Mechanisms of Adhesion in Geckos[1]

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SYNOPSIS. The extraordinary adhesive capabilities of geckos have challenged explanation for millennia, since Aristotle first recorded his observations. We have discovered many of the secrets of gecko adhesion, yet the millions of dry, adhesive setae on the toes of geckos continue to generate puzzling new questions and valuable answers. Each epidermally-derived, keratinous seta ends in hundreds of 200 nm spatular tips, permitting intimate contact with rough and smooth surfaces alike. Prior studies suggested that adhesive force in gecko setae was directly proportional to the water droplet contact angle (θ), an indicator of the free surface energy of a substrate. In contrast, new <u>theory</u> suggests that adhesion energy between a gecko seta and a surface (W_{GS}) is in fact proportional to $\sqrt{(1 + \cos\theta)}$, and only for $\theta > 60°$. A reanalysis of prior data, in combination with our recent study, support the van der Waals hypothesis of gecko adhesion, and contradict surface hydrophobicity as a predictor of adhesion force. Previously, we and our collaborators measured the force production of a single seta. Initial efforts to attach a seta failed because of improper 3D orientation. However, by simulating the dynamics of gecko limbs during climbing (based on force plate data) we discovered that, in single setae, a small normal preload, combined with a 5 μm displacement yielded a very large adhesive force of 200 microNewton (μN), 10 times that predicted by whole-animal measurements. 6.5 million setae of a single tokay gecko attached maximally could generate 130 kg force. This raises the question of how geckos manage to detach their feet in just 15 ms. We discovered that simply increasing the angle that the setal shaft makes with the substrate to 30° causes detachment. Understanding how simultaneous attachment and release of millions of setae are controlled will require an approach that integrates levels ranging from molecules to lizards.

INTRODUCTION

Geckos seem to defy gravity as they run along smooth vertical surfaces at up to 20 body lengths per second (Autumn *et al.*, 1999*a*), and even upside down on the ceiling. 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, Book IX, Part 9). How geckos adhere has been a gripping topic of scientific research for well over a century (Cartier, 1872; Haase, 1900; Gadow, 1901; Weitlaner, 1902; Schmidt, 1904; Hora, 1923; Dellit, 1934; Mahendra, 1941; Maderson, 1964; Ruibal and Ernst, 1965; Hiller, 1968, 1969, 1975; Gennaro, 1969; Russell, 1975, 1986; Williams and Peterson, 1982; Stork, 1983; Schleich and Kästle, 1986; Irschick *et al.*, 1996; Autumn *et al.*, 2000; Liang *et al.*, 2000; Autumn *et al.*, 2002). Rapid locomotion on a vertical surface requires the ability to generate parallel (frictional) forces equal to or greater than body weight (Fig. 1A). Detachment is perhaps even more important than attachment. After all, even the most common household adhesives are more than sufficient to hold statically the weight of a large gecko (50 g), but repeated and rapid detachment without significant detachment forces is beyond the capability of any current synthetic adhesive. The secret of geckos' adhesive capabil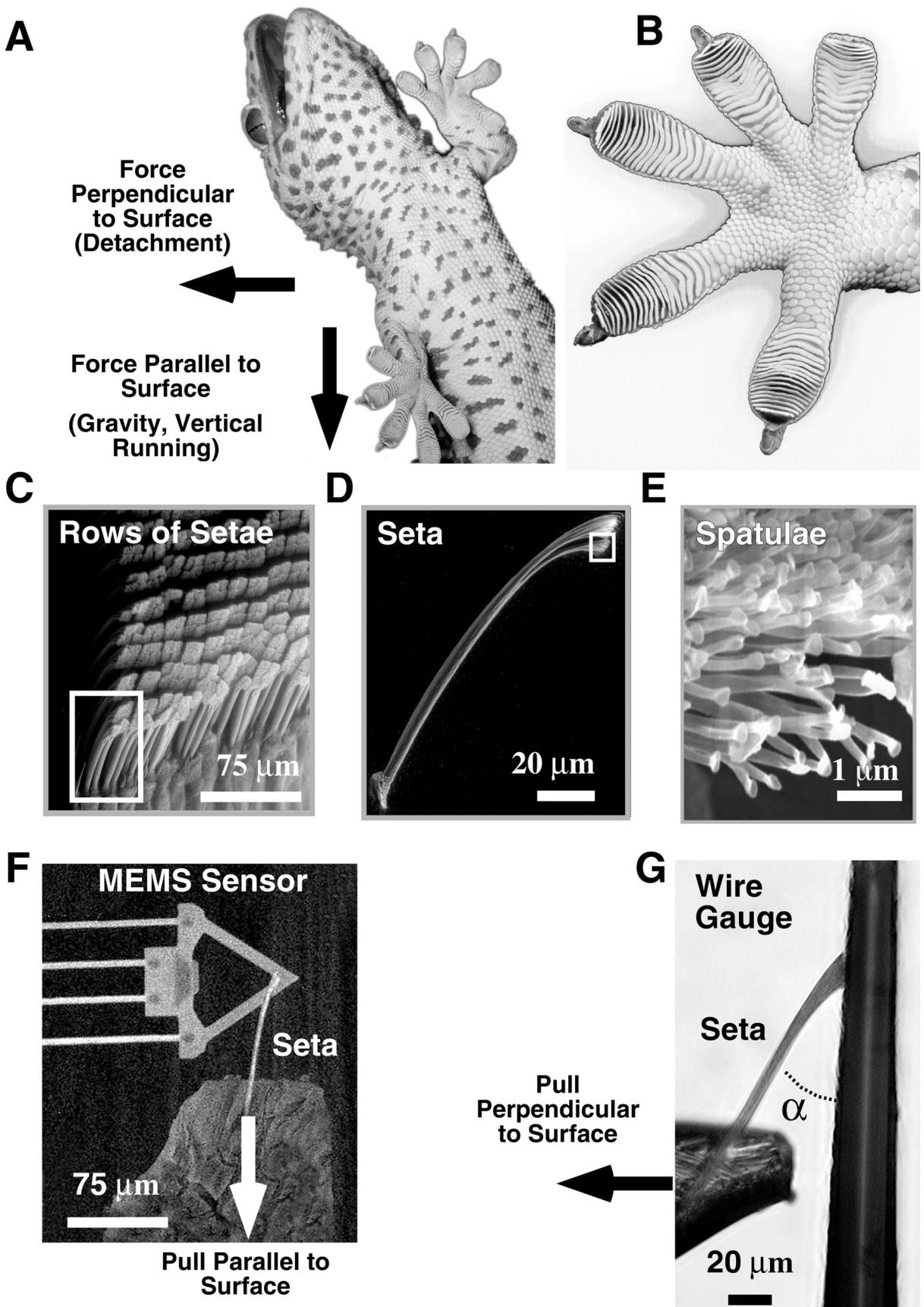ities lies in the structure and function of their feet (Russell, 2002) and in the adhesive toe pads borne on the underside of each digit. These pads consist of a series of modified lamellae (scansors; Fig. 1B), each one covered with uniform arrays of similarly-oriented hair-like bristles (setae; Fig. 1C) formed from β-keratin (Wainwright *et al.*, 1982; Russell, 1986). A single seta of the tokay gecko (*Gekko gecko*; Fig. 1D) is approximately 100 microns in length and 5 microns in diameter (Ruibal and Ernst, 1965; Russell, 1975; Williams and Peterson, 1982). The setae of the tokay gecko (as well as most others) branch at the tips into 100–1,000 structures known as spatulae (Fig. 1E). A single spatula consists of a stalk with a flattened, roughly triangular end, where the apex of the triangle connects the spatula to its stalk. Spatulae are approximately 200 nm at their widest edge (Ruibal and Ernst, 1965; Williams and Peterson, 1982). While the tokay is currently the best studied of any adhesive gecko species, there exist many hundreds of species with adhesive toe pads, encompassing an impressive range of morphological variation at the seta, scansor, and toe levels, which has yet to be fully characterized. The results discussed in this paper are based predominantly on observations of isolated tokay gecko setae and whole-animal dynamics of the house gecko *Hemidactylus garnoti*, which shares the tokay's setal morphology (but not its toe morphology).

