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New Species of Lungless Salamanders of the Genus *Pseudoeurycea* (Amphibia: Caudata: Plethodontidae) from Veracruz, Mexico

By

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CONTENTS

ABSTRACT Field studies in the mountains of central Veracruz, Mexico, resulted in discovery of two previously undescribed species of salamanders of the genus *Pseudoeurycea*, a member of the plethodontid tribe Bolitoglossini. A population previously identified as *Pseudoeurycea nigromaculata* is described as a new species, *P. lynchi*. This species, known from three localities, is the apparent sister taxon of *P. nigromaculata*, based on morphological and allozymic similarities and phylogenetic analysis of mitochondrial DNA sequence data. A species with some scansorial propensities, *P. lynchi* occurs mainly under the bark of fallen logs and in and under decaying wood. This species is a member of a relatively rich local community in cloud forest habitat at elevations of 2100–2200 m. The other new species, named *P. naucampatepetl*, is a salamander related to *Pseudoeurycea gigantea*, which we remove from the synonymy of *Pseudoeurycea bellii*. This new species is an attractive animal with a striking color pattern that has inexplicably eluded detection despite extensive collecting in the region. Although *P. naucampatepetl* is strikingly distinct in color pattern from *P. gigantea* and occurs at higher elevations (ca. 3000 m), the two species are closely allied by allozymic and mtDNA characters. The two new species are components of a rich salamander fauna distributed along a local transect on the slopes of Cerro Cofre de Perote.

Key Words: Amphibia; Caudata, Mexico; Veracruz, taxonomy; new species.

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RESUMEN Estudios de campo en las montañas de la región central del estado de Veracruz, México resultaron en el descubrimiento de dos especies nuevas de salamandras pletodontidas, del género *Pseudoeurycea*. Una población, previamente asignada a *P. nigromaculata* se reconoce como especie nueva, *P. lynchi*. Esta especie, conocida para tres localidades, es aparentemente el grupo hermano de *P. nigromaculata*. Dicha relación está basada en datos morfológicos, y también en el análisis de secuencias de ADN mitochondrial y aloenzimas. *Pseudoeurycea lynchi* es una especie con rasgos trepadores que generalmente se encuentra bajo la corteza de troncos caídos o debajo de madera podrida. Esta especie forma parte de una comunidad relativamente rica del bosque nublado, en altitudes de aproximadamente 2100–2200 m. La segunda nueva especie, *P. naucampatepetl*, se relaciona con *P. gigantea*, una especie que se encontraba en la sinonimia de *P. bellii* y que en este trabajo se restablece como un taxon válido. El nuevo taxon a posee una coloración atractiva y un patrón característico, pero había pasado desapercibida a pesar de los muestreos intensivos efectuados en la región a través de los años. Aunque *P. naucampatepetl* difiere drásticamente de *P. gigantea* en la coloración, los datos de ADN mitocondrial y de aloenzimas sugieren una estrecha relación entre ambos táxones. Las dos especies nuevas son parte de la extensa fauna de salamandras que se distribuyen a lo largo de un transecto en las faldas del cerro Cofre de Perote, Veracruz, México.

PALABRAS CLAVES: Amphibia; Caudata, México; Veracruz; taxonomía; especies nuevas.

INTRODUCTION

While studying distributions of tropical salamanders along elevational transects throughout Middle America (Wake et al., 1992), a number of specimens could not be identified. Many tropical plethodontids are confusingly similar in morphology, so comparative biochemical methods are now routinely being used to determine species limits (e.g. Hanken and Wake, 1994). One transect (the Veracruz Transect; Wake et al., 1992), located in the mountains of central Veracruz, Mexico, between Cerro Cofre de Perote and Jalapa, has a large elevational span (1000–4000 m) and includes habitats that range from lowland deciduous forest through cloud forest and pine-oak forest. Although located in a relatively well studied region, this transect yielded new taxa (*Thorius minydemus* and *T. munificus*) and specimens of other taxa that either represented new species or led to the identification of problems with the existing classifications of different taxa (such as the genus *Chiropterotriton*, discussed by Darda, 1994). Here we describe two additional species from this region, both members of the large and taxonomically difficult genus *Pseudoeurycea*. Whereas the two new species of *Thorius* were difficult to recognize in part because of their small size and cryptic morphological differentiation, the new species of *Pseudoeurycea* are morphologically, as well as biochemically distinct, and each has a distinctive color pattern.

ACKNOWLEDGMENTS

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MATERIALS AND METHODS

The descriptions follow the format used by Lynch and Wake (1989) for other species in the genus *Pseudoeurycea*, and include the same basic characters and measurements. Larger measurements were taken using a dial calipers (to the nearest 0.1 mm), but measurements of feet, toes and some head dimensions (e.g., additional measurements of the holotype), as well as tooth counts (ankylosed teeth only), were taken under a stereoscopic microscope equipped with an eyepiece reticle. All measurements are in mm. The distance from the tip of the snout to the poste-

rior end of the vent is treated as standard length (SL). Color notes are based on field notes taken from living specimens.

