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A NEW GENUS AND SPECIES OF PLETHODONTID  
SALAMANDER FROM CHIAPAS, MEXICO

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DAVID B. WAKE AND JERRY D. JOHNSON

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TWO NEW SPECIES OF *PSEUDOEURYCEA*  
(AMPHIBIA: CAUDATA) FROM OAXACA, MEXICO

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JAMES F. LYNCH AND DAVID B. WAKE

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# A NEW GENUS AND SPECIES OF PLETHODONTID SALAMANDER FROM CHIAPAS, MEXICO

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DAVID B. WAKE<sup>1</sup> AND JERRY D. JOHNSON<sup>2</sup>

**ABSTRACT.** A new species of plethodontid salamander from the mountains of northern Chiapas, Mexico, is so distinct from all described species that it is placed in a new genus. This taxon, *Ixalotriton niger*, is known only from a small patch of cloud forest near Berriozábal, Chiapas. This slender, active, scansorial species has very long arms, legs, and digits, and it has broadly expanded terminal phalanges that have hook-like processes. The tail is long and slender. All specimens are nearly uniformly black. The only species that resembles the new species in morphology is *Nyctanolis pernix*, another long-legged, slender, scansorial form from nuclear Central America. However, *Nyctanolis* differs from all other tropical genera, including *Ixalotriton*, in having divided premaxillary bones, an ancestral trait. In most osteological characters *Ixalotriton* resembles members of *Pseudoeurycea*, a group thought to be paraphyletic. The habitat of the new genus is rapidly disappearing and immediate conservation measures are required if this novel species is to survive.

**RESUMEN.** Una nueva especie de salamandra plethodóntida de las montañas del norte de Chiapas, México, es tan diferente de todas las descritas que se la coloca en un nuevo género. Este taxon, *Ixalotriton niger*, se conoce solamente de una pequeña área de bosque nublado cerca de Berriozábal, Chiapas. Esta especie es elongada, activa y trepadora, posee miembros anteriores y posteriores y dígitos largos, y falanges terminales ensanchadas con procesos en forma de gancho. La cola es larga y fina. Todos los ejemplares son casi uniformemente negros. La única especie que se le asemeja en morfología es *Nyctanolis pernix*, otra salamandra elongada de patas largas y trepadora de América Central. Sin embargo, *Nyctanolis*, a diferencia de todos los demás géneros tropicales, incluyendo *Ixalotriton*, posee huesos premaxilares divididos, un rasgo ancestral. En la mayoría de los caracteres osteológicos *Ixalotriton* se parece a *Pseudoeurycea*, un grupo considerado parafilético. El habitat de este nuevo género está desapareciendo rápidamente, y se requieren medidas de conservación inmediatas para que esta nueva especie sobreviva.

## INTRODUCTION

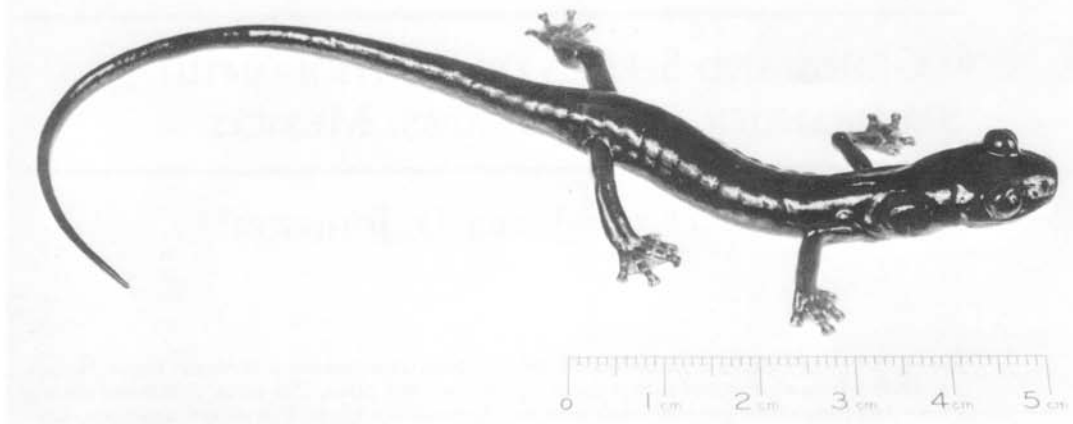
In January, 1973, J.D. Johnson collected a series of highly active, arboreal salamanders in a humid forest in northwestern Chiapas, Mexico. Subsequent visits to this area have resulted in additional specimens, but despite a substantial amount of field-work the species has not been found elsewhere. Upon examining preserved specimens in 1973, D.B. Wake recognized that they represented a distinct species. During the intervening years we have sought to determine the most appropriate genus in which to place this species. Wake and Lynch (1976, Appendix) referred this undescribed species to *Chi-*

*ropterotriton* beta. Subsequently, the beta species group was divided and the species were assigned to two new genera (*Dendrotriton* and *Nototriton* Wake and Elias, 1983), and the new species did not fit well into either of them. At a later date a superficially similar species was discovered in Chiapas and adjacent Guatemala, and for a time we thought that these two species formed a natural group. However, detailed anatomical study revealed that the second species (placed in a new genus, *Nyctanolis* Elias and Wake, 1983) differed from all tropical salamanders in having paired premaxillary bones, a character considered to be of significant cladistic importance (Wake, 1966; Wake and Larson, 1987). At this point it became evident that among currently recognized genera only *Pseudoeurycea* could possibly accommodate this new taxon. However, *Pseudoeurycea* contains a diverse group of species and is suspected to be paraphyletic (Wake and Elias, 1983). To add this unique new taxon to such a heterogeneous conglomerate would be both inappropriate and uninformative. The new taxon and *Pseudoeurycea* share no unique synapomorphies.

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1. Department of Zoology and Museum of Vertebrate Zoology, University of California, Berkeley, California 94720; Research Associate in Herpetology, Natural History Museum of Los Angeles County, Los Angeles, California 90007.

2. Department of Biology, El Paso Community College, El Paso, Texas 79998, and Department of Biological Sciences, University of Texas at El Paso, El Paso, Texas 79968.



**Figure 1.** Photograph of a live *Ixalotriton niger* new genus, new species, MVZ 158822, collected at the type-locality. This individual has a parasite-induced tumor on the side of the neck.

Accordingly, we have chosen to place this unique new species in a new genus.

### *Ixalotriton* new genus

**TYPE-SPECIES.** *Ixalotriton niger* new species.

**DIAGNOSIS.** A genus of plethodontid salamanders belonging to the subfamily Plethodontinae, tribe Bolitoglossini, supergenus *Bolitoglossa*. Members of *Ixalotriton* are relatively large, with long legs, fingers, toes, and tails. The genus differs from the only similar taxon, the stouter *Nyctanolis*, in having a single premaxillary bone and in lacking any dorsal markings on its solid black ground color. No other tropical salamanders have such long legs or large hands and feet (when adpressed to the body the legs overlap for 2 to more than 4 costal interspaces). In addition, *Ixalotriton* differs from *Chirotrotitron* in lacking septomaxillary bones and having a fifth metatarsal smaller than the fourth, and from *Bolitoglossa* in having a sublingual fold. *Ixalotriton* is most similar to *Pseudoeurycea* in osteology but differs from all members of that genus in having very long limbs, digits, and tail. The new genus differs from all other members of the supergenus *Bolitoglossa* by the combination of its large size, generalized osteological structure, and long limbs, digits, and tail.

**ETYMOLOGY.** From *ixalos*, Greek, meaning bounding or springing, in reference to its behavior; and *triton*, Greek, a commonly used term for salamanders. The gender is masculine.

### *Ixalotriton niger* new species

Figures 1–4

**HOLOTYPE.** Museum of Vertebrate Zoology (MVZ) 158823, an adult female from 12 km (7.5 mi) NW Berriozábal, Chiapas, Mexico, elevation

ca. 1,068 m, collected on December 26, 1980, by Jerry D. Johnson.

**PARATYPES.** MVZ 143837–38, 158822, 160952–58, 160960–63, 184891–92 (cleared and stained); Natural History Museum of Los Angeles County (LACM) 137512; Laboratory for Environmental Biology, University of Texas at El Paso (UTEP) 5796–98; same locality data as holotype, collected on different dates.

**DIAGNOSIS (measurements in millimeters).** See Generic Diagnosis. A large, slender species (standard length, SL, of ten adult males 53.2–59.7, mean 56.6; nine adult females 51.1–58.9, mean 54.4) with a long, strongly tapered, slender tail (SL/tail length of six adult males 0.64–0.74, mean 0.68; seven adult females 0.7–0.88, mean 0.76) and long limbs and digits (when adpressed to the sides of the trunk the fore and hind limbs overlap for 2.5 to more than 4, mean 3.7, costal grooves in ten adult males, and 2 to 4, mean 3, in nine adult females). The head is broad and flat (SL/head width of ten adult males 5.8–6.2, mean 6.0; nine adult females 5.9–6.8, mean 6.4). There are large numbers of very small premaxillary–maxillary (ten adult males have left plus right totals of 78–150, mean 120; nine adult females have 110–143, mean 125) and vomerine (ten adult males have left plus right totals of 31–47, mean 40; nine adult females have 37–52, mean 42) teeth. Coloration of the species is distinctive—all specimens are a solid, glossy black by day (becoming brown by night), with a little white pigment in the snout region and red-tinted (probably from the dense capillary beds) toe tips.

**DESCRIPTION.** This is a moderately large, slender species with a broad, depressed head and large, strongly protuberant, prominent eyes (Fig. 1). The snout is rather long and broad, and is strongly flattened. The nostrils and white-tipped nasolabial protuberances are small in both sexes, but more broad-

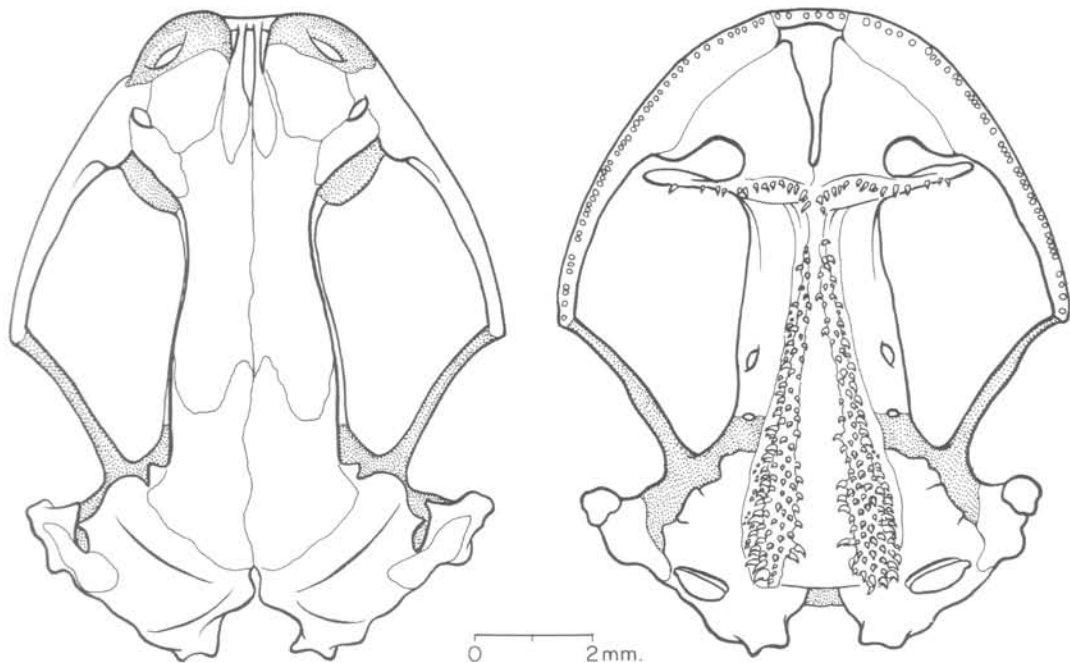


Figure 2. Dorsal and ventral views of the skull of *Ixalotriton niger* new genus new species, MVZ 184892. Cartilage is stippled.

