DISTRIBUTION OF SALAMANDERS ALONG ELEVATIONAL TRANSECTS IN MEXICO AND GUATEMALA

David B. Wake, Theodore J. Papenfuss
Museum of Vertebrate Zoology,
University of California, Berkeley, California 94720, USA

James F. Lynch
Smithsonian Institution,
Edgewater, Maryland 21037, USA

Abstract

Salamanders are widely distributed in Mesoamerica, and over 100 species have been described from the region. The organization of salamander communities in the tropics have been studied along five elevational transects, one each in Veracruz, Oaxaca, and Chiapas, and two in Guatemala. Many species maintain local allopatry or parapatry through differences in elevational distribution. Within a given elevational zone, species usually differ by microhabitat preferences or body size. High species diversity, a high degree of elevational limitation and geographic restriction, and marked microhabitat specialization all are characteristic of salamanders that occur in cloud forest formations at elevations between 1000 m and 2800 m. The relatively few species found at higher elevations tend to occur in high density and to be ecologically generalized. Species diversity is also reduced in the tropical lowlands, but species there are invariably specialized in morphology for specialized arboreal or fossorial life. There is strong evidence for independent adaptive radiations in each of the five transect areas, and species assemblages appear to be very old. The limited faunal interchange that has occurred among the regions sampled by the transects has been via lowland dispersal routes.

Introduction

A striking difference between the faunas of the paleotropics and neotropics is the unique presence of salamanders in the latter region (Darlington, 1957; Wake, 1970). Lungless salamanders of the family Plethodontidae are abundant and diverse in the New World tropics, especially in Mesoamerica, where over 100 species are known. Features of this group that may help to explain its unique success in tropical environments include the achievement of true terrestriality through loss of aquatic larvae, the adoption of a metabolically conservative way of life, and the evolutionary development of an extremely efficient, highly projectile tongue (Hanken et al., 1980).

Tulane Studies in Zoology and Botany, Supplementary Publication number 1, 1992. Manuscript revised May, 1991.

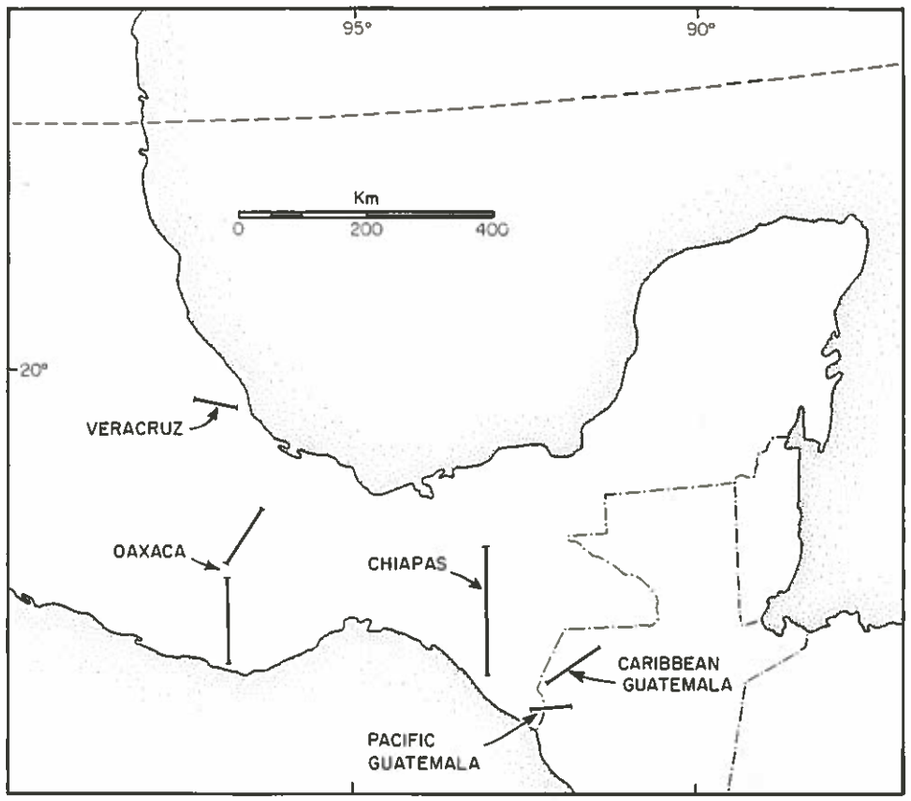

Figure 1. Location of Transects in Mexico and Guatemala.

For some years we have been studying the geographical ecology of Mesoamerican salamanders. In an earlier publication (Wake & Lynch, 1976) we identified three major foci of salamander diversity and abundance in Mesoamerica—the southeastern margins of the Mexican Plateau and adjacent uplands (our Mexican center), the mountainous core of Chiapas and western Guatemala (our Nuclear Central American center), and the mountains of Costa Rica and western Panama (our Talamancan center). In each area we have studied ecological and behavioral interactions of salamanders within local communities, as well as broader biogeographic, tectonic and phylogenetic relationships. We have concentrated on Guatemala (Lynch & Wake, 1975, 1978; Wake & Lynch, 1976, 1982; Elias, 1984), but have conducted field work throughout the Mesoamerican region (Wake, 1987; Papenfuss & Wake, 1987).

In this paper we present a preliminary summary of ongoing studies in Mexico and Guatemala. A general conclusion of Wake and Lynch (1976) was that in a given tropical region the salamander component of local communities was organized primarily on the basis of elevational zonation. Indeed, for western Guatemala we estimated that about three-fourths of the potential associations of species pairs are precluded by allopatric or parapatric elevational distributions.

This pattern, which stands in marked contrast to the broad sympatry often observed in extratropical salamanders, seemed to provide one possible mechanism for the seemingly paradoxical increase in numbers of species that this fundamentally Holarctic group has undergone in the tropics. Our present studies have as one goal the testing of our earlier hypothesis that elevational zonation is a major mechanism for maintaining high species diversity in tropical plethodontids. Because tropical salamanders tend to have specialized habitat requirements, combined with poor dispersal abilities, they should prove to be useful indicators of areas of potential special interest for other organisms. The present patterns of distribution and diversity of these salamanders are likely to have historical explanations that may apply to various other taxa as well.

Study Areas and Methods

We selected five areas for transect studies of salamander distribution (Figure 1) based on high topographic relief and the presence of high numbers of species and individuals. Two of the five areas are located near sites from which earlier workers had already reported data on elevational zonation (cf. Gadow, 1905, for Veracruz; Schmidt, 1936, for western Guatemala); the other three are in areas that were relatively or completely unstudied when we began our work.

