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# ADAPTIVE RADIATION OF SALAMANDERS IN MIDDLE AMERICAN CLOUD FORESTS[1]

## DAVID B. WAKE[2]

### ABSTRACT

Tailed amphibians, or salamanders, occur in the tropics only in the New World, where they are concentrated primarily in Middle America and northwestern South America. All are members of the family Plethodontidae, the lungless salamanders. As recently as 1926 only 30 species of tropical salamanders were known, and all were placed in a single genus. Today 11 genera are recognized. All occur in Middle America, and over 140 species have been described. Many local tropical regions are very rich in numbers of species, and as many as 21 species may be present along a single altitudinal gradient. Community organization of species of salamanders in the tropics differs from that in temperate regions in that species of tropical salamanders tend to be segregated into discrete elevational zones, with any given species restricted to a narrow elevational band. Within elevational zones, species are segregated by major habitat type, then by microhabitat, body size, and finally trophic and behavioral features. Cloud forests at middle elevations, from about 750 m to 2,500 m, are especially rich in salamanders, in both diversity and density. In Nuclear Central America nearly 50% of arboreal bromeliads in a local sample (N = 903) contained salamanders. Some species are found almost exclusively in bromeliads, and over 30 salamanders have been encountered in a single bromeliad. Farther south, in Costa Rica, cloud forests harbor salamanders in bromeliads as well as in arboreal and terrestrial moss mats. Extreme microhabitat specialization enriches the Costa Rican fauna to the maximum number of species present locally anywhere in the tropics. In the relatively lower latitudes (e.g., Costa Rica and Panama) the proportion of species occurring at lower elevations increases compared with Mexican and Guatemalan transects.

Bromeliads and moss mats in the mid-elevational wet and rain forests are ideal microhabitats for these insectivorous, direct developing amphibians. Bromeliads offer abundant food resources, egg deposition sites, protection from predation, and microenvironments buffered against temperature extremes and low humidity. Salamanders are top carnivores in the bromeliad microhabitat.

The extensive adaptive radiation of plethodontid salamanders in Middle America has featured both convergent and parallel evolution. The mid-elevational cloud forests, with their rich epiphytic assemblages and highly dissected topography, have been of great significance in speciation, morphological and behavioral diversification, geographical ecology, and historical biogeography of tropical plethodontid salamanders.

The cloud forests of Middle America are home to a unique group of vertebrates—lungless, climbing salamanders that belong to the family Plethodontidae. By "cloud forest" I refer rather loosely to those forest assemblages which form in the presence of fog. Clouds condense at varying elevational levels in Middle America, depending on many local and regional factors such as temperature of the water of the nearest ocean, topography, rainfall patterns, and wind direction (Grubb & Whitmore, 1966; Myers, 1969). In general, cloud forests form between elevations of about 800 and 2,700 m. Both upper and lower boundaries shift with climatic changes, with the lowest occurring along humid slopes in the low latitudes and the highest being found in the northern tropics along the Pacific slopes.

Cloud forests offer ideal conditions for tropical salamanders, all of which are nonaquatic, direct developing species. Although they do not breed in water, these organisms nevertheless require moist conditions for activity, and the cloud forest

environments are effectively buffered from des-
iccating conditions as well as from extremes of
temperature. In addition, these forests typically
support abundant epiphytes that are used exten-
sively by salamanders.

There are more than 140 species of pletho-
dontid salamanders in the New World tropics;
about 80% occur in Middle America (Wake &
Lynch, 1976; Frost, 1985). What makes them
unusual is their great diversity in the New World
tropics and their total absence from the Old World
tropics. Middle America has been the setting for
an extensive, unique adaptive radiation that has
remained very localized.

The success of these species can be measured
against that of salamanders generally. World-
wide, there are about 350 species of salamanders
divided among nine families (Frost, 1985). Eight
families are restricted to North Temperate re-
gions. Over 200 of the species are members of
the family Plethodontidae, the only group of sal-
amanders to radiate in tropical regions. All trop-
ical species of salamanders are members of the
supergenus *Bolitoglossa* (Wake, 1966), which
contains 11 genera and about 40% of the species
of salamanders in the world. The supergenus is
exclusively New World in distribution and does
not occur north of Mexico.

The plethodontids have a curious distribution,
with two primary areas of evolutionary diver-
sification: North America with concentration in
the Appalachian region, and Middle America
(Fig. 1). In eastern North America are found three
major groups of plethodontids, two of which have
life histories involving an aquatic larval stage.
The Middle American region contains members
of a fourth major group, the tribe Bolitoglossini,
members of which have a uniphasic life history
featuring direct development without a larval
stage (Wake, 1966). The other two supergenera
in the Bolitoglossini occur in California and Or-
egon (and possibly in Alaska and Mexico), and
on Sardinia, the Italian mainland, and a tiny
portion of southeastern France.

I have argued elsewhere that the absence of an
aquatic larval stage facilitated occupancy of the
relatively densely crowded, predator-rich tropics
(Wake, 1966; Hanken et al., 1980). A unique
feeding mechanism and an associated behavioral
repertoire (Lombard & Wake, 1977, 1986; Roth
& Wake, 1985a, 1985b), which could evolve its
particular characteristics only in a group lacking
aquatic larvae, may have aided in the successful
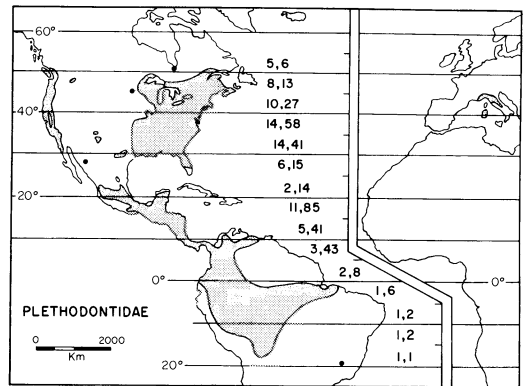radiation of the tropical species. Those animals



FIGURE 1. Latitudinal gradient of generic and species
diversity in the salamander family Plethodontidae. The
numbers of genera (first figure) and species (second
figure) that occur in zones of five degrees latitude are
indicated. Data are available from the author. Unde-
scribed species for which descriptions are being pre-
pared have been included.

use a highly specialized, extremely fast tongue
projection mechanism to capture moving prey
at a considerable distance, and thus they are able
to feed on a wide array of invertebrate animals.

We still know relatively little about the tropical
plethodontids. The authoritative work of Dunn
(1926) listed but 30 species and placed them all
in a single genus. Taylor (1944) recognized the
generic diversity of the group (seven genera), but
four additional genera were described as recently
as 1983 (Elias & Wake, 1983; Wake & Elias,
1983), and about one-half of the 140 species have
been described since 1950. Not surprisingly, most
published work has dealt with taxonomy and
systematics, although there has been some re-
search on life history (Vial, 1968; Houck, 1977a,
1977b) and geographical ecology (Schmidt,
1936a; Martin, 1958; Wake & Lynch, 1976; Wake
et al., 1987).

The present paper attempts to evaluate the role
of epiphytic communities in the evolution of the
neotropical salamanders. I summarize infor-
mation that my research collaborators and I have
gathered over the past 15 years. In particular, I
examine the results of transect studies from Mex-
ico to Costa Rica and concentrate on an area that
appears to have been of critical importance for
salamanders, the mid-elevation cloud forests.

ECOLOGICAL GEOGRAPHY AND SYSTEMATICS

Salamanders in the tropics have diversified in
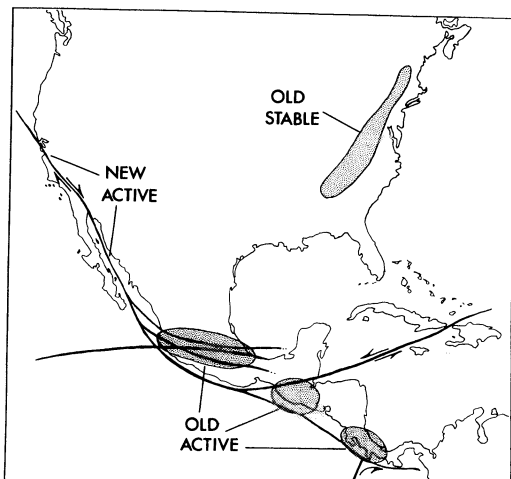three major regions, each characterized by a rel-

atively ancient tectonic core, high topographic diversity, and high tectonic activity along some borders. From north to south, these regions are: 1) the southeastern margins of the Mexican Plateau and the highlands of northern Oaxaca, 2) Nuclear Central America, and 3) Talamancan Central America (Wake & Lynch, 1976; Fig. 2). Each region is characterized by species richness and a high degree of endemism (Savage, 1982). For example, *Chiropterotriton, Lineatriton, Thorius,* and *Parvimolge* are endemic to region 1, and *Pseudoeurycea* occurs mainly in region 1 with only a few species in region 2. *Dendrotriton, Bradytriton,* and *Nyctanolis* are endemic to region 2, and the great majority of the species of the beta assemblage of the large genus *Bolitoglossa* occur there. The few species of *Bolitoglossa* beta which occur in regions 1 and 3 are members of distinct subgroups (see Papenfuss et al., 1983). The genus *Oedipina* is centered in re-



FIGURE 3. *Chiropterotriton arboreus,* a bromeliad-dwelling salamander from near Zacualtipán, Hidalgo, Mexico. This species has the typical features of a bromeliad specialist: a long prehensile tail, relatively long legs, large hands and feet with widely spread digits, and frontally directed eyes. The fine divisions on the scale are mm.

gion 3, and only one species extends as far north as Chiapas. The alpha assemblage of *Bolitoglossa* is centered in region 3 and areas to the south, but a distinct species group extends northwestward to the other two regions. The genus *Nototriton* is something of a puzzle (see below). It has species in all three regions.

