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Three New Species of Minute Salamanders (*Thorius*: Plethodontidae) from Guerrero, México, Including the Report of a Novel Dental Polymorphism in Urodeles

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Three new species of minute lungless salamanders of the Mexican genus *Thorius* (Plethodontidae) are described from montane forests in the Sierra Madre del Sur of Guerrero. Each species is distinguished from congeners by a combination of body size, external morphology, osteology, dental traits, and proteins. *Thorius omiltemi* and *T. grandis* are among the largest species within the genus; standard length (SL) approaches or exceeds 30 mm in many adults. *Thorius infernalis* is much smaller (SL < 19 mm). Adult *T. grandis* display an extreme, unique sexual dimorphism involving the presence/absence of maxillary teeth and several related features of cranial osteology. Protein (allozyme) data for *T. omiltemi* and *T. grandis* reveal substantial levels of genetic differentiation relative to species in Veracruz, Puebla, and Oaxaca. Comparable genetic data are unavailable for *T. infernalis*. The three species collectively define a broad elevational range, from high elevation *T. omiltemi* and *T. grandis* (2200–2700 m and 2495–3360 m, respectively) to lower montane *T. infernalis* (1140 m). Description of several additional species of plethodontid salamanders from central montane Guerrero underscores the region's rich herpetological diversity, which includes many endemic species of both amphibians and reptiles.

Se describen tres especies nuevas de salamandras mexicanas del género *Thorius*, las cuales habitan el bosque de montaña de la Sierra Madre del Sur en el estado de Guerrero, México. Cada especie se distingue de sus congéneres por una combinación de caracteres que incluyen: tamaño total del cuerpo, morfología externa, osteología, caracteres dentales y proteínas. *Thorius omiltemi* y *T. grandis* alcanzan longitudes mayores a 30 mm, lo cual las sitúa dentro de las especies más grandes dentro del género. En contraste, *Thorius infernalis* alcanza una longitud máxima de sólo 19 mm. Los adultos de *T. grandis* poseen un dimorfismo sexual extremo, incluyendo la presencia o ausencia de dientes maxilares, así como varios aspectos relacionados con la osteología del cráneo. Los datos de proteínas de *T. omiltemi* y *T. grandis* revelan una diferenciación genética substancial con aquellas especies de Veracruz, Puebla y Oaxaca. Se carece de informacion genética para *T. infernalis*. Las tres especies en conjunto presentan una amplia distribución altitudinal, desde elevaciones de 2200–2700 msnm y 2495–3360 msnm para *T. omiltemi* y *T. grandis*, respectivamente, a elevaciones de 1140 msnm para *T. infernalis*. La descripción de varias especies de salamandras pletodóntidas, para la zona montañosa del estado de Guerrero, enfatiza la diversidad herpetológica de la zona, la cual incluye muchos taxa endémicos tanto de anfibios como de reptiles.

THE total number of species of living organisms formally recognized represents only a small fraction of existing biological diversity (Hammond, 1992). Ongoing description of new species is common even in many groups that are seemingly well known taxonomically, including vertebrates. In amphibians alone, the total number of formally described, valid species increased by 13% in the seven-year period between 1985 and 1992 (Frost, 1985; Duellman, 1993), and many more new species continue to be described in all three Recent orders (e.g., Nussbaum and Hinkel, 1994; Mendelson, 1997; Campbell and Smith, 1998). Some of the increase in numbers of species can be traced to changing definitions of species and species concepts (de Queiroz and Gauthier, 1994; Frost and Hillis, 1990; Ghiselin, 1997) and to more frequent use of sophisticated molecular tools for defining species boundaries (Hillis et al., 1996). Both methodological refinements have led to finer subdivision of what earlier—based on more traditional methods—were regarded as single species (Highton et al., 1989; Good and Wake, 1992). Yet, many other new species follow the discovery of previously unknown forms, especially in biogeographic provinces that have never been inventoried adequately.

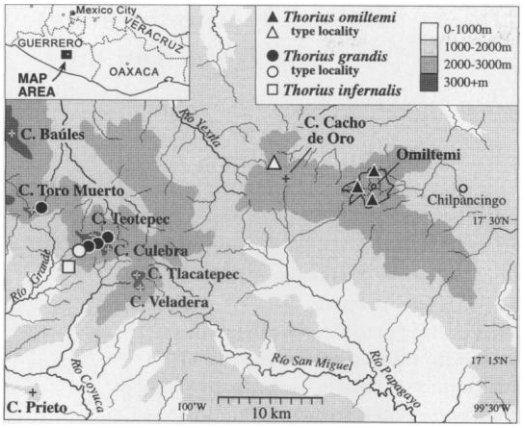

Fig. 1. Map of central Guerrero, México, showing known distributions of three new species of *Thorius*. *Thorius infernalis* is known only from the type locality, which lies within lower montane forest (elev. 1140 m). Ranges of *T. grandis* and *T. omiltemi* are somewhat more extensive, but each is centered around Cerro Teotepec/Cerro Toro Muerto and Cerro Cacho de Oro/Omiltemi, respectively. Neither species has been taken at elevations below 2200 m. The irregular line around the village of Omiltemi is the state park boundary. Cerro Cacho de Oro is named Cerro Yohualatzco on some earlier maps. Adapted with permission from Adler (1996).

In this paper, we describe three new species of minute lungless salamanders of the Mexican genus *Thorius* (Plethodontidae) from montane forests in the Sierra Madre del Sur of Guerrero (Fig. 1). This is a region of high diversity for herpetological fauna; many endemic species of both amphibians (Adler, 1965; Adler and Dennis, 1972; Savage, 1984) and reptiles (Smith, 1972; Smith and Savitzky, 1974; Myers and Campbell, 1981) have been described over the last 35 years. Although the existence of *Thorius* in Guerrero has been known to herpetologists for decades (Adler 1965; Freeman, 1977; Saldaña de la Riva and Pérez Ramos, 1987), identification of these salamanders to the species level has been hampered by the generally poor understanding of the taxonomy and systematics of the group overall (Wake and Lynch, 1976; Hanken, 1983a). Recently, two of us completed systematic revisions of *Thorius* from two centers of species diversity in the states of Veracruz, Puebla, and northern Oaxaca (Hanken and Wake, 1994, 1998). These studies resolve much of the previous taxonomic uncertainty, thereby allowing us to confidently formulate descriptions of the Guerreran *Thorius* as comprising three new species based on both morphological and molecular criteria. These new species bring to 22 the total number of valid, formally described species of *Thorius* known throughout its range in southern México. This, in turn, represents a more than doubling of the number of species in the genus recognized as recently as six years ago (Duellman, 1993).

Materials and Methods

Measurements were made using digital or dial calipers or a dissecting microscope fitted with an ocular micrometer; standard 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) and Hanken and Wake (1994, 1998); see Wake and Elias (1983) for comparisons with other tropical genera. Counts of presacral (trunk) vertebrae do not include the first, or atlas, vertebra. Tooth counts are based on cleared-and-stained specimens when available; all alcoholic specimens were examined for the presence of maxillary teeth. Numbers of maxillary and vomerine teeth in each holotype are provided 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 Autonoma de México, México, DF).