ly based and pronounced in the males. Snouts of both sexes are similar, and there is only a moderate extension anteriorly beyond the tip of the lower jaw. All males have a round mental gland that, while prominent, never has a diameter more than about one-third the width of the head. The broad, flattened head is much broader than any other part of the body. The ratio of maximum head width to head depth at the angle of the jaw generally exceeds 3. An unpigmented groove extends below the anterior and middle parts of the eye, following its curvature, but this groove does not communicate with the lip. The large eyes stand out prominently above the head, but they extend only slightly, if at all, beyond its lateral margins. A weakly defined postorbital groove extends posteriorly from behind the eye as a shallow depression which meets the upper end of the nuchal groove. The nuchal groove proceeds ventrally at the angle of the lower jaw and proceeds across the gular region, at first as a well-marked groove and then as an indistinct slight depression. The small vomerine teeth are arranged in a long series that is a flattened curve lying almost perpendicular to the midline. The series curves slightly posteriorly at the lateral end, and there is a sharp bend near the midline where the series ends by becoming directed toward the posterior vomerine tooth patch. The tooth series extends well beyond the lateral margin of the internal naris. Medially the two series do not come into contact, and there is a small gap between the posteromedial end of the series and the posterior patch. The patch is similar to that which occurs in other members of

the supergenus *Bolitoglossa*, being shaped like an inverted teardrop. It is bilaterally symmetrical and each half contains in excess of 75 tiny teeth. The result is a large shagreen-like surface on the roof of the mouth that extends posteriorly, beyond the glottis, into a kind of pouch. Maxillary and premaxillary teeth are numerous. The maxillary teeth extend posteriorly in a long series that ends at approximately the level of the posterior margin of the opening for the eye. The maxillary and premaxillary teeth are similar in size and morphology, and there is no evident break in the series on adjacent bones. Both premaxillary and maxillary teeth are small. The premaxillary teeth are relatively few—six in each of the cleared and stained animals. The premaxillary teeth of males are usually not differentiated from maxillary teeth, or from premaxillary teeth of females; but in some of the males, including one of the cleared and stained animals, the premaxillary teeth can be large. In the cleared and stained animal there are six teeth on the premaxillary bone and three of them are large. The middle tooth is exceptionally long, over five times the length of the typical crown, and it is moncuspid, with the labial cusp apparently absent. The tongue pad is nearly round and lies at the end of a distinct pedicel. There is no anterior attachment, and the tongue has the boletoid form characteristic of the supergenus *Bolitoglossa*. A large, fleshy sublingual fold is present.

The trunk and tail of this species are slender and cylindrical. There is a distinctly shortened segment at the base of the tail, which is slightly constricted

at this point, but the tail can also be autotomized distally. The tails are very long, slender, and strongly tapered, becoming very narrow and whip-like near the tip. The postiliac spot is distinct in some individuals and indistinct in others. The limbs are extremely long. The hands and feet are large, with long digits. The limb segments are exceptionally long and slender. There is a moderate amount of webbing at the base of the digits. The webbing extends to the level of about the middle of the first phalanx of the longest digit of both hands and feet. All but the first digit of both hands and feet have broadly expanded, flattened tips. The fingers are, in order of decreasing length, 3,4,2,1; the toes, 3,4,2-5,1.

**MEASUREMENTS OF THE HOLOTYPE** (in millimeters). Head width 8.6; snout to gular fold (head length) 13.2; head depth at posterior angle of jaw 3.5; eyelid length 3.8; eyelid width 2.0; anterior rim of orbit to snout 3.3; horizontal orbit diameter 3.4; interorbital distance 2.7; distance between vomerine teeth and parasphenoid tooth patch 0.5; snout to forelimb 16.8; distance separating internal nares 3.0; distance separating external nares 3.0; snout projection beyond mandible 0.8; snout to posterior angle of vent (SL) 58.2; snout to anterior angle of vent 53.8; axilla to groin 31.0; tail length 81.6; tail width at base 3.2; tail depth at base 3.8; forelimb length (to tip of longest toe) 18.2; hindlimb length 19.2; width of right hand (across digits, from tip of innermost to tip of outermost digits) 5.1; width of right foot 7.5.

**COLORATION.** In life (by day) the animals have a glossy black color that is very dark dorsally, and the venter is a lighter, dark gray color. The ground color lightens to a brown appearance at night. The nasolabial protuberances are inconspicuously lightened, due to a reduction in melanin concentration. The dark iris has some golden-brown highlights. The toe tips appear reddish, evidently due to the low concentration of melanin and the presence of extensive vascularization. In alcohol the black coloration has lightened to varying degrees, but the contrast between the darker dorsum and the somewhat lighter venter persists. There are two relatively depigmented areas, which appear as lightened patches, near the front of the head, and these are more prominent in males than in females. The hands and feet also are very dark in color, although a bit lighter than the middorsal part of the trunk.

**OSTEOLOGY.** Information has been derived from two cleared and stained specimens (MVZ 184891-92, a male and a female, respectively) and from radiographs of the type-series. Dorsal and ventral views of the skull are illustrated (Fig. 2).

The skull is exceptionally broad and flattened, and the anterior cranial elements are not tightly articulated; the skull appears to be rather loosely organized anterior to the eyes. The bones are all well defined, but several of them are thin. The single premaxillary bone bears a rather narrow dental process and is relatively small, especially in comparison

with the paired premaxillary bones found in *Nyctanolis*. The premaxillary is either loosely articulated, or makes no contact at all, with the maxillary bones. The premaxillary has no palatal process. Frontal processes of the premaxillary are slender and they arise near each other, but separately. The internasal fontanelle is small and narrow. Near the dorsal surface of the skull the premaxillary frontal processes become flattened and somewhat expanded, and the expanded portions may come into contact on the midline. The expanded portions extensively overlap the facial region of the frontal bones, but they have no or extremely limited contact with the nasals. The frontal processes terminate rather far posteriorly, behind the nasals and at the level of, or even posterior to, the bony rim of the orbits. The moderately large nasals are protuberant in males, in which an anteromedial lobe extends forward beyond the premaxillary and dentaries to be the anteriormost part of the skull. In females the nonprotuberant nasals are rather quadrangular in shape. The nasals have almost no articulations with other bones but are flattened, scale-like elements that lie on top of the cartilaginous nasal capsules. There is a weak articulation with the facial portion of the frontal, and the anterolateral lobe is slightly overlapped by the facial lobe of the maxillary. No septomaxillaries have been found. Prefrontal bones are relatively well developed. These rectangular elements are between one-third and one-half the size of the nasals, and they have extensive articulation with the frontals and the facial lobes of the maxillaries. They may make a slight contact with the nasals. The nasolacrimal duct passes between the front end of the prefrontal, the lateral lobe of the nasal, and the facial lobe of the maxillary. The facial lobe of the maxillary is normally incised to provide space for the duct, and the anterior face of the prefrontal is normally concave, and may be incised, to accommodate the duct. The duct passes over the dorsal surface of the prefrontal, which is somewhat depressed and grooved anterolaterally. The maxillary bones are large and well developed, with relatively well-developed facial lobes and palatal shelves. The bones are well articulated to both the prefrontals and the vomers. The dental portion of the maxillary extends almost to the posterior limit of the eye, where it terminates in a relatively sharp point. The maxillaries bear a long series of small, bicuspid teeth.

The vomers are large and well developed. The intervomerine fontanelle is relatively small and is abruptly pinched off posteriorly, where the two vomers are well articulated to each other. The preorbital processes of the vomers are long and well developed, but relatively slender. They extend beyond the lateral margins of the vomer bodies and bear teeth in a long, relatively straight row to about the level of the lateral border of the bony opening for the nares (but well lateral to the internal nares themselves). The vomerine teeth are of about the same size as the maxillary teeth.

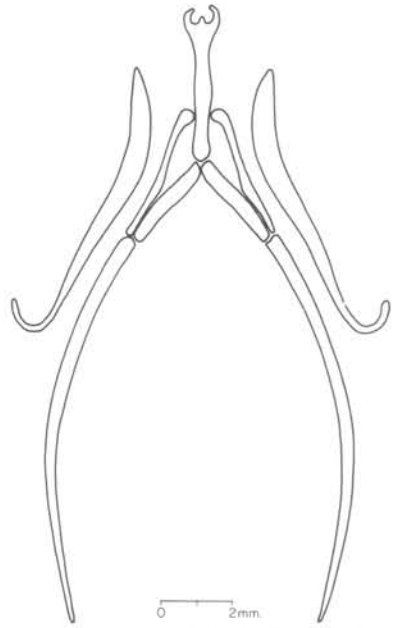
Frontals and parietals are broad, well-developed bones that are firmly articulated with each other in a complex, interlocking network, with large lateral lobes of the frontals overlapping the parietals and small medial lobes of the parietals overlapping the frontals. The paired frontals and the paired parietals are tightly articulated to each other along the midline, and here, too, the articulation involves interlocking portions of the elements. The facial portion of each frontal is relatively large and contributes importantly to the anterior part of the skull. The parietal is a simple bone but it does have a slight ventrolateral tab, characteristic of the supergenus, overlying the cartilaginous portion of the braincase immediately posterior to the orbitosphenoid. The interorbital region of the skull is rather broad, although it is somewhat narrower anteriorly than posteriorly.

The parasphenoid is large and relatively broad anteriorly, with a blunt anterior tip. The orbitosphenoids are rather vertical in orientation, although tipped medioventrally. Posterior vomerine teeth are borne in long, relatively narrow patches that become increasingly well separated from each other posteriorly. The teeth in these patches are somewhat smaller than the maxillary teeth. In the two cleared and stained specimens there are totals of 154 and 192 teeth in the two patches. The otic capsules are large and well developed, and there are distinct rounded ridges which mark the paths of the enclosed semicircular canals. There are no crests, but there is a small spur directed laterally, over the anterodorsal process of the squamosal. The operculum has a short, but distinct, columnar stilus. The stout, well-developed quadrates are connected to the otic capsules by broad squamosals and by the cartilaginous suspensorium. The squamosals are broad dorsally, with a distinct anterior process. Posterodorsally the squamosal bears a large, lobed process that lies over the posterolateral part of the otic capsule.

The lower jaw has a long, slender dentary that bears a very long series of small teeth, similar in size to those on the maxillary. There are 67–72 and 59–61 dentary teeth in the two cleared and stained animals. The prearticular is well developed and has a coronoid process that is bent mediodorsally.

The hyobranchial apparatus is relatively generalized in structure for a member of the supergenus *Bolitoglossa* (Fig. 3). The apparatus is entirely cartilaginous. There is no urohyal. The basibranchial bears relatively short radii that are continuous with it, and there is a small but distinct and partially discontinuous lingual cartilage. The epibranchials are long, approximately 3 times the length of the basibranchial. The first ceratobranchials are extremely slender, whereas the second ceratobranchials are relatively stout. The long ceratohyals have a generalized form, with no anterior extensions or medial processes. The blade is relatively broad and flattened, with a bluntly sharp anterior terminus.

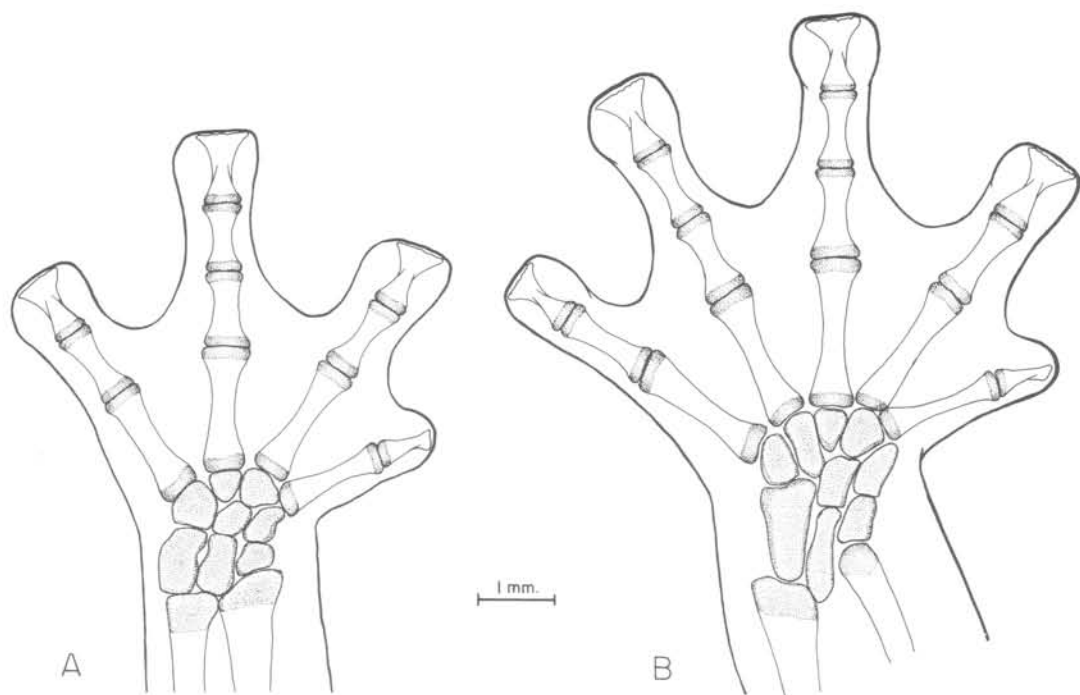
The vertebrae have a generalized structure with



**Figure 3.** Dorsal view of the hyobranchial apparatus (totally cartilaginous) of *Ixalotriton niger* new genus, new species, MVZ 184892. The ceratohyals have been moved laterally for purposes of illustration.

no especially distinctive features. Spindle-shaped intervertebral cartilages join the adjacent vertebrae, which appear to have bony husks that are tapered toward the center and thus appear amphicoelous. There is a single atlas, 14 trunk, one sacral, two caudosacral, and a variable number of caudal vertebrae. The atlas bears a pair of posterolaterally directed processes on the ventrolateral margins of the centrum, but there are no other ventral processes of note. A low dorsal crest is present on the neural arch of the first three to four trunk vertebrae. Transverse processes on the trunk vertebrae arise and remain separated for their entire length, and the rib heads also are separate structures. Ribs are borne on all trunk vertebrae but the last, and only the first and last pairs of ribs are noticeably shortened relative to the remainder. While ribs are relatively long, a rib on a mid-trunk vertebrae is slightly shorter than the distance across the transverse processes, and that distance in turn is slightly less than the length of the centrum. Spinal nerve routes are like those of other members of the supergenus *Bolitoglossa* (Elias and Wake, 1983).

