Gecko Adhesion as a Model System for Integrative Biology, Interdisciplinary Science, and Bioinspired Engineering

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Keywords

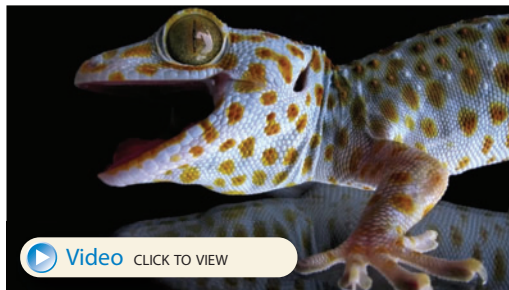geckos, adhesion, morphology, ecology, engineering

Abstract

Geckos possess a superlative climbing adaptation in the form of hierarchical arrays of adhesive nanostructures on the underside of their toes. These structures permit rapid, robust, and reliable adhesion to nearly any substrate during full-speed locomotion. We review the fundamental principles and properties of this system, describe its ecological and evolutionary aspects, and offer our assessment of the field alongside suggestions for future research in this direction.

INTRODUCTION

Over two millennia ago, Aristotle commented on the ability of geckos to "run up and down a tree in any way, even with the head downwards" (Aristotle 1910). How geckos adhere has attracted substantial and sustained scientific scrutiny for over two centuries (Cartier 1872, Dellit 1934, Dewitz 1882, Schmidt 1904, Simmermacher 1884, Wagler 1830). This review focuses on gecko adhesion as a model system for integrative biology, interdisciplinary science, and bioinspired engineering. A robust understanding of how geckos adhere to surfaces has involved the study of an integrated hierarchy of mechanisms at scales ranging from atoms to whole animals. Recent progress in gecko adhesion research has been made by working at the interfaces of biology, physics, and materials science. We review how the gecko adhesive system functions through the integration of intermolecular forces at the atomic scale, contact mechanics at the nanometer scale, a hierarchy of compliant contact elements at the micron and millimeter scales, and locomotion biomechanics at the whole-animal scale. We then identify several promising ecological and evolutionary contexts in which further study of conspicuous patterns of variation would likely yield significant insights about the gecko adhesive system relevant to a broad range of investigators, including biologists, physicists, material scientists, engineers, and others. Recent discoveries of broadly applicable physical mechanisms underlying gecko adhesion (Autumn et al. 2002b, 2006a,c; Hansen & Autumn 2005) led to a rapid expansion of research in biology, physics, materials science, and nanoscience. Remarkably, the study of a humble lizard has deepened our understanding of the fundamental nature of adhesion and friction (Autumn et al. 2000, Gao et al. 2003, Gravish et al. 2010, Jagota & Bennison 2002, Puthoff et al. 2013) and fueled innovations ranging from industrial and biomedical adhesives to climbing robots (Clark et al. 2008, Cutkosky 2006, Sameoto et al. 2008).

The multiscale organization of the adhesive system (see **Video 1**) of the tokay gecko is shown in **Figure 1**. A single seta (often referred to as a fibril) of the tokay gecko is approximately 110 μm in length and 4.2 μm in diameter (Ruibal & Ernst 1965, Russell 1975, Williams & Peterson 1982). Setae are similarly oriented and uniformly distributed on the scansors, creating a fibrillar adhesive surface. Setae branch at the tips into 100–1,000 more structures (Ruibal & Ernst 1965, Schleich & Kästle 1986) known as spatulae. A single spatula consists of a stalk with a thin, roughly triangular end, in which the apex of the triangle connects the spatula to its stalk. Spatulae are approximately 0.2 μm in length and also in width at the tip (Ruibal & Ernst 1965, Williams & Peterson 1982). Although the tokay is currently the best studied of any adhesive gecko species, there are over a

Video 1

Zoom into the tokay gecko's adhesive system from the macro- to nanoscales. For information on the helium ion scanning electron microscopy technique used in this video, see Yang et al. (2011). To view the video, access this article on the Annual Reviews website at **www.annualreviews.org**.
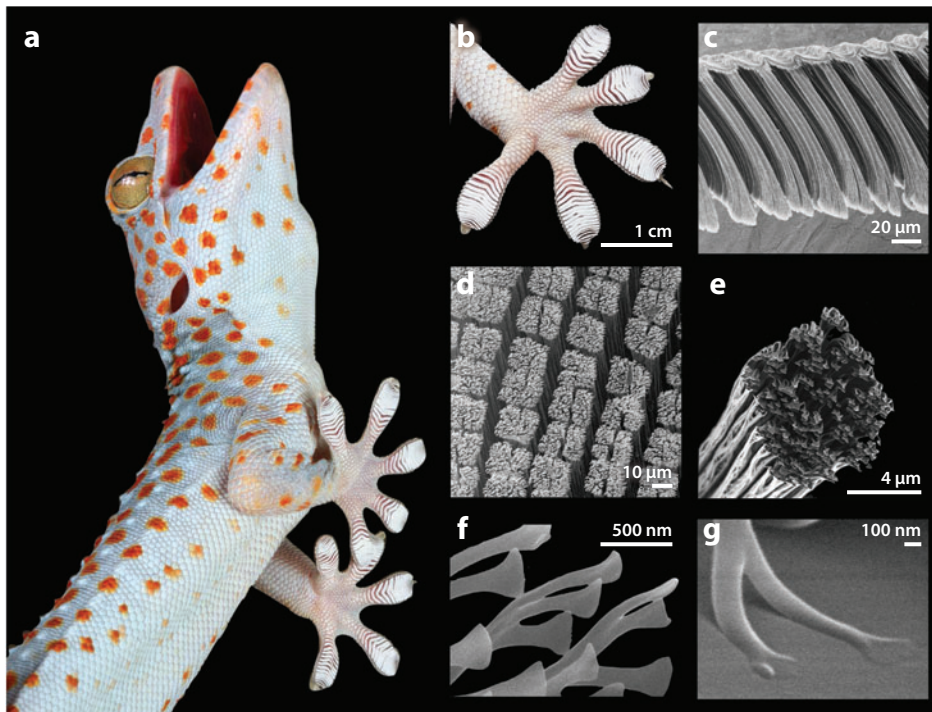
Figure 1

Structural hierarchy of the gecko adhesive system (see also **Video 1**): (*a*) ventral view of a tokay gecko (*Gekko gecko*) climbing a vertical glass surface; (*b*) ventral view of the foot of a tokay gecko, showing a mesoscale array of seta-bearing scansors (adhesive lamellae); (*c*) cross-sectional micrograph through an isolated setal array. The setae are tilted and curve proximally near the tip; (*d*) microscale arrays of setae are arranged in a grid-like pattern on the ventral surface of each scansor. Each diamond-shaped structure is the branched end of a group of four setae clustered together in a tetrad; (*e*) nanoscale array of hundreds of spatular tips branching from a single gecko seta; (*f*) the terminal spatular branches are widened and flattened at the tip; and (*g*) these flat faces interface with the substrate to produce strong attachment.

thousand species (Han et al. 2004) with adhesive toe pads, encompassing an impressive range of morphological variation at the spatula, seta, scansor, and toe levels (Arzt et al. 2003; Autumn & Peattie 2002; Maderson 1964; Irschick et al. 1996; Peterson & Williams 1981; Ruibal & Ernst 1965; Russell 1975, 1981, 1986; Schleich & Kästle 1986; Stork 1983; Williams & 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 & Williams 1981, Ruibal & Ernst 1965), and in scincid lizards of the genus *Prasinohaema* (Irschick et al. 1996, Williams & Peterson 1982). However, much of what is known is based on studies of a single species: the tokay gecko (*Gekko gecko*). The degree of variation in function among species remains an open question, and future studies are likely to yield valuable insights to biologists, material scientists, and engineers alike.

The fibrillar adhesive system of geckos dates back at least 100 Ma, as evidenced by the sophisticated toe pads found in the fossil gecko *Yantarogekko balticus*, a specimen preserved in amber (Arnold & Poinar 2008, Bauer et al. 2005). Geckos diverged from other lizard clades nearly 200 Mya, coming to be one of the most diverse (>1,400 species) groups of extant terrestrial vertebrates in the world. Moreover, the evolution of morphological variation in toe pads and supporting

structures of the integrated system (Russell 2002) has been subject to many repeated independent gains and losses (Gamble et al. 2012; see **Figure 2**). In select systems, we are only beginning to understand how putative environmental factors, such as climate change, are potentially related to gain, reduction, and loss of adhesive toe pads (Lamb & Bauer 2006). As more detailed phylogenetic information becomes available, hypotheses about the ecological and evolutionary circumstances influencing the gain, loss, and variability of toe pads become testable at both broad and narrow taxonomic scales.

