

Properties, Principles, and Parameters of the Gecko Adhesive System

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“The designers of the future will have smarter adhesives that do considerably more than just stick” –Fakley 2001

1. Summary

Gecko toe pads are sticky because they feature an extraordinary hierarchy of structure that functions as a smart adhesive. Gecko toe pads (Russell 1975) operate under perhaps the most severe conditions of any adhesives application. Geckos are capable of attaching and detaching their adhesive toes in milliseconds (Autumn et al. 2005 (in press)) while running with seeming reckless abandon on vertical and inverted surfaces, a challenge no conventional adhesive is capable of meeting. Structurally, the adhesive on gecko toes differs dramatically from that of conventional adhesives. Conventional pressure sensitive adhesives (PSAs) such as those used in adhesive tapes are fabricated from materials that are sufficiently soft and sticky to flow and make intimate and continuous surface contact (Pocius 2002). Because they are soft and sticky, PSAs also tend to degrade, foul, self-adhere, and attach accidentally to inappropriate surfaces. Gecko toes typically bear a series of scensors covered with uniform microarrays of hair-like setae formed from β -keratin (Russell 1986; Wainwright et al. 1982), a material orders of magnitude stiffer than those used to fabricate PSAs. Each seta branches to form a nanoarray of hundreds of spatular structures that make intimate contact with the surface.

Functionally, the properties of gecko setae are as extraordinary as their structure: the gecko adhesive is 1) directional, 2) attaches strongly with minimal preload, 3) detaches quickly and easily (Autumn and Peattie 2002; Autumn et al. 2000), 4) sticks to nearly every material, 5) does not stay dirty (Hansen and Autumn 2005) or 6) self-adhere, and 7) is nonsticky by default. While some of the principles underlying these seven functional

properties are now well understood, much more research will be necessary to fully map out the parameters of this complex system.

2. 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/Thompson 1918). How geckos adhere has attracted substantial and sustained scientific scrutiny (Arzt et al. 2003; Autumn and Peattie 2002; Autumn et al. 2000; Autumn et al. 2002b; Cartier 1872b; Dellit 1934; Gadow 1901; Gennaro 1969; Hansen and Autumn 2005; Hiller 1968; Hiller 1969; Hiller 1975; Hora 1923; Huber et al. 2004; Irschick et al. 1996; Maderson 1964; Mahendra 1941; Ruibal and Ernst 1965; Russell 1975; Russell 1986; Schleich and Kästle 1986; Schmidt 1904; Stork 1983; Weitlaner 1902; Williams and Peterson 1982). The unusual hairlike microstructure of gecko toe pads has been recognized for well over a century (Braun 1878; Cartier 1872a; Cartier 1872b; Cartier 1874). Setal branches were discovered using light microscopy (Schmidt 1904), but the discovery of multiple split ends (Altevogt 1954) and spatular nanostructure (Ruibal and Ernst 1965) at the tip of each seta was made only after the development of electron microscopy.

A single seta of the tokay gecko is approximately 110 microns in length and 4.2 microns in diameter (Ruibal and Ernst 1965; Russell 1975; Williams and Peterson 1982) (Fig. 1). Setae are similarly oriented and uniformly distributed on the scensors. Setae branch at the tips into 100-1000 more structures (Ruibal and Ernst 1965; Schleich and Kästle 1986) 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 microns in length and also in width at the tip (Ruibal and Ernst 1965; Williams and Peterson 1982). 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, scensor, and toe levels (Arzt et al. 2003; Autumn and Peattie 2002; Irschick et al. 1996; Maderson 1964; Peterson and Williams 1981; Roll 1995; Ruibal and Ernst 1965; Russell 1975; Russell 1981; Russell 1986; Russell and Bauer 1988; Russell and Bauer 1990a; Russell and Bauer 1990b; Schleich and Kästle 1986; Stork 1983; Williams and Peterson 1982). 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; Peterson and Williams 1981; Ruibal and Ernst 1965), and in scincid lizards of the genus *Prasinohaema* (Irschick et al. 1996; Williams and Peterson 1982). This chapter aims broadly at identifying the known properties of the gecko adhesive system, possible underlying principles, and quantitative parameters that affect system function. However, much of what is known is based on studies of a single species –the tokay gecko (*Gekko gecko*)– and the degree of variation in function among species remains an open question that should be kept in mind.

3. Adhesive properties of gecko setae

Two front feet of a tokay gecko (*Gekko gecko*) can withstand 20.1 N of force parallel to the surface with 227 mm² of pad area (Irschick et al. 1996). The foot of a tokay bears approximately 3,600 tetrads of setae per mm², or 14,400 setae per mm² (Schleich and Kästle 1986; pers. obs.). 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). However, single setae proved both much less sticky and much more sticky than predicted by whole animal measurements, under varying experimental conditions, implying that attachment and detachment in gecko setae are mechanically controlled (Autumn et al. 2000).

3.1. Properties (1) anisotropic attachment and (2) high adhesion coefficient (μ')

Using a newly developed micro-electromechanical systems (MEMS) force sensor (Chui et al. 1998), Autumn and collaborators (2000) measured the adhesive and shear force of a single isolated gecko seta. Initial efforts to attach a single seta failed to generate forces above that predicted by Coulomb friction because of the inability to achieve the proper orientation of the seta in six degrees of freedom. The angle of the setal shaft was particularly important in achieving an adhesive bond. Strong attachment occurred when using proper orientation and a motion based on the dynamics of gecko legs during climbing (based on force plate data; Fig. 2; (Autumn et al. 2005 (in press))). A small normal preload force yielded a shear force of $\sim 40\mu$ N, six times the force predicted by whole-animal measurements (Irschick et al. 1996). The small normal preload force, combined with a 5 μ m proximal shear displacement yielded a very large shear force of 200 μ N, 32 times the force predicted by whole-animal measurements (Irschick et al. 1996) and 100 times the frictional force measured with the seta oriented with spatulae facing away from the surface (Autumn et al. 2000). The preload and drag steps were also necessary to initiate significant adhesion in isolated gecko setae, consistent with the load dependence and directionality of adhesion observed at the whole-animal scale by Haase (1900) and Dellit (1934). The ratio of preload to pulloff force is the adhesion coefficient, μ' , which represents the strength of adhesion as a function of the preload (Bhushan 2002). In isolated gecko setae, a 2.5 μ N preload yielded adhesion between 20 μ N (Autumn et al. 2000) and 40 μ N (Autumn et al. 2002b) and thus a value of μ' of between 8 and 16.

3.1.1. Large safety factor for adhesion and friction?

All 6.5 million (Irschick et al. 1996; Schleich and Kästle 1986) setae of a 50 gram Tokay gecko attached maximally could theoretically generate 1300 N (133 kg force) of shear force –enough to support the weight 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 (20N; (Irschick et al. 1996)). Only less than 0.04% of a gecko's setae attached maximally are needed to support its weight of 50 grams on a wall. At first glance, gecko feet seem to be enormously overbuilt by virtue of a safety margin of at least $(20 \text{ N} / 0.5 \text{ N}) - 1 = 3900\%$.

However, it is unlikely that all setae are able to achieve the same orientation simultaneously. The proportion of spatulae attached may be greatly reduced on rough surfaces (particularly those with roughness on the same scale as spatulae or setae) (Persson and Gorb 2003). On dusty or exfoliating surfaces, attachment to a well-anchored substrate will not be possible for every seta. Geckos may use a significant portion of their safety margin while withstanding high winds during tropical storms, resisting predator attack, or recovering adhesion after a fall (Autumn and Peattie 2002; Hecht 1952; Pianka and Sweet 2005; Russell 1976; Vinson and Vinson 1969).

Geckos have been observed to recover from a fall by re-attaching their toes to leaves or branches as they plummet (Pianka and Sweet 2005; Vitt and Zani 1997). A simple calculation suggests that recovery from a fall may require a large proportion of a gecko's safety margin of adhesion or friction. Consider a 50 gram gecko falling from rest. If the gecko attaches a foot to a vertical surface after it has fallen 10 cm (neglecting air resistance) it will be moving at 0.44 m/s. If the foot is able to produce 5 N of friction, the gecko will be able to come to a stop in 0.005 s after sliding 1.1 cm. In this theoretical example, recovering from a fall of the very modest distance of 10 cm would require 50% of the shear capacity of one foot based on whole animal measurements (Irschick et al. 1996) but still less than 4% of the theoretical maximum shear stress calculated for single setae (Autumn and Peattie 2002).

3.2. Property (3) low detachment force

The surprisingly large forces generated by single setae raised the question of how geckos manage to detach their feet in just 15 ms (Autumn et al. 2005 (in press)) with no measurable detachment forces (Autumn et al. 2005 (in press)). We discovered that simply increasing the angle that the setal shaft (α) makes with the substrate to 30° causes detachment (Autumn et al. 2000). We proposed that as the angle of the setal shaft increases, sliding stops and stress increases at the trailing edge of the seta, causing fracture of the seta-substrate bonds (Autumn et al. 2000) and returning the seta to the unloaded default state. This scenario is supported by models of setae as cantilever beams (Gao et al. 2005; Sitti and Fearing 2003; Spolenak et al. 2005) and by finite element modeling (FEM) of the seta (Gao et al. 2005). FEM simulation of the single seta pulloff experiment in Autumn et al. (2000) revealed more than an order of magnitude decrease in adhesive force as α increased from 30° to 90° . The FEM simulation also identified a transition from sliding to peeling that occurs at $\alpha = 30^\circ$, consistent with cantilever beam-based models (Sitti and Fearing 2003) and empirical observations that setae slide at $\alpha < 30^\circ$ but detach at $\alpha > 30^\circ$ (Autumn et al. 2000). Thus the gecko adhesive can be thought of as the first known *programmable adhesive*. Preload and drag steps turn on and modulate stickiness while increasing the shaft angle to 30° turns off stickiness.

3.3. Integration of body and leg dynamics with setal attachment and detachment

How attachment and detachment of millions of setae during locomotion are integrated with the function of the sensor, toe, foot, leg, and body remains a topic of interest and

ongoing research (Autumn et al. 2005 (in press); Autumn and Peattie 2002; Autumn et al. 2005; Gao et al. 2005; Russell 1986; Russell 2002). Since gecko setae require a preload in the normal axis for adhesion, large forces could potentially be associated with attachment of the foot. The tremendous adhesive capacity of gecko setae suggests that large forces could also occur during detachment. In fact, no measurable ground reaction forces were associated with either attachment or detachment during vertical climbing on a force plate of the house gecko *Hemidactylus garnoti* (Autumn et al. 2005 (in press)), indicating that these actions are either mechanically decoupled from the center of mass in this species, or result in forces so small as to be undetectable. Russell (2002) suggested that in the tokay (*Gekko gecko*), the perpendicular preload and $5\ \mu\text{m}$ drag requirements (Autumn and Peattie 2002; Autumn et al. 2000) are controlled by hydrostatic pressure in the highly derived blood sinuses, and lateral digital tendon system, respectively. However, control of inflation and deflation of the sinuses remains to be demonstrated. This mechanism would not be available to those species that lack blood sinuses.

Setal preload and drag could also be a consequence of force development during the stride (Fig. 2). The force necessary to bend even thousands of setae into an adhesive orientation is probably quite small (at most 10mN (Autumn and Peattie 2002)) and possibly below the threshold of the force plate used (Autumn et al. 2005 (in press)). Another possibility is that attachment is a reversal of the peeling process of toe detachment, which may be decoupled from the center of mass. The gecko's foot may approach the substrate without pressing into it and re-apply the adhesive by unrolling its toes like a new year's party favor. This process is called digital hyperextension (Russell 1975; Russell 2002). In this case, setal preload forces would be spread out over time, and would likely be far below the 1mN resolution of force plates used in measurements of whole body and single leg dynamics of small animals (Biewener and Full 1992).

