



INVITED PAPER

Going Out on a Limb: How Investigation of the Anoline Adhesive System Can Enhance Our Understanding of Fibrillar Adhesion

Austin M. Garner,^{1,*†} Michael C. Wilson,[‡] Anthony P. Russell,[§] Ali Dhinojwala,^{*,‡} and Peter H. Niewiarowski^{*,†}

*Integrated Bioscience Program, The University of Akron, Akron, OH 44325-3908, USA; [†]Department of Biology, The University of Akron, Akron, OH 44325-3908, USA; [‡]Department of Polymer Science, The University of Akron, Akron, OH 44325-3909, USA; [§]Department of Biological Sciences, University of Calgary, Calgary, AB T2N 1N4, Canada

¹E-mail: amg149@zips.uakron.edu

Synopsis The remarkable ability of geckos to adhere to a wide-variety of surfaces has served as an inspiration for hundreds of studies spanning the disciplines of biomechanics, functional morphology, ecology, evolution, materials science, chemistry, and physics. The multifunctional properties (e.g., self-cleaning, controlled releasability, reversibility) and adhesive performance of the gekkotan adhesive system have motivated researchers to design and fabricate gecko-inspired synthetic adhesives of various materials and properties. However, many challenges remain in our attempts to replicate the properties and performance of this complex, hierarchical fibrillar adhesive system, stemming from fundamental, but unanswered, questions about how fibrillar adhesion operates. Such questions involve the role of fibril morphology in adhesive performance and how the gekkotan adhesive apparatus is utilized in nature. Similar fibrillar adhesive systems have, however, evolved independently in two other lineages of lizards (anoles and skinks) and potentially provide alternate avenues for addressing these fundamental questions. Anoles are the most promising group because they have been the subject of intensive ecological and evolutionary study for several decades, are highly speciose, and indeed are advocated as squamate model organisms. Surprisingly, however, comparatively little is known about the morphology, performance, and properties of their convergently-evolved adhesive arrays. Although many researchers consider the performance of the adhesive system of *Anolis* lizards to be less accomplished than its gekkotan counterpart, we argue here that *Anolis* lizards are prime candidates for exploring the fundamentals of fibrillar adhesion. Studying the less complex morphology of the anoline adhesive system has the potential to enhance our understanding of fibril morphology and its relationship to the multifunctional performance of fibrillar adhesive systems. Furthermore, the abundance of existing data on the ecology and evolution of anoles provides an excellent framework for testing hypotheses about the influence of habitat microstructure on the performance, behavior, and evolution of lizards with subdigital adhesive pads.

They are good, but not good enough

Considering the variation and variability of real-world surfaces, new multifunctional adhesives that reversibly adhere to surfaces of varying form and substance (e.g., surface roughness, chemistry, softness) and under non-ideal conditions are in considerable demand. Nature has been generating such multifunctional adhesives for tens of millions of years, one example being the subdigital adhesive pads of some lizards. Gecko subdigital adhesive pads possess arrays of β -keratin fibrils (setae) that terminate in nanoscale, triangular-shaped tips (spatulae) (Maderson 1964; Ruibal and Ernst 1965) that

foster adhesion, primarily via van der Waals intermolecular forces, when intimate contact is made with a surface (Autumn et al. 2002) (Fig. 1A–D). The gecko adhesive system is multifunctional (e.g., self-cleaning, anti-wetting, reusable) and can operate under an array of conditions (Autumn et al. 2014; Niewiarowski et al. 2016). Consequently, hundreds of gecko-inspired synthetic adhesives have been designed and fabricated, attempting to incorporate some of the structural attributes of the gekkotan adhesive system, such as scansors (Lee et al. 2009), spatulae (Northen et al. 2008; Seo et al. 2014; Xue et al. 2014), fibril leaning angle (Lee et al. 2008;