Some biochemical data are reported. Tissues were extracted from freshly sacrificed specimens and stored at -76 °C. For some of the DNA studies, tail tips were stored in 95% ethanol. Allozyme methods follow Lynch and Wake (1989). Mitochondrial DNA results are reported from the much larger but as yet unpublished study of Parra-Olea (1999), and in general follow laboratory and data analytical methods used in García-París and Wake (2000).

DESCRIPTIONS OF NEW SPECIES

Pseudoeurycea lynchi new species
Veracruz Green Salamander

Pseudoeurycea nigromaculata- Smith, Smith and Werler, 1952:251

Holotype.—Museum of Vertebrate Zoology (MVZ) 230994, an adult female from the top of Cerro San Pedro at Loma Alta Microwave Station, 6 km ENE Chiconquiaco, Veracruz, Mexico (19°45.3' N, 96°46.9' W, 2160 m elevation), collected by G. Parra-Olea, M. García-París, and D. B. Wake, on October 15, 1997.

Paratypes.—MVZ 230995–231000 (6 specimens), same data as holotype; MVZ 158821, 158824–25, 178841–43, 203669–70, 203672- 203675 (12 specimens), KU 290071 from forest west of La Joya, Veracruz, Mexico (19°36.9'N, 97°01.9'W, elevation 2120 m); UIMNH 21808, 21811, 21814, " 3 miles" (4.8 km) E Las Vigas, Veracruz, Mexico.

Referred specimens.—MVZ 231001–05, same data as holotype (subadults and juveniles).

Diagnosis.—This relatively small species of *Pseudoeurycea* is distinguished from all other members of the genus by its greenish to yellow-green coloration. It is further distinguished from *Pseudoeurycea nigromaculata* by its more robust habitus and somewhat fewer maxillary (average 75 versus 89 in adults) and more numerous vomerine (average 36 versus 31 in adults) teeth, and from *Pseudoeurycea leprosa* by its broader head, larger hands and feet, longer limbs, and more robust habitus.

Description.—Relatively small species; SL in 5 adult males 40.6–48.3 ($\bar{x}$ = 43.6), in 14 females 41.2–53.5 ($\bar{x}$ = 47.5) with relatively robust habitus; head relatively broad, (males 16–17% SL in males, 14–16% SL in females); dorsal surface of head slightly but evidently pitted; snout broadly rounded, more truncate in males than in females; neck region ill-defined, only slightly narrower than head; eyes moderate in size, only slightly protuberant. Parotoid glands not evident. Costal folds 13, counting one each in axilla and groin. Limbs relatively long; digits typically meet when limbs appressed to side of trunk in males, or separated by no more than one-half costal interspace; in females, adpressed limbs fail to meet by one-half to one and one-half costal interspaces. Hands and feet relatively well developed, digits relatively long and slender for *Pseudoeurycea*, bearing small subterminal pads; fifth toe well developed but much shorter than the fourth. Digits in order of decreasing length: fingers 3-2-4-1; toes 3-4-2-5-1; slight basal webbing present. Tail missing in many of the specimens; when present, 86 to 115% ($\bar{x}$ = 99%) SL; tail relatively stout, tapering rather abruptly toward tip. Maxillary teeth small 63–88 ($\bar{x}$ = 75) in males, 63–94 ($\bar{x}$ = 74) in females; premaxillary teeth 2–7 ($\bar{x}$ = 3.8) and enlarged in adult males, 10–15 ($\bar{x}$ = 12.1) and smaller in females; vomerine teeth in long rows, 25–40 ($\bar{x}$ = 31.2) in males, 26–39 ($\bar{x}$ = 31.7) in females.

Coloration: The preserved specimens are generally dark, with slate ground color and a dark venter. The dorsal ground color is overlain with gray, to silver-gray, to a bright silver wash that is interrupted by many small rounded to larger irregularly shaped openings through which the darker ground color shows through. In most individuals there is a thin pale color stripe joining the eyes that has the shape of a very shallow "V" pointed posteriorly. The head is often darker than the trunk, while the tail is paler than the trunk and has a bright yellowish tip. The limbs generally are the same gray color as the dorsum. The gular area is slightly paler than the venter of the trunk, and the tail venter is the same slate-black as the trunk (Fig. 1).

The coloration in life contrasts greatly with that of the preserved animals. The dorsum is dark green, green-ochre, pale yellow-green, or tannish yellow (Fig. 2), usually with many black spots and short streaks. Generally the tail is paler than the trunk and has a bright yellow to reddish orange tip. The dorsum appears to have a black ground color overlain by yellowish-green or ochre, with black spots or streaks showing through the paler overlay. The venter is black. A distinct, shallow V-shaped yellowish band is present between the eyes in some individuals. The limb insertions generally are greenish yellow. The iris is coppery gold.

