

Gecko adhesion: evolutionary nanotechnology

Kellar Autumn and Nick Gravish

Phil. Trans. R. Soc. A 2008 **366**, 1575-1590 doi: 10.1098/rsta.2007.2173

References	This article cites 84 articles, 18 of which can be accessed free http://rsta.royalsocietypublishing.org/content/366/1870/1575.ful l.html#ref-list-1
Rapid response	Respond to this article http://rsta.royalsocietypublishing.org/letters/submit/roypta;366/ 1870/1575
Email alerting service	Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click here

To subscribe to *Phil. Trans. R. Soc. A* go to: http://rsta.royalsocietypublishing.org/subscriptions



Gecko adhesion: evolutionary nanotechnology

By Kellar Autumn* and Nick Gravish

Department of Biology, Lewis & Clark College, Portland, OR 97219, USA

If geckos had not evolved, it is possible that humans would never have invented adhesive nanostructures. Geckos use millions of adhesive setae on their toes to climb vertical surfaces at speeds of over 1 m s^{-1} . Climbing presents a significant challenge for an adhesive in requiring both strong attachment and easy rapid removal. Conventional pressure-sensitive adhesives (PSAs) are either strong and difficult to remove (e.g. duct tape) or weak and easy to remove (e.g. sticky notes). The gecko adhesive differs dramatically from conventional adhesives. Conventional PSAs are soft viscoelastic polymers that degrade, foul, self-adhere and attach accidentally to inappropriate surfaces. In contrast, gecko toes bear angled arrays of branched, hair-like setae formed from stiff, hydrophobic keratin that act as a bed of angled springs with similar effective elastic modulus to that of PSAs. Setae are self-cleaning and maintain function for months during repeated use in dirty conditions. Setae are an anisotropic 'frictional adhesive' in that adhesion requires maintenance of a proximally directed shear load, enabling either a tough bond or spontaneous detachment. Gecko-like synthetic adhesives may become the glue of the future—and perhaps the screw of the future as well.

Keywords: gecko; adhesion; friction; contact mechanics; nanotechnology

The designers of the future will have smarter adhesives that do considerably more than just stick.

(Fakley 2001)

1. Introduction

Over two millennia ago, Aristotle commented on the ability of the gecko to 'run up and down a tree in any way, even with the head downwards' (Aristotle 350 BCE (1918)). Geckos, the world's supreme climbers, are capable of attaching and detaching their adhesive toes in milliseconds while running with apparently reckless abandon on vertical and inverted surfaces. More complete reviews of gecko adhesion can be found in recent volumes (Autumn 2006*a*,*b*; Bhushan & Sayer 2007).

A single seta (figure 1d) of the tokay gecko (figure 1a) is approximately 110 µm in length and 4.2 µm in diameter (Ruibal & Ernst 1965; Russell 1975; Williams & Peterson 1982). Setae are similarly oriented and uniformly

* Author for correspondence (autumn@lclark.edu).

One contribution of 7 to a Theme Issue 'Nanotribology, nanomechanics and applications to nanotechnology II'.



Figure 1. Structural hierarchy of the gecko adhesive system. Images (a, b) provided by Mark Moffett. (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 a mesoscale array of seta-bearing scansors (adhesive lamellae). (c) Microscale array of setae are arranged in a nearly grid-like pattern on the ventral surface of each scansor. In this scanning electron micrograph, each diamond-shaped structure is the branched end of a group of four setae clustered together in a tetrad. (d) Cryo-SEM image of a single gecko seta (image by S. Gorb and K. Autumn). Note individual keratin fibrils comprising the setal shaft. (e) Nanoscale array of hundreds of spatular tips of a single gecko seta. (f) Synthetic spatulae fabricated from polyimide at UC Berkeley in the laboratory of Ronald Fearing using nanomoulding (Campolo *et al.* 2003).

distributed in arrays (figure 1c) on approximately 20 leaf-like scansors of each toe (figure 1b). Each set branches to form a nanoarray of hundreds of spatular structures (figure 1e) that make intimate contact with the surface. 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 & Ernst 1965; Williams & Peterson 1982). Gecko setae are formed primarily of beta-keratin (Maderson 1964; Russell 1986; Alibardi 2003) with some alpha-keratin components (Rizzo et al. 2006). While the tokay is currently the best studied of any adhesive gecko species, there are over a thousand species of gecko (Han et al. 2004), encompassing an impressive range of morphological variation at the spatula, seta, scansor and toe levels (Maderson 1964; Ruibal & Ernst 1965; Russell 1975, 1981, 1986; Peterson & Williams 1981; Williams & Peterson 1982; Stork 1983; Schleich & Kästle 1986; Russell & Bauer 1988, 1990a, b; Roll 1995; Irschick et al. 1996; Autumn & Peattie 2002; Arzt et al. 2003). Setae have even evolved on the tails of some gecko species (Bauer 1998). Remarkably, setae have evolved convergently in iguanian lizards of the genus Anolis (Braun 1879; Ruibal & Ernst 1965; Peterson & Williams 1981) and in scincid lizards of the genus Prasinohaema (Williams & Peterson 1982; Irschick et al. 1996).

2. Mechanics of setal attachment and detachment

Two front feet of a tokay gecko (*Gekko gecko*) can withstand 20.1 N offorce parallel to the surface with 227 mm² of pad area (Irschick *et al.* 1996). The foot of a tokay bears approximately 3600 tetrads of setae mm⁻² or 14 400 setae mm⁻² (Schleich & Kästle 1986). Consequently, a single seta should produce an average force of 6.2 μ N and an average shear stress of 0.090 N mm⁻² (0.9 atm). Using a newly developed microelectromechanical system (MEMS) force sensor (Chui *et al.* 1998), we (Autumn *et al.* 2000) measured the adhesive and shear force of a single isolated gecko seta. Isolated setae did not adhere initially, leading us to hypothesize that a chemical component secreted by the gecko might be required for setal adhesion, as is the case for many insects (Gillett & Wigglesworth 1932; Edwards & Tarkanian 1970; Lee *et al.* 1986; Lees & Hardie 1988; Brainerd 1994). Instead, we discovered that attachment and detachment in gecko setae are controlled mechanically through the unique structural design of setae (Autumn *et al.* 2000; Gravish *et al.* 2008).

