TWO NEW SPECIES OF PLETHODONTID SALAMANDERS (GENUS NOTOTRITON) FROM MEXICO

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RESUMEN

Wake y Elias (1983) encontraron que el género de salamandra Chiropterotriton (Plethodontidae) es polifilético. Dos nuevos géneros, Dendrotriton y Nototriton, fueron establecidos para aquellas especies presentes al sur y al oriente del Istmo de Tehuantepec, previamente incluidas en Chiropterotriton. En este trabajo se informa del descubrimiento del género Nototriton en México y de la definición de cuatro grupos de especies. Se describen dos nuevas especies: Nototriton alvarezdeltoro, habitante del declive caribeño de la Mesa Central de Chiapas, y N. adelos, único miembro del grupo adelos, habitante de la ladera caribeña de la Sierra de Juárez, Oaxaca. El grupo nasalis también se presenta en Guatemala y Honduras, mientras que los grupos picadoi y richardi se conocen sólo de Costa Rica. N. adelos es de especial interés ya que se encuentra en simpatría con el género norteño Chiropterotriton.

ABSTRACT

The plethodontid salamander genus Chiropterotriton was found to be polyphyletic by Wake and Elias (1983). Two new genera, Dendrotriton and Nototriton, were created for those species south and east of the Isthmus of Tehuantepec which formerly were included in Chiropterotriton. In this paper the discovery of the genus Nototriton in Mexico is announced, and four species groups are defined. Two new species are described: Nototriton alvarezdeltoro from the Caribbean Escarpment of the Mesa Central of Chiapas, a member of the nasalis group, and N. adelos from the Caribbean slopes of the Sierra de Juarez of Oaxaca, the only member of the adelos group. The nasalis group is also known from Guatemala and Honduras. The picadoi and richardi groups occur only in Costa Rica. N. adelos is of special interest because it occurs in sympatry with the northern genus Chiropterotriton.
Mexico has a rich diversity of tailed amphibians, Order Caudata, and the majority of the species are lungless salamanders of the Family Plethodontidae. Despite a moderate amount of scientific work with Mexican salamanders, the group remains relatively poorly known. Smith and Smith (1976) considered salamanders to be the least well known of the major groups of Mexican amphibians and reptiles and predicted that many additional species and genera would be discovered. Their prediction has already been validated in part by recent descriptions of new genera and species of plethodontids (Wake and Elias, 1983; Lynch, Wake, and Yang, 1983; Papenfuss, Wake, and Adler, 1983; Elias and Wake, 1983). In this paper we report the first record of the plethodontid genus *Nototriton* from Mexico and describe two new species from the states of Oaxaca and Chiapas.

The genus *Nototriton* was described relatively recently (Wake and Elias, 1983) and it is a poorly known group previously thought to range from Guatemala to Costa Rica. Because there has been a complex taxonomic history of this genus, and because its status as a monophyletic group is still somewhat in doubt, we believe that it is important that we present an historical summary of our knowledge of this group of species and their taxonomy.

Sixty years ago, Emmet Reid Dunn (1926) recognized 31 species of neotropical salamanders, all placed in the genus *Oedipus* Tshudi (1838). Eighteen years after Dunn's monograph, 76 species were recognized (Taylor, 1944). The genus *Oedipus* had been suppressed by Taylor (1940) because it was preoccupied by *Oedipus* Berthold (1827), an orthopteran genus. Taylor included four species of small Mexican salamanders in the revived genus *Thorius* Cope (1869), and placed the remaining neotropical species in the genus *Bolitoglossa* Duméril, Bibron, and Duméril (1854).

The more than two-fold increase in named species between 1926 and 1944 resulted almost entirely from field work by Smith and Taylor in Mexico (22 species), Schmidt in Guatemala and Honduras (10 species), and Stuart in Guatemala (3 species). In retrospect it seems surprising that such an array of morphologically well-differentiated species was placed in the single genus *Bolitoglossa*. In addition to non-specialized terrestrial forms, there were elongate, short-legged fossorial species as well as arboreal species, some with fully webbed feet, all included in *Bolitoglossa*. Far less differentiated species in North Ameri-
ca (for example, species in the genera *Plathodon, Ensatina* and *Aneides*) had long been separated at the generic level.

