exceptionally effective reversible adhesive system for so called “dry adhesion” that works without any sticky fluid involved. In geckos, the dry adhesive system consists of a multitude of keratinous setae that branch at the tips and are arranged in lamella on the toes (Rizzo et al., 2006). In spiders, the dry adhesive system for locomotion is located on the most distal leg parts (pretarsi) and made up of chitinous setae bundled in the so-called scopula claw tuft. From each of these setae, a multitude of microtrichia branch off, which are...
arranged densely close to the seta tips and face the substrate (Niederegger and Gorb, 2006; Schaber et al., 2019). As in geckos, the terminal contact elements of the setae are flat and thin platelet-shaped spatulae.

Adhesion of the dry attachment systems is enhanced by shearing, which promotes alignment of the spatulae with the substrate surface and increases the contact area for attractive van der Waals forces (Wulf and Gorb, 2013; Flennor et al., 2020). In the gecko, the adhesive force of a single seta strongly depends on its sliding in contact with a substrate. The adhesive force ranged from 0.6 µN without sliding, to 13.6 µN with sliding, and 194 µN at 5 µm sliding and a preload of 15 µN. Assuming that all setae were simultaneously and maximally attached, these data indicated an adhesive force of 100 N of the single gecko foot (Autumn et al., 2000). In the jumping spider Evracha arcuata, the adhesive force of a single spatula was measured to be 38 nN. The assumption that all spatulae were in contact resulted in an adhesive force that could support 173 times the body weight of the animal (Kesel et al., 2003; Kesel et al., 2004). In the Central American wandering spider species Cupiennius salei, which was also used in the present study, the adhesion of a single leg scopula on glass when shear force was applied was found to be 35 µN, which would suffice to hold an adult female animal on a vertical surface. However, the vertical pull-off force without shear preload was zero (Wohlfart et al., 2014). The arrangement of the spatulae on the setae was previously explained to be most important for the spider’s traction forces on different micro-rough substrates in the species Philodromus dispar (Wulf and Gorb, 2012a).

Up to now, the adhesive forces of the single spider setae that make up the adhesive scopula on the claw tufts of the spider remained unknown. To find out more on the interplay of the adhesive setae with different kinds of substrates, here we examined the morphology of the claw tuft and the setae and measured adhesion forces of individual setae on various characterized substrates with different surface energies and roughness and at different setal contact angles on glass.

MATERIALS AND METHODS

Animal Sample Preparation

Air-dried exuviae of the last molt of female wandering spiders of the species Cupiennius salei (Barth, 2002) were used for reflected light microscopy and scanning electron microscopy. Individual setae were plucked in the center of the pretarsal scopulae from automatized legs of adult female specimen that were bred and raised in the Department of Functional Morphology and Biomechanics at Kiel University and kept at temperatures between 20 and 25°C and relative humidity of 70–100%. For in vivo examination of adhesion, spiders were anesthetized and fixed upside-down to a sample holder using adhesive tape.

Surface Samples

Different rough surfaces with the same surface chemistry were fabricated in a two-step casting technique. First, casts were taken from glass slides, polishing papers with different defined roughness (P0.05, P1, P3, P9, and P12; Buehler Ltd., Lake Bluff, IL, United States) and sand papers (P800, P1500, P2500; Bauhaus GmbH, Mannheim Germany) using polyvinyl siloxane (Coltène President light body; Coltène Whaledent AG, Altstätten, Switzerland). In the second step, these negative impressions were cast using epoxy resin (low viscosity kit; Electron Microscopy Sciences, Hatfield, PA, United States). The smooth surfaces for testing adhesion at different surface energies were uncoated glass slides, silicon wafers, polytetrafluoroethylene (PTFE; Goodfellow Ltd. Huntingdon, United Kingdom), and epoxy resin casts of glass slides.

Microscopy

Reflected light microscopy was performed using a Leica M205A microscope equipped with a Leica DFC420 camera (Leica Microsystems GmbH, Wetzlar, Germany) in multifocus imaging mode. For scanning electron microscopy, single setae were fixed to the sample holders using conductive carbon adhesive tape. Whole pretarsi were additionally mounted using conductive carbon cement (LEIT-C; Plano GmbH, Wetzlar, Germany). The samples were examined without sputter coating using a Hitachi S-4800 (Hitachi Ltd., Tokyo, Japan) scanning electron microscope at an acceleration voltage of 3 kV or sputter coated with 10 nm gold-palladium using a Hitachi TM3000 at 15 kV. Plucked single setae were inspected in 70% ethanol cover slipped on glass slides using a transmitted light microscope (Axioplan; Carl Zeiss Microscopy GmbH, Jena, Germany) equipped with a digital camera (AxioCam MRc).

