

Five New Species of Minute Salamanders, Genus *Thorius* (Caudata: Plethodontidae), from Northern Oaxaca, Mexico

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Five new species of diminutive salamanders of the endemic Mexican genus *Thorius* (Plethodontidae) are described from the Sierra de Juárez in northern Oaxaca. The species are diagnosed by adult body size, external proportions, dentition, osteology and coloration. The three species that have been studied using protein electrophoresis are genetically unique; all differ from *T. macdougalli*, the only species of the genus previously known from these mountains. Each of the six species studied has distinct geographic and elevational ranges, and there is a complex pattern of geographic overlap and replacement. As many as three species co-occur locally at elevations up to 2955 m on Cerro Pelón, and each species is sympatric with at least one other. One species descends to approximately 800 m, which is the lowest known elevational record for the genus. The new taxa include the full size range of the genus, with two large and three small species.

AMONG the many impressive aspects of the Mexican herpetofauna is the rate at which new urodele taxa, including both species and genera, continue to be discovered and described (Wake and Elias, 1983; Lynch and Wake, 1989; Wake and Johnson, 1989). This may be attributed to at least two reasons: first, the access by herpetologists to poorly collected regions, especially montane cloud forest habitats which are characterized by a high degree of endemism (Wake and Lynch, 1976); and second, the advent of molecular tools, which frequently offer greater resolution than standard taxonomic characters, such as morphology, for revealing cryptic species (Wake, 1981).

For the last several years, we have pursued genetic and morphological studies of what is perhaps the most enigmatic Mexican genus, *Thorius*. These plethodontid salamanders have represented a continuous source of frustration, if not confusion, to systematic herpetologists for decades. The primary reason for this lies in their small size—they are among the smallest extant tetrapods—which has impeded efforts to accurately and reliably define species boundaries. As studies of comparative and evolutionary biology require an accurate phylogenetic framework, we have expended considerable effort in attempting to resolve taxonomic uncertainty in the genus. By combining the results of an electrophoretic analysis of population samples from throughout the range of the genus in southern

Mexico (Hanken, 1983) with the study of external morphology and osteology (Hanken, 1982, 1984, 1985), we have reduced appreciably the taxonomic uncertainty. In this report, we present the first installment of our findings, specifically concerning the species of *Thorius* from the Sierra de Juárez in southern Oaxaca. This mountain range is home to at least six species of *Thorius*, all of which are endemic to this region and only one of which has been described previously.

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. Whole-mount skeletal preparations were stained for bone and cartilage using alizarin red S and Alcian blue 8GX, respectively (Klymkowsky and Hanken, 1991). Osteological descriptions use the cranial character states and mesopodial patterns described by Hanken (1982, 1984); see Wake and Elias (1983) for comparisons with other tropical genera. All tooth counts are based on cleared-and-stained specimens. Institutional abbreviations are as listed in Leviton et al. (1985).

Thorius aureus n. sp.
Golden Thorius

Holotype.—MVZ 85966, an adult female from 0.7 mi (rd.) E Cerro Pelón from point where road crosses top, Oaxaca, México, collected by R. W. McDiarmid and R. D. Worthington, 20 Jan. 1969.

Paratypes.—All from Oaxaca, México: MVZ 85956-58 (three specimens), 85960, 85961, 85968-70 (three specimens), 85972, 85973, 85975, same data as the holotype; MVZ 85978, 85979, same data as the holotype, except collected 21 Jan. 1969; MVZ 112175, 112179, 112181, 112182, 112184, 52 km (Hwy. 175) NE of Guelatao, collected by T. J. Papenfuss, 5 Aug. 1974; MVZ 114690, Cerro Pelón, near Hwy. 175, 108.9 km (rd.) N jct. Pan Am Hwy. at Oaxaca City, collected by J. F. Lynch, 24 Jan. 1974; MVZ 183332, 187179-84 (six specimens), 187189-91 (three specimens), 32.4 mi N Guelatao on Hwy. 175, elev. 2515 m, collected by H. B. Shaffer, 8 July 1978; MVZ 187003-9 (seven specimens), Hwy. 175, 33.5 mi N Guelatao, elev. 8120 ft, collected by J. Hanken, 21 July 1976; MVZ 187185-87 (three specimens), Hwy. 175, 31.8 mi N Guelatao, 1 km N Cerro Pelón from where road crosses top, collected by J. Hanken, 21 July 1976; LACM 58663, 31.2 mi N Guelatao, elev. 9600 ft, collected by D. Paulson, 5 Aug. 1965. Some of the above specimens are cleared and stained.

Diagnosis.—This is a large, robust species of *Thorius*, distinguished from all other members of the genus by the following combination of traits: well-ossified skull, short limbs, teeth present on the maxillary bones, golden-yellow dorsal stripe, slightly enlarged nostril, and pale venter. It differs from sympatric associates as follows: from *T. macdougalli* and *T. arboreus* by its larger size, lighter coloration and the presence of maxillary teeth; from *T. boreas* by its lighter coloration and the presence of maxillary teeth.

Description.—This is one of the largest species in the genus: 21 adult males, 21.1–29.3 mm SL, mean 25.9 mm; 20 adult females, 22.6–34.9 mm SL, mean 29.1 mm. Heads are relatively narrow, especially in females (SL is 6.8–8.9 times head width in 10 adult males, mean 8.1; 8.3–9.7, mean 8.9, in 10 adult females). The snout is rounded in females but somewhat more pointed in males. The nostril is oval (the major axis is between 1.3 and 2.0 times the minor axis,

mean 1.6) but only slightly enlarged for a member of this genus. A suborbital groove intersects the lip on each side. Teeth are well developed and more numerous in females than males: premaxillary teeth range from 0 to 5 (mean 2.1) in males and from 3 to 7 (mean 5.2) in females; maxillary teeth range from 9 to 21 (mean 13.2) in males and from 11 to 34 (mean 21.0) in females; vomerine teeth range from 6 to 11 (mean 8.0) in males and from 6 to 11 (mean 8.5) in females. The trunk is relatively robust for this genus. Limbs are relatively short; limb interval ranges from 6 to 7.5 (mean 6.4) in males and from 7 to 7.5 (mean 7.4) in females. Hands are very small, and feet are small and narrow (hind foot width varies from 1.0 to 1.4 mm, mean 1.2 mm); the first and fifth digits of the pes are short and poorly developed. Fingers, in order of decreasing length, are 3-2-1-4; toes are 3-2-4-1-5. The postiliac gland is prominent. Tails that are apparently unregenerated exceed standard length, which is as little as 0.86 times tail length in males.

Measurements of the holotype (in millimeters).—Head width 3.7; snout to gular fold (head length) 5.0; head depth at posterior angle of jaw 2.7; eyelid width 0.8; eyelid length 1.2; anterior rim of orbit to snout 1.3; horizontal orbit diameter 1.2; interorbital distance 1.3; snout to forelimb 8.2; distance separating external nares 0.8; major axis of nostril 0.5; minor axis of nostril 0.3; snout projection beyond mandible 0.2; snout to posterior angle of vent (standard length) 34.0; snout to anterior angle of vent 32.5; axilla to groin 20.6; tail length 32.2; tail width at base 3.2; tail depth at base 3.1; forelimb length (to tip of longest toe) 3.4; hind limb length 3.4; hand width 0.9; foot width 1.5.

Coloration of the holotype (in alcohol).—This is a light brown animal with a broad, golden-tan stripe extending from the snout to the tail tip. The stripe is broadest over the head and becomes pinched over the shoulders, forming an hourglass shape; it is sharply edged dorsolaterally by dark brown coloration, which fades gradually along the flanks. The stripe is also marked by a series of subdued brown chevrons which point anteriorly; the chevrons fade over the tail. The venter is pale and unmarked. Limbs are light below, the same color as flanks above. The iris is charcoal.

Coloration in life.—Based on field notes by J. Hanken for MVZ 187003-9; see also Figure 1A. There is a prominent gold dorsal stripe, either