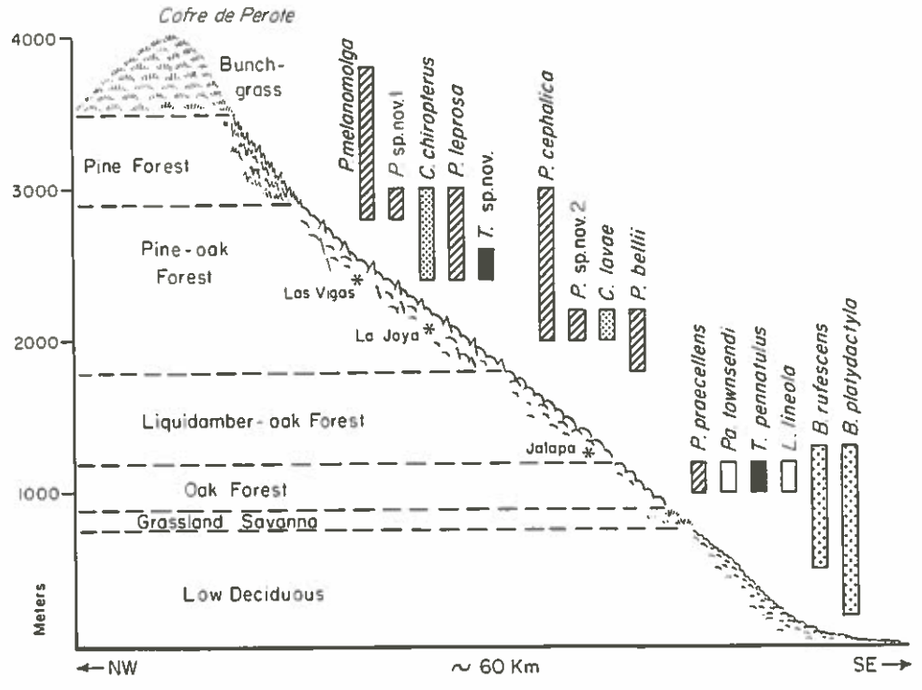

Figure 2. Veracruz transect. Abbreviations: B., *Bolitoglossa*; C., *Chiropterotriton*; L., *Lineatriton*; Pa., *Parvimolge*; P., *Pseudoeurycea*; T., *Thorius*.

The Veracruz transect extends eastward about 75 km from the vicinity of Cofre de Perote to the Gulf lowlands near the city of Veracruz, Mexico. This transect encompasses approximately 4000 m of elevation, and includes habitats that range from lowland deciduous forest through cloud forest and pine-oak forest to open bunchgrass.

The Oaxaca transect, the longest of the five, extends more than 200 km from the northern lowlands of Oaxaca across the continental divide to the Pacific Coast.

Our Chiapas transect extends northwest from Tapachula, on the Pacific Coastal Plain of Chiapas, Mexico, across the Sierra Madre, through the Grijalva Valley, then across the Central Plateau, before terminating in the lowlands of northern Chiapas. This transect is about 150 km long.

The Pacific Guatemala transect extends NE from the Pacific lowlands in the vicinity of Tapachula, Chiapas, Mexico, to the top of Volcan Tajumulco (elevation 4200 m), in western Guatemala. A great deal of information, much of it as yet unpublished, exists for this transect area, which was the site of intensive study for several years (Wake & Lynch, 1976). Since our earlier work we have extended the lower limits of this transect nearly to sea level, and its total length is now about 50 km.

The Caribbean Guatemala transect, a somewhat extended version of the area studied by Elias (1984), runs NE from the Sierra de Cuilco (elevation 3100 m) of western Guatemala to the Sierra de los Cuchumatanes (elevation 3200 m), and then into the northern foothills. It has a length of about 100 km.

The general rationale and methodology of our elevational studies have been outlined by Wake and Lynch (1976). The transects are strips of territory with a maximum width of approximately 10 km. We have used all available distributional information, including data and materials gathered by us, published records, and specimen data in major museums.

The vertical bars in our figures indicate the maximal known elevational range for each species on each major elevational gradient within a given transect. Although we have made repeated collections of most species, all of our transects contain species that are known from only a few individuals, and few species have been studied in sufficient detail to permit us to quantify abundance and distribution in great detail.

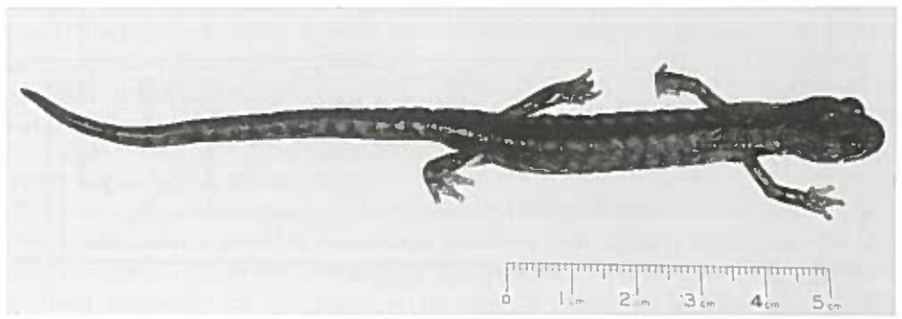

Figure 3. *Pseudoeurycea melanomolga* from Veracruz transect above Las Vigas.

The figures show only the most general vegetational associations, based on published data where available (e.g., Schmidt, 1936; Gómez-Pompa, 1973; Breedlove, 1973) and on our observations.

Results

A substantial degree of elevational zonation is indeed typical of rich salamander communities in the tropics, at least in Mesoamerica. In the following section each of the five transect studies will be examined in greater detail.

Veracruz (Transect One)—This area has suffered the greatest degree of habitat degradation as a result of human disturbance. Nevertheless, we have found 15 salamander species, three of them undescribed, along the transect (Figure 2).

An upland representative, *Pseudoeurycea melanomolga* (Figure 3), which occurs alone over the upper 500 m of the transect (3000-3500 m), strongly resembles its close relative *P. gadovii*, which reaches the highest elevation yet recorded for salamanders (over 5000 m), on nearby Volcan Orizaba (Swan, 1973). Both are relatively large, terrestrial salamanders that occur under rocks and logs, as well as in vertical banks and ledges. At about 3000 m, at the upper limits of pine-oak forest, a community of five species is encountered. Four of these are members of the genus *Pseudoeurycea*, a group of generalized, mainly terrestrial salamanders that is widespread in the highlands of Mexico and Guatemala. All five species are broadly sympatric, but show subtle differences in their habitat and microhabitat preferences. For example, *P. cephalica* is found under rocks and logs in more open areas whereas *P. leprosa* prefers rotting wood within heavy forest. The species also differ markedly in abundance. An undescribed species of *Pseudoeurycea* is uncommon, whereas *P. leprosa* is abundant, almost from its first

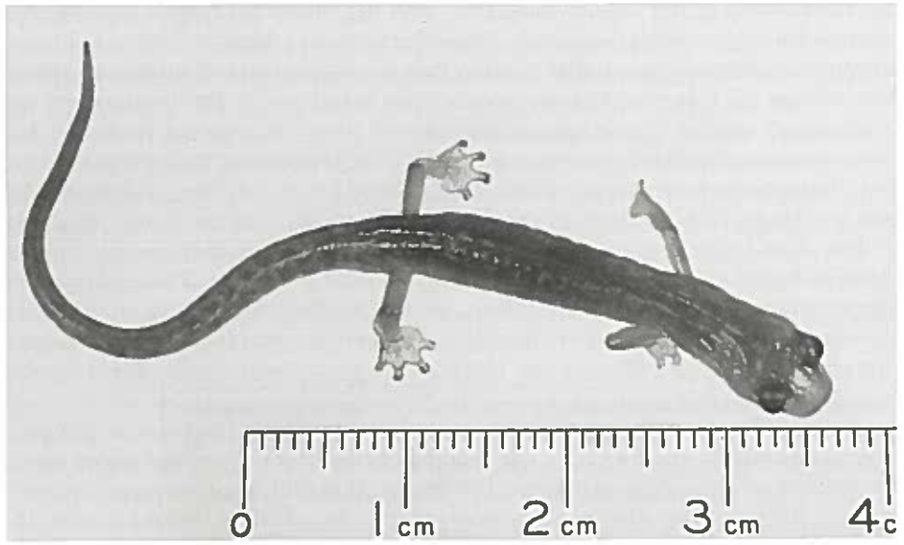

Figure 4. *Chiropterotriton lavae* from Veracruz transect at La Joya.

appearance on the transect. The most specialized ecologically of these five sympatric species is *Chiropterotriton chiropterus*, which in this region is found under the bark of logs and fallen branches.

