Salamander Invasion of the Tropics

No longer restricted to aquatic habitats, lungless salamanders dispersed southward and achieved their greatest diversity

by James Hanken, James F. Lynch, and David B. Wake

What is evolutionary success? Perhaps the most obvious example is an adaptive radiation: the divergence of members of a single lineage into a number of different ecological niches or adaptive roles. This divergence can involve changes of morphology, physiology, ecology, and behavior. By investigating adaptive radiations, we can learn the causes and limitations of evolutionary change.

In many ways, salamanders might seem unlikely subjects for the study of adaptive radiation. As is typical of most amphibians, salamanders must maintain a moist skin and are frequently restricted to aquatic sites in or near ponds, streams, and seepages or under moist logs or leaf litter in humid forests. Because salamanders are ectothermic (cold-blooded), their energetic needs are slight—usually only a fraction of those of birds and mammals. They can feed infrequently and remain inactive for long periods; this, plus their usually small size, makes them inconspicuous. For these reasons, some biologists have dismissed them as rare and of little ecological significance.

Despite their apparent low profile, in many habitats salamanders are the most abundant vertebrates. For example, salamanders in a New Hampshire forest were found to exceed birds and mammals in both numbers and biomass. Further, salamanders display a variety of body shapes and sizes, ranging from inch-long species to an Asian genus whose members attain lengths of five feet. Some salamanders are fully aquatic, others are partly so, and many are fully terrestrial. Most species have well-developed legs and feet, but some groups have tiny limbs, and others lack hind limbs entirely. Some salamanders are subterranean, while others spend their entire lives far above the ground in the canopy of tropical forests.

One of many lungless salamanders of Central America is Bolitoglossa mexicana, *native to Belize. Geologic events that fragmented populations helped to create a diversity of salamander species in this region.*

Raymond A. Mendez

The approximately 325 species of living salamanders are divided among nine families. However, more than 200 species belong to one family, the Plethodontidae, or lungless salamanders, and about 150 of these, or nearly half of all salamanders, are members of one subgroup, the tribe Bolitoglossini, or, literally translated from Greek, the "mushroom-tongued" salamanders. Salamanders as a group arose in the Northern Hemisphere, and virtually all living nonbolitoglossine salamanders are confined to the north temperate portions of Asia, Europe, and North America. In contrast, all but about a dozen bolitoglossines live at tropical latitudes in Middle and South America. How can we account for this successful invasion of the tropics?

The earliest lungless salamanders were descendants of stream-dwelling salamanders of the ancient Appalachian highlands of eastern North America. The most primitive living lungless salamanders are still found in stream habitats in the Appalachians where they maintain a 100-million-year-old life history pattern. Semiaquatic adults mate and deposit eggs at streamside. Carnivorous aquatic larvae that emerge from these eggs later metamorphose into terrestrially adapted adults that leave the water. This reproductive pattern, although typical of many other amphibians, constrains ecological and evolutionary diversification. Most important is the restriction of such amphibians to areas where aquatic breeding habitat is at least periodically available. Dependence on aquatic breeding sites also limits the ability of amphibians to disperse through areas without free surface water.

Exceptions to this life history pattern are rare in most salamander families. One alternative is demonstrated by a few species of the European genus *Salamandra*, in which females do not deposit eggs, but instead retain them in the oviduct where development proceeds. Young emerge either as well-developed aquatic larvae or fully metamorphosed terrestrial salamanders.

Many lungless salamanders, including all bolitoglossines, have evolved a different means of eliminating the restrictive aquatic larval stage. These salamanders retain the primitive pattern of laying eggs, but the eggs are deposited in moist, protected terrestrial sites where the female broods them for a long period (up to eight months in some species). At hatching, a fully functional salamander emerges, having achieved complete independence from aquatic habitats.

