



Geometric and allometric constraints on animal evolution: surface, volume, mass and the limits of viable size

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Abstract. Animal evolution is fundamentally constrained by geometric and allometric relationships governing how surface area, volume, and mass scale with body size. Because surface area increases with the square of linear dimensions while volume and mass increase with the cube, changes in size alter physiological, mechanical, and metabolic performance in predictable ways. These geometric principles underlie critical biological processes, including heat exchange, diffusion, structural support, and metabolic rate, and help explain why animals cannot exist at arbitrarily small or large sizes. Classic metabolic scaling relationships, often approximating a three-quarter power law, illustrate how energy use, growth, lifespan, and reproduction systematically vary with body mass. Mechanical constraints further require disproportionate reinforcement of support structures in larger organisms, while miniaturization is limited by minimum functional requirements of organs such as the nervous and reproductive systems. In addition, ecological, developmental, and population-genetic factors interact with physical constraints to define viable size ranges and evolutionary trajectories. Although allometric relationships retain some evolutionary flexibility, they channel morphological and physiological diversification within bounded limits. Together, geometric scaling and allometric principles define a constrained region of viable phenotypic space, explaining both the diversity of animal forms and the absence of biologically unfeasible sizes and designs.

Key Words: allometry, animal morphology, body size evolution, evolutionary constraints, geometric scaling, mechanical constraints, metabolic scaling, miniaturization limits, size-shape relationships, surface area-to-volume ratio.

Introduction. Animal evolution unfolds under strict physical and geometric constraints. As organisms change in size, their surface area, volume and mass do not scale proportionally, producing systematic changes in physiology, morphology and life history known as allometric patterns. These scaling relationships define ranges of viable body sizes and shapes, and explain why animals cannot simply be scaled copies of each other at arbitrarily small or large sizes. Modern research integrates classic geometric arguments with metabolic, ecological, developmental and population-genetic perspectives to explain why evolution produces regular size-related “designs”, but also why not all imaginable sizes and forms are realized in nature (Harrison et al 2022; Glazier 2023; Lindstedt & Hoppeler 2023; White & Marshall 2023).

The purpose of this mini-review is to synthesize current knowledge on how geometric and allometric scaling relationships constrain animal evolution by shaping physiological performance, structural design, and the limits of viable body size.

Geometric foundations: surface area, volume and the 2/3 law. Basic geometry predicts that if shape is preserved, linear dimensions scale with body length L , surface area with L^2 , and volume (and thus mass, assuming constant density) with L^3 (Figure 1). Consequently, surface area A should scale with body volume V as $A \propto V^{2/3}$. This 2/3 power-law has long been used to explain constraints on heat exchange, diffusion and mechanical support (Lindstedt & Hoppeler 2023). Recent whole-organism analyses in sharks demonstrate that body surface area scales with volume very close to the 2/3 expectation across a 19,000-fold mass range, providing rare direct confirmation of this geometric law at the whole-animal level (Gayford et al 2025).

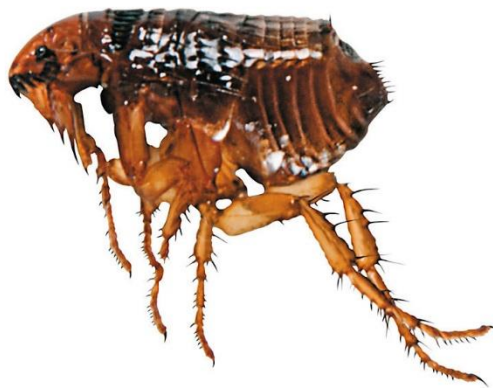


Figure 1. The legs of a flea the size of an elephant would break under the weight of its body (source: <https://www.newswire.ca/news-releases/know-your-flea-facts-810312685.html>).

Because many crucial biological processes occur across surfaces (e.g. gas exchange, nutrient uptake, heat loss) while demand arises from volumes (i.e. numbers of cells and total metabolism), the decline of surface area-to-volume ratio with increasing size creates fundamental problems for large animals. These problems can be mitigated by internal folding of exchange surfaces, changes in shape and behavior, or shifts in physiology, but cannot be eliminated (Lindstedt & Hoppeler 2023; Gayford et al 2025). At the small end, miniaturization is limited because some organs and tissues, particularly the nervous and reproductive systems, cannot shrink indefinitely without loss of function (Polilov & Makarova 2017). Thus, geometry alone implies upper and lower size limits beyond which viable animals are impossible without radical design changes.