The first caudosacral vertebra has transverse processes that are relatively long and straight and are oriented mainly laterally and a little posteriorly. The processes of the second caudosacral vertebra are considerably shorter, and they usually make a distinct posterior bend about mid-way along their length. These processes are always substantially shorter than those of the first vertebra. These processes arise fairly far anteriorly on the second cau-



**Figure 4.** Dorsal view of the right hand (A) and right foot (B) of *Ixalotriton niger* new genus, new species, MVZ 184891. Cartilage is stippled.

dosacral vertebra, in front of the midpoint. The second caudosacral vertebra is the first to bear a complete haemal arch, but it lacks a haemal spine. The transverse processes of the first caudal vertebra are long and slender and are oriented sharply anterolaterally, arising from the extreme anterior end of the vertebra. They extend forward approximately to the level of the midpoint of the second caudosacral vertebra, but they do not overlap the processes of that vertebra. Transverse processes of succeeding vertebrae are located in the far anterior position, and they become progressively short posteriorly. However, they are readily apparent at least until the twentieth vertebra.

Individual caudal vertebrae are long and slender. Complete tails are rare, but in the cleared and stained specimen with a complete tail there are 48 vertebrae. There is a slight change in length at vertebra 37 which suggests that even in this animal there might have been loss of the tail tip early in life. Other animals that appear to have complete tails have between 48 and 52 trunk vertebrae.

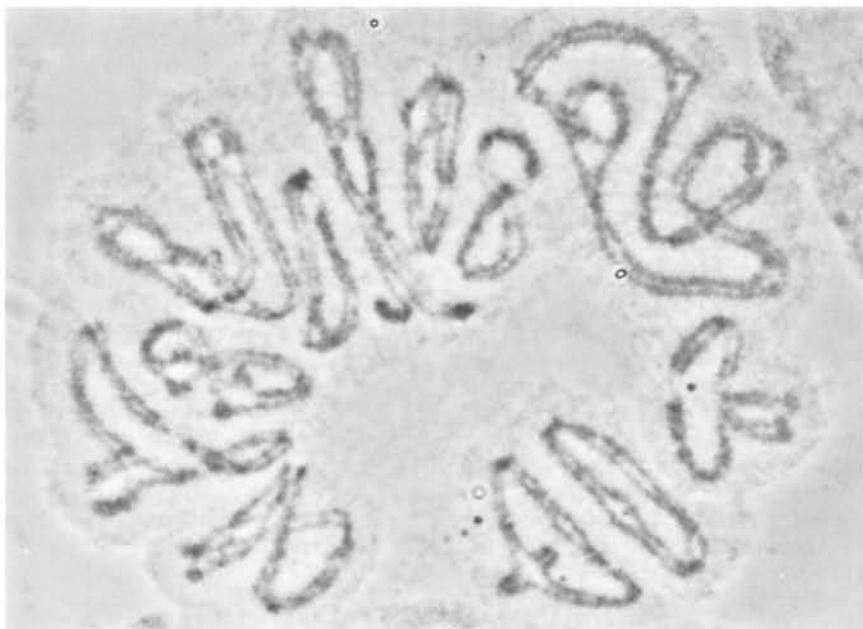
The exceptionally long limbs contain individual bones that are long and slender. They are simple elements with no special processes. No tibial spur has been seen, although there is a low ridge in the area where it is normally found. The large hands and feet bear long digits made up of well-developed metacarpals, metatarsals, and phalanges (Fig. 4). The phalangeal formula is 1,2,3,2 for the hand and 1,2,3,3,2 for the foot. The very long metapodial elements and all but the terminal phalanges are

simple cylindrical bones. The three longest fingers and the four longest toes have terminal phalanges that are highly specialized in structure. These elements are strongly flattened and expanded distally, so that they are more than twice the basal diameter of the phalanx. The expanded portion is bent downward, so as to form a cup-like depression on its underside. The outer margin of the phalanx extends into the skin and is serrated. On the underside of each terminal phalanx, just a little distal from the bony proximal end of the element, is a low knob, which serves as the point of insertion of the digital tendon and provides a mechanical advantage in bending the toe tip.

The carpal and tarsal arrangements are those characteristic of primitive plethodontids and are found in various other members of the supergenus *Bolitoglossa*, such as *Pseudoeurycea* (Wake and Elias, 1983, fig. 7A). There are eight carpals and nine tarsals. Distal tarsal 5 is smaller than distal tarsal 4, and it does not articulate with the centrale.

**KARYOTYPE.** James Kezer examined the chromosomes of one male and has kindly provided the following information and photograph. The haploid chromosome number is 13, as in all other members of the supergenus *Bolitoglossa* (Fig. 5). There is no male heteromorphism of the kind that has been found in *Oedipina*, *Nototriton*, *Dendrotriton*, and *Thorius* (Leon and Kezer, 1978; S.K. Sessions, pers. comm.). The particular individual examined had a reciprocal translocation, which is rare in salamanders. The ring of four chromosomes formed





**Figure 5.** Karyotype of *Ixalotriton niger* new genus, new species, prepared and photographed by James Kezer. N = 13. Note that this individual has a reciprocal translocation, and this diplotene spread has a ring of four chromosomes.

at diakinesis (Fig. 5) includes a deeply interstitial chiasma, which is frequently present in bolitoglossines. Because only one individual has been examined, it is not known if this phenomenon is characteristic of the species.

**HABITAT AND BEHAVIOR.** *Ixalotriton niger* inhabits a moist evergreen forest at about 1,100 m elevation on the Caribbean versant of the Northern Highlands physiographic region of Chiapas, Mexico (described by Müllerried, 1957, and Breedlove, 1973). The area where salamanders were collected surrounds an abandoned oil well (Pozo Turipache) and is locally known as "Linda Vista." The locality is approximately 3 km NW of "El Suspiro," an abandoned coffee finca. Coffee is cultivated extensively in the area, and that activity has resulted in the cutting of much of the native forest vegetation. The locality is part of the southernmost ridge of the Northern Highlands that extends from Sumidero Canyon, north of Tuxtla Gutiérrez, Chiapas, westward to southeastern Oaxaca. Clouds gather consistently along this ridge as moist air flows from the Gulf of Mexico, located approximately 180 km to the north. Clouds usually cover the area beginning in mid- to late afternoon and lasting through early morning hours. During the dry season, clouds are sometimes absent. Rainfall data are not available for the type-locality, but records from Villahermosa, Tabasco, and Palenque, Chiapas, which are also located on the Caribbean versant, indicate a seasonal pattern of rainfall with a rainy season from early summer through late fall (Wernstedt, 1972). In the region of the type-locality, winter rains usually are associated with frontal systems

("nortes"), which periodically sweep in from the north. Even during the winter dry season sufficient precipitation falls to maintain moist conditions in the leaf litter on the forest floor, and in some years rainfall may be heavy. We estimate that rainfall averages around 3,000 mm per year. Temperatures at night reach as low as 14 C at night and as high as 32 C during the day. Average temperatures range from 17 C at night to 23 C during the day. The lowest temperatures occur during winter "nortes" and the highest temperatures are recorded during spring periods of the dry season (April and May).

The substratum located in the area is composed of rough, jagged limestone containing many sinks and crevices. The karst topography results in almost total absence of surface water.

Vegetation at the type-locality is montane rainforest, as classified by Breedlove (1973). The forest physiognomy is composed of two canopies of straight-trunked, large to medium-sized trees, with an understory of broad-leaved forbs and ferns. The larger trees usually have great burdens of epiphytic plants such as philodendrons, bromeliads, and orchids, which are more numerous on branches higher in the canopy. Most tree trunks and limbs are covered with a growth of mosses, sometimes in conjunction with small ferns and vascular plants, and fungi. The understory plants have become more abundant in recent years, probably due to the effects of cutting large trees, which allows more sunlight to penetrate to the forest floor.

The microhabitat requirements and behavior of *Ixalotriton niger* are mostly unknown. All specimens were collected during the winter months of

December and January, when "nortes" produced precipitation or heavy cloud cover. Extensive searches during summer months revealed no salamanders of this species. Most individuals, including the holotype, were found on the trunks of large and medium-sized trees, although a few were on leaves of understory forbs, and two individuals were found crawling on limestone boulders. All individuals were collected at night. It is unknown if the salamanders spend daytime hours in the cracks and holes of the limestone substratum or if they descend at night from moist habitats in canopy epiphytes (e.g., bromeliads). The former is supported by the number of individuals found on lower vegetation and on the limestone boulders. In addition, Dennis E. Breedlove (pers. comm.) has found no salamanders in epiphytes during field investigations of vegetation of the area.

The escape behavior observed during capture of *Ixalotriton niger* primarily consisted of leaping away from a tree trunk or off of an understory leaf. The jumping action is similar to that of *Anolis*. The tail appears to be used as a spring. In the laboratory the animals had quick movements, relative to most salamanders, and they were observed to leap from one end of a container to the other. As is common in tropical plethodontids, the tail autotomizes near the base, but perhaps more readily than in most species. During capture some salamanders lost distal segments of the tail. When captured by hand, salamanders secreted a noxious-smelling, sticky substance. Charles A. Ely developed a skin rash after handling a specimen, possibly an effect of the secretion.

The only other commonly observed members of the herpetofaunal community at the type-locality were a frog (*Eleutherodactylus stuarti*) and a lizard (*Anolis parvicirculata*). When *Ixalotriton niger* was active, it was more abundant than these species. The number of salamanders, observed on recent visits, was low, likely a result of continued cutting of natural vegetation. The following species of amphibians and reptiles have been collected from the vicinity of the type-locality: salamanders—*Bolitoglossa mexicana*, *B. occidentalis*; frogs—*Agalychnis moreleti*, *Anotheca spinosa*, *Eleutherodactylus rhodopis*, *E. stuarti*, *Smilisca baudinii*, *S. cyanostricta*, and an undescribed species of leptodactylid frog; lizards—*Anolis laevis*, *A. parvicirculata*, *A. petersi*, *Celestus rozellae*, *Laemantius longipes*, *Lepidophyma flavimaculatum*, *Sceloporus internasalis*, *S. variabilis*, *Sphenomorphus assatus*, *Xenosaurus grandis*; snakes—*Imantodes cenchoa*, *Lampropeltis triangulum*, *Leptodeira septentrionalis*, *Leptophis mexicanus*, *Micrurus elegans*, *Ninia diademata*, *N. sebai*, *Pliocercus elapoides*, *Pseustes poecilonotus*, *Rhadinaea decorata*, *Stenorrhina degenhardtii*. Johnson *et al.* (1977) discussed some of the species occurring at this locality.

Amphibians and reptiles that are most likely to share microhabitat with *Ixalotriton niger* include the species of *Bolitoglossa* and *Eleutherodactylus* listed above, as well as *Anolis parvicirculata*, *A.*

*laevis*, *Celestus rozellae*, *Sphenomorphus assatus*, and *Xenosaurus grandis*. In addition, *Imantodes cenchoa* often was encountered while we were searching for salamanders in low vegetation and on limestone boulders, and it may prey upon the species.

