PII: S0964-1726(04)75934-0

Smart Mater. Struct. 13 (2004) 512-518

Getting a grip on spider attachment: an AFM approach to microstructure adhesion in arthropods

Antonia B Kesel^{1,3}, Andrew Martin¹ and Tobias Seidl²

- ¹ University of Applied Sciences, Institute for Technical Zoology and Bionics, D-28199 Bremen, Germany
- ² University of Zurich, Institute for Zoology, Department of Neurobiology, CH-8057 Zurich, Switzerland

E-mail: akesel@bionik.hs-bremen.de

Received 25 June 2003, in final form 12 January 2004 Published 19 April 2004 Online at stacks.jop.org/SMS/13/512

Offine at stacks.top.org/stvis/15/312

DOI: 10.1088/0964-1726/13/3/009

Abstract

Although the spider exoskeleton, like those of all other arthropods (spiders, insects and crustaceans), consists of an extremely non-adhesive material known as cuticle, some spider species produce astonishingly high adhesive forces using cuticular appendages. Unlike other arthropods, they do not rely on sticky fluids but use a different strategy: the miniaturization and multiplication of contact elements. In this study the number of contact elements (setules) in the species Evarcha arcuata was determined at 624 000 with an average contact area of 1.7×10^5 nm². The total area of contact in this species measured 1.06×10^{11} nm². By using atomic force microscopy it was shown that a single setule can produce an adhesive force of 41 nN perpendicular to a surface. Thus with a total adhesive force $F_a = 2.56 \times 10^{-2}$ N and an average body mass of 15.1 mg, this species possesses a safety factor (adhesive force F_a /force for weight F_m) of 173. The tenacity σ (ultimate tensile strength) amounts to 0.24 MPa. Due to the extreme miniaturization of the contact elements it is assumed that van der Waals forces are the underlying adhesive forces, although final evidence for this has yet to be provided. The present study was performed in order to clarify the fundamental basics of a biological attachment system and to supply potential input for the development of novel technical devices.

1. Introduction

A striking feature of biological materials is their enormous variability of chemical and physical characteristics although they are usually based on only a handful of different molecular components. The properties of biological materials vary considerably depending on the combination and configuration of these basic components. Due to their multifunctionality, biologically inspired materials have become of great interest for technological applications.

One of the most interesting biological materials is the arthropod cuticle. This cuticle is the exoskeleton of such

animals as crustaceans, insects and spiders and represents a rigid barrier between the inner media of the animals and the surrounding environment. As a material it incorporates two main components: the crystalline polymer chitin and a multitude of proteins and lipids. In combination, these two components form a fibrous composite with the long chain polymeric fibre chitin embedded in a matrix of structured proteins and lipids. Minor changes in this basic molecular set-up lead to a broad spectrum of macroscopic chemical, physical and mechanical behaviours. Elasticity given in terms of the Young's modulus for example is documented at 10^3-10^{10} Pa (Neville 1975, Wainwright *et al* 1976, Vincent 1990). Furthermore, numerous layers of cuticular material may be organized in such a way that layers vary in chitin fibre

³ Author to whom any correspondence should be addressed.

