

A SEVENTH SPECIES OF MINUTE SALAMANDER (*THORIUS*: PLETHODONTIDAE) FROM THE SIERRA DE JUÁREZ, OAXACA, MÉXICO

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ABSTRACT: We describe a new terrestrial species of minute lungless salamander of the Mexican genus *Thorius* (Plethodontidae) from montane pine-oak forests in the Sierra de Juárez of north central Oaxaca, México. The new species is distinguished from congeners by a combination of body size, external morphology, osteology, and dental traits, and it is well differentiated genetically from other named species for which data are available. This is the seventh endemic species of *Thorius* reported from the Sierra de Juárez, and known localities are geographically isolated from those of all other species. Discovery of another new species of plethodontid salamander from Oaxaca enhances the state's standing as a preeminent center of herpetological diversity within both México and Mesoamerica.

Key words: Miniaturization; Taxonomy; Biogeography; Osteology

MESOAMERICA is one of the world's biodiversity hotspots; both the relative and absolute numbers of species and the degree of endemism are exceeded by few other terrestrial habitats (Myers et al., 2000). Approximately 40% of the nearly 3000 species of tetrapod vertebrates reported from Mesoamerica are endemic to this region, and they represent more than 4% of the total number of tetrapod species known worldwide. Within Mesoamerica, geographic patterns of species richness vary among taxa. For amphibians and reptiles, an important center of biological diversity is the Mexican state of Oaxaca. Indeed, the richness of Oaxaca's herpetofauna, which includes more than one-third of all species of amphibians and reptiles found in México, is exceeded only by Costa Rica (Casas-Andreu et al., 1996).

One of the groups that has helped to establish the biological importance of both Mesoamerica and Oaxaca is the terrestrial salamander genus *Thorius* (Plethodontidae). *Thorius* is endemic to México, where it is restricted to four states along the southeastern edge of the Mexican plateau—Oaxaca, Veracruz, Puebla, and Guerrero (Wake and Lynch, 1976). Although the genus was first described >130 yr ago (Cope, 1869), as recently as 1993 it

comprised only nine formally described species (Duellman, 1993). In the last several years, the number of valid, named species has more than doubled to 22, including five new species described from Oaxaca (Hanken and Wake, 1994, 1998; Hanken et al., 1999). There remain, however, many populations of *Thorius* that cannot be confidently or easily assigned to any known species, and which are believed to represent undescribed species (Hanken, 1980, 1983; Hanken and Wake, 1998). Several of these populations exist at remote montane localities in northern and western Oaxaca, and are poorly represented in most museum collections. Here, we formally describe a new species of *Thorius* based on large series of specimens collected from adjacent localities at the extreme northwestern edge of the Sierra de Juárez of northern Oaxaca (Fig. 1). This species, which is both morphologically and genetically distinct from all congeners, further enhances Oaxaca's standing as an important center of herpetological diversity within both México and Mesoamerica.

MATERIALS AND METHODS

Measurements were made using digital or dial calipers or a dissecting microscope fitted with an ocular micrometer; standard

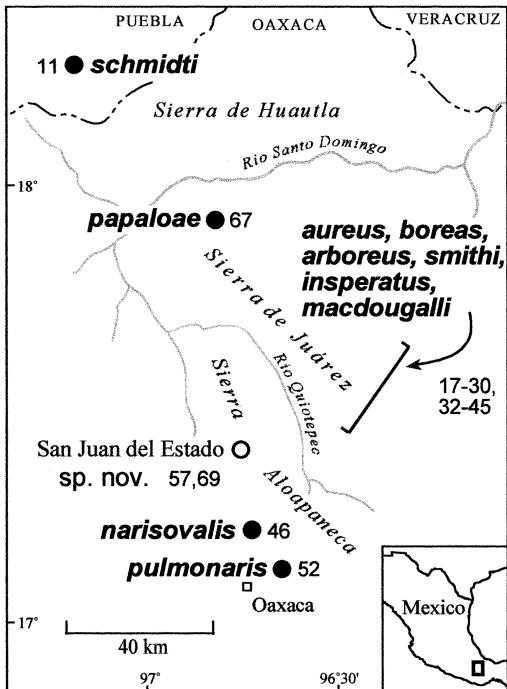


FIG. 1.—Map of north-central Oaxaca, México, showing the type localities (closed circles, bracket) of *Thorius papaloae* and its geographically closest congeners. *Thorius papaloae* is known from several localities near the village of Concepción Pápolo. All lie within montane pine-oak forest at elevations ranging between 2500 and 2850 m. The open circle denotes the locality of two sympatric populations of *Thorius* from 15 km northeast of the village of San Juan del Estado, 2550 m elevation. Neither of these populations can be referred to any named species; each likely represents an additional, undescribed species. Location of main map area in southeastern México is depicted in inset at lower right. Populations are numbered according to Hanken (1983).

