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Biology of Tiny Animals: Systematics of the Minute Salamanders (*Thorius*: Plethodontidae) from Veracruz and Puebla, México, with Descriptions of Five New Species

James Hanken and David B. Wake

Minute plethodontid salamanders, genus *Thorius*, are far more diverse taxonomically than has been recognized previously. Populations of these salamanders from the Mexican states of Veracruz and Puebla are assigned to 10 species, five of which are described as new. Combinations of morphological and allozymic characters are used to sort the species and to make initial assessments of relationships. Valid existing names include *Thorius pennatulus*, *T. troglodytes*, *T. dubitus*, and *T. schmidti*. *Thorius narismagnus*, from the Sierra de Los Tuxtlas, which previously was considered to be a disjunct subspecies of *T. pennatulus*, is elevated to species rank. *Thorius maxillabrochus* is treated as a subjective junior synonym of the sympatric *T. schmidti*. New taxa include *Thorius lunaris*, *T. magnipes*, *T. minydemus*, *T. munificus*, and *T. spilogaster*. All 10 species can be distinguished by morphological characters, but the distinctiveness of the taxa is bolstered by allozymic characters and by extensive sympatry. As many as three, and possibly four, species occur in sympatry, with some evidence of segregation by microhabitat (arboreal vs terrestrial). Adult body sizes span the range known for the genus, from very small in *T. pennatulus* (maturing at < 16 mm standard length) to large in *T. lunaris* (adults reaching > 31 mm). Collectively these species display a wide elevational distribution, from less than 1000 m (*T. pennatulus*, *T. narismagnus*) to more than 3000 m (*T. lunaris*, *T. spilogaster*). Discovery of these new species adds to the rich herpetological diversity of east-central México and underscores its importance as a principal center of radiation of tropical plethodontid salamanders.

Las salamandras diminutas del género *Thorius* (familia Plethodontidae) son mucho mas diversas taxonomicamente de lo que se había reconocido previamente. Poblaciones de estas salamandras en los estados de Veracruz y Puebla en México, se asignan a diez especies, cinco de las cuales son nuevas para la ciencia. Combinaciones de caracteres morfológicos y de aloenzimas son usadas para discriminar especies y proponer relaciones filogenéticas. Los nombres válidos existentes incluyen *Thorius pennatulus*, *T. troglodytes*, *T. dubitus*, y *T. schmidti*. *Thorius narismagnus*, anteriormente considerado subespecie de *T. pennatulus* es elevado a nivel de especie. *Thorius maxillabrochus* se reconoce como sinónimo ("subjective junior synonym") de la especie simpática *T. schmidti*. Los nuevos taxa incluyen *Thorius lunaris*, *T. magnipes*, *T. minydemus*, *T. munificus*, y *T. spilogaster*. Las diez especies se pueden distinguir mediante caracteres morfológicos, la distinción de los taxa se refuerza con caracteres de aloenzimas y por simpatría extensa. Tres o posiblemente cuatro especies ocurren en simpatría, con alguna evidencia de segregación en microhabitat (arbóreo y terrestre). La longitud total del cuerpo incluye el intervalo conocido para el género, desde muy pequeños como *T. pennatulus* (adultos 16 mm longitud estandar) hasta grandes como *T. lunaris* (adultos 31 mm longitud estandar). Estas especies se encuentran en un gradiente altitudinal amplio, desde elevaciones menores de 1000 metros (*T. pennatulus*, *T. narismagnus*) hasta elevaciones mayores de 3000 metros (*T. lunaris*, *T. spilogaster*). El descubrimiento de estas nuevas especies enriquece la diversidad herpetológica de la zona centro oriental de México y enfatiza su importacia como centro principal de la radiación de las salamandras tropicales de la familia Plethodontidae.

> *These little things showed a predilection for living in a proverbially precarious position, namely, "between the bark and the wood" of decaying pine-trees, amongst the boring-dust of beetles and maggots (Gadow, 1908:55).*

> *I have examined the presumed cotypes in the National Museum. . .. The first of these consists of several body fragments with part of the head. The snout is missing, part of the jaws cannot be discovered. I find none of the limbs, and cannot be certain that the species belongs to the genus* Thorius. *[Another specimen] consists of a head and part of the neck, and a fragment with several vertebrae. This is possibly a specimen of* Thorius *. . .. [The third specimen] consists of a small fragment of the body of a salamander [which] cannot be certainly placed in the genus* Thorius *(Taylor, 1941:106).*

SALAMANDERS of the endemic Mexican genus *Thorius* are among the smallest tailed tetrapods; they are a preeminent example of the evolutionary phenomenon of miniaturization (Hanken, 1986; Wake, 1992; Hanken and Wake, 1993). Phylogenetic decrease of adult body size in *Thorius* has been accompanied by pervasive and extreme modifications in morphology, which provide important insights into the design constraints of the vertebrate body as well as more general mechanisms of morphological evolution (Hanken, 1985; Roth et al., 1990; Wake, 1991). Yet, the same features that make these salamanders compelling subjects for studies of scaling, developmental biology, and functional morphology have seriously impeded attempts to resolve the taxonomic and systematic biology within the group. Many skeletal components that provide useful characters for differentiating species in other urodele taxa are extremely reduced or absent in *Thorius* and therefore of little or no taxonomic value. Intraspecific variability of other characters often is so great as to obscure interspecific differences, even when they exist. Molecular techniques for establishing species identity and assessing phylogenetic relationships independent of morphology provide a potential solution to the taxonomic problems associated with miniaturization in *Thorius* and other similar groups (e.g., *Chiropterotriton*—Darda, 1994; *Nototriton*—Good and Wake, 1993). Indeed, an earlier protein electrophoretic analysis of *Thorius* revealed substantial levels of genetic differentiation among most recognized species, as well as the existence of several additional species yet to be described (Hanken, 1980, 1983a). Moreover, once species boundaries are accurately delineated by molecular criteria, distinguishing morphological features can be defined (Hanken, 1982, 1984; Hanken and Wake, 1994).

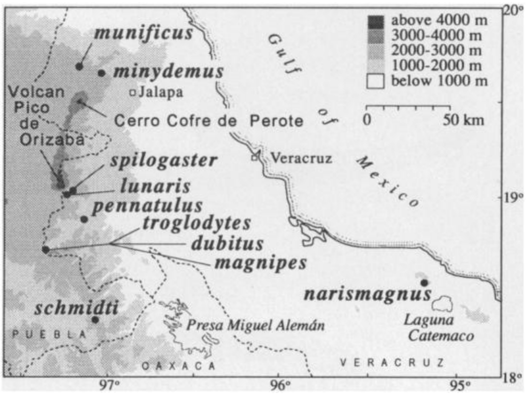

Fig. 1. Topographic map showing the type localities (closed circles) of the 10 recognized species of *Thorius* in the states of Veracruz and Puebla, México. All but one species are known only from within the general vicinity of their respective type localities. *Thorius pennatulus*, a lowland species, has a somewhat more extensive range in west-central Veracruz (see text).

Recently, we incorporated genetic, morphological, and ecological data into a review of the systematic biology of *Thorius* from the Sierra de Juárez in northern Oaxaca, including the description of five new species (Hanken and Wake, 1994). Here, we present a comparable study of the genus in the adjacent states of Veracruz and Puebla (Fig. 1). This complex geologic and biogeographic area lying at the southeastern edge of the Mexican plateau is home to at least 10 species of *Thorius*, including five that are formally described here for the first time. Recognition of these new species, in combination with the results of other recent taxonomic studies, affects the status and composition of several species described earlier. Accordingly, we present a brief account of each remaining species, emphasizing traits that have proven useful in differentiating taxa in these two states.

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

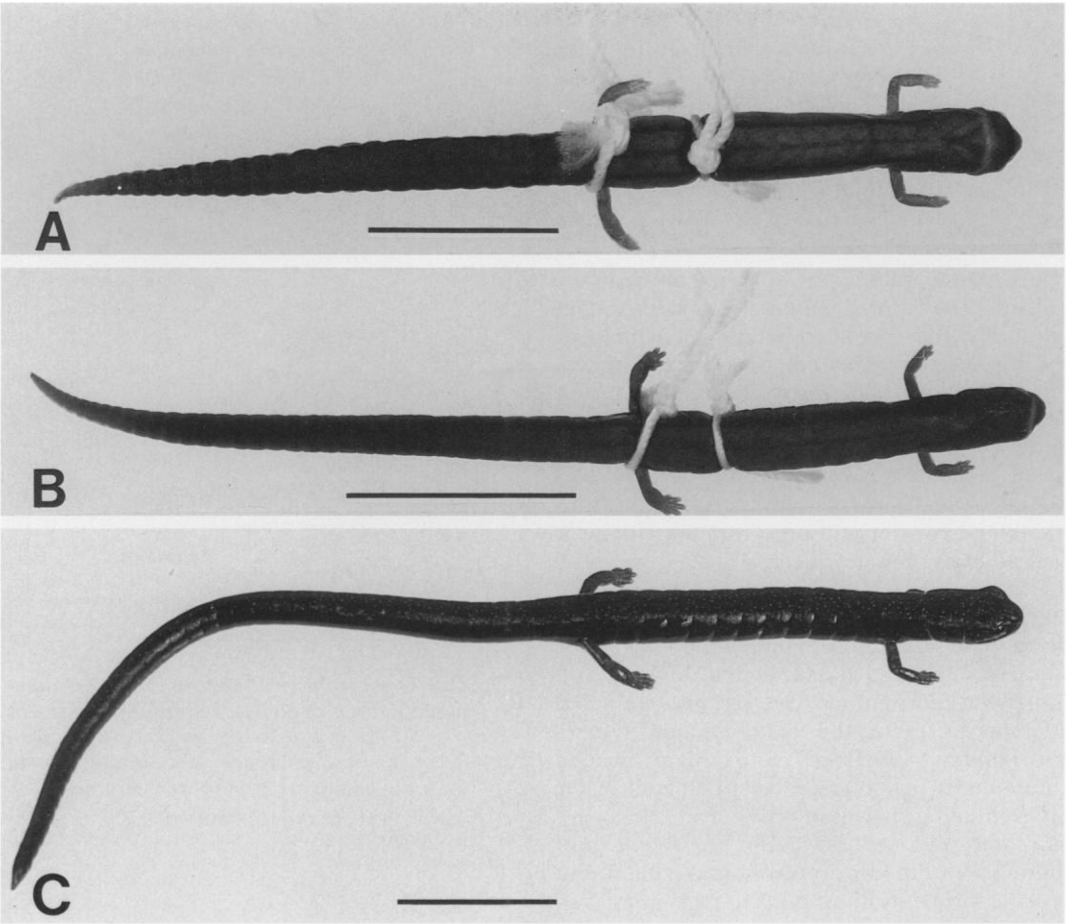

Fig. 2. Photographs of two new, sympatric species of *Thorius* from Volcán Orizaba, Ver. (A) Holotype of *T. spilogaster*, MVZ 183109, an adult female. (B) Holotype of *T. lunaris*, MVZ 183292, an adult female. (C) Live *T. lunaris*, same data as the holotype (museum number unavailable). Scale bar = 1 cm.

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); see Wake and Elias (1983) for comparisons with other tropical genera. Nearly all of the mesopodial patterns found in the 10 valid species of *Thorius* from Veracruz and Puebla that are recognized here also occur in a single species, *T. schmidti*; they are illustrated in the account for that species (see below). Counts of presacral (trunk) vertebrae do not include the first, or atlas, vertebra. Tooth counts are based on cleared-and-stained specimens unless indicated otherwise; 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).

Thorius spilogaster, n. sp.

Spotted *Thorius*

Figure 2A

Holotype.—MVZ 183109, an adult female from the forest above Xometla, Veracruz, México, elevation 8600–8640 ft, collected by J. Hanken, D. Eakins, and C. Ceron, 23 July 1976.

Paratypes.—All from Veracruz, México: MVZ 183097, 183100, 183104–7 (four specimens), 183114, 183116–17 (two specimens), 187091–97 (seven specimens), 187102, same data as the holotype; MVZ 114606, 114609, 114612, 114614–15 (two specimens), 114618, 114624, 114631, MZFC 8598–99 (two specimens), same locality as the holotype, elevation 2710–25 m, collected by J. F. Lynch, 22 January 1974; MVZ 183085–87 (three specimens), 183089–90 (two specimens), 183093, 187071–80 (10 specimens), and 187082–90 (nine specimens), canyon approximately 1 km southeast of El Berro (approximately 15 km by air southwest of Pico de Orizaba), elevation 2500 m, collected by J. Hanken, H. B. Shaffer, and C. Ceron, 2 February 1976; BMNH 1903.9.30.320–21 (two specimens), 1903.9.30.323, near Xometla, collected by H. Gadow, July 1902; KU 106896, 106928, Pico de Orizaba (Xometla), elevation 2545 m, collected by C. Ceron, D. Rubin, and H. L. Freeman, 21 June 1966; LACM 117700, 117714, 117735, 117795, 117814, 117833, 117851, 117916, near Xometla, 8 mi by road north-northwest of Perla, collected by R. W. McDiarmid, D. B. Wake, M. Ceron Sr., M. Ceron Jr., and C. Ceron, 2–4 April 1970. Some specimens are cleared and stained or have had tissue removed for protein comparisons.

Diagnosis.—This is a moderately sized species of *Thorius*, which differs from most other members of the genus, including sympatric *T. lunaris*, by the following combination of traits: maxillary teeth; conspicuous ventral spotting; moderately sized, oval nostril; small frontoparietal fontanelle; and modal mesopodial and phalangeal patterns in the hind limb. Although small, *T. spilogaster* is relatively robust with a well-developed head and large eyes. It can be distinguished from *T. schmidti* and *T. minydemus*, the only other two species of *Thorius* in Veracruz and Puebla that have maxillary teeth, by combinations of traits including adult body size, nostril size and shape, foot proportions, ventral coloration, and/or protein differences.

Description.—Adult standard length of this moderately sized species averages 21.9 mm in 10 males (range 19.9–23.6) and 23.7 mm in 14 females (range 19.4–26.7). The head is relatively broad in males—SL averages 6.9 times head width (range 6.3–7.5)—but only moderately wide in females (mean 7.3, range 6.3–8.3). Jaw muscles are large and prominent; their outlines are very visible externally. Snouts are relatively short and bluntly rounded or pointed. Nostrils are oval and of moderate size for the genus; the mean ratio of major to minor axes equals 1.4 in both sexes (range 1.2–1.7 in males, 1.1–1.6 in females). Eyes are 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 2–3 premaxillary teeth in adult males (mean 2.1) and 4–6 (mean 5.4) in females. Maxillary teeth average 14.8 in males (range 7–20) and 24.2 in females (range 19–29). Vomerine teeth average 9.2 in males (range 6–13) and 8.8 (range 5–12) in females. Limbs are moderately long; limb interval averages 4.5 in males (range 4–5.5) and 5.2 in females (range 4–6). 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 to bluntly pointed. 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 standard length; mean SL divided by tail length equals 1.09 in males (range 0.93–1.35) and 1.02 in females (range 0.91–1.08). The mental gland is present in large adult males and is round to moderately elliptical (maximum dimensions: 1.1 mm wide, 1.3 mm long). The postiliac gland is prominent externally.

Coloration varies little from the holotype. Most specimens have a prominent, brown-to-tan dorsal stripe that is bordered on each side by a dark, wavy line. Chevrons are found within the stripe of some specimens. Conspicuous light spots are present ventrally, including the gular region and belly, and the tip of the snout usually is white. The iris is dark brown.

Measurements of the holotype (in millimeters).—Head width 3.4; snout to gular fold (head length) 4.1; head depth at posterior angle of jaw 2.4; eyelid width 0.8; eyelid length 1.5; anterior rim of orbit to snout 0.9; horizontal orbit diameter 1.2; interorbital distance 1.6; distance separating external nares 0.8; major axis of nostril 0.44; minor axis of nostril 0.32; snout projection beyond mandible 0.3; snout to posterior angle of vent (standard length) 24.9; snout to anterior angle of vent 23.5; snout to forelimb 6.5; axilla to groin 15.1; limb interval 4; shoulder width 2.7, tail length 24.9; tail width at base 2.8; tail depth at base 2.8; forelimb length (to tip of longest toe) 4.4; hind-limb length 4.2; hand width 0.7; foot width 0.9. Numbers of teeth: premaxillary 5; maxillary 16–17; vomerine 5–6.

Coloration of the holotype (in alcohol).—The dorsal and lateral ground color is medium brown. A conspicuous, tan dorsal stripe arises just behind the eyes and extends the full length of the body and tail. It is narrowest across the shoulders; lateral borders are slightly wavy behind that point. The stripe is bordered dorsolaterally by prominent, dark brown lines. Lateral surfaces of the body and tail are uniformly medium brown, with whitish spots ventrolaterally. Ventral surfaces are a little lighter than lateral surfaces and are prominently marked by numerous whitish spots that are mainly round and somewhat smaller than the pupil. The spots are most prominent and largest in the gular region; they coalesce in the posterior part of the tail to form a light-colored network. Limbs are medium brown with some lighter highlights. The snout, face, and upper eyelids are medium to dark brown; there is a faint, light spot on the tip of the snout. The iris is dark brown.

Coloration in life.—Based on field notes by J. Hanken for MVZ 183094–118, 187091–97, and 187102 and by J. F. Lynch for MVZ 114606, 114609, 114612, 114614–15, 114618, 114624, 114631, and MZFC 8598–99 (all from Xometla); the dorsal stripe ranges from brown, to tan, to golden; lateral regions are blackish grey; the venter is a medium brownish gray. Conspicuous white flecks are concentrated at the chin, on lateral portions of the venter, and on the underside of the tail.

Osteology.—This description is based on data from 27 partial-to-complete skeletons. The skull is well developed, especially in MVZ 187092, 187095, and 187097. Ascending processes of the premaxillary bone are stout and typically remain separate from one another (character 1, state a), although they articulate in the midline in a few specimens (state b). The processes articulate firmly, and overlap substantially, with the facial processes of the frontal bones. Facial processes usually are well separated from the maxillary bones in ventral view (character 2, state a), but the two elements overlap slightly in a few specimens (state b). The premaxilla bears teeth in all adults (character 8, state b). The nasal bone is relatively large and triangular or rectangular in shape (character 3, states b–c); it frequently articulates or even fuses with the facial process of the maxilla (character 4, states b–c) and with the frontal. The prefrontal bone is relatively broad and frequently articulates or even fuses with the nasal, especially in males (character 5, states b–d). It is separate from the facial process of the maxilla in most specimens (character 6, state a), but the two elements occasionally articulate (state b). Septomaxillary bones are absent in most specimens (character 7, state a) but are rarely present on one or both sides (states b–c). The maxilla is relatively stout and bears numerous teeth (character 9, state b). The vomer is short and bears a very short preorbital process, which resembles that in *T. munificus*. There are relatively few vomerine teeth; they are arranged in a short, crescentic pattern, which is different from both *T. munificus* and *T. lunaris*. The frontal fontanelle is narrow; the parietal fontanelle, although conspicuous, is narrower than in some other species (its breadth equals 0.30–0.48, mean 0.41, 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 present and well developed (spinous).