Peeling may reduce detachment and attachment forces, but may limit speed during vertical climbing. If toe peeling and uncurling in climbing geckos requires some minimum time, then speed cannot be increased by reducing contact time as is typical in level running. *Hemidactylus garnoti* increased velocity by increasing stride length (Autumn et al. 2005 (in press)). Attachment and detachment occupied a constant value of approximately 20 ms.

3.4. Molecular mechanism of gecko adhesion

While setal structures of many gecko species are well documented, a complete understanding of what makes them adhere has been more elusive. At the turn of the 20th Century, Haase (1900) noted that attachment is load-dependent and only occurs in one direction: proximally along the axis of the toe. Haase was also the first to suggest that geckos stick by intermolecular forces (*Adhäsion*), noting that under this hypothesis the attractive force should increase as the space between the feet and the substrate decreases. However, at least seven possible mechanisms for gecko adhesion have been discussed over the past 175 years.

3.4.1. Unsupported mechanisms: glue, suction, electrostatics, microinterlocking, and friction

Since geckos lack glandular tissue on their toes, sticky secretions (Dewitz 1882) were ruled out early in the study of gecko adhesion (Cartier 1872a; Simmermacher 1884; Wagler 1830). The hypothesis that the toe pads acted as suction cups was first proposed by Wagler (1830), who classified geckos as amphibians. The hypothesis that individual setae act as miniature suction cups was first under debate in the insect adhesion literature (Blackwall 1845; Hepworth 1854). Dewitz argued against suction as an explanation for gecko adhesion (1882), but Simmermacher (1884) considered suction to be the most likely mechanism. However, there are no data to support suction as an adhesive mechanism, and the adhesion experiments carried out in a vacuum by Dellit (1934) suggest that suction is not involved. Measurements of 9 atm of adhesive stress (Autumn et al. 2002b) strongly contradict the suction hypothesis. Despite substantial evidence against it, the suction hypothesis has been surprisingly tenacious in the popular literature (e.g. (Gennaro 1969)). Electrostatic attraction (Schmidt 1904) was another hypothesized mechanism for adhesion in gecko setae. Experiments using X-ray bombardment (Dellit 1934) eliminated electrostatic attraction as a necessary mechanism for setal adhesion since geckos could still adhere to metal in ionized air. However, electrostatic effects could enhance adhesion even if another mechanism is operating (Maderson 1964).

Setae are recurved such that their tips point proximally, leading Dellit (1934) to hypothesize that setae act as micro- or nanoscale hooks, catching on surface irregularities (microinterlocking). Mahendra (1941) suggested that setae were analogous to the pitons of a climber's boot. Microinterlocking was challenged by the ability of geckos to adhere while inverted on polished glass. This mechanism could play a secondary role under some conditions, but the presence of large adhesive forces on a molecularly smooth SiO₂ MEMS semiconductor (Autumn et al. 2000) demonstrates that surface irregularities are not necessary for adhesion. The friction hypothesis (Hora 1923) can be dismissed since by definition, friction only acts in shear (Bhushan 2002), and therefore cannot in itself explain the adhesive capabilities of geckos on inverted surfaces.

3.4.2. Potential intermolecular mechanisms: van der Waals and Capillary Forces

Using the greatly enhanced resolution of electron microscopy, Ruibal and Ernst (1965) described the spatular structures at the setal tips. They concluded that spatulae were unlikely to function like the spikes on climbing boots and postulated that the spatulae lie flat against the substrate while the seta is engaged. It was clear to them that these flattened tips increased the realized contact area. Ruibal and Ernst (1965) concluded that gecko adhesion was the result of molecular interactions, not mechanical interlocking. The turning point in the study of gecko adhesion came with a series of experiments (Hiller 1968; Hiller 1969) that suggested that the surface energy of the substrate, rather than its texture, determined the strength of attachment. By providing evidence that intermolecular forces were responsible, Hiller paved the way for the application of modern methods of surface science (Israelachvili 1992) in studies of gecko adhesion (Autumn and Peattie

2002; Autumn et al. 2000; Autumn et al. 2002b; Hansen and Autumn 2005; Huber et al. 2004).

Hiller (1968; 1969; 1975) showed that shear force was correlated with the water droplet contact angle of the surface, and thus with the surface energy of the substrate, providing the first direct evidence that intermolecular forces are responsible for attachment in geckos.

Intermolecular capillary forces are the principal mechanism of adhesion in many insects (Brainerd 1994; Edwards and Tarkanian 1970; Gillett and Wigglesworth 1932; Lee et al. 1986; Lees and Hardie 1988), frogs (Emerson and Diehl 1980; Green 1981; Hanna and Barnes 1991) and even mammals (Rosenberg and Rose 1999). Unlike many insects, geckos lack glands on the surface of their feet (Bellairs 1970; Cartier 1872b). However, this does not preclude the role of capillary adhesion (Baier et al. 1968; Israelachvili 1992; Stork 1980; von Wittich 1854, quoted directly in Simmermacher 1884) since layers of water molecules are commonly present on hydrophilic surfaces at ambient humidities, and can cause strong attraction between surfaces. The observation (Hiller 1968; Hiller 1971; Hiller 1975) that geckos cannot adhere to polytetrafluoroethylene (PTFE; Teflon) is consistent with the capillary hypothesis, since PTFE is strongly hydrophobic. Indeed, the apparent correlation between adhesive force and hydrophobicity (water contact angle) (Hiller 1968; Hiller 1971; Hiller 1975) suggested that the polarity of the surface might be an important factor in the strength of adhesion (Autumn and Peattie 2002).

A non-mutually-exclusive alternative mechanism is van der Waals force (Autumn et al. 2000; Stork 1980). Van der Waals force is strongly dependent on the distance between surfaces, increases with the polarizability of the two surfaces, and is not related directly to surface polarity (Israelachvili 1992). The observation (Hiller 1968) that geckos cannot adhere to PTFE is consistent with both van der Waals and capillary hypotheses, since PTFE is weakly polarizable and hydrophobic.

3.4.3. Contact angle estimates of surface energy

Hiller's experiments (1968; 1969; 1975) were groundbreaking because they provided the first direct evidence for adhesion *sensu stricto*. The precise nature of the adhesion remained unknown until 2002 (Autumn and Peattie 2002; Autumn et al. 2002b). The intermolecular attraction between any fluid droplet and a surface is due to a combination of dispersive (van der Waals) and polar components (Israelachvili 1992; Pocius 2002). Water contact angle by itself cannot be used to determine the relative contributions of van der Waals and polar interactions. Complete liquid droplet contact angle analyses require a series of fluids ranging from dispersive (e.g. methylene iodide) to primarily polar (e.g. water) in order to partition the relative contributions of the different intermolecular forces (Baier et al. 1968; Israelachvili 1992; Pocius 2002). However, it is possible to test the hypothesis that van der Waals forces are sufficient for gecko adhesion by reanalyzing Hiller's data to linearize the relationship between water contact angle and adhesion energy (Autumn and Peattie 2002). Hiller's data (Hiller 1968; Hiller 1969; Hiller 1975)

when linearized (Autumn and Peattie 2002), yield a strong correlation between force and adhesion energy for $\theta > 60^\circ$, consistent with the van der Waals hypothesis.

3.5. Property (4) material independent adhesion

3.5.1. Testing the van der Waals and capillary adhesion hypotheses

To test directly whether capillary adhesion or van der Waals force is a sufficient mechanism of adhesion in geckos, Autumn and colleagues (Autumn et al. 2002b) measured the hydrophobicity of the setal surface and measured adhesion and friction on two polarizable semiconductor surfaces that varied greatly in hydrophobicity. If capillary adhesive forces dominate, we expected a lack of adhesion on the strongly hydrophobic surfaces. In contrast, if van der Waals forces are sufficient, we predicted large adhesive forces on the hydrophobic, but polarizable GaAs and Si MEMs surfaces. In either case we expected strong adhesion to the hydrophilic SiO₂ control surfaces. We showed that tokay gecko setae are ultrahydrophobic (160.9°; (Autumn and Hansen 2005 (in press); Autumn et al. 2002b)), probably a consequence of the hydrophobic side groups of β -keratin (Bereiter-Hahn et al. 1984). The strongly hydrophobic nature of setae suggests that they interact primarily via van der Waals forces whether water is present or not.

Shear stress of live gecko toes on GaAs ($\theta = 110^\circ$) and SiO₂ ($\theta = 0^\circ$) semiconductors was not significantly different, and adhesion of a single gecko seta on the hydrophilic SiO₂ and hydrophobic Si cantilevers differed by only 2%. These results reject the hypothesis that polarity (as indicated by θ) of a surface predicts attachment forces in gecko setae, as suggested by Hiller (1968; 1969), and are consistent with reanalysis of his data using adhesion energies (Autumn and Peattie 2002). Since van der Waals force is the only mechanism that can cause two hydrophobic surfaces to adhere in air (Israelachvili 1992), the GaAs and hydrophobic semiconductor experiments provide 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. Setal adhesion is strong on polar and nonpolar surfaces, perhaps because of the strongly hydrophobic material they are made of, and due to the very large contact areas made possible by the spatular nanoarray. Gecko setae thus have the property of *material independence*: they can adhere strongly to a wide range of materials, largely independently of surface chemistry.

3.5.2. The role of water in gecko adhesion

Property (4), material independent adhesion, does not preclude an effect of water on gecko adhesion 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 because of the complexity of the system. An excellent example of the difficulty of interpreting the effect of water on gecko adhesion is a study by Sun et al. (2005) that used a model of interaction of two hydrophilic surfaces as a function of humidity to predict greatest adhesion due to capillary forces at 70 to 80% relative humidity (RH). Sun et al. measured greater adhesion in gecko spatulae at 70% RH than in dry air. However the

theory and methods of this study leave room for interpretations other than that favored by its authors. While the parameters and assumptions of the capillary model were not presented in their paper, it is clear that this hydrophilic-hydrophilic model is not applicable to gecko setae since they are strongly hydrophobic (Autumn and Hansen 2005 (in press); Autumn et al. 2002b). It is well known that hydrophobic-hydrophobic interactions in air are due solely to van der Waals force. Plant surfaces are generally hydrophobic (Holloway 1969; Jeffree 1986), as are gecko setae. The property of largely material independent adhesion in gecko setae is due to the ubiquity of van der Waals forces, so even if capillary forces could occur between gecko setae and a hydrophilic substrate, it has already been shown that this is not necessary for gecko adhesion (Autumn et al. 2002b).

It is interesting to consider the possibility that adsorbed water could act as an interlayer, with van der Waals forces acting between setae and water, while H-bonds and polar interactions could dominate between water and the substrate. Water could reduce adhesion on rough surfaces by preventing spatular penetration into gaps, thus decreasing the contact fraction (Persson and Gorb 2003). Alternatively, a fluid interlayer could enhance adhesion on rough surfaces by filling in gaps and increasing the contact fraction. The property of material independence predicts that the primary effect of water would be to alter the contact fraction, not adhesion energy. The effect of water on adhesion and friction in gecko setae will be a challenging and productive research area.

3.5.3. Dominance of geometry in vdW interactions

The theoretical magnitude of van der Waals force between a planar substrate and a circular planar spatula of radius R (Israelachvili 1992) is: $F_{vdw} = \frac{AR^2}{6D^3}$, and for a planar substrate and a curved spatula of radius R : $F_{vdw} = \frac{AR}{6D^2}$, where A represents the Hamaker constant, D is the gap distance (typically 0.2 nm for solids in contact). A is a function of the volume and polarizability of the molecules involved.

