

Phylogenetic analysis of the scaling of wet and dry biological fibrillar adhesives

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Edited by John G. Hildebrand, University of Arizona, Tucson, AZ, and approved September 26, 2007 (received for review August 10, 2007)

Fibrillar, or “hairy,” adhesives have evolved multiple times independently within arthropods and reptiles. These adhesives exhibit highly desirable properties for dynamic attachment, including orientation dependence, wear resistance, and self-cleaning. Our understanding of how these properties are related to their fibrillar structure is limited, although theoretical models from the literature have generated useful hypotheses. We survey the morphology of 81 species with fibrillar adhesives to test the hypothesis that packing density of contact elements should increase with body size, whereas the size of the contact elements should decrease. We test this hypothesis in a phylogenetic context to avoid treating historically related species as statistically independent data points. We find that fiber morphology is better predicted by evolutionary history and adhesive mechanism than by body size. As we attempt to identify which morphological parameters are most responsible for the performance of fibrillar adhesives, it will be important to take advantage of the natural variation in morphology and the potentially suboptimal outcomes it encompasses, rather than assuming evolution to be an inherently optimizing process.

contact splitting | fibrillar adhesion | setae | phylogeny | independent contrasts

Geckos are best known for using their subdigital fibrillar adhesive to scale vertical and overhanging, smooth or rough surfaces with ease. Yet, “dry” fibrillar adhesives are not unique to geckos but can be found in anoles, skinks, and spiders. Some insects also bear hairy pads but augment them with “wet” sticky secretions. Although the adhesive mechanisms may differ, the similarities in their morphology have led researchers to create models in search of universal relationships between structure and function across all fibrillar adhesive organisms (1). Such relationships, if found, would do much to guide our understanding of how fibrillar adhesives function, to determine how they benefit or limit the organisms using them and to offer clear design principles for the engineers attempting fabrication of such adhesives (2–10).

Contact splitting is one important principle of fibrillar adhesives predicted by several models including fracture mechanics (11, 12) and Johnson-Kendall-Roberts theory (JKR) (13, 14). This principle suggests that a given amount of surface area detaches with higher adhesive forces (or work) if it is divided into smaller, more numerous contact elements (14). Contact splitting is, at minimum, a byproduct of fibrillar adhesives, which are by definition densely packed fine structures. Geckos and several other organisms seem to capitalize further on the advantages of contact splitting by terminally branching into many flattened tips, termed “spatulae,” of considerably smaller radius than the stalks themselves (Fig. 1). Despite the growing body of physical and mathematical literature modeling fibrillar adhesion, there have been few direct tests of the models’ predictions on the biological specimens (14–22) and even fewer that attempt to describe or account for the variation in adhesive morphology seen in nature (23–25).

Arzt *et al.* (24) hypothesize that organisms take advantage of contact splitting to overcome the unfavorable geometric scaling of body mass with adhesive pad area. Using JKR theory, they

estimate the pull-off force (F_c) of a field of n hemispherical contact elements with diameter s in contact with a smooth surface to be

$$F_c = n \frac{3}{4} \pi s \gamma, \quad [1]$$

where γ is the adhesion energy per area. Contacts are square-packed, and their diameter is inversely proportional to the square root of contact density. It is assumed that adhesive pad area per unit mass decreases with size according to geometric similarity. This mass-specific decrease is predicted to drive a compensatory increase in contact density and a corresponding decrease in seta and contact diameter to support increasing body mass. Given these assumptions, Arzt *et al.* (24) hypothesize that spatular density should increase with body mass to the $2/3$ power across all fibrillar adhesive organisms and that spatular width should decrease with body size to the $-1/3$ power. They survey a variety of fibrillar adhesive organisms (nine flies, five beetles, two spiders, one heteropod, three geckos, and one anole) to test their hypothesis, but did not include the effects of evolutionary history, setal branching, or adhesive mechanism (dry versus wet, or secretion-aided adhesion) in their analysis. Because the hypothesis is a logical, compelling, and important one, we decided to retest their prediction using a phylogenetic approach that considers more species over a wider range of body mass and setal morphology.