Taylor (1944) finally sorted the 71 species of *Bolitoglossa* he recognized into seven genera, but North American herpetologists were slow to accept his taxonomy. Twenty species were referred, or tentatively referred, to *Bolitoglossa*. Two old generic names were resurrected. Seven species of elongate, terrestrial salamanders were placed in *Oedipina* Keferstein (1868), and a single Costa Rican form was placed in *Haptoglossa* Cope (1893). This species later was synonymized with *Oedipina uniformis* by Brame (1968). Taylor placed the remaining species in four new genera: *Magnadigita* (later synonymized back into *Bolitoglossa* by Wake and Brame, 1963), with 14 species; *Parvimolge*, a monotypic genus; *Pseudoeurycea* with 18 species; *Chiropterotriton* with 11 species.

All but three of Taylor’s species of *Chiropterotriton* occur in upland areas of central Mexico. Only his *C. xolocalcae* (Chiapas), *C. bromeliacae* (Guatemala), and *C. nasalis* (Honduras) are found south of the Isthmus of Tehuantepec. Taylor speculated that “When the Central American countries south of Guatemala are better explored herpetologically it seems likely that the genus will be traced farther to the south than it is now known” (Taylor, 1944, p. 218). Four years later Taylor (1948) described *C. abscondens* from Costa Rica. This species was later synonymized with *C. picadoi* (Wake and Lynch, 1976), a form known to Taylor (1944), but not referred to any of his seven genera as a result of the poor state of preservation of the specimens he examined. Taylor (1949) referred to the species as *Pseudoeurycea?* (stet.) *picadoi* and in 1952 finally assigned it to *Chiropterotriton* and stated that “The relationship of this species is, I believe, undoubtedly with the species I have described as *Chiropterotriton abscondens*” (Taylor, 1952, p. 705).

In a study of *Chiropterotriton* of northeastern Mexico, Rabb (1958) briefly noted that “the species south of the Isthmus of Tehuantepec differ somewhat in skeletal anatomy and may be subgenerically separable from the species of northern Mexico.” Rabb (1960) described *C. megarhinus* from northwestern Chiapas. He suggested that members of the genus from south of the Isthmus fell into two osteologically recognizable groups. He placed *C. megarhinus, C. xolocalcae* from southwestern Chiapas, and *C. bromeliacae* from northwestern Guatemala in one group and the more southern *C. nasalis* from Honduras, and *C. pi-
cadoi and C. abscondens, both from Costa Rica, in a second group. He stated "the pattern of speciation for the southern Chiropterotriton, in light of the distribution of the characteristics mentioned above, reflects a single invasion from the north followed by at least two radiations in the new territory".

Wake (1966), in a detailed study of plethodontid salamander osteology, examined four species of Chiropterotriton from north of the Isthmus of Tehuantepec and four from south of the Isthmus. He found that the northern (and presumably more primitive) species usually have prefrontals, septomaxillae, tibial spurs and vomerine preorbital processes. These elements were lacking in various combinations in the southern species.

Lynch and Wake (1975) described C. cuchumatanus and C. rabbi from western Guatemala and placed them in the C. bromeliacia group (along with C. megarhinus and C. xolacalcae). The bromeliacia group was defined as Chiropterotriton with a generalized Pseudoeurycea-like tarsal arrangement, but differing from all Pseudoeurycea in lacking prefrontal bones. Lynch and Wake stated that the closest relatives of the bromeliacea group were the Honduran species C. nasalis and C. barbouri. They also suggested that, as an alternative hypothesis to Rabb (1960), the species of Chiropterotriton occurring south of the Isthmus of Tehuantepec may "represent an autochthonous evolutionary radiation from a generalized Pseudoeurycea-like ancestor."

Wake and Lynch (1976) referred to all species north of the Isthmus as Chiropterotriton alpha and all species south of the Isthmus as Chiropterotriton beta. They suggested that each group merited generic status. Within Chiropterotriton beta, two species groups were recognized. The bromeliacia group contained the five species of Lynch and Wake (1975) and the picadoi group included C. picadoi, C. barbouri, C. nasalis, and C. richardi, a rare Costa Rican species that originally had been placed in the genus Parvimolge by Taylor (1949).