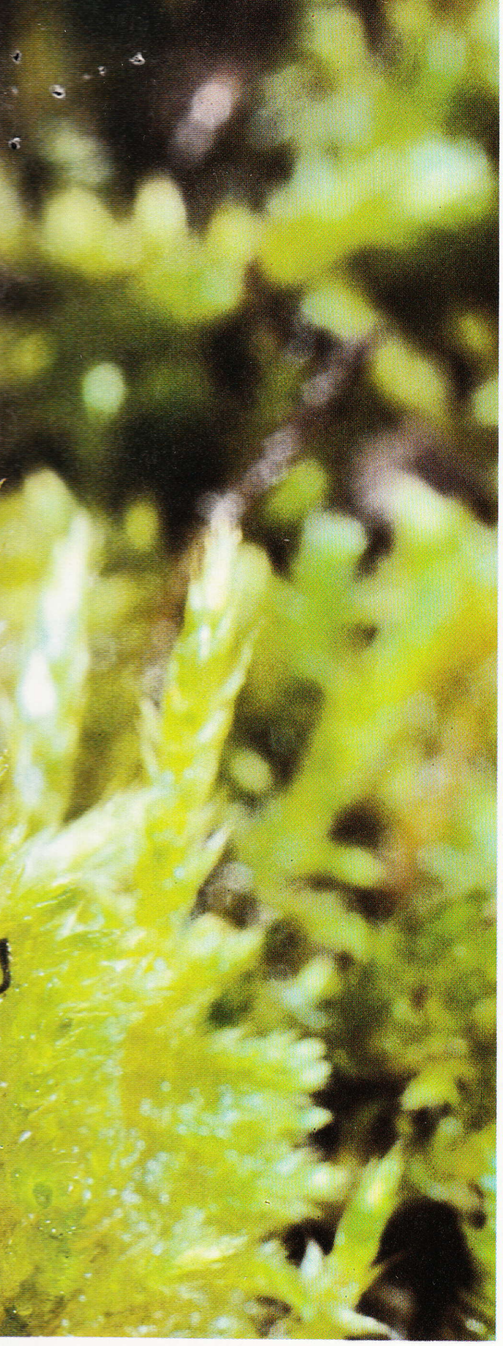
With this fully terrestrial reproductive mode, ancestral lungless salamanders dispersed across the humid temperate forests that covered most of North America during late Mesozoic and early Cenozoic times, ultimately extending west to the Pacific coast and south into the New World tropics. Subsequent episodes of mountain building and climatic change caused much of the temperate forest to disappear from the western half of North

America in favor of more arid habitats, eliminating lungless salamanders from virtually all of the mid-continental region and northern Mexico.

Today, isolated survivors of these events give us some idea of the enormous and nearly continuous distribution that lungless salamanders must have enjoyed in the past. Relict species still may be found in pockets of favorable humid habitat in New Mexico, Oklahoma, Texas, and Arkansas, while in California's Mojave Desert, several distinctive species have recently been discovered leading precarious lives around tiny springs and seepages in otherwise uninhabitable mountains. Most startling is the present distribution of the genus *Hydromantes,* one of the two genera of nontropical bolitoglossines. The western North American ancestors of *Hydromantes* dispersed into Asia via the Bering land bridge across the northern Pacific Ocean and extended their range to the west and south until they reached the Mediterranean region. Today, we find two of the five species of *Hydromantes* inhabiting caves and crevices in limestone areas of northern Italy, southern France, and the island of Sardinia, while the remaining three species are restricted to the mountains of central and northern California.

A great expanse of inhospitable arid country at present separates the lungless salamanders of temperate North America from those of the tropics. The northernmost members of the tropical assemblage include several generalized species of the genera *Pseudoeurycea* and *Chiropterotriton* that live at high elevations in Mexico's northern mountains. In morphology and ecology, these animals resemble the presumed ancestors of all tropical salamanders. These ancestral forms continued their southward invasion via mountainous dispersal routes, leaving descendants throughout all of Middle America and much of South America as far as Bolivia.

The adaptive radiation of salamanders in the tropics has produced more than 150 known species assigned to nine distinct genera. As many as sixteen species may inhabit a single tropical mountain. Salamanders in the tropics are perhaps most abundant in mountainous areas, but they also are well represented at intermediate and low elevations, with the proportion of lowland species increasing southward.