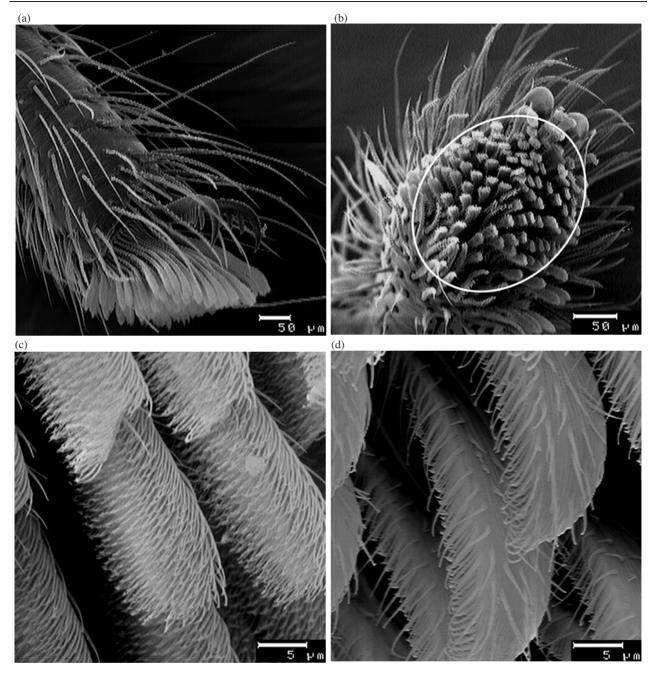


Figure 1. (a) A scanning electron microscope (SEM) micrograph of the foot of the jumping spider *E. arcuata*. In addition to the tarsal claws (CI), a scopula (Sc) is found at the tip of the foot. The long hairs which are distributed over the entire foot are mechanosensitive receptors (Mr), elements of the sense of touch, and as such needed for the perception of underlying substrates as well as prey. (b) A ventral view of the scopula reveals the scopula's differentiation into single hairs (setae) as visible in this SEM micrograph. The additionally plotted oval represents the estimated scopula area (here: $3.2 \times 10^4 \ \mu m^2$). (c) At larger magnifications it becomes clear that single setae are densely covered with numerous setules. The setule density averages 2.1×10^6 setules mm⁻² ($\pm 1.0 \times 10^6$, n = 48). (d) An overview of the setae shows that setule density is clearly much lower on the upper side of the setae and that the sporadic setules taper off to a point (see (e)). It is very likely that the function of these setules lies in the prevention of adhesion between neighbouring setules and setae, which, so to speak, act as spacers. (e) Contrary to the setules on the upper side of the setae, the setules on the seta underside not only show a higher density but also broaden toward the end and end in a sail-like area, as can be seen at larger magnifications. (f) The terminal setule areas represent the spider's elements in direct contact with the substrate. An average setule area of $1.7 \times 10^5 \ \text{nm}^2$ ($\pm 0.34 \times 10^5 \ \text{nm}^2$, n = 7) was obtained from the above SEM micrograph.

orientation. The resulting laminate can be optimally designed for specific purposes and positional demands.

Usually the surface of the multilayered cuticle is sealed with a topographically microconfigured wax layer. These surfaces are reportedly non-wettable (water repellent) and

show extremely low adhesion (Beament 1960, Ghiradella and Radigan 1974, Wagner *et al* 1995, Seidl *et al* 2001). Such behaviour is however at variance with the requirements for the adhesion of certain body parts, especially the feet, to any underlying surface.

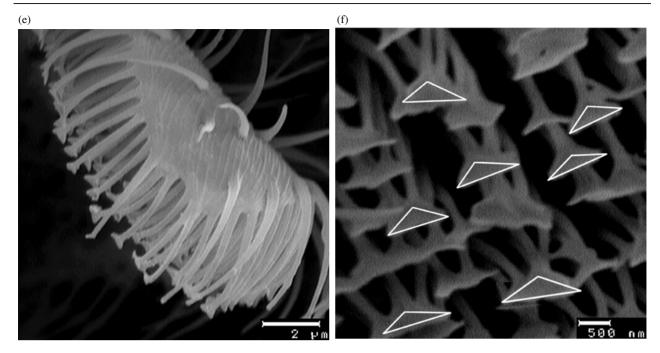


Figure 1. (Continued.)

In order to overcome this limitation, animals have developed numerous strategies which all aim at compensating for isolating cuticular characteristics. In addition to having claws and clamp-like structures, insects, for example, secrete oily fluids that mediate the contact with a substrate and support the adhesion occurring (Hasenfuss 1977, Bauchhenß 1979, Walker et al 1985, Gorb 1998, Attygalle et al 2000). In contrast to this, spiders do not produce any adhesive fluids, but gain and keep contact with substrates using 'dry adhesion'. Whilst on rough surfaces spiders, like insects, use their claws as attachment devices, adhesion to comparably smooth surfaces is achieved due to an ultrastructured morphology of the spider's footpads or, more precisely, claw tufts (scopulae). Prior to our approach, no efforts at quantifying the actual efficiency of this attachment system have been made. The microgeometry of the spider's claw tufts was studied via a scanning electron microscope and additionally the adhesive force F_a produced by the cuticular contact elements (setules) was verified using atomic force microscopy (AFM). By applying the force spectroscopy mode of the AFM it is possible to register local surface characteristics (Binnig et al 1986, Radmacher et al 1994). This technique allows a new approach towards determining the adhesive properties of single-terminal contact structures in arthropods.