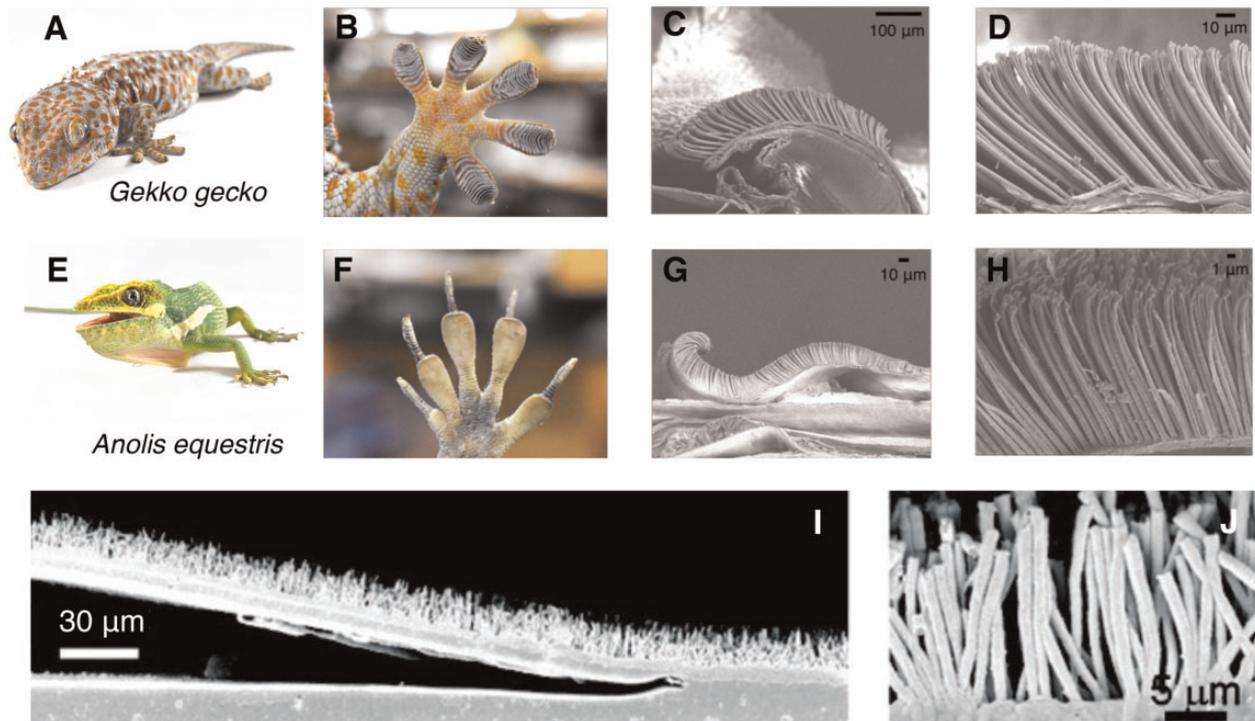


Fig. 1 The gekkotan and anoline adhesive system. (A) A whole-animal view of *Gekko gecko*. (B) Ventral view of *G. gecko* subdigital adhesive pads. (C) Representative setal array of *G. gecko*. (D) *G. gecko* setae. (E) A whole-animal view of *Anolis equestris*. (F) Ventral view of *A. equestris* subdigital adhesive pads. (G) Representative setal array of *A. equestris*. (H) *A. equestris* setae. (I–J) An exemplar gecko-inspired synthetic adhesive complete with lamellae and fibrils similar in morphology and size to the anoline adhesive system. Panels I and J adapted with permission from Lee et al. (2009). Copyright 2009 American Chemical Society.

Parness et al. 2009; Jeong et al. 2010), compliance of the dermis and properties of the digital tendon system (Bartlett et al. 2012; King et al. 2014; Gilman et al. 2015; King and Crosby 2015), and hierarchy (Northen et al. 2008; Greiner et al. 2009; Jeong et al. 2009; Murphy et al. 2009; Lee et al. 2012; Rong et al. 2014). Thus far, however, gecko-inspired synthetic adhesives have fallen short of matching the multifunctionality of their natural counterpart (Niewiarowski et al. 2016). A potential explanation for this is that most gecko-inspired adhesives are assembled from fibrils that do not accurately mimic the complex, hierarchical nature of gecko setae. Although some researchers have managed to fabricate, at best, pillars on pillars (Murphy et al. 2009), the technology to replicate the complex, branching nature of gecko setae is not yet available. Pad-bearing anoles, however, have independently evolved setal fields that consist of unbranched fibrils with a single spatulate tip (Ruibal and Ernst 1965; Williams and Peterson 1982) similar in morphology to single-pillared gecko-inspired adhesives (Fig. 1E–J). Examining anoline subdigital adhesive pads and their properties could help address the morphological and functional disparity between the naturally configured gecko setae and their gecko-inspired synthetic counterparts.

In this short perspective, we briefly review the pertinent literature concerning the anoline subdigital adhesive system, consider how its investigation could improve our understanding of fibrillar adhesion, and provide some initial hypotheses and questions for pursuit in future studies. Our main objective is to encourage discussion and suggest areas of future inquiry, such that we can begin to take full advantage of the diversity of lizard fibrillar adhesive structures; understand the relationships between morphology, performance, ecology and behavior; and develop biologically-inspired adhesives that can accurately capture the multifunctional properties of their natural counterparts.

Anolis lizards, their convergently evolved adhesive system, and the corresponding gaps in our knowledge

Anolis lizards are considered classic examples of convergence because distantly-related species of anoles share similar behavioral and morphological traits associated with specialization for a particular microhabitat (a concept known as ecomorphology) (Williams 1972; Losos 1990a, 2011). For example, anoles found in the crowns of tree canopies

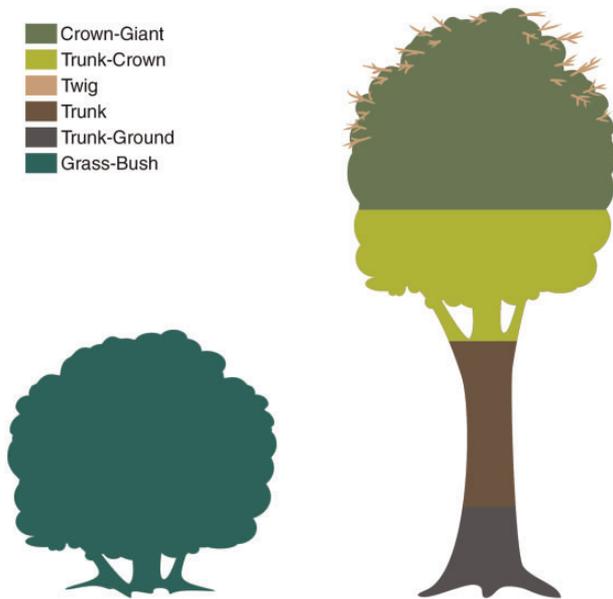


Fig. 2 *Anolis* ecomorph microhabitats. Each color represents the typical microhabitat occupied by the six *Anolis* ecomorph categories, each of which is named for the microhabitat it generally inhabits. Based on previous work detailing the scaling relationships between clinging ability, toe pad area, and perch height of different anole ecomorphs (Elstrott and Irschick 2004) and observations from fibrillar adhesion design maps (Spolenak et al. 2005), hypotheses can be generated that predict how the different ecomorphs may vary in subdigital microstructure. Considering that smaller bodied anoles (e.g., trunk-ground, trunk, and grass-bush anoles) adhere relatively better than larger bodied anoles, we might expect those smaller ecomorphs to possess setal morphologies and properties that result in greater adhesive ability, such as smaller spatulae, smaller aspect ratios closer to 10, setal elastic modulus between 0.1 and 10 GPa, and greater setal density (as suggested by Spolenak et al. 2005).