Results and Discussion

The data shown by Arzt *et al.* (24) in support of their scaling hypotheses assume that all taxa have evolved independently. If we make the same assumption with our expanded dataset, we would also conclude that spatular density increases significantly with body mass, although to the 0.50 power, significantly less than the predicted $2/3$ [$P < 0.001$; $r^2 = 0.47$; 95% confidence limits (CL) = 0.38, 0.62; Fig. 2*a* and Table 1]. Phylogenetically uncorrected or raw species values (SV) would suggest that spatular width varies significantly with body mass to the -0.27 power ($P < 0.0001$; $r^2 = 0.44$; 95% CL: -0.35 , -0.20 ; Fig. 2*c* and Table 2), not significantly different from the $-1/3$ prediction ($P = 0.11$).

After correcting for the fact that some species are more closely related phylogenetically than others, we found that no parameter describing setal morphology scaled with body size to an exponent significantly different from zero (spatula density, $P = 0.16$, Fig. 2*b*; spatula width, $P = 0.072$, Fig. 2*d*; seta length, $P = 0.63$; seta width, $P = 0.30$). Furthermore, neither phylogenetically cor-

Author contributions: A.M.P. and R.J.F. designed research; A.M.P. performed research; A.M.P. analyzed data; and A.M.P. and R.J.F. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

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This article contains supporting information online at www.pnas.org/cgi/content/full/0707591104/DC1.

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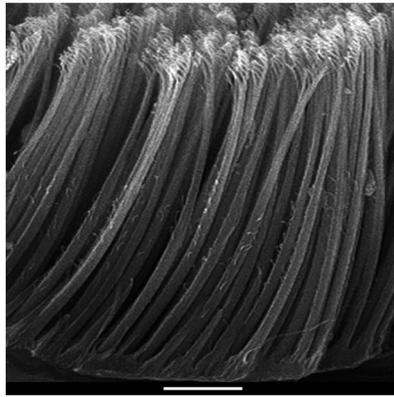
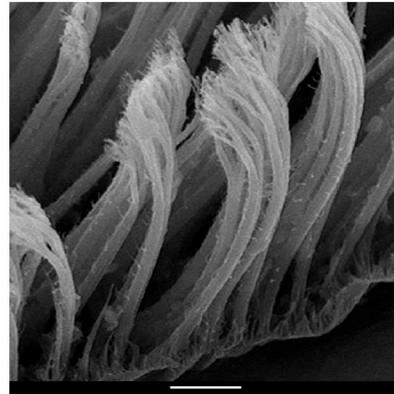
Rhacodactylus leachianus (300 g)*Sphaerodactylus glaucus* (0.3 g)

Fig. 1. Setal morphology of two gecko species varying by three orders of magnitude in body mass but by only 2-fold in density of contact elements (spatulae). (Scale bars, 10 μm .)

rected nor uncorrected values for spatula density and spatula width scaled with body mass to an exponent significantly different from zero when partitioned into wet (SV: density, $P = 0.30$; width, $P = 0.54$) and dry adhesive organisms (SV: density, $P = 0.086$; width, $P = 0.19$; Fig. 2 *a* and *c* and Tables 1 and 2). Our

expanded dataset revealed that within groups of related taxa, there were no strong trends relating spatular density or width with body mass (Figs. 1 and 3). By partitioning corrected values according to setal branching structure, we found that the assumed inverse relationship between spatular density and spatula

