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COMMENTARY

Sticking to the story: outstanding challenges in gecko-inspired adhesives

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ABSTRACT

The natural clinging ability of geckos has inspired hundreds of studies seeking design principles that could be applied to creating synthetic adhesives with the same performance capabilities as the gecko: adhesives that use no glue, are self-cleaning and reusable, and are insensitive to a wide range of surface chemistries and roughness. Important progress has been made, and the basic mechanics of how 'hairy' adhesives work have been faithfully reproduced, advancing theory in surface science and portending diverse practical applications. However, after 15 years, no synthetic mimic can yet perform as well as a gecko and simultaneously meet of all the criteria listed above. Moreover, processes for the production of inexpensive and scalable products are still not clearly in view. Here, we discuss our perspective on some of the gaps in understanding that still remain; these gaps in our knowledge should stimulate us to turn to deeper study of the way in which free-ranging geckos stick to the variety of surfaces found in their natural environments and to a more complete analysis of the materials composing the gecko toe pads.

KEY WORDS: Gecko, Biomimicry, Biologically inspired, Adhesive

Introduction

It is now 15 years since Autumn and colleagues manipulated the adhesion of isolated gecko setae (see Glossary) (Autumn et al., 2000), unleashing a torrent of studies on the design and function of gecko-inspired synthetic adhesives. The ability of geckos to cling to a wide variety of surfaces (Fig. 1A–E) has long held the fascination of scientists and casual observers, especially in tropical environments, the native habitats of many of the world's >1000 species of gecko. Geckos are also found in deserts and temperate environments, and at least half of the species have adhesive toe pads (Fig. 1F) made up of hierarchically structured, hair-like surfaces that provide the 'stick' (see below). Although laboratory-scale mimics of gecko toe pads can already match or exceed the capacity of geckos to generate strong adhesive and low pull-off forces (Kwak et al., 2011; Hu and Xia, 2012), gecko-inspired adhesives that simultaneously capture all of the performance characteristics seen in geckos (e.g. self-cleaning, reliability, reusability and functionality on wet and rough surfaces) remain elusive (Autumn et al., 2014). Why? We believe that there are three gaps in our understanding which contribute to the shortcomings of the gecko-inspired synthetic adhesives that have been produced to date: (1) incomplete theory and data on the mechanics of fibrillar adhesives in non-ideal circumstances (e.g. on wet, dirty and/or rough surfaces), (2) limited understanding of the contribution to performance made by the gecko adhesive materials (skin, lipids, etc.) as distinct from their structure and (3) lack of quantitative and qualitative data on or analysis of behavior, function and performance of free-ranging geckos on natural substrates (Fig. 1). Closing these three gaps will require an expanded area of study that not only builds on existing work but also shifts our attention to the features of gecko adhesion that have been relatively ignored: the material composition of gecko setae and the variation in performance shown by geckos observed in natural environments or in laboratory settings that mimic natural environments. One reason to close these gaps, aside from the inherent value of knowledge about the biological system, is very self-evident: gecko-inspired synthetic adhesives would address many of the shortcomings of current design and technology in pressure-sensitive adhesives. Although the imagery of people scaling walls using 'gecko-gloves and -shoes' may seem like something from science fiction, there are many potential applications for strong and repeatedly reversible attachment that works on almost any kind of surface, even in a vacuum and without leaving any residue. Whether in the form of transfer devices used in manufacturing (Jeong et al., 2014), in the fastening and heat dissipation of components in electronic devices (Ge et al., 2007; Badge et al., 2011) or in providing traction for mobile search and rescue robots (Kim et al., 2008), there appear to be many openings for gecko-inspired adhesives to replace existing adhesive technologies, as well as opportunities to create entirely new markets.

In this Commentary, we explore what we consider to be conspicuous examples of gaps in current knowledge that fall into the three areas outlined above. Given that gecko adhesion emerges within a system that includes complex features of the animal as well as features of the substrates and environment with which the animal interacts, any particular example does not necessarily fit neatly within one single area. Consequently, we present our perspective as a collection of readily accessible examples where our understanding is still very incomplete. It seems clear to us that much work remains to be done before we can achieve the interdependent goals of designing gecko-inspired synthetic adhesives with the multivariate performance characteristics seen in geckos, and testing robust hypotheses of the ecological and evolutionary significance of adhesion in gecko biology.