A , the Hamaker constant, for materials interacting in dry air is typically approx. 10^{-19} J. Altering the chemical composition of one or both surfaces can alter A , which can be as low as approx. one half to one third this value for some polymer-polymer interactions (e.g. PTFE or polystyrene), and as high as five times this value for some metal-on-metal interactions. In water, A can be reduced by an order of magnitude. Nevertheless, the variation in A is only about an order of magnitude while gap distance and contact area may vary by six or more orders of magnitude without macroscopically visible changes at the interface. Moreover, the effects of gap distance are exponential to a power of at least two. Thus adhesive surface effects due to van der Waals interactions are a function primarily of geometry not chemistry. A van der Waals mechanism for adhesion in gecko setae suggests that continuum theory models of the mechanics of surface contact (Johnson 1985) may be applicable. Then again, since the complex structure of setae and spatulae differs dramatically from the ideal curved and planar surfaces used in contact

mechanics models, one might question the validity of models based on simple geometries to the function of gecko setae.

3.5.4. JKR model of spatulae

The mechanics of contact have been modeled using continuum theory and highly simplified geometries. For example the Johnson, Kendall, Roberts (JKR; (Johnson et al. 1973)) model considers the force F required to pull an elastic sphere of radius R from a planar surface. The predicted adhesion force is given by, $F = (3/2)\pi R\gamma$, where γ is the adhesion energy between the sphere and the surface. Using values of $R = 100$ nm and $\gamma = 50$ mJ/m², the predicted force for a gecko spatula is $F = 23.6$ nN, approx. twice the value measured by AFM (Huber et al. 2004) (Table 1).

Another test of the validity of the JKR model is to begin with the forces measured in single setae, and then calculate the size of the JKR sphere (Autumn et al. 2002b). Adhesion is ~ 40 μ N per seta on silicon cantilever surfaces (Table 1). The setal tip is approx. 43 μ m² in area (Autumn and Gorb 2005, pers. obs.), therefore the adhesive stress (σ) was ~ 917 kPa. If the spatulae are packed tightly, $\sigma \approx (3/2) \pi R\gamma / \pi R^2 = (3/2) \gamma / R$. Using a typical adhesion energy for van der Waals surfaces ($\gamma = 50$ to 60 mJ/m²), solving for the predicted radii (R) of individual spatulae using empirical force measurements: $R = (3/2) \gamma / \sigma = 82$ to 98 nm, (164 to 196 nm in diameter). This value is remarkably close to empirical measurements of real gecko spatulae (200 nm in width) (Autumn et al. 2000; Ruibal and Ernst 1965) yet obviously spatulae are not spherical (Fig. 1E). Note that the preceding estimate of R using the JKR model differs from that of Autumn and colleagues' (2002b) in that they estimated the area of one seta using setal density, and arrived at a similar but somewhat lower value for σ . The confirmation that the JKR model predicts similar magnitudes of force as observed in setae suggested the extraordinary conclusion that adhesion can be enhanced simply by splitting a surface into small protrusions to increase surface density (Autumn et al. 2002b) and that adhesive stress is proportional to $1/R$ (Arzt et al. 2002). This model is supported by a comparative analysis of setae in lizards and arthropods (Arzt et al. 2003) (see Section 6.1).

3.5.5. Kendall peel model of spatulae

Spatulae may also be modeled as nanoscale strips of adhesive tape (Hansen and Autumn 2005; Huber et al. 2004; Spolenak et al. 2004). Using the approach of Kendall (1975), $F = \gamma w$, assuming there is negligible elastic energy storage in the spatula as it is pulled off, and where w is the width of the spatula, and γ is the adhesion energy as for the JKR model. Empirical measurements of spatular adhesion (Huber et al. 2004) suggest that each spatula adheres with approx. 10 nN force. Using a value of $\gamma = 50$ mJ/m², typical of van der Waals interactions the Kendall peel model predicts a spatular width of 200 nm, remarkably close to the actual dimension (Autumn et al. 2000; Ruibal and Ernst 1965).

Theoretical considerations suggest that generalized continuum models of spatulae as spheres or nanotape are applicable to the range of spatula size and keratin stiffness of setae found in reptiles and arthropods (Spolenak et al. 2004). Interestingly, at the 100 nm

size scale the effect of shape on adhesion force may be relatively limited (Gao and Yao 2004; Spolenak et al. 2004). However, at sizes above 100 nm and especially above 1 μm , Spolenak et al. (2004) concluded that shape should have a very strong effect on adhesion force. A phylogenetic comparative analysis of attachment force in lizards and insects will be an important test of this hypothesis.

4. Anti-adhesive properties of gecko setae

Paradoxical as it may seem, there is growing evidence that gecko setae are strongly anti-adhesive. Gecko setae do not adhere spontaneously to surfaces, but instead require a mechanical program for attachment (Autumn et al. 2000). Unlike adhesive tapes, gecko setae 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 seem to stay dirty.

4.1. Properties (5) self-cleaning and (6) anti-self-adhesion

Dirt particles are common in nature (Little 1979), yet casual observation suggests that geckos' feet are quite clean (Fig. 1B). Sand, dust, leaf litter, pollen, and plant waxes would seem likely to contaminate gecko setae. Hair-like elements on plants accumulate micron-scale particles (Little 1979) that could come into contact with gecko feet during climbing. Indeed, insects must cope with particulate contamination that reduces the function of their adhesive pads (Gorb and Gorb 2002), and spend a significant proportion of their time grooming (Stork 1983) in order to restore function. On the other hand, geckos have not been observed to groom their feet (Russell and Rosenberg 1981), yet apparently retain the adhesive ability of their setae during the months between shed cycles. How geckos manage to keep their toes clean while walking about with sticky feet has remained a puzzle until recently (Hansen and Autumn 2005). While self-cleaning by water droplets has been shown to occur in plant (Barthlott and Neinhuis 1997) and animal (Baum et al. 2002) surfaces, no adhesive had been shown to self-clean.

Gecko setae are the first known self-cleaning adhesive (Hansen and Autumn 2005). Tokay geckos with 2.5 μm radius microspheres applied to their feet recovered their ability to cling to vertical surfaces after only a few steps on clean glass. We contaminated toes on one side of the animal with an excess of 2.5 μm radius silica-alumina microspheres and compared the shear stress to that of uncontaminated toes on the other side of the animal. Prior researchers had suggested that geckos' unique toe peeling motion (digital hyperextension) might aid in cleaning of the toe pads (Bauer et al. 1996; Russell 1979), so we immobilized the geckos' toes and applied them by hand to the surface of a glass force plate to determine if self-cleaning could occur without toe peeling. After only 4 simulated steps on a clean glass surface, the geckos recovered enough of their setal function to support their body weight by a single toe (Hansen and Autumn 2005). To test the hypothesis that self-cleaning is an intrinsic property of gecko setae and does not require a gecko, we isolated arrays of setae and glued them to plastic

strips. We simulated steps using a servomanipulation system we called RoboToe. We compared shear stress in clean setal arrays to that in the same arrays with a monolayer of microspheres applied to their adhesive surfaces. Self-cleaning of microspheres occurred in arrays of setae isolated from the gecko. Again as for live gecko toes, isolated setal arrays rapidly recovered the shear force lost due to contamination by microspheres. We hypothesized that the microspheres were being preferentially deposited on the glass substrate, and did not remain strongly attached to the setae.

Contact mechanical models suggest that it is possible that self-cleaning occurs 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 (Fig. 3)(Hansen and Autumn 2005). The models suggest that self-cleaning may in fact require γ of spatulae to be relatively low (equal to or less than that of the wall), perhaps constraining the spatula to be made of a hydrophobic material. So, geckos may benefit by having setae made of an anti-adhesive material: decreasing γ decreases adhesion energy of each spatula but promoting self-cleaning should increase adhesion of the array as a whole by maximizing the number of uncontaminated spatulae. If γ were to be increased by supplementing van der Waals forces with stronger intermolecular forces such as polar or H-bonding, it is likely that self-cleaning and anti-self properties would be lost. Thus the self-cleaning and anti-self properties may represent a sweet spot in the evolutionary design space for adhesive nanostructures.

4.2. Property (7) nonsticky default state

The discovery that maximal adhesion in isolated setae requires a small push perpendicular to the surface, followed by a small parallel drag (Autumn et al. 2000), explained the load dependence and directionality of adhesion observed at the whole-animal scale by Haase (1900) and Dellit (1934), and was consistent with the structure of individual setae and spatulae (Hiller 1968; Ruibal and Ernst 1965). In their resting state, setal stalks are recurved proximally. When the toes of the gecko are planted, the setae may become bent out of this resting state, flattening the stalks between the toe and the substrate such that their tips point distally. This small preload and a micron-scale displacement of the toe or scensor proximally may serve to bring the spatulae (previously in a variety of orientations) uniformly flush with the substrate, maximizing their surface area of contact. Adhesion results and the setae are ready to bear the load of the animal's body weight.

To test the hypothesis that the default state of gecko setal arrays is to be nonsticky, Autumn and Hansen (2005 (in press)) estimated the fraction of area able to make contact with a surface in setae in their unloaded state. Only less than 6.6% of the area at the tip of a seta is available for initial contact with a smooth surface, and 93.4% is air space. 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 (Autumn et al. 2002b; Hansen and Autumn 2005; Irschick et al. 1996) and isolated setae (Autumn et al. 2000; Autumn et al. 2002b; Hansen and Autumn 2005). Thus gecko setae may be nonsticky by

default because only a very small contact fraction is possible without mechanically deforming the setal array.

How much does the contact fraction increase during attachment? While there are no empirical measurements of the number of spatulae in contact as a function of adhesion (or friction) force, it is possible to estimate from measurements of single setae. Empirical measurements and theoretical estimates of spatular adhesion (Arzt et al. 2003; Autumn et al. 2000; Autumn et al. 2002b; Hansen and Autumn 2005; Huber et al. 2004; Spolenak et al. 2004) suggest that each spatula generates approx. 10 to 40 nN with approx. $0.02\mu^2$ area, or approx. 500 to 2000 kPa. A single seta on a Si MEMs cantilever can generate approx. 917 kPa (Table 1). The value of 10 nN adhesion measured in single spatulae using an AFM (Huber et al. 2004) implies that 4000 spatulae would need to be attached to equal the peak adhesion force ($40\mu\text{N}$) measured in single setae (Autumn et al. 2002b). However, each seta contains not more than approx. 100 to 1000 spatulae ((Ruibal and Ernst 1965; Schleich and Kästle 1986)). Therefore a spatular force of 40 nN is more appropriate for a conservative estimate of setal contact fraction during attachment. In the case of a spatular adhesion force of 40 nN, the adhesive stress is 2000 kPa. Therefore a contact fraction of 46% is required to yield the setal stress. This suggests that unless the force of adhesion of a spatula has been greatly underestimated, the contact fraction must increase from 6% to 46%, or by approx. 7.5-fold, following preload and drag.