While the structures of many gecko setae are well documented, a full understanding of their function has been more elusive. Haase (1900) noted that adhesion 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

A

Force Perpendicular to Surface (Detachment)

Force Parallel to Surface (Gravity, Vertical Running)

B

C

Rows of Setae

75 μm

D

Seta

20 μm

E

Spatulae

1 μm

F

MEMS Sensor

Seta

75 μm

Pull Parallel to Surface

G

Wire Gauge

Seta

α

Pull Perpendicular to Surface

20 μm

forces (*Adhäsion*), noting that under this hypothesis the attractive force should increase as the space between the feet and the substrate decreases. Setae are recurved such that their tips point proximally, leading Dellit (1934) to hypothesize that setae act like hooks, catching on surface irregularities (microinterlocking). Ruibal and Ernst (1965) later postulated that, while the seta is engaged, the spatulae lie flat against the substrate. It was clear to them that these flattened tips increased the realized contact area, increasing frictional force. This was an important step in understanding setal mechanics but it did not significantly change predictions associated with a microinterlocking hypothesis. This implied that adhesion should be stronger on rougher surfaces, and that inverted locomotion should be difficult, if not impossible, since friction (in the classical sense) only operates parallel to the plane of locomotion, leaving no vertical force component to oppose gravity.

The turning point in the study of gecko adhesion came with a series of experiments by Hiller (1968), who suggested that the material properties of the substrate, rather than its texture, determined the strength of gecko adhesion. In demonstrating that adhesion was a molecular phenomenon rather than a mechanical one, his discovery effectively refuted the microinterlocking and friction hypotheses and paved the way for the research we describe here.

MECHANICS OF GECKO ADHESION

In a phylogenetic comparison of the forces produced by pad-bearing lizards, Irschick *et al.* (1996) showed that two front feet of a tokay gecko (*Gekko gecko*) produced 20.1 N of force parallel to the surface with 227 mm^2 of pad area. The foot of a tokay bears approximately 3,600 tetrads of setae per mm^2, or 14,400 setae per mm^2 (Schleich and Kästle, 1986; personal observation). Consequently, a single seta should produce an average force of 6.2 μN, and an average shear stress of 0.090 N mm^{-2} (0.9 atm). (Note that Autumn *et al.* (2000) used a value of 5,000 setae per mm^2 taken from Ruibal and Ernst (1965). In this paper, we use the more accurate value of 14,400 setae per mm^2 (Schleich and Kästle [1986]; we have confirmed this

figure with our own observations.) The difficulty of first isolating and manipulating a single seta, and then finding an instrument capable of measuring micronewton forces in two dimensions, complicated our attempt to demonstrate how the function of a single seta might contribute to adhesion at the organismal level. We will now describe how we confronted these difficulties in our experimental procedure.

