

Integrative biology of sticky feet in geckos

Eric R. Pianka^{1*} and Samuel S. Sweet²

Summary

Geckos have gained ecological access to novel microhabitats by exploiting intermolecular van der Waals forces, which allow them to climb smooth vertical surfaces. They use microscopic surface-based phenomena to thrive in a macroscopic mass- and kinetic energy-based world. Here we detail this as a premier example of integrative biology, spanning seven orders of magnitude and a lot of interesting biology. Emergent properties arising from molecular adhesion include several adaptive radiations that have produced a great diversity of geckos worldwide. *BioEssays* 27:647–652, 2005.

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Hierarchical biology and emergent properties

Biology has a complex hierarchical organization. Biologists study phenomena that range across vastly different spatial and temporal scales, from molecules to cells to organisms to populations to communities and entire ecosystems (Fig. 1). Additionally, biological processes integrate the statistical outcomes of billions of years of evolutionary experiments, each replicated uncounted times, in creating macroevolutionary patterns of adaptation and diversity. Emergent properties arise at each level. For example, glycolysis is a property shared by some metabolic pathways, but it is not a property of any given molecule. Dominance or recessiveness are exhibited by some genes but not by nucleotides. Sexual behavior is a property shared by some organisms but not of a gene. Sex ratio, gene frequency and population density are parameters of groups of organisms but not of single animals. Food web connectance and species diversity are properties of a community but are not a property of a population. Adaptive radiations are properties of lineages, but not a property of any given species.

As biology expands its scope, there has been an increasing tendency to focus narrowly within this hierarchy of scale, and reductionism is widely embraced. Unfortunately, some reductionistic biologists consider higher-level biology to be

some sort of mysticism, which is clearly not true. The influence of evolution transcends scale, such that properties of molecules can in fact affect population biology of whales or, equally validly, mechanisms of eukaryotic gene regulation have been shaped by functional “value judgments” applied by ecosystem dynamics operating over hundreds of millions of years. Natural selection is not constrained by scale and integrates all of biology.^(1,2)

Mass-related phenomena

Living organisms span a size range exceeding 21 orders of magnitude (in volume, 10^8 in length), and they inhabit physical environments that vary in scale by about 10^{25} . While physical laws are constant across scales, their relative magnitudes change greatly with size, creating both challenges and opportunities for organismal design and function. For example, many “supply” functions viewed at a meso-scale are surface-limited, whereas the “demands” they must serve are functions of volumes. Isometric scaling of objects results in surface areas that scale as the $2/3$ power of volume, with rapid consequences for the need to preserve functional equivalence at different sizes.

More generally, we are impressed by the implications of a synthesis outlined by Went,⁽³⁾ adapted here as Fig. 2. Assuming that surface-area-related events (such as cohesion, diffusion, radiation, surface tension, electrostatic forces and intermolecular attraction) scale as some characteristic length squared, that volume-related events (such as oxygen or nutrient demand, or heat production) scale as the same length cubed, and that kinetic energy scales as at least length⁵ (in the simple case of $F = ma$, where $m \propto$ volume and $a \propto$ length² as, for example with a falling pole hinged at the base), the relative importances of surface-, volume- and movement-related physical forces vary greatly across the range of size of organisms and their component structures. In a skin-out context, the physical world in which a mite must survive differs greatly from that confronting a gecko, which differs again from the world as experienced by a rhinoceros.

Went⁽³⁾ argued that organisms occupy either surface-dominated or volume-dominated physical worlds, and that many aspects of the biology of organisms reflect adaptations to physical size alone [see also Haldane⁽⁴⁾ and Bonner⁽⁵⁾ for related discussions]. This concept is easily extended to the realm of substructures (i.e. the physiology, anatomy and

¹Integrative Biology C0930, University of Texas, Austin.