Lynch and Wake (1978) described C. veraepacis from Baja Verapaz, Guatemala and placed it in the nasalis group, changing the name from the picadoi group but keeping the composition. They noted that the nasalis group showed more morphological and ecological diversity than the bromeliacia group and could be subdivided into three parts. First, a northern group of arboreal species that is well defined osteologically (C. nasalis, C. barbouri, and C. veraepacis).
Second, the Costa Rican *C. picadoi*, which is similar in some osteological features to the first group, but differs in some other osteological features as well as in external morphology and ecology. Third, the Costa Rican *C. richardi*, an elongate, short legged semifossorial species.

Maxson and Wake (1981) used the immunological technique of microcomplement fixation to examine albumin evolution in *Chiropterotriton*. Immunological distance between *C. multidentatus* (alpha) and *C. bromeliacia* (beta) was greater than between either of these species and most species of *Pseudoeurycea* examined. They argued that the separation of *Chiropterotriton* alpha and beta was ancient, perhaps in excess of 50 million years. Within *Chiropterotriton* beta, two members of the *bromeliacia* group (*C. rabbi* and *C. cuchumatanus*) were relatively close to *C. bromeliacia*, with immunological distances of 14 and 21 (approximately 8 and 12 million years). However, when the albumin of two other members of *Chiropterotriton* beta (*C. nasalis* and *C. veraepacis*) was compared to *C. bromeliacia* antiserum, the immunological distances were 64 and 67, suggesting a time separation in excess of 35 million years. Neither of the Costa Rican species was examined.

Wake and Elias (1983), using mainly osteological characters, reviewed the status of all of the genera of tropical plethodontids. The genus *Chiropterotriton* was found to be polyphyletic and two new genera were described for the forms living south of the Isthmus of Tehuantepec. The *bromeliacia* group of *Chiropterotriton* beta was placed in the new genus *Dendrotriton* and the *picadoi* group (exactly equivalent to what they called the *nasalis* group) was placed in the new genus *Nototriton*. *Bolitoglossa diminuta* Robinson (1976) was included in *Nototriton*, but *C. richardi* was included with reluctance because of its unusual combination of primitive and derived characters. Wake and Elias found no unique synapomorphies for *Nototriton*, and stated that it may be paraphyletic.

The six species assigned to *Nototriton* occur in isolated populations in cloud forests at moderate elevations (ca. 1,000 - 3,000 m) from the Meseta Central of Costa Rica to eastern Guatemala, with a hiatus in the lowlands of Nicaragua and eastern Honduras (Fig. 1). Most species are known from few specimens and occur only in limited geographic areas. The two new species described below extend the range of the genus north into Mexico.

One of the new species occurs north of the Isth-
The distribution of the species of *Nototriton* in Middle America. The ranges shown are generalized from locality data available in the literature or from museum records.

mus of Tehuantepec, in local sympatry with both *Chiropterotriton* and *Thorius*. This species, known only from four specimens, is so small that in the ten years since they were first discovered the specimens were misidentified as members of the genus *Thorius*. We name this species
Nootriton adelos New Species

Figure 2

The holotype of *Nootriton adelos*, MVZ 112226, an adult male from 65 km NE Guelatao, Oaxaca, Mexico. Scale bar is 25 mm.


*Paratypes.*—MVZ 112225, same locality and date as the holotype; MVZ 183359, 0.5 km S. Vista Hermosa (along Hwy. 175), Oaxaca, Mexico, 1530 m. Collected by James Hanken on February 7, 1976; University of Rome (uncatalogued), La Hesperanza (La Esperanza), Tuxtepec, Oaxaca, Mexico, 1900 m. Collected by V. Sbordoni on August 8, 1973.

*Diagnosis.*—A member of the genus *Nootriton* differing from other members of the genus (Table 1) by the following combination of characters: tail relatively short (1.05-1.19 times SL); foot width
narrow (.06 times SL); nostril diameter moderate (.016-.019 times SL); combined limb length moderate (.40-.45 times SL).

Description of Holotype.—This adult (Fig. 2) male has a rounded snout and moderate nostrils that tilt slightly upward. The distinct nasolabial grooves extend from the posterior margin of each nostril to the lip. The suborbital grooves angle beneath the eyes and end in shallow pockets below the posterior margins of the eyes; they do not intersect the lip. The eyes are moderate and when viewed from above protrude slightly beyond the jaw. There is a single pre-maxillary tooth, 26 maxillary teeth, and 6 vomerine teeth. The limbs are short (though of moderate length for the genus) and are separated by 4 costal grooves when appressed along the body. The hands and feet are small with extensive fusion of digits. On each hand the first digit is fused to the second and the fourth digit to the third. The tips of digits two and three are free. On each foot the first digit is fused to the second and the fifth digit to the fourth. The tips of digits two, three, and four are free. Concave disks are present on the underside of the free digit tips on both hands and feet. The distinct costal folds extend from just lateral of the middorsal line onto the venter. The relatively short tail, which is only slightly constricted at the base, tapers gradually.