In their account of the specimens from Las Vigas, Veracruz, Smith et al. (1952:251) noted dorsal coloration to be blue-gray dorsally, with "distinct but exceedingly variable black spots, blotches, or linear markings." They described the dorsal surface of the posterior part of the trunk and the distal tip of the tail to be paler in most specimens; the venter and chin were reported to be unmarked blue-black.

Measurements of holotype (in mm): Head width 7.9; head depth 5.1; eyelid length 2.7; eyelid width 1.9; ante-

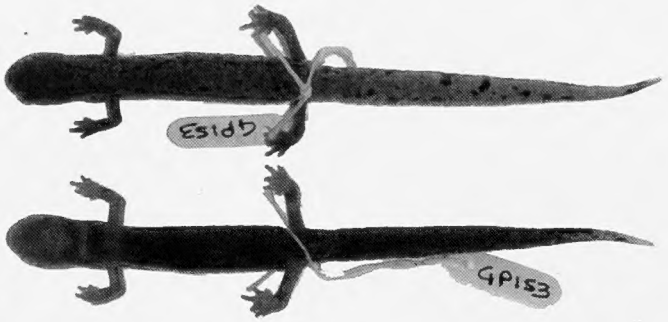

Fig. 1. Holotype of *Pseudoeurycea lynchi*, MVZ 230994, SL 49.8 mm. Dorsal and ventral views of the preserved specimen bearing the collector's field label.

rior rim of orbit to snout 2.3; interorbital distance 2.5; distance between corners of eyes 3.3; snout to forelimb 15.6; nostril diameter 0.2; distance between external nares 2.0; projection of snout beyond mandible 0.4; snout to gular fold 11.7; width across shoulders 6.2; snout to posterior angle of vent 49.8; snout to anterior angle of vent 46.5; axilla to groin 26.4; tail length 49.0; tail depth at base 4.7; tail width at base 4.7; forelimb length 11.3; width of hand 3.6; hind limb length 12.6; width of foot 4.7; length of longest (third) toe 2.0; length of fifth toe 1.0. Numbers of teeth: premaxillary 14; maxillary 36/33; vomerine 13/14.

Distribution.—This species is known from the central Sierra Madre Oriental where it may range widely. The type locality at Cerro San Pedro (2160 m) is about 6 km ENE from the town of Chiconquiaco, and the species also has been found at elevations of 2050–2300 m near the escarpment on the slopes of mountains close to Cerro Cofre de Perote in and near the village of La Joya, and a nearby site at somewhat higher elevations than La Joya. We tentatively assign specimens from an area to the northwest of these localities, in the state of Puebla (near the town of Xocoyolo, ca. 20°00' N, 97°32' W; specimens to be deposited in collections of Universidad Nacional Autónoma de México), to this species.

Natural History.—This species occurs in cloud forest where it is found only in, or under, decaying wood and under the bark of logs. In the La Joya area, the salamanders were in relatively densely wooded areas where they were encountered under the bark of pine logs varying in size from a few cm to about 50 cm in diameter. Smith et al. (1952) recorded two specimens in a huge rotten log and six others beneath pine logs. On Cerro San Pedro most specimens were found in or under decaying logs in a mesophilic forest dominated by oaks. One adult was under a fallen mat of moss and other epiphytes. Few bromeliads were observed in this forest, but many vines are present.

The vegetation and salamander fauna at the type locality is similar to that at La Joya, although the soil differs. La Joya lies in an area of extensive lava flow, and the surface of the ground is mainly coarse pumice-like rock with interspersed humus. Rock in the area is mined for road construction material. Deforestation is also occurring, and the unusual fauna (e.g., the bromeliad dwelling *Chiropterotriton lavae* is known only from La Joya) at the site is at risk of destruction. The forest at Cerro San Pedro is less disturbed, but it is a small remnant (estimated at 1.5-2 ha) isolated on the top of a peak. The soil is a rich humus with only a little exposed rock. Unexplored forest occurs to the east.

Co-occurring species of salamanders at La Joya include *Pseudoeurycea gigantea*, *P. cephalica*, *Chiropterotriton lavae*, and *Thorius minydemus*. On Cerro San Pedro co-occurring species include *P. gigantea*, *T. minydemus* (Parra-Olea and García-París, 1999), and an apparently undescribed species of *Chiropterotriton*.

Etymology.—This species is named to honor the memory of Dr. James F. Lynch, friend and long-time collaborator, who was one of the rediscoverers of this taxon at La Joya and who was to have been a co-author on this paper until his untimely death in 1998.

Pseudoeurycea naucampatepetl new species

Cofre de Perote Salamander

Holotype.—Museum of Vertebrate Zoology (MVZ) 158941, an adult male from a roadside bank along the road to Las Lajas Microwave Station, 15 km (by rd) S Highway 140 from Las Vigas, Veracruz, Mexico (19°35.5' N, 97°05.7' W, 3000 m elevation), collected by T. J. Papenfuss, October 24, 1981.