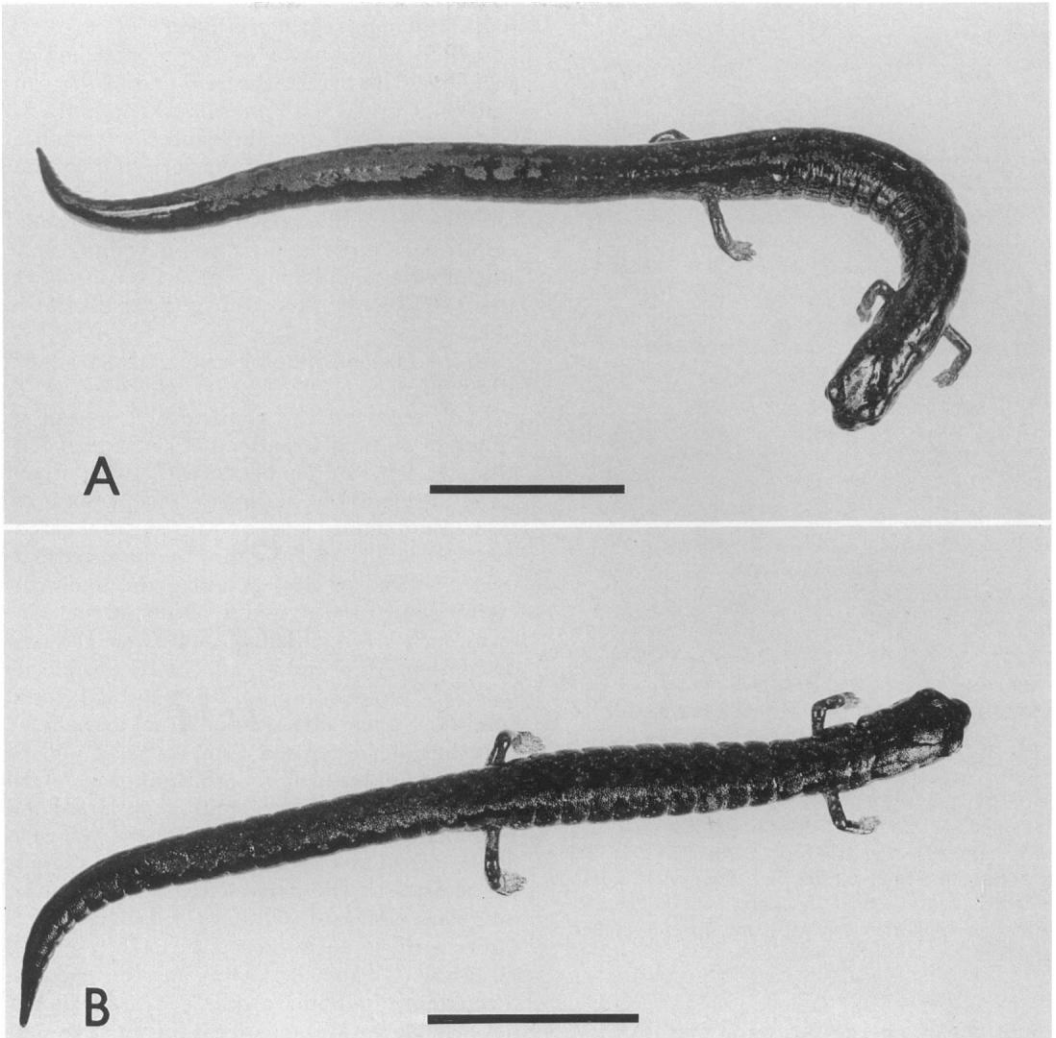


Fig. 1. Photographs of adult *Thorius*. (A) *T. aureus*, 32.4 mi (rd.) N Guelatao, elev. 2515 m, collected 8 July 1978 by H. B. Shaffer; (B) *T. boreas*, 33 km (rd.) N Guelatao, elev. 2940 m, collected 20 Nov. 1974 by D. B. Wake. Museum numbers are unavailable for either specimen. Scale bar equals 1 cm.

solid or variably interrupted by dark markings along the midline. The venter is pale. Lateral surfaces have light flecking.

Osteology.—This description is based on data from 21 partial to complete skeletons. The skull of a single specimen is illustrated in Figures 2C, 3C, a maxillary bone of that specimen in Figure 4A, and its fore- and hind limb skeletons in Figure 5B, 5G.

The skeleton is well ossified; individual bones are generally larger than in other species of the genus. The skull has a relatively broad premaxillary bone that overlaps and usually articulates

with the maxillary bones (character 2, states c and d). The ascending processes of the premaxillary are fused for about one-half their length, but they enclose a small fontanelle immediately above the pars dentalis and below the area of fusion (character 1, intermediate between states b and c). Nasals are relatively well developed and are expanded over the cartilaginous nasal capsules (character 3, state c); they also contact the ascending process of the maxillary bones (character 4, state b). The relatively small prefrontals do not contact the maxillaries (character 6, state a), from which they are separated by the foramen of the nasolacrimal duct,

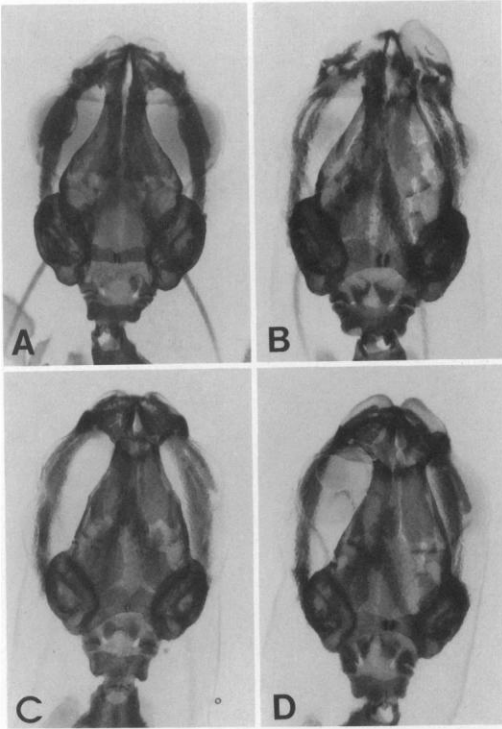


Fig. 2. Photographs of skulls of four species of *Thorius*, cleared and double stained for bone and cartilage. (A) *T. arboreus*, MVZ 187011, an adult female, 20.0 mm SL. (B) *T. macdougalli*, MVZ 186790, an adult male, 20.5 mm SL. (C) *T. aureus*, MVZ 187189, an adult female, 29.8 mm SL. (D) *T. boreas*, MVZ 187165, an adult female, 28.9 mm SL. All images are printed to approximately the same size; see Figure 3 for scale.

which lies along the posterior margin of the nasal. The prefrontals usually articulate with the nasals (character 5, state c), but in a few instances the articulation is slight, and in three specimens there is no contact (state b). There are no septomaxillaries (character 7, state a). The premaxillary bears teeth (character 8, state b), except in one adult male. The maxillaries are relatively large and stout and bear numerous teeth (character 9, state b).

The dorsal fontanelle is relatively small for *Thorius*, but large in relation to that in other tropical salamander genera. The fontanelle is very narrow and ill-defined between the frontals but is wider and more evident between the parietals, where its breadth is from 0.13–0.44, mean 0.32, times the maximum skull width across the parietals. There are no otic crests, and there is no columellar process on the operculum. The relatively well-developed squamosal bears a cylindrical and relatively stout post-

squamosal process. The vomer bears a distinct, tooth-bearing preorbital process.

Each vertebra has a well-developed, mineralized condyle on the anterior end of the centrum that fits into a mineralized cotyle in the posterior end of the more anterior vertebra. Regional organization of the vertebral column includes one cervical, 15 trunk, one sacral, two caudosacral, and a variable number of caudal vertebrae. The tibia has a well-developed spur at its proximal end that is either free distally or attached by a thin bony web to the shank of the tibia.

Mesopodial morphology is relatively generalized. Hanken (1982, *T. aureus* identified as "*T. sp. D*") reported carpal pattern I present in 76.9% of 39 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. Other carpal patterns, each with additional fusions, were II (fused distal carpals 1-2 and 3), 12.9%; III (distal carpals 3 and 4 plus centrale), 7.8%; and VII (fused centrale 1 plus radiale, fused distal carpals 1-2 plus centrale, and fused distal carpals 3 and 4), 2.5% and unique to *T. aureus*. Hanken reported tarsal pattern I (again the most generalized and presumably the ancestral state for the genus) in 82.9% of 39 tarsi examined. It contains eight elements, with one derived state in relation to outgroup genera: fused distal tarsals 4 and 5. Other patterns encountered were III (fused distal tarsals 1-2 and 3), 11.8%; and V (fused intermedium plus fibulare), 5.8%. Most specimens have the ancestral phalangeal formulae of 1-2-3-2, 1-2-3-3-2, but frequently phalanges are extremely small, and one fewer phalanx is encountered in the outermost and sometimes in more interior digits. The terminal phalanges of finger three and toe three are terminally expanded, and frequently so are those of adjacent digits.

Mineralization of the ends of long bones and mesopodial elements proceeds progressively with size and sexual maturation, as in other species of the genus (Hanken, 1982). The second ceratobranchials and basibranchials are mineralized in one adult female (MVZ 187189, 29.8 mm SL). There are no hyobranchial mineralizations in other specimens.

Comparisons to other taxa.—This is one of the most distinctive species in the genus. It is readily distinguished from its sympatric congeners by color pattern alone, because it is a brightly col-