Functional studies examining the relationship between variation in toe pad morphology and ecological factors, such as species habitat preferences and geographic distribution, predate by at least 30 years our current understanding of both the detailed mechanics of fibrillar adhesives and well-resolved phylogenetic hypotheses for relationships among and within major gecko clades (Irschick et al. 1996; Russell 1975, 1979; Russell & Bauer 1988a,b). Most of this literature was concentrated in morphological and anatomical journals, and much of the data and analyses primarily interpreted anatomy and related function, as they revealed hypotheses about phylogenetic relationships (Russell 1979). However, research on the gecko adhesive system entered a new phase between the years 2000 and 2012, marked by breakthroughs in instrumentation enabling measurements of the adhesive force of a single gecko seta (Autumn et al. 2000) as well as advances in understanding locomotion biomechanics, contact mechanics, and intermolecular forces.

Over the past 15 years, there has been a rapid accumulation of publications concerning the mechanistic basis and functional-morphological units of the gecko adhesive system at millimeter, micron, and nanometer scales literally probing intermolecular-scale mechanics at the contact interface. The keywords "gecko adhesion" return just five citations in 2001 from the Web of Knowledge™ database. By 2005, there were nearly 100 publications accumulating per year, with corresponding citations rising exponentially to approximately 3,000 per year by 2012. By and large, studies to date are comprised of analyses at the micro- and nanoscale elucidating the mechanics of adhesion, especially as such knowledge might relate to design and fabrication of gecko-inspired synthetic adhesives (GSAs). Currently, a wide variety of materials and fabrication techniques have successfully equaled or exceeded the performance capacity of the gecko adhesive system in a single dimension: to generate large adhesive forces with relatively low pull-off forces (Hu & Xia 2012, Kwak et al. 2011), at least in laboratory-scale production.

Interestingly, advances in our understanding of functional mechanics of gecko adhesion at multiple length scales have proceeded nearly in parallel with studies of gecko phylogenetic relationships based on molecular data sets. In contrast to long-standing but occasionally problematic phylogenies based on morphological data, molecular phylogenies suggest multiple independent origins and high lability of the gecko adhesive system (Feng et al. 2007, Gamble et al. 2012, Han et al. 2004). These two research streams (functional morphology and phylogenetic), largely carried out independently, now make it feasible to link functional morphology at all length scales with ecological performance studies within an evolutionary biogeographic framework. Such an integrative approach (Autumn et al. 2002a, Irschick et al. 2013) is likely to lead to new insights not only about the history and basis of success of the gecko adhesive system but also to extrapolation for new approaches in bioinspired design, fabrication, and application of GSAs.

Most of our understanding about the structure and function of the gecko adhesive system has arisen from highly focused work mostly in well-controlled laboratory settings. We expect the next wave of findings to come from work that expands the focus to include ecological and evolutionary questions, especially as posed by studies of geckos in their natural environments. We hope our review helps reveal the very broad platform of both basic and applied study provided by this extraordinary biological system, including opportunities for synthesis and integration across physics, chemistry, biology, engineering, materials science, and design.
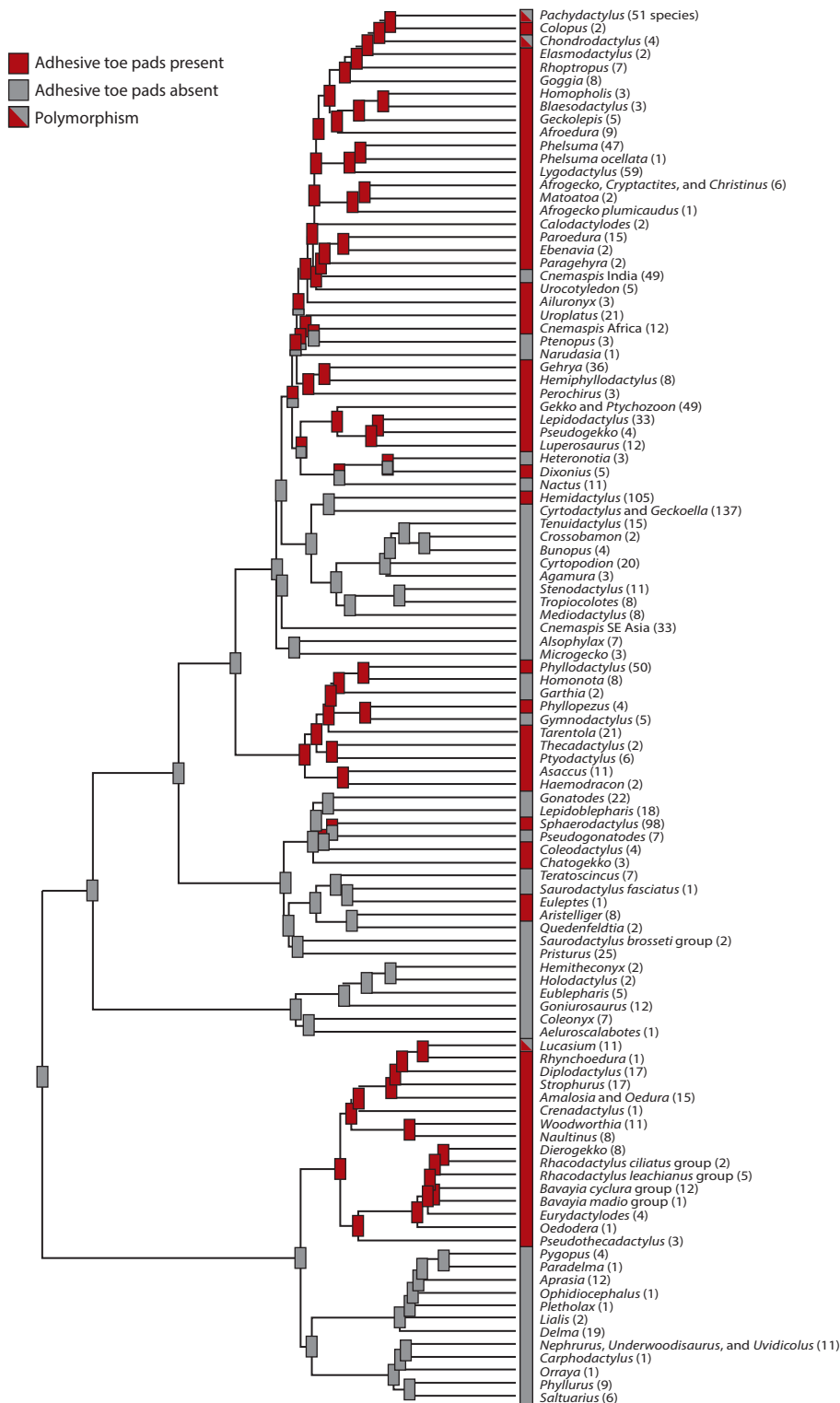
Adhesive toe pads present
Adhesive toe pads absent
Polymorphism

Pachydactylus (51 species)
Colopus (2)
Chondrodactylus (4)
Elasmodactylus (2)
Rhoptropus (7)
Goggia (8)
Homopholis (3)
Blaesodactylus (3)
Geckolepis (5)
Afroedura (9)
Phelsuma (47)
Phelsuma ocellata (1)
Lygodactylus (59)
Afrogecko, Cryptactites, and *Christinus* (6)
Matoatoa (2)
Afrogecko plumicaudus (1)
Calodactylodes (2)
Paroedura (15)
Ebenavia (2)
Paragehyra (2)
Cnemaspis India (49)
Urocotyledon (5)
Ailuronyx (3)
Uroplatus (21)
Cnemaspis Africa (12)
Ptenopus (3)
Narudasia (1)
Gehrya (36)
Hemiphyllodactylus (8)
Perochirus (3)
Gekko and *Ptychozoon* (49)
Lepidodactylus (33)
Pseudogekko (4)
Luperosaurus (12)
Heteronotia (3)
Dixonius (5)
Nactus (11)
Hemidactylus (105)
Cyrtodactylus and *Geckoella* (137)
Tenuidactylus (15)
Crossobamon (2)
Bunopus (4)
Cyrtopodion (20)
Agamura (3)
Stenodactylus (11)
Tropiocolotes (8)
Mediodactylus (8)
Cnemaspis SE Asia (33)
Alsophylax (7)
Microgecko (3)
Phyllodactylus (50)
Homonota (8)
Garthia (2)
Phyllopezus (4)
Gymnodactylus (5)
Tarentola (21)
Thecadactylus (2)
Ptyodactylus (6)
Asaccus (11)
Haemodracon (2)
Gonatodes (22)
Lepidoblepharis (18)
Sphaerodactylus (98)
Pseudogonatodes (7)
Coleodactylus (4)
Chatogekko (3)
Teratoscincus (7)
Saurodactylus fasciatus (1)
Euleptes (1)
Aristelliger (8)
Quedenfeldtia (2)
Saurodactylus brosseti group (2)
Pristurus (25)
Hemitheconyx (2)
Holodactylus (2)
Eublepharis (5)
Goniurosaurus (12)
Coleonyx (7)
Aeluroscalabotes (1)
Lucasium (11)
Rhynchoedura (1)
Diplodactylus (17)
Strophurus (17)
Amalosia and *Oedura* (15)
Crenadactylus (1)
Woodworthia (11)
Naultinus (8)
Dierogekko (8)
Rhacodactylus ciliatus group (2)
Rhacodactylus leachianus group (5)
Bavayia cyclura group (12)
Bavayia madio group (1)
Eurydactylodes (4)
Oedodera (1)
Pseudothecadactylus (3)
Pygopus (4)
Paradelma (1)
Aprasia (12)
Ophidiocephalus (1)
Pletholax (1)
Lialis (2)
Delma (19)
Nephrurus, Underwoodisaurus, and *Uvidicolus* (11)
Carphodactylus (1)
Orraya (1)
Phyllurus (9)
Saltuarius (6)

Figure 2

Evolutionary gain and loss of adhesive toe pads in geckos inferred from a molecular phylogeny based on nuclear and mitochondrial genes (modified from Gamble et al. 2012 with permission). Note that adhesive toe pads are the derived condition and that gain and loss has occurred multiple times across the clade (see Gamble et al. 2012 for a detailed hypothesis based on parsimony).