length (SL) was measured from the anterior tip of the snout to the posterior angle of the vent. Limb interval equals the number of costal interspaces between the tips of appressed fore- and hind limbs, measured in one-half increments (e.g., 3, 4.5). Whole-mount skeletal preparations were stained for bone and cartilage using alizarin red S and Alcian blue 8GX, respectively (Klymkowsky and Hanken, 1991). Osteological descriptions use the cranial character states and mesopodial patterns described and illustrated by Hanken (1982, 1984, 1985), Hanken and Wake (1994, 1998), and Hanken et al. (1999);

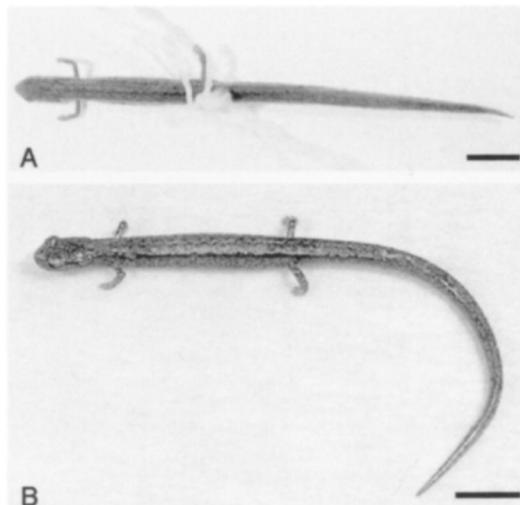


FIG. 2.—Photographs of *Thorius papaloae*. (A) Holotype, MVZ 183468, an adult female. Photo by D. Wake. (B) Live specimen, collected at the type locality by J. Hanken and H. B. Shaffer, 15 February 1976 (museum number unavailable). Photo by J. Hanken. Scale bars = 0.5 cm.

see Wake and Elias (1983) for comparisons with other tropical genera. Counts of presacral (trunk) vertebrae do not include the first, or atlas, vertebra. Except for the holotype, tooth counts are based on cleared-and-stained specimens; all alcoholic specimens were examined for the presence of maxillary teeth. Numbers of vomerine teeth in the holotype are provided separately for right and left sides; these counts are summed for other individuals. Institutional abbreviations are as listed in Leviton et al. (1985) except for MZFC (Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México, México, D.F.).

DESCRIPTION OF NEW SPECIES

Thorius papaloae sp. nov. Pápolo Minute Salamander

Holotype.—MVZ 183468, an adult female from 8 km (road) NE of Concepción Pápolo, Oaxaca, México, elevation 2670 m, collected 15 February 1976 by J. Hanken and H. B. Shaffer (Fig. 2A).

Paratypes.—All from Oaxaca, México: MVZ 183470, 183473, 183475, 187052–69 (18 specimens), same data as the holotype;

MVZ 183479, 183483, 183485–6 (two specimens), 183493–94 (two specimens), 183496, 183504–5 (two specimens), 183508, 183510, MCZ A-134202–3 (two specimens), MZFC 12630–31 (two specimens), same data as the holotype, except 11 km (road) NE of Concepción Pápaló, elevation 2820 m; MVZ 183518, same data as the holotype, except 15 km (road) NE of Concepción Pápaló, elevation 2850 m; LACM 121728–29 (two specimens), 121731, 121733, 121737–38 (two specimens), approximately 14 mi E of Santos Reyes Pápaló (likely identified incorrectly, should instead be Concepción Pápaló—see Remarks), elevation 2500 m, collected 3 August 1975 by T. W. Taylor and A. D. Lau. Some specimens are cleared and stained or have had tissue removed for protein comparisons.

Diagnosis.—This is a small species of *Thorius* with large, elliptical nostrils, no maxillary teeth, and a relatively long tail (Fig. 2B). Most specimens have prominent paratoid glands. It is distinguished from all other small species of *Thorius* from the Sierra de Juárez that lack maxillary teeth, as follows: from *T. macdougalli* in having somewhat larger hands and feet, a slightly narrower head, more vomerine teeth, and premaxillary teeth in most females, and in lacking a mottled dorsal coloration; from *T. insperatus* by having narrower, more elongate nostrils; from *T. arboreus* in having larger adult size, a larger, more elongate nostril, and a more obscure dorsal coloration; and from *T. pulmonaris* in having smaller adult size and a relatively shorter tail. The predominant tarsal pattern is different from the one found in most other species, and there are significant protein (allozyme) differences.