Paratypes.—MVZ 171521, MVZ 172131, MVZ 173436, KU 290072, all from the immediate vicinity of the holotype, collected at different times at elevations of 2880–3000 m.

Diagnosis.—This relatively small member of the *Pseudoeurycea bellii* complex is distinguished from all other described taxa by its relatively slender habitus and distinctive color pattern and hue, which consists of a pair of prominent, pink, rather than orange spots on the head, a pair of similarly colored triangular shoulder spots, a series of ten pairs of small costal spots, and a distinctive broad U-shaped (apex oriented posteriorly) spot complex just posterior to the limb insertions (see Fig. 2 and color description, p. 6).

Description.—Moderately robust species attaining moderately large size (largest male 82.1 mm in SL; smallest male 67.6 mm in SL having a mental gland suggesting sexual maturity; largest female 82.9 mm SL). Head prominent with large, relatively protuberant eyes and broadly rounded, large snout. Head broad (14.3–16.0%, $\bar{x}$ = 15.4% SL), moderately long (22–24% SL); parotoid glands not evident; mental gland prominent, round in holotype. Cos-

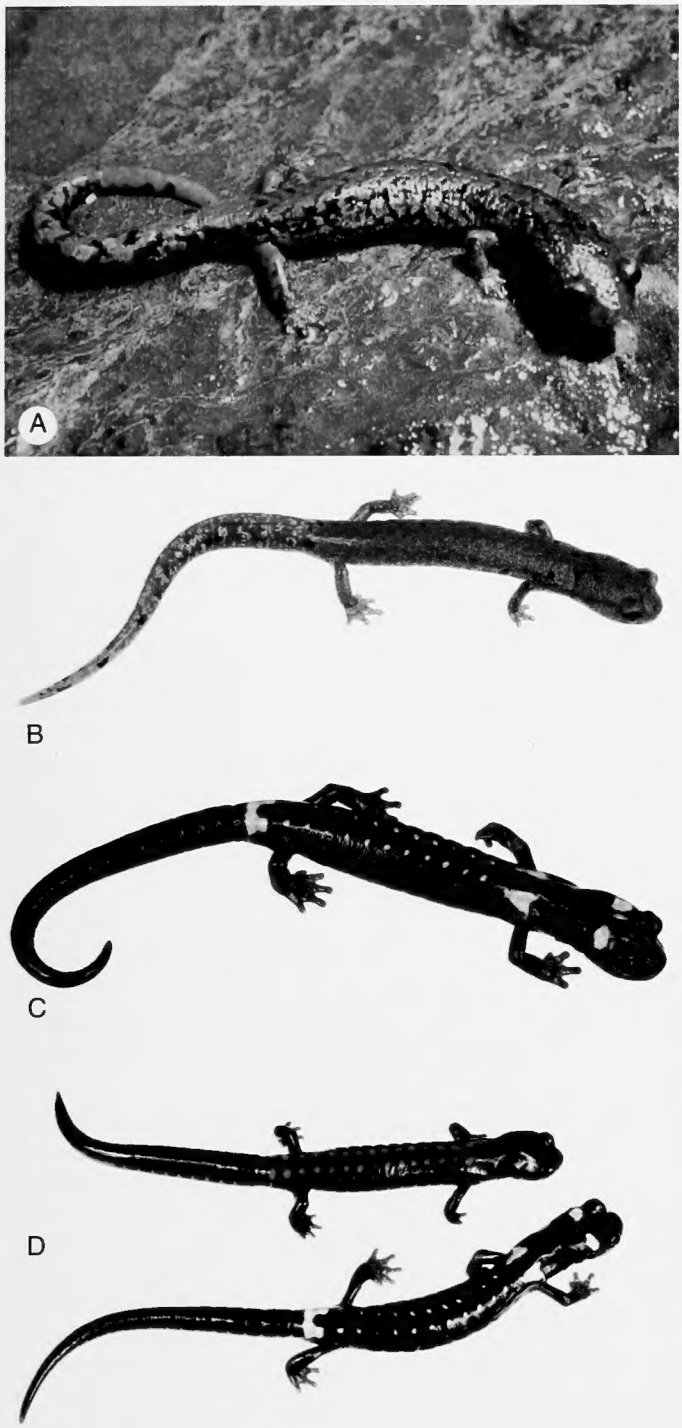

Fig. 2. *Pseudoeurycea* from central Veracruz, Mexico. A. *Pseudoeurycea lynchi*, MVZ 231000, subadult female, SL 38.5 mm, from Loma Alta, top of Cerro San Pedro, Veracruz, Mexico. B. *Pseudoeurycea nigromaculata*, MVZ 185977, subadult female, SL 35.5 mm, from Cerro Chicahuaxtla, Cuautlapan, Veracruz, Mexico. C. *Pseudoeurycea naucampatepetl*, MVZ 158941 (holotype), adult male, SL 76.4 mm, from Las Lajas Microwave Station, Veracruz, Mexico. D. Top, *Pseudoeurycea gigantea*, MVZ 158715 (missing, unknown size and sex) from La Joya, Veracruz, Mexico. Bottom, *Pseudoeurycea naucampatepetl* MVZ 158941, adult male, SL 76.4 mm, from Las Lajas Microwave Station, Veracruz, Mexico.