*Ixalotriton niger* may be endangered, especially if it is a localized species that occurs only in the vicinity of the type-locality, where the forest is rapidly being cut for agricultural purposes and lumber. We predict that the natural forest in this area will be completely destroyed within the next few years, if this has not already occurred. Removal of the forest likely will result in the extinction of *I. niger*, which apparently has both a restricted geographic range and narrow habitat and microhabitat tolerances.

**RANGE.** The species is known only from the immediate vicinity of the type-locality in northwestern Chiapas, Mexico.

**ETYMOLOGY.** The name *niger*, Latin, is chosen because of the uniformly dark blackish color of the species.

## DISCUSSION

The relationships of *Ixalotriton* are obscure, and we have withheld publication of this taxon for some time while we have attempted to obtain specimens for biochemical studies and have searched for additional populations. *Ixalotriton* is clearly a member of the supergenus *Bolitoglossa*, for it possesses all of the critically important features of the tongue that characterize that group (Lombard and Wake, 1977), as well as the synapomorphic karyotype, with a haploid chromosome number of 13 (Leon and Kezer, 1978; Elias and Wake, 1983). However, the relationships of *Ixalotriton* within that supergenus are less clear.

Wake and Elias (1983) listed 18 potentially useful characters for cladistic analysis of the tropical plethodontid genera. Of these characters, seven are apparently autapomorphies that are useful only in defining monotypic genera but are not otherwise informative. One of these characters, the presence of unusually long limbs, is shared with *Nyctanolis* and is a potential synapomorphy for these two genera. The remaining 11 are synapomorphies for two or more genera. *Ixalotriton* has three of these derived traits: no tibial spur (shared with *Dendrotriton* and *Oedipina*), no septomaxillary bones (shared with *Bolitoglossa*, *Bradytriton*, *Lineatriton*, *Nototriton*, *Nyctanolis*, *Parvimolge*, *Oedipina*, and *Thorius*), and a single premaxillary bone (shared with all but *Nyctanolis*). The only one of these characters that appears to be informative is the presence of a single premaxillary bone, which serves to link it cladistically to all genera except *Nyctanolis*, the one genus it resembles most closely in overall structure and habits. In fact, one of its other potential synapomorphies is the only derived trait previously listed for *Nyctanolis*, very long legs.

The two remaining traits are not very useful for they are known to vary within genera. Derived con-

ditions were coded by Wake and Elias (1983) on the basis of presence in all species of the generic unit under consideration. Thus, in order to qualify as an apomorphy a trait had to occur in all members of the genus, but in order to qualify as a plesiomorphy for that genus it only had to appear in a single species. Accordingly, the absence of septomaxillaries and the absence of a tibial spur in *Ixalotriton* are not appropriately viewed as synapomorphies that link the taxon to any other group. The combination of four apomorphies is unique, however.

The limits of the genus *Pseudoeurycea* could be expanded to accommodate *Ixalotriton*, but for several reasons we believe that such an action would be counterproductive. First, we strongly suspect (Wake and Elias, 1983) that *Pseudoeurycea* is paraphyletic. The reason why it would be possible to expand the concept of that genus and include the new species in it is that *Pseudoeurycea* has neither unique synapomorphies nor any unique combination of synapomorphies. *Pseudoeurycea* does share one synapomorphy (single premaxillary bone) with all tropical genera except *Nyctanolis*. We expect *Pseudoeurycea* to be broken into smaller monophyletic groups as additional information becomes available, but such a move may be slow in coming because many species are poorly known and it is increasingly difficult to obtain specimens for study. Available information concerning biochemical differentiation of the species currently assigned to *Pseudoeurycea* (Maxson and Wake, 1981; Wake and Yang, unpubl.) indicates that the group is old and highly diversified, but diagnostic osteological and other morphological traits have been very difficult to identify. We know that the majority of the species of *Pseudoeurycea* lack septomaxillary bones, and some populations of *P. cephalica* lack tibial spurs, so it is not difficult to imagine a species of *Pseudoeurycea* also evolving extremely long limb bones and large hands and feet. The closest relatives of *Ixalotriton* ultimately may prove to be some (but not all) species of the paraphyletic *Pseudoeurycea* (or possibly *Nyctanolis*, another genus ambiguously associated with *Pseudoeurycea*, see Lynch and Wake, 1989). Our description of *Ixalotriton* is a stage in the anticipated subdivision of what might be termed the "*Pseudoeurycea* complex."

Very little tissue has been available for biochemical analysis (see Lynch and Wake, 1989), but some comments can be made concerning immunological analysis. Linda Maxson, using the technique of quantitative micro-complement fixation, has made some preliminary measurements of albumin differentiation in *Ixalotriton* relative to two species of *Pseudoeurycea* (*P. smithi*, *P. brunnata*), and single species of *Chiropterotriton* (*C. multidentatus*), *Dendrotriton* (*D. bromeliacia*), and *Bolitoglossa* (*B. rostrata*) for which antisera have been prepared. No antisera have been available for *Ixalotriton*, so all comparisons are unidirectional. The measurements of albumin immunological distance (see Maxson and Wake, 1981) from each of these anti-

sera to *Ixalotriton* are, in order of presentation (above), 65, 65, 89, greater than 110, and 113. These are all large distances. If one accepts the current estimate from the concept of a molecular evolutionary clock that 100 immunological distance units accumulate every 55–60 million years (Maxson and Wilson, 1975), the minimal time of divergence of *Ixalotriton* from any of the above taxa is on the order of 35 million years. There are, however, immunological differences considerably greater than 65 within *Pseudoeurycea*. In a five-by-five matrix of reciprocal comparisons of *P. bellii*, *P. brunnata*, *P. cephalica*, *P. leprosa*, and *P. smithi*, six of the 20 entries exceeded a value of 65, and two more exceeded 60 (Maxson and Wake, 1981). However, most of the great distances involved species of *Pseudoeurycea* other than those considered here and species that are unlikely prospects as far as possible relationship to *Ixalotriton* is concerned. By contrast, comparisons to members of other genera disclosed immunological distances of from 71 (*Dendrotriton bromeliacia*) to 88 (*Chiropterotriton multidentatus*). Dr. Maxson also has provided some unpublished data for immunological comparisons of the albumin of the poorly known *Bradytriton* and *Nyctanolis*. The former is a short-limbed terrestrial species that is an unlikely relative of *Ixalotriton*, but the latter is a potential relative. Albumin immunological distances to the five reference antisera used in comparisons with *Ixalotriton* all exceeded 90 (the only measurements less than 100 were of *Bradytriton* and *Nyctanolis* to *P. brunnata*). The distance from *Ixalotriton* to *P. brunnata* is 65, but from *Nyctanolis* to *P. brunnata* is 90. There are no data for the distance between *Ixalotriton* and *Nyctanolis*, but it is very unlikely that these genera have evolved in exactly the same direction from *P. brunnata*.

*Ixalotriton* and *Nyctanolis* appear to have evolved independently toward arboreal and scansorial life in cloud forests in nuclear Central America. The relationships of *Nyctanolis* have been discussed in detail by Elias and Wake (1983) and Wake and Elias (1983), who concluded that the genus is the sister-group of the remainder of the supergenus *Bolitoglossa*. The critical character is the paired premaxillary bones of *Nyctanolis*, a plesiomorphous trait not found in any other member of the supergenus *Bolitoglossa*. It was on the basis of this character that Wake and Elias (1983) fixed the root of the cladogram for the supergenus. The character is relatively complex and well understood. But there are also other reasons for thinking that *Nyctanolis* might be an early derivative of the ancestral stock. It has a poorly differentiated tail-breakage region and a large, stout, generalized skull. Several osteological features differentiate *Ixalotriton* from *Nyctanolis*. Not only is the premaxillary bone of *Ixalotriton* single, but the premaxillary region of the skull has a different construction from that of *Nyctanolis*. In *Ixalotriton* the frontal processes are close together and the internasal fontanelle is small. The hyobranchial apparatus and the tail base region of

*Ixalotriton* are more similar to structure in *Pseudoeurycea* than in *Nyctanolis*, and although the limbs, hands, and feet of *Ixalotriton* and *Nyctanolis* are rather similar in overall structure, *Ixalotriton* lacks a tibial spur. Accordingly, we believe that ecologically driven convergence is the most likely reason for the general morphological and ecological similarity of the genera. The alternative to this interpretation is a sister-group arrangement for *Ixalotriton* and *Nyctanolis*, based solely on the limb characters, and this would require a reversal of the premaxillary character in *Nyctanolis* (see also discussion of relationships in Lynch and Wake, 1989).

Nuclear Central America has a remarkably diverse salamander fauna, including four endemic genera (*Nyctanolis*, *Bradytriton*, *Dendrotriton*, and *Ixalotriton*), as well as representatives of *Oedipina*, *Bolitoglossa* (both alpha and beta assemblages), *Pseudoeurycea*, and *Nototriton*. It clearly has been an important area, not only of diversification and adaptive radiation, but also of survival of what increasingly appear to be ancient lineages (Wake and Lynch, 1976; Wake, 1987).

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During the last decade and a half many individuals have assisted us in our quest for information concerning the biology of *Ixalotriton niger*. However, none were more responsible for the initial discovery and early period of study of this species than Dr. Charles A. Ely and Jan Ely, Fort Hays State University, Hays, Kansas. Their unselfish willingness to include a fledgling undergraduate herpetologist (J.D. Johnson) in their Mexican ornithological expeditions was one of those actions that determines the direction of a person's life. The friendship that originated during those years is cherished. We are honored to dedicate this description of a new species of salamander to Chuck and Jan Ely.

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# TWO NEW SPECIES OF *PSEUDOEURYCEA* (AMPHIBIA: CAUDATA) FROM OAXACA, MEXICO

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JAMES F. LYNCH<sup>1</sup> AND DAVID B. WAKE<sup>2</sup>

**ABSTRACT.** *Pseudoeurycea saltator* and *P. parva* are described from the mountains of Oaxaca, in southern Mexico. These new species are small, arboreal forms that inhabit bromeliads in two widely separated areas of cloud forest on opposite sides of the Isthmus of Tehuantepec. Morphological and protein comparisons suggest that although the two new forms are similar in external morphology, they are distinct species and are only distantly related to other *Pseudoeurycea*. Discovery of these new taxa complicates interpretation of cladistic relationships among Middle American plethodontid salamanders of the genera *Pseudoeurycea*, *Ixalotriton*, and *Nyctanolis*.

**RESUMEN.** Se provee la descripción de *Pseudoeurycea saltator* y *P. parva*, de las montañas de Oaxaca, en el sur de México. Estas nuevas especies son pequeñas formas arbóreas que viven en bromelias en dos áreas ampliamente separadas de bosque nublado en lados opuestos del Istmo de Tehuantepec. Comparaciones morfológicas y de proteínas sugieren que, aunque similares en morfología externa, estas dos formas son especies diferentes, lejanamente relacionadas con otras *Pseudoeurycea*. El descubrimiento de estos nuevos taxa complica la interpretación de las relaciones cladísticas de las salamandras plethodontidas de los géneros *Pseudoeurycea*, *Ixalotriton*, y *Nyctanolis*.

## INTRODUCTION

With 24 described species, *Pseudoeurycea* ranks second only to *Bolitoglossa* (68 species) in species diversity among the 12 neotropical genera of the salamander family Plethodontidae (Wake and Lynch, 1976; Wake and Elias, 1983). Whereas *Bolitoglossa* occurs from sea level to nearly 3,000 m elevation in humid habitats throughout the New World tropics, *Pseudoeurycea* is restricted to Mexico and Guatemala, and with few exceptions its species occur only above 1,200 m (Fig. 1). *Pseudoeurycea* can be abundant locally, but most species have limited geographic ranges. Consequently, discovery of new taxa can be expected as more mountain ranges become accessible (e.g., Regal, 1966; Bogert, 1967; Lynch *et al.*, 1983; Wake *et al.*, 1989).

Here we describe two distinctive new plethodontid species that we tentatively assign to the genus *Pseudoeurycea*. Whereas these new forms complicate the systematics of an already problematic genus (Wake and Lynch, 1976; Maxson and Wake, 1981; Elias and Wake, 1983; Wake and Elias, 1983; Wake and Johnson, 1989), they also shed new light

on the evolutionary, ecological, and biogeographic relationships among the species groups of *Pseudoeurycea*, and between that genus and its closest relatives, *Dendrotriton*, *Ixalotriton*, and *Nyctanolis*. We first describe the new species, and then discuss their relationships.