Description.—This is a small species; adult standard length averages 20.4 mm in 10 males (range 19.0–23.2) and 21.6 mm in 10 females (20.1–23.4). The head is relatively broad; SL averages 7.2 times head width in males (range 6.5–7.5) and 7.4 in females (6.7–8.4). Snouts are pointed. Nostrils are large and elliptical; the mean ratio of major to minor axes equals 1.7 (range 1.5–2.0) in males and females. Eyes are moderately large and protrude slightly

beyond the margin of the jaw in dorsal view. A suborbital groove intersects the lip on each side of the head. There are 1–2 premaxillary teeth in adult males (mean 1.8) and 0–5 teeth in females (mean 2.2). There are no maxillary teeth. Vomerine teeth average 6.1 in both males (range 4–10) and females (4–8). Limbs are moderately long; limb interval averages 3.6 in males (range 3–4) and 4.5 in females (4–6). Hands and feet are relatively well developed and moderately broad; foot width averages 1.0 in males (0.9–1.1) and 1.1 in females (0.9–1.2). Digits 1 and 4 (hand) and 1 and 5 (foot) are short, but the central digits are relatively long and have rounded tips. Fingers, in order of decreasing length, are 3–2–4–1; toes are 3–2–4–5–1. The tail is moderately long (exceeds standard length) and tapered; mean SL divided by tail length equals 0.85 in two males (range 0.83–0.86) and 0.92 in six females (0.75–1.06). A round and relatively prominent mental gland is present in most adult males (maximum dimensions: 1.2 mm wide, 1.0 mm long). The postiliac gland is small and pale, and it is relatively inconspicuous externally in some adults. Paratoid glands are prominent in most specimens, but less so in a few others.

This is a relatively dark species, with some indication of an obscure dorsal band in most individuals. Specimens with the lightest band have a herringbone pattern middorsally. The venter, while dark, is lighter than the flanks, and the underside of the tail is especially light. The gular region is marked with numerous white spots. Many individuals have a light nuchal spot, and some have a pair of light streaks over the shoulders.

Measurements of the holotype (in millimeters).—Head width 3.0; snout to gular fold (head length) 3.9; head depth at posterior angle of jaw 1.8; eyelid width 0.7; eyelid length 1.5; anterior rim of orbit to snout 1.0; horizontal orbit diameter 1.0; interorbital distance 1.7; distance separating external nares 0.8; major axis of nostril 0.5; minor axis of nostril 0.3; snout projection beyond mandible 0.5; snout to posterior angle of vent (standard length) 22.1; snout to anterior angle of vent 20.8; snout

to forelimb 6.0; axilla to groin 13.0; limb interval 6.0; shoulder width 2.0; tail length 29.3; tail width at base 2.0; tail depth at base 2.2; forelimb length (to tip of longest toe) 3.7; hind limb length 4.7; hand width 0.7; foot width 0.9. Numbers of teeth: premaxillary 2; maxillary 0; vomerine 6–8. The right foot is partly regenerated.

Coloration of the holotype (in alcohol).—The ground color of the head, body, and tail is dark blackish-brown. It is darkest along the flanks of the trunk and tail. An obscure brown dorsal stripe with indistinct borders begins on the nape and extends posteriorly onto the proximal portion of the tail. The venter is pale brown with scattered white spots in the gular region; the ventral spots become indistinct in the trunk. Limbs are a slightly lighter brown than the rest of the animal, and the hands and feet are even less densely pigmented. Costal grooves, the gular fold, and the extension of the fold onto the neck all stand out because of their lack of pigment. Otherwise, there are no distinguishing marks of any kind. The paratoid gland is prominent.

Coloration in life.—Based on field notes by J. Hanken (18 February 1976): In juveniles, the solid dorsal stripe is interrupted by a median dark line. In adults, it is reduced to a dark, herringbone pattern.

Osteology.—This description is based on data from 18 adult skeletons. The skull is very poorly ossified, even relative to most other species of *Thorius*. Some cranial characters are sexually dimorphic, with males typically less developed than females. The degree of contact between ascending processes of the premaxillary bone is highly variable. The processes remain separate from one another in half of the specimens (character 1, state a), but in the other specimens they range from barely articulating to fusing along more than half of their length (states b–d). Dental processes of the premaxilla are separate from the maxilla in all males and most females (character 2, state a). In a few females, the two elements overlap slightly in ventral view but do not articulate (state b). The premaxilla bears teeth in all specimens but one (character 8, state b). The