(‘crown-giants’) display large body size, short-limbs, well-developed subdigital adhesive pads, and long tails, which likely correlate with increased performance in the tree tops (Losos 1990a, 1990b, 2011). Crown-giant anoles are one of six “ecomorph” categories of Caribbean *Anolis* lizards, with each ecomorph being morphologically and behaviorally distinct from the others (Losos 1990a, 1990b, 2011) (Fig. 2). The repeated convergence of *Anolis* ecomorphs has led to anoles being recognized as a model system for studying the interactions between form, function, and behavior (Losos 1994; 2011; Mahler et al. 2013). Evolutionary convergence is a useful guide for bio-inspired design, as the repeated evolution of similar traits signifies viable solutions to common environmental problems (Fish and Beneski 2014). As such, anoles are prime candidates for the study of fibrillar adhesion.

Despite anoles being recognized as model systems for ecological and evolutionary explorations, their

uniquely derived adhesive system has not been investigated to anywhere near the extent of the more complex gecko manifestation (Losos 2011; Autumn et al. 2014; Niewiarowski et al. 2016; Russell 2017; Niewiarowski et al. 2017; Russell and Eslinger 2017), even though it has, on several occasions, been advocated to be an evolutionary key innovation (Peterson 1983; Warheit et al. 1999; Pinto et al. 2008; Losos 2011; Crandell et al. 2014). Nevertheless, several studies have documented gross aspects of setal morphology (Table 1) (Ruibal and Ernst 1965; Peterson and Williams 1981; Williams and Peterson 1982; Peterson 1983; Peattie and Full 2007), others have investigated adhesive clinging performance on smooth laboratory substrates (Irschick et al. 1996; Elstrott and Irschick 2004; Bloch and Irschick 2005; Irschick et al. 2005a; Garner et al. 2017), and yet others have correlated morphology and performance of anoline subdigital adhesive pads with habitat use (Macrini et al. 2003; Elstrott and Irschick 2004; Irschick et al. 2005a, 2005b). Morphological studies have revealed that (1) anoline setae are shorter, thinner, and present in higher density compared to those of geckos; and (2) each seta ends in a single spatulate tip that is over three times wider than gecko spatulae (Ruibal and Ernst 1965; Peterson and Williams 1981; Williams and Peterson 1982; Peterson 1983; Peattie and Full 2007; Losos 2011). Clinging ability on smooth laboratory substrates has been documented (Irschick et al. 1996; Elstrott and Irschick 2004; Bloch and Irschick 2005; Irschick et al. 2005a; Garner et al. 2017), and in general, it appears that clinging performance of *Anolis* is not markedly inferior to that of geckos (Irschick et al. 1996). Gross toe pad size and clinging ability on smooth laboratory substrates appear to be correlated with habitat use in several species of *Anolis*, suggesting that anoline ecology may be a determining factor in the size and performance of their subdigital adhesive pads (Macrini et al. 2003; Elstrott and Irschick 2004; Irschick et al. 2005a, 2005b), but the properties and performance of the *Anolis* adhesive system under ecologically-relevant conditions remain largely unknown.

Morphometric data pertaining to anoline setae have been collected from only 15 of the over 300 species of anoles (Losos 2011). Additionally, setal field configuration and variation across the proximo-distal axis of the toe pad and the potential consequences of this for adhesion within populations and species of *Anolis* have not been explored, although such data have been collected for a number of gekkonid species (Russell et al. 2007; Johnson and Russell 2009; Russell and Johnson 2014).

Table 1 Currently available morphometric data for anoline setae. Note that only 15 species are represented by these data, and all variables (setal density, setal length, setal diameter, tip width, and tip area) are reported for only two of these species (denoted with **)

Species	Density (setae/ μm^2)	Length (μm)	Diameter (μm)	Tip width (μm)	Tip area (μm^2)	Sources
<i>Chamaeleolis chamaeleontides</i> ^a	1	18.4–18.6	0.56–0.58	–	0.206–0.377	(1)
<i>Chamaeleolis porcus</i> ^b	1	22.3	0.53	–	0.264	(1)
<i>Chamaelinorops barbouri</i> ^c	0.5–0.6	5.0–8.4	0.47–0.56	–	0.6–1.472	(1)
<i>Phenacosaurus heterodermus</i> ^d	1.2	13.7–14.8	0.41–0.46	–	0.214–0.308	(1)
<i>Anolis cuvieri</i>	0.9–1.4	22.4–27.2	0.51–0.65	–	0.184–0.253	(1)
<i>Anolis cuvieri</i> **	1	22.4	0.51	0.729	0.229	(2)
<i>Anolis sheplani</i>	1.1–1.2	11.8–12.6	0.39–0.41	–	0.220–0.279	(1)
<i>Anolis occultus</i>	1.4	11	0.49	–	0.237	(1)
<i>Anolis</i> sp. n. near <i>eulaemus</i>	1	20.4	0.57	–	0.593	(1)
<i>Anolis valencienni</i>	1.1–1.4	15.3–17.2	0.40–0.47	–	0.171–0.209	(1)
<i>Anolis carolinensis</i>	0.83	21	0.5	0.87	–	(3, 4)
<i>Anolis equestris</i>	0.7	30	–	–	–	(3, 4)
<i>Anolis lineatopus</i>	0.51	–	–	1	–	(3, 4)
<i>Anolis sagrei</i>	1.7	20	–	0.75	–	(3, 4)
<i>Anolis homolechis</i>	–	20	–	–	–	(3)
<i>Anolis annectens</i> **	1.0–2.0	20	0.48	0.73	0.211	(5)

Sources: (1) Peterson (1983), (2) Williams and Peterson (1982), (3) Ruibal and Ernst (1965), (4) Peattie and Full (2007), and (5) Peterson and Williams (1981).