Mechanism of setal attachment

Using new microelectromechanical systems (MEMS) force measurement techniques (Chui *et al.*, 1998), Autumn *et al.* (2000) measured the force production of a single gecko seta (Fig. 1F). Initial efforts to attach a single seta failed to generate adhesive forces above that predicted by friction because we could not achieve the proper orientation of the seta in 6 degrees of freedom (*i.e.*, translation in, and rotation about, all three axes). The angle of the setal shaft was particularly important in achieving an adhesive bond (Fig. 1G). When we simulated the dynamics of gecko limbs during climbing (based on force plate data; Autumn *et al.*, 1999*a, b*), we discovered that a small normal preload force (Fig. 2A) yielded a shear force of ~40 μN, six times the force predicted by whole-animal measurements (Irschick *et al.*, 1996). Proper orientation, preload, and drag yielded 10 to 20 times the frictional force measured with the seta oriented with spatulae facing away from the surface (Fig. 2B). The small normal preload force (Fig. 2A), combined with a 5 μm displacement yielded a very large shear force of 200 μN, 32 times the force predicted by whole-animal measurements (Irschick *et al.*, 1996; Fig. 2C). The discovery that maximal adhesion in isolated setae requires a small push perpendicular to the surface, followed by a small parallel drag, explained the load dependence and directionality of adhesion observed at the whole-animal scale by Dellit (1934), and was consistent with the hypothesis that the structure of individual setae and spatulae is such that a small preload and rearward displacement is necessary to engage adhesion (Ruibal and Ernst, 1965; Hiller, 1968). In their resting state, setal stalks are recurved proximally. When the toes of the gecko are planted, we believe

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FIG. 1. Gecko adhesive structures and methods used to measure setal adhesive function. Images (A) and (B) by Mark Moffett. Figure modified from Autumn *et al.* (2000), *Nature*.

A) Ventral view of a tokay gecko (*Gekko gecko*) climbing a vertical glass surface. Arrows represent the forces acting on the gecko's feet as it climbs.

B) Ventral view of the foot of a tokay gecko, showing seta-bearing scansors.

C) 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. Box shows seta enlarged in (D).

D) Single isolated gecko seta used in measurements in Autumn *et al.* (2000). Box shows spatulae enlarged in (E).

E) Spatular tips of a single gecko seta.

F) Isolated seta adhering to a micro-electromechanical system (MEMS) cantilever capable of measuring forces parallel and perpendicular to the surface. Arrow shows direction of manipulation during the experiment, simulating parallel forces generated during vertical locomotion of the gecko.

G) Single seta adhering to a 25 μm aluminum bonding wire capable of measuring detachment force perpendicular to the surface. Arrow shows direction of manipulation during the experiment, simulating perpendicular movement during detachment of the foot. (α is the angle between the setal stalk and the wire.
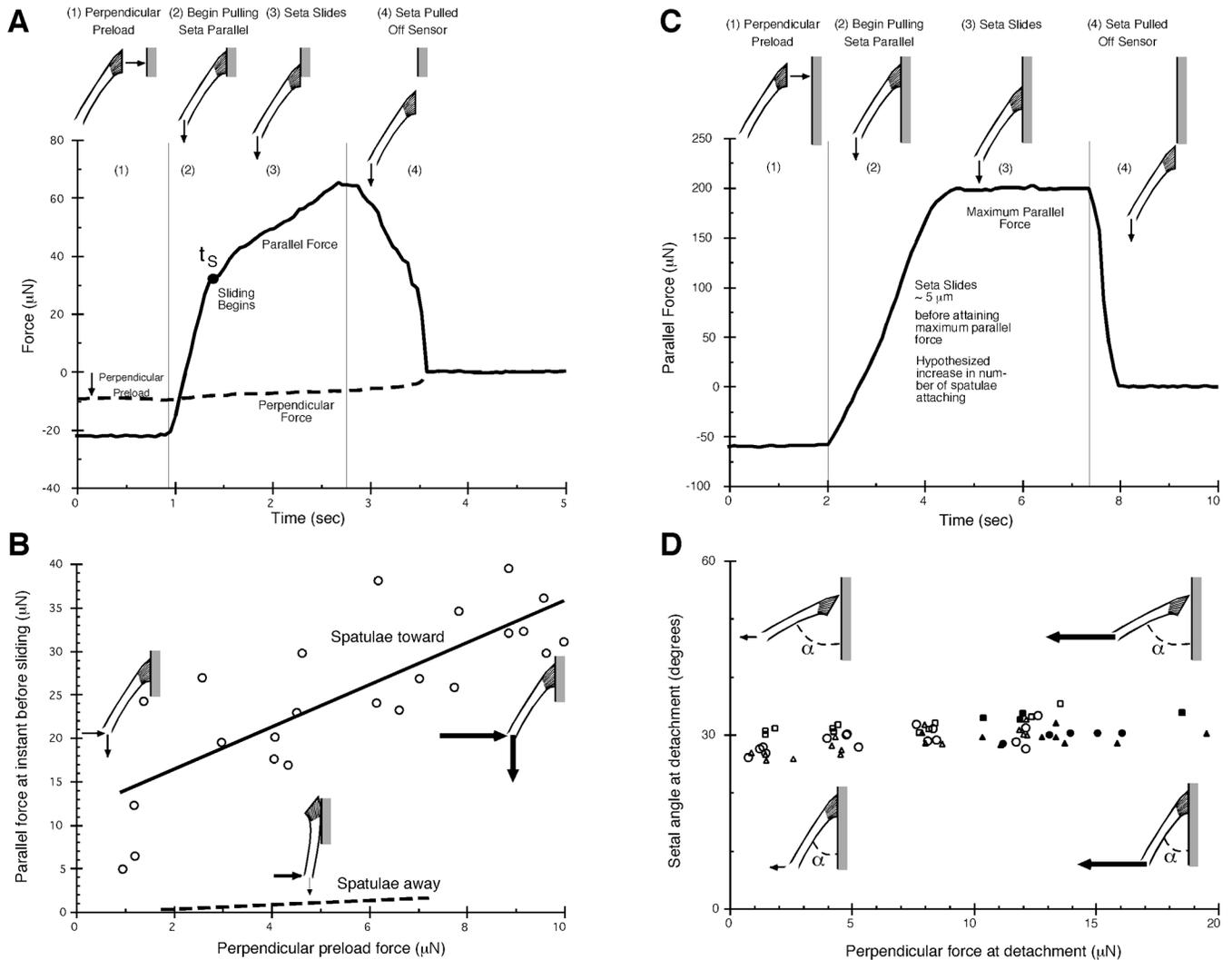
FIG. 2. Single seta measurements. Figure modified from Autumn *et al*. (2000), *Nature*.