Close encounters

That the stickiness of geckos on dry, clean, smooth surfaces (such as glass or acrylic used in many laboratory assays) arises mostly from van der Waals forces (see Glossary) – a source of weak attraction caused by intermolecular interactions when two surfaces come into intimate contact (Israelachvili, 1991) – is not generally disputed (Autumn and Peattie, 2002; Autumn et al., 2014). In fact, reliance on van der Waals attraction is perceived to be the core feature underlying the success of geckos using adhesive locomotion in so many different contexts (Autumn et al., 2014). Many geckos have

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Glossary

Contact angle hysteresis
Differences in the advancing and receding contact angles formed between a water droplet and a surface. The contact angle hysteresis arises because of chemical heterogeneity and/or surface roughness. This measure can be used to help characterize properties of the surface such as roughness.

Digital hyperextension
The capacity for distal elements of the digits of many geckos to flex or bend in the dorsal as well as ventral direction.

Effective modulus
The elastic modulus of a heterogeneous material that accounts for the elastic properties of the individual components as well as their geometrical arrangement.

Nanobubbles
A gas phase present at the interface between water and a hydrophobic material that is observable as bubbles that can be tens to hundreds of nanometers in diameter.

Setae
Small hair-like structures ~1–5 µm in diameter and up to ~100 µm long. These high aspect ratio extensions of the epidermis in geckos can be organized in fields or patches on the ventral surfaces of the feet (lamellae) and the tip of the tail.

Spatulae
Very small (hundreds of nanometers in length) plate-like termini of the setae that arise from multi-level branching near the end of the main stalk, providing the contact surface for van der Waals attraction in adhesion.

Superhydrophobic
A state of very high water repellency seen in the 'lotus effect' that is associated with a measure called the 'water contact angle' equaling or exceeding 150 deg.

van der Waals forces
Non-covalent, non-ionic intermolecular weak forces that can be either attractive or repulsive.

specialized 'hair-like' structures called setae on the ventral surfaces of their toes, and the setae of many geckos terminate in nano-scale plates called spatulae (see Glossary; Fig. 2). The setae make intimate contact with the substrate possible through a principle called 'contact splitting' (Peattie and Full, 2007). The concept of contact splitting is used to explain why small fibers (such as the gecko setae) stick more strongly than larger fibers. If we assume a hemispherical tip, then the actual effective contact area of the curved surface increases with decreasing fiber size, and this is referred to as contact splitting. The fact that fibrillar structures can inhibit crack propagation might also explain why hairy structures of a certain size stick better than flat surfaces. In geckos, the shape, size and effective modulus (see Glossary) of the spatulae may play an important role in increasing the adhesive contact area to maximize the van der Waals adhesion (Arzt et al., 2003). This principle is also observed in the adhesive structures of many invertebrates. The setae and spatulae of many geckos provide millions of potential points of contact with a substrate (Maderson, 1964; Williams and Peterson, 1982). Individually, the force of attraction at each spatula is quite small, but together the spatulae can produce very significant whole-animal forces. Indeed, early theoretical work estimated that the toe pad area of an average-sized tokay gecko (*Gekko gecko*) could generate up to 130 kg of force through these 'close encounters' (Autumn and Peattie, 2002).

Other factors that might contribute to adhesion in geckos have been explored and debated even as we accrue more and more

