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THE SALAMANDERS OF GUERRERO, MEXICO, WITH DESCRIPTIONS OF FIVE NEW SPECIES OF *PSEUDOEURYCEA* (CAUDATA: PLETHODONTIDAE)

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ABSTRACT Five new species of plethodontid salamanders, all belonging to the genus *Pseudoeurycea* (*ahuitzotl, mixcoatl, tenchalli, teotepec,* and *tlahcuiloh*), are described from higher elevations (2200–3425 m) in the Sierra Madre del Sur of western Guerrero, Mexico. The geographic and elevational distributions of the eight species of plethodontids in the genera *Bolitoglossa, Pseudoeurycea,* and *Thorius* known in western Guerrero are reviewed and compared with salamander distributions in Oaxaca. A key to Guerreran salamanders is provided.

Key words: Caudata; Plethodontidae; *Pseudoeurycea;* New species; *Thorius; Bolitoglossa;* Guerrero; Mexico.

RESUMEN Cinco especies nuevas de salamandras plethodontida, todas en el género *Pseudoeurycea* (*ahuitzotl, mixcoatl, tenchalli, teotepec,* y *tlahcuiloh*), son descritas de las elevaciónes altas (2200–3425 m) de la Sierra Madre del Sur del oeste de Guerrero, México. Las distribuciones geográficas y elevacionales de las ocho especies de plethodontida en los géneros *Bolitoglossa, Pseudoeurycea,* y *Thorius* conocidas en el oeste de Guerrero son revisadas y ellos se comparan a las distribuciones de las salamandras en Oaxaca. Una clave a las salamandras de Guerrero es provista.

Palabras claves: Caudata; Plethodontidae; *Pseudoeurycea;* Especies nuevas; *Thorius; Bolitoglossa;* Guerrero; México.

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> "A more difficult question is the apparent absence of Newts [here meaning plethodontid salamanders] on the terrain of gneiss and granite which covers so large a portion of southern Guerrero and Oaxaca. For months have we searched Guerrero during the rainy season ... but it was in vain."—Hans Gadow (1905)

> "Thus south of the Balsas River there is an area that can boast of 64 species [of amphibians and reptiles] not to be found elsewhere in México; and, save for one species, a total absence of salamanders." —Edward H. Taylor (1942)

The mountains of central Guerrero and southern Oaxaca—the Sierra Madre del Sur, a continuation of the Sierra Madre Occidental of western Mexico—are separated from the Transverse Volcanic Range by the xeric valley of the Río Balsas (Fig. 1, inset). As noted by Taylor, it was recognized by 1942 that this region south of the Balsas had a high degree of endemism, yet the herpetological surveys conducted up to that time had covered only low to moderate elevations, because localities in the highlands, with one major exception, were not accessible to collectors. That special case was Omiltemi (sometimes spelled Omilteme), a settlement located about 17 km due west of Chilpancingo at an elevation of 2360 m (Fig. 1). Herbert H. Smith and his wife, who collected for the "Biologia Centrali-Americana" biological survey, visited the area in the late 1880s, and during 1902–1904, Hans Gadow, an English naturalist with a special interest in herpetology, also collected amphibians and reptiles there. Edward W. Nelson and Edward A. Goldman, who conducted extensive surveys in Mexico and made collections for the National Museum in Washington, visited Omiltemi in 1903. At the times that these collectors visited Omiltemi, it was a cattle ranch and consisted of a few scattered huts that also served as a halfway station along the trail from Chilpancingo to copper mines located in the high mountains farther west; later, Omiltemi became a lumber camp, but today it is part of the 3600-ha Omiltemi State Ecological Park (Luna Vega and Llorente Bousquets, 1993). The dense forests in the

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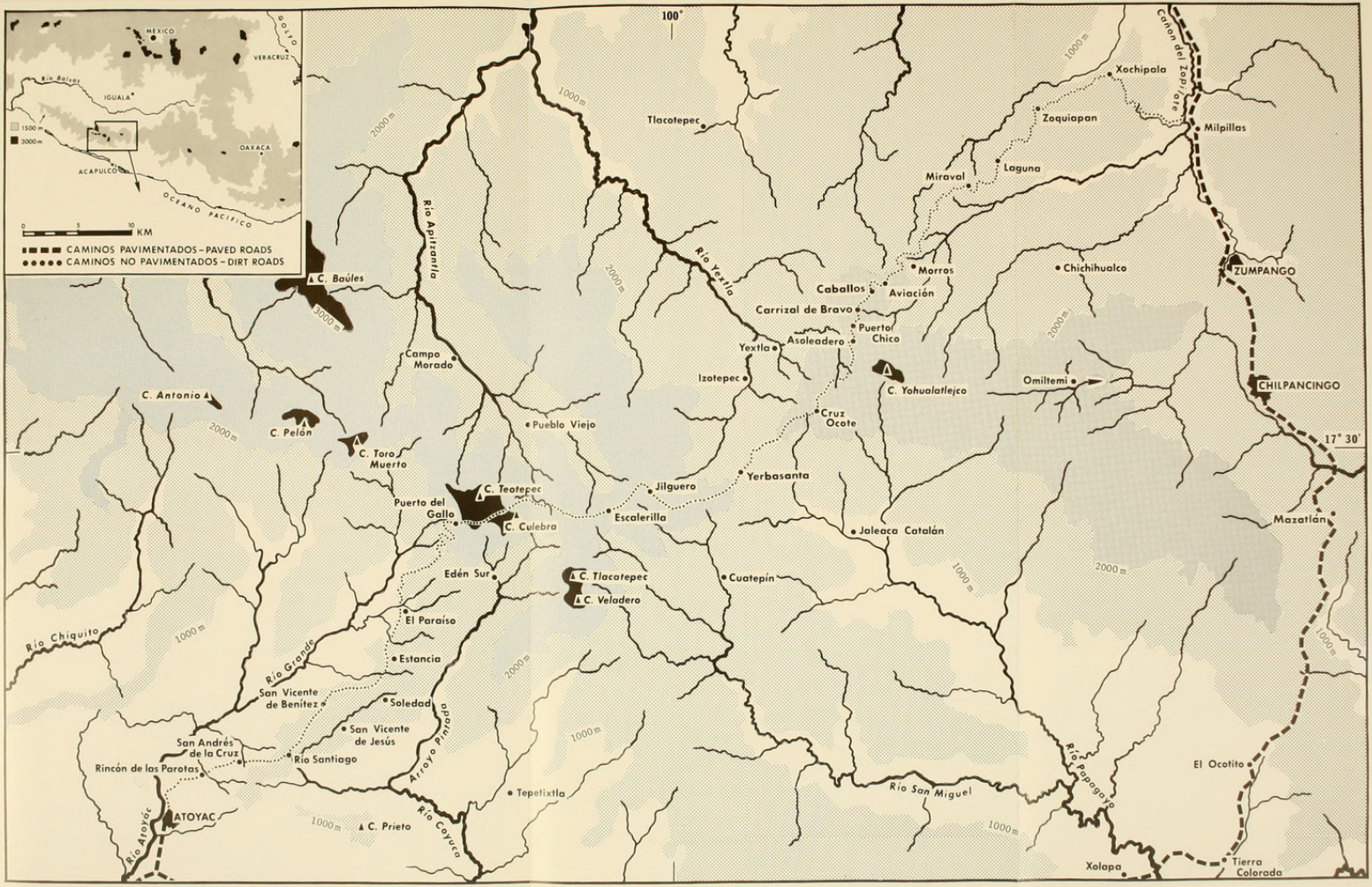
Fig. 1 (foldout map, opposite). Elevational map of the Sierra Madre del Sur of western Guerrero, Mexico. The then-unpaved route between Atoyac de Álvarez and Milpillas is mapped as it existed during the 1960s and 1970s, when the specimens described in this paper were collected. During that time, the roads primarily were used by logging trucks that were headquartered at the lumber camp of Puerto del Gallo (now abandoned). Today, the northern segment of this road is paved and extends from Casa Verde (just north of Milpillas) to Filo de los Caballos where it turns northwestward and ends at Tlacotepec. The main eastern access to Cerro Teotepec today is by paved road from just north of Chilpancingo via Chichihualco, Corral de Bravo, Yerbasanta, and Jilguero. From Atoyac, a paved road now extends almost the entire distance to Puerto del Gallo, but along a partly different route. The scale for the larger map is given in the inset, which also illustrates the isolation of the western Sierra Madre del Sur from the Transverse Volcanic Range by means of the broad, dry valley of the Río Balsas.


MEXICO
GOLFO
VERACRUZ
Río Balsas
IGUALA
1500 m
3000 m
OAXACA
ACAPULCO
OCEANO PACIFICO
0 5 10 KM
CAMINOS PAVIMENTADOS – PAVED ROADS
CAMINOS NO PAVIMENTADOS – DIRT ROADS
100°
Cañon del Zopilote
Xochipala
Zoquiapan
Milpillas
Tlacotepec
Laguna
Miraval
Río Apitzantla
Río Yextla
Morros
Chichihualco
ZUMPANGO
Caballos
Aviación
Carrizal de Bravo
Puerto Chico
Asoleadero
Yextla
Izotepec
C. Yohualatlejco
Omiltemi
CHILPANCINGO
C. Baúles
Campo Morado
C. Antonio
C. Pelón
C. Toro Muerto
Pueblo Viejo
Cruz Ocote
17° 30'
C. Teotepec
Puerto del Gallo
C. Culebra
Jilguero
Escalerilla
Yerbasanta
Jaleaca Catalán
Mazatlán
Edén Sur
C. Tlacatepec
C. Veladero
Cuatepín
El Paraíso
Río Chiquito
Río Grande
Estancia
San Vicente de Benítez
Soledad
San Vicente de Jesús
San Andrés de la Cruz
Rincón de las Parotas
Río Santiago
Arroyo Pinzanda
Río Papagayo
El Ocotito
Tepetixtla
Río San Miguel
ATOYAC
Río Atoyac
C. Prieto
Río Coyuca
Xolapa
Tierra Colorada
1000 m
2000 m

area—then as now—consist largely of pine and oak, with some ash mixed in, and there are numerous meadows and streams. Taken together, the Smiths and Gadow collected 22 species of amphibians and reptiles in the Omiltemi region, but they obtained only one species in common (Gadow, 1908).