A) Submaximal force of single seta parallel to the surface with a known perpendicular preload, as a function of time. Perpendicular preload is designated by the dashed line. t_s represents the time when the seta began to slide off the sensor. The initial perpendicular force need not be maintained during the subsequent pull. Diagrams show the stages of setal movement corresponding to the force record from the MEMS cantilever (Fig. 1F). Arrows indicate the direction of applied force to the seta. Vertical arrow indicates a parallel force, and a horizontal arrow indicates a perpendicular force.

B) Setal force parallel to the surface during attachment as a function of perpendicular preload force. Setal force was taken to be the adhesive force at the time just prior to sliding (t_s; Fig. 2A). The solid line represents a seta with spatulae projecting toward the surface. The dashed line represents the setal force with spatulae projecting away from the surface (parallel force = 0.25 perpendicular preload −0.09; r^2 = 0.64; F = 13; df = 1,9; P = 0.007). The force produced by the inactive, non-spatular region increased with normal or perpendicular force, typical of materials with a coefficient of friction equal to 0.25. The perpendicular preloading force that could be applied attained a maximum (near 15 μN), because greater forces resulted in the setal buckling.

C) Maximal force after a maximum preload (≈15 μN) of a single seta parallel to the surface as a function of time. Diagrams show the stages of setal movement corresponding to the force record from the MEMS cantilever (Fig. 1F). Arrows indicate the direction of force applied to the seta. Vertical arrow indicates a parallel force; horizontal arrow indicates a perpendicular force. The maximum force (~200 μN) following the small rearward displacement (≈5 μm) was 32 times that predicted from maximal whole animal estimates (see text). The large increase in force during the rearward displacement may be caused by an increase in the number of spatulae contacting the surface.

D) Change in the orientation of the setae may facilitate detachment. Setal angle (α) with the surface at detachment as a function of perpendicular force. Filled symbols represent seta pulled away from the surface until release. Open symbols represent seta held at a constant force as angle is increased. Each symbol shape represents a different seta. Data collected with wire gauge (Fig. 1G). Setal angle at detachment changed by only 15% over the entire range of perpendicular forces. This observation is consistent with an adhesive model where sliding stops when pulling at greater than the critical setal angle and hence stress can increase at a boundary, causing fracture of the contact.

that the setae are 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 scansor 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.

All 6.5 million (Schleich and Kästle, 1986; Irschick et al., 1996) setae of a 50 g tokay gecko attached maximally could theoretically generate 1,300 N (133 kg force) of adhesive 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). Less than 0.04% of a gecko's setae attached maximally are needed to support its weight of 50 g on a wall. At first glance, gecko feet seem to be enormously overbuilt. On further consideration, however, there are some clear advantages to possessing as many setae as possible (at which point we might ask what factors actually limit a gecko's adhesive capacity). 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; Autumn and Gorb in preparation). On dusty or exfoliating surfaces, attachment to a well-anchored substrate will not be possible for every seta. Large forces generated by perturbations during locomotion (e.g., recovering from a fall, predator avoidance, or station-keeping in high winds) may also utilize a greater proportion of geckos' adhesive capacity.

Mechanism of setal detachment

The surprisingly large forces generated by single setae raised the question of how geckos manage to detach their feet so rapidly (15 ms; Autumn et al., 1999a) with no measurable detachment forces (Autumn et al., 1999b). We discovered that increasing the angle between the setal shaft and the substrate beyond 30° caused detachment (Autumn et al., 2000; Fig. 1G; Fig. 2D). It is likely that as the angle of the setal shaft increases, stress increases at the trailing edge of the seta, causing fracture of the spatula-substrate bonds. Similarly, at the scansor level, geckos' unusual toe peeling behavior (digital hyperextension; Russell, 1975, 1981) may aid in reducing or eliminating detachment forces by detaching only a small number of setae at any moment. How this peeling behavior results in reaching the critical angle of detachment is still unclear, but the two are almost certainly linked.