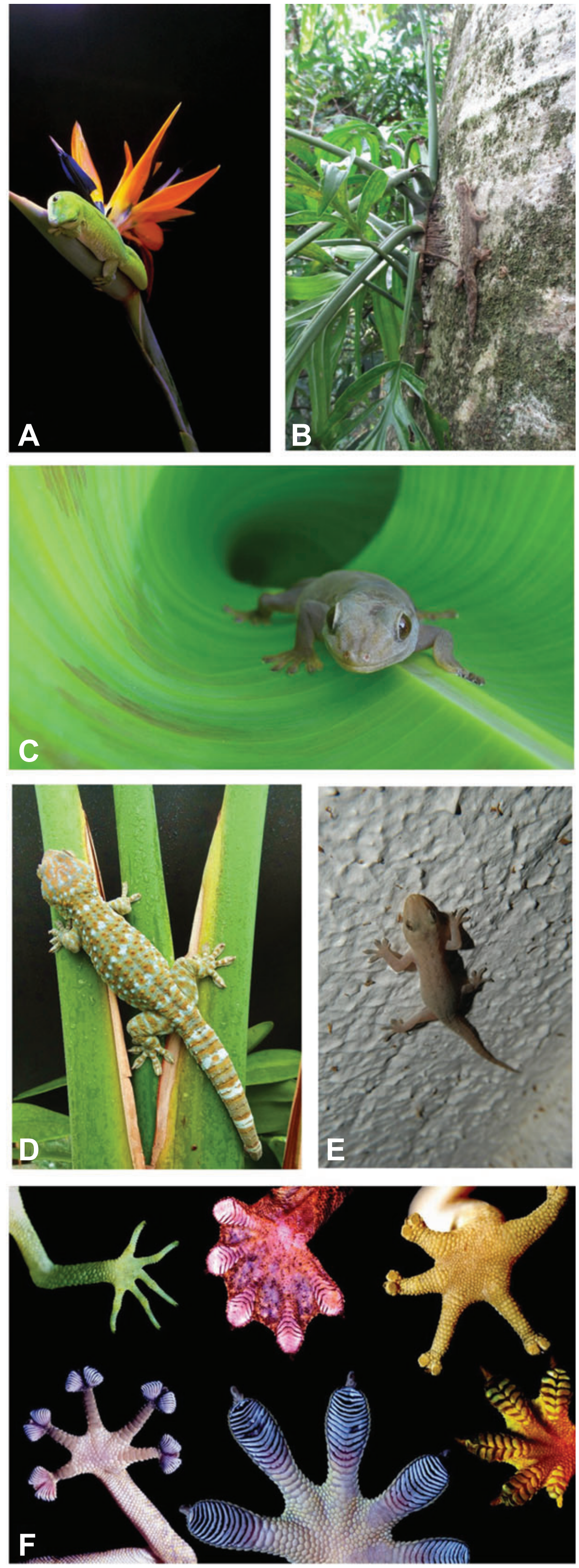

Fig. 1. Geckos can effectively cling to a wide variety of surfaces. (A) Day gecko on a bird of paradise. (B) Oceanic gecko on the bark of a tree. (C) Golden gecko scaling a banana leaf. (D) Tokay gecko on a wet palm leaf. (E) House gecko on a masonry wall. (F) A sample of diversity in gecko toe pad gross morphology – there is also micro- and nano-scale morphological variation that is not shown here. Toe pad image courtesy of ©Paul D. Stewart.

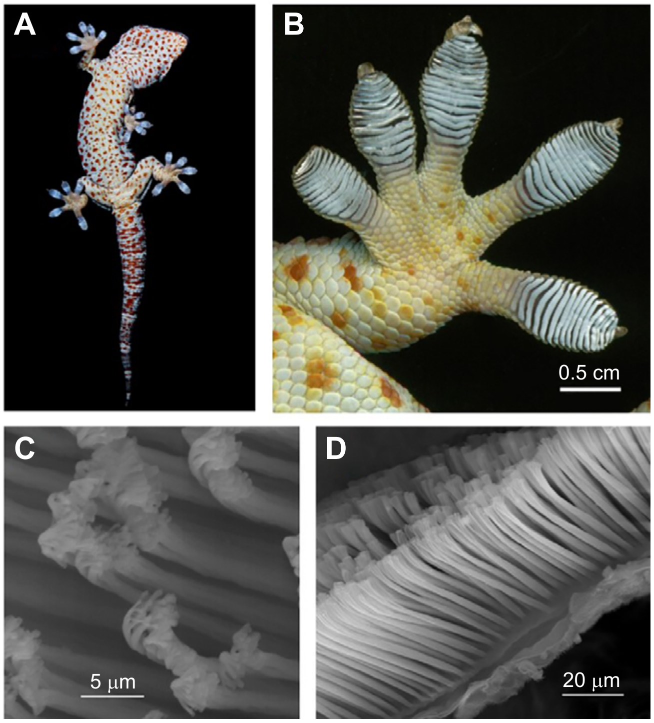

Fig. 2. An overview of the hierarchical nature of the gecko adhesive system. (A) A ventral view of a tokay gecko on glass, showing the toe pads. (B) Lamellae on the gecko toe pads. (C) The setae that make up the lamellae. (D) The flattened tips of branched setae (spatulae).

evidence for the central role of van der Waals forces in adhesion and our understanding of these forces increases. Two prominent examples of other factors potentially contributing to gecko adhesion include contact electrification (Izadi et al., 2014) and capillary forces (Huber et al., 2005; Sun et al., 2005; Bhushan, 2007; Kim and Bhushan, 2008; Puthoff et al., 2010; Wolff and Gorb, 2012). Contact electrification is a phenomenon in which electric charges move between surfaces that come into contact with each other, such that one surface forms a net negative and the other a net positive charge. Capillary forces are forces of attraction that arise from the formation of liquid bridges (in the case of geckos, the liquid is water) between two surfaces brought into contact. The role of contact electrification in gecko adhesion is still poorly understood and has not received much attention, whereas capillary forces have been more continuously and broadly studied. In both cases, however, it is likely that further research examining the dynamics of adhesion of whole animals on more complex surfaces than are typically used in laboratory assays (smooth, dry, clean glass or plastic) will lead to a more integrative view of gecko adhesion.