In the unloaded state, gecko setae are recurved proximally (towards the animal's body), with the tips bearing the spatular nanoarrays misaligned with the substrate. (In figure 1*d*, the left edge of the figure represents the approximate orientation of a vertical surface relative to an unloaded seta during climbing.) When the toes of the gecko are planted, the setae bend out of this resting state, flattening the stalks between the toe and the substrate such that their tips point distally (away from the animal's body). This small preload and an approximate 10 µm proximal displacement (Gravish et al. 2008) of the toe or scansor may serve to bring the spatulae (previously in a variety of orientations) uniformly flush with the substrate, pulling the setal shaft in tension. We discovered that adhesion in isolated setae requires a small push perpendicular to the surface, followed by a small parallel drag (Autumn et al. 2000). Dragging setae in shear pulls the spatula in tension resulting in large friction and adhesion forces (Tian *et al.* 2006). When properly oriented, preloaded and dragged, a single seta can generate 200 μ N in shear (Autumn *et al.* 2000) and 40 μ N in adhesion (Autumn *et al.* 2002), over three orders of magnitude more than that required to hold the animal's body weight (Autumn & Peattie 2002). All 6.5 million setae on the toes of one gecko attached simultaneously could lift 133 kg. Given the surprisingly large attachment forces generated by their setae, it is remarkable that geckos are able to detach their feet in just 15 ms with no measurable detachment forces (Autumn et al. 2006b).

Detachment of individual setae is accomplished by increasing the angle that the setal shaft makes with the substrate above 30° (Autumn *et al.* 2000). This is consistent with models of setae as cantilever beams (Sitti & Fearing 2003; Gao *et al.* 2005; Spolenak *et al.* 2005; Autumn 2006*b*, Autumn *et al.* 2006*c*) and with finite-element modelling of the seta (Gao *et al.* 2005). Elastic energy storage may be maximized for shaft angles near 35° ; however, such a low resting setal angle may inhibit rough surface compliance (Federle 2006). Optimum detachment of setae occurs when the base is displaced at an approximate right angle to the setal shaft (approx. 130° ; Gravish *et al.* 2008). High-angle detachment results in distal elastic unloading of the attached setae causing spontaneous detachment to occur. It is probable that as the angle of the setal shaft increases, the spatular forces are reduced (Tian *et al.* 2006) as the stress increases causing easy fracture of the spatula–substrate bonds (Autumn *et al.* 2000).



Figure 2. Force space of isolated gecko setal arrays on a glass surface. (a) Setal array during load (1), drag (2) and pull (3) (LDP) against the curvature of the setal shafts. F_{\perp} and F_{\parallel} followed a path along the Coulomb friction cone (dashed line of slope $1/\mu$). (b) LDP with curvature of the setal shafts. F_{\perp} and F_{\parallel} followed a path that began initially along the friction cone. As adhesion developed, forces converged on $F_{\perp} = -F_{\parallel} \tan \alpha^*$, where $\alpha^* \approx 30^\circ$ (dotted line).

3. Frictional adhesion

Amontons' first law states that the relationship of shear force (friction, F_{\parallel}) to normal load (F_{\perp}) is a constant value, μ (the coefficient of friction): $F_{\parallel} = \mu F_{\perp}$; friction is determined by the normal load. When setae are dragged across a surface against their natural curvature (the 'non-adhesive' direction), they do not adhere and instead exhibit typical Amontons friction (Autumn et al. 2006a; figure 2a). In tokay gecko setae, the friction coefficient on glass is approximately 0.3, a typical value for dry solid-solid interactions. In contrast, when dragged along their natural curvature (the 'adhesive' direction; figure 2b), setae exhibit a response that violates Amontons' first law. Adhered setae maintain strong static and kinetic friction even while under tensile loading and adhesion is determined by friction. Because detachment occurs at a shaft angle above 30° , a shear force must be maintained that is sufficient to keep the shaft at an angle below 30° . This relationship is $F_{\parallel} \ge -F_{\perp}/\tan 30$ or approximately $F_{\parallel} \ge -2F_{\perp}$. The requirement of shear force to maintain adhesion is an advantage because it provides precise control over adhesion via friction (shear force: Autumn et al. 2006a), allowing strong attachment and easy removal.

Amontons' second law predicts that μ is independent of the area of contact (Bhushan 2002; Ringlein & Robbins 2004). In contrast, shear stress in setae increases greatly with a decrease in contact area suggesting that at larger scales fewer spatulae are attached and/or the contact fraction within spatulae is reduced. Figure 3 illustrates the scaling of friction and adhesion from the spatular to the whole body level. It is unknown whether stress is spread uniformly across the toe or foot (Russell 2002) or there are stress concentrations on the setal arrays of a few scansors. The force of only 2% of setae, and only 25% of setal arrays, are required to yield the maximum shear stresses measured at the whole animal level (Irschick *et al.* 1996). However, at the setal level, it appears that most spatulae must be strongly attached to account for theoretical and empirical values of adhesion, suggesting that the seta is highly effective at making contact with a smooth surface.



Figure 3. Stress versus area in the gecko adhesive hierarchy modified from Autumn (2006*b*). Open circles represent measurements of adhesion and open squares represent measurements of friction. A JKR model prediction for spatular adhesion (23.6 nN) and the measured value for spatular pull off of 10 nN (Huber *et al.* 2005*a*) are too low to explain the 40 μ N adhesive force of a single seta. However, our new theoretical analysis of van der Waals (vdW) adhesion and friction (Tian *et al.* 2006) suggests that adhesion of a spatula can be increased by two orders of magnitude when the angle of pull is reduced from 90° to 10°. The van der Waals model predictions for spatular shear force at 10° pull angle are also consistent with measured values of shear force in single setae.

The relationship between friction and adhesion at the spatular level is a topic of current interest. In a recent study, we considered the coupling of friction and adhesion at the spatular scale (Tian *et al.* 2006) and showed that the contact geometry at the peel zone of a spatula becomes more favourable for *both* adhesion and friction, as spatulae are pulled at lower angles (below 30°). Our 'peel zone' model yielded predicted spatular forces of 70 nN adhesion and 400 nN friction when pulled at an angle of 10° , representing the forces during attachment of the setae. With a pull angle of 90° , representing detachment of the seta, our model predicted a force of 16 nN adhesion close to the 10 nN reported by Huber *et al.* (2005*a*) for spatulae pulled at approximately 90° (figure 3). Thus, frictional adhesion occurs at the spatular level as well as at the setal level, allowing adhesion to be controlled via the shear force.

