

Diversity of Costa Rican Salamanders

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Diversification and Species Richness in a Small Area

There are many more species of salamanders in Costa Rica than one would expect from the study of Old World tropical environments, because salamanders have thrived only in the New World tropics. Nearly all are members of a single clade, the supergenus (sg) *Bolitoglossa* (Plethodontidae: Plethodontinae: Bolitoglossini), which is restricted to Middle and South America. Its sister group is the sg *Batrachoseps*, which ranges from Baja California to the Columbia River, mainly west of the Sierra Nevada–Cascades mountain systems; the sister group of these two taxa is the sg *Hydromantes*, which occurs in California and the central Mediterranean region (Jackman et al. 1997). What never ceases to amaze me is that this tropical clade is not only species-rich, containing more than 200 species, nearly half of all currently recognized species of Caudata, but its impressive adaptive radiation is concentrated in Middle America, the smallest part of the Neotropical region. Surprisingly, only about 10% of the members of the clade are South American, and only 2 of the 13 currently recognized genera reach that continent. However, despite the proximity to South America, Costa Rica (and western Panama, which largely shares the same fauna) has a large and diverse salamander fauna. Although it may seem inappropriate to select an apparently arbitrary geographic subdivision for a faunal analysis, in reality Talamancan Central America (montane western Panama with Costa Rica; Wake and Lynch 1976) is an area of high salamander endemism and historical integrity. The older mountain areas and all of the central, eastern, and southern parts of present-day Costa Rica lie on the Chorotega Plate, with antecedents dating to 65 million years before the present (Coates and Obando 1996; Coates 1997; Burnham and Graham 1999). The region has enjoyed a largely separate history, sharply delimited from South America until about 3 million years ago,

and having fleeting and intermittent connection to the Chortis section of the complicated Caribbean Plate, from which it is separated largely by the currently land-positive region of the Nicaraguan Depression (fig. 3.1).

Talamancan Central America is the lowest latitude at which salamanders occur in any degree of diversity, yet it is the site of some of the richest local salamander faunas in the world. I believe it has been an important staging ground for salamander evolution.

AN UNLIKELY ADAPTIVE RADIATION

Salamanders are associated with northern continents and have been throughout their long evolutionary history (Savage 1973). All ten salamander families occur in north temperate areas today, and only the Plethodontidae has undergone any significant tropical diversification (Wake 1966, 1970, 1987). Within the Plethodontidae, one subfamily (Desmognathinae), two of three tribes in the other (Hemidactyliini and Plethodontini of the Plethodontinae), and two (*Batrachoseps* and *Hydromantes*) of the three supergenera in the last tribe (Bolitoglossini) are exclusively North Temperate in origin. Thus tropical plethodontids would appear to be an unlikely prospect for adaptive radiation. Compounding the problem is the fact that all bolitoglossines undergo direct development and have abandoned aquatic larvae, thereby restricting themselves to only some of the array of habitats used by other salamanders. For example, in the Appalachian Mountains of eastern North America, salamander diversity is high in large part because species occur in rivers, streams, ponds, springs, and seeps—habitats avoided by tropical bolitoglossines.

Although it is impossible to reconstruct details of the evolutionary history of the tropical bolitoglossines, two factors appear to be associated with their success. The first is direct development, which, while constraining them to only certain ecologies, at the same time removes them from many competitive and high-predation environments. Direct development also makes it possible for these salamanders to avoid breeding migrations and to maintain permanent small home ranges. Not having to move much during their lifetime, tropical bolitoglossines can use such specialized microhabitats as arboreal bromeliads and arboreal moss mats and balls.

A second feature that has been important in the success of tropical salamanders is their extraordinarily specialized feeding system, which involves excellent vision and a long, fast tongue (Wake and Deban 2000). This system combines high visual acuity with biomechanical attributes that enable an animal to feed rapidly, with high accuracy and wide-range directionality, on prey that might be a great distance from the predator's head (approximately 40% of snout-vent length). Perhaps most important, this specialized tongue permits the salamander to remain hidden and thus to feed with stealth.