Classic allometry: metabolic scaling and the 3/4 power law. The most famous evolutionary pattern linked to size is metabolic allometry. Across species, whole-organism metabolic rate B typically scales with body mass M as $B = aM^b$, where b is usually between 2/3 and 1, but often near 3/4 for many groups, and mass-specific metabolic rate B/M therefore declines in larger animals (Gavrilov et al 2022; Harrison et al 2022; Glazier 2023; Lindstedt & Hoppeler 2023). This hypometric scaling emerges for basal/resting metabolism, field metabolism and maximal metabolic rates, and is tightly linked to scaling of numerous life history and physiological traits, including growth rate, lifespan, reproduction and cellular properties (Harrison et al 2022; Lynch et al 2022; Pettersen et al 2022; Glazier 2023; Lindstedt & Hoppeler 2023).

Constraint-based theories have attributed the 3/4 power law to the geometry of resource-transport networks, limits of surface area for exchange, or heat dissipation constraints (Harrison et al 2022; Glazier 2023; White & Marshall 2023). However, large comparative datasets reveal considerable variation in exponents across taxa. Among tetrapods, standard metabolic rate scales with $b \approx 3/4$ in mammals, $b < 3/4$ in birds, and $b > 3/4$ in amphibians and reptiles, reflecting differences in thermoregulation, phylogeny

and the geological timing of clade origin (Gavrillov et al 2022). At the broadest eukaryotic scale, metabolic and ecological traits such as abundance, growth and mortality follow interrelated scaling laws, but with exponents that vary among groups and are sometimes inconsistent with simple metabolic-constraint models, suggesting important roles for growth dynamics, ecology and evolutionary history (Hatton et al 2019; Lynch et al 2022).

Why all sizes and shapes are not viable: mechanical and structural constraints.

As body mass increases, the forces acting on bones, muscles and connective tissues scale faster than the cross-sectional areas that resist them if isometric proportions are maintained. Galileo first drew attention to this paradox, which implies that large animals must have disproportionately thicker, more robust support structures to avoid mechanical failure (Lindstedt & Hoppeler 2023). Allometric studies confirm that limb bones and other load-bearing structures often scale hypermetrically ($b > 1$ for diameter vs. length, or $> 2/3$ for cross-sectional area vs. mass), reflecting the need to maintain safety factors in larger animals (Lindstedt & Hoppeler 2023; Harrison et al 2022).

Similar constraints apply to specialized structures such as adhesive pads. Adhesion-based climbing relies on sufficient pad area to support body weight; across 225 species from mites to geckos, adhesive pad area increases with extreme positive allometry relative to body mass, requiring about a 200-fold rise in relative pad area from the smallest to largest climbers (Labonte et al 2016). Within closely related taxa, pad area tends to scale closer to isometry when phylogeny is controlled, implying that such dramatic changes in surface allocation are constrained by developmental and anatomical limits (Labonte et al 2016). The fact that very large animals do not use adhesion-based climbing reflects a real size limit imposed by the need to devote an unfeasibly large fraction of body surface to pads.

Cranial morphology illustrates similar trade-offs. Mammalian craniofacial evolutionary allometry (CREA) describes a pattern where larger species often have relatively longer, more gracile faces and smaller braincases compared to smaller relatives (Mitchell et al 2024). This seems paradoxical because more gracile skulls appear mechanically weaker. Recent work suggests that in many clades, larger species can produce required absolute bite forces with lower stress because of their size, allowing selection to favor lighter, more gracile skulls for reasons such as sensory function or locomotor performance. Where large species adopt feeding strategies that demand higher bite forces (e.g. hard-object feeding), this pattern reverses and large animals evolve stouter faces (Mitchell et al 2024). Thus, mechanical and functional demands impose context-dependent constraints on how size and shape can co-evolve.

