SMALL WONDERS

For Some Species, Reduced Size Is the Key to Survival

by JAMES HANKEN

IN 1912, the *American Naturalist* published a short, curious article entitled "The Range of Size in the Vertebrates," in which a zoologist, Arthur W. Henn, of Indiana University, provided a veritable who's who of the largest and smallest fishes, amphibians, reptiles, birds, and mammals, both living and long since perished. His registry included examples of giantism (the eighty-five-foot blue whale, *Balaenoptera musculus*, "the bulkiest vertebrate which has ever existed") and dwarfism (*Microsorex hoyi*, the pygmy shrew, which measures about three inches from snout to tail).

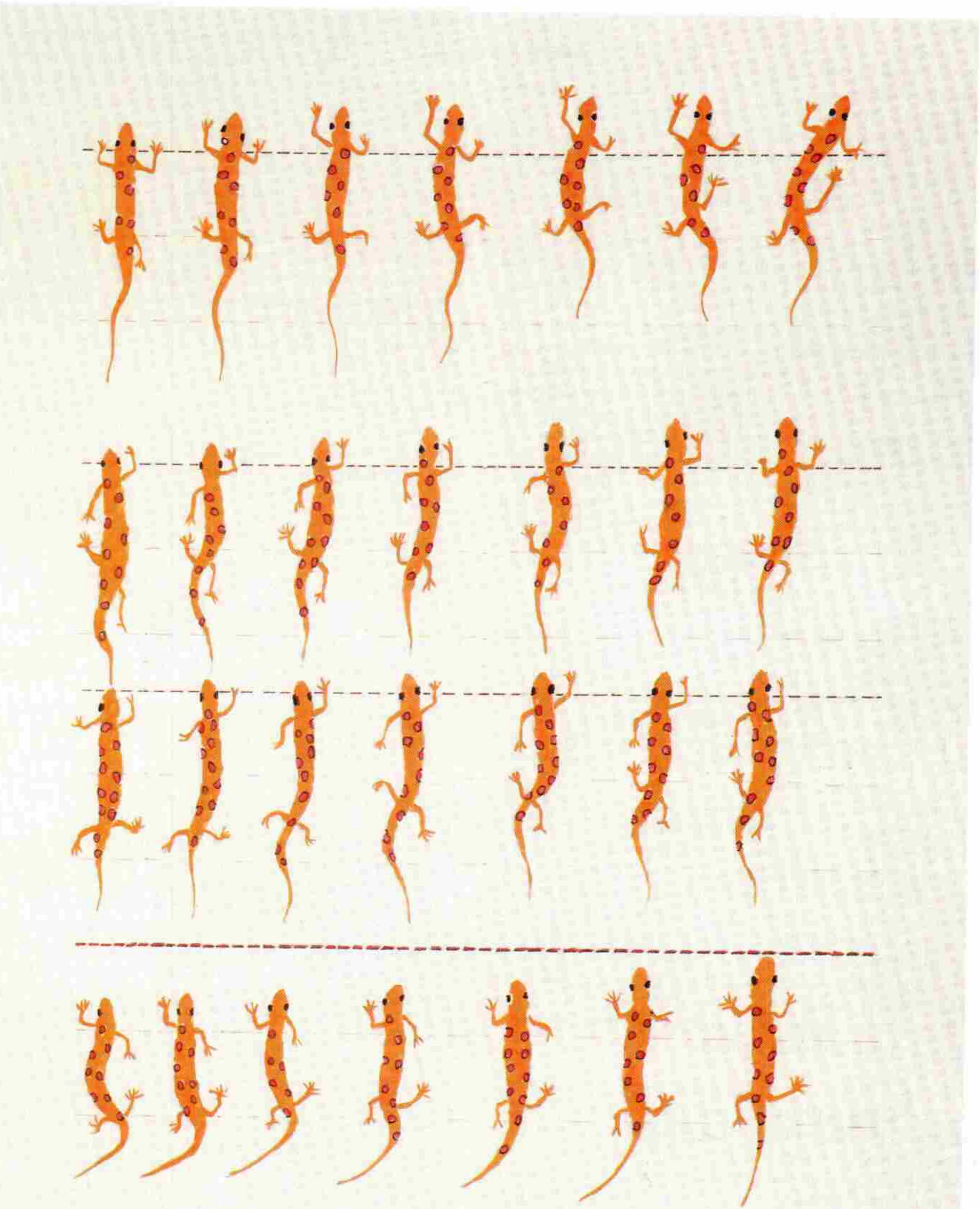
No mere chronicler of nature's eccentricities, Henn paused here and there in his list to advance a comment, his most discerning being that extreme size at either end of the scale invariably exacts a heavy, often fatal, toll. Thus, we are told that extravagant energy needs, coupled with an undersized brain, brought about the demise of the immense dinosaur *Atlantosaurus*. And in the case of such insectivores as the pygmy shrew, one of the most primitive mammals, that smallness is an unmistakable sign that the species is outmoded, an indictment Henn extended to tiny representatives of many other groups as well.