Table 1   Clinging capabilities of some gecko species (from Irschick et al. 1996)[a]

Species	n	Body mass (g)	Pad area (mm²)	Clinging force (N)
Hemidactylus frenatus	15	3.0 ± 0.21	25.3 ± 1.34	1.0 ± 0.08
Hemidactylus turcicus	5	2.1 ± 0.28	21.5 ± 1.69	0.8 ± 0.24
Gehyra oceanica	11	7.9 ± 0.50	69.1 ± 3.22	4.7 ± 0.31
Gehyra mutilata	9	1.7 ± 0.09	18.1 ± 1.17	0.8 ± 0.04
Lepidodactylus lugubris	8	1.4 ± 0.05	12.1 ± 0.58	0.9 ± 0.09
Gekko gecko	6	43.4 ± 1.48	227.1 ± 10.81	20.04 ± 1.33

[a]Error estimates are the standard error of the mean.

ADHESIVE PROPERTIES OF GECKO SETAE AND THEIR UNDERLYING MECHANISMS

Animal-Level Adhesion Overview

The adhesive toe pads of many gecko species are capable of supporting the animals on inclined, vertical, and even inverted surfaces. **Table 1** contains experimental data on gecko body mass, adhesive pad area, and ultimate clinging force. The most impressive entry is that of the tokay gecko (*G. gecko*), whose body mass exceeds 40 g and whose clinging force capability exceeds its body weight by a factor of ≈50. Toe pad area is correlated with clinging ability (Irschick et al. 1996). The concept is complicated somewhat by the fact that there is tremendous variation in the morphological characteristics of the toe pads and setal arrays. **Table 2** contains data on the seta-level characteristics of eight species. The foot of the tokay gecko bears approximately 14,000 setae mm⁻². This setal density is roughly half that of the mourning gecko, *Lepidodactylus lugubris*, though the clinging force/pad area ratios for these species are similar. Peattie & Full (2007) tested scaling hypotheses related to spatular density and found little to indicate that there was any relationship between density and the body mass of the animal. Taken together, these two studies suggest that increased demands on clinging capacity with increasing body size can be met in several nonmutually exclusive ways both within and among species.

Despite these morphology/performance complications, there are some basic mechanical truths that can be derived from the above data. From a whole-animal perspective, a single *G. gecko* seta should produce an average clinging force of ∼10 μN, corresponding to an average shear stress (force parallel to the contact surface) of 0.2 N·mm⁻². When this force is further divided among the terminal branches of the hierarchical setae (≈500 spatulae per seta), we obtain 10 nN per

Table 2   Essential setal morphology data from some gecko species (from Peattie 2007)

Species	Setal length (μm)	Setal width (μm)	Setal density (mm⁻²)
Gehyra mutilata	78	2.8	31,000
Gehyra oceanica	86	2.3	24,000
Lepidodactylus lugubris	62	2.4	24,000
Gekko gecko	110	4.0	14,000
Pachydactylus bibronii	120	3.5	16,000
Phelsuma madagascariensis	82	3.0	28,000
Rhacodactylus leachianus	52	1.0	110,000
Tarentola mauritanica	116	4.0	11,000

spatula. This result gives us some indication of the basic scale of the forces that operate in the gecko adhesion system. The essence of the geckos' adhesive capabilities is the multiplicative effect produced when a vast number of small, individually adhesive nanostructures are deployed at an interface simultaneously.
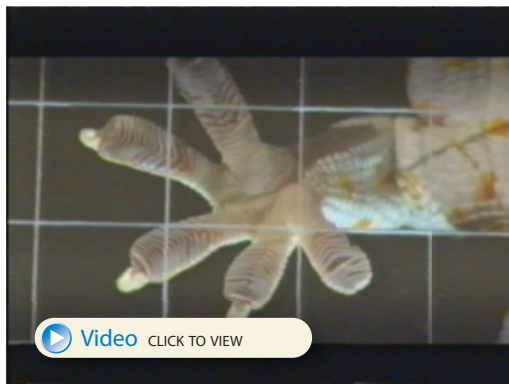
Anisotropic Attachment

How the gecko deploys this complex, multiscale system effectively has been revealed by microscopic measurements. Using a microelectromechanical force sensor, Autumn and collaborators (Autumn et al. 2000) measured the adhesive and shear forces produced by an isolated gecko seta in a number of different configurations. Simply pressing a seta into the surface and removing it vertically failed to generate adhesive forces. However, when the seta was placed in contact with the force sensor and a suite of mechanical conditions was met, strong adhesion and friction forces resulted. The mechanical requirements (see **Video 2**) for adhesion of an isolated tokay gecko seta were (*a*) a slight vertical load, (*b*) a micrometer-scale drag parallel to the surface, (*c*) a drag in the direction of curvature of the seta, and (*d*) maintenance of the setal shaft at an angle below 30°. This "load-drag-pull" attachment pathway produced shear forces of ∼40 µN, six times the force predicted by whole-animal measurements above. The small normal preload force combined with a 5-µm proximal shear displacement yielded a very large shear force of 200 µN, 32 times the force predicted by whole-animal measurements. Furthermore, these significant forces could only be maintained if the angle α between the setal stalk and the substrate was less than 30°.

The preload, extension, and drag steps were necessary to initiate significant adhesion in isolated gecko setae. This result is consistent with the load dependence and directionality of adhesion

Mechanically controllable adhesion
Autumn+ 2000 *Nature*
unloaded "default" state
100 µm
1. Preload
2. Drag
3. Perpendicular Pull
▶ Video CLICK TO VIEW
adhered state
detachment

Video 2

Video and animation illustrating the mechanical requirements for attachment and detachment of a single isolated gecko seta (Autumn et al. 2000). The video shows a single seta glued to a minutien pin. The vertical bar at the left side is a 25-µm aluminum wire force gauge. Initial attempts to adhere a single isolated seta to a surface failed because we simply touched the tip of the seta into the surface and pulled away vertically. Instead, a slight preload force, followed by a micrometer-scale drag along the direction of curvature of the seta (i.e., toward the rear of the animal) switches the spatulae from their default unloaded state to the adhered state. The seta can now sustain a perpendicular pull because the adhesive van der Waals forces at the spatula tips resist detachment. Detachment occurs when the angle between the setal shaft and the surface exceeds 30°. This experiment illustrates the mechanical program for attachment and detachment required for controllable adhesion in gecko setae. To view the video, access this article on the Annual Reviews website at **www.annualreviews.org**.

Video 3

Toe peeling (digital hyperextension) during climbing by a tokay gecko. The motion of gecko toes is superficially similar to that of peeling tape. However, because adhesion of gecko toes is governed by the micro-mechanics of their setae, a tape peeling model can be rejected (Autumn et al. 2006a). In contrast to the peeling of tape, gecko toes function by "frictional adhesion": Pull-off forces increase linearly with shear load and detach when the angle of the resultant force exceeds 30° relative to the surface. To view the video, access this article on the Annual Reviews website at **www.annualreviews.org**.

observed at the whole-animal scale by Haase (1900) and Dellit (1934). The load-pull-drag attachment pathway and critical detachment angle α also provide an explanation for the role played by hyperextension of the gecko's toes (see **Video 3**) during locomotion (Autumn et al. 2006b, Russell 1975, Wagler 1830). The "roll on" attachment motion directs the setal-bearing scansors along the load-pull-drag pathway and establishes strong adhesion and shear forces. The "roll off" motion directs the angle of the setal arrays on each scansor toward values $\alpha > 30°$, and rapid, spontaneous detachment results.