By the 1960s, 30 species had been collected in and around Omiltemi (Davis and Dixon, 1959; 1961; 1965), and because Omiltemi is at a relatively high elevation, it was suspected that the species found in that region were generally representative of the highlands of western Guerrero. In fact, Omiltemi itself is in the pine-oak ecological zone but below the cloud forest, which begins some 2–3 km to the west and which envelopes the lower slopes of the higher peaks in the Sierra Madre del Sur (Fig. 1). Some of these higher peaks are Cerro Yohualatlejco (3150 m) about 50 km west of Omiltemi, and, farther west, Cerro Baúles (3020 m), and the highest peak in the sierra, Cerro Teotepec (3550 m). The height of Teotepec is given as 3350–3700 m in various sources, but I have utilized here the elevation given on the latest Mexican government topographical map (Americas series, scale 1:250,000, Zihuatanejo section NE 14–7, published by Detenal, Mexico City).

I visited these higher areas to the west of Omiltemi in 1964 and again in 1969, when I took advantage of an actively used logging road extending west from a point just north of Milpillas ("Casa Verde," a settlement along the highway, 34 km N Chilpancingo) to Puerto del Gallo (a then-active lumber camp), and thence south to the town of Atoyac de Álvarez near the Pacific coast. Many new species of amphibians and reptiles were discovered on these trips by me and my colleagues and by several other biologists who visited the area in the succeeding years. To date, only two of these new species were later collected in the Omiltemi area (*Hyla mykter* [J. A. Campbell, pers. comm.] and *Sceloporus adleri* [Flores-Villela and Muñoz Alonzo, 1993]), but both are rare in that region.

The inference that the Omiltemi herpetofauna was representative of that in the mountains of western Guerrero has turned out to be especially untrue for the salamander fauna. The only salamander reported in the literature to occur at Omiltemi—the "one species" alluded to by Taylor—is the wide-ranging *Pseudoeurycea bellii*, a large species first collected at Omiltemi by H. H. Smith more than a century ago. Specimens of *Thorius* were later reported from several localities along the Milpillas-to-Atoyac road and from near Omiltemi. These represent the most northerly distribution of this genus of miniature salamanders in Pacific-coast Mexico (Adler, 1965; Myers and Campbell, 1981; Saldaña de la Riva and Pérez Ramos, 1987; Flores-Villela and Muñoz Alonzo, 1993); all Guerreran populations of this genus are assigned to a single, as-yet-unnamed species (Hanken, 1983), but see discussion below. *Bolitoglossa hermosa*, which has the most northerly

distribution of any Pacific-coast species of *Bolitoglossa*, was described from specimens collected at several sites northeast of Atoyac (Papenfuss et al., 1983). The purpose of this paper is to describe five additional salamanders, all assigned to the generalized bolitoglossine genus *Pseudoeurycea*, from localities in the western highlands of Guerrero, and to summarize the distributions of salamanders in Guerrero.

The plethodontid genus *Pseudoeurycea* Taylor, 1944, presently consists of 28 nominal species. (Liner [1994] listed 27 Mexican species, three of which also occur in Guatemala; another, *P. exspectata,* is restricted to Guatemala.) This group of species ranges from western Tamaulipas in the northeast, and eastern Sonora in the northwest of Mexico, through eastern and southern Mexico and into western Guatemala, although most individual species have limited geographic ranges. Biochemical differentiation of the species of *Pseudoeurycea* indicates that the group is old and highly diversified (Lynch et al., 1977, 1983; Lynch and Wake, 1989), and it has been difficult to determine diagnostic morphological and osteological traits for the genus. There are few characters that bind this assemblage of species together. Members of the genus share no uniquely derived osteological traits, and possess a single osteological synapomorphy (fused premaxillae, a condition shared with most other Neotropical plethodontids); *Pseudoeurycea* is characterized primarily by its lack of the various derived traits that characterize other, closely related plethodontid genera (Wake and Elias, 1983).

Wake and Lynch (1976) mainly used morphological criteria to recognize five species groups for the 22 species of *Pseudoeurycea* then known. However, an extensive immunological study, based on quantitative microcomplement fixation techniques which utilized 18 species (Maxson and Wake 1981), concluded that there was significant conflict between the morphological and immunological data, and that many species were incorrectly assigned to species group. These results and subsequent starch-gel electrophoretic data suggest the existence of ancient phyletic divisions within the genus *Pseudoeurycea,* which may be paraphyletic and possibly polyphyletic (Lynch and Wake, 1989). Therefore, it is premature to assign the new species described in this paper to properly defined species groups. However, it is my hope that their description will contribute to a better understanding of diversity within the "*Pseudoeurycea* complex" which, in turn, may lead to the construction of a natural classification.

MATERIALS AND METHODS

All measurements were made to the nearest 0.1 mm with dial calipers. Because of marked ontogenetic changes in tooth numbers and body proportions (e.g., increase in number of teeth, proportional shortening of legs, and

lengthening of tails with age), it was necessary to calculate relative proportions for comparisons between species in the diagnoses as follows: *relative limb length* (combined length of right arm and right leg divided by the standard length [SL; snout to posterior end of vent]), *relative tail length* (length from posterior end of vent to tip of tail divided by SL), *relative head width* (maximum head width divided by SL), and *relative head length* (length from tip of snout to center of gular fold divided by SL). Other definitions are head length (tip of snout to center of gular fold) and tail length (posterior angle of vent to tip of tail). Descriptions of color and pattern in the diagnoses are based on specimens preserved in alcohol. Diagnoses and descriptions are given in the form that has become the standard for neotropical salamanders, as developed by David B. Wake and his colleagues. (See Literature Cited, papers by Hanken, Lynch, Papenfuss, and Wake.)

Museum collections are identified as follows: AMNH, American Museum of Natural History; KU, Natural History Museum, The University of Kansas; MVZ, Museum of Vertebrate Zoology, University of California at Berkeley; UMMZ, Museum of Zoology, The University of Michigan; USNM, National Museum of Natural History, Washington; and UTA, University of Texas at Arlington. Comparisons of the new taxa were made to the species mentioned in this paper using specimens in all of these museums, except for USNM, and from materials collected personally.

The names given to the new species are all derived from Classical Nahuatl, the Aztec language. All are nouns in apposition to the generic name.

TAXONOMY

Pseudoeurycea ahuitzotl new species
Imperial Salamander (Tlaconete Imperial)
Figures 2A, B and 3A

Holotype.—KU 182509, an adult male, from 9.4 km (by road) NE of Puerto del Gallo (an abandoned lumber camp), Guerrero, Mexico, at an elevation of 3296 m on the southern slope of Cerro Teotepec (17°28' N, 100°08' W). One of three specimens collected at this site on 6 August 1979 by Jonathan A. Campbell. (See Remarks concerning type locality.)

Paratypes.—KU 182507–508, same data and collector.

Diagnosis.—*Pseudoeurycea ahuitzotl* is a moderately large-sized species (to 67.0 mm SL) of *Pseudoeurycea* with a large head, long limbs, large hands and feet, a relatively slender body, and a moderately thick tail of average length. In general proportions and color pattern, it superficially resembles *P. gadovii* of Puebla and Veracruz, but differs most notably in

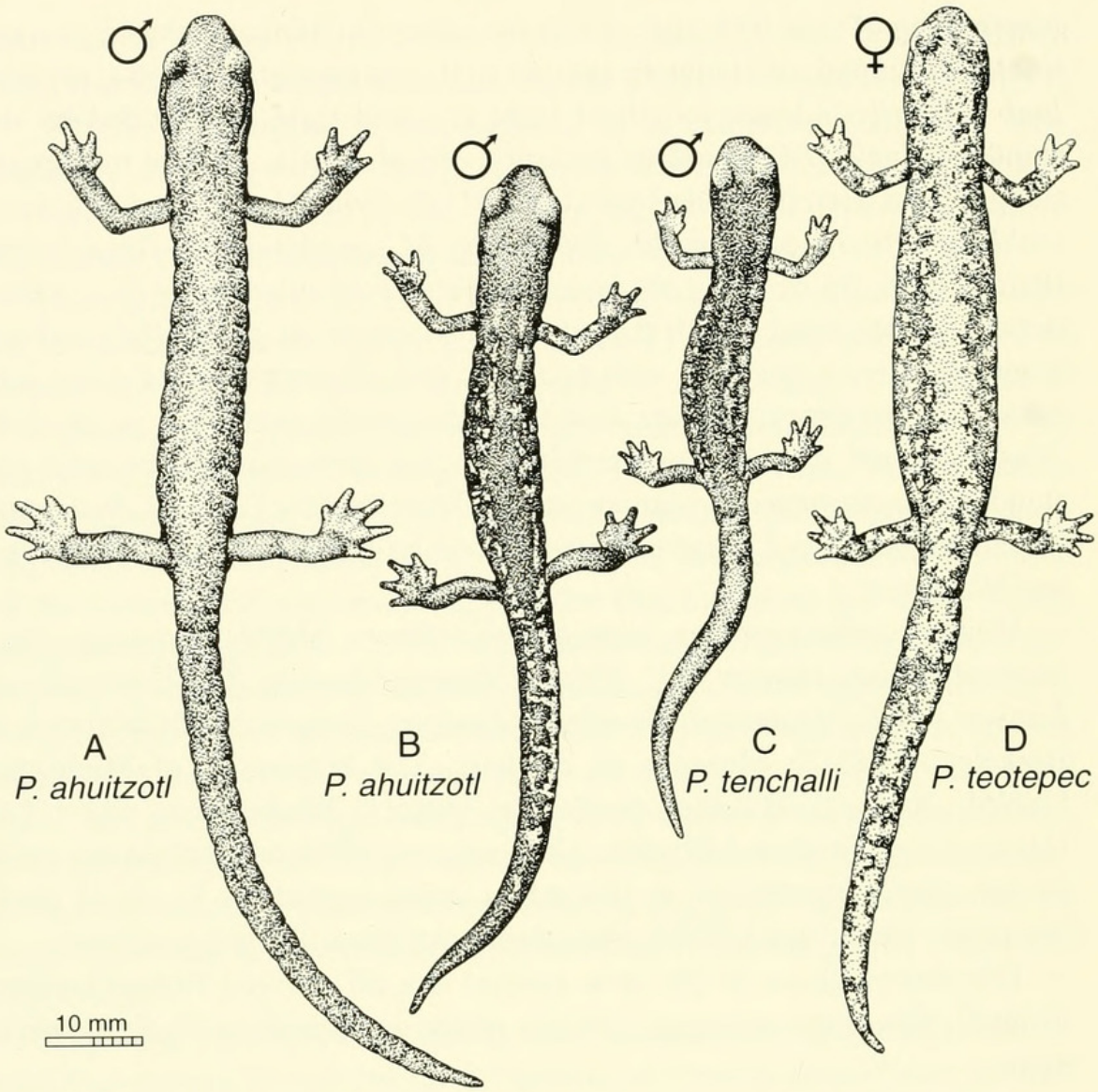


Fig. 2. Dorsal views of new species of *Pseudoeurycea* from Guerrero: *P. ahuitzotl* (**A:** male, KU 182509, holotype; **B:** male, KU 182507, paratype); *P. tenchalli* (**C:** male, KU 182505, holotype); *P. teotepec* (**D:** female, UMMZ 125896, holotype). Drawings by David M. Dennis.