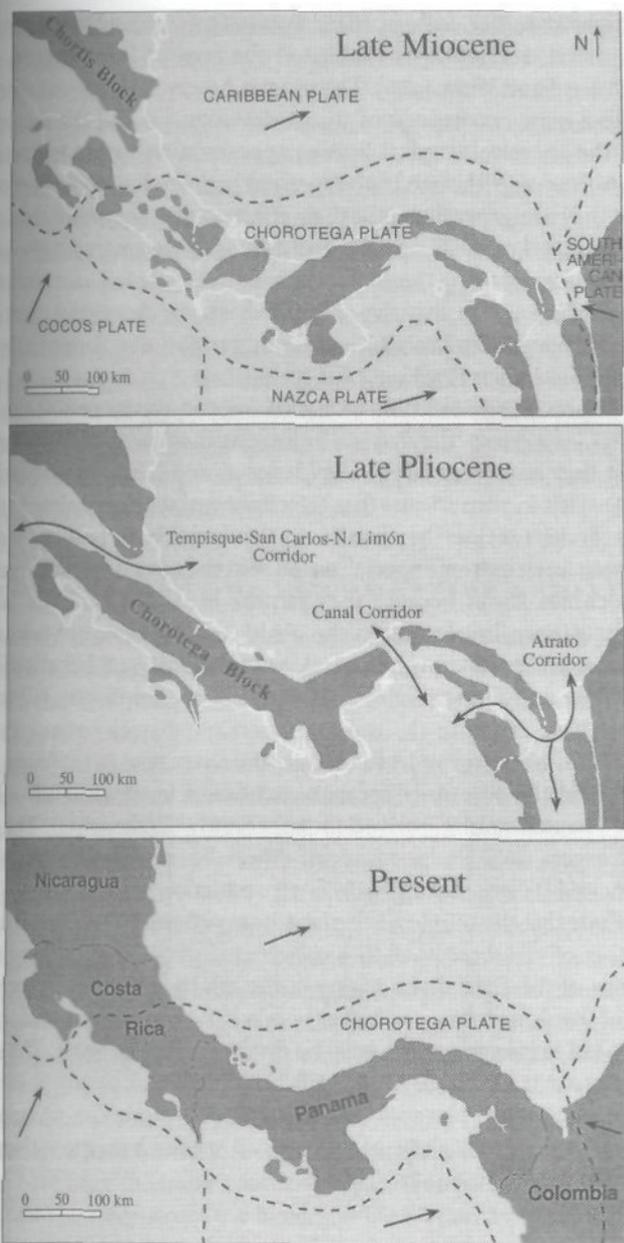


Figure 3.1 Reconstructions of the isthmian region of Lower Central America from Late Miocene to the present. Redrawn with modifications from Coates and Obando 1996.

One might consider each of these features to represent a key innovation. However, direct development evolved at the level of *Bolitoglossini*, or even lower (Lombard and Wake 1986). The tongue, however, is unique to the sg *Bolitoglossa*. The joint occurrence of direct development and the extraordinary tongue in the ancestral tropical lineage appears in retrospect to have been of special significance. Although both represent high levels of specialization, at the same time they are generalizing in their effects in that they freed the lineage of prior constraints (i.e., life historical) and gave access to environments and habitats, and new ways of using them. Access, followed by ecological innovation, led to new ways of life and to adaptive radiation based on elevational zonation, new patterns of habitat and microhabitat use, and possibly new community interactions (Wake and Lynch 1976).

Other factors were doubtless of significance in the success of the tropical salamanders. As a group, the tropical bolitoglossines have large genomes, which means that they have very large cells (Sessions and Larson 1987; Sessions and Kezer 1991). This in turn means that they have extraordinarily low basal metabolic rates (Feder 1983) so they live life in slow motion, so to speak. Again, this might be seen as an extreme specialization, but the advantage that is general for the group comes about because they require little food. Another factor that seems to have been important to the clade is the presence of tail autotomy, involving a complex of morphological, physiological, and behavioral specializations (Wake and Dresner 1967). All tropical species display tail autotomy, which must have arisen in the immediate ancestral stock because there is no specialized autotomy region in the sequential sister taxa *Batrachoseps* and *Hydromantes*, and the autotomy mechanisms found in the distantly related *Ensatina* and *Hemidactylium* evolved independently (Wake 1991a). The tail is an important organ, used for locomotion (especially in arboreal settings) and for fat storage, and its loss directly affects reproduction (Maiorana 1976), so one must conclude that the universality of autotomy attests to its survival value. The fixed number of vertebrae in all tropical genera but one may be associated with the presence of the specialized region at the tail base. In species with variable numbers of trunk vertebrae, asymmetry is relatively common, and in such instances the tail breakage pattern may be disabled (Frolich 1991). The species of *Oedipina* have extraordinarily long tails that may break at any point; perhaps this feature resulted in relaxation of the former constraint on variation in vertebral numbers, and they alone of the tropical species have more than 14 trunk vertebrae.

WHY SO MANY SPECIES?