Integration of setal mechanics, functional morphology of the foot, and dynamics of locomotion

It is important to emphasize that without integrating dynamics at a larger scale (body and legs), the function of the seta would likely still remain unknown. This underscores the importance of an integrative approach to answering biological questions (Lauder, 1991; Savageau, 1991; Ryan et al., 1998; Dickinson et al., 2000; Autumn et al., 2002). How attachment and detachment of millions of setae during locomotion is integrated with the function of the scansor, toe, foot, leg, and body remains a topic of great interest and ongoing research (Sponberg et al., 2001; Russell, 2002). Russell has suggested that in the tokay (*Gekko gecko*), the perpendicular preload and 5 μm drag requirements (Autumn et al., 2000) are controlled by hydrostatic pressure in the highly derived blood sinuses, and lateral digital tendon system, respectively (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., 1999a, b), indicating that these actions are either mechanically decoupled from the center of mass in this species, or so small as to be undetectable.

The absence of detachment forces is consistent with (1) the mechanism of detachment and (2) the anatomy of the foot. Geckos peel their toes up and away from the substrate (digital hyperextension) rather than attempting to detach an entire foot at once, much like removing a piece of tape. Peeling minimizes peak forces by spreading detachment out over time. Since the muscles responsible for digital hyperextension (interossei dorsales; Russell, 1975) are located in the foot, detachment does not have to be coupled mechanically to the center of mass, as would be the case if the gecko used its leg musculature to break the adhesive bonds in the foot.

The absence of attachment forces is a more complicated issue, with at least three possible explanations. As Russell (2002) has suggested, inflation of the digital blood sinuses (such as those present in individuals of *Hemidactylus* and *Gekko*) may satisfy the preload requirement of the setae during attachment without generating measurable forces acting on the center of mass. 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.

A second potential explanation is that setal preload and drag are a consequence of force development during the stride. Climbing geckos use all four feet similarly to produce positive fore-aft forces parallel to the surface that propel the gecko upwards (Autumn et al., 1999b). Left legs apply a force to the right while right legs apply a force to the left. Therefore, all four feet pull medially, probably dragging the setae to engage them fully, increasing the force of attachment (Autumn et al., 1999b). However, geckos' front legs pull the center of mass into, while hind legs push the center of

mass away from, the vertical substrate (Autumn *et al.*, 1999*b*), generating a net moment pitching the anterior toward the surface and counteracting the tendency of the head to fall away from the surface (Alexander, 1992). Front legs do not push into the vertical substrate during or after foot contact. Thus, these results do not support the hypothesis that the setae become preloaded as a consequence of force development during the stride. While this is possible for the hind feet, it is difficult to reconcile with the negative normal forces produced by the front feet (Autumn *et al.*, 1999*b*), unless the attachment force is so small as to be undetectable. The force necessary to bend even thousands of setae into an adhesive orientation is probably quite small (by our estimate, at most 10 mN). In this case, we may have observed no measurable attachment forces simply because we cannot measure them.

A third possibility is that attachment is a reversal of the peeling process of toe detachment, which we believe to be decoupled from the center of mass. The gecko's foot may approach the substrate without pressing into it, re-applying its adhesive by gradually extending (unrolling) its toes against the surface, at which point they are ready to bear the load of the animal's weight. In this case, setal preload forces would be spread out over time, and would likely be far below the resolution of our force plate (±1 mN).

MOLECULAR MECHANISM OF GECKO ADHESION

While the mechanism of setal attachment and detachment in geckos is now understood in mechanical terms (Autumn *et al.*, 2000), the molecular mechanism underlying adhesion in setae has remained unclear. Adhesion can be caused by at least 11 different types of intermolecular surface forces at the interface between solids (Israelachvili, 1992; Gay, 2002), and cannot always be distinguished from friction, a complicated phenomenon in and of itself (Persson, 1999). The study of surface forces is currently an active area of research (Kinloch, 1987; Israelachvili, 1992, 2001; Christenson, 1993; Noy *et al.*, 1995; Thomas *et al.*, 1995; Gay and Leibler, 1999; Kunzig, 1999). The complexity of the problem stems from the difficulty of knowing what materials are actually interacting at the molecular scale (Israelachvili, 1992; Persson, 1999). Thus it is not surprising that adhesion in geckos has remained a challenging problem.

Unsupported mechanisms: glue, suction, electrostatics, and microinterlocking

Since geckos lack glandular tissue on their toes, sticky secretions were ruled out early in the study of gecko adhesion (Wagler, 1830; Cartier, 1874; Simmermacher, 1884). The idea that the individual setae acted as miniature suction cups was first debated in the insect adhesion literature (Blackwall, 1845; Hepworth, 1854), but was later proposed for gekkonid lizards by Simmermacher (1884). However, there are no data to support suction as an adhesive mechanism, and the adhesion experiments carried out in a vacuum by Del-

lit (1934) suggest that suction is not involved. Furthermore, our measurements of 10 atm of adhesion pressure (Autumn *et al.*, 2000) strongly contradict the suction hypothesis.

Electrostatic attraction (Schmidt, 1904) is another possible mechanism for adhesion in gecko setae. Experiments using X-ray bombardment (Dellit, 1934) eliminated electrostatic attraction as a necessary mechanism for setal adhesion since the geckos were still able to adhere in ionized air. However, electrostatic effects could possibly enhance adhesion even if another mechanism is operating (Maderson, 1964).