^aCurrently *Anolis chamaeleonides*;

^bCurrently *Anolis porcus*;

^cCurrently *Anolis barbouri*;

^dCurrently *Anolis heterodermus*.

How anoles can enhance our fundamental understanding of fibrillar adhesion

We believe that the anoline adhesive system provides a viable research avenue for enhancing many aspects of our understanding of fibrillar adhesion. First, anoline setal form more closely resembles that of the synthetic fibrillar adhesives currently able to be generated (Fig. 1) (Autumn 2006), and thus may provide a more effective means of benchmarking the performance of synthetic fibrillar adhesives. Because of this, investigation of anole fibrillar adhesion may allow us to not only assess how these synthetic adhesives perform in relation to their closest natural model, but also provide context for the impact of hierarchically-branched fibrillar structures (as seen in geckos) on adhesive performance and multifunctionality of fibrillar adhesive systems. Furthermore, the similarity between anoline setae and our current gecko-inspired synthetic fibrillar adhesives will allow us to tune synthetic adhesives to, and beyond, the morphological variation observed in the natural system, which will then allow us to investigate the role of the configuration of entire setal fields on fibrillar adhesive performance and its associated multifunctional properties.

The role of hierarchical branching in natural fibrillar adhesive systems possessed by geckos was initially explored 14 years ago by Yao and Gao (2006), who showed that the fractal-like branching geometry of gecko setae contributes significantly to strong adhesion, as well as easy release, of gecko toe pads. Many subsequent studies have focused on the various ways in which adhesive fiber characteristics can covary with hierarchical branching, including parameters such as fiber aspect ratio, fibril system effective elastic modulus, tip shape, contact splitting, and contact area (Brodoceanu et al. 2016). Theories of contact mechanics, as they apply to fibrillar systems in general and geckos in particular, can differentially emphasize the importance of parameters that covary with branching. Because of this, our ability to draw design principles from the gecko adhesive system by comparing its performance to that of simplified synthetic versions is easily thwarted. For example, many synthetic mimics of gecko setae are fabricated from polymer fibers with low modulus and large contact size compared to gecko setae because of limitations in molding techniques and material properties of the fibers (Röhrig et al. 2012). Although technologies on the horizon, such as laser lithography (Tricinci et al. 2018), will make it possible to mimic the hierarchical

branching structure of gecko setae, we also need natural setal models that are unbranched (e.g., *Anolis* setae) to enable factorial experimental designs to be used to examine effects on adhesion that result from the covariance of aspect ratio, degree of hierarchical branching, effective and inherent elastic modulus, and other parameters. Using such models to delimit the parameter space explored by experiments should help accelerate discovery of the design space occupied by vertebrate fibrillar systems and the translation of such designs into robust synthetic mimics.

Furthermore, anole setae more closely resemble the iconography of the theoretical models of substrate contact that are used to predict the mechanics of fibrillar adhesion (Johnson et al. 1971; Kendall 1975). The Johnson–Kendall–Roberts (JKR) model calculates the pull-off forces of two elastic spherical solids (Johnson et al. 1971), although most modern applications use a hemispherical probe in contact with a planar surface (Fig. 3A) (Johnson and Sridhar 2001; Gao et al. 2005; Yao and Gao 2006), whereas the Kendall tape peeling model predicts the adhesion of an elastic tape being peeled from a surface at a particular angle (θ) (Fig. 3B) (Kendall 1975). Although these theories have been used to explain gecko adhesion (Autumn et al. 2002; Hansen and Autumn 2005; Huber et al. 2005; Autumn et al. 2006; Yao and Gao 2006), they fail to account for (or oversimplify) the potential impact of the complex, branching structure of gekkotan setae on adhesive force production of both the individual fibrils and the whole organism. For example, the JKR and Kendall tape peeling models have been used to estimate adhesive performance of spatulae (Autumn et al. 2014). This becomes problematic, however, when the number of spatulae in contact with a surface is unknown for a single seta. Because of this, relationships between whole toe pad and single seta or spatula adhesion become difficult to interpret. Anoles, however, incorporate at least one fewer layer of the adhesive hierarchy (because their setae bear only one spatula on a single, unbranched stalk rather than hundreds to thousands of spatulae on multiply-branched stalks). If single seta measurements from anoles can be obtained, comparisons can easily be made with the JKR and Kendall tape peeling models. If these models can accurately estimate anoline single seta adhesion, then they could be used to estimate adhesion of setae in a variety of conditions. It is possible, however, that these adhesion models may not be ideal for explaining fibrillar adhesion because they make a number of critical assumptions that may not be particularly relevant to fibrillar adhesive systems (e.g.,