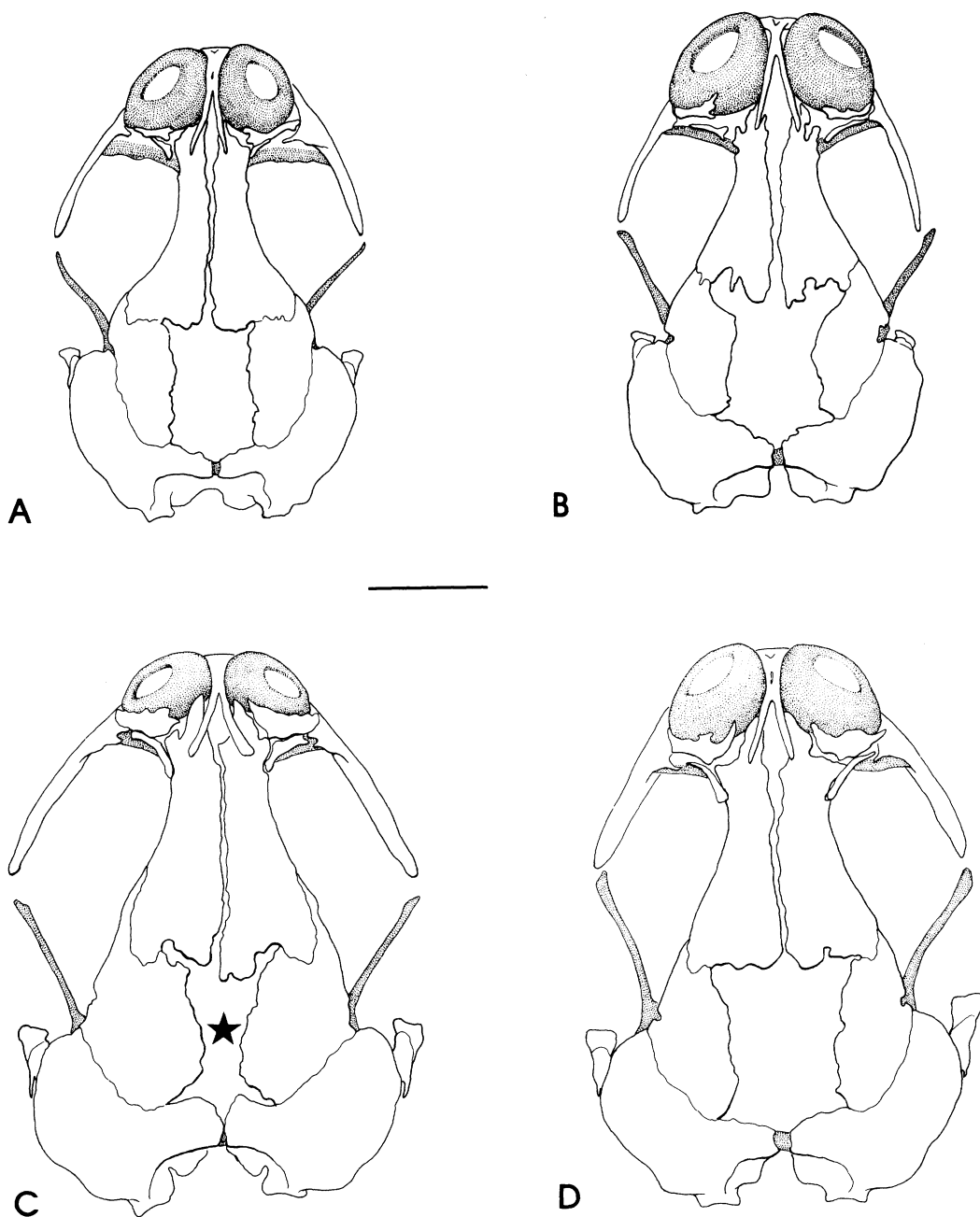


Fig. 3. Drawings of skulls of four species of *Thorius*, based on specimens in Figure 2; all are dorsal views. (A) *T. arboreus*; (B) *T. macdougalli*; (C) *T. aureus*; (D) *T. boreas*. *Thorius aureus* has the most heavily ossified skull of these species; note, for example, the relatively small dorsal fontanelle (star). Bones are shown in outline; cartilage is stippled. Scale bar equals 1 mm.

ored species and the others are generally much darker. It is substantially larger than both *T. macdougalli* and *T. arboreus* but about the same size as *T. boreas*. None of the sympatric congeners has maxillary teeth. Nostrils are smaller and slightly more round than those of *T. boreas*. Limbs of *T. aureus* are shorter, relative to body

size, than those of the sympatric species. The species resembles *T. schmidti* of Puebla and central Veracruz in coloration and size, and in having numerous maxillary teeth, but it is readily distinguished from that taxon by numerous protein differences (see below), by its larger nostril, and by having a more extensively ossified skull.

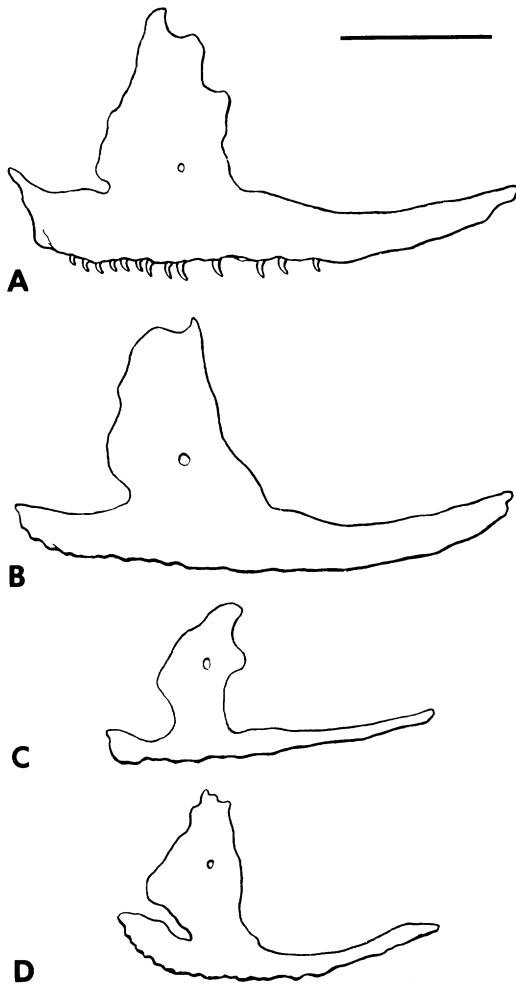


Fig. 4. Morphology of the maxillary bone in four species of *Thorius*, based on specimens in Figure 2; left lateral views, anterior is to the left. (A) *T. aureus* (note teeth); (B) *T. boreas*; (C) *T. arboreus*; (D) *T. macdougalli*. The bones depicted generally are typical for each species, although there is considerable intraspecific variation in the degree of articulation between the maxillary and adjacent bones. Scale bar equals 0.5 mm.

In particular, the cranial fontanelle between the parietal bones is smaller in *T. aureus* than in *T. schmidti*. Limbs are relatively shorter in *T. aureus* (limb interval exceeds six costal grooves) than in *T. schmidti* (limb interval less than six grooves). The skull of *T. aureus* lacks septo-maxillary bones, which occur variably in some species (Hanken, 1984), but in other respects it is the most fully developed in the genus. The cranial fontanelle may be as small as 0.13 times the maximum width of the skull across the parietals (it may be as great as 0.55 times the skull

width in adults of such large species as *T. narisovalis*).

Habitat and range.—*Thorius aureus* is known only from the type locality and nearby localities along Hwy. 175 on the north slopes of Cerro Pelón, a prominent massif of the Sierra de Juárez (Figs. 6A, 7). It is a terrestrial species and has been collected in montane pine-oak-fir forest and upper cloud forest habitats (Hanken, 1983; Wake, 1987; Wake et al., 1992). The recorded elevational range is 2475–2930 m. It is sympatric with both *T. macdougalli* and *T. boreas* at upper elevations (see notes for *T. boreas*) and with *T. arboreus* at lower elevations.

Etymology.—The species name is derived from the Latin word *aureus*, meaning golden or splendid, in recognition of the distinctive and attractive golden dorsal stripe that is characteristic of this species.

Thorius arboreus n. sp.
Arboreal Thorius

Holotype.—MVZ 196078, an adult female from 10.9 km (rd.) W La Esperanza, along Hwy. 175, Oaxaca, México, elev. 2060 m, collected by D. Darda and P. Garvey, 20 Nov. 1983.

Paratypes.—All from Oaxaca, México: MVZ 158915, 65 km NE Guelatao on Hwy. 175, elev. 6480 ft, collected by T. J. Papenfuss, 27 Aug. 1975; MVZ 183349, 187010, 187011, Hwy. 175, 33.6 mi N Guelatao, elev. 2380 m, collected by H. B. Shaffer, 8 July 1978; MVZ 183350, 187012, 187013, Hwy. 175, 34.7 mi (rd.) N Guelatao, elev. 7660 ft, collected by J. Hanken, 21 July 1976; MVZ 183353, 40.5 mi N Guelatao on Hwy. 175, collected by H. B. Shaffer, 8 July 1978; MVZ 112210, 65 km NE Guelatao on Hwy. 175, collected by T. J. Papenfuss, 22 Aug. 1974; MVZ 131440, 16 km (rd.) S Vista Hermosa on Hwy. 175, elev. 2050 m, collected by J. F. Lynch, 21 Nov. 1974; MVZ 178844, 66 km N Guelatao on Hwy. 175, elev. 2100 m, collected by D. B. Wake, 19 Oct. 1981. Some of the above specimens are cleared and stained.

Diagnosis.—This is one of the smallest species of *Thorius*, distinguished from other members of the genus by the following combination of traits: small size, slender habitus, ornate dorsal coloration, no maxillary teeth, and semiarboreal habits. It is distinguished from its only sympatric associate, *T. aureus*, by being smaller and more slender, and in lacking maxillary teeth. It most closely resembles *T. macdougalli* in mor-

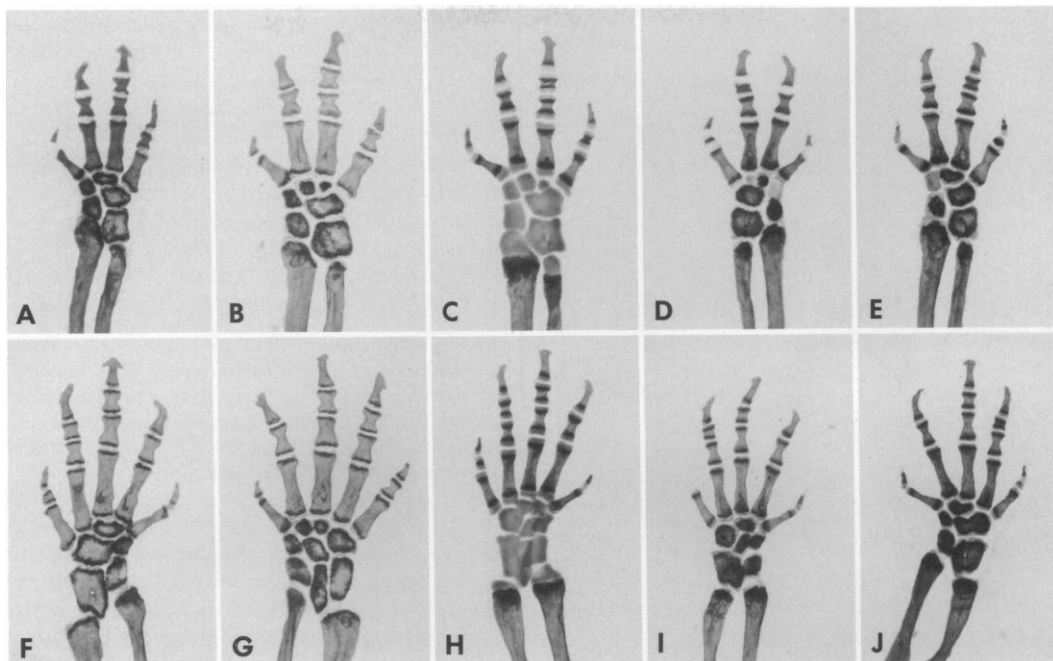


Fig. 5. Mesopodial morphology in four species of *Thorius*; same cleared-and-stained specimens as in Figure 2. (A) Right hand of *T. arboreus*, carpal pattern II. This specimen and most of the others have fully ossified mesopodials, and the ends of long bones are mineralized. (B) Right hand of *T. aureus*, carpal pattern I. (C) Right hand of *T. boreas*, carpal pattern I; mesopodial elements are unmineralized. (D) Left hand of *T. macdougalli*, carpal pattern I. (E) Right hand of *T. macdougalli* (same specimen as in D), carpal pattern II. (F) Left foot of *T. arboreus*, tarsal pattern VIII. (G) Right foot of *T. aureus*, tarsal pattern I. (H) Left foot of *T. boreas*, tarsal pattern I; mesopodial elements are unmineralized. (I) Left foot of *T. macdougalli*, tarsal pattern VI. (J) Right foot of *T. macdougalli* (same specimen as in I), tarsal pattern VIII. Images are printed to approximately the true size.

phology and allozymes but is distinguished from that taxon by its smaller size, smaller feet, and rounded nostril.