The idea that the evolution of *decreased* body size, or miniaturization, is insignificant, or even detrimental, to a species' survival was a popular theme in evolutionary biology long before publication of Henn's paper. And this view is at least partially justified. To take one example: During the Pleistocene epoch, a two-million-year period that ended about ten thousand years ago, the elephant populations of numerous islands evolved into dwarf species. These insular groups, ranging on islands in the Mediterranean, in the Malay Archipelago, and in the Channel Islands off the California coast, attained heights (at the shoulder) of only three feet, compared with twelve feet or more in continental species. As in other cases of miniaturization recorded by paleontologists, the elephants' decrease in size was most often interpreted as an evolutionary response to the regressive circumstances confronted by animals who became isolated on islands: shrunken, less diverse habitats favored reduced populations and small animals capable of surviving on fewer resources. But those who actually studied the fossil remains of the extinct island elephants and other dwarf species found no evidence to suggest that miniaturization contributed in any way to evolutionary success. On the contrary, as Henn suggested, miniaturization appeared to be symptomatic of decline.

This view persisted until about thirty years ago, when evolutionary biologists started to take a closer look at miniaturized animals, especially those whose size approached the limit at which a particular body plan can perform the functions characteristic of that creature. They found that novel morphological structures—the raw material for evolutionary variation—appear more frequently in diminutive species than in standard populations. As much as this reappraisal helped remove the stigma associated with miniaturization, it did not address the fundamental questions of how variation originates and of how, after arising in a single individual, a novel structure becomes established in a population or even characteristic of an entire species. In answering these questions for vertebrates—in particular, for salamanders of the genus *Thorius*—we have learned that, far from being an evolutionary dead end, miniaturization can serve as a detour around the obstacles nature normally places in the way of novelty and can thus enhance survival.

A MINIATURE is not merely something small; it is a small object that is functionally equivalent to the larger object from which it derives or after which it is patterned. Predictably, reducing size without sacrificing essential characteristics poses any number of design problems, the severity of which corresponds to the complexity of the object undergoing change. Manufacturing a tiny version of a rubber ball is a simple task because a ball is a compositionally simple object. But miniaturization of, say, a 1930 Philco box radio requires that its internal structure—based on vacuum tubes that will no longer work if reduced in size—be redesigned altogether, to rely on transistors or, better yet, on integrated circuits. Scaling down something as complicated as a vertebrate demands even more ingenious solutions, two of which were first described in 1954, by the German biologist Bernhard Rensch in his book *Evolution Above the Species Level*.

The first solution concerns the organs or tissues that an animal can effectively do without. In many species undergoing miniaturization, organs are discarded or reduced to mere vestiges, and the functions they served are either abandoned or assumed by remaining organs. An example of the latter is seen in the tiny Panamanian spider *Micro-*



Nancy Graves, Diagonal Sequence of Limb Movements in a Newt, *1971* *mygale diblemma,* which lacks the so-called book lungs, found in many larger spiders. For an animal of its size—adult males are only one thirty-second of an inch long—an internal respiratory system is not as efficient for transporting gases as is simple diffusion through the spider's skin. Such cutaneous exchange can suffice in a tiny creature, in which all cells are relatively close to the surface, but would not be satisfactory in a larger animal because the distances that dissolved substances would have to travel are too great.

Rensch's second solution to the problems posed by miniaturization centers on morphological structures that must be retained if the animal is to survive. In this case, the only way to diminish size below the functional limit of a given design is to alter the design itself so that, like the transistor that replaces the vacuum tube, it will serve the same function but in a more parsimonious and efficient fashion. Although the jumping spider *Portia fimbriata,* with a body about one-eighth of an inch long, is substantially larger than the Panamanian spider, its size nonetheless poses a problem: unlike *Micromygale,* which has only two eyes rather than the eight of larger, related species, the jumping spider can ill afford a reduction in the size or number of its eyes because of their preeminent role in discriminating between prey and mates. David S. Williams and Peter McIntyre, of the Australian National University, in Canberra, recently described a unique fovea, or pit, in the retina of *Portia* 's anterior median eyes that magnifies the image transmitted by the cornea. The effect is similar to that of a telephoto lens but without an equivalent change in focal length. Thus, a design alteration allows *Portia* to maintain visual acuity despite a reduction in the retina's size that otherwise would hinder sight.