Surface Characterization

The surface energy and its polar and disperse shares were characterized on the four different smooth substrates using a contact angle measurement system (OCA20; DataPhysics Instruments, Filderstadt, Germany). The contact angle of three different liquids (double distilled water, diiodomethane, ethylene glycol) was measured on ten random spots of each substrate. The polar and disperse shares of the surface energy were calculated using the software of the instrument, and the mean values determined for each substrate.

For roughness characterization, 3D surface measurements were performed using a white light interferometer (NewView 6k; Zygo Corporation, Middlefield, Connecticut, United States). Using the software MetroPro (version 8.1.5) of the instrument, height maps were plotted and their surface roughness determined in µm as the root mean square deviation of the roughness profile (rms roughness).

Adhesion Force Measurements

Piezo-electric force sensing cantilevers (FMT-120b; Kleindiek Nanotechnik, Reutlingen, Germany) mounted on a micromanipulator (MM3A; Kleindiek Nanotechnik, Reutlingen, Germany) were calibrated by pushing the tip against a calibrated spring. Calibration curves were plotted from the cantilever deflection measured using white light interferometry and recordings of the corresponding voltage signal from the force measurement amplifier (FMS-01; Kleindiek Nanotechnik, Reutlingen, Germany). The sensitivities of the cantilevers were in the range between
2.7 μN V\(^{-1}\) and 6.5 μN V\(^{-1}\) (linear regression coefficients \(R^2 \geq 0.995\)).

The adhesion force measurements were performed under a reflected light microscope (LMS310; Carl Zeiss Microscopy GmbH, Jena, Germany) equipped with a digital camera (BLS 5 MP; BMS microscopes b.v., Capelle aan den IJssel, Netherlands). The cantilevers with single setae glued to their tips using polyvinyl siloxane as well as the substrates were arranged in side view. For the tests, the cantilevers were pushed vertically onto the substrate up to a force of 0.5 μN using the software NanoControl 3.1 (Kleindiek Nanotechnik, Reutlingen, Germany) and immediately pulled off. The sampling rate of the analogue/digital converter was set to 10 kHz and the data smoothened by a moving average calculation of 100 data points. The adhesion peaks just before the loss of contact between the setae and the substrate were used for further analysis. All measurements were performed at temperatures between 22.8°C and 26.1°C and at relative humidity between 31 and 58.7%. For statistical analysis the software SigmaPlot (12.5; Systat Software, Inc. San Jose, CA, United States) and R Studio (R Studio Inc. Boston, United States) were used.

**RESULTS**

**Morphology of the Pretarsus**

Besides the adhesive setae of the scopula, on the pretarsus there are two claws for clamping on compliant and rough substrates. Additionally, in between of the claws there is a much shorter middle hook. The ventral side of the pretarsus is two-lobed and densely covered by the adhesive setae (Figure 1A). The seta tips of the pad form a rather flat sole-like surface that well gains contact with a substrate surface (Figure 1B). The setae show an increased curvature in their distal parts so that the angles at which their tips approach a substrate increase from approximately 45° in the proximal part of the scopula up to approximately 90° in the most distal part (Figure 1C).

**Morphology of the Adhesive Setae**

Using SEM on partly shaved pretarsi showed highly ordered regular arrangement of the setae of the scopulae. The single setae are densely covered with branching microtrichia. In the uppermost 30 μm of the seta, its shape appears flatter and the density of microtrichia increases, especially on the ventral side facing the substrate upon contact (Figure 2A). The distance between the seta tips amounts to 10–15 μm (Figure 2B). On the ventral side, the microtrichia of the tip regions consist of less than 1 μm thick narrowing stalks with flattened ends, the spatulae, that are responsible for building up contact with the substrate and generating adhesion force (Figure 2C). No spatulae were found on the dorsal sides of the setae. In the SEM, after some exposure to the electron beam, the previously separated spatulae attracted each other and congregated.