Description.—This may be the smallest species of *Thorius*; adult standard length averages 17.0 mm (range 16.1–18.4) in four males and 17.2 mm (range 15.2–20.0) in seven females. The body is very slender. The head is relatively wide with a bluntly pointed snout and is distinct from the anterior portion of the trunk; mean ratio of standard length to head width equals 6.7 in both sexes (range 6.1–7.3). The nostril is of moderate size and is round to slightly oval; the mean ratio of major axis to minor axis equals 1.3 (range 1.0–1.7). Nasolabial lobes are small and obscure. Eyes are moderately large and protrude beyond the jaw margins in dorsal view. A suborbital groove intersects the lip on each side. There are very few teeth. Two males each have one premaxillary tooth; mean number for females equals 0.5 (range 0–1). Mean number of vomerine teeth equals six in males (range 5–7) and 4.5 in females (range 4–5). There are no

maxillary teeth. Limbs are relatively long; limb interval equals four in one male and 3.4 in females (range 2–4.5). Hands and feet are narrow, and the digits are syndactylous with rounded tips (when free); the outermost digits are small and indistinct. Fingers, in order of decreasing length, are 3-2-1-4; toes are 3-2-4-1-5. The postiliac gland is a distinct pale spot. The tail is long and tapers progressively from its midpoint to its tip.

Measurements of the holotype (in millimeters).—Head width 2.4; snout to gular fold (head length) 3.1; head depth at posterior angle of jaw 1.5; eyelid width 0.5; eyelid length 1.4; anterior rim of orbit to snout 0.9; horizontal orbit diameter 1.0; interorbital distance 0.7; snout to forelimb 5.1; distance separating external nares 0.5; major axis of nostril 0.45; minor axis of nostril 0.38; snout projection beyond mandible 0.2; snout to posterior angle of vent (standard length) 17.6; snout to anterior angle of vent 16.4; axilla to groin 9.8; tail length 19.3; tail width at base 1.5; tail depth at base 1.7; forelimb length (to

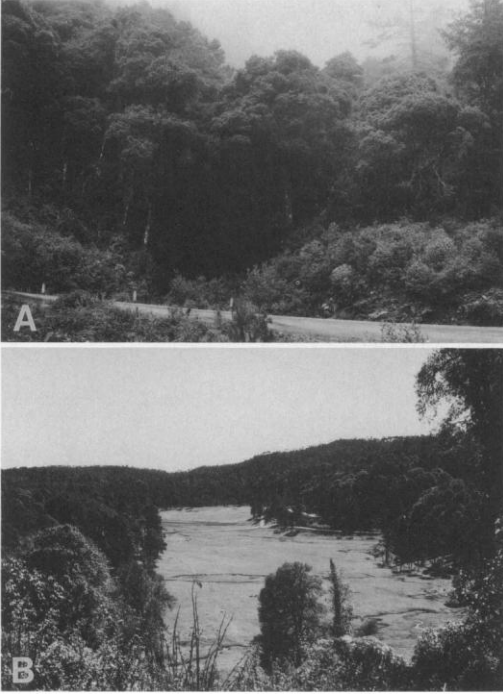


Fig. 6. Type localities of two new species of *Thorius*. (A) 51 km N Guelatao along Hwy. 175, the type locality of *T. aureus*, in July 1976. Here a deep ravine crosses the highway 1 km north of the crest of Cerro Pelón (recorded as 0.7 mi E Cerro Pelón on some specimen tags). Two additional congeneric species—*T. macdougalli* and *T. boreas*—occur at this site, which also is the type locality for *Pseudoeurycea juarezi* (Regal, 1966). (B) Llano de las Flores, 25–26 km N Guelatao along Hwy. 175, the type locality of *T. boreas*, in Feb. 1976. The view is from the highway at the north end of the meadow, looking south. This also is a collection locality for *T. macdougalli*. Both species have been taken on the forest floor and under the bark of fallen logs, especially at the forest edge.

tip of longest toe) 2.2; hind limb length 3.4; hand width 0.6; foot width 0.8.

Coloration of the holotype (in alcohol).—The dorsum is a dark golden brown, mottled with darker brown. A dark band arises in the nasal region, passes along the side of the head, narrows to a wavy line that rises over the shoulder, and dips to the dorsolateral margin of the trunk. From here, it extends caudal to the hind limbs where it dips sharply ventrolaterally and then rises to a midlateral position at the tail base. It then extends uninterrupted for a distance three-quarters of the length of the tail, at which point it begins to break up and extend as a series of dots to the tail tip. There is a distinct light saddle over the caudosacral region. The venter is

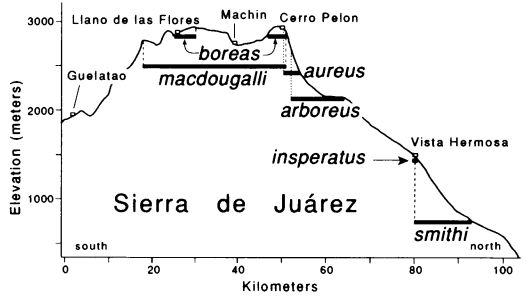


Fig. 7. Distribution of six species of *Thorius* along a line transect crossing the Sierra de Juárez, Oaxaca, México, from south (left) to north (right). Horizontal bars indicate the absolute known elevational and geographic limits for each species. *Thorius insperatus* is known from only the type locality.

generally lighter than the dorsum, with the greatest amount of pigment over the gular region and extending halfway back along the body. Large guanophores are spotted on the gular region, the breast region, and for a short distance behind the insertion of the forelimb. The dorsum is boldly marked along the midline with small chevronlike markings at each vertebral position. Limbs are much lighter than the body. There are some whitish spots on the tip of the snout and immediately below the eye.

Coloration in life.—Based on field notes by J. Hanken for MVZ 183349 and MVZ 187010-11. There is a reddish dorsal stripe, but only one animal has the ornate pattern (dorsolateral margins of stripe “pinched” over the shoulders) generally characteristic of the species; the other animals have a “normal” stripe.

Osteology.—Four complete skeletons have been available for this species. In general, the skeleton closely resembles that of *T. macdougalli* (Hanken, 1982, 1984) and is less well developed than that of either *T. aureus* or *T. boreas*. Skulls of the two larger individuals (both adult females) have a broad premaxillary bone that reaches the maxillaries (character 2, state b; Figs. 2A, 3A), but the bone is narrower (state a) in the two smaller specimens (both males). The ascending processes are fused basally (character 1, state c) in both females but are mainly unfused (state b) in the two males. The premaxillary bears a single tooth in three specimens (character 8, state b) and lacks teeth in a fourth (state a). Nasals generally are small (character 3, state b) but are larger (state c) in one female. The nasals meet the ascending processes of the maxillaries in three individuals (character 4, state

b) but fail to do so (state a) in one male. The slender maxillaries are toothless (character 9, state a; Fig. 4C). The relatively well-developed prefrontals articulate with the nasal (character 5, state c), but they are separated from the ascending processes of the maxillaries by the foramen of the nasolacrimal duct (character 6, state a). There are no septomaxillary bones (character 7, state a).

There is a narrow frontal fontanelle, but the parietal fontanelle is large (equals 0.38–0.42 times the maximum skull width across the parietals in three measurable specimens). There is no otic crest and no columellar process on the operculum. The postsquamosal process is well developed and spinous. The vomer has a very short but distinct preorbital process, and teeth are borne nearly to the tip.

Vertebrae are similar to those described for *T. aureus* but smaller. A tibial spur is absent in one female but present as a semiattached process in the remaining individuals. The four specimens have carpal patterns I (one specimen) or II (Fig. 5A; Hanken, 1985, *T. arboreus* identified as “*T. sp. E*”). Tarsi have patterns VII, with six separate elements and two fusion combinations (intermedium plus fibulare, and distal tarsals 4 and 5 plus centrale), or VIII (like VII, but with fused distal tarsal 1-2 plus 3; Fig. 5F). The ancestral phalangeal formulae (1-2-3-2, and 1-2-3-3-2) are present in some specimens, but reduced formulae (1-2-3-1 and 1-2-3-2-1) are also found. One female has 1-2-3-2 in one carpus and 1-2-2-2 in the other (1-2-3-3-2 for both tarsi).

All mesopodials are ossified in one female, which also has the epibranchials mineralized near their articulation with the ceratobranchials. Mesopodials are cartilaginous in the other individuals.

Comparisons to other taxa.—This very small species is most similar in morphology and proteins to *T. macdougalli*, a species that is widespread to the south but only barely occurs on the upper, north-facing slopes of the Sierra de Juárez. There is about one km in road distance between the closest known localities of the two taxa; but, in this short interval, the road drops nearly 200 m in elevation, the harsh climatic regime of the peaks ameliorates, and the vegetation becomes tall and lush, with the trees laden with bromeliads and other epiphytes. We have never taken *T. macdougalli* in arboreal settings, but all *T. arboreus* for which data exist have been taken in this microhabitat. Furthermore, *T. arboreus* is smaller, with smaller feet, it has a more rounded nostril, and it has a different color pattern

than *T. macdougalli*. The longest toe of *T. arboreus* has an expanded “T” shape (Fig. 5F). *Thorius macdougalli* is stockier in proportions and typically has a bright nuchal spot, whereas the slender *T. arboreus* has a colorful pattern with a dorsal band that has a distinctive dorsolateral boundary. This is the only species in this mountain range that has arboreal habits. Some species (of uncertain taxonomic status) in central Veracruz and eastern Puebla occur in arboreal microhabitats, but these species differ in coloration and proteins (Hanken, 1983).