"Overdesigned" Adhesion System

If all 6.5 million setae on the toes of a tokay gecko could be deployed simultaneously, a clinging force of $\approx$1,300 N (133-kg force) would result; this is enough to support the weight of two humans. This calculation suggests that a tokay gecko only needs to have $\approx$3% (roughly one scansor's worth) of its setae deployed to generate the 20 N of force reported in **Table 1**. Only 0.04% of the setae are required to support its 50-g mass on a wall. In engineering terms, gecko feet possess a factor of safety of at least 20 N/0.5 N = 40. However, it is unlikely that all setae are able to contribute to the animal's clinging ability simultaneously. First, the proportion of spatulae capable of attachment may be greatly reduced on rough surfaces (particularly whose feature sizes are on a similar scale as the spatulae or setae). Second, on dusty or exfoliating surfaces, attachment will be inhibited and contamination of the adhesive toe pads can produce temporary impairment of adhesive performance. Third, in certain dire circumstances, such as during extreme weather events, combat, or digit loss, geckos may experience an effective reduction in the factor of safety (Autumn & Peattie 2002, Hecht 1952, Irschick et al. 2006, Vinson & Vinson 1969).

When geckos fall or leap between perches they require rapid and failsafe reattachment (Pianka & Sweet 2005, Vitt & Zani 1997), and it is under such circumstances that the gecko adhesive system is pushed to its limit. Consider a 50-g gecko falling from rest. After it has fallen 10 cm, it will be moving at 0.44 m·s^{-1}. If a single foot is capable of producing 5 N of friction force, attachment of this foot can bring the falling gecko to rest after 0.005 s. During this interval, the gecko will have

slid 1.1 cm down the face of the arresting surface. Under these reasonable physical assumptions, recovering from a brief fall requires 50% of the shear capacity of one foot (based on whole-animal measurements), which is still less than 4% of the theoretical maximum shear stress possible (based on single seta measurements) (Autumn & Peattie 2002). A recently discovered dynamic response to sliding in gecko setae may aid in preventing and recovering from falls (Gravish et al. 2010, Puthoff et al. 2013).

Detachment

The surprisingly large forces indicated by single-seta measurements raise the question of how geckos manage to detach their feet in just 15 ms with no measurable detachment forces or significant displacement of their center of mass (Autumn et al. 2006b). The answer to this question is related to the setal inclination angle α. Simply increasing the angle that the setal shaft makes with the substrate to 30° causes spontaneous detachment (Autumn et al. 2000). The forces produced in the gecko's setal arrays have two components. The first is an in-plane (or shear) force $F_\parallel$, and the other is an out-of-plane adhesion (or normal) force $F_\perp$. The mechanics of detachment (see **Video 3**) are superficially similar to those of tape peeling (Kendall 1975), but there are crucial differences. A piece of tape is pulled with a force F at an angle α with respect to the surface it is stuck to, $F_\perp = -F \sin \alpha$ and $F_\parallel = F \cos \alpha$. According to the tape-peeling model, there is a critical angle α^* (alpha star) at which peeling/detachment occurs for a given force F. This critical angle depends on the surface energy, the elastic modulus of the tape, and the tape geometry. The implication of this theory is that the maximum pull-off force occurs when a positive shear force is present ($\alpha^* < 90°$); however, continued increase of shear force results in decreased pull-off force resulting from elastic stretching of the film.

In contrast to tape peeling, tokay gecko setal arrays exhibit pull-off forces that increase linearly with shear load (Autumn et al. 2006a). Furthermore, as we discovered earlier in studies of single isolated setae, gecko arrays cannot sustain any pull-off force in the absence of shear, as peeling tape can. Tape is tacky and resists 90° pull-off, but gecko setae detach spontaneously when lifted vertically. Gecko adhesion obeys principles that have more in common with fundamental friction laws (Autumn et al. 2006a). In Coulombic friction, the friction force obtained is proportional to the applied normal load, or $F_\parallel \leq -\mu F_\perp$, where μ is the coefficient of friction. Tokay gecko setal arrays obey a criterion whereby the apparent adhesive force $F_\perp$ is determined by the in-plane (friction) component $F_\parallel$, i.e., $F_\perp \leq -F_\parallel \tan \alpha^*$. For the tokay gecko we have $\alpha^* = 30°$. Because $F_\parallel$ has an upper limit, the value at which sliding initiates, $F_\perp$ is necessarily limited. This kind of inverse friction is called frictional adhesion (Autumn et al. 2006a). Example data (see **Videos 4** and **5**) from isolated setal arrays are shown in **Figure 3**.

Unlike tape peeling, frictional adhesion permits a vanishing value of $F_\perp$. This allows a foot to separate from a surface with essentially zero contact forces at the actual instant of detachment. This is exactly the behavior required for rapid locomotion, and it has been confirmed experimentally (Autumn et al. 2006b). Though the frictional adhesion concept was derived from data acquired from tokay geckos and their isolated setal arrays, the same principles have been observed for the giant day gecko, *Phelsuma grandis* (or *Phelsuma madagascariensis*), whose setal architecture is similar to that of *G. gecko* (Hagey et al. 2013), suggesting that this is a general principle of setal function.

Microscopic Mechanism of Gecko Adhesion

The attachment/detachment mechanics of the adhesive setal structures give the gecko climbing system many of its superlative properties, but there are other crucial aspects of the system that

Video 4 and 5

Sample data and videomicroscopy demonstrating anisotropic frictional adhesion in isolated tokay gecko setal arrays (Autumn et al. 2006a). In each video, the upper section shows in side view an array of ~10,000 setae taken from one scansor of a toe. A multiaxis sensor measures the forces acting on the setal array. Nanopositioners move a glass substrate through load, drag, and pull steps. The lower left sections of the videos show the time course of shear (*green*) and normal (*blue*) forces. Positive normal forces represent compression, whereas negative normal forces represent adhesion. The sign of shear force is arbitrary and represents sliding to the left or right. The lower right sections show force space, a plot of shear force on the horizontal axis versus normal force on the vertical axis.

Video 4 shows how gecko setae are slippery, not sticky, when pushed away from the animal, against the direction of curvature of the setae (this is the opposite direction geckos use when they climb). In the lower left, a compression force (*blue line*) develops during the load step. Friction (shear force) is approximately 0.25 of the compression force, as expected for conventional friction of hard dry materials in contact. There is no measurable adhesion when setae are pushed against their curvature: This is the anti-adhesive direction.

Video 5 shows how gecko setae adhere when preloaded and dragged along the direction of curvature of the setae (this is in the same direction geckos use when they climb). In the lower left, the normal force (*blue line*) is compressive initially during the load step, but immediately following the drag step, strong adhesion occurs (negative normal force) and the setae are drawn into tension. Notably, adhesion is sustained even as the setae slide across the substrate. The lower right plot illustrates frictional adhesion: Adhesion is coupled to friction, and the resultant force angle is approximately 30°. Adhesion is controlled by the shear force. During the pull step, shear force decreases, and adhesion returns to zero without the tacky behavior common to conventional adhesive tapes. To view the video, access this article on the Annual Reviews website at **www.annualreviews.org**.

require examination. As noted previously, the contribution of individual spatular contacts to the overall clinging force is around 10 nN per spatula. What, exactly, is the origin of the forces that bind these nanostructures to the surface? This question has been continually revisited throughout the history of research on these animals but resolved conclusively only recently.

The prevailing opinion on the matter is historically nonuniform, and explanations, such as adhesive secretions (Dewitz 1882), suction (Gennaro 1969, Simmermacher 1884, Wagler 1830), electrostatic attraction (Schmidt 1904), microinterlocking (the "climber's boot" hypothesis) (Dellit 1934, Mahendra 1941), and strong friction (Hora 1923), have been advanced. All these explanations have been dismissed credibly. Micrographic studies of gecko feet revealed no secretory glands (Cartier 1872, 1874; Simmermacher 1884), and inverted locomotion is not possible via a frictional mechanism, no matter how strong. Suction effects cannot explain the sustained adhesion in a vacuum (Dellit 1934) nor can an apparent adhesive stress that exceeds one atmosphere (Autumn & Peattie 2002). Electrostatic adhesion cannot persist in an ionized atmosphere, but geckos remain attached in such environments (Dellit 1934). Finally, microinterlocking is only possible on surfaces
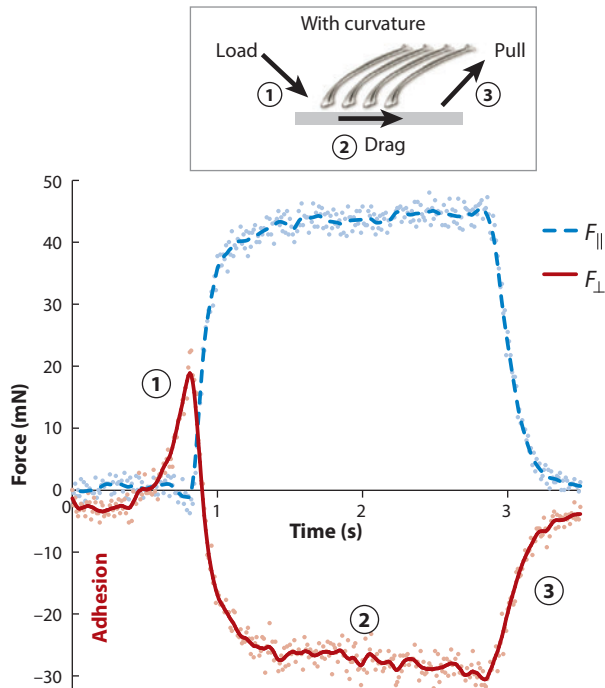
Frictional adhesion in isolated tokay gecko setal arrays (see also **Videos 4** and **5**). Lateral forces generate and sustain adhesion forces during a load-pull-drag attachment sequence. (By convention, adhesive forces are shown negative.)

with some roughness, and geckos can stick to surfaces that are atomically smooth (Autumn et al. 2000).