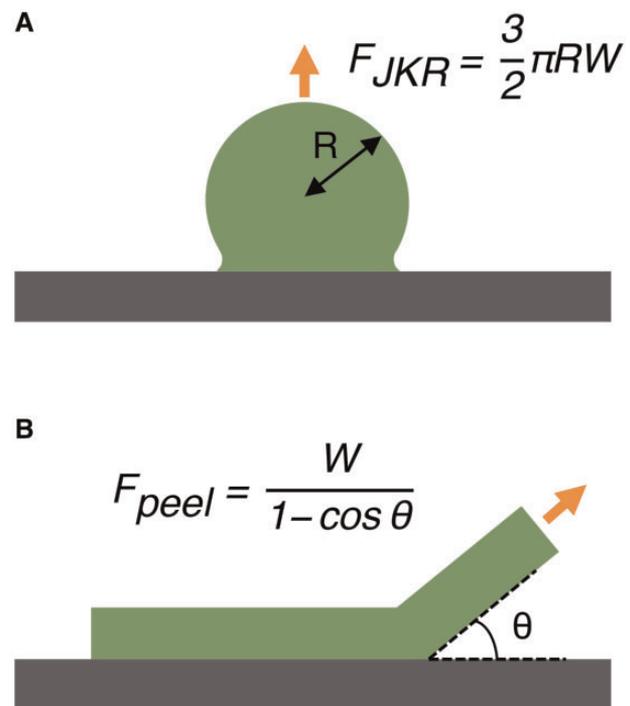


Fig. 3 Example of two theoretical models previously used to explain gecko adhesion. These models more closely accord with the morphology of anoline setae. **(A)** Modern applications of the JKR model predict the pull-off force (F_{JKR}) of an elastic sphere in contact with a planar surface. R represents the radius of the sphere and W represents the work of adhesion (Johnson et al. 1971). **(B)** The Kendall tape peeling model predicts the force required to peel an elastic tape at angle (θ) from a planar surface. W denotes the work of adhesion (Kendall 1975). These models have been historically used to explain the adhesion of gecko setae with multiple spatulae (Autumn et al. 2014), but this is problematic when the number of spatulae in contact with the surface at any given point in time is unknown. If the adhesive force of a single anole seta/spatula can be measured and evaluated against the predictions of the JKR and Kendall tape peeling models, these models, if validated, could be used to model the adhesion and other properties of anoline setae under a variety of conditions.

normal pull-off and spherical tip geometry in the JKR model or steady-state peeling in the Kendall tape peeling model). Nevertheless, comparisons between anoline setal adhesion and the adhesion models currently employed in fibrillar adhesion literature may assist in identifying limitations of the current models, adapting such models for fibrillar adhesion specifically, or developing new models that better represent the mechanics and properties of fibrillar adhesive systems.

Gekkotan and anoline adhesive systems have long been advocated to be key innovations that permitted niche expansion and subsequent diversification in these taxa (Peterson 1983; Warheit et al. 1999; Losos 2011; Gamble et al. 2012; Autumn et al. 2014), but few

empirical data support these notions (Autumn et al. 2014; Niewiarowski et al. 2016). Understanding how adhesive systems are derived and utilized in nature can not only increase our understanding of the evolutionary and ecological origins of such systems, but also provide information that can be employed in the design and fabrication of synthetic fibrillar adhesives (Niewiarowski et al. 2016). Historically, research on lizard fibrillar adhesion has mostly focused on the function, structure, and mechanics of the gekkotan adhesive system under controlled laboratory conditions. However, several studies have advocated integrated evolutionary and ecological investigations of fibrillar adhesion (Russell 2002; Autumn et al. 2014; Niewiarowski et al. 2016, 2017). Employing ecological and evolutionary data, several persistent questions regarding lizard adhesive systems could be made more tractable, such as: What surfaces are utilized in their natural habitats and what are the conditions of those surfaces (e.g., wet, dry, rough, smooth, dirty, clean, etc.)? When is such a system actually utilized in nature (i.e., engaged)? What are the relationships between the morphology and performance of such systems and what is their relationship to evolutionary fitness? Does habitat microstructure correlate with adhesive system morphology, performance, and evolution? Are such adhesive systems truly key innovations? The data necessary to begin answering these questions are currently lacking for geckos (Niewiarowski et al. 2016), but the many decades of ecological and evolutionary investigation of *Anolis* lizards provide a potentially fruitful backdrop for addressing such questions.

Hypotheses and areas of future inquiry

In this section, we offer several potential hypotheses and concepts for future inquiry. First, we begin with a number of hypotheses/areas for future work that take a hierarchical form (i.e., the results of each study inform the design/focus of the subsequent studies).

First, the “single foot hair” measurements made by Autumn et al. (2000) have, to our knowledge, never been repeated for any other geckos, and have never been analyzed in terms of how many spatulae contribute to the overall adhesive force that was recorded. We do not know where the “single foot hair” came from on the foot and do not know how many spatulae it had or how many of them contributed to the force outputs obtained. All statements since then about the adhesive function of an individual seta have been extrapolated from that study. Because anoline setae only have a single spatula (of larger size than that of geckos), attachment by a seta

will be directly relatable to the force that the seta can generate and should be interpretable directly in terms of the JKR and Kendall adhesion models. Employing the spatula dimensions of *Anolis* it should be possible to predict what forces can be generated by a single setal shaft with a single tip of known dimensions and with known material properties of the setal shaft. In this way, anoles may be much more directly applicable for relating force production of toe pads to the setae that they bear.

Given that single anole setal forces could be predicted, then by calculating the number of setae on a toe pad, entire foot, or entire animal, and measuring clinging performance, we should be able to assess the percentage of all setae/spatulae actually engaged. Thus, clinging performance should be able to be related to surface structure (such as roughness) in terms of the proportion of setae/spatulae that can make contact at any one time. Subsequently, we can begin to ask and answer some of the more ecological and evolutionary questions alluded to above. For example, we should be able to measure toe pad size, seta, and spatula numbers for different ecomorphs (ideally of the same monophyletic radiation) and relate these data to clinging ability and to the nature of surfaces naturally exploited. Predictions, using the rich anole ecology literature, should be able to be made about performance, surface structure, and intrageneric adaptation.