Early zoogeographic biases combined with inadequate collecting led to the perception of tropical salamanders as northern invaders that had "trickled" down into the tropics. Dunn (1926) placed all 30 species then recognized in a single genus, and several of his species groups later proved to be polyphyletic. For example, he united all elongate animals into one group, and all small, bromeliad dwellers into another, thereby obscuring the extensive parallelism and convergence that have occurred. Even after Taylor's (1944) generally progressive division of the genus *Oedipus* into several genera, the bias of recent
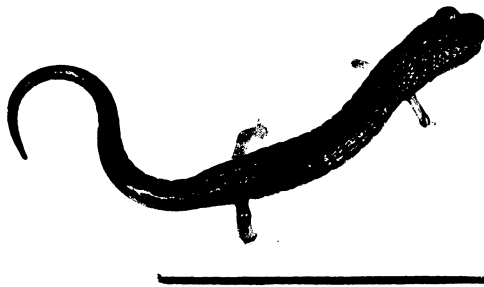


FIGURE 4. *Dendrotriton xolocalcae,* a bromeliad-dwelling salamander from the upper slopes of Cerro Ovando, Chiapas, Mexico. This bromeliad specialist shares many gross structural similarities with species that occupy similar microhabitats (Figs. 3, 5). The scale bar is 25 mm.
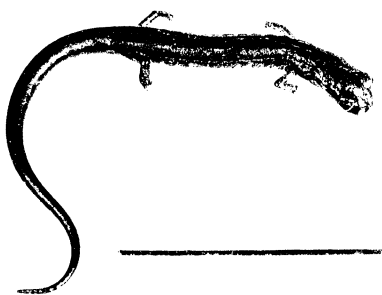
FIGURE 5. *Nototriton veraepacis,* a bromeliad-dwelling salamander from 10.5 km N Santa Cruz, Zacapa, Guatemala, in the Sierra de las Minas. Compare this species with unrelated bromeliad specialists in Figures 3 and 4. The scale bar is 25 mm.

penetration from the north persisted. The genus *Chiropterotriton* as recognized prior to 1983 provides an example. Its species mainly are bromeliad specialists living in cloud forests, and they are superficially similar in external morphology (Figs. 3–5). Both Rabb (1960) and Wake (1966) recognized that members of the genus differed substantially in osteology, but they chose to interpret this as increasing divergence and specialization toward the south. This especially instructive case is relevant to the main theme of this paper and is developed further below.

Species once assigned to *Chiropterotriton* are typically small, slender, long tailed, acrobatic forms, that are common inhabitants of cloud forests in Mexico, Nuclear Central America, and



FIGURE 7. Distribution of the genus *Dendrotriton.* Species of this genus are bromeliad specialists restricted to cloud forests. All occupy small geographic ranges, and only *D. rabbi* occurs in more than one of the isolates indicated here (Elias, 1984).

Costa Rica (Figs. 3–5). Based on their study of comparative osteology, Lynch & Wake (1975, 1978) recognized that the species below the Isthmus of Tehuantepec formed a cladistically distinct group, which they termed *Chiropterotriton* beta. The latter group was found to include at



FIGURE 6. Probable distribution of the genus *Chiropterotriton.* Most species occur in cloud forests, and a number utilize bromeliads as microhabitats. The generalized ranges were derived by grouping known localities into potentially contiguous units, based on forest distribution. Information gathered by David M. Darda and the author.
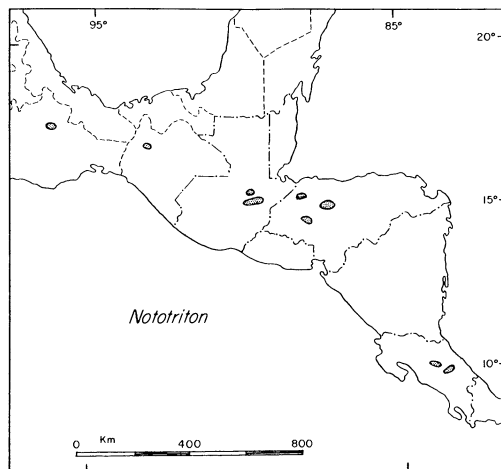


FIGURE 8. Distribution of the genus *Nototriton.* This genus may not be a monophyletic group. The species are all small and resemble one another in many external morphological and ecological features. All of the species inhabit cloud forests, but the Costa Rican species use moss mats as a primary microhabitat, while the Guatemalan and Honduran species are bromeliad specialists. The Chiapan and Oaxacan records are based on recently discovered and as yet undescribed species.
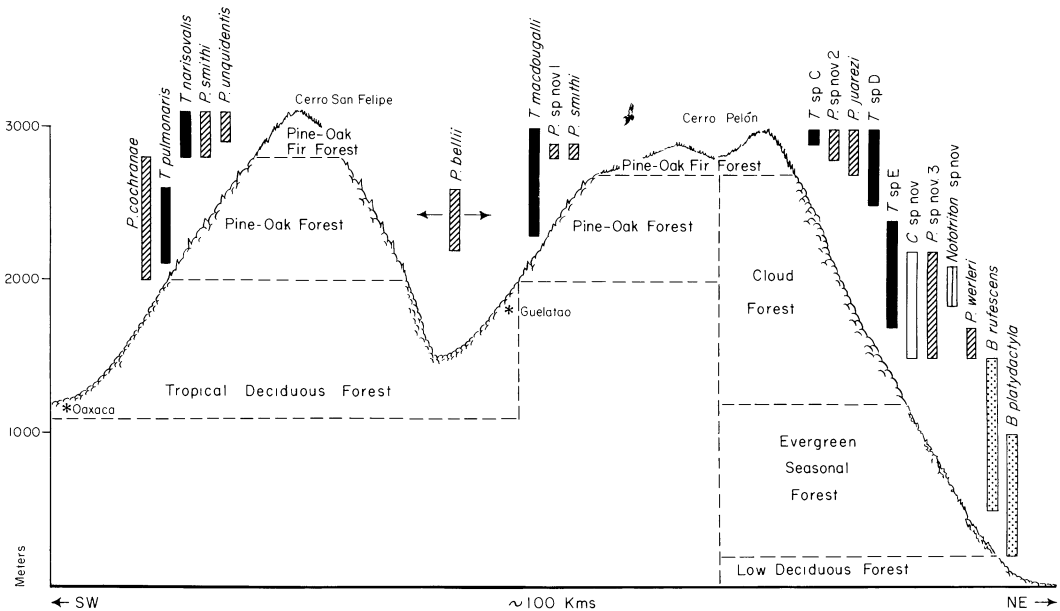
FIGURE 9.   Distribution of plethodontid salamanders along the Northern Oaxacan transect, about 100 km in length, extending north-northeastward from Ciudad de Oaxaca, over Cerro San Felipe and the Sierra de Juarez to the vicinity of Tuxtepec, Oaxaca, Mexico. The northern slopes of the Sierra de Juarez are occupied by an extensive cloud forest which offers habitat to numerous species of salamanders. Updated version of diagram presented by Wake et al. (1987).

least two distinct subgroups, an interpretation subsequently supported by molecular biological data (Maxson & Wake, 1981). The two southern groups finally were given generic status as *Dendrotriton* and *Nototriton* by Wake & Elias (1983), who noted that *Nototriton* might prove to be paraphyletic. Some species of each of the three genera resulting from the subdivision of *Chiropterotriton* include members that are very similar in external morphology. Because the species are very small (frequently <40 mm in head plus body length), the critical differences in morphology can be difficult to detect. The species of the three genera typically have small ranges, and the widely disjunct ranges offer little opportunity for sympatry. These salamanders are found mainly in isolated cloud forests, and several of them remain rare and poorly known.

Until recently we thought that *Chiropterotriton, Dendrotriton,* and *Nototriton* were exclusively allopatric (Figs. 6–8). *Chiropterotriton* occurs as 11 or more discrete geographic isolates in eastern Mexico, north of the Isthmus of Tehuantepec. *Dendrotriton* is found only in Nuclear Central America, mainly on Pacific slopes, but also in some internal regions of Caribbean drainage. *Nototriton* is the southernmost of this group,

and it occurs in regions of Caribbean drainage. An undescribed Oaxacan species of *Nototriton* occurs in sympatry with an undescribed species of *Chiropterotriton,* an association that was unexpected. Both were discovered as a result of detailed studies of vertical zonation along a transect (Fig. 9). Our knowledge of the groups probably remains far from complete, even at the alpha taxonomic level, but they clearly offer fascinating opportunities for the study of convergent evolution.

Lynch & Wake (1978) showed that bromeliad-inhabiting species currently placed in the genera *Dendrotriton* and *Nototriton* resemble each other very closely in external morphology. The bromeliad-dwelling species of *Nototriton* are more similar to bromeliad-dwelling species of *Dendrotriton* in external morphology (evaluated by methods of multivariate morphometrics) than to semi-fossorial congeners that live in moss mats on soil banks. These distantly related species have converged so that they share body forms that are especially well suited for life in bromeliads. Indeed, if *Nototriton* is, as I believe, paraphyletic it is possible that we actually have underestimated the true amount of evolutionary convergence.

The three genera discussed above are commonly encountered inhabitants of cloud forests and epiphytes. Other tropical salamander genera also contain cloud forest inhabitants, and many use epiphytes as their main microhabitats. Some of these, such as the Nuclear Central American *Nyctanolis* and *Bradytriton,* are recently discovered and their habits are very poorly known (Elias, 1984). The monotypic Mexican genera *Parvimolge* and *Lineatriton* (the latter an elongate fossorial form that utilizes moss mats to some degree; Fig. 11) are relatively rare within their restricted ranges, which lie at the lower margins of cloud forests. Some species of the Mexican genus *Thorius* occasionally occur in bromeliads; an undescribed species from the northern slopes of the Sierra de Juarez in Oaxaca seems to occur primarily in bromeliads (undescribed species E, fig. 9 in Hanken, 1983). The remaining genera (*Pseudoeurycea, Bolitoglossa,* and *Oedipina*) have numerous species that are inhabitants of cloud forests.

*Pseudoeurycea* is widespread in Mexican and southwestern Guatemalan cloud forests, but most species are terrestrial and are not often found in epiphytes. The only described species that are bromeliad specialists are *P. firscheini* (Werler & Smith, 1952; Shannon & Werler, 1955b) and *P. nigromaculata* of Veracruzian cloud forests (unpubl. data, contra Taylor, 1941). An undescribed species from our Northern Oaxacan transect (Fig. 9) uses arboreal microhabitats, and an additional undescribed species from our San Marcos transect (Wake & Lynch, 1976: 30) uses bromeliads consistently.