4. Van der Waals adhesion in gecko setae

The adhesive setal structures of many gecko species are well documented; however, a comprehensive understanding of what produces setal adhesion has remained elusive. At the turn of the twentieth century, Haase (1900) noted that

K. Autumn and N. Gravish

attachment is load dependent and occurs only in one direction: proximally along the axis of the toe. He was also the first to suggest that geckos stick by intermolecular forces (*Adhäsion*). However, his suggestion was far from conclusive and at least seven possible mechanisms for gecko adhesion have been discussed over the past 175 years: glue, suction, interlocking, friction, static electricity, capillary forces and van der Waals adhesion. All but the latter two mechanisms had been rejected by 1969, and there was strong evidence that gecko adhesion was in part determined by surface energy (Hiller 1968, 1969, 1975; Autumn & Peattie 2002).

To test whether capillary adhesion or van der Waals force is a sufficient mechanism of adhesion in geckos, Autumn *et al.* (2002) measured adhesion and friction on two polarizable semiconductor surfaces that varied greatly in hydrophobicity. If capillary adhesive forces dominate, a lack of adhesion would be expected on strongly hydrophobic surfaces. In contrast, shear stress of live gecko toes on hydrophobic GaAs semiconductors was not significantly different from that on hydrophilic SiO_2 semiconductors, and adhesion of a single gecko seta on the hydrophilic SiO_2 and hydrophobic Si cantilevers differed by only 2%. They found that gecko setae are strongly hydrophobic with a water drop contact angle of 160.9°. Since van der Waals force is the only mechanism that can cause two hydrophobic surfaces to adhere in air (Israelachvili 1992: Parsegian 2006: Lamoreaux 2007), the semiconductor experiments provided direct evidence that van der Waals force is a sufficient mechanism of adhesion in gecko setae, and that water-based capillary forces are not required. Van der Waals force is largely independent of surface chemistry and highly dependent on the distance between surfaces; thus it can be said that gecko adhesion depends more on geometry than on chemistry. This discovery paved the way for fabrication of synthetic gecko adhesives from a variety of materials. Gecko keratin proteins are not required for fabrication of gecko-like adhesives; Autumn et al. (2002) used silicone and polyester to fabricate the first prototype synthetic gecko spatulae that exhibited limited gecko-like adhesion at the nanoscale.

The discovery that gecko adhere by van der Waals forces does not preclude an effect of water under some conditions. Water is likely to alter contact geometry and adhesion energies when present between hydrophobic (e.g. spatula) and hydrophilic (e.g. glass) surfaces, but it is exceedingly difficult to predict what the effect will be in gecko setae owing to the complexity of the system. Water may increase (Huber et al. 2005b; Sun et al. 2005) or decrease (Mizutani et al. 2005) adhesion (Kim & Bhushan 2008). While high humidity can result in an increase in adhesion in gecko spatulae, Huber *et al.* (2005b) rejected 'true' capillary forces involving a water bridge since only a few monolayers of water were present at the spatula–substrate interface—even at high humidity. Instead, they concluded that humidity (i) modifies the contact geometry, increasing adhesion and (ii) decreases the van der Waals Hamaker constant, reducing adhesion. These two effects counteracted each other to yield an increase in adhesion from 7 nN at low humidity to 12 nN at high humidity. These results support prior work (Autumn et al. 2002) showing that geckos can adhere solely by van der Waals forces, and that van der Waals adhesion is the primary mechanism of adhesion in geckos (Bhushan & Sayer 2007). It is well known that hydrophobic-hydrophobic interactions in air are due solely to van der Waals force (Israelachvili 1992). For arboreal geckos climbing on hydrophobic plant surfaces (Hollowav 1969;

Jeffree 1986), it is not clear whether humidity effects are important. However, even in this case, it is possible that prolonged exposure to high humidity or bulk water could cause changes in the setal keratin, possibly altering stiffness or even causing overturning to reveal more hydrophilic side chains.

5. Self-cleaning

Paradoxically, there is growing evidence that gecko setae are both strongly adhesive and strongly anti-adhesive. Self-adhesion is a common frustration when the adhesive surface of sticky tapes is folded together. Interestingly, gecko setal arrays do not self-adhere. Pushing the setal surfaces of a gecko's feet together does not result in strong adhesion. Also unlike conventional adhesives, gecko setae do not remain dirty. Gecko setae are the first known self-cleaning adhesive (Hansen & Autumn 2005). Tokay gecko feet contaminated with 2.5 μ m radius microspheres recovered their ability to cling to vertical surfaces only after a few steps on clean glass. Similarly, isolated setal arrays self-cleaned by repeated contact with a clean surface. Contact mechanical models suggest that it is possible that self-cleaning a dirt particle to the substrate and those attracting the same particle to one or more spatulae (Hansen & Autumn 2005). Particle rolling may also contribute to self-cleaning (Hui *et al.* 2006).

6. Comparison of gecko setae and conventional adhesives

Conventional adhesives are used extensively for industrial and residential applications (Pocius 2002). Adhesives come in many forms including tapes, hotmelt glues or curable liquid adhesives that harden through chemical reactions or exposure to UV light (Pocius 2002). All adhesives including gecko setae and the above examples must be able to spread over a surface to achieve intimate molecular contact (Kinloch 1987; Pocius 2002). Conventional adhesives are designed to flow in a liquid-like fashion spontaneously initiating intimate molecular contact (Kinloch 1987; Pocius 2002). Gecko setae however gain intimate molecular contact through the hierarchical branching of the adhesive from seta to spatula (Northen & Turner 2005; Autumn 2006b; Bhushan et al. 2006; Kim & Bhushan 2007a, 2007b; Kim et al. 2007). Additionally, the fibrillar structure of the gecko adhesive results in an effective elastic modulus ($E_{\rm eff} \sim 100$ kPa; figure 4; Autumn et al. 2006c) that is approximately equal to the Dahlquist stiffness criterion for tack ($E \leq 100$ kPa at 1 Hz) in pressure-sensitive adhesives (PSAs; Dahlquist 1969).

PSAs, such as tape, are the closest synthetic comparison to the gecko adhesive, having noticeable similarities yet equally noteworthy differences. Both adhesives adhere under light pressure without the use of chemicals, have elastic moduli below 100 kPa (Dahlquist 1969; Pocius 2002; Autumn *et al.* 2006*c*) and are capable of repeated use (Autumn *et al.* 2000; Gay 2002; Creton 2003). Van der Waals forces are responsible for the adhesion of both gecko setae (Autumn *et al.* 2002) and PSAs (Newby & Chaudhury 1998; Gay 2002; Creton 2003). However, gecko setae have significant advantages over PSAs, including the abilities to

Phil. Trans. R. Soc. A (2008)



Figure 4. Young's modulus (E) of materials including approximate values of bulk β -keratin and effective modulus (E_{eff}) of natural setal arrays. Adapted with permission from Autumn *et al.* (2006*c*). A value of $E \approx 100$ kPa (measured at 1 Hz) is the upper limit of the Dahlquist criterion for tack, which is based on empirical observations of pressure-sensitive adhesives (PSAs; Dahlquist 1969; Pocius 2002). A cantilever beam model (Sitti & Fearing 2003) predicts a value of E_{eff} near 100 kPa, as observed for natural setae and PSAs. It is notable that geckos have evolved E_{eff} close to the limit of tack. This value of E_{eff} may be tuned to allow strong and rapid adhesion, yet prevent spontaneous or inappropriate attachment (Autumn & Hansen 2006).

resist self-adhesion and particulate contamination (Hansen & Autumn 2005). PSAs deform plastically during detachment (Creton & Fabre 2002) while gecko setae deform elastically during load–unload cycles (Autumn *et al.* 2006*c*; Gravish *et al.* 2008).