2. Materials and methods

2.1. Biological materials

Analyses were performed on spiders of the species *Evarcha arcuata* Clerck. This species is a member of the family of jumping spiders (Salticidae) and as such hunts down its prey without building any kind of web. Thus the scopulae are notedly differentiated in jumping spiders (Hill 1977, Roscoe and Walker 1991).

Specimens were collected near Saarbrücken (southwestern Germany) and body mass was determined. Subsequently specimens were kept frozen prior to SEM preparation.

AFM analyses were carried out on untreated specimens that were collected directly before experimental measurements.

2.2. Experiments

Scanning electron microscopy. Whole specimens were dehydrated in ascending acetone concentrations (70%, 80%, 90%, 100%), cleansed by ultrasound and critical-point dried (Bal-Tec CPD 030 Critical Point Dryer). Single legs were then mounted on plates and sputter-coated with gold (Bal-Tec SCD 005 Sputter Coater). Samples were examined in high vacuum in a Zeiss DSM 940A scanning electron microscope at 10–15 kV.

Atomic force microscopy. In order to carry out adhesion measurements via the AFM whole, freshly collected and untreated individuals were supinely embedded in 5 min epoxide resin (R&G GmbH, Waldenbuch, Germany). Scopula hairs were kept free of the embedding material. As a covering layer of epoxy resin would have altered the mechanical behaviour of the scopula hairs, the capillary rise of the fluid resin was avoided by having a short curing time (approximately 1.5 min) prior to the application of the specimens. Measurements were conducted under ambient conditions (23 °C, 45% air humidity).

Point spectroscopic analyses were carried out using a commercial AFM (Topometrix Exporer[®], Controller Software SPMLab 4.01). Two different cantilevers were used: cantilever 1 (C1) with a spring constant of 5.95 N m⁻¹ ($s_d = 0.095 \text{ N m}^{-1}$; $n_{C1} = 5$) and cantilever 2 (C2) with a spring constant of 0.6 N m⁻¹ ($s_d = 0.079 \text{ N m}^{-1}$;

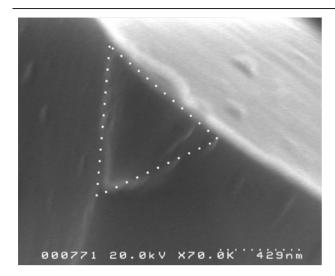


Figure 2. The flattened probe tip of cantilever C1. The tip area drawn in this figure only represents the tip area used in our assumptions. The tip area of 3.6×10^5 nm² was calculated, thereby taking the viewing angle in SEM micrographs into account.

 $n_{\rm C2}=10$). Prior to measurements both probe tips were modified and both cantilevers were calibrated. In order to create a constant area of contact between probe tips and the samples, the probe tips were flattened by repeatedly driving them against a glass plate. Probe tip areas were examined and measured via the SEM (C1 = 3.6×10^5 nm²; C2 = 0.8×10^5 nm²; figure 2) and later assumed as areas of contact between the probe and sample. This simplification allowed an estimation of the adhesion occurring (probe tip areas are not necessarily contact areas; see the results and discussion). The cantilevers' spring constants were calibrated by repeatedly applying pieces of aluminium foil of known weight to the probe tips using a micromanipulator. Cantilever deflection and weight application were correlated.

The probes were driven at a velocity of $0.5~\mu m~s^{-1}$ and in passing along a predetermined path $z~(\Delta z:~200{\text -}400~n m;$ maximum error: $\pm 4~n m$) were slowly brought into contact with the sample and subsequently retracted. This procedure was recorded by a linearized scanner (EX 179807) via a strain gauge. Contact was established perpendicular to the underside of the scopula and due to the probe's low driving velocity the applied load during this phase was taken as quasi-static (Burnham and Kulik 1999).

Cantilever deflection was plotted as a load–displacement curve directly related to the probe's path and later transformed into force values, according to the calibration of the instrumental set-up prior to measurements (maximum AFM-internal measurement error: 10%). Further data processing did not occur in this study. The absolute values of the pull-off forces plotted in the load–displacement curves represent the spontaneous detachment of the probe and sample and thus the adhesive force F_a established during contact (figure 3) (Radmacher *et al* 1994). The ultimate tensile strength of the adherent–adhesive system (tenacity σ) in relation to the contact area was calculated according to registrations. Only load–displacement curves with a clearly defined single pull-off event were taken into account for further considerations and calculations.