nasal bone is thin, rod-like, and confined to the posterior edge of the nasal capsule, especially in males (character 3, state b). In some males and many females, it is slightly broader and extends somewhat anteriorly over the nasal capsule (state c). The nasal and the maxilla barely articulate in most specimens (character 4, state b), but they are separate in a few specimens (state a) and fuse to one another on one side of one specimen (state c). The prefrontal bone is slender. It remains separate from the nasal in nearly all females (character 5, state b) but contacts the nasal in all males (state c). In all specimens but one, the prefrontal does not extend ventral to the dorsal border of the nasolacrimal foramen; thus, it remains well separated from the maxilla (character 6, state a). In one specimen, the prefrontal extends posteriorly beyond the nasolacrimal foramen to articulate with the maxilla (state b). Septomaxillary bones are absent in nearly all specimens (character 7, state a). In one specimen, they are represented by a tiny sliver of bone at the edge of each external naris (state c).

The maxillary bone is delicate—long and slender—and lacks teeth (character 9, state a). In one specimen (MVZ 187064), the right maxilla appears to have been broken and partly repaired; a cartilaginous callus bridges the fracture site. The vomer is reasonably well developed. A short to very short preorbital process is present in all specimens but one and bears teeth. There are relatively few vomerine teeth, which are arranged in a short row. The frontal fontanelle is relatively narrow for *Thorius*; the parietal fontanelle is wide (its breadth equals 0.44–0.67, mean 0.52, times the maximum skull width across the parietals). Otic crests are lacking, and there is no columellar process on the operculum. The postsquamosal process is well developed. Hyobranchial cartilages are mineralized in only three specimens (and only the basibranchial).

All specimens have 14 presacral vertebrae. Typically, all trunk vertebrae but the last bear ribs, but in a few specimens the last trunk vertebra has only a partial rib. The limbs are slender but well developed.

The tibial spur is present as an attached crest in most specimens, but it ranges from well developed to absent in those remaining.

Mesopodial morphology is variable, although the frequency of non-modal variants is somewhat lower than in most other species of *Thorius*. Asymmetry, however, is common: nearly 40% of the specimens have a different carpal or tarsal pattern between right and left sides. Carpal pattern I predominates in the forelimb (94% of adult carpi examined). This pattern contains six separate elements, with two derived states in relation to outgroup genera: fused intermedium plus ulnare, and fused distal carpal 4 plus centrale. It is the most generalized pattern observed in *Thorius* and is the likely ancestral state for the genus. Two other carpal patterns, each with additional or different fusions relative to pattern I, are each found in a single adult (one side only): II (fused distal carpals 1–2 and 3), 3%, and VIII (like II, but with the centrale fused to the intermedium-ulnare instead of distal carpal 4, and centrale 1 fused to the first metatarsal), 3%. Pattern VIII is unique to *T. papaloae*.

The modal tarsal pattern is V, 75%. This pattern contains seven separate elements, with two derived states in relation to outgroup genera: fused intermedium and fibulare, and fused distal tarsals 4 and 5. Tarsal pattern VII, with one additional fusion relative to pattern V (fused distal tarsal 4–5 and centrale), is present at a moderate frequency, 19%. Pattern I (like V, but with separate intermedium and fibulare), the presumed ancestral pattern for *Thorius* that predominates in many species, is found on only one side of one adult, 3%. The tarsal pattern could not be scored in one abnormal foot that had only four toes.

The digital skeleton also is highly variable, especially in the hind limb, including several instances of phalangeal loss and gain. The predominant phalangeal formula in the hand is 1-2-3-2 (86% of adult carpi). 1-2-3-1 and 2-2-3-2 are rare variants, 3% each; the formula could not be counted in two hands that were damaged during preparation, 3%. The modal formula in the foot is 1-2-3-3-2, 53%; 1-2-3-3-1 is a com-



FIG. 3.—Concepción Pápolo, Oaxaca, 15 February 1976. The type series of *Thorius papaloae* was collected from terrestrial microhabitats within forested slopes like those visible in the background, between 8 and 15 km by road NE of the village. Photo by J. Hanken.

mon variant, 22%. Three other formulae (1-2-3-2-2, 1-2-3-2-1, and 1-2-3-4-1) are rare, 3–6% each; a few other feet were damaged during preparation, 14%. Limb bone epiphyses and mesopodial elements are mineralized in most adults.