At the turn of the twentieth century, Haase (1900) noted that attachment is load-dependent and only occurs in one direction: proximally along the axis of the toe. Haase suggested that geckos stick by intermolecular forces ("Adhäsion"), i.e., proximity-dependent forces. Using electron microscopy, Ruibal & Ernst (1965) first described the spatular structures on the terminal branches of the seta (cf. **Figure 1***e*). They concluded that the spatulae were most likely to engage with an underlying surface on their comparatively large, flat faces, an interpretation that emphasizes the forces acting at the interface between two solids. Later, Hiller (Hiller 1968, 1969) revealed that the surface energy of the substrate, rather than its texture, determined the strength of attachment. [A reanalysis of Hiller's results by Autumn & Peattie (2002) reconciled a discrepancy between these and more recent data (Autumn et al. 2002b) on the relationship between gecko adhesion and surface energy.] By explicitly demonstrating that molecular forces were predominantly responsible, Hiller paved the way for the application of modern methods of surface science in studies of gecko adhesion (Autumn & Hansen 2006; Autumn & Peattie 2002; Autumn et al. 2000, 2002b; Huber et al. 2005a).

Van der Waals Forces

Intermolecular forces take many forms, including the forces in chemical bonds and the forces between ions, polar molecules, and nominally nonpolar but polarizable species. Setting aside the

(covalent, ionic, hydrogen) bonding forces, the forces that remain are the dipole-dipole, and van der Waals forces. Van der Waals forces act between nondipolar molecules, between a fixed dipole and a nondipolar molecule, and between a rotating dipole and either another rotating dipole or a nondipolar molecule. What these van der Waals interactions share is an attraction caused by resonant fluctuations in the e-fields of the two molecules. They are referred to as the weak intermolecular forces because the forces scale as 1/(separation distance)[7]. [The electrostatic force between ions, for instance, scales as 1/(separation distance)[2].]

It is the van der Waals forces that provide the essential sticking force between the terminal spatulae and the underlying surface, given the evidence against the other possibilities (Puthoff et al. 2010) and the fact that van der Waals forces are consistent with existing measurements and observations (Autumn & Peattie 2002, Autumn et al. 2000). The van der Waals force is strongly dependent on the distance between objects, increases with the bulk polarizability of the two objects, and is not related directly to surface polarity/chemistry (Israelachvili 1992). For example, the observation (Hiller 1968) that geckos cannot adhere strongly to Teflon® is consistent with the van der Waals mechanism, because Teflon® is only weakly polarizable. The fact that the gecko's adhesion system operates on physical principles that are essentially independent of the chemistry of the two surfaces involved is what makes the gecko's climbing ability universal. As further evidence, consider that the β-keratin that the gecko's setal arrays are primarily composed of is a hydrophobic, i.e., nonpolar, material. Because the van der Waals force is the only force that can cause two hydrophobic surfaces to adhere in air (Israelachvili 1992), geckos should be able to stick to other hydrophobic surfaces, such as the hydrophobic semiconductor gallium arsenide. Indeed, they do (Autumn & Peattie 2002, Autumn et al. 2002b, Huber et al. 2005b, Puthoff et al. 2010).

Capillary Forces

Another effect of intermolecular forces on adhesion worth mentioning is the surface tension of a liquid and the associated capillary effects. Water-based capillarity can contribute to adhesion forces via the Laplace pressure, which is the effective pressure difference between the two different sides of a curved interface between phases, such as that which the water pooled at the interface between bodies might exhibit. This pressure, and hence the resulting force, is proportional to the surface tension of the liquid (Israelachvili 1992). The aforementioned hydrophobic/hydrophobic adhesion experiments (Autumn et al. 2002b) indicated that capillarity is not necessary for the gecko's climbing system to operate, but the presence or absence of the additional capillary/fluid forces would have ramifications for ecological studies and engineered adhesive efforts.

Recent studies have shown that gecko adhesion increases with relative humidity (Niewiarowski et al. 2008) and it has been proposed that surface hydration (capillarity) is important (Huber et al. 2005b) or even necessary (Sun et al. 2005) for gecko adhesion. These studies raise a number of questions. The humidity-dependent adhesion forces at low temperatures suggest that setae must be hydrophilic, despite evidence that water droplets do not wet gecko feet and roll off easily upon tilting, and it is not clear why humidity has a strong influence on the adhesion forces only at low temperatures. Capillary-based interpretations predict that the adhesion forces at fixed humidity should be proportional to the absolute temperature (Kim & Bhushan 2008), and these predictions do not agree with the experimental observations (Huber et al. 2005b, Niewiarowski et al. 2008). Resolution of these questions will likely require examination of the manner in which water interacts with the substrate and seta at the nanoscale level.

A partial resolution of these questions was provided by Puthoff et al. (2010), who confirmed that contact forces increase with humidity in isolated gecko setal arrays but not because of capillary effects. Contrary to the predictions of a capillary mechanism, contact forces and humidity

effects were similar on hydrophobic and hydrophilic substrates. These results do not agree with mechanisms involving capillarity but suggest that the mechanical properties of keratin are affected strongly by humidity. Mechanical testing of single gecko setae and scansor scales showed that as humidity increased, elastic modulus decreased while internal friction increased. These results suggested that capillarity is absent or has a limited role in the adhesion of geckos under humid conditions. Rather, humidity softens and plasticizes setal β-keratin, which increases true contact area and adhesion forces.

PHYSICAL MODELING OF ADHESIVE NANOSTRUCTURES

The Work of Adhesion

Van der Waals forces are the result of atomic-scale interactions between microscopic entities/molecules, but their influence can be expanded to describe interactions between macroscopic bodies. Using mathematical techniques resembling summation or integration, the van der Waals force between bodies of various shapes and spatial configurations can be derived. An important example is the attractive force between two opposing surfaces. This force scales as 1/(separation distance)^3 per unit area of the surfaces. To remove the adjacent surfaces to some large separation distance, an amount of work W, also measured on a per-unit-area basis, is required. W is called the work of adhesion and is recorded in joules per square meter. The work of adhesion is a factor in all adhesion mechanics solutions and reflects the amount of "stick" between macroscopic bodies.

Adhesion Mechanics Modeling of Spatulae

The mechanics of contact and adhesion have a long history, but the more recent results of Johnson, Kendall, and Roberts (JKR) reconsidered classic contact mechanics with surface forces added (Johnson et al. 1971). When the surface energy is introduced, contacting spheres under no applied compressive load can exhibit a nonzero contact area. Furthermore, the tensile force F required to pull them apart can be determined analytically. For a sphere of radius R adhered to a plane, $F_{JKR} = (3/2)\pi RW$. The JKR geometry is shown in **Figure 4a**. The JKR result can furnish a rough estimate of the gecko adhesion force. Taking a value of R similar to the dimensions of a spatula (100 nm) and a value of W typical of van der Waals–only surface forces (50 mJ·m^{-2}), the predicted pull-off force is $F_{JKR} = 23.6$ nN. This value is approximately twice that of the estimate from the animal-level forces, as well as twice that of the value measured directly using atomic force microscope techniques (Huber et al. 2005a), though it is positioned at the correct order of magnitude.

