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# Ultrahydrophobicity indicates a non-adhesive default state in gecko setae

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Abstract Geckos may represent the world's most demanding adhesives application. The adhesive setae on the toes of climbing geckos must adhere strongly yet avoid fouling or attachment at inappropriate times. We tested the hypothesis that gecko setae are non-adhesive in their unloaded default state by comparing the water droplet contact angle  $(\theta)$  of isolated setal arrays to the smooth surface of eye spectacle scales of tokay geckos (Gekko gecko). At equilibrium,  $\theta$  was  $98.3 \pm 3.4^{\circ}$  in spectacle scales of live geckos and  $93.3 \pm 3.5^{\circ}$  in isolated spectacles. Isolated setal arrays were ultrahydrophobic, with  $\theta$  of 160.6  $\pm$  1.3° (means  $\pm$  SD). The difference in  $\theta$ of setal arrays and smooth spectacles indicates a very low contact fraction. Using Cassie's law of surface wettability, we infer that less than 6.6% of the surface of unloaded setae is solid and at least 93.4% is air space. We calculated that the contact fraction must increase from 6.6% in the unloaded state to 46% in the loaded state to account for previously measured values of adhesion. Thus gecko setae may be non-sticky by default because only a very small contact fraction is possible without mechanically deforming the setal array.

Keywords Adhesion  $\cdot$  Contact mechanics  $\cdot$ Locomotion · Reptilia · Nanotechnology

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# Abbreviations



# **Introduction**

Conventional pressure sensitive adhesives (PSAs) such as those used in adhesive tapes are fabricated from materials that are sufficiently soft and sticky to be considered tacky (Dahlquist [1969\)](#page-6-0). When PSAs are applied gently to a substrate, adhesion forces cause the PSA to flow and make intimate and continuous surface contact. Tack is the ability of adhesive forces to selfdeform a material to increase contact area with a substrate. Because they are tacky, PSAs also tend to foul, self-adhere, and attach accidentally to inappropriate surfaces.

The toes of arboreal pad-bearing geckos (Russell [1975](#page-6-0)) are perhaps the world's most demanding adhesives application. Geckos are capable of attaching and <span id="page-1-0"></span>detaching their adhesive toes in milliseconds (Autumn et al. [2006\)](#page-6-0) while running with seemingly reckless abandon on vertical and inverted surfaces. The adhesive structure on gecko toes differs dramatically from that of conventional adhesives. In most species, the toe pads consist of a series of scansors covered with uniform arrays of hair-like bristles formed from  $\beta$ -keratin (Wainwright et al. [1982;](#page-7-0) Russell [1986](#page-6-0)). A single seta of the tokay gecko is approximately  $110 \mu m$  in length and 5 µm in diameter (Ruibal and Ernst [1965;](#page-6-0) Russell [1975;](#page-6-0) Williams and Peterson [1982\)](#page-7-0) (Fig. 1). Setae are similarly oriented and uniformly distributed on the scansors. Setae branch at the tips into 100–1,000 more structures known as spatulae. A single spatula consists of a stalk with a thin, roughly triangular end, where the apex of the triangle connects the spatula to its stalk. Spatulae are approximately  $0.2 \mu m$  in length and also in width at the tip (Ruibal and Ernst [1965](#page-6-0); Williams and Peterson [1982\)](#page-7-0).

Avoiding inappropriate attachment forces during climbing (Autumn et al. [2005\)](#page-6-0) is perhaps as important

as attachment itself. A small amount of most common household PSAs is more than sufficient to hold the mass of a large gecko (50 g). However, conventional PSAs are designed to bond spontaneously on contact, and it is amusing to consider the difficulties a gecko would have in climbing through a forest canopy with duct tape on its toes.

