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A NEW LONG-TAILED RATTLESNAKE (VIPERIDAE) FROM GUERRERO, MEXICO

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Abstract: A distinctive new species of rattlesnake is described from the western versant of the Sierra Madre del Sur of Guerrero, Mexico. This long-tailed rattlesnake cannot be confused with any other species of rattlesnake and is most similar to *Crotalus stejnegeri* and *C. lannomi*. The Guerrero species possesses a strikingly distinct color pattern and differs from all other rattlesnakes in aspects of lepidosis. Mexico continues to be the origin of newly discovered species that provide important insights into the evolution or ecology of particular groups. A few examples from recent decades include *Exiliboa placata*, a monotypic, relictual dwarf boa (Bogert, 1968), *Rhadinophanes monticola*, a monotypic, highland colubrid (Myers and Campbell, 1981), and *Pseudoeurycea aquatica*, the only aquatic bolitoglossine salamander (Wake and Campbell, 2001).

Resumen: Se describe una especie nueva de serpiente de cascabel de la vertiente oeste de la Sierra Madre del Sur de Guerrero, México. Esta cascabel de cola larga, se distingue fácilmente de otras especies de cascabel y es muy similar a *Crotalus stejnegeri* y *C. lannomi*. Esta nueva especie del estado de Guerrero posee un patrón de coloración característico y una lepidosis cefálica que la distingue de otras especies de cascabel conocidas.

Key words: Crotalus ericsmithi; Long-tailed rattlesnakes; Guerrero; Mexico; New species; Reptilia; Serpentes; Squamata

With almost 1200 described species of amphibians and reptiles (Flores-Villela and Canseco-Márquez, 2004), the biodiversity of Mexico continues to astound herpetologists. Not surprisingly, many of the new species being discovered are secretive and cryptic species such as salamanders and fossorial snakes as well as nocturnal species such as hylids. However, some of the new species being discovered provide especially important insights into the evolution or ecology of particular groups. A few examples from recent decades include *Exiliboa placata*, a monotypic, relictual dwarf boa (Bogert, 1968), *Rhadinophanes monticola*, a monotypic, highland colubrid (Myers and Campbell, 1981), and *Pseudoeurycea aquatica*, the only known aquatic bolitoglossine salamander (Wake and Campbell, 2001). Herein we describe a new long-tailed rattlesnake that may provide a better understanding into the evolution of rattlesnakes.

Since the monumental monographs of Gloyd (1940) and Klauber (1972), the conventional wisdom among many taxonomists has been that rattlesnakes were well-known taxonomically with few new species likely to be discovered, although perhaps previously known populations might be reallocated and elevated to species status (e.g., Dorcas, 1992). Indeed this has been largely true. For example, in the most recent comprehensive treatment of rattlesnakes (Campbell and Lamar, 2004), the Neotropical rattlesnakes were partitioned into three species: *C. totonacus*, *C. simus*, and *C. durissus*, and *C. oreganus* was regarded as distinct from *C. viridis*. Grismer (2002) suggested that many of the populations of rattlesnakes on Pacific or Gulf of California islands be recognized full species, including *C. ruber lorenzoensis*, *C. mitchellii angelensis*, *C. m. muertensis*, *C. molossus estebanensis*, and *C. oreganus calginus*. Only two distinctly new species of rattlesnakes have been discovered and described in the last half-century: *C. lannomi* (Tanner, 1966) and *C. tancitarensis* (Alvarado-Diaz and Campbell, 2004).

The Sierra Madre del Sur in Guerrero has not been as well surveyed as many other parts of Mexico but nevertheless has been visited by many herpetologists over the last century who

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have amassed a relatively large number of specimens now distributed in various museums. In the late 1880s, Herbert H. Smith and his wife assembled a collection in that state that was used by various authors in preparing volumes of Biologia Centrali-Americana. Edward W. Nelson and Edward A. Goldman made collections in Guerrero from 1894 to 1903, most of which are deposited in the United States National Museum. Most of their travels in Guerrero were along the Mexico City to Acapulco road and Pacific coastal plain, but they did visit Omiltemi and other highlands in the Sierra Madre del Sur. Hans Gadow and his wife made two trips to Mexico in 1902 and 1904, respectively, spending time in Guerrero, including the highlands around Omiltemi. During the latter part of the 1800s and the early decades of the 1900s, the professional collector Wilmot W. Brown made collections of vertebrates in many parts of Mexico, including Guerrero, for a number of museums, and some of the reptiles were subsequently obtained by the University of Kansas and reported by Hall (1951). Expeditions in the Chilpancingo region over the course of several summers from 1952 to 1958 were led by William B. Davis of Texas A&M University, and the results were reported by Davis (1954) and Davis and Dixon (1959, 1961, 1965). In the 1960s, Kraig Adler led trips that made collections mostly along the road running from the Balsas Basin up though Puerto del Gallo near Cerro Teotepec and down the Pacific versant to Atoyac. Material garnered by Adler was published, in part, in Adler (1965, 1996), Adler and Dennis (1972), and Smith and Savitsky (1974). In the 1970's, the senior author visited Guerrero a number of times, assembling a collection that was partially reported in Campbell (1989), Campbell and Armstrong (1979), and Myers and Campbell (1981), and, more recently, from 2002 to 2004 Campbell led several expeditions into Guerrero. More recently, the results of a herpetological survey of the Omiltemi region was reported by Flores and Muñoz-Alonzo (1993).