Spatulae may also be modeled as nanoscopic strips of adhesive tape (Hansen & Autumn 2005, Huber et al. 2005a, Spolenak et al. 2005). Using the approach of Kendall (1975), $F_{peel} \approx Wb/(1 - \cos\theta)$, where b is the width of the spatula, θ is the angle at which the tape is pulled, and we assume there is negligible elastic energy storage in the spatula. The peel geometry is shown in **Figure 4b**. This approach provides richer mechanics than those of the JKR model, because it incorporates a distinct dependence on the detachment direction. The peel zone model of adhesion is an extension of the Kendall peel model that places additional emphasis on the nanometer-scale aspects of adhesion (Pesika et al. 2007, Tian et al. 2006), namely, the influence of the curvature of the peeling film in the region over which intermolecular forces act. The peel zone model predicts $F_{peel} \approx 2Wb\theta/\pi$ $(1 - \cos\theta)\sin\theta$. Note that, when $\theta = 90° = \pi/2$ rad, the result is the same as for the Kendall solution. Also, as θ becomes small, F increases rapidly. Using a value of $W = 50$ mJ·m^{-2} and

a Sphere on plane (JKR) model   **b** Thin-film peel model

$$F_{JKR} = \frac{3}{2}\pi RW$$

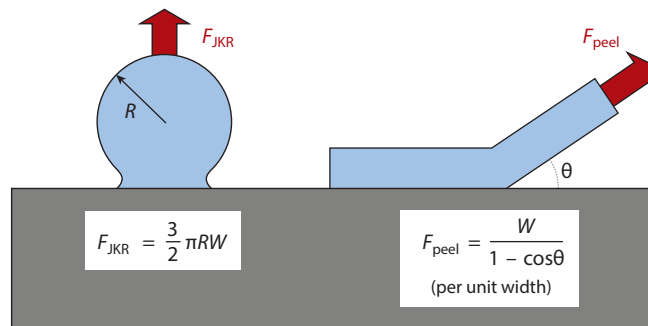$$F_{peel} = \frac{W}{1 - \cos\theta}$$

(per unit width)

Figure 4

Basic adhesion mechanics models. (*a*) The Johnson-Kendall-Roberts (JKR) model describes the force required to detach an adhered sphere of radius *R*. (*b*) The thin-film peel model describes the force at which an adhered film, pulled at an angle θ, will detach. Both models involve the work of adhesion (*W*).

$\theta = 90°$, the peel models predict a spatular width of $b = 200$ nm for $F_{peel} \sim 10$ nN, which is consistent with the actual dimension (Autumn et al. 2000, Rizzo et al. 2006, Ruibal & Ernst 1965).

Empirical measurements of spatular adhesion (Huber et al. 2005a) suggest that each spatula adheres with approximately 10 nN force when pulled at a peel angle of 90°. At ~500 spatulae per seta, these data predict a setal adhesive force of 5 μN. We know from the experiments of Autumn et al. (2000), however, that single-seta forces exceed 40 μN. The discrepancy arises because the detachment pathways in the spatula- and seta-level experiments are different. Pull-off in the single-spatula measurements was vertical, and the tape-peeling mechanics indicate that this force represents a lower bound. The tape-peeling models indicate large forces at shallow detachment angles, and a peel angle of <30° is required to account for the 10× difference in the spatular and setal force measurements. Furthermore, these detachment conditions are very likely those represented in the whole-animal clinging force measurements, because those measurements were made by dragging on the animal rather than lifting it.

STRUCTURE/PROPERTIES/PERFORMANCE RELATIONSHIPS

Setal Development, Structure, and Arrangement

The adhesive setae of geckos are highly specialized keratinous epidermal derivatives that develop on the underside of the gecko's toe pads (Maderson 1964) and in some species on the underside of the tail (Bauer 1998). They are formed during the maturation of the outermost layer of epidermal cells in the skin (Alibardi 2002, Maderson 1964). Setae are their full length and are exposed to the exterior when the old epidermal layer of the skin is shed. The arrangement of the setae on the outer, cornified layer of tissue shows considerable variation. Setae are sometimes grouped into square arrangements of four fibrils, though many species have a more uniform distribution (Peattie 2007). Their branching depths are typically in the range of 4–6 bifurcations. Given these different architectural parameters—length, diameter, spacing, grouping, and branching depth—a wide variety of setal-array morphologies are possible.

Both during (Alibardi & Toni 2005) and after (Rizzo et al. 2006) development, the majority component of the setae is β-keratin. The 8–16-kDa β-keratins found in the setae are somewhat

smaller than those comprising typical lizard scales, and it is presumed that this difference is what makes them suitable for incorporation into long, axially oriented structures (Alibardi & Toni 2005, Toni et al. 2007). The setal arrays also contain a measurable amount of lipid materials (Alibardi et al. 2011, Hsu et al. 2011). Setal β-keratin is quite stiff for a nonmineralized biomaterial, with an elastic modulus in the range of 1–4 GPa (Huber et al. 2008, Peattie et al. 2007, Prowse et al. 2011). At first glance, the material appears to be entirely unsuitable for an adhesive system (Autumn & Hansen 2006) because it is hard and low in surface energy. Indeed, lizard scales, which are also made of β-keratin, are slippery, not sticky. However, when arranged in arrays of freestanding, angled fibers rather than as a bulk solid, the effective elastic modulus of β-keratin is significantly lower (Autumn et al. 2006c, Pesika et al. 2009a) and is similar to that of the polymers used in adhesive tapes. Furthermore, there is evidence that the modulus is a property that is conserved across species, an indication that strictly morphological changes are required to change functionality (Peattie et al. 2007).

Antientanglement, Antifouling, and Self-Cleaning Capabilities of Gecko Setae

Another crucial aspect of gecko adhesive performance is the ability of the adhesive structures to maintain function during repeated use in contaminant-rich environments. There are three principles at work here: antientanglement, antifouling, and self-cleaning. Antientanglement is the intrinsic resistance of the setae to becoming entangled with each other, whereas antifouling and self-cleaning refer to the capability of the setal arrays to resist and shed contamination, respectively. As described above, the failsafe operation of the gecko adhesion system relies on the animal's ability to deploy its millions of setae uniformly and simultaneously, and this ability is impaired if the fibrils become entangled, self-adhere, or are prevented from making intimate contact with the substrate because of the mechanical interference of accumulated contaminants.

Although the setal fibrils are composed of a stiff material, they are quite flexible overall by virtue of their slender geometry. A valid question is, Why do the forces that produce adhesion between the fibrils and the substrate not produce adhesion between adjacent fibrils? This type of fiber entanglement or lateral collapse (Jagota & Bennison 2002) would have a profoundly deleterious influence on setal performance. A partial answer to the question of self-adhesion is that the attractive intermolecular/surface forces are opposed by elastic restoring forces within the fibrils (Sitti & Fearing 2003). Fibrils that are separated by larger distances (measured at the base) must bend to a greater degree to adhere to one another. There are also untested hypotheses that the adhesive forces vary with position on the seta; this would lead to a situation in which the shaft of the fiber is less sticky than the tip.

During locomotion, the gecko's toes contact surfaces that might have a dusting of particles or that may delaminate under small applied loads. These fine contaminants would occupy a similar length scale (0.1–100 μm) as the features on the underside of the toes and may intercalate into the subdigital structures. Furthermore, no gecko has ever been observed grooming its feet, so we are faced with the question of how the adhesive system can operate continuously without becoming hopelessly fouled. The gecko's feet both resist contamination and spontaneously clean themselves (Hansen & Autumn 2005, Hui et al. 2006). The mechanical principle at work here is that the contact forces between the contaminant and the substrate are typically greater than those between the contaminant and the fibers in the setal array. In addition to these quasistatic self-cleaning mechanisms, dynamic effects related to digital hyperextension (Hu et al. 2012) and contaminant rolling (Hui et al. 2006) are possible. **Figure 5** shows how gecko feet and setal arrays recover shear force capability after contamination, alongside images of the contaminated and cleaned
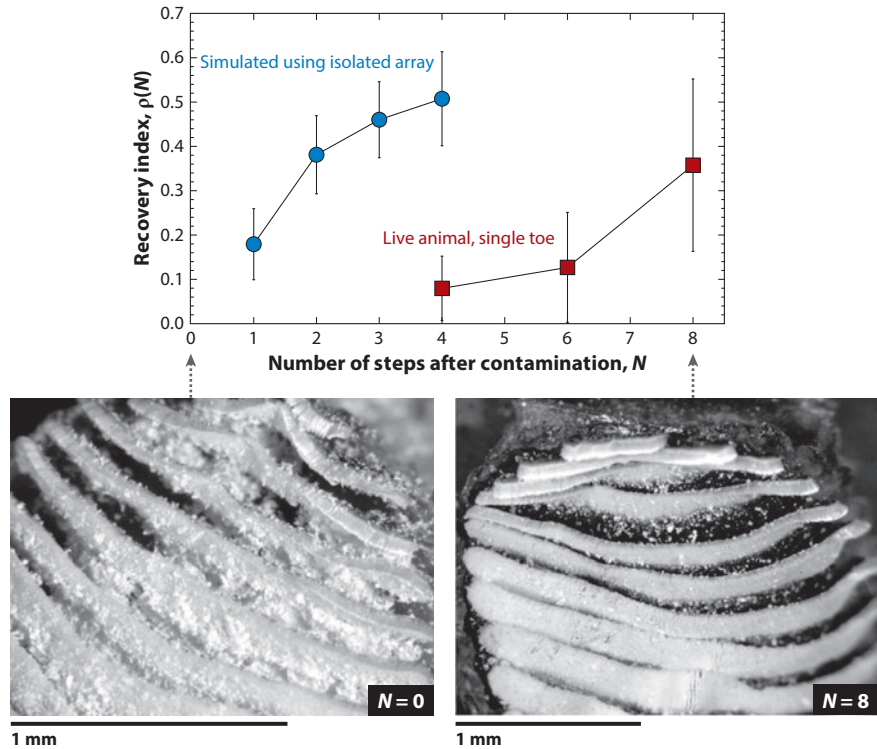
Figure 5

Recovery of shear force in tokay gecko toes and isolated setal arrays after contamination. The recovery index $\rho(N)$ describes how forces recover after a number of real or simulated steps. The images show how contaminants are shed spontaneously from the bottom of the toe after a number of steps on a clean surface.

setal arrays. The recovery index $\rho(N) = (F_N - F_1)/(F_0 - F_1)$ relates the clinging force in the uncontaminated state F_0 to the clinging force F_N after N postcontamination steps.