having longer limbs and digits, a longer head with a more rectangular snout, and males with mental-gland clusters that are significantly wider than long. Moreover, in *P. ahuitzotl,* the paired rows of spots on the dorsum are lost at a smaller size and the large spot present on each shoulder (anterior to the forearm) in *gadovii* is lacking altogether. *Pseudoeurycea ahuitzotl* differs from the Guerreran species of *Pseudoeurycea* described in this paper as follows. (1) From *P. teotepec,* it differs in possessing a generally gray color (instead of chocolate brown) and lacks prominent iridophore patches on the venter (present in *P. teotepec*). *Pseudoeurycea ahuitzotl* also possesses relatively longer limbs (a ratio of 0.54 and 0.58 in the 2 adult specimens of *P. ahuitzotl* vs. 0.46 in the single available adult specimen of *P. teotepec*). (2) From *P. tlahcuiloh,* it differs in dorsal color pattern (mottled streaks and spots of various shades of brown present in *P.*

tlahcuiloh, lacking in *P. ahuitzotl*) and in having a paler venter (blackish brown belly and throat in *P. tlahcuiloh*). The mental gland in males is noticeably wider than long (round to only slightly wider than long in *P. tlahcuiloh*). The tail is relatively thicker in *P. ahuitzotl,* and the limbs are relatively longer (0.54 and 0.58 in the 2 adult males of *P. ahuitzotl* [57.2 and 67.0 mm SL] vs. a mean of 0.52 in 5 adult *P. tlahcuiloh* [56–62 mm SL]). (3) From *P. tenchalli,* it differs in its larger adult size (57.2 and 67.0 mm SL in the 2 adult male *P. ahuitzotl* vs. 41.6 mm SL in the single available adult male of *P. tenchalli*). The mental gland is nearly twice as wide as long in *P. tenchalli* compared to its narrower condition in *P. ahuitzotl. Pseudoeurycea ahuitzotl* possesses more vomerine (23 and 27 in the 2 adult *P. ahuitzotl* vs. 21 and 22 in the 2 adult *P. tenchalli*) and premaxillary-maxillary teeth (45 and 53 in the adults of *P. ahuitzotl* vs. 36 and 42 in adult *P. tenchalli*). (4) From *P. mixcoatl,* it differs in possessing a gray ground color (pale brown with tiny darker brown spots in *P. mixcoatl*). The mental gland is much wider than long in *P. ahuitzotl* (round to only slightly wider than long in *P. mixcoatl*) and the digits lack expanded tips (slightly expanded at tips in *P. mixcoatl*). From *P. bellii, P. ahuitzotl* differs most notably in color pattern; the general color of *ahuitzotl* in preservative is gray (instead of black) and, in adults, the dorsum of the body lacks prominent markings; in *P. bellii*, the dorsum bears two longitudinal rows of discrete orange-to-red spots including a pair on the occiput, and these markings exist throughout an individual's life.

Description of holotype (in mm).—An adult male of 67.0 SL, with two large, well-formed testicular lobes on each side. Head length 14.0; maxi-

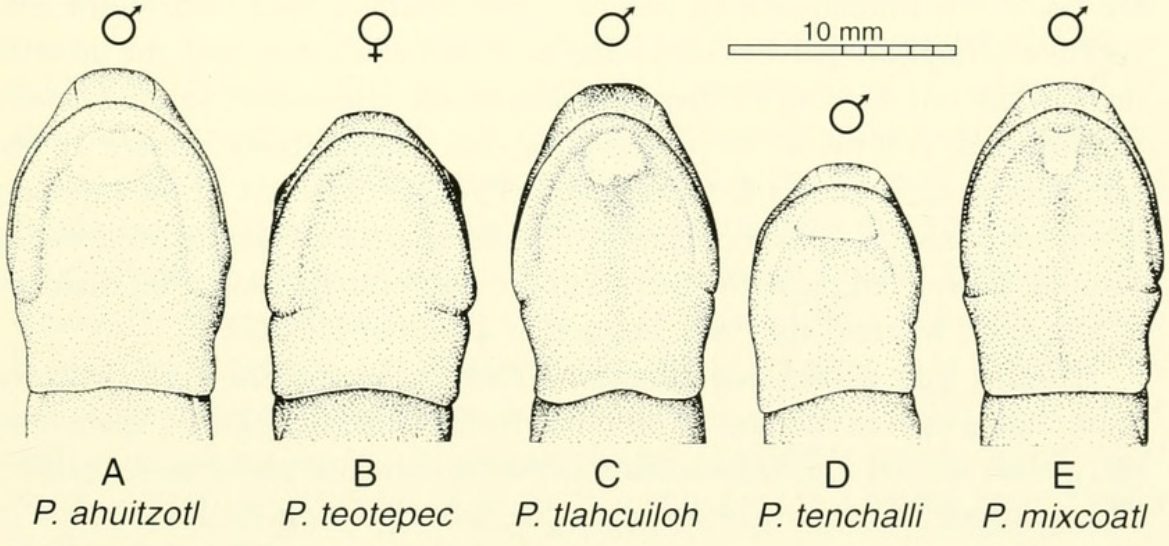


Fig. 3. Throat regions of new species of *Pseudoeurycea* from Guerrero: *P. ahuitzotl* (**A:** male, KU 182509, holotype); *P. teotepec* (**B:** female, UMMZ 125896, holotype); *P. tlahcuiloh* (**C:** male, KU 221955, holotype); *P. tenchalli* (**D:** male, KU 182505, holotype); *P. mixcoatl* (**E:** male, KU 221957, holotype). No males of *P. teotepec* are known. Drawings by David M. Dennis.

mum head width 10.0; head depth at posterior angle of jaw 5.1; upper eyelid length 4.2; upper eyelid width 2.5; anterior rim of orbit to snout 4.3; horizontal length of orbit 2.1; interorbital distance 3.0; projection of snout beyond lower jaw 1.4; mental gland slightly bilobed bilaterally, its width 4.3, and length 2.6; distance separating external nares 3.7; distance separating internal nares 2.5; distance between vomerine teeth and parasphenoid tooth patch 1.0; number of premaxillary-maxillary teeth 46; number of vomerine teeth 23; axilla to groin 35.4; anterior-to-posterior angle of vent 6.0; snout to insertion of arm 18.6; length of right arm 18.4; length of right leg 17.7; width of right hand 5.9; width of right foot 7.5; tail length 62.3; tail width at base 4.3; tail depth at base 4.3.

Coloration in life: According to the collector's field notes, the animals were "dark brownish black with rust-colored markings."

Coloration in alcohol: Dorsum gray with scattered, small, paler, irregular patches of iridophores, especially on back and sides of body; tail with fewer patches and these mostly concentrated near its base. Venter paler gray, especially throat, mental gland, and soles of hands and feet.

Variation.—The smallest male (48.9 mm SL) is immature and lacks well-formed testicular lobes. The smaller mature male (57.2 mm) has one large and one partially formed testicular lobe on each side, whereas the largest male (67.0 mm) has two well-formed lobes. Both have well-developed mental-gland clusters. Given the sexual size dimorphism in species of *Pseudoeurycea*, the females of *P. ahuitzotl* would be expected to exceed 75 mm SL.

The smaller mature male has more pronounced, irregular patches of iridophores on the back, especially in the dorsolateral and lateral areas of the body. The immature male has two longitudinal rows of fairly discrete, spotlike iridophore patches down the back and extending onto the anterior third of the tail. In both of these specimens, the iridophore patches have a salmon-pink coloration in preservative. The dorsal body pattern in the immature male is reminiscent of that in *P. bellii* (in terms of the numbers and sizes of spots), but specimens of *P. bellii* also have discrete spots on the occiput. Moreover, these rows of spots are absent in the two adult males of *P. ahuitzotl,* whereas they are retained in adults of *P. bellii.*

Habitat and associated species.—These salamanders were collected under fallen logs in an open fir-pine-oak forest with bunchgrass. Specimens of *Thorius* sp. and *Porthidium barbouri* were collected at the same locality. The holotype of *Pseudoeurycea teotepec* was taken on the same slope of Cerro Teotepec, but at an elevation about 125 m higher. (See below.)

Etymology.—Ahuitzotl (?–1502), King of Tenochtitlán, was Aztec ruler at the time that Guerrero was conquered.

Remarks.—Although the type locality was mapped by Campbell (1988) as being on the northern slope of Cerro Teotepec, he assured me (in litt., 25

January 1995) that these salamanders were collected on the southern slope, "near the ridge where the road reaches its highest point on Cerro Teotepec." Thus, the distance given from Puerto del Gallo is along the road to Milpillas.

Pseudoeurycea teotepec new species

Teotepec Salamander (Tlaconete de Teotepec)

Figures 2D, 3B

Holotype.—UMMZ 125896, an adult female, from the southern slope of Cerro Teotepec (17°28' N, 100°08' W), above the highest crest of the Milpillas–Atoyac Road on Cerro Teotepec just east of Puerto del Gallo (an abandoned lumber camp), Guerrero, Mexico, at an elevation of about 3425 m, collected on 10 August 1964 by Theodore J. Cohn and Jean Cohn. (See Remarks concerning type locality.)