Second, our laboratories have begun comprehensive examinations of the morphometrics and configuration of anoline setal fields, and we have formulated hypotheses based on what is already known about gecko setal morphology. Johnson and Russell (2009) investigated the setal field configuration of a number of gekkonid species in the genus *Rhoptropus* and found that setal length increases distally both within and between scansors. They hypothesized that the variation in length may permit simultaneous detachment of setae during active distoproximal hyperextension (i.e., the characteristic distal-to-proximal peeling of the subdigital pads of most geckos). In contrast to most geckos, anoles peel their subdigital adhesive pads in the opposite direction (i.e., in a proximal-to-distal direction) (Russell and Bels 2001). Thus, if distoproximal hyperextension in geckos is the main driving factor of variation in setal length, we might expect to observe markedly different setal field configuration in anoles or even reverse trends (i.e., increases in setal length proximally versus distally).

Third, a number of macromorphological features of *Anolis* lizards vary in conjunction with their typical microhabitat (i.e., ecomorph category) including

limb length, tail length, gross body size, and number of lamellae (Beuttell and Losos 1999; Losos 2011). Whether subdigital microstructure also varies with habitat use, however, has not been studied (Losos 2011). Toe pad area and clinging ability both appear to correlate positively with perch height, yet it is currently unknown whether setal morphometrics also vary with perch height, clinging ability, or ecomorph type (Elstrott and Irschick 2004; Losos 2011). Interestingly, Elstrott and Irschick (2004) found that anoline clinging ability scales as predicted by isometry ($M^{0.67}$), which results in a functional disparity in clinging ability between small and large anoles (i.e., small anoles cling relatively better than larger anoles). Considering these are size-corrected observations and that variation in adhesive pad area does not explain 100% of the variation in clinging ability, subdigital microstructure may vary between different anoline ecomorphs. Specifically, we may expect smaller bodied anoles (e.g., trunk-ground, trunk, grass-bush anoles; Fig. 2) to possess setal morphologies that result in stronger adhesion relative to their body size. Adhesion design maps (Spolenak et al. 2005) may be helpful for generating morphological predictions, as they suggest that adhesive stress increases with decreases in tip radius (spatula size), materials with elastic moduli between 0.1 and 10 GPa, and structures with aspect ratios between 3 and 10. Setal morphology of different anole ecomorphs could be explored within this framework to examine whether setal morphology also varies within the well-established ecomorph paradigm; studies that our laboratories are currently undertaking.

Conclusions

Although the past two decades of intensely focused research on the gekkotan adhesive system has led to numerous influential discoveries about fibrillar adhesion, there are still major gaps in our understanding for which parallel investigation of the anoline adhesive system may be more suited. For example, studying the single fibril morphology of anoline setae may permit us to address why the observed discrepancy between the multifunctional properties of gecko-inspired synthetic adhesives and the natural gekkotan adhesive system is so great (Niewiarowski et al. 2016). Furthermore, the collective evolutionary and ecological data available for *Anolis* lizards will allow better tracking of the finer details of organism–environment–function interactions. We encourage communal, transdisciplinary investigation of the morphology, performance, and behavior of anoles

with respect to their subdigital adhesive pads to increase our comprehension of biological adhesive systems. Furthermore, we posit that investigation of this system will also assist in further pursuing questions about lizard fibrillar adhesive systems that are seemingly otherwise intractable.

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References

- Autumn K. 2006. How gecko toes stick. *Am Sci* 94:124–32.
- Autumn K, Dittmore A, Santos D, Spenko M, Cutkosky M. 2006. Frictional adhesion: a new angle on gecko attachment. *J Exp Biol* 209:3569–79.
- Autumn K, Liang YA, Hsieh ST, Zesch W, Chan WP, Kenny TW, Fearing R, Full RJ. 2000. Adhesive force of a single gecko foot-hair. *Nature* 405:681–5.
- Autumn K, Niewiarowski PH, Puthoff JB. 2014. Gecko adhesion as a model system for integrative biology, interdisciplinary science, and bioinspired engineering. *Annu Rev Ecol Evol Syst* 45:445–70.
- Autumn K, Sitti M, Liang YA, Peattie AM, Hansen WR, Sponberg S, Kenny TW, Fearing R, Israelachvili JN, Full RJ. 2002. Evidence for van der Waals adhesion in gecko setae. *Proc Natl Acad Sci U S A* 99:12252–6.
- Bartlett MD, Croll AB, King DR, Paret BM, Irschick DJ, Crosby AJ. 2012. Looking beyond fibrillar features to scale gecko-like adhesion. *Adv Mater* 24:1078–83.
- Beuttell K, Losos JB. 1999. Ecological morphology of Caribbean anoles. *Herpetol Monogr* 13:1–28.
- Bloch N, Irschick DJ. 2005. Toe-clipping dramatically reduces clinging performance in a pad-bearing lizard (*Anolis carolinensis*). *J Herpetol* 39:288–93.
- Brodoceanu D, Bauer C, Kroner E, Arzt E, Kraus T. 2016. Hierarchical bioinspired adhesive surfaces—a review. *Bioinspir Biomim* 11:051001.
- Crandell KE, Herrel A, Sasa M, Losos JB, Autumn K. 2014. Stick or grip? Co-evolution of adhesive toepads and claws in *Anolis* lizards. *Zoology* 117:363–9.
- Elstrott J, Irschick DJ. 2004. Evolutionary correlations among morphology, habitat use and clinging performance in Caribbean *Anolis* lizards. *Biol J Linn Soc Lond* 83:389–98.
- Fish FE, Beneski JT. 2014. Evolution and bio-inspired design: natural limitations. In: Goel AK, McAdams DA, Stone RB, editors. *Biologically inspired design: computational methods and tools*. London: Springer London. p. 287–312.
- Gamble T, Greenbaum E, Jackman TR, Russell AP, Bauer AM. 2012. Repeated origin and loss of adhesive toepads in geckos. *PLoS One* 7:e39429.