*Bolitoglossa,* with 68 currently recognized species, has by far the greatest geographic range of the tropical salamander genera (from Veracruz, Mexico, to Brazil, Bolivia, and Peru). Many of the species in Nuclear Central America are cloud forest specialists, and they frequently occur in bromeliads. Over one-half of the *B. engelhardti* encountered during an intensive investigation of an elevational transect on the lower slopes of Volcán Tajumulco, western Guatemala, were found in bromeliads, and *B. franklini* is also a frequent inhabitant of bromeliads (Wake & Lynch, 1976). Most records for *Bolitoglossa* in bromeliads refer to members of the beta assemblage (e.g., Stuart, 1943). Some of these occur north of the Isthmus of Tehuantepec (the northern limits of Nuclear Central America), including *B. hermosa* (Papenfuss et al., 1983), from the Pacific slopes of Guerrero, Mexico, and the widespread Gulf-Caribbean slope species *B. rufescens* (Taylor & Smith, 1945), which ranges from San Luis Potosí, Mexico, to Honduras. The only two species of the beta assemblage that reach Costa Rica (*B. alvaradoi, B. arborescandens*) have been taken in bromeliads (Taylor, 1954; unpubl. data).

Occurrence of members of the large alpha assemblage of *Bolitoglossa* in bromeliads is less well documented. The distribution of this group is centered in the Talamancan region and in northern Colombia; only the *mexicana* group (Wake & Lynch, 1976) occurs as far north as the eastern margins of the Mexican Plateau and Nuclear Central America. The *mexicana* group is found mainly in the lowlands, and there are no records of the species being found in bromeliads in cloud forests. Two members of the group, *B. platydactyla* and *B. mexicana,* have been recorded from bromeliads, mainly at elevations of <500 m (Taylor & Smith, 1945). There are scattered reports of *Bolitoglossa* alpha in cloud forest bromeliads in Talamancan Central America and regions to the south (e.g., *B. borburata* near Rancho Grande, Venezuela, Trapido, 1942; *B. lignicolor,* Dunn, 1937; *B. subpalmata,* Robinson, 1977; *B. taylori,* Wake et al., 1970). But in Costa Rica, where the assemblage is well represented, there are surprisingly few records of its occurrence in bromeliads (Robinson, 1977), although we now know that some species are common in such microhabitats (see below).

Several species of the alpha assemblage of *Bolitoglossa* are associated with arboreal microhabitats in cloud forests. The only known adult of *Bolitoglossa diminuta* was collected with an egg mass in a mat of liverworts (Robinson, 1976; recent examination of the tiny holotype, which lacks a sublingual fold, suggests that this species should remain in *Bolitoglossa,* contra Wake & Elias, 1983). Other species associated with moss mats covering tree trunks and branches include *B. marmorea* of Panama (Wake et al., 1973) and an undescribed species sympatric with *B. diminuta.*

The final genus, *Oedipina,* is widespread in cloud forest habitats in Costa Rica, the center of its diversity (Brame, 1968). These salamanders are elongate, mainly fossorial species that include some relatively specialized arboreal climbers in lowland forests (e.g., *O. parvipes*). The species that occur at intermediate elevations in cloud forests typically are found in moss mats covering downed vegetation and soil banks.

Information in the above paragraphs makes

clear that there has been an extensive adaptive radiation of salamanders in the New World tropics, but the age of this radiation remains unknown. Since the initial effort of Dunn (1926), subsequent studies have for the most part suggested progressively earlier dates for the entry of salamanders into the region (Martin & Harrell, 1957, is a striking exception), and until recently an Early or Middle Tertiary origin of the group was accepted (Wake & Lynch, 1976). But biochemical and immunological studies in the last decade have shown that even within genera there has been very great genic differentiation, which implies relatively great age for the separation of the lineages studied (Hanken, 1983; Hanken & Wake, 1982; Larson, 1983, 1984; Lynch et al., 1983; Maxson & Wake, 1981; Papenfuss et al., 1983; Wake & Lynch, 1982). Progress has been made in defining monophyletic groups, but I believe that we have not yet achieved a robust cladistic hypothesis for the group (Wake & Elias, 1983), mainly because of the extensive parallelism and convergence that have obscured patterns. Nevertheless, Hendrickson (1986) has attempted to interpret the history of the group by combining what is known about likely cladistic patterns with knowledge of the geological history of the region in a vicariance biogeography study. He suggested that salamanders which gave rise to the tropical radiation first separated from those in the Appalachia area by rifting of an ancient Maya terrane from Appalachia or by a post-Middle Jurassic to Mid-Cretaceous marine transgression. In general he argues for much older times of separation than previous authors, based both on arguments from earth history and from his belief (although he has not studied these salamanders directly) that the extensive radiation of the tropical salamanders must have taken a long time. I cannot discuss this provocative study in detail here, but it is important to understand that available evidence suggests that salamanders and habitats have coevolved in areas that became present-day Middle America for a very long time.

## SALAMANDERS AND EPIPHYTES

The epiphytic component of cloud forests offers two major classes of microhabitats for salamanders—arboreal bromeliads and moss mats (which are complex and contain diverse ferns, club mosses, and roots, stems, and entire small angiosperms). These microhabitats, particularly bromeliads, are used on occasion by other vertebrates: frogs (especially *Hyla* and *Eleutherodactylus*), lizards (especially *Abronia*), and snakes (e.g., *Bothrops schlegeli*). However, with the exception of a few species of frogs whose tadpoles are clearly adapted for life in the water of tank bromeliads, only salamanders rely on epiphytic plants as their main microhabitats, and salamanders are far more common in bromeliads than are any other vertebrates.

The density of salamanders in bromeliads is difficult to document. As many as 34 *Dendrotriton xolocalcae* have been found in a single bromeliad in Chiapas, Mexico (Taylor & Smith, 1945), but until recently we have had few quantitative data to indicate the frequency of occurrence of salamanders in bromeliads. Although one of the first reports of salamanders living in bromeliads was from Costa Rica (Picado, 1913), the general impression has been that salamanders are not common in bromeliads (Robinson, 1977). Bromeliads have been thought to be more important for salamanders in Mexico, Guatemala, and Honduras. In an early account, Gadow (1908) reported that a Mexican species of *Pseudoeurycea* leads a "partly arboreal life, their favorite hunting and hiding-places being in the clusters of epiphytic plants, such as tillandsias, orchids and the climbing phyllodendrons." Schmidt (1936a, 1942) described bromeliad-dwelling salamanders as relatively abundant in Guatemala and Honduras, apparently more so than in Costa Rica and Panama (Dunn, 1937).

In contrast to the above generalization, salamanders in Costa Rica use moss mats more commonly than do salamanders farther to the north and west. The genera *Nototriton* and *Oedipina* use moss mats extensively in Costa Rica, but apparently rarely do so in northern Middle America. To the north and west *Oedipina* is mainly fossorial, and *Nototriton* is associated mainly with bromeliads (an exception may be a poorly known, undescribed species from Chiapas that has been taken in a moss-covered bank).

There is a general morphology that characterizes most bromeliad-dwelling salamanders (Figs. 3–5). They typically are small animals (usually < 50 mm body length) with long, prehensile tails, long limbs with widely spread digits, and frontally directed eyes. They are acrobatic climbers and are very adept in a three dimensional environment. Some larger salamanders use bromeliads on occasion, but the true specialists usually approximate the above description.

Occupants of moss mats are less characteristic

in morphology. In general they are slender and have relatively short legs. The Appendix contains a list of species which have been reported to occur in bromeliads and moss mats. It also contains a few species known by me to have such habits, but which as yet are not reported in the literature. This list does not differentiate between species that specialize on these microhabitats and those that are but casual occupants.

## COMMUNITY ORGANIZATION

For nearly 15 years my colleagues (James F. Lynch and Theodore J. Papenfuss) and I have been engaged in a broadly based survey of geographical ecology and community organization of the salamanders of Mesoamerica (Wake & Lynch, 1976; Wake et al., 1987). We established a series of line transects in Mexico, Guatemala, and Costa Rica and conducted intensive sampling over a multi-year period along each of them.

By far the most intensively studied of these transects is located in extreme southwestern Guatemala and adjacent Mexico, between San Marcos, Guatemala, and Tapachula, Chiapas, Mexico. Our San Marcos transect extends from the continental divide, down the Pacific slopes of Volcán Tajumulco, to the Pacific coastal plain. Here we have documented the presence of a rich salamander fauna comprised of 15 species, ranging from near sea level to nearly 4,000 m. This transect has provided an opportunity to study the ecological organization of this group of species, relative to each other and to various physical and biotic factors. An earlier study (Wake & Lynch, 1976) presented a general overview of our results, and a recent report (Wake et al., 1987) updates the main patterns of distribution. A summary of our primary results and data relevant to the use of epiphytes by salamanders is presented here.

Schmidt (1936a) collected seven species of salamanders on the slopes of Volcán Tajumulco and inferred the presence of two additional species. He outlined their main patterns of vertical distribution and presented comparisons with the nine species then known from Veracruz, Mexico. His basic conclusion was that zonation was sharper in Guatemala than in Mexico.

We (Wake & Lynch, 1976; Wake et al., 1987) found eight additional species on the Guatemalan transect and confirmed the main elements of Schmidt's preliminary analysis. We recognized four elevational assemblages of salaman-

ders, including a lower cloud forest (1,600–2,400 m) group of four and an upper cloud forest (2,400–2,800 m) group of seven species. These ten species (one is present in both elevational belts) are restricted not only in elevational zonation, but also in geographic distribution; none of the species occurs beyond the limits of the southwestern Guatemalan volcanoes and the adjacent Sierra Madre of Chiapas, Mexico. The region between 1,600 m and 2,800 m is occupied by Evergreen Cloud Forest (above about 1,900 m) and Montane Rain Forest, using the terminology of Breedlove (1981), who also has characterized these formations floristically.

Within elevational zones we examined differential use of major habitat types. For example, some species are more common in edge situations, and some favor small clearings and open spaces, while others are found throughout the dense forest. Within a major habitat we examined the use of specific microhabitats. We recognized four categories: ground-dwelling (beneath logs, rocks, and other surface objects), log-dwelling (within and under the bark of logs and stumps), arboreal (within a leaf-axil microhabitat, including bromeliads), and fossorial (within subterranean passageways). We found no moss mat specialists and therefore did not recognize this microhabitat category. Within microhabitats we paid special attention to differences in body size and in trophic specializations (morphology of the jaws and teeth). The primary modes of ecological segregation of the 15 species are indicated in Table 1. Here a one-sided matrix of potential co-occurrence of the species records our assessment of primary segregation ordered according to decreasing spatial proximity of the segregated species: elevation, habitat, microhabitat, size, and trophic specialization. Nearly three-fourths of the potential sympatric associations of the 15 species are precluded by differences in elevational distribution, and habitat or microhabitat differences separate all but nine of the remaining paired associations. Of the nine pairs of species which show elevational, habitat, and microhabitat sympatry, eight differ importantly by size. The ninth case involves congeneric species similar in size and morphology, except that one species has about half as many substantially larger maxillary teeth and enlarged jaw muscles.