Habitat and range.—*Thorius arboreus* is known only from the type locality and other nearby cloud forest localities along Hwy. 175 on the Atlantic drainage of the Sierra de Juárez (Fig. 7). It is sympatric with *T. aureus* at upper elevations (e.g., 52 km N Guelatao, 2755 m), where it has been collected only one km (by road) from both *T. macdougalli* and *T. boreas*. The lowest recorded elevation is 2170 m.

Etymology.—The species name is derived from the Latin word *arbor*, meaning tree, in recognition of the arboreal habits of this species, which is frequently found in the leaf axils of bromeliads, both on the ground and on trees.

Thorius boreas n. sp.
Boreal Thorius

Holotype.—MVZ 162202, an adult male from Llano de las Flores, along Hwy. 175, 25–26 km NE Guelatao, Oaxaca, México, collected by T. J. Papenfuss, 12 Aug. 1975.

Paratypes.—All from Oaxaca, México: MVZ 85985, 85995, 11.7 mi SW Cerro Pelón on Tuxtepec-Oaxaca rd., 17 mi NE Ixtlan de Juárez, collected by R. W. McDiarmid, 21 Jan. 1969; MVZ 112169, 22 km N Guelatao along Hwy. 175, collected by T. J. Papenfuss, 5 Aug. 1974; MVZ 131363, 33 km (rd.) N Guelatao along Hwy. 175, elev. 2940 m, collected by D. B. Wake, 20 Nov. 1974; MVZ 162188-98 (11 specimens), 162203, 162204, 162244, 162250, same data as the holotype; MVZ 183327, 187162-64 (three specimens), same locality as the holotype, elev. 2830 m, collected by J. F. Lynch, 21 July 1976; MVZ 186999, 187000, 29.1 km N Guelatao along Hwy. 175, elev. 2890 m, collected by H. B. Shaffer, 29 June 1978; MVZ 187161, same locality as the holotype, elev. 2950 m, collected by J. Hanken, 9 Feb. 1976; MVZ 183528, 187165-68 (four specimens), 18.9 mi (rd.) N Guelatao along Hwy. 175, elev. 9470 ft, collected by J. Hanken, 19 July 1976; MVZ 187169-

73 (five specimens), same locality as the holotype, elev. 9340 ft, collected by J. Hanken, 20 July 1976; MVZ 187174-78 (five specimens), Cerro Pelón, 31.8 mi N Guelatao, 1.0 km E from where Hwy. 175 crosses top, collected by J. Hanken, 21 July 1976; LACM 58669, 58670, 18.8 mi N Guelatao, elev. 10000 ft, collected by D. Paulson, 5 Aug. 1965. Some of the above specimens are cleared and stained.

Diagnosis.—This is a large, robust species of *Thorius* distinguished from other members of the genus by the following combination of traits: very dark dorsal and ventral coloration, large size, relatively large nostril, no maxillary teeth, and protein variants. It is distinguished from sympatric congeners as follows: from *T. aureus* by its darker coloration and larger nostril, and in lacking maxillary teeth; from *T. macdougalli* by its larger size, more robust habitus, and smaller nostril.

Description.—This is a large, robust species; adult standard length averages 27.4 mm (range 25.1–29.9) in 21 males, and 29.7 mm (range 24.7–34.9) in 20 females. The head is relatively narrow; standard length averages 7.7 times head width in males, 8.4 times head width in females. Snouts are bluntly pointed in females and more sharply pointed in males. Nostrils are large and oval; the mean ratio of major axis to minor axis equals 1.8 (range 1.4–2.3). Eyes are small and barely protrude beyond the jaw margins in dorsal view. A suborbital groove intersects the lip on each side. There are few premaxillary teeth (range 2–3, mean 2.2 in males; range 2–6, mean 4.3 in females), moderate numbers of vomerine teeth (range 8–11, mean 9.9 in males; range 7–11, mean 9.3 in females), and no maxillary teeth. Limbs are moderately long for the genus; limb interval averages 5.9 in males and 6.5 in females. Hands and feet are of moderate size. Only the two longest fingers and the three longest toes are free at their tips, and these tips are rounded rather than pointed in adults. Fingers, in order of decreasing length, are 3-2-5-1; toes are 3-4-2-5-1. The distinction between folds and grooves along the trunk and tail is especially well marked. The postiliac gland is obscure. The tail is robust and does not taper noticeably until its tip.

Coloration varies little from that of the holotype. This generally is a very dark species, especially dorsally and laterally; coloration lightens somewhat ventrally. There often are obscure dorsal markings in the form of a faint, somewhat lighter dorsal stripe with wavy borders. This dorsal stripe may have light chevrons

or partial chevrons associated with successive costal grooves. There is a scattering of small white dots along the ventrolateral margins of the trunk, but typically there are few or no spots in the gular area or on the venter of the trunk or tail. The mental gland is a prominent, light colored protuberance. The iris is charcoal.

Measurements of the holotype (in millimeters).—Head width 3.5; snout to gular fold (head length) 4.5; head depth at posterior angle of jaw 2.1; eyelid width 0.8; eyelid length 1.7; anterior rim of orbit to snout 1.5; horizontal orbit diameter 1.2; interorbital distance 1.0; snout to forelimb 7.4; distance separating external nares 0.9; major axis of nostril 0.84; minor axis of nostril 0.36; snout projection beyond mandible 0.6; snout to posterior angle of vent (standard length) 27.7; snout to anterior angle of vent 26.2; axilla to groin 15.0; tail length 28.5; tail width at base 2.1; tail depth at base 2.4; forelimb length (to tip of longest toe) 3.5; hind limb length 3.9; hand width 1.0; foot width 1.3.

Coloration of the holotype (in alcohol).—This is a dark gray animal, especially laterally; the venter is a lighter, charcoal color. An obscure ebony dorsal stripe extends from the level of the eyes to the base of the tail where it gradually disappears. There are small, ventrolateral and gular guanophores. The mental gland is whitish. Nasolabial protuberances are pronounced and unpigmented at their tips. Limbs are dark basally but lighter distally.

Coloration in life.—Based on field notes by J. Hanken for MVZ 18699-700; see also Figure 1B. There is a broad dorsal stripe, which is not very conspicuous because of its dark brown color and “herring-bone” pattern. The venter is black with slight, very fine light speckling.

Osteology.—This description is based on data from 22 partial to complete skeletons. This large species has a relatively well-ossified skeleton. However, the bones are slightly smaller and less robust than those of *T. aureus* of similar size, with the exception of the nasal, which is larger (Figs. 2C, 3C). The premaxillary bone is sexually dimorphic; it is narrow and slightly (if at all) overlaps the maxillary in males (character 2, states a and b) but broadly and extensively overlaps or articulates with the maxillary in females (states c and d). The ascending processes of the premaxillary are partially fused, usually for about one-half of their length (character 1, state c) but less in some specimens (intermediate between states b and c) and more in another

(state d); in eight specimens a small and obscure fontanelle is enclosed by the processes below the zone of fusion. Premaxillary teeth are present on all adult specimens (character 8, state b). The moderately large (but very small in comparison with other bolitoglossine salamanders) nasals contact the ascending processes of the maxillaries (character 4, state b). The prefrontals are moderately large for the genus and are crescentic in shape; they typically overlap the frontals, and narrowly articulate with the nasals (13 individuals, with asymmetrical contact in two others; character 5, state c). In most specimens, they are separated from the ascending processes of the maxillaries (character 6, state a) by the foramen of the nasolacrimal duct. However, in one individual, the prefrontal contacts the maxillary (state b) on both sides, and, in two others, there is contact on one side. The maxillaries are relatively well developed but lack teeth (character 9, state a). There are no septomaxillary bones (character 7, state a; Fig. 4B).

There is a narrow frontal fontanelle (about the same size as in *T. aureus*, or slightly broader) and a relatively broad parietal fontanelle (which appears larger than in *T. aureus* but measures about the same, having a breadth of 0.23–0.44, mean 0.32, times the maximum skull width across the parietals). There is no otic crest, and there is no columellar process on the operculum. The postsquamosal process is well developed. The vomers have a short, toothed pre-orbital process.

Vertebrae resemble those of *T. aureus* in morphology and number. A tibial spur is present in most specimens; it is attached by a bony web to the tibia in 10 specimens, free distally in eight specimens, and reduced to a crest in three others. Ends of long bones and condyles on the anterior end of vertebral centra are ossified in adults. Mesopodial morphology is relatively generalized (Fig. 5C, H). Hanken (1982; *T. boreas* identified as "*T. sp. C*") reported carpal pattern I (see above description of *T. aureus*) in 87.5% of 40 carpi examined; remaining specimens had patterns II (10%) and III (2.5%). Tarsal pattern I was found in all but one of 40 tarsi examined (97.1%); one tarsus had pattern III (2.8%).

All mesopodials are ossified in three adults, but some elements are ossified in four other specimens. The basibranchial is mineralized in two specimens that have fully ossified mesopodials, but otherwise there are no hyobranchial mineralizations.

Comparisons to other taxa.—This is a large, stout species of *Thorius* that is readily distinguished

from its equally large, sympatric associate, *T. aureus*, by its darker coloration, absence of maxillary teeth, and elongate nostril. It is less readily distinguished morphologically from *T. narisovalis*, a large, dark species from the region of Cerro San Felipe, in the mountain range immediately to the south of the Sierra de Juárez. In general, *T. boreas* is larger and has a larger and more elongate nostril than *T. narisovalis*. *Thorius pulmonaris* is another species from the Cerro San Felipe region, which generally occurs at lower elevations than *T. boreas*, but it is smaller and has a somewhat larger nostril. Both species from Cerro San Felipe differ in many protein variants from *T. boreas* (Hanken, 1983).