In the vicinity of Las Vigas (elevation 2450 m), in a rich pine-oak forest, a somewhat different assemblage of four species is encountered. Two of the upland species of *Pseudoeurycea* (*P. melanomolga* and the undescribed species) have dropped out, and a diminutive, undescribed member of the terrestrial genus *Thorius* is locally abundant. Moving down the escarpment to the vicinity of the village of La Joya (elevation 2100 m), one encounters a different four-species community. The giant *P. bellii*, a highly terrestrial to fossorial species, is found here, together with the much smaller and also terrestrial *P. cephalica*. A third sympatric *Pseudoeurycea* is still smaller and more slender. This undescribed species appears to be a microhabitat specialist—it has been collected only inside rotting logs and under their loose bark. A more extreme microhabitat specialist—the bromeliad-dwelling *Chiropterotriton lavae* (Figure 4)—is the fourth member of this assemblage. The La Joya site is an especially interesting one; although it is highly modified by human activities, all four species can still be found in the backyards of local inhabitants.

The region below 1800 m has been extensively modified by human activities, and there are only a few steep canyons where present-day conditions approximate natural ones. There is a 500 m interval (1500-2000 m) on the transect from which we have not collected any salamanders, but we expect they persist in residual patches of habitat. Despite gaps in our information, we know that a substantial change in the salamander fauna occurs between La Joya and the vicinity of Jalapa (elevation 1400 m), where six species co-occur. *Pseudoeurycea praecellens*, a close relative of *P. cephalica*, is found in terrestrial situations. There are three diminutive species: the elongate burrowing *Lineatriton lineola* (Figure 5), the tiny terrestrial *Thorius pennatulus*, and the somewhat larger, terrestrial to semi-arboreal *Parvimolge townsendi*. These four species appear to have very limited elevational distributions in this vicinity: they are known only from a canyon near the village of Teocelo. The two remaining members of this community are widespread species whose ranges extend well into the adjacent lowlands, and for a considerable distance north and south of the Jalapa area. *Bolitoglossa rufescens* is a diminutive arboreal species with fully webbed hands and feet, and *B. platydactyla* is a large, fully webbed, long-tailed species of both arboreal and terrestrial habits. The latter species is unusually tolerant of human disturbance and has been collected in large numbers within the city limits of Jalapa. These two species are commonly encountered under banana leaf sheaths, a non-native microhabitat commonly used by lowland salamanders. We have no distributional information for elevations below 500 m at this latitude, but both species occur at sea level in southern Veracruz.

Oaxaca (Transect Two)—Some information concerning this transect was published recently (Wake, 1987), in the mistaken belief that the present paper would be published first. The northern 100 km of this 220 km transect (Figure 6) extend from the City of Oaxaca northward over two distinct upland masses, the mountains surrounding Cerro San Felipe, and, farther to the north, the Sierra de Juarez (represented by Cerro Pelon in Figure 6). The two massifs are separated

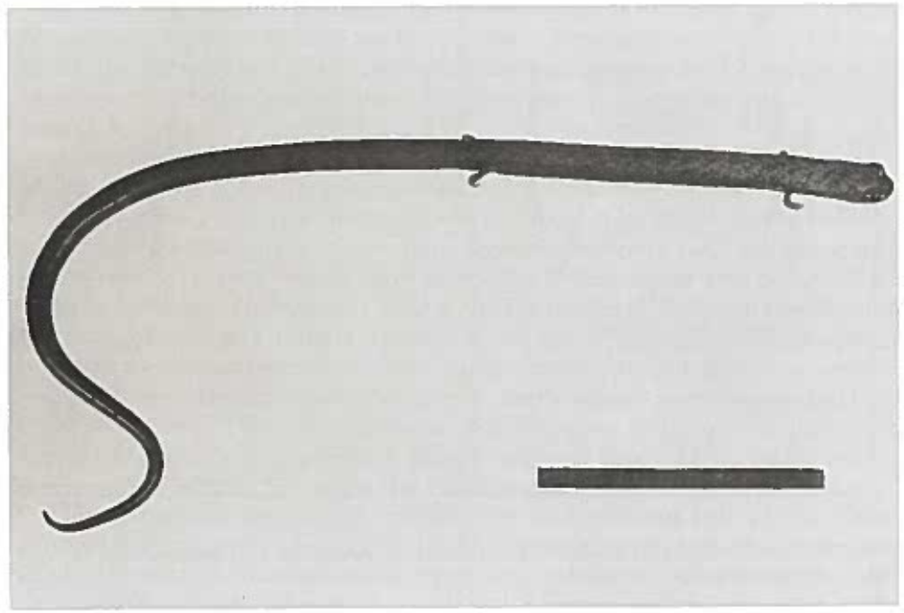

Figure 5. *Lineatriton lineola* from Barranca de San Miguel, Veracruz. Scale is equal to 25 mm.

by the subhumid valley of the Rio Grande. At least 19 species of salamanders occur along this northern half of the Oaxaca transect. From 2800 m to the top (3200 m) of Cerro San Felipe, three species co-occur: *Pseudoeurycea smithi, P. unguidentis*, and *Thorius narisovalis*. Two of the three species occur in a variety of terrestrial microhabitats (e.g., under and inside logs, under rocks, in crevices), but *P. unguidentis* is a microhabitat specialist that lives mainly under the bark of logs (Lynch et al., 1977). In the Sierra de Juarez there are 7 species above 2800 m, 3 of which are found mainly on the drier south-facing interior slopes, and four on the wetter Caribbean face. As on Cerro San Felipe, all are mainly terrestrial members either of the genera *Pseudoeurycea* or *Thorius*. Only two species (*P. smithi* and *P. bellii*) are shared between the Sierra de Juarez and Cerro San Felipe.