Species density in restricted geographic areas is greater for tropical bolitoglossines than that typical of most temperate zone clades of salamanders. If one

considers only strictly terrestrial species, there can be substantially more species of salamanders on a rich elevational tropical gradient than on a temperate one, often as many as 14–18 or more local species (Wake and Lynch 1976; Wake 1987; Wake et al. 1992). The main factors related to this species richness are the narrow elevational and geographic ranges of the species. Many of the species are restricted to relatively high cloud forests, and the lower margins of their ranges lie above the levels of the passes in mountain chains. Furthermore, Middle America is a tectonically dynamic area, with much land movement and extensive volcanism having occurred in the last 60–70 million years, especially since mid-Tertiary (Coates and Obando 1996; Coates 1997; fig. 3.1), the time inferred from genetic distances (e.g., García-París and Wake 2000) among taxa to have been the main period of species formation. There have been associated breakups and new formations of cloud forest, and accordingly abundant opportunity for fragmentation of species ranges and local ecological specialization associated with new opportunities (e.g., García-París, Good, et al. 2000). Geographic and allopatric species formation has resulted.

GENERAL GEOGRAPHY OF THE ADAPTIVE RADIATION

Salamanders in the Neotropics are concentrated in four areas: the eastern and southern margins of the Mexican Plateau; the mountainous regions of Chiapas, Guatemala, and western and central Honduras (termed Nuclear Central America by Wake and Lynch 1976); the mountainous regions of Costa Rica and western Panama (Talamancan Central America of Wake and Lynch 1976); and less important, the mountains of northwestern South America. Recent molecular phylogenetic studies (Parra-Olea 1999; García-París and Wake 2000; Parra-Olea and Wake 2001) are giving definition to the cladistic structure of the radiation. A major conclusion is that Nuclear Central America contains the largest number of clades and the largest number of endemic clades (e.g., *Dendrotriton*, *Cryptotriton*, *Bradytriton*, *Nyctanolis*, *Ixalotriton*, and several clades within *Bolitoglossa*), although the southeastern margins of the Mexican Plateau and associated mountains in northern Oaxaca also harbor many clades, including some that are species-rich and endemic. Notable endemics are *Chiropterotriton* and *Thorius*, which may be two of the earliest branches of the tropical bolitoglossines (Parra-Olea 1999). The geographically central and northern regions of tropical America have been more important in the long history of bolitoglossines than have been the more southerly areas of radiation. An attempt (Hendrickson 1986) to reconstruct the historical biogeography of the tropical salamanders was hampered by the lack of a robust phylogenetic hypothesis. At present we have a large database of mtDNA sequences that we expect will give more resolution and aid in future reconstructions of historical biogeography. The most basal lineages in various phylogenetic analyses are always north-

ern, either eastern Mexico or Nuclear Central America (Parra-Olea 1999; García-París and Wake 2000; D. B. Wake, unpub. data), and these areas appear to have been the primary centers for the adaptive radiation of the tropical bolitoglossines.

NO MID-DOMAIN EFFECT

Recently Lees et al. (1999) and Colwell and Lees (2000) identified a mid-domain effect in biogeographic analysis, an artifact of the tendency for ranges of species to pile up in the middle of any preset boundaries. They propose that the mid-domain effect be treated as a kind of null model to test against alternative hypotheses of species richness. This is not the place for a detailed examination of this hypothesis for tropical salamanders, but because the effect is a challenge to any biogeographic hypotheses about species richness, I present here only a few observations. If one takes 20° N and S as the rough outer bounds of distribution of the sg *Bolitoglossa*, only a small fraction (approximately 10%) of its species occur in South America, and no more than 10 species (counting all possible described and undescribed species known to me) occur between 0° and 20° S. Accordingly, the mid-domain hypothesis is rejected for the tropical bolitoglossines as a whole. On a more local scale, for example, along elevational transects such as that presented in preliminary form herein, a more formal analysis of the patterns is required but it may be premature.

Costa Rican Salamanders

A BIT OF HISTORY

Tropical salamanders have been known for at least 180 years, and Costa Rican species have been studied since Keferstein (1868) and Gray (1868) almost simultaneously described the same species (now *Oedipina uniformis*). Later history is reviewed by Taylor (1952a). Dunn made personal visits to Costa Rica and Panama, described some new species, and revised others (summarized in Dunn 1926). Taylor spent a few months in 1947 in continual fieldwork and described many new species, especially in his general review of the salamander fauna (Taylor 1952a). Neither Dunn nor Taylor worked along the Panamanian border region to any extent. Taylor (1952a) recorded 22 species of salamanders from Costa Rica. These were placed in six genera: *Chiropterotriton* (restricted to Mexico by Wake and Elias 1983; Costa Rican species now in *Nototriton*), *Magadigita* (synonymized with *Bolitoglossa* by Wake and Brame 1963a), *Bolitoglossa*, *Parvimolge* (restricted to Mexico by Wake and Elias 1983; Costa Rican species now in *Nototriton*), *Haptoglossa* (synonymized with *Oedipina* by Brame 1968), and *Oedipina*. Work by Jay Savage and his group on the entire Costa Ri-