Six species on the transect commonly occur in arboreal microhabitats (in order of frequency in such microhabitats, from most frequent to least): *Bolitoglossa occidentalis, Dendrotriton bromelia-*

TABLE 1. Primary modes of ecological segregation among species that occur along the San Marcos transect. Species arranged in approximate order of appearance from high to low elevations. In order of decreasing spatial proximity: E = elevation; H = habitat; M = microhabitat; S = size; T = trophic specializations. From Wake & Lynch (1976).

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1. *P. rex* | | | | | | | | | | | | | | | |
| 2. *P.* sp. | (E) M | | | | | | | | | | | | | | |
| 3. *P. brunnata* | E | M | | | | | | | | | | | | | |
| 4. *P. goebeli* | E | M | T? | | | | | | | | | | | | |
| 5. *B. rostrata* | H, S | (H) M | (E) H | (E) H | | | | | | | | | | | |
| 6. *B. resplendens* | E | (H) M | (H) M | (H) M | (E) H | | | | | | | | | | |
| 7. *D. bromeliacia* | E | E | M | M | E | M | | | | | | | | | |
| 8. *B. morio* | E | (H) M | H | H | (E) H | (M) S | (E) H | | | | | | | | |
| 9. *B. franklini* | E | E | E | E | E | E | (M) S | | | | | | | | |
| 10. *B. flavimembris* | E | E | E | E | E | E | M | E | M | | | | | | |
| 11. *B. engelhardti* | E | E | E | E | E | E | S, T? | E | S | M | | | | | |
| 12. *B. occidentalis* | E | E | E | E | E | E | E | E | E | E | E | | | | |
| 13. *B. salvinii* | E | E | E | E | E | E | E | E | E | E | E | M, S | | | |
| 14. *O. ignea* | E | E | E | E | E | E | E | E | E | E | E?, M | M | M, S | | |
| 15. *B. flaviventris* | E | E | E | E | E | E | E | E | E | E | E | S | E | E | |
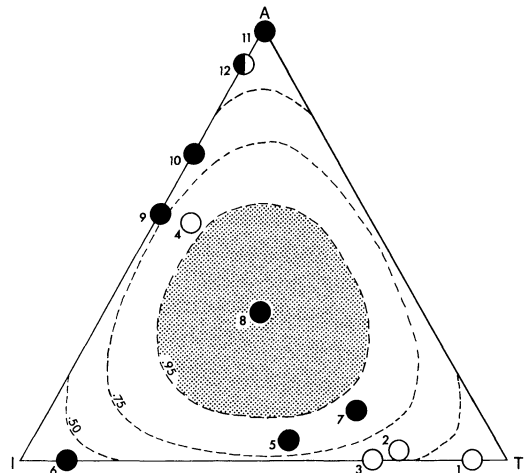


FIGURE 10. Proportional diagram indicating use of microhabitats by 12 species on the San Marcos transect. The dashed lines are isodiversity contours based on occurrences of approximately 1,100 salamanders. Microhabitats were scored as follows: A = arboreal bromeliads; T = under rocks, logs and debris, on the surface of the soil; I = under bark of stumps and standing trees, and inside fallen logs. Open symbol = *Pseudoeurycea*; half-closed symbol = *Dendrotriton*; closed symbol = *Bolitoglossa*. 1, *P. rex*; 2, *P. brunnata*; 3, *P. goebeli*; 4, *P.* sp.; 5, *B. morio*; 6, *B. flavimembris*; 7, *B. rostrata*; 8, *B. resplendens*; 9, *B. franklini*; 10, *B. engelhardti*; 11, *B. occidentalis*; 12, *D. bromeliacia*. Numbers 2 through 10, and 12, are cloud forest inhabitants. Figure from Wake & Lynch (1976).

cia, *B. engelhardti*, *B. franklini*, *Pseudoeurycea* sp., and *B. resplendens* (Fig. 10). All but the first, which occurs at relatively low elevations, are present in the cloud forest and make extensive use of bromeliads. *Bolitoglossa occidentalis* is a small, mainly lowland species that occurs in bromeliads, but it is most commonly found now within the so-called "coffee zone," where it occurs in agricultural plantings of bananas.

James F. Lynch and I are preparing a detailed ecological account of our work in this transect, and with his permission I present here some of our data concerning use of bromeliads in cloud forests by the above listed species. When we first visited this area in 1969 primary forest extended to roadside and bromeliads were abundant. When we last visited the cloud forest region in 1980 the forest had been removed and pasture occupied nearly the entire area between 1,500 m and 2,700 m. Below 1,500 m traditional coffee plantations, which feature large shade trees and extensive plantings of bananas, had given way to a near monoculture of coffee grown in hedgerows without any suitable cover for arboreal salamanders.

TABLE 2.  Relative abundance of salamanders in bromeliads, San Marcos transect.

| Elevation | Wet Season[1] | Dry Season[2] | Combined |
|---|---|---|---|
| Below 1,750 m | — | 3/25 = 0.12[3] | 3/25 = 0.12 |
| 1,750–2,000 m | 6/39 = 0.15 | 41/75 = 0.55 | 47/114 = 0.41 |
| 2,000–2,250 m | 48/239 = 0.20 | 29/64 = 0.45 | 77/303 = 0.25 |
| 2,250–2,500 m | 89/121 = 0.74 | 140/191 = 0.73 | 229/312 = 0.73 |
| 2,500–2,750 m | 81/25 = 0.72 | 27/30 = 0.90 | 45/55 = 0.82 |
| Above 2,750 m | 14/73 = 0.19 | 13/21 = 0.62 | 27/94 = 0.29 |

[1] May–September.
[2] November–February.
[3] Number of salamanders/number of bromeliads.

Salamanders are common inhabitants of bromeliads along the San Marcos transect (Table 2). We found salamanders in approximately every second bromeliad we opened. These bromeliads, primarily members of the genera *Tillandsia* and *Vriesia,* were located relatively low in the trees.

Salamanders in southwestern Guatemala are most abundant in bromeliads at elevations between 2,250 and 2,750 m. From these elevations down to approximately 1,700 m, bromeliads remain relatively common, and there are bromeliads present at elevations up to approximately 3,000 m. All of the bromeliad specialists occur in the cloud forest (roughly 1,500–2,750 m), even though bromeliads are found both above and below that formation. Above the cloud forest those species that use bromeliads at lower elevations (e.g., *Bolitoglossa rostrata, Pseudoeurycea rex*) shift almost entirely to terrestrial microhabitats. Salamanders are consistently more abundant in bromeliads during the dry season than during the wet season, except in the heart of the cloud forest (2,250–2,500 m), where there is less seasonality than elsewhere.

Martin Feder accompanied us on one trip to our transect and studied the thermal ecology of some of the cloud forest salamanders (Feder, 1982). He found that bromeliads, even in the cloud forest, afford cooler and more stable temperatures than microhabitats in immediately surrounding areas. Bromeliad-dwelling salamanders appear not to thermoregulate behaviorally or physiologically, because thermal diversity in their microhabitats is so low as to offer little opportunity for such behavior. As is usual for salamanders, there is a high correlation between body temperatures of salamanders and prevailing microenvironmental conditions (Feder & Lynch, 1982), so the more stable the microenvironment, the less variable will be the temperature of the salamander. The tropical salamanders contrast sharply with more northern plethodontids in having very limited ability to undergo thermal acclimation (Feder, 1978, 1982). This may be either the cause or the effect of the high fidelity to elevational zone and microhabitat displayed by many of these species (Feder, 1983).

The data and analyses in Tables 3–5 indicate that the distribution of salamanders per bro-

TABLE 3.  Distribution of salamanders in bromeliads, San Marcos transect, 16 January 1972, 2,400 m elevation.[1]

| Number of Salamanders per Bromeliad | Frequency |
|---|---|
| 0 | 15 |
| 1 | 10 |
| 2 | 8 |
| 3 | 3 |
| 4 | 1 |
| 5 | 1 |
| 6 | 1 |
| 8 | 1 |

[1] These data are for 55 *Dendrotriton bromeliacia* and three *Bolitoglossa franklini* taken from a sample of 40 bromeliads ($\bar{x}$ = 1.45 salamanders per bromeliad).

TABLE 4.  Distribution of salamanders in bromeliads, San Marcos transect, 18 January 1972, 2,300–2,350 m.[1]

| Number of Salamanders per Bromeliad | Frequency |
|---|---|
| 0 | 12 |
| 1 | 8 |
| 2 | 10 |
| 3 | 7 |
| 4 | 1 |
| 5 | 2 |

[1] These data are for 59 *Dendrotriton bromeliacia* and four *Bolitoglossa franklini* collected in a sample of 40 bromeliads ($\bar{x}$ = 1.58 salamanders per bromeliad).

TABLE 5.   Test for randomness, combined data from Tables 3 and 4.[1]

| Number of Salamanders per Bromeliad | Observed Frequency | Expected Frequency (Poisson) |
|---|---|---|
| 0 | 27 | 17.5 |
| 1 | 18 | 26.6 |
| 2 | 18 | 20.2 |
| 3 | 10 | 10.3 |
| 4 | 2 ⎫ | 3.9 ⎫ |
| 5 | 3 ⎪ | 1.2 ⎪ |
| 6 | 1 ⎬ 7 | 0.3 ⎬ 5.5 |
| 7 | — ⎪ | 0.1 ⎪ |
| 8 | 1 ⎭ | 0.0 ⎭ |

Chi-square (goodness of fit) = 8.50 with 4 df
$0.05 > P > 0.1$

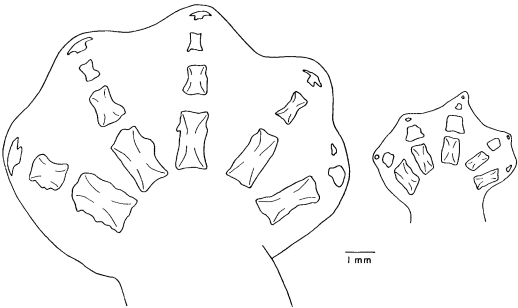[1] Data for 121 salamanders collected from 80 bromeliads ($\bar{x} = 1.52$ salamanders per bromeliad).