Descriptions of New Species

Thorius omiltemi n. sp.

Omiltemi Minute Salamander

Figure 2A–B

Holotype.—MVZ 110916, an adult female from 3.2 km SW of Carrizal de Bravos, Guerrero, México, elevation 2400 m, collected by T. J. Papenfuss, 31 August 1973.

Paratypes.—All from Guerrero, México: MVZ 57116–17, 57119, 4.8 km W of Omiltemi, elevation 2500 m; MVZ 110624, 110656, 110664, 110673, 110694, 110697–98, 110700, 110703–4, 110706, 110913–15, 110919, 110921–22, 187014–31, 187070, same locality as the holotype, although some elevations are listed as 2520 m; MVZ 110902, 110906, 110908, 0.7 km

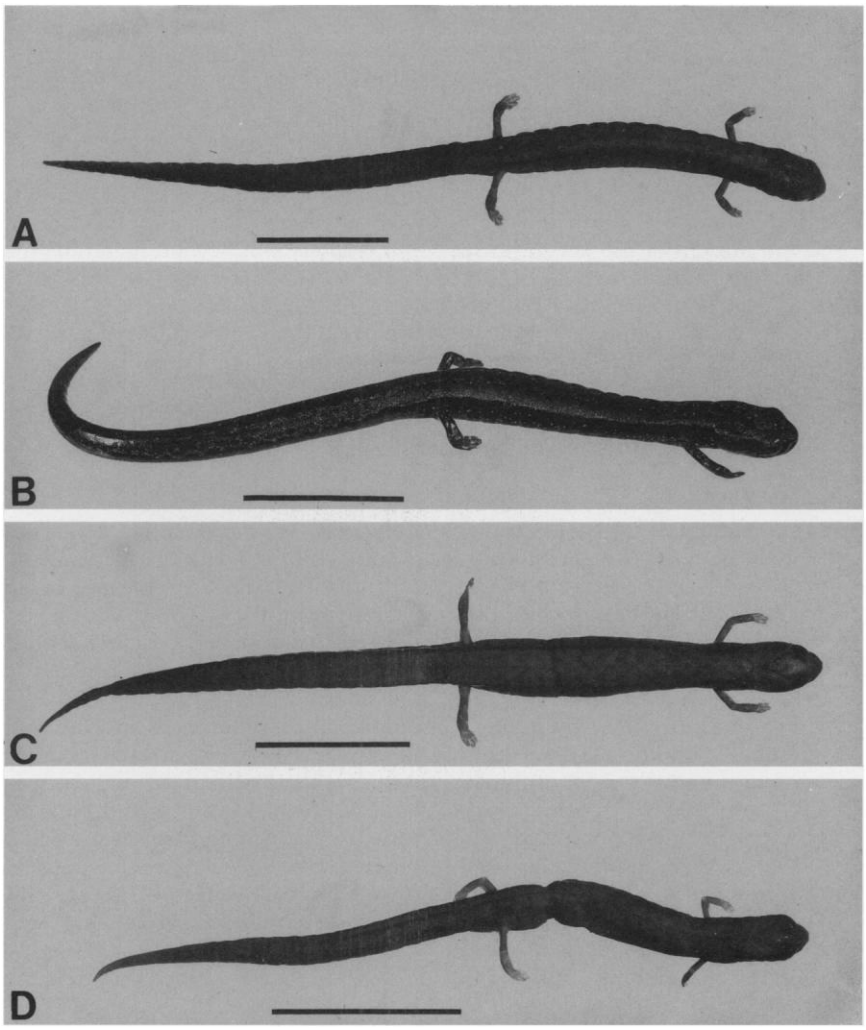

Fig. 2. Photographs of three new species of *Thorius* from Guerrero. (A) Holotype of *T. omiltemi*, MVZ 110916, an adult female. (B) Live *T. omiltemi*, collected at the type locality by J. Hanken, 31 July 1976 (museum number unavailable). (C) Holotype of *T. grandis*, MVZ 183384, an adult female. (D) Holotype of *T. infernalis*, MVZ 183426, a subadult male. Constrictions along the trunk in C and D are artifacts of museum tags, which were removed temporarily to photograph the specimens. Scale bars = 1 cm.

southwest of Carrizal de Bravos, elevation 2200 m; UMMZ 222368–69, logging road between Puerto Chico and Asoleadero, elevation 2500–2580 m; MZFC 2954, 2954-2, and 2954-6, 5 km north Zona Trincheras, Parque Ecológico Estatal Omiltemi, Chilpancingo, elevation 2800 m. Some specimens are cleared and stained or have had tissue removed for protein comparisons.

Diagnosis.—This is a large, dark, and robust species of *Thorius*, which differs from most other members of the genus by the following combination of traits: large body size, dark dorsolateral coloration, moderately large feet with discrete toes and broadly rounded digital tips, relatively short tail, and maxillary teeth absent in most adults. Compared to *T. grandis*, *T. omiltemi* is stouter and more robust across the shoulders and has a relatively broader and longer (in males) head, somewhat shorter limbs, and more elongate nostrils. It also lacks the extreme sexual dimorphism that is characteristic of *T. grandis*.

Description.—This is a large species; adult SL averages 24.9 mm in 10 males (range 24.2–26.5) and 27.3 mm in 10 females (26.5–29.6). The head is relatively broad; SL averages 7.2 times head width in both sexes (range 6.4–8.0 in

males, 6.8–8.3 in females). SL is 5.2 times head length in males (range 4.8–5.6) and 5.8 in females (4.9–6.3). Snouts are bluntly pointed. Nostrils are elongate, especially in females, and of moderate size for the genus; the mean ratio of major to minor axes equals 1.63 in males (range 1.3–2.0) and 2.25 in females (1.7–3.0). Eyes are relatively small and protrude only 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 0–6 teeth in females (mean 3.3). Maxillary teeth are absent in all males and present in only two of 20 females (mean 0.9); the latter two specimens have three and 15 teeth, respectively. Vomerine teeth average 6.1 in males (range 4–8) and 7.1 in females (range 3–10). Limbs are relatively short; limb interval averages 5.5 in males (range 4.0–5.5) and 5.8 in females (range 5.0–6.5). Hands and feet are narrow. Digits are fused for much of their length but are free at their tips, which are broadly rounded and even expanded. Fingers, in order of decreasing length, are 3-2-4-1; toes are 3-4-2-5-1. The tail is stout near the base and tapers posteriorly. It is rounded in cross-section and about as long as SL; mean SL divided by tail length equals 1.02 in males (range 0.85–1.33) and 1.12 in females (range 0.89–1.15). The mental gland is present in large adult males and is round to moderately elliptical (maximum dimensions: 1.0 mm wide, 1.0 mm long). The postiliac gland is prominent externally. Many specimens have dermal glands with enlarged external openings distributed over the back of the head and other dorsal body surfaces, including the trunk and the tail.