Prevention of inappropriate attachment is not due to weakness of the adhesive. All 6.5 million (Schleich and Kästle [1986](#page-6-0); Irschick et al. [1996\)](#page-6-0) setae of a 50-g tokay gecko attached maximally could theoretically generate 1,300 N of shear force—enough to support 133 kg, about the mass of two humans. This suggests that a gecko need only attach 3% of its setae to generate the greatest forces measured in the whole animal [20 N for two feet; (Irschick et al. [1996\)](#page-6-0)]. Only less than 0.04% of a gecko's setae attached maximally are needed to support its mass of 50 g on a wall. Indeed the adhesive toes of Phelsuma are sufficiently tenacious that dead individuals remained adhered to the leaves of trees following a hurricane (Vinson and Vinson [1969](#page-7-0)). The

Fig. 1 Gecko adhesive structures. a Ventral view of a tokay gecko (Gekko gecko) climbing a vertical glass surface. b Ventral view of the foot of a tokay gecko, showing seta-bearing scansors. c Setae are arranged in a nearly grid-like array on the ventral surface of each scansor. d Single isolated gecko seta. Circle shows spatulae enlarged in (e). e Spatular tips of a single gecko seta



Setal array

surprisingly large forces generated by gecko setae underscore the question of how geckos manage to avoid inappropriate attachment of their adhesive toes.

Do gecko setae minimize contact in their default state?

Isolated gecko setae have not been observed to adhere spontaneously to surfaces. ''Preloading'', a small push perpendicular to the surface, followed by a micrometer scale parallel drag, may be necessary to switch setae from an unloaded default state to an adhered state. Previously we showed that proper orientation, preload, and drag of single isolated setae increases attachment forces by 10–20-fold (Autumn et al. [2000](#page-6-0)). This discovery explains the load dependence and directionality observed at the whole animal scale by Dellit ([1934\)](#page-6-0), and is consistent with the structure of individual setae and spatulae (Ruibal and Ernst [1965;](#page-6-0) Hiller [1968\)](#page-6-0). It also suggests a hypothesis addressed by this study: we hypothesize that gecko setal arrays are non-sticky in their default state. We hypothesize further that the non-sticky default state is due primarily to structure—setae do not adhere spontaneously to surfaces because their surface topology while unloaded may prevent contact by a large fraction of the setal area.

Estimating contact fraction using Cassie's law of surface wettability

Water droplet contact angle  $(\theta)$  methods provide a measure of surface energy  $(y)$  available for adhesive bonding at a surface. Water droplet contact angle can be used as an index of hydrophobicity, with more hydrophobic surfaces having greater values of  $\theta$ .  $\cos(\theta)$  represents the interaction energy between water and the substrate, relative to the self-energy of water. For example, polytetrafluoroethylene (PTFE) has a large value of  $\theta$ =104–111°, indicating that it is hydrophobic, and suggesting that PTFE possesses a low  $\gamma$ .

In this study, we compared  $\theta$  in tokay gecko setal arrays to  $\theta$  of the smooth surface of the spectacle, which is an optically clear  $\beta$ -keratin scale covering the eye. Assuming that the  $\beta$ -keratin surfaces (Maderson [1964;](#page-6-0) Stewart and Daniel [1972;](#page-7-0) Bereiter-Hahn et al. [1984;](#page-6-0) Fraser and Parry [1996](#page-6-0); Alibardi [2003\)](#page-6-0) of setae and spectacle are hydrophobic ( $\theta > 60^{\circ}$ ) and similar in  $\gamma$ , we can apply Cassie's law of surface wettability (Cassie and Baxter [1944](#page-6-0); Chen et al. [1999;](#page-6-0) Patankar [2003,](#page-6-0) [2004](#page-6-0); Gao and Jiang [2004\)](#page-6-0) to determine the area fraction composed of solid and air at the seta–water interface:

$$
\cos\left(\theta_{\text{seta}}\right) = f_{\text{solid}}\cos\left(\theta_{\text{spec}}\right) - f_{\text{air}}\tag{1}
$$

It follows that since  $f_{\text{solid}} + f_{\text{air}} = 1$ ,

$$
f_{\text{solid}} = \frac{1 + \cos\left(\theta_{\text{seta}}\right)}{1 + \cos\left(\theta_{\text{spec}}\right)},\tag{2}
$$

where  $f_{\text{solid}}$  and  $f_{\text{air}}$  are the fractions of surface area occupied by setae and air, respectively.  $\theta_{\text{seta}}$  and  $\theta_{\text{spec}}$ are the water droplet contact angles on setal array and smooth spectacle.