Comparative measurements were also conducted on glass as well as the embedding medium (epoxide resin; resin curing time approximately 1 h under ambient conditions).

3. Results

Scanning electron microscopy

The electron microscopic examination of the spider's feet revealed that a scopula is composed of many single scopula hairs (setae; figures 1(a) and (b)) which again are covered by an immense number of cuticular processes (setules; figures 1(c) and (d)). These setules are broadened toward their distal ends and eventually form a sail-like, triangular surface area of 1.7×10^5 nm² ($\pm 0.34 \times 10^5$ nm², n=7; figures 1(e) and (f)). It is these setules that represent the direct contact points or rather the areas of contact with a substrate. With an average density of 2.1×10^6 ($\pm 1.0 \times 10^6$, n=48) setules mm² (see figure 1(f)) and an estimated area of 0.037 mm² (± 0.01 mm², n=4) per scopula (figure 1(b)), the total number of setules per foot can be calculated at 78 000. Thus all eight feet combined are provided with a total of 624 000 points of contact with a given surface.

Atomic force microscopy

When applying point spectroscopy in order to determine the adhesive force F_a (figure 3) it was first presumed that full contact was achieved between the surfaces of the probe and the setule. Further aspects were considered in order to determine force values. For cantilever C1, the probe tip area measured was 3.6×10^5 nm², larger than the average terminal surface area of the setules $(1.7 \times 10^5 \text{ nm}^2)$. Consequently, for all further considerations concerning data registered with cantilever C1, it was assumed that the relevant contact area was that of the terminal setule surface. Registered forces were therefore related to this surface area. In the case of cantilever C2 the contact area of the probe tip was clearly smaller than the terminal setule contact area. Therefore, the registered force values were set in relation to the probe tip area $(0.8 \times 10^5 \text{ nm}^2)$.

Average adhesion forces of $F_{\rm a}=38.11$ nN (± 14.73 nN, n=45, C1) and $F_{\rm a}=43.71$ nN (± 12.51 nN, n=50, C2) per setule were obtained from the recorded load–displacement curves (table 1). These two mean values are not significant (Utest (Mann and Whitney 1947); p<0.01), so it was concluded that the spring constants had no measurable influence on the registered adhesion values. Thus, in the course of the following discussion, the averaged value of the adhesive force is taken as $F_{\rm a}=41$ nN.

With an estimated number of 78 000 contact points per scopula a single foot could produce an adhesive force of 3.2×10^{-3} N when in maximum contact with an underlying surface. Provided that all eight feet or rather all eight scopulae are in full contact with a substrate, adhesion normal to the surface would amount to 2.56×10^{-2} N and the tenacity σ , as the ratio of adhesive force to contact area, could be calculated at 2.4×10^5 N m $^{-2}$ or 0.24 MPa.

The average body mass of *E. arcuata* was measured at 15.1 mg (± 1.96 mg, n=8); the average force of weight of this species averages at $F_{\rm m}=1.48\times 10^{-4}$ N. As a result of the AFM measurements and neglecting the inaccuracies due to

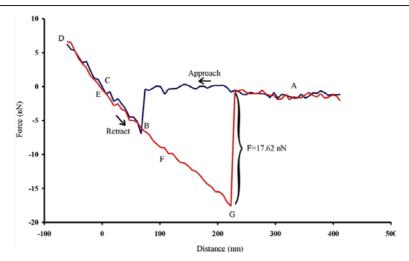


Figure 3. The force—distance curve of an AFM cantilever (C2) on a setule. The curve shows all the typical features. A: the probe is approaching the sample but not yet in contact. B: due to long range attractive forces a transient instability occurs and the probe and sample are brought into contact by 'snap-in'. C: the probe is pressed into the sample with ascending force. D: the force reaches its maximum; retraction starts. E: the force between the probe and sample decreases until the probe sticks to the sample by adhesion (F). G: the force of the cantilever equals the force of adhesion; the probe and sample are separated abruptly ('pull-off'). (This figure is in colour only in the electronic version)

Table 1. Average forces of adhesion on several materials using two different cantilevers. Three samples were tested with cantilever 1 (C1); comparative measurements between two probes (C1 and C2) were conducted on setules. Force measurements were set into relation with single-setule contact areas.