Diagnosis.—*Pseudoeurycea teotepec* is a medium-sized species (to 62.2 mm SL) of *Pseudoeurycea* with a short head, very short limbs, small hands and feet, a thick body, and a thick tail of very short length. In general proportions and color pattern, it superficially resembles *P. cochranae* of Oaxaca, but differs most notably in having a relatively longer tail (ratio of 0.82 in the single available specimen, a female [62.2 mm SL], vs. a range of 0.66–0.74 [mean, 0.69] in a sample of 5 female *P. cochranae* [57.0–63.4 mm SL]) and in possessing larger hands and feet. From the Guerreran species of *Pseudoeurycea* described in this paper, *P. teotepec* differs in the following characters. (1) The head is shorter (the head of the single specimen of *P. teotepec* [62.2 mm SL] is 12.2 mm long, whereas the heads of the 11 largest specimens of *P. ahuitzotl, P. tlahcuiloh*, and *P. mixcoatl* [57.0–67.0 mm SL] range in length from 13.0–15.3 mm [mean, 13.8]). (2) The limbs of *P. teotepec* are relatively shorter (in *P. teotepec*, a ratio of 0.46 vs. 0.51–0.58 [mean, 0.55] in the same 11 specimens of *P. ahuitzotl, P. tlahcuiloh,* and *P. mixcoatl*). (3) The tail is relatively shorter (in *P. teotepec*, a ratio of 0.82 vs. 0.93–1.04 [mean, 0.99] in 9 of the same 11 specimens of *P. ahuitzotl, P. tlahcuiloh,* and *P. mixcoatl* having tails that are not regenerated). From *P. tenchalli*, which matures at a much smaller size and, thus, cannot be compared at similar sizes, *P. teotepec* differs in having a much bolder dorsal pattern, a generally brown color (not gray, as in *P. tenchalli*), and a dark throat (not lighter than the belly). From *P. bellii, P. teotepec* differs in lacking the two longitudinal rows of discrete orange-to-red spots on the occiput and dorsum of the body and in having a brown ground color (rather than black).

Description of holotype (in mm).—An adult female of 62.2 SL, with large eggs. Head length 12.2; maximum head width 9.2; head depth at posterior angle of jaw 5.0; upper eyelid length 4.0; upper eyelid width 2.9; anterior rim of orbit to snout 3.8; horizontal length of orbit 4.0; interorbital

distance 2.2; projection of snout beyond lower jaw 1.2; distance separating external nares 2.9; distance separating internal nares 2.0; distance between vomerine teeth and parasphenoid tooth patch 0.8; number of premaxillary-maxillary teeth 55; number of vomerine teeth 23; axilla to groin 36.1; anterior to posterior angle of vent 3.9; snout to insertion of arm 16.6; length of right arm 14.2; length of right leg 14.5; width of right hand 4.5; width of right foot 5.7; tail length 50.7; tail width at base 4.9; tail depth at base 5.1.

Coloration in life: Examination of 35-mm color transparencies reveals the dorsum to be black with slightly greenish, cream-colored iridophore patches (having an overall lichenlike appearance), which are especially pronounced on sides of body (thus producing a faint dorsal stripe), limbs, and on entire length of tail. Venter black with a few tiny, widely scattered, cream-colored iridophore patches with the largest at the tip of the tail.

Coloration in alcohol: Dorsum chocolate brown with paler patches on sides; top of head and center of back lighter. Venter paler brown, with a few scattered tiny light flecks.

Habitat and associated species.—The holotype was under a moist log in a small patch of heavy pine-fir forest with much moss and low weeds, and with bunchgrass in open areas. Specimens of *Sceloporus adleri* were collected in rocky areas nearby (Smith and Savitzky, 1974) and the type series of *Pseudoeurycea ahuitzotl* and specimens of *Thorius* sp. were taken about 125 and 65 m lower, respectively, on the same slope of Cerro Teotepec. (See above.)

Etymology.—Teotepec, the name of the highest peak in the Sierra Madre del Sur, is derived from the Nahuatl words *teôtl* (deity or god) and *tepêtl* (mountain).

Remarks.—Concerning the type locality, the museum register recorded "3150–3450 m, 79 road miles west of Xochipala," but the collectors' field notes state "halfway to road" from their previous entry, which was at the peak of Teotepec; thus, 3425 m may be the best estimate. According to my measurement, the crest of the road (3300 m), above which the holotype was collected, is at a point about 11.3 km E (by road) Puerto del Gallo.

Pseudoeurycea tlahcuiloh new species

Green-flecked Salamander (Tlaconete de Lunares Verdes)

Figures 3C and 4A, B

Holotype.—KU 221955, an adult male, from the eastern approaches to Cerro Teotepec (17°28' N, 100°08' W), along the Milpillas–Atoyac Road, 50.3 km (by road) W Cruz Ocote, Guerrero, Mexico, at an elevation of 9725 feet (= 2966 m). One of two specimens collected at this site 25–26 June 1971 by Howard L. Freeman and Leo A. Cross, Jr. (See Remarks concerning type locality.)

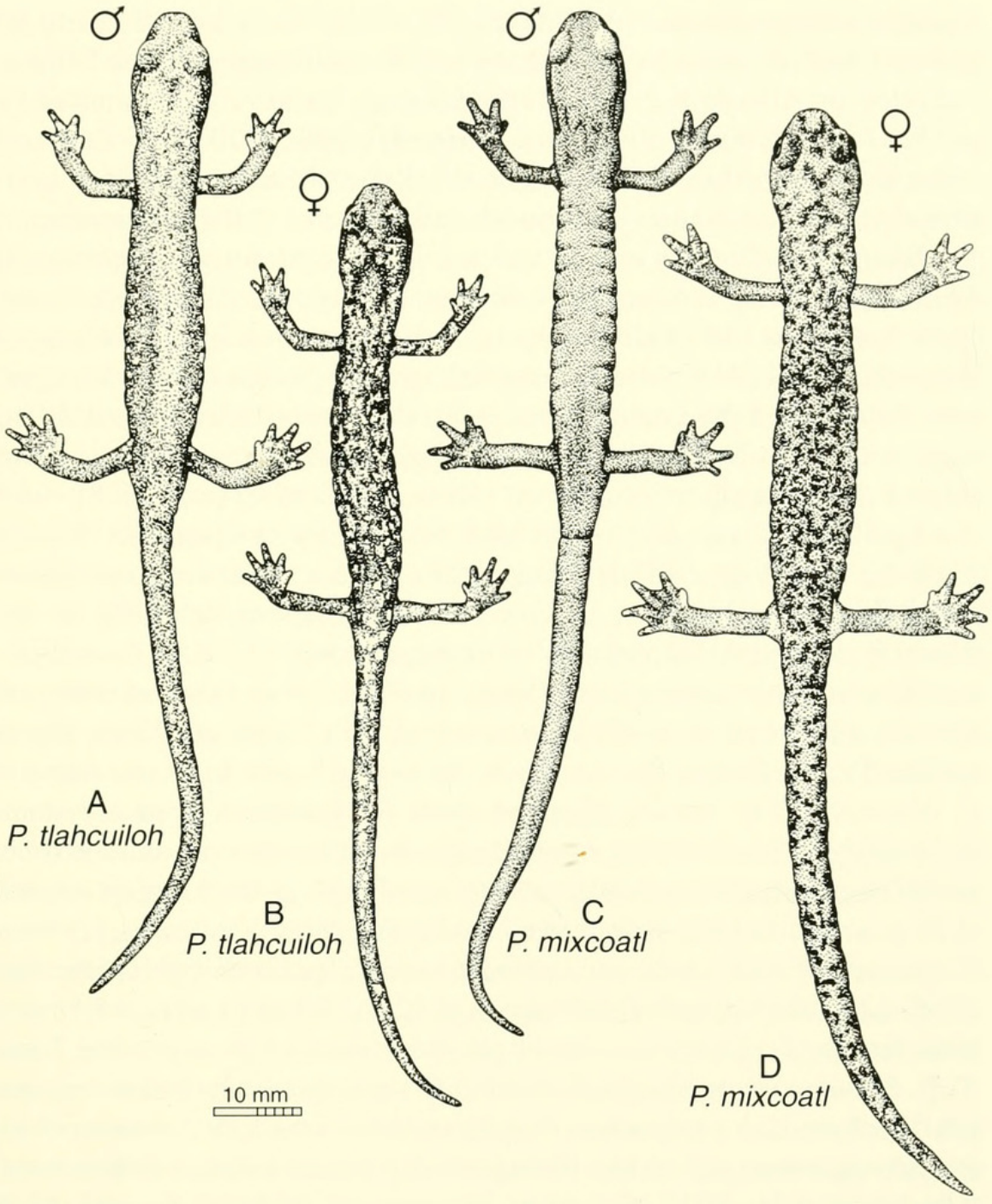


Fig. 4. Dorsal views of new species of *Pseudoeurycea* from Guerrero: *P. tlahcuiloh* (**A:** male, KU 221955, holotype; **B:** female, MVZ 222470, paratype); *P. mixcoatl* (**C:** male, KU 221957, holotype; **D:** female, MVZ 162162, paratype). Drawings by David M. Dennis.

Paratypes.—USNM 342490, same data as holotype; MVZ 222469, 29.5 km (by road) W Cruz Ocote, 8740 feet (= 2666 m); and UTA A-45578, MVZ 222470–471, KU 221956, USNM 342489, UMMZ 21101–102, AMNH A142152–153, all 36.8 km (by road) W Cruz Ocote, 8775–8900 feet (= 2676–2715 m). All specimens were taken along the Milpillas–Atoyac Road, on the eastern approaches to Cerro Teotepec, by Howard L. Freeman, Leo A. Cross, Jr., and Michael Gerardi.

Referred specimens.—UMMZ 211003–019, from 1 km SE Puerto del Gallo (17°29' N, 100°11' W), just south of Cerro Teotepec, about 2400 m, collected by Alfredo Sartorius Z. (See Variation.) MVZ field number TP 14551, from a clearing just above Puerto del Gallo, 8200 ft (= 2501 m), collected by Theodore J. Papenfuss and J. Robert Macey. (Specimen is not available for examination and was identified from a color transparency.)