- Gao H, Wang X, Yao H, Gorb S, Arzt E. 2005. Mechanics of hierarchical adhesion structures of geckos. *Mech Mater* 37:275–85.
- Garner AM, Lopez SM, Niewiarowski PH. 2017. Brown anole (*Anolis sagrei*) adhesive forces remain unaffected by partial claw clipping. *Acta Herpetologica* 12:133–7.
- Gilman CA, Imburgia MJ, Bartlett MD, King DR, Crosby AJ, Irschick DJ. 2015. Geckos as Springs: mechanics Explain Across-Species Scaling of Adhesion. *PLoS One* 10:e0134604.
- Greiner C, Arzt E, Del Campo A. 2009. Hierarchical gecko-like adhesives. *Adv Mater* 21:479–82.
- Hansen WR, Autumn K. 2005. Evidence for self-cleaning in gecko setae. *Proc Natl Acad Sci U S A* 102:385–9.
- Huber G, Gorb SN, Spolenak R, Arzt E. 2005. Resolving the nanoscale adhesion of individual gecko spatulae by atomic force microscopy. *Biol Lett* 1:2–4.
- Irschick DJ, Austin CC, Petren K, Fisher RN, Losos JB, Ellers O. 1996. A comparative analysis of clinging ability among pad-bearing lizards. *Biol J Linn Soc Lond* 59:21–35.
- Irschick DJ, Carlisle E, Elstrott J, Ramos M, Buckley C, VanHooydonck B, Meyers J, Herrel A. 2005. A comparison of habitat use, morphology, clinging performance and escape behaviour among two divergent green anole lizard (*Anolis carolinensis*) populations. *Biol J Linn Soc Lond* 85:223–34.
- Irschick DJ, VanHooydonck B, Herrel A, Meyers J. 2005. Intraspecific correlations among morphology, performance and habitat use within a green anole lizard (*Anolis carolinensis*) population. *Biol J Linn Soc Lond* 85:211–21.
- Jeong HE, Lee J-K, Kim HN, Moon SH, Suh KY. 2009. A nontransferring dry adhesive with hierarchical polymer nanohairs. *Proc Natl Acad Sci U S A* 106:5639–44.
- Jeong HE, Lee J-K, Kwak MK, Moon SH, Suh KY. 2010. Effect of leaning angle of gecko-inspired slanted polymer nanohairs on dry adhesion. *Appl Phys Lett* 96:043704.
- Johnson K, Kendall K, Roberts A. 1971. Surface energy and the contact of elastic solids. *Proc R Soc Lond A Math Phys Sci* 324:301–13.
- Johnson K, Sridhar I. 2001. Adhesion between a spherical indenter and an elastic solid with a compliant elastic coating. *J Phys D Appl Phys* 34:683.
- Johnson MK, Russell AP. 2009. Configuration of the setal fields of *Rhoptropus* (Gekkota: Gekkonidae): functional, evolutionary, ecological and phylogenetic implications of observed pattern. *J Anat* 214:937–55.
- Kendall K. 1975. Thin-film peeling-the elastic term. *J Phys D Appl Phys* 8:1449–52.
- King DR, Bartlett MD, Gilman CA, Irschick DJ, Crosby AJ. 2014. Creating gecko-like adhesives for “real world” surfaces. *Adv Mater* 26:4345–51.
- King DR, Crosby AJ. 2015. Optimizing adhesive design by understanding compliance. *ACS Appl Mater Interfaces* 7:27771–81.
- Lee DY, Lee DH, Lee SG, Cho K. 2012. Hierarchical gecko-inspired nanohairs with a high aspect ratio induced by nanoyielding. *Soft Matter* 8:4905–10.
- Lee J, Bush B, Maboudian R, Fearing RS. 2009. Gecko-inspired combined lamellar and nanofibrillar array for adhesion on nonplanar surface. *Langmuir* 25:12449–53.
- Lee J, Fearing RS, Komvopoulos K. 2008. Directional adhesion of gecko-inspired angled microfiber arrays. *Appl Phys Lett* 93:191910.
- Losos JB. 1990. Ecomorphology, performance capability, and scaling of West Indian *Anolis* lizards: an evolutionary analysis. *Ecol Monogr* 60:369–88.
- Losos JB. 1990. The evolution of form and function: morphology and locomotor performance in West Indian *Anolis* lizards. *Evolution* 44:1189–203.
- Losos JB. 1994. Integrative approaches to evolutionary ecology: *Anolis* lizards as model systems. *Annu Rev Ecol Syst* 25:467–93.
- Losos JB. 2011. Lizards in an evolutionary tree: ecology and adaptive radiation of anoles. Berkeley (CA): University of California Press.
- Macrini TE, Irschick DJ, Losos JB. 2003. Ecomorphological differences in toepad characteristics between mainland and island anoles. *J Herpetol* 37:52–8.
- Maderson P. 1964. Keratinized epidermal derivatives as an aid to climbing in gekkonid lizards. *Nature* 203:780–1.
- Mahler DL, Ingram T, Revell LJ, Losos JB. 2013. Exceptional convergence on the macroevolutionary landscape in island lizard radiations. *Science* 341:292–5.
- Murphy MP, Kim S, Sitti M. 2009. Enhanced adhesion by gecko-inspired hierarchical fibrillar adhesives. *ACS Appl Mater Interfaces* 1:849–55.
- Niewiarowski PH, Stark AY, Dhinojwala A. 2016. Sticking to the story: outstanding challenges in gecko-inspired adhesives. *J Exp Biol* 219:912–9.
- Niewiarowski PH, Stark AY, Dhinojwala A. 2017. A bibliometric analysis of gecko adhesion: a view of its origins and current directions. In: Heepe L, Xue L, Gorb SN, editors. Bio-inspired structured adhesives. Cham, Switzerland: Springer. p. 1–19.
- Northern MT, Greiner C, Arzt E, Turner KL. 2008. A Gecko-inspired reversible adhesive. *Adv Mater* 20:3905–9.
- Parness A, Soto D, Esparza N, Gravish N, Wilkinson M, Autumn K, Cutkosky M. 2009. A microfabricated wedge-shaped adhesive array displaying gecko-like dynamic adhesion, directionality and long lifetime. *J Roy Soc Interface* 6:1223–32.
- Peattie A, Full R. 2007. Phylogenetic analysis of the scaling of wet and dry biological fibrillar adhesives. *Proc Natl Acad Sci U S A* 104:18595–600.
- Peterson J. 1983. The evolution of the subdigital pad of *Anolis* 2. Comparisons among the iguanid genera related to the anolines and a view from outside the radiation. *J Herpetol* 17:371–97.
- Peterson JA, Williams EE. 1981. A case history in retrograde evolution: the Onca lineage in anoline lizards: II. Subdigital fine structure. *Bull Mus Comp Zool* 149:215–68.
- Pinto G, Mahler DL, Harmon LJ, Losos JB. 2008. Testing the island effect in adaptive radiation: rates and patterns of morphological diversification in Caribbean and mainland *Anolis* lizards. *Proc R Soc Lond B Biol Sci* 275:2749–57.
- Röhrig M, Thiel M, Worgull M, Hölscher H. 2012. 3D direct laser writing of nano- and microstructured hierarchical gecko-mimicking surfaces. *Small* 8:3009–15.
- Rong Z, Zhou Y, Chen B, Robertson J, Federle W, Hofmann S, Steiner U, Goldberg-Opppenheimer P. 2014. Bio-inspired