Miniaturization and the lower size limit. At very small sizes, organ systems confront geometric and developmental constraints that prevent indefinite miniaturization. Detailed 3D reconstructions of insect body and organ volumes show that most systems can preserve relative size across a broad body-size range, indicating considerable scaling flexibility. However, the relative volume of the nervous and reproductive systems increases dramatically as body size decreases, so that in the smallest beetles and wasps, nervous tissue and gonads occupy a large fraction of body volume (Polilov & Makarova 2017). These systems require a minimum number and size of cells to remain functional; they cannot simply be scaled down proportionally. As a result, further miniaturization would demand either radical simplification of nervous systems and reproductive anatomy or would push below a threshold of viability (Polilov & Makarova 2017).

Similar issues appear at the cellular level. Larger animal species and sexes often have larger cells with lower surface area-to-volume ratios, which reduces the total membrane area per unit mass and thereby lowers the energetic cost of maintaining ion gradients, supporting lower mass-specific metabolic rates (Schramm et al 2021). Conversely, extremely small animals would require small, membrane-rich cells with high surface area-to-volume ratios, dramatically increasing the cost of homeostasis. This metabolic burden contributes to the instability or rarity of extremely miniature body plans, reinforcing lower size limits through energetic as well as anatomical constraints (Glazier 2023; Schramm et al 2021).

Metabolic, temporal and ecological constraints on size evolution. Beyond geometry and mechanics, time and ecology limit the sizes and life histories that are evolutionarily viable. A “time perspective” on scaling emphasizes that biological rates and durations - development, reproduction, aging - must fit within the finite time window imposed by mortality (Glazier 2023, 2024). Mortality-based theory posits that high extrinsic mortality in small, vulnerable organisms favors fast growth and early reproduction, whereas lower mortality in larger, better-protected organisms allows slower, longer lives; this framework helps explain observed ranges of body-mass exponents for many traits (Glazier 2023, 2024). Because mortality is itself size-dependent and environment-dependent, not all combinations of size and pace of life are evolutionarily attainable.

Across all eukaryotes, maximum growth rates show contrasting size-scaling patterns: in heterotrophic bacteria they increase with size, while in eukaryotes they decrease with size and do so more weakly than predicted by physical-constraint models (Lynch et al 2022). Genomic and population-genetic analyses suggest that in large, complex eukaryotes, growth-diminishing mutations with small effects accumulate more readily due to stronger random genetic drift, limiting the achievable performance of large-bodied forms (Lynch et al 2022). This introduces a population-genetic constraint on body size evolution that interacts with geometric and energetic factors.

At macroevolutionary scales, studies of tetrapods reveal that both the normalization constant and scaling exponent of metabolic rate evolved over geological time, with consistent differences between ectothermic and endothermic classes (Gavrilov et al 2022). Endotherms such as birds and mammals exhibit higher mass-specific metabolic rates but slower increases of metabolism with size than ectotherms, reflecting both internal design evolution and changing ecological roles (Gavrilov et al 2022). Broad cross-eukaryote analyses further show that mortality and growth rates scale with body mass with exponents near $-1/4$, whereas abundance and metabolism often scale near $\pm 3/4$ within groups, but ± 1 across all eukaryotes, pointing to deep, group-specific constraints on how energy, time and size are linked (Hatton et al 2019; Glazier 2023).

Allometry as both constraint and opportunity. A central question is whether scaling patterns represent hard constraints that restrict evolution, or flexible outcomes shaped by optimization under selection. Work on metabolic scaling shows that both views have merit. Constraint-based models highlight geometric, network and heat-dissipation limits, but optimization-based approaches demonstrate that metabolic exponents and normalization constants can emerge from selection to maximize lifetime reproductive success under life-history trade-offs, without invoking strict physical ceilings (Harrison et al 2022; White & Marshall 2023). Allometry thus reflects a combination of unavoidable physical geometry, developmental and genetic architecture, and adaptive fine-tuning within those limits.