5. Modeling adhesive nanostructures

5.1. Effective modulus of a setal array

The gecko adhesive is a microstructure in the form of an array of millions of high aspect ratio shafts. The effective elastic modulus, E_{eff} , (Persson 2003; Sitti and Fearing 2003) is much lower than the Young's modulus (E) of β -keratin. Thus arrays of setae should behave as a softer material than bulk β -keratin. E of beta-keratin in tension is approx. 2.5 GPa in bird feathers (Bonser and Purslow 1995) and 1.3 to 1.8 GPa in bird claws (Bonser 2000). Young's moduli of lizard beta keratins in general (Fraser and Parry 1996) and gecko beta keratins in particular (Alibardi 2003) remain unknown at present. The behavior of a setal array during compression and relaxation will depend on the mode(s) of deformation of individual setae. Bending is a likely mode of deformation (Simmernacher 1884) (Fig. 1D), and a simple approach is to model arrays of setae as cantilever beams (Glassmaker et al. 2004; Hui et al. 2004; Persson 2003; Sitti and Fearing 2003; Spolenak et al. 2005). One might question the applicability of models based on a simple geometry for the complex, branched structure of the seta. However, as with the JKR and Kendall models (Sections 3.5.4 and 3.5.5) applied to spatulae, the simple cantilever model is surprisingly well supported by empirical measurements of setal arrays (Geisler et al. 2005).

The cantilever model of a single seta (Campolo et al. 2003; Sitti and Fearing 2003) is based on a cantilever beam under a lateral load, F at its tip. The resulting tip displacement

due to bending is $\Delta = \frac{FL^3}{3EI}$, where L is the length, E is the elastic modulus of the material, and I is the area moment of inertia of the cantilever (Gere and Timoshenko 1984) (Fig. 4A). The lateral bending stiffness K_y is given by

$$K_y = \frac{3EI}{L^3} = \frac{3\pi R^4 E}{4L^3}, \quad (5.1)$$

for a cylindrical cantilever of radius R , $I = \frac{\pi R^4}{4}$. For a cantilever at an angle ϕ to the substrate and under a normal load, F_n , the resolved force lateral to the cantilever is $F = F_n \cos \phi$ (Fig. 4B). This results in a lateral tip displacement of $\Delta = \frac{F_n \cos(\phi)L^3}{3EI}$, and a normal tip displacement of $\Delta_n = \Delta \cos \phi = \frac{F_n \cos^2(\phi)L^3}{3EI}$.

Next, to derive an effective elastic modulus (E_{eff}) for a model setal array, in the cantilever system above, we use Hooke's law, $\sigma = E_{eff}\epsilon$, where σ and ϵ are the applied stress and resulting strain in the normal axis, respectively. The normal strain is $\epsilon = \Delta_n / L_n$ (Fig. 4B), where $L_n = L \sin \phi$.

Now, for an array of cantilevers with density D (meter⁻²) in parallel at an angle ϕ and under a normal stress σ , the normal force acting on each cantilever tip is $F_n = \sigma / D$. The resulting normal displacement of the array is $\Delta_n = \frac{\sigma \cos^2(\phi)L^3}{3EID}$. Thus,

$\epsilon = \frac{\sigma \cos^2(\phi)L^2}{3EID \sin \phi}$, and the stress over the cantilever array is

$\sigma = \frac{E_{eff} \sigma \cos^2(\phi)L^2}{3EID \sin \phi}$. Dividing by σ and Solving for E_{eff} we reach a general equation for the effective stiffness of a cantilever array,

$$E_{eff} = \frac{3EID \sin \phi}{\cos^2(\phi)L^2}. \quad (5.2)$$

For a cylindrical cantilever, we can substitute EI in Eqn. 5.2 for $\frac{K_y L^3}{3}$ using Eqn. 5.1, yielding,

$$E_{eff} = \frac{K_y L D \sin \phi}{\cos^2 \phi}. \quad (5.3)$$

For a tokay seta-size cylindrical cantilever of $R = 2.1 \mu\text{m}$, $L = 110 \mu\text{m}$, $E = 1 \text{ GPa}$, the bending stiffness from Eqn. 5.1 is $K_y = 0.0344 \text{ N/m}$. For $E = 2 \text{ GPa}$, $K_y = 0.0689 \text{ N/m}$.

I will now calculate the shaft angle ϕ (see Fig 4B) required to yield an effective stiffness of 100 kPa (the upper limit of Dahlquist's criterion) (Dahlquist 1969; Pocius 2002). A

typical tokay setal array has approx 14,000 setae per mm^2 and $D = 1.44 \times 10^{10} \text{ m}^{-2}$. Using Eqn. 5.3, a value of $\phi = 50^\circ$ is required for $E = 1 \text{ GPa}$, and $\phi = 36.65^\circ$ for $E = 2 \text{ GPa}$ to yield $E_{\text{eff}} = 100 \text{ kPa}$.

We measured the forces resulting from deformation of isolated arrays of tokay gecko (*Gekko gecko*) setae to determine E_{eff} and test the validity of the cantilever model. We found that E_{eff} of tokay gecko setae falls near 100 kPa, close to the upper limit of Dahlquist's criterion for tack (Fig. 5)(Geisler et al. 2005). Additionally, we observed values of ϕ for tokay gecko setae near 43° , further supporting the validity of the cantilever model (Fig. 4; (Geisler et al. 2005)).

5.2. Rough surface and antimatting conditions

The cantilever model predicts that a high density of setae should be selected for in increasing adhesive force of setal arrays. Firstly, it follows from the JKR model (Arzt et al. 2003; Autumn et al. 2002b) that packing in more spatulae should increase adhesion in an array of setae. Secondly, the cantilever model suggests that thinner setal shafts should decrease E_{eff} , and promote a greater contact fraction on rough surfaces (Campolo et al. 2003; Jagota and Bennison 2002; Persson 2003; Persson and Gorb 2003; Scherge and Gorb 2001; Sitti and Fearing 2003; Spolenak et al. 2005; Stork 1983). The cantilever model also suggests that longer and softer setal shafts, and a lower shaft angle ϕ will result in better adhesion on rough surfaces because these parameters will reduce E_{eff} . On a randomly rough surface, some setal shafts should be bent in compression (concave), while others will be bent in tension (convex). The total force required to pull off a setal array from a rough surface should therefore be determined by the cumulative adhesive force of all the attached spatulae, minus the sum of the forces due to elastic deformation of compressed setal shafts.

If setae mat together (Stork 1983), it is likely that adhesive function will be compromised. Interestingly, the same parameters that promote strong adhesion on rough surfaces should also cause matting of adjacent setae (Glassmaker et al. 2004; Hui et al. 2004; Persson 2003; Sitti and Fearing 2003; Spolenak et al. 2005). The distance between setae and the stiffness of the shafts will determine the amount of force required to bring the tips together for matting to occur. It follows from the cantilever model that stiffer, shorter, and thicker stalks will allow a greater packing density without matting. As is the case for self-cleaning (Hansen and Autumn 2005), setae should be made of materials with lower surface energy to prevent self-adhesion and matting. Satisfying both antimatting and rough surface conditions may require a compromise of design parameters. Spolenak et al. (2005) devised "design maps" for setal adhesive structures, an elegant approach to visualizing the parametric tradeoffs needed to satisfy the rough surface and antimatting conditions while at the same time maintaining structural integrity of the material.

6. Scaling

Small and large organisms are dominated by different forces (McMahon and Bonner 1983). Inertial forces usually dwarf adhesive forces in organisms gecko-size and above. Geckos are unusual among macroscale organisms in having adhesive forces dominate their world. The astonishing adaptive radiation in geckos and their unique ecologies can be seen as an emergent property of integration across seven orders of magnitude in size (Pianka and Sweet 2005) –from the nanoscale spatula and the microscale seta to the mesoscale scensors and the macroscale body (Fig. 1).

While it is tempting to focus on the smallest level in the gecko adhesive system, integration of multiple levels in the compliance hierarchy is needed to achieve reliable and controllable adhesion and friction. Self-cleaning adhesive nanostructures cannot adhere if they never get near the surface. Compliant scensors and the compliant adipose or vascular tissue underlying the scensors may be important in spreading the load during foot placement (Russell 1986; Russell 2002). The complex morphology and musculature of the toes, feet, and limbs play a critical role in bringing the compliant scensors to bear upon the substrate in the appropriate manner, and in detaching them without large forces (Russell 1975). Simulation studies of animal-like climbers suggest that tuning limb compliance correctly is much more important for climbing than for running. In particular, the ratios of linear and torsional compliances at the foot and ankle have an enormous effect on climbing stability and efficacy (Autumn et al. 2005).

6.1. Scaling of pad area and spatular size

Shear force of the two front feet of pad-bearing lizards (geckos, anoles and skinks) is highly correlated with pad area, even when the effects of body size and phylogeny are accounted for (Irschick et al. 1996). However, there is significant variation in shear force among taxa of similar size and pad area, suggesting that other factors are important in determining the strength of the setal adhesive. The JKR model (Arzt et al. 2003; Autumn et al. 2002b) predicts that larger spatulae should result in lower forces, and this is supported by an inverse correlation between body mass and the size of the spatula or setal tip in lizards and arthropods (Arzt et al. 2003). It seems clear that geckos have superior adhesion and friction in comparison to other seta-bearing species, and one likely reason is small spatular size.

6.2. Scaling of stress

Amontons' first law states that the relationship of shear force (friction) to load is a constant value, μ (the coefficient of friction). Amontons' second law predicts that μ is independent of the area of contact (Bhushan 2002; Ringlein and Robbins 2004). When pulled in shear (Autumn et al. 2000; Autumn et al. 2002b), gecko setae seem to violate Amontons' laws, as do tacky polymers where the forces of adhesion can be much greater than the external load. Shear stress in setae increases greatly with a decrease in contact

area A , suggesting that at larger scales, fewer spatulae are attached and/or the contact fraction within spatulae is reduced (Fig. 6; Table 1). The scaling of shear stress, τ , is exponential and scales as $\log \tau = 1.14 - 0.24 \log A$ ($R^2 = 0.99$). It is unknown whether stress is uniformly spread across the toe or foot (Russell 2002), or if there are high stress concentrations on the setal arrays of a few scensors. 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. 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. If each spatula can generate 10 to 40 nN, it would take 1000 to 4000 spatulae to yield the 40 μ N of adhesion measured in single setae. However, each seta bears only 100 to 1000 spatulae. Clearly further work is needed to resolve this discrepancy. The relationship between adhesion and friction also demands further investigation. Existing data suggest that friction at the seta level is about two to four times the adhesion.

7. Comparison of conventional and gecko adhesives

Conventional adhesives are materials that are used to join two surfaces. Typically, adhesives are liquids that are chemically compatible with both surfaces and have sufficiently low viscosity that wetting of the surfaces occurs either spontaneously or with a small amount of pressure (Baier et al. 1968; Kinloch 1987; Pocius 2002). Surface treatments are often needed to raise the interfacial energies between one or both surfaces and the adhesive. Liquid hard-set adhesives (e.g. epoxy or cyanoacrylate glues) flow easily during application, but cure to make a strong, permanent bond. Because they are stiff when cured, hard-set adhesives can resist plastic creep caused by sustained loading. However, hard-set adhesives are single-use: their bonds must be broken or dissolved for removal and once broken, hard-set adhesives do not rebond.

Conventional pressure sensitive adhesives (PSAs) are fabricated from soft, tacky, viscoelastic materials (Gay 2002; Gay and Leibler 1999; Pocius 2002). Tacky materials are those that exhibit spontaneous plastic deformation that increases true area of contact with the surface at the molecular scale. Theoretical considerations (Creton and Leibler 1996) agree with Dahlquist's (Dahlquist 1969; Pocius 2002) empirical observation that a Young's modulus (E) below 100 kPa (at 1 Hz) is needed to achieve a high contact fraction with the substrate. Additives known as tackifiers are commonly used to promote plastic deformation in PSAs during contact (Pocius 2002). PSAs such as masking tape or sticky notes are capable of repeated attachment and detachment cycles without residue because the dominant mechanism of adhesion is weak intermolecular forces. PSAs adhering with weak intermolecular forces can require much more energy to pull off of surfaces than do rigid adhesives relying on strong chemical bonds. As soft polymeric adhesives are pulled apart from a surface, polymer chains or bundles of polymers chains can be elongated into pillars in a process known as crazing. The total fracture energy can greatly exceed the sum of all the bond energies at the interface since work must be done on the craze as well as to break adhesive bonds at the interface. Thus the strong adhesion

in polymeric adhesives results from long bonds rather than from strong bonds (Persson 2003). However, because they are soft polymeric materials, PSAs are prone to creep, degradation, self-adhesion, and fouling.