- hierarchical polymer fiber–carbon nanotube adhesives. *Adv Mater* 26:1456–61.
- Ruibal R, Ernst V. 1965. The structure of the digital setae of lizards. *J Morphol* 117:271–93.
- Russell AP. 2002. Integrative functional morphology of the gekkotan adhesive system (Reptilia: Gekkota). *Integr Comp Biol* 42:1154–63.
- Russell AP. 2017. The structure of anoline (Reptilia: Dactyloidae: *Anolis*) toe pads in relation to substratum conformity. *Acta Zoologica* 98:300–9.
- Russell AP, Bels V. 2001. Digital hyperextension in *Anolis sagrei*. *Herpetologica* 57:58–65.
- Russell AP, Eslinger A. 2017. A whole lamella perspective on the origin of the epidermal free margin of *Anolis* (Reptilia: Dactyloidae) toe pads. *J Morphol* 278:360–8.
- Russell AP, Johnson MK. 2014. Between a rock and a soft place: microtopography of the locomotor substrate and the morphology of the setal fields of Namibian day geckos (Gekkota: Gekkonidae: *Rhoptropus*). *Acta Zoologica* 95:299–318.
- Russell AP, Johnson MK, Delannoy SM. 2007. Insights from studies of gecko-inspired adhesion and their impact on our understanding of the evolution of the gekkotan adhesive system. *J Adhes Sci Technol* 21:1119–43.
- Seo S, Lee J, Kim K-S, Ko KH, Lee JH, Lee J. 2014. Anisotropic adhesion of micropillars with spatula pads. *ACS Appl Mater Interfaces* 6:1345–50.
- Spolenak R, Gorb S, Arzt E. 2005. Adhesion design maps for bio-inspired attachment systems. *Acta Biomater* 1:5–13.
- Tricinci O, Eason EV, Filippeschi C, Mondini A, Mazzolai B, Pugno NM, Cutkosky MR, Greco F, Mattoli V. 2018. Approximating gecko setae via direct laser lithography. *Smart Mater Struct* 27:075009.
- Warheit KI, Forman JD, Losos JB, Miles DB. 1999. Morphological diversification and adaptive radiation: a comparison of two diverse lizard clades. *Evolution* 53:1226–34.
- Williams E, Peterson J. 1982. Convergent and alternative designs in the digital adhesive pads of scincid lizards. *Science* 215:1509–11.
- Williams EE. 1972. The origin of faunas. evolution of lizard congeners in a complex island fauna: a trial analysis. In: Dobzhansky T, Hecht MK, Steere WC, editors. *Evolutionary Biology*. Vol. 6. New York (NY): Springer. p. 47–89.
- Xue L, Iturri J, Kappl M, Butt H, Jr, del Campo A. 2014. Bioinspired orientation-dependent friction. *Langmuir* 30:11175–82.
- Yao H, Gao H. 2006. Mechanics of robust and releasable adhesion in biology: bottom-up designed hierarchical structures of gecko. *J Mech Phys Solids* 54:1120–46.