Measurements (in mm).—Head width 3.1; snout to gular fold 3.9; snout to posterior angle of vent 21.1; axilla to groin 11.5; tail 25.1; forelimb length 3.8; hind limb length 4.7; width of right foot 1.2.

Coloration in Alcohol.—The backround color on the dorsal surface of the head, trunk, and tail is brown. Tan iridophores form an irregular veil-like network over the head, body, and on to the tail. There is a dorsal cream colored stripe on each side that starts on the head at a point above the gular fold, curves inward toward the midline above each arm, then curves dorsolaterally onto the side, and stops abruptly at the second costal groove. Lateral to each cream colored stripe, a dark brown stripe runs from the second costal groove along the side of the trunk and neck, then just anterior to the gular fold, the stripe curves upward on to the dorsolateral edge of the head and continues over the orbit to the anterior margin of the orbit. The sides of the trunk are a darker brown than the dorsum. This contrast gives the appearance of a vague, lighter dorsal stripe. The venter is light brown with scattered cream flecks on the tail and belly. The chin is cream
with irregular light brown blotches. The limbs are light brown with scattered cream flecks. The three paratypes resemble the holotype in coloration. In the University of Rome specimen, the dorsum is tan with small paired brown spots above each costal groove. The tail is pale yellow with broken lateral brown stripes and a mid-dorsal brown stripe on the anterior part of the tail that breaks up into spots more posteriorly.

**Habitat.**—All four specimens were obtained in humid cloud forest on the Caribbean slopes of the Sierra de Juarez between 1530 and 2050 m. The holotype and MVZ 12225 were found inside arboreal bromeliads. At this site (elev. 2050 m) *Nototriton* is uncommon, at least during August. Only two were found after opening about 200 bromeliads. Two other salamanders, both undescribed, (*Pseudoeurycea* sp. and *Chiropterotriton* sp.) were common in bromeliads. Some 30 of each were taken. A single *Thorius* sp. was found under a rock. On additional visits to this locality in Nov. 1974, July 1976, April 1980, and Oct. 1981 no *Nototriton* were found although other salamanders were obtained.

**Etymology.**—The species name is the Greek word *adelos*, meaning unseen or obscure, in reference to its having been overlooked and its relative obscurity.

A second species of *Nototriton* has been discovered on the Caribbean slopes of the Mesa Central of Chiapas, Mexico. We name this species

*Nototriton alvarezdeltoroi* New Species

**Holotype.**—Museum of Vertebrate Zoology (MVZ) 158942. An adult male from 21.5 miles (34.6 km) N (by Mex. Hwy. 195) of Jitotol, Chiapas, Mexico, ca. 1550 m (5100 feet). Found at night crawling up a moss bank on August 14, 1976, by Theodore J. Papenfuss and Robert L. Seib.

**Paratype.**—MVZ 201396, Puerto del Viento, 13 km NW Pueblo Nuevo Solistahuacan, Chiapas, Mexico (we believe that this is the same locality as that for the holotype, even though this locality is recorded as "6,000 ft."). Collected July 21, 1972 by Dennis E. Breedlove.
The holotype of *Nototriton alvarezdeltoroi*, MVZ 158942, an adult male from 21.5 miles (34.6 km) N Jitotol, Chiapas, Mexico. Scale bar is 25 mm.

**Diagnosis.**—A member of the genus *Nototriton* differing from other members of the genus (Table 1) by the following combination of characters: tail relatively short (1.08-1.21 times SL); foot width moderate (.08 times SL); nostril diameter large (.024-.026 times SL); combined limb length moderate (.44-.45 times SL).