**Seta Adhesion at Different Contact Angles**

The individual setae used for the force measurements were plucked from the mid-region of the scopula. The three randomly selected setae clearly showed different curvatures and tip shapes (Figures 3A–C). For the determination of a significant angle for the measurements of adhesion on different substrates, the adhesion forces of the individual setae were measured at different contact angles with smooth glass (Figures 3D–F, 4). Seta 1 showed increasing adhesion with decreasing contact angles. With 412 ± 15 nN (mean ± standard deviation; \(n = 12\) measurements), adhesion was highest at an angle of 38°. However, because of the curvature of the seta, this angle could only be reached at the edge of the glass substrate. Therefore, the naturally more realistic angle of 45° was used for the further measurements. The measurements of adhesion for seta 2 showed a peak force of 277 ± 13 nN at approximately 61°, a smaller peak of 187 ± 16 nN at 72°, and constantly high values between 232 ± 10 nN and 319 ± 7 nN in the range from 83° to 97°. Here, the angle of 85° close to the force maximum was selected for the further measurements. The adhesion values of seta 3 did not vary as much as those of setae 1 and 2 and they were in the range between 120 ± 11 nN and
Seta Adhesion to Surfaces With Different Surface Energies

Substrate Surface Properties

The $\text{rms}$ roughness values for the four smooth substrates were $0.006 \pm 0.002 \mu m$ for the glass, $0.131 \pm 0.011 \mu m$ for the epoxy resin mold of the glass surface, $0.002 \pm 0.001 \mu m$ for the silicon, and $0.014 \pm 0.001 \mu m$ for the PTFE surface (mean values ± standard deviations of measurements on five different areas of the substrates).

The contact angles of water on the different smooth substrates indicated the strongest hydrophilicity for the glass surface with a contact angle of $31.9 \pm 11.6^\circ$ (mean ± standard deviation; $n = 10$). The epoxy resin and silicon surfaces were slightly hydrophilic with contact angles of $85.2 \pm 1.6^\circ$, and $84.9 \pm 4.6^\circ$, respectively. The PTFE surface showed hydrophobic properties with a contact angle of water of $103.9 \pm 3.8^\circ$.

The surface energies calculated from the contact angles of the different liquids showed the highest value for the hydrophilic glass surface with a total of $59.24 \text{ J m}^{-2}$ dominated by a polar share of $44.13 \text{ J m}^{-2}$ (74.5%), and a dispersive share of $15.11 \text{ J m}^{-2}$ (25.5%). The total values of the surface energy and the distribution of its shares were similar for the epoxy resin and the silicon surface. The values for the epoxy resin were $30.33 \text{ J m}^{-2}$ dominated by a dispersive share of $25.26 \text{ J m}^{-2}$ (83.3%), and a polar share of $5.07 \text{ J m}^{-2}$ (16.7%). The surface energy of the silicon surface was $28.45 \text{ J m}^{-2}$ with a dispersive share of $22.70 \text{ J m}^{-2}$ (79.8%) and a polar share of $5.75 \text{ J m}^{-2}$ (20.2%). The lowest value of surface energy was found for the hydrophobic PTFE with $18.07 \text{ J m}^{-2}$ as the sum of $16.61 \text{ J m}^{-2}$ (91.9%) dispersive and $1.46 \text{ J m}^{-2}$ (8.1%) polar shares (Figure 5A).

Adhesion Forces on Smooth Substrates With Different Surface Energies

The highest adhesive force of the setae was measured on the glass with $263 \pm 86 \text{ nN}$ (mean ± standard deviation; $N = 3$ setae, $n = 108$ measurements) and a median value of $262 \text{ nN}$. The mean adhesion force on the epoxy resin surface was $156 \pm 56 \text{ nN}$ and a median of $142 \text{ nN}$; that to the silicon amounted to $174 \pm 61 \text{ nN}$ and a median of $188 \text{ nN}$. The weakest adhesion was found on the PTFE substrate with $82 \pm 53 \text{ nN}$ (median $81 \text{ nN}$). A box plot of the results is shown in Figure 5B. Kruskal-Wallis one way analysis of variance (ANOVA) on ranks indicated very high statistically significant difference ($p < 0.001$) of the adhesion values between the substrates. An all pairwise multiple comparison procedure (Tukey test) of the data on a significance level of $p < 0.05$ yielded significant differences between all the surfaces except for silicon and the epoxy resin. Figures 5C,D clearly show increasing seta adhesion with increasing polarity of the substrates and no or little influence of the dispersive shares. Correlation statistics for the influence of relative humidity using the Spearman method gained a not significant $p$ value of 0.0992 for all measurements, which were performed in a humidity range between 31 and 58.7%.