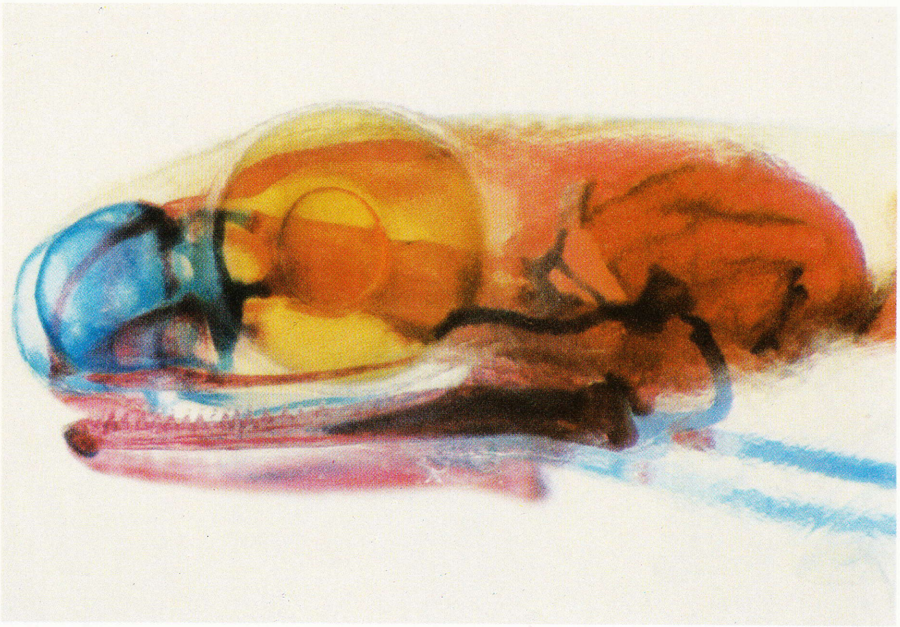


James Hanken

In southern Mexico and Guatemala more than 40 percent of the species are found, at least in part, below 5,000 feet and 14 percent occur below 1,500 feet. Farther south in Costa Rica, Panama, and northwestern South America, more than 85 percent of the species occur below 5,000 feet, and fully a third of the species live below 1,500 feet.

This information will help dispel the belief that tropical salamanders are restricted to high, mountainous areas with climates and habitats similar to cool, temperate forests. Salamanders are both diverse and locally common in the lowland forest where they thrive in conditions that are, by anyone's standards, truly tropical. Temperatures are characteristically high and rainfall may be highly seasonal, limiting activity by salamanders to only a portion of the year.

Although ecologists argue over the causes and effects of tropical diversity, a given tropical habitat will generally have more predators, parasites, and competitors than a corresponding temperate habitat. By conducting field studies we have attempted to understand how tropical salamanders have not only managed to invade tropical communities but to flourish in them. One important aspect concerns community structure. In North America, coexistence of similar species is achieved by a number of mechanisms. For example, in salamander-rich areas of the Appalachians, the species in a local community are about equally divided between aquatic and terrestrial forms. In species with aquatic



