

# MINIATURIZATION OF BODY SIZE: Organismal Consequences and Evolutionary Significance

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## *Abstract*

Miniaturization, or the evolution of extremely small adult body size, is a widespread phenomenon in animals. It has important consequences for both organismal biology and phyletic diversification above the species level. The miniaturized phenotype is a complex combination of ancestral and derived traits, including reduction and structural simplification, increased variability, and morphological novelty. Many features likely represent secondary consequences of size decrease, which may be the result of selection primarily for small body size or some related attribute such as life history characteristics. In some cases, miniaturization has resulted in novel bauplans associated with the origin of higher taxa. Evaluation of causes and consequences of miniaturization should consider obvious features of physical size as well as less obvious, but biologically important, features such as genome and cell size.

## INTRODUCTION

Body size is among the most important determinants of organismal function and ecological role (58, 97). Biologists have expended considerable effort in

documenting patterns of size distribution and evolutionary size change among organisms (76, 141), as well as in analyzing the consequences of size and size change for various biological attributes (4a, 9, 78, 125). One especially significant trend in the evolution of body size is miniaturization, or extreme phylogenetic size decrease. Yet, with the exception of a few early studies (e.g. 107, 108), the broad significance of miniaturization for organismal biology and evolution, including its high frequency among major groups of animals, has been largely unappreciated. In this review we summarize the phenomenon of miniaturization in animals, focusing on both the mechanisms and morphological consequences of size decrease and the implications of these features for various aspects of organismal biology and phylogeny. We hope to promote recognition of the prominent role played by miniaturization in evolutionary processes in both vertebrates and invertebrates, and especially phyletic diversification above the species level.

## THE PHENOMENON OF MINIATURIZATION

### *What is Miniaturization?*

Miniaturization is the evolution of extremely small body size within a lineage. It is a phylogenetic statement, implying that the group under consideration evolved from a larger ancestor. Yet, miniaturization involves not only small body size per se, but also the consequent and often dramatic effects of extreme size reduction on anatomy, physiology, ecology, life history, and behavior—the costs of size decrease, and its compensations. We consider the “critical size” for miniaturization to be that at which important physiological or ecological functions such as feeding, locomotion or reproductive biology are affected, necessitating a major change in the way an organism deals with its ancestral adaptive zone. Some instances of miniaturization may represent a minimum body size below which further size decrease is not permitted because of the design limitations of a given bauplan.

Biological parameters vary widely with respect to how they scale with body size, as do physiological systems with respect to the range of body sizes over which they function efficiently (125). Hence, it should rarely be possible to identify a single critical size for any group of closely related organisms, let alone for a higher taxonomic group such as vertebrates. There also is no strict criterion for distinguishing miniaturization from other, less severe instances of size reduction, which lie along the same body-size continuum. The distinction between miniaturized and nonminiaturized taxa may even be somewhat arbitrary (31, 65). In freshwater teleostean fishes, a standard length (snout to base of caudal fin) of 25–26 mm has been used as the maximum

size for miniature species (164); this represents one-fourth to one-fifth the average size of living teleosts (87). Other complicating factors include cell size and number in relation to body and organ size (121, 122; see discussion below), and physiology. For example, the endothermic metabolism of birds and mammals dictates a larger minimum adult body size compared to ectotherms (9, 46, 125). Consequently, while many instances of evolutionary size decrease are known, especially for mammals (66, 104, 123, 131, 135, 153a), miniaturization is more common, and certainly more extreme, in fishes, amphibians, and reptiles. In these, adults may be as small as 8–10 mm standard length and weigh as little as 2–8 mg (29, 169).