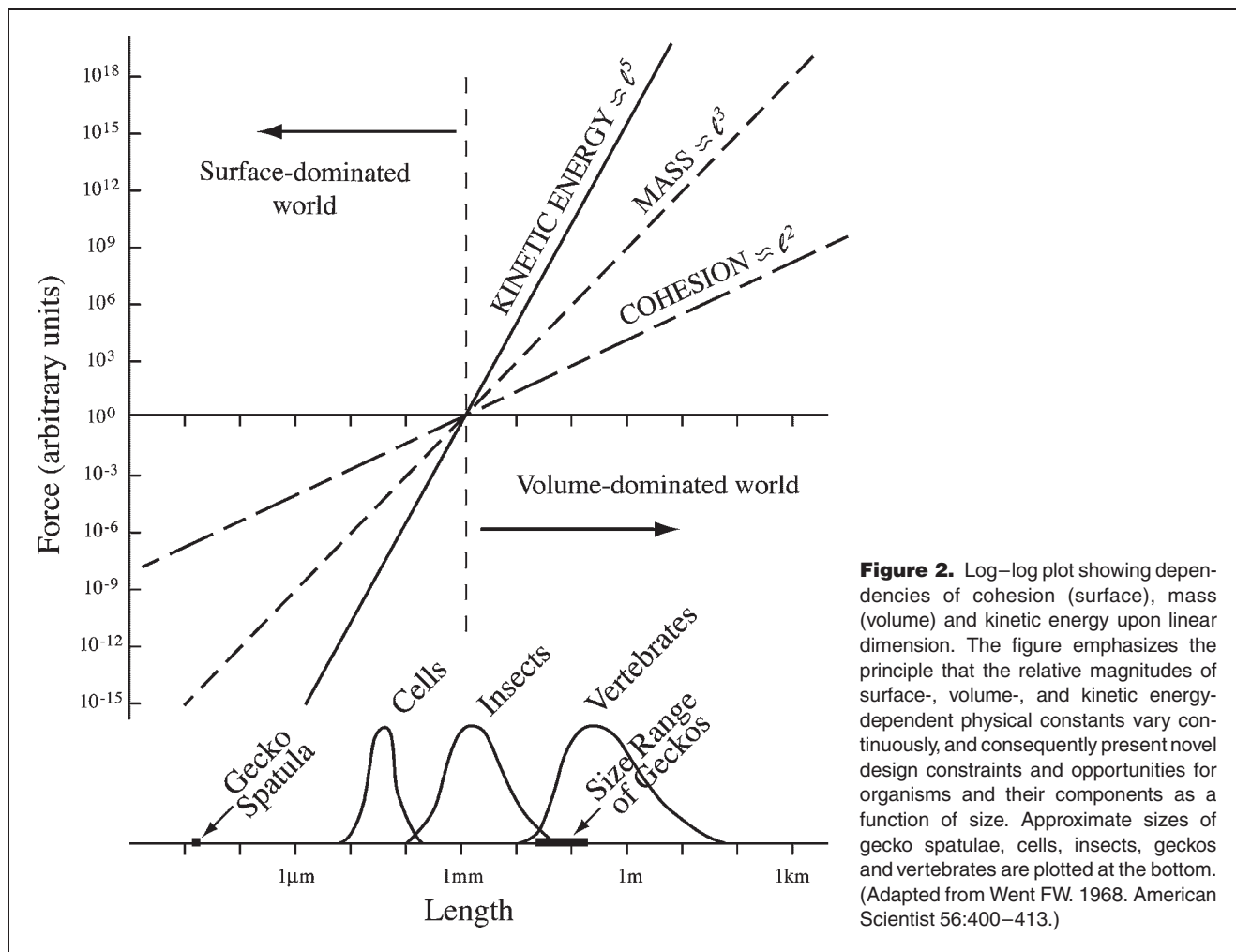
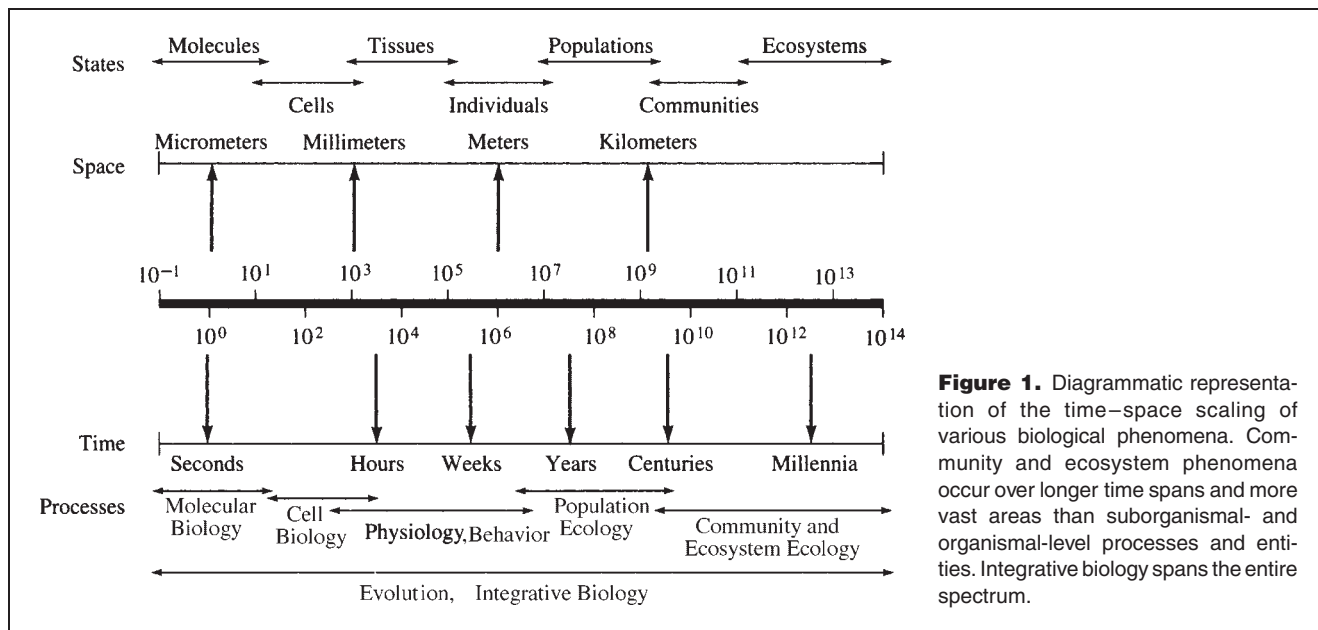
²Biological Sciences, Ecology, Evolution & Marine Biology, University of California, Santa Barbara.