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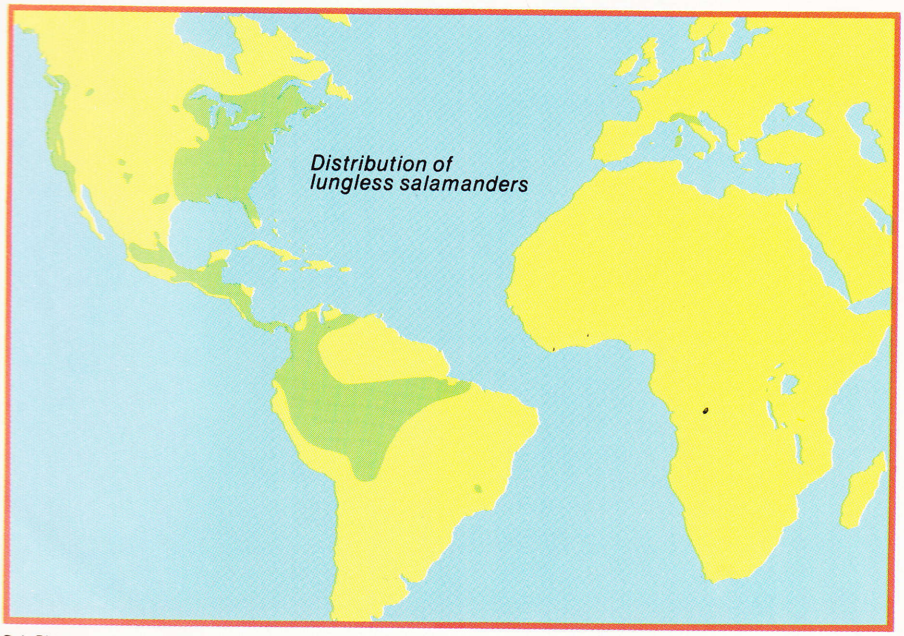
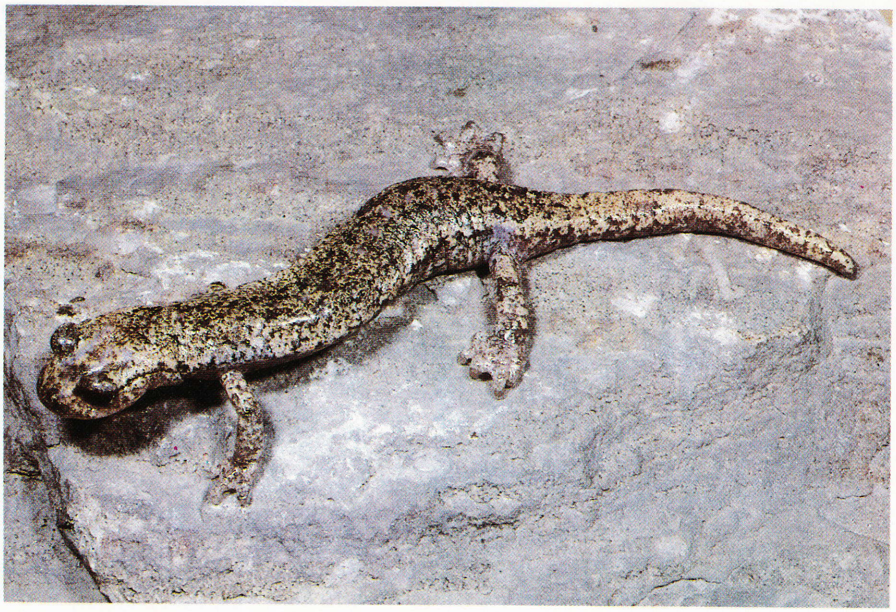


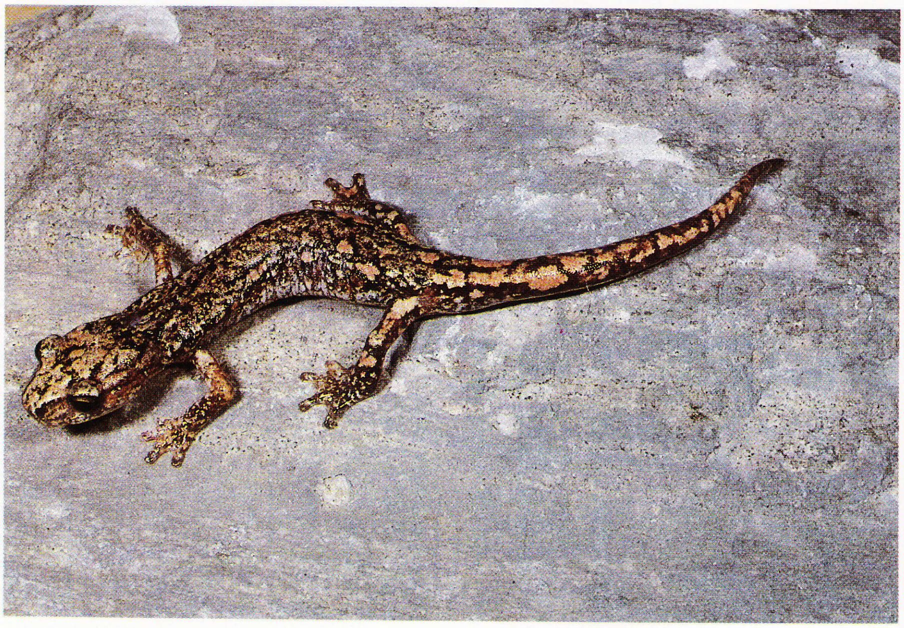
Bob Ritter

In ten milliseconds the salamander Bolitoglossa adspersa, *above left, found in Colombia, can fire its tongue a third the length of its body, capture an insect, and return the prey to its mouth. The long tongue makes it largely unnecessary for bolitoglossine salamanders to pursue prey. The photomicrograph, above, shows an artificially colored specimen of the smallest, tailed tetrapod species,* Thorius pennatulus. *Behind the large eye characteristic of small tropical salamanders is the otic capsule (dark red), the structure that controls balance and hearing.*