### *How Common is Miniaturization?*

Examples of miniaturization are numerous and taxonomically diverse (73, 107, 108). They include a variety of living and extinct invertebrates, such as foraminiferans (69), nemertines (55), annelids (110, 165), brachiopods (60), molluscs (59, 96, 101, 124, 127, 138, 143, 146, 149), arachnids (100, 105, 166, 167), crustaceans (47, 91, 128), insects (7, 18, 23, 56), echinoderms (84, 85, 140, 152), and ascidians (83). Vertebrate examples include a large number of teleost fishes (5, 81, 87, 88, 93–95, 115–118, 139, 145, 151, 161–164, 168, 169), amphibians (20, 29, 32, 33, 36, 37, 42–45, 137, 148, 159, 171), reptiles (14, 27, 35, 102, 111–113), birds (106, 170), and mammals (25, 28, 38, 86, 134). Indeed, it is difficult to propose any major metazoan taxon that doesn't offer an example.

Miniaturization is especially common in certain environments. For example, "Gigantism, together with bizarreness, and dwarfing are two striking features of the Antarctic and deep-sea biotas" (65, p. 336). In the Antarctic, 61% of bivalve molluscs are sexually mature at less than 10 mm; maximum adult size of some minute species is 1.1 mm (124). Entire communities of reduced or even miniaturized species include the interstitial or meiofauna (50, 142) and many island faunas (72, 102, 123). (Islands also provide classic examples of gigantism; 138a).

Quantifying the frequency of miniaturization, however, is problematic; one of the main reasons is the lack of a simple criterion for recognizing it in individual taxa. Nevertheless, individual estimates are informative, and surprisingly high. Using the size criterion discussed above, at least 85 species of South American freshwater fishes are regarded as miniature, representing 5 orders, 11 families, and 40 genera (164).

Even more difficult is quantifying the number of times miniaturization has evolved. Because of the homoplasy that frequently accompanies size decrease in closely related groups, miniaturized taxa may be regarded incorrectly as monophyletic, representing a single instance of reduction. This is exemplified

by pygmy squirrels ("Nannosciurinae"; 86), mites (Acari; 153), and "archiannelid" worms (165a). Basing any tabulation of the number of times miniaturized body size has evolved on its distribution among major taxa thus is likely to underestimate the actual number. When phylogenetic hypotheses are robust, the frequency of evolution of miniaturization is surprisingly high. A critical size of 30 mm standard length yields at least 10 genera of plethodontid salamanders in which miniaturization has evolved independently, involving a total of at least 20 species (157).

### *Developmental Basis of Body Size Decrease*

The developmental mechanisms that mediate evolutionary change in body size have been addressed in a number of recent studies (46, 75, 77, 79, 132, 133). Virtually all discuss developmental mechanisms in terms of heterochrony, and they take as their point of departure either the "clock model" of Gould (30) or the subsequent, more formal scheme of Alberch et al (2). Both models attempt to characterize the ontogenetic and phylogenetic relations among age, body size, and one or more aspects of "shape" or developmental stage, and both try to evaluate the possible processes and results of heterochronic change.

Several important generalizations regarding miniaturization emerge from these studies. First, adult body size decrease may result from various perturbations to the ancestral ontogeny; each case requires its own heterochronic analysis. Precocious cessation of growth (i.e. ancestral patterns of growth in mass and allometry unchanged, but duration of growth truncated, termed *progenesis* or *time hypomorphosis*; 132, 133) and reduction in growth rate (ancestral rate of growth in mass reduced, but pattern of allometry and duration of growth unchanged, termed *rate hypomorphosis*) are perhaps the most straightforward processes for achieving body size decrease, but other perturbations, e.g. extension of the growth period, could also be associated with size decrease (46).

Secondly, the consequences of size decrease for adult morphology may be highly variable, depending on the kind of ontogenetic scaling and developmental processes involved. Identical changes may result from different perturbations. Thirdly, the relevant ontogenetic data for evaluating possible mechanisms of size decrease (including size- and age-specific growth rates, age at sexual maturity, and developmental sequences for various structures) are rarely known, especially for fossil organisms (75, 77).

Finally, and following from the above considerations, it may be impossible to identify reliably and unambiguously the specific developmental perturbation underlying many instances of miniaturization. Adult morphology may be a poor guide to these processes; i.e. it is risky to infer process from pattern.