A high value of  $\theta_{\text{seta}}$  would support the hypothesis that the gecko setae have low surface energy in an unloaded state.  $\theta_{\text{seta}} \gg \theta_{\text{spec}}$  would yield a small contact fraction,  $f_{\text{solid}}$ , supporting the hypothesis that a low surface energy in an unloaded state is due primarily to structure.

#### Methods

Water droplet contact angle measurement on gecko setal arrays and spectacles

#### Contact angles on isolated setal arrays

We carefully peeled single setal arrays from five restrained, non-molting tokay geckos (Gekko gecko) using the methods of Hansen and Autumn ([2005\)](#page-6-0). Using cyanoacrylate gel glue, these setal arrays were affixed, setal side up (Fig. 2), to glass slides that had been previously cleaned with acetone and ethanol. The fixed setal arrays were oriented such that the setae formed a flat surface on which contact angles could be measured.



Fig. 2 Schematic of experimental procedure. We used a waxtipped pipette to apply small deionized water droplets to the surface of isolated tokay gecko setal arrays fixed to a glass substrate. The water droplet contact angle  $(\theta)$  is the angle between the substrate plane and a tangent to the droplet at the point of contact

<span id="page-3-0"></span>To measure water droplet contact angle, we placed a right-angle prism (Newport Corporation, Irvine, CA, USA) under a microscope (Nikon SMZ1500) and positioned the glass slide with the fixed setal array in front of the prism so that both top view and the reflected side view were visible. This dual-view setup allowed us to measure the droplet contact angle from the side while correctly positioning the droplet within the field of view of the microscope. We placed deionized water droplets of variable size (approximately 0.5– 2 mm diameter) onto the setal array using a fine waxtipped capillary tube. Images  $(2,048\times1,536$  pixels) of each droplet at  $72\times$  magnification were captured on a digital camera (Nikon Coolpix 995; Fig. 3). Images were taken during three droplet stages: increasing volume, constant volume, and decreasing volume. These stages yielded advancing, equilibrium, and receding droplet contact angles (Chen et al. [1999](#page-6-0)). Angles were measured in Canvas 8 (Deneba, ACD, Saanichton, British Columbia, Canada). All measurements were completed within 24 h of isolating the setal array.

#### Contact angles on intact spectacle scales

We affixed the spectacle scale from the shed skin of two healthy tokay geckos to glass slides in the same manner as for setal array. Spectacles were dissected into smaller pieces before gluing to allow them to flatten. Advancing, equilibrium, and receding contact angles were measured and analyzed as for the setal array. All measurements were completed within 24 h of shedding.

Using a custom-made mount, we rotated the microscope in the experimental setup by  $90^\circ$  in order to measure water droplet contact angles on the large spectacle scales of five live, restrained, horizontally resting tokay geckos. The horizontal orientation of the microscope resulted in a side view of the droplet on the spectacle similar to that from the right-angle prism mentioned previously. We positioned the pipette tip just above the spectacle and allowed small droplets to fall onto the surface and captured images of constantvolume droplets. From these we measured equilibrium contact angles using the analysis methods described above. We did not measure dynamic angles in order to avoid possible injury to the animals' eyes from the pipette tip.

Equilibrium water contact angle  $(\theta)$  of isolated gecko

# **Results**



Fig. 3 Representative images of deionized water droplets (0.5– 2 mm diameter) on isolated tokay gecko setal array (a) and eye spectacle scale (b). Note that the *bright arcs* on the water droplets are reflections of the microscope illuminator. Mean  $\theta$  on isolated setal arrays was  $160.6 \pm 1.30^{\circ}$  (SD). In contrast,  $\theta$  on smooth spectacle scales was  $93.3 \pm 3.51^{\circ}$  (SD). The large difference in  $\theta$  between setal arrays and smooth spectacles suggests that the ultrahydrophobic nature of setal arrays is due to the highly rough surface topology that permits only a small (~6%) contact fraction with the water droplets