It's a rough world out there

Although the role of the hierarchical compliance of the gecko adhesive system in allowing good contact and strong van der Waals attraction with surfaces of varying roughness (Fig. 1A–E) was recognized early in the study of gecko adhesion (Autumn and Peattie, 2002; Persson and Gorb, 2003), the most common laboratory test substrates have been glass, acrylic and similarly smooth materials. Work in the laboratory, as well as with free-ranging geckos, has explored the effects of surface roughness on adhesion and synthetic design in only limited ways, probably because roughness is a deceptively complex parameter; real surfaces vary in roughness over many length scales, making the characterization of roughness non-trivial (Persson and Gorb, 2003). Basic theory and laboratory work on the effects of controlled roughness on gecko adhesion (Persson and Gorb, 2003; Huber et al., 2007; Persson, 2007; Greiner et al., 2009; Peng and Chen, 2011) have made an important contribution to our thinking about the design of the gecko adhesive system, especially as it relates to safety factors (Pugno and Lepore, 2008; Gillies and Fearing, 2014; Russell and Johnson, 2014). Safety factors in a system reflect the capacity of that system to perform beyond expected or normal limits in ideal circumstances (Hawkes et al., 2015). For example, when all the spatulae of a gecko come into contact with a substrate, adhesive forces are estimated to be >1000-fold greater than what is needed to support the gecko's body weight (Russell and Johnson, 2014). Limits to the theoretical performance of the system on rough substrates have been revealed in laboratory assays of dynamic performance like sprinting (Vanhooydonck et al., 2005), and through analysis of the degree of mismatch between critical setal dimensions and typical substrate roughness profiles and habitat associations in some species (Johnson et al., 2005; Russell and Johnson, 2007, 2014). However, because natural substrates vary randomly over many length scales as a function of the area measured, and given the hierarchical compliance of the gecko toe pad, we still do not have clear expectations about how the gecko adhesive system may have evolved in different ways to adapt to different substrates (Gillies et al., 2014). Recent work, however, is beginning to combine evolutionary and ecological approaches to advance our understanding of gecko adhesion (Russell et al., 2015). There are emerging hypotheses about the origins of adhesive structures in geckos that address multiple levels in what is a fundamentally complex hierarchical system (involving spatulae, setae, toe pads and skeletal and connective tissue of the feet, etc.). Currently, functional analyses relating variation in gecko adhesive morphology to variations in performance on variably rough substrates are limited to a few studies on hard substrates, yet geckos also commonly traverse and stick to both rough and smooth soft substrates (Russell and Johnson, 2014; Collins et al., 2015). At the very least, it will be interesting to see whether there are patterns of variation in gecko adhesive systems or design principles that emerge from studying geckos using rough substrates that are predominately hard or soft (Stark et al., 2015c).