*Correspondence to: Eric Pianka, Integrative Biology C0930, University of Texas, Austin, TX 78712-1064.

E-mail: pianka@mail.utexas.edu

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molecular biology of tissues and organs.⁽⁶⁾ Additionally, and less intuitively, we suggest that behavior and population biology, and perhaps community and ecosystem structure and dynamics also have emergent properties that are highly dependent on scale.^(7–9) The intersection point in Went's⁽³⁾ conceptual model is a neutral node that lies between about 1 and 10 mm in body length—the size of most insects—and it may be no accident that biodiversity peaks at about this interval of scale.⁽¹⁰⁾

Ideas about the central role of size in biology are not new,^(11–14) but they seldom receive the prominence their generality deserves, perhaps because size is seen as being an *attribute* rather than a *principle*. In fact, size is second only to evolution in the ranks of organizing principles in biology. No general synthesis of the biological implications of size has yet been formulated, perhaps precisely because of difficulties in assessing the scope and significance of emergent properties that arise from billions of independent evolutionary experiments at every level in the vast hierarchy. Even the mechanisms underlying relatively robust scale dependencies such as the $V^{0.75}$ rule of interspecific scaling of resting metabolic rate admit to several explanations, such as the rate-limiting step models in MacMahon's⁽¹⁵⁾ derivation from elastic similarity principles, or West et al.'s^(16,17) focus on the single constraint of fractal-like geometries of space-filling distribution systems,⁽¹⁸⁾ or alternatively, as derived from an incremental, cascade-like process with no single rate-limiting step.^(19,20)

Whatever mechanisms underlie scale dependencies, their emergent properties may in fact convey novel insights and contribute towards more inclusive models (e.g. Brown et al.⁽²¹⁾); for an excellent discussion of the prospects and pitfalls of emergent properties in integrative biology, see Valentine.⁽²²⁾ However, it is also true that biological models in the volume-dominated world collide squarely with Richard Levins's⁽²³⁾ observation that, whereas useful models simultaneously embody reality, generality and precision, nature seems to be determined to allow us only any two of that trio!