Seta Adhesion on Substrates With Different Roughness

Morphology and Roughness of the Test Substrates

The surface P0 (glass mold) was smooth. The white light interferometric height maps showed increasing grain sizes,

179 ± 6 nN at angles from 49° to 80°. The lowest adhesive force of 99 ± 8 nN was measured at an angle of 85°. At higher angles, adhesion increased again, and 88° was chosen for the measurements on different substrates (Figure 4).
height differences, and irregularities of the surface structures from P0.05 to P12 (molds of polishing papers). Small granules were visible in the molds of the polishing papers P3, P9, and P12 in addition to the larger asperity structures. The shapes of the grains of the sand paper molds SP1 and SP2 were more distinct. In SP2 the grains were larger compared to those in SP1 and
The sand paper mold SP3 showed the highest degree of irregularity having smaller but more densely arranged grains of different shapes (Figure 6). The mean \( r_{ms} \) roughness values of these nine different rough substrate surfaces are plotted in Figure 7A.

### Adhesion Forces on Different Rough Substrates
Adhesive forces of individual setae considerably differed on all tested surfaces and no general trend is indicated by the data (Figure 7B). For seta 1, the mean values of adhesion force were the highest on all substrates except for P3. For seta 1, there was a trend toward stronger adhesion to surfaces with increasing \( r_{ms} \) roughness up to \( 533 \pm 249 \) nN (\( n = 36 \)) on substrate SP3. In addition, the standard deviations increased with increasing mean values of adhesion force. Adhesion values obtained for seta 2 were generally lower (<200 nN) than those of seta 1. Seta 2 did not show any trend of adhesion force on the differently rough substrates, with mean values between \( 67 \pm 31 \) nN on substrate P12 and \( 160 \pm 48 \) nN on substrate P3. Adhesion forces of seta 3 were the lowest on all substrates with the minimum values of \( 34 \pm 13 \) nN on the relatively smooth substrate P1 and \( 34 \pm 16 \) nN on the rough SP2. The maximum value of \( 100 \pm 24 \) nN was measured on the smooth substrate P0. Without considering the individual setae, a statistical comparison of all pooled values using a pairwise \( t \)-test and a Tukey HSD test indicated that the adhesion force on the substrates P0,05 and SP2 was significantly lower than on all other substrates and significantly higher on SP3.

### DISCUSSION
The examination of the general morphology of the pretarsus of *Cupiennius salei* in the present study showed the claws and the two lobed claw tufts of scopula setae. This finding confirms those of previous authors (Wolff and Gorb, 2013; Labarque et al., 2017). It enables the spider to use the specific attachment mechanism dependent on the geometry and the mechanical properties of the substrate. The claws are assumed to enable clamping on soft or very rough surfaces, whereas the adhesive setae are used for adhesion to smoother and hard surfaces (Figures 1B,C). The setae themselves are covered with differently shaped microtrichia. The microtrichia with pointed tips along the shaft can be interpreted as spacers similar to those of other spider species (Eggs et al., 2015) and avoid that the setae to stick to each other. The increased density of the spatula-shaped microtrichia in the tip region and their arrangement toward the substrate make them well suited to make contact with a surface during locomotion. This hierarchical structure of the pretarsal attachment system of spiders is different from the structure of fibrillary adhesive systems of insects, e.g. in
beetles and earwigs, which are made up of shorter, unbranched setae on the tarsi (Haas and Gorb, 2004; Gilet et al., 2018).

On the smooth substrates with different surface energy, the setae adhered best to the glass, which also exhibited the highest hydrophilicity and a highest amount the polar shares of surface energy (Figure 5). For adhesion, the polar shares are responsible for hydrogen bonds between two materials. The disperse shares result in attractive van der Waals forces (Autumn et al., 2002). On the epoxy resin and the silicon surface that are only slightly hydrophilic and for which the amount of disperse shares of surface energy are similarly high, the adhesive force of the setae dropped down to approximately two thirds of that on glass. On the hydrophobic and non-polarizable PTFE substrate, the adhesive forces of the setae was lowest and approximately 30% of those on glass.