**Description of Holotype.**—This adult male (Fig. 3) has a blunt snout and large nostrils that point forward. The nasolabial grooves extend from the posterior margin of each nostril to the lips. The suborbital grooves curve beneath the eyes and extend two-thirds the distance to the posterior end of the orbit; they do not intersect the lip. The eyes are moderate and when viewed from above protrude slightly beyond the jaw. There are three premaxillary teeth, 49 maxillary teeth, and 9 vomerine teeth. The limbs are moderate in length and, when appressed along the body, are separated by four costal grooves. The hands and feet are moderate with extensive webbing of the digits. On each hand the tips of digits two, three, and
four are free. On each foot the tips of digits two, three, four, and five are free. The costal folds extend from just lateral of the middorsal line onto the venter. The relatively short tail is slightly constricted at the base and tapers gradually.

**Measurements (in mm).**—Head width 3.9; snout to gular fold 5.0; snout to posterior angle of vent 26.6; axilla to groin 15.2; tail 32.1; forelimb length 5.8; hind limb length 6.3; width of right foot 2.1.

**Coloration in life.**—The dorsum of the body and tail is rich reddish brown with a very obscure, irregularly bordered, narrow dorsal stripe. There is a pair of light tan patches at the tail base. A few white iridophores surround gland openings on dorsum and tail. There are extensive single cell whitish iridophores ventro-laterally with some grouped into 4 or 5 cell masses. Some greenish chromatophores are present around the chin. The venter is nearly clear with punctate melanophores and a few widely spaced iridophores. The limbs are orange and the toes have clear, colorless tips.

**Habitat.**—This species is known only from the type locality, a small stream that crosses the highway 3.7 miles (6.1 km) below Puerto del Viento on the Caribbean Escarpment of the Mesa Central of Chiapas. At Puerto del Viento there is an abrupt change in vegetation type from pineoak forest to cloud forest. Most of the cloud forest has been cut and only tiny patches remain in stream canyons and on steep slopes. The holotype was found at night crawling up a moss covered rock face about 3 meters above the ground. The only other species of salamander recorded from the area is *Bolitoglossa mexicana*.

**Etymology.**—This species is named to honor Miguel Alvarez del Toro, the leading authority on the herpetology of Chiapas and a man who is dedicated to preserving natural habitats in that state.

**DISCUSSION**

The discovery of species assignable to *Nototriton* in a region so remote from other members of the genus (see Fig. 1) surprised us. Tropical bolitoglossine salamanders are a highly derived group, specialized in using free projectile tongues for feeding and in having direct terrestrial development. The group as a whole is character-
ized by relative structural simplification, with loss and fusion of osteological elements, and it seems that relatively few options for the evolution of novel structures remain. As a result, phylogenesis has involved extensive parallelism and coverage (Wake, 1966; Wake and Elias, 1983), which makes recognition of monophyletic units difficult.

Nototriton, as recognized by Wake and Elias (1983), is a fairly diverse group of rare, secretive, and poorly-known species. It was easily diagnosed in relation to groups with which it co-occurred. The species of Nototriton all are small and can be unambiguously distinguished from Oedipina by having only 14 trunk vertebrae (a plesiomorphic condition), and from Bolitoglossa by having a sublingual fold (also plesiomorphic). Internal morphological details distinguish species of Nototriton from Dendrotriton (see Wake and Elias, 1983; Lynch and Wake, 1978), but most members of the latter genus also have distinctly larger hands and feet than do species of Nototriton. The two species described herein are somewhat different from previously described Nototriton, and we were hesitant to assign them to that genus. The question of generic assignment has been made more difficult by the shortage of material and the unavailability of skeletal preparations. The latter problem has been partially circumvented by our use of radiographs.

The Chiapan species, N. alvarezdeltoroi, is very similar in external morphology to Guatemalan and Honduran members of the genus, all of which occur in cloud forests in areas of Caribbean drainage. In addition, radiographs reveal what we have come to recognize as a unique synapomorphy of a new nasalis species group, here defined as comprising N. alvarezdeltoroi, N. barbouri, N. nasalis, and N. veraepacis. This group has nasal and prefrontal bones of approximately equal size, with a nasal bone that is relatively small for all bolitoglossine genera, and with a prefrontal bone that is pierced, or very strongly evacuated along its anterior border near its contact with the maxillary, for the passage of the nasolacrimal duct (illustrated in Lynch and Wake, 1978). In this group the external nares are large (except in N. barbouri, where they are only slightly enlarged) and they are rotated so that they aim anterodorsolaterally (what is unusual is the dorsal tilting, not found to nearly the same degree in Dendrotriton and Thorius). Thus, even in the absence of more detailed osteological information, the generic placement of N. alvarezdeltoroi seems appropriate.