Diagnosis.—*Pseudoeurycea tlahcuiloh* is a medium-sized species (to 61.8 mm SL) of *Pseudoeurycea* with an average-sized head and limbs, large hands and feet, a slender body, and a long, slender tail. In general proportions and color pattern, it superficially resembles *P. leprosa*, a species distributed from central Veracruz to the state of Mexico, but differs most notably in having a dark throat (light in *P. leprosa*), a longer and thinner tail (a length ratio mean of 0.95 in *P. tlahcuiloh* [range 0.81–1.03; $n = 10$; 40.1–61.8 mm SL] vs. 0.85 in Pueblan *P. leprosa* [range 0.78–0.95; $n = 8$; 51.1–57.2 mm SL]), and a larger head with a more pronounced neck. From the other Guerreran species of *Pseudoeurycea* described in this paper, *P. tlahcuiloh* differs in the following features. (1) From *P. ahuitzotl*, it differs in dorsal color pattern (large specimens of *P. ahuitzotl* with gray dorsum, not brown as in *P. tlahcuiloh*, and with lighter markings largely confined to the flanks). The venter is darker (light gray belly and throat in *P. ahuitzotl*). The mental gland of male *P. tlahcuiloh* is nearly round (noticeably wider than long in *ahuitzotl*); the tail is thinner, and the limbs are relatively shorter (a length ratio mean of 0.52 in the 5 largest adult *P. tlahcuiloh* vs. 0.54 and 0.58 in the 2 available adult *P. ahuitzotl*). (2) From *P. teotepec*, it differs in having a longer head (6 specimens of *P. tlahcuiloh* [52.5–62.0 mm SL] with head lengths of 12.6–13.7 mm [mean, 13.1] vs. a head length of 12.2 mm in the single specimen of *P. teotepec* [62.2 mm SL]). *Pseudoeurycea tlahcuiloh* has relatively longer limbs (in the 5 largest adult *P. tlahcuiloh* a ratio mean of 0.52 vs. 0.46 in the lone *P. teotepec*) and a relatively longer tail (in the 10 largest adult *P. tlahcuiloh*, a ratio mean of 0.95 [range 0.81–1.03] vs. 0.82 in *P. teotepec*). (3) From *P. tenchalli*, *P. tlahcuiloh* differs in its much larger adult size, in having a brown ground color (not gray, as in *P. tenchalli*), a dark throat (not lighter than belly), and the presence of a nearly round mental gland in males (nearly twice as wide as long in *P. tenchalli*). (4) From *P. mixcoatl*, it differs in dorsal color pattern (*P. tlahcuiloh* much more strongly patterned with light and dark patches and possessing light areas on the occiput). The gular fold bears a light edge (dark in *P. mixcoatl*), and the tail is thinner (widest at the base in *P. tlahcuiloh*, but usually thickest posterior to it in *P. mixcoatl*). The average number of premaxillary-maxillary teeth is greater in *P. tlahcuiloh* (46–58 teeth [mean, 54.0] in the 11 largest specimens [40.1–61.8 mm SL] vs. 34–56 teeth [mean, 43.6] in the 15 largest *P. mixcoatl* [41.0–65.4 mm

SL]). From *P. bellii*, *P. tlahcuiloh* differs in lacking the two longitudinal rows of discrete orange-to-red spots on the occiput and back, and in having a brown, rather than black, ground color.

Description of holotype (in mm).—An adult male 58.2 SL, with one long, well-developed testicular lobe on each side. Head length 13.5; maximum head width 9.2; head depth at posterior angle of jaw 4.6; upper eyelid length 4.0; upper eyelid width 2.4; anterior rim of orbit to snout 4.0; horizontal length of orbit 2.0; interorbital distance 2.4; projection of snout beyond lower jaw 1.4; mental gland irregularly roundish, its width 2.3, and length 2.0; distance separating external nares 3.1; distance separating internal nares 2.3; distance between vomerine teeth and parasphenoid tooth patch 1.1; number of premaxillary-maxillary teeth 45; number of vomerine teeth 27; axilla to groin 30.8; anterior-to-posterior angle of vent 5.4; snout to insertion of arm 18.4; length of right arm 15.4; length of right leg 16.6; width of right hand 5.1; width of right foot 6.1; tail length 58.0; tail width at base 3.7; tail depth at base 3.7.

Coloration in life: Examination of a 35-mm color transparency reveals the dorsum and sides of the head, body, limbs, and tail to be black, with small, dark brown blotches; on the sides of the body and on the tail, the blotches are light metallic brown. The digits are light brown. There are numerous tiny green flecks on the dorsal surfaces.

Coloration in alcohol: Dorsum dark brown, mottled with irregular small patches of iridophores, especially on sides of body; occiput slightly lighter brown; patches of iridophores along entire length of tail. Venter of body and tail blackish brown; throat same color, but with distinct, lighter edge to gular fold; soles of hands and feet cream. When freshly preserved, specimens from 1 km SE Puerto del Gallo were brownish-black with distinct, tiny greenish flecks on dorsum of body, limbs, and tail.

Variation.—The two sexually mature males (50.1 and 58.2 mm SL) have well-developed mental-gland clusters and testicular lobes; the four mature females are 52.4–61.8 mm SL (mean, 57.2). There is considerable variation in the boldness of the mottled dorsal pattern, the pale area on the occiput, and the pale-edged gular fold, irrespective of sex. The throat of some specimens is darker, with a few tiny lighter areas.

The specimens from 1 km SE Puerto del Gallo are poorly preserved, contorted, and brittle; hence, they have not been used in calculations of any meristic data in this description.

Habitat and associated species.—The type locality is a wet oak-pine-fir forest; one of two specimens of *Pseudoeurycea tlahcuiloh* collected here was under bark and the other under a log on the ground. The area had been logged and burned, but there was abundant cover for salamanders. The paratypes were collected in pine-oak-birch forests that were less moist than

those at the type locality; the salamanders were found in rotting logs and under bark of both standing and fallen trees. The specimens from 36.8 km W Cruz Ocote were collected on a steep slope above a cascading stream. The lowest locality (2666 m) had stands of birch mixed with pine and oak; "the area was wet from rains [when the specimen of *P. tlahcuiloh* was collected], but [is] seasonally more xeric" (Freeman, 1976). The specimens from 1 km SE Puerto del Gallo were under fallen, rotting trees. At four of these localities (29.5, 36.8, and 50.3 km W Cruz Ocote and in the clearing just above Puerto del Gallo), specimens of *Thorius* also were found beneath bark.

Etymology.—The Nahuatl word *tlahcuiloh* (painter or artist) is given in honor of my long-time friend, colleague, and field companion in Mexico and elsewhere, David M. Dennis, whose artistic and photographic skills have so greatly enriched our discipline.

Remarks.—According to my calculations, the type locality would lie approximately 17.6 km (by road) E Puerto del Gallo (an abandoned lumber camp), 5.1 km (by road) east of the crest of the road on Cerro Teotepec, and 15.0 km (by road) W Escalerilla.

Pseudoeurycea tenchalli new species
Bearded Salamander (Tlaconete con Barba)
Figures 2C, 3D

Holotype.—KU 182505, an adult male from 6.4 km (by road) SW Caballos (17°39' N, 99°50' W), Guerrero, Mexico, at an elevation of 2560 m. One of two specimens collected at this site on 4 August 1979 by Jonathan A. Campbell. (See Remarks concerning type locality.)

Paratype.—KU 182506, same data and collector.

Diagnosis.—*Pseudoeurycea tenchalli* is a small species (to 41.6 mm SL) of *Pseudoeurycea* with a wide head, short limbs, large hands and feet, a body of average girth, and a moderately thick tail of average length. In size and general proportions, it superficially resembles *P. anitae* of Oaxaca, but differs most notably in having a slightly narrower head, fewer maxillary-premaxillary teeth, and an unspotted body and tail. *Pseudoeurycea tenchalli* differs from all of the other Guerreran species of *Pseudoeurycea* described herein in the following features. (1) It matures at a smaller size (41.6 mm SL in the single available mature specimen vs. the smallest mature males of *P. ahuitzotl* [57.2 mm], *P. tlahcuiloh* [50.1 mm], and *P. mixcoatl* [52.7 mm]; single specimen of *P. teotepec*, a mature female [62.2 mm]). (2) *Pseudoeurycea tenchalli* has a relatively wider head (head-length:SL ratio of 0.20 and 0.18 in the 2 specimens of *P. tenchalli* vs. range of 0.14–0.17 [mean, 0.15] in adult *P. ahuitzotl, P. teotepec, P. tlahcuiloh,*

and *P. mixcoatl*). In addition, *P. tenchalli* differs from individual species in the following features. (1) From *P. ahuitzotl,* it differs in adult males having a mental gland that is nearly twice as wide as long, in contrast to its narrower condition in *P. ahuitzotl*. *Pseudoeurycea tenchalli* possesses fewer vomerine (21 and 22 in *P. tenchalli* vs. 23 and 27 in the 2 adult *P. ahuitzotl*) and premaxillary-maxillary teeth (36 and 42 in the same 2 *tenchalli* vs. 45 and 53 in adult *P. ahuitzotl*). (2) From *P. teotepec,* it differs in having a faintly patterned, gray dorsum (vs. boldly marked brown in *P. teotepec*), and a throat that is lighter than the belly (equally dark in *P. teotepec*). (3) From *P. tlahcuiloh,* it differs in having a gray ground color (not brown, as in *P. tlahcuiloh*), a light throat (dark like the belly in *P. tlahcuiloh*), and in males having a mental gland that is nearly twice as wide as long (nearly round in *P. tlahcuiloh*). (4) From *P. mixcoatl,* it differs in having a gray ground color (not brown, as in *P. mixcoatl*), and in males having a mental gland that is nearly twice as wide as long (nearly round in *P. mixcoatl*). From *P. bellii*, *P. tenchalli* differs in being gray in color (instead of black) and in lacking the two longitudinal rows of discrete orange-to-red spots on the occiput and back.

Description of holotype (in mm).—An adult male 41.6 SL, with one well-formed testicular lobe on each side. Head length 10.0; maximum head width 7.3; head depth at posterior angle of jaw 3.8; upper eyelid length 3.0; upper eyelid width 1.9; anterior rim of orbit to snout 3.4; horizontal length of orbit 1.7; interorbital distance 2.2; projection of snout beyond lower jaw 1.0; mental gland oblong, its width 4.1, and length 2.2; distance separating external nares 2.5; distance separating internal nares 1.8; distance between vomerine teeth and parasphenoid tooth patch 0.4; number of premaxillary-maxillary teeth 38; number of vomerine teeth 21; axilla to groin 22.8; anterior to posterior angle of vent 3.8; snout to insertion of arm 13.5; length of right arm 11.3; length of right leg 10.4; width of right hand 3.8; width of right foot 4.7; tail length 34.6; tail width at base 3.0; tail depth at base 3.3.

Coloration in life: According to the collector's field notes, the smaller specimen was "dark brown with tan markings" and the larger one was "uniformly black."

Coloration in alcohol: Dorsum gray with faint light patches of iridophores on body and along entire length of tail. Venter of body lighter gray; throat, soles of hands and feet, and midline of tail pale cream.