## CONSEQUENCES OF MINIATURE BODY SIZE FOR THE ORGANISM

The consequences of miniaturization for organismal biology are ubiquitous and profound; virtually every attribute, from physiology (78, 125, 154), to behavior (18), to ecology (50), may be affected. Here we emphasize the morphological consequences of size decrease, which are among the most conspicuous and frequently documented features; they also mediate, or even dictate, many of the changes observed in other aspects of the phenotype. We restrict our treatment to three classes of effects—reduction and structural simplification, morphological novelty, and increased morphological variability—which are most relevant to our subsequent discussion of the evolutionary significance of miniaturization.

### *Reduction and Structural Simplification*

The most common effect of miniaturization on morphology is reduction and structural simplification. This is manifest in many ways, ranging from general underdevelopment to the loss of individual organs or even entire organ systems (19, 30, 50, 107, 108). Among vertebrates, examples from the skeleton are perhaps the most numerous (46). In salamanders of the genus *Thorius*, the adult skull lacks several bones found in related genera of larger animals (44). Many of the bones remaining are so poorly developed that they fail to articulate with any other and leave many important nonskeletal components, such as the brain, largely unprotected (43). Many species are virtually toothless. Such examples may indicate an especial lability or size-dependence of skeletal tissues, but equally dramatic examples of reduction and simplification involving other components, e.g. the brain and sense organs, have also been described (64, 121, 122, 145).

One interesting and conspicuous difference between vertebrates and many invertebrate groups involves the tendency for wholesale loss of major organ systems as a consequence of, if not a prerequisite for, extreme body size reduction. This remarkably common and seemingly facile option in invertebrates may involve one (usually males) or both sexes (108, 110, 142, 143). Such alterations of the basic bauplan typically are associated with dramatic changes to the organism's way of life, including ecology, life history, and behavior (73); they frequently involve the evolution of parasitism (52, 149). Deepsea ceratioid anglerfishes (99) provide a comparable example from vertebrates, which otherwise evince a bias towards miniaturization without loss of major functions.

The reduced and simplified adult morphology that characterizes many miniaturized taxa often bears a strong resemblance to subadult, or even

embryonic, stages of larger close relatives. This resemblance typically is the primary evidence used to define the morphology of many miniaturized species as paedomorphic, and as having evolved via precocious truncation of the ancestral developmental program (30). However, the "juvenile" adult morphology of many miniaturized forms is rarely a perfect replicate of any stage of the presumed ancestral ontogeny (38, 59, 132, 165b). Instead, it often constitutes variable, and sometimes opposite, effects of size reduction on different tissues within the same organism. In amphibians, skeletal reduction (assessed by the size, shape, or configuration of individual cartilages or bones) is often correlated with excessive development (e.g. hyperossification) of the same tissues (42, 46, 148). Moreover, cases are known from both vertebrates (95) and invertebrates (73) in which reduced and simplified adult morphology results from resorption of structures that are partly or even fully formed at earlier ontogenetic stages.

### *Morphological Novelty*

There is a consistent association between extreme phylogenetic body size decrease and morphological novelty. This association seemingly cuts across all major taxa, including many marine forms (10, 59, 73, 90, 142), insects (56), and vertebrates (42, 43, 45, 88, 113, 117, 118, 162). Examples comprise a series of remarkable and sometimes bizarre structures, ranging from the priaprium, a bilaterally asymmetric, subcephalic copulatory organ derived from the pelvic fins in the minute phallostethid fishes of southeast Asia (94, 95, 115), to the "ciliated" wing characteristic of tiny adult featherwing beetles (Trichopterygidae), which are as short as 0.25 mm (23, 56).

The evolution of some novel features is readily tied to size decrease. In vertebrates, for example, there is a negative allometric relationship between the size of the inner ear and head and body size. When this conservative relationship is extrapolated to extremely small heads, as in several lineages of miniaturized amphibians and reptiles, the now prominent inner ear effects gross and novel rearrangement of the adjacent skull, and especially the jaw suspension, often with important functional consequences (14, 43, 111, 113).