How gecko feet work and some natural history

The hierarchical structure of biology can be illustrated using gecko adhesive toe lamellae as a focal point. At one end of this spectrum, in the surface-dominated world, the proximate mechanism for adhesion is intermolecular van der Waals forces. At the other end of the spectrum (for geckos) are the myriad ecological and evolutionary benefits conferred in the volume-dominated world by such sticky feet, which have resulted in several major adaptive radiations. In between, individual geckos live out their daily lives, catching prey, escaping predators, mating and laying eggs.

Geckos can run up a pane of glass and even run upside down across a ceiling using clinging scansorial toe pads, which can provide amazingly powerful purchase. Boys in Malaysian towns use large geckos to play practical jokes and steal

hats⁽²⁴⁾ by tying a string around a gecko which is then lowered from a second story window on to the hat of an unsuspecting person walking past below—the gecko grabs hold of the hat with its toe pads and claws and the boy reels in the string along with the gecko and the hat (Fig. 3).

Scanning electron micrographs of the digital pads of some geckos show literally millions of elaborate very fine hairlike setae,⁽²⁵⁾ each bearing tiny hooks and hundreds of spatulae, which allow these lizards to gain purchase on almost any surface including very smooth ones.⁽²⁶⁾ A single individual gecko can have almost a billion spatulae. Several mechanisms of adhesion have been proposed, including suction, glue, electrostatic attraction and friction. Gecko feet still stick in a vacuum, eliminating suction. Gecko feet have no glands, making glue most unlikely. Experiments using x-rays to ionize air have eliminated the possibility of electrostatic attraction. A smooth pane of glass offers very little in the way of friction, although friction would certainly be quite important when climbing on any rough surface.

In an interesting study of gecko setae, scientists removed a single seta from a large Tokay gecko and glued it to an extremely fine pin.^(27,28) Each seta ends in hundreds of spatulae which press up and conform to the substrate (Fig. 4). Direct forces of setal attachment were measured with an extremely tiny micro-electro-mechanical sensor (a “dual-axis piezoresistive cantilever fabricated on a single-crystalline silicon wafer”). Earlier work had rejected two previously proposed mechanisms of attachment, suction and friction,⁽²⁹⁾ and had succeeded in demonstrating that intermolecular forces provided adhesion. Autumn et al.⁽³⁰⁾ demonstrated that hydrophobic gecko toes adhere to molecularly smooth hydrophobic surfaces, providing direct support that van der Waals forces are involved. Van der Waals forces are mutually induced dipolar attractions that occur when e-fields of nonpolar



Figure 3. Underside of the foot of a Tokay gecko *Gekko gecko* showing adhesive toe lamellae (Photo by Chris Mattison).

molecules get very close. Like electrostatic forces, van der Waals forces act between molecules, but they can even act between nonpolar (or non-charged) molecules. Van der Waals forces require exceedingly intimate contact between a gecko's spatulae and the surface, and they are extremely weak at distances greater than atomic distance gaps. These authors estimate that, if a gecko's entire billion spatulae were simultaneously engaged with substrate molecules, the force holding a gecko to the substrate would be about 40 atmospheres (about 40 kg per cm²). Only about 0.03% of gecko setae will support a gecko's entire body weight!⁽²⁸⁾ Indeed, gecko feet have been claimed to be "overdesigned".⁽³¹⁾ One of our colleagues made an interesting and highly relevant observation while collecting in Amazonia with a graduate student (Laurie J. Vitt, personal communication). His graduate student (Pete Zani) was in a tree 30 meters above ground searching epiphytic bromeliads for frogs and lizards when a gecko (*Thecadactylus*) jumped out and came parachuting down. Vitt was on the ground watching the falling gecko, preparing to catch it as it landed. But, about 7 meters above ground, the gecko reached out with one foot and gained purchase on a leaf of an adjacent tree, then scrambled into it, thus evading capture. This incident suggests that most spatulae are probably not in adhesive contact with the substrate much of the time, and suggests that gecko toes may not be "overdesigned" at all.

Aaron Bauer (personal communication) suggests that climbing geckos as a group may appear to be overdesigned for "standard" locomotor purposes, but this increased factor of safety permits them to deal with extraordinary loads encountered under rare circumstances, such as in the *Thecadactylus* example above. This overdesign might then serve as the basis for further selection for new biological roles.