Water, water everywhere

As continuing research investigates ways to model and mimic gecko adhesion, evidence suggests that adhesion to substrates like those encountered by free-ranging geckos could be considerably more complex than that observed in the laboratory. A prime example is the 'contamination' of natural surfaces with water (Fig. 1D), whether as adsorbed layers that are ubiquitous on many surfaces under ambient conditions, or as surface droplets; in fact, geckos might even encounter submerged substrates (Stark et al., 2012). The effects of water on gecko adhesion, especially those due to adsorbed layers of water that form when ambient humidity is greater than zero, have been debated for many years (Losos, 1990; Huber et al., 2005; Sun et al., 2005; Niewiarowski et al., 2008). Early versions of this debate focused mainly on a desire to distinguish between van der Waals and capillary forces of adhesion as general explanations of how geckos stick. Interestingly, it has been shown that the mechanical properties of the setae themselves are affected by humidity variation, providing a potential explanation for the observed effects of humidity on adhesion (Puthoff et al., 2010; Prowse et al., 2011). Furthermore, such studies remind us that many of the >1000 species of geckos (Han et al., 2004) live in environments with high relative humidity where wet surfaces are probably ubiquitous. However, only a handful of studies have examined gecko adhesion on wet substrates, and the results are not simple to understand. Indeed, in addition to the way humidity can affect the mechanical properties of setae, the effects of water at the contact interface also vary depending upon the surface chemistry of the substrate, substrate roughness and whether the setae are in their default un-wetted, superhydrophobic state (see Glossary) (Stark et al., 2012, 2013, 2014a,b, 2015a,b; Badge et al., 2014). The default wetting state for gecko setae is that they repel water, but that state is not stable. Indeed, extended contact of the setae with water, and other kinds of conditions (e.g. brief contact under high adhesive force), can lead to the setae 'wetting'. Theoretical models have been developed to predict and explain the wetting behavior of materials, and several studies reveal the inherent complexities and limitation of current theory, but also show the potential opportunities for novel applications (Nosonovsky and Bhushan, 2008; Wang et al., 2012). In general, once the setae are wet, they no longer adhere to surfaces as they do when they are dry. For example, when glass (a smooth hydrophilic surface) is sprayed with water or submerged underwater, the ability of geckos to adhere is drastically reduced; this effect is exacerbated if the normally superhydrophobic gecko toe pads become wetted due to the contact with water (Stark et al., 2012). In contrast, when hydrophobic substrates are sprayed with water or submerged, the superhydrophobic toe pads of geckos have considerable capacity to exclude water from the contact interface – thereby maintaining high adhesion (Stark et al., 2013) – as long as the toe pads themselves do not become wetted (Fig. 3). Robust adhesive capabilities arise when both the substrate and the toe pads are hydrophobic, a condition that may reflect the typical situation encountered by geckos when they move across leafy vegetation in their natural environments. It is also interesting to note that if the default state of the toe pads was hydrophilic instead of hydrophobic, they would wet immediately in the presence of surface water – a condition that we know compromises whole-animal adhesion irrespective of the chemistry of the substrate (Stark et al., 2012, 2014b; Badge et al., 2014). It is striking that, in the gecko system, we do not see another possible situation where toe pads are permanently superhydrophobic, at least not among the species studied so far. However, when setae are coated with a nanometer-thick permanently hydrophobic layer, they remain superhydrophobic (and non-wetting), and their adhesion performance on hydrophobic substrates is indefinitely uncompromised (Badge et al., 2014).

Fig. 3. The interaction of gecko toe pads with the substrate in the presence and absence of water. The schematic top panels show the interaction of toe pads with substrates in air (left) and with hydrophobic and hydrophilic substrates in the presence of water (indicated by the blue color; center and right, respectively). In the un-wetted state, toe pads exclude water on the hydrophobic but not on the hydrophilic surface. The lower panel shows water beading up around the hydrophobic residue left on a glass surface after a gecko removed its adhered foot during walking.

These studies raise several interesting points. First, the surface chemistry of the substrates that geckos move across is likely to be a significant factor in the performance of their adhesive toe pads if surface water is present. Second, why is the material that the toe pads are made from (β-keratin and lipids) not permanently superhydrophobic and non-wetting, i.e. why are a gecko's toe pads ultimately wettable? Is it impossible for a hierarchical biological material to be permanently non-wetting? Would a permanently superhydrophobic and non-wetting toe pad have reduced performance in other dimensions, such as compliance, self-cleaning or reusability? We have no idea which of these two obvious possibilities (or others not yet proposed) is more likely. Further research will be needed to address these possibilities and to extend our understanding to the design of synthetic mimics of the gecko system.

Is it surprising that, beyond anecdotal accounts, we do not yet understand how water affects gecko adhesion? Perhaps, but it is almost certainly related to two distinct yet interrelated limitations of the current literature. First of all, data on the ecology and natural history of geckos, especially relating to detailed information about the nature and condition of the substrates that geckos move across, are quite limited (Collins et al., 2015). Second, there is still ongoing debate about the mechanisms of gecko adhesion. Consider the recent study proposing that contact electrification is more important than van der Waals forces in determining gecko adhesion (Izadi et al., 2014), or a second study which suggests that, underwater, nanobubbles (see Glossary) – rather than fundamental thermodynamic contributions arising from two contacting surfaces in water – play a role in adhesion (Peng et al., 2014). Both of these shortcomings in understanding the gecko adhesive system will ultimately limit our ability to use the relevant principles of design and consequent function to create synthetic mimics.

Down and dirty

Similar to the challenges with rough substrates, dirty substrates pose a significant and very real problem for geckos in their natural environment (Fig. 4). Dirt particles may not only cause misalignment and matting among the setae but also interrupt the close contact between setae and the substrate that is necessary for adhesion. Laboratory experiments that measure gecko and/or gecko-inspired synthetic adhesion to clean substrates fail to consider the non-pristine substrates that both of these systems will encounter when in regular day-to-day use. Luckily for the gecko, the adhesive system has both a passive and an active self-cleaning mechanism. First, the simple action of pressing the setae into contact with a surface removes dirt particles of most sizes; only small particles remain trapped inside the setal mats (Hansen and Autumn, 2005).