photographs by James Hanken



These two salamanders, Hydromantes platycephalus *from Sonora Pass, California, right, and* H. italicus *from Liguria, Italy, below, belong to a genus with a remarkably disjunct distribution. The North American ancestors of* Hydromantes *dispersed into Asia, eventually reaching the Mediterranean. Mountain-building processes and climatic changes eliminated the habitat of the lungless salamanders so that only five species of* Hydromantes *are found today. Relict populations of two of the present species persist in caves and rock crevices in northern Italy, southern France, and Sardinia. The other three species survive in the mountains of central and northern California.*



reproduction, larval development may occur in springs, streams, or ponds, and breeding seasons may differ from species to species. Thus, both spatial and temporal overlap of larvae and, presumably, larval competition are reduced. Species that occur in the same habitat at the same time frequently differ in body size, and this is correlated with differences in the kinds and size of animal prey taken. All of these mechanisms may reduce competition between coexisting species.

Tropical salamander communities are different. As we have noted, all tropical salamanders are fully terrestrial, so separation along an aquatic-terrestrial gradient is not possible. Instead, two types of vertical segregation are especially important.

First, each tropical species has a narrow, precisely defined altitudinal distribution that frequently matches the complex, yet regular, elevational zonation of tropical plant communities. In this way, species present on the same mountain may actually never occur together because of nonoverlapping elevational distributions. Although altitudinal layering also occurs in temperate regions, it is never as pronounced as in tropical habitats.

At any given elevation and habitat, further sorting is achieved by different species living at different heights above or below the forest floor. Some burrow, others confine their activity to the ground surface, while many literally take to the trees where epiphytic plants, especially bromeliads, are favored retreats. Lacking a functional root system, bromeliads attach themselves to the trunks and limbs of trees and obtain necessary moisture and nutrients from the atmosphere. Like salamanders, bromeliads thrive in areas with excessive humidity, particularly the cool, fogbound cloud forest that cloaks the slopes of many tropical mountains. There, a diverse community of salamanders and other small animals has evolved in the aerial swamp created by the upward-directed, tightly overlapping leaves of bromeliads. The association between salamanders and bromeliads is hardly casual. Some salamander species occur nowhere else, and local densities can be great—as many as thirty-four salamanders have been found inside a single bromeliad in a Mexican cloud forest. We have found salamanders in bromeliads as high in trees as we have been able to search, and examination of recently felled trees (an all-too-common sight in the tropics) has revealed salamanders at least 100 feet above the ground.

Distinctive habits and habitat preferences of salamanders are often associated with morphological specialization, and several species, or even whole genera, are highly modified to survive in tropical environments. Arboreal montane species usually have small, flattened bodies that allow them to squeeze between tightly overlapping bromeliad leaves. Such species also possess a moderately prehensile tail and partially webbed hands and feet that adhere readily to wet leaf surfaces, providing great climbing ability. Burrowing forms have tiny limbs and extremely elongate bodies

The evolution of a terrestrial life style preadapted bolitoglossine salamanders for survival in rugged tropical areas where free-standing water is scarce.

and tails that almost make them vertebrate worms. Members of the genera *Thorius* and *Parvimolge* are true miniatures. Living among leaf litter and bark on the forest floor, some adults may be only one inch in total length. This brings them very near the minimum size limit for vertebrates, and they possess various skeletal and sensory modifications to accommodate their reduced size.

The most specialized of all tropical salamanders live in the wet lowland forest. During the day most species conceal themselves in bark crevices, leaf axils, or other relatively inaccessible sites. Emerging only at night, they cling to a tree trunk, plant stem, or leaf surface in wait of prey. (This behavior explains why even experienced field biologists have tended to overlook lowland tropical salamanders.) Ground-dwelling salamanders are scarce in the lowland tropics; almost all lowland species are either arboreal or subterranean. Arboreal lowland salamanders are even more highly specialized than their relatives in the montane cloud forest. A fully prehensile tail and extensive webbing, which in effect turns the hands and feet into suction cups, allow a salamander to suspend itself, even upside down, from stems and leaves.