can herpetofauna began in 1958 and has continued to the present. Arden Brame revised *Oedipina* (1968), synonymizing eight species recognized by Taylor (1952a) and naming four new ones. Jim Vial's doctoral research (Vial 1968) dealt mainly with the ecology of tropical salamanders, in particular *Bolitoglossa pesrubra* (most of the populations he studied are now placed in *B. pesrubra*, although those from lower elevations belong to an undescribed species). Vial also conducted some systematic studies; he synonymized two of Taylor's species of *Bolitoglossa* (Vial 1966; his conclusion was rejected by García-París, Good, et al. 2000, on the basis of molecular data) and described one new species (Vial 1963). I made my first trip to Costa Rica with the Savage group in 1961 and worked with Brame on some of the materials (Wake and Brame 1963b), but apart from brief trips in 1971 and 1973, I did not return for further studies until the mid-1980s. My associates and I continued fieldwork until 1994, and we hope to continue our investigations in the future.

THE SPECIES OF COSTA RICAN SALAMANDERS

Systematics

At present at least 45 species of salamanders are known to occur in Costa Rica. This total includes seven species of *Bolitoglossa* and one of *Oedipina* that are undescribed but will be soon (table 3.1). Of these undescribed species, three were announced in a preliminary manner by García-París, Good, et al. (2000). The recently described *Bolitoglossa anthracina* occurs within a few kilometers of the Costa Rican border (Brame et al. 2001), and two or three additional Panamanian species (one or two as yet undescribed) occur within 50 km of the border. Thus a realistic estimate of the number of species in the country is 45–48, or more than double Taylor's (1952a) number.

Many cryptic or morphologically very similar species of plethodontid salamanders have been recognized (e.g., Highton 2000). With few exceptions, the species I discuss here are not cryptic but are morphologically, genetically, and ecogeographically distinct. We are just now beginning to recognize cryptic species in tropical America, and the number of species is certain to increase.

If one includes western Panama with Costa Rica, the fauna of the region is surprisingly cohesive and highly endemic, not only at the species level but also at the level of clades of salamanders and other amphibians and reptiles (Savage 1982; Campbell 1999). In large part this is the result of the restriction of many species to upland habitats (the Talamancan herpetofauna of Savage 1982), and the fact that the region has had a history of independence from uplands to the north and west (Nuclear Central America) and to the south and east (the northwestern reaches of the Andes) (Coates and Obando 1996; Coates 1997; fig. 3.1). The Costa Rican species belong to three major clades, *Nototriton*,

Table 3.1 Salamanders known from or anticipated to be found in Costa Rica

| Clade name | Described Costa Rican species | Undescribed Costa Rican species | Panamanian species |
|---------------------|-------------------------------|---------------------------------|--------------------|
| <i>Nototriton</i> | | | |
| <i>picadoi</i> | 5 | | |
| <i>richardi</i> | 2 | | |
| <i>Oedipina</i> | | | |
| <i>Oedipina</i> | 11 | | |
| <i>Oedopinola</i> | 3 | 1 | 2 |
| <i>Bolitoglossa</i> | | | |
| <i>alvaradoi</i> | 1 | | |
| <i>mexicana</i> | 2 | | |
| <i>subpalmata</i> | 11 | 7 | |
| "Eladinea" | 2 | | 2 |
| Total | 37 | 8 | 4 |

Oedipina, and *Bolitoglossa*, each well-supported monophyletic groups based on recent published and unpublished molecular and morphological evidence. *Nototriton*, as revised by García-París and Wake (2000), includes seven Costa Rican species in two clades: a *picadoi* group, including five species, and a *richardi* group, including two species (Good and Wake 1993). A sixth member of the *picadoi* group occurs in Nicaragua (Köhler 2002; relationships based on unpublished mtDNA data from G. Parra-Olea and D. B. Wake), but otherwise the clades are endemic to Costa Rica. Although the two clades of *Nototriton* are well supported, their relationship to a third clade, in Guatemala and Honduras, is unresolved. A combined analysis of all available mtDNA data weakly supports a sister group relationship of the Costa Rican clades (García-París and Wake 2000). The presence of two of the three species groups in Costa Rica suggests that this part of Middle America might have been the center of origin and that the northern clade represents a zoogeographic dispersal. This hypothesis is attractive to me because three other clades of miniaturized salamanders (*Bradytriton*, *Cryptotriton*, *Dendrotriton*), all related to *Nototriton* but none to its sister taxon, and none of them sister taxa of each other, are endemic to Nuclear Central America. I consider it unlikely that one more miniaturized clade might have independently arisen in that region.