Habitat and range.—*Thorius boreas* is known only from the type locality and other localities along Hwy. 175 both north and south of the crest of Cerro Pelón in the Sierra de Juárez (Figs. 6B, 7). It has been taken in sympatry with *T. macdougalli* at several localities in and near Llano de las Flores (Fig. 6B) and with both *T. macdougalli* and *T. aureus* in a deep ravine that crosses Hwy. 175 one km north of the crest of Cerro Pelón (Fig. 6A). It is a terrestrial species that occupies primarily pine-oak-fir forest. Recorded elevations are between 2850 and 2950 m.

Etymology.—The species name is derived from the Greek word *boreas*, meaning the north wind, in recognition of the elevational range of this species, which is confined to the cool montane peaks at elevations above 2850 m.

Thorius smithi n. sp.
Smith's *Thorius*

Holotype.—MVZ 150590, a female from 0.5 mi (rd.) SW Vista Hermosa along Hwy. 175, Oaxaca, México, collected by J. E. Cadle, 14 July 1977.

Paratypes.—MZFC 5316, 1–2 km SW Metates, Oaxaca, México, elev. approximately 800 m, collected by J. R. Mendelson, III, and A. Nieto, 19 July 1992.

Diagnosis.—This is a small species of *Thorius* with a dull dorsal stripe and maxillary teeth. It is distinguished from congeners in the Sierra de Juárez as follows: from *T. macdougalli* and *T. arboreus* by its more rounded nostril and in having maxillary teeth; from *T. boreas* by its smaller adult size, more rounded nostril, and maxillary teeth; from *T. aureus* by its small size, more rounded nostril, and darker ventral coloration;

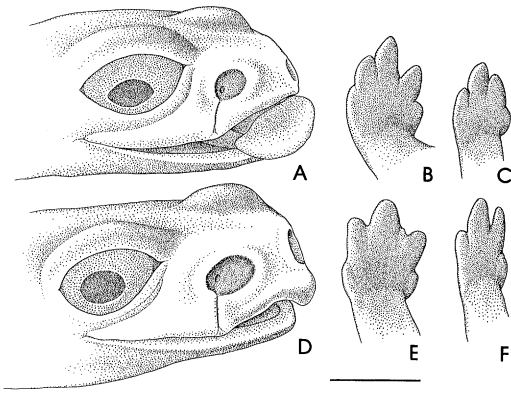


Fig. 8. Diagnostic features of two new species of *Thorius*. (A–C) *T. smithi*, MZFC 5316 (paratype). (D–F) *T. insperatus*, KU 66799 (holotype). Left hands (C, F) and feet (B, E) are shown in dorsal view; the tongue protrudes slightly from the mouth in A. Scale bar equals 1 mm.

and from *T. insperatus* by having maxillary teeth and pointed toe tips.

Description.—This is a small, slender species; standard lengths of the two known specimens, both females, are 20.3 and 20.4 mm. The narrow head has a somewhat truncate but bluntly pointed snout; standard length averages 7.4 times head width. The relatively large, round-to-slightly elongate nostrils have a ratio of major axis to minor axis of 1.1–1.3 (Fig. 8A). Nasolabial grooves extend through a cutaneous enlargement that has only a slight ventral lobe. The eyes are of moderate size and, when viewed from above, protrude only slightly beyond the margin of the jaw. A suborbital groove curves beneath the eyes and intersects the lip below the posterior margin of the orbit. Each specimen has three premaxillary teeth. Maxillary teeth range from 16 to 21, and there are 6 to 9 vomerine teeth. Limbs are relatively long; limb interval ranges from 3.5 to 4. The hands and feet are very small (Fig. 8B, C). The tips of the longest digits are pointed, and the outermost digits are barely differentiated and have no free tips. Fingers, in order of decreasing length, are 3-2-1-4; toes are 3-2-4-1-5. The postiliac gland is pale and obscure. The relatively long tail, which exceeds standard length in one specimen, is very slender and tapers progressively along its entire length to a sharply pointed tip.

This is a generally dark salamander with an obscure, light dorsal stripe that extends from the level of the eyes onto the tail. The ground color is a rich dark brown. The light stripe is

bordered by a dark dorsolateral band that extends onto the tail. The flanks and venter are lighter, with numerous white spots (approximately 0.1–0.2 mm in diameter), especially in the gular region. The limbs are the same rich dark brown as the flanks, and they too have some small white spots. The iris is charcoal.

Measurements of the holotype (in millimeters).—Head width 2.9; snout to gular fold (head length) 3.8; head depth at posterior angle of jaw 1.6; eyelid width 0.5; eyelid length 1.0; anterior rim of orbit to snout 1.3; horizontal orbit diameter 1.2; interorbital distance 1.1; snout to forelimb 5.9; distance separating external nares 0.6; major axis of nostril 0.45; minor axis of nostril 0.41; snout projection beyond mandible 0.2; snout to posterior angle of vent (standard length) 20.3; snout to anterior angle of vent 18.3; axilla to groin 11.0; tail length 20.2; tail width at base 1.5; tail depth at base 1.9; forelimb length (to tip of longest toe) 3.6; hind limb length 4.5; hand width 0.7; foot width 1.1.

Comparisons to other taxa.—Most species of *Thorius* lack maxillary teeth. *Thorius smithi* can be distinguished from the three described species that have maxillary teeth as follows: from *T. aureus*, which occurs at higher elevations on the northern flanks of Cerro Pelón, by its much smaller size and darker coloration; from *T. schmidtii*, which occurs in Puebla, well to the north of the Sierra de Juárez, by its more rounded nostrils and smaller size; and from *T. maxillibrochus*, which is sympatric with *T. schmidtii*, by its smaller size, narrower feet, and more pointed toe tips. It is distinguished from its only sympatric associate, *T. insperatus*, by having maxillary teeth and by having pointed, rather than rounded, toe tips.

Habitat and range.—*Thorius smithi* extends to lower elevations than any *Thorius* reported to date. It is known only from cloud forest and tropical forest localities along Hwy. 175 between approximately 800 and 1550 m elev. (J. E. Cadle's field notes record the elevation of the collection locality above Vista Hermosa as 1440 m. However, the elevation of Vista Hermosa is approximately 1500 m, and we believe that 1550 m is a more accurate estimate of the elevation of this locality.) Both known specimens were collected on the ground—the holotype in a pile of wood chips, the paratype under a rock.

Etymology.—The species name honors H. M. Smith, in recognition of his unparalleled con-

tributions to Mexican herpetology, including the taxonomy of *Thorius*.

Thorius insperatus, n. sp.
Surprise *Thorius*

Holotype.—KU 66799, an adult male from Vista Hermosa, Oaxaca, México, collected by J. B. Tulecke on 14 Aug. 1961. The species is known from the unique holotype.

Diagnosis.—This is a small, slender species of *Thorius* distinguished from other members of the genus by the following combination of traits: dark brown color with light dorsal stripe; small size; large, elongate nostril; and no maxillary teeth. It is distinguished from its sympatric congener, *T. smithi*, by its lighter dorsal coloration, its rounded rather than pointed toe tips, and in lacking maxillary teeth.

Description of the holotype.—This apparently adult male, 19.5 mm SL, represents a small species. The narrow head has a swollen, rounded snout and is only slightly broader than the anterior trunk. Standard length is about seven times head width. The nostrils are very large and oval; the major axis is 1.5 times the minor axis (Fig. 8D). The nasolabial region is swollen and contains a well-defined nasolabial groove extending through a broad lobe on the upper lip. The moderately large eyes protrude slightly beyond the margin of the jaw when viewed from below. The suborbital groove curves beneath the eyes and intersects the lip below the posterior margin of the orbit. There are seven vomerine teeth and no premaxillary or maxillary teeth. Limbs are relatively long; limb interval equals 3.5. The hands and feet are narrow but well developed; the longest digits (fingers 2 and 3 and toes 2, 3, and 4) have rounded tips that are distinct and free from the otherwise syndactylous nature of the hands and feet (Fig. 8E, F). Fingers, in order of decreasing length, are 3-2-4-1; toes are 3-2-4-1-5. The postiliac gland is pale and clearly evident. The tail is broken from the body (post-preservational) and apparently was damaged during capture (broken at the midway point). The tail is relatively stout and long, tapering along its entire length. A mental gland is ill-defined.

Measurements of the holotype (in millimeters).—Head width 2.8; snout to gular fold (head length) 3.5; head depth at posterior angle of jaw 1.8; eyelid width 0.6; eyelid length 1.4; anterior rim of orbit to snout 1.0; horizontal orbit diameter 1.1; interorbital distance 1.1; snout to forelimb

5.8; distance separating external nares 0.5; major axis of nostril 0.6; minor axis of nostril 0.4; snout projection beyond mandible 0.4; snout to posterior angle of vent (standard length) 19.5; snout to anterior angle of vent 17.9; axilla to groin 11.1; tail length 21.2; tail width at base 2.2; tail depth at base 1.9; forelimb length (to tip of longest toe) 3.6; hind limb length 4.2; hand width 0.7; foot width 1.2.

Coloration of the holotype (in alcohol).—The specimen is in very good condition, but, after 30 years of preservation, it has faded to a dark brown with a light tan dorsal stripe. The stripe extends from the back of the head onto the base of the tail, where it merges with the background coloration. A few flecks of light pigment are present on the flanks of the trunk. The venter is slightly lighter than the lateral surfaces. Obscure white spots are present on the gular region and on the anterior part of the trunk venter. The iris is charcoal.

Coloration in life.—From field catalog of W. E. Duellman: "ground color gray-brown with light gray flecks. Olive tan on dorsal surfaces of body and tail."