PSAs are soft viscoelastic solids (Gay & Leibler 1999; Gay 2002; Pocius 2002; Creton 2003) that can be divided into two categories: permanent and removable PSAs. Permanent PSAs are designed for both structural and non-structural applications requiring a tenacious adhesive that can form tough bonds (Creton 2003). Removable PSAs are not typically used structurally since the weak adhesion that allows for easy removal also would result in failure under light structural loading (Creton 2003). Conversely, a large adhesive toughness enables structural loading, yet makes removal very difficult. Thus, in the design of PSAs, there is a trade-off between the ability to support heavy loading and ease of removal (Pocius 2002; Creton 2003).

Gecko setae function as both a permanent and a removable adhesive. Within 15 ms, climbing geckos are able to switch from producing large attachment forces to detaching efficiently with no lost kinetic energy (Autumn *et al.* 2006*b*). Anisotropic *frictional adhesion* (Autumn *et al.* 2006*a*) is a key to the gecko's smart adhesive (Fakley 2001) capabilities and should be considered a basic benchmark for gecko-like synthetics.

Single-axis detachment force measurements of PSAs during peeling, shearing or vertical pull off typically determine a PSA's loading capabilities (Pocius 2002). However, the gecko adhesive does not peel in the conventional sense (Kendall 1975) and has a complex interplay of friction and adhesion (which we termed *frictional adhesion*; Autumn *et al.* 2006*a*). Thus, pull off measurements must include a shear component (Autumn *et al.* 2000, 2006*a*). Unlike PSAs, gecko setae are non-adhesive

Gecko adhesion: evolutionary nanotechnology



Figure 5. To determine the adhesive properties of gecko setae, we measured two-dimensional forces while dragging in both proximal and distal directions. (a) Side view of a gecko toe illustrating the distal ('non-adhesive') and proximal ('adhesive') directions. The distal direction is away from the animal while the proximal direction is towards the animal. (b) Load-drag-pull (LDP) tests consist of a vertical load (L) to predetermined depth, a directional drag (D) while the vertical position is maintained and finally a vertical pull off (P) removing the adhesive from the surface. Setal arrays dragged in the proximal direction adhere and generate large friction forces. The adhesive force is controlled by friction and is sustained during shear sliding. (c) Distal dragging of setal arrays results in low friction and a compressive normal force. Setal arrays obey Amontons' law of friction in the distal direction with a coefficient of friction of $\mu \approx 0.25$ -0.3.

in their default state (Autumn & Hansen 2006) and require a small vertical preload followed by a proximal shear (Autumn *et al.* 2000) before adhesion occurs. Thus, adhesion of a gecko setal array cannot be measured using standard single-axis PSA measurement techniques; instead, a special double-axis testing system is required (see methods of Gravish *et al.* (2008)).

We developed the load-drag-pull (LDP) test (figure 5; Autumn *et al.* 2006*a*) to measure the basic function of natural and synthetic gecko adhesive samples (Autumn *et al.* 2007). An initial vertical preload to a predetermined depth is required to achieve sample substrate contact. Once loaded in compression, the sample is dragged in shear at a constant velocity over a set distance either proximally or distally while maintaining constant vertical displacement. Distal dragging (against setal curvature) produces standard Amontons/Coulomb friction forces (and no adhesion), with a coefficient of friction of

$$\mu = \frac{F_{\parallel}}{F_{\perp}},$$

and where the two-dimensional resultant force vector lies in quadrant II of the force space (figure 2a).

During proximal dragging (with setal curvature), adhesion occurs and the twodimensional forces produce a resultant vector in quadrant IV of the force space (figure 2b). The largest adhesion to friction ratio determines the critical angle of

detachment (α^*) as given by

$$\alpha^* = \arctan\left(\frac{F_{\perp}}{F_{\parallel}}\right).$$

After dragging, samples are removed from the surface along a set angle. The proximal and distal LDP tests are a simple method to compare the frictional adhesion properties of natural and synthetic samples (Autumn *et al.* 2007).

7. Gecko-like synthetic adhesives

Using a nanostructure to create an adhesive (figure 1f) is a novel and bizarre concept. It is possible that if it had not evolved, humans would never have invented it. Gecko-like synthetic adhesives (GSAs) are under rapid development (see del Campo & Arzt (2007) for review) and with each generation more gecko-like properties will emerge. Initial attempts at creating GSAs consisted of using dimpled or porous surfaces as moulding template negatives to create vertical fibrillar adhesives (Autumn et al. 2002; Geim et al. 2003; Sitti & Fearing 2003). Autumn et al. (2002) created the first such mould using an atomic force microscope tip to indent a wax surface serving as the moulding template for polydimethylsiloxane and polyester. Moulded synthetic spatulae approximated the nanoscale adhesive function of natural spatulae (Autumn et al. 2002), as predicted by the Johnson– Kendall-Roberts (JKR) model (Johnson et al. 1971), but recent theoretical considerations suggest that spherical contacts may have significant disadvantages (Spolenak et al. 2004; Tian et al. 2006). Larger scale moulding of GSAs yielded macroscale adhesion (Geim et al. 2003; Sitti & Fearing 2003; Glassmaker et al. 2004; Peressadko & Gorb 2004). However, these materials lack the anisotropy and relative ease of attachment and detachment of the natural gecko adhesive.