Materials and Methods

Protocols for making scale counts and definitions of external morphological features follow Campbell and Lamar (2004) and Klauber (1972). The body and tail were measured using a meter stick to the nearest 1 mm, and the head, fang, and rattle were measured using a vernier caliper to the nearest 0.1 mm. The number of particular bilateral structures are designated right/left. The primary maps from which geographic names and distances were obtained are the topographic maps (1:1,000,000) issued by the Dirección General de Geografía, México. For recognizing various vegetation zones in Mexico we use the designations of Leopold (1950). The type-specimen was preserved in buffered formalin diluted to 10% of stock solution and tissues were taken for subsequent study. This specimen was placed in 70% ethanol within 10 days of collection. Colors in life are described from an excellent series of digital photographs taken in the field of the live specimen and deposited in the UT–Arlington Digital Collection (UTADC). We have examined the types of *Crotalus lannomi* and *C. stejnegeri*, as well as most known specimens of *C. stejnegeri* (see Appendix I). We have had available an excellent series of photographs for several specimens of *C. stejnegeri*. Various dimensions have been published previously for some of these specimens. For the sake of consistency, we have retaken all of these, often finding mensural differences, albeit usually minor.

Field parties from UT Arlington and the Universidad Nacional Autónoma de México have collaborated on a number of forays into lesser known regions of Mexico since 2001, resulting in the discovery of many new species of amphibians and reptiles (e.g., Canseco-Márquez et al., 2007; Meik et al., 2006). One of the major participants has been Eric N. Smith-Urrutia. He was responsible for collecting the only known individual of the new taxon described herein. In recognition of his continuing diligence in the field, we designate it as:

Crotalus **ericsmithi** *sp. nov.*

Holotype.—An adult male (UTA R-55372) from Carretera La Laguna–Bajitos de la Laguna, Guerrero, Sierra Madre del Sur, Mexico, 1037 m (Fig. 1). The coordinates for this locality are 17.55330° N, 100.77472° W. The type was collected as it crawled along the