Habitat and range.—*Thorius papaloae* is known only from the vicinity of the type locality, which lies at the northwestern edge of the Sierra de Juárez in north-central Oaxaca, México, northeast of the village of Concepción Pápolo (Figs. 1, 3). Recorded elevations range from 2500 to 2850 m. The dominant natural habitat is pine or pine-oak forest (Binford, 1989). Goldman (1951:220–221) discussed the local terrain, vegetation and climate of this region, which he visited with E. W. Nelson 15–24 October 1894. According to field notes of J. Hanken (15 and 18 February 1976), most salamanders were collected under cover objects on the forest floor. Specimens collected at 15 km NE of Concepción Pápolo were found beneath the bark on fallen pine logs in a small clearing alongside the road. While this occurred during the winter dry season, moist microhabitats were common on north-facing wooded slopes with abundant cover. Several specimens of *Pseudoeurycea* are the only other salamanders collected at these localities (e.g., MVZ 137002, LACM 121722–27; tentatively assigned to *P. smithi*).

Etymology.—The species name refers to the village of Concepción Pápolo, which is very near the type locality. *Pápolo* (Span.) is a pungent digestive herb eaten raw by the sprig with many Mexican foods. The word is derived from *papalotl*, which means “butterfly” in Nahuatl, the language of the Aztecs.

Remarks.—Genetic variation in *T. papaloae* and relationships to congeners were examined using protein electrophoresis by Hanken [1980, 1983; populations 67–68, listed as *T. sp. G* (part)]. Evolutionary consequences of miniaturization of adult body size for appendicular morphology were examined by Hanken (1982, 1985; *T. sp. G*). Original data for the type specimens from MVZ, MCZ, and MZFC misidentifies the village of Concepción Pápolo as “Santos Reyes Pápolo,” a different village that lies only a few kilometers away, due to a faulty road map for Oaxaca State in wide use at the time of collection. The revised (correct) village name used in locality data above is derived from newer and improved topographic maps for this region, and was confirmed during field work by J. Hanken, D. Wake, G. Parra-Olea, and M. García-París in summer 1999. We believe that the same error applies to the remaining type specimens from LACM, which were collected within a year of the former specimens “on [the] road to Santa María Pápolo . . . approximately 14 mi. E of Santos Reyes Pápolo” (letter from A. Brame to D. Wake, 22 October 1975). According to newer maps, the village of Santa María Pápolo is accessible by road only from Concepción Pápolo and not from Santos Reyes Pápolo. The earliest record of *T. papaloae* is a single specimen (USNM 047797) collected by E. W. Nelson and E. A. Goldman from “near Reyes, Oaxaca,” elevation 3048 m, on 20 October 1894. “Reyes, Oaxaca” has been identified as Santos Reyes Pápolo (Binford, 1989; Goldman, 1951), and is thus very near the type locality.

DISCUSSION

Recognition of *Thorius papaloae* as a new species is justified by its large degree of genetic differentiation from other named species, by the substantial geo-

graphic distance of known localities from populations of its nearest congeners, and by subtle but characteristic morphological features.

Thorius papaloae is genetically distinct from all named species of *Thorius* in northern Oaxaca and adjacent Puebla for which allozyme data are available (Table 1; Fig. 4). Levels of genetic differentiation (Nei genetic distance, D_N ; Nei, 1972) are comparable to or exceed those that are typically seen among congeneric species of plethodontid salamanders (e.g., Highton, 2000). In contrast, two populations of *T. papaloae* from 8 and 11 km NE of Concepción Pápolo are virtually identical genetically; D_N equals 0.014 (n equals 20 specimens each). *Thorius boreas* from the Sierra de Juárez in Oaxaca is the most similar to *T. papaloae*, but even this distance is very large— D_N equals 0.64—and there are seven fixed allelic differences. Adults of *Thorius boreas* also are much larger and more robust, and they are osteologically distinct. The next most similar species are *T. macdougalli*, also from the Sierra de Juárez, and *T. pulmonaris* from Cerro San Felipe in the Sierra Aloapaneca. Each of these species has a D_N to *T. papaloae* of 0.68, which includes six or seven fixed differences and major frequency differences at 2–3 additional loci. *Thorius pulmonaris* is a larger species, and whereas *T. macdougalli* resembles *T. papaloae* in some morphological features, the two latter species differ in dental characters and external coloration. Three other Oaxacan species (*T. aureus*, *T. narisovalis*, and *T. arboreus*) each have a D_N to *T. papaloae* of around 0.8. *Thorius aureus* and *T. narisovalis* are much larger species; *T. aureus* also has maxillary teeth and a distinctive cranial morphology. *Thorius arboreus* is smaller and has a different external coloration than *T. papaloae*, and it occurs at much lower elevations. Finally, *T. schmidti*, from southeastern Puebla and extreme northern Oaxaca (Hanken and Wake, 1998; García-París and Parra-Olea, 1999), has a D_N of 1.24, with 10 fixed allelic differences. It is a much larger species and has maxillary teeth.