Oedipina has at least 14 Costa Rican species, plus an undescribed species, by far the most species of this genus that occur in any of the Middle American countries. There are two additional species in the Caribbean lowlands of adjacent Panama. Of these 17 species, 11 are members of the subgenus *Oedipina* and

the remainder are in the subgenus *Oedopinola*. The subgenera are clades, distinct on the basis of morphological and allozymic data (Good and Wake 1997) as well as mtDNA (García-París and Wake 2000) evidence (although *Oedopinola* is not as well supported by mtDNA as is *Oedipina*). Both of these clades are represented outside Costa Rica. *Oedipina* ranges from Guatemala to central Panama but is clearly centered on Costa Rica, to which most of the species are restricted. *Oedopinola* is less well known but more widely distributed, ranging from Chiapas, Mexico, to Ecuador. However, the facts that both subgenera occur in the country, and that most species in each subgenus occur in the country, suggest again that this part of Middle America might have witnessed the origin and most of the diversification of this clade. Furthermore, the deepest genetic divergences, between the two subgenera and also within each subgenus, occur in Talamancan Central America (García-París and Wake 2000).

Bolitoglossa, the largest of the tropical genera, has 23 (possibly more) species in Costa Rica. These belong to three main clades, one that includes nearly all of the Costa Rican species and all of the Panamanian and South American species as well, and two other clades with northern affinities, each containing but a single Costa Rican species. Although *Bolitoglossa* is the largest clade of salamanders (81 species currently recognized), the number of species found in Costa Rica is exceptionally high, greater than the number found in any other country. Analysis of mtDNA sequences (M. García-París, G. Parra-Olea, and D. B. Wake, unpub. data) reveals that most of the species are members of a major clade that corresponds well with the informal grouping labeled *Bolitoglossa* alpha (Wake and Lynch 1976). The major difference is that this grouping does not include the *B. mexicana* group, whose exclusion from *Bolitoglossa* alpha was forecast by Papenfuss et al. (1983).

Most Costa Rican and western Panamanian taxa belong to a group that I believe to be monophyletic that contains three clades. One of these includes species allied to *Bolitoglossa subpalmata*, and a second includes a diverse assortment of mainly upland species associated with the Talamancan mountain system. (I refer to these collectively as the *subpalmata* clade in table 3.1.) The third, a southern clade, includes all of the species in South America, several in Panama, and two that reach Costa Rica. This I call the Eladinea clade, a name that is available for this or even a more inclusive clade should *Bolitoglossa* eventually be subdivided (Miranda-Ribeiro 1937; the name *Eladinea estheri*, now considered a synonym of *B. altamazonica*, was assigned to specimens from Utinga at Belém, Pará, Brazil).

The *Bolitoglossa subpalmata* clade has recently been studied by García-París, Good, et al. (2000), who identified five species: *B. subpalmata* itself, which is associated mainly with the Cordillera Central and the Cordillera de Guanacaste and neighboring ranges, and the remaining species, all Talamancan, including the well-known *B. pesrubra* (which until its recent reclassification was known as

B. subpalmata), the most studied and best known of the tropical salamanders. Two more species are associated with the northern part of the Talamancas, *B. gracilis* and an undescribed species. Four other undescribed members occur in the Panama–Costa Rica border region.

The second clade is less cohesive and far more diverse in morphology and ecology. It includes several taxa that occur in sympatry with members of the *subpalmata* group in the northern Talamancas, including three species that are found in sympatry with *Bolitoglossa subpalmata*. In order of decreasing abundance they are *B. cerroensis*, a larger species, *B. sooyorum*, a slightly larger species, and the very much larger but rare *B. nigrescens*. This subclade is morphologically diverse and includes the largest (*B. robusta*) and smallest (*B. diminuta*) species in the entire genus, as well as both fully terrestrial and fully arboreal forms. Several undescribed species are known, including one from the northern portion of the Talamancas and another from the Panama–Costa Rica border region.

Many species from Panama and all of the South American members of the genus belong to the Eladinea clade, which has the most southerly distribution of any in the genus. The northernmost representative of this clade is *Bolitoglossa colonnea*, which ranges as far north as the northeastern lowlands (it is present at La Selva; Donnelly 1994a). Another member of the clade in the Costa Rica–Panama border region is *B. schizodactyla*, which is known from the Bocas del Toro lowlands and ranges east beyond the Panama Canal. The clade might have originated in eastern Panama, where other species occur, and the two representatives in Costa Rica likely arrived via lowland dispersal.

Recent molecular evidence suggests that *Bolitoglossa lignicolor* and *B. striatula* are the southernmost members of the *B. mexicana* clade (García-París, Parra-Olea, et al. 2000). All members of this clade are lowland forms, and the largest number of species occurs in Nuclear Central America. Presumably these species (which are not sister taxa) or their forerunners spread to the south via lowland routes after final connection of the Chortis and Chorotega plates (fig. 3.1).