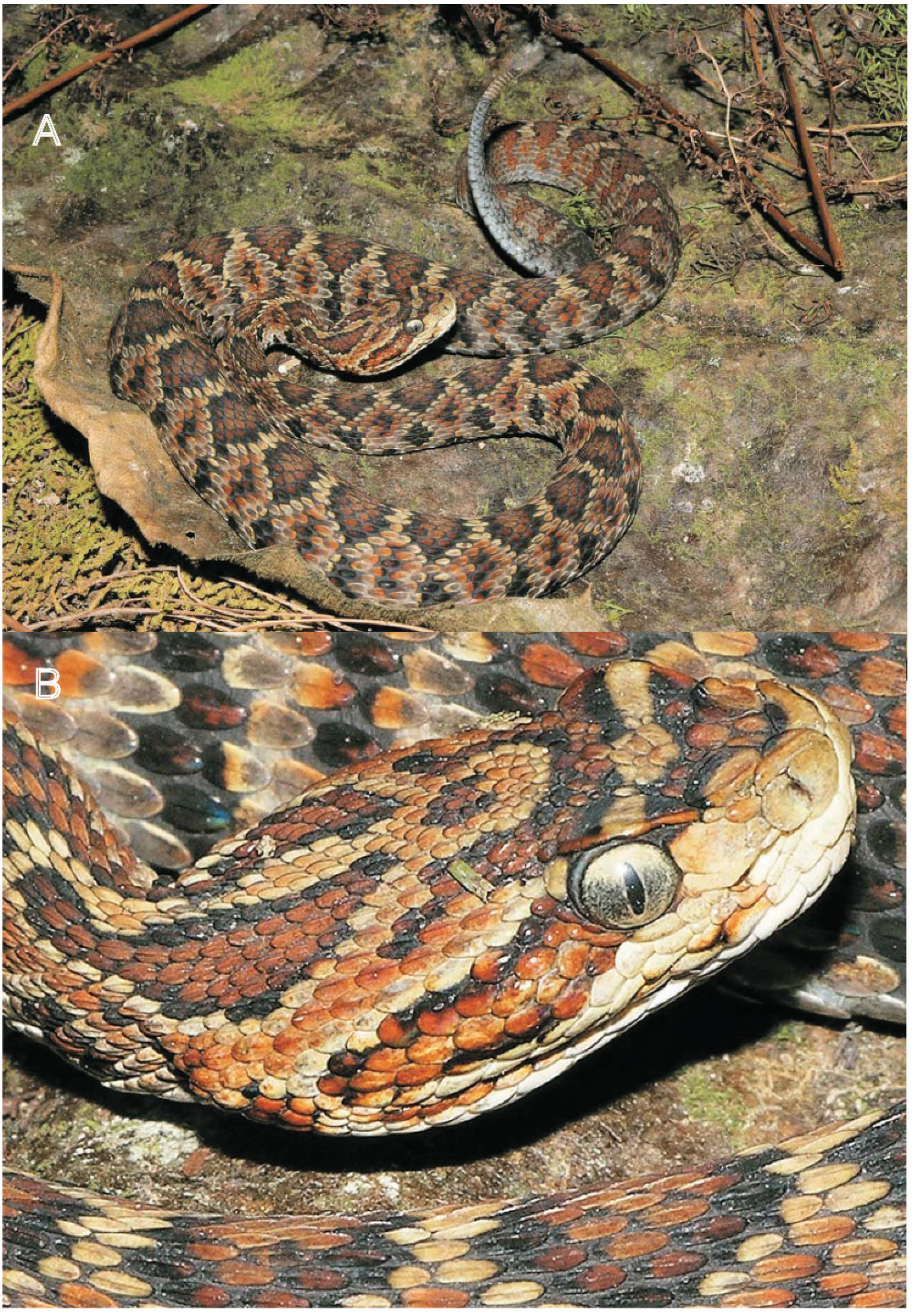

FIG. 1.—(A) body and (B) head of holotype of *Crotalus ericsmithi*, UTA R-55372, 54.0 cm TL.

side of a small dirt road at 2015 h. The field party included E. N. Smith, C. Sheehy, U. García, R. Jadin, A. Acevedo, and J. C. Blancas.

Diagnosis.—Distinguished from all other rattlesnakes except *C. stejnegeri* and *C. lannomi* in having a long tail (15.9% of TL in adult male holotype) with a tiny rattle (proximal rattle segment 2.2 mm in holotype). Canthals relatively large and separated by two (anteriorly) or a single (posteriorly) small scales (canthals moderately small and separated by two or three large scales in *C. stejnegeri* and *C. lannomi*); intersupraoculars relatively small, 5 (somewhat smaller, 6–8, rarely 5, in *C. stejnegeri*; large and flat, 4, in *C. lannomi*); first pair of infralabials mostly separated by the mental (in broad contact in *C. stejnegeri* and *C. lannomi*); the second pair of infralabials in broad contact with chinshields (often excluded or in narrow contact in *C. stejnegeri*); ventrals 172 in single male (172–178 in male *C. stejnegeri*); subcaudals 41 (42–45 in male *C. stejnegeri*); hemipenis with spines on proximal portion of lobes grading abruptly to calyces and large ridged calyces covering apex of each lobe (spines gradually grading to calyces and distal portion of lobe smooth in *C. stejnegeri*). The type of *C. ericsmithi* has a longer tail (15.9% of TL) and proportionally smaller rattle (proximal segment 2.2 mm) than any known species of rattlesnake.

In *C. lannomi* the dorsal head and body markings appear to be slightly more boldly outlined in black than the other two species of long-tailed rattlesnakes and the dark lower border of the postocular stripe continues beneath and in front of the eye to merge with the dark border of the snout blotch; the postocular stripe reaches the rictus, whereas it is separated from the rictus by the ultimate supralabial in *C. ericsmithi*. In *C. lannomi* the pale bar across the middle third of the supraocular is not well defined and black markings on these scales are irregular. *Crotalus lannomi* has two (vs. one in *C. ericsmithi*) occipital spots.

Crotalus lannomi differs from *C. stejnegeri* by having fewer prefoveals (5 vs. 7–8), fewer intersupraoculars (4 vs. 7–8), and fewer middorsal body blotches (31 vs. 34–43).

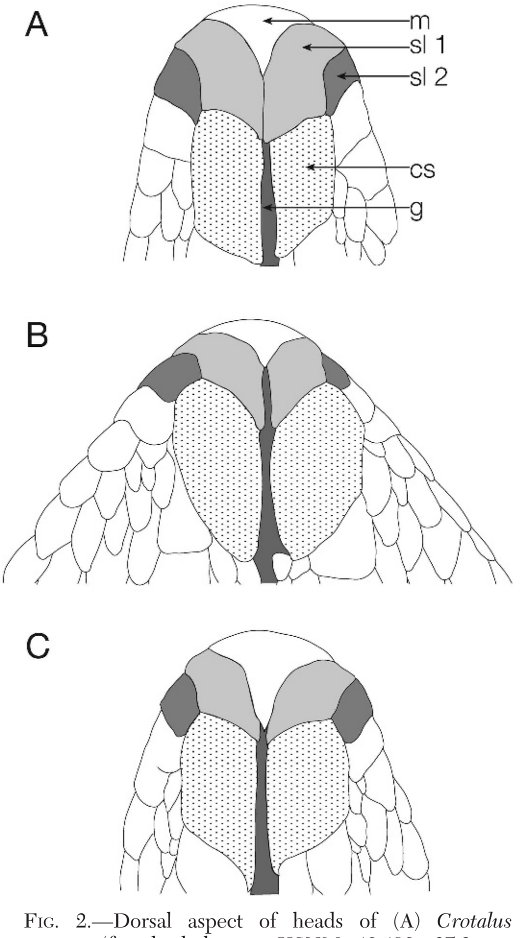

FIG. 2.—Dorsal aspect of heads of (A) *Crotalus stejnegeri* (female holotype, USNM 46,486, 27.3 mm head length); (B) *C. lannomi* (female holotype, BYU 23,800, 31.8 mm head length); and (C) *C. ericsmithi* (male holotype, UTA R-55372, 25.0 mm head length), showing differences in scalation. Dark grey, internasals; medium grey, prefrontals, pale gray, intersupraoculars at about midlevel of supraoculars.