Coloration is dark blackish-brown dorsolaterally but becomes progressively lighter ventrally. A somewhat paler, golden-brown dorsal stripe extends from the nape to the base of the tail in many specimens. In some specimens, the stripe is a lively golden tan, whereas in others it is obscure and may have a fine, middorsal dark line. A few specimens have a herring-bone pattern within the stripe. Lateral borders between the stripe and either flank are irregular, but occasionally there is a nearly straight line along the trunk separating the stripe from the darker flank. There are numerous white spots ventrolaterally and ventrally, especially in the gular and pectoral regions, to a lesser extent on the tail, and rarely on the belly. Limb insertions tend to be lighter than the rest of the limbs. About half the specimens have a bright nuchal spot, and in some the nuchal gland is lightly pigmented. Snouts typically are black, and the iris is dark.

Measurements of the holotype (in millimeters) and tooth counts.—Head width 3.6; snout to gular fold (head length) 4.9; head depth at posterior angle of jaw 2.4; eyelid width 0.6; eyelid length 1.5; anterior rim of orbit to snout 1.0; horizontal orbit diameter 1.3; interorbital distance 2.2; distance separating external nares 0.7; major axis of nostril 0.6; minor axis of nostril 0.2; snout projection beyond mandible 0.7; SL 29.6; snout to anterior angle of vent 26.7; snout to forelimb 7.1; axilla to groin 17.2; limb interval 6.0; shoulder width 2.6, tail length 31.1; tail width at base 2.1; tail depth at base 2.5; forelimb length (to tip of longest toe) 4.0; hind limb length 4.0; hand width 1.0; foot width 1.2. Numbers of teeth: premaxillary 3; maxillary 4–11; vomerine 4–6.

Coloration of the holotype (in alcohol).—The ground color is a dark blackish brown. It is darkest dorsolaterally and becomes progressively lighter onto the medium-brown venter. The dorsum of the head becomes increasingly dark toward the snout, which is essentially black, as are dorsal surfaces of the eyelids. Tips of the nasolabial protuberances and the upper lip are unpigmented. A narrow, irregularly bordered, dark-tan band extends from the nape to the base of the tail. Ventrally, there are scattered white flecks in the gular region and a very few on the trunk. Flecks become more numerous on the ventral surface of the tail but are still widely scattered. The iris is black.

Coloration in life.—Based on field notes by J. Hanken (2 Aug. 1976) for MVZ 183360–63, 187014–31, and 187070 (Carrizal de Bravos): Most specimens have a dorsal stripe that ranges from brick red to brown, sometimes tan. The stripe is faint in at least one specimen, which in this respect resembles *T. spilogaster* (Veracruz). There is abundant whitish flecking on the venter and flanks. The specimen illustrated (Fig. 2B) has a distinct dorsal stripe that is separated from the lighter flanks by a well demarcated, straight border. The stripe becomes diffuse on the tail and develops an irregular border. The head bears a Y-shaped, dorsal groove that is darker than surrounding areas. According to Freeman (1977), specimens from the Asoleadero region have a light brown-bronze dorsal stripe with thin tan-cream margins and a dark brown to black middorsal groove. The stripe extends from the occiput to the tail. The head is flecked with silvery white and has a blackish brown, Y-shaped mark. Flanks are blackish-brown grading to grey-brown ventrolaterally, with flecks of white. The venter is greyish-brown

with scattered flecks and small whitish spots. Additional color notes are provided in field notes by W. Riemer for MVZ 57116–19 (Omiltemi): The dorsal stripe is golden brown in two larger animals, red brown in a smaller one. Sides have a heavy suffusion of very pale blue specks decreasing in number ventromedially.

Osteology.—This description is based on 20 cleared-and-stained specimens (MVZ 110624, 187014–31, and 187070). The skull is relatively well developed. Ascending processes of the premaxillary bone usually arise separately and remain apart for their entire lengths (character 1, state a), but each of the other character states (b–d) appears in at least one specimen. Facial processes of the premaxilla and maxilla overlap in ventral view and articulate directly in most females (character 2, state d), but they overlap broadly and do not articulate in two females (state c), and overlap only slightly in another (state b). This character is sexually dimorphic, and the two elements fail to overlap (state a) in all males but one, in which they slightly overlap (state b). The premaxilla bears teeth in all adults (character 8, state b) but one (state a). The nasal bone is relatively well developed and broad in most individuals (character 3, state c), extending somewhat over the posterior portion of the cartilaginous nasal capsule. It is fragmented in a few individuals. The nasal and the maxilla articulate to some degree in all individuals (character 4, state b). The prefrontal bone is relatively well developed and articulates with the nasal in all females and most males (character 5, state c). The bones do not articulate in two males (state b). The prefrontal and maxilla are separated and do not overlap in most specimens (character 6, state a), but the bones articulate in a few of the males (state b). Septomaxillary bones are absent in all specimens (character 7, state a) except one female in which the bone is present on one side only (state c). The maxilla is relatively well developed anteriorly but becomes extremely attenuate posteriorly (Fig. 3). It lacks teeth (character 9, state a) in all specimens but one female, which has just two teeth on one side and one on the other (state b; Fig. 3). The vomer is well developed and bears a small but distinct preorbital process. There are moderate numbers of vomerine teeth, which occur in a short, curved row. They extend onto the preorbital process in four females and six males. The frontal fontanelle is relatively narrow for *Thorius*; the parietal fontanelle is moderately wide (its breadth equals 0.40–0.66, mean 0.50, 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 unmineralized.

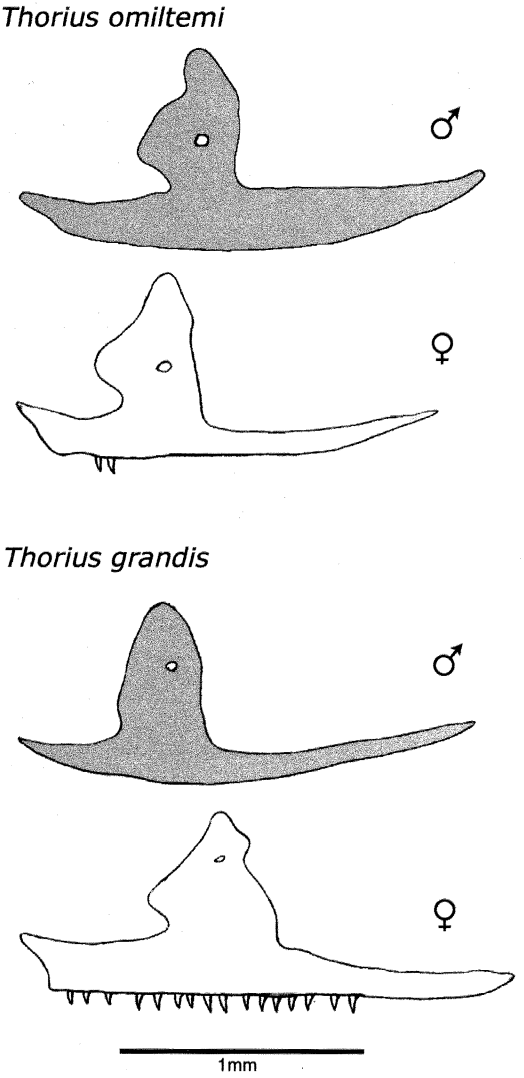

Fig. 3. Sexual dimorphism in cranial osteology and dentition in *Thorius grandis*, compared to *T. omiltemi*. Maxillary bones are depicted in left lateral view; anterior is to the left. Maxillary bones lack teeth in most adult *T. omiltemi* and in all male *T. grandis*, but all female *T. grandis* possess large numbers of maxillary teeth. The maxillary bone also is generally more robust and has a straighter ventral margin when teeth are present. Specimens depicted: *T. omiltemi*—MVZ 187022 (male), MVZ 187016 (female, and the only specimen with maxillary teeth among 20 cleared-and-stained adults of this species); *T. grandis*—MVZ 187032 (male), MVZ 187038 (female).