Bolitoglossa beta of Wake and Lynch (1976), although not as cohesive a unit as they envisioned, includes most of the species in the genus that occur in Nuclear Central America. The Costa Rican *B. alvaradoi*, a poorly known species from middle-elevation cloud forests mainly on the northeastern slopes of the Cordillera Central, is allied (on the basis of sharing a derived tail base morphology and in mtDNA sequences) with more northern members of the assemblage, although it has no close relatives (M. García-París, G. Parra-Olea, and D. B. Wake, unpub. data).

General Ecology

All tropical plethodontids are nocturnal predators, and with one exception (Wake and Campbell 2001), all are strictly terrestrial throughout life. Direct development with no free-living larval stage is the exclusive life-history mode. Ecological differentiation among related species is associated mainly with different elevational limits and differences in locomotion and microhabitat use (Wake and Lynch 1976; Wake 1987; Wake et al. 1992). Throughout Middle America, local elevational transects extending from sea level to over 3,000 m support as many as 18 species, but relatively few species are strictly syntopic (e.g., the maximum number is 7 of the 15 species that occur along the best-studied transect, in western Guatemala; Wake and Lynch 1976). Elevational zonation is evident in the Cordillera Central (Wake 1987) and the Cordillera de Talamanca (Wake 1987; García-París, Good, et al. 2000), the latter region being as rich in species as any place in Middle America. There are 18 species in a relatively local region on the Caribbean slopes of the part of the Cordillera de Talamanca known as Cerro de la Muerte. Recent work has also shown extensive elevational stratification in a broad, less well-studied transect across the continent near the Costa Rica–Panama border (J. Hanken, D. B. Wake, and J. M. Savage, unpub. results; fig. 3.2), which is the southernmost region of relatively high salamander diversity. I estimate that 22 species occur along this transect, although most are poorly known. In northern parts of Middle America, only 2 or 3 species are found in any lowland locality below 500 m in elevation, but in the Costa Rica–Panama border region there are 4 species on the Osa Peninsula and nearby lowlands (*Bolitoglossa colonnea*, *B. lignicolor*, *Oedipina pacificensis*, *O. alleni*), and across the cordillera on the Atlantic side, in the Bocas del Toro region and adjoining Costa Rica, there are 5 species (*B. colonnea*, *B. biseriata*, *B. schizodactyla*, *O. maritima*, and an undescribed *Oedipina*). Thus, at the southernmost limit of high salamander diversity, tropicality is most strongly expressed, and species packing is such that the largest local salamander faunas encountered anywhere in Middle America are found, even though only a small subset of the rich diversity of tropical clades is represented. Conditions at mid-elevations appear ideal for members of the genus *Nototriton*, but they are not known from the region. (One poorly preserved specimen possibly assignable to this genus but not currently identifiable was collected in the Fortuna region.) If this clade were present, there could well be one or two additional cloud forest species.

Salamanders are present to the tops of the highest mountains in the Costa Rica–Panama border zone, and there are three species that occur above 3,000 m. The largest number of species (six) is found in cloud forests between 1,500 and 2,500 m, but the maximal number of strictly syntopic montane species is four (near Las Tablas).

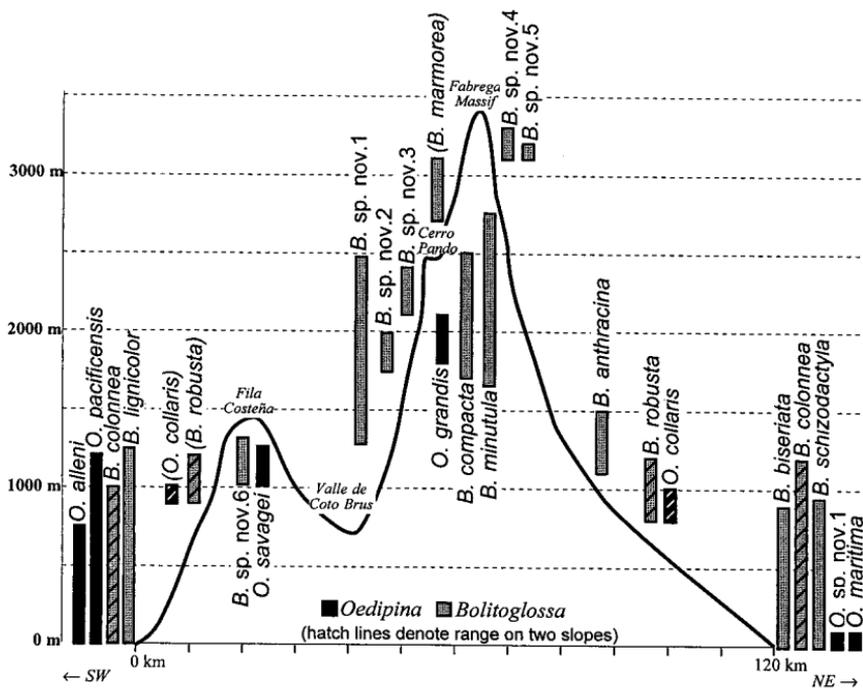


Figure 3.2 Distribution of plethodontid salamanders along an imaginary transect across the continent from the vicinity of Golfito, Costa Rica, on the Pacific Coast (southwest, at left) to the vicinity of Altirima, Bocas del Toro, Panama (northeast, at right). Total known elevational distribution of species in this region is shown. Some species occur on both sides of the mountains, but a number are restricted to upland regions. Undescribed species are indicated by letter designations.