GSAs may someday match, or even exceed, the performance of natural gecko setae. Current GSAs mimic the fibrillar structure of setae but match few, if any, of the seven benchmark functional properties of natural gecko adhesives: anisotropic attachment; high pull off to preload ratio; low detachment force; material independence; self-cleaning; anti-self-matting; and non-sticky default state (Autumn 2006b). The growing list of benchmark properties (Autumn 2006b) can be used to evaluate the degree of gecko-like function of synthetic prototypes. For example, consider the adhesion coefficient, $\mu' = F_{adhesion}/F_{preload}$, as a metric for gecko-like adhesive function. By this criterion, the material of Geim *et al.* (2003) is not gecko-like since it required a very large preload of 50 N to yield 3 N and 0.3 atm of adhesion, yielding a value of $\mu' = 0.06$. The synthetic setae of Northen & Turner (2005) perform significantly better with $\mu' = 0.125$, but still well below the benchmark of real gecko setae where $\mu' = 8-16$.

Multiwalled carbon nanotubes (MWCNTs) are a promising GSA technology (Tong *et al.* 2005; Yurdumakan *et al.* 2005; Zhao *et al.* 2006). Each nanotube grown to a length of 50–100 μ m with a diameter of 10–20 nm could function as individual spatulae. Nanoscale adhesion measurements of a MWCNT-based GSA produced nanoscale detachment stresses up to 16 MPa (Yurdumakan *et al.* 2005), 35 times the adhesive stress measured in a single gecko seta (Autumn *et al.* 2000, 2002). However macroscale adhesion of this MWCNT-based adhesive was absent, due to the difficulty of achieving coplanar surface alignment

1584

(Yurdumakan *et al.* 2005). The limitations of MWCNT GSAs illustrate the importance of hierarchical branching (Northen & Turner 2005; Bhushan *et al.* 2006; Kim & Bhushan 2007*a*, 2007*b*; Kim *et al.* 2007) in gecko setae, in which spatula initiate sub-nanometre contact and setal shafts provide compliance to achieve a high contact fraction on non-coplanar surfaces.

Effective design of gecko-like adhesives will require deep understanding of the principles underlying the properties observed in the natural system. For example, synthetic setae that can attach without substantial preloads will probably require angled rather than vertical shafts (Sitti & Fearing 2003; Aksak *et al.* 2007; Kim & Bhushan 2007*c*) to promote a bending rather than buckling mode of deformation. Simultaneous measurements of friction and adhesion (Autumn *et al.* 2006*a*) will be important in assessing the degree of gecko-like (anisotropic, controllable) adhesive function in synthetic materials. Understanding of the gecko adhesive system is developing rapidly, enabling truly gecko-like synthetic dry adhesives with anisotropic frictional adhesion (Autumn *et al.* 2006*a*) and self-cleaning (Hansen & Autumn 2005) properties. The first synthetics to achieve anisotropic frictional adhesion (Autumn *et al.* 2007) and limited self-cleaning (Gorb *et al.* 2006) have recently been developed, and the future of gecko adhesives seems bright.

8. Applications for gecko-inspired adhesive nanostructures

Applications abound for a dry self-cleaning adhesive that does not rely on soft polymers or chemical bonds (Naik & Stone 2005). Biomedical applications such as endoscopy and tissue adhesives (Pain 2000; Menciassi & Dario 2003) are one example. However, any materials chosen for synthetic setae in biomedical applications would need to be non-toxic and non-irritating (Baier *et al.* 1968). Other applications include MEMS switching (Decuzzi & Srolovitz 2004), wafer alignment (Slocum & Weber 2003), micromanipulation (Pain 2000) and robotics (Autumn et al. 2005; Kim et al. 2007). Since a nanostructure could be applied directly to a surface, it is conceivable that gecko-like structures could replace screws, glues and interlocking tabs in many assembly applications, such as automobile dashboards or mobile phones. Adhesive nanostructures relying on van der Waals forces should be able to rebond dynamically following fracture, allowing for self-repair. With a clever joint design that takes advantage of frictional adhesion (Autumn *et al.* 2006a), self-disassembly for repair and recycling should also be possible. Self-cleaning adhesive nanostructures have the potential to reduce dramatically our reliance on cleaning solvents and surface preparation, reducing cost and environmental impact.

Sports applications such as fumble-free football gloves or rock climbing aids (Irving 1955) could be revolutionary. Using gecko technology to climb is not a new idea. In a seventeenth century Indian legend, Shivaji and his Hindu warriors used adhesive lizards from the Deccan region as grappling devices to scale a shear rock cliff and mount a surprise attack on a Maharashtrian clifftop stronghold (Ghandi 2002). The legendary climb was even depicted in a 1923 historical film, *Sinhagad* (although in this version of the legend it was Shivaji's military commander, Tanaji, who used geckos to assail the fortress; Varma 2005).

K. Autumn and N. Gravish

It is remarkable that the study of a humble lizard is contributing to understanding the fundamental processes underlying adhesion and friction (Fakley 2001; Urbakh *et al.* 2004) and providing biological inspiration for the design of novel adhesives and climbing robots (Autumn *et al.* 2005; Kim *et al.* 2007). The broad relevance and applications of the study of gecko adhesion underscore the value of basic curiosity-based research.