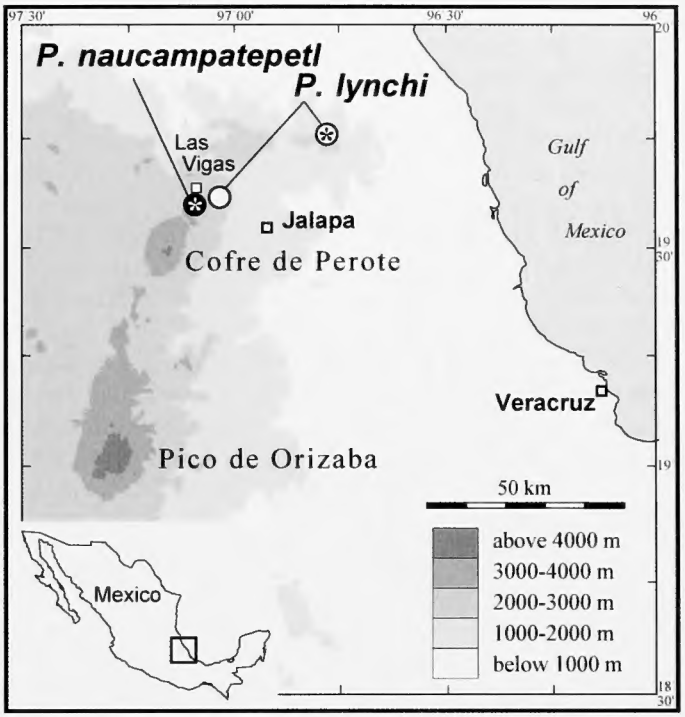

Fig. 3. Eastern Mexico showing topographic relief and localities for the two species of *Pseudoeurycea* described herein. Type localities are indicated by stars.

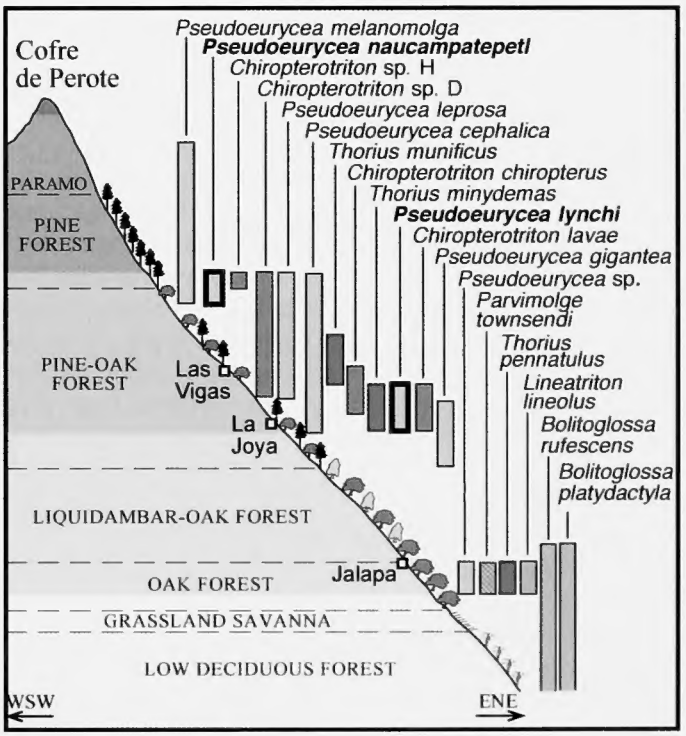

Fig. 4. View of an imaginary generalized transect extending eastward from Cofre de Perote to the lowlands east of Jalapa and Teocelo, Veracruz, Mexico, showing dustributional limits of 18 species of salamanders. Information is lacking from the heavily populated areas near and immediately above Jalapa.

tal folds 13, counting one each in the axilla and groin. Limbs long, robust, combined limb length 47–51% SL); adpressed limbs either meet, slightly overlap, or slightly fail to overlap in males and fail to overlap by one to one-half costal folds in females. Fifth toe relatively prominent for a member of this genus; digits well developed, moderately long, with no appreciable basal webbing; subterminal pads well developed; fingers in order of decreasing length 3-2-4-1; toes in order of decreasing length 3-4-2-5-1. Tail short, relatively slender, tapering gradually to a blunt tip; complete tails 74–84% SL in two males and 75–79% SL in two females. Premaxillary teeth slightly enlarged, 3–4 in males; premaxillary teeth not distinguishable from maxillary teeth in females; maxillary teeth small, moderately numerous; total number of maxillary and premaxillary teeth 68–98 ($\bar{x}$ = 79.8); vomerine teeth in long rows, 37–44 ($\bar{x}$ = 41) in males, 26–46 ($\bar{x}$ = 36) in females.