In contrast to the soft polymers of PSAs, the adhesive on the toes of geckos is made of hard protein (β -keratin) with E four to five orders of magnitude greater than the upper limit of Dahlquist's criterion. Therefore, one would not expect a β -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, E_{eff} (Glassmaker et al. 2004; Hui et al. 2004; Jagota and Bennison 2002; Persson 2003; Sitti and Fearing 2003; Spolenak et al. 2005) is much lower than E of bulk β -keratin. The effective modulus of gecko setal arrays is close to 100 kPa (Geisler et al. 2005). Gecko setal arrays possess some of the properties of PSAs although the bulk material properties of β -keratin place it in the class of stiff, nonviscous materials (Fig. 5) (Creton and Leibler 1996; Dahlquist 1969; Gay 2002; Gay and Leibler 1999; Jagota and Bennison 2002; Persson 2003; Persson and Gorb 2003; Pocius 2002; Sitti and Fearing 2003).

There is emerging evidence that an array of gecko setae can act like a tacky, deformable material, while individual setae and spatulae retain the structural integrity of stiff protein fibers. This may enable the gecko adhesive to tolerate heavy, repeated use without creep or degradation. Indeed theoretical considerations suggest that the fibrillar structure of the gecko adhesive can be thought of as a permanent craze (Jagota and Bennison 2002; Persson 2003) that can raise the fracture energy relative to a solid layer of adhesive material. As with polymer crazes, setal structures under stress could store energy elastically in each seta of the array, and then as setae are pulled off, elastic energy could be dissipated internally without contributing to propagation of the crack between the adhesive and substrate (Hui et al. 2004; Jagota and Bennison 2002; Persson 2003). Unlike polymer crazes, setal structures may dissipate energy primarily elastically rather than plastically.

Gecko setae do not bond spontaneously on contact, as do PSAs. Gecko setae have a nonsticky default state (Autumn and Hansen 2005 in press), and require mechanical deformation to initiate adhesion and friction (Autumn and Peattie 2002; Autumn et al. 2000). Again in contrast to PSAs, gecko setae are anisotropic and possess a built-in release mechanism. Setae are sticky when forces are directed with the curvature of the shaft, and release when forces are directed away from the curvature of the shaft (Autumn and Peattie 2002; Autumn et al. 2000; Gao et al. 2005).

8. Gecko-inspired synthetic adhesive nanostructures

Using a nanostructure to create an adhesive is a novel and bizarre concept. It is possible that if it had not evolved, humans would never have invented it. With the inspiration of biology, the first generation of adhesive nanostructures is being developed (Fig. 1F). The

growing list of benchmark properties –seven of which are presented in this chapter– can be used to evaluate the degree of geckolike function of synthetic prototypes. By these criteria, synthetic setae (Autumn et al. 2002b; Geim et al. 2003; Northen and Turner 2005; Peressadko and Gorb 2004; Sitti and Fearing 2003) are at a very early stage, and none has significantly geckolike properties. For example, consider the adhesion coefficient, $\mu' = F_{\text{adhesion}} / F_{\text{preload}}$, as a metric for geckolike adhesive function. By this criterion, the material of Geim et al. (2003) is not geckolike since it required a very large preload of 50 N to yield 3N and 0.3 atm of adhesion, yielding a value of $\mu' = 0.06$. The synthetic setae of Northen and Turner (2005) perform significantly better with a $\mu' = 0.125$, but still well below the benchmark of real gecko setae where $\mu' = 8$ to 16. Effective design of geckolike adhesives will require deep understanding of the principles (Table 2) underlying the properties observed in the natural system. For example, synthetic setae that can attach without substantial preloads will likely require angled rather than vertical shafts (Sitti and Fearing 2003) to promote a bending rather than buckling mode of deformation.

Applications abound for a dry self-cleaning adhesive that does not rely on soft polymers or chemical bonds. Biomedical applications such as endoscopy and tissue adhesives (Menciassi and Dario 2003; Pain 2000) are one example. However any materials chosen for synthetic setae in biomedical applications would need to be nontoxic and nonirritating (Baier et al. 1968). Other applications include MEMS switching (Decuzzi and Srolovitz 2004), wafer alignment (Slocum and Weber 2003), micromanipulation (Pain 2000), and robotics (Autumn et al. 2005). Since a nanostructure could be applied directly to a surface, it is conceivable that geckolike structures could replace screws, glues, and interlocking tabs in many assembly applications such as automobile dashboards or mobile phones.

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 17th century Indian legend, Shivaji and his Hindu warriors used adhesive lizards from the Deccan region as grappling devices to scale a sheer rock cliff and mount a surprise attack on a Maharashtrian cliff-top stronghold (Ghandi 2002).

9. Future directions in the study of the gecko adhesive system

Adhesion in geckos remains a sticky problem that is generating at least as many new questions as answers. Much of the fertility of this area stems from an integration of biology, physics, and engineering. For example, the relationship between friction and adhesion is one of the most fundamental issues in surface science (Luan and Robbins 2005; Ringlein and Robbins 2004). One of the most striking properties (Table 2) of the gecko adhesive system is the coupling between adhesion and friction. Without a shear load, setae detach easily. Indeed, without shear loading of opposing toes or legs, a gecko could not hang from the ceiling. Integration of the macroscale system with the as yet undefined relationship between friction and adhesion at the nanoscale could yield important design principles for natural and synthetic setal structures.

Natural surfaces are rarely smooth, and an important next step will be to measure empirically the effect of surface roughness (Vanhooydonck et al. 2005) on friction and adhesion in gecko setae to test the predictions of the new generation of theoretical models for rough surface contacts with micro and nanostructures (Persson and Gorb 2003). Under real-world conditions where surfaces are fractal (Greenwood 1992; Persson and Gorb 2003), compliance is required at each level of the gecko adhesive hierarchy: spatula, seta, lamella, toe, and leg. Models including a spatular array at the tip of a seta have not yet been developed. Similarly, models of lamellar structure will be needed to explain function on roughness above the micron scale.

Biological diversity of setal and spatular structure is high and poorly documented. Basic morphological description will be required. Theory predicts that tip shape affects pulloff force less at smaller sizes (Gao and Yao 2004), so it is possible that part of spatular variation is due to phylogenetic effects, but material constraints such as tensile strength of keratin must be considered as well (Autumn et al. 2002b; Spolenak et al. 2005). The collective behavior of the setal array will be a productive research topic (Gao and Yao 2004). Diversity of the array parameters, density, dimension, and shape is great but not well documented. In particular, the shape of setal arrays on lamellae demands further investigation. Phylogenetic analysis (Harvey and Pagel 1991) of the variation in setal structure and function will be required to tease apart the combined effects of evolutionary history, material constraints, and adaptation (Autumn et al. 2002a).

The molecular structure of setae is not yet known. Setae are made primarily of β -keratin, but a histidine-rich protein or proteins may be present as well (Alibardi 2003). One possible role of non-keratin proteins is as a glue that holds the keratin fibrils together in the seta (Fig. 1D) (Alibardi 2003). This suggests a possible role of genes coding for histidine-rich protein(s) in tuning the material properties of the setal shaft. The outer molecular groups responsible for adhesion at the spatular surface will also be an important topic for future research.

Clearly there is great desire to engineer a material that functions like a gecko adhesive, yet progress has been limited. A biomimetic approach of attempting to copy gecko setae blindly is unlikely to succeed due to the complexity of the system (Fig. 1) and the fact that evolution generally produces satisfactory rather than optimal structures. Instead, development of biologically inspired adhesive nanostructures will require careful identification and choice of design principles (Table 2) to yield selected geckolike functional properties. As technology and the science of gecko adhesion advance, it may become possible to tune design parameters to modify functional properties in ways that have not evolved in nature.

It is remarkable that the study of a 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. Indeed the broad relevance and applications of the study of gecko adhesion underscore the importance of basic, curiosity based research.

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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.

Altevogt R. (1954). Probleme eines Fußes. *Kosmos* 50, 428-430.

Aristotle. (350 B.C.E. (1918)). *Historia animalium* translated by Thompson, D'A.W.: Oxford, The Clarendon Press.

Arzt E, Enders S and Gorb S. (2002). Towards a micromechanical understanding of biological surface devices. *Zeitschrift Fur Metallkunde* 93, 345-351.

Arzt E, Gorb S and Spolenak R. (2003). From micro to nano contacts in biological attachment devices. *Proc. Natl. Acad. Sci USA* 100, 10603-10606.

Autumn K and Hansen W. (2005 (in press)). Ultrahydrophobicity indicates a nonadhesive default state in gecko setae. *Journal of Comparative Physiology A-Sensory Neural & Behavioral Physiology*.

Autumn K and Peattie A. (2002). Mechanisms of adhesion in geckos. *Int. Comp. Bio.* 42, 1081-1090.

Autumn K, Liang YA, Hsieh ST, Zesch W, Chan W-P, Kenny WT, Fearing R and Full RJ. (2000). Adhesive force of a single gecko foot-hair. *Nature* 405, 681-685.

Autumn K, Ryan MJ and Wake DB. (2002a). Integrating historical and mechanistic biology enhances the study of adaptation. *Quarterly Rev. Biology* 77, 383-408.

Autumn K, Sitti M, Peattie A, Hansen W, Sponberg S, Liang YA, Kenny T, Fearing R, Israelachvili J and Full RJ. (2002b). 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, Saranlı U et al. (2005). Robotics in scansorial environments.

Proceedings of SPIE 5804, 291-302.

Autumn, K., Hsieh ST, Dudek DM, Chen J, Chitaphan C and Full RJ. (2005 (in press)). Dynamics of geckos running vertically. *Journal of Experimental Biology*.

Baier RE, Shafrin EG and Zisman WA. (1968). Adhesion: mechanisms that assist or impede it. *Science* 162, 1360-1368.

Barthlott W and Neinhuis C. (1997). Purity of the sacred lotus, or escape from contamination in biological surfaces. *Planta (Heidelberg)* 202, 1-8.

Bauer AM. (1998). Morphology of the adhesive tail tips of carphodactylid geckos (Reptilia: Diplodactylidae). *Journal of Morphology* 235, 41-58.

Bauer AM, Russell AP and Powell GL. (1996). The evolution of locomotor morphology in *Rhoptropus* (Squamata: Gekkonidae): functional and phylogenetic considerations. *African journal of herpetology* 45, 8-30.

Baum C, Meyer W, Stelzer R, Fleischer L-G and Siebers D. (2002). Average nanorough skin surface of the pilot whale (*Globicephala mela*, Delphinidae): considerations on the self-cleaning abilities based on nanoroughness. *Marine Biology* 140, 653-657.

Bellairs A. (1970). *The Life of Reptiles*. New York: Universe Books.

Bereiter-Hahn J, Matoltsy AG and Richards KS. (1984). *Biology of the Integument 2: Vertebrates*. New York, NY: Springer-Verlag.

Bhushan B. (2002). *Introduction to tribology*. New York: John Wiley and Sons.

Biewener AA and Full RJ. (1992). Force platform and kinematic analysis *Biomechanics: Structures and Systems A Practical Approach*. IRL at Oxford University Press, New York, pp. 45-73.