| | | Absolute force | | Force/setule | | Force/area | | |
|--------------------------------------|----------------------|-------------------------------------|----------------------------------|--------------|--------------------|------------------------------|------------------------------|----------------------|
| Sample | Probe | Mean (nN) | SD (nN) | Mean (nN) | SD (nN) | Mean (MPa) | SD (MPa) | n (—) |
| Glass Epoxide Setula Setula | C1 C1 C1 C2 | 1315.53 443.72 38.11 20.67 | 22.85 149.20 14.73 5.91 | | 14.73 12.50 | 3.65 1.23 0.22 0.26 | 0.06 0.41 0.09 0.07 | 20 19 45 50 |

^a Marked values are obtained from separate measurements and therefore treated separately. As the two values are not significant, the averaged value (41 nN) of the two was used for further calculations.

simplifications, we conclude that *E. arcuata* is roughly able to compensate its 173-fold body mass when in full contact with a given surface.

4. Discussion

The spider's impressive ability to cling to overhanging, smooth surfaces is based on the miniaturization and ultrastructure of a cuticular attachment system. The superiority of the spider attachment system is most obvious when compared to the closest and most comparable biological model: insects. As already mentioned, the cuticle is the exoskeleton material of all arthropods, yet adhesion in insects is not as strong as in spiders even though insect adhesion is additionally supported by a fluid. Safety factor values (calculated from data given) for insect adhesion merely lie between 1.5 (American cockroach Periplaneta americana; Pell, cited in Walker (1993)) and 50 (knotgrass leaf beetle Chrysolina polita; Stork (1983)). Higher values of over 100 have only been documented for cocktail ants (Crematogaster spec.; Federle et al (2000)). Similarly, the tenacity of insect attachment devices amounts to values between $\sigma = 2$ kPa (bush cricket *Tettigonia viridissima*; Jiao et al (2000)) and $\sigma = 30$ kPa (blowfly Calliphora vomitoria;

Walker (1993)) whereas in the spider species studied it stands out at 0.24 MPa.

Surprisingly, a comparably competitive system is found not in other arthropods but in a group of reptiles: the attachment systems of spiders and geckoes show astounding similarities. Just like for spiders, strong adhesion for geckoes is achieved by an ultrastructured apparatus with extremely miniaturized contacting elements (Ruibal and Ernst 1965, Hiller 1968, Stork 1983). Branched hairs and a progressive structural miniaturization, broadened contact elements as well as the absence of adhesive secretions are characteristic features of both the gecko and the spider attachment system. Tenacity values for geckoes are documented at $\sigma = 576$ kPa (Autumn *et al* 2000)—within the order of magnitude, comparable to $\sigma = 240$ kPa discussed for *E. arcuata*.

Whereas the surface tension of the adhesive fluid has been identified as one of the physical principles forming the basis of wet adhesion, van der Waals forces have recently been discussed in the context of the dry adhesive system of geckoes (Autumn *et al* 2000, 2002). Point spectroscopy, as carried out in this study, is an adequate method for determining van der Waals forces (Hartmann 1991); thus the measured 41 nN can be interpreted as the average van der Waals force of an isolated

setule contact area. As these short ranged forces are relatively independent of the contacting materials, isolating properties of the cuticle could be neglected. Yet whether or not animals rely on these weak forces *in vivo* has still to be verified.

The van der Waals interaction however does not allow contacting surfaces to be separated by more than a few nanometres. This nanoscaled proximity could be attained by the present spider scopula. Hierarchical organization of tarsal elements in arthropods is not unusual, yet in E. arcuata differentiation reaches a level which is clearly superior to that of insects. Progressive setal branching and miniaturization in this jumping spider not only increase the possible contact area but also provide the attachment system with a high flexibility, allowing a detailed replication of any underlying surface relief. Insects with setose attachment systems lack setal branching and are only supplied with between 5000 and 42 000 contact hairs (syrphid fly Episyrphus balteatus; Gorb (1998); blowfly Caliphora vomitoria; Walker et al (1985)). Furthermore, comparatively large contact surfaces of 2.6 μ m² (Gorb 1998) do not possess the necessary degree of miniaturization required for van der Waals interaction with the substrate.