All specimens have 14 presacral vertebrae.

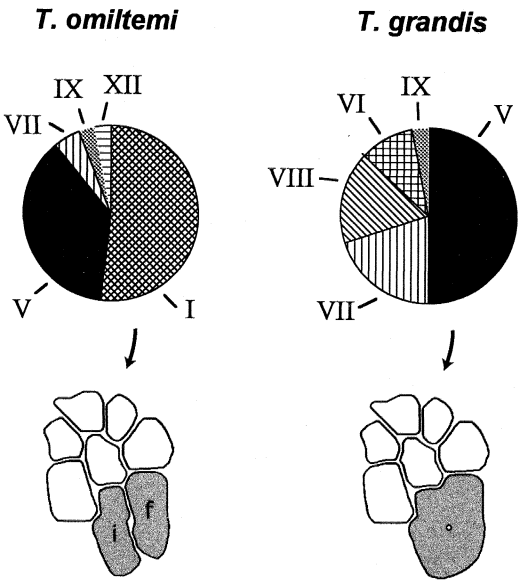

Fig. 4. Interspecific variation in limb-skeletal morphology between *Thorius omiltemi* and *T. grandis*. Pie diagrams depict frequencies of alternate tarsal patterns (roman numerals, described in text), based on 20 specimens (equals 40 tarsi) per species. The predominant tarsal pattern in each species is depicted below its corresponding pie diagram. The two patterns differ solely regarding the condition of the intermedium (i) and fibulare (f), which are fused in *T. grandis* but separate in *T. omiltemi*. Carpal pattern frequencies are similar between the two species, which differ principally in the presence of rare variants.

Typically, all trunk vertebrae but the last bear ribs, but in a few specimens the last trunk vertebra has a partial rib. The limbs are relatively robust. The tibial spur ranges from free to attached in approximately equal frequencies.

Mesopodial morphology is variable. Carpal pattern I predominates in the forelimb (76% 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 fusions relative to pattern I, are also present in adults: II (fused distal carpals 1-2 and 3; 21%) and IV (fused intermedium-ulnare plus centrale; 3%). Carpal pattern IV is known only in *T. omiltemi*. The modal tarsal pattern is I (52%; Fig. 4). This pattern contains eight separate elements, with one derived state in relation to outgroup genera: fused distal tarsals 4 and 5. As with carpal pattern I, it is the presumed ancestral pattern and predominates in many species of *Thorius*. However, pattern V (like I, but with fused intermedium and fibulare) is also common (37%). Three additional tarsal patterns, each with additional fusions relative to pattern I, are present at low frequencies: VII (fused distal tarsal 4-5 and centrale; 5%), IX (fused distal tarsals 3 and 4-5 plus centrale; 3%), and XII (fused intermedium and fibulare plus centrale; 3%). Tarsal pattern XII is known only in *T. omiltemi* and is reported here for the first time. Asymmetry is common; at least three-fourths of the specimens have a different carpal or tarsal pattern between right and left sides. The digital skeleton also is highly variable, including many instances of phalangeal loss. The predominant phalangeal formula in the hand is 1-2-3-2 (60% of adult carpi). 1-2-3-1 is a common variant (32%); 1-2-2-1 is rare (8%). The modal formula in the foot is 1-2-3-3-1 (65% of adult tarsi); 1-2-3-2-1 and 1-2-3-3-2, the typical formula in *Thorius*, are rare variants (24% and 10%, respectively). Limb bone epiphyses and mesopodial elements are mineralized in many adults.

Comparisons to other taxa.—*Thorius grandis*, a second large-bodied species from high-montane forests of central Guerrero, differs from *T. omiltemi* in several respects. Most *T. grandis* have a V- to Y-shaped mark on the dorsum of the head, which is absent or at best weakly developed in most *T. omiltemi*. They also generally lack the conspicuous dorsal glands with relatively large openings that are characteristic of many *T. omiltemi*. Also, *T. grandis* has extreme sexual dimorphism of adult cranial morphology (hyperossification and maxillary teeth present in females only) that is less conspicuous in *T. omiltemi*. Finally, the two species differ in several proteins. *Thorius infernalis*, the only other congeneric species from Guerrero, is much smaller and is found at much lower elevation than either *T. grandis* or *T. omiltemi*. See account of *T. grandis* for comparison with species that have maxillary teeth, which are rarely present in adult *T. omiltemi*.

Habitat and range.—*Thorius omiltemi* is a terrestrial species of montane forests in the Sierra Madre del Sur of central Guerrero west of Chilpancingo (Fig. 1). Recorded localities are from Cerro Cacho de Oro (elev. 2200–2673 m) and from near the village of Omiltemi, within the Omiltemi State Ecological Park (elev. 2200–2700 m). Localities on Cerro Cacho de Oro are between Carrizal de Bravos and Asoleadero (an abandoned lumber camp and sawmill) along the original road between Atoyac de Álvarez

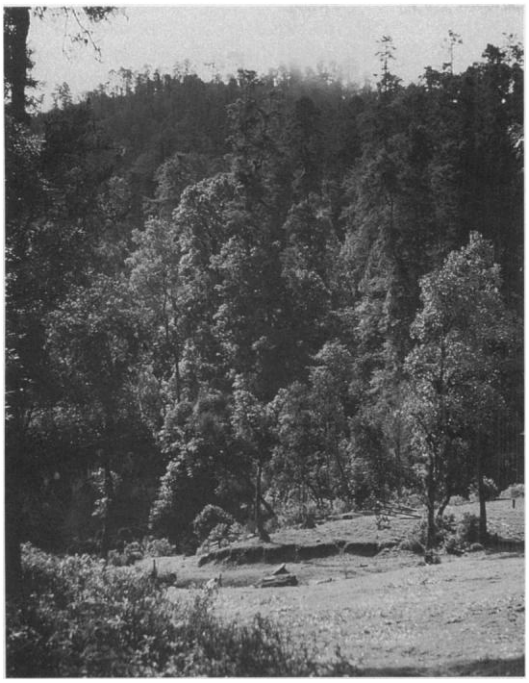

Fig. 5. Type locality of *Thorius omiltemi*, 3.2 km southwest of Carrizal de Bravos, Guerrero, in June 1964. The site is known locally as Asoleadero, an abandoned lumber camp and sawmill, and is also the type locality for *Hyla chryses*, *Sceloporus adleri*, and *Pseudoeurycea mixcoatl*. Specimens of *Thorius* were collected beneath bark on fallen logs and under loose bark on the forest floor. Since this photograph was taken, the forest has been largely cleared (Adler, 1996:18). Photo courtesy of K. Adler.

and Milpillas (now Mexican highway 196). They include oak-pine-fir cloud forest and pine-oak forest (Adler, 1965, 1996; Fig. 5), where salamanders may be locally abundant (field notes of J. Hanken, 31 July 1976; Freeman, 1977). Specimens have been collected from inside, underneath, and beneath the bark of fallen logs. Recent collections near Omiltemi are from pine-alder forest (Flores-Villela and Muñoz Alonso, 1993). According to field notes by W. Riemer for MVZ 57116–19 (4.8 km west of Omiltemi), specimens were taken in fallen, rotting logs in "semi-open mixed pine-oak forest on steep slope" and in a canyon bottom within a "dense broadleaf forest."