Blackwall J. (1845). On the means by which walk various animals on the vertical surface of polished bodies. *Annals of Natural History* XV, 115.

Bonser RHC. (2000). The Young's modulus of ostrich claw keratin. *Journal of Materials Science Letters* 19, 1039-1040.

Bonser RHC and Purslow PP. (1995). The Young's modulus of feather keratin. *Journal of Experimental Biology* 198, 1029-1033.

Brainerd EL. (1994). Adhesion force of ants on smooth surfaces. *American Zoologist* 34, 128A.

Braun M. (1878). Zur Bedeutung der Cuticularborsten auf den Haftlappen der Geckotiden. *Arb. Zool.-Zoot. Inst. Würzburg* 4, 231-237.

Braun M. (1879). Über die Haftorgane an der Unterseite der Zehen bei Anolius. *Arb. Zool.-Zoot. Inst. Würzburg* 5, 31-36.

Campolo D, Jones SD and Fearing RS. (2003). Fabrication of gecko foot-hair like nano structures and adhesion to random rough surfaces. In *IEEE Nano 2003 Aug 12-14, San Francisco*.

- Cartier O. (1872a). Studien über den feineren Bau der Epidermis bei den Geckotiden. *Verhandlungen der Würzburger Phys.-med. Gesellschaft* 1, 239-258.
- Cartier O. (1872b). Studien über den feineren Bau der Haut bei den Reptilien. I. Abt. Epidermis der Geckotiden. *Arb. Zool. Inst. Würzburg* Bd. 1, 83-96.
- Cartier O. (1874). Studien über den feineren Bau der Epidermis bei den Reptilien. II. Abtheilung. Ueber die Wachstumserscheinungen der Oberhaut von Schlangen und Eidechsen bei der Häutung. *Arb. Zool.-Zoot. Inst. Würzburg* 1, 239-258.
- Chen JJ, Peattie AM, Autumn K and Full RJ. (2005 (in press)). Differential leg function in sprawled-posture quadrupedal trotters. *Journal of Experimental Biology*.
- Chui BW, Kenny TW, Mamin HJ, Terris BD and Rugar D. (1998). Independent detection of vertical and lateral forces with a sidewall-implanted dual-axis piezoresistive cantilever. *Appl. Phys. Lett.* 72, 1388-1390.
- Creton C and Leibler L. (1996). How does tack depend on contact time and contact pressure? *Journal of Polymer Science: Part B: Polymer Physics* 34, 545-554.
- Dahlquist CA. (1969). Pressure-sensitive adhesives. In Patrick RL (ed.) *Treatise on Adhesion and Adhesives*, Vol. 2. Dekker, New York, pp. 219-260.
- Decuzzi P and Srolovitz DJ. (2004). Scaling laws for opening partially adhered contacts in MEMS. *Journal of Microelectromechanical Systems* 13, 377-385.
- Dellit W-D. (1934). Zur anatomie und physiologie der Geckozehe. *Jena. Z. Naturw.* 68, 613-656.
- Dewitz H. (1882). Wie ist es den Stubenfliegen und vielen anderen Insecten möglich, an senkrechten Glaswänden emporzulaufen? *Sitz. Ges. naturf. Freunde*, 5-7.
- Edwards JS and Tarkanian M. (1970). The adhesive pads of heteroptera: a re-examination. *Proceedings of the Royal Entomological Society London* 45, 1-5.
- Emerson SB and Diehl D. (1980). Toe pad morphology and mechanisms of sticking in frogs. *Biological Journal of the Linnaean Society* 13, 199-216.
- Fakley M. (2001). Smart Adhesives. In *Chemistry & Industry*, pp. 691-5.
- Fraser RDB and Parry DAD. (1996). The molecular structure of reptilian keratin. *International Journal of Biological Macromolecules* 19, 207-211.
- Gadow H. (1901). *The Cambridge Natural History* Vol. 8 Amphibia and Reptiles. London: McMillan and Co.
- Gao H and Yao H. (2004). Shape insensitive optimal adhesion of nanoscale fibrillar structures. *Proc. Nat. Acad. Sci. U. S. A.* 101, 7851-7856.
- Gao HJ, Wang X, Yao HM, Gorb S and Arzt E. (2005). Mechanics of hierarchical adhesion structures of geckos. *Mechanics of Materials* 37, 275-285.
- Gay C. (2002). Stickiness -some fundamentals of adhesion. *Int. Comp. Bio.* 42, 1123-

1126.

Gay C and Leibler L. (1999). Theory of tackiness. *Physical review letters* 82, 936-939.

Geim AK, Dubonos SV, Grigorieva IV, Novoselov KS and Zhukov AA. (2003). Microfabricated adhesive mimicking gecko foot-hair. *Nature Materials* 2, 461-463.

Geisler B, Dittmore A, Gallery B, Stratton T, Fearing R and Autumn K. (2005). Deformation of isolated gecko setal arrays: bending or buckling? 2. Kinetics. In *Society for Integrative and Comparative Biology, San Diego*.

Gennaro JGJ. (1969). The gecko grip. *Natural History* 78, 36-43.

Gere JM and Timoshenko SP. (1984). *Mechanics of materials*. Independence, KY: Thomson Brooks/Cole.

Ghandi M. (2002). The ugly buglies. *Swagat* January 2002.

Gillett JD and Wigglesworth VB. (1932). The climbing organ of an insect, *Rhodnius prolixus* (Hemiptera, Reduviidae). *Proceedings of the Royal Society London, Series B* 111, 364-376.

Glassmaker NJ, Jagota A, Hui CY and Kim J. (2004). Design of biomimetic fibrillar interfaces: 1. Making contact. *J. R. Soc. Lond. Interface* 1, 1-11.

Gorb EV and Gorb SN. (2002). Attachment ability of the beetle *Chrysolina fastuosa* on various plant surfaces.

Green DM. (1981). Adhesion and the toe-pads of treefrogs. *Copeia* 4, 790-796.

Greenwood JA. (1992). Problems with rough surfaces. In Singer IL and Pollock HM (eds.) *Fundamentals of Friction: Macroscopic and Microscopic Processes*. Kluwer, Dordrecht, pp. 57-76.

Haase A. (1900). Untersuchungen über den Bau und die Entwicklung der Haftlappen bei den Geckotiden. *Archiv. f. Naturgesch.* 66, 321-345.

Han D, Zhou K and Bauer AM. (2004). Phylogenetic relationships among gekkotan lizards inferred from Cmos nuclear DNA sequences and a new classification of the Gekkota. *Biological Journal of the Linnaean Society* 83, 353-368.

Hanna G and Barnes WJP. (1991). Adhesion and detachment of the toe pads of tree frogs. *Journal of Experimental Biology* 155, 103-125.

Hansen W and Autumn K. (2005). Evidence for self-cleaning in gecko setae. *Proc. Nat. Acad. Sci. U. S. A.* 102, 385-389.

Harvey PH and Pagel MD. (1991). *The comparative method in evolutionary biology*. Oxford: Oxford Univ. Press.

Hecht MK. (1952). Natural selection in the lizard genus *Aristelliger*. *Evolution* 6, 112-124.

Hepworth J. (1854). On the structure of the foot of the fly. *Quarterly Journal of*

Microscopical Science 2, 158-163.

Hiller U. (1968). Untersuchungen zum Feinbau und zur Funktion der Haftborsten von Reptilien. Z. Morph. Tiere 62, 307-362.

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. (1971). Form und Funktion der Hautsinnesorgane bei Gekkoniden. Forma et functio 4, 240-253.

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. Annals of applied Biology 63, 145-153.

Hora SL. (1923). The adhesive apparatus on the toes of certain geckos and tree frogs. J. Proc. Asiat. Soc. Beng. 9, 137-145.

Huber G, Gorb S, Spolenak R and Arzt E. (2004). Resolving the nanoscale adhesion of individual gecko spatulae by atomic force microscopy. Biology Letters (in press).

Hui CY, Glassmaker NJ, Tang T and Jagota A. (2004). Design of biomimetic fibrillar interfaces: 2. Mechanics of enhanced adhesion. J. R. Soc. Lond. Interface 1, 12-26.

Irschick DJ, Austin CC, Petren K, Fisher R, Losos JB and Ellers O. (1996). A comparative analysis of clinging ability among pad-bearing lizards. Biological Journal of the Linnean Society 59, 21-35.

Irving RLG. (1955). A history of British Mountaineering. London: B.T. Batsford, Ltd.

Israelachvili J. (1992). Intermolecular and Surface Forces. New York: Academic Press.

Jagota A and Bennison S. (2002). Mechanics of adhesion through a fibrillar microstructure. Int. Comp. Bio. 42, 1140-1145.

Jeffree C. (1986). The cuticle, epicuticular waxes and trichomes of plants, with reference to their structure, functions and evolution. In Juniper B and Southwood RS (eds.) Insects and the Plant Surface. Edward Arnold Publishers Ltd., London, pp. 23-64.

Johnson KL. (1985). Contact mechanics. Cambridge: University of Cambridge Press.

Johnson KL, Kendall K and Roberts AD. (1973). Surface energy and the contact of elastic solids. Proceedings of the Royal Society London, series A 324, 310-313.

Kendall K. (1975). Thin-film peeling -the elastic term. J. Phys. D: Appl. Phys. 8, 1449-1452.

Kinloch AJ. (1987). Adhesion and adhesives: science and technology. New York: Chapman and Hall.

Lee YI, Kogan M and Larsen JRJ. (1986). Attachment of the potato leafhopper to soybean plant surfaces as affected by morphology of the pretarsus. Entomol. exp. appl.

42, 101-107.

Lees AD and Hardie J. (1988). The organs of adhesion in the aphid *megoura viciae*. *Journal of Experimental Biology* 136, 209-228.

Little P. (1979). Particle Capture by Natural Surfaces. *Agricultural Aviation* 20, 129-144.

Luan B and Robbins MO. (2005). The breakdown of continuum models for mechanical contacts. *Nature* 435, 929-932.

Maderson PFA. (1964). Keratinized epidermal derivatives as an aid to climbing in gekkonid lizards. *Nature* 203, 780-781.

Mahendra BC. (1941). Contributions to the bionomics, anatomy, reproduction and development of the Indian house gecko *Hemidactylus flaviviridis* Ruppell. Part II. The problem of locomotion. *Proc. Indian Acad. Sci., Sec. B* 13, 288-306.

McMahon TA and Bonner JT. (1983). *On Size and Life*. New York: Scientific American Library.

Menciassi A and Dario P. (2003). Bio-inspired solutions for locomotion in the gastrointestinal tract: background and perspectives. *Philosophical Transactions Of The Royal Society Of London Series A-Mathematical Physical And Engineering Sciences* 361, 2287-2298.

Northen MT and Turner KL. (2005). A batch of fabricated dry adhesive. *Nanotechnology* 16, 1159-1166.

Pain S. (2000). Sticking power. *New Scientist* 168, 62-67.

Peressadko A and Gorb SN. (2004). When less is more: Experimental evidence for tenacity enhancement by division of contact area. *Journal Of Adhesion* 80, 247-261.

Persson BNJ. (2003). On the mechanism of adhesion in biological systems. *Journal of Chemical Physics* 118, 7614-7621.

Persson BNJ and Gorb S. (2003). The effect of surface roughness on the adhesion of elastic plates with application to biological systems. *Journal of Chemical Physics* 119, 11437.

Peterson JA and Williams EE. (1981). A case study in retrograde evolution: the *onca* lineage in anoline lizards. II. Subdigital fine structure. *Bulletin of the Museum of Comparative Zoology* 149, 215-268.