All specimens have 14 presacral vertebrae, but there is variation in the number of presacral ribs. Limbs are weak, although long-bone epiphyses and mesopodial elements are mineralized in many adults. The tibial spur ranges from free (nine specimens), to attached (eight), to crest (three).

Mesopodial morphology is highly variable and, in the hind limb, distinctive (Table 1). Carpal pattern I predominates in the forelimb (78% 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), 18%; and III (fused distal carpals 3 and 4 plus centrale), 5%. A fourth pattern, V (fused distal carpals 1-2, 3, and 4 plus centrale), is present on both sides of one of seven immature specimens. In the tarsus, the modal pattern is V (fused intermedium and fibulare), 56%, but pattern VII (like V, but with fused distal tarsal 4-5 and centrale) is also common, 33%. 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 rare, 5%. Two additional tarsal patterns each are present at a low frequency, 3%: II (fused distal tarsal 4-5 and centrale), and VIII (like VII, but with fused distal tarsals 1-2 and 3). Asymmetry is common; approximately half of the specimens have a different carpal or tarsal pattern on right and left sides. The predominant phalangeal formula in the hand is 1-2-3-2; 1-2-3-1 is a rare variant. The modal formula in the foot is 1-2-3-3-1; 1-2-3-2-1 and 1-2-3-3-2, the typical formula in *Thorius*, are rare variants.

Comparisons to other taxa.—Maxillary teeth are a symplesiomorphy for the genus *Thorius* that occurs in only five species. *Thorius aureus* has other

TABLE 1. DISTRIBUTION OF CARPAL[a] AND TARSAL[b] PATTERNS AMONG NINE OF THE 10 SPECIES OF *Thorius* IN VERACRUZ AND PUEBLA. Closed circles denote the modal patterns in each species. Mesopodial data are unavailable for *T. minydemus.*

	Carpal patterns						Tarsal patterns								
Species	I	II	III	V	IX	X	I	II	III	V	VI	VII	VIII	X	XI
dubitus	●	●					●		●						
lunaris	●	○					●		○						
magnipes	●	○					●								
munificus	●	○					○		○	●	○				
narismagnus	○		●									●	●		
pennatulus	○	●	○									●	○		
schmidti	●	○	○	○		○	●	○		○	○	○		○	○
spilogaster	●	○	○	○			○	○		●		○	○		
troglodytes	●	○	○		○		●			○					

[a] I: u-i, r, c1, d1-2, d3, d4-c; II: u-i, r, c1, (d1-2)-d3, d4-c; III: u-i, r, c1, d1-2, d3-(d4-c); V: u-i, r, c1, (d1-2)-d3-(d4-c); X: u-i, r, c1-(d1-2), d3-(d4-c); XI: u-i, r, c1, d1-2, d3, d4, c. u, ulnare; i, intermedium; r, radiale; c, centrale; c1 = centrale 1, d, distal carpal.

[b] I: i, f, t, c, c1, d1-2, d3, d4-5; II: i, f, t, c1, d1-2, d3, c-(d4-5); III: i, f, t, c, c1, (d1-2)-d3, d4-5; V: i-f, t, c, c1, d1-2, d3, d4-5; VI: i-f, t, c, c1, (d1-2)-d3, d4-5; VII: i-f, t, c1, d1-2, d3, c-(d4-5); VIII: i-f, t, c1, (d1-2)-d3, c-(d4-5); X: i, f, t, c1, (d1-2)-d3, c-(d4-5); XI: i-c, f, t, c1, d1-2, d3-d4. i, intermedium; f, fibulare; t, tibiale; c, centrale; c1, centrale 1; d, distal tarsal.

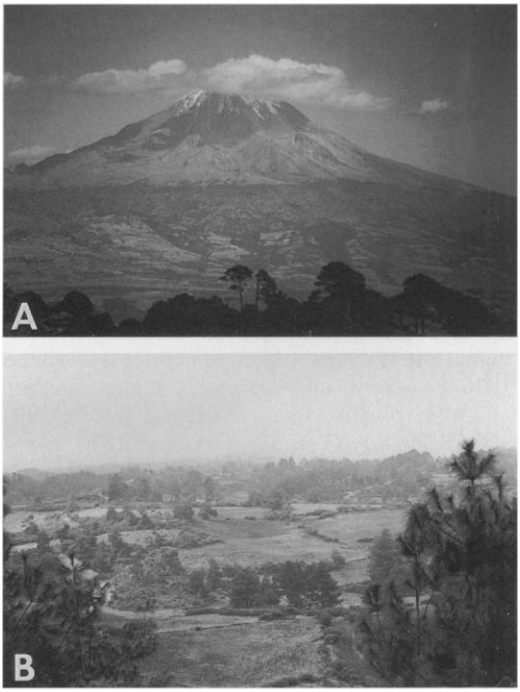

Fig. 3. Localities and habitats of two new species of *Thorius* from Volcán Orizaba, Ver. (A) Volcán Orizaba, December 1978. *Thorius spilogaster* and *T. lunaris* occupy forest habitats between 2500 and 2725 m on the south and southeast flanks. The photograph is taken from 12 km east of San Felipe, Ver. (foreground), a collecting locality for *T. magnipes* and *T. troglodytes.* (B) Canyon approximately 1 km southeast of El Berro, February 1976. *Thorius spilogaster* and *T. lunaris,* two terrestrial species, occur in microsympatry.

plesiomorphic states that are lacking in the other four species, such as a small dorsal fontanelle and large adult body size. It also has a unique color pattern. *Thorius spilogaster* and *T. schmidti* share a unique combination of derived tarsal patterns and spotted ventral coloration; both also have a golden or brown, as opposed to black, dorsal coloration. There are, however, subtle morphological differences between them. *Thorius spilogaster* is slightly smaller than *T. schmidti* and has smaller hands and feet with less discrete digits and pointed rather than rounded digit tips. It also has a smaller, rounder nostril; more marked sexual dimorphism; a more prominent dorsal light band that has brassy highlights; and more prominent and consistent ventral white spotting. The two species differ in several proteins. Adult *T. smithi* and *T. minydemus* are much smaller than *T. spilogaster,* and only some *T. minydemus* have maxillary teeth.

Habitat and range.—*Thorius spilogaster* is known from localities near the villages of El Berro and Xometla, Ver., on the south and southeast flanks of Volcán Orizaba (Figs. 1, 3). It is sympatric with *T. lunaris* at both sites but has not been collected near Texmola, a village west of El Berro that is a third locality for *T. lunaris.* Recorded elevations range from 2500–2725 m (9000–10,000 ft, according to Gadow, 1905). According to field notes by J. Hanken, both species were collected at El Berro (3 Feb. 1976) along the north-facing wall of a canyon within the few remaining clumps of pine-oak forest (most of the canyon slope was otherwise cleared for farming). At Xometla (23 July 1976), they were found in partially cut-over pine forest. In spite of warm and dry conditions on both days, 50–60 adults were taken at each locality from terrestrial microhabitats under the bark of stumps, under large fallen logs, and especially within piles of wood chips and shavings (see also introductory quote from Gadow, 1908). According to D. B. Wake, the two species were equally common at Xometla on 2 April 1970, when he and R. W. McDiarmid observed more than 300 specimens in apparently identical microhabitats (small surface cover and leaf litter). J. F. Lynch (22 Jan. 1974) did not detect any microhabitat differences between the two species at Xometla but noted *T. spilogaster* as being slightly more common than *T. lunaris* (38 of 63 specimens observed).

The locality recorded for KU 106818, a single specimen that we identify as *T. spilogaster*, is Puebla border west of Cumbres de Acultzingo, elevation 2151 m, 22 June 1966. This site is at or very near Puerto del Aire, the type locality of *T. troglodytes*, *T. dubitus*, and *T. magnipes*. We have examined large series of specimens from Puerto del Aire and adjacent localities and have found no others that can be referred to *T. spilogaster*. Accordingly, we believe that this specimen may have been collected near Xometla, which was visited the previous day by the same collectors, and that it may have been mixed inadvertently with specimens from Puerto del Aire.

Etymology.—The species name is a conjunction of two Greek words, *spilos* (a spot, blemish) and *gaster* (the belly, stomach), in reference to the characteristic spotted ventral coloration. The name has been used informally by herpetologists in reference to this species for more than 25 years; its exact origin is unknown (J. Kezer, pers. comm.).

Remarks.—Gadow (1905, 1908, 1910) collected *Thorius* from near Xometla at the turn of the century. He identified them as *T. pennatulus*, the only species of *Thorius* recognized at that time, and also claimed to distinguish males from females based on nostril size: "This tiny Newt, less than two inches in length and thinner than a match, with weak limbs and reduced digits, shows a peculiar dimorphism of the size of the nostrils. They are very large and open in the males, much smaller in the females" (Gadow, 1905:202). *Thorius pennatulus* is now known to be an exclusively lowland species that does not occupy the montane forest at Xometla. Instead, Gadow's sample includes both new species that occur at this locality, which differ in nostril size and shape (large nostriled *T. spilogaster* vs small nostriled *T. lunaris*). We suggest that Gadow recognized the existence of these two forms but mistook them for different sexes of the same species. Taylor (1941:107) was the first person to suggest that *Thorius* from Xometla belong to a species other than *T. pennatulus*.

Genetic variation in *T. spilogaster* and the species' relationships to congeners were examined using protein electrophoresis by Hanken (1980, 1983a; populations 8–9, listed as *T. maxillabrochus* or *T. schmidti*). Evolutionary consequences of miniaturization of adult body size for cranial and appendicular morphology were examined by Hanken (1982, 1984, 1985; listed as *T. schmidti*). Large numbers of additional specimens of this species reside at MVZ, KU, and LACM.

Thorius lunaris, n. sp.

Crescent Nostriled *Thorius*

Figure 2B–C

Holotype.—MVZ 183292, an adult female from 1.5 km by road west of Texmola, on southwestern slopes of Volcán Orizaba, Veracruz, México, elevation 2640 m, collected by J. Hanken, H. B. Shaffer, and C. Ceron, 2 February 1976.

Paratypes.—All from Veracruz, México: MVZ 183282, 183291, 183294–96 (three specimens), 183298, 183300–1 (two specimens), 183307–9 (three specimens), 186963–70 (eight specimens), 186972–77 (six specimens), same data as the holotype; MVZ 183218–20 (three specimens), 183222–24 (three specimens), 183228, 187081, canyon approximately 1 km southeast of El Berro (approximately 15 km by air southwest of Pico de Orizaba), elevation 2500 m, collected by J. Hanken, H. B. Shaffer, and C. Ceron, 2 February 1976; MVZ 183313–15 (three specimens), 183318–20 (three specimens), 187098–101 (four specimens), 187188, forest above Xometla, elevation 8600–8640 ft, collected by J. Hanken, D. Eakins, and C. Ceron, 23 July 1976; MZFC 8600–8601 (two specimens), forest above Xometla, elevation 2710–25 m, collected by J. F. Lynch, 22 January 1974; BMNH 1903.9.30.317–19 (three specimens), Xometla, collected by H. Gadow, July 1902; LACM 117955, near Xometla, collected by R. W. McDiarmid, 30 September 1969; LACM 117996, 118003, 118008, 118010, 118046, 118055, 118060, 118065–66 (two specimens), near Xometla, 8 mi by road north-norhwest of Perla, collected by R. W. McDiarmid, D. B. Wake, M. Ceron Sr., M. Ceron Jr., and C. Ceron, 2 April 1970; KU 106707, 106759, Pico de Orizaba (Xometla), elevation 2545 m, collected by C. Ceron, D. Rubin, and H. L. Freeman, 21 June 1966. Some specimens are cleared and stained or have had tissue removed for protein comparisons.

Diagnosis.—This is a large species of *Thorius*, which is distinguished from other members of the genus by the following combination of traits: no maxillary teeth; plain (unmarked) belly; small, crescent-shaped nostril in many adults; prominent parotoid gland; moderately long limbs and large feet; and long, slender tail. It is readily distinguished from adults of sympatric *T. spilogaster*, which are smaller and stouter, have maxillary teeth, a spotted belly, a larger, more oval nostril, a relatively shorter tail, smaller feet, a smaller parietal fontanelle, different modal tarsal and foot phalangeal patterns, and typically lack septomaxillary bones. It differs from biochemically similar *T. munificus* in adult body size, nostril shape, presence/absence of the parotoid gland, relative limb length, modal tarsal patterns, cranial osteology, and protein variants.

Description.—Adult standard length of this large, sexually dimorphic species averages 26.3 mm in nine males (range 21.7–29.7) and 28.5 mm in 16 females (range 25.2–31.9). The head is relatively narrow; SL averages 8.0 times head width in males (range 7.1–8.3) and 8.3 times head width in females (range 7.6–9.4). Snouts are bluntly pointed. Nostril shape is highly variable; the mean ratio of major axis to minor axis is 1.6 in males (range 1.3–2.0) and 1.5 in females (range 1.2–2.7). There appears to be an ontogenetic shift in nostril size and shape; most large adults have a small, comma-shaped nostril, whereas many smaller individuals have a relatively large, oval nostril. Large males with well-developed mental glands have a swollen upper lip and enlarged nasolabial protuberances. Eyes are small; they either do not or just barely reach 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 males (mean 2.2) and 1–4 in females (mean 2.1). Vomerine teeth average 13.0 in males (range 10–16) and 9.9 in females (range 7–17). There are no maxillary teeth. Limbs are moderately long; limb interval averages 4.6 in males (range 4–5) and 5.3 in females (range 4–6). Hands and feet are relatively large with well-demarcated digits. Only the two longest fingers and three longest toes are free at their tips, which are rounded rather than pointed in adults. Fingers, in order of decreasing length, are 3-2-4-1; toes are 3-(2-4)-1-5. There are marked subdigital pads on digits 2–4; they are also evident on digits 1 and 5 of the largest specimens. The tail is relatively long and exceeds standard length in most specimens; mean SL divided by tail length equals 0.89 in males (range 0.75–1.07) and 0.88 in females (range 0.66–1.52). The mental gland is white; the postiliac gland is visible.

Overall coloration is very dark. A dark-brown to brownish-tan dorsal band is conspicuous on some specimens but obscure on others. Many specimens have white flecks limited to the gular region; some have additional faint, tiny white spots on the snout, limbs, and, rarely, the venter. The iris is blackish brown.

Measurements of the holotype (in millimeters).—Head width 3.9; snout to gular fold (head length) 5.3; head depth at posterior angle of jaw 2.7; eyelid width 0.7; eyelid length 2.0; anterior rim of orbit to snout 1.5; horizontal orbit diameter 1.1; interorbital distance 2.0; distance separating external nares 1.3; major axis of nostril 0.24; minor axis of nostril 0.12; snout projection beyond mandible 0.6; snout to posterior angle of vent (standard length) 30.8; snout to anterior angle of vent 28.6; snout to forelimb 7.9; axilla to groin 18.0; limb interval 4.5; shoulder width 2.9; tail length 36.0; tail width at base 2.9; tail depth at base 2.9; forelimb length (to tip of longest toe) 4.8; hind-limb length 5.8; hand width 1.0; foot width 1.5. Numbers of teeth: premaxillary 2; maxillary 0-0; vomerine 9-10.

Coloration of the holotype (in alcohol).—The ground color of dorsal and lateral surfaces is blackish brown. A broad dorsal band arises on the nape and extends onto the base of the tail. The band is dark brown with some lighter highlights, for example, on the occiput. The head is dark brownish-black without light spots; there are obscure, white spots between the eyes and on the snout. The venter is lighter than lateral surfaces and has a melanic network, but it generally appears gray-brown. The gular region is the lightest ventral surface and has many obscure white spots. Otherwise, the venter is unmarked. Limbs are dark brown with some distal mottling. The general color of the tail is blackish brown, although it is somewhat lighter ventrally with some pale spots near the tip.

Coloration in life.—Based on field notes by J. Hanken for MVZ 183279–310 and 186963–79 (Texmola), some specimens display the dorsal stripe characteristic of *Thorius*, but others are almost completely dark above and below (Fig. 2C). For MVZ 185403–18 and 187103 (Xometla), faint, brassy dorsal stripe; faint whitish speckling on dark venter; no lateral flecking. D. B. Wake (2 April 1970) also noted two color morphs of this species at Xometla: one very dark dorsally and ventrally, with brassy iridophores that form an indistinct dorsal stripe; the second with a brown stripe and a uniformly black belly.

Osteology.—This description is based on data from 20 partial-to-complete adult skeletons. The skull is relatively well developed. Ascending processes of the premaxillary bone arise separately and remain so for their entire lengths in all specimens but one (character 1, state a), in which they are partly fused (state c). The processes overlap extensively with the facial processes of the frontal bones. The facial process of the premaxilla is well separated from the maxillary bone in ventral view in all females (character 2, state a), but the two elements overlap or articulate in nearly all males (states b–d). The premaxilla bears teeth in all adults (character 8, state b). The nasal bone is well developed (character 3, states b–c) and frequently articulates with the relatively large facial portion of the maxilla anterior to the foramen for the nasolacrimal duct (character 4, state b). The prefrontal bone is small and crescent-shaped (character 5, state d) and usually does not contact the maxilla (character 6, state a). Septomaxillary bones are present on both sides in most specimens (character 7, states b–c) but are absent on one or both sides in a few others (state a). Even when maximally developed, they are extremely tiny. The maxilla is slender and toothless (character 9, state a). The vomer is relatively well developed and bears a moderate number of teeth, which are arranged in an elongate row that extends onto a pronounced preorbital process. The frontal fontanelle is narrow; paired frontal bones occasionally articulate in the midline. The parietal fontanelle is broad but not as much as in some other species; its breadth equals 0.43–0.64, mean 0.57, 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 (spinous).

All specimens have 14 presacral vertebrae except MVZ 187100, in which two adjacent vertebrae are fused. The tibial spur ranges from free (two specimens), to attached (five), to crest (three). Limb bone epiphyses and mesopodial elements, and rarely the hyobranchial skeleton, are mineralized in many adults.