In other instances of miniaturization the link between size decrease and novelty is not as easily defined. Its existence, however, is reinforced by the parallel or convergent evolution of similar, if not identical, modifications in disparate lineages that have evolved small size. For example, the ciliated wing morphology of most featherwing beetles, which is an aerodynamically functional design at the tiny body sizes involved (17, 78), has evolved independently "in the most minute members of unrelated groups" (23, p. 14). These include both moths (23, 78) and wasps, such as the "fairy flies" (Mymaridae), which, at as little as 0.21 mm long, are the smallest known insects (56).

A causal explanation for the striking correlation between miniaturization and novelty may lie in part in the effect of size reduction on the morphogenetic mechanisms of pattern formation, many of which are size dependent (45). A simple decrease in the size of an embryonic organ primordium, for example, can effect dramatic change in adult morphology (1); moreover, such changes do not require any change in the underlying developmental mechanism.

Novelty is often superimposed on reduction and simplification (42–44, 46, 85, 121, 156). Among ammonites, miniature paedomorphic species may be nearly indistinguishable from the juvenile stages of outgroups, but more typically they display novel or unique features at maturity that seem unrelated to paedomorphosis (59). Other species display traits thought to result from a termination of growth without a cessation of development. This reinforces the generalization that the evolution of small size, even when it involves paedomorphosis, is more than simple truncation of the ancestral ontogeny. Instead, it is the outcome of a complex interplay of size, developmental mechanisms, functional demand, and historical contingency (60, 133–135).

### *Increased Morphological Variability*

There are few examples of a third consequence of miniaturization—increased morphological variability within species (44, 46, 72). When present, the variation is related to reduction or morphological novelty. For example, it frequently involves late-forming structures, whose development is precociously truncated as part of an overall pattern of reduction via paedomorphosis. This results in extensive intrapopulational, and sometimes even intraindividual (right-left), variation in the presence/absence of a given element, e.g. the septomaxillary bone in salamanders of the genus *Thorius* (44). Other instances of increased variability are not obviously related to developmental truncation, but instead involve novel features that have themselves arisen during miniaturization (42, 45).

## EVOLUTIONARY SIGNIFICANCE OF MINIATURIZATION

### *Phylogenetic Perspectives*

Some clades are more successful than others in terms of the number and diversity of component taxa and longevity. Founders of successful clades are more often small than large, and size increase within lineages (Cope's Rule) is more common than size decrease (41, 58, 63, 76, 89, 141). One reason that successful clades arise at small size may be simply that most available ancestors are small (21, 141). Conversely, when morphological novelty commonly associated with miniaturization involves fundamental changes to



the bauplan, entirely new patterns of organization may result (see below). Indeed, miniaturization has been postulated as a key feature in the evolution of many major taxa, including the earliest reptiles (11, 12), snakes (113, 114), lizards (12, 13), lissamphibians (3, 4, 15, 82), bivalves (127), and several "mesozoan" phyla (8). There is a temporal asymmetry in the pattern of phyletic size change in the fossil record; body size increase within clades is characteristically gradual, but size decrease may be abrupt (39–41) and often attributed to paedomorphosis (39, 53). Small size of the members of basal groups may account for many gaps in the fossil record. Ancestors of modern amphibians (Lissamphibia), for example, may have been among the smallest of Paleozoic amphibians (4, 14, 15).

### *Morphological Perspectives*

Miniaturization has at least three general consequences for morphological evolution. In extreme cases it can lead to changes in bauplan. Even when the bauplan is maintained, miniaturization can promote the evolution of novel developmental and morphological relationships. Finally, it often results in morphological homoplasy, which can complicate phylogenetic analyses and obscure the evolutionary impact of size decrease.