The interior of Oaxaca is drier than the coastal slopes; salamanders are scarce at elevations below 2800 m at inland localities, and apparently absent below 2000 m. However, on the humid Caribbean slope salamanders are found virtually to sea level (although our transect does not extend below 500 m). Some gaps on the Caribbean slope of our Oaxaca transect (for example, at around 2500 m, Figure 6) are doubtless collecting artifacts, but a substantial turnover in species occurs between 2800 m and 2000 m. At the latter elevation, an area of cloud forest, there are four species, two apparently undescribed, assignable to the genera *Thorius, Pseudoeurycea, Nototriton*, and *Chiropterotriton* (for more details concerning the *Thorius* from this area see Hanken, 1983; *Nototriton adelos* was described recently by Papenfuss & Wake, 1987, and *Pseudoeurycea saltator* by Lynch & Wake, 1989). All are microhabitat specialists and show arboreal tenden-

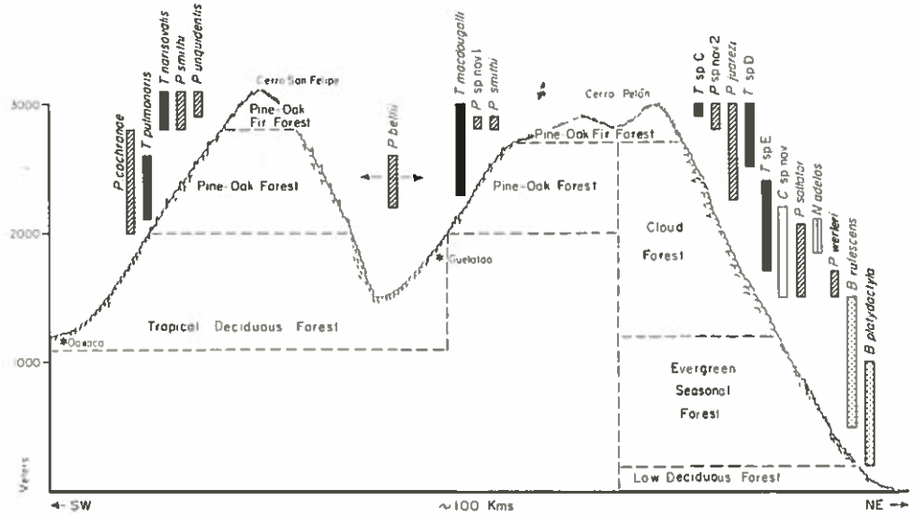

Figure 6. Northern Oaxaca transect. Abbreviations: B., *Bolitoglossa*; C., *Chiropterotriton*; N., *Nototriton*; P., *Pseudoeurycea*; T., *Thorius*.

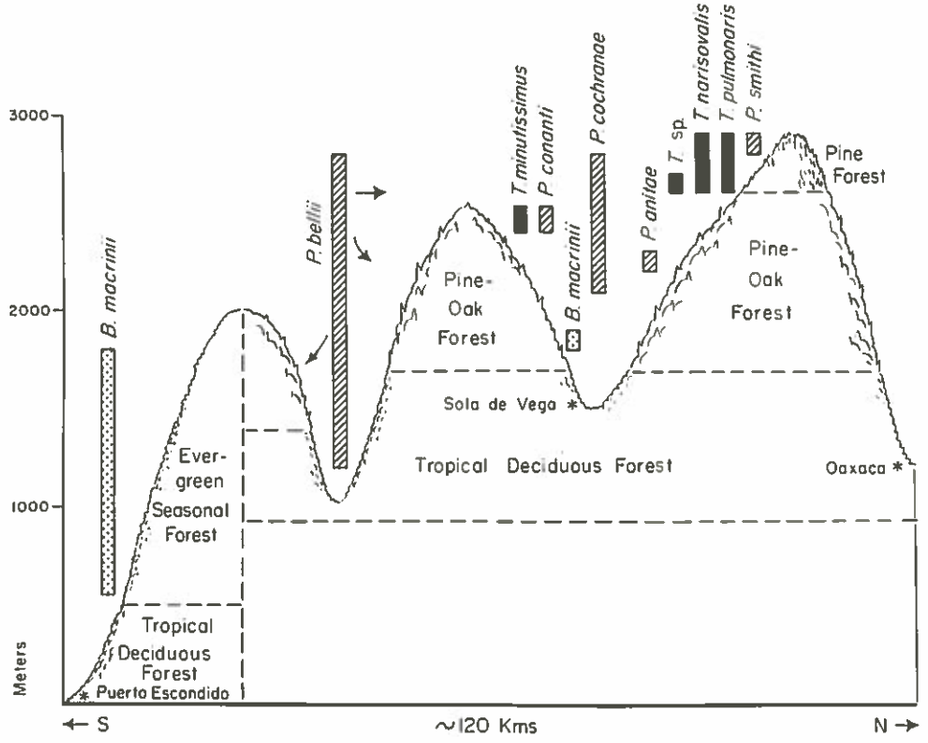

Figure 7. Southern Oaxaca transect. Abbreviations: B., *Bolitoglossa*; P., *Pseudoeurycea*; T., *Thorius*.

cies, occurring beneath the bark of fallen tree trunks or branches, and in arboreal bromeliads. At about 1400 m the uppermost representatives of the Gulf lowland fauna are encountered. Two arboreal *Bolitoglossa*, apparently conspecific with *B. rufescens* and *B. platydactyla* of the Veracruz transect, range from this level to the base of the transect.

We have less complete information concerning the southern (Pacific) segment of the Oaxaca transect (Figure 7). We found 10 species in this region, and we believe that few, if any, additional species remain to be discovered. The richest salamander community is at elevations around 2500 m in pine-oak forest south of the city of Oaxaca, where three species of *Pseudoeurycea* and two of *Thorius* occur in sympatry. We indicate (Figure 7) three species of *Thorius* at this elevation, but no more than two of these co-occur at any one place. As we move southward to lower elevations four of the five species drop out and four new ones are added. The maximum number of species that co-occur at any single site below 2500 m is three. The only species of *Bolitoglossa* on the southern part of the Oaxaca transect is *B. macrinii*, a mainly arboreal form whose range extends downward to at least 500 m on the Pacific versant (Papenfuss et al., 1983).

The most extreme habitat specialist on the southern half of the Oaxaca transect is *Pseudoeurycea anitae* (Figure 8), a species found only in a limited area of limestone caves. In contrast, the most widespread and generalized species on the transect is *P. bellii* (Figure 9), which occurs in generally lower and drier sites than most other species of *Pseudoeurycea*.

Chiapas (Transect Three)—There is little distributional information for salamanders from the subhumid central portion of this transect (Figure 10), but we have considerable data for the Pacific Slope of the Sierra Madre, the Central Plateau and its northern (Caribbean) slope. We record 15 species from the Chiapas transect, 7 from the southern and 8 from the northern parts. No species are shared between the two sections, but there are pairs of close relatives. For example, arboreal members of the *Bolitoglossa* alpha group (*Bolitoglossa flaviventris*, *B. mexicana*) and diminutive members of the arboreal *Bolitoglossa* beta group (*B. occidentalis*, *B. rufescens*) are present in each area.