ing values of  $\theta$  were significantly smaller than advancing and equilibrium values (ANOVA,  $F=15.7$ ;  $df=2$ , 9; P=0.001).  $\theta$  of live gecko spectacles was 5% greater than in isolated samples (Table [1\)](#page-4-0). Equilibrium water contact angle  $(\theta)$  of gecko setal arrays was  $160.6 \pm 1.30^{\circ}$  (*n*=10; mean  $\pm$  SD), 72% greater than for isolated spectacles, and 63% greater than on the spectacles of live geckos (Fig. 3). Equilibrium, advancing, and receding values of  $\theta$  of setal arrays did not differ significantly (ANOVA,  $F=1.02$ ;  $df=2$ , 27;  $P=0.37$ ).

Contact angle hysteresis, the difference between advancing and receding contact angles, was  $1.4^\circ$  for setal arrays and  $18.6^{\circ}$  for isolated spectacles.

<span id="page-4-0"></span>**Table 1** Mean  $\pm$  SD of equilibrium, advancing, and receding water droplet contact angles  $(\theta)$ 

	$\theta_{\rm ea}$	$\theta_{adv}$	$\theta_{rec}$
Setal array	$160.6 \pm 1.30$	$160.7 \pm 3.65$	$159.3 \pm 2.04$
	(10)	(10)	(10)
Spectacle,	$93.3 \pm 3.51$	$96.0 \pm 1.91$	$77.4 \pm 7.68$
isolated	(6)	(3)	(3)
Spectacle, live	$98.3 \pm 3.89$ (5)		

Number of samples is in parentheses

Using Eq. 2, and  $\theta_{eq}$  of spectacles of live geckos, the estimated contact fraction  $(f_{solid})$  of setal arrays is 0.066. Using  $\theta_{eq}$  of isolated spectacles, the estimated contact fraction  $(f_{\text{solid}})$  of setal arrays is 0.060.

## **Discussion**

## Ultrahydrophobicity

There are two principle measures of ultrahydrophobicity, high equilibrium water droplet contact angle  $($ >150 $^{\circ}$ ) and low contact angle hysteresis [typically only a few degrees (Johnson and Dettre [1963;](#page-6-0) Chen et al. [1999\)](#page-6-0)]. The latter is considered by some to be the definitive measure of hydrophobicity (Johnson and Dettre [1963](#page-6-0); Wolfram and Faust [1978](#page-7-0); Chen et al. [1999\)](#page-6-0). Low contact angle hysteresis indicates that a water droplet is unlikely to become energetically pinned to the substrate; the droplet will readily roll off the surface at a small tilt angle. We found that gecko setae are ultrahydrophobic by both criteria ( $\theta$  =160.6°, hys-teresis=1.4°; Fig. [3](#page-3-0)a; Table 1), as predicted for  $\beta$ -keratin structures (Wainwright et al. [1982;](#page-7-0) Bereiter-Hahn et al. [1984;](#page-6-0) Russell [1986\)](#page-6-0). In contrast, spectacle scales are not ultrahydrophobic ( $\theta$  =93.3–98.3°, hystere-sis=18.6°; Fig. [3](#page-3-0)b; Table 1). Considering that both surfaces are composed of  $\beta$ -keratin, we conclude that the ultrahydrophobicity of setal arrays is due to their microstructure.

Gecko setae: a smart adhesive that is non-sticky by default

Typically, adhesives are liquids that are chemically compatible with both surfaces and that have sufficiently low viscosity that wetting of the surfaces occurs either spontaneously or with a small amount of pressure (Kinloch [1987;](#page-6-0) Pocius [2002\)](#page-6-0). Surface treatments are often needed to raise the interfacial energies between one or both surfaces and the