Novelty associated with miniaturization may be responsible for distinctiveness, even bauplan reorganization, in newly established clades (73, 109, 142). The interstitial fauna has attracted particular attention; many taxa, such as the phyla Gnathostomulida and Loricifera (both comprised of species of very small size), may have been founded by miniaturized and possibly paedomorphic species (68, 73). A minute (2–4 mm long) worm discovered recently, (*Jennaria pulchra*), is thought to be an annelid, but it lacks circular muscle and a coelom; it may illustrate how acoelomates arose from coelomates during the pre-Cambrian radiation of the Bilateria (110). The pseudocoelomate condition characteristic of many other phyla also may have arisen by paedomorphosis from an ancestral coelomate bauplan (8, 109a). Minute polychaete worms, for example, have lost intersegmental septa, and the coelomic fluid is continuous among segments; in many species the coelomic lining also has been lost, producing a homoplastic pseudocoelomate condition (109a). The four enigmatic "mesozoan" phyla (Placozoa, Monoblastozoa, Rhombozoa, and Orthonectida) have a generally simple organization but also display odd, specialized features that may be consequences of secondary simplification (8, 34a, 141a, 154a). Finally, basic body organization of the smallest known species of monoplacophoran mollusc (genus *Micropilina*; maximum length 0.92 mm) is so poorly defined as to lead one author to question whether the group even has a meaningful bauplan (48a). In all these examples, novel bauplans may have evolved as a consequence of size decrease.

Miniaturization may promote novelty when tissues and organs reach limits



imposed by the physical world (17), or by exploiting the potential of underlying developmental processes (31). Its full evolutionary potential is realized when a novel feature leads to additional novelty during subsequent phyletic diversification. Seilacher (127) postulates "morphogenetic shunting" in the evolution of soft-bodied oysters, in which miniaturization initially produces fundamental changes in the mechanisms of shell morphogenesis. Descendant lineages, including small and large forms, subsequently display a wide array of novel shell types that are manifestations of the modified morphogenetic system. These novel configurations, in turn, facilitate ecological diversification. Additional invertebrate examples include some bizarre features of miniaturized phyla, e.g. the complex head of loriciferans (49). In salamanders, an extreme case of miniaturization resulted in the loss of a biomechanically important cartilage and erosion of vertebrae, but subsequent evolution produced new and fully functional organizations (67, 155, 156, 158).

Homoplasy (phylogenetic convergence, parallelism, and reversal) often accompanies miniaturization (25, 114). Mites (Acari), among the smallest of complex terrestrial metazoans, may have been derived independently from several ancestral arachnid clades (153), which evolved "convergently to capitalize on miniaturization and the acarine Bauplan" (8, p. 503). At lower taxonomic levels, homoplasy is rampant in the appendicular and cranial skeleton of miniaturized frogs and salamanders (20, 45, 46, 148, 156). A striking example is the repeated reduction and loss of the first digit of the hind limb in frogs and the fifth digit in salamanders (1, 29, 37).

A special kind of homoplasy related to miniaturization is compensatory convergence, which involves the evolution of similar features that compensate for detrimental effects of size decrease (159). Within a morphologically diverse taxon, repeated instances of miniaturization result in convergent specializations because the same developmental rules are in effect. Examples include cranial organization in pygmy squirrels (86), hyperossification in amphibians (46), and reinforcement of the body wall by the development of a spiracular skeleton in many meiofaunal taxa (142, 143).

### *Ecological and Behavioral Perspectives*

There are many ecological correlates of miniaturization, especially involving life history. In general, extreme body size decrease is associated with a reduction in fecundity and an increase in egg size (32, 126, 136). This trend is taken to its logical extreme in some species of miniaturized animals in which females produce only a single large egg per clutch (23). The possible role of life history features in the evolution of miniaturization is discussed below.