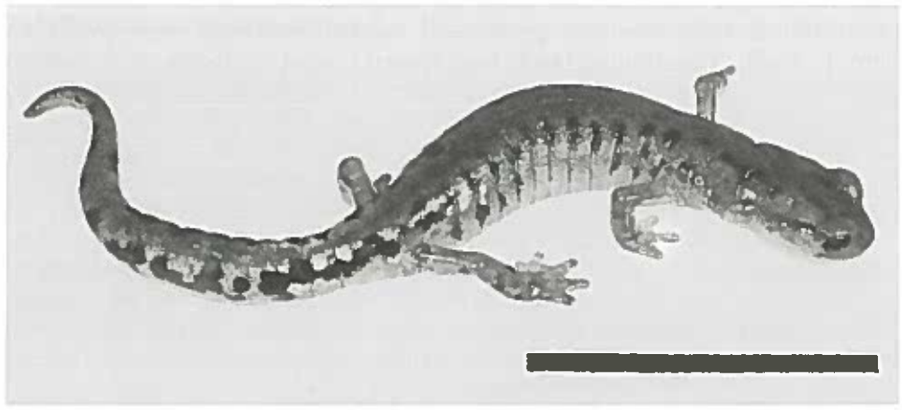

Figure 8. *Pseudoeurycea anitae* from San Vincente Lachixio, Oaxaca. Scale is equal to 25 mm.

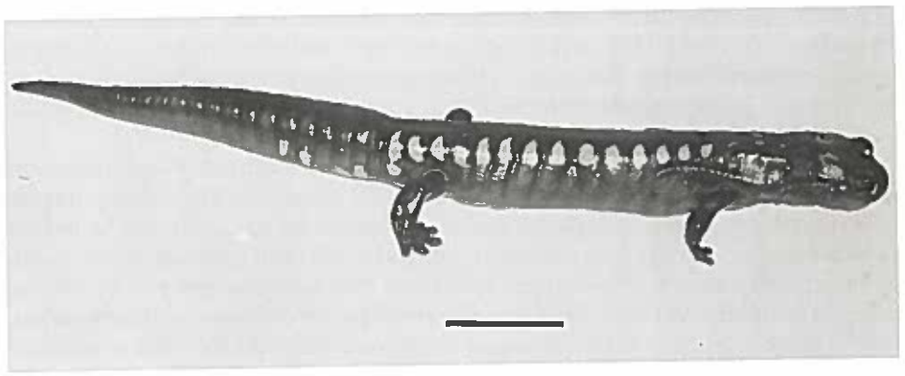

Figure 9. *Pseudoeurycea bellii* from Putla de Guerrero, Oaxaca. Scale is equal to 25 mm.

In the limited area above 2800 m in the Sierra Madre there are three species. Two of these (*P. brunnata* and *P. goebeli*) are members of the mainly terrestrial genus *Pseudoeurycea*, which we have come to expect at high elevations based on our observations in Veracruz and Oaxaca. However, the third species (*Bolitoglossa franklini*) belongs to a genus that is not part of the upland fauna north of the Isthmus of Tehuantepec. In cloud forest between 2500 m and 1600 m on the Pacific Slope there is a three-species community which includes largely arboreal forms: two relatively widely distributed *Bolitoglossa* (*B. franklini* and *B. engelhardti*), and an endemic, the diminutive bromeliad specialist, *Dendrotriton xolocalcae*. Only two species occur below 1600 m—the large arboreal *B. flaviventris* and the small arboreal *B. occidentalis*.

On the northern part of the Chiapas transect there are three species of *Bolitoglossa* (*B. lincolni*, *B. rostrata*, and *B. hartwegi*) all related to Guatemalan species. The rare *Nototriton alvarezdeltoroi* is found at the 2000 m level, just below the elevation where two highland forms disappear. *Bolitoglossa mexicana* (Figure 11) occurs from sea level to surprisingly high elevations (nearly 2000 m) in this area, and ranges nearly to sea level. At about 1000 m we find a strikingly specialized, recently described genus and species, *Ixalotriton niger* (Wake & Johnson, 1989). This shining black, long-legged species is capable of unusually rapid locomotion (including jumping), and lives on vertical surfaces, such as tree trunks and rock faces. *Bolitoglossa rufescens* appears slightly below this elevation and ranges down to the Gulf coastal plain. Finally, at about 300 m a highly specialized, elongate, burrowing member of the genus *Oedipina* appears. The lowland community also includes a large and a small species of *Bolitoglossa*.

Pacific Guatemala (Transect Four)—Major features of the salamanders of this transect have been described previously (Wake & Lynch, 1976) (Figure 12). We find 15 species here, as opposed to 7 on the analogous section of the nearby Chiapas transect. The higher species diversity probably reflects the greater extent of suitable upland habitat, especially cloud forest, and the direct continuity of the transect with the Guatemalan Plateau. Six of the seven species found on the Pacific Slope of transect three also occur on transect four; the seventh (*Dendrotriton xolocalcae*) is represented by a sister species (*D. bromeliacia*).

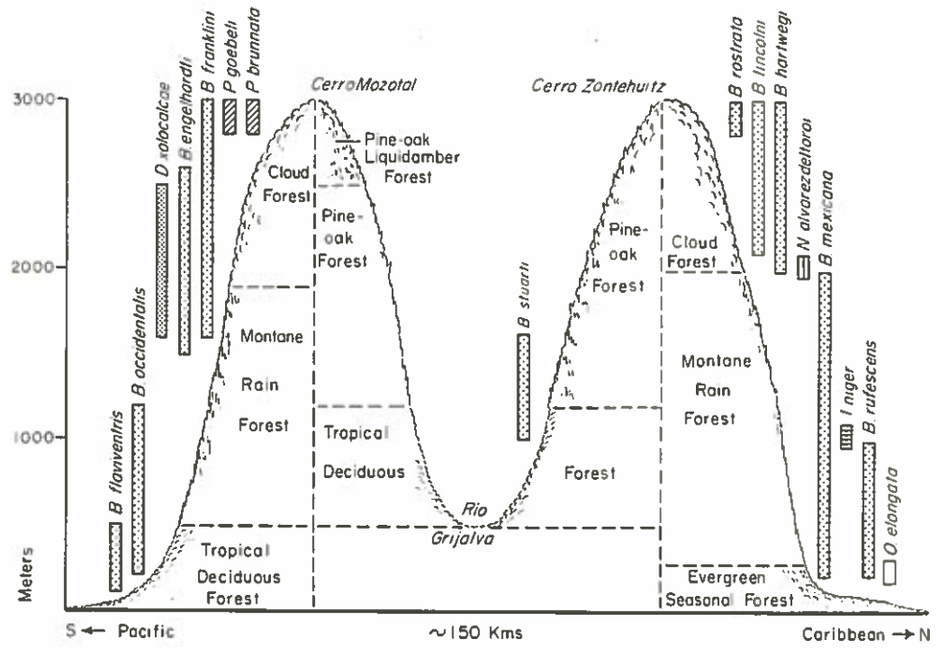

Figure 10. Chiapas transect. Abbreviations: B., *Bolitoglossa*; D., *Dendrotriton*; I., *Ixalotriton*; N., *Nototriton*; O., *Oedipina*; P., *Pseudoeurycea*.