Rate Effects

The gecko adhesion system also exhibits novel rate-dependent behavior that enables stronger attachment during landing after a fall or leap and allows strong adhesion even while sliding. Ordinarily, dry, hard materials slip more easily as they slide more rapidly, in part due to wear caused by rubbing. Gecko adhesive fibrils are dry and hard, but they become stickier as they slide more rapidly and do not wear out even after sliding as much as 300 meters (Gravish et al. 2010; Puthoff et al. 2010, 2013). Stable frictional adhesion forces in sliding gecko setae may emerge from the stochastic stick-slip of a large population of individual fibrils with high resonant frequencies. Similarly, wear resistance may be a consequence of stick-slip motion that minimizes rubbing. Models suggest that setae are small and stiff enough to recover from detachment and reattach to the surface in under a microsecond. The smooth, rate-dependent sliding observed in gecko setae may be a consequence of millions of uncorrelated stick-slip events. Moreover, each seta is small enough to be affected by thermal energy, raising the possibility that rate-enhancement is in part due to thermal kinetics (Gravish et al. 2010, Puthoff et al. 2013). Interestingly, these results

provided some of the first empirical support for theories of stick-slip dynamics shared by processes ranging from atomic friction and earthquakes.

EFFECT OF BULK WATER ON GECKO ADHESION

Adhesion of gecko setae is reduced in water by about threefold (Pesika et al. 2009b). However, there is only a small reduction in friction when setae are submerged. These results are consistent with a reduction of the magnitude of the van der Waals forces by the aqueous medium and are inconsistent with a capillary mechanism of adhesion (see the section above titled Capillary Forces). When exposed to a water droplet for 20 min, the setal array switches from an ultrahydrophobic Cassie state (Autumn & Hansen 2006), with a contact angle of 160°, to a Wenzel state, in which the array is flooded (Wenzel 1949). This is caused by a subtle but significant change in water droplet contact angle of the bulk keratin surface from 96° to ~86°, suggesting that a shift in the hydrophilic/lyophilic balance occurs, caused by a shift in conformation of amino acid residues at the setal surface (Pesika et al. 2009b) or other types of restructuring of the surface groups of setae (Hsu et al. 2011). Stark and colleagues (Stark et al. 2012) studied the effect of water submersion on the toes of live geckos. Gecko toes are ultrahydrophobic and resist wetting via a plastron of air. After prolonged exposure to water, or when conditions favor transition of the toe pads between the Cassie and Wenzel state, the scansors become flooded as the toe pad is wetted. This substantially reduces the ability of geckos to stick to a hydrophilic glass substrate. The effect of surface water on the clinging ability of whole animals also appears to depend on the surface chemistry of the substrate. As long at toe pads remain in the Cassie state (unwetted) there are no differences between wet and dry adhesion on surfaces that are hydrophilic, intermediately wetting, or hydrophobic (Stark et al. 2013). However, a wet hydrophilic surface, such as glass, appears to more rapidly promote transition of the toe pad to a Wenzel state, significantly compromising the whole-animal clinging force (Stark et al. 2013).

It is difficult to completely reconcile the animal-level effects on the basis of studies at the scale of individual setae or setal arrays because in the animal-level studies it is not possible to separate the adhesion and friction components of the setae and spatulae due to the mechanics of the toe and seta (Tian et al. 2006). Moreover, at the whole-animal scale, adhesion to Teflon® is about fivefold higher when wet compared with dry. Aside from how geckos cope with wet toes, this effect suggests some interesting engineering applications in microfluidics, sensing, bioengineering, and many other areas, including nonslip shoe soles and automobile tires. Furthermore, there is a need for more empirical and theoretical work exploring the role of surface chemistry and composition of the setae on gecko adhesion at multiple scales and in nonideal environments. In particular, if lipids found in gecko setae confer a hydrophobic surface chemistry to setae, this could have implications for wettability and clinging performance on wet substrates (Stark et al. 2012, 2013).

FUNCTIONAL MORPHOLOGY, ECOLOGY, EVOLUTION, AND GECKO-INSPIRED ADHESIVES

Although the focus of the past decade on the biophysics and biomechanics of the gecko adhesive system has spawned diverse research on fibrillar adhesives, including natural adhesives found in other animals, such as insects and spiders (Creton & Gorb 2007; Federle 2006; Gorb 2008, 2009; Varenberg et al. 2010), as well as pushed the frontiers of study and knowledge about surfaces in contact with one another (tribology), we still know very little about the ecological and evolutionary contexts that have given rise to these capabilities. However, conspicuous variation in toe pad size and morphology and its association with performance variation or observed

ecological characteristics have long been a source of study and speculation. For example, species from two arboreal genera of carphodactyline geckos from New Caledonia exhibit variation in whether their toe pads are divided or not, although the internal structures of the toe pad system (tendons, sinuses, and musculature) are highly conserved (Bauer & Russell 1990). Because the ecological characteristics of these species are not well known and the suspected variation has not been quantified, we can only speculate about the potential relationship between form and function in the adhesive locomotion of these two species.

Aside from broad comparisons across taxa, such as the testing of expected scaling functions between adhesive toe pad size and body size (Peattie & Full 2007) or functional consequences of morphological variation in independently evolved adhesive toe pads in unrelated lineages (anoles and geckos) (Irschick et al. 1996, 2006), we have only just started to examine explicit hypotheses about the ecological significance of variation in adhesive toe pads and their evolutionary implications. Just as technological advances have made it possible to study micro- and nanoscale interactions between spatula and substrate, new molecular phylogenies have made it possible to test explicit hypotheses about the association of toe pad variation with specific environmental factors. Indeed, the rate at which phylogenetic hypotheses are being generated and evaluated is unprecedented, especially for nonmodel organisms (Ekblom & Galindo 2011). For instance, in the Gekkota, variation in and evolution of adhesive toe pads are great and labile, respectively (Gamble et al. 2012).

Toe pads have evolved independently at least 11 times and have been lost 9 times (cf. **Figure 2**). Although it has been assumed and argued that adhesive toe pads are a key innovation in the adaptive diversity and radiation of geckos (Vitt & Pianka 2005), in at least one study estimates of speciation and extinction rates associated with the presence or absence of toe pads showed no significant differences between clades that have toe pads and those that don't. One interpretation is that toe pads by themselves do not a gecko make. Rather, toe pads may be a single trait within a suite of traits linked to the success of geckos. For example, geckos are often considered as successfully invading new niches compared with other squamates due to correlated innovations involving nocturnality, aboreality, adhesive locomotion, and highly sensitive visual and olfactory prey discrimination. Interestingly, geckos have become an important focus of study of continental biogeography, especially as their genomes and morphology may have preserved a record of response to cyclic climate changes during the Miocene (∼20 Ma), driving continental scale expansion and contraction of deserts and mesic refugia (Pepper et al. 2011a,b). Especially in Australia, sustained shrinkage and isolation of mesic refugia in a continuously expanding central arid zone have left a clear genetic signal of restricted gene flow among populations in mesic forested habitat refugia embedded in an otherwise arid scrub or desert landscape.

Such information presents an extraordinary opportunity to connect macroscale biogeographic patterns of species divergence, radiation, and hypotheses of key innovations to microevolutionary studies of performance, behavior, and adaptation in geckos. At least two study systems seem particularly well primed for delivering the kind of synthetic and integrated tests of adaptive evolution envisioned by the expansion of the evo-devo framework to one which connects genes, morphology, function, and resource use (Irschick et al. 2013): geckos in the *Pachydactylus* and *Phelsuma* species groups. The former includes a southern, arid-distributed subgroup of 73 species in six genera distributed on the African continent that display wide variation in lamellar morphology. The latter group is a single genus of more than 40 species of arboreal geckos native or endemic to Madagascar, the Seychelles, and Mascarene and Comoros Islands. *Phelsuma* spp. have been the subject of intensive phylogenetic and biogeographic analyses as they relate to testing hypotheses of adaptive radiation (Radtkey 1996). In both of these examples, many of the

ingredients for synthesis and integration (Irschick et al. 2013) already exist, although significant challenges remain. We review salient features of both these systems below.