Variation.—The larger specimen (41.6 mm SL) is mature and has a single, well-formed testicular lobe on each side. Given the sexual size dimorphism in species of *Pseudoeurycea*, female *P. tenchalli* would be expected to exceed 45 mm SL. The smaller male (30.8 mm SL) lacks any external evidence of a mental-gland cluster; its dorsal ground color is a brownish-gray and it almost entirely lacks the dorsal iridophore patches

present in the holotype.

Habitat and associated species.—The two specimens were under logs in a disturbed pine-oak forest at a location just below the lower limit of the cloud forest. Other species taken at this site were *Eleutherodactylus* sp., *Thorius* sp., *Sceloporus formosus, S. mucronatus*, and *Mesaspis gadovii*. Saldaña de la Riva and Pérez Ramos (1987) reported the following species from the Caballos region: *Eleutherodactylus omiltemanus, E. nitidus, Anolis liogaster, Sceloporus stejnegeri, Eumeces brevirostris, Rhadinaea taeniata, Thamnophis chrysocephalus, T. godmani,* and *Crotalus intermedius*. The paratypes of *Pseudoeurycea mixcoatl* were collected near Carrizal de Bravo, in areas close to Caballos, but in distinctly wetter habitats. (See below.)

Etymology.—The Nahuatl word *tênchalli* (chin) is used in reference to the enormous mental-gland cluster on the chin of mature males of this species.

Remarks.—Caballos, a settlement near the type locality, has been known under a variety of names during the last 30 years, including Puentecilla, Filo de Caballos, and Filo de los Caballos.

Pseudoeurycea mixcoatl new species

Brown-streaked Salamander (Tlaconete Rayado Marrón)

Figures 3E and 4C, D

Holotype.—KU 221957, an adult male from Asoleadero (an abandoned lumber camp and sawmill; 17°36' N, 99°52' W), Guerrero, Mexico, at an elevation of 8500 ft (= 2600 m), collected 22–23 June 1971 by Howard L. Freeman and Leo A. Cross, Jr. (See Remarks concerning type locality.)

Paratypes.—MVZ 110899–0901, 0.6 km (by road) SW Carrizal de Bravo (17°37' N, 99°50' W), 2200 m; MVZ 132881–893 and 162162–172, 4 km (by road) SW Carrizal de Bravo, 8460 ft (= 2580 m), Guerrero, Mexico, all collected by Theodore J. Papenfuss. (See Remarks about localities.)

Diagnosis.—*Pseudoeurycea mixcoatl* is a medium-sized species (to 65 mm SL) of *Pseudoeurycea* with an average-sized head and limbs, large hands and feet, a slender body, and a long, moderately thick tail. In general proportions and color pattern, it superficially resembles *P. unguidentis* of Oaxaca, but differs most notably in having males with simple premaxillary teeth (vs. the strongly hooked premaxillary teeth of *P. unguidentis*, the teeth of which also are distinctly bicuspid) and in having a dark belly and throat (throat lighter than dorsum in *P. unguidentis*). From the other Guerreran species of *Pseudoeurycea* described herein, *P. mixcoatl* differs in the following features. (1) From *P. ahuitzotl,* it differs in having a pale brown dorsum with tiny, darker brown spots (not an unspotted, gray

dorsum as in *P. ahuitzotl*). The mental gland of male *P. mixcoatl* is round to only slightly wider than long (noticeably wider than long in *P. ahuitzotl*), and the digits have slightly expanded tips (not expanded in *P. ahuitzotl*). (2) From *P. teotepec,* it differs in having a longer head (head lengths of 13.0–15.3 mm [mean, 13.7 mm] in 7 adults [52.7–65.4 mm SL] vs. a head length of 12.2 mm in the single specimen of *P. teotepec* [62.2 mm SL]). The limbs are relatively longer (in *P. mixcoatl*, ratios of 0.52–0.58 [mean, 0.54] in the same 7 adults vs. 0.46 in the specimen of *P. teotepec*), and the tail is relatively longer (in *P. mixcoatl*, ratios of 0.94–1.04 [mean, 0.98] in the same adults, except one with a regenerated tail, vs. 0.82 in *P. teotepec*). (3) From *P. tlahcuiloh,* it differs in dorsal color pattern (*P. mixcoatl* less strongly patterned and lacking light areas on the occiput). *Pseudoeurycea mixcoatl* has a dark-edged gular fold (light-edged in *P. tlahcuiloh*), a thick tail (in *P. mixcoatl* tail usually thickest posterior to base, but tail widest at base in *P. tlahcuiloh*), and possesses a smaller average number of premaxillary-maxillary teeth (34–56 teeth [mean, 43.6] in the 15 largest *P. mixcoatl* [41.0–65.4 mm SL] vs. 46–58 teeth [mean, 54.0] in the 11 largest *P. tlahcuiloh* [40.1–61.8 mm SL]). (4) From *P. tenchalli,* it differs in having a brown ground color (not gray or grayish-brown, as in *P. tenchalli*). *Pseudoeurycea mixcoatl* has a relatively narrower head (range of 0.14–0.15 [mean, 0.15] in 7 adults vs. 0.20 and 0.18 in the two available specimens of *P. tenchalli*), and it matures at a larger size (smallest mature male *P. mixcoatl* 52.7 mm SL, whereas the single mature male of *P. tenchalli* 41.6 mm SL). From *P. bellii,* it differs in lacking the two longitudinal rows of discrete orange-to-red spots on the back and occiput.

Description of holotype (in mm).—An adult male 57.4 SL, with one large, well-formed testicular lobe on each side. Head length 13.5; maximum head width 8.6; head depth at posterior angle of jaw 5.3; upper eyelid length 3.7; upper eyelid width 2.8; anterior rim of orbit to snout 4.0; horizontal length of orbit 2.3; interorbital distance 2.5; projection of snout beyond lower jaw 1.3; mental gland squarish, its width 1.9, and length 1.9; distance separating external nares 3.2; distance separating internal nares 2.2; distance between vomerine teeth and parasphenoid tooth patch 0.1; number of premaxillary-maxillary teeth 45; number of vomerine teeth 31; axilla to groin 30.0; anterior to posterior angle of vent 4.8; snout to insertion of arm 17.0; length of right arm 15.0; length of right leg 15.5; width of right hand 5.4; width of right foot 6.2; tail length 58.3; tail width at base 3.4; tail depth at base 4.1.

Coloration in alcohol: Dorsum pale brown with tiny, darker brown spots, often configured approximately into longitudinal lines, especially down the midline of the back; spots generally longer than wide. Some light patches on the tail, irregular in position. Venter lighter brown than dorsum, especially on throat, soles of hands and feet, and on tail; edge of gular fold

dark like throat; no markings on venter except for some faint spots on throat.

Variation: Among four sexually mature males with mental-gland clusters and well-developed testicular lobes, the range in SL is 52.7–60.7 mm, in eight mature females, 44.2–65.4. There is considerable variation in dorsal pattern, ranging from some specimens that are nearly uniform brown with faint indication of spotting to others that are strongly marked with dark brown spots.

Habitat and associated species.—The holotype was in a crevice under a log on the ground. The general area of Asoleadero, the type locality, was described as a moist, oak-pine-fir cloud forest, dominated by large, bromeliad-ladened oaks (Adler, 1965). Asoleadero also is the type locality of *Hyla chryses* and *Sceloporus adleri.* Specimens of *Eleutherodactylus saltator, Hyla mykter, Thorius* sp., *Sceloporus formosus, S. grammicus, Mesaspis gadovii,* and *Pituophis lineaticollis* also have been collected in the same forest (Adler, 1965; Adler and Dennis, 1972; Adler, unpubl. observ.; Saldaña de la Riva and Pérez Ramos, 1987). *Pseudoeurycea bellii* also is known from Asoleadero (MVZ 110617). Asoleadero has now been "ruined by bulldozing for gravel for the new road" (T. J. Papenfuss, pers. comm.). The paratypes were taken in wet oak-pine-fir forest, where they were under bark of fallen oak and fir trees, beneath bark of vertical oak stumps, and in one instance, under a piece of oak bark on the ground; all were under loosened bark on fresh, not rotten logs. Other species taken at these sites include *Pseudoeurycea bellii, Anolis* sp., *Mesaspis* sp., two species of *Sceloporus, Thamnophis* sp., and *Ophyrachus undulatus*. Saldaña de la Riva and Pérez Ramos (1987) reported the following species from the region of Carrizal de Bravo: *Anolis liogaster, Sceloporus formosus, S. grammicus, Mesaspis gadovii, Eumeces brevirostris, Pituophis lineaticollis,* and *Thamnophis chrysocephalus*. The types of *Pseudoeurycea tenchalli* were collected near Caballos (description above), in an area near Carrizal de Bravo, but the habitat at the former site is drier than that at the latter.

Etymology.—The Nahuatl word *mixcoatl* is derived from *mixtli* (cloud) and *côâtl* (sometimes meaning serpent, but here, companion), in reference to the cloud-forest habitat of this species.

Remarks.—Asoleadero is between Caballos and Cruz Ozote, along a section of road that has now been abandoned; the collector recorded the altitude as "about 8400 feet," but I have measured it as about 2600 m. Carrizal de Bravo sometimes is mapped as Corral de Bravo. The locality 4 km (by road) SW Carrizal was given as "northwest" in the collector's notes, but on inquiry I am informed that "southwest" is correct (T. J. Papenfuss, pers. comm).

KEY TO THE SALAMANDERS OF WESTERN GUERRERO

The following key applies to the species known from western Guerrero; some characteristics may not apply to other species in the genus outside Guerrero. Generic characteristics follow Wake and Elias (1983).