Salamanders occur from 3900 m to sea level on this transect. Above 2900 m we find a two-species community of mainly terrestrial or log-dwelling forms—*Pseudoeurycea rex*, which occurs alone over an extensive elevational range (3200-3900 m), and *Bolitoglossa rostrata*, a species also present at the highest elevations of the Central Plateau of transect three. Between 2600 and 2800 m we find 8 species, but because of habitat and microhabitat differences no more than five of these are normally microsympatric (Wake & Lynch, 1976). Four species of *Pseudoeurycea* occur in this zone, but *P. rex* rarely occurs together with the other

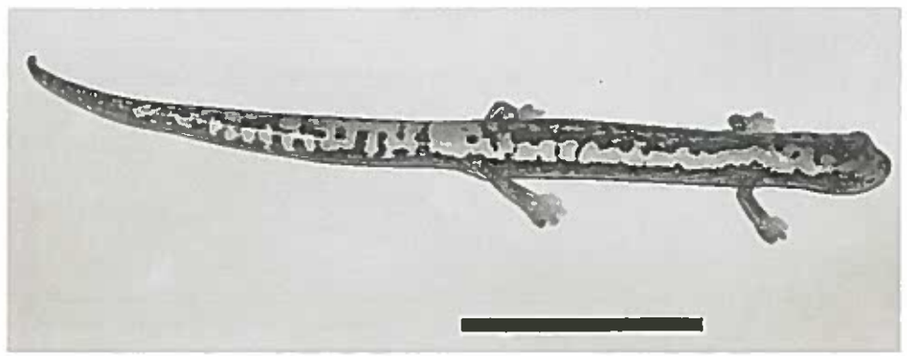

Figure 11. *Bolitoglossa mexicana* from vicinity of Tapilulua, Chiapas. Scale is equal to 25 mm.

three, which are microsympatric at somewhat lower elevations. There are also three *Bolitoglossa,* two of which (*B. lincolni, B. rostrata*) occur at high elevations on the northern part of transect three. The third (*B. morio*) is a widely distributed member of the fauna of the Guatemalan Plateau. The final species (*Dendrotriton bromeliacia*) is a diminutive bromeliad specialist.

A mid- to low-elevational cloud forest assemblage of four species occurs together over an elevational range of about 400 m (1700-2100 m). This group includes the above-mentioned *Dendrotriton* and three species of *Bolitoglossa* (*B. flavimembris, B. engelhardti, B. franklini*), two of which also occur on the Pacific Slope of transect three.

There is an abrupt faunal break near the base of the cloud forest (about 1600 m), below which different species with marked microhabitat and morphological specializations occur. At 1000 m three species coexist: the large arboreal *Bolitoglossa salvinii* (a *Bolitoglossa* alpha), the small arboreal *B. occidentalis* (a *Bolitogossa* beta), and an elongate, burrowing member of the genus *Oedipina* (Figure 13). At the lowest elevations on this transect we find only *B. flaviventris*, another member of the alpha-group.

Caribbean Guatemala (Transect Five)—We have little to add to the review of this region by Elias (1984). This transect can be considered a northeastward continuation of transect four. There are about 15 species of salamanders on this

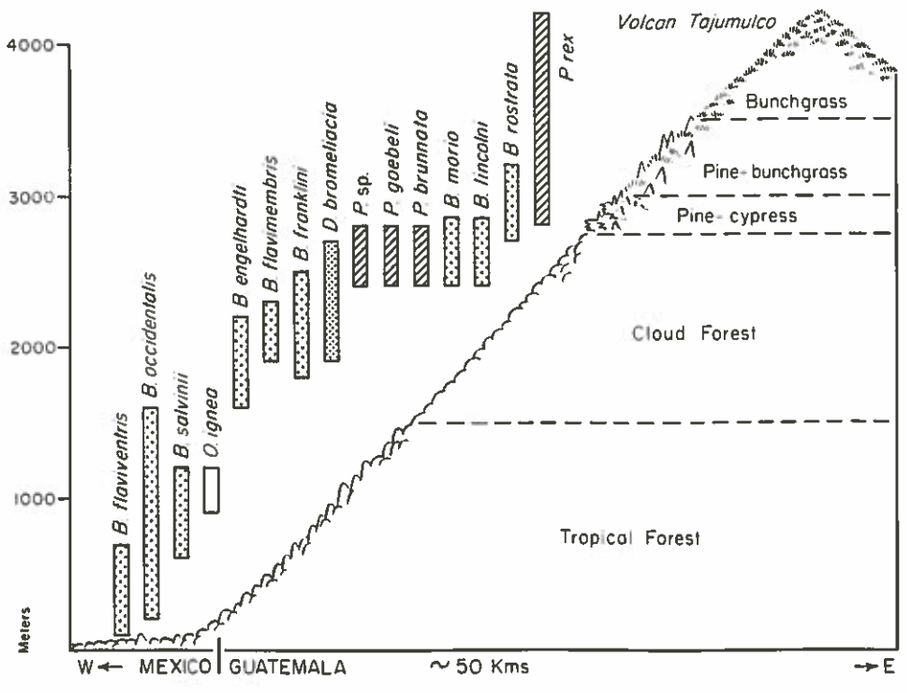

Figure 12. Pacific Guatemala transect. Abbreviations: B., *Bolitoglossa*; D., *Dendrotriton*; O., *Oedipina*; P., *Pseudoeurycea*.

transect (Figure 14), the same as on transects one and four, but the level of generic diversification (five genera) on transect five is exceeded only by the six genera that occur on the Veracruz transect.

Pseudoeurycea rex is found at elevations above 3000 m in both the Cuilcos and the Cuchumatanes. The Cuilcos, a small and isolated range, are relatively depauperate, with only four species of salamanders. Maximum local diversity is seen at about 2600 m where three species co-occur: *Bolitoglossa morio* and *B. lincolni* (both present on transect four), and *Dendrotriton rabbi* (which has sister species on transects three and four). No species occurs below 2000 m, but *B. stuarti* is known from the general vicinity and might be expected between 1600 and 2000 m.

In the Cuchumatanes there is a rich salamander fauna consisting of 13 species. At the 3000 m level both *Pseudoeurycea rex* and *Bolitoglossa rostrata* are abundant in terrestrial and rotten-log microhabitats. Below this point we have only fragmentary information. There are two species of *Dendrotriton,* one of which (*D. rabbi*) also occurs in the Cuilcos, but they are not sympatric. Four species of *Bolitoglossa* occur between 2000 and 2500 m. One of these (*B. morio*), also is present on transect four, while another (*B. lincolni*) is present in the Cuilcos and on transects three and four (cf. Wake & Lynch, 1982). The other two species of *Bolitoglossa* have unexpectedly great elevational ranges and may be taxonomic composites. One is referred to *B. hartwegi*, a species present at higher elevations on the inner portion of transect three. The other, *B. cuchumatana*, is a regional endemic.