Etymology.—The species name recognizes Omiltemi State Ecological Park, which includes the earliest known collecting locality for *Thorius* in the state of Guerrero (four specimens collected 28 April and 1 May 1950 by W. Riemer and F. Pitelka, MVZ 57116–19).

Remarks.—Freeman (1977) identified specimens from Cerro Cacho de Oro as an undescribed species. Saldaña de la Riva and Pérez Ramos (1987) discuss *T. omiltemi* as *T. narisovalis* (part). Adler (1996; Fig. 5) depicts the geographic and elevational distribution of *T. omiltemi* from Cerro Cacho de Oro and Omiltemi (identified as *Thorius* undescribed species) vis-à-vis other plethodontid salamanders recorded from central and western Guerrero.

Genetic variation in *T. omiltemi* and the species' relationships to congeners were examined using protein electrophoresis by Hanken [1980, 1983a; population 58, listed as *T.* sp. F (part)] and M. J. Mahoney (unpubl.). Evolutionary consequences of miniaturization of adult body size for appendicular morphology were examined by Hanken (1982, 1985; listed as *T.* sp. F). Large numbers of additional specimens reside at MVZ and MZFC, with others at KU and UMMZ.

Thorius grandis n. sp.

Grand Minute Salamander

Figure 2C

Holotype.—MVZ 183384, an adult female from Puerto del Gallo, Guerrero, México, elevation 2500 m, collected by T. J. Papenfuss, 22 December 1976.

Paratypes.—All from Guerrero, México: MVZ 183366–68, 183381–83, 183386–87, 183389–90, 183392–93, 183401, 183404–5, 183408–9, 187032–51, same data as the holotype; MVZ 183417–18, Cerro Teotepec, 9 km (road) northeast of Puerto del Gallo, elevation 3109 m; UTA A-4107, 1.6 km north of Puerto del Gallo, elevation 2743 m; UMMZ 222366–67, 11.3 km (road) east of Cerro Teotepec, elevation 2850 m; KU 182519, 182521–22, 9.5 km (road) northeast of Puerto del Gallo, elevation 3296 m. Some specimens are cleared and stained or have had tissue removed for protein comparisons.

Diagnosis.—This is among the largest and most sexually dimorphic species of *Thorius*. It differs from most other members of the genus by the following combination of traits: very large body size, moderately long limbs, oval nostrils, and maxillary teeth that are present (and numerous) in adult females but typically absent in males. It differs from its geographically closest congener, *T. omiltemi*, in having somewhat longer limbs; different coloration, including a broader and more prominent dorsal stripe; a narrower and shorter (in males) head, larger

and less elongate nostrils; indistinct dorsal glands; and many maxillary teeth in females.

Description.—This is a very large species; adult SL averages 27.0 mm in 10 males (range 22.3–28.6) and 27.6 mm in 10 females (24.4–30.6). The head is moderately wide in both sexes—SL averages 7.8 times head width in males (range 7.2–8.2) and 7.5 in females (7.4–8.7). SL averages 5.5 times head length in males (range 5.1–6.4) and 5.8 in females (5.4–6.3). Snouts are bluntly pointed. Nostrils are oval and of moderate size for the genus; the mean ratio of major to minor axes equals 1.40 in both males and females (range 1.3–1.7). Eyes are of moderate size 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 2–3 premaxillary teeth in adult males (mean 2.2) and 3–8 teeth in females (mean 5.5). Maxillary teeth are present in all females (mean 27.8, range 19–37) but in only 1 of 10 males (mean 0.2, range 0–2). Vomerine teeth average 7.1 in males (range 4–9) and 8.5 in females (7–10). Limbs are moderately long; limb interval averages 4.8 in males (range 3.5–5.5) and 5.3 in females (4.0–6.0). Hands and feet are moderately broad. Digits are joined at the base but free distally; the longest finger and toe are expanded distally and have bluntly rounded tips. Fingers, in order of decreasing length, are 3-2-4-1; toes are 3-(2≈4)-5-1. The tail is stout and tapers posteriorly. It is rounded in cross-section and only rarely exceeds SL; mean SL divided by tail length equals 1.01 in males (range 0.97–1.13) and 1.11 in females (1.0–1.34). The mental gland is present in large adult males and is round to moderately elliptical (maximum dimensions: 1.3 mm wide, 1.2 mm long). The postiliac gland is prominent externally.

Dorsolateral coloration is medium brown. All specimens have a prominent dorsal stripe (Fig. 2C), which is slightly broader than in *T. omiltemi*; about half the specimens have a distinctive ventrolateral excursion from the stripe immediately behind the shoulder. Tiny white spots are scattered over the head and dorsal surfaces. The spots become dense ventrolaterally, forming a kind of "frosting," and then give way to sparser, larger spots ventrally, especially in the gular region. Most specimens have a dark V- or Y-shaped mark on the top of the head, which extends posteriorly as a thin median line. This distinctive color pattern is only weakly developed or absent in the remaining specimens. The iris is dark.

Measurements of the holotype (in millimeters) and tooth counts.—Head width 3.2; snout to gular fold (head length) 4.6; head depth at posterior angle of jaw 2.2; eyelid width 0.7; eyelid length 1.2; anterior rim of orbit to snout 1.2; horizontal orbit diameter 1.1; interorbital distance 1.7; distance separating external nares 0.7; major axis of nostril 0.5; minor axis of nostril 0.4; snout projection beyond mandible 0.4; SL 26.0; snout to anterior angle of vent 23.6; snout to forelimb 6.4; axilla to groin 15.4; limb interval 5.0; shoulder width 2.4, tail length 25.0; tail width at base 2.3; tail depth at base 3.0; forelimb length (to tip of longest toe) 3.6; hind limb length 4.0; hand width 0.9; foot width 0.9. Numbers of teeth: premaxillary 5; maxillary 10–13; vomerine 4–6.

Coloration of the holotype (in alcohol).—The ground color is medium brown. A moderately broad, golden-tan dorsal band extends from behind the eyes to the tip of the tail. It broadens at the back of the head to include the weakly developed parotoid glands but narrows over the shoulders. It broadens again at the level of the second costal interspace (behind the arm), retracts to the standard width at the third interspace, and is broader again posteriorly. The band is bordered dorsolaterally by medium brown pigment of the flanks, which is darkest alongside the band. The ground color of the flanks becomes progressively lighter onto the venter, which is light brown with abundant, irregularly shaped, small white flecks. These flecks are organized into more discrete spots, about 20 in number, in the gular region. White flecking extends to the tip of the tail on the ventral surface and onto the ventrolateral flanks. Limb insertions are light tan; the rest of each limb is medium brown with some white flecking. A distinctive, dark Y-shaped mark extends from the eyes to the midline near the nape; it ends at a slight nuchal pit. The tip of the snout is darker than the rest of the head and is the same color as the cheeks. There is some white flecking on the upper lips. Eyelids are dark brown; the iris is black.