## SPECIES ACCOUNTS

### *Pseudoeurycea saltator* new species

Figure 2

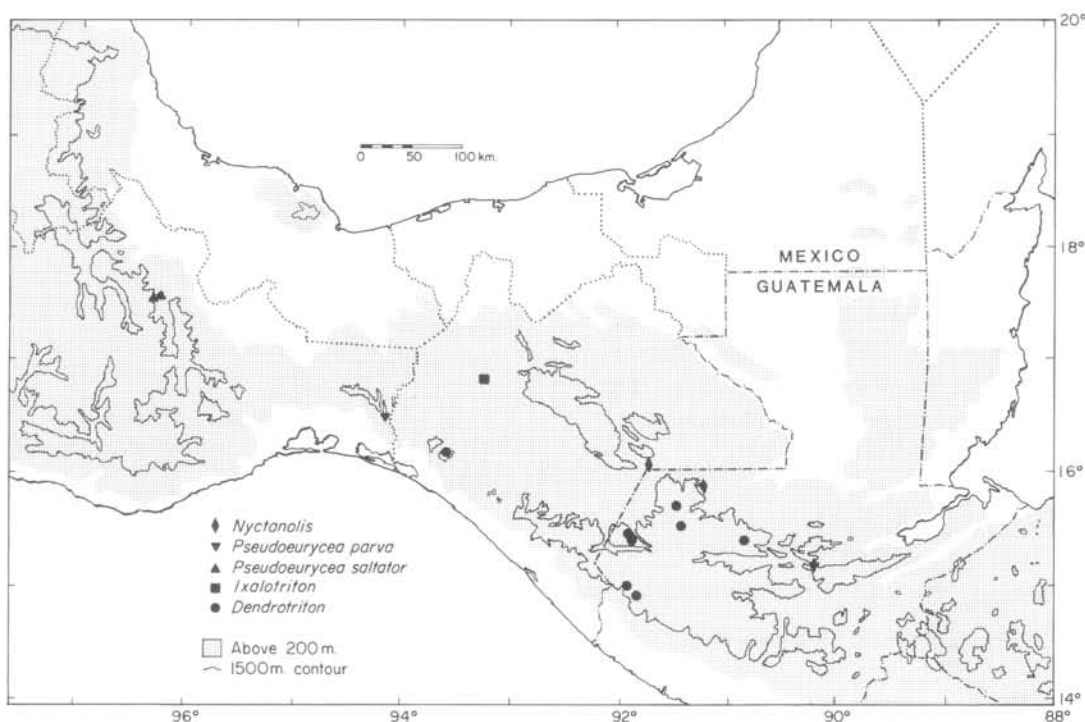
**HOLOTYPE.** MVZ 131102, an adult male collected under the bark of a fallen log in cloud forest just west of highway 175, 16 km (by road) S Vista Hermosa, Oaxaca, Mexico (1,970 m), November 21, 1974 by D.B. Wake, J.F. Lynch, and T.J. Papenfuss.

**PARATYPES.** MVZ 112227–37, 114398, 132876–80, 147259–63 (147260 is cleared and stained), 162283 (23 specimens) all within 1 km of the holotype (1,950–2,050 m) on W side of highway 175; University of Kansas (KU) 136478–99, 136512 (23 specimens) along highway 175, 4–15 km S Vista Hermosa, Oaxaca, Mexico (1,580–1,970 m); University of Texas at Arlington (UTA) A-2869–70 (2 specimens) 27 mi [= 43 km] S Valle Nacional; UTA A-3593 25 km S Valle Nacional; Natural History Museum of Los Angeles County (LACM) 137514, same data as holotype.

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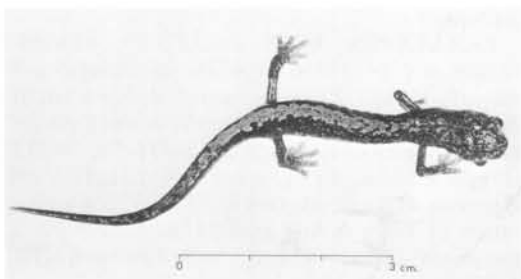
1. Smithsonian Environmental Research Center, Edgewater, Maryland 21037.

2. Museum of Vertebrate Zoology, University of California, Berkeley, California 94720; Research Associate in Herpetology, Natural History Museum of Los Angeles County, Los Angeles, California 90007.



**Figure 1.** Southern Mexico and Guatemala with the distribution indicated of the two species of *Pseudoeurycea* described in this paper. All known localities for the genera *Nyctanolis*, *Ixalotriton*, and *Dendrotriton*, which are potential relatives of these two new species, are also indicated.

**DIAGNOSIS.** *Pseudoeurycea saltator* is one of the smallest species in the genus. Standard length (SL), the distance from the snout to the posterior angle of the vent, is generally less than 45 mm (maximum = 45 mm for males, 48 mm for females;  $n = 42$ ). In its gracile external proportions and dorsally striped color pattern, *P. saltator* somewhat resembles *P. longicauda* and *P. juarezi*. The former species, which is restricted to western portions of the Transverse Volcanic Range of central Mexico (Lynch *et al.*, 1983), is much larger than *P. saltator* (males to 62 mm, females to 65 mm) and has relatively shorter limbs (combined length of the fore limb and hind limb divided by the SL averages 0.48 in *P. longicauda* vs. 0.56 in *P. saltator*). Both *P. saltator* and *P. longicauda* have long tails for the



**Figure 2.** Photograph of a living *Pseudoeurycea saltator* new species (MVZ 132880), collected at the type-locality.

genus (in both species, mean ratio of tail length divided by SL is greater than 1.0 in adults of average SL). Compared with *P. juarezi*, which occurs at higher elevations (2,200–2,900 m) just south of the range of *P. saltator*, the new species is smaller (median SL of the largest third of our sample = 44 mm vs. 49 mm for *P. juarezi*) and has a relatively longer tail (relative tail length = 1.05 vs. 0.96 for *P. juarezi*), more vomerine teeth (projected mean at a common SL of 45 mm = 28 vs. 23 for *P. juarezi*), and more maxillary + premaxillary teeth (projected mean at SL of 45 mm = 86 vs. 78 for *P. juarezi*). The new species also differs from *P. juarezi* in color pattern. *Pseudoeurycea saltator* has a uniformly dark gray dorsal ground color that is invariably overlain by a paler mid-dorsal stripe. A diagnostic feature of the color pattern of all adults and subadults is the presence of conspicuous white or cream-colored pigmentation at the tip of the tail. In contrast, the highly variable color pattern of *P. juarezi* includes a light dorsal ground color that is marked by conspicuous dark spots and a very irregular dorsal stripe (Regal, 1966); in addition, *P. juarezi* lacks a white tail tip. These two parapatric species differ greatly in electrophoretically determined traits of various proteins (see below). In external appearance, *P. saltator* is most similar to another newly discovered *Pseudoeurycea* that is described below. Diagnostic features separating these two taxa are listed in the description of the second species.

**MEASUREMENTS OF THE HOLOTYPE (mm).** Maximum head width, 6.0; head length (snout to gular fold), 9.2; head depth at posterior angle of jaw, 3.2; eyelid length, 2.5; eyelid width, 1.7; anterior rim of orbit to snout, 2.5; interorbital distance, 2.0; distance between vomerine teeth and parasphenoid tooth patch, 0.0; distance separating internal nares, 1.6; distance separating external nares, 2.1; snout projection beyond mandible, 0.8; snout to fore limb, 11.0; snout to anterior angle of vent, 34.1; snout to posterior angle of vent (SL), 36.8; axilla to groin, 19.1; tail length, 36.4; tail width at base, 36.4; tail depth at base, 3.0; fore limb length, 10.2; hind limb length, 11.2; width of right hand, 2.8; width of right foot, 3.7; number of premaxillary teeth, 5; number of maxillary teeth, 60; number of vomerine teeth, 28.

**COLORATION OF THE HOLOTYPE IN ALCOHOL.** The ground color is gray-black dorsally, grading to pale gray ventrally. The underside of the tail is darker than either the belly or the chin. A narrow but conspicuous mid-dorsal stripe extends from the scapular region to the tip of the tail, which is depigmented and appears white. The dorsal stripe varies in color from tan in the trunk region to gray-white on the tail. In the head region the dorsal stripe is broken into obscure flecks. Small white iridophores are scattered across the entire ventral surface but are larger and more concentrated on the chin, tail, and sides than on the belly. Coloration in life was similar, but the light iridophores were more distinct.

**VARIATION.** As in other species of *Pseudoeurycea*, the sexes of *P. saltator* overlap broadly in SL, body proportions, and coloration. However, females reach a somewhat larger overall size than do males ( $P < 0.05$ ; Mann-Whitney U-test), and the four largest individuals in our sample of 43 are females. The basic color pattern, which varies little among individuals, features a light-colored mid-dorsal stripe on a gray-black background. The dorsal stripe typically originates in the occipital or scapular region and extends posteriorly to encompass most or all of the length of the tail. The stripe varies in color from pale cream through various shades of tan, brown, or gray and is lighter posteriorly on some individuals. The margins of the dorsal stripe vary from nearly straight to ragged or scalloped. In some individuals scattered dark concentrations of melanin are present along the margins of the stripe. A consistent feature of the color pattern is the white tail tip, which is evident in all but the smallest of the available specimens. The ventral surface is paler than the dorsum and is invariably marked by small, scattered white iridophores. These iridophores are larger and more abundant in the lateral region and on the chin and tail than on the belly.

As is typical in plethodontids, there is marked ontogenetic variation in most proportional and meristic characters. Compared to juveniles (projected to a standard SL = 30 mm), adults (projected to a

standard SL = 45 mm) have more maxillary-premaxillary teeth (mean = 86 vs. 66), more vomerine teeth (mean = 28 vs. 22), relatively longer limbs (hind limb plus fore limb, divided by SL = 0.57 vs. 0.52), and relatively longer tails (tail length divided by SL = 1.05 vs. 0.81).

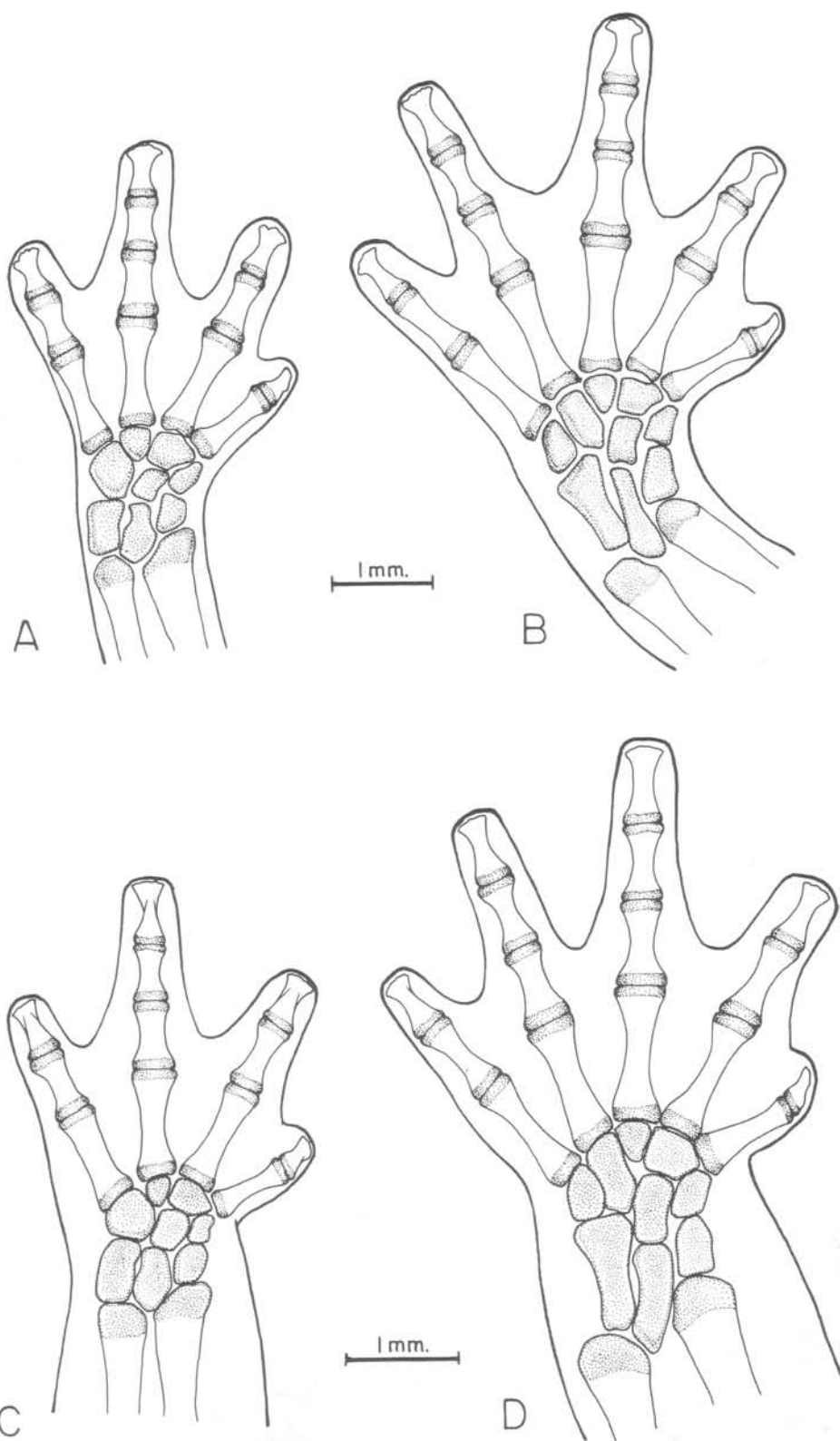
**OSTEOLOGY.** Information was obtained from one cleared and doubly stained male (MVZ 147260, 36.4 mm SL). The skull is compact and well ossified. The single premaxillary has a relatively broad but slender pars dentalis that bears four long, spine-like teeth; each tooth has a specialized tip consisting of a long, recurved labial cusp that extends well beyond the distinct but tiny lingual cusp and forms a minute hook-like structure. The configuration of the tooth is similar to the condition illustrated by Taylor (1941:59) for *P. unguidentis* and *P. smithi*, also Oaxacan species.