Comparisons to other taxa.—It is unusual for species of *Thorius* in the Sierra de Juárez to occur at elevations below 2000 m, so it was surprising to discover not one but two species in the same elevational zone (approximately 1500 m) near the lower end of the Cerro Pelón transect. Syntopic *T. insperatus* and *T. smithi* differ in nostril and digit shape and by the presence or absence of maxillary teeth. *Thorius insperatus* is much smaller than *T. aureus* and *T. boreas*, which occur at higher elevations on the same transect. It also lacks the distinctive coloration and habitat of *T. arboreus*, whose mean body size is slightly smaller than the single known specimen of *T. insperatus*. *Thorius macdougalli* is a more robust salamander with a more elongate nostril; it occurs at higher elevations mainly on the south side of the transect. The only other species of *Thorius* known to occur at relatively low elevations along the Atlantic drainage are *T. penatulus* and *T. narismagnus*, which occur at slightly below 1000 m in neighboring Veracruz. These two small species are distinct from *T. insperatus* in having smaller, round nostrils.

Habitat and range.—*Thorius insperatus* is known from the unique holotype, which was collected from beneath a log in the lower cloud forest near the hamlet of Vista Hermosa.

Etymology.—The species name is derived from the Latin word *insperatus*, meaning unexpected, or not even hoped for, in recognition of the authors' surprise at the discovery, made only as the present paper was being prepared, that not one but two species of *Thorius* coexist at lower elevations of the north side of the Cerro Pelón transect.

REDESCRIPTION

The original description of *T. macdougalli* (Taylor, 1949) was thorough, but the taxon was compared only to *T. pulmonaris*. Accordingly, we present a brief redescription, emphasizing the traits that have proven useful in discriminating taxa in the Sierra de Juárez.

Thorius macdougalli Taylor, 1949

Holotype.—AMNH 52136, collected on Cerro de Humo, Maquiltianguis, Oaxaca, México, by T. C. MacDougall on 2 March 1945.

Diagnosis.—This is a small species of *Thorius* with large, elongate nostrils and no maxillary teeth. It is distinguished from sympatric associates as follows: from *T. boreas* by its smaller size and larger nostril; and from *T. aureus* by its smaller size, darker coloration, and much larger nostril. It is distinguished from its parapatric relative *T. arboreus* by its slightly larger size and larger, more elongate nostril. It is distinguished from all other species of *Thorius* by a combination of allozymic, osteological, and external morphological traits (Hanken, 1982, 1983, 1984; Figs. 2B, 3B, 4D, 5D, 5E, 5I, 5J).

Description.—This is a small but stocky species; adult standard length averages 20.2 mm (range 17.5–22.6) in 12 males, and 21.2 mm (range 17.6–26.5) in 11 females. The head is moderately wide for the genus; standard length averages 7.0 times head width in males, and 7.1 times head width in females. Snouts are bluntly to sharply pointed. Nostrils are large and oval; the mean ratio of major axis to minor axis is 1.8 in males (range 1.7–2.2) and 1.7 in females (range 1.4–1.9). The eyes are small and barely protrude beyond the jaw margins in dorsal view. A suborbital groove intersects the lip on each side. There are no premaxillary or maxillary teeth in females and no maxillary teeth in males; males have 2–3 premaxillary teeth. There are very few vomerine teeth (4–5 in each sex). Limbs are relatively long; limb interval averages 3.0 in males and 3.8 in females. Feet are of moderate size for the genus. The fingers and toes

are well developed; the tips of the two middle fingers and three middle toes are broadly rounded and well separated from one another.

Coloration (in alcohol).—This species has a dark brownish-black ground color with a dorsal mottling of lighter coloration or a light dorsal stripe. The venter is covered with abundant small whitish flecks or spots, especially in the throat and gular region. A distinctive feature is the almost invariable presence of a small, bright, tan-to-golden nuchal spot.

DISCUSSION

Allozyme data.—Hanken (1980, 1983) examined genetic differentiation among populations of *Thorius* assayed by protein electrophoresis. In this section, we summarize these data with respect to the four species of *Thorius* from the Sierra de Juárez for which such data exist—*T. macdougalli*, *T. aureus*, *T. boreas*, and *T. arboreus*. No biochemical data are available for either *T. smithi* or *T. insperatus*.

Each of the four species displays protein variation among conspecific populations. Genetic distances (Nei, 1972) within *T. macdougalli* (populations 18–30, all from the Sierra de Juárez) range from 0.011–0.392 (mean 0.147); the large values result from clinal patterns of allozyme variation in the high elevation populations (Hanken, 1983, Fig. 4). Comparable distance values within the remaining species are as follows: *T. boreas* (populations 32–36) 0.035–0.210, mean 0.125; *T. aureus* (populations 37–39) 0.005–0.071, mean 0.046; and *T. arboreus* (populations 40–44) 0.044–0.271, mean 0.170. Given the relatively small known geographic ranges of both *T. boreas* and *T. arboreus*, and, hence, the small distance between conspecific localities, the level of interpopulational variation within each of these species is relatively great. As with *T. macdougalli*, this divergence is the result of extensive clinal variation within each species. Even these large genetic distances, however, are exceeded by some measured among populations of the more extensively sampled *T. macdougalli* in the same area.

Protein data for interspecific comparisons among populations from the Sierra de Juárez are presented in Table 1. Genetic distance (based on samples of five or more specimens) between species ranges from a mean of 0.26 between *T. macdougalli* and *T. arboreus* to 0.97 between *T. macdougalli* and *T. boreas*. The smallest pairwise distance between individual populations of different species is 0.20 (population 27, *T. mac-*

TABLE 1. GENETIC DIFFERENTIATION AMONG SPECIES OF *Thorius* IN THE SIERRA DE JUÁREZ (BASED ON HANKEN, 1980). Above diagonal, mean Nei genetic distance between species (range in parentheses), based on population samples of five or more specimens. Below diagonal, proteins showing fixed differences between species (bold-face) or nearly fixed differences, i.e., variants shared by only some populations at frequencies of 0.25 or less. Diagonal, number of populations sampled per species.

	<i>macdougalli</i>	<i>boreas</i>	<i>aureus</i>	<i>arboreus</i>
<i>macdougalli</i>	n = 13	0.97 (0.61–1.02)	0.88 (0.61–1.02)	0.26 (0.20–0.32)
<i>boreas</i>	Pt-2, Gapdh, Gpi, Lap, Mdh-1, Got-1, Mpi	n = 5	0.30 (0.23–0.40)	0.77 (0.65–0.92)
<i>aureus</i>	Lap, Gapdh, Gpi, Mpi, Mdh-1	Pt-2, Gapdh	n = 3	0.59 (0.54–0.64)
<i>arboreus</i>	Gpi^a	Pt-2, Gapdh, Mdh-1	Gapdh, Mdh-1	n = 6

^a An *arboreus* variant is present in one *macdougalli* population at a frequency of 0.06.

dougalli vs population 41, *T. arboreus*); the largest distance is 1.12 (population 27, *T. macdougalli* vs population 36, *T. boreas*). Moreover, fixed differences involving at least two and as many as six different allozymes characterize each pairwise species comparison (Table 1). These genetic differences, combined with the numerous instances of sympatry which involve as many as three species with no indication of interbreeding (Table 5 in Hanken, 1983), and with the morphological differences discussed earlier, affirm the distinctiveness of each species. Some pairwise genetic distances within *T. macdougalli* and *T. arboreus* exceed some pairwise distances between populations of the two species. We regard this as an artifact of the extensive clinal variation within each species, which are otherwise clearly distinct.

In phenograms of 69 populations of *Thorius* from throughout the range of the genus in southern Mexico, the two large (*T. aureus*, *T. boreas*) and two of the small (*T. macdougalli*, *T. arboreus*) species from the Sierra de Juárez cluster together (fig. 2 in Hanken, 1983). These species are more similar to one another than to other taxa. These two species pairs, however, cluster with each other only after linking with several other species from outside the Sierra de Juárez. We do not attempt any phylogenetic analysis of the protein data here, because we deal primarily with only a small subset of the genus. However, there is no reason to believe that the species in the Sierra de Juárez represent a single clade.

Morphological data.—Species of *Thorius* have long been regarded as extremely difficult to distinguish morphologically (e.g., Gehlbach, 1959). We believe that a large part of this perceived

difficulty emanates from the failure to accurately distinguish sympatric taxa. Once such taxa are differentiated on biochemical grounds (Hanken, 1983), characteristic morphological traits can be found for nearly all species. Features that are especially effective in this regard are color pattern, adult body size, nostril size and shape, and the presence or absence of maxillary teeth. There also are significant osteological differences (Hanken 1982, 1984, 1985).

Distribution of salamanders in northern Oaxaca.—

We have confined this taxonomic study to the six species of *Thorius* that exist along the northern part of Transect Two of Wake et al. (1992), the region of Oaxaca that has been most thoroughly investigated in terms of local salamander distribution and taxonomy. In Figure 7, we outline the distribution of these species in relation to elevation for the Sierra de Juárez, correcting and extending previous representations (Hanken, 1983; Wake, 1987; Wake et al., 1992).

We recognize a total of eight named species of *Thorius* (and possibly one unnamed) along a nearly straight transect from Oaxaca City north through Guelatao and Vista Hermosa to Tuxtepec. Immediately north of Oaxaca City, two species occur at different elevational ranges over an extensive area on Cerro San Felipe: the large (males reach 27 mm SL, females may exceed 31 mm SL), small-nostrilled *T. narisovalis*, and the somewhat smaller, large-nostrilled *T. pulmonaris*. There is then a distributional gap to about 10 km (by rd.) south of Guelatao (2230 m elev.), where *Thorius* is again found. This population is known from a single specimen, which is severely deformed apparently by a parasitic infestation. It is distinct in allozymes from all described species of *Thorius* (Nei D greater than

0.5); the most genetically similar species on the transect is nearby *T. macdougalli*, from which it differs by three fixed differences and which otherwise is not known from elevations below 2760 m (Hanken, 1983). *Thorius macdougalli*, however, is known to display strong geographic differentiation in proteins (Hanken, 1983); and, in the absence of morphological data, we tentatively assign this population to *T. macdougalli*.