Crotalus lannomi appears to have a somewhat stouter body than either *C. ericsmithi* or *C. stejnegeri*.

Description of holotype.—Rostral broader than high (3.0 × 2.2 mm); internasals 2, in contact medially, large and wing-shaped, broadly convex over most of scale; canthals 2, large with diagonal striations, separated by 2 scales anteriorly and by a single scale posteriorly (Fig. 2); intersupraoculars 5 at midlevel of supraoculars; loreals 2/2, lower slightly higher than long, upper longer than high (Fig. 3); 2/1 small scales intervening

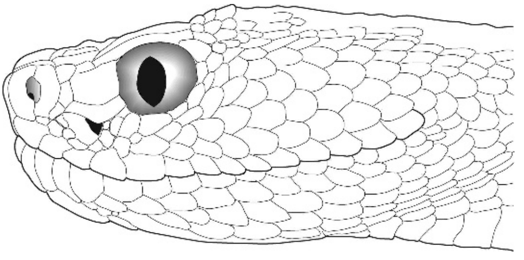

FIG. 3.—Lateral aspect of head of holotype of *Crotalus ericsmithi* (UTA R-55372), showing details of scalation. Head length 25.0 mm.

between upper preocular and/or loreals and canthals; prefoveals 5/6, anterior scale intervening between first supralabial and postnasal, precluding contact between these two scales; prenasal contacting internasal above and first supralabial below; naris in postnasal just posterior to edge of prenasal suture, postnasal contacting internasals, loreals, and two prefoveals; preoculars 2, upper largest and about twice as high as lower, upper contacting supraocular but not canthal, lower long and narrow, deflected upwards at about midlevel, forming upper border of pit; pit about midway between level of eye and naris, located entirely below line from middle of eye to naris; suboculars 3/3, anterior subocular roundish, others horizontally elongate; number of scale between eye and margin of lip 4/3 including suboculars and infralabials; supralabials 12/14; infralabials 14/15, one scale on right side the result of fusion of two scales (partially dividing suture); mental produced posteriorly to mostly preclude contact between first pair of infralabials (Fig. 4); dorsal scale rows 27–25–19; preventrals 2; ventrals 172; subcaudals 41, none divided; rattle-fringe scales 8; tail bearing 9 rattle segments; hemipenis long and slender, partially everted organ extending 5 subcaudals; deeply bifurcated, base of organ mostly nude, spines numerous covering proximal portion of lobes; transition from spines to papillate fringes relatively abrupt; ridges of calyces extending to distal end of organ.

Measurements of holotype.—The holotype is an adult male, 54.0 cm in total length (TL), with a tail length of 8.6 cm (15.9% of total). The head is 25.0 mm long from the front face of the rostral to the angle of the jaw and 14.8 mm at the widest point near rictus. The eye is relatively large; the horizontal distance across the eye is 4.0 mm (16% of the head length). The width of the proximal rattle segment is 2.2 mm.

Color pattern of holotype in life.—Snout medium brown with irregularly black-edged dark brown marking from posterior of internasals extending posteriorly and bifurcating with branches extending to anterior portion of supralabials; dark marking extending from about posterior third of supraoculars and across top of head, extending posteriorly for 3–4 scales and continuing laterally onto parietal region for 6–8 scales as branches 2–3 scales wide, this marking dark-edged, especially anteriorly and posteriorly; pale crossbar across the top of the head involving about the middle third of the supraoculars, accentuated by the dark edging of the markings on snout and parietals; dark spot encompassing 9 scales in mid-parietal region; pair of dark-edged paravertebral strips beginning in parietal region and extending posteriorly about 12 scales on right side and 13 scales on left, left blotch confluent with first body blotch; paravertebral blotches expanded to 6–7 scales wide on posterior portion of head, no more than 2–3 scales more posteriorly; iris yellow with black stippling; orange postocular stripe black-edged above and below, extending from lower posterior border of eye to level just above ultimate supralabial; most of side of head below canthus, eye, and postocular stripe mostly white with sparse black stippling; in region below eye supralabials with some irregular black pigment on upper portions of some of these scales and adjacent interoculabials.