Frontal processes of the premaxilla arise independently and remain separated; these stout processes expand distally as they diverge. The processes overlap the frontal in a strong articulation, and they surround a moderately large fontanelle. The maxillaries are long and slender and bear 38 and 40 small bicuspid teeth. Septomaxillaries are absent. The nasals are relatively small, rectangular in shape, and are at most weakly articulated with the frontals and prefrontals. The well-developed prefrontal bones have areas about two-fifths those of the nasals. The nasolacrimal duct is surrounded by a distinct evagination in the anteromedial margin of the prefrontal and a corresponding depression in the posterolateral margin of the nasal. The frontals and parietals are firmly ankylosed on the midline; there is no frontal-parietal fontanelle. A parietal "spur" is only moderately developed, and there is no ventrally directed tab. There are no crests on the otic capsules, and only one small laterally placed spine is present on one side. Vomers are weakly ankylosed for a short distance posteriorly, behind the relatively large internasal fontanelle. Preorbital processes of the vomers are long and extend beyond the body of the bone; 13–14 teeth extend beyond the lateral margins of the internal nares. The posterior vomerine tooth patches are widely separated and narrow; each contains about 65 small, bicuspid teeth. There is a well-developed, short, rod-like columella attached to the operculum.

There is an atlas, 14 trunk vertebrae (13 of them rib-bearing), 1 sacral, 2 caudosacral, and 31 caudal vertebrae. The first caudal vertebra is shorter than the second caudal or the second caudosacral and bears elongated, unbranched processes that extend sharply anteriorly. However, these processes are not especially slender or otherwise specialized as compared with the situation in other tropical plethodontids. The tail is slender. Distinct transverse processes are present on all but the small last two caudal vertebrae.

Hands and feet are typical of *Pseudoeurycea*. There is a very short, truncated tibial spur. The tarsals have the arrangement typical of the genus





**Figure 3.** Drawings of the left hand (A) and left foot (B) of a paratype of *Pseudoeurycea saltator* new species (MVA 147260), and of the left hand (C) and left foot (D) of a paratype of *Pseudoeurycea parva* new species (MVZ 202294). Cartilage is stippled.



(Wake, 1966; Wake and Elias, 1983), with distal tarsal 5 being smaller than distal tarsal 4. The middle three digits of the foot are much longer than the others. Terminal phalanges are well developed and distally expanded (Fig. 3), and the distal portion is somewhat cupped. There is a small process to which the digital tendon is attached.

The hyoid apparatus is typical for the genus. No lingual cartilage is evident.

**DISTRIBUTION.** *Pseudoeurycea saltator* has been collected along a 27-km section of highway 175 that traverses the humid Caribbean-facing slope of the Sierra de Juárez, in north-central Oaxaca, Mexico (Fig. 1).

**HABITAT AND HABITS.** Most specimens have been found inside arboreal bromeliads, some as much as 8 m above the ground. A few individuals have been collected under the loose bark of downed logs. The type-locality, a steep north-facing ridge, supports a luxuriant growth of evergreen cloud forest and receives abundant precipitation even during the winter "dry" season. Extensive cloud forest is present east and west of the type-locality, but the native forest has been severely disturbed or removed by cattle ranching and coffee cultivation at the northern (*i.e.*, lower) limit of the known distribution, in the vicinity of the settlement of Vista Hermosa.

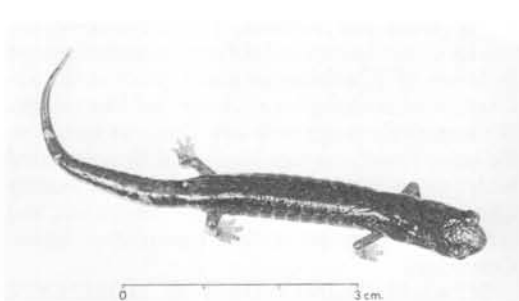
Amphibians associated with *P. saltator* at higher elevations (ca. 1,800 m) include at least five hylid (*Hyla chaneque*, *H. dendroscarta*, *H. mixe*, *Ptychohyla ignicolor*) and leptodactylid (*Eleutherodactylus* sp.) frogs and three species of plethodontid salamanders (*Nototriton adelos*, *Chiropetrotriton* sp., *Thorius* sp.), all cloud-forest endemics. At the lower limit of its distribution, in the vicinity of Vista Hermosa (ca. 1,500 m elevation), *P. saltator* occurs with the same *Chiropetrotriton*, a fully-webbed species of *Bolitoglossa* of the *rufescens-occidentalis* complex, a *Pseudoeurycea* tentatively identified as *P. werleri*, an unidentified species of *Thorius*, and at least seven species of hylids (*Agalychnis moreleti*, *Anotheca spinosa*, *Hyla arboreascandens*, *H. dendroscarta*, *H. echinata*, *Ptychohyla ignicolor*, *P. leonhardschultzei*).

In comparison with other members of the genus, *P. saltator* is active and fast-moving. The specific name *saltator* is Latin for leaper or dancer and refers to the unusual ability of this species to jump when attempting to elude capture. To our knowledge, the only other tropical plethodontids that combine rapid locomotion and well-developed jumping abilities are members of two recently discovered monotypic genera, *Nyctanolis* (Elias and Wake, 1983) and *Ixalotriton* (Wake and Johnson, 1989).

### *Pseudoeurycea parva* new species

Figure 4

**HOLOTYPE.** MVZ 196101, an adult male collected by Ken Lucas inside an arboreal bromeliad on a ridge SE Cerro Baul, 21 km W Rizo de Oro,



**Figure 4.** Photograph of a living *Pseudoeurycea parva* new species (MVZ 194330), collected at the type-locality.

Chiapas, Mexico (ca. 1,600 m). The type-locality is just within the eastern border of the state of Oaxaca.

**PARATYPES.** MVZ 196102, 196444–45 (3 specimens), 202294 (cleared and stained) same locality as holotype; MVZ 163823–25, 177823–24 (5 specimens), 16.8 km (by rd) NW Rizo de Oro (1,650–1,860 m); MVZ 194330–31 (2 specimens), Cerro Baul, 37 km (by rd) W Rizo de Oro; California Academy of Sciences (CAS) 164157–62 (6 specimens), Cerro Baul, 19 km W Rizo de Oro; LACM 137513, same locality as holotype.

**DIAGNOSIS.** This is the smallest known member of the genus. None of the 17 available specimens exceeds 40 mm SL, and all individuals with SL greater than 35 mm appear to be sexually mature. The combination of small size and a distinctive color pattern (brown dorsal stripe and lichenous white spots on the tail) easily separates this species from all other *Pseudoeurycea*, except *P. saltator*. Compared with the latter species, *P. parva* is smaller (median SL of the largest third of the sample = 39 mm in *P. parva* vs. 44 mm in *P. saltator*) and has a proportionately shorter tail (tail length projected to a common SL of 42 mm = 0.93 SL in *P. parva* vs. 1.02 SL in *P. saltator*). About half the specimens of *P. parva* lack a dorsal stripe, and when present the stripe is more obscure than in *P. saltator*. In the latter species, the dorsal pattern is formed by a heavily pigmented swath of iridophores; in contrast, the dorsal pattern of *P. parva* results from reduction in the density of melanin pigmentation in the mid-dorsal region. While *P. parva* lacks the diagnostic white tail tip found in *P. saltator*, most individuals possess conspicuous white or tan iridophore patches along the tail. There is often a pale patch on the rostrum.

In general appearance and ecology, *P. parva* somewhat resembles an oversized *Dendrotriton* (see also Wake and Elias, 1983) but differs from members of that genus in possessing prefrontal bones (see below, Osteology) and in lacking enlarged nostrils in both the juvenile and adult stages (Lynch and Wake, 1975). Both *P. parva* and *P. saltator* share some morphological and behavioral similarities with two recently discovered monotypic genera, *Nyctanolis* (Wake and Elias, 1983) and *Ixalo-*

*triton* (Wake and Johnson, 1989). However, the mosaic of similarities and differences argues against inclusion of *P. saltator* in either genus in the absence of more definitive evidence (see Discussion). We tentatively assign both new Oaxacan species to the genus *Pseudoeurycea* based on their generalized body proportions, configuration of the toes (middle digits are markedly longer than the outer ones), and retention of primitive skeletal features (see below, Osteology).

**MEASUREMENTS OF THE HOLOTYPE (mm).** Maximum head width, 6.4; head length, 9.3; depth at posterior angle of jaw, 3.1; eyelid length, 2.7; eyelid width, 1.5; anterior rim of orbit to snout, 2.9; interorbital distance, 2.5; distance between vomerine teeth and parasphenoid tooth patch, 0.1; snout to insertion of fore limb, 11.7; distance separating internal nares, 2.1; distance separating external nares, 2.4; snout projection beyond mandible, 0.9; snout to anterior angle of vent, 35.8; snout to posterior angle of vent (SL), 38.1; axilla to groin, 20.4; tail length, 38.9; tail width at base, 3.3; tail depth at base, 3.2; width of right hand, 3.1; width of right foot, 4.3; number of premaxillary teeth, 2; number of maxillary teeth, 80; number of vomerine teeth, 30.

**COLORATION OF THE HOLOTYPE IN ALCOHOL.** The ground color is dark gray-brown; the mid-dorsal region is lightened, forming an indistinct medium-brown stripe. The mid-dorsal stripe has a "dirty" appearance, due to a suffusion of small melanophores over unpigmented tissue. The dorsal stripe extends over the length of the tail, where it is overlain by large, scattered white iridophore patches. The belly is pale gray with scattered inconspicuous white flecks. Larger, more abundant white flecks are present in the lateral region of the trunk. The ventral surface of the tail is darker than the belly and has fewer iridophores. The chin is cream-colored, with a suffusion of tiny melanophores. The holotype, an adult male, possesses a well-developed kidney-shaped mental gland whose long axis is parallel to the anterior mandibular margin.

**VARIATION.** The dorsal ground color is dark brown or gray-brown in all specimens, but there is considerable individual variation in both the degree of development and the coloration of the mid-dorsal stripe. Some animals have a well-defined, contrasting stripe, others have only a slight reduction in the darkness of the ground coloration in the mid-dorsal region, and a few lack any dorsal pattern. Where present, the dorsal stripe varies in color from creamy white to dark brown, apparently depending on the degree of melanin reduction. Most individuals have at least a few conspicuous lichenous white spots scattered over the tail, but these spots vary in size and abundance. In general, individuals with reduced melanism in the mid-dorsal region also tend to be depigmented on the snout, parietal area, and limb bases. A suffusion of tiny white iridophores is invariably present on the ven-

ter, and somewhat larger white iridophores are concentrated in the lateral region of the trunk.