Costa Rican cloud forest salamanders use microhabitats that are often not used elsewhere in Middle America, in particular, leaf litter (*Nototriton richardi*, *N. tapanti*) and moss mats, often including liverworts and other epiphytes as well (several species of *Nototriton* and *Oedipina*, *Bolitoglossa gracilis*, and *B. diminuta*). Furthermore, although bromeliads are used (Wake 1987), they are not used as commonly as in cloud forests to the north.

Costa Rican salamander diversity is not widely appreciated because one of the areas of intense research focus, La Selva Biological Station, is relatively depauperate in salamanders, and those present are rarely encountered (Donnelly 1994a). The three species at La Selva, *Oedipina gracilis* (this species, formerly referred to as *O. uniformis*, was resurrected by García-París and Wake 2000), *O. cyclocauda* (previously misidentified as *O. pseudouniformis*), and *Bolitoglossa colonneae*—are all essentially unstudied ecologically (Donnelly 1994a). A fourth species, *B. alvaradoi*, is known from an adjoining site, but it is rarer than the

other three. At the higher-elevation Monteverde cloud forest region there is a larger salamander fauna: *Oedipina uniformis*, *O. poelzi*, *Nototriton gamezi* (commonly identified as *N. picadoi* or *N. abscondens* but recognized as a new, endemic species by García-París and Wake 2000), *Bolitoglossa subpalmata*, and *B. robusta* (Pounds 2000), but these species have proven difficult to find and study. The species most commonly encountered by biologists in Costa Rica is *B. pesrubra* (formerly known as *B. subpalmata*), which has been studied ecologically (e. g., Vial 1968) and has been seen by many students in the Organization for Tropical Studies (OTS) classes during visits to the Cerro de la Muerte region over the years. What is not so generally appreciated is that this is only one of four species that occur at high elevations on the Cerro, although in recent years *B. cerroensis* has been commonly found at the Querici site used by OTS classes. Salamanders are also uncommon at other biological stations in tropical America, such as Barro Colorado, where only two species are known to occur, both of which are *Oedipina* (Ibáñez et al. 1999). Thus, the common but erroneous impression that tropical salamanders are rare tends to be reinforced.

Patterns of Species Formation

Herpetologists have mainly accepted the standard allopatric (dichopatric) model of species formation, and there is substantial empirical support (e.g., Lynch 1989). The general assumption is that species form as a result of fragmentation of once continuous geographic ranges followed by selection associated with local conditions in the fragments. Stochastic factors also play a role, so that in time two or more differentiates arise from one ancestral form. Vicariance events, as a result of which populations find themselves in changed circumstances because of tectonic movements, climate change, and volcanism, likely play important roles in species formation in salamanders, as they do in frogs (cf. Lynch 1989). Salamanders of the genus *Nototriton* offer a particularly vivid example. Within both the *richardi* and *picadoi* species groups, pairs of species are segregated into northern Talamancan and Central Cordilleran components, with current species in both groups being endemic to one but not both areas, which suggests a common vicariant event (Good and Wake 1993). There has been further species formation in the *picadoi* group, with one species (*abscondens*) associated with the large central volcanos, another to the northwest, in the main mass of the Cordillera de Guanacaste at Monteverde, and two more (*guanacaste* and an undescribed species from central Nicaragua) associated with small volcanos farther to the north and west. A final species (*major*) in the *picadoi* group is found to the southeast, in the upland mass near Moravia de Chirripo. A third species group (*barbouri*) in the genus is known from eastern Guatemala and western Honduras, on the north side of the Nicaraguan Depression. One possible scenario is that a widespread ancestral form was sepa-

rated on either side of the Nicaraguan Depression, and this led to the establishment of two species groups. A third arose in the south, most likely in association with the Miocene archipelago that was the emergent manifestation of the Chorotega Plate (Coates and Obando 1996). The relationships of the three species groups are unresolved, although most often the *richardi* and *picadoi* groups are considered to be sister taxa (Good and Wake 1993; García-París and Wake 2000). The related but more basal taxa *Cryptotriton* and *Dendrotriton*, as well as the enigmatic but somehow related *Bradytriton*, are restricted to areas north of the Nicaraguan Depression and likely arose in Nuclear Central America. Perhaps the *barbouri* group dispersed northward from Talamancan Central America, and retention of generalized morphology and ecology enabled coexistence with the more specialized resident groups.