adhesive. Conventional PSAs are fabricated from soft viscoelastic materials that satisfy Dahlquist's (Dahlquist [1969;](#page-6-0) Pocius [2002](#page-6-0)) criterion for tack, a Young's modulus, E, of 300 kPa or less. Tacky materials are those that exhibit spontaneous plastic and elastic deformation that increase true area of contact with the surface at the molecular scale. Additives known as tackifiers are commonly used to promote plastic deformation in PSAs during contact (Pocius [2002](#page-6-0)). In contrast, the adhesive on the toes of geckos is made of  $\beta$ -keratin, a stiff material with E four to five orders of magnitude greater than the upper limit of Dahlquist's criterion. Therefore, one would not expect a  $\beta$ -keratin structure to function as a PSA by readily deforming to make intimate molecular contact with a variety of surface profiles. However, since the gecko adhesive is a microstructure in the form of an array of millions of high aspect ratio shafts (setae) the effective elastic modulus, Eeff (Persson [2003;](#page-6-0) Sitti and Fearing [2003](#page-7-0); Persson et al. [2005;](#page-6-0) Spolenak et al. [2005](#page-7-0)) is much lower than E of bulk  $\beta$ -keratin (Bonser and Purslow  $1995$ ; Bonser  $2000$ ).  $E_{\text{eff}}$  of gecko setal arrays is the subject of a separate study (Geisler et al. [2005](#page-6-0)).

Adhesion and friction between two molecularly smooth coplanar surfaces can be large (Baier et al. [1968](#page-6-0); Johnson [1985](#page-6-0)) since all molecules of both surfaces can interact at the sub-nanometer scale. The area fraction of sub-nanometer interactions is reduced when one or both surfaces are rough. Thus, roughness greatly decreases adhesion between rigid bodies (Baier et al. [1968](#page-6-0); Johnson [1985](#page-6-0); Israelachvili [1992;](#page-6-0) Gay and Leibler [1999](#page-6-0)). However, given sufficient preload pressure, plastic and elastic deformation can create areas of contact between rough surfaces that approach or exceed that of smoother surfaces (Johnson [1985\)](#page-6-0). The performance of gecko setal adhesives is due largely to the billions of spatulae (Fig. [1e](#page-1-0)) on compliant stalks that can conform to a substrate sufficiently well to approach the behavior of smooth surfaces in coplanar contact—even when the substrate is rough—without large preload pressure (Autumn et al. [2000](#page-6-0), [2002;](#page-6-0) Autumn and Peattie [2002](#page-6-0); Persson and Gorb [2003\)](#page-6-0). The Johnson–Kendall–Roberts model (Johnson et al. [1973](#page-6-0)) suggests that smaller spatulae increase adhesion pressure, assuming dense packing on the surface (Arzt et al. [2002,](#page-6-0) [2003](#page-6-0); Autumn and Peattie [2002](#page-6-0); Autumn et al. [2002](#page-6-0)).

## Minimizing contact in the default state

Assuming that the  $\beta$ -keratin surfaces (Maderson [1964;](#page-6-0) Stewart and Daniel [1972;](#page-7-0) Bereiter-Hahn et al. [1984;](#page-6-0) Fraser and Parry [1996;](#page-6-0) Alibardi [2003](#page-6-0)) of setae and spectacle are similar in surface energy  $(y)$ , our results suggest that the setal array is highly rough in its default state. Using Eq. 2, we calculate that less than 6.6% ±0.009 (SD) of setal area is available for initial contact with a smooth surface. This suggests that, initially, during a gecko's foot placement, the contact fraction of the distal region of the setal array must be very low. Yet the dynamics of the foot must be sufficient to increase the contact fraction substantially to achieve the extraordinary values of adhesion and friction that have been measured in whole animals (Irschick et al. [1996;](#page-6-0) Autumn et al. [2002](#page-6-0); Hansen and Autumn [2005\)](#page-6-0) and isolated setae (Autumn et al. [2000](#page-6-0), [2002](#page-6-0); Hansen and Autumn [2005\)](#page-6-0).