Thirty-six orange, black-edged dorsal body blotches, black-edging most distinct over most of body but becoming narrower on posterior part of body; dark borders edged with pale yellowish gray, this edging most conspicuous on anterior two-thirds of body; on anterior part of body blotches elongate, much longer than wide (6–7 scales long and 7–8 scales wide); at midbody dorsal blotches about 11 scales wide and most are 3.5–4 scales long; on posterior of body dorsal blotches are 7–10 scales wide and 3 scales long; dorsal blotches bordered by single row of yellowish scales;

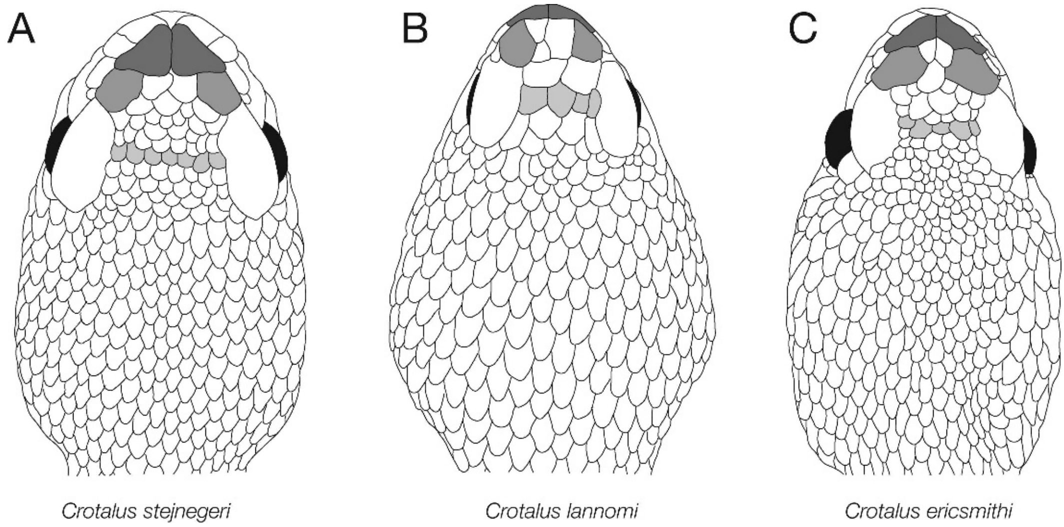

FIG. 4.—Ventral aspect of head of (A) *Crotalus stejnegeri*, UTA R-6234; (B) *C. lannomi*, BYU 23,800; and (C) *C. ericsmithi*, UTA R-55372, showing differences in scalation. Shape of lower jaw of *C. lannomi* somewhat distorted during preservation. Abbreviations as follows: m, mental; sl 1, first supralabial; sl 2, second supralabial; cs, chinshield; g, midventral gular fold.

each dorsal body blotch offset laterally with distinct black blotch, mostly on scale rows 2–5 but some extending to scale row 1 and others onto row 6; distinctive small dark umber blotches heavily suffused with black about halfway up flanks at levels midway between dorsal blotches, bordered by bright orange on surrounding scales; dorsal ground color of tail pale blue-gray; 16 tail rings, containing much orange pigment on proximal third of tail, posteriorly grading to mostly darker gray; proximal rattle segment dark gray.

Venter of head nearly immaculate, except for mental, the first two pairs of infralabials, and all infralabials posterior to the seventh scale in the series, which have sparse black stippling; ultimate three infralabials with orange pigment; venter pearly white on anterior of body but grading into gray posteriorly, especially laterally, owing to gray smudging; small black ventrolateral blotches below lateral blotches on scales rows 1 or 1 and 2 extending onto lateral portion of ventrals, and other irregularly spaced very small black blotches restricted to lateral portion of ventrals; dark ventral blotches becoming more irregular on posterior half of body; venter of tail medium gray with narrow black-edging on border of subcaudals, black-edging mostly on outer lateral third of anterior subcaudals and may extend across the venter of the tail on distal subcaudals.

Habitat.—The type of *C. ericsmithi* was collected in low elevation, dry pine forest. Pines in this area are sparsely distributed and there is an under story of grass and shrubs. The type-locality lies at 1037 m and represents a low elevation for pines in the area. Slightly lower on the slopes, pines give way to a thick tropical deciduous forest.

Etymology.—We take pleasure in naming this species for Eric N. Smith, a talented young scientist with a propensity for making exciting discoveries through arduous fieldwork. We have known him from his days as a junior high school student in Guatemala through his career as an undergraduate and graduate student, postdoctoral fellow, research associate, and tenure-track colleague.

DISCUSSION

The slender-bodied, long-tailed species of *Crotalus* are among the most distinctive of rattlesnakes. In his description of *C. stejnegeri*, Dunn (1919) provided the following one sentence diagnosis: "A small *Crotalus* with a long slender tail, a very small rattle with the first pair of lower labials long and produced backwards broadly in contact behind the symphysial." This simple diagnosis served well to distinguish *C. stejnegeri* from all other species of rattlesnakes known at the time. *Crotalus lannomi* was distinguished from *C. stejnegeri* by features presented by Tanner (1966). With the addition of *C. ericsmithi*, bringing the number of species of long-tailed rattlesnakes to three, it has become necessary to expand the diagnoses for these species slightly; they may be distinguished easily by the following key.