There are alternatives in specific cases to dichopatric species formation, however attractive it may be as a general model. The most likely is allopatric species formation (Endler 1977), which was recently invoked to explain the local buildup of species in the *Bolitoglossa subpalmata* species group in the northern Cordillera de Talamanca (García-París, Good, et al. 2000). Within this group there has been allopatric species formation, with *B. subpalmata* being separated in the northern mountains of Costa Rica (Cordillera Central, Cordillera de Guanacaste) from the remaining species, in the Cordillera de Talamanca. However, within the latter region there are three species that are parapatrically distributed, each with a distinctive ecological association and a unique elevational distribution. And within the most widespread species, *B. pesrubra*, there is extensive local differentiation in genetic markers and color pattern. These patterns suggest that local adaptation may be the driving force in leading to the differentiation of taxa in association with the dramatic ecological changes that occur with elevational change in the region.

HISTORICAL BIOGEOGRAPHY

On the basis of the large numbers of species now present and the degree of morphological, ecological, and genetic differentiation they display, salamanders must have been in Talamancan Central America for much of the Tertiary. However, many of the lineages present in Nuclear Central America are absent, and most of the clades of salamanders that are found in Costa Rica (e.g., *Nototriton*, *Oedipina*, *Oedopinola*, two of the three main clades of *Bolitoglossa*) also have representatives in Nuclear Central America. Thus although there is high species diversity in Talamancan Central America, the fauna is relatively depauperate with respect to major clades and also with respect to major endemic clades (one in *Bolitoglossa*, two species groups in *Nototriton*). This suggests that it was relatively difficult for salamanders to reach the terrain associated with the Chorotega Plate, but once there they thrived. Some dispersal events might have

occurred relatively recently. For example, *B. alvaradoi* has its closest relatives (none very close) to the north, and *B. striatula* and *B. lignicolor* are members of the *mexicana* group, widely distributed in Nuclear Central America and Mexico. These species could have dispersed through lowland routes that are not available for most tropical species (i.e., those restricted to montane forests). Although species of *Oedipina* are widely distributed to the north and south of Talamancan Central America, all clades and most species of that genus occur here, and it is likely that the lineage originated here (see also Brame 1968).

PROSPECTS

One would like to think that we are close to having a complete list of species of salamanders of Costa Rica, but I fear that such optimism is premature. Large areas of Costa Rica remain from which salamanders are virtually unknown, even though they are almost certain to be present. I have in mind the Caribbean slopes of the Cordillera de Talamanca in the eastern part of the country, from which only a handful of salamanders have been collected. Yet among these there are at least two specimens I cannot identify to species and that may well represent undescribed taxa. A number of species of *Bolitoglossa* are about to be described, and there is every reason to suspect that more species will be found in other areas that have been as yet relatively little studied. Several species (including undescribed forms) are known from very small samples (e.g., *B. anthracina* from but three specimens), and some are known only from one collecting event. It is difficult to know whether the rarity of certain species (i.e., *B. sooyorum* and *Oedipina paucidentata*, not seen for many years) is the result of recent declines, to loss of habitat, to failure of herpetologists to use specialized searching methods, or simply to the secretiveness of the species. Some species seem to be truly rare, for there has been abundant opportunity for them to have been found by extensive fieldwork in different parts of the country. More than 50 years after its description, *Nototriton richardi* is known from about 15 specimens, and yet individuals continue to appear from time to time. *Bolitoglossa alvaradoi* is known from fewer than 10 specimens over the same time span. In neither case is loss of habitat likely to be the main reason for rarity. However, *B. sooyorum* and *B. nigrescens*, both from Cerro de la Muerte, may well be rare because of habitat modification. In recent years there is the more ominous phenomenon of decline in amphibian populations in general, and especially in Costa Rica and western Panama (Pounds et al. 1996; Lips 1998, 1999; Pounds 2000). Without doubt the once abundant populations of *B. pesrubra* on Cerro de la Muerte have been strongly affected. Whereas these salamanders were once incredibly abundant along the Pan American Highway, they can now scarcely be found at all. For me this is the most dramatic case of declining salamander populations in Costa Rica.

The Talamancan Central America region has been a major staging ground for salamander evolution. The bulk of the salamander fauna can be traced ultimately to more northern zones, but at least one major clade, *Oedipina*, may have originated and undergone its most dramatic radiation here. Importantly, this region supplied the lineages that successfully occupied South America when that continent became physically accessible.

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