1. Distinct groove between eye and lip present; skull incompletely ossified ..... *Thorius* species
   Groove between eye and lip absent; skull completely ossified 2

2. Sublingual fold absent; hands and feet nearly fully webbed, digits indistinct ..... *Bolitoglossa hermosa*
   Sublingual fold present; hands and feet not fully webbed, digits distinct 3

3. Two rows of distinct, large spots down middle of back (sometimes lateral pairs joined to form chevrons) and with spots on occiput ..... *Pseudoeurycea bellii*
   Rows of distinct spots on back and occiput absent 4

4. Broad head in adults (head width/SL 0.18–0.20); mental-gland cluster nearly twice as wide as long in males ..... *Pseudoeurycea tenchalli*
   Narrower head in adults (head width/SL 0.14–0.17); mental-gland cluster round or only slightly wider than long in males (condition unknown in *P. teotepec*) 5

5. Short tail in adults over 55 mm SL (tail length/SL 0.82); short head and short limbs with small hands and feet ..... *Pseudoeurycea teotepec*
   Longer tail in adults over 55 mm SL (tail length/SL 0.93–1.04); longer head and longer limbs with larger hands and feet 6

6. Tail moderate length in adults over 55 mm SL (tail length/SL 0.93); long limbs (combined length of arm plus leg/SL 0.54–0.58 [mean, 0.56] in adults over 57 mm SL); body dark brownish black with rust-colored markings in life ..... *Pseudoeurycea ahuitzotl*
   Tail long in adults over 55 mm SL (tail length/SL 0.94–1.04); shorter limbs (combined length of arm plus leg/SL 0.51–0.58 [mean, 0.53] in adults over 57 mm SL); body various shades of brown but without rust-colored markings in life 7

7. Dorsum of body brown with irregular darker streaks (and tiny green flecks in life); occiput lighter brown; gular fold pale-edged; tail widest at its base ..... *Pseudoeurycea tlahcuiloh*
   Dorsum of body brown with small darker streaks (commonly arranged in longitudinal lines down midline); occiput not paler; gular fold not pale-edged; tail widest beyond its base ..... *Pseudoeurycea mixcoatl*

THE DISTRIBUTION AND BIOGEOGRAPHY OF SALAMANDERS IN WESTERN GUERRERO

Eight species of salamanders—all of them members of the family Plethodontidae—presently are known from Guerrero.[1] All occur in a segment of the Sierra Madre del Sur that is bounded by the Pacific Ocean to the south, by the semidesert basin of the Río Balsas to the west and north, and to the east by a low, xeric pass at the approximate longitude of Chilpancingo. This pass separates the western part of the Sierra Madre from the rest of the range in the Guerreran-Oaxacan highlands to the east (Fig. 1). The highest point along this low pass is about 6 km N Chilpancingo, where the elevation is about 1450 m. Thus, for animals that are largely restricted to mesic habitats, this western segment of the sierra effectively is isolated from mesic habitats in surrounding regions. All but one of the Guerreran species of salamanders are endemic to this most western segment of the Sierra Madre del Sur Physiographic Region. The exception is *Pseudoeurycea bellii*, which has the largest range of any Middle American salamander (from eastern Sonora and western Tamaulipas to Oaxaca), but *P. bellii* may consist of more than one species because populations "are deeply differentiated from one another genetically" (Wake et al., 1992).

Within this segment of the Sierra Madre del Sur, several major factors affect the distribution of salamanders. The axis of the mountains lies in a general east-west direction. Along the coast, the prevailing winds throughout the year are on-shore and generally to the east, as based on measurements made at Acapulco, but inland—in the region occupied by the sierra—the wind direction changes to northwest (Page, 1930; Vivó Escoto, 1964). The result is that the moisture-laden winds from over the Pacific Ocean are interrupted by the sierra; thus, the moisture falls almost entirely on the Pacific slopes, thereby producing a rain-shadow effect in the arid Balsas Depression to the north. The windward side of the mountain chain has dense, mesic, deciduous forests at the lower elevations and oak-pine cloud forests at higher levels, whereas on the opposite (leeward) side, the deciduous forests are more xeric, less dense, and extend to higher elevations (Fig. 5). Cloud forest is more restricted or non-existent on most leeward slopes. In detail, the situation is more complex because of outlying peaks, deep canyons, and other physical features that tend to channel cloud movements. For example, the forests below Puerto del Gallo are directly

[1]There are no published records of salamanders in eastern Guerrero. However, in an unpublished thesis, Saldaña de la Riva and Pérez Ramos (1987) reported "*Pseudoeurycea* sp." from Cerro Pico del Aguila in the Sierra de Malinaltepec of southeastern Guerrero, near the Oaxacan border.

exposed to the Pacific and are cloud-covered mostly in the afternoons when clouds tend to move onto the slopes, but these clouds usually dissipate later in the day. On the other hand, at Asoleadero, which is somewhat sheltered from the Pacific behind Cerro Yohualatlejco, the clouds tend to remain for longer periods, sometimes for days or even weeks at a time, and can cause light rain to fall almost continuously. Moreover, the ecotones between vegetation types, which are shown as discrete boundaries in Figure 5, are in fact complex interdigitations that depend on local features such as exposure and slope that facilitate the reception and retention of moisture.

With the exception of *Bolitoglossa hermosa* and a single population of *Thorius* at 1140 m (discussed below), all other Guerreran salamanders apparently are confined to mesic habitats at elevations above 1700 m. It should be stated, however, that the near absence of salamanders from along the mesic transect below Puerto del Gallo may be an artifact of limited collecting. Compared to the rather extensive collecting by several persons at the higher elevations, relatively few have worked the area below Puerto del Gallo; most of my own field work in this area was concentrated on collecting frogs along stream courses. Unfortunately, the prospects for filling in distributional information are dim, given the extensive loss of high-elevation forests and salamander habitat by logging operations and erosion, as well as a widespread fire which destroyed much of the forest in the sierra west of Chilpancingo during 1982–1983 (Campbell, 1988).

In general, the seven species living at higher elevations are fairly unspecialized with respect to habitat and tend to be found beneath logs or bark (cf. discussion of *Thorius*, below). None has been found in more extreme microhabitats, such as bromeliads, caves, or in rock outcrops, although these habitats have been searched. However, more careful observations on the ecology of these species probably will reveal subtle differences in microhabitat. *Bolitoglossa hermosa*, generally found at low elevations, is at least occasionally a bromeliad inhabitant; one specimen was taken from a spiny bromeliad 2.5 m from the ground. A series of 23 was "found on the ground in leaf litter among coffee plants" (Papenfuss et al., 1983). At higher elevations, the amphibian inhabitants of arboreal bromeliads are frogs of the genera *Hyla* and *Eleutherodactylus*.

So far as is known, the eight species are rather restricted in vertical range. One specimen of *Bolitoglossa hermosa,* given to me by a logging company administrator, reportedly was collected at about 2465 m. However, this would mean an altitudinal range for *B. hermosa* of 1700 m, which is greater than that recorded for any species of *Bolitoglossa*. Therefore, this locality requires confirmation. Except for *Thorius* (which may comprise more than a single species as discussed below) and the wide-ranging *Pseudoeurycea bellii*, none of the high-elevation species has a vertical range greater than 550 m, although admittedly the data available for some

species are quite limited.

With one exception, the only salamander species found sympatrically are *Thorius* with single species of *Pseudoeurycea* (*bellii, ahuitzotl, tenchalli, tlahcuiloh,* and *mixcoatl,* and a near sympatry with *teotepec*). *Thorius* differs from *Pseudoeurycea* by having much smaller body and head sizes and, presumably, they feed on smaller prey. This is true even for the smallest species of *Pseudoeurycea—P. tenchalli*—which has a much broader head than do sympatric *Thorius* of comparable standard length. In snakes, Shine (1991) showed that feeding costs are disproportionately greater for the smallest prey eaten. Like snakes, salamanders are gape-limited predators and swallow their prey whole; feeding efficiency is presumably maximized when body size is closely related to the body sizes of their most common prey. *Pseudoeurycea bellii* and *P. mixcoatl* occur sympatrically at Asoleadero (2600 m) and at a site 0.6 km SW Carrizal de Bravo (2200 m). Thus, *P. tenchalli, P. mixcoatl,* and *P. bellii* occur in the same general region—between Caballos and Carrizal de Bravo—within no more than 2 or 3 km of each other; these three species have significantly different adult sizes. The type locality of *P. tenchalli* is in a relatively dry oak-pine forest, whereas *P. bellii* and *P. mixcoatl* are found in wetter habitats and often in cloud forest. A near sympatry also occurs on the south slope of Cerro Teotepec, where *P. ahuitzotl* and *P. teotepec* exist within about 125 m of elevation of each other (3296 and 3425 m, respectively).

David B. Wake and his colleagues have been studying the geographical ecology of Mesoamerican salamanders for many years (summarized in Wake et al., 1992) by conducting detailed studies along elevational transects. Their results allow comparisons to the distributional pattern of Guerreran salamanders, although data on the latter are more limited. Nevertheless, some similarities and contrasts can be discerned when comparing

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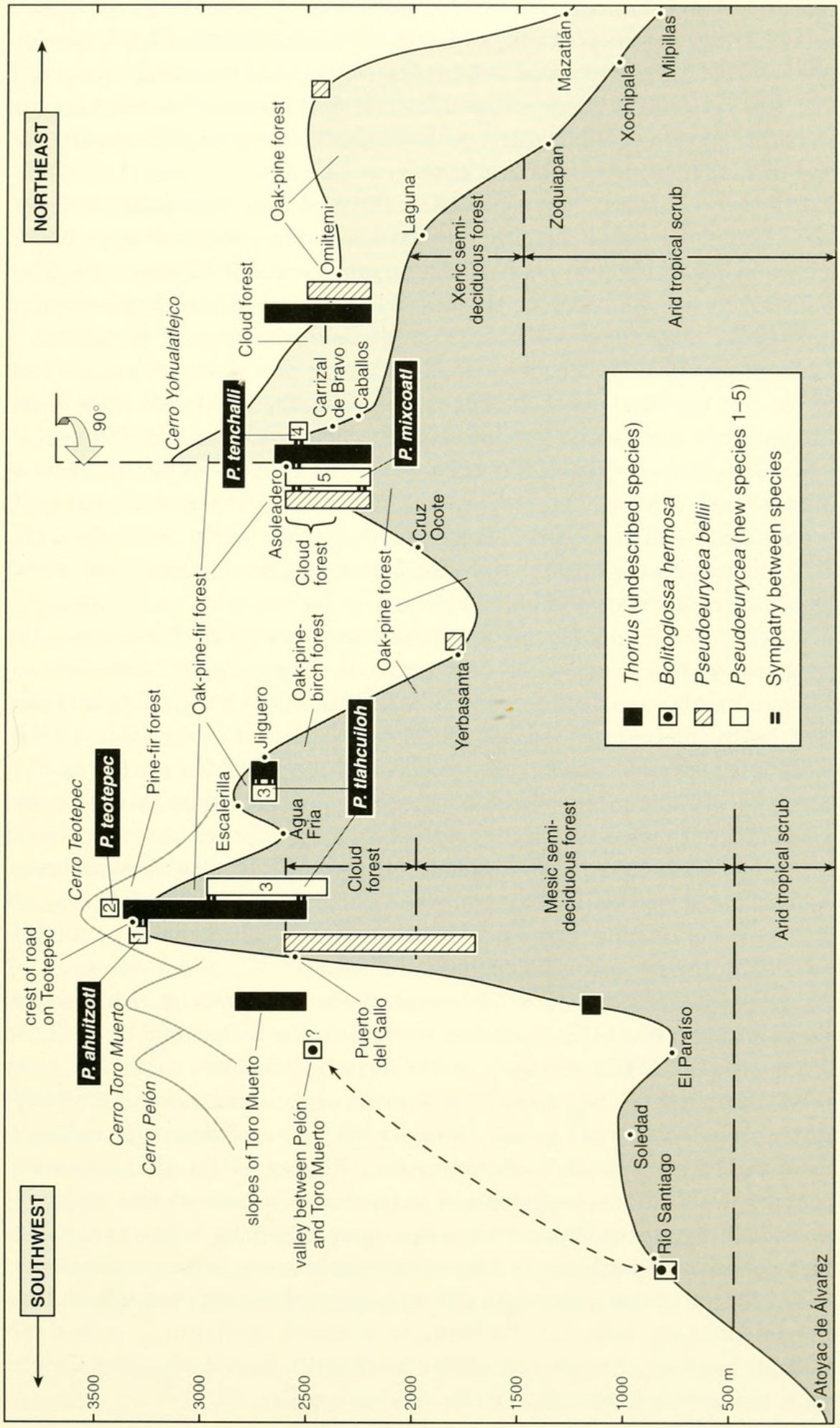
Fig. 5 (opposite page). Elevational transect through the Sierra Madre del Sur of western Guerrero, Mexico. The transect follows the route between Atoyac de Álvarez and Milpillas, shown in Figure 1. The straight-line distance between these two points is about 113 km, but by road is 238 km. The vertical axis is exaggerated. The transect is illustrated as if viewed from Xolapa, in the lower right corner of Figure 1; thus, it primarily shows the windward (Pacific) side of the sierra. The transect including Cerro Yohualatlejco and Omiltemi is shaded differently to emphasize that this ridge actually is positioned to the south of the route that includes Asoleadero and is nearly perpendicular to it (refer to Fig. 1); note that Asoleadero really is on the northwestern slope of Yohualatlejco. The approximate vertical distribution of the various vegetational communities is shown (see text for further details), as well as the vertical distribution and location of the salamander species (*Bolitoglossa hermosa, Thorius* sp., and 6 species of *Pseudoeurycea*). All records of plethodontid salamanders recorded from western Guerrero are plotted on this transect.