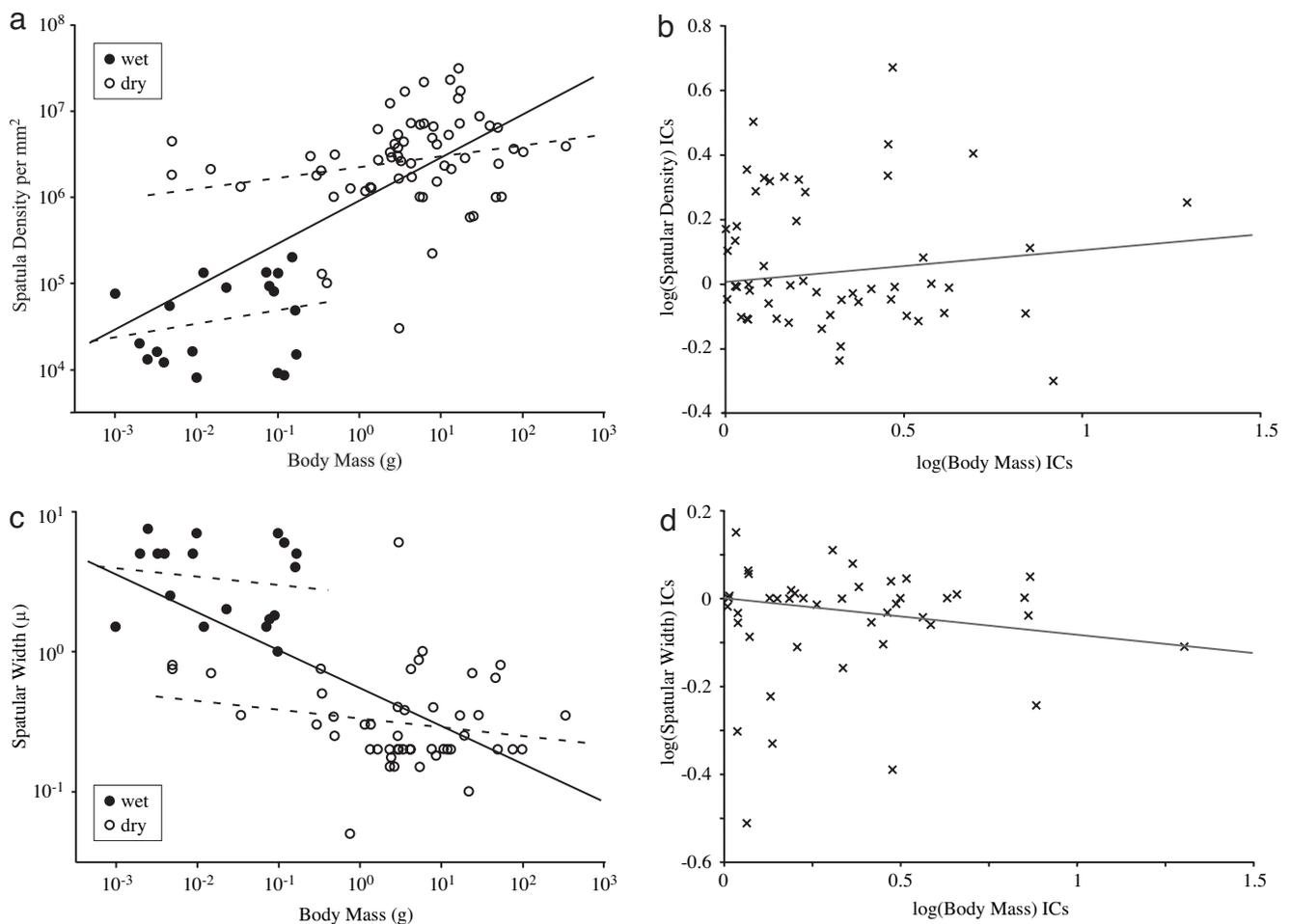


Fig. 2. Linear regression on species values compared with independent contrasts (ICs). Solid lines represent regressions through the pooled dataset. Dashed lines represent partitioned (wet/dry) data. (a) Log–log plot of spatular density versus body mass for 81 taxa. (b) Phylogenetically corrected values for spatular density versus body mass. (c) Log–log plot of spatular width (μm) versus body mass (g) for 67 taxa. (d) Phylogenetically corrected values for spatular width versus body mass.

Table 1. Regression results for spatula-density versus body-mass analyses

Partition	Scaling exponents		Comparison of analyses
	Raw species values	Phylogenetically corrected (ICs)	
Dry	0.13 (ns); 95% CL (−0.020, 0.27); $P = 0.08$; $df = 61$	0.064 (ns); 95% CL (−0.13, 0.26); $P = 0.50$; $df = 37$	ns
Wet	0.16 (ns); 95% CL (−0.16, 0.47); $P = 0.30$; $df = 18$	0.093 (ns); 95% CL (−0.10, 0.29); $P = 0.32$; $df = 15$	ns
Branched	0.22 (+); 95% CL (0.052, 0.38); $P = 0.014$; $df = 43$	−0.030 (ns); 95% CL (−0.25, 0.19); $P = 0.78$; $df = 22$	*
Unbranched	0.29 (+); 95% CL (0.089, 0.43); $P = 0.006$; $df = 36$	0.12 (ns); 95% CL (−0.024, 0.26); $P = 0.10$; $df = 31$	*
Pooled	0.50 (+); 95% CL (0.38, 0.62); $P < 0.001$; $df = 80$	0.10 (ns); 95% CL (−0.036, 0.24); $P = 0.14$; $df = 53$	*