During the evolution of tropical salamanders, a premium has been placed on adaptations that reduce activity and make the most of available energy. A prime example involves prey capture. Most nontropical lungless salamanders ingest insects, millipedes, and snails by partially flipping out a sticky tongue, then retrieving it with the prey item attached. Simultaneously, the salamander may lunge forward and seize its victim in its jaws, especially when the prey is large. Because the front of the tongue is anchored to the lower jaw, the back of the tongue is flipped out at the prey. This resembles the movement of a clenched fist resting palm up on a table top as the fingers are first quickly outstretched and then reclenched. The anterior attachment of the tongue means that prey can be attacked only at close range.

In contrast to this primitive pattern, the tropical salamanders have evolved a highly protrusible tongue that can be fired accurately for long distances at astonishingly high speeds. Careful laboratory measurements have shown that in the genus *Bolitoglossa* the tongue can be extended to about a third of a salamander's body length and returned to the mouth with a captured prey in as few as ten milliseconds. The evolution of this efficient prey-capturing system has required a complete reorganization of the musculature and skeleton of the tongue to allow the mushroom-shaped tongue, now no longer attached in front, to be catapulted from the mouth. As an additional refinement, bolitoglossines have developed the ability to control the direction of tongue projection. Thus, the salamander need not directly face or actively pursue its prey. A highly modified tongue structure means that a salamander can instead wait for prey to approach within its increased firing range.

Regional species diversity of tropical salamanders is greatest in areas that are geologically most active. To fully understand the regional patterns of adaptation and diversity in salamanders, we must consider geologic factors as well as behavior and morphology. Throughout much of Middle and South America large-scale tectonic processes, ranging from massive volcanic activity to lateral slippage of continental plates, have created new habitat, destroyed previously habitable areas, erected barriers to dispersal, and fragmented once continuous salamander distributions.

A particularly good example of the connection between geologic events and biotic diversity and distribution is seen in the genus *Chiropterotriton.* Eight species of this group are found in wet montane forests of Guatemala and adjacent Mexico and Honduras. Morphological, genetic, and ecological evidence agree that these species are more closely related to one another than to any other salamanders, insofar as they share a common ancestor. Each species is confined to its own mountain range or cluster of ranges, and no two species occur together. For tens of millions of years, this part of northern Central America has been the scene of violent geologic activity. The region straddles the juncture of three major crustal plates, and massive fault scarps crisscross a landscape dotted with some of the most spectacular volcanoes on earth. Originally continuous upland areas, some of which date from the early Cenozoic period, have been repeatedly fragmented by lateral faults, and large upland sections have been moved hundreds of miles from their original locations. Any ancestral *Chiropterotriton* species that inhabited the continuous upland habitat would have been fragmented into numerous subpopulations, each separated by impassible lowland barriers. Some of these isolated populations doubtless went extinct, but others continued to evolve independently, so that now each is sufficiently differentiated to qualify as a distinct species.

Why have salamanders experienced such a major adaptive radiation in the tropics? We can suggest the following explanations: (1) The prior evolution of a fully terrestrial life history preadapted bolitoglossine salamanders for life in the tropics, particularly in rugged, mountainous areas where free surface water is scarce, (2) limited activity, slow metabolism, and a simple, yet efficient, feeding mechanism allow salamanders to make slight energetic demands on an environment and invade and occupy otherwise closed tropical communities, (3) morphological specializations, including a diversity of locomotor patterns, (4) the availability of distinctly tropical microhabitats, especially arboreal bromeliads, enables more species to be packed into a given habitat, (5) restriction of species distributions to the narrow elevational zones of climate and vegetation characteristic of tropical environments increases local diversity, and (6) the extraordinarily high intensity of geologic activity in Middle America and northern South America has promoted the formation of new species, thereby increasing regional diversity.

Tropical salamanders provide an unusually favorable opportunity to study patterns of evolution. Our effort has spanned more than a decade, and has at various times included the collaboration of anatomists, physiologists, taxonomists, ecologists, biochemists, and geneticists. It is sad to note that thoughtless devastation of fragile tropical habitats by humans threatens to obliterate many of the most interesting pages of this story before they can be read. □

Extensive webbing on the feet of this specialized species, Bolitoglossa mexicana, *creates a suction cup effect, enabling the salamander to suspend itself from stems and leaves.*

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