FIGURE 11.   Outlines of the left hind foot of two lowland species of *Bolitoglossa* from Pacific coastal Guatemala. The digits and bony phalanges are indicated in each. *Bolitoglossa salvinii* is a large species (this specimen is 67.5 mm, snout-vent length) with extensive webbing and is capable of generating suction in arboreal situations. *Bolitoglossa occidentalis* is a diminutive species (this specimen is 38.7 mm, snout-vent length) with feet that superficially appear to be webbed, but in reality are just incompletely developed (paedomorphic) as suggested by the strong gradient in phalangeal structure within each digit.

meliad is not significantly different from random. However, there is at least a suggestion that there might be an excess of bromeliads that lack salamanders, as well as a deficiency of bromeliads containing single salamanders. Thus, there might be a tendency toward clumping under conditions of high salamander abundance.

Bromeliads might seem to be a near perfect microhabitat for salamanders, in terms of food availability, thermal stability, and constancy of humidity. But concentration of salamanders in bromeliads might attract predators. Spiders and salamanders are the top resident carnivores within bromeliads, and they do not prey on each other very extensively. Some arboreal snakes forage widely and may be important, although infrequent, predatory visitors to bromeliads; birds might also be important predators. All tropical salamanders have a specialized autotomy zone at the base of the tail, and Shaffer (1978) examined tail loss frequency as a rough index of relative predation pressure on 10 species of salamanders from the San Marcos transect (parts of tails may be lost in intraspecific aggressive encounters, but these species are not known to be very aggressive). He found an inverse correlation between rates of tail loss and elevation, and we know that snake densities also decrease with elevation. Two of the three cloud forest species commonly found in bromeliads (*Dendrotriton bromeliacia, Bolitoglossa franklini*) had the second and third highest tail loss percentages of the species studied (the highest was the ar-

boreal lowland species *B. occidentalis*). Although exposure to predation may be a relative cost for living in bromeliads, the cost is apparently outweighed by other advantages, such as those mentioned above.

Although bromeliad dwellers in cloud forest habitats differ greatly in morphology, ecology, and behavior from even the most arboreal North American plethodontids (e.g., *Aneides*), they are not the most extremely specialized species on the San Marcos transect. At elevations below about 1,400 m the cloud forests, and the lower cloud forest salamander fauna, are absent. A new salamander community appears at about 1,000 m, composed of three extreme morphological and ecological specialists. This community includes a relatively large and a relatively small arboreal species of the genus *Bolitoglossa* and an elongate fossorial species of the genus *Oedipina*.

*Bolitoglossa salvinii*, a large species, is an active, climbing animal with a long prehensile tail and large hands and feet with extensive interdigital webbing (Fig. 11). These animals, which frequent surfaces of *Heliconia* and other large-leafed plants on moist evenings, are capable of producing suction with their large hands and feet (Alberch, 1981).

*Bolitoglossa occidentalis*, the small species, has small hands and feet that appear to be fully webbed. In reality the hands and feet manifest incomplete development, a phenomenon known

as paedomorphosis that affects a number of features of the organism (Wake, 1966; Wake & Brame, 1969; Alberch et al., 1979; Alberch & Alberch, 1981). Such similarly affected features include a relatively short and strongly tapered tail, as well as a reduction in skull ossification. The hands and feet are essentially "embryonic," with digits that show a strong gradient of development (Fig. 11). Although these animals do not generate suction with their hands and feet (Alberch, 1981), they are very agile, partly as a result of their small size. They have an extensive ventral surface area (body, limb, and tail) relative to their mass, so they "stick" to moist plant surfaces by surface tension. Apparently these salamanders are virtually restricted to leaf axil retreats. They especially favor *Heliconia* and both cultivated and feral banana plants (*Musa* spp.). Smith (1945) reported finding *Bolitoglossa rufescens* (very similar in morphology and ecology to its close relative *B. occidentalis*) to be abundant in red bananas (he found about 250 per hour) at a Veracruzian site. These animals are adept at climbing small tendrils, stems, and strands of moss.

Members of the small species of *Bolitoglossa* are encountered only rarely in terrestrial sites, and the large species, while occasionally found on the ground (e.g., crossing roads on rainy nights), also are basically arboreal. (An exception may be the very large species *B. dofleini,* which can be very common in terrestrial situations.) But another group of lowland species, the very elongate, short-legged genus *Oedipina,* is found only at and beneath the surface of the ground. Species of *Oedipina* are elongated as a result of the addition of trunk and especially tail vertebrae, and they have bizarre long tails (Fig. 12). In addition to their extremely short legs and tiny hands and feet, they have heads and bodies of very small diameters; all of these features facilitate use of root channels and underground burrows.

The San Marcos transect is special because more species of salamanders occur there than in any other area of the Pacific Versant in Middle America. Volcán Tajumulco (4,200 m) is attached to the Guatemalan Plateau at about the 3,000 m level, so on both sides of the volcano there are substantial areas of moderate elevation which trap moisture and thereby create favorable salamander habitat. To the south and east the Plateau gradually lowers and rainfall declines. In the vicinity of Guatemala City, Volcán Agua (over
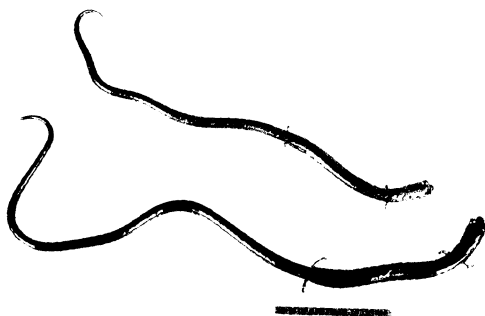


FIGURE 12.    *Lineatriton lineola* (top), from near Fortín de las Flores, Veracruz, Mexico, and *Oedipina ignea* (bottom), from Finca Santa Julia, near San Rafael Pie de la Cuesta, San Marcos, Guatemala. The scale bar is 25 mm. These extremely elongated species are semi-fossorial to fossorial in habit, and have evolved convergently.

3,700 m) towers over the Plateau, to which it is attached along only its northern flank at a low elevation (about 1,000 m). The contrast in salamander faunas between Volcán Tajumulco and Volcán Agua is great. Only three species have been collected on the slopes of Agua. There is a single high elevation member of the genus *Pseudoeurycea* (*P. goebeli*), one low elevation species of the genus *Bolitoglossa* (*B. salvinii,* a large, fully webbed species), and a middle elevation generalized species of the genus *Bolitoglossa* (*B. morio*). All three of these species also are present on the San Marcos transect. There is a well-developed cloud forest with abundant bromeliads on Volcán Agua, but the forest is localized and it is isolated from similar habitats to the north and west by low elevations covered by drier vegetation types. In 1969 we opened about 600 bromeliads on Volcán Agua, but found only two salamanders! This contrasts sharply with the data presented earlier for the San Marcos transect. *Bolitoglossa morio,* the species we encountered, is a widespread and relatively common inhabitant of ground and log microhabitats in forested areas of the Guatemalan Plateau. On the San Marcos transect it is found only at the top of the cloud forest and in drier broadleaf forest above, where the edge of the Plateau contacts Volcán Tajumulco. Here the species occurs occasionally in bromeliads (Fig. 10). On Volcán Agua, although *B. morio* remains uncommon in bromeliads and apparently has not modified its microhabitat utilization patterns in any dramatic way, its elevational range is 1,300–2,500 m. At this site, where *B. morio* is the only salamander
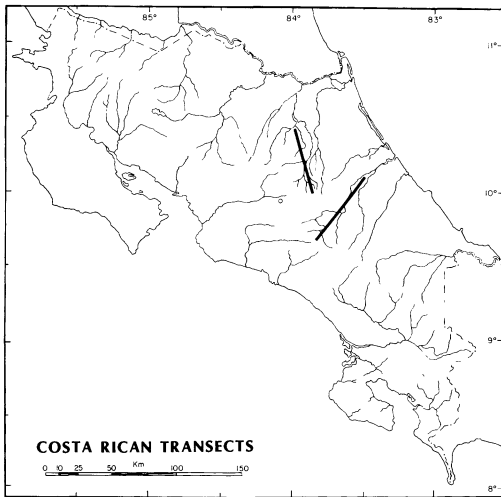
FIGURE 13. Map of Costa Rica indicating the location of the Irazú and Tapantí transects illustrated in Figures 14 and 15.

present, it occupies an elevational range that accommodates ten species on the San Marcos transect. The patterns of species distribution in the tropics (this example, but see below also) are probably determined by combinations of physiological constraints (in relation to physical factors in the environment) as well as such interspecific interactions as predation and competition.

### COMPARATIVE ASPECTS OF COMMUNITY ORGANIZATION

Until recently most fieldwork by my group has been in Mexico and Guatemala (for general summaries see Wake & Lynch, 1976; Wake et al., 1987). In general, the results of our detailed studies of the San Marcos transect have been mirrored in other areas (cf. Fig. 9). Typically only one or two species occur at elevations above 3,500 m; as one moves lower the number of species present in a given habitat increases dramatically at about 3,000 m and continues to be relatively high until the lower limit of the cloud forest is reached. At elevations below 1,000 m the number of species present typically declines, and at sea level the largest number of species definitely known to be present is four on the Osa Peninsula of Costa Rica, where there are two species of *Bolitoglossa* and two species of *Oedipina*. Possibly five species occur together at sea level in the region of Bocas del Toro, Panama (Wake et al., 1973 and unpubl. data), and in northeastern

Costa Rica seven species are known from elevations below 1,000 m, but not in local sympatry (see below). The proportion of the total salamander fauna present in the lowlands increases at lower latitudes within Middle America (see Table 5 in Wake & Lynch, 1976). There is evidence of increased "tropicality" (that is, of closer packing of species in communities and increased numbers of species present locally) as one moves into the deep tropics. Finally, however, in northwestern South America this trend stops, perhaps because plethodontids are not thought to have dispersed into South America until late Pliocene times (Wake & Lynch, 1976; Hanken & Wake, 1982). Except in the Chocó and the flanks of the northern Cordilleran regions of Colombia, the number of salamander species present in lowland sites in South America is not known to exceed two, even in such biotically rich forests as those of the Río Palenque area of Ecuador.