Osteology.—This description is based on 20 cleared-and-stained specimens (MVZ 187032–51). The skull, and especially the jaws, shows extreme sexual dimorphism; individual bones are more fully developed and adjacent bones are more completely articulated in females. Ascending processes of the premaxillary bone are relatively stout; they may be separate (character 1, state a) or partly fused (states c and d). Premaxillae are well separated from the maxillary

bones in all males (character 2, state a), but these bones are firmly articulated in all females (state d). The premaxilla bears teeth in all adults (character 8, state b). The nasal bone is relatively well developed (character 3, state c) and extends anteriorly over at least the posterior edge of the cartilaginous nasal capsule. The prefrontal bone is always a separate ossification, but it usually articulates with the nasal (character 5, state c). It is well separated from the maxilla in males (character 6, state a), but these elements articulate in most females (state b). The foramen for the nasolacrimal duct is incised in the posterior border of the nasal and is frequently bordered posteriorly by the prefrontal in females. In males, there usually is no bony posterior border to this foramen. Septomaxillary bones are absent in most specimens (character 7, state a) but present in a few males and females (state b). The maxilla in females is a robust bone that bears many teeth (character 9, state b), but it is slender, irregularly shaped, and toothless in nearly all males (state a; Fig. 3). The vomer is well developed and bears a preorbital process that varies from small to relatively well developed, but this process never extends to the posterior border of the internal nares. There are moderate numbers of vomerine teeth, which are typically arranged in a short row. The frontal fontanelle is very narrow; the bones may contact one another at the midline. The parietal fontanelle, while wider than the frontal fontanelle, is still relatively narrow for *Thorius* (its breadth equals 0.29–0.59, mean 0.38, times the maximum skull width across the parietals). Otic crests are lacking, and there is a short columellar process on the operculum in many specimens. The postsquamosal process is present and well developed. The nasal capsule and some hyobranchial cartilages (basibranchial and second ceratobranchial) are partly mineralized in a few specimens, and even the procoracoid cartilages are mineralized in one specimen.

All specimens have 14 presacral vertebrae. Typically, all trunk vertebrae but the last bear ribs, but in some specimens the last trunk vertebra has a partial rib. Limbs are relatively well developed, with ossified condyles. The tibial spur ranges from free in a few specimens to attached in most. Mesopodial elements are mineralized in many adults.

Mesopodial morphology is variable. Carpal pattern I predominates in the forelimb (70% of adult carpi examined). This pattern contains six separate elements, with two derived character 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 fusions relative to pattern I, are also present in adults: II (fused distal carpals 1-2 and 3; 27%) and III (fused distal carpals 3 and 4 plus centrale; 3%). In the tarsus, pattern I (eight elements, with one derived state in relation to outgroup genera: fused distal tarsals 4 and 5), the presumed ancestral pattern which predominates in many species of *Thorius*, is absent. Instead, the modal pattern is V (fused intermedium and fibulare; 50%), but patterns VI (like V, but with fused distal tarsals 1-2 and 3; 10%), VII (like V, but with fused distal tarsal 4-5 and centrale; 20%), and VIII (like VII, but with fused distal tarsals 1-2 and 3; 17%) occur at moderate frequencies (Fig. 4). Tarsal pattern IX (like VII, but with fused distal tarsals 3 and 4-5 plus centrale) occurs at a very low frequency (3%). Asymmetry is common; approximately one-third of the specimens have a different carpal or tarsal pattern between right and left sides. The predominant phalangeal formula in the hand is 1-2-3-2; 1-2-3-1 is the only variant, found in 15% of adult carpi. The modal formula in the foot is 1-2-3-3-1, although it is found in fewer than half of adult tarsi. 1-2-3-2-1, 1-2-3-2-2, and 1-2-3-3-2, the typical formula in *Thorius*, are common variants.

Comparisons to other taxa.—Maxillary teeth are plesiomorphous for *Thorius* and are found in seven species: *T. spilogaster, T. schmidti, T. aureus, T. smithi, T. grandis, T. omiltemi,* and *T. minydemus* (some adults only of the last three). The extreme sexual dimorphism in dentition immediately differentiates *T. grandis* from all species except *T. omiltemi* and *T. minydemus*. The latter is a much smaller and little known species from Veracruz. *Thorius aureus* resembles *T. grandis* in possessing several additional plesiomorphic character states that are lacking in most other species, such as a small frontoparietal fontanelle and large adult body size. However, in addition to having maxillary teeth in adult males, *T. aureus* has a unique color pattern and a small, circular nostril (vs elongate in *T. grandis*). See account for *T. omiltemi* for additional comparisons between *T. grandis* and its two congeners from Guerrero.

Habitat and range.—*Thorius grandis* is a terrestrial species of montane forests in the Sierra Madre del Sur of central Guerrero northeast of Atoyac de Álvarez (Fig. 1). Most recorded localities are from the flanks of Cerro Teotepec (2500–3360 m). The easternmost of these lo-

Fig. 6. Collecting locality for *Thorius grandis*, 3.2 km east of the type locality at Puerto del Gallo, Guerrero, in December 1969. The site is known locally as La Victoria in honor of an important Mexican revolutionary battle. *Thorius* were common here, especially in the forest and deep inside moist pine logs. Other species taken include *Sceloporus adleri* and *Eleutherodactylus saltator* (K. Adler, pers. comm.). Photo courtesy of K. Adler.

calities is near Jiguero, 29.5 km (by road) west of Cruz Ocote; the westernmost is from the vicinity of Puerto del Gallo, an abandoned lumber camp (Fig. 6). An additional locality is from Cerro Toro Muerto, about 10 km (by air) to the northwest of Cerro Teotepec. Adler (1996, Fig. 5) and Saldaña de la Riva and Pérez Ramos (1987) note the elevation of this locality as lying between 2000 and 2500 m, but collection data associated with the three known specimens (IBH 06463, 06463-2, and 06463-3) list the elevation simply as 2495 m. Habitats for *T. grandis* include pine-fir and pine-oak-fir forests at high elevations, and bamboo-tree fern cloud forest at lower elevations (Adler, 1996; Myers and Campbell, 1981). According to field notes by J. A. Campbell (1.6 km north of Puerto del Gallo; 21 May 1974), UTA A-4107 was collected under a log in pine-oak forest. Additional specimens from several localities have been collected from inside and beneath the bark of fallen, rotting logs (Adler, 1965; Saldaña de la Riva and Pérez Ramos, 1987). Large numbers of specimens were taken from beneath bark on fallen and dead standing trunks of fir trees, and others from under logs and in cracks and crevices in well-rotted logs in fir and pine forest (Freeman, 1977).

Etymology.—The species name is derived from the Latin word, *grandis* (large, great, magnificent), in reference to the very large adult body size (for *Thorius*), which frequently exceeds 30 mm SL.