Friction (Hora, 1923) and microinterlocking (Dellit, 1934; the ''climber's boot'' model of Mahendra, 1941) may also play a secondary role, but the ability of geckos to adhere while inverted on polished glass, and the presence of large adhesive forces on a molecularly smooth SiO_2 MEMS semiconductor (Autumn *et al.*, 2000) show that surface irregularities are not necessary for adhesion, and may in fact be an impediment (Autumn and Gorb, in preparation)

Potential intermolecular mechanisms: van der Waals and capillary forces

Hiller (1968, 1969, 1975) showed that adhesive 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 adhesion in geckos. Ongoing research is now directed toward understanding the precise nature of these intermolecular forces.

Intermolecular capillary forces are the principal mechanism of adhesion in many insects (Gillett and Wigglesworth, 1932; Edwards and Tarkanian, 1970; Lee *et al.*, 1986; Lees and Hardie, 1988; Brainerd, 1994; Dixon *et al.*, 1990), frogs (Emerson and Diehl, 1980; Green, 1981; Hanna and Barnes, 1991) and even mammals (Rosenberg and Rose, 1999). Unlike these animals, geckos lack glands on the surface of their feet (Wagler, 1830; Cartier, 1872; Dellit, 1934; Mahendra, 1941). This in itself does not preclude the role of thin film capillary adhesion (von Wittich, 1854, quoted directly in Simmermacher, 1884; Stork, 1980; Scherge and Schaefer, 1998) since a monolayer of water molecules (presumably present in the environment) can cause strong attraction between surfaces (Baier *et al.*, 1968; Israelachvili, 1992). The apparent inverse correlation between adhesive force and hydrophobicity, as inferred from the water droplet contact angle (Hiller, 1968) suggests that the polarity of the surface might be an important factor in the strength of adhesion (Fig. 3). Two points are worth noting with regard to this hypothesis: (1) Such a monolayer would have to be ubiquitous and relatively pure in continuous patches in order for the gecko to take advantage of it, and (2) Hiller (1968) did not favor a capillary mechanism for gecko adhesion since adhesive force did not decrease completely to zero on all hydrophobic surfaces.

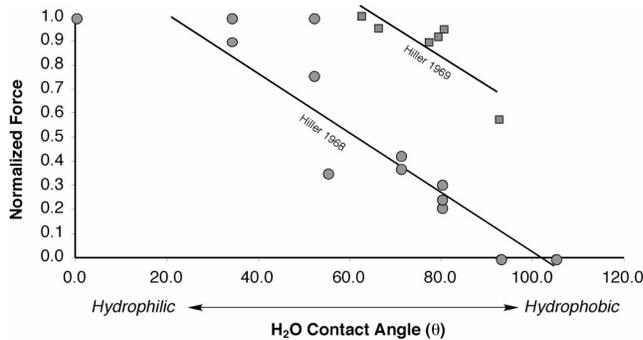An alternative mechanism is that geckos adhere by

FIG. 3. Normalized force versus surface polarity (measured by water droplet contact angle, θ) from Hiller (1968, 1969). Hiller's (1968) measurements of whole geckos on surfaces of varying polarity (circles) showed a correlation between polarity and force (y = −0.012x + 1.26; R^2 = 0.85). In a separate study, Hiller (1969) found a weakly significant correlation between force and surface polarity on polyethylene films modified with corona discharge (squares; y = −0.012x + 1.79; R^2 = 0.69).

van der Waals interactions alone (Stork, 1980; Autumn et al., 2000). This is a very intriguing hypothesis since van der Waals interactions are the weakest of all intermolecular forces, but also the most universal. An adhesive utilizing these very weak interactions would be capable of sticking to nearly any natural surface. However, a vast number of these interactions would have to operate simultaneously in order to generate a significant amount of force. That is, there must be a large, real contact area between the organism and the substrate. The highly branched setae on gecko toes may be suited for maximizing contact area. If this is the case, setal morphology would have a greater effect on force of adhesion than surface chemistry of the seta or substrate. In other words, the geometry of the adhesive would be more important than the chemistry.

The strength of van der Waals attractions is highly dependent on the distance between surfaces, increases with the polarizability of the two surfaces, and is not directly proportional to surface polarity (Israelachvili, 1992). The observation that geckos cannot adhere to Polytetrafluoroethylene (PTFE; Hiller, 1968) is consistent with the van der Waals hypothesis, since PTFE is only weakly polarizable.

The following equation estimates the force (per area) due to van der Waals interactions between two planar surfaces (Israelachvili, 1992):

$$\text{Force per area (N m}^{-2}) = \frac{A}{6\pi D^3} \qquad (1)$$

In this equation, A represents the Hamaker constant, a function of the volume and polarizability of the molecules involved. For most solids and liquids, the Hamaker constant lies between 4×10^{-20} and 4×10^{-19} J, so it cannot affect an estimate of force by more than a power of ten. Far more important to the estimate is the separation distance (D) between the two surfaces since force of adhesion scales inversely with the third power of this distance. This implies that at small sep-

arations, strong forces of adhesion can occur, but for each power of ten increase in the distance, the force of adhesion decreases 1,000 fold. Assuming the Hamaker constant to be of a typical value (1×10^{-19} J), and the spatular surface area to be approximately 2×10^{-14} m^2 (Ruibal and Ernst, 1965; Williams and Peterson, 1982; personal observation) the force of adhesion of a single seta with 100 spatulae increases from 11 μN to 11 mN as the separation distance decreases from 1 nm to 0.1 nm. The actual force of adhesion of a single seta can reach almost 200 μN (Autumn et al., 2000). This would correspond to a separation distance of 0.38–0.81 nm (assuming 100–1,000 spatulae/seta). The actual magnitude of this gap distance remains unknown.