Key to the Species of Long-tailed Rattlesnakes

1. First pair of infralabials in narrow posterior contact (may be separated by interstitial skin of gular fold); lateral blotches distinctly bordered by bright orange ..... *Crotalus ericsmithi*
- First pair of infralabials in broad contact (may be separated by interstitial skin of gular fold); orange color on flanks, if present, confined to a few scattered scales 2

2. Internasals large and broadly triangular; intersupraoculars 6–8 (rarely 5); dorsal body blotches 34–43 .... *Crotalus stejnegeri*
- Internasals small and slender; intersupraoculars 4 (only 2 anteriorly); dorsal body blotches 31 .... *Crotalus lannomi*

The species of long-tailed rattlesnakes share a number of similarities. All species have two moderately sized loreals, one situated above another, but sometimes additional smaller scales, referred to as loreals by some authors, are located anterior or posterior to the upper loreal. The pattern of these species consists of pale bordered dorsal blotches that are offset laterally by darker blotches. *Crotalus ericsmithi* has a color pattern containing distinctive bright orange, and in life some specimens of *C. stejnegeri* may have a very reduced amount of orange coloration, usually limited to a few scattered scales on the flanks. The color in life of *C. lannomi* has not been described, but based on the preserved type and comparing it to preserved specimens of *C. stejnegeri*, the coloration of these species appear to be similar. Even after more than 40 yr in preservative, the centers of the dorsal blotches have a faint orange-brown cast in *C. lannomi*. Long-tailed rattlesnakes are moderate in size, with adults ranging from about 50 to 75 cm in TL (the maximum recorded length in *C. stejnegeri* is 72.4 cm). All species of long-tailed rattlesnakes lack teeth on the palatine and have unusually long fangs.

Molecular analyses will undoubtedly reveal answers about the phylogenetic position of this long-tailed species with other rattlesnakes. While beyond the scope of this description to delve too speculatively into the evolution of rattlesnakes, the discovery of *C. ericsmithi* provides the opportunity to revisit certain basic questions.

Why have long-tailed rattlesnakes remained so rare? The three species of long-tailed rattlesnakes are known from very small geographic regions (two of the species remain known only from the type). The reason for these restricted ranges are not readily apparent, and to some extent must be attributed to a sampling artifact. Certainly a careful consideration of topography, climate, and vegetation cover provides no compelling reason why these species should have such small ranges. All three species occur in the low to moderately elevated foothills of the Pacific versant of Mexico. The northernmost species, *C. stejenegeri* occurs only in a small portion of the Sierra Madre Occidental in western Sinaloa and adjacent Durango. Only about a dozen specimens of *C. stejnegeri* have reached museum collections (see Appendix I for localities of specimens examined). Despite its rarity in museums, early collections well over a century ago contained representatives of this species. The original description by Dunn (1919) mentioned three specimens, two from Plomosas, Sinaloa, and one from Ventanas, Durango, collected by Alfonse Forrer and reported by Boulenger (1896). The latter locality lies near the Sinaloa border at about 610 m. Forrer had been commissioned by the British Museum to collect zoological material in western Mexico and the United States immediately after the American Civil War (Breninger, 1899). The type-material was collected near Plomosas, Sinaloa, by Nelson and Goldman during their extensive biological explorations of Mexico for the United States Department of Agriculture (material deposited in the USNM). They visited the region about Plomosas from July 13–20 1897, which Goldman (1951) described as being from 2500 to 3000 ft [762–914 m) with nearby flanking ridges reaching 4000 ft [1219 m] and vegetation similar to that of the adjacent lowlands ("Arid Lower Tropical Zone"). For his monograph of rattlesnakes Gloyd (1940) had only these three individuals available. Subsequently, two additional specimens from near Yamoriba, Durango, were reported by Klauber (1952) who stated that they "were found on the border of a pine forest, at the upper edge of a canyon dissecting a plateau".

In the decades of the 1960s and 1970s, three individuals of *C. stejnegeri* were taken from Mexico Highway 40 that extends between the cities of Durango and Mazatlán. Hardy and McDiarmid (1969) reported a specimen collected 2.2 km northeast of Santa Lucía at 1155 m. McDiarmid et al., (1976) reported two specimens, one taken from 10 and the other 10–15 mi northeast of Concordia. The latter individual they reported was found only about 3.3 km west of where the pine zone begins. The specimen figured by Harris and Simmons (1978) was collected 10–15 mi [16–24 km] northeast of Concordia on a road which undulates through tropical deciduous forest at elevations of 800–1100 m.

Despite intensive efforts by one of us (JAC) over a period of several years in the 1970s to obtain additional material of *C. stejnegeri*, only three individuals were secured. These were found near the type-locality in August 1976 at an elevation of 1000–1100 m. These specimens are deposited in UT-Arlington and were included in the treatise on Mexican rattlesnakes by Armstrong and Murphy (1979). These snakes were taken in large jumbles of boulders at the base of high bluffs in tropical deciduous forest (see Fig. 4 in Armstrong and Murphy, 1979). The only other sympatric rattlesnake was *C. basiliscus*, but *C. lepidus* was taken along the crests of these bluffs on which open stands of pines were the dominant tree.