Thus gecko setae may be non-sticky by default because only a very small contact fraction is possible without mechanically deforming the setal array. Prior observations (Autumn et al. [2000](#page-6-0)) suggested that attachment requires a ''mechanical program'' (preload and drag) to initiate adhesion and high friction. Indeed the strength of frictional interaction can be programmed by modulating the amount of preload and/or drag (Autumn et al. [2000\)](#page-6-0), perhaps determining the number of spatulae brought into contact. Bending is a likely mode of deformation of setae (Persson [2003](#page-6-0); Sitti and Fearing [2003;](#page-7-0) Spolenak et al. [2005\)](#page-7-0). It is likely that bending of the setal shaft during preload and drag acts to promote spatular contact at the tip (Fig. [1d](#page-1-0)). The force associated with deformation of setal arrays is the subject of another study (Geisler et al. [2005](#page-6-0)).

# Maximizing contact in the adhered state

Empirical and theoretical estimates of spatular adhesion (Autumn et al. [2000,](#page-6-0) [2002](#page-6-0); Arzt et al. [2003;](#page-6-0) Spolenak et al. [2004;](#page-7-0) Hansen and Autumn [2005;](#page-6-0) Huber et al. [2005\)](#page-6-0) suggest that each spatula generates approximately 10–40 nN with approximately 0.02  $\mu$ m<sup>2</sup> area, or approximately 500–2,000 kPa. A single seta can generate 40  $\mu$ N over approximately 43  $\mu$ m<sup>2</sup> of area (unpublished data), or approximately 917 kPa of adhesive stress. Using the higher spatular force of 40 nN to provide a conservative estimate of setal contact area, we calculate 917/2,000 kPa=0.46 contact fraction. This suggests that unless the force of adhesion of a spatula has been greatly underestimated, the contact fraction must increase by approximately 7.5 fold following preload and drag in order to account for our prior measurements of 917 kPa of adhesive stress.

### Implications for self-cleaning

Strongly adhesive materials are not unusual (see Pocius [2002](#page-6-0) for review), nor are very weakly adhesive surfaces that are ultrahydrophobic (Barthlott and Neinhuis [1998](#page-6-0)). The gecko adhesive system is unique in that it combines strong adhesive capabilities and avoidance of inappropriate adhesion. The very low surface energy of unloaded gecko setae may aid in avoiding inappropriate adhesion not only to nearby surfaces, but to dirt particles as well. The results of this study suggest that like water droplets, dirt particles may not adhere strongly to the setal surface in the unloaded default state.

Highly hydrophobic rough surfaces can be washed clean by water droplets. This is known as the lotus effect (Barthlott and Neinhuis [1997,](#page-6-0) [1998;](#page-6-0) Neinhuis [1997](#page-6-0)) and is observed for plants with micro-rough epicuticular wax layers, for nano-rough pilot whale skin (Globicephala melas) (Baum et al. [2002](#page-6-0)), and possibly for the feet of non-adhesive gecko species (e.g., Stenodactylus khobarensis) (Russell [1979\)](#page-6-0). This study showed that non-adhered setal surfaces are highly non-wettable. Thus non-adhering setae should exhibit the lotus-like wet self-cleaning characteristic of non-adhesive micro- or nano-rough surfaces. Particles contacting the unloaded surface should wash away easily in the presence of water. However it is not known if geckos' feet often become wet.

We have shown previously that gecko setae are capable of self-cleaning from dirt particles even when strongly adhered to numerous spatulae in the loaded state (Hansen and Autumn [2005](#page-6-0)). Self-cleaning may occur by an energetic disequilibrium between the adhesive forces attracting a dirt particle to the substrate and those attracting the same particle to one or more spatulae.

Thus, there are three related self-cleaning mechanisms that can be utilized by natural and engineered adhesive nano-structures: (1) setae can form an ultrahydrophobic surface that resists unwanted adhesion, (2) setae may become cleaner by the lotus effect if they encounter water, and (3) setae may self-clean during normal use (Hansen and Autumn [2005\)](#page-6-0). All three mechanisms are due to a micro- and nano-rough topology that reduces adhesion with solid and liquid surfaces.