Throughout Middle America, salamanders are found in cloud forests. In Mexico and in Nuclear Central America, cloud forest salamanders make extensive use of bromeliads as microhabitats, even at the extreme northeastern limits of the range of the supergenus *Bolitoglossa* in the Gómez Farías region of Tamaulipas (where cloud forests also reach their northern limit; Martin, 1958). But the manner in which cloud forest microhabitats are utilized changes in Costa Rica. The Costa Rican salamander fauna justifiably has been considered one of the best known in the tropics, thanks primarily to the work of Taylor (1952, 1954). However, very little has been reported concerning microhabitat utilization and patterns of co-occurrence of Costa Rican species. Only four species are reported to occur in bromeliads (Robinson, 1977), although many more species are known to inhabit cloud forests.

Recently I have been investigating the systematics and distribution of Costa Rican salamanders in some detail. I have focused attention on two general transects (Figs. 13–15). Results for Costa Rica are preliminary, because major sections of these generalized transects have yet to be searched thoroughly. Nevertheless, certain marked contrasts with more northerly transects are apparent.

A dominant theme in the history of studies of tropical salamanders has been that the species which are the most conservative ecologically and the most primitive phylogenetically occur in Mexico, and that there is both increased specialization and a decline in the number of species
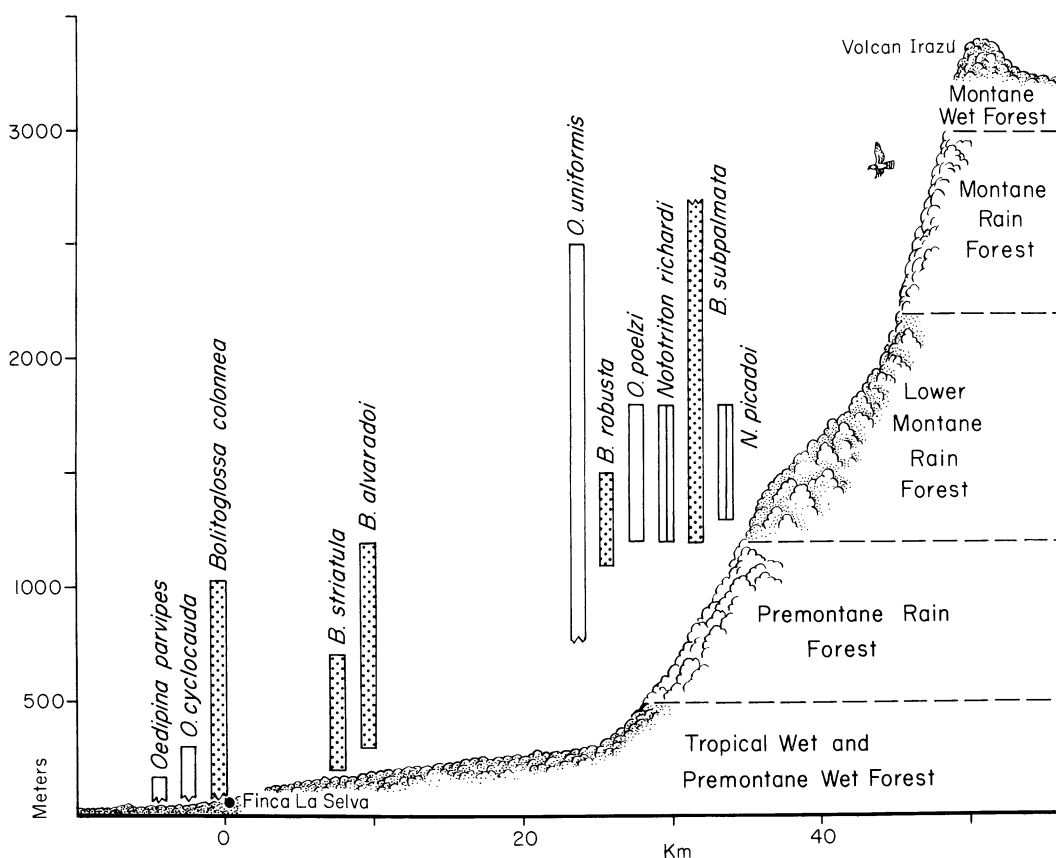
FIGURE 14. Vertical distribution of plethodontid salamanders along the Irazú transect, extending about 55 km from Finca La Selva to Volcán Irazú, Costa Rica.

to the south (Dunn, 1926; Taylor, 1944, 1952; Brame & Wake, 1963; Wake, 1966; Wake & Lynch, 1976). Even though Wake & Lynch (1976) documented the presence of a large number of species below 10° latitude, we continued to espouse the traditional view of relics in the north (e.g., *Chiropterotriton priscus* of Coahuila and Nuevo León, Mexico) and increasingly derived forms to the south. The recent discovery of the most primitive known genus of tropical plethodontid in Guatemala (Elias & Wake, 1983) and a fresh analysis of relationships of new and existing groups (Wake & Elias, 1983) have forced me to re-evaluate my earlier views. It now seems likely that salamanders have been in the tropics of present-day Middle America for a very long time, possibly throughout the Tertiary (see above section on Ecological Geography and Systematics). Middle elevations doubtless have been important areas of both survival and radiation in the group, and we have discovered that patterns of microhabitat utilization differ dramatically between Mexico and Nuclear Central America on one hand, and Talamancan Central America on the other.

Perhaps the most striking difference between the above regions is the presence of a rich fauna associated with moss mats in the cloud forests of Talamancan Central America. As noted earlier (Table 2), salamanders are sometimes very abundant in cloud forests of northern Middle America, where many species utilize bromeliads (Wake & Lynch, 1976). In Veracruz, Mexico, and in Nuclear Central America, elongate, fossorial species of *Lineatriton* and *Oedipina* occur only at elevations below the lower limit of cloud forest. In contrast, elongate members of the genus *Oedipina* are well represented in Costa Rican and Panamanian cloud forests, extending upwards to elevations in excess of 2,000 m (Figs. 14, 15). Here they utilize moss mats covering soil banks, downed logs, and stumps. Furthermore, living
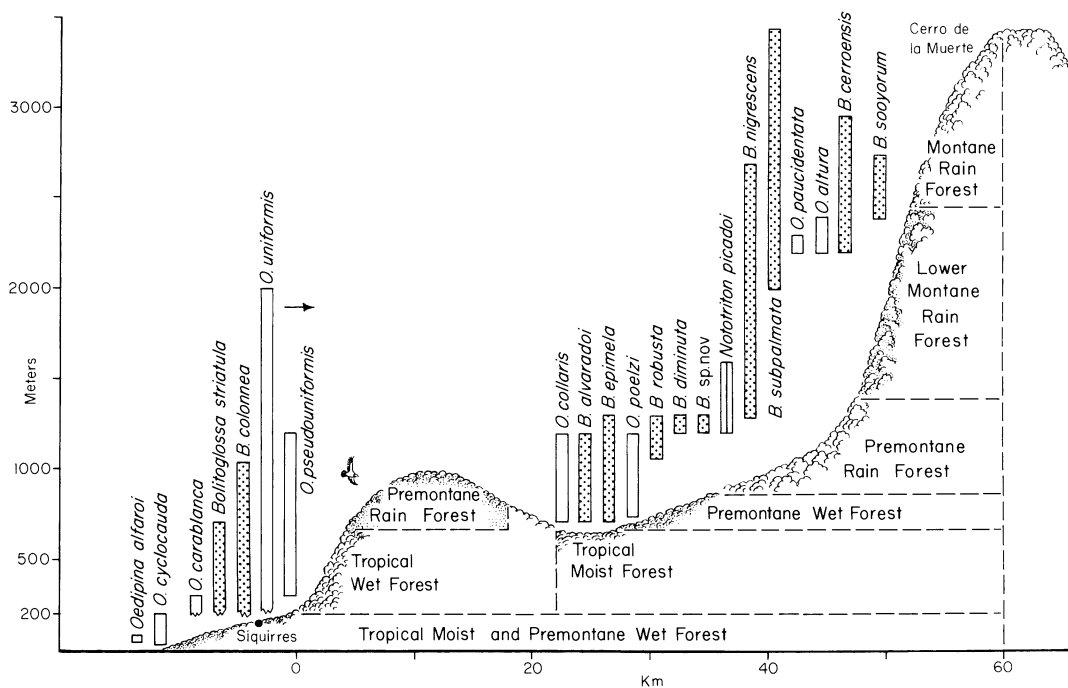
FIGURE 15. Vertical distribution of plethodontid salamanders along a generalized Tapantí transect, which extends between Siquirres and Cerro de la Muerte, Costa Rica. This region, about 60 km long, contains more species of plethodontid salamanders than any known area in tropical America.

in moss mats in these cloud forests are species of *Nototriton,* a genus that is mainly confined to bromeliads in Nuclear Central America. There is even an undescribed Costa Rican species of *Bolitoglossa* that has been taken only in moss surrounding twigs on trees and shrubs in cloud forests. This substantial fauna represents an ecological component that is rare (e.g., *Dendrotriton cuchumatanus* occurs in moss mats in Guatemala, Lynch & Wake, 1975) or is missing in cloud forests of Nuclear Central America.

The two Costa Rican transects offer some interesting contrasts. Both extend up the Caribbean slopes from near sea level to elevations well above 3,000 m. The first (Fig. 14), the Irazú transect, extends from the vicinity of Finca La Selva for about 55 km to the peak of Volcán Irazú. Salamander distributions along this transect are poorly known except for the region between 1,000 and 2,500 m. For example, Scott et al. (1983) listed two species of *Oedipina* from Finca La Selva, but study of specimens from the area suggests that three occur there. The taxonomy of the group is difficult, but it may be that none of the three are the species listed. (Note that only two species are indicated on Fig. 14.) There are pres-

ently 11 species of salamanders (in three genera) known from this transect. As with the more northerly transects, only one species (*Bolitoglossa subpalmata*) is likely to occur at elevations of >3,000 m (and I cannot document its presence at that elevation as yet, although I expect it may be found). However, in contrast with more northerly transects (cf. Wake et al., 1987), there are at least five species present at elevations of <500 m. Eight species occur in cloud forest between 750 and 2,000 m, including two species that specialize on moss mat microhabitats (the two species of *Nototriton;* see also comments in Taylor, 1954), two others that utilize moss mats extensively but also use burrows in soil (the two species of *Oedipina*), and two *Bolitoglossa* (*B. subpalmata, B. robusta*) that I have found in moss mats, although other microhabitats are used more frequently. Both *B. subpalmata* (at this elevation) and *B. alvaradoi* use bromeliads.