Mesopodial morphology is generalized, and there is little variation in comparison to that seen in most other species of *Thorius* (Table 1). Carpal pattern I predominates in the forelimb (90% of adult carpi examined); pattern II occurs at low frequency (10%). Tarsal pattern I predominates in the hind limb (87%); pattern III (fused distal tarsals 1-2 and 3) occurs at low frequency (13%). Mesopodial asymmetry is also rare. In the hand, the predominant phalangeal formula is 1-2-3-2; a single specimen has only three fingers (1-2-3) on each side. The lone regular phalangeal formula in the foot is 1-2-3-3-2; a few feet are malformed and not readily scored.

Comparisons to other taxa.—*Thorius lunaris* is most closely related to *T. munificus* based on protein comparisons (Hanken, 1983a; Table 2). Both species are dark with a somewhat lighter dorsal stripe and plain ventral coloration, and both lack maxillary teeth. The dorsal stripe, however, seems to be more conspicuous in *T. munificus*, which also lacks the gular flecking that is seen occasionally in *T. lunaris*. Adult *T. munificus* are significantly smaller, lack the distinctive comma-shaped nostril found in most adult *T. lunaris*, and have more extensive interdigital webbing. The two species differ in several skeletal features (e.g., carpal and tarsal variants and frequencies, presence/absence of septomaxillary bones, shape of the preorbital process of the vomer, size of ascending processes of the premaxillary bone), although there are few discrete differences.

Habitat and range.—*Thorius lunaris* is known from localities near the villages of Texmola, El Berro, and Xometla, Ver., on the south and southeast flanks of Volcán Orizaba (Figs. 1, 3–4). It is sympatric with *T. spilogaster* at the latter two sites but is the only species of *Thorius* known from Texmola. Recorded elevations range from 2500–2640 m. According to field notes by J. Hanken (3 Feb. 1976), specimens from Texmola were collected from within a small patch of pine-oak forest that was surrounded by cleared agricultural fields. The surface of the forest floor was dry, but approximately 50 specimens were taken from terrestrial microhabitats under the bark of stumps, under large fallen logs, within leaf litter, and especially within piles of wood chips. See account for *T. spilogaster* for habitat notes.

Etymology.—The species name is a conjunction of two Latin words, *lunaris* (crescent-shaped) and *naris* (nostril), in reference to the distinctive and characteristic nostril shape.

TABLE 2. GENETIC DIFFERENTIATION AMONG NINE OF 10 SPECIES OF *Thorius* IN VERACRUZ AND PUEBLA (DATA FROM HANKEN, 1980). Above diagonal, mean pairwise Nei genetic distance (D_N) between species (range in parentheses), baesd on population samples of five or more specimens each. Below diagonal, numbers of enzyme 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 unavailable for *T. minydemus*.

Species	*pennatulus*	*naris-magnus*	*dubitus*	*troglodytes*	*spilogaster*	*schmidti*	*magnipes*	*lunaris*	*munificus*
pennatulus (1)	—	0.39	1.00	1.16 (1.1–1.3)	0.95 (0.9–1.0)	0.99 (1.0–1.0)	0.85	1.07 (1.0–1.1)	1.0
narismagnus (1)	**2,** 2[1]	—	0.75	1.03 (1.0–1.1)	0.73 (0.7–08)	0.95 (0.9–1.0)	0.95	0.84 (0.8–0.9)	0.92
dubitus (1)	**9,** 0[2]	**8,** 0[3]	—	0.43 (0.4–0.5)	0.80 (0.8–0.9)	0.88 (0.8–0.9)	0.56	1.33 (1.3–1.4)	1.42
troglodytes (3)	**9,** 1[4]	**9,** 0[5]	**3,** 2[6]	—	0.68 (0.6–0.9)	0.68 (0.6–0.8)	0.89 (0.8–0.9)	1.17 (1.1–1.3)	1.27 (1.2–1.3)
spilogaster (2)	**9,** 1[7]	**6,** 1[8]	**7,** 1[9]	**4,** 3[10]	—	0.60 (0.6–0.6)	1.23 (1.2–1.3)	1.08 (1.0–1.2)	1.1 (1.1–1.2)
schmidti (2)	**8,** 0[11]	**8,** 2[12]	**7,** 2[13]	**5,** 2[14]	**4,** 4[15]	—	1.4 (1.4–1.4)	0.98 (0.9–1.1)	0.99 (0.9–1.1)
magnipes (1)	**7,** 0[16]	**9,** 0[17]	**5,** 1[18]	**6,** 1[19]	**8,** 1[20]	**10,** 1[21]	—	1.38 (1.4–1.4)	1.49
lunaris (3)	**7,** 2[22]	**6,** 2[23]	**7,** 3[24]	**6,** 3[25]	**9,** 1[26]	**7,** 3[27]	**8,** 2[28]	—	0.25 (0.2–0.3)
munificus (1)	**9,** 0[29]	**8,** 1[30]	**11,** 0[31]	**9,** 1[32]	**8,** 1[33]	**8,** 2[34]	**11,** 0[35]	**2,** 0[36]	—

[1] IDH-1, PEP, MDH-2, AAT-1. Enzymes abbreviated according to Murphy et al. (1996).
[2] CAP, GAPDH, MPI, LDH-1, LDH-2, IDH-1, MDH-1, MDH-2, AAT-1.
[3] CAP, GAPDH, LDH-1, LDH-2, MDH-1, MDH-2, PEP, MPI.
[4] GP-2, CAP, PEP, GAPDH, LDH-1, LDH-2, MDH-1, MDH-2, AAT-1, G3PDH.
[5] CAP, GAPDH, LDH-1, LDH-2, MDH-1, MDH-2, PGM, PEP, MPI.
[6] GP-2, MDH-1, MPI, G3PDH, PEP.
[7] PEP, GP-2, IDH-1, LDH-1, LDH-2, AAT-1, GAPDH, MDH-1, MDH-2, MPI.
[8] GP-2, GAPDH, LDH-1, LDH-2, MDH-1, PEP, MPI.
[9] GP-2, CAP, MPI, MDH-2, LDH-1, LDH-2, PEP, MDH-1.
[10] CAP, MDH-2, LDH-1, LDH-2, G3PDH, PEP, MPI.
[11] GP-2, GAPDH, G3PDH, LDH-1, AAT-1, MPI, MDH-1, MDH-2.
[12] GP-2, PEP, LDH-1, LDH-2, MPI, MDH-1, MDH-2, GAPDH, IDH-1, G3PDH.
[13] GP-2, CAP, MPI, MDH-1, LDH-1, LDH-2, GAPDH, IDH-1, G3PDH.
[14] CAP, GAPDH, MPI, LDH-1, LDH-2, G3PDH, PEP.
[15] GAPDH, MDH-2, LDH-1, MPI, IDH-1, LDH-2, G3PDH, PEP.
[16] CAP, GAPDH, PGM, LDH-1, LDH-2, MDH-1, MDH-2.
[17] CAP, GAPDH, MPI, LDH-1, LDH-2, MDH-1, MDH-2, PEP, PGM.
[18] CAP, GAPDH, MPI, MDH-2, PGM, PEP.
[19] GP-2, GAPDH, MPI, MDH-1, CAP, G3PDH, MDH-2.
[20] GP-2, GAPDH, MPI, MDH-2, CAP, PEP, LDH-1, LDH-2, MDH-1.
[21] GP-2, CAP, PGM, GAPDH, MDH-1, MDH-2, LDH-1, LDH-2, PEP, MPI, G3PDH.
[22] GP-2, GAPDH, PEP, LDH-1, IDH-1, MDH-1, MDH-2, PGM, MPI.
[23] GP-2, GAPDH, LDH-1, MDH-1, MDH-2, PEP, AAT-1, MPI.
[24] GAPDH, MDH-2, GP-2, LDH-1, MPI, LDH-2, AAT-1, MDH-1, PGM, PEP.
[25] GP-2, CAP, MDH-2, GAPDH, LDH-1, LDH-2, PGM, G3PDH, MPI.
[26] GP-2, GAPDH, MDH-1, MDH-2, CAP, MPI, PEP, LDH-1, LDH-2, G3PDH.
[27] GP-2, GAPDH, PEP, AAT-1, LDH-1, MPI, LDH-2, IDH-1, PGM, G3PDH.
[28] GAPDH, MDH-2, GP-2, MPI, LDH-1, LDH-2, AAT-1, CAP, MDH-1, PGM.
[29] IDH-1, MDH-1, MDH-2, PGM, PEP, MPI, LDH-1, GP-2, GAPDH.
[30] GP-2, GAPDH, PEP, LDH-1, MDH-1, MDH-2, PGM, MPI, AAT-1.
[31] AAT-1, GAPDH, GP-2, PEP, MDH-1, MDH-2, CAP, MPI, LDH-1, LDH-2, PGM.
[32] GP-2, GAPDH, LDH-1, LDH-2, CAP, MDH-2, PEP, MPI, PGM, G3PDH.
[33] GP-2, GAPDH, MPI, LDH-1, LDH-2, PGM, AAT-1, PEP, G3PDH.
[34] GP-2, GAPDH, PEP, LDH-1, LDH-2, PGM, AAT-1, MPI, IDH-1, G3PDH.
[35] GP-2, GAPDH, MPI, MDH-1, MDH-2, CAP, PGM, PEP, LDH-1, LDH-2, AAT-1.
[36] PEP, PGM.

Remarks.—Genetic variation in *T. lunaris* and the species' relationships to congeners are examined using protein electrophoresis by Hanken (1980, 1983a; populations 13–15, *T.* sp. B). Large numbers of additional specimens of this species reside in MVZ, KU, and LACM.

Thorius munificus, n. sp.

McDiarmid's *Thorius*

Figure 5A

Holotype.—MVZ 183274, an adult female from

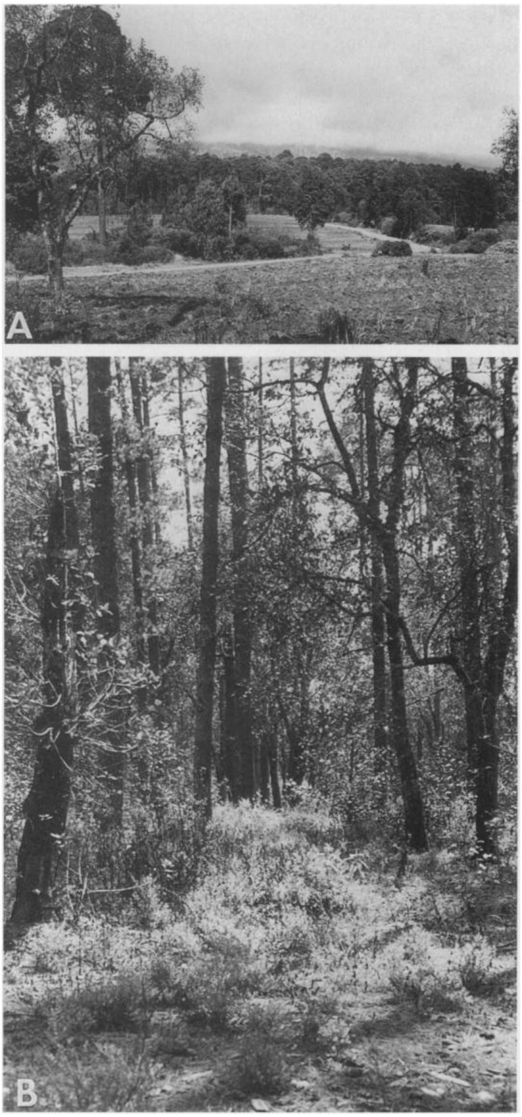

Fig. 4. (A) Type locality of *Thorius lunaris*, 1.5 km west of Texmola, Ver., February 1976. Only a single species of *Thorius* has been collected at this locality. (B) Forest at (A). Specimens were taken under cover objects on the forest floor, including small wood chips visible in the foreground.

Mexican Hwy. 140, 4.5 km by road west of Las Vigas, Veracruz, México, elevation 2420 m, collected by J. F. Lynch, T. J. Papenfuss, and D. B. Wake, 25 July 1976.

Paratypes.—All from Veracruz, México: MVZ 183255–73 (19 specimens), 183277, 186998, same data as the holotype; USNM 497640–41 (two specimens), MZFC 8596–97 (two specimens), same locality as the holotype, elevation 2400 m, collected by T. J. Papenfuss and S. S. Sweet, 17 Dec. 1972; MVZ 183241, 183244, 183247–48 (two specimens), 186980–97 (18 specimens), Mexican Hwy. 140 at Las Vigas, elevation 2525 m, collected by J. Hanken and H. B. Shaffer, 17 February 1976. Some of the above specimens are cleared and stained or have had tissue removed for protein comparisons.

Diagnosis.—This is a moderately sized species of *Thorius*, which is distinguished from other members of the genus by the following combination of traits: no maxillary teeth; dark, nondescript coloration; roundish-oval nostril; long limbs and tail; compact skull with a very large frontoparietal fontanelle, and tarsal variants. It differs from the biochemically similar but nevertheless distinct *T. lunaris*, which is substantially larger and has a comma-shaped nostril, prominent parotoid gland, relatively shorter limbs, more elongate skull with an enlarged preorbital process on the vomer bone and larger ascending processes of the premaxillary bone, and a different modal tarsal pattern.

Description.—Adult standard length of this moderately sized species averages 23.2 mm in 11 males (range 20.5–25.4) and 23.6 mm in 14 females (range 19.9–25.9). The head is moderately wide; SL averages 7.5 times head width in males (range 6.9–7.8) and 7.6 times head width in females (range 7.1–8.4). Snouts are bluntly pointed. Nostrils are oval in shape; the mean ratio of major axis to minor axis equals 1.3 both in males (range 1.1–1.5) and in females (range 1.1–1.6). Eyes are small and barely intersect the margin of the jaw in dorsal view. A suborbital groove intersects the lip on each side of the head. There is a prominent parotoid gland on each side of the neck above the protuberance marking the posterior tip of the epibranchial cartilage. There are 0–2 premaxillary teeth in males (mean 1.7) and 0–3 in females (mean 1.1). Vomerine teeth average 8.2 in males (range 6–11) and 9.1 in females (range 8–10). There are no maxillary teeth. Limbs are relatively long; limb interval averages 4.0 in males and 3.8 in females (range 3–5 in both sexes). Hands and feet are moderately long. Only the two longest fingers and three longest toes are free at their tips, which are rounded rather than pointed in adults. Fingers, in order of decreasing length, are 3-2-4-1; toes are 3-(2-4)-(1-5). The tail is long and slender; mean SL divided by tail length equals 0.95 in males (range 0.76–1.19) and 0.86 in females (range 0.76–1.00). The postiliac gland is evident, but the mental gland is faint or indistinct. Secondary sexual

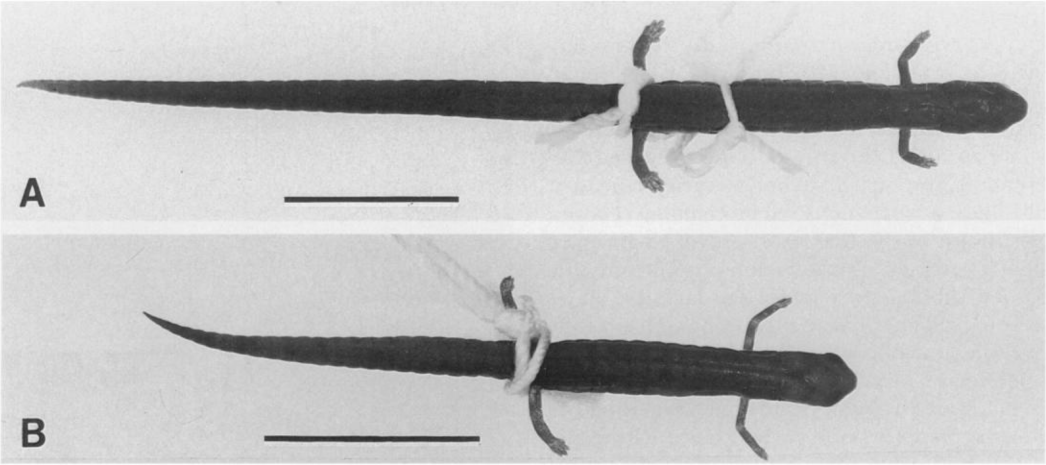

Fig. 5. Photographs of two new species of *Thorius* from northern Veracruz. (A) Holotype of *T. munificus*, MVZ 183274, an adult female. (B) Holotype of *T. minydemus*, MVZ 131444, an adult male. Scale bar = 1 cm.

characters are inconspicuous in males; sexual dimorphism is slight.

Coloration varies little from the holotype; the dorsal band is more evident on some specimens than others. Some large males are very dark and have dark pigment concentrated in the grooves between the digits. Spots on the head are always very faint. The iris is black.

Measurements of the holotype (in millimeters).—Head width 3.1; snout to gular fold (head length) 4.7; head depth at posterior angle of jaw 2.2; eyelid width 0.6; eyelid length 1.4; anterior rim of orbit to snout 1.0; horizontal orbit diameter 1.1; interorbital distance 1.7; distance separating external nares 0.8; major axis of nostril 0.36; minor axis of nostril 0.28; snout projection beyond mandible 0.5; snout to posterior angle of vent (standard length) 25.9; snout to anterior angle of vent 24.6; snout to forelimb 7.3; axilla to groin 15.3; limb interval 3.5; shoulder width 2.3; tail length 33.5; tail width at base 2.2; tail depth at base 2.6; forelimb length (to tip of longest toe) 4.0; hind-limb length 4.2; hand width 0.8; foot width 1.3. Numbers of teeth: premaxillary 1; maxillary 0-0; vomerine 3–4.

Coloration of the holotype (in alcohol).—Dorsal and lateral ground color is a dark blackish-brown. A faint, dark brown dorsal band extends from the nape onto the tail. The venter is lead-gray and lighter than lateral surfaces. There are numerous white spots ventrally from the gular region to the level of the sternum and scattered spots more posteriorly. The tail is unmarked. Distal surfaces of the limbs have some light-colored spots. Faint white spots are present between the eyes and on the snout. The iris is black.

Coloration in life.—According to field notes by D. B. Wake (25 July 1979), specimens collected from 6 km west of Las Vigas had a tan-gold dorsal stripe and at least superficially resembled *T. troglodytes* from Puerto del Aire.