Pianka ER and Sweet S, S. (2005). Integrative biology of sticky feet in geckos. *BioEssays*, 647-652.

Pocius AV. (2002). *Adhesion and adhesives technology: an introduction*. 2nd edition. Munich: Hanser Verlag.

Ringlein J and Robbins MO. (2004). Understanding and illustrating the atomic origins of friction. *American Journal Of Physics* 72, 884-891.

Roll B. (1995). Epidermal fine structure of the toe tips of *Sphaerodactylus cinereus*. *Journal of*

Zoology 235, 289-300.

Rosenberg HI and Rose R. (1999). Volar adhesive pads of the feathertail glider, *Acrobates pygmaeus* (Marsupialia; Acrobatidae). *Canadian Journal of Zoology* 77, 233-248.

Ruibal R and Ernst V. (1965). The structure of the digital setae of lizards. *Journal of Morphology* 117, 271-294.

Russell AP. (1975). A contribution to the functional morphology of the foot of the tokay, *Gekko gecko* (Reptilia, Gekkonidae). *Journal of Zoology London* 176, 437-476.

Russell AP. (1976). Some comments concerning the interrelationships amongst gekkonine geckos. In Bellairs AdA and Cox CB (eds.) *Morphology and Biology of Reptiles*. Academic Press, London, pp. 217-244.

Russell AP. (1979). Parallelism and integrated design in the foot structure of gekkonine and diplodactyline geckos. *Copeia* 1979, 1-21.

Russell AP. (1981). Descriptive and functional anatomy of the digital vascular system of the tokay, *Gekko gecko*. *Journal of Morphology* 169, 293-323.

Russell AP. (1986). The morphological basis of weight-bearing in the scansors of the tokay gecko (Reptilia: Sauria). *Canadian Journal of Zoology* 64, 948-955.

Russell AP. (2002). Integrative functional morphology of the gekkotan adhesive system (Reptilia: Gekkota). *Integrative and Comparative Biology* 42, 1154-1163.

Russell AP and Bauer AM. (1988). Paraphalangeal of gekkonid lizards: a comparative survey. *Journal of Morphology* 197, 221-240.

Russell AP and Bauer AM. (1990a). *Oedura* and *Afroedura* (Reptilia: Gekkonidae) revisited: similarities of digital design, and constraints on the development of multiscansorial subdigital pads? *Memoirs of the Queensland Museum* 29, 473-486.

Russell AP and Bauer AM. (1990b). Digit I in pad-bearing gekkonine geckos: alternate designs and the potential constraints of phalangeal number. *Memoirs of the Queensland Museum* 29, 453-472.

Russell AP and Rosenberg HI. (1981). Self-grooming in *Diplodactylus spinigerus* (Reptilia: Gekkonidae) with a brief review of such behaviour in reptiles. *Can. J. Zool.* 59, 564-566.

Scherge M and Gorb SN. (2001). *Biological Micro- and Nanotribology: Nature's Solutions*. Berlin: Springer.

Schleich HH and Kästle W. (1986). Ultrastrukturen an Gecko-Zehen (Reptilia: Sauria: Gekkonidae). *Amphibia-Reptilia* 7, 141-166.

Schmidt HR. (1904). Zur Anatomie und Physiologie der Geckopfote. *Jena Z. Naturw.* 39, 551.

Simmermacher G. (1884). Haftapparate bei Wirbeltieren. *Zool. Garten* 25, 289-301.

- Sitti M and Fearing RS. (2003). Synthetic gecko foot-hair micro/nano structures as dry adhesives. *Journal of Adhesion Science and Technology* 17, 1055-1073.
- Slocum AH and Weber AC. (2003). Precision passive mechanical alignment of wafers. *Journal of Microelectromechanical Systems* 12, 826-834.
- Spolenak R, Gorb S, Gao HJ and Arzt E. (2004). Effects of contact shape on the scaling of biological attachments. *Proceedings Of The Royal Society Of London Series A-Mathematical Physical And Engineering Sciences* 461, 305-319.
- Spolenak R, Gorb S and Arzt E. (2005). Adhesion design maps for bio-inspired attachment systems. *Acta Biomaterialia* 1, 5-13.
- Stork NE. (1980). Experimental analysis of adhesion of *Chrysolina polita* (Chrysomelidae: Coleoptera) on a variety of surfaces. *Journal of Experimental Biology* 88, 91-107.
- Stork NE. (1983). A comparison of the adhesive setae on the feet of lizards and arthropods. *Journal of Natural History* 17, 829-835.
- Sun W, Neuzil P, Kustandi TS, Oh S and Samper VD. (2005). The nature of the gecko lizard adhesive force. *Biophys. J.* 89, L14-L17.
- Urbakh M, Klafter J, Gourdon D and Israelachvili J. (2004). The nonlinear nature of friction. *Nature* 430, 525-528.
- Vanhooydonck B, Andronescu A, Herrel A and Irschick DJ. (2005). Effects of substrate structure on speed and acceleration capacity in climbing geckos. *Biological Journal of the Linnean Society* 85, 385-393.
- Vinson J and Vinson J-M. (1969). The saurian fauna of the Mascarene islands. *Bull. Maurit. Inst.* 6, 203-320.
- Vitt LJ and Zani PA. (1997). Ecology of the nocturnal lizard *Thecadactylus rapicauda* (Sauria: Gekkonidae) in the Amazon region. *Herpetologica* 53, 165-179.
- von Wittich. (1854). Der Mechanismus der Haftzehen von *Hyla arborea*. *Archiv für Anatomie und Physiologie*, 180.
- Wagler J. (1830). *Natürliches System der Amphibien*. München: J. G. Cotta'schen Buchhandlung.
- Wainwright SA, Biggs WD, Currey JD and Gosline JM. (1982). *Mechanical Design in Organisms*. Princeton: Princeton University Press.
- Weitlaner F. (1902). Eine Untersuchung über den Haftfuß des Gecko. *Verhdl. Zool. Bot. Ges. Wien* 52, 328-332.
- Williams EE and Peterson JA. (1982). Convergent and alternative designs in the digital adhesive pads of scincid lizards. *Science* 215, 1509-1511.

Figure legends

Figure 1. Structural hierarchy of the gecko adhesive system. Images (A) and (B) by Mark Moffett. **A.** Ventral view of a tokay gecko (*Gekko gekko*) climbing a vertical glass surface. **B.** Ventral view of the foot of a tokay gecko, showing a mesoscale array of seta-bearing scensors (adhesive lamellae). **C.** Microscale array of setae are arranged in a nearly grid-like pattern on the ventral surface of each scensor. 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.** Micrograph of a single gecko seta assembled from a montage of five Cryo-SEM images (Image by Stas 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 lab of Ronald Fearing using nanomolding (Campolo et al. 2003).

Figure 2. Single-leg ground reaction forces in running geckos (*Hemidactylus garnoti*). **A.** During level running, geckos' front legs produce deceleratory ground reaction forces while their hind legs produce acceleratory forces (Autumn et al. 2005 (in press)). All legs push away from the body, producing ground reaction forces aimed through the joints toward the center of mass, minimizing joint moments, and possibly stabilizing the animal as it runs. Circles with dots represent positive ground reaction forces normal to the surface. During level running these represent the forces that support the animal's weight. **B.** During vertical climbing, geckos have similar kinematics, but alter dramatically their kinetics in comparison to level running (Chen et al. 2005 (in press)). While climbing, all legs accelerate the body up the wall, and all legs pull in toward the center of mass, engaging the adhesive setae and claws. Front limbs pull away from the surface and hind limbs push into the surface, producing a torque that tips the head toward the wall, counteracting the tendency of the animal's head to pitch back as it climbs.

Figure 3. Model of self-cleaning in gecko setae from Hansen and Autumn (2005). If we model spatulae as nanoscale strips of adhesive tape (Kendall 1975) that peel during detachment, the particle-spatula pulloff force is given by $F_{ps} \approx 2R_s \gamma_{ps}$, where γ_{ps} is the adhesion energy at the dirt particle – spatula interface, and $2R_s$ is the width of the spatula, and assuming negligible elastic energy storage. The pulloff force of the dirt particle from a planar wall, using the Johnson, Kendall, Roberts (JKR) model (Johnson et al. 1973) is $F_{pw} = \frac{3}{2} \pi R_p \gamma_{pw}$, where γ_{pw} is the adhesion energy of the particle to the wall. N represents the number of spatulae attached simultaneously to each dirt particle to achieve energetic equilibrium.

Figure 4. Free body diagram of (A) cantilever beam and (B) angled cantilever beam based on the model of Sitti and Fearing (2003). This model is similar to that of Persson (2003) who used a spring-based approach.

Figure 5. Young's modulus (E) of materials including approximate values of bulk β -keratin and effective modulus (E_{eff}) of natural setal arrays (Geisler et al. 2005). 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 (Eqn. 5.3; Sitti and 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.

Figure 6. Stress versus area in the gecko adhesive hierarchy. See [Table 1](#) for numerical values and literature sources. JKR and Kendall model predictions for spatular adhesive stress (triangles) bound the measured value of Huber et al. (2005). Text below the X-axis shows the level in the gecko adhesive hierarchy ([Fig. 1](#))

Table 1. Scaling of adhesion and friction stresses in tokay gecko setae. Stress decreases approximately exponentially (Fig. 6), or approximately linearly on a log-log scale. The Kendall peel model prediction uses a square spatula of 100 nm on a side. The JKR model prediction uses a spherical spatula with 100 nm radius. Both predictions use an adhesion energy of $W = 50 \text{ mJ/m}^2$. Note that the similarity of area between single toe and single foot is due to the use of larger geckos in the single toe measurements.

Scale	Mode	Force	Area	Stress (kPa)	Stress (atm)
Single spatula (Huber et al. 2005)	Adhesion	10 nN	$0.02 \mu^2$	500	4.9
JKR model prediction for single spatula	Adhesion	23.56 nN	$0.0314 \mu^2$	750	7.4
Kendall peel model prediction for single spatula	Adhesion	10.00 nN	$0.04 \mu^2$	250	2.5
Single seta (Autumn et al. 2000)	Adhesion	$20 \mu\text{N}$	$43.6 \mu^2$	458	4.5
Single seta (Autumn et al. 2002)	Adhesion	$40 \mu\text{N}$	$43.6 \mu^2$	917	9.0
Single seta (Autumn et al. 2000)	Friction	$200 \mu\text{N}$	$43.6 \mu^2$	4585	45.2
Setal array (Hansen & Autumn 2005)	Friction	0.37 N	0.99 mm^2	370	3.7
Single toe (Hansen & Autumn 2005)	Friction	4.3 N	0.19 cm^2	226	2.2
Single foot (Autumn et al. 2002)	Friction	4.6 N	0.22 cm^2	186	1.8
Two feet (Irschick et al. 1996)	Friction	20.4 N	2.27 cm^2	90	0.9

Table 2. Properties, principles, and parameters of the gecko adhesive system. This table lists known properties of the gecko adhesive, proposed principles (or models) that explain the properties, and model parameters for each property. JKR refers to the Johnson, Kendall, Roberts model of adhesion (Johnson et al. 1973).