Crotalus lannomi was described over 40 yr ago, and since that time one of us (JAC) has made multiple trips attempting to find additional specimens. Despite spending a collective total of over 30 days at the type-locality (1.8 mi west of Puerto Los Mazos, Jalisco), the species was not rediscovered. The crest of the ridge near Los Mazos at a little over 1000 m

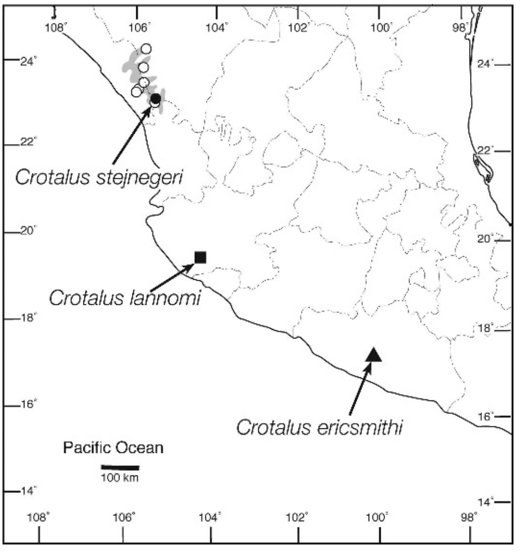

Fig. 5.—Map of western Mexico showing distributions for *Crotalus stejnegeri*, *C. lannomi*, and *C. ericsmithi*. Type-localities indicated by solid symbols.

down the Pacific versant to an elevation of about 500 m was carefully surveyed. The type-locality of *C. lannomi* lies in the ecotone between lowland tropical deciduous forest and the more mesic highland forest which is present on the crest near Puerto Los Mazos. The type-locality is characterized by an abundance of a species of short oak with huge leaves that contribute to the thick leaflitter found beneath most of these trees. Species found at this locality include such typically lowlands species as *Hyla arenicolor*, *Sceloporus utiformis*, *Leptodeira splendida*, and *Heloderma horridum*, and species associated more with the uplands as *Norops nebulosus*, *Elgaria kingii*, and *Thamnophis cyrtopsis*.

The type-locality for *C. ericsmithi* is more than 500 km from that for *C. lannomi* and more than 800 km from the nearest locality (which happens to be the type-locality) for *C. stejnegeri* (Fig. 5). The type-locality for *C. ericsmithi* lies to the south of the Balsas Basin that forms the low entrenchment extending from the Pacific Coast inland across much of central Mexico. The lower elevations of the Río Balsas Valley are covered mostly with arid tropical scrub and represent a formidable barrier not only to montane species but also many of the foothill species occurring in tropical deciduous forest. *Crotalus ericsmithi* was found at 1037 m in a region of scattered pines on relatively open hillsides. This is near the lower limit for conifers in the area and the habitat grades into tropical deciduous forest within a short distance down the hill. *Crotalus ericsmithi* may be restricted to a small range on the southern slopes of the Sierra Madre del Sur and may be rare as well. We hope that scientists are able to obtain sufficient additional material before the region becomes even further degraded owing to human activity so that we may learn more about the variation and natural history of this unusual rattlesnake.

All long-tailed rattlesnakes may be considered lower montane species with narrow elevational distributions that fall, at least in part, within the zone where tropical deciduous forest grades into oak or pine-oak forests characteristic of higher elevations. *Crotalus stejnegeri*, the only one of these species known from more than a single specimen, has a vertical distribution of about 500–1200 m (Campbell and Lamar, 2004). The lowest elevations are represented by specimens from near Concordia. These individuals were collected during the rainy season in the Río Concordia drainage, which is noted for its torrential flash flooding that regularly stops all traffic on Mexico Highway 40. Individuals from the vicinity of Santa Lucía and Plomosas represent the highest records for *C. stejnegeri* in regions covered by the upper edge of tropical deciduous forest or in open pine-oak forest. Five specimens of *C. stejnegeri* have been taken from the vicinity of Plomosas. Three of these (UTA) were taken from upper tropical deciduous forest and two (USNM) were apparently taken slightly higher in "oak woods," according to data associated with the type-specimens.

Activity patterns are poorly known for many reptiles, including most rattlesnakes. Our knowledge of the activity patterns of long-tailed rattlesnakes is sketchy at best. Specimens of *C. stejnegeri* from Plomosas, Sinaloa, were found near large rocks or burrows during the early morning hours following heavy thunderstorms the previous night. An individual from near Concordia was taken actively crawling on the road at nightfall when the air temperature was 24 C (McDiarmid et al., 1976). Individuals of *C. stejnegeri* (Hardy and McDiarmid, 1969) and *C. lannomi* (Tanner, 1966) were found as road kills. The type of *C. ericsmithi* was taken well after dark (2015 h) as it crawled along the side of a small, unpaved mountain road. It appears that long-tailed rattlesnakes are similar to many other lowland rattlesnakes and will bask when environmental conditions are sufficiently humid and cool, but retreat to relatively deep shelter as soon as daytime temperatures become hot or during dry periods. For the most part we suspect they are active mostly after dark.