Each analysis was conducted on species values and ICs by using pooled and partitioned datasets (dry/wet, branched/unbranched). P values indicate whether the exponent is significantly different from zero. The rightmost column indicates where results from phylogenetic analyses were significantly different from nonphylogenetic analyses. +, significant and positive relationship; *, analyses yielded significantly different conclusions; ns, no significant relationship or no significant difference between analyses.

width was only present across unbranched setae (95% CL: −0.78, −0.38; $P < 0.001$). The spatular density of branched setae did not scale predictably with spatula size (95% CL: −0.24, 0.50; $P = 0.45$) but was in general much greater than that of unbranched setae.

The hypothesis that larger animals should benefit from higher spatular density is the most reasonable null model. In fact, available data appear to support the notion. Among fibrillar adhesive organisms, certain geckos have attained their relatively large size because they inherited from their ancestors especially small, densely packed spatulae. Both the largest living and extinct geckos (*Rhacodactylus leachianus* and *Hoplodactylus delcourti*; ref. 26) belong to a clade of geckos whose current members possess the highest spatular densities of all organisms with setae. However, miniaturized geckos (various *Sphaerodactylus* spp., at <1 g, rank among the smallest of the tetrapods; ref. 27) share the same spatular morphology and density as many of their much larger relatives (Fig. 1). To invoke a scaling law, body mass must predominately determine adhesive morphology, and morphology must not be constrained by ancestry. It appears that natural selection has driven gekkonid body size in divergent directions under divergent pressures, rather than larger and larger as their spatular morphology alone might allow. This result yields new predictions. For instance, we can hypothesize that the smaller organisms within each group possess an advantage. Animals with lower body mass may either enjoy a higher safety factor or require less total pad area per body mass than their larger relatives.

Our results question the assumption that natural selection has acted to increase spatular density solely due to increased static normal forces during station-keeping. Considering that even large Tokay geckos hang easily by a single toe (20) and that the shear force generated at that toe fails under a load 10–20 times their body weight (14), it is unlikely that the adhesive performance of most organisms is limited by the static support of their body mass. Geckos running up a vertical surface at nearly one meter per second attach their adhesive pads in 5 ± 2 ms and detach them in 15 ± 4 ms (28). Peak shear forces exceed twice

body weight at midstance. Adhesive function depends on how effectively single setae, arrays, toes and feet all function synergistically during dynamic attachment and detachment, not just the density and size of contact elements. Additional variation is likely present for species that live on different substrates, because attachment to rougher surfaces may depend on, among other things, seta length, angle, and curvature, as well as effective seta, array, and toe compliance (12, 21, 29–32). The setae of arthropods are made of cuticle, which can vary in stiffness from 1 kPa to tens of GPa (33), whereas reptile setae are likely confined to a narrow range of high elastic moduli (25). Furthermore, most animals do not use fibrillar adhesives exclusively but are aided by alternative attachment mechanisms such as claws. Finally, each taxon must grow through a range of body sizes during its lifespan, with undetermined constraints on its adhesive pad morphology as it develops. Although it is not unreasonable to choose body mass as a proxy for adhesive force, direct simultaneous measurements of shear and normal forces will contribute far more to our eventual understanding of fibrillar adhesive mechanics.