Besides the large number of 624 000 setules, the cuticle's material properties might additionally support contact mechanics, despite the previously discussed isolating characteristics. A soft and deformable material with viscous as well as elastic properties would not only enhance countersurface replication but also allow a high number of attachment-As already mentioned, the cuticular detachment cycles. fibre composite displays a high variability in this respect. Cuticle elasticity has been analysed and values for the Young's modulus cover several orders of magnitude. Tensile strength has been determined at 10-100 MPa (Jensen and Weis-Fogh 1962, Ker 1977) and material hardness is documented at 200-400 MPa (Hillerton et al 1982, Kreuz et al 2000). Provided that these material characteristics apply to the attachment system in jumping spiders, the animals are equipped with the structural and the material prerequisites for an efficient interaction with a substrate.

Data obtained from force spectroscopy only comprise measurements with a force applied perpendicular to the attachment system. Yet in other biological systems adhesion is stronger when not only a normal load but also a parallel force component is applied. In both wet and dry adhesive systems, friction induced shear stress values τ easily exceed measured tenacity values σ : tenfold (Walker 1993, Autumn et al 2000). Frictional forces clearly dominate over all other adhesive forces that might contribute to attachment. This can also be expected for E. arcuata although adequate experiments have yet to be performed.

Of course the great safety factor of over 170 represents an ideal value, for which the full contact of all 624 000 contact points is required. Comparable measurements conducted on geckoes revealed that such an ideal value is easily reduced to approximately one tenth under environmental conditions (Irschick *et al* 1996). Analogue reductions can also be expected in the case of jumping spiders: the hunting way of life and its associated dynamics, substrate contamination, wear of the cuticular attachment apparatus and numerous other influences should contribute to a considerable decrease of adhesive capacities. In this context the question of detachment

also arises. Despite the large adhesive forces, spiders are not permanently stuck to their environment. It is unlikely that all 624 000 setules are in contact with a substrate at the same time and observations have shown that not even all eight feet are simultaneously in contact with the ground. Even if this were the case, the total adhesive force could easily be overcome by subsequently detaching single setules and not the whole foot at once. Such a peeling behaviour has been suggested for geckos as well as for flies (Niederegger and Gorb 2003).

5. Conclusions

Despite the simplifications mentioned, this study stands as a successful first approach to a biological system that has so far not been characterized in such detail. 'Spider-Post-Its' obtain their high efficiency through the smart realization of a hierarchically structured, microconfigured design utilizing a highly adaptive, smart material and momentary reproductions of these systems have to be seen as quite rudimentary trials (e.g. Autumn et al 2002). Adequate materials as well as production techniques have yet to be developed, if the astounding attachment system of spiders is to be realized as a technical product. Adhesives fabricated according to the constructive guidelines of the spider foot presented here could be of major significance. Due to the underlying physical principle of van der Waals interaction, adhesion becomes independent not only of material characteristics but also of conditions of the surroundings and could even occur in outer space vacuum.

Acknowledgments

We would like to thank Professor Dr Uwe Hartmann (Institute of Experimental Physics, Saarland University, Saarbrücken, Germany) for access to the atomic force microscope. This study was supported by the Federal Ministry of Education, Science and Technology (BMB+F), Germany, to ABK (Bionik-Kompetenz-Netz).

References

Attygalle A B, Aneshansley D J, Meinwald J and Eisner T 2000 Defense by foot adhesion in a chrysomelid beetle (*Hemisphaerota cyanea*): characterisation of the adhesive oil Zoology **103** 1–6

Autumn K, Liang Y A, Hsieh S T, Zesch W, Chan W P, Kenny T W, Fearing R and Full R J 2000 Adhesive force of a single gecko foot-hair *Nature* **405** 684–8

Autumn K, Sitti M, Liang Y A, Peattie A M, Hansen W R, Sponberg S, Kenny T W, Fearing R, Israelachvili J N and Full R J 2002 Evidence for van der Waals adhesion in gecko setae *Proc. Natl Acad. Sci. USA* **99** 12252–6

Bauchhenß E 1979 Die Pulvilli von *Calliphora erythrocephala* (Diptera, Brachycera) als Adhäsionsorgan *Zoomorph.* **93** 99–123

Beament J W L 1960 Wetting properties of insect cuticle *Nature* **186** 408–9

Binnig G, Quate C F and Gerber C 1986 Atomic force microscope *Phys. Rev. Lett.* **56** 930–3

Burnham N A and Kulik A J 1999 Surface forces and adhesion Handbook of Micro/Nano Tribology ed B Bhushan (Boca Raton, FL: CRC Press)

Federle W, Rohrseitz K and Hölldobler B 2000 Attachment forces of ants measured with a centrifuge: better 'wax-runners' have a poorer attachment to a smooth surface *J. Exp. Biol.* **203** 505–12