Experimental evolution and artificial selection show that some allometric relationships can evolve rapidly, but are stabilized by internal constraints. In *Drosophila*, intense selection over just 26 generations shifted the allometric slope linking wing shape to size to the extremes seen among 111 species, demonstrating substantial evolutionary potential. Yet when selection stopped, the slope reverted toward its ancestral value, a reversal only partly attributable to genetic recombination, suggesting pleiotropic internal selection that maintains preferred allometries (Bolstad et al 2015). Similar studies of fossil sticklebacks reveal that static allometries can evolve over thousands of years, but remain strong predictors of long-term evolutionary trajectories for many traits, supporting the idea that allometry both channels and constrains diversification (Voje et al 2022).

Ontogenetic studies in monitor lizards and allies show that the magnitude and direction of developmental allometric trajectories vary across clades and habitats, indicating that ontogenetic allometry is evolutionarily labile and often adaptive rather than purely constraining (Pavón-Vázquez et al 2022). Nevertheless, the range of possible ontogenetic changes seems bounded by optimal values, consistent with stabilizing selection around functionally workable growth trajectories (Pavón-Vázquez et al 2022). Together, these lines of evidence indicate that while size–shape–function relationships are not absolutely fixed, the accessible region of phenotypic space is delimited by intertwined geometric, mechanical, physiological, developmental and ecological constraints.

Evolutionary patterns of body size and the “right size” problem. Global patterns of body-size evolution illustrate how physical constraints interact with ecology. The island rule describes a tendency for small species to evolve gigantism and large species dwarfism on islands, moving toward intermediate sizes that may be “optimal” under insular conditions. A massive phylogenetic meta-analysis across mammals, birds, reptiles and amphibians shows that the island rule is pervasive, but modulated by climate, island size and isolation, and differs in strength among vertebrate classes (Benítez-López et al 2021). Such patterns echo Haldane’s and others’ ideas about “being the right size”: environmental and ecological conditions define local optima, while geometric and physiological constraints ensure that those optima fall within a feasible size window.

Climate-induced body-size changes also underline the complexity of size evolution. Long-term data from a migratory bird show decreases in body mass and some linear dimensions over three decades of warming, consistent with Bergmann’s and Allen’s rules, but no evidence that smaller individuals have higher survival or fecundity; in some traits, larger birds actually fare better (Romano et al 2025). These results suggest that observed size changes may often reflect developmental plasticity or non-adaptive responses within constrained reaction norms, rather than straightforward adaptive evolution toward a new optimum.

At macroevolutionary scales, analyses of mammalian brain–body allometry reveal that shifts in scaling slopes and intercepts underlie major transitions in brain evolution, often driven by changes in body size rather than brain size alone (Smaers et al 2021). This finding undermines simplistic interpretations of relative brain size and highlights how fundamental allometric relationships can themselves evolve, while still being bounded by the need to maintain viable ratios of neural tissue, body mass and energy supply.

Conclusions. Across the tree of life, the evolution of animals is shaped by the interplay of surface, volume and mass, manifesting in pervasive allometric patterns. Geometric relationships fix how surface area and volume scale with size, imposing inescapable trends in surface area-to-volume ratio. These trends underlie constraints on gas exchange, heat balance, diffusion, mechanical support and organ miniaturization, and help explain why animals cannot be arbitrarily small or large. Metabolic, temporal, ecological and population-genetic considerations further restrict the range of viable sizes and shapes, while developmental and genetic architecture channels the directions in which size and form can co-evolve.

Although allometric relationships are not perfectly rigid and can evolve in response to selection, they represent enduring “rules of design” that both enable and limit evolutionary innovation. Viable animals occupy a constrained region of size–shape–function space defined jointly by geometry, physics, biology and ecology. Beyond that region, the necessary combinations of surface, volume, mass and time are incompatible with life, and thus absent from evolutionary history.

Conflict of interest. The authors declare that there is no conflict of interest.

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 Accessed: October, 2025.

Received: 22 October 2025. Accepted: 29 November 2025. Published online: 30 December 2025.

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How to cite this article:

Oroian C., Balint C., Popescu M., Bora F. D., Petrescu-Mag I. V., Rusu T., 2025 Geometric and allometric constraints on animal evolution: surface, volume, mass and the limits of viable size. *ELBA Bioflux* 17(1):34-40.