With such powerful forces, one might expect geckos to be plastered against their substrates and unable to move. Indeed, during a powerful cyclone on Mauritius,⁽³²⁾ *Phelsuma* day geckos were actually beaten to death by the furious flapping of leaves they were on—but these dead geckos nevertheless remained firmly attached to the leaves! How do geckos manage to break such strong bonds? How do they control their powerful feet and toes? Autumn et al.⁽²⁷⁾ liken the complex behavior of toe uncurling during attachment to blowing up an inflating party favor, whereas toe peeling during detachment is analogous to removing a piece of tape from a surface. Setae operate under very fine motor control over a mechanical program: preload and drag are needed for attachment, and a 30° shaft angle is required for easy detachment,^(27,33) Setae are directional and are only sticky in a distal direction.⁽²⁷⁾ Detachment is complex—during running, geckos peel their toes away from a smooth surface (Fig. 5). Toe peeling may have two effects. First, it could put an individual seta in an orientation or at a critical angle that aids in its release. Second, toe peeling concentrates the detachment force on only a small subset of all attached setae at any instant.⁽²⁷⁾

Autumn et al.⁽²⁷⁾ comment that the natural technology of gecko foot hairs could provide biological inspiration for future design of remarkably effective re-usable dry adhesives (velcro³?!). Perhaps one day, people will climb cliffs and buildings wearing gloves made of simulated gecko toe lamellae—but if so, natural selection will hold the patent! Manufacture of such small, closely packed arrays mimicking gecko setae has been attempted using nanotechnology, but the resulting sticky tape quickly became clogged with all sorts of debris. Recent experiments using tiny alumina-silica microspheres have shown that gecko feet clean themselves with each step a gecko takes.⁽³⁴⁾ Self-cleaning appears to occur by an energetic

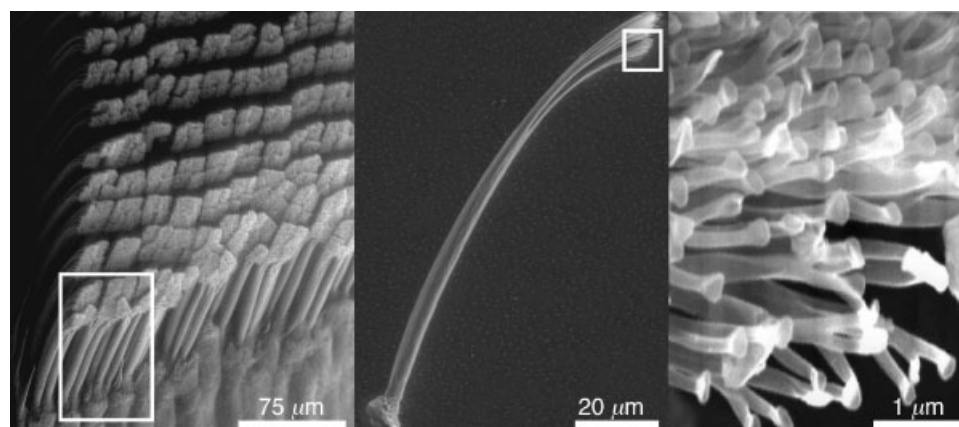


Figure 4. Scanning EMs of parts of a *Gekko gecko* foot pad at increasing levels of magnification, showing rows of setae on a toe (left), an individual seta (center), and the very tiny terminal branches of a seta, the spatulae (right). (From Autumn K et al. 2000. *Nature* 405:681–685 with permission).



Figure 5. Toes unpeeling just before a *Gekko smithii* jumps (Photo by Chris Mattison).

disequilibrium between adhesive forces attracting a dirt particle to the substrate versus those attracting the same particle to one or more spatulae. Dirt particles stick to the substrate, leaving cleaner spatulae behind.