Coloration: This is a strikingly colored species that resembles its close relatives in the *Pseudoeurycea bellii* complex in general pattern, but differs significantly from all members of that complex in the color and the arrangement of the pale spots. It is basically a solid black species with bright pink to pinkish-cream dorsal spots arranged in a characteristic pattern (Fig. 2). The dorsum is conspicuously marked on the back of the head with a pair of rounded spots about the diameter of the eyeball. A small middorsal spot lies in the nuchal region (fragmented in the holotype), followed by an unmarked space to the level of the forelimbs, where a pair of large spots is located. These have the form of an inverted, rather elongated triangle. These large spots are followed by 11 pairs of small spots (10 dorsolaterally on the trunk intercostal areas, one immediately above the hind limbs). A conspicuous U-shaped mark (apex posteriorly oriented) in the caudosacral region terminates well before the prominent groove marking the autotomy plane at the base of the tail. This U-shaped mark appears to be formed from the coalescence of four spots; the two posterior spots have further coalesced across the dorsal midline. There is only minor variation from this pattern. In one individual, the triangular spot joins the first paired spot unilaterally. In two individuals, the pairs of spots are very small and the posterior ones are obscure. The larger spots tend to be pink and the smaller ones cream. The venter is pale to dark gray, and the mental glands are pale gray.

Measurements of holotype (in mm): Head width 12.2; head depth 6.2; eyelid length 5.0; eyelid width 2.8; anterior rim of orbit to snout 4.0; interorbital distance 3.0; snout to forelimb 22.8; nostril diameter 0.3; distance between internal nares 2.8; distance between external nares 4.7; projection of snout beyond mandible 1.9; snout to gular fold 17.8; width across shoulders 9.2; snout to posterior angle of vent 76.4; snout to anterior angle of vent 71.6; axilla to groin 40.6; tail length 64.5; tail depth at base 5.7; tail width at base 5.3; forelimb length 17.0; width of hand 6.8; hind-limb length 19.1; width of foot 7.8; length of longest (third) toe 3.2; length of fifth toe 2.3. Numbers of teeth: premaxillary 3; maxillary 36/42; vomerine 20/24.

Distribution.—This species is known only from along a narrow ridge extending east from Cofre de Perote and terminating in a small peak (Cerro Volcancillo) at the type locality, in the Sierra Madre Oriental in central Veracruz, México (Fig. 3).

Natural History.—All specimens of this species were found by scraping the surface of roadside banks, which consisted of moist soil with a somewhat dry outer crust, under which the salamanders were found. Most of the banks were shaded. The animals rolled out onto the ground and were languid at the cool temperatures (± 13° C). *Pseudoeurycea melanomolga*, *P. leprosa*, and *P. cephalica* were found in the same banks. Of these, *P. leprosa* was the most common locally and *P. cephalica* the least common. In the neighboring forest, a member of the *Chiropterotriton chiropterus* complex occurred.

The type locality is a peak (Cerro Volcancillo on some maps) on the east side of Cofre de Perote. The peak is connected by a ridge that extends south for a few km and then extends west to join the main slope of Cofre de Perote. The peak is separated from Cofre de Perote by a steep valley extending northeastward, rapidly to lower elevation, where it intersects the road between Las Vigas and Jalapa. The peak is only about 5 km by air above Las Vigas, although the road distance is about 15 km. The peak supports pine-oak forest with alder, *Arbutus*, *Baccharis*, and bunch grass in cleared areas. Because of extensive cutting of the forest, most of the trees are relatively small second growth. Some large firs are present. They are remnants of the original vegetation, now largely replaced by secondary forest.

Etymology.—The specific name of this species is the Náhuatl name "Naucampatépetl" for Cerro Cofre de Perote, of which the type locality is a satellite peak.

Remarks.—The species is known from a small sample; repeated attempts to find additional specimens have failed and we describe the new species at this time so that the biodiversity of this important region can be more fully understood. Members of the *Pseudoeurycea bellii* complex are typically the largest of the tropical plethodontids. Possibly this species reaches a larger size than suggested by available specimens because females of *Pseudoeurycea* are usually larger to much larger than males, whereas our largest male and female of *P. naucampatepetl* are about the same size.