Thorius macdougalli occurs continuously from about 18 km south of Guelatao to just beyond the high point on the road (locally known as Cerro Pelón) on the north-facing slopes of the Sierra de Juárez. This species has the most extensive range of any *Thorius* in this region, extending upward to elevations of 2955 m. Populations similar in morphology to *T. macdougalli* are known to occur south and east of this transect, and Hanken (1983) studied a population from the vicinity of Totontepec that is more similar genetically to *T. macdougalli* (Nei D is 0.38–0.48) than to any other species (with the exception of a geographically remote population of uncertain taxonomic status from Guerrero). We assign these Oaxacan populations to *T. macdougalli*.

A complex pattern of sympatry and species replacement occurs along this part of the transect. In two disjunct zones above 2850 m elev.—in the vicinity of Llano de las Flores and on Cerro Pelón—the larger, darker and more robust *T. boreas* occurs in microsympatry with *T. macdougalli*. At the top of Cerro Pelón, and for a short distance along the northern slope of that mountain, a third species, *T. aureus*, occurs in microsympatry with the others over an elevational range of about 50 m and a linear geographic distance of at most a few hundred meters. All three species are terrestrial. Both *T. boreas* and *T. macdougalli* drop out slightly above the 2900 m level on the north slope, but *T. aureus* continues on for another 3.5 linear kilometers, down to 2475 m elev. A few hundred meters beyond the lowest known locality of *T. boreas* and *T. macdougalli*, the first *T. arboreus* are encountered (at 2755 m elev.). This species is found most frequently in bromeliads growing either on the ground or in trees and occasionally under the bark of logs. There are no authenticated records of *T. arboreus* taken in or on the ground.

For about two linear kilometers along the north slope, down to an elevation of 2475 m, the ranges of the large, colorful, terrestrial *T. aureus* and the small, dark, mainly arboreal *T. arboreus* overlap. At this point, the former species drops out, and the latter is found exclusively for another 11 km, where it has been found at

an elevation of 2170 m. Despite extensive searches, no populations of *Thorius* have been found between here and Vista Hermosa (approximately 1500 m elev.), where *T. smithi* and *T. insperatus*, two small, terrestrial species, occur together. *Thorius insperatus* is known only from a single site, but *T. smithi* also has been taken below Vista Hermosa near Metates, approximately 800 m elev. This is the lowest known elevation for any species of *Thorius*.

The highest elevations of the Sierra de Juárez (above 2850 m) are populated by three species of *Thorius* and from one to three species of *Pseudoeurycea* (all may be undescribed, although one has been assigned to *P. smithi*; Wake et al., 1992). An additional species, *P. bellii*, occurs to the south of Cerro Pelón at relatively high elevations. From the top of Cerro Pelón northward to the lowlands in the vicinity of Tuxtepec, as many as 15 species are known. These include the three species of *Thorius* mentioned above and an apparently undescribed species of *Pseudoeurycea* that resembles *P. smithi* (of Cerro San Felipe) in some aspects of its morphology but is larger and more muscular in appearance; all occur in the vicinity of the summit along the main highway. As one proceeds downslope to the north, *P. juarezi* (which overlaps in elevation with the other *Pseudoeurycea*) is encountered first then *T. arboreus*. *Pseudoeurycea juarezi* is not found below 2000 m elev., and, at the lower extreme of the distribution of *T. arboreus*, one encounters a new mix of species in a cloud forest habitat rich in bromeliads. A single specimen included in the analysis of genetic variation in *Thorius* (Hanken, 1983, population 45) was remarkably distinct from all other samples and subsequently proved to be assignable to *Nototriton adelos* (Papenfuss and Wake, 1987). This genus was not known to occur in Mexico at the time of Hanken's study. *Nototriton adelos* is microsympatric with *T. arboreus* and an undescribed species of *Chiropterotriton* (Darda, 1994), all of which are found in bromeliads. A fourth species, the largest of this community, is *Pseudoeurycea saltator*; it is found in bromeliads but also under the bark of logs. All four of these species display at least semiarboreal tendencies. In the immediate vicinity of Vista Hermosa, at 1500 m elev., the forest has been badly disrupted by human disturbance, but we believe that the four species mentioned above are replaced by four others: *T. insperatus*, *T. smithi*, a species tentatively identified as *Pseudoeurycea werleri* (otherwise known only from high elevations in the Los Tuxtlas area of coastal Veracruz), and a small species with fully webbed hands and feet that appears to be an unde-

scribed species of *Bolitoglossa* (related to the *B. rufescens-occidentalis* complex which is mainly found at elevations below 1000 m elsewhere). Although *T. smithi* has been traced down to about 800 m, the other species are known only from the vicinity of Vista Hermosa, and all are known from small samples. In the lowlands near Tuxtepec, both *B. rufescens* and *B. platydactyla* are known.

The 15 species found on this relatively local transect is about the same number that one finds on transects of similar length in east-central Veracruz, extreme western Guatemala—eastern Chiapas, Caribbean Guatemala, and the Tapan-ti-Cerro de la Muerte region of Costa Rica (Wake, 1987; Wake et al., 1992), although the latter has more species if one extends the transect into the lowlands, a relatively large geographic distance from the upper part of the transect. On all of these transects, salamanders are relatively easy to find (or were in the recent past) at elevations above 2000 m but become progressively more difficult to find at lower elevations, especially near the transition between the lower cloud forest and the adjacent evergreen lowland forest. Our samples of the low elevation *Thorius* are rather typical in size of samples of other salamanders that occur between 1500 and 800 m, which is the least known and understood elevational zone as far as tropical salamanders are concerned.

ACKNOWLEDGMENTS

The following people provided access to and valuable information concerning specimens in their personal or institutional collections: R. Bezy, J. Cadle, C. Cole, W. Duellman, H. Freeman, R. Inger, H. Marx, R. McDiarmid, J. Mendelson, C. Myers, A. Nieto, H. Voris, J. Wright, and R. Zweifel. Several people helped collect specimens in the field, especially D. Darda, D. Eakins, T. Hetherington, J. Lynch, T. Papenfuss, S. Sessions, and H. Shaffer. H. Smith provided comments on the manuscript. K. Klitz prepared the line drawings; J. Hendel produced Figure 1. Research support was provided by NSF grant BSR 90-19810 (to DBW), and by the Museum of Vertebrate Zoology, the Center for Latin American Studies, and Sigma Xi (Alpha chapter), University of California, Berkeley. The Direccion General de la Fauna Silvestre, México, provided collecting permits.

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(JH) DEPARTMENT OF ENVIRONMENTAL, POPULATION, AND ORGANISMIC BIOLOGY AND

UNIVERSITY MUSEUM, UNIVERSITY OF COLORADO, BOULDER, COLORADO 80309-0334; AND (DBW) MUSEUM OF VERTEBRATE ZOOLOGY, UNIVERSITY OF CALIFORNIA, BERKELEY, CALIFORNIA 94720. Send reprint requests to JH. Submitted: 15 March 1993. Accepted: 18 Aug. 1993. Section editors: D. Cundall and F. Irish.

Copeia, 1994(3), pp. 590-597

Assessment of Genetic Introgression between Two Pupfish Species, *Cyprinodon elegans* and *C. variegatus* (Cyprinodontidae), after More than 20 Years of Secondary Contact

ALICE F. ECHELLE AND ANTHONY A. ECHELLE

Allozyme analysis of three diagnostic gene loci revealed little evidence of genetic introgression after more than 20 years of contact between two pupfishes (*Cyprinodon elegans* and *C. variegatus*) in Lake Balmohrea, an artificial impoundment in west Texas. *Cyprinodon elegans* is native to spring-fed waters in the area, whereas *C. variegatus* was introduced into Lake Balmohrea in the 1960s. The two species contact one another near the mouth of a canal connecting spring flows with the lake. Within the canal, genotypes expected of *C. elegans*, *C. variegatus*, F₁ hybrids, and backcross progeny represented 7%, 85%, 5%, and 3%, respectively, of the pupfish collected. In lake areas outside the canal, all individuals were classified morphologically as *C. variegatus*, and genotypes typical of *C. elegans* were absent. There was only meager evidence of introgression in the lake population of *C. variegatus* outside the area of contact between the two species.

HYBRIDIZATION and genetic introgression following anthropogenic introduction of nonnative fishes is often cited as an important threat to native fishes in western North America (Allendorf and Leary, 1988; Echelle, 1991). The pupfishes (Cyprinodontidae: *Cyprinodon*) in the deserts of southwestern United States and northern Mexico are particularly vulnerable to hybridization following secondary contact. Pupfish species in this region are often restricted to a single drainage or spring system where there are no other indigenous pupfishes. Thus, hybridization with introduced pupfish can lead to rapid genetic changes in the original population (Hubbs, 1980; Echelle and Connor, 1989). Further, laboratory studies have generally demonstrated low levels of sexual isolation and high genetic compatibility between morphologically divergent species of *Cyprinodon* (Turner and Liu, 1977; Cokendolpher, 1980; Villwock, 1982).

Three exceptions to the general rule of allopatry between native pupfishes are found in Mexico: (1) *C. atratus* and *C. bifasciatus* in Cuatro Ciénegas, Coahuila (Miller, 1968); (2) *C. pachycephalus* and *C. eximius*, in Ojo de San Diego, Chihuahua; and (3) a flock of five species in Laguna Chichancanab, Quintana Roo (Humphries, 1984). The genetic consequences in these instances of sympatry have received little attention, although hybridization has been suggested for each of the three situations (Miller, 1968; Humphries and Miller, 1981; Minckley and Minckley, 1986). In addition, there is evidence that hybridization between divergent forms may have been important in the evolution of pupfishes in the Death Valley region (Echelle and Dowling, 1992; Echelle and Echelle, 1993).

The introduction of *C. variegatus* (sheepshead minnow) into the range of *C. elegans* (Comanche Springs pupfish) prompted the first detailed study of pupfish hybridization under field con-