Behavioral evolution, accompanied by homoplasy, often accompanies miniaturization; examples include behavioral simplification in copepods

(128), and modifications of mating behavior in fishes (81, 93, 94, 115, 162), salamanders (103), frogs (22, 32, 34), and mammals (61). Behavioral complexity in ants is related to the  $3/2$  power of brain volume, which is allometrically related to head width (18). Because in ants head width also is a good measure of body size, miniaturization of these insects leads to behavioral simplification.

## PROBLEMS IN THE STUDY AND ANALYSIS OF MINIATURIZATION

### *Phylogenetic Issues*

Comparative biology must proceed within a rigorous phylogenetic framework (6, 48), and tools for phylogenetic reconstruction and analysis are readily available (70). Heterochrony and homoplasy both figure prominently in discussions of miniaturization, yet explicit phylogenetic hypotheses are necessary before either class of phenomena may be invoked or analyzed effectively (24, 48, 156, 158, 160). Heterochrony and homoplasy interconnect in the case of paedomorphic parallelism, in which related clades in essence back down (in a phylogenetic sense) inherited and thus largely common ontogenetic trajectories. Particularly confounding are the many instances of reversal in which plesiomorphic states are restored; when organismal-wide, or global, paedomorphosis is involved, there may be profound difficulty in determining whether taxa are basal or highly derived (50, 85, 163, 165b).

Another challenge to phylogenetic analysis is posed when the miniaturized, adult morphology is so specialized (as a result of reduction, simplification, compensation, novelty, etc) as to obscure affinities with any other known taxon; many such groups are taxonomic enigmas (36, 44, 57, 84, 109, 112, 117, 161). Characters derived from DNA sequences and other nonmorphological features are often required to resolve these formidable problems.

### *Factors Promoting the Evolution of Miniaturization*

As evolutionary biologists, we seek causes for miniaturization in environmental factors that favor small body size. In ecology and evolutionary biology, however, causality is difficult to ascertain (98). The adult morphology of many miniaturized species is so poorly developed, including reduction, structural simplification, and increased variability, that it is hard to envision these features as the main target of selection (4, 26, 44). Instead, they may represent nonadaptive (but not necessarily maladaptive) by-products of size decrease that is promoted by selection for some other attribute (38, 74). Many specialized niches or habitats demand tiny body sizes, such as the spaces

between sediment particles (the meiofauna; 50, 142), and life as external parasites or commensals on parts of already small organisms (e.g. mites that live on the wing bases of insects; 73), or as commensals, inquilines, or internal parasites (e.g. pearl fishes; 147, 150). In many other instances of miniaturization, the factors promoting size decrease are more elusive. Because body size is a critical variable in most studies of population biology and community ecology (97), adaptive explanations related to life history evolution need to be explored (35, 69, 133).

It is possible to integrate life history theory, selection theory, and ideas of heterochrony in regard to miniaturized species. Early sexual maturation, which may be favored in unpredictable or unstable environments, may come at the expense of subsequent growth and differentiation and result in progenesis (time hypomorphosis) (30, 80). Indeed, claims of progenesis abound in the literature on miniaturization (e.g. 165b). Yet, as discussed above, other processes that do not involve precocious reproduction, such as rate hypomorphosis, may also result in small size and paedomorphic morphology. These processes are rarely considered (132, 133). A careful phylogenetic analysis is required for each clade to determine if age at first reproduction is advanced in the miniaturized lineage. Moreover, subsequent evolution may extend the time to first reproduction, obscuring the proximal evolutionary process originally responsible for size decrease.

An alternative model for the evolution of miniaturization based on selection primarily for life history attributes comes from Matsuda (73). It involves both environmentally induced phenotypic plasticity and subsequent genetic assimilation. According to this model, environmentally induced increase in egg size leads to the incorporation of larval or other juvenile stages into the period of intraovular development. In extreme cases, this condensation of the ancestral ontogeny results in tiny hatchlings that are structurally adult, thereby providing an easy transition to miniaturization. Such "direct development" is characteristic of many taxa of miniaturized animals within lineages that primitively display a complex life history (51, 73).