The number of lamellae comprising the adhesive toe pads of climbing, rock-dwelling, terrestrial, sand-dwelling, and burrowing *Pachydactylus* geckos distributed in southern African habitats is correlated with a gradient of variation in climbing requirements and the potential for fouling (inversely related) presented by the substrates of the different habitats (Lamb & Bauer 2006). Among 38 species included in a detailed and well-resolved molecular phylogeny, there are 3 independently evolved conditions of complete or nearly complete loss of toe pads in burrowing specialists, and 5 independently evolved reductions (by 50% or more relative to ancestral forms) of toe pad lamellae in terrestrial forms (including sand-dwelling species) (Lamb & Bauer 2006). As pointed out by the authors, the size of the species group and the diversity of habitats and functional morphological variation observed provide a robust opportunity to examine the mechanics of adaptive differentiation as it relates to adhesive toe pads.

However, a very significant challenge remains in mapping the observed morphological variations (e.g., including but not necessarily limited to number of lamellae) in function, performance and resource use differences. Ironically, such links have not yet received enough study such that we can construct specific and testable hypotheses. This is not to say that functional morphological analysis of gecko adhesion has not been studied in related contexts, such as the effects of substrate type (Johnson & Russell 2009), roughness (Russell & Johnson 2007), and slope/orientation (Russell & Higham 2009), but rather that the rate of progress and variety of those studies has lagged far behind the micro- and nanomorphological analyses associated with the many more studies focused on applications to synthetic adhesives. Indeed, several studies near the beginning of the explosion of research linking micro- and nanomorphology from gecko systems to design and production of synthetics highlighted such functional morphological-ecological relationships as key to understanding the ecology and evolution of gecko adhesive locomotion (Bauer & Russell 1991, Russell 2002).

Interest in the mechanisms driving adaptive radiation in species groups like geckos in the genus *Phelsuma* has surged in the past decade (Losos 2010) as the integration of ecological, phylogenetic, and biogeographical data has become more feasible. The confluence of these same factors, noted above, bodes well for new insights into not only the ecology and evolution of gecko adhesion but our ability to abstract new design principles relevant to the design of synthetic mimics that can perform as well or better than geckos. Perhaps not surprisingly, gaps in our understanding of the details regarding how the natural systems function likely limit our understanding of how the radiations unfolded as well as explain what more we need to know to produce a synthetic adhesive that can do all a gecko can do. Indeed, although micro- and nano-mechanical empirical and theoretical studies of the adhesive systems of geckos has created a substantial industry around fibrillar adhesive models and design (Hu & Xia 2012, Jagota & Bennison 2002, Zhou et al. 2012), further progress likely depends on a deep mechanistic understanding of presumptive key innovations (i.e., toe pads) as they function in ecologically relevant contexts. For example, studies of the adaptive radiation of diurnal day geckos inhabiting island systems of the southwest Indian Ocean (Madagascar, Seychelles, and the Comoros and Mascarene Islands) (Radtkey 1996) suggest correlations among body size and perch type and height are common to *Phelsuma* and the independent Caribbean *Anolis* (Harmon et al. 2007). It remains to be determined whether variation among *Phelsuma* species in one of the likely key innovations underlying the radiation of adhesive toe pads is relevant to ecological divergence and coexistence. Relevant ecomorphological hypotheses seem obvious, but only a few studies have explored these issues. For example, in *Rhoptropus*, a genus of rock-dwelling geckos closely related to *Phelsuma*, six ecologically similar species of seven species

studied (Johnson & Russell 2009) show little variation in characteristics, such as toe pad and setal size, shape and density, or habitat associations. However, the seventh species is distinct from the rest in both habitat associations and toe pad characteristics: *Rhoptropus afer* is a highly terrestrial member of the genus and has short setae and relatively small toe pads (as well as several other distinct morphological characters associated with cursorial locomotion). Such differences are not unexpected and are consistent with variation seen among more distantly related species, such as *G. gecko* and *P. grandis* (Hagey et al. 2013). It seems logical to expect that, for a taxon in which adhesive toe pads have been identified as directly or indirectly related to success and high species diversity across the clade (Losos 2010), variation in toe pad structure and function, at various length scales, might be associated with characteristics like behavior, performance, and habitat preferences that reflect ecological opportunity. However, the necessary data and analyses to test functional hypotheses about toe pad variation (at length scales including individual setae and spatula up to whole toes, feet, and animals) and how it relates to ecological performance and fitness are not currently available (Hagey et al. 2013). Nevertheless, existing ecomorphology studies of *Phelsuma* are intriguing for several reasons. First, hypertrophied epiphyses of the digits are a defining characteristic of the genus, and variation in the extent of hypertrophy has been associated with specific habitat associations (e.g., arboreal versus rock-dwelling) (Russell & Bauer 1990). Second, there is ample evidence that radiations of *Phelsuma* species on different islands across their range show niche partitioning (e.g., perch height and diameter) that is analogous to that seen in independent radiations of another group of adhesive-padded lizards (*Anolis*) (Losos 2010). Third, in contrast to *Anolis*, *Phelsuma* does not necessarily show the same types of morphological correlates of niche partitioning, such as variation in limb proportions, tail length, and toe pad size (Losos 2010). One way this has been interpreted is that the adhesive toe pads of day geckos, being more sophisticated and functionally superior for vertical and inverted locomotion (Irschick et al. 2006), obviate a response by other components of the locomotor system as a way of compensating for unique challenges of moving across different substrates and orientations associated with species in the *Phelsuma* radiations (Losos 2010). However, questions about how toe pad variation may be correlated to *Phelsuma* niche partitioning based on substrate texture and vegetation type (Harmon et al. 2007) seem ripe for investigations testing links between genes, morphology, performance, fitness, and resource use (Irschick et al. 2013) in the adaptive radiations of geckos.

CONCLUSION

This review by necessity mentions only a small part of the rapidly growing literature on gecko adhesion, a fertile new field at the interfaces of biology, physics, materials science, and engineering. We conclude with some future directions that we predict will be especially fruitful.

We hope our new field continues to grow in the spirit of friendly, open collaboration. The number of permutations of coauthors in recent publications suggests that this will be so, and the future of gecko adhesion as an interdisciplinary model system seems bright.

FUTURE ISSUES

1. Natural surfaces vary in roughness and surface chemistry, and an important next step will be to measure these effects on friction and adhesion in gecko setae. Biological diversity of setal and spatular structure is high and poorly documented. Basic morphological study of setae and spatulae will be required, but the study of variation in—and the genes

coding for—materials properties and surface chemistry will be productive research topics. Diversity of array parameters, such as density, dimension, and shape, is great but not well documented. In particular, the shape of setal arrays on lamellae and toes demands further investigation.

2. Phylogenetic analysis of the variation in setal structure and function must tease apart the combined effects of evolutionary history, material constraints, and adaptation (Autumn et al. 2002a). The gecko fibrillar system has evolved repeatedly over the past 100 Ma across a vast array of ecological contexts, leading to what may be optimal combinations of potentially conflicting performance characteristics, such as strong adhesion, compliance, resilience, and self-cleaning. This last observation should be both sobering and exciting for there is undoubtedly an enormous amount of untapped knowledge embedded in the more than 1,400 species of geckos about which we know very little. If the past 15 years could be characterized as a highly successful campaign of laboratory-based tribology/adhesion research, the next phase will most likely be defined by a return to and integration of curiosity and observation of the great diversity of free-ranging geckos in their equally diverse ecological contexts (Pianka & Sweet 2005, Russell 2002).

3. There is great desire to engineer a material that functions like the gecko adhesive. A biomimetic approach of attempting to copy gecko setae directly is unlikely to succeed owing to the complexity of the system (cf. **Figure 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 to yield selected gecko-like functional properties. Indeed, hundreds of gecko-inspired synthetic adhesives have been proposed, fabricated, and tested (Kwak et al. 2011). Although GSAs have exceeded the capabilities of the model system in single dimensions, particularly adhesive strength (Lee & Bhushan 2012), achieving the multidimensional performance capabilities of the native gecko adhesive system remains a formidable challenge (Hagey et al. 2013). Significant empirical, theoretical, and fabrication challenges must be overcome before GSAs match all the seven benchmark functional properties of natural gecko adhesives (Autumn 2006): anisotropic attachment, high pull-off to preload ratio, low detachment force, material independence and rough surface compatibility, self-cleaning, antiself-matting, and nonsticky default state.

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