- Ghiradella H and Radigan W 1974 Collembolan cuticle: wax layer and anti-wetting properties *J. Insect Physiol.* **20** 301–6
- Gorb S N 1998 The design of the fly adhesive pad: distal tenent setae are adapted to the delivery of an adhesive secretion *Proc. R. Soc.* B **265** 747–52
- Hartmann U 1991 van der Waals interaction between sharp probes and flat sample surfaces *Phys. Rev.* B **43** 2404–7
- Hasenfuss I 1977 Die Adhäsionsflüssigkeit bei Insekten *Zoomorph*. **87** 51–64
- Hill D E 1977 The pretarsus of salticid spiders *Zool. J. Lin. Soc.* **60** 319–38
- Hiller U 1968 Untersuchungen zum Feinbau und zur Funktion der Haftborsten von Reptilien Z. Morph. Tiere 62 307–62
- Hillerton J E, Reynolds S E and Vincent J F V 1982 On the indentation hardness of insect cuticle *J. Exp. Biol.* **96** 45–52
- Irschick D J, Austin C C, Petren K, Fisher R N, Losos J B and Ellers O 1996 A comparative analysis of clinging ability among pad-bearing lizards *Biol. J. Lin. Soc.* **59** 21–35
- Jensen M and Weis-Fogh T 1962 Biology and physics of locust flight: V. Strength and elasticity of locust cuticle *Phil. Trans. R.* Soc. B 245 137–69
- Jiao Y, Gorb S and Scherge M 2000 Adhesion measured on the attachment pads of *Tettigonia viridissima* (Orthoptera, Insecta) *J. Exp. Biol.* 203 1887–95
- Ker R F 1977 Some structural and mechanical properties of locust and beetle cuticle *PhD Thesis* University of Oxford
- Kreuz P, Kesel A B, Kempf M, Göken M, Vehoff H and Nachtigall W 2000 Mechanische Eigenschaften biologischer Materialien am Beispiel Insektenflügel *Biona-Report 14* ed A Wisser and W Nachtigall (Mainz: Akad. Wiss. Lit.) pp 201–2
- Mann H B and Whitney D R 1947 On a test of whether one of two random variables is stochastically larger than the other *Ann. Math. Stat.* **18** 50–60

- Neville A C 1975 *Biology of the Arthropod Cuticle* (New York: Springer)
- Niederegger S and Gorb S 2003 Tarsal movements in flies during leg attachment and detachment on a smooth substrate *J. Insect Physiol.* **49** 611–20
- Radmacher M, Fritz M, Cleveland J P, Walters D A and Hansma P K 1994 Imaging adhesion forces and elasticity of lysozyme adsorbed on mica with the atomic force microscope Langmuir 10 3809–14
- Roscoe D T and Walker G 1991 The adhesion of spiders to smooth surfaces Bull. Brit. Arachnol. Soc. 8 224-6
- Ruibal R and Ernst V 1965 The structure of the digital setae of lizards *J. Morphol.* **117** 271–94
- Seidl T, Göken M and Kesel A B 2001 Mikrokonfigurierte Wachsauflagen der Insektenkutikula: Ein Beispiel multifunktionaler Oberflächenbeschichtungen *Biona-Report 15* ed A Wisser and W Nachtigall (Mainz: Akad. Wiss. Lit.) pp 335–9
- Stork N E 1983 Experimental analysis of adhesion of *Chrysolina* polita (Chrysomelidae: Coleoptera) on a variety of surfaces *J. Exp. Biol.* **88** 91–107
- Vincent J F V 1990 Structural Biomaterials (Princeton, NJ: Princeton University Press)
- Wagner T, Neinhuis C and Barthlott W 1995 Wettability and contaminability of insect wings as a function of their surface sculptures *Acta Zool.* 77 213–25
- Wainwright S A, Biggs W D, Currey J D and Gosline J M 1976 Mechanical Design in Organisms (London: Arnold)
- Walker G 1993 Adhesion to smooth surfaces by insects—a review Int. J. Adhesion Adhesives 13 3–7
- Walker G, Yule A B and Ratcliffe J 1985 The adhesive organ of the blowfly, *Calliphora vomitoria*: a functional approach (Diptera: Calliphoridae) *J. Zool. Lond.* A **205** 297–307