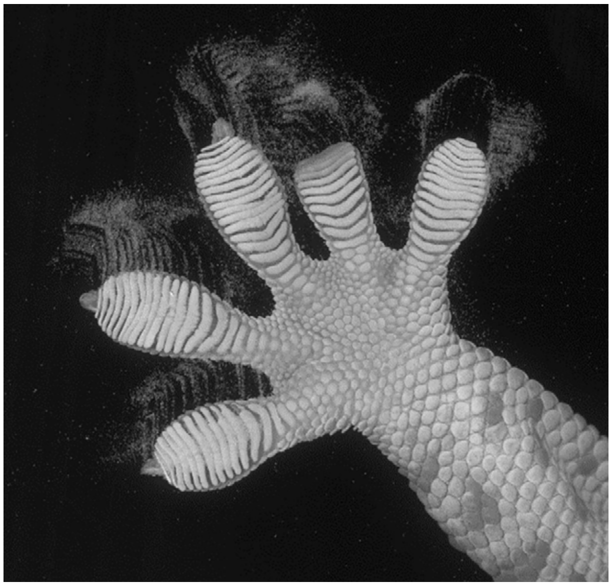

Fig. 4. Self-cleaning of gecko toes by digital hyperextension. The image shows the toes of a tokay gecko peeling off a glass sheet after the toe pads were exposed to fine sand. This digital hyperextension acts as an active self-cleaning mechanism, causing sand to be left on the glass as the toes separate from the substrate.

Second, the impressive digital hyperextension mechanism (see Glossary) that geckos use to peel their adhesive setae from a substrate also functions as an active self-cleaning mechanism (Fig. 4), whereby dirt particles are rapidly expelled as the toes peel backwards with every step (Hu et al., 2012). Incidentally, this active mechanism may also help to remove water from wetted toe pads (Stark et al., 2014b). Thus, simply by walking or running, a gecko removes dirt and debris from its toe pads to regain or maintain adhesion after fouling. Whereas the active self-cleaning mechanism appears to be related to the natural peeling behavior of the toes, the passive self-cleaning mechanism is likely to be a function of the surface chemistry and structure of the setal mats. In particular, to aid passive removal of dirt particles, the setae may benefit from a surface chemistry that is hydrophobic rather than hydrophilic. It is worth noting that the self-cleaning property of gecko skin is not restricted to the adhesive toe pads, a feature which may be particularly important for terrestrial geckos moving among ground-level detritus (Watson et al., 2015). Although terrestrial geckos are often pad-less, the ability to self-clean dirt from the body and/or the adhesive toe pads has clear advantages. It is not yet known whether there is variation in cleaning performance or cleaning mechanism related to the nature of the microhabitats used by different species of geckos (e.g. sand, dirt, plant matter, bark, waxy leaves, etc.).

A second component of self-cleaning that has not been investigated in the natural system but has been of great interest in the synthetic design of surfaces and adhesives is self-cleaning with water. Because gecko toe pads are superhydrophobic and have a low contact angle hysteresis (see Glossary), such that water droplets roll off the pad when it is tilted by only 2–3 deg (Autumn and Hansen, 2006), they have the potential to exhibit the 'lotus effect'. Though never directly tested in the natural gecko adhesive system, the lotus effect is a paired water-repellency and self-cleaning mechanism named after the lotus leaf, which remains clean when growing from the depths of muddy ponds (Bhushan and Jung, 2011). Owing to the hierarchical structuring and chemistry of the lotus leaf, the leaf is superhydrophobic with a low contact angle hysteresis, similar to the gecko's adhesive toe pad. As a droplet of water rolls from the leaf at low angles, it takes dirt particles with it, essentially self-cleaning the surface of the leaf as it emerges from the murky water. While it remains to be seen whether the lotus effect plays a role in the self-cleaning of the natural adhesive system of the gecko, the ability of gecko toe pads to become wetted could hinder this wet self-cleaning mechanism. Thus, similar to adhesion in wet environments, self-cleaning of the toe pads by the lotus effect is likely to rely on the toe pads staying dry.