### *The Meaning and Measurement of Size*

Biologists typically measure organisms against a physical standard and express size in related units—\_inches, meters, etc. These estimates of "physical size" are very effective for describing many biological phenomena, such as the allometric scaling of morphological and physiological variables relative to body size during both ontogeny and phylogeny (125). Such an approach implicitly assumes that a common scaling principle can be used across a wide range of organisms (e.g. 97), except in extreme cases where constraints of the physical world intervene (e.g. the effects of very low Reynolds numbers;



17). Other basic features of organismal design, however, may also qualify this assumption. For example, metazoans are made up of modular units—cells—which, with the exception of some types such as neurons, have a predictable and typical size within a given organism and tissue (4a). However, because of the strong, positive correlation between cell size and genome size, and because genome size may vary widely among taxa, cell size may differ significantly between even closely related species (92, 144). There is, in turn, a complicated relationship between genome/cell size and metabolic and developmental rates (16, 130). As a result, species that are the same physical size but have different genome and cell sizes likely also differ in ways that significantly affect morphogenesis, growth, and adult morphology. Analysis of organismal size and size change thus becomes a consideration not simply of physical size, but also of a more elusive concept—biological size.

This has direct bearing on the study of miniaturization. In some groups, miniaturization may have been achieved by cell size decrease (65). In others, extensive genome and cell size variation complicates tremendously even basic comparisons of body size among taxa. In two amphibian groups well known to us, Anura and Caudata, genome size varies by an order of magnitude among species (54, 62, 71, 129, 130). The variation is especially large in salamanders, in which genome size ranges approximately from 14 to 100 pg DNA per haploid genome (vs 1–19 pg DNA in frogs). For these taxa physical size is misleading, although for most other tetrapods, which have genomes smaller than 5 pg DNA/haploid nucleus and relatively little variation (92), it is appropriate. Because the tiny salamanders of the plethodontid genus *Thorius* have a large genome (ca. 25 pg DNA/haploid nucleus; 129, 130) and, hence, large cells, they are even smaller with respect to developmental mechanics and structuralist principles of design and self-organization; their morphology is among the most profoundly specialized in vertebrates (42, 44, 121, 156).

Even physically large organisms can be “biologically small” if their genomes are sufficiently large. Two of the three living genera of lungfishes (Dipnoi), which have by far the largest genomes in vertebrates (92), show evidence of secondary simplification of the nervous system as well as other traits that have been interpreted as pedomorphic (120). The plethodontid salamander genus *Hydromantes* has the largest genome of any terrestrial salamander (129, 130). Although all species are moderately large (head and trunk length exceeds 60 mm), they have among the most simplified brains of any vertebrates (119, 121). *Hydromantes* belongs to the speciose tribe Bolitoglossini, which itself is characterized by a high degree of secondary simplification, loss of ancestral structures, and novel organization and morphology (158). These features have been attributed mostly to the large genomes characteristic of these salamanders, which result in a biological, but largely nonphysical miniaturization (157).



## SUMMARY AND CONCLUSIONS

Miniaturization is a common phylogenetic trend that has immediate and far-reaching consequences for organismal and evolutionary biology. The miniaturized phenotype is a complex combination of ancestral and derived traits; morphological correlates include reduction and structural simplification, increased variability, and novel structural configurations. Many of these features likely represent secondary consequences of precocious truncation of ancestral ontogenetic trajectories. Such truncation may result from selection primarily for small body size or some related attribute (e.g. life history characteristics). Other features are not readily explained by developmental truncation, but instead likely represent direct results of size decrease, i.e. scaling effects. Effects on adult morphology may obscure phylogenetic relations to other, nonminiaturized taxa; this taxonomic confusion is often compounded by homoplasy and character reversal. In extreme instances, miniaturization has resulted in novel bauplans associated with the origin of higher taxa. Evaluation of the causes and consequences of miniaturization should play an integral role in the search for explanation of the biology of small animals, which should consider both obvious (e.g. physical size) and nonobvious (e.g. genome and cell size) features.

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