Genetic distances from *T. papaloae* to

TABLE 1.—Genetic differentiation between *Thorius papaloae* and several of its geographically closest congener (Fig. 1). D_N , Nei (1972) genetic distance between populations; **Fixed**, numbers of protein loci showing fixed differences between species (boldface) or nearly fixed differences, i.e., variant alleles are shared by two or more populations at frequencies of 0.25 or less; **n**, numbers of individuals sampled per population. Allozyme data (Hanken, 1980, 1983) are unavailable for *T. smithi* and *T. insperatus*, two additional species from the Sierra de Juárez, Oaxaca (Hanken and Wake, 1994).

Species	Locality	Population ¹	n	D_N to <i>T. papaloae</i>	Fixed
Uncertain	San Juan del Estado, Oaxaca	69	9	0.41	4, 3²
Uncertain	San Juan del Estado, Oaxaca	57	10	0.50	5, 2³
<i>T. boreas</i>	Sierra de Juárez, Oaxaca	36	10	0.64	7, 0⁴
<i>T. pulmonaris</i>	Cerro San Felipe, Oaxaca	52	3	0.68	6, 3⁵
<i>T. macdougalli</i>	Sierra de Juárez, Oaxaca	30	17	0.68	7, 2⁶
<i>T. aureus</i>	Sierra de Juárez, Oaxaca	37	9	0.80	7, 2⁷
<i>T. narisovalis</i>	Cerro San Felipe, Oaxaca	46	20	0.80	8, 0⁸
<i>T. arboreus</i>	Sierra de Juárez, Oaxaca	41	8	0.81	7, 2⁹
<i>T. schmidti</i>	Zoquitlán, Puebla	11	6	1.24	10, 2¹⁰

¹ Populations are numbered according to Hanken (1983). The reference population for *T. papaloae* (67) is from the type locality (n = 20).

² CAP, *Ldh-1*, *Mdh-2*, PEP, *Aat-1*, *Gp-2*, *Idh-2*. Enzymes are abbreviated according to Murphy et al. (1996).

³ GAPDH, CPI, C3PDH, *Ldh-1*, PEP, *Aat-1*, *Mdh-2*.

⁴ CAP, *Cp-2*, CPI, G3PDH, *Ldh-1*, *Mdh-1*, PEP.

⁵ CAP, GAPDH, CPI, *Ldh-1*, MPI, PEP, *Aat-1*, *Idh-1*, *Mdh-1*.

⁶ CAP, GAPDH, CPI, G3PDH, *Ldh-1*, MPI, PEP, *Aat-1*, *Mdh-1*.

⁷ *Aat-1*, CAP, GAPDH, CPI, C3PDH, *Mdh-1*, *Mdh-2*, *Idh-2*, PEP.

⁸ *Aat-1*, CAP, *Gp-2*, G3PDH, *Ldh-1*, *Mdh-1*, *Mdh-2*, PEP.

⁹ CAP, GAPDH, CPI, G3PDH, *Ldh-1*, *Mdh-1*, PEP, *Aat-1*, *Mdh-2*.

¹⁰ CAP, GAPDH, *Gp-2*, CPI, G3PDH, *Ldh-1*, *Mdh-1*, *Mdh-2*, MPI, PEP, *Idh-1*, *Ldh-2*.

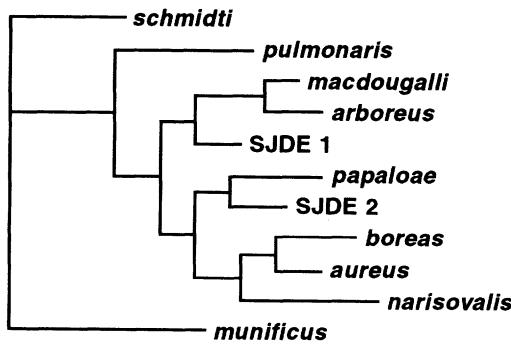


FIG. 4.—Neighbor-joining phylogram among *Thorius papaloae* and the nine geographically closest congeners in north-central Oaxaca and adjacent Puebla for which allozyme data are available (Fig. 1; Table 1). The dendrogram was produced by analyzing a matrix of Nei genetic distances (D_N) with the program Neighbor in PHYLIP, version 3.57c (J. Felsenstein, University of Washington, Seattle, unpublished 1995). It is intended to depict only the relative magnitude of genetic differences among taxa, not phylogenetic relationships. SJDE 1 and SJDE 2 are two sympatric, undescribed species from near San Juan del Estado, in the Sierra Aloapaneca, Oaxaca (Hanken 1980, 1983; populations 57 and 69, respectively). *Thorius munificus* from northern Veracruz is included as an outgroup, although the overall branching sequence is unrooted. Alternate branching schemes among these and additional populations based on allozyme data are presented in Hanken (1983).