For the gecko seta, it has been shown that its adhesion purely relies on van der Waals forces, because the adhesive forces were the same on polarizable hydrophilic and hydrophobic substrates and confirmed the model prediction (Autumn et al., 2002). For a single Gecko spatula, however, adhesion increased with increasing relative air humidity and substrates with increasing hydrophilicity (Huber et al., 2005), and the authors suggested monolayers of water being adsorbed between the spatulae and the substrate leading to additional capillary forces. For the spider setae, here we show stronger adhesion on the hydrophilic glass surface with a high polar share of surface energy, which makes the influence of thin layers of water on the adhesion strength likely. For different spider species with scopulae, the capillary forces between the thin water layer on a substrate and the scopula hairs were found to be most important for their adhesion (Homann, 1957). On the polarizable epoxy resin and the silicon substrate, which mainly exhibit disperse shares of surface energy, the adhesion of the spider setae is still fair. Together with the presence of adhesive force on the hydrophobic non-polarizable PTFE substrate, these findings lead to the conclusion that a combination of van der Waals forces and hydrogen bonds between polar substrates and the spatulae is responsible for the adhesion of the attachment setae of Cupiennius salei on substrates with different surface energies. Capillary forces may also play an important role especially at higher relative humidity, because it has been shown that the shear adhesion of the spider Philodromus dispar on an epoxy resin substrate was highest at a relative humidity of 60% (Wolff and Gorb 2012b).

The tests for seta adhesion on differently rough surfaces were performed on the same material of epoxy resin molds to avoid different chemistry of the substrates. The small adhesion forces of the setae to the P0.05 substrate likely result from its rms roughness of 396 nm and the size of the spatulae. This roughness may be too small for the single spatulae to form proper contact. For the reduced adhesion to the SP2 surface, the interplay between the substrate morphology and the seta size likely is the limiting factor. The grains on the SP2 substrate appear

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**FIGURE 6 | (A–I)** White light interferometric height maps of the tested epoxy resin surfaces with increasing rms roughness.
spherically shaped and spread on a rather flat surface. For an approaching seta, it is crucial whether it hits a grain and which aspect of the seta tip – the one with or the one without the spatula – gets in contact on top or at the edges of the grain. If the seta tip makes contact with its spatula-free side at the edges of the grains, adhesion forces will be low. It can be assumed that the surface morphology of the SP2 substrate strongly inhibits proper contact making of the spatulae. The statistically significantly increased adhesion value of the setae on the roughest substrate SP3 results from the high adhesion force of the seta 1. Both seta 2 and seta 3 on SP3 do not show values higher than on other substrates. The obvious different adhesion of different setae to the substrates with different roughness indicates that most likely the tip shape and the distribution of the spatulae plays the key role for the attachment of the individual setae. Neighboring setae plucked from the center of the claw tuft scopula showed four different tip shapes and arrangements of the tip microtrichia in four randomly selected setae (Figure 8A).

Shear force applied on an already attached seta, however not sliding the seta, was shown to largely increase the pull-off force from 3.6 µN up to 25 µN by the alignment of a large number of spatulae with a smooth glass surface (Flenner et al., 2020). In the present study, no shear force was applied on the three individual tested setae. Therefore, we measured the result of the arrangement of the spatulae, which spontaneously aligned with the substrate structures upon contact. For such an adhesive behavior, the tip shapes and the arrangement of the microtrichia and spatulae of the seta is crucial for the adhesive force generation. The tip shapes of the three individual tested setae clearly differed (Figures 8B–D), as most likely did the arrangement of the spatulae. As can be seen in Figure 4, adhesion on glass greatly differed at different contact angles of the setae. The mostly higher adhesion forces of seta 1 at the angle of 45° may be the result of the orientation of the spatula-rich side of the setae toward the structural features of the rough substrates. The higher number of the flexible microtrichia and spatulae are more likely to find proper surface features to attach. For seta 2 and seta 3, the angles of 85°, and 88°, respectively, were also selected within ranges of high adhesion for the respective setae. However, their adhesion on differently rough surfaces was low compared to that of seta 1. For seta 2, at the chosen angle of 85°, likely only the microtrichia next to the tip contacted the substrate with their sides. This lead to alignment and adhesion of a smaller number of spatulae and less adhesive force compared to seta 1. Seta 3 showed the lowest adhesion on the differently rough epoxy resin surfaces. Considering the angle of 88° chosen for the measurements and the rounded shape of the tip, it appears likely that seta 3 contacted the surface with the backbone and not with the ventral side, rich in spatula-shaped microtrichia, which resulted in reduced attachment forces.