Cloud forest vegetation extends to lower elevations on the Atlantic slopes of the Cuchumatantes (ca. 1000 m) than on the Pacific versant of transect four (ca. 1500 m), and six species occur in the area just above the cloud line in the Cuchumatantes. Five of these (*Bolitoglossa hartwegi, B. cuchumatana, B. jacksoni, Bradytriton silus, Nyctanolis pernix*) are essentially sympatric, and all six are habitat specialists. The four *Bolitoglossa* have extensively webbed feet, and are arboreal, semi-arboreal or log-dwelling in habit. Both *B. jacksoni* and *B. mulleri* belong to the *Bolitoglossa* alpha complex; the other two species of *Bolitoglossa* are members

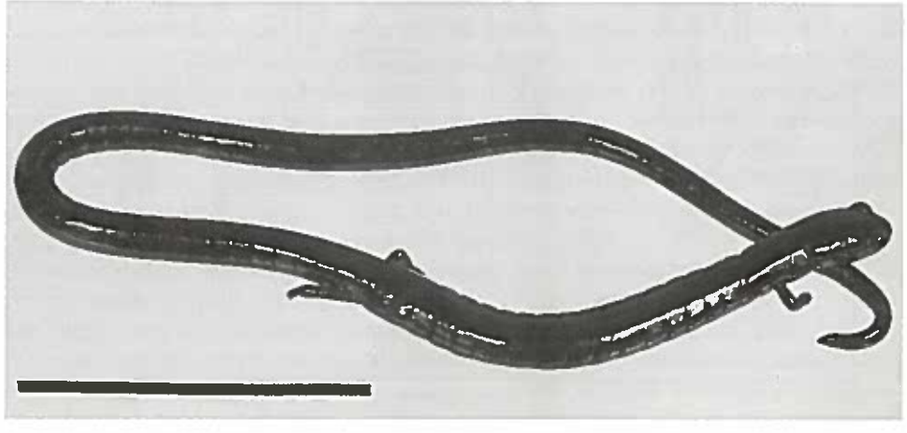

Figure 13. *Oedipina ignea* from Finca Santa Julia, San Marcos, Guatemala. Scale is equal to 25 mm.

of the beta complex. Both the terrestrial *Bradytriton* and the scansorial *Nyctanolis* are members of monotypic genera that were discovered by Elias (Elias & Wake, 1983; Wake & Elias, 1983), and appear to have very limited distributions. The final species on transect five is the widely distributed *Bolitoglossa rufescens*, which is found below 1000 m. Additional field work at low elevations doubtless would reveal the presence of a lowland member of the large *Bolitoglossa* alpha group (probably the widely distributed *B. mexicana*), and an elongate burrowing member of *Oedipina* (possibly *O. ignea*).

Discussion

Data from four additional transects support the major generalizations presented by Wake and Lynch (1976) concerning the nature of tropical salamander communities. There is well-developed elevational zonation of the species on all of these areas. Most species at intermediate elevations have relatively limited elevational, as well as geographic, distributions. The species that occur at high elevations often have both great elevational ranges and relatively broad geographic distributions, and they are among the most terrestrial of the tropical salamanders. In these features they resemble terrestrial extratropical plethodontids (e.g., *Plethodon, Ensatina*) more than do any other tropical forms.

The richest local communities in any given region occur at middle to high elevations, in areas of high topographic diversity. Usually these are humid mountains that support cloud forest vegetation or similar wet forest. In general, then, optimal habitat for tropical salamanders in northern Mesoamerica is wet montane evergreen forests at elevations between 1000 m and 2800 m.

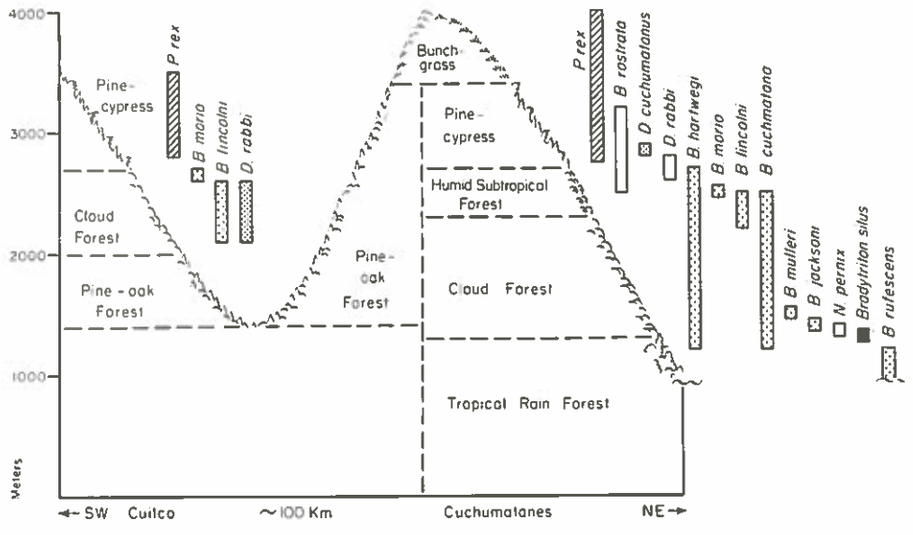

Figure 14. Caribbean Guatemala transect. Abbreviations: B., *Bolitoglossa*; D., *Dendrotriton*; N., *Nyctanolis*; P., *Pseudoeurycea*.

In the richest local salamander communities, distinct morphological and microhabit differences separate most locally sympatric forms. The commonest modes of segregation are vertical position (fossorial, terrestrial, crevice- or bark-dwelling, arboreal), although body size (implying feeding differences) is also important. In the lowlands, arboreal and highly fossorial species predominate. Log-dwelling, crevice- and log-inhabiting, and bromeliad-dwelling forms are commonest at mid-elevations, and fully terrestrial forms (under-log or under-rock) are mainly found at the highest elevations.

There are some distinct phylogenetic-geographic correlates of community composition. Members of the genus *Pseudoeurycea* generally occur in terrestrial habitats at high elevations, and tend to be most diverse north of the Isthmus of Tehuantepec. Local and regional endemics are usually found in cloud forest, and are often microhabitat specialists as well. Lowland communities in these regions typically contain at least one large species of *Bolitoglossa* alpha (a mainly southern group) and one small species of *Bolitoglossa* beta.

We continue to be surprised by the high diversity of tropical salamanders in Mesoamerica. Our studies have disclosed numerous previously undetected taxa including undescribed genera. Even in such relatively well-known areas as Veracruz we have found undescribed species. Recent work (Elias & Wake, 1983; Wake & Elias, 1983; Elias, 1984; Papenfuss & Wake, 1987; Wake, 1987) has revealed that Nuclear Central America is a major center for salamander diversity, and has suggested that it may be a refugium where members of several relatively ancient lineages have persisted into the present time.

Broad outlines of relationships have begun to take form (Wake & Elias, 1983) but many uncertainties remain, in part because of the continued discovery of novelties, but also because of the very extensive morphological and ecological convergence that appears to have characterized the phylogeny of tropical salamanders. Biochemical and immunological studies (e.g., Maxson & Wake, 1981; Larson, 1984) will be crucial in unraveling the phylogeny of this complex group. It is already clear, however, that, except for the nearby transects three and four, there has been relatively little interchange of species among the regions studied. For example, there are two endemic genera on our Caribbean Guatemalan transect that do not occur on the two nearby Pacific-slope transects. Except for a few widely distributed lowland forms, there are few species shared between any of the transects except three and four. Published (Wake & Lynch, 1982) and unpublished work indicates that populations of several of these shared species (e.g., *Pseudoeurycea bellii, Bolitoglossa rostrata*) are deeply differentiated from one another genetically. Species in the lowlands do tend to have broader distributions than do upland ones, but these species, too, show unexpectedly deep genetic differentiation regionally (Larson, 1983).