Both kinds of morphological adjustment—organ loss accompanied by a transfer of functions, and organ redesign—occur in the genus *Thorius,* a group of some fifteen species of terrestrial and arboreal salamanders native to the montane forests of southern Mexico. *Thorius* is of particular interest because its members are so tiny; in some species, the length of adult males (which, in general, are smaller than females) is little more than an inch and a quarter, of which nearly half is tail. Moreover, *Thorius* is slight compared with its ancestors; the genus exemplifies the evolutionary trend toward dwarfism. Together with a few species of frogs that are even tinier than *Thorius,* these amphibians define the lower end of the size range reached by vertebrates in their more than four-hundred-million-year history.

GIVEN THE FUNCTIONAL PROBLEMS posed by miniaturization, one would expect *Thorius* to possess all manner of novel morphological features, and, indeed, it does. Its vertebrae and skull, its brain and eyes, and the highly specialized projectile tongue it uses to capture prey are only a few of the structures that have been redesigned to suit the constraints imposed by miniaturization. Of particular interest is *Thorius*'s modified limb structure, which differs greatly from the ancestral structure in some species and less so in others; thus, the skeleton is an intermediate form that allows one to trace the development of new patterns and to test hypotheses about the way they appeared and became established.

In most vertebrates, all members of a given species possess the same number and arrangement of limb elements. The same holds true for closely related species (both a human foot and a chimpanzee foot possess twenty-six parts), but the figure may vary greatly among distantly related taxa. Indeed, some of the most important transformations of the vertebrate limb, such as the evolution of the five-fingered arm from the fin of ancestral fishes, involved changes in the number of skeletal elements and their spatial configuration. In short, skeletal features go a long way toward defining what differentiates one species from another—which fact underscores the peculiarity of *Thorius.*

Instead of a single wrist pattern characteristic of all species in the genus, or even of all members of a species, specimens of *Thorius* have been found to have nine configurations that separate the two bones of the salamander's lower arm from the four digits of its hand. Fourteen species of *Thorius* have at least two of these different skeletal patterns, and three species have as many as four. And all of the arrangements involve fewer wrist elements than the eight that were present in ancestors of the genus; some species possess as few as four distinct wristbones, whereas others have as many as seven.

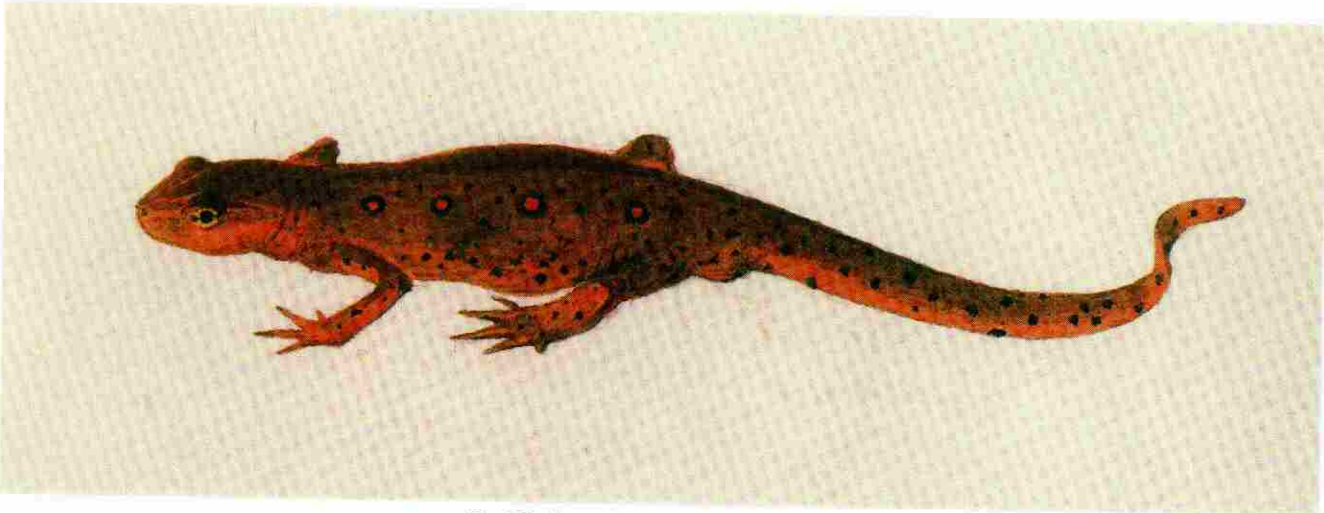
The most unexpected aspect of this increased variation is the high degree of structural asymmetry within individual salamanders: in as many as half the members of a species, the number of wristbones on a salamander's right side differs from that on the left. Many of the novel limb patterns within a single population of *Thorius*—or, indeed, within an individual salamander—are as different from one another as the patterns that differentiate one species from another or, in higher taxonomic groupings, one genera, or even family, from another.