SOUTHWEST
NORTHEAST
3500
3000
2500
2000
1500
1000
500 m
Atoyac de Álvarez
Río Santiago
Soledad
El Paraíso
Puerto del Gallo
Mesic semi-deciduous forest
Arid tropical scrub
Cloud forest
Agua Fría
Escalerilla
Jilguero
Oak-pine-birch forest
Oak-pine forest
Yerbasanta
Cruz Ocote
Asoleadero
Oak-pine-fir forest
Pine-fir forest
Cerro Teotepec
crest of road on Teotepec
P. ahuitzotl
P. teotepec
P. tlahcuiloh
P. tenchalli
P. mixcoatl
Cerro Toro Muerto
Cerro Pelón
slopes of Toro Muerto
valley between Pelón and Toro Muerto
90°
Cerro Yohualatlejco
Cloud forest
Oak-pine forest
Omiltemi
Carrizal de Bravo
Caballos
Laguna
Xeric semi-deciduous forest
Zoquiapan
Mazatlán
Xochipala
Milpillas
Arid tropical scrub
Thorius (undescribed species)
Bolitoglossa hermosa
Pseudoeurycea bellii
Pseudoeurycea (new species 1–5)
Sympatry between species

the Guerreran transect to the two Oaxacan transects conducted by Wake's group. The general topography of the three transects is remarkably similar. All have a similar horizontal extent: Guerrero (113 km), northern Oaxaca (ca. 100 km), and southern Oaxaca (ca. 120 km). Each is dissected by one or two deep valleys; the highest peaks are in the range of 3000 m, and one end of each transect is near sea level.

All three transects have species of *Bolitoglossa, Pseudoeurycea,* and *Thorius*, but the transect in northern Oaxaca also has representatives of two additional plethodontid genera (*Chiropterotriton* and *Nototriton*). All three transects share one species, the ubiquitous *P. bellii*, which is found most commonly at moderate elevations in all three transects. The species of *Bolitoglossa* in all transects occur at the lowest elevations and, in the case of the two transects along the Pacific coast, on the windward sides of the ridge nearest the ocean. (The lone exception is an isolated population of *B. macrinii* from near Sola de Vega, Oaxaca.) The greatest species richness in all three transects is above 2000 m. As pointed out by Peterson et al. (1993), montane habitats in Mexico (cloud forest, pine-oak forest) have the greatest endemism among terrestrial vertebrates in general, which has direct implications for conservation efforts.

There are also some notable differences among three transects. The species diversity varies widely: Guerrero (8 species, but see discussion of *Thorius* below), southern Oaxaca (10), and northern Oaxaca (21, including two newly discovered species of *Thorius* [Hanken and Wake, 1994]). Additional species may be discovered, but I think that the greater species diversity of the northern Oaxaca transect is real and probably reflects the proximity of this transect to the confluence of a number of mountain ranges that might have served as past routes of dispersal during more mesic times.

Within the combined Oaxacan transects there are 26 species; only six species occur on more than one mountain ridge: (1) the isolated population of *Bolitoglossa macrinii* mentioned above; (2) the wide-ranging *Pseudoeurycea bellii;* (3) *P. cochranae* in the mountains on either side of the city of Oaxaca; (4) *P. smithi* on both Cerro San Felipe and Cerro Pelón in the northern Oaxaca transect and in the mountains just south of the city of Oaxaca; and (5) two species of *Thorius* in the mountains immediately surrounding the city of Oaxaca. Several of these populations may represent undescribed species (D. B. Wake, in litt., 18 May 1995). This mountain-specific distribution—in Oaxaca as in Guerrero—is remarkable when one considers that the valleys between the various pairs of ridges in the three transects are not particularly deep. However, because tropical salamanders generally are stenotopic and are able to tolerate only rather limited environmental variation (with *P. bellii* being an apparent exception if, in fact, it is a single species), they are restricted altitudinally; thus, these valleys apparently act as barriers to most of the various species.

Given this last point, it is perhaps noteworthy that Hanken (1983) regarded all Guerreran *Thorius* as belonging to a single species, even though he examined specimens from the two major uplifts in the Guerreran transect. In the Oaxacan transects there are 10 species of *Thorius*, and those on adjacent ridges are different species, with the two exceptions noted above. If Hanken's interpretation is correct, it implies that the valley in the Guerreran transect (at about 1700 m, between Yerbasanta and Cruz Ocote; Fig. 1), has not been sufficient to maintain genetic isolation of the *Thorius* in the two uplifts. The area between Yerbasanta and Cruz Ocote is, in fact, quite a narrow and dry ridge and presently is an unsuitable environment for the high-elevation *Thorius* that are confined to moist habitats. Alternately, larger samples of *Thorius* from either side of the valley may reveal consistent differences and separate species status.

In my experience, during the dry season *Thorius* in the Asoleadero area tend to live in more exposed places such as under the bark of fallen pine logs or under pine bark in the forest, whereas those in the Cerro Teotepec area were deep inside moist pine logs and especially in logs covered with moss. This apparent ecological difference may simply represent the more consistently moist environment around Asoleadero during the dry season. Freeman (1976), who conducted an extensive ecological study of *Thorius* in the western Sierra Madre del Sur during the wet season, concluded that there were statistically significant differences in microhabitat selection between populations at Cerro Teotepec and Asoleadero. He noted (1976:164–165) that *Thorius* in the Asoleadero region were "inhabitants of mesic cloud forests ... [and] were most often found within rotted logs and to a lesser extent beneath logs," whereas the form in the Cerro Teotepec area "is found in pine and fir forest habitat ... [and] prefers living beneath bark on fallen dead trees and to a lesser extent is found within and beneath logs."

In addition to these montane localities for *Thorius*, specimens also are known from a significantly lower elevation. Two specimens (MVZ 183425–426) were collected at a site 13.7 km (by road) NE El Paraíso (along the Atoyac–Puerto del Gallo Road), 1140 m, by John E. Cadle in November 1977. They were under separate logs along a small stream surrounded by riparian vegetation that had been partly cleared and planted with coffee. Associated species included *Eleutherodactylus ?rugulosus, Hyla pinorum, Ptychohyla leonhardschultzei, Anolis liogaster*, and *Leptodeira septentrionalis* (J. E. Cadle, pers. comm.). Given the low elevation and the distinctively lowland association of species, these *Thorius* well may represent a separate species from those in the highlands (lowest locality, 2200 m).

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LITERATURE CITED

Adler, K. 1965. Three new frogs of the genus *Hyla* from the Sierra Madre del Sur of México. Occas. Pap. Mus. Zool. Univ. Michigan 642:1–18.

Adler, K., and D. M. Dennis. 1972. New tree frogs of the genus *Hyla* from the cloud forests of western Guerrero, México. Occas. Pap. Mus. Nat. Hist. Univ. Kansas 7:1–19.

Campbell, J. A. 1988 (1989). The distribution, variation, natural history, and relationships of *Porthidium barbouri* (Viperidae). Acta Zool. Mex., new ser. 26:1–32.

Davis, W. B., and J. R. Dixon. 1959. Snakes of the Chilpancingo region, Mexico. Proc. Biol. Soc. Washington 72:79–92.

Davis, W. B., and J. R. Dixon. 1961. Reptiles (exclusive of snakes) of the Chilpancingo region, Mexico. Proc. Biol. Soc. Washington 74:37–56.

Davis, W. B., and J. R. Dixon. 1965. Amphibians of the Chilpancingo region, México. Herpetologica 20:225–233.

Flores-Villela, O., and A. Muñoz Alonzo. 1993. Anfibios y reptiles, pp. 411–442 *in* Luna Vega, I., and J. Llorente Bousquets (eds.), Historia Natural del Parque Ecológico Estadal Omiltemi, Chilpancingo, Guerrero, México. México: Univ. Nac. Autón. México.

Freeman, H. L. 1976. *Systematics and Evolutionary Trends of the Mexican Salamander Genus* Thorius *Cope, 1869 (Amphibia: Plethodontidae)*. Doctoral dissertation. Newark: Rutgers Univ.

Gadow, H. 1905. The distribution of Mexican amphibians and reptiles. Proc. Zool. Soc. London 1905:191–244.