References

- Aksak, B., Murphy, M. & Sitti, M. 2007 Adhesion of biologically inspired vertical and angled polymer microfiber arrays. *Langmuir* 23, 3322–3332. (doi:10.1021/la062697t)
- 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. (doi:10.1016/S0040-8166(03)00050-8)
- Aristotle 350 BCE 1918 Historia animalium translated by Thompson, D'A.W. Oxford, UK: The Clarendon Press.
- Arzt, E., Gorb, S. & Spolenak, R. 2003 From micro to nano contacts in biological attachment devices. Proc. Natl Acad. Sci. USA 100, 10 603–10 606. (doi:10.1073/pnas.1534701100)
- Autumn, K. 2006a How gecko toes stick. Am. Sci. 94, 124-132. (doi:10.1511/2006.2.124)
- Autumn, K. 2006b Properties, principles, and parameters of the gecko adhesive system. In Biological adhesives (eds A. Smith & J. Callow), pp. 225–255. Berlin, Germany: Springer.
- Autumn, K. & Hansen, W. 2006 Ultrahydrophobicity indicates a nonadhesive default state in gecko setae. J. Comp. Physiol. A: Sens. Neural Behav. Physiol. 192, 1205–1212. (doi:10.1007/ s00359-006-0149-y)
- Autumn, K. & Peattie, A. 2002 Mechanisms of adhesion in geckos. Int. Comp. Biol. 42, 1081–1090. (doi:10.1093/icb/42.6.1081)
- Autumn, K., Liang, Y. A., Hsieh, S. T., Zesch, W., Chan, W.-P., Kenny, W. T., Fearing, R. & Full, R. J. 2000 Adhesive force of a single gecko foot-hair. *Nature* 405, 681–685. (doi:10.1038/ 35015073)
- Autumn, K. et al. 2002 Evidence for van der Waals adhesion in gecko setae. Proc. Natl Acad. Sci. USA 99, 12 252–12 256. (doi:10.1073/pnas.192252799)
- Autumn, K. et al. 2005 Robotics in scansorial environments. Proc. SPIE 5804, 291–302. (doi:10. 1117/12.606157)
- Autumn, K., Dittmore, A., Santos, D., Spenko, M. & Cutkosky, M. 2006a Frictional adhesion: a new angle on gecko attachment. J. Exp. Biol. 209, 3569–3579. (doi:10.1242/jeb.02486)
- Autumn, K., Hsieh, S. T., Dudek, D. M., Chen, J., Chitaphan, C. & Full, R. J. 2006b Dynamics of geckos running vertically. J. Exp. Biol. 209, 260–272. (doi:10.1242/jeb.01980)
- Autumn, K., Majidi, C., Groff, R., Dittmore, A. & Fearing, R. 2006c Effective elastic modulus of isolated gecko setal arrays. J. Exp. Biol. 209, 3558–3568. (doi:10.1242/jeb.02469)
- Autumn, K., Gravish, N., Wilkinson, M., Santos, D., Spenko, M. & Cutkosky, M. 2007 Frictional adhesion of natural and synthetic gecko setal arrays. In Proc. 30th Annual Meeting of the Adhesion Society, pp. 58–60.
- Baier, R. E., Shafrin, E. G. & Zisman, W. A. 1968 Adhesion: mechanisms that assist or impede it. Science 162, 1360–1368. (doi:10.1126/science.162.3860.1360)
- Bauer, A. M. 1998 Morphology of the adhesive tail tips of carphodactyline geckos (Reptilia: Diplodactylidae). J. Morphol. 235, 41–58. (doi:10.1002/(SICI)1097-4687(199801)235:1<41:: AID-JMOR4>3.0.CO;2-R)

Bhushan, B. 2002 Introduction to tribology. New York, NY: Wiley.

Bhushan, B. & Sayer, R. A. 2007 Gecko feet: natural attachment systems for smart adhesion. In Applied scanning probe methods, vol. 7 (eds B. Bhushan & H. Fuchs). Biomimetics and industrial applications, pp. 41–76. Heidelberg, Germany: Springer.

- Brainerd, E. L. 1994 Adhesion force of ants on smooth surfaces. Am. Zool. 34, 128A.
- Braun, M. 1879 Über die Haftorgane an der Unterseite der Zehen bei Anolius. Arb. Zool. Zoot. Inst. Würzburg 5, 31–36.
- Campolo, D., Jones, S. D. & Fearing, R. S. 2003 Fabrication of gecko foot-hair like nano structures and adhesion to random rough surfaces. In *IEEE Nano 2003 August 12–14*, vol. 2, pp. 856–859. San Francisco, CA: IEEE.
- Chui, B. W., Kenny, T. W., Mamin, H. J., Terris, B. D. & Rugar, D. 1998 Independent detection of vertical and lateral forces with a sidewall-implanted dual-axis piezoresistive cantilever. *Appl. Phys. Lett.* **72**, 1388–1390. (doi:10.1063/1.121064)
- Creton, C. 2003 Pressure-sensitive adhesives: an introductory course. MRS Bull. 28, 434-439.
- Creton, C. & Fabre, P. 2002 Tack. In Adhesion science and engineering, vol. I: the mechanics of adhesion (eds D. Dillard & A. Pocius), pp. 535–576. Amsterdam, The Netherlands: Elsevier.
- Dahlquist, C. A. 1969 Pressure-sensitive adhesives. In *Treatise on adhesion and adhesives*, vol. 2 (ed. R. L. Patrick), pp. 219–260. New York, NY: Dekker.
- Decuzzi, P. & Srolovitz, D. J. 2004 Scaling laws for opening partially adhered contacts in MEMS. J. Microelectromech. Syst. 13, 377–385. (doi:10.1109/JMEMS.2004.824889)
- del Campo, A. & Arzt, E. 2007 Design parameters and current fabrication approaches for developing bioinspired dry adhesives. *Macromol. Biosci.* 7, 118–127. (doi:10.1002/mabi. 200600214)
- Edwards, J. S. & Tarkanian, M. 1970 The adhesive pads of heteroptera: a re-examination. Proc. R. Entomol. Soc. Lond. 45, 1–5.
- Fakley, M. 2001 Smart adhesives. Chem. Ind. 5, 691–695.
- Federle, W. 2006 Why are so many adhesive pads hairy? J. Exp. Biol. 209, 2611–2621. (doi:10. 1242/jeb.02323)
- Gao, H. J., Wang, X., Yao, H. M., Gorb, S. & Arzt, E. 2005 Mechanics of hierarchical adhesion structures of geckos. *Mech. Mater.* 37, 275–285. (doi:10.1016/j.mechmat.2004.03.008)
- Gay, C. 2002 Stickiness—some fundamentals of adhesion. *Int. Comp. Biol.* **42**, 1123–1126. (doi:10. 1093/icb/42.6.1123)
- Gay, C. & Leibler, L. 1999 Theory of tackiness. Phys. Rev. Lett. 82, 936–939. (doi:10.1103/ PhysRevLett.82.936)
- Geim, A. K., Dubonos, S. V., Grigorieva, I. V., Novoselov, K. S. & Zhukov, A. A. 2003 Microfabricated adhesive mimicking gecko foot-hair. *Nat. Mater.* 2, 461–463. (doi:10.1038/ nmat917)
- Ghandi, M. 2002 The ughly buglies. Swagat January 2002.
- Gillett, J. D. & Wigglesworth, V. B. 1932 The climbing organ of an insect, *Rhodnius prolixus* (Hemiptera, Reduviidae). Proc. R. Soc. B 111, 364–376. (doi:10.1098/rspb.1932.0061)
- Glassmaker, N. J., Jagota, A., Hui, C. Y. & Kim, J. 2004 Design of biomimetic fibrillar interfaces: 1. Making contact. J. R. Soc. Interface 1, 1–11. (doi:10.1098/rsif.2004.0004)
- Gorb, S., Varenberg, M., Peressadko, A. & Tuma, J. 2006 Biomimetic mushroom-shaped fibrillar adhesive microstructure. J. R. Soc. Interface 4, 271–275. (doi:10.1098/rsif.2006.0164)
- Gravish, N., Wilkinson, M. & Autumn, K. 2008 Frictional and elastic energy in gecko adhesive detachment. J. R. Soc. Interface. 5, 339–348. (doi:10.1098/rsif.2007.1077)
- Haase, A. 1900 Untersuchungen über den Bau und die Entwicklung der Haftlappen bei den Geckotiden. Arch. Naturgesch. 66, 321–345.
- Han, D., Zhou, K. & Bauer, A. M. 2004 Phylogenetic relationships among gekkotan lizards inferred from Cmos nuclear DNA sequences and a new classification of the Gekkota. *Biol. J. Linn. Soc.* 83, 353–368. (doi:10.1111/j.1095-8312.2004.00393.x)
- Hansen, W. & Autumn, K. 2005 Evidence for self-cleaning in gecko setae. Proc. Natl Acad. Sci. USA 102, 385–389. (doi:10.1073/pnas.0408304102)