Eccentric skeletons would deserve no more than passing notice were it not for the huge imbalance between the factors that favor such novelty in natural populations and those that discourage it. Some degree of morphological change is inevitable with each generation of a species. The variation may result from internal forces (as in the mutations that arise from unprecedented genetic combinations after the fusion of sperm and egg) or from large-scale environmental influences (as when an embryo is exposed to extreme cold or heat, for example, and forms differently from the way it would at a more moderate temperature). Finally, changes may appear as a type of "developmental noise"; minute random differences in appearance between the right and left sides of an organism, for example, can sometimes be caused by variations in the chemicals found in different parts of an egg.

Opposing these sources of variation is a powerful force: natural selection, the process by which a particular structure, because of its utility, achieves greater proportional representation in successive generations at the same time that other, less serviceable designs diminish in abundance or disappear entirely. Natural selection thus exercises a generally reductive effect on variation, filtering maladapted forms from the population.

In *Thorius,* the tiny Mexican salamander with maverick wrists, it would seem that either the factors favoring novelty are unusually strong or those discouraging it are atypically weak. Both statements, it turns out, are true.

With respect to skeletal variation, the rate at which new forms arise in *Thorius* so exceeds the norm that it points to a previously unappreciated source of morphological novelty (in addition to mutation, environmental influence, and developmental noise), called scale dependence. Evidence for scale dependence as a source of morphological novelty derives, in part, from mathematical models that describe the development of patterns as different as the arrangement of feathers on a bird's wing and the alternating rings of pigment on a raccoon's tail. Most of these models make clear that pattern formation is a function of the size of a developing structure and, most critically, of the number of cells available for the growth of tissues. In *Thorius*—as in any vertebrate that has undergone miniaturization—size reduction is accompanied by a decrease in the number of cells that make up the limb. But since bone development requires a minimum number of cells, reducing their total number to a level even slightly below that threshold results in the formation of fewer elements and, consequently, an alternate skeletal arrangement. The effect is pronounced in *Thorius*, because the minute creature virtually teeters on the edge of salamandrine existence; with a body that approaches the absolute minimum size for a vertebrate, it is profoundly affected by incremental changes in the number of cells available for skeletal formation and thus displays an unusually high rate of morphological novelty.



Karl Bodmer, Salamander, *c. 1832–34*

If scale dependence explains the increased frequency of variation in *Thorius,* how does such seemingly capricious variation survive the severe pruning of natural selection? Imagine, for the sake of comparison, an equivalent range of deviant skeletal patterns in, say, a lion or a hawk. How might the lion's ability to chase and pounce on a gazelle be affected by the presence of three pieces of surplus bone in each of its ankles? Would a redtail's flight be as effortless if its left wing were deprived of two elements? Surely the movements of such animals would be hobbled in ways that would render them less capable of living well enough and surviving long enough to perpetuate their kind. It seems, however, that in the tiny limb of *Thorius,* skeletal variants impose no ill effects on the salamanders that bear them. Indeed, the novel patterns are functionally neutral. This is especially true for the asymmetrical individuals whose left and right limbs are differently structured: dissimilarities in gait have never been observed. Even more unusual, no correlation exists between habitat, type of locomotion, and skeletal novelty; the wrist patterns and movements of tree-dwelling salamanders are indistinguishable from those of their terrestrial cousins.

These observations are not meant to suggest that the influence of natural selection has been eliminated. Presumably, if a skeletal pattern that impaired locomotion appeared, seriously undermining the adaptive success of the individuals bearing it, it would diminish in frequency and eventually disappear. But in *Thorius,* the variant patterns are about equally adaptive; no one configuration is so utilitarian as to exclude all others—the typical progression of events in larger salamanders. Because *Thorius*'s nine different wrists are invisible to natural selection, they are not winnowed from the species as they would be if the tiny vertebrate were as large as a lion or a hawk.

Thus, miniaturization establishes the conditions necessary both for the initial appearance of alternate morphological types and for their subsequent maintenance throughout a population. A miniature species, like *Thorius,* is a kind of living laboratory in which experimentation with novel morphological forms is sheltered from the normal stresses of evolution. But these laboratories are no mere basement workshops in which nature indulges in anatomical whimsy and superfluous tinkering. All the while that the tiny Mexican salamander is inventing new ways of doing things, it is building repertoires of alternate structural designs that become available for subsequent adaptation and evolutionary diversification. Reduced size provides a means for evolutionary bridges between distinct morphological arrangements—bridges that are impossible for larger organisms to build. In *Thorius,* it seems as if miniaturization is not a last-ditch effort to stave off the inevitable in an evolutionary endgame but a shrewd gambit that increases the species' chances of survival. By sacrificing size, the tiny Mexican salamander has gained longevity. ●

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