I expect that more species will be found on the Irazú transect, in part because of the unusually high numbers of species present on the Tapantí transect (Fig. 15). The latter transect is far more generalized in its boundaries than the first, and is essentially a broad (ca. 20 km) swath of ter-

ritory extending about 60 km from the vicinity of Siquirres to the summit of Cerro de la Muerte. The Tapantí transect is not a straight line, but twists somewhat to encompass sites where some of the rarer species are known to occur. There is extensive habitat disturbance along this transect (for example, in the vicinity of Turrialba), and I justify weaving together an indirect transect as an attempt to demonstrate the potential number of species one might reasonably expect to find on a continuous altitudinal transect under pristine conditions. The Tapantí transect thus offers a greater diversity of habitats than does the Irazú transect and one might expect more species to be present. To my surprise, the Tapantí transect is the richest that I have found in the tropics, with 21 species. There are only 26 species of plethodontids known from Costa Rica (Scott et al., 1983; their list and mine differ slightly but we obtain the same total number of species), and that about 80% of them occur along this transect attests to its richness.

The Tapantí transect has a higher number of species (seven) occurring below 500 m than does the Irazú transect, and in both Panama and Nicaragua another species (*Oedipina collaris*) occurs at elevations of <500 m (Brame, 1968), so there is the likelihood that an eighth species eventually will be found. *Bolitoglossa alvaradoi* apparently occurs at elevations of <500 m elsewhere in Costa Rica. Thus, as many as nine species might be expected in the lowlands in the area crossed by this transect.

Thirteen species occur in the cloud forest of the Tapantí transect, if we accept 750–2,000 m as its elevational bounds. In fact, cloud forest conditions exist almost to 3,000 m, although in general cloud forests are less well defined in Costa Rica and Panama than farther to the north (Myers, 1969). This transect contains the richest cloud forest salamander fauna found anywhere in the tropics. Here, too, I have probably underestimated the number of species present. At least one more species of *Bolitoglossa* may be present, and the two poorly known highland species of *Oedipina* may well extend to lower elevations, since the genus as a whole is strongly concentrated at lower elevations. Two species of *Bolitoglossa* (an undescribed species and *B. diminuta,* Robinson, 1976) use mats of vegetation including mosses and liverworts that surround twigs and branches of trees. Several other species use bromeliads and moss mats, but no quantitative data are available. In the forests of Refugio

Tapantí there is an especially rich epiphyte fauna, and this is the locality where the largest number of species are found. However, in marked contrast to the situation in the cloud forest on our San Marcos transect, the density of individual species is uniformly low on this transect. This situation of high species diversity and low density of individual species is one more indication of the increased "tropicality" of the Costa Rican salamander fauna.

The contrast between the cloud forest that occurs at around 1,000 m and the forest around 3,000 m on this transect is sharp. At high elevations the density of *Bolitoglossa subpalmata* is extraordinarily great, on the order of 9,000/ha (Vial, 1968). Four species occur in sympatry at around 2,500 m; in my experience *B. subpalmata* is about 100 times more common than *B. cerroensis,* about 1,000 times more common than *B. sooyorum,* and about 10,000 times more common than *B. nigrescens*! Doubtless there is a collecting artifact involved, but the first species is remarkably abundant and the last has been, at the very least, elusive. The high density of a single species at high elevation is a common theme in tropical salamander biology.

*Bolitoglossa subpalmata,* which can be exceedingly abundant at high elevations in Costa Rica, displays a marked shift in microhabitat utilization and a reduction in abundance at lower elevations. The species is primarily grounddwelling at high elevation, although it also uses bromeliads. I have collected *B. subpalmata* from bromeliads 30 m above ground level in an oak tree at 3,000 m elevation. At elevations of <2,000 m the species becomes increasingly common in bromeliads and is encountered only infrequently in terrestrial situations. This species can be extraordinarily persistent in the face of even drastic habitat change, so long as bromeliads remain. An anecdote illustrates this point. An old collecting locality in the Montes de Aguacate, west of San José, was visited recently. Only tiny fragments of forest remain at this site, at about 1,500 m. Salamanders were common residents of bromeliads in one forest fragment where trees were being felled. We opened 130 bromeliads and found 55 salamanders, including 14 adults and a subadult in a single bromeliad. As many as three adults were found in the axil of a single leaf. This is a graphic demonstration of the suitability of bromeliads as microhabitat for salamanders, especially under conditions of great habitat modification. I have had similar expe-

riences with *Chiropterotriton lavae* in fragments of cloud forest above Jalapa, Veracruz, Mexico, and with *Bolitoglossa morio* in an area devastated by volcanic activity on Volcán Pacaya, Guatemala.

It is still too early to generalize very extensively from our comparative transect studies. We have come to be suspicious of species with broad elevational ranges (such as *O. uniformis*, Figs. 14, 15), and these deserve careful taxonomic re-evaluation, for most species occur within rather narrow elevational limits. We also have come to expect few extreme highland or lowland species, but there are more lowland species at low latitudes. Cloud forests and salamanders are most abundant at mid-elevations.

## Factors Influencing Salamander Speciation and Radiation

Species of plethodontid salamanders characteristically display a high degree of genetic fragmentation (Larson et al., 1984; Larson, 1984). Larson (1984) has argued that a general pattern for the history of population structure in plethodontids is that following origination they expand gradually and contiguously into regions to which they have ecological access. Later, as a result of climatic change which may result from many proximal causes, their populations become fragmented into islands among which there is little or no genetic exchange. Subsequent climatic changes may lead to re-establishment of ecological access to areas separating isolated populations. This may lead either to renewed genetic exchange or, depending on the level of genetic divergence and its effect on isolating mechanisms or mate recognition systems, to a variety of interactions. There may be a hybrid swarm, a narrow hybrid zone, a narrow zone of overlap with occasional hybridization, partial sympatry with boundaries set by competitive interactions, or coexistence with different ecological requirements. All of these interactions have been documented among plethodontids. The many studies of population structure based on electrophoretic analysis of proteins, together with studies of distribution, phylogenetic history, and biogeography (reviewed by Larson, 1984), suggest that geographic or allopatric speciation by subdivision is the common mode in plethodontids. There are similarities with the concept of "taxon cycles" (Wilson, 1961; Ricklefs & Cox, 1972), which usually have involved examples from island

chains. These postulated cycles of expansion and contraction of geographic ranges and population densities would establish the setting for the kind of speciational processes I envision having taken place among the tropical salamanders.

The two primary factors in the history of the tropical salamander fauna probably have been the combination of adaptation of species to cloud forest environments and the long, complex history of tectonic activity in Middle America. There are some relatively stable areas, such as the ancient core of Nuclear Central America, where the upper and lower boundaries of the cloud forest have shifted, but where cloud forest in a broad sense probably has been present for much of the Tertiary and Quaternary periods (see discussion in Wake & Lynch, 1976). However, there are many other areas where tectonic movements and associated volcanic activity have been so great and so persistent that cloud forests have been only an ephemeral presence, shifting almost constantly.

The three foci for salamander radiation in the tropics (Fig. 2) all have stable, ancient tectonic core areas surrounded by regions of great tectonic activity. (For summary of tectonic history, see Hendrickson, 1986.) These areas have been cited by other workers as having phylogenetically distinctive faunal components. For example, Savage (1982) stated:

> I now believe that the distinctive montane herpetofaunas of the southern Sierras of Mexico, Nuclear Central America, and the Talamanca area developed more or less *in situ* from ancestors that "rode" the uplifted areas and evolved with them. Each endemic montane area then represents an uplifted island biota vicariated from a more or less similar sea of widely distributed ancestors.

Nuclear Central America (Fig. 16) illustrates the ideas outlined above. That region has as its core the ancient Sierra de los Cuchumatanes, located on the southern part of the North American plate. The area has been characterized as the Middle American Megathrust by Plafker (1976), because it is the conjunction of three major plates. The Cocos plate, to the southwest, is being subducted near the intersection of the North American and Caribbean plates (for evidence of the widespread influence of this phenomenon see Singh et al., 1985). The latter is being forced eastward by the combined plate movements, and a small western tip of the plate is effectively "caught" between the North American and the Cocos plates. The zone between the Caribbean
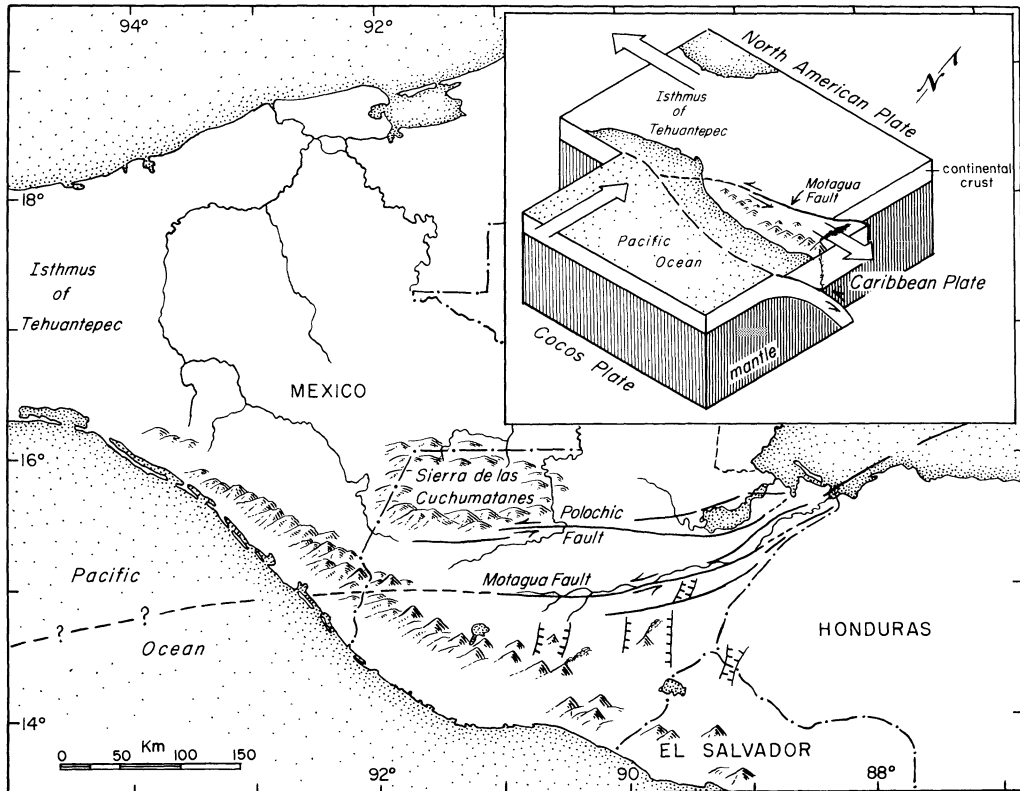
FIGURE 16. Nuclear Central America. A generalized diagram illustrating relationship of the core region, north of the Polochic Fault, to the intersection of three crustal plates. The margins of the core region are areas of intense tectonic activity because of the complex geology of the region. Nuclear Central America has been an area both of preservation of apparently ancient lineages, because of the continued stability of the core, and of speciation of cloud forest forms, due in large part to the fragmentation and reassembly of areas of cloud forest. Inspired by and based largely on Plafker (1976).