K. Autumn and N. Gravish

- Hiller, U. 1968 Untersuchungen zum Feinbau und zur Funktion der Haftborsten von Reptilien. Z. Morphol. Tiere 62, 307–362. (doi:10.1007/BF00401561)
- Hiller, U. 1969 Correlation between corona-discharge of polyethylene-films and the adhering power of Tarentola *M. mauritanica* (Rept.). Forma et functio 1, 350–352.
- Hiller, U. 1975 Comparative studies on the functional morphology of two gekkonid lizards. J. Bombay Nat. Hist. Soc. 73, 278–282.
- Holloway, P. 1969 The effects of superficial wax on leaf wettability. Ann. Appl. Biol. 63, 145–153.
- Huber, G., Gorb, S., Spolenak, R. & Arzt, E. 2005a Resolving the nanoscale adhesion of individual gecko spatulae by atomic force microscopy. *Biol. Lett.* 1, 2–4. (doi:10.1098/rsbl.2004.0254)
- Huber, G., Mantz, H., Spolenak, R., Mecke, K., Jacobs, K., Gorb, S. & Arzt, E. 2005b Evidence for capillarity contributions to gecko adhesion from single spatula nanomechanical measurements. *Proc. Natl Acad. Sci. USA* **102**, 16 293–16 296. (doi:10.1073/pnas.0506328102)
- Hui, C. Y., Shen, L., Jagota, A. & Autumn, K. 2006 Mechanics of anti-fouling or self-cleaning in gecko setae. In Proc. 29th Annual Meeting of the Adhesion Society, Inc.
- Irschick, D. J., Austin, C. C., Petren, K., Fisher, R., Losos, J. B. & Ellers, O. 1996 A comparative analysis of clinging ability among pad-bearing lizards. *Biol. J. Linn. Soc.* 59, 21–35. (doi:10. 1006/bijl.1996.0052)
- Irving, R. L. G. 1955 A history of British mountaineering. London, UK: B. T. Batsford Ltd.
- Israelachvili, J. 1992 Intermolecular and surface forces. New York, NY: Academic Press.
- Jeffree, C. 1986 The cuticle, epicuticular waxes and trichomes of plants, with reference to their structure, functions and evolution. In *Insects and the plant surface* (eds B. Juniper & R. S. Southwood), pp. 23–64. London, UK: Edward Arnold Publishers Ltd.
- Johnson, K. L., Kendall, K. & Roberts, A. D. 1971 Surface energy and the contact of elastic solids. Proc. R. Soc. A 324, 310–313. (doi:10.1098/rspa.1971.0141)
- Kendall, K. 1975 Thin-film peeling—the elastic term. J. Phys. D: Appl. Phys. 8, 1449–1452. (doi:10.1088/0022-3727/8/13/005)
- Kim, T. W. & Bhushan, B. 2007a Adhesion analysis of multi-level hierarchical attachment system contacting with a rough surface. J. Adhes. Sci. Technol. 21, 1–20. (doi:10.1163/15685610 7779976097)
- Kim, T. W. & Bhushan, B. 2007b Effect of stiffness of multi-level hierarchical attachment system on adhesion enhancement. Ultramicroscopy 107, 902–912. (doi:10.1016/j.ultramic.2006.11.008)
- Kim, T. W. & Bhushan, B. 2007c Optimization of biomimetic attachment system contacting with a rough surface. J. Vac. Sci. Technol. A 25, 1003–1012. (doi:10.1116/1.2435389)
- Kim, T.-W. & Bhushan, B. 2008 The adhesion model considering capillarity for gecko attachment system. J. R. Soc. Interface 5, 319–327. (doi:10.1098/rsif.2007.1078)
- Kim, S., Spenko, M., Trujillo, S., Heyneman, B., Mattoli, V. & Cutkosky, M. R. 2007 Whole body adhesion: hierarchical, directional and distributed control of adhesive forces for a climbing robot. In *IEEE International Conference on Robotics and Automation, Rome, Italy*, pp. 1268–1273.
- Kinloch, A. J. 1987 Adhesion and adhesives: science and technology. New York, NY: Chapman and Hall.
- Lamoreaux, S. 2007 Casimir forces: still surprising after 60 years. *Phys. Today* **60**, 40–45. (doi:10. 1063/1.2711635)
- Lee, Y. I., Kogan, M. & Larsen, J. R. J. 1986 Attachment of the potato leafhopper to soybean plant surfaces as affected by morphology of the pretarsus. *Entomol. Exp. Appl.* 42, 101–107. (doi:10. 1007/BF00343535)
- Lees, A. D. & Hardie, J. 1988 The organs of adhesion in the aphid *Megoura viciae*. J. Exp. Biol. **136**, 209–228.
- Maderson, P. F. A. 1964 Keratinized epidermal derivatives as an aid to climbing in gekkonid lizards. Nature 203, 780–781. (doi:10.1038/203780a0)
- Menciassi, A. & Dario, P. 2003 Bio-inspired solutions for locomotion in the gastrointestinal tract: background and perspectives. *Phil. Trans. R. Soc. A* 361, 2287–2298. (doi:10.1098/rsta.2003. 1255)