Osteology.—This description is based on data from 19 partial-to-complete adult skeletons. This species has a relatively weak skeleton, even in comparison to other *Thorius*; the skull is compact. Ascending processes of the premaxillary bone are very slender. They remain separated along their entire length in most specimens (character 1, state a) but articulate medially or fuse slightly in a few specimens (states b–c). They overlap the small facial processes of the frontal bones. Facial processes of the premaxilla are well separated from the maxillary bones in ventral view in all males but one (character 2, state a), but these bones overlap or articulate in nearly all females (states b and d). The premaxilla bears teeth in six of eight adult females and in 10 of 11 adult males (character 8, state b). These teeth are enlarged in males. Dental processes are nearly separate (divided premaxilla) in a single specimen, MVZ 186995. The nasal bone is substantially larger than the prefrontal and varies from being thin and crescent-shaped to rectangular (character 3, states b–c). It typically articulates with the facial process of the maxilla (character 4, state b), although occasionally these bones are separate. The prefrontal in most males is small and crescent-shaped and separate from both the nasal and maxilla (character 5, state b; character 6, state a). In females, it is somewhat larger and shows a tendency to articulate with both the nasal (character 5, state c) and the facial process of the maxilla (character 6, state b), as well as with the facial process of the frontal bone. Degree of articulation among these bones varies considerably among specimens. Septomaxillary bones are present on both sides in only a single specimen (character 7, state b) and on only one side in a few others. Most specimens lack the bones entirely (state a). The maxillary bone has a well-developed facial process, but the dental process is slender or even sinuous and toothless (character 9, state a). Vomers are well developed but widely separated posteriorly, except where the dental rows come together; the preorbital process is present but short. There are relatively few vomerine teeth, which are are arranged in a short row. The frontal fontanelle is narrow, but the parietal fontanelle is very broad; its breadth equals 0.49–0.69, mean 0.60, 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 discrete.

All specimens have 14 presacral vertebrae. The tibial spur is highly variable, ranging from absent (five specimens), to rudimentary (four specimens), to rudimentary with knob (one specimen), to free (one specimen), to attached (six specimens), to crest with attached spur (two specimens). Limb bone epiphyses and mesopodial elements are mineralized in many adults.

Mesopodial morphology is highly variable, especially in the hind limb (Table 1). Carpal patterns I and II occur at nearly identical frequencies in the adult forelimb (51% and 49%, respectively). The modal tarsal pattern is V (39%), but three additional patterns occur at low to moderate frequencies: I, 33%; III, 14%; and VI (like III, but with fused intermedium and fibulare), 14%. Asymmetry is extremely common; three-fourths of the specimens have a different carpal or tarsal pattern on each side, and nearly half have asymmetric carpal and tarsal patterns. The predominant phalangeal formula in the hand is 1-2-3-2 (occasionally 1-2-3-1). In the foot, the predominant formula is 1-2-3-3-2 (occasionally 1-2-3-3-1).

Comparisons to other taxa.—See account for *T. lunaris* for a comparison between this species and *T. munificus*, its closest relative based on protein comparisons. *Thorius minydemus* from the vicinity of La Joya to the east is smaller and lighter colored; has a large, round-to-oval nostril; and has maxillary teeth in some adults.

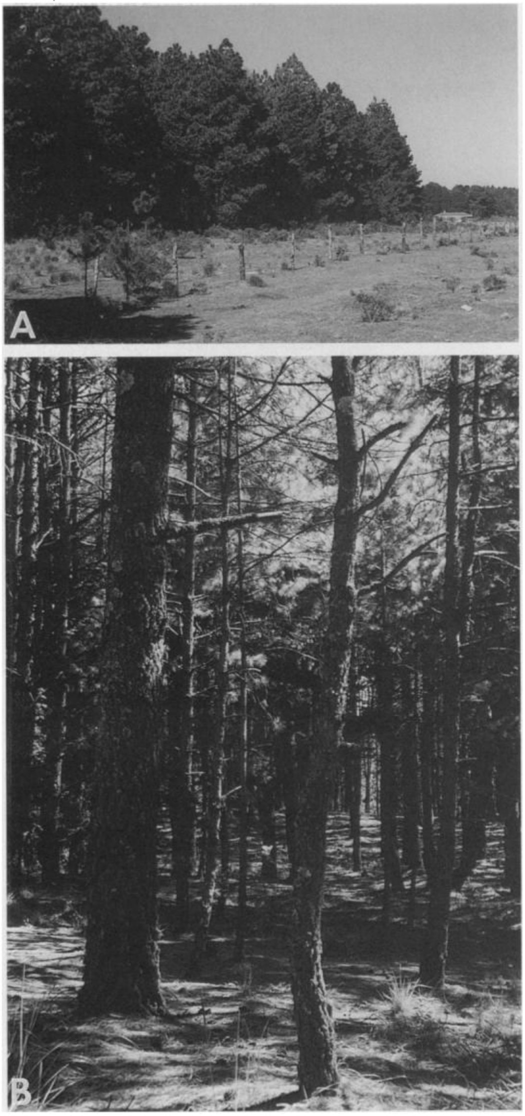

Fig. 6. (A) Type locality of *Thorius munificus*, 4 km west of Las Vigas, Ver., February 1976. Only a single, terrestrial species of *Thorius* has been collected at this locality. (B) Forest at (A). Local villagers regularly collect fallen branches and dead logs for firewood, resulting in a near total absence of large, wooden cover objects on the forest floor.

Habitat and range.—*Thorius munificus* is known from Las Vigas, Ver. (19°35'18"N, 97°05'34"W), and from adjacent localities within a few kilometers both east and especially west (Figs. 1, 6). Recorded elevations range from 2380–2525 m (included in Wake et al., 1992, fig. 2, as *Thorius* sp. nov.). All specimens have been collected in terrestrial microhabitats within pine or pine-oak forest. According to field notes by D. B. Wake, the locality at 4.5 km west of Las Vigas (25 July

1976) comprises dense pine woods with a few oaks and abundant representation of plants characteristic of temperate woodlands in northern North America, including the genera *Pteridium, Adianthum, Monotropa,* and *Lupinus,* as well as herbaceous ericaceous species and saprophytic orchids. Large numbers of *T. munificus* were observed under the abundant ground cover, which mainly comprised pine logs and branches. The site located 6 km west of Las Vigas (25 July 1979) was a mixed woodland of oak, pine, and madrone, with abundant shrubby *Baccharis* and again with *Monotropa* and other ericaceous plants. Salamanders of several species (*T. munificus, Pseudoeurycea leprosa, P. cephalica,* and *Chiropterotriton chiroptera*) were "incredibly abundant" under the bark of fallen logs and on the ground in litter and under logs and fallen branches.

Etymology.—The species name is derived from the Latin word *munificus,* meaning bountiful, or generous. The species is dedicated in honor of Roy W. McDiarmid, in recognition of his longstanding interests in and contributions to the biology of tropical salamanders, especially those of Veracruz, México, and who has graciously shared his knowledge and insights with us on many occasions.

Remarks.—Genetic relationships of *T. munificus* to congeners was examined using protein electrophoresis by Hanken (1980, 1983a; population 16, *T.* sp. B). Levels of genetic variability among populations of *T. munificus* are unknown. Evolutionary consequences of miniaturization of adult body size for appendicular morphology in *T. munificus* were examined in Hanken (1982, 1985; *T.* sp. B). Large numbers of additional specimens of this species reside in MVZ.

Thorius minydemus, n. sp.

Minute *Thorius*

Figure 5B

Holotype.—MVZ 131444, an adult male from the vicinity of La Joya (19°38′08″N, 97°09′13″W), Mexican Hwy. 140, Veracruz, México, elevation 2230 m, collected by J. F. Lynch, D. B. Wake, and T. J. Papenfuss, 24 November 1974.

Paratypes.—All from Veracruz, México: UIMNH 21816–20 (five specimens), 3 mi east of Las Vigas, collected by J. Werler, 16 January 1950.

Diagnosis.—This is among the smallest species of *Thorius.* It is distinguished from other members of the genus by the following combination of traits: small size; maxillary teeth in some adults; large, round-to-oval nostril; long legs; narrow foot with pointed, syndactylous digits; short tail; dorsal stripe; and white-spotted venter. It is most similar to *T. pennatulus,* from which it differs in having a shorter tail, larger nostril, longer legs, and maxillary teeth in some adults.

Description.—This description is based primarily on data from two adult males (MVZ 131444, the holotype, and UIMNH 21816) and one female (UIMNH 21818). Complete measurements could not be obtained from the remaining paratypes, which are poorly preserved. Although very small, this species is characterized by a relatively robust habitus; adult standard length averages 18.2 mm in males (range 17.1–19.2) and 21.3 mm in the female. The head is relatively broad; SL averages 6.6 times head width in males (range 6.4–6.8) and is 6.9 times head width in the female. Snouts are bluntly pointed in the female and more sharply pointed in males. Nostrils are relatively large and round to slightly oval; the mean ratio of major axis to minor axis equals 1.2 in males (range 1.1–1.2) and 1.3 in the female. Eyes are relatively large and protuberant; their outline extends beyond the margin of the head in dorsal view. A suborbital groove intersects the lip on each side of the head. There are 1–2 premaxillary teeth in males (mean 1.5) and three in the female. Vomerine teeth average 5.5 in males (range 5–6); there are nine in the female. A moderate number of maxillary teeth (19) are present in the female; males have few or no teeth (range 0–3). Limbs are relatively long and slender; limb interval averages 3.5 in males (range 3–4) and is 4.0 in the female. Hands and feet are very small; the hand is so short and narrow as to be barely distinguishable from the distal limb. Toes are distinct; all are free or partly free at their tips. The third finger and toe are sharply pointed and much longer than adjacent digits, which are bluntly pointed. The fourth finger and fifth toe are barely distinguishable externally. Fingers, in order of decreasing length, are 3-2-4-1; toes are 3-2-4-1-5. The tail is relatively short and stout in males; mean SL divided by tail length equals 1.07 (range 1.03–1.10). The tail is missing from the female specimen.

Coloration of paratypes appears to resemble that of the holotype (dark with a dorsal stripe and ventral white spotting), although some specimens are faded. The iris is very dark brown to black. The mental gland is relatively large and ovoid. The postiliac gland is barely perceptible.

Measurements of the holotype (in millimeters).—Head width 2.5; snout to gular fold (head length) 3.3; head depth at posterior angle of jaw 1.9; eyelid width 0.5; eyelid length 1.2; anterior rim of orbit to snout 0.9; horizontal orbit diameter 0.9; interorbital distance 1.2; distance separating external nares 0.5; major axis of nostril 0.52; minor axis of nostril 0.44; snout projection beyond mandible 0.4; snout to posterior angle of vent (standard length) 17.1; snout to anterior angle of vent 15.9; snout to forelimb 5.0; axilla to groin 9.4; limb interval 2.5; shoulder width 2.2; tail length 15.5; tail width at base 1.6; tail depth at base 1.8; forelimb length (to tip of longest toe) 3.8; hind-limb length 3.9; hand width 0.3; foot width 0.5. Numbers of teeth: premaxillary 1; maxillary 0-0; vomerine 2–3.

Coloration of the holotype (in alcohol).—The dorsal ground color is dark brown on either side of a lighter-brown dorsal band. The dark color is pinched inward over the shoulders. Ventrolateral surfaces are dark brown with many white flecks. The belly is lighter, with a network of moderate-sized white spots here and on the throat. The small mental gland is distinct.

Coloration in life.—No data.

Osteology.—No skeletal preparations are available.

Comparisons to other taxa.—Four other described species of *Thorius* have maxillary teeth: *T. aureus* and *T. smithi* from the Sierra de Juárez in northern Oaxaca, *T. schmidti* from Zoquitlán in extreme southeastern Puebla, and *T. spilogaster* from Pico de Orizaba, Ver. All except *T. smithi* exist at higher elevations and are much larger than *T. minydemus*. *Thorius smithi* is a small species, but it is found in cloud- and tropical-forest localities at much lower elevations. Lowland *T. pennatulus*, another very tiny species, has a longer, more slender tail, relatively shorter limbs, and lacks maxillary teeth in all adults. See account for *T. munificus* for a comparison between this species and the geographically close *T. minydemus*.

Habitat and range.—The type series of *T. minydemus* are from the vicinity of the village of La Joya, Ver., approximately 21 km northwest of the city of Jalapa and 3 km east of the town of Las Vigas (Fig. 1). Recorded elevation for La Joya varies between 2100 and 2250 m. Based on field notes of D. B. Wake (23 Oct. 1981), the type locality is at the lower elevational range of mixed pine-oak forest in this region. It is a marginal "cloud forest," consisting of oaks and pines growing on poor soil in an area of extensive lava flows. Bromeliads are abundant, especially in the oaks. Two additional specimens are referred to this species, KU 26140 and 26159. Both were collected by W. W. Dalquest from Las Vigas, elevation 8500 ft, 16 October 1948. Although Las Vigas is the principal locality for *T. munificus*, there is no indication from our own field experience that this species and *T. minydemus* occur in sympatry. The exact collection locality of Dalquest's specimens is unknown.

Etymology.—The species name, used as an adjective, is a conjunction of two Greek words, *minys* (small) and *demas* (body, frame), in reference to the extremely tiny adult body size of these animals, which are small even in comparison to most other *Thorius*.

Remarks.—No data are available regarding the genetic relationships of *T. minydemus* to congeners. The type locality is included in the Veracruz transect used to analyze plethodontid biogeography by Wake et al. (1992), but *T. minydemus* was then unknown and is not mentioned in that study. Paratypes are listed under *T. pennatulus* by Smith et al. (1952); all five specimens are in a poor state of preservation.

Thorius magnipes, n. sp.

Big-Footed *Thorius*

Figure 7A

Holotype.—MVZ 114514, an adult female from 4 km south of Puerto del Aire, Veracruz, México, elevation 2475 m, collected by J. F. Lynch, C. Kimmel, and J. Kezer, 21 January 1974.

Paratypes.—All from Veracruz, México: MVZ 114515–18 (four specimens), same data as the holotype; MVZ 85948–49 (two specimens), 2 mi by road south of Puerto del Aire, collected by R. W. McDiarmid, 17 January 1969; MVZ 129657–58 (two specimens), 205071, LACM 118719–21 (three specimens), 2 mi by road south of Puerto del Aire, collected by R. W. McDiarmid, D. B. Wake, and C. Ceron, 3 April 1970; MVZ 185392–96 (five specimens), 186960–62 (three specimens), 3.2 km south of Puerto del Aire, collected by J. Hanken, D. B. Wake, and J. F. Lynch, 24 July 1976; USNM

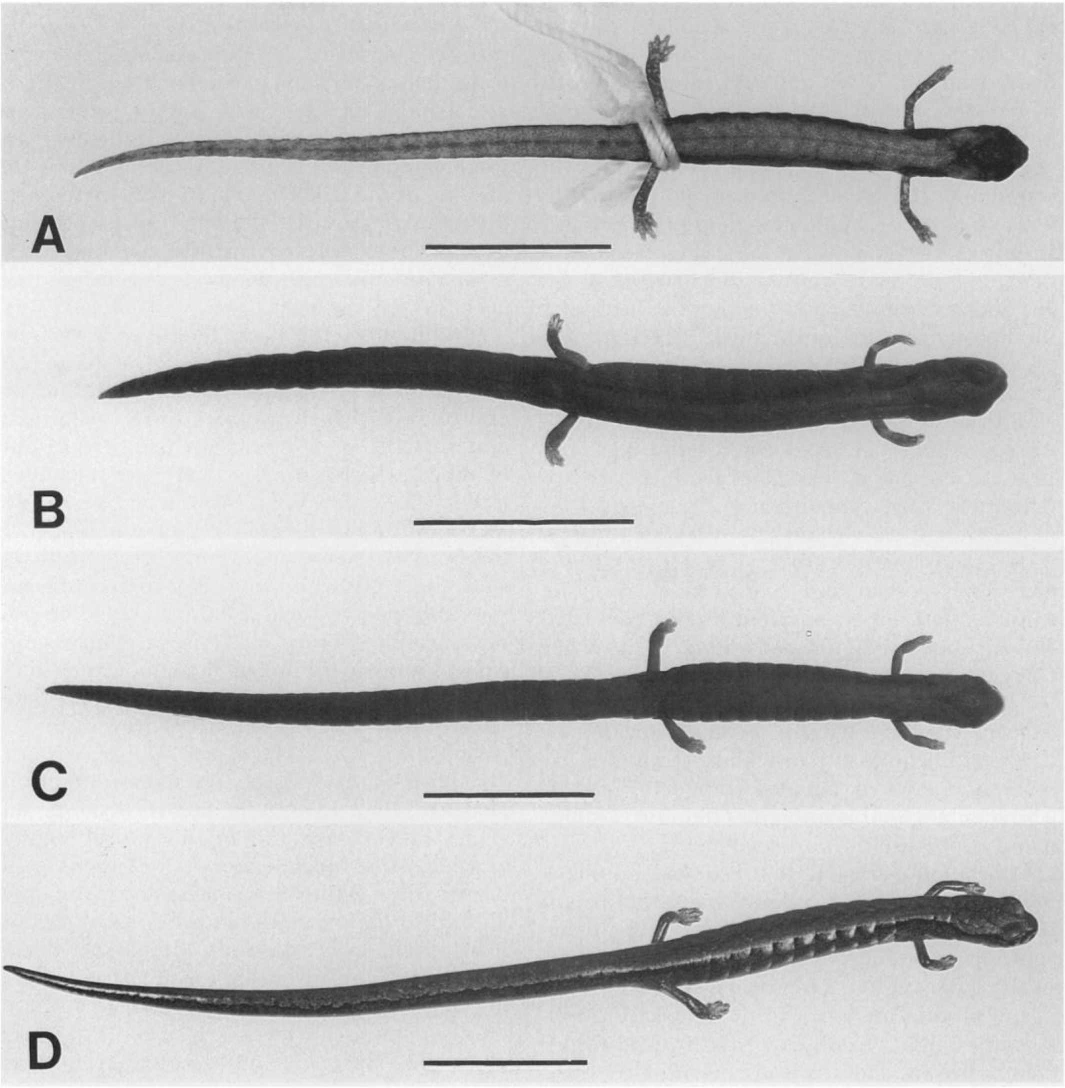

Fig. 7. Photographs of three species of *Thorius* that occur in sympatry west of Acultzingo, Ver. (A) Holotype of *T. magnipes*, MVZ 114514, an adult female. (B) *T. dubitus*, MVZ 114551, and (C) *T. troglodytes*, MVZ 114580, both adult females from 4 km south of Puerto del Aire. (D) Live *T. troglodytes*, 10–12 km east of San Felipe, collected 24 July 1976 by J. Hanken (museum number unavailable). Scale bar = 1 cm.

224769, 1.9 mi by road south of Puerto del Aire, collected by R. W. McDiarmid, 2 September 1975; MVZ 150541–42 (two specimens), 150554–55 (two specimens), 150559–60 (two specimens), 150563, 150572, 150575, MZFC 8602, 10.9 mi (Mexican Rte. 150) west of Acultzingo, then 14.8 mi east by dirt road, elevation 2640 m, collected by J. E. Cadle, 11 July 1977. Some of the above specimens are cleared and stained or have had tissue removed for protein comparisons.