Show us what you're made of

Gecko setae are epidermal structures and have conventionally and exclusively been modeled as β-keratin. However, geckos are part of a lineage of tetrapods (sauropsids) whose success in dealing with desiccating terrestrial environments has involved many modifications to the skin (Chang et al., 2009). Gecko skin is actually a complex, dynamic, heterogeneous, multi-layered material, and there is evidence that lipids (fat) and proteins are both present at the contact interface (Alibardi et al., 2011; Hsu et al., 2012). It is not yet clear whether the composition of the epidermis in toe pads is differentiated or specialized in a way that is related to the highly specific adhesive function of the toe pad, but there is evidence that specific keratins are associated with the setae (Alibardi, 2013). Furthermore, analysis of the molecular dynamics of the interaction between lipids and proteins in the setae and the skin shows that there is a difference between adhesive toe pad epidermis and epidermis from other regions of the body, suggesting that structural differences, in addition to the chemical difference in proteins, may occur (Jain et al., 2015). Available evidence suggests that surface lipids contribute to the superhydrophobic default state of the adhesive toe pads and their remarkable ability to avoid transitioning to a wetted state even under an extended period of time at elevated pressure (Stark et al., 2013; Badge et al., 2014). Despite the relative stability of the superhydrophobic nature of gecko toe pads, some evidence suggests that, in the presence of water, surface groups at the contact interface change and reorient, shifting from predominately methyl groups on the lipids to methylene (Pesika et al., 2009; Hsu et al., 2012). What this dynamic shift means for adhesion is unknown, and how lipids specifically, and the heterogeneous composition of toe pad epidermis in general, contribute to adhesion and other performance characteristics of the gecko toe pads remains to be seen.

Ain't nothing like the real thing

Gecko-inspired synthetic adhesives have already found multiple applications, including use in climbing robots (Kim et al., 2008), heat dissipation, improved fabrication in the electronics industry (Mengüç et al., 2012) and biomedical adhesives (Lee et al., 2007; Mahdavi et al., 2008). The list of new potential applications is growing rapidly as the technology is improving (Kwak et al., 2011; Hu and Xia, 2012). Gecko-inspired adhesives have also been proposed as a means to help the design of microfluidic chips (Wasay and Sameoto, 2015), as reversible adhesives for diapers (Ross et al., 2014), to provide better grip for tires (Stark et al., 2014b) and even perhaps for hanging your television (Bartlett et al., 2012). To a large extent, these successes reflect dramatic progress in mimicking the shape and length scales of gecko setae using synthetic materials such as polymers and carbon nanotubes (CNTs; Fig. 5) (Ge et al., 2007; Qu et al., 2008). Although the adhesive strength of some synthetic mimics surpasses that of the natural system (for example, multi- and single-walled CNTs can exceed 100 N cm^{-2} or about

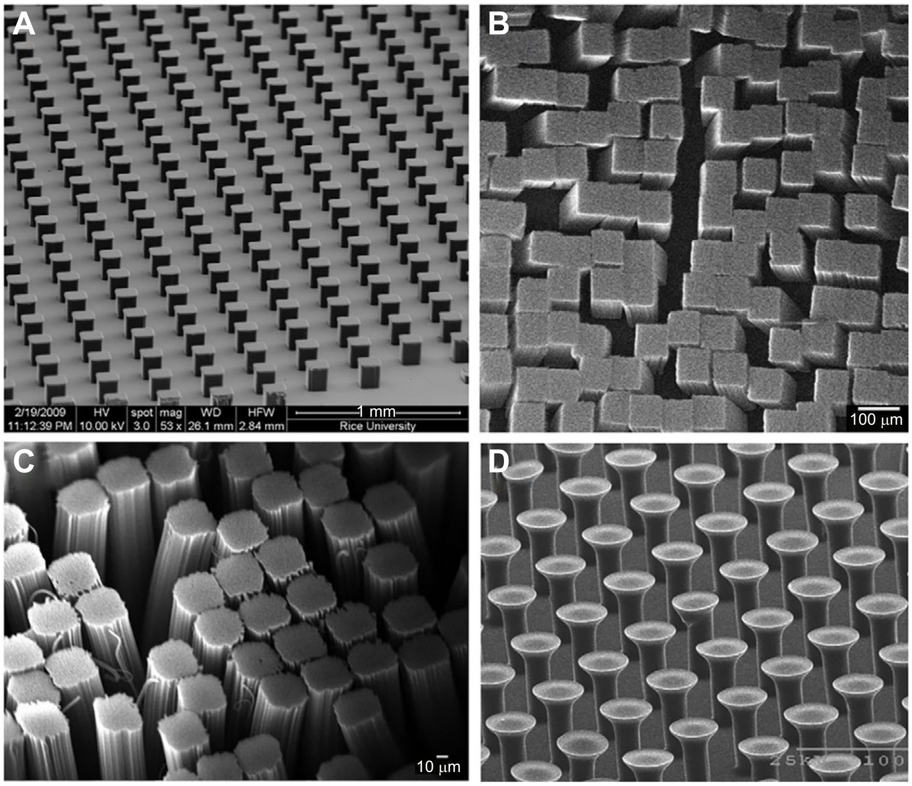

Fig. 5. Examples of gecko-inspired synthetic adhesives. (A–C) Carbon nanotube areas shown at three different magnifications. Picture credit: A.D. (D) An array of mushroom-tipped polyurethane pillars (Murphy et al., 2009). Scale bar in D, 100 µm. Picture credit: Metin Sitti.