Sexual dimorphism is not evident in our limited sample, but there is statistically significant (determined according to methods of Lynch and Wake, 1975) ontogenetic variation in most proportional and meristic characters. Compared with standardized juveniles (character values projected to a common SL = 25 mm), standardized adults (projected to a common SL = 40 mm) have more maxillary + premaxillary teeth (80 vs. 60), more vomerine teeth (50 vs. 28), relatively longer limbs (combined length of fore limb and hind limb, divided by SL = 0.54 vs. 0.45), and relatively longer tails (tail length divided by SL = 0.91 vs. 0.62).

**OSTEOLOGY.** Information has been obtained from a cleared and stained adult female MVZ 202294 (40 mm SL). The skull is well developed, and the articulations are generally extensive and firm. The relatively stout premaxillary bone has a relatively broad, undivided pars dentalis that carries 6 bicuspid teeth. The latter are of moderate size (larger than the maxillary teeth) but are unspecialized in morphology. Frontal processes arise separately and remain separated, but they lie close together and enclose a narrow fontanelle. The processes are expanded distally, where they overlap the frontals in a firm articulation. The long and slender maxillary bones carry 32 and 33 small bicuspid teeth. These bones are rather firmly articulated to the premaxilla, the nasals, and the prefrontals. The nasals are broadly triangular in shape and of moderate size. Only a posterior tab overlaps the frontal. Septomaxillaries are absent. The prefrontals are somewhat elongate and articulate firmly with both the maxillaries and the frontals. Each prefrontal is about one-third the area of a nasal bone. The nasolacrimal duct passes between the nasal, prefrontal, and maxilla, and each bone is somewhat evacuated along the relevant margin, especially the prefrontal. Frontals and parietals are moderately ankylosed on the midline; there is only an extremely small frontal-parietal fontanelle. The parietal "spur" is only modestly developed, and there is no ventrally directed tab. Small lateral otic crests are present. Squamosals are notably large and are firmly articulated to the otic capsule. The vomers are barely ankylosed to each other posteriorly, and anteriorly the widely separated bones embrace a moderately large internasal fontanelle. Each of the long preorbital processes bears 13 teeth, which extend to the lateral margin of the internal nares. The posterior vomerine patches are narrow and well separated, and each bears about 45–50 small bicuspid teeth. The operculum bears a distinct, but very small, rod-like columella.

There is an atlas, 14 trunk vertebrae (13 of them rib-bearing), 1 sacral, 2 caudosacral, and 30 caudal vertebrae. The first caudal vertebra is weakly specialized for tail autotomy. It is only slightly shorter than the neighboring vertebrae on each side, and its transverse processes are shorter than those on

Table 1. Samples used in electrophoretic study of proteins.

Sample number	Species	Locality
1	<i>P. brunnata</i>	San Marcos, Guatemala
2	<i>P. goebeli</i>	San Marcos, Guatemala
3	<i>P. juarezi</i>	52 km NE Guelateo, Oaxaca, Mexico
4	<i>P. rex</i>	San Marcos, Guatemala
5	<i>P. rex</i>	Cerro Mozotal, Chiapas, Mexico
6	<i>P. smithi</i>	Cerro San Felipe, Oaxaca, Mexico
7	<i>D. bromeliacia</i>	San Marcos, Guatemala
8	<i>N. pernix</i>	Finca Chiblac, Huehuetenango, Guatemala
9	<i>I. niger</i>	12 km N Berriozabal, Chiapas, Mexico
10	<i>P. saltator</i>	65 km NE Guelateo, Oaxaca, Mexico
11	<i>P. parva</i>	Cerro Baul, 16.8 km NW Rizo de Oro, Oaxaca, Mexico

the first few caudal vertebrae, an unusual condition. Transverse processes of the first caudal vertebra are only slightly swept forward from near the anterior end of the vertebra. Transverse processes are distinct on all but the last two, tiny caudal vertebrae.

The hands and feet are typical for *Pseudoeurycea*, except that there is no sign of a tibial spur. Terminal phalanges have moderate distal expansion (Fig. 3).

The hyobranchial apparatus is generally typical of the genus, but there is a distinct, well-developed lingual cartilage on the basibranchial.

**RANGE.** *Pseudoeurycea parva* has been collected only on and around Cerro Baul, a relatively isolated 2,000-m peak that lies along the continental divide just east of the Isthmus of Tehuantepec (Fig. 1). The cluster of known localities is in easternmost Oaxaca, 5–10 km west of the state border with Chiapas. Access to the area is from Chiapas, via the Pan-American highway and a rough track from the settlement of Rizo de Oro. Topographic maps indicate the existence of poorly explored montane areas, some of them higher and more extensive than Cerro Baul, just west of the type-locality. Assuming these uplands also support cloud forest, *P. parva* may have a somewhat larger range than present records indicate. Nevertheless, the low-lying, subhumid Isthmus of Tehuantepec, less than 25 km W of Cerro Baul, constitutes a major distributional barrier (Fig. 1). East of the type-locality, elevations drop below 1,500 m for nearly 50 km, before rising to 2,000 m at Cerro Tres Picos, near Tonalá, Chiapas. The salamander fauna at Cerro Tres Picos includes an endemic *Dendrotriton* (*D. megarhinus*) and an undescribed large *Bolitoglossa* of the *franklini* species-group (Wake and Lynch, 1982), but *P. parva* has not been found there.

**HABITAT AND HABITS.** All specimens of *P. parva* have been collected inside arboreal bromeliads within cloud forest at elevations ranging from 1,500 to 1,900 m. The large tank-type bromeliads used by the species have been identified as species of *Vriesia* and *Tillandsia* (D. Breedlove, pers. comm.). The only other salamander reported from Cerro Baul, a small *Bolitoglossa* of the *rufescens*-

*occidentalis* group, also occurs inside arboreal bromeliads. The specific name *parva* is a Latin word meaning small.

PROTEIN COMPARISONS

METHODS

Both *P. parva* and *P. saltator* are distinctive morphologically, and their recognition as valid species does not depend on biochemical data. However, we have employed starch-gel electrophoresis of proteins as an independent means for assessing the degree of genetic differentiation of the two new species. In the future we hope to address problems of paraphyly (and possibly polyphyly) within *Pseudoeurycea* (Wake and Lynch, 1976; Maxson and Wake, 1981; Wake and Elias, 1983). Here, we consider three narrower questions. (1) Are *P. saltator* and *P. parva* close phyletic relatives? (2) Which other species of *pseudoeurycea* are most closely related to the two new species? (3) Does discovery of *P. parva* and *P. saltator* provide insight into the cladistic relationships among *Pseudoeurycea*, *Ixalotriton*, *Nyctanolis*, and *Dendrotriton*?

The procedures we employed for study of proteins have been described in detail elsewhere (Lynch *et al.*, 1977, 1983; Wake and Lynch, 1982). Briefly, we used horizontal starch-gel electrophoresis to analyze variation in 13 proteins in the two new species and in five described species of *Pseudoeurycea* (*P. brunnata*, *P. goebeli*, *P. juarezi*, *P. rex*, *P. smithi*), one species of *Dendrotriton* (*D. bromeliacia*), *Nyctanolis pernix*, and *Ixalotriton niger* (Table 1). An additional four proteins were analyzed for some taxa. Only two specimens from each population were used for most comparisons. The various taxa are sufficiently well differentiated that even small samples should provide useful information (Gorman and Renzi, 1979). Indeed, they are so distant from one another cladistically that they have few similarities, and even these should be considered suspect. A practical difficulty is that so many cross comparisons are required that tissue extracts are often exhausted before questions of protein identity are resolved.

Table 2. Proteins and conditions of analysis.

Enzyme	Enzyme commis- sion number	Locus	Buffer	Voltage and time run
Phosphogluconate dehydrogenase	1.1.1.44	pgdh	Tris maleate with NADP in gel	100 V (3.5 h)
Adenosine deaminase	3.5.4.4	ada	Tris maleate with NADP in gel	100 V (3.5 h)
Glycerol-3-phosphate dehydrogenase	1.1.1.8	gpd	Tris maleate with NADP in gel	100 V (3.5 h)
Isocitrate dehydrogenase	1.1.1.42	icdh-1,2	Tris citrate, pH 8.0	130 V (4 h)
Mannose phosphate isomerase	5.3.1.8	mpi	Tris citrate, pH 8.0	130 V (4 h)
Iditol dehydrogenase	1.1.1.14	iddh	Tris citrate, pH 8.0	130 V (4 h)
Phosphoglucomutase	2.7.5.1	pgm-1,2	Tris citrate, pH 8.0	130 V (4 h)
Phosphoglucose isomerase	5.3.1.9	pgi	Tris citrate, pH 7.0	180 V (3 h)
Leucine aminopeptidase	3.4.11.1	lap	Tris citrate, pH 7.0	180 V (3 h)
Malate dehydrogenase	1.1.1.37	mdh-1,2	Tris citrate, pH 7.0	180 V (3 h)
Aspartate aminotransferase	2.6.1.1	aat	LiOH	300 V (3 h)
Tripeptide aminopeptidase	3.4.11.4	pep-b	LiOH	300 V (3 h)
Dipeptidase	3.4.13.11	pep-c	LiOH	300 V (3 h)
Lactate dehydrogenase	1.1.1.27	ldh	Poulik	250 V (3 h)

RESULTS

The comparison of 13 proteins yielded 70 presumptive genetic alleles ( $x = 5.4$  per locus); the comparison of 17 proteins yielded 101 alleles ( $x = 5.9$  per locus), but there were difficulties in accu-

rately scoring the four additional proteins in some samples. The following discussion is based on the results of the more reliable 13-locus study, except where otherwise noted (Tables 2 and 3). We fully realize that this is too low a number of proteins to be of critical value in determining phylogenetic pat-

Table 3. Allele frequencies for 13 allozyme loci. Lowercase letters in the body of the table refer to electrophoretically distinguishable alleles. For abbreviations see Table 2.

Locus	Species sample number (see Table 1)						
	1 (n = 2)	2 (n = 2)	3 (n = 2)	4 (n = 2)	5 (n = 3)	6 (n = 2)	7 (n = 2)
pgdh	d (1.00)	b (1.00)	c (0.250) d (0.750)	c (0.750) d (0.250)	c (0.333) d (0.667)	b (1.00)	e (1.00)
icdh-1	c (1.00)	h (0.750) i (0.250)	f (1.00)	g (0.750) h (0.250)	h (0.333) i (0.667)	d (1.00)	a (1.00)
icdh-2	a (1.00)	b (1.00)	b (1.00)	b (1.00)	b (1.00)	a (1.00)	a (1.00)
mpi	b (1.00)	b (1.00)	a (0.250) b (0.750)	c (1.00)	a (0.167) b (0.833)	b (1.00)	d (1.00)
iddh	d (1.00)	e (1.00)	b (1.00)	e (1.00)	c (1.00)	e (1.00)	e (1.00)
pgm-1	b (1.00)	d (1.00)	c (1.00)	b (1.00)	b (1.00)	b (1.00)	b (1.00)
pgm-2	c (1.00)	d (1.00)	b (1.00)	c (1.00)	c (1.00)	c (1.00)	c (1.00)
pgi	d (1.00)	d (1.00)	a (0.250) b (0.750)	d (1.00)	d (1.00)	d (1.00)	b (1.00)
lap	c (1.00)	d (1.00)	a (0.250) c (0.750)	c (1.00)	c (1.00)	b (1.00)	f (1.00)
aat	e (1.00)	f (1.00)	e (1.00)	f (1.00)	f (1.00)	e (1.00)	c (1.00)
pep-b	b (1.00)	a (0.250) c (0.750)	c (0.750) d (0.250)	b (1.00)	b (1.00)	b (1.00)	c (1.00)
pep-c	b (1.00)	c (0.250) e (0.500) g (0.250)	c (1.00)	d (0.500) f (0.500)	c (0.667) e (0.167) g (0.167)	e (1.00)	g (1.00)
ldh	c (1.00)	c (1.00)	b (0.250) c (0.750)	f (1.00)	e (1.00)	c (1.00)	b (1.00)

terns. However, the data demonstrate the distinctiveness of the species and serve to generate hypotheses of relationship. For practical reasons of comparison with the now-extensive literature on protein evolution in salamanders, we present Nei genetic distances, but we recognize that at the levels of differentiation we have found, any distant measure has little reliability as an exact measure.