RESULTS OF BIOCHEMICAL STUDIES

Some data are available from unpublished studies of allozymes and mitochondrial DNA sequences (cytochrome *b*, 16S rDNA for both species and also ND4 for *Pseudoeurycea lynchi*) for both of the new species. The mtDNA data set, which includes approximately 1822 base pairs was used in a general phylogenetic analysis of *Pseudoeurycea* (Parra-Olea, 1999). In both parsimony and maximum-likelihood analyses of the combined data for the three mitochondrial genes, *P. lynchi* is the sister taxon of *P. leprosa* (parsimony bootstrap 100%, decay index 23), but *P. nigromaculata* was not available in this study. Only data for 16S are available for *P. nigromaculata*, and *P. lynchi* is about equally similar to it (K2P values of 0.024–0.026) and to *P. leprosa* (K2P values of 0.018–0.030). This slowly evolving gene is not of much use in determining relationships within what we consider to be the *P. leprosa* species group, but a neighbor-joining analysis reveals a cluster containing *P. lynchi* and *P. nigromaculata* as sister taxa, both basal to *P. leprosa* (bootstrap 95 for monophyly of this haplotype clade).

Only cyt *b* sequence is available for *Pseudoeurycea naucampatepetl* (two specimens). A parsimony analysis of the *P. bellii* group (Parra-Olea, 1999) shows that *P. naucampatepetl* is the sister taxon of *P. gigantea*, from nearby La Joya (bootstrap 94, decay index 7). The two taxa have a K2P value of 0.040–0.049, whereas the K2P values to *P. bellii* exceed 0.071.

Allozyme data for *Pseudoeurycea lynchi* are from an unpublished data set (Frelow and Wake); Lynch and Wake (1989) published some of these data. The study compared 20 allozymic loci of *P. lynchi* (La Joya, Veracruz, n= 6) with *P. nigromaculata* (Cerro Chicahuaxtla, Veracruz, n = 7), several populations of *P. leprosa* (Las Vigas, Veracruz, n = 5; Río Frío, México, n = 5; Xometla, Veracruz, n = 5), *P. juarezi* (from Sierra de Juárez, Oaxaca, n = 5), *P. saltator* (Sierra de Juárez, Oaxaca, n = 5), and *P. parva* (Cerro Baúl, Oaxaca, n = 2). The genetic distance (Nei, 1972) between *P. lynchi* and *P. nigromaculata* is 0.580. Genetic distances between *P. lynchi* and *P. leprosa* range from 0.897 (Xometla) to 1.068 (Las Vigas). All comparisons of *P. lynchi* to other taxa have genetic distances exceeding 1.5. Genetic distances of *P. nigromaculata* to *P. leprosa* exceed 1.0, and all comparisons of *P. parva, P. juarezi,* and *P. saltator* to *P. nigromaculata, P. lynchi,* and *P. leprosa* exceed 1.0. Fixed differences exist between *P. nigromaculata* and *P. lynchi* at the following loci: 6-PGD, ME, LAP, and MDH-2. There are nearly fixed differences at two additional loci, and major frequency differences at other loci.

Allozyme data are available for *Pseudoeurycea naucampatepetl* from an unpublished data set (Frelow and Wake) for 21 loci comparing *P. bellii* (from Nevado de Toluca region, México, n = 4), *P. gigantea* (La Joya, Veracruz, n = 6), *P. naucampatepetl* (topotypes, n = 2), *P. gadovii* (Parque Nacional La Malinche, Puebla, n=3) and *P. melanomolga* (sympatric with *P. naucampatepetl*, n = 3). Genetic distances (Nei, 1972) from *P. naucampatepetl* are 0.112 to *P. gigantea*, 0.181 to *P. bellii*, 1.343 to *P. melanomolga*, and 1.140 to *P. gadovii*. The genetic distance between our samples of *P. gigantea* and *P. bellii* is 0.035, and between *P. melanomolga* and *P. gadovii* is 0.229. A fixed difference exists between *P. naucampatepetl* and *P. gigantea* for ME2, and between *P. naucampatepetl* and *P. bellii* for ME2 and LAP. An allele (frequency 0.5) for ICD2 in *P. naucampatepetl* is not found in either *P. bellii* or *P. gigantea*.

DISCUSSION

The two species described herein have been known for some time (Wake et al., 1992) but have not been described previously because of small sample sizes and uncertainties concerning distinctiveness of taxa. Recent fieldwork was successful in obtaining additional samples of *Pseudoeurycea lynchi* but not of *P. naucampatepetl*. Because we have been able to add information from DNA sequences to allozymic data collected earlier, we feel confident in describing these new species.