Diagnosis.—This is a moderately sized species of *Thorius*, which is distinguished from other members of the genus by the following combination of traits: no maxillary teeth; white spotting in the gular region; very large, elongate nostrils; very long limbs; large hands and feet with splayed digits; laterally compressed tail; and arboreal tendencies. It is distinguished from sympatric congeners as follows: from *T. dubitus* by its larger adult body and foot size, larger nostril, and relatively longer tail; and from *T. troglodytes* by its much broader feet and larger nostril.

Description.—Adult standard length of this moderately sized species averages 23.0 mm in 12 males (range 20.6–26.9) and 21.8 mm in 16 females (range 18.2–24.4). The head is moderately wide; SL averages 7.2 times head width in males (range 6.7–7.8) and 7.3 times head width in females (range 6.5–8.4). Snouts are bluntly pointed in most adults but truncated in some males. Nostrils are very large, elongate, and prominent; the mean ratio of major axis to minor axis equals 1.4 in males (range 1.1–1.6) and 1.5 in females (range 1.3–2.3). Eyes are prominent and protrude beyond the margin of the jaw in dorsal view. A suborbital groove intersects the lip on each side of the head. There are two premaxillary teeth in each of three adult males and 4–8 (mean 6.7) vomerine teeth; these teeth could not be counted in the lone cleared-and-stained female paratype, which has a damaged head. There are no maxillary teeth. Limbs are extremely long; limb interval averages 2.4 in males (range 1.5–3) and 2.9 in females (range 2–4). Hands and feet are large and broad. Digits are widely spread and free at their tips; the three longest fingers and four longest toes have conspicuous subdigital pads. Fingers, in order of decreasing length, are 3-2-4-1; toes are 3-4-2-5-1. The tail is long and slender and typically exceeds standard length; mean SL divided by tail length equals 0.85 in males (range 0.79–0.90) and 0.90 in females (range 0.75–1.13). The mental gland is unpigmented; the postiliac gland is obscure in most specimens.

Coloration varies little from the holotype. Most specimens have a dorsal band that is narrowest over the shoulders; a tiny, light nuchal spot; light-colored parotoid glands; white spots in the gular region; and a white spot on the tip of the snout. The dorsal stripe ranges from conspicuous (light) to obscure (dark). The venter is light brown. The iris is gray brown.

Measurements of the holotype (in millimeters).—Head width 3.1; snout to gular fold (head length) 4.1; head depth at posterior angle of jaw 1.9; eyelid width 0.6; eyelid length 1.6; anterior rim of orbit to snout 1.4; horizontal orbit diameter 1.2; interorbital distance 1.8; distance separating external nares 0.7; major axis of nostril 0.64; minor axis of nostril 0.48; snout projection beyond mandible 0.4; snout to posterior angle of vent (standard length) 22.3; snout to anterior angle of vent 21.2; snout to forelimb 6.5; axilla to groin 13.4; limb interval 3.5; shoulder width 2.0; tail length 29.2; tail width at base 1.8; tail depth at base 2.0; forelimb length (to tip of longest toe) 4.5; hind-limb length 5.1; hand width 1.0; foot width 1.6. Numbers of teeth: premaxillary 0; maxillary 0-0; vomerine 4–4.

Coloration of the holotype (in alcohol).—The dorsal surface comprises a light golden-tan, broad band that extends the entire length of the body. The band is suffused with darker brown over the posterior part of the head, and there are some light brown segmental marks along the midline of the tail. The band is constricted over the shoulders but is expanded posteriorly and over the head, where it includes the moderately prominent parotoid glands. It is bordered on each side by a dark brown, wavy line that extends about two-thirds the length of the tail before breaking up. This produces a sharp contrast between the dorsal golden band and lateral surfaces, which are dark brown. Ventrolateral surfaces have numerous white spots and blotches, which sometimes interconnect. Ventral surfaces are light brown, with extensive white spotting in the gular region and especially the last third of the tail. Limbs are light brown with numerous white spots that interconnect at the limb base to form a lighter area. The postiliac gland is obscure. There are prominent white spots on the tip of the snout and along the posterior margins of the nostrils and nasolabial protuberances. The iris is gray-brown.

Coloration in life.—Based on field notes by J. Hanken (MVZ 185392–96 and 186960–62) and D. B. Wake (3 April 1970), the dorsal color is variable. Most specimens have a copper-to-gold dorsal stripe with a conspicuous herringbone pattern of darker markings, whereas others are nearly solid brownish-black with brassy flecks. The venter is relatively dark with a strong marking of ventral guanophores.

Osteology.—This description is based on data from four partial-to-complete skeletons. (The snout of MVZ 186961, a female, is badly damaged and many cranial characters cannot be scored.) This species has a poorly developed skull, especially anteriorly. Ascending processes of the premaxillary bone articulate or fuse slightly along less than one-half their length, enclosing a large to moderate internasal fontanelle (character 1, states b–c). Facial processes are well separated from the maxillary bones in ventral view in two specimens (character 2, state a), but these bones overlap in one (state b). The premaxilla bears two teeth in all three adult males (character 8, state b). The nasal bone is thin in two specimens (character 3, state b) but broader in a third (state c). It is separate from the facial process of the maxilla in two specimens (character 4, state a), but these bones articulate in two others (state b). The nasal does not contact the frontal. The prefrontal bone is slender and typically does not contact either the nasal (character 5, state b) or the facial process of the maxilla (character 6, state a). Septomaxillary bones are present on both sides in all three males (character 7, states b–c). The maxillary bone is moderately well developed but lacks teeth (character 9, state a). Vomers are distinctive: the preorbital process is very short and arranged diagonally toward the midline. There are few vomerine teeth, which are arranged diagonally toward the midline. The frontoparietal fontanelle ranges from narrow to wide, but it could not be measured accurately because the enclosing bones are extremely thin and delicate and very hard to see. Otic crests are lacking, and there is no columellar process on the operculum. The postsquamosal process is stout.

All specimens have 14 presacral vertebrae. The tibial spur is never free but instead is either attached (one specimen) or attached with crest (two specimens).

Mesopodial morphology is generalized, with relatively little variation and no asymmetry among the four specimens (Table 1). Carpal pattern I predominates in the forelimb (75% of adult carpi examined); pattern II occurs at moderate frequency (25%). All tarsi display pattern I. The sole phalangeal formula in the hand is 1-2-3-2. The modal formula in the foot is 1-2-3-3-2 (the three middle toes of MVZ 186962 are broadly spatulate); formulae could not be determined for three feet, which are malformed.

Comparisons to other taxa.—*Thorius magnipes* is sympatric with two congeneric species at the type locality. Adult *T. dubitus* are smaller and have shorter limbs, narrower feet, and a relatively shorter tail (which is less than or equal to SL). They also generally lack the light nuchal spot found in most *T. magnipes*. Adult *T. troglodytes* are slightly larger than *T. magnipes* and have shorter limbs, narrower feet, and a somewhat longer tail. Most preserved adult specimens can be assigned readily to species by using these external morphological features. Nevertheless, many subadult specimens cannot be identified with certainty without protein data (see Remarks). There also are microhabitat differences among these species, at least at the type locality: *T. magnipes* is exclusively arboreal (it has been collected on the ground elsewhere), whereas both *T. dubitus* and *T. troglodytes* are terrestrial. *Thorius arboreus*, from the Sierra de Juárez of northern Oaxaca, is the only other arboreal species in the genus. It is much smaller than *T. magnipes* and has much smaller hands and feet and a more ornate dorsal coloration.

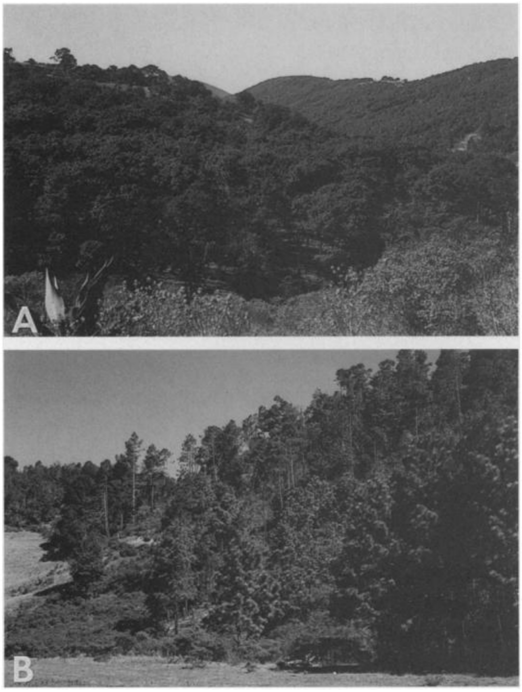

Fig. 8. Forest habitats of three species of *Thorius* from localities west of Acultzingo, Ver., February 1976. (A) Four kilometers south of Puerto del Aire, the type locality of *T. magnipes*, an arboreal species. Two terrestrial species, *T. dubitus* and *T. troglodytes*, also occur at this locality. (B) Twelve kilometers east of San Felipe, locality of *T. magnipes* and *T. troglodytes*.

Habitat and range.—*Thorius magnipes* is known from the vicinity of the type locality, which is approximately 3 km west of the village of Acultzingo, Ver., and from near the village of San Felipe, Pue., several kilometers to the southeast (e.g., MVZ 150541–42; Figs. 1, 8). All known localities lie within Veracruz but are very close to the border with Puebla. The predominant vegetation type is pine-oak cloud forest, which is characteristic of these and other localities that lie along the southeastern edge of the Mexican plateau. Recorded elevations range from 2475–2800 m. All specimens from the type locality were collected in arboreal microhabitats (e.g., bromeliad leaf axils). Specimens from near San Felipe were taken on the ground under rocks and litter and inside piles of wood chips (field notes of J. E. Cadle, 11 July 1977). See description of *T. troglodytes* for additional notes on habitat.

Etymology.—The species name is a conjunction of two Latin words, *magnus* (great) and *pes* (a foot), in reference to the very large feet and limbs, which readily distinguish this species from all congeners.

Remarks.—Genetic relationships of *T. magnipes* to congeners were examined using protein electrophoresis by Hanken (1980, 1983a; population 12, *T.* sp. A). Levels of genetic variability among populations of *T. magnipes* are unknown. Evolutionary consequences of miniaturization of adult body size for appendicular morphology in *T. magnipes* were examined by Hanken (1985; *T.* sp. A).

Status of Other Species of *Thorius* in Puebla and Veracruz

Thorius dubitus (Taylor, 1941)

Figure 7B

Thorius dubitus Taylor, 1941:108. Holotype: FMNH 100039 (formerly EHT-HMS 17751): "summit of mountain about two miles south of Acultzingo, Veracruz (near Puebla line)," México.

Reference sample.—All from Veracruz, México: MVZ 85725, 2 mi by dirt road south of Puerto del Aire; MVZ 114361, 114551, 114556–57 (two specimens), 114562, 114589–91 (three specimens), 114600–114601 (two specimens), 4 km south of Puerto del Aire; MVZ 182625, 182631–33 (three specimens), 182635–36 (two specimens), 182639–40 (two specimens), 185397, 186778, 3.2 km south of Mexican Hwy. 150 at Puerto del Aire. Some of the above specimens are cleared and stained or have had tissue removed for protein comparisons.

Diagnosis.—This is a small, robust species of *Thorius*, which has a distinct, greenish (in life) dorsal stripe; relatively large, elongate nostrils; moderately long limbs; and a relatively short, stocky tail. It is distinguished from sympatric associates as follows: from *T. magnipes* by its duller dorsal coloration, smaller size, shorter limbs and much smaller hands and feet; and from *T. troglodytes* by its smaller adult body size, shorter and stockier tail, relatively larger nostril, dorsal gland openings of homogeneous size, and greenish (vs brick red) dorsal stripe. It is distinguished from all other species of *Thorius* by a combination of allozymic, skeletal, and external morphological traits (Hanken, 1982, 1983a, 1984).

Description.—Adult standard length of this small species averages 19.8 mm in 10 males (range 18.2–21.7) and 20.6 mm in 10 females (range 18.1–22.0). The head is moderately wide; SL averages 7.2 times head width in males (range 6.2–8.7) and 7.6 times head width in females (range 7.0–8.3). Snouts are rounded to bluntly pointed. Nostrils are relatively large and elongate; the mean ratio of major axis to minor axis is 1.4 in males (range 1.2–1.6) and 1.5 in females (range 1.2–1.8). The eyes are somewhat protuberant and extend beyond the margin of the jaw in dorsal view, especially in males. A suborbital groove intersects the lip on each side of the head. The single cleared-and-stained specimen, a male, has two premaxillary teeth, six vomerine teeth, and no maxillary teeth. Limbs are relatively long; limb interval averages 3.5 in males (range 2.5–4) and 4.6 in females (range 4–5). Feet are relatively well developed. The middle two fingers and the middle three toes are much longer than the outer digits. Adjacent digits are free from one another only at their tips, which are rounded except in some smaller individuals in which they are slightly pointed. There are poorly developed subterminal pads on some of the larger specimens. The tail is relatively short and only rarely exceeds standard length; mean SL divided by tail length equals 1.23 in males (range 1.01–1.69) and 1.16 in females (range 0.99–1.32). The tail is round (in cross-section) in smaller specimens, and quadrangular to somewhat laterally compressed in larger specimens.

Coloration in alcohol.—Based on MVZ 114562, this is a dark brownish-black animal with a lighter dorsal band. The dorsal band originates behind the eyes and extends to the tip of the tail. It is very broad over the posterior portion of the head (including the parotoid glands), is constricted over the shoulders, expands rapidly on the second costal interspace behind the forelimb, and then constricts again posteriorly. There frequently are dark chevrons in the upper parts of the costal grooves in the middle of the back. The dorsal band is bordered laterally by a dark, wavy line. Below the wavy line, the flanks of the body and tail are dark blackish-brown. The dark-brown venter is extensively marked with small whitish spots, especially in the gular and sternal regions. The spots extend upward along the flanks of the body where they coalesce, so that the ventrolateral margins of the trunk have an almost continuous whitish stripe. The venter of the tail is also spotted extensively, even more so than the gular region. Limbs are dark brown with a few light spots. The iris is lead gray.

Margins of the dorsal band vary from wavy to straight in other specimens, but the band is always bordered by a dark line and is usually pinched over the shoulders. Nearly all specimens have the extensive ventral spotting, which coalesces to form a ventrolateral stripe along each flank.

Coloration in life.—Based on field notes by J. Hanken for MVZ 182624–32, most specimens have a greenish dorsal stripe.

Osteology.—This description is based on data from a single complete skeleton (MVZ 186776). The skeleton is weakly ossified; the skull is very poorly developed. Ascending processes of the premaxillary bone articulate along part of their length and then diverge (character 1, state b). The premaxillary is separated from the maxillary bone by a small gap (character 2, state a). The premaxillary bears two teeth (character 8, state b), which are long and hooked. The nasal bone is thin and rodlike (character 3, state b) and separate from the maxillary (character 4, state a). Prefrontals are slender, rodlike bones lying immediately anterior to the eye. They are separate from both the nasal (character 5, state b) and the maxillary (character 6, state a). There are no septomaxillary bones (character 7, state a). Maxillaries are slender and lack teeth (character 9, state a). Vomers are small but moderately well developed; there are seven vomerine teeth arranged in a short row. The preorbital process is represented on one side by a tiny projection that bears a single tooth and on the other side by a somewhat longer process that bears two teeth. The frontoparietal fontanelle is very large, but it cannot be measured accurately because surrounding bones are very thin and faintly stained. Otic crests are absent, and there is no columellar process on the operculum. The postsquamosal process is present.

All specimens have 14 presacral vertebrae. Limbs are relatively well developed; the longest digits on each hand and foot have well-developed terminal phalanges. The tibial spur is represented by a low crest on each side. Hyobranchial and mesopodial elements are not mineralized.

Mesopodial morphology is generalized but variable, including right-left asymmetry of both fore- and hind limbs (Table 1). The two carpi display patterns I and II; the two tarsi display patterns I and III. Hand phalangeal formulae are 1-2-3-2 and 1-2-3-1. The right foot has only four toes (1-2-3-3), and the outermost toe is very wide. The left foot has five toes (1-2-3-3-1), but toes 4 and 5 share a single metatarsal.

Habitat and range.—*Thorius dubitus* is known only from the vicinity of the type locality near Puerto del Aire, which is approximately 3 km west of the village of Acultzingo, Ver., very close to the Puebla border (Fig. 1, 8A). Recorded elevations range from 2380–2475 m. *Thorius dubitus* is an exclusively terrestrial species; see description of *T. magnipes* for habitat notes.

Remarks.—*Thorius dubitus* is sympatric with at least two congeners in the vicinity of Puerto del Aire: *T. troglodytes*, another exclusively terrestrial species; and *T. magnipes*, which is found both on the ground and in arboreal microhabitats. A third sympatric species may also be present, as a single specimen of *T. spilogaster* (KU 106818) is recorded from this locality. We have, however, examined hundreds of specimens of *Thorius* from this locality and others nearby and failed to identify other specimens of *T. spilogaster*, locality data for this specimen may be in error. Sympatry of three species of *Thorius* is also known from the Sierra de Juárez in northern Oaxaca (Hanken and Wake, 1994); sympatry involving four congeners has not been reported previously.

Genetic relationships of *T. dubitus* to congeners were examined using protein electrophoresis by Hanken (1980, 1983a). Levels of genetic variability among populations of *T. dubitus* are unknown.

Thorius troglodytes (Taylor, 1941)

Figure 7C–D

Thorius troglodytes Taylor, 1941:110. Holotype: FMNH 100112 (formerly EHT-HMS 17791): "along old road on mountains about two miles south of Acultzingo, Veracruz," México.

Reference sample.—Veracruz, México: MVZ 85698–700 (three specimens), 85716, 85723, 2 mi by dirt road south of Puerto del Aire; MVZ 106754, 106759, 106762, Puerto del Aire; MVZ 114521, 114528, 114534–35 (two specimens), 114537, 114540, 114546, 114554, 114559, 114580, 114582, 114586, 4 km south Puerto del Aire. Puebla, México: MVZ 186939–43 (five specimens), 12 km E of San Felipe; MVZ 186944–57 (14 specimens), 10 km E of San Felipe; MVZ 186959, 7.4 mi east-southeast of San Felipe. Some of the above specimens are cleared and stained or have had tissue removed for protein comparisons.

Diagnosis.—This is a large species of *Thorius* with a long tail and an elongate nostril. It is distinguished from sympatric associates as follows: from *T. magnipes* by its more robust habitus and prominent parotoid glands; and from *T. dubitus* by its larger size, longer and more slender tail, dorsal gland openings of homogeneous size, and darker coloration. It is distinguished from all other species of *Thorius* by a combination of allozymic, skeletal, and external morphological traits (Hanken, 1982, 1983a, 1984).