Although variation in setal morphology cannot be predicted by body mass, we can identify some trends by taking into account the history, presence or absence of setal branching, and adhesive mechanism of each taxon. Hierarchical structure (branching) has been predicted to confer multiple advantages, including decreased self-adhesion (1, 34), orientation dependence (35) and increased tolerance to rough surfaces (36, 37). Our results indicated that branching allows higher packing density of smaller spatulae compared with unbranched setae. Animals using dry adhesives possessed spatular densities one to three orders of magnitude greater than those with wet adhesives (Fig. 2a), and much smaller spatula size (Fig. 2c). Beetles and flies surveyed in our study possess spatular tips 1–10 μm wide, whereas geckos possess spatulae ≈ 200 nm in width, and spider and anole spatulae fall between 350 nm to 1 μm . Federle (1) has suggested that secretions compensate for larger spatulae in insects, specifically on substrates with finer roughness scales than the width of the spatula, where the fluid can bridge small scale gaps. Because secretions predate hairy adhesives in insects, and be-

Table 2. Regression results for spatula-width versus body-mass analyses

Partition	Scaling exponents		Comparison of analyses
	Raw species values	Phylogenetically corrected (ICs)	
Dry	−0.064 (ns); 95% CL (−0.16, 0.031); $P = 0.19$; $df = 48$	−0.075 (ns); 95% CL (−0.21, 0.058); $P = 0.26$; $df = 28$	ns
Wet	−0.060 (ns); 95% CL (−0.26, 0.14); $P = 0.54$; $df = 17$	−0.031 (ns); 95% CL (−0.15, 0.087); $P = 0.59$; $df = 14$	ns
Branched	0.040 (ns); 95% CL (−0.045, 0.13); $P = 0.32$; $df = 33$	0.040 (ns); 95% CL (−0.11, 0.19); $P = 0.59$; $df = 15$	ns
Unbranched	−0.17 (−); 95% CL (−0.27, −0.062); $P = 0.003$; $df = 32$	−0.11 (ns); 95% CL (−0.22, 0.007); $P = 0.065$; $df = 27$	*
Pooled	−0.27 (−); 95% CL (−0.35, −0.20); $P < 0.001$; $df = 66$	−0.086 (ns); 95% CL (−0.18, 0.007); $P = 0.068$; $df = 42$	*

For an explanation, see the legend of Table 1. +, significant and positive relationship; −, significant and negative relationship; *, analyses yielded significantly different conclusions; ns, no significant relationship or no significant difference between analyses.

from the literature (refs. 16, 23, 24, and 47–88; N. E. Stork, unpublished data; SI Table 3). We included data from species in Arzt *et al.* (24), but those data were based on our own observations or alternate sources.

Phylogenetic and Statistical Analyses. We calculated independent contrasts (40) from log-transformed data using CAIC version 2.6.9 (89), which outputs ordinary least squares (OLS) regression statistics (slope, r^2 , P value) and notifies the user of outliers, as well as any statistical or evolutionary assumptions violated by the data. We calculated regressions on phylogenetically uncorrected species values for comparison. All 81 taxa were included in the spatular density versus body mass analysis. Sixty-seven taxa were available for the spatular width versus body mass scaling analysis. The phylogenetic hypothesis used to generate independent contrasts is a conservative (consensus) composite tree assembled from phylogenies published for the constituent groups (geckos, refs. 90–98; *Anolis*, ref. 99; squamates, refs. 100 and 101; spiders, refs. 102 and 103; hexapods, ref. 104; beetles, based on

refs. 105 and 106; flies, refs. 107 and 108; SI Fig. 4). Where no phylogenetic information was available for a species, the current accepted taxonomic relationship was used. Because statistically supported branch lengths were lacking, we compared results across four trees with the same topology but with widely varying branch lengths transformations (Equal, Grafen, Nee, and Pagel; constructed with Mesquite version 1.12, ref. 109). Because there were no significant differences across branch-length assumptions for any analysis, all plots and statistics representing phylogenetic analyses assume equal branch lengths for simplicity.

We thank Kellar Autumn, Chris Conroy, Jens Vindum, Walter Federle, Ed Florence, Ted Garland, Sheila Patek, Shai Revzen, and Nigel Stork. Funding was provided by National Science Foundation Nanoscale Interdisciplinary Research Teams Grant 0304730, Defense Advanced Research Projects Agency/Space and Naval Warfare Systems Command Grant N66001-03-C-8045, the American Association of University Women, the National Science Foundation Graduate Research Fellowship Program, and the University of California, Berkeley, Integrative Biology Department.

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