Adaptive radiations of geckos

Several major groups of geckos (about 116 genera, over 1100 species) are recognized,⁽³⁵⁾ usually treated as families or subfamilies. Eublepharids are presumed to be the most-basal geckos because they possess movable eyelids, whereas all other geckos have a fused, transparent lower eyelid, termed a spectacle. All eublepharids (6 genera, 25 species) are terrestrial and none has adhesive toe pads. This widespread group is thought to be ancient and the sister group to all other geckos (Fig. 6). Hence, the common ancestor of all other geckos presumably was terrestrial and padless. Other geckos are placed in two major clades, the gekkonids (77 genera, about 800 species) and the diplodactylids (20–21 genera, about 150 species). Gekkonids include the cosmopolitan gekkonines (72 genera, about 670 species) as well as the New World padless sphaerodactylines (5 genera, about 133 species). Some gekkonines are terrestrial without adhesive toe pads, but many others are arboreal and possess adhesive toe pads. Diplodactylids (22 genera, about 150 species) occur only in the Australian region (Australia, New Guinea, New Caledonia, and New Zealand) and include the pygopodids (6 genera, about 35 species), an elongate snake-like lineage without forelimbs and only vestigial hindlimbs, as well as more typical carphodactylines and diplodactylines. Carphodactylines (5 genera, 24 species) are padless (although many do climb), whereas Diplodactylines (11 genera, 110 species) all possess adhesive toe pads, ranging from a single pair of small distal lamellae in terrestrial species to complex, fully-developed adhesive toe pads in those that climb (Aaron Bauer, personal communication).

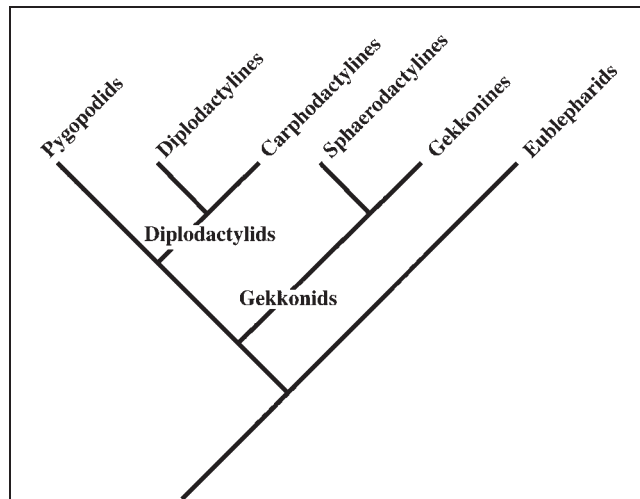


Figure 6. Phylogenetic relationships of major lineages of geckos based on both morphological and molecular systematic studies (From Han D, Zhou K, Bauer AM. 2004 Biol J Linn Soc 83:353–368, with assistance from Aaron Bauer, pers comm).

Lamellar adhesive toe pads adapted for clinging have arisen independently several times within different lineages of climbing geckos (including both gekkonines and diplodactylines), each of which has undergone its own adaptive radiation as a result.^(35–37) As gecko phylogeny becomes better resolved, we will finally be able to estimate the number of times adhesive toe pads have arisen. Scansorial toe pads have also been lost as some gekkonines reverted back to terrestriality.⁽³⁶⁾ Sticky toe lamellae have arisen independently in iguanian lizards (polychrotine anoles,⁽³⁸⁾ which have also undergone a major adaptive radiation (over 300 species). Several species of arboreal New Guinean skinks (*Lipinia leptosoma* and three species of *Prasinohaema*) have evolved ruffled adhesive toe pads, but only one species, *Prasinohaema virens*, has true setae.^(39,40) For unknown reasons, this lineage has not yet diversified. Similar structures have evolved in various arthropods (including spiders, kissing bugs, beetles, and flies) for holding on to prey, mates, and/or vertical surfaces,^(30,41–45) but comparative micro-anatomical studies have yet to be undertaken.

Conclusions

Most of the inhabitants of Went's⁽³⁾ volume-dominated world that climb or cling do so by muscular gripping, often with the aid of sharp recurved claws. However, such solutions fail on many smooth surfaces (such as most leaves, or the stems of many plants), as do the suction-based foot structures of many frogs and some salamanders. Geckos and a few other lizard lineages have gained ecological access to novel microhabitats in the volume-dominated world by exploiting aspects of the surface-dominated world: size-scaling limitations of van der

Waals forces appear to have less to do with the mass of the animal that they can support than with ecological opportunities for life on vertical surfaces. Much of the evolutionary diversity of climbing geckos can be argued to be an emergent property of events occurring at a molecular scale, as integrated across seven orders of magnitude in setal, lamellar and limb design, and utilized in an environment where the gulf between the magnitudes of surface forces and kinetic energy seems at first glance to be prohibitive.

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