Although these taxa occur in one of the regions of México most frequented by salamander collectors, both are uncommon and have largely eluded earlier collectors. The earliest report of *Pseudoeurycea lynchi* is that of Smith et al. (1952), who discovered eight specimens 3 miles (4.8 km) east of Las Vigas, which would place the locality about midway between La Joya and Las Vigas (the two villages are separated by about 8.5-9.0 km). They considered their material to be *P. nigromaculata*. We are familiar with that species at the type locality near Orizaba, Veracruz. It is an arboreal animal that is more gracile and is colored differently from *P. lynchi*; it usually does not have a greenish or ochre coloration, but instead is red, orange, or yellowish-orange, especially on the dorsum of the posterior trunk and the tail. Our two molecular data sets are in agreement in identifying *P. nigromaculata* as the most likely sister taxon of *P. lynchi*. However, there is substantial genetic differentiation of the taxa (allozyme genetic distance in excess of 0.5, with many fixed differences), and there are significant differences in mtDNA sequences (Parra-Olea 1999; see above). The only other close relatives are *P. leprosa* and possibly the enigmatic *P. firscheini*. We have compared the mtDNA and allozymes of *P. lynchi* with *P. leprosa* but samples of the rare *P. firscheini* were not available for biochemical comparisons. Whereas *P. leprosa* and *P. lynchi* form

a monophyletic group in combined analyses of mtDNA sequences (Parra-Olea, 1999), we only were able to obtain sequences of 16S for *P. nigromaculata* and have not been able to make equal comparisons of the three species. Based on 16S and allozymes, we feel confident in identifying *P. nigromaculata* and *P. lynchi* as sister taxa, and based on the combined analysis of all mtDNA sequences we predict that these two taxa form a monophyletic clade with *P. leprosa*, which, however, is a highly differentiated taxon (Lynch et al., 1983) that may require further systematic revision in the future. We think that *P. firscheini* is also a member of this clade based on similarities in morphology and distribution.

Whereas *Pseudoeurycea lynchi* is well differentiated from all other taxa in morphology, allozymes and mtDNA, *P. naucampatepetl* differs from its close relatives mainly in morphology. Fortunately we have a good series of *P. gigantea* from only about 5 km from its type locality; P. *naucampatepetl* and *P. gigantea* differ dramatically both in distribution of spots and in the color of the spots (Fig. 2). The spots of *P. gigantea* are deep red-orange, whereas those of *P. naucampatepetl* are pink or pinkish-cream. Both species are members of the *P. bellii* group, but within that group *P. naucampatepetl* stands apart from other members by lacking reddish to red-orange markings (Fig. 2). The distribution and arrangement of the marks is variable within the group but always involves chevron-like markings, or fragments of chevron spots along the trunk. The arrangement in *P. naucampatepetl* is unique in several respects, including the U-shaped mark in the pelvic region and the small spots along the trunk.

Two of the specimens of *Pseudoeurycea naucampatepetl* are badly emaciated, and one has deformed hands and feet. It is possible, but unlikely, that what we call *P. naucampatepetl* is a local phenotypic variant, but if so, the degree of genetic differentiation is high for such a small geographic distance. Finally, we note that genetic distances within the *P. bellii* complex are generally much larger than reported here (unpublished data); allozymic genetic distances between several populations exceed 1.0. Accordingly, we think that the complex contains a number of species. *Pseudoeurycea gigantea* has been treated as a synonym of *P. bellii* by some authors (e.g., Wake and Lynch, 1976), but we prefer to recognize *P. gigantea* as a distinct species.

The Las Vigas-La Joya-Las Lajas region has a large and complex salamander fauna. Wake et al. (1992) characterized the region, which they called the Veracruz Transect, and listed nine species (four named subsequently as *Thorius minydemus*, *T. munificus*, *Pseudoeurycea lynchi*, and *P. naucampatepetl*) at, or above, elevations of 2000 m. We present a revised version of the transect in Fig. 4. We now report 18 species in the area; 12 of these occur at, or above, 2000 m. Of these 18 species, three remain unnamed. Darda (1994) reported four species of *Chiropterotriton*, and although we can readily identify two as known species, we are unable to verify that his species H and D are unnamed taxa. He found species D and *C. chiropterus* in sympatry, but at that locality we found only one species (based on mitochondrial markers). The species identified as *C. chiropterus* by Wake et al. (1992) may be three species. If we accept Darda's determinations, there are 12 species that occur above 2000 m. Lower on the same transect an additional six species occur. The 18 species inhabiting this transect make it one of the richest local transects known. Fifteen species of salamanders were reported by Hanken and Wake (1994) from a local segment of the Northern Oaxaca Transect of Wake et al. (1992), and we know of additional species from that site. There are 15 species on the Pacific Guatemala Transect of Wake et al. (1992), and 18 species on the transect from Cerro de la Muerte through Tapantí, Costa Rica (García-París et al., 2000).

One might think that the mountains of central Veracruz, which have been explored extensively for well over a century, would be well known herpetologically, but in the past few years many species of salamanders and even snakes have been described. We think that we are now close to having a complete list, but taxonomic problems continue and doubtless a few additional species will be described. Most of the recently described species were known as populations, some of them for over a century, and their recognition as distinct species is the result of biochemical analyses that have only recently been undertaken. However, some are truly new, previously unknown species, such as *Pseudoeurycea naucampatepetl*. This region of high biodiversity is rapidly changing because of human activities and some species of vertebrates may well become extinct before they are discovered.

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