The question of generic assignment is not so
clear for *N. adelos*. This tiny species was mistaken for a species of *Thorius* until recently, and only the discovery of *N. alvarezdeltoroii* in Chiapas made the assignment of *N. adelos* to *Nototriton* a reasonable possibility. The first problem was to clearly separate this species from the various species of *Thorius* (some undescribed), which occur either in sympatry or very nearby and are about the same size as *N. adelos*. *Thorius* is rarely encountered in bromeliads, which suggests an ecological separation between the two genera, but one of the few *Thorius* we have collected in bromeliads happened to be in the vicinity of the type locality of *N. adelos*. All species of *Thorius* share an apomorphous state, unique in the family Plethodontidae: a cutaneous groove below the eye intersects the upper lip. This condition is not found in *N. adelos*. All *Thorius* have a distinctive, posteriorly oriented spur on the squamosal to which the stapes attaches, another apomorphous state, and this is absent in *N. adelos*. The small size of the species makes these differences relatively difficult to detect, and Hanken (1984), who studied genetic variation in a number of populations and species of the genus *Thorius*, mistakenly included the new species in his study. His population number 45 showed marked differences from nearby members of the genus, and he listed it as an unidentified species. Fortunately, he preserved a voucher specimen of this population (now MVZ 183359), which is a specimen of *N. adelos*.

It is even more difficult to reject assignment of *N. adelos* to either *Chiropterotriton* (which occurs sympatrically with it) or *Parvimolge* (known from not too distant parts of Veracruz, near the city of Orizaba). The foot of the new species is not shaped like that of *Chiropterotriton*, and partial dissection of one specimen has revealed that distal tarsals 4 and 5 are fused, an apomorphous condition not present in either *Chiropterotriton* or *Dendrotriton* (see illustration in Wake and Elias, 1983, Fig. 7). *Parvimolge* is a monotypic genus, and its single species is a small, short-legged and short-tailed animal with a relatively stocky habitus, and it typically has mineralized mesopodial elements. *N. adelos* is a relatively long-tailed species and is very slender; its mesopodials are not mineralized. There are also other reasons for choice of *Nototriton*. While our radiographs are not definitive, it is very likely that *N. adelos* has fused frontal processes on the preaxillary, an apomorphous state found in all members of *Nototriton* except *N. richardi* of Costa Rica. Taking all of the foregoing information into consideration, we conclude that *N. adelos* is most appropriately placed in *Nototriton*. 

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Lynch and Wake (1978) predicted that when additional information became available it would be possible to divide what is now known as Nototriton into three groups: a nasalis group, which we have defined above; a picadoi group, currently containing only one species, N. picadoi from Costa Rica, which has large nasals, has preorbital processes of the vomer, and does not have the prefrontal pierced by the nasolacrimal duct; and a richardi group, also containing only one species, N. richardi from Costa Rica, which is diminutive with syndactyloous hands and feet and has frontal processes of the premaxillary which arise separately. We also add a fourth group, the adelos group, containing only N. adelos. This group is characterized by its diminutive size and the near fusion of the digits of the hands and feet. We know that N. adelos has relatively large nasal bones and lacks vomerine preorbital processes, but have little additional osteological information. Table 1 includes information useful in separating the species of Nototriton.

Finally, we will comment briefly on the status of the species described as Bolitoglossa diminuta by Robinson (1976). This species was placed in Nototriton (Wake and Elias, 1983) because it was small and slender, and did not resemble other Bolitoglossa. The holotype is the only adult known and no osteological information has been available. We recently reexamined this specimen and radiographs of it. Based on the absence of the sublingual fold and the presence of external and internal foot morphology similar to that of other members of the genus, we return it to Bolitoglossa.

ACKNOWLEDGMENTS

We thank officials of the Direccion General de la Fauna Silvestre for providing collecting permits which enabled us to study in Mexico. Silvio Bruno kindly brought the material in the collections of the University of Rome to our attention and sent us the material. James D. Dixon, Robert L. Seib, and James Hanken assisted with the field work. We thank J. Coop for his cooperation. Gene M. Christman prepared Figure 3. James F. Lynch provided useful review of the manuscript. This research has been supported by NSF grant BSR 8305763.
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