Description.—Adult standard length of this large and robust species averages 23.5 mm in 10 males (range 21.2–24.9) and 24.8 mm in 10 females (range 22.8–27.4). The head is moderately wide, but there is no conspicuous constriction between the head and trunk; SL averages 7.4 times head width in males (range 6.8–7.9) and 7.6 times head width in females (range 7.1–8.2). Snouts are bluntly pointed. Nostrils are relatively small and oval; the mean ratio of major axis to minor axis is 1.6 in males (range 1.4–1.7) and 1.5 in females (range 1.3–1.8). The eyes do not protrude 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 males (mean 1.9) and 0–5 in females (mean 2.6). Vomerine teeth average 5.7 in males (range 3–8) and 6.0 in females (range 5–7). There are no maxillary teeth. Limbs are relatively short; limb interval averages 4.9 in males (range 4.5–5.5) and 5.8 in females (range 5.5–6.5). Feet are relatively narrow. The two middle fingers and three middle toes are much longer than the outer digits; the longest digits have discrete subterminal pads. Digit tips are bluntly rounded; only the tips of the longest digits are free (unwebbed). The tail is rounded in cross-section and relatively long, typically exceeding standard length; mean SL divided by tail length equals 0.82 in males (range 0.76–0.93) and 0.81 in females (range 0.73–0.95). There is a prominent parotoid gland.

Coloration in alcohol.—Based on MVZ 114521, a broad, light-brown dorsal band extends from the nuchal groove to the base of the tail, where it becomes diffuse. The rest of the tail is a dark brownish-black, as are the dorsum and flanks of the head and body, especially anterior to the eyes. The region below and behind the eye and anterior parts of the flanks have a few widely scattered, light-brown spots. The venter is light brown with some darker areas along the midline. The gular region is especially light with some faint whitish spots. Margins of the lips are much lighter. Limbs are light brown with a few scattered white spots, some of which coalesce. The iris is black; the lower eyelid is very light.

Coloration is remarkably uniform in this species; most specimens vary little from the above account. The overall impression is of a dark, brownish animal, with some specimens being almost uniformly dark brownish-black and others having a nearly tan stripe; the dorsal band is always lighter than lateral surfaces. There is variation in the degree to which the band contrasts or blends in with the lateral surfaces.

Coloration in life.—Based on field notes by J. Hanken for MVZ 183141–62 and 186944–57 (10 km east San Felipe), there is a variably colored dorsal stripe ranging from olive, to brick, to tan. The venter is dark but somewhat translucent, with fine, white speckling that is more abundant ventrolaterally than along the midline. For MVZ 183211–16 (3.2 km south Puerto del Aire), the dorsal stripe is brick-red (most specimens) or greenish.

Osteology.—This description is based on data from 20 partial-to-complete skeletons. This species has a relatively well-developed, well-ossified skeleton, including the skull. The premaxillary bone is separate from the maxillary in all males (character 2, state a), but the two elements overlap or articulate in nearly all females (states b–d). Ascending processes of the premaxilla are strongly developed; they typically remain separate from one another (character 1, state a), although they barely articulate in five specimens (state b) and fuse along less than one-half their length in two males (state c). The premaxillary bears 1–5 teeth in all specimens (character 8, state b) except one female, which lacks teeth (state a). The nasal bone is broad and extends over much of the cartilaginous nasal capsule (character 3, state c). It articulates with the ascending process of the maxillary in the majority of specimens (character 4, state b), but these elements are separate in most others (state a); they are fused on one side of a single specimen (state c). Prefrontal bones are present, well developed, and typically separate from the nasals (character 5, state b), although these two elements are in contact in a few specimens (state c). The prefrontal is separate from the maxillary in all specimens (character 6, state a). Septomaxillary bones are absent in most females (character 7, state a) but present on one or both sides in most males (states b and c). Maxillaries are elongate but lack teeth (character 9, state a). Vomers are well developed; the preorbital process is variable—distinct and rodlike in some specimens but very short in others. There are 3–8 vomerine teeth, which are arranged in short rows extending to the tip of the preorbital process. The frontoparietal fontanelle is enormous; its breadth equals 0.42–0.61, mean 0.52, times the maximum skull width across the parietals. In larger specimens, there is a tiny otic crest behind the junction of the horizontal and anterior semicircular canals. There is no columellar process on the operculum; the postsquamosal process is present and well developed.

All specimens have 14 presacral vertebrae. The tibial spur ranges from well developed and free in most specimens (16 of 20), to attached (three), to crest (one). At least some mesopodials are mineralized in many specimens. The hyobranchial apparatus typically is unmineralized.

Mesopodial morphology is generalized in most specimens, but several variants occur at very low frequencies (Table 1). Carpal pattern I predominates in the forelimb (92% of carpi examined), but three additional patterns—II, III, and IX—each occur in a single limb (3%). Pattern IX (distal carpal 4 separate from centrale) is unique to *T. troglodytes*. Tarsal pattern I predominates in the hind limb (92%); pattern V occurs at low frequency (8%). Mesopodial asymmetry is rare. Modal phalangeal formulae are 1-2-3-2 (hand) and 1-2-3-3-2 (foot), but some hands and feet have fewer elements in one or more digits.

Habitat and range.—*Thorius troglodytes* is known from the vicinity of the type locality near Puerto del Aire, which is approximately 3 km west of the village of Acultzingo, Ver., and from localities 10–12 km east of the village of San Felipe, Pue., southeast of the type locality (Figs. 1, 8). All known localities lie within Veracruz but are very close to the border with Puebla. Recorded elevations range from 2380–2800 m. It is an exclusively terrestrial species. According to field notes by J. F. Lynch (21 Jan. 1974), the locality at 4 km south of Puerto del Aire is a pine-oak forest; salamanders were abundant under wood chips as well as under and inside logs, under the bark of logs, and under rocks. According to J. Hanken (2 and 6 Feb. 1976), the locality at 12 km east of San Felipe comprised steep canyon slopes adjacent to cleared fields. The slopes were covered with mixed pine and chaparral vegetation, whereas salamanders were taken from under fallen logs, rocks, and wood chips. There was a more mesic pine-oak forest at 10 km east of San Felipe, where salamanders were collected from under fallen logs and among the soil of the road bank. See the description of *T. magnipes* for additional habitat notes.

Remarks.—*Thorius troglodytes* is sympatric with at least two congeners in the vicinity of Puerto del Aire: *T. dubitus*, another terrestrial species; and *T. magnipes*, which is found both on the ground and in arboreal microhabitats. (See accounts for *T. spilogaster* and *T. dubitus* for discussion of a possible third sympatric congener at Puerto del Aire.) *Thorius troglodytes* is the most abundant of these species. Only *T. magnipes* has been taken with *T. troglodytes* at the nearby San Felipe localities. Genetic variation in *T. troglodytes* and the species' relationships to congeners are examined using protein electrophoresis by Hanken (1980, 1983a). The three population samples of *T. troglodytes* surveyed genetically are very similar, even though adults from the San Felipe localities are considerably larger (mean SL equals 27.2 for females, range 25.3–28.9; and 24.4 for males, range 22.0–25.9) than those from the type locality at Puerto del Aire. Evolutionary consequences of miniaturization of adult body size for appendicular morphology in *T. troglodytes* are examined in Hanken (1982, 1985).

Thorius schmidti (Gehlbach, 1959)

Figure 9

Thorius schmidti Gehlbach, 1959:203. Holotype: USNM 140295: 4 mi west of Zoquitlán, Puebla, México, at 8400 ft.
Thorius maxillabrochus: Gehlbach, 1959:205.
Thorius schmidti: Hanken, 1983a:1051–1073.
Thorius schmidti: Frost, 1985:605.

Reference sample.—All from Puebla, México: MVZ 183059, 183066, 183070–77 (eight specimens), 183079–82 (four specimens), 186919–34 (16 specimens), 9 km by road west of Zoquitlán; MVZ 183084, 186935–38 (four specimens), 10 km by road west of Zoquitlán; MVZ 196085–86 (two specimens), 14.4–11.0 km by road southwest of Zoquitlán. Some of the above specimens are cleared and stained.

Diagnosis.—This is a moderately large, sexually dimorphic species of *Thorius* with a relatively short tail. It is distinguished from other species of *Thorius* with maxillary teeth as follows: from *T. aureus* by its smaller size, darker coloration, larger and more elongate nostril, and larger frontoparietal fontanelle; from *T. smithi* by its larger size, shorter tail, and more elongate nostril; from *T. spilogaster* by its larger size, larger and more elongate nostril, larger hands and feet with more discrete digits and rounded rather than pointed digit tips, less conspicuous ven-

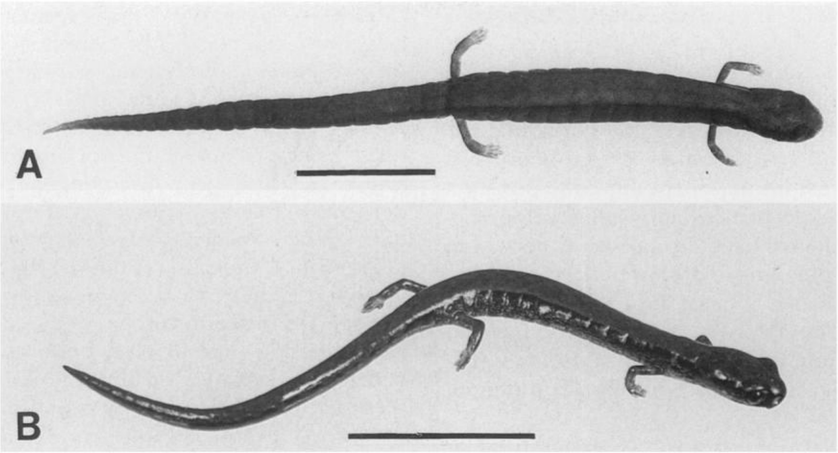

Fig. 9. Photographs of *Thorius schmidti* from 9–10 km west of Zoquitlán, Pue. (A) MVZ 183074, an adult female. (B) Live specimen, collected 16 February 1976 by J. Hanken (museum number unavailable). Scale bar = 1 cm.

tral spotting, and by substantial protein differences; and from *T. minydemus* by its larger size and relatively shorter limbs, more elongate nostril, and greater number of maxillary teeth. It is distinguished from all other species of *Thorius* by a combination of allozymic, skeletal, and external morphological traits (Hanken, 1982, 1983a, 1984).

Description.—Adult standard length of this moderately large species averages 22.5 mm in eight males (range 19.0–24.5) and 25.5 mm in nine females (range 21.8–29.5). The head is of moderate width; SL averages 7.2 times head width in males (range 6.7–7.9) and 7.5 times head width in females (range 7.1–7.9). Snouts are rounded to bluntly pointed. Nostrils are large and elongate; the mean ratio of major axis to minor axis is 1.3 in males (range 1.1–1.3) and 1.5 in females (range 1.2–1.9). The eyes are moderately protuberant and extend only slightly beyond the margin of the jaw in ventral view. A suborbital groove intersects the lip on each side of the head. There are 1–2 premaxillary teeth in males (mean 1.9) and 4–7 in females (mean 5.4). Vomerine teeth average 6.5 in males (range 4–10) and 8.0 in females (range 4–10). Maxillary teeth average 13.9 in males (range 7–19) and 22.6 in females (range 17–29). Limbs are of moderate length; limb interval averages 4.4 in males (range 3.5–5.5) and 5.2 in females (range 4–6). Hands and feet of adults are moderately large, with well-defined, rounded digital tips on the two (hand) and three (feet) longest digits. The tail is relatively short and stout; mean SL divided by tail length equals 1.12 in six females (range 1.00–1.21) and 1.16 in the only male reference specimen with an intact tail. The mental gland is large and raised, longer than broad, and characteristically unpigmented; the parotoid gland is discrete.

Coloration in alcohol.—All specimens have a tan-to-brown dorsal stripe that is bordered laterally by a dark line of pigment. Many have a herringbone pattern down the length of the stripe. The venter is generally gray to gray-brown, and lighter than the dorsum. There is extensive white flecking ventrally, especially in the gular area, which often extends onto the ventrolateral margins of the belly.

Coloration in life.—No data.

Osteology.–This description is based on data from 20 partial-to-complete skeletons. This species has a well-ossified skeleton. The skull is well articulated, and there is considerable sexual dimorphism. Ascending processes of the premaxillary bone are separate or barely articulate in most specimens (character 1, states a–b), but they are fused along less than one-half their length in a few others (state c). The premaxillary is usually separate from the maxillary in ventral view (character 2, state a), but the two bones overlap or articulate in a few specimens (states b–d). The premaxillary bears teeth in all adults (character 8, state b). The nasal bone is broadly expanded in all females and most males (character 3, state c) but slender in a few males (state b). It fails to overlap the maxillary in all males but one (character 4, state a), whereas in every female but one it overlaps the maxillary and in one female the elements are fused

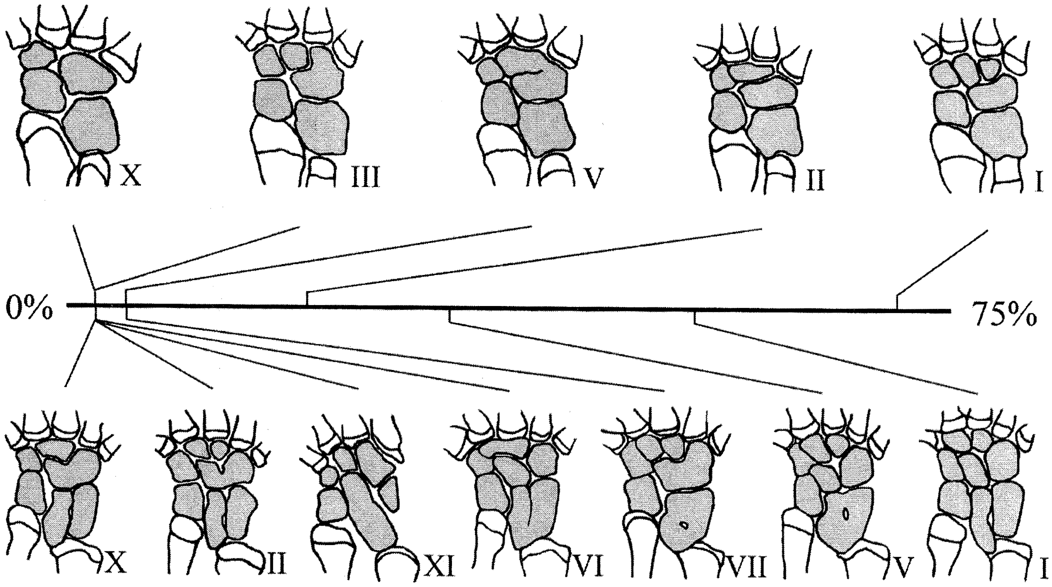

Fig. 10. Mesopodial variation in 20 adult *Thorius schmidti* from 9–10 km west of Zoquitlán, Pue. Relative frequencies of the 12 carpal- and tarsal-pattern variants are depicted above and below the horizontal line, respectively. Most of the patterns occur in at least one other species of *Thorius* in Veracruz and Puebla (see text). A few rare variants found in these species, but not observed in *T. schmidti*, are not illustrated.

(states b–c). The prefrontal bone is separate from the nasal in all males but in only one female (character 5, state b). It articulates with the nasal in most females, and in two specimens the bones are fused on one side (states c–d). The prefrontal is separate from the maxillary in all males and most females (character 6, state a), but the two elements overlap in three females (state b). Septomaxillary bones are relatively well developed on both sides of a single female (character 7, state c), but they are absent in all other specimens. Maxillaries are stout and bear numerous, relatively large teeth (character 9, state b). The vomer is well developed, although the preorbital process is short, stout, and blunt-tipped. It bears teeth arranged in a short, curved row. The frontoparietal fontanelle is broad, especially in males. Its breadth equals 0.38–0.49, mean 0.42, times the maximum skull width across the parietals in females; 0.43–0.58, mean 0.48, in males. Otic crests are low, and there is no columellar process on the operculum. The postsquamosal process is well developed.

All specimens have 14 presacral vertebrae; there is variation in the number of presacral ribs. The tibial spur ranges from large, free, and distinct (four of 20 specimens), to distinct but attached (14 specimens), to crest (two specimens). Mineralization is common in mesopodial cartilages, but typically absent in hyobranchial elements.

Mesopodial morphology is extremely variable; a total of 12 different carpal or tarsal arrangements coexist in a single sample of 20 adults drawn from two adjacent populations (Fig. 10; Table 1). Carpal pattern I predominates in the forelimb (70% of carpi examined), but II also is common (20%). Three patterns—III, V, and X—occur in one or two limbs each (2.5–5%). Pattern X (like III but with fused centrale 1 and distal carpal 1–2) is unique to *T. schmidti* and is reported here for the first time. Tarsal pattern I predominates in the hind limb (52.5%), but V also is common (32.5%). Five patterns—II, VI, VII, X, and XI—occur in one or two limbs each (2.5–5%). Patterns X (like VIII but with separate intermedium and fibulare) and XI (like IV but with distal tarsals 3 and 4 fused and distal tarsal 5 absent) are unique to *T. schmidti* and are reported here for the first time. Asymmetry is common; nearly one-half of the specimens have a different carpal or tarsal pattern on each side. Some specimens display the primitive phalangeal formulae, 1-2-3-2 (hand) and 1-2-3-3-2 (foot), but there is extensive variation involving reduction in the numbers of phalanges and digits, especially in the hind limb.

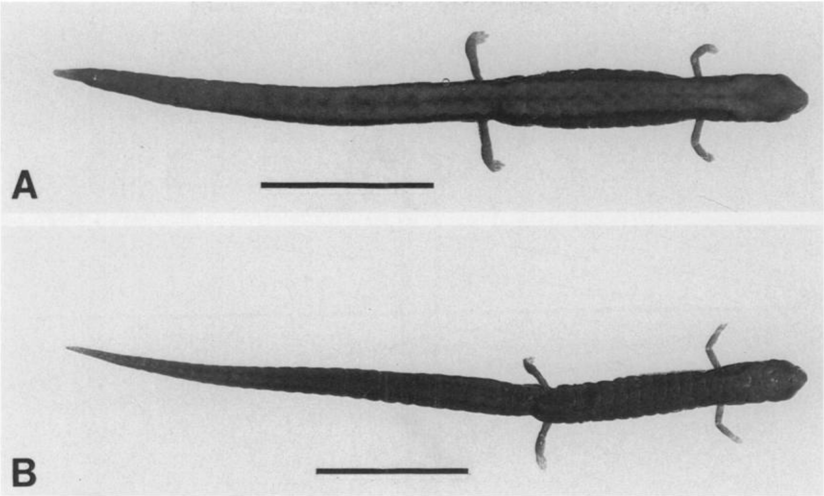

Fig. 11. Photographs of two species of *Thorius* from montane-lowland Veracruz. (A) *Thorius pennatulus*, MVZ 85834, an adult female from 1.4 mi southwest of Huatusco. (B) *Thorius narismagnus*, MVZ 128928, an adult male from Volcán San Martín. Scale bar = 1 cm.