remaining species in Oaxaca and Puebla, and to all species in Veracruz and Guerrero, are similarly large; they range from 0.41–1.63 (Hanken, 1980, 1983). *Thorius papaloae* also is morphologically distinct from two diminutive, poorly known species from the Sierra de Juaréz for which allozyme data are not available (Hanken and Wake, 1994). It differs from *T. smithi* in lacking maxillary teeth, and from both *T. smithi* and *T. insperatus* in having narrower and more elongate nostrils. Moreover, neither of the latter two species is known from elevations above 1550 m, whereas *T. papaloae* has not been taken below 2550 m.

Hanken (1980, 1983) used allozyme data to assign tentatively one of two sympatric populations from near San Juan del Estado, in the Sierra Aloapaneca, Oaxaca (T. sp. G, population 69), to the same species as populations from near Concepción Pápolo, which are herein described as *T. papaloae*. Indeed, each of the two populations from San Juan del Estado is more similar genetically to *T. papaloae* than is any other species of *Thorius*, named or unnamed (Table 1, Fig. 4). Based on preliminary morphological analysis (Hanken and

Wake, unpublished), we regard both populations from San Juan del Estado as distinct from those at Concepción Pápaló, so at this time the known range of *T. papaloae* is confined to the vicinity of the type locality. Neither population from San Juan del Estado can be confidently assigned to any named species of *Thorius*. Their identities, along with those of several remaining enigmatic and geographically disparate populations from southern and western Oaxaca, are currently under investigation and will be considered in a subsequent paper.

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RESUMEN

Se describe una especie nueva de salamandra de la familia Plethodontidae del género *Thorius* del bosque de Pino-Encino de la Sierra de Juárez en el Estado de Oaxaca, México. Esta salamandra se diferencia de sus congéneres por una combinación de caracteres morfológicos que incluyen tamaño total del cuerpo, osteología y características de la dentición. Asimismo esta especie está bien diferenciada genéticamente. Esta es la séptima especie endémica de *Thorius* de la Sierra de Juárez, aunque ésta se encuentra geográficamente aislada de las otras especies de la región. El descubrimiento de una especie nueva de salamandra de la familia Plethodontidae para el Estado de Oaxaca, incrementa la relevancia del Estado como un centro importante de diversidad herpetológica para México y Mesoamerica.

LITERATURE CITED

- BINFORD, L. C. 1989. A distributional survey of the birds of the Mexican state of Oaxaca. *Ornithological Monographs* 43:1–418.
- CASAS-ANDREU, G., F. R. MÉNDEZ-DE LA CRUZ, AND J. L. CAMARILLO. 1996. Anfibios y reptiles de Oaxaca. Lista, distribución y conservación. *Acta Zoológica Mexicana* (n.s.) 69:1–35.
- COPE, E. D. 1869. A review of the species of the Plethodontidae and Desmognathidae. *Proceedings of the Academy of Natural Sciences of Philadelphia* 1869:93–118.
- DUELLMAN, W. E. 1993. *Amphibian Species of the World: Additions and Corrections*. Museum of Natural History, University of Kansas, Special Publication 21:i–iii, 1–372.
- GARCÍA-PARÍS, M., AND G. PARRA-OLEA. 1999. Range extension of *Thorius schmidti* (Amphibia: Plethodontidae) in México. *Rev. Biol. Trop.* 47:627–628.
- GOLDMAN, E. A. 1951. Biological investigations in México. *Smithsonian Miscellaneous Collections* 115:1–476.
- HANKEN, J. 1980. Morphological and Genetic Investigations of Miniaturization in Salamanders (Genus *Thorius*). Ph.D. Dissertation, University of California, Berkeley, California, U.S.A.
- . 1982. Appendicular skeletal morphology in minute salamanders, genus *Thorius* (Amphibia: Plethodontidae): growth regulation, adult size determination, and natural variation. *Journal of Morphology* 174:57–77.
- . 1983. Genetic variation in a dwarfed lineage, the Mexican salamander genus *Thorius* (Amphibia: Plethodontidae): taxonomic, ecologic, and evolutionary implications. *Copeia* 1983:1051–1073.
- . 1984. Miniaturization and its effects on cranial morphology in plethodontid salamanders, genus *Thorius* (Amphibia: Plethodontidae). I. Osteological variation. *Biological Journal of the Linnean Society* 23:55–75.
- . 1985. Morphological novelty in the limb skeleton accompanies miniaturization in salamanders. *Science* 229:871–874.
- HANKEN, J., AND D. B. WAKE. 1994. Five new species of minute salamanders, genus *Thorius* (Caudata: Plethodontidae), from northern Oaxaca, México. *Copeia* 1994:573–590.
- . 1998. Biology of tiny animals: systematics of the minute salamanders (*Thorius*: Plethodontidae) from Veracruz and Puebla, México, with descriptions of five new species. *Copeia* 1998:312–345.
- HANKEN, J., D. B. WAKE, AND H. L. FREEMAN. 1999. Three new species of minute salamanders (*Thorius*: Plethodontidae) from Guerrero, México, including the report of a novel dental polymorphism in urodeles. *Copeia* 1999:917–931.
- HIGHTON, R. 2000. Detecting cryptic species using allozyme data. Pp. 215–241. In R. C. Bruce, R. G. Jaeger, and L. D. Houck (Eds.), *The Biology of Plethodontid Salamanders*. Kluwer Academic/Plenum Publishers, New York, New York, U.S.A.
- KLYMKOWSKY, M. W., AND J. HANKEN. 1991. Whole-