- Mizutani, K., Egashira, K., Toukai, T. & Ogushi, J. 2005 Adhesive force of a spider mite, Tetranychus urticae, to a flat smooth surface. Nihon Kikai Gakkai Ronbunshu, C Hen/Trans. Japan Soc. Mech. Eng., Part C 71, 2094–2099.
- Naik, R. R. & Stone, M. O. 2005 Integrating biomimetics. *Mater. Today* 8, 18–20. (doi:10.1016/ S1369-7021(05)71077-4)
- Newby, B. M. Z. & Chaudhury, M. K. 1998 Friction in adhesion. Langmuir 14, 4865–4872. (doi:10. 1021/la9802901)
- Northen, M. T. & Turner, K. L. 2005 A batch of fabricated dry adhesive. Nanotechnology 16, 1159–1166. (doi:10.1088/0957-4484/16/8/030)
- Pain, S. 2000 Sticking power. New Sci. 168, 62-67.
- Parsegian, V. 2006 Van der Waals forces, a handbook for biologists, chemists, engineers, and physicists. New York, NY: Cambridge University Press.
- Peressadko, A. & Gorb, S. N. 2004 When less is more: experimental evidence for tenacity enhancement by division of contact area. J. Adhes. 80, 247–261. (doi:10.1080/00218460490430199)
- Peterson, J. A. & Williams, E. E. 1981 A case study in retrograde evolution: the onca lineage in anoline lizards. II. Subdigital fine structure. Bull. Mus. Comp. Zool. 149, 215–268.
- Pocius, A. V. 2002 Adhesion and adhesives technology: an introduction, 2nd edn. Munich, Germany: Hanser Verlag.
- Ringlein, J. & Robbins, M. O. 2004 Understanding and illustrating the atomic origins of friction. Am. J. Phys. 72, 884–891. (doi:10.1119/1.1715107)
- Rizzo, N., Gardner, K., Walls, D., Keiper-Hrynko, N., Ganzke, T. & Hallahan, D. 2006 Characterization of the structure and composition of gecko adhesive setae. J. R. Soc. Interface 3, 441–451. (doi:10.1098/rsif.2005.0097)
- Roll, B. 1995 Epidermal fine structure of the toe tips of Sphaerodactylus cinereus. J. Zool. 235, 289–300.
- Ruibal, R. & Ernst, V. 1965 The structure of the digital setae of lizards. J. Morphol. 117, 271–294. (doi:10.1002/jmor.1051170302)
- Russell, A. P. 1975 A contribution to the functional morphology of the foot of the tokay, *Gekko gecko* (Reptilia, Gekkonidae). J. Zool. Lond. 176, 437–476.
- Russell, A. P. 1981 Descriptive and functional anatomy of the digital vascular system of the tokay, Gekko gecko. J. Morphol. 169, 293–323. (doi:10.1002/jmor.1051690305)
- Russell, A. P. 1986 The morphological basis of weight-bearing in the scansors of the tokay gecko (Reptilia: Sauria). Can. J. Zool. 64, 948–955.
- Russell, A. P. 2002 Integrative functional morphology of the gekkotan adhesive system (Reptilia: Gekkota). *Integr. Comp. Biol.* 42, 1154–1163. (doi:10.1093/icb/42.6.1154)
- Russell, A. P. & Bauer, A. M. 1988 Paraphalangeal elements of gekkonid lizards: a comparative survey. J. Morphol. 197, 221–240. (doi:10.1002/jmor.1051970208)
- Russell, A. P. & Bauer, A. M. 1990a Digit I in pad-bearing gekkonine geckos: alternate designs and the potential constraints of phalangeal number. *Mem. Queensl. Mus.* 29, 453–472.
- Russell, A. P. & Bauer, A. M. 1990b Oedura and Afroedura (Reptilia: Gekkonidae) revisited: similarities of digital design, and constraints on the development of multiscansorial subdigital pads? *Mem. Queensl. Mus.* 29, 473–486.
- Schleich, H. H. & Kästle, W. 1986 Ultrastrukturen an Gecko-Zehen (Reptilia: Sauria: Gekkonidae). Amphib.-Reptil. 7, 141–166.
- Sitti, M. & Fearing, R. S. 2003 Synthetic gecko foot-hair micro/nano structures as dry adhesives. J. Adhes. Sci. Technol. 17, 1055–1073. (doi:10.1163/156856103322113788)
- Slocum, A. H. & Weber, A. C. 2003 Precision passive mechanical alignment of wafers. J. Microelectromech. Syst. 12, 826–834. (doi:10.1109/JMEMS.2003.820289)
- Spolenak, R., Gorb, S., Gao, H. J. & Arzt, E. 2004 Effects of contact shape on the scaling of biological attachments. Proc. Math. Phys. Eng. Sci. 461, 305–319. (doi:10.1098/rspa.2004.1326)
- Spolenak, R., Gorb, S. & Arzt, E. 2005 Adhesion design maps for bio-inspired attachment systems. Acta Biomater. 1, 5–13. (doi:10.1016/j.actbio.2004.08.004)

K. Autumn and N. Gravish

- Stork, N. E. 1983 A comparison of the adhesive setae on the feet of lizards and arthropods. J. Nat. Hist. 17, 829–835. (doi:10.1080/00222938300770641)
- Sun, W., Neuzil, P., Kustandi, T. S., Oh, S. & Samper, V. D. 2005 The nature of the gecko lizard adhesive force. *Biophys. J.* 89, L14–L17. (doi:10.1529/biophysj.105.065268)
- Tian, Y., Pesika, N., Zeng, H., Rosenberg, K., Zhao, B., McGuiggan, P., Autumn, K. & Israelachvili, J. 2006 Adhesion and friction in gecko toe attachment and detachment. *Proc. Natl Acad. Sci. USA* 103, 19 320–19 325. (doi:10.1073/pnas.0608841103)
- Tong, T., Zhao, Y., Delzeit, L., Majidi, C., Groff, R. E., Reddy, P., Majumdar, A., Kashani, A. & Meyyappan, M. 2005 Compressive properties of dense vertically aligned multi-walled carbon nanotube arrays. In NANO2005 ASME Integrated Nanosystems: Design, Synthesis & Applications, Berkeley, CA, 14–16 September 2005.
- Urbakh, M., Klafter, J., Gourdon, D. & Israelachvili, J. 2004 The nonlinear nature of friction. Nature 430, 525–528. (doi:10.1038/nature02750)
- Varma, S. R. 2005 Plot summary for Sinhagad (1923). In *IMDB*, vol. 2005. See http://www.imdb. com/title/tt0249962/plotsummary.
- Williams, E. E. & Peterson, J. A. 1982 Convergent and alternative designs in the digital adhesive pads of scincid lizards. *Science* 215, 1509–1511. (doi:10.1126/science.215.4539.1509)
- Yurdumakan, B., Raravikar, N. R., Ajayanb, P. M. & Dhinojwala, A. 2005 Synthetic gecko foothairs from multiwalled carbon nanotubes. *Chem. Commun.* 2005, 3799–3801. (doi:10.1039/ b506047h)
- Zhao, Y., Tong, T., Delzeit, L., Kashani, A., Meyyappan, M. & Majumdar, A. 2006 Interfacial energy and strength of multiwalled-carbon-nanotube-based dry adhesive. J. Vac. Sci. Technol. B 24, 331–335. (doi:10.1116/1.2163891)