Van der Waals and capillary adhesion are not mutually exclusive mechanisms. Although water at the seta-substrate interface would increase the gap distance and therefore reduce the strength of van der Waals adhesion, the diameter of a single water molecule (0.3 nm) remains well within the range of van der Waals attraction (Israelachvili, 1992). Thus, in the presence of a thin film of water, it is conceivable that the two mechanisms are working in tandem. As more layers of water molecules intervene, however, resistance to shear forces across the fluid is provided solely by its viscosity (Baier et al., 1968). Water does not have a high viscosity and therefore cannot withstand high shear forces. Therefore, capillary forces are strong in the normal direction and weak in the parallel direction, whereas the opposite is true of setal adhesion. Empirically, setae have demonstrated stronger resistance to shear forces than to normal forces (Autumn et al., 2000), suggesting that if capillary adhesion occurs, the films involved would have to be relatively thin.

The extent to which a thin film of water will form over the available interfacial area is dependent on the relative vapor pressure. At extremely low humidity, capillary adhesion will be weak due to lack of adsorbed water on substrates. At high humidity, water begins to saturate the interstices of rough surfaces, acting as a lubricant (Israelachvili, 1992). This can be described as the sand castle effect: one cannot build a sand castle out of sand that is either very dry or very wet. Dry sand does not adhere because the wetted interfacial area is too low. Very wet sand does not adhere because the radius of the water meniscus between particles approaches the size of the particle itself, and capillary forces decline toward zero (Israelachvili, 1992). If geckos were to rely solely on capillary adhesion for attachment, setal function could be constrained by relative humidity of the habitat. However, since pad-bearing gecko species are found in habitats ranging from tropical rain forests to dry, rocky desert, humidity does not seem to have a strong influence on effective adhesion in nature.

A reanalysis of the relationship between water contact angle and gecko adhesion

Since Hiller's (1968, 1969) data correlate the strength of setal adhesion with the polarity of the surface as indicated by the water droplet contact angle (θ; Fig. 3), it is reasonable to consider capillary action a likely mechanism of adhesion. However, recent advances in the understanding of intermolecular surface forces (Israelachvili, 1992) allow us to revisit Hiller's data (Hiller, 1968, 1969) and ask if they support *only* a capillary adhesive mechanism. The adhesion energy (W) between two identical solid surfaces is related to the contact angle (θ) of a liquid droplet on the surface via the Young-Dupré equation, $\gamma_L(1 + \cos\theta) = W$, where γ_L is the surface tension (or energy) of the liquid (L) in units of mN/m (or mJ/m^2). However, if the two adhering surfaces are different materials, as for gecko setae (G) on a substrate surface (S), the interfacial adhesion energy (W_{GS}) bears no simple linear relation to the liquid (water) contact angle. The relationships can now be expressed as, $\gamma_L(1 + \cos\theta_{LG}) = W_{GG}$ and $\gamma_L(1 + \cos\theta_{LS}) = W_{SS}$, and by the thermodynamic relation (Israelachvili, 1992): $W_{GS} = 1/2W_{GG} + 1/2W_{SS} - \gamma_{GS}$, where γ_{GS} is the interfacial tension of the setae-substrate interface, and W_{GG} and W_{SS} are the cohesion energies of setal and substrate materials, respectively. An approximate relation, valid when the two adhering surfaces are nonpolar and interact with each other only via van der Waals dispersion forces, is (Israelachvili, 1992): $W_{GS} = \sqrt{W_{GG}W_{SS}}$. Replacing W_{GG} and W_{SS} with the above equations gives: $W_{GS} = \gamma_L\sqrt{(1 + \cos\theta_{LG})(1 + \cos\theta_{LS})}$, and a correlation between adhesion energy (W_{GS}) and water droplet contact angle on the substrate (θ_{LS}) may be expressed as

$$W_{GS} = \sqrt{\gamma_L W_{GG}(1 + \cos\theta_{LS})} \qquad (2)$$

Thus, for $\gamma_L = 72$ mJ/m^2 (for water) and $W_{GG} = 60$ mJ/m^2 (a typical value for a nonpolar van der Waals solid) we theoretically expect W_{GS} to vary monotonically from $W_{GS} \approx 93$ mJ/m^2 for $\theta_{LS} = 0°$ to $W_{GS} \approx 66$ mJ/m^2 for $\theta_{LS} = 90°$ to $W_{GS} = 0$ for $\theta_{LS} = 180°$. This correlation, however, is expected to hold *only* when the substrate surface is hydrophobic ($\theta > 60°$). A reanalysis of Hiller's data (Hiller, 1968, 1969; Fig. 4) using Equation 1 in fact supports the van der Waals hypothesis with a strong correlation between force and adhesion energies for $\theta > 60°$.