- mount staining of *Xenopus* and other vertebrates. *Methods in Cell Biology* 36:419–441.
- LEVITON, A. E., R. H. GIBBS, JR., E. HEAL, AND C. E. DAWSON. 1985. Standards in herpetology and ichthyology: part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia* 1985:802–832.
- MURPHY, R. W., J. W. SITES, JR., D. G. BUTH, AND C. H. HAUFER. 1996. Proteins: isozyme electrophoresis Pp. 51–120. In D. M. Hillis, C. Moritz, and B. K. Mable (Eds.), *Molecular Systematics*, 2nd ed. Sinauer Associates, Sunderland, Massachusetts, U.S.A.
- MYERS, N., R. A. MITTERMEIER, C. G. MITTERMEIER, G. A. B. DA FONSECA, AND J. KENT. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853–858.
- NEI, M. 1972. Genetic distance estimates between populations. *American Naturalist* 106:283–292.
- WAKE, D. B., AND P. ELIAS. 1983. New genera and a new species of Central American salamanders, with a review of the tropical genera (Amphibia, Caudata, Plethodontidae). *Contributions in Science, Natural History Museum of Los Angeles County* 345:1–19.
- WAKE, D. B., AND J. F. LYNCH. 1976. The distribution, ecology, and evolutionary history of plethodontid salamanders in tropical America. *Science Bulletin, Natural History Museum of Los Angeles County* 25:1–65.

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A NEW TOAD OF THE *BUTO MARGARITIFER* COMPLEX (AMPHIBIA: BUFONIDAE) FROM NORTHWESTERN VENEZUELA

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ABSTRACT: We describe a new species of toad of the *Bufo margaritifer* complex from the state of Falcón, Venezuela. This new species differs from the other members of the complex by the following combination of characters: medium-size (snout–vent length mean in 11 males 61.2 mm, in two females 72.9 mm), presence of a bony knob at the angle of the mouth, heel reaching the posterior margin of the tympanum when hindlimbs are adpressed forward, tibia length/snout–vent length ratio ranging from 0.40–0.45, toes almost fully webbed, tarsal fold absent, cephalic crests protuberant and thick, supratympanic crest visible and projecting slightly obliquely from body (slightly more pronounced in females), and neural spines generally distinct (except in some males).

Key words: Amphibia; Anura; *Bufo margaritifer* complex; Bufonidae; Taxonomy; Venezuela

AT PRESENT, one of the most complex taxonomic problems within Neotropical Bufonidae involves the members of the *Bufo margaritifer* (Laurenti, 1768) complex (as identified by Hass et al., 1995). Hoogmoed (1989a) stated: (1) the name *Bufo 'typhonius'* (Linnaeus, 1758) is not applicable to the species it is associated with at the moment, (2) the name probably was originally based on a specimen currently assigned to the genus *Rana* (*R. tigerina* Daudin, 1802), (3) *Bufo margaritifer* would be the correct name for the

taxon with large cephalic crest, occurring in the Guianas, and (4) the name '*typhonius*' should be suppressed. In spite of Hoogmoed's (1989a) arguments, some herpetologists still consider *Bufo 'typhonius'* valid (Duellman and Schulte, 1992; Vélez, 1995) perhaps because of a lack of a review of the *B. margaritifer* complex (Köhler and Lötters, 1999, and references cited therein) and/or type series for *B. margaritifer*. Hoogmoed (1986, 1989a,b, 1990) removed or synonymized 13 of the 17 species names which had been associ-