Salamanders appear to be exceptionally good biogeographic indicators, as recognized long ago by Stuart (1950). Biochemical data suggest that extant species are often very old. Because salamanders have such low vagility, they tend to disperse little, even over geological periods of time. They are capable of maintaining relatively high population densities, and can survive extreme degrees of regional habitat modification, as long as small pockets of natural habitat (or suitable artificial substitutes) remain available.

ACKNOWLEDGMENTS

Many individuals have provided assistance in the field, or with data or specimens. In addition to those acknowledged in Wake & Lynch (1976), we thank J. Campbell, C. Ceron, M. Ceron, D. Darda, P. Elias, M. Feder, J. Hanken, E. Koford, J. Johnson, R. Seib, S. Sessions, H. B. Shaffer, and T. A. Wake. In addition to the institutions previously acknowledged we thank the curators of the Vertebrate Collection of the University of Texas at Arlington. We especially thank officials associated with the Direccion General de la Fauna Silvestre (Mexico) and INAFOR (Guatemala) for providing collecting permits. Illustrations were prepared by Gene M. Christman and photography is by J. Hendel, of the Scientific Photographic Laboratory of this university. This research has been supported by grants from the National Science Foundation (current grant BSR86-19630), the Annie M. Alexander fund of the Museum of Vertebrate Zoology, and the Center for Latin American Studies of the Berkeley campus.

LITERATURE CITED

BREEDLOVE, D. E. The phytogeography and vegetation of Chiapas (Mexico). *In* A. Graham, ed. Vegetation and Vegetational History of Northern Latin America, Chap. 5, pp. 149-165. Elsevier Scientific Publishing Co., Amsterdam.

DARLINGTON, P. J., JR. Zoogeography: The Geographical Distribution of Animals. John Wiley and Sons, New York.

ELIAS, P. 1984. Salamanders of the northwestern highlands of Guatemala. Contrib. Sci. Mus. Nat. Hist. Los Angeles Co. 348: 1-20.

ELIAS, P. & D. B. WAKE. 1983. *Nyctanolis pernix*, a new genus and species of plethodontid salamander from northwestern Guatemala and Chiapas, Mexico. *In* A. G. J. Rhodin & K. Miyata, eds. Advances in Herpetology and Evolutionary Biology: Essays in Honor of Ernest E. Williams, pp. 1-12. Mus. Comp. Zool., Cambridge, Mass.

GADOW, H. 1905. The distribution of Mexican amphibians and reptiles. Proc. Zool. Soc. London 2: 191-244.

GOMEZ-POMPA, A. 1973. Ecology of the vegetation of Veracruz. *In* A. Graham, ed. Vegetation and Vegetational History of Northern Latin America, Chap. 4, pp. 73-148. Elsevier Scientific Publishing Co., Amsterdam.

HANKEN, J. 1983. Genetic variation in a dwarfed lineage, the Mexican salamander genus *Thorius* (Amphibia: Plethodontidae): taxonomic, ecologic and evolutionary implications. Copeia 1983: 1051-1073.

HANKEN, J., J. F. LYNCH, & D. B. WAKE. 1980. Salamander invasion of the tropics. Nat. Hist. 89(12): 46-53.

LARSON, A. 1983. A molecular phylogenetic perspective on the origins of a lowland tropical salamander fauna. I. Phylogenetic inferences from protein comparisons. Herpetologica 39: 85-99.

———. 1984. Neontological inferences of evolutionary pattern and process in the salamander family Plethodontidae. *In* M. K. Hecht, B. Wallace, & G. T. Prance, eds. Evolutionary Biology, Vol. 17, Chap. 4, pp. 119-217. Plenum Publ. Corp., New York.

LYNCH, J. F. & D. B. WAKE. 1975. Systematics of the *Chiropterotriton bromeliacea* group (Amphibia: Caudata), with description of two new species from Guatemala. Contrib. Sci. Mus. Nat. Hist. Los Angeles Co. 265: 1-45.

———. 1978. A new species of *Chiropterotriton* (Amphibia: Caudata) from Baja Verapaz, Guatemala, with comments on relationships among Central American members of the genus. Contrib. Sci. Mus. Nat. Hist. Los Angeles Co. 194: 1-22.

———. 1989. Two new species of *Pseudoeurycea* (Amphibia: Caudata) from Oaxaca, Mexico. Contrib. Sci. Mus. Nat. Hist. Los Angeles Co. 411: 11-22.

LYNCH, J. F., S. Y. YANG, & T. J. PAPENFUSS. 1977. Studies of neotropical salamanders of the genus *Pseudoeurycea*, I: Systematic status of *Pseudoeurycea unguidentis*. Herpetologica 33: 46-52.

MAXSON, L. R. & D. B. WAKE. 1981. Albumin evolution and its phylogenetic implications in the plethodontid salamander genera *Pseudoeurycea* and *Chiropterotriton*. Herpetologica 37: 109-117.

PAPENFUSS, T. J. & D. B. WAKE. 1987. Two new species of plethodontid salamanders (genus *Nototriton*) from Mexico. Acta Zool. Mex. n.s. 21: 1-16.

PAPENFUSS, T. J., D. B. WAKE, & K. ADLER. 1983. Salamanders of the genus *Bolitoglossa* from the Sierra Madre del Sur of southern Mexico. J. Herp. 17: 295-307.

SCHMIDT, K. P. 1936. Guatemalan salamanders of the genus *Oedipus*. Zool. Ser. Field Mus. Nat. Hist. 322: 15-22.

STUART, L. C. 1950. A geographic study of the herpetofauna of Alta Verapaz, Guatemala. Contrib. Lab. Vert. Biol. Univ. Michigan 45: 1-77.

SWAN, L. 1973. Star Mountain of Mexico. Pacific Discovery 26: 1-9.

WAKE, D. B. 1970. The abundance of diversity of tropical salamanders. Am. Nat. 104: 211-213.

———. 1987. Adaptive radiation of salamanders in Middle American cloud forests. Ann. Missouri Bot. Gard. 74: 242-264.

WAKE, D. B. & P. ELIAS. 1983. New genera and a new species of Central American salamanders, with a review of the tropical genera (Amphibia, Caudata, Plethodontidae). Contrib. Sci. Mus. Nat. Hist. Los Angeles Co. 345: 19.

WAKE, D. B. & J. D. JOHNSON. 1989. A new genus and species of plethodontid salamander from Chiapas, Mexico. Contrib. Sci. Mus. Nat. Hist. Los Angeles Co. 411: 1-10.

WAKE, D. B. & J. F. LYNCH. 1976. The distribution, ecology, and evolutionary history of plethodontid salamanders in tropical America. Bull. Los Angeles Co. Mus. Nat. Hist. Vol. 25.

———. 1982. Evolutionary relationships among Central American salamanders of the *Bolitoglossa franklini* group, with a description of a new species from Guatemala. Herpetologica 38: 257-272.