The smallest value in the genetic distance matrix ( $D_N = 0.3$ ; 3 fixed allelic differences) separates two geographically isolated populations of *P. rex*. The smallest  $D_N$  value for between-species comparisons ( $D_N = 0.5$ ; 5 fixed allelic differences) separates *P. brunnata* and *P. smithi*. At the opposite extreme, several values exceed  $D_N = 1.5$ , the maximum being 4.1 (12 fixed allelic differences) between *P. goebeli* and *P. parva*. The degree of genetic differentiation between *P. parva* and *P. saltator* ( $D_N = 0.8$ ; 6 fixed allelic differences) is substantial in comparison to other salamander genera (Highton and Larson, 1979; Larson, 1984; Larson et al., 1981). In the 17-locus comparison, the degree of differentiation between *P. parva* and *P. saltator* increases to  $D_N = 1.0$ , with 10 of 17 loci having apparent fixed allelic differences. The proteins we examined of the two new species are more similar to one another than they are to any other species of *Pseudoeurycea* or to the other genera included in our comparison.

Table 3. Extended.

Species sample number			
8 (n = 2)	9 (n = 2)	10 (n = 2)	11 (n = 2)
f (1.00)	a (1.00)	c (1.00)	a (1.00)
b (1.00)	e (1.00)	f (1.00)	b (1.00)
a (1.00)	a (1.00)	c (1.00)	a (1.00)
d (1.00)	b (1.00)	a (1.00)	a (0.500) c (0.500)
a (1.00)	c (1.00)	d (1.00)	d (1.00)
d (1.00)	a (0.500) b (0.500)	b (1.00)	b (1.00)
d (1.00)	a (1.00)	a (1.00)	a (1.00)
c (1.00)	b (1.00)	b (1.00)	b (1.00)
f (1.00)	d (1.00)	e (1.00)	b (1.00)
a (1.00)	a (1.00)	b (1.00)	b (0.750) d (0.250)
c (0.500) d (0.500)	c (1.00)	c (1.00)	c (0.750) d (0.250)
c (1.00)	a (1.00)	c (1.00)	a (0.250) b (0.750)
a (1.00)	b (1.00)	b (0.750) d (0.250)	a (1.00)

Other than *P. saltator*, the species of *Pseudoeurycea* most similar to *P. parva* is *P. brunnata* ( $D_N = 1.0$ ; 8 fixed allelic differences); relative to *P. saltator*, the most similar species other than *P. saltator* is *P. juarezi* ( $D_N = 1.0$ ; 10 fixed allelic differences). There is substantial asymmetry in these results in that *P. saltator* is much more differentiated from *P. brunnata* ( $D_N = 1.9$ ; 11 fixed allelic differences) than is *P. parva*. Conversely, *P. parva* is more highly differentiated from *P. juarezi* ( $D_N = 2.3$ ; 10 fixed allelic differences) than is *P. saltator*.

The two species that are least differentiated from *Ixalotriton* are *P. parva* ( $D_N = 0.9$ ; 6 fixed allelic differences) and *P. saltator* ( $D_N = 1.1$ ; 8 fixed allelic differences). *Nyctanolis* is more similar to *Ixalotriton* ( $D_N = 1.3$ ; 9 fixed allelic differences) than are the remaining species of *Pseudoeurycea* in our sample. However, the species most similar to *Nyctanolis* is *P. parva* ( $D_N = 1.1$ ; 9 fixed allelic differences), followed by *Ixalotriton*, then a group of 4 species of *Pseudoeurycea*, including *P. saltator* ( $D_N = 1.5-1.6$ ). *Dendrotriton* differs substantially from all other taxa (minimum  $D_N = 1.4$ ).

DISCUSSION

As currently constituted, the genus *Pseudoeurycea* is a taxonomic category of convenience. Its species, many of which are rather generalized in morphology, share no uniquely derived osteological traits. Instead, the species assigned to *Pseudoeurycea* are characterized mainly by their lack of the derived traits that define other plethodontid genera (Wake and Elias, 1983). Electrophoretic analysis of proteins (Lynch et al. 1977, 1983; data presented herein; unpubl. data) and immunological studies (Maxson and Wake, 1981) indicate the existence of ancient phyletic divisions within *Pseudoeurycea*, but difficulties in obtaining fresh specimens of key taxa have made comprehensive biochemical comparisons impossible. In addition, few, if any, morphological traits are unambiguously correlated with biochemical patterns of similarity. Finally, there are a number of undescribed species that may affect the construction of new generic or subgeneric categories, as well as nominal species (e.g., *P. bellii*) that may constitute species groups.

Several species that may be related to *Pseudoeurycea* have been assigned to new genera (*Ixalotriton*, *Nyctanolis*, *Dendrotriton*) on the basis of a few rather accentuated morphological differences that may not accurately reflect cladistic relationships. Some species-groups of *Pseudoeurycea* (sensu lato) may be closer cladistically to these genera than they are to each other (Maxson and Wake, 1981). Our protein data suggest the possibility that one or both of the two new species may be closer to *Ixalotriton* or *Nyctanolis* than to at least some other species of *Pseudoeurycea*.

Comparative osteological information provides conflicting indications of relatedness. For example, *Dendrotriton* differs from some *Pseudoeurycea* (in-

cluding the two new species) and from *Ixalotriton* and *Nyctanolis* in having septomaxillae (a plesiomorphic trait also found in certain species of *Pseudoeurycea*; see Wake and Elias, 1983), and from all species of these genera in lacking prefrontals and having large nostrils as juveniles and large openings of the olfactory sac throughout life (synapomorphies). *Nyctanolis* has divided premaxillary bones, an attached lingual cartilage, and tibial spurs, all plesiomorphic traits. All other genera of tropical plethodontid salamanders have a single premaxillary bone, a synapomorphy (Elias and Wake, 1983). Free lingual cartilages (an apomorphy) are found in *Ixalotriton*, *Dendrotriton*, and some *Pseudoeurycea*, including *P. parva*, but lingual cartilages are absent (another apomorphy that may be derived from the free lingual cartilage or may be independent of it) in other *Pseudoeurycea*, including *P. saltator*. Tibial spurs are present in most species of *Pseudoeurycea*, including *P. saltator*, but are absent (an apomorphy) in *Dendrotriton*, *Ixalotriton*, and *P. parva*. In one very specialized and apomorphic trait, the possession of enlarged, hook-like premaxillary teeth (Taylor, 1941), *P. saltator* differs from *P. parva* and all other neotropical salamanders except *P. smithi* and *P. unguidentis*, two species from northern Oaxaca.

Thus, while the protein evidence favors a hypothesis of relatively close relationship between the two new species, the morphological evidence suggests that *P. saltator* is clearly aligned with *Pseudoeurycea*, whereas *P. parva* is more isolated cladistically. The latter species may be more closely related to species currently assigned to other genera (e.g., *Ixalotriton*) than to the remainder of the genus *Pseudoeurycea*.

The group of species and genera considered here may represent cladistic fragments of a basal radiation in the supergenus *Bolitoglossa*. The deep genetic differentiation of the group and the ambiguous nature of the morphological data suggest a complex pattern of mosaic evolution. As a result, it is impossible to present a well-supported cladistic hypothesis at the present time.

## HISTORICAL BIOGEOGRAPHY

Recent discoveries of new salamander species and genera in southeastern Mexico and adjacent Guatemala (e.g., Lynch and Wake, 1975, 1978; Wake and Lynch, 1982; Elias and Wake, 1983; Wake and Elias, 1983; Elias, 1984; Wake and Papenfuss, 1987; Wake and Johnson, 1989), and systematic revision of known genera (Wake and Elias, 1983), have strengthened our earlier conclusion (Wake and Lynch, 1976) that the mountains of nuclear Central America and the adjacent highlands of Oaxaca are major evolutionary centers for neotropical plethodontids. However, we previously emphasized the importance of the relatively young (Pliocene-Pleistocene) volcanic highlands of nuclear Central America as centers of species proliferation (Wake

and Lynch, 1976), whereas it has become increasingly evident that the ancient (pre-Cretaceous) geologic core of the region has been the site of a much older and more profound phyletic radiation. Since 1976, four new plethodontid genera (*Bradytriton*, *Dendrotriton*, *Ixalotriton*, *Nyctanolis*) have been discovered to be endemic to a limited area of ancient mountains in Chiapas and adjacent Guatemala; five other widespread plethodontid groups (*Bolitoglossa*-alpha, *Bolitoglossa*-beta, *Nototriton*, *Oedipina*, *Pseudoeurycea*) occur in the same region, which thus contains representatives of all generic groups of plethodontids that occur anywhere in nuclear Central America (Wake and Lynch, 1976; Wake and Elias, 1983). Only the Orizaba region of Veracruz, Mexico, with seven generic-level groups (*Bolitoglossa*-alpha, *Bolitoglossa*-beta, *Pseudoeurycea*, *Chiropterotriton*, *Lineatriton*, *Parvimolge*, *Thorius*) approaches the generic diversity of the plethodontid fauna of eastern Chiapas and western Guatemala. Although the precipitous Atlantic slope of Oaxaca, where *P. saltator* occurs, lies between these two major centers of endemism and diversity, the Atlantic highlands of Oaxaca are separated from nuclear Central America by the low-lying, sub-humid Isthmus of Tehuantepec. The mountains of northern Oaxaca are rich in endemic plethodontid species (Wake, 1987; Wake *et al.*, 1988), but the salamander fauna of the area is not distinctive at the generic level; five of the six generic groups that occur in northern Oaxaca (*Bolitoglossa*-alpha, *Bolitoglossa*-beta, *Pseudoeurycea*, *Chiropterotriton*, *Thorius*) also are found in the Orizaba region. The sole exception is the recently described *Nototriton adelos* Wake and Papenfuss, 1987, whose affinities lie to the southeast, in nuclear Central America.

Despite earlier views that the Isthmus of Tehuantepec was the locus of a Tertiary marine portal (e.g., Stuart, 1966), geologists now believe the area has been land-positive since at least the Cretaceous (Malfait and Dinkelman, 1972). Nevertheless, the isthmian region must have formed a long-standing distributional barrier for animals that require cool, humid conditions (Halffter, 1987). Two lowland species of *Bolitoglossa* (*B. mexicana*, *B. rufescens*) occur on both sides of the Isthmus, but no montane species does so. Indeed, the only species-groups of high-elevation salamanders with representatives east and west of the Isthmus are the *gadovii* group of *Pseudoeurycea* (*sensu* Maxson and Wake, 1979) and, possibly, two recently described species of *Nototriton* (Papenfuss and Wake, 1987). Apart from *P. parva*, just five species of *Pseudoeurycea* range east of the Isthmus of Tehuantepec: *P. brunnata*, *P. expectata*, *P. goebeli*, *P. rex*, and an undescribed Guatemalan species (Wake and Lynch, 1976). All are found at high elevations (above 2,500 m) in Guatemala and easternmost Chiapas, usually in terrestrial microhabitats. Our analysis of protein data suggests that this assemblage is only distantly related to *P. saltator* and *P. parva*.

Both *P. parva* and *P. saltator* have ambiguous

relationships to other *Pseudoeurycea* and to allied genera. *Pseudoeurycea parva* resembles *Dendrotriton* in habitus, and is intermediate in overall size between the largest *Dendrotriton* and the next smallest *Pseudoeurycea*. The habitat/microhabitat association of *P. parva* (arboreal bromeliads in mid-elevation cloud forests) is typical of *Dendrotriton* (Wake and Lynch, 1976; Lynch and Wake, 1975, 1978) but unusual in *Pseudoeurycea*, most species of which inhabit terrestrial microhabitats at high elevations (Wake and Lynch, 1976). Three allopatric *Dendrotriton* (*D. bromeliacia*, *D. xolocalcae*, *D. megarhinus*) occupy the three known isolates of montane cloud forest along the Pacific versant between western Guatemala and the range of *P. parva*, a fact consistent with the hypothesis that both groups comprise remnants of a once continuous range. On the Atlantic versant, the ecological roles of *Dendrotriton* and *P. parva* are filled by *D. rabbi* in west-central Guatemala, *Nyctanolis* in western Guatemala and adjacent Chiapas, *Ixalotriton* in central Chiapas, and *P. saltator* in central Oaxaca. Again, the fact that none of the eight species of small to medium-sized arboreal specialists are sympatric is consistent with the hypothesis that a breakup of formerly continuous areas of cloud forest stranded ancestors of these salamanders within isolated areas of favorable habitat on the margins of the ancient core of nuclear Central America.

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