Habitat and range.—*Thorius schmidti* is known only from the type locality and adjacent forest localities west of the village of Zoquitlán in southern Puebla (Fig. 1). The recorded elevational range is 2560–2760 m. It is an exclusively terrestrial species; according to field notes by J. Hanken (18 Feb. 1976), specimens from 9 km west of Zoquitlán were collected on the ground of a steep, shaded, east-facing slope within dense pine-oak forest with abundant litter of pine needles. Similar habitat conditions are reported by Gehlbach and Collette (1957).

Remarks.—Two sympatric species of *Thorius* were originally described from near Zoquitlán, *T. schmidti* and *T. maxillabrochus* (Gehlbach, 1959). Subsequently, Gehlbach came to doubt the existence of more than one species from this locality (letter to R. C. Stebbins, 6 July 1966). This latter suggestion is supported by many lines of evidence. First, only one species was detected in the electrophoretic survey of samples from two localities near Zoquitlán by Hanken (1980, 1983a). Second, because few species of *Thorius* have maxillary teeth, the probability of finding two sympatric species with maxillary teeth is low. Finally, the original description was based on perceived differences in nostril size and shape, which are subject to considerable intraspecific and intrapopulational variation. We believe that only one species exists at Zoquitlán. Because the name *schmidti* is favored in recent usage (Hanken, 1983a; Hanken and Wake, 1994), we regard the name *maxillabrochus* as a subjective junior synonym.

Genetic variation in *T. schmidti* and the species' relationships to congeners are examined using protein electrophoresis by Hanken (1980, 1983a; populations 10–11). Analysis of morphological consequences of miniaturization of adult body size in *T. schmidti* in Hanken (1982, 1984) corresponds instead to *T. spilogaster*.

Thorius pennatulus (Cope, 1869)

Figure 11A

Thorius pennatribus: Anon., 1869:222.
Thorius pennatulus Cope, 1869:111. Holotype: USNM 6341, the largest of six specimens with this number, now lost: "Orizava," México.
Oedipus pennatulus: Dunn, 1922:5.
Oedipus pennatulus: Dunn, 1926:374.
Thorius pennatulus: Taylor, 1941:107. USNM 111017 designated as neotype.
Thorius pennatulus pennatulus: Shannon and Werler, 1955:364.
Thorius pennatulus: Malnate, 1971:348. ANSP 1269 provisionally included as surviving syntype.
Thorius pennatulus: Smith et al., 1988:210.
Thorius pennatulus: Anon., 1990:168.

Reference sample.—All from Veracruz, México: MVZ 85729–30 (two specimens), 85732, 85737, 85739, 85741, 85750, 85770, 85778, 85795, 85812, 85819–21 (three specimens), 85827–28 (two specimens); 106586, 106590, 150589, 186903–906 (four specimens), 222385, 222387, 222389–90 (two specimens), 222392, Cuautlapan; MVZ 85832, 85834–36 (three specimens), 85840, 85842, 1.4 mi by road southwest of Huatusco. Some of the above specimens are cleared and stained or have had tissue removed for protein comparisons.

Diagnosis.—This is a tiny species of *Thorius* with a small, round nostril, relatively long limbs with small feet, and a long tail. It is distinguished from *T. narismagnus* by its relatively shorter tail, lighter coloration, and protein differences; from *T. minydemus* by its longer tail, relatively shorter limbs, and absence of maxillary teeth; and from *T. insperatus* by its somewhat smaller and rounder nostrils. It is distinguished from all other species of *Thorius* by a combination of allozymic, skeletal, and external morphological traits (Hanken, 1982, 1983a, 1984).

Description.—Adult standard length of this tiny species averages 17.9 mm in 12 males (range 15.5–19.3) and 18.5 mm in 10 females (range 16.9–21.4). The head is relatively broad; SL averages 7.0 times head width in males (range 6.2–7.4) and 7.1 times head width in females (range 6.5–7.7). Snouts are short and pointed. Nostrils are round to slightly oval; the mean ratio of major axis to minor axis is 1.06 in males (range 1.00–1.11) and 1.03 in females (range 1.00–1.11). Nostrils are relatively small in both sexes but slightly larger in males (mean length of major axis 0.41 mm) than in females (0.39 mm), despite the males' smaller average body size. The eyes, though small, are prominent and extend beyond the margin of the head in ventral view. A suborbital groove intersects the lip on each side of the head. There are 1–2 premaxillary teeth in males (mean 1.2) and 2–4 teeth in females (mean 2.8). Vomerine teeth average 6.4 in males (range 5–8) and 6.2 in females (range 6–7). There are no maxillary teeth. Limbs are relatively long; limb interval averages 4.3 in males (range 3–5.5) and 4.6 in females (range 3.5–5.5). Hands and feet are narrow; digits are short and the longest ones are pointed. The tail is relatively long, typically much longer than standard length; mean SL divided by tail length equals 0.83 in males (range 0.60–1.08) and 0.80 in females (range 0.70–0.96). The parotoid gland is discrete, but the mental gland is indistinct, even in large adult males. In terms of external characters, this is among the least sexually dimorphic of any species in the genus.

Coloration in alcohol.—Based on MVZ 85834, a broad, tan to golden-brown dorsal band extends posteriorly from the back of the head nearly to the tip of the tail. The band is bordered by especially dark pigment, which makes the band stand out. The lateral ground color is dark brown, which grades into the light-brown venter. There is extensive white spotting ventrolaterally and ventrally. The spots become relatively large near the forelimb insertions and anteriorly onto the gular region; the largest spots are slightly smaller than the diameter of the nostril. Limbs are light brown dorsally. The head is medium-tan dorsally; lateral portions are brown except near the tip of the snout, which becomes light gray. The iris is gray-black.

Coloration in life.—Based on field notes by J. Hanken for MVZ 186902, there is a brownish dorsal stripe with a fine, black-and-brown herringbone pattern. The venter is dark with fine white flecking.

Osteology.—This description is based on data from 12 partial-to-complete skeletons. The skull is weakly developed. Bony elements are small and slender, especially anteriorly, yet those elements tend to be well ossified. The very slender ascending processes of the premaxillary bone arise separately and remain separate for their entire lengths (character 1, state a), except in one specimen in which they barely articulate anterior to the internasal fontanelle (state b). The premaxilla is separate from the maxillary bone on either side in nearly all specimens (character 2, state a); the two elements overlap slightly but do not articulate on one or both sides in two specimens (state b). There are 2–4 (mean 2.8) premaxillary teeth in females and 1–2 (mean 1.2) teeth in males (character 8, state b). The nasals in most specimens are thin, rodlike bones located far posteriorly on the cartilaginous nasal capsule (character 3, state b); they are broad on one or both sides in a few specimens (state c). The nasal and maxilla are separate on both sides in most specimens (character 4, state a); they are fused (state c) or articulate (state b) on one side in two specimens. In some specimens (e.g., MVZ 85729), the nasal sends a process posteriad, around the nasolacrimal foramen. In other specimens, the foramen pierces the facial process of the maxilla. Most specimens have the prefrontal bone separate from or barely articulating with the nasal (character 5, states b–c, respectively). These two bones are fused on both sides of one specimen and on one side of two others (state d); the prefrontal is absent from the other side of one of the latter two specimens (state a). In one specimen, the prefrontal on one side is divided in two. The prefrontal and maxilla are separate in all specimens (character

6, state a). Septomaxillary bones are present and well developed on both sides in one specimen (character 7, state c). A very small (barely visible) septomaxilla is present on both sides of one specimen and on one side in three others (state b). Maxillary bones, while slender, often have a well-developed facial process and lack teeth (character 9, state a). Vomers are relatively well developed with a small, toothed preorbital process. There are 6–7 vomerine teeth in females (mean 6.2) and 5–8 in males (mean 6.4) and they are arranged in a short row.

Paired frontal bones articulate medially in several specimens; the parietal fontanelle is of small-to-moderate size (its breadth equals 0.35–0.49, mean 0.44, times the maximum skull width across the parietals in females; 0.45–0.59, mean 0.53, in males). There is a well-developed ventrolateral parietal tab, but the parietal fails to reach the occipital arch posteriorly. Otic crests are absent and there is no columellar process on the operculum. The postsquamosal process is well developed.

All specimens but one have 14 presacral vertebrae; there is variation in the number of presacral ribs. MVZ 222389 has only 13 presacral vertebrae. The first presacral vertebra is fused to the atlas and bears a rib on one side; a free-floating rib is present on the other side. One vertebra appears to be missing entirely. The tibial spur is free in one specimen; in others the spur is either attached or reduced to a low crest. Hyobranchial elements are mineralized in some specimens, especially the second ceratobranchials and, less commonly, the proximal portion of the epibranchial. An occasional specimen (e.g., MVZ 85840) has additional mineralization of the nasal capsular cartilage dorsal to the premaxillary bones.

Mesopodial morphology is generalized in the forelimb but distinctive in the hind limb. The modal carpal pattern is II (54%), but pattern I is also common (46%). Pattern III, although not represented in the above reference sample, is present in one of 37 carpi scored from an additional 19 specimens from Cuautlapan (Hanken, unpubl. data), for an overall frequency of less than 2%. Pattern VII predominates in the hind limb (64%); pattern VIII occurs at a moderate frequency (36%). Although neither tarsal pattern is unique to *T. pennatulus*, each is rare or absent in most other species. Presence of both patterns at moderate to high frequencies is a distinctive feature of *T. pennatulus* shared only with *T. arboreus* from Oaxaca (Hanken and Wake, 1994). Asymmetry is common; nearly two-thirds of the specimens examined have a different carpal or tarsal pattern on each side. Modal phalangeal formulae are 1-2-3-2 (hand) and 1-2-3-3-2 (foot). Some specimens have one fewer phalanx in the outermost digit (i.e., 1-2-3-1, 1-2-3-3-1).

Habitat and range.—*Thorius pennatulus* is known from a number of forest localities in lowland Veracruz (Fig. 1). Elevations range from about 1000 m between Orizaba and Cordoba, to almost 2000 m near Soledad Atzompa (KU 154630–33). It is an exclusively terrestrial species; according to field notes by D. Wake (3 April 1970) and J. Hanken (31 Jan. 1976), specimens in Cuautlapan were found under rocks, inside and under rotting logs, and among the leaf litter at the base of banana trees. Northernmost samples are from the vicinity of Teocelo (approximately 1000 m), which is approximately 15 km south of Jalapa and near, but much lower in elevation than, the type locality of *T. minydemus.* (These samples are the basis for including *T. pennatulus* in the Veracruz transect of Wake et al., 1992, fig. 2). We assign specimens from Teocelo to *T. pennatulus* based on their general morphological similarity to specimens from more southerly localities. Dunn (1926: 375) referred montane populations of *Thorius* from widely scattered localities in Oaxaca (Cerro San Felipe) and Veracruz (Xometla) to *T. pennatulus*, but these populations belong to different species (e.g., see Remarks for *T. spilogaster*).

Remarks.—This taxon is now restricted to the former subspecies, *T. p. pennatulus*, following elevation to specific rank of the disjunct population from the Sierra de Los Tuxtlas, which had been recognized as a second subspecies of *T. pennatulus* (*T. narismagnus*—see below). Genetic relationships of *T. pennatulus* to congeners were examined using protein electrophoresis by Hanken (1980, 1983a; population 1, listed as *T. p. pennatulus*). Levels of genetic variability among populations of *T. pennatulus* are unknown. Evolutionary consequences of miniaturization of adult body size for cranial and appendicular morphology in *T. pennatulus* were examined by Hanken (1982, 1983b, 1984).

Thorius narismagnus (Shannon and Werler, 1955)

Figure 11B

Thorius pennatulus narismagnus Shannon and Werler, 1955:364. Holotype: FAS 4780: "3500–4000 feet altitude on the slopes of Volcán San Martín," Veracruz, México.

Thorius narismagnus: Hanken and Wake, 1994: 585.

Reference sample.—All from Veracruz, México: MVZ 128922–23 (two specimens), 128925–26 (two specimens), 128928–30 (three specimens), 128933–36 (four specimens), 128938, 128940, 201383, SE slope of Volcán San Martín; MVZ 183034–35 (two specimens), southwest slopes of Volcán San Martín, along trail from San Andres Tuxtla. Some of the above specimens are cleared and stained or have had tissue removed for protein comparisons.

Diagnosis.—This is a small species of *Thorius* with a long tail and large, round nostrils. It is distinguished from other members of the genus by the following combination of traits: small body size, no maxillary teeth, round nostrils, long legs, and very long tail. It is most similar to *T. pennatulus*, from which it differs by its relatively longer tail and limbs, stouter habitus, broader head and blunter snout, darker coloration, narrower foot, and predominant carpal pattern. Other similar species include *T. minydemus*, which has maxillary teeth and a short tail; *T. smithi*, which has an elongated nostril and maxillary teeth; and *T. insperatus*, which has an elongated nostril and lighter dorsal coloration.

Description.—Adult standard length of this small species averages 18.3 mm in 10 males (range 16.6–20.8) and 17.8 mm in four females (range 16.7–19.2). The head is relatively broad; SL averages 6.7 times head width in males (range 6.0–7.6), 6.5 times head width in females (range 6.0–7.1). Snouts are relatively broad and blunt in females and more pointed in males. Nostrils are relatively large and nearly round; the mean ratio of major axis to minor axis equals 1.1 in both males (range 1.0–1.2) and females (range 1.0–1.1). Eyes are moderately sized and protrude slightly beyond the margin of the head in ventral view. A suborbital groove intersects the lip on each side of the head. The two males each have a single premaxillary tooth, 4–5 vomerine teeth, and no maxillary teeth. There were no cleared-and-stained female specimens on which to count teeth. Limbs are relatively long and slender; limb interval averages 3.4 in males (range 2–4) and 3.8 in females (range 3–4). Hands and feet are narrow; the third finger and toe are substantially longer than remaining digits and are sharply pointed. Fingers, in order of decreasing length, are 3-2-4-1; toes are 3-4-2-5-1. The tail is relatively long; mean SL divided by tail length equals 0.68 in males (range 0.64–0.80) and 0.72 in females (range 0.67–0.76). The mental gland is round to ovoid. The postiliac gland is obscure.

Coloration in alcohol.—The dorsal ground color is a very dark brown. A relatively obscure, lighter-brown dorsal band extends from the head onto the base of the tail; it is bordered by very dark dorsal pigment. The ventral ground color is lighter and is covered by abundant whitish flecks and spots. The iris is dark brown.

Coloration in life.—Based on field notes by J. Hanken for MVZ 183028–35, there is a brownish dorsal stripe with a fine, black-and-brown herringbone pattern. The venter is dark with fine white flecking.

Osteology.—This description is based on data from two complete skeletons (MVZ 183034–35, both adult males). This species has a poorly developed skeleton. Ascending processes of the premaxillary bone are separate along their entire lengths in one specimen (character 1, state a); the second specimen (MVZ 183034) lacks an ascending process on the right side. Premaxillaries are well separated from the maxillary bones in ventral view (character 2, state a). The premaxilla bears one tooth in each specimen (character 8, state b). The nasal bone is relatively narrow and located in a far posterior position just anterior to the eye (character 3, state b). It is relatively broad on one side of one specimen (MVZ 183035), approaching character state c. The nasals articulate narrrowly with the maxilla (character 4, state b). The prefrontal bone is present and articulates with the nasal (character 5, state c). It does not, however, articulate with the maxilla (character 6, state a). A tiny septomaxillary bone is present on only the right side in one specimen (character 7, state c; MVZ 183035). It is lacking entirely in the other specimen (state a). The maxillary bone is very slender and lacks teeth (character 9, state a); the facial process is relatively well developed. Vomers are slender and narrowly articulate with each other posteriorly; there is no preorbital process. There are 4–5 vomerine teeth. Frontal bones are relatively well developed and articulate medially in one specimen (MVZ 183034); they are poorly developed and well separated in the other. The frontoparietal fontanelle is large; its breadth equals 0.57–0.65, mean 0.61, times the maximum skull width across the parietals. The parietal falls short of the occipital arch posteriorly. Otic crests are lacking, and there is no columellar process on the operculum. The postsquamosal process is well developed.

Both specimens have 14 presacral vertebrae. Tibial spurs are partially fused in one specimen (MVZ 183035) and reduced to a low crest in the other. Nearly all mesopodials are mineralized in one specimen (MVZ 183035), but none is mineralized in the other. Second ceratobranchials are mineralized in one specimen (MVZ 183035). No other hyobranchial elements are mineralized in either specimen.

Mesopodial morphology is variable, even among the limbs of just two specimens (i.e., 4 carpi and 4 tarsi). Carpal pattern III predominates in the forelimb (75%); pattern I is present in one limb (25%). Tarsal patterns VII and VIII are present in two limbs each (50%). Asymmetry is common; carpal or tarsal patterns differ between right and left sides in three of the four pairs of limbs. Phalangeal formulae are 1-2-3-2 (hand) and 1-2-3-3-2 (foot), although in all limbs terminal phalanges of the outermost digits are not or only barely ossified.

Habitat and range.—*Thorius narismagnus* is disjunct from all congeners. It is known only from the forested slopes of Volcán San Martín, in the Sierra de Los Tuxtlas, Veracruz, México (Fig. 1). Recorded elevations range from 890–1200 m. It is an exclusively terrestrial species; according to field notes by J. Hanken (7 Feb. 1976), specimens were collected from under rotten logs and among leaf litter on the forest floor, especially under fallen bromeliads.

Remarks.—*Thorius narismagnus* was originally described as a subspecies of *T. pennatulus* (Shannon and Werler, 1955). It is, however, geographically, morphologically, and genetically distinct from that species and was treated as a separate species by Hanken and Wake (1994). In completing the present study, we evaluated all available data concerning species of *Thorius* that occur in Veracruz and adjacent parts of Puebla and Oaxaca. We conclude that *T. narismagnus* is most appropriately recognized as a valid, distinct species. The taxon was said to differ from *T. pennatulus* in having larger nostrils and a dorsal coloration that is darker than the lateral coloration (Shannon and Werler, 1955). The general coloration of specimens in our (larger) reference sample is darker than that of *T. pennatulus*, but we cannot verify that nostrils are larger in *T. narismagnus*. We can, however, cite additional morphological differences between the species: *T. narismagnus* is slightly larger, has a longer tail and limbs, and its predominant carpal pattern (III) is a rare variant in *T. pennatulus*.