and North American plates is outlined by the Motagua and Polochic fault zone. This has been an area of intense tectonic activity for millions of years and Plafker (1976) has estimated that at least 200 km of lateral movement of plates along this fault zone has occurred since the Miocene. The western tip of the Caribbean plate, trapped between the other plates, is being ripped, or decoupled (Plafker, 1976). Grabens have formed, with small volcanic cones rising within them. Parallel to the Pacific versant, above the zone where the earth's mantle is being pierced by the subducted Cocos plate, the famous Guatemalan volcanoes are lined up. Volcán Tajumulco and Volcán Tacaná lie at the northwestern corner of the Caribbean plate, where the three plates meet. In this topographically complex zone of maximal geological turbulence, the largest number of co-occurring species of salamanders in Middle America is found, along our San Marcos transect.

The relatively stable upland of the Sierra de los Cuchumatanes is in many ways an even more interesting area than the Pacific volcanic belt. We began fieldwork in this area in 1974, at a time when only two species of salamanders were known from the Caribbean slopes of the Cuchumatanes, despite a number of brief collecting trips by different herpetologists. Results of our investigations have been summarized by Elias (1984), who found 13 species of salamanders in this region (see also Wake et al., 1987). As elsewhere in Middle America, the cloud forest is of special interest, for six species with narrow elevational ranges occur just above the cloud line, here located at about 1,300 m. Two new genera of salamanders were discovered in this cloud forest

(Elias & Wake, 1983; Wake & Elias, 1983), including the exceptional *Nyctanolis,* a morphologically primitive genus which appears to be the sister group of all other tropical salamanders. Thus, on the one hand, the ephemeral cloud forests of the tectonically active and topographically complex margins of the Cuchumatan uplands have contributed to speciation and led to the highly disjunct distributional patterns illustrated previously for *Dendrotriton* and *Nototriton* (Figs. 7, 8). On the other hand, the more stable cloud forests on the northeastern slopes of the core of the Cuchumatan region have served as refugia for what must be extremely ancient lineages.

CONCLUSIONS

We still have much to learn about the salamanders of the New World tropics, and even the best known areas of Middle America have yielded many recent surprises. Earlier misconceptions concerning the probable history and ecology of tropical salamanders have led to underestimates of the age and diversity of the group and have contributed to our relative ignorance of the ecology of the cloud forest and lowland species, especially the arboreal and fossorial forms. New species are being discovered more rapidly than they can be described, for many species are known from small series. Our knowledge of the comparative osteology and of molecular evolution of this group, while still fragmentary, is sufficient to demonstrate that parallelism and convergence are rampant.

This, in turn, implies both that there may be only a limited number of ecological roles available to tropical salamanders, and that there may be functional and developmental-historical constraints which impose limits on the evolutionary potential of the group. An especially clear case of convergence is the elongation associated with fossorial life in the genera *Oedipina* (from south and east of the Isthmus of Tehuantepec) and *Lineatriton* (from north of the Isthmus) (Fig. 12). The former has become elongate by increasing the numbers of vertebrae; the latter by increasing the length of the individual vertebrae, which are identical in number (in the trunk) to all tropical genera except *Oedipina* (Tanner, 1950; Wake & Lynch, 1976). Earlier in this paper I highlighted the convergence in the *Chiropterotriton-Dendrotriton-Nototriton* assemblage. Within *Bolitoglossa* webbing of hands and feet has evolved both convergently (Alberch & Alberch, 1981) and in

parallel (Wake, 1966; Wake & Brame, 1969; Larson, 1983; Elias, 1984). These phenomena have made phylogenetic analysis very difficult, for any phylogenetic hypothesis requires extensive convergence, parallelism, or evolutionary reversal (Wake & Elias, 1983).

Epiphytes appear to have been significant factors in the evolution of tropical salamanders. The convergence in morphology and behavior of bromeliad-dwelling salamanders is one indication of this importance, and the extent to which bromeliads and moss mats are utilized as microhabitats is another. It is also significant that salamanders persist in the face of great environmental change so long as fragments of forest with the preferred microhabitats remain.

The tropical salamanders, which originated from a Laurasian ancestral group (Savage, 1973), are a marked exception to a common pattern of tropical origin and subsequent temperate invasion. Late in the history of salamanders as a group, but nevertheless a very long time ago (perhaps at the beginning of Tertiary), they invaded the area that has become modern Middle America. Compared with salamanders generally, the tropical salamanders have been phenomenally successful. But now their survival and, indeed, the survival of much of the diversity of tropical ecosystems is at risk, for the lowland forests and the middle elevation cloud forests that harbor most tropical salamanders are being cleared at rates that almost defy belief. Not a tree is standing over extensive parts of our San Marcos transect, which was in an almost pristine state as recently as 1969. In a single human lifetime the results of perhaps a hundred million years of evolution will have been dramatically changed, if not extinguished.

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## APPENDIX I

Use of bromeliads and moss mats by neotropical salamanders. All species known to occur in either of these microhabitats are listed below. Literature references do not include all observations for a given species, but either the first or the best documented example. Where no publication exists field notes or notes from museum collections made by the author are cited.

Bromeliad Occurrence:

| | |
|---|---|
| *Bolitoglossa alvaradoi* | DBW notes |
| *B. arborescandens* | Taylor (1954) |
| *B. borburata* | Trapido (1942) |
| *B. cuchumatana* | Stuart (1943), Elias (1984) |
| *B. dunni* | Schmidt (1942) |
| *B. engelhardti* | Schmidt (1936a), Wake & Lynch (1976) |
| *B. flavimembris* | DBW notes |
| *B. franklini* | Taylor (1941), Wake & Lynch (1976) |
| *B. hartwegi* | Wake & Brame (1969), Elias (1984) |
| *B. helmrichi* | Schmidt (1936a) |
| *B. hermosa* | Papenfuss et al. (1983) |
| *B. jacksoni* | Elias (1984) |
| *B. lignicolor* | Dunn (1926) |
| *B. lincolni* | Wake & Lynch (1976), Elias (1984) |
| *B. meliana* | Wake & Lynch (1982) |
| *B. mexicana* | Taylor & Smith (1945) |
| *B. minutula* | Wake et al. (1973) |
| *B. morio* | Wake & Lynch (1976), Elias (1984) |
| *B. mulleri* | Stuart (1943) |
| *B. nicefori* | Brame & Wake (1963) |
| *B. occidentalis* | Shannon & Werler (1955a) |
| *B. odonnelli* | Stuart ("probably," 1948) |
| *B. platydactyla* | Taylor & Smith (1945) |
| *B. ramosi* | Brame & Wake (1972) |
| *B. resplendens* | Wake & Lynch (1976) |
| *B. rostrata* | Wake & Lynch (1976) |
| *B. rufescens* | Schmidt (1936a), Taylor & Smith (1945) |
| *B. savagei* | Ruthven (1922) |
| *B. subpalmata* | Dunn (1937) |
| *B. taylori* | Wake et al. (1970) |
| *B. vallecula* | Brame & Wake (1963) |
| *B. walkeri* | Brame & Wake (1972) |
| *B. yucatana* | DBW notes |
| *Chiropterotriton arboreus* | Rabb (1955) |
| *C. chiropterus* | DBW notes |
| *C. chondrostega* | Martin (1958) |
| *C. lavae* | Taylor (1942) |
| *C. multidentatus* | Martin (1958) |
| *Dendrotriton bromeliacia* | Schmidt (1936a), Wake & Lynch (1976) |
| *D. megarhinus* | Rabb (1960) |
| *D. rabbi* | Lynch & Wake (1975), Elias (1984) |
| *D. xolocalcae* | Taylor (1941) |
| *Nototriton barbouri* | Schmidt (1936b) |

APPENDIX I.  Continued

| | |
|---|---|
| *N. nasalis* | Dunn (1926), Schmidt (1942) |
| *N. picadoi* | Picado (1913) |
| *N. veraepacis* | Lynch & Wake (1978) |
| *Pseudoeurycea bellii* | DBW notes from T. J. Papenfuss |
| *P. brunnata* | Wake & Lynch (1976), and DBW notes |
| *P. exspectata* | Stuart (1954) |
| *P. firscheini* | Werler & Smith (1952), Shannon & Werler (1955b) |
| *P. goebeli* | Schmidt (1936a), and DBW notes |
| *P. leprosa* | DBW notes |
| *P. nigromaculata* | DBW notes |
| *P. scandens* | Walker (1955), Martin (1958) |
| *P. smithi* | DBW notes from T. J. Papenfuss |
| *Thorius dubitus* | DBW notes |

Moss Mat Occurrence:

| | |
|---|---|
| *Bolitoglossa diminuta* | Robinson (1976—in a liverwort mat) |
| *B. marmorea* | Wake et al. (1973) |
| *B. subpalmata* | Taylor (1952) |
| *Dendrotriton cuchumatanus* | Lynch & Wake (1975) |
| *Nototriton picadoi* | Taylor (1954) |
| *N. richardi* | DBW notes |
| *Nyctanolis pernix* | Elias & Wake (1983) |
| *Oedipina poelzi* | Brame (1963) |
| *O. pseudouniformis* | Brame (1968) |
| *O. uniformis* | Brame (1968) |
| *Pseudoeurycea rex* | Elias (1984) |
| *P. scandens* | Martin (1958) |
| *P. werleri* | Shannon & Werler (1955a) |
| *Thorius dubitus* | Taylor (1941) |