Remarks.—Freeman (1977) recognized specimens from Cerro Teotepec as a distinct species. Saldaña de la Riva and Pérez Ramos (1987) discuss *T. grandis* as *T. narisovalis* (part). Adler (1996, Fig. 5) depicts the geographic and elevational distribution of *T. grandis* on Cerro Teotepec and Cerro Toro Muerto (identified as *Thorius* undescribed species) vis-à-vis other plethodontid salamanders recorded from central and western Guerrero.

Genetic variation in *T. grandis* and the species' relationships to congeners were examined using protein electrophoresis by Hanken [1980, 1983a; populations 59–60, listed as *T.* sp. F (part)] and M. J. Mahoney (unpubl.). Large numbers of additional specimens of this species reside at MVZ, with others at KU, UMMZ, and UTA. The paratype specimen of *Rhadinophanes monticola*, a small colubrid snake from 1.6 km north of Puerto del Gallo, contained two or three specimens of *T. grandis* in its stomach (Myers and Campbell, 1981).

Thorius infernalis n. sp.

Atoyac Minute Salamander

Figure 2D

Holotype.—MVZ 183426, an adult male from 13.7 km northeast (road from Atoyac to Puerto del Gallo) of El Paraiso, Guerrero, México, elevation 1140 m, collected by J. E. Cadle, 18 November 1977.

Paratype.—MVZ 183425, an adult female. Same data as the holotype.

Diagnosis.—This is a small species of *Thorius*, less than 20 mm SL, which differs from most other members of the genus by the following combination of traits: small body size with a relatively long tail; narrow head with a pointed snout and relatively small, elliptical nostrils; relatively short limbs with narrow feet and pointed toe tips; light dorsal stripe; and no maxillary teeth. It is distinguished from *T. omiltemi* and *T. grandis*, the only other species of *Thorius* known from Guerrero, by its much smaller adult body size, narrower head, more pointed snout, shorter limbs, and syndactylous toes with pointed toe tips.

Description.—This is a small species; SL is 18.8 and 18.6 mm in the male and female, respectively. Both specimens are maturing adults (see below). The head is relatively broad in the male—SL is 7.0 times head width—but only moderately wide in the female (7.2). Snouts are pointed. Nostrils are elliptical and of moderate

size for the genus; the mean ratio of major to minor axes equals 1.41 (1.5 in male, 1.3 in female). Eyes are of moderate size for the genus and protrude slightly beyond the margin of the jaw in dorsal view. A suborbital groove intersects the lip on each side of the head. The male has a single premaxillary tooth and five vomerine teeth. The female lacks premaxillary teeth but has seven vomerine teeth. Neither specimen has maxillary teeth. Limbs are relatively short; limb interval equals 5.5 in each specimen. Hands and feet are narrow. Digits are syndactylous; only the two longest fingers and three longest toes are free at their tips, which are pointed. Fingers, in order of decreasing length, are 3-2-4-1; toes are 3-4-2-5-1. The male's tail is stout and tapers posteriorly. It is rounded in cross section and is slightly longer than the body; SL divided by tail length equals 0.94. The tail is broken in the female. The postiliac gland is prominent externally. Lateral body surfaces are relatively dark. A pale dorsal stripe extends anteriorly onto the nape but becomes obscure on the tail. The venter is paler than the flanks and is especially pale in the gular region. The iris is dark.

The holotype is a sexually maturing (i.e., small adult) male based on both external and internal criteria. A mental gland is evident but obscure and cannot be measured, and the anterior walls of the cloaca are papillate. Vasa deferentia are relatively large. Testes are small, unpigmented, and unlobed, but they show lobules, which denote the onset of sexual maturation. The paratype is a maturing female. Ovaries contain ovules of different sizes; some are modestly enlarged with yolk.

Measurements of the holotype (in millimeters) and tooth counts.—Head width 2.7; snout to gular fold (head length) 3.3; head depth at posterior angle of jaw 1.6; eyelid width 0.5; eyelid length 1.1; anterior rim of orbit to snout 0.8; horizontal orbit diameter 1.0; interorbital distance 1.3; distance separating external nares 0.6; major axis of nostril 0.3; minor axis of nostril 0.2; snout projection beyond mandible 0.4; SL 18.8; snout to anterior angle of vent 17.5; snout to forelimb 5.2; axilla to groin 10.3; limb interval 5.5; shoulder width 1.9, tail length 20.1; tail width at base 1.5; tail depth at base 1.8; forelimb length (to tip of longest toe) 2.9; hind limb length 3.4; hand width 0.6; foot width 0.7. Numbers of teeth: premaxillary 1; maxillary 0; vomerine 2-3.

Coloration of the holotype (in alcohol).—This specimen is clearly faded. Although generally golden brown, it is darker along the flanks and lighter both dorsally and ventrally. An obscure band extends from the head to the base of the tail. There are white spots in the gular region and a few scattered, irregular marks on other ventral surfaces. The iris is gray.

Comparisons to other taxa.—This is the smallest and least known of the three Guerreran species of *Thorius*. Both *T. omiltemi* and *T. grandis* are larger species restricted to much higher elevations in the Sierra Madre del Sur (approximately 2200 m and above, vs 1140 m for *T. infernalis*). Maxillary teeth are present in some adults of both species but are lacking in *T. infernalis*. Salamanders assigned to *T. minutissimus* from near Sola de Vega, in the Sierra Madre del Sur of Oaxaca (Hanken, 1983a), are larger, have a more elongate nostril and have rounded, rather than pointed, toe tips. Three species of *Thorius* occur at elevations as low as or lower than *T. infernalis*: *T. pennatulus*, *T. narismagnus*, and *T. smithi*, all from the Caribbean versant. All are small species like *T. infernalis*, but all three have rounded nostrils, and *T. smithi* has maxillary teeth. All other congeneric species typically are found at much higher elevations (> 2000 m).

Habitat and range.—*Thorius infernalis* is known only from the type locality, which lies within the Sierra Madre del Sur of central Guerrero along the original road between Atoyac de Álvarez and Milpillas (Adler, 1996; Fig. 1). According to field notes by J. E. Cadle (18 Nov. 1977), the locality is an area of steep slopes adjacent to a small stream. Hillsides are planted with coffee; riparian vegetation grows along the stream. The hillsides had recently been cleared of undergrowth, leaving much fresh-cut vegetation on the ground, in addition to a few logs and rocks to turn. The two specimens were taken under different logs in the afternoon. Adler (1996) lists associated species of amphibians and reptiles.

Etymology.—The species name is derived from the Latin word, *infernalis* (of the lower world), in reference to the low elevational occurrence of the species in comparison to most congeners. The name also refers to the distinction of the nearby city Atoyac de Álvarez as the hottest geographical location in North America (average annual maximum temperature 29.7 C; Anonymous, 1974).

Remarks.—This species is known from only two specimens, and there are no allozyme data for use in assessing its genetic relationships to other

TABLE 1. GENETIC DIFFERENTIATION AMONG TWO SPECIES OF *Thorius* FROM GUERRERO (*T. omiltemi* AND *T. grandis*) AND TWO FROM SOUTHWESTERN OAXACA (*T. minutissimus*, *T.* SP. UNCERTAIN), MÉXICO (BASED ON HANKEN, 1980 1983a). Above diagonal, mean pairwise Nei genetic distance between species (D_N; range in parentheses), based on population samples of five or more specimens each.[a] Below diagonal, 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). Numbers of populations sampled per species are listed in the left column. Data are not included for the pairwise comparison between the two Oaxacan species and are unavailable for *T. infernalis*, a third species from Guerrero.