DISCUSSION

Allozyme data.—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. In this section, we summarize these results as they pertain to the nine species of *Thorius* from Veracruz and Puebla for which such data exist—*T. pennatulus, T. narismagnus, T. dubitus, T. troglodytes, T. spilogaster, T. schmidti, T. magnipes, T. lunaris,* and *T. munificus* (Table 2). No data are available for *T. minydemus.*

Hanken's *T. schmidti* was deeply divided genetically; Nei genetic distance (D_N; Nei, 1972) ranged from 0.58 to 0.62 between two populations from near Zoquitlán, Pue., the type locality, and two populations from Volcán Orizaba, here named *T. spilogaster.* There are fixed allelic differences between *T. schmidti* and *T. spilogaster* at four allozyme loci and nearly fixed differences at four others. Pairwise D_N between conspecific populations of each species are less than 0.1. Neither species is very similar genetically to any other species. Genetic distance between *T. spilogaster* and *T. troglodytes* equals 0.68 (four fixed differences), but all other pairwise comparisons between *T. spilogaster* and other species are much larger. For most comparisons D_N exceeds 1.0, and there are from six to nine fixed differences. Similarly, D_N between *T. schmidti* and *T. troglodytes* equals 0.68 (five fixed differences), whereas nearly all other pairwise comparisons involving *T. schmidti* are much larger and include from six to nine fixed differences; D_N equals 0.61 between *T. schmidti* and a population of uncertain species identity from near Tlaxiaco, Oax., a long distance to the south and west. [Both populations of *T. schmidti* from near Zoquitlán, which included topotypic specimens, were genetically homogeneous, leading Hanken (1983a) to conclude that this species and *T. maxillabrochus* are conspecific.]

Earlier work also showed that a second species, here named *T. lunaris,* is sympatric with *T. spilogaster* on Volcán Orizaba. There are fixed allelic differences between the two species at nine allozyme loci, and one additional locus is nearly fixed; D_N equals 1.0–1.2. Although *T. lunaris* also is genetically distinct from the allopatric and morphologically distinct *T. munificus,* the genetic distances are substantially smaller (D_N = 0.23–0.28; Hanken, 1980). There are, however, two fixed differences. These two species are well separated genetically from all other *Thorius*; all pairwise genetic distances between either species and any other member of the genus exceed 0.8.

Hanken (1983a) detected three sympatric species near Puerto del Aire: *T. troglodytes, T. dubitus,* and a third species named here, *T. magnipes.* Genetic distance (D_N) between *T. troglodytes* and *T. dubitus* equals 0.43 (range 0.39–0.45), with fixed differences at three loci and nearly fixed differences at two others. Interestingly, these two species are more similar to one another than to any other species; pairwise D_N between *T. dubitus* or *T. troglodytes* and all other taxa exceed 0.75 and 0.5, respectively. *Thorius magnipes* appears to have no close genetic relatives. It is most similar to the sympatric *T. dubitus;* D_N equals 0.56, with five fixed differences and one nearly fixed difference. Genetic distances to all other species exceed 0.85; D_N to the sympatric *T. troglodytes* equals 0.89 (range 0.84–0.94), with six fixed differences and one nearly fixed difference.

Recognition of *T. narismagnus* as a distinct species from *T. pennatulus* is warranted by a combination of morphological and genetic differences. Genetic distance (D_N) between the two taxa equals 0.39, including fixed allelic differences at two allozyme loci and nearly fixed differences at two others. Each species is well differentiated from all other *Thorius.* Genetic distances to other species from this geographic region exceed 0.73 (*T. narismagnus*) and 0.85 (*T. pennatulus*); pairwise values to species outside this region are at least as large (Hanken, 1983a).

Detailed phylogenetic analysis of the allozyme data is beyond the scope of this paper but is being undertaken separately (Mahoney, unpubl.). In an earlier phenetic analysis based on genetic distances (D_N), Hanken (1983a, fig. 2) showed that several species from Veracruz and Puebla cluster together in pairs, each typically with no near neighbors. These included *T. lunaris* and *T. munificus, T. troglodytes and T. dubitus, T. spilogaster* and *T. schmidti,* and *T. pennatulus* and *T. narismagnus.* The latter three species pairs clustered with *T. magnipes* in a UPGMA phenogram that included all sampled populations of *Thorius; T. lunaris* and *T. munificus* were well separated from all other taxa. Neighbor-joining analysis based on genetic distances among the same nine species from Veracruz and Puebla retains three of the four species pairs from the earlier UPGMA analysis: *T. lunaris* and *T. munificus, T. spilogaster* and *T. schmidti,* and *T. pennatulus* and *T. narismagnus* (Fig. 12). Unlike the earlier analysis, however, *T. dubitus* first pairs with *T. magnipes* before these two species cluster with *T. troglodytes.*

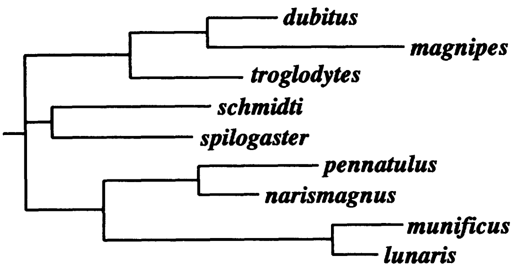

Fig. 12. Neighbor-joining analysis of the nine species of *Thorius* from Veracruz and Puebla for which there are allozyme data (i.e., all species except *T. minydemus*). The dendrogram was produced by analyzing a matrix of Nei genetic distances (D_N) with the program Neighbor in PHYLIP, version 3.5c (J. Felsenstein, University of Washington, Seattle, unpubl., 1993). It is intended to depict only the relative magnitude of genetic differences among taxa, not phylogenetic relationships.

Morphological data.—Taxonomy and systematic relationships within *Thorius* have vexed herpetologists for much of the nearly 160-year interval that has elapsed since the genus was first described by Cope in 1869 (Hanken, 1983a; Hanken and Wake, 1994). Much of the difficulty can be traced to the inability to reliably delineate species boundaries based exclusively on morphological criteria. In our studies, biochemical data (see above) have provided the necessary insights into patterns of geographic variation and phylogenetic relationship, including several instances of sympatric species, that have allowed us to confidently and unambiguously differentiate congeneric species. Moreover, once such taxa are distinguished on biochemical grounds, characteristic morphological traits can be found for nearly all species. Morphological features that are especially effective include adult body size, limb and tail proportions, dorsal and ventral coloration, nostril size and shape, and the presence or absence of maxillary teeth. There also are significant skeletal differences (Hanken, 1982, 1984; Hanken and Wake, 1994; Table 1).

The ability to distinguish species morphologically is well illustrated by the three sympatric species found at Puerto del Aire, Ver. *Thorius dubitus* and *T. troglodytes,* two terrestrial species, were originally described by Taylor (1941), who differentiated them on the basis of adult body size and several subtle aspects of external morphology, including tail shape, dorsal coloration, and skin texture. Subsequently, additional specimens of *Thorius* were collected from arboreal microhabitats at this same locality. These specimens were tentatively identified as a third, un-

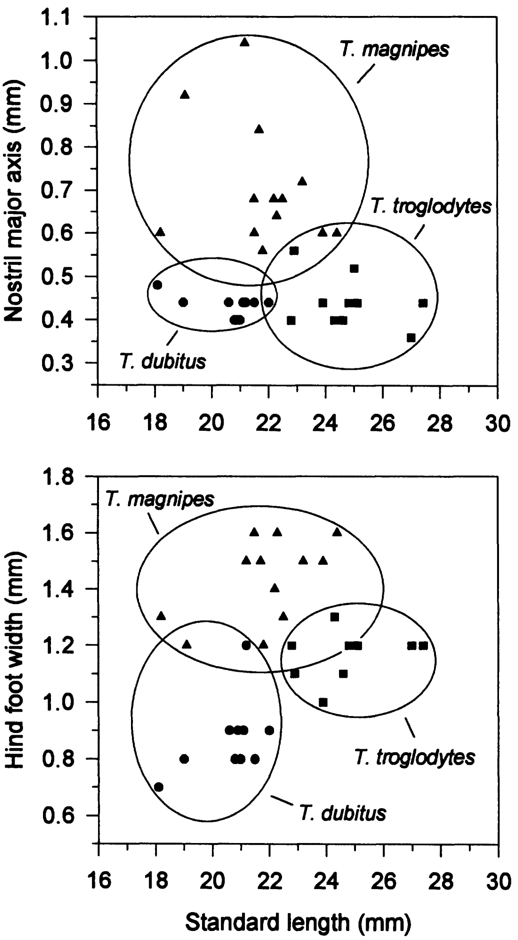

Fig. 13. Bivariate plots of maximal nostril opening (major axis; top) and hind foot width (bottom) versus adult body size (standard length) for the three sympatric species of *Thorius* at Puerto del Aire, Ver. ● = *T. dubitus*; ■ = *T. troglodytes*; ▲ = *T. magnipes*. Data are for females only; comparable data for adult males display basically the same distribution and separation among species. Ellipses are drawn by eye to include all data points for a given species.

described species based on the relative size of the limbs, which appeared to be significantly larger than those in either *T. dubitus* or *T. troglodytes* (R. W. McDiarmid, pers. comm.). Allozyme analysis confirmed the distinctiveness of all three populations at Puerto del Aire, both from one another and from all other described species (Hanken, 1983a; see above); the third, arboreal species is here described as *T. magnipes*. Bivariate plots of external measurements, in turn, validate both Taylor's original differentiation of *T. dubitus* from *T. troglodytes* and subsequent field herpetologists' differentiation of both species from sympatric *T. magnipes*, based only on external morphology (Fig. 13). *Thorius troglodytes* generally is larger and has a wider foot than *T. dubitus*. *Thorius magnipes* overlaps considerably both *T. dubitus* and *T. troglodytes* in body size, but it generally has a much larger nostril and wider foot than either terrestrial species.

At the same time, our results highlight the extensive intraspecific variability that is exhibited by many morphological characters in *Thorius*. For example, a total of 15 different mesopodial patterns are displayed collectively by the 10 species found in Veracruz and Puebla (Table 1). In some species (e.g., *T. munificus* and *T. narismagnus*), modal patterns are distinctive and taxonomically useful. Twelve of the 15 patterns, however, coexist in a single sample of 20 adult *T. schmidti* (Fig. 10). Modal patterns in *T. schmidti* are the same ones found in most other species and are of little taxonomic use. Such variability underscores the extensive and profound consequences for body organization and development that are associated with miniaturization in this lineage of vertebrates (e.g., Wake and Larson, 1987; Hanken, 1993; Roth et al., 1995). It also helps to account for the considerable difficulty that has attended earlier attempts at taxonomic analysis based exclusively on morphology. Without an independent means of assessing species identity (e.g., allozymes), it may be nearly impossible to distinguish a priori those morphological characters that are useful taxonomically from those that are not.

Distribution of salamanders in Veracruz and Puebla.—This is the second in our series of taxonomic studies of *Thorius*. This genus constitutes a large and difficult group in which to discern species identities and relationships. By organizing our work geographically, we take advantage of several instances of sympatry, which provide insight into the morphological and ecological differentiation of the lineage. Previously, we dealt with species from a single elevational transect in northern Oaxaca (Hanken and Wake, 1994); here we treat species along the Atlantic versant of Veracruz. Our point of departure is the allozyme analysis of Hanken (1983a), which documented several localities in this region where species occur in sympatry. This reliable method for assessing taxonomic differentiation in sympatry aided our discovery of morphological characters that diagnose the taxa. These and subsequent analyses led to our current recognition of 10 species in Veracruz and neighboring areas in Puebla. We outline the known distribution of these species in Figure 1, extending previous representations (Hanken, 1983a).

To link this paper to the earlier work by Hanken (1983a), we briefly summarize his designations. Hanken's species A is *T. magnipes*, which occurs in sympatry with two other species at Puerto del Aire, *T. dubitus* and *T. troglodytes*. Species B comprises two new species: *T. lunaris*, from the southern flanks of Volcán Orizaba; and *T. munificus*, from the lower slopes of Cofre de Perote. We have subdivided Hanken's *T. schmidti*; northern populations are described here as *T. spilogaster*. We recognize *T. pennatulus* and *T. narismagnus* (formerly *T. p. narismagnus*) as distinct species. *Thorius minydemus*, the other new species described here, was unknown to Hanken.

Distribution of these species can perhaps be best understood by considering two generalized elevational transects—one to the north, starting in the vicinity of Cofre de Perote; the other in the south, at the pass above Acultzingo. The northern transect was outlined in general terms by Wake et al. (1992), who recognized 15 species of salamanders in the area. Their "*Thorius* sp. nov.," known from the vicinity of Las Vigas (2400–2600 m), is *T. munificus*. *Thorius pennatulus* was shown to occur at lower elevations (approximately 1000–1200 m) near Teocelo. Here we add a third species, *T. minydemus*, which occurs at an intermediate elevation (approximately 2200–2400 m) at La Joya. There is as yet no known sympatry among species of *Thorius* in this area, although each of the above species coexists with at least three species from other plethodontid genera.

The southern transect is more complicated than the northern one. It starts with several different combinations of highland species. Sympatric *T. lunaris* and *T. spilogaster* are found at elevations between 2500 m and 2725 m on the southern flanks of Volcán Orizaba. Three additional sympatric species—*T. troglodytes*, *T. dubitus*, and *T. magnipes*—occur between 2450 and 2800 m to the south, at Cumbres de Acultzingo (Puerto del Aire). (See Remarks for *T. spilogaster* and *T. dubitus* regarding a possible fourth species at Puerto del Aire.) Two of these species (*T. troglodytes* and *T. magnipes*) extend to a slightly lower elevation (approximately 2400 m) near San Felipe. Finally, these species are replaced further south by a single, high-elevation form, *T. schmidti*, in the Sierra de Zongolica at Zoquitlán (2560–2760 m). As in the northern transect, *T. pennatulus* is found at lower elevations (1000–2000 m) to the east. Then there is a large geographic gap to Volcán San Martín, near the Atlantic coast, the only known locality for a second lowland species, *T. narismagnus* (890–1200 m).

Discovery of additional species of *Thorius* reinforces the characterization of Veracruz-Puebla-northern Oaxaca as a major focus of evolutionary activity for Neotropical salamanders (Wake and Lynch, 1976, region four), and appreciably adds to the high numbers of both species and endemism within it.

Status of systematic treatments of Thorius taxa.—With the completion of the present study and our previous work (Hanken and Wake, 1994), we have addressed the taxonomy and systematics of more than 40 of the 69 populations examined by Hanken (1980, 1983a). Based on these analyses we recognize a total of 19 named species of *Thorius*. This leaves more than 20 populations still to be considered, and these include only three named taxa—*T. narisovalis*, *T. pulmonaris*, and *T. minutissimus*. Hanken (1983a) identified two additional candidate species—species F (Guerrero) and species G (western Oaxaca)—but genetic differentiation is so great that it seems likely that several more species will be found. Work in progress considers Guerreran populations (J. Hanken, D. B. Wake, and H. L. Freeman, unpubl.), but many problematic Oaxacan populations remain to be studied.

KEY TO THE SPECIES OF *Thorius* IN VERACRUZ AND PUEBLA

1A. Maxillary teeth present in adults 2
1B. Maxillary teeth absent in adults 4
2A. Adults small—SL $<$ 20 mm in males, $<$ 23 mm in most females .... *T. minydemus* (part)
2B. Adults moderate-size; SL $>$ 20 mm in most males, $>$ 23 mm in most females 3
3A. Prominent ventral white spotting; hands and feet relatively small; digit tips pointed .... *T. spilogaster*
3B. Inconspicuous ventral white spotting; hands and feet relatively large; digit tips rounded .... *T. schmidti*
4A. Adults small—SL $<$ 21 mm in all or most males, $<$ 22 mm in all or most females 5
4B. Adults moderate-size to large—SL $>$ 21 mm in all or most males, $>$ 22 mm in all or most females 9
5A. Nostril round; tail length exceeds SL 6
5B. Nostril elongate; tail shorter or longer than SL 7
6A. Tail long—SL divided by tail length usually $>$ 0.75; head narrow—SL divided by head width usually $\geq$ 7.0; snout pointed; light dorsal coloration .... *T. pennatulus*
6B. Tail very long—SL divided by tail length usually $\leq$ 0.75; head broad—SL divided by head width usually $<$ 7.0; snout blunt; dark dorsal coloration; Sierra de Los Tuxtlas .... *T. narismagnus*
7A. Hind-foot width usually $>$ 1.2 mm; tail length $\geq$ SL .... *T. magnipes* (part)

7B. Hind-foot width usually < 1.2 mm; tail length < SL 8
8A. Head moderately wide to narrow—SL divided by head width usually ≥ 7.0; nostril elongate—ratio of major axis to minor axis usually ≥ 1.3; hands and feet moderately wide .... *T. dubitu*
8B. Head broad—SL divided by head width usually ≤ 7.0; nostril round to slightly oval; hands and feet very narrow .... *T. minydemus* (part)
9A. Limbs relatively long—limb interval ≤ 3 in males, ≤ 3.5 in females .... *T. magnipes* (part)
9B. Limbs moderate length to short—limb interval ≥ 3 in most males, ≥ 3.5 in females 10
10A. Adults large—SL ≥ 25 mm in all or most males, ≥ 26 mm in females 11
10B. Adults moderate-size—SL ≤ 25 mm in most males, ≤ 26 mm in females 12
11A. Hind-foot width ≥ 1.2 mm; nostril crescent-shaped .... *T. lunaris*
11B. Hind-foot width ≤ 1.2 mm; nostril oval, elongate .... *T. troglodytes* (part)
12A. Limbs moderate length—limb interval usually ≤ 4.5 .... *T. munificus*
12B. Limbs short—limb interval usually ≥ 4.5 .... *T. troglodytes* (part)

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(JH) DEPARTMENT OF ENVIRONMENTAL, POPULATION, AND ORGANISMIC BIOLOGY AND UNIVERSITY MUSEUM, UNIVERSITY OF COLORADO, BOULDER, COLORADO 80309-0334; AND (DBW) DEPARTMENT OF INTEGRATIVE BIOLOGY AND MUSEUM OF VERTEBRATE ZOOLOGY, UNIVERSITY OF CALIFORNIA, BERKELEY, CALIFORNIA 94720-3160. E-mail: (JH) James.Hanken@Colorado.edu. Send reprint requests to JH. Submitted: 29 April 1997. Accepted: 29 Oct. 1997. Section editors: D. Cundall and F. Irish.