Even when taking the highest adhesive value of 830 nN into account and assuming that all 18,800 setae (∼2,350 per leg; Wolff and Gorb, 2012c) of the spider were in contact with a substrate, the resulting adhesive force of approximately 16 mN could not support the body weight (∼3.6 g) of an adult female spider. Since Cupiennius salei easily climbs vertical surfaces and is able to walk upside-down also on smooth surfaces, there must be mechanisms of adhesion other than those examined in the single setae in the present study. Interestingly, the adhesive setae are not rigidly fixed in the pretarsal cuticle. In the natural situation, the movability of the setae toward the substrate is strictly limited by a stopper-like structure of the basal hair shaft directly at the insertion of the seta in its socket (Figure 9). This stopper keeps the position of the seta fixed in its position in the socket at dorsad movements of the claw tuft to facilitate pulling-off. On the dorsal (distal) side of the socket, however, there is some space that allows a seta deflection by approximately 6–7° when placed onto a substrate. In our experiments, the setae were well fixed to the stiff silicon cantilevers. In the natural situation, the flexibility of the seta suspension in the pretarsal cuticle may help each individual seta of the claw tuft to find better contact with the structural features of the substrate and consequently a good place to adhere. This movability of the setae also supports their
shearing in order to bring more adhesive spatulae in contact with the substrate (see Flenner et al., 2020), which likely resulted in the better adhesion of Cupiennius, when opposing leg pairs were in contact with the ground at pulling-off the whole spider (Wohlfart et al., 2014). Considering the previously measured 25 µN adhesive force of a single attachment seta preloaded in shear, 1,400 setae in contact (which is less than two thirds of the setae of a single leg) would suffice for an adult female Cupiennius salei to adhere on smooth glass. Interestingly, adhesion of the whole scopula claw tuft was zero at vertical pulling-off even after shearing (Wolff and Gorb, 2013; Wohlfart et al., 2014). In the present study the single setae did show adhesive forces at vertical pulling-off on all the different substrates tested. These results indicate that the specific movements of the individual setae of the claw tuft may be most important for making adhesive contact with the substrate.

The results of the present study indicate a distribution of different adhesive tip shapes of the adhesive setae, which likely represents an adaptation of the spider attachment system for efficient interaction with substrates of different roughness. The cuticle of Cupiennius salei has been reported to have an effective Young’s modulus of 18 GPa (Blickhan and Barth, 1985). For the individual seta, the specific structural arrangement of the mechanically stiffer dorsal seta backbone (Schaber et al., 2019) and the softer ventral “brush” of spatula-shaped microtrichia is crucial for adhesion at certain angles with the substrate. It can be assumed that the individual morphology of each individual seta and its position within the scopula orchestration are optimized for maximal adhesion on natural substrates with many different properties as found in the habitat of the spider.

FIGURE 8 | (A) Transmitted light microscopic side view of a bunch of neighboring attachment setae plucked from the center of the pretarsal scopula. Different tip shapes (arrows) are clearly visible (B–D) Reflected light microscopic images of the tips of the setae used for the adhesion measurements in the experimental setup. The arrows point to the tips of the seta backbone.

FIGURE 9 | SEM images of the bases of pretarsal adhesive setae and their insertion into the cuticle in a vertically dissected exuvia cuticle. (A) On the left are the most proximal parts of the adhesive setae. At their insertion in the cuticle, the hair shaft is narrowed and a stopper-like structure is situated on the ventral (lower) aspect. Distal and proximal refer to the arrangement the claw and the leg. (B) Magnified cuticle insertion region of the setae. The asterisk exemplary marks the pivot point of a seta for dorsad (upward) deflections.

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The individual variability of the morphology of the spider attachment setae, which is strongly interdigitated with their adhesive performance, has been shown here for the first time. Furthermore, we reveal the importance of examining the relevant different length and force scales for understanding the functionality of specific structures in the entire adhesive system of the spider. This knowledge can lead to new bioinspired materials with outstanding properties such as nanostructured reversible residue-free dry adhesives e.g. based on cellulose nanofibers (Schaber et al., 2018), carbon nanotubes (Blushan et al., 2008; Schaber et al., 2015a; Schaber et al., 2015b; Su et al., 2020; Yang et al., 2020) or other polymeric materials (Xue et al., 2012; Pattantyus-Abraham et al., 2013; Xue et al., 2013; Borodich and Savencu 2017; Di Tan et al., 2020).

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

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AUTHOR CONTRIBUTIONS

CS and SG conceived of the research. CS and BP designed the experiments. BP conducted the experiments and analyzed the data. BP, CS, and SG interpreted the data. BP wrote the first draft. CS edited the draft and wrote the manuscript. SG and CS revised the manuscript. All authors read and approved the final manuscript.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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