Species	*omiltemi*	*grandis*	*minutissimus*	*Uncertain*
omiltemi (1)	—	0.21 (0.18–0.24)	0.40 (0.38–0.44)	0.53 (0.44–0.60)
grandis (2)	**1**, 1[b]	—	0.39 (0.37–0.44)	0.37 (0.24–0.51)
minutissimus (3)	**3**, 2[c]	**3**, 0[d]	—	—
uncertain (3)	3, 2[e]	**1**, 1[f]	—	—

[a] Populations are numbered according to Hanken (1980, 1983a): *T. omiltemi* (58), *T. grandis* (59–60), *T. minutissimus* (64–66), *T.* sp. Uncertain (61–63).
[b] LDH-1, MPI. Enzymes abbreviated according to Murphy et al. (1996).
[c] GP-2, CAP, G3PDH, LDH-1, MPI.
[d] GP-2, CAP, LDH-1.
[e] CAP, GAPDH, LDH-1, AAT-1, MPI.
[f] LDH-1, CAP.

species. Adler (1996) suggested that these specimens represented a separate species from high-elevation populations (*T. omiltemi* and *T. grandis*) based on their low elevational range and the "lowland association" of sympatric amphibians and reptiles. He also (Fig. 5) depicts the geographic and elevational distribution of *T. infernalis* (identified as *Thorius* undescribed species) vis-à-vis other plethodontid salamanders recorded from central and western Guerrero.

DISCUSSION

Allozyme comparisons.—Hanken (1980, 1983a) used protein electophoresis to examine genetic differentiation among 69 populations of *Thorius* distributed throughout the range of the genus in southern México. Here we summarize these results as they pertain to *T. omiltemi* and *T. grandis* (Hanken's *T.* sp. F, populations 58 and 59–60, respectively; Table 1). No data are available for *T. infernalis*.

Thorius omiltemi and *T. grandis* are more similar to each other biochemically than either is to any other species. Mean pairwise genetic distance (D_N; Nei, 1972) between populations of the two species equals 0.21 (0.18–0.24). This value is nearly twice that obtained between two populations of *T. grandis* separated by a distance of approximately 9 km (populations 59 vs 60; D_N equals 0.11). There are fixed allelic differences between the species at one allozyme locus and significant differences in allelic frequencies at a second (Table 1). Populations from these two species were tentatively identified as a single species, *T.* sp. F, by Hanken (1983a) because they clustered together in a phenetic (UPGMA) analysis based on genetic distance. Recognition of two species was suggested earlier by Freeman (1977), based on analysis of external morphology, and is warranted at this time by their genetic and morphological distinctiveness, including osteology (see above). This decision is supported by a recent phylogenetic analysis of Hanken's (1983a) original allozyme data, in which populations from these two species do not cluster as sister taxa (M. J. Mahoney, unpubl.).

Salamanders from southern and western Oaxaca are more similar in allozymes to *T. grandis* and *T. omiltemi* than other members of the genus (D_N as low as 0.24). One of the Oaxacan species (populations 64–66) comprises small adults and has been assigned to *T. minutissimus* (Hanken, 1983a). The other Oaxacan populations (61–63) comprise relatively large animals that lack maxillary teeth and which likely represent an undescribed species. The mean D_N between the two Guerreran species (*T. omiltemi* and *T. grandis*) and the apparently undescribed Oaxacan species equals 0.42; pairwise interspecific values range from 0.24–0.60 (mean values are 0.37 to *T. omiltemi* and 0.53 to *T. grandis*). Genetic distances to all other congeners are large; in Hanken's UPGMA dendrogram clustering all 69 populations sampled (Hanken, 1983a; Fig. 2), the above four species joined the

remaining species at $D_N > 0.5$. Genetic distances to species in Veracruz and Puebla typically exceed 1.0.

Morphological novelty.—Perhaps the most unusual morphological feature of the three new species of *Thorius* described from Guerrero is the pronounced cranial and dental polymorphism in *T. grandis*. Adult females have large numbers of maxillary teeth and relatively strong, firmly articulated skulls. In sharp contrast, males lack maxillary teeth entirely and have weakly formed skulls. These sex-based differences are much less pronounced in *T. omiltemi*, in which adult females only rarely have maxillary teeth, and are not seen at all in *T. infernalis*, which appears to lack maxillary teeth in both sexes. Although sexual dimorphism involving various external features and premaxillary teeth is a common phenomenon in plethodontid salamanders (Wake, 1966; Staub and Paladin, 1997), dimorphism in skeletal morphology is rare (e.g., *Aneides hardii*; Wake, 1963) and usually does not involve presence or absence of maxillary teeth. Cranial and dental polymorphism in *T. grandis* provides yet another example of the pervasive association between morphological novelty and miniaturization in *Thorius* (Hanken, 1983b, 1985; Hanken and Wake, 1993).

Maxillary teeth are present in all adults of four species of *Thorius* (*T. schmidti, T. aureus, T. smithi*, and *T. spilogaster*) and absent from all but three of the remaining species (Hanken and Wake, 1994, 1998). Limited data for *T. minydemus* suggest that this species may also possess a dental polymorphism similar to that seen in *T. grandis* and *T. omiltemi*. Based on outgroup comparisons (Wake, 1966), presence of maxillary teeth represents the ancestral character state for the genus, with absence of teeth a derived state. The distant phylogenetic relationships and geographic distributions among species with or without maxillary teeth suggests that one or both traits may have evolved numerous times within the genus. This topic will be addressed in a separate analysis.

Distribution of salamanders in Guerrero.—Early herpetological investigations of Guerrero underestimated the diversity of urodeles. Gadow, for example, failed to find any salamanders at all: "For months have we searched Guerrero during the rainy season (there are thousands of places which, if they were on the Eastern slope, would yield an abundance of Newts), but it was in vain" (1905:204). Since the 1950s, however, numerous fieldworkers have encountered representatives of three genera (*Bolitoglossa, Pseudoeurycea*, and *Thorius*) in the Sierra Madre del Sur (Wake and Lynch, 1976; Papenfuss et al., 1983; Adler, 1996).

Discovery of *T. infernalis* at relatively low elevation shows that the genus is not restricted to cool montane forests, and we suspect that it is far more widely distributed than is known at present. Searches should be made especially in extreme eastern Guerrero and western Oaxaca in an attempt to link the two areas of known distribution in central Guerrero and western and southern Oaxaca. In the Sierra Madre del Sur, *Thorius* apparently is widely distributed in fir-pine-oak montane forest above 2500 m; the main physiographic feature isolating *T. grandis* from *T. omiltemi* is a depression in the mountain crest that falls to approximately 1700 m near the headwaters of the Río Yextla and the Río Papagayo, between Cerro Teotepec and Cerro Cacho de Oro (Adler, 1996; Fig. 1). We expect *Thorius* to be found in mountains west and north of Cerro Toro Muerto, especially in the remote, extensive uplands around Cerro Baúles.

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