two times typical gecko adhesion strength; see Hu and Xia, 2012, and note that adhesion strength estimates vary substantially depending on the measurement techniques used), the performance gap, compared with gecko adhesion, remains extraordinary (Autumn et al., 2014; Tao et al., 2015). The world in which geckos live is often humid and wet, and always dirty, and synthetic designs are only just beginning to capture the breadth of the gecko performance. The knowledge that a gecko's setae are covered with hydrophobic lipids is helpful for the design of synthetic materials that will have a better grip in wet environments (Soltannia and Sameoto, 2014; Defante et al., 2015). Likewise, understanding the role of hyperextension in cleaning adhesive toe pads may help in designing synthetic materials that remain clean. Although some initial progress has been made in designing self-cleaning surfaces (Lee and Fearing, 2008; Sethi et al., 2008), the performance of current designs still falls short of what is needed for practical applications. Finally, synthetic materials also face additional challenges in that it is difficult to manufacture large quantities of material at prices that can compete with existing and cheaper technologies. For successful application of new gecko-inspired technologies, we need rapid progress in innovative methods such as roll-to-roll processing, as well as the design of economical ways to manufacture synthetic gecko adhesives.

It's the ecology, stupid

The diversity of gecko toe shapes and sizes is bewildering (Fig. 1F), but perhaps not unexpected for a species group that is widely believed to have diversified because of a major innovation: adhesive locomotion (Losos, 2010; Gamble et al., 2012). Early work on the complex morphology and functional anatomy of gecko toes (Russell, 1973, 1979; Russell and Bauer, 1988, 1989), and recent studies on phylogeographic patterns associated with climate and habitat changes on landscape scales (Lamb and Bauer, 2006; Gamble et al., 2011; Pepper et al., 2011, 2013; Oliver et al., 2014), reveals a conspicuous opportunity to study the performance consequences of variations in toe pad size, shape, material composition and function (Autumn et al., 2014). Indeed, compared with phylogeographic studies, new species accounts and descriptions, and laboratory-based analysis of toe pad adhesive mechanics of just a few species, it is notable that ecological or evolutionary studies that examine toe pad structure–function of free-ranging geckos are very rare (but see Russell and Johnson, 2007, 2014; Collins et al., 2015). A search using Web of Science® and key words such as 'gecko+habitat+substrate+preference' returns dozens of studies with only anecdotal and qualitative information about the natural surfaces that geckos select during activity and inactivity. In general, such studies have not simultaneously considered questions relating to the functional morphology of adhesive toe pads. Specific studies that reconstruct the evolutionary history of a radiation driven by a major innovation (Harmon et al., 2008) or that link morphological variation to the optimization of ecological performance and design principles for biologically inspired mimics would be highly informative (Russell and Higham, 2009; Higham and Russell, 2010; Russell and Johnson, 2014; Collins et al., 2015; Higham et al., 2015). We predict that when ecologists who are interested in basic biology and autecology of geckos increase their collaborations with researchers working on gecko adhesion in laboratory settings, there will be a new wave of findings that advance our understanding of gecko ecology and evolution as well as of gecko-inspired synthetic adhesives.

Conclusions

The adhesive systems of geckos and the diversity and ecological success of these species has driven more than a decade of vigorous study by ecologists and material scientists alike. We believe that this work has laid the foundation for at least two major forthcoming breakthroughs. First, tests of specific hypotheses about the evolution of the adhesive system as a key innovation are likely to rapidly increase in number. Second, greater attention to the study of the natural or semi-natural conditions under which geckos use their adhesive systems, combined with an expanded analysis of other dimensions related to performance (e.g. materials, chemistry and optimization parameters) is likely to help bridge the gap between the performance of synthetic materials and that of geckos. This will also involve a greater appreciation of how synthetic materials provide exquisite models with which to test mechanistic biological and/or ecological hypotheses (Autumn, 2007; Russell et al., 2007). Indeed, the quest for gecko-inspired adhesives is a specific example of how design inspiration drawn from natural systems is not a one-way or one-sided enterprise. On the contrary, advances in our understanding of the basic biology are both fueled and directed by the practical application of this biology, emphasizing that basic and applied study are not independent activities, and that interdisciplinary collaboration, though difficult, is also critical for the advancement of this and many other fields.

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Author contributions
All authors contributed equally to the preparation of this manuscript

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