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#### References

- Alibardi L (2003) Ultrastructural autoradiographic and immunocytochemical analysis of setae formation and keratinization in the digital pads of the gecko Hemidactylus turcicus (Gekkonidae, Reptilia). Tissue Cell 35:288–296
- Arzt E, Enders S, Gorb S (2002) Towards a micromechanical understanding of biological surface devices. Z Metallkunde 93:345–351
- Arzt E, Gorb S, Spolenak R (2003) From micro to nano contacts in biological attachment devices. Proc Natl Acad Sci USA 100:10603–10606
- Autumn K, Peattie A (2002) Mechanisms of adhesion in geckos. Integr Comp Biol 42:1081–1090
- Autumn K, Liang YA, Hsieh ST, Zesch W, Chan W-P, Kenny WT, Fearing R, Full RJ (2000) Adhesive force of a single gecko foot-hair. Nature 405:681–685
- Autumn K, Sitti M, Peattie A, Hansen W, Sponberg S, Liang YA, Kenny T, Fearing R, Israelachvili J, Full RJ (2002) Evidence for van der Waals adhesion in gecko setae. Proc Natl Acad Sci USA 99:12252–12256
- Autumn K, Buehler M, Cutkosky M, Fearing R, Full RJ, Goldman D, Groff R, Provancher W, Rizzi AA, Saranli U, et al. (2005) Robotics in scansorial environments. Proc SPIE 5804:291–302
- Autumn K, Hsieh ST, Dudek DM, Chen J, Chitaphan C, Full RJ (2006) Dynamics of geckos running vertically. J Exp Biol 209:260–272
- Baier RE, Shafrin EG, Zisman WA (1968) Adhesion: mechanisms that assist or impede it. Science 162:1360–1368
- Barthlott W, Neinhuis C (1997) Purity of the sacred lotus, or escape from contamination in biological surfaces. Planta 202:1–8
- Barthlott W, Neinhuis C (1998) The lotus-effect: a paradigm for the use of a natural design for technical application. Am J Bot 85:6
- Baum C, Meyer W, Stelzer R, Fleischer L-G, Siebers D (2002) Average nanorough skin surface of the pilot whale (Globicephala melas, Delphinidae): considerations on the selfcleaning abilities based on nanoroughness. Mar Biol 140:653–657
- Bereiter-Hahn J, Matoltsy AG, Richards KS (1984) Biology of the integument 2: vertebrates. Springer, Berlin Heidelberg New York
- Bonser RHC (2000) The Young's modulus of ostrich claw keratin. J Mater Sci Lett 19:1039–1040
- Bonser RHC, Purslow PP (1995) The Young's modulus of feather keratin. J Exp Biol 198:1029–1033
- Cassie A, Baxter S (1944) Wettability of porous surfaces. Trans Faraday Soc 40:546–551
- Chen W, Fadeev AY, Hsieh MC, Oner D, Youngblood J, McCarthy T (1999) Ultrahydrophobic and ultralyophobic surface: some comments and examples. Langmuir 15:3395– 3399
- Dahlquist CA (1969) Pressure-sensitive adhesives. In: Patrick RL (ed) Treatise on adhesion and adhesives, vol 2. Dekker, New York, pp. 219–260
- Dellit W-D (1934) Zur Anatomie und Physiologie der Geckozehe. Jena Z Naturw 68:613–656
- Fraser RDB, Parry DAD (1996) The molecular structure of reptilian keratin. Int J Biol Macromol 19:207–211
- Gao X, Jiang L (2004) Water-repellent legs of water striders. Nature 432:36
- Gay C, Leibler L (1999) Theory of tackiness. Phys Rev Lett 82:936–939
- Geisler B, Dittmore A, Gallery B, Stratton T, Fearing R, Autumn K (2005) Deformation of isolated gecko setal arrays: bending or buckling? 2. Kinetics. Society of Integrative and Comparative Biology, San Diego
- Hansen W, Autumn K (2005) Evidence for self-cleaning in gecko setae. Proc Natl Acad Sci USA 102:385–389
- Hiller U (1968) Untersuchungen zum Feinbau und zur Funktion der Haftborsten von Reptilien. Z Morphol Tiere 62:307–362
- Huber G, Gorb S, Spolenak R, Arzt E (2005) Resolving the nanoscale adhesion of individual gecko spatulae by atomic force microscopy. Biol Lett 1:2–4