Properties	Principles	Parameters
1. Anisotropic attachment (Autumn et al. 2000)	Cantilever beam (Autumn et al. 2000; Sitti & Fearing 2003; Spolenak et al. 2004; Geisler & Autumn in prep) Low effective stiffness (Sitti & Fearing 2003; Persson 2003; Geisler & Autumn in prep)	Shaft length, radius, density (Sitti & Fearing 2003)
2. High μ' (pulloff/preload) (Autumn et al. 2000)		Shaft angle (Sitti & Fearing 2003)
3. Low detachment force (Autumn et al. 2000)		Shaft modulus (Sitti & Fearing)
		Spatular shape (Persson & Gorb 2003; Spolenak, Gorb, Gao, Arzt 2004)
4. Material independence (Autumn et al. 2002; Hiller 1968,9)	van der Waals (vdW) mechanism (Autumn et al. 2002)	Spatular size (Arzt, Gorb, Spolenak 2003)
	JKR-like contact mechanics (Autumn et al. 2002; Arzt et al. 2002,3)	Spatular Shape (Gao & Yao 2004; Spolenak, Gorb, Gao, Arzt 2004)
	Nanoarray (divided contact) (Autumn et al. 2002; Gao et al. 2004)	Spatular density (Arzt, Gorb, Spolenak 2003; Peattie 2004)
5. Self-cleaning (Hansen & Autumn 2005)	Nanoarray (divided contact)	Spatular bulk modulus
6. Anti-self	Small contact area Nontacky spatulae	Particle size, shape, surface energy
7. Nonsticky default state (Autumn & Hansen in review)	Hydrophobic, vdW spatulae	Spatular size, shape, surface energy

Fig. 1

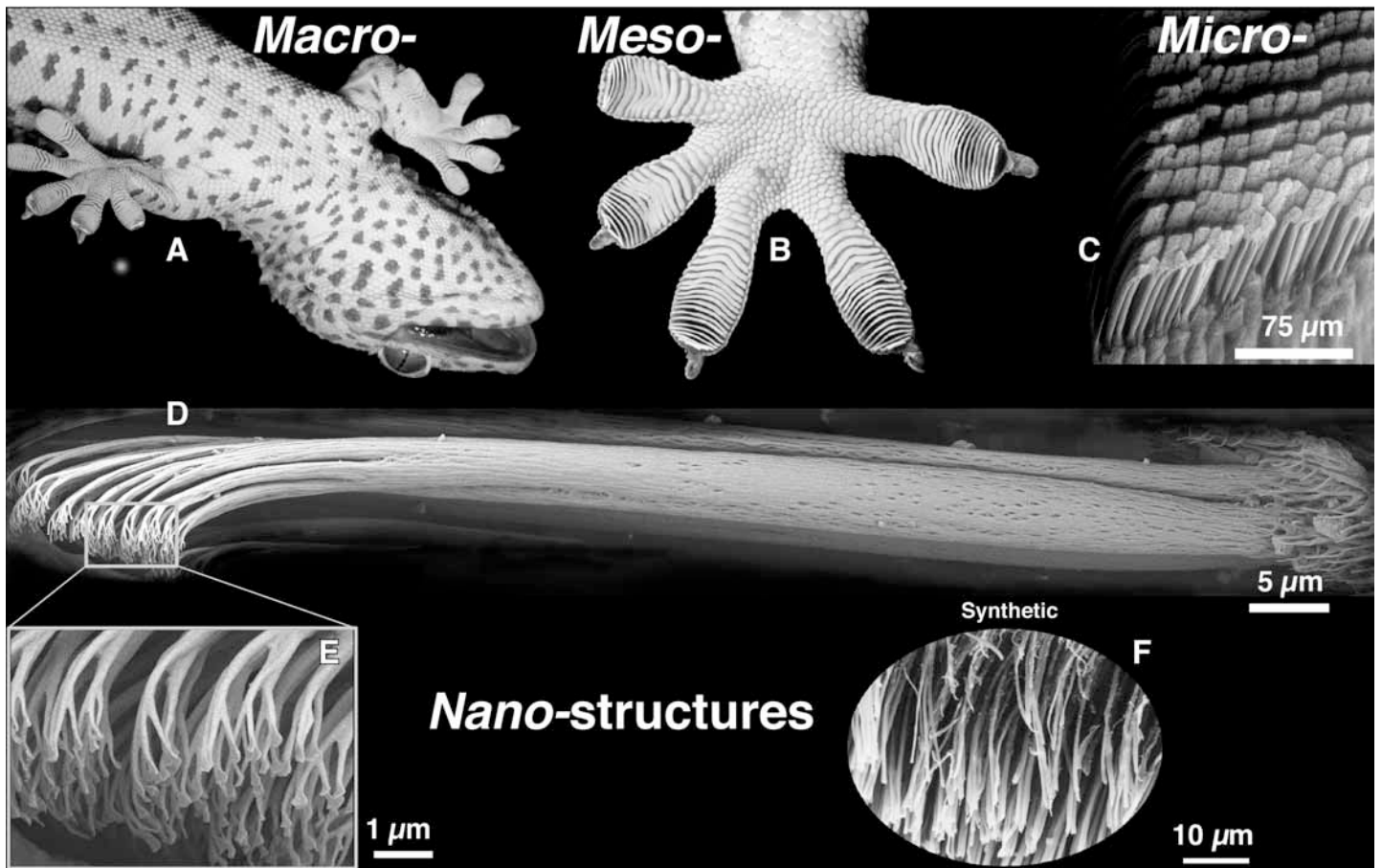


Fig. 2

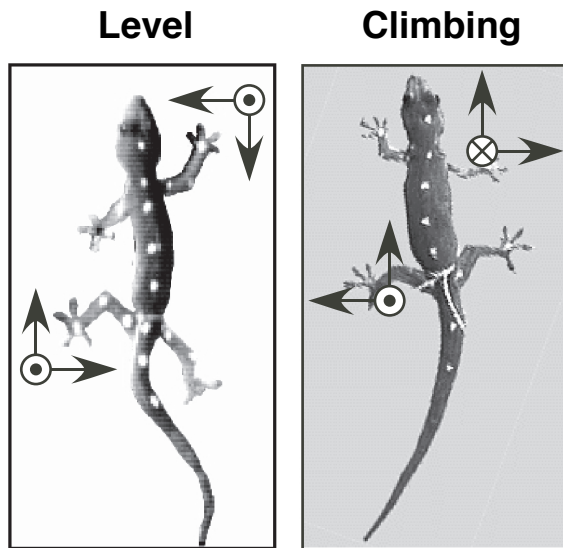


Fig. 3

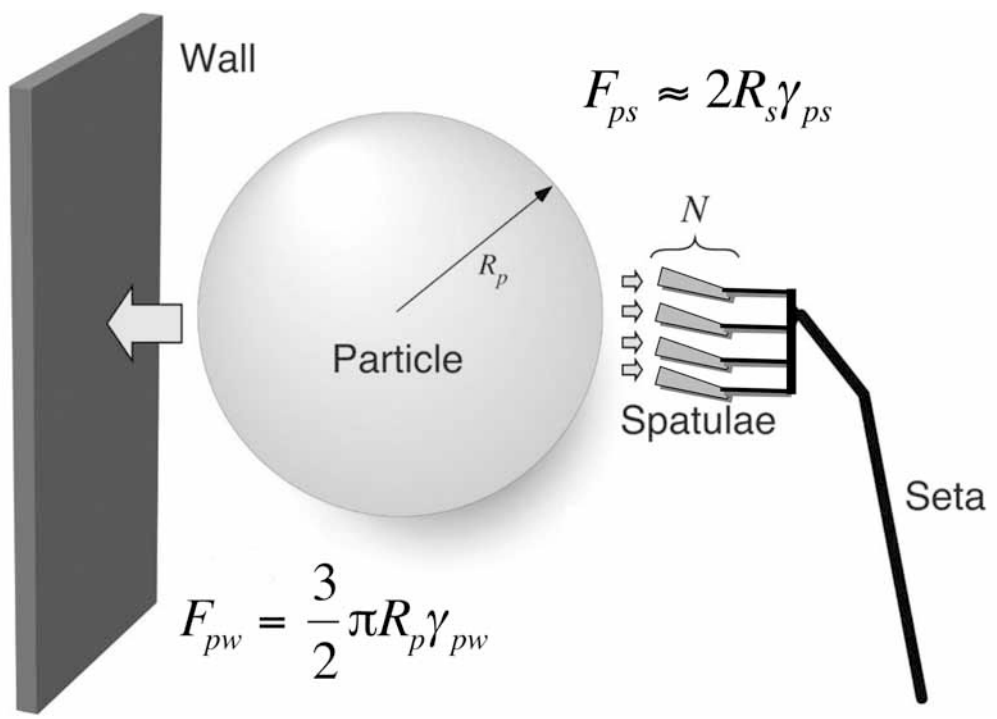


Fig. 4

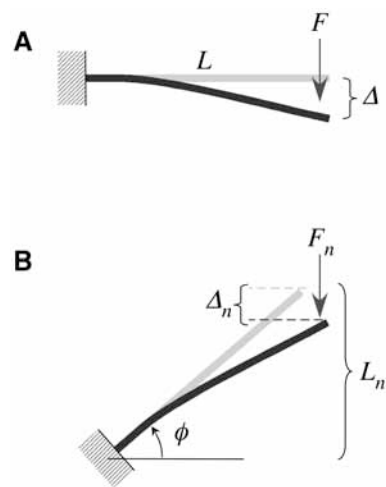


Fig. 5

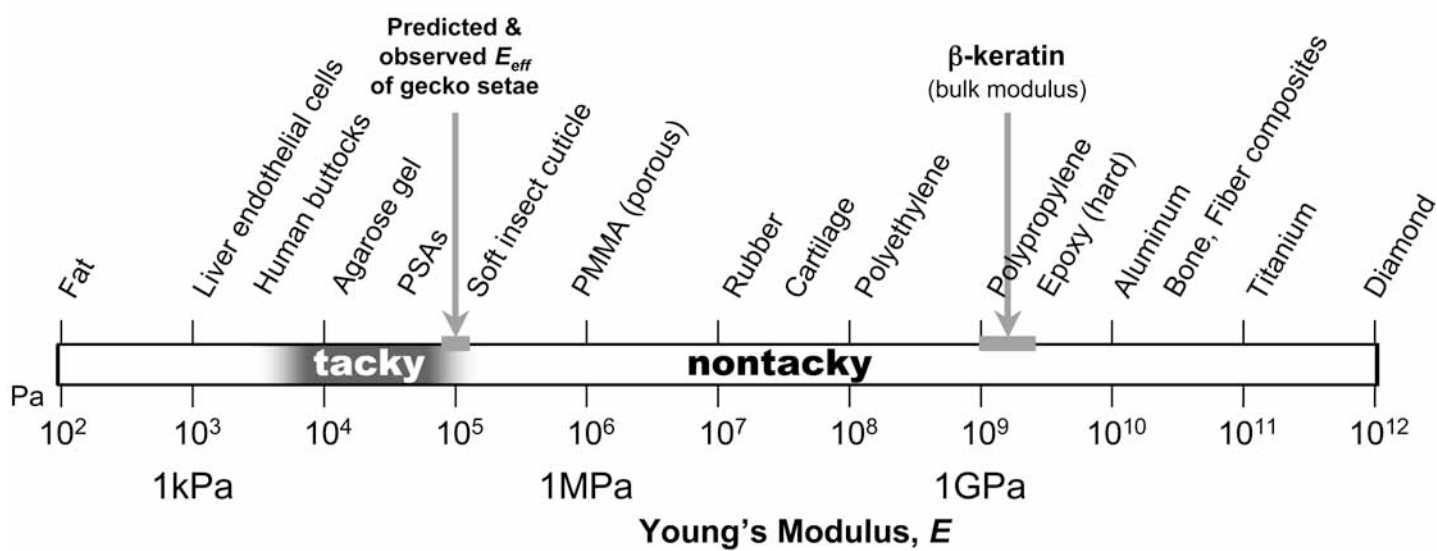


Fig. 6