Testing the van der Waals and capillary adhesion hypotheses

To test directly whether capillary adhesion or van der Waals force is the primary mechanism of adhesion in geckos, we measured the hydrophobicity of the setal surface, and measured adhesion on two polarizable semiconductor surfaces that varied greatly in hydrophobicity (Autumn *et al.*, 2002). We measured the parallel force of single gecko toes on a gallium arsenide (GaAs) semiconductor surface that is highly hydrophobic ($\theta = 110°$). As a control, we measured parallel
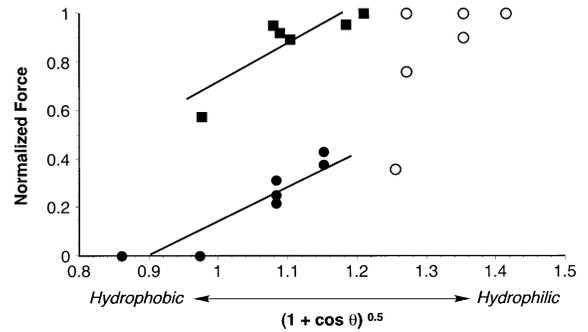

FIG. 4. Reanalysis of Hiller's previous measurements of geckos adhering to surfaces of varying surface polarity (θ water droplet contact angle of surface; Hiller, 1968, 1969). Normalized force versus adhesion energy approximated by $\sqrt{(1 + \cos\theta)}$. The apparent correlation between force and θ (Fig. 3) suggested that adhesion in geckos was a function of θ. It is now known (Israelachvili, 1992) that if one of two adhering surfaces is hydrophilic ($\theta < 60°$; open circles), their adhesion energy bears no simple relationship to the liquid (water) contact angle of either surface. However, for hydrophobic surfaces ($\theta > 60°$) adhering by van der Waals forces (see Eqn. 2) the adhesion energy is approximately proportional to $\sqrt{(1 + \cos\theta)}$. Thus, the correlations between force and adhesion energy for hydrophobic surfaces (closed circles: y = 1.41x − 1.27; R^2 = 0.83; closed squares: y = 1.60x − 0.88; R^2 = 0.73) support the hypothesis that geckos adhere by van der Waals forces.

force on the strongly hydrophilic ($\theta = 0°$) silicon dioxide (SiO$_2$) semiconductor surface. We also compared the perpendicular force of single isolated gecko setae on hydrophilic (SiO$_2$, $\theta = 0°$) and hydrophobic (Si, $\theta = 81.9°$) micro-electro-mechanical-systems (MEMS) force sensors. If wet, capillary adhesive forces dominate, we expected a lack of adhesion on the strongly hydrophobic GaAs and Si MEMS surfaces. In contrast, if van der Waals forces dominate, 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 SiO$_2$ semiconductor and MEMS control surfaces.

We showed that tokay gecko setae are strongly hydrophobic (160.9°; Autumn *et al.*, 2002), probably a consequence of the hydrophobic side groups of ß-keratin (Gregg and Rogers, 1984). Parallel stress of live gecko toes on GaAs and SiO$_2$ semiconductors was not significantly different, and adhesion of a single gecko seta on the hydrophobic and hydrophobic MEMS cantilevers differed by only 2%. These results reject the hypothesis that water contact angle (θ) of a surface predicts attachment forces in gecko setae, as suggested by Hiller (1968, 1969), and are consistent with our reanalysis (above). Since van der Waals force is the only mechanism that can cause hydrophobic surfaces to adhere in air (Israelachvili, 1992), the GaAs and hydrophobic MEMS semiconductor experiments provide direct evidence that van der Waals force is the mechanism of adhesion in gecko setae, and that water-based capillary forces are not significant.

CONCLUSION AND FUTURE DIRECTIONS

Gecko setae are a novel type of adhesive in that the strength of adhesion depends largely on geometry

rather than on surface chemistry. Many secrets of setal form and function remain: The feet of geckos captured in nature are usually clean (*e.g., Stenodactylus khobarensis*; Russell, 1979), and the possibility exists that gecko setae are actually self-cleaning. We have yet to uncover the design principles underlying the variation in, and multiple convergent evolutions of setal, scansor, and foot structures in geckos (Russell, 1972, 1976, 1979; Bauer and Russell, 1990), and in convergent setal adhesive systems in anoles (Peterson and Williams, 1981), skinks (Williams and Peterson, 1982), and insects (Gillett and Wigglesworth, 1932; Edwards and Tarkanian, 1970; Nachtigall, 1974; Bauchhenss and Renner, 1977; Hill, 1977; Rovner, 1978; Stork, 1980, 1983; Walker *et al.*, 1985; Wigglesworth, 1987; Roscoe and Walker, 1991; Betz, 1996; Gorb, 1998, 2001; Attygalle *et al.*, 2000; Eisner and Aneshansley, 2000; Koelsch, 2000; Gorb *et al.*, 2001; Gorb and Beutel, 2001; Scherge and Gorb, 2001). It is clear that gecko setae are vastly overbuilt for adhesion to smooth ideal surfaces under static conditions. This may not be the case for natural surfaces, or for dynamic conditions such as for running, jumping, and falling. Characterization of the surfaces and loading regimes seta-bearing animals experience in nature will be necessary before we can address the question of how much of a safety factor exists in the gecko adhesive system. Study of the setal adhesive system requires an extraordinary degree of integration across scales and disciplines—from quantum mechanics to biomechanics— and highlights the benefits of an integrative approach to biology.

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