- Irschick DJ, Austin CC, Petren K, Fisher R, Losos JB, Ellers O (1996) A comparative analysis of clinging ability among pad-bearing lizards. Biol J Linn Soc 59:21–35
- Israelachvili J (1992) Intermolecular and surface forces. Academic, New York
- Johnson KL (1985) Contact mechanics. Cambridge University Press, Cambridge
- Johnson RE, Dettre RH (1963) Contact angle hysteresis I. Study of an idealized rough surface, chapter 7. In: Fowkes FM (ed) Advances in chemistry series, vol 43, American Chemical Society, Washington DC, pp. 112–129
- Johnson KL, Kendall K, Roberts AD (1973) Surface energy and the contact of elastic solids. Proc R Soc Lond A 324:310–313
- Kinloch AJ (1987) Adhesion and adhesives: science and technology. Chapman & Hall, New York
- Maderson PFA (1964) Keratinized epidermal derivatives as an aid to climbing in gekkonid lizards. Nature 203:780–781
- Neinhuis C (1997) Characterization and distribution of waterrepellent, self-cleaning plant surfaces. Ann Bot 79:667–677
- Patankar NA (2003) On the modeling of hydrophobic contact angles on rough surfaces. Langmuir 19:1249–1253
- Patankar NA (2004) Mimicking the lotus effect: influence of double roughness structures and slender pillars. Langmuir 20:8209–8213
- Persson BNJ (2003) On the mechanism of adhesion in biological systems. J Chem Phys 118:7614–7621
- Persson BNJ, Gorb S (2003) The effect of surface roughness on the adhesion of elastic plates with application to biological systems. J Chem Phys 119:11437
- Persson BNJ, Albohr O, Tartaglino U, Volokitin AI, Tosatti E (2005) On the nature of surface roughness with application to contact mechanics, sealing, rubber friction and adhesion. J Phys Condens Matter 17:R1–R62
- Pocius AV (2002) Adhesion and adhesives technology: an introduction, 2nd edn. Hanser Verlag, Munich
- Ruibal R, Ernst V (1965) The structure of the digital setae of lizards. J Morphol 117:271–294
- Russell AP (1975) A contribution to the functional morphology of the foot of the tokay, Gekko gecko (reptilia, gekkonidae). J Zool (Lond) 176:437–476
- Russell AP (1979) Parallelism and integrated design in the foot structure of gekkonine and diplodactyline geckos. Copeia 1979:1–21
- Russell AP (1986) The morphological basis of weight-bearing in the scansors of the tokay gecko (reptilia: Sauria). Can J Zool 64:948–955
- Schleich HH, Kästle W (1986) Ultrastrukturen an Gecko-Zehen (reptilia: Sauria: Gekkonidae). Amphib-Reptil 7: 141–166
- <span id="page-7-0"></span>Sitti M, Fearing RS (2003) Synthetic gecko foot-hair micro/nano structures as dry adhesives. J Adhes Sci Technol 17:1055– 1073
- Spolenak R, Gorb S, Gao HJ, Arzt E (2004) Effects of contact shape on the scaling of biological attachments. Proc Royal Soc Lond A 461:305–319
- Spolenak R, Gorb S, Arzt E (2005) Adhesion design maps for bio-inspired attachment systems. Acta Biomater 1:5–13
- Stewart G, Daniel R (1972) Scales of the lizard gekko gecko: surface structure examined with the scanning electron microscope. Copeia 1972(2):252–257
- Vinson J, Vinson J-M (1969) The saurian fauna of the Mascarene Islands. Bull Maurit Inst 6:203–320
- Wainwright SA, Biggs WD, Currey JD, Gosline JM (1982) Mechanical design in organisms. Princeton University Press, Princeton
- Williams EE, Peterson JA (1982) Convergent and alternative designs in the digital adhesive pads of scincid lizards. Science 215:1509–1511
- Wolfram E, Faust R (1978) Liquid drops on a tilted plate, contact angle hysteresis and the young contact angle. In: Padday JF (ed) Wetting, spreading, and adhesion. Academic, London, pp. 213–226