Are characters purported previously to be primitive really so, and what are the relationships of the long-tailed species with each other and other species of rattlesnakes? The length of the tail and rattle size are nonindependent characters that probably do not provide evidence for rattlesnake relationships. Previously it had been assumed that rattlesnakes were derived from ancestors with long slender tails and that this character was primitive or degenerate (Klauber, 1952, 1972; Tanner, 1966). This notion has been dispelled by more recent studies that have demonstrated a relatively basal placement for vipers in the evolution of snakes (Vidal and Hedges, 2002), and most primitive snakes have short tails. Rattle size may be subject to relatively rapid evolution as demonstrated by the presence of considerable variation in closely related, isolated populations of rattlesnakes (Campbell and Armstrong, 1979). Contrary to previous assertions, the presence of a long, slender tail and tiny rattle in rattlesnakes may be a derived character, and this feature alone does nothing to place these snakes within the framework of rattlesnake evolution. If this feature is indeed plesiomorphic, it does not provide evidence for the monophyly of long-tailed rattlesnakes.

Besides a long tail and small rattle, similarities of the three species of long-tailed rattlesnakes include a rostral wider than high (erroneously stated to be higher than wide in *C. stejnegeri* by Tanner, 1966, and illustrated as such by Gloyd, 1940: pl 29), a relatively high number of ventrals compared to many other small montane species of rattlesnakes (171–178; but a feature shared with many of the larger rattlesnakes); slender habitus and moderate in overall size (50–75 cm), canthals

TABLE 1.—Selected mensural, scalation, and color pattern characteristics for long-tailed species of rattlesnakes. Where two ranges of figures are given, males are above females.

Characters	*Crotalus ericsmithi*	*Crotalus stejnegeri*	*Crotalus lannomi*
Maximum known TL	54.0 cm (male)	72.4 cm (female)	63.8 cm (female)
Tail length/TL	Male, 15.9%	Males, 10.4–14.5%	
		Female, 9.7%	Female, 10.7%
Dorsal body blotches	36	32–43	31
Internasals	Relatively narrow	Broad	Very narrow
Canthals	Canthals large and posterolaterally expanded; separated by 1 scale	Canthals moderate in size; usually separated by 3 scales, rarely 2	Canthals moderate in size; separated by 2 scales
Intersupraoculars	5	5–8	2 anteriorly; 4 at midlevel
First pair infralabials	In narrow contact midventrally, greatly tapering towards midline	In broad contact midventrally, not tapering towards midline	In broad contact midventrally, not tapering towards midline
Dorsal scales at midbody	25	25–27	27
Ventrals	Male,172	Males, 172–178	—
		Females, 171–176	Female, 176
Subcaudals	Male, 41	Males, 42–45	—
		Females, 36–37	Female, 37
Dorsal body blotches	35	34–43	31
Tail bands	16	13–16	—

not in contact at dorsal midline, separated by 1–3 scales (these canthals also may be appropriately considered to be prefrontals as pointed out by Campbell and Lamar, 2004).

There has been general agreement by most researchers that rattlesnakes originated in Mexico (Klauber, 1972) or, more specifically, the Mexican Plateau (Armstrong and Murphy, 1979; Gloyd, 1940). Based mostly on inferences of mustelid and procyonid predators, Greene (1997) suggested that ancestral rattlesnakes evolved in regions of talus slopes, and based on cladistic methodology Bremer (1992) and Place and Abramson (2004) suggested the most probable ancestral area of rattlesnakes was the Sierra Madre Occidental of Mexico in pine-oak forest; these forests represent a habitat and area corresponding to the present-day distribution of *C. stejnegeri*. *Crotalus lannomi* occurs on the western versant of the highlands associated with the Transverse Volcanic Cordillera, and *C. ericsmithi* is on the Pacific versant of the Sierra Madre del Sur.

Long-tailed rattlesnakes are intermediate in some respects for traits often used to characterize rattlesnakes. Long-tailed rattlesnakes cannot be considered to be either a highland or lowland species nor can they be considered to be restricted to either tropical deciduous forest or pine-oak forest, vegetational associations that grade into each other in the foothills of western Mexico, but which are considerably different in terms of structural heterogeneity, humidity, and temperature. As first pointed out by Klauber (1952), many of the morphological characters of *C. stejnegeri*, including elevated number of dorsal scale rows, high number of ventrals, numerous dorsal head scales, do not closely resemble small species of montane rattlesnakes that show opposite tendencies.

We suggest the following standard English and Spanish names for these snakes: Sinaloan Long-tailed Rattlesnake—Cascabel Cola-larga de Sinaloa (*C. stejnegeri*), Autlán Long-tailed Rattlesnake—Cascabel Cola-larga de Autlán (*C. lannomi*), and Guerreran Long-tailed Rattlesnake—Cascabel Cola-larga de Guerrero (*C. ericsmithi*).

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APPENDIX I

Records for Long-Tailed Rattlesnakes

Crotalus ericsmithi: **Guerrero**: see data herein. *Crotalus lannomi*: **Jalisco**: 1.8 mi W of the pass, Puerto Los Mazos, *or* 22 mi W by road from the Río Tuxcacuesco, a branch of the Río Armeria, on Mexican Highway No. 80 (BYU 23800–holotype). *Crotalus stejnegeri*: **Durango**: Ventanas (BM 83.4.16.64, photographs only available); ca. 6 mi N Yamoriba, 24° 12 ½′ N, 105° 47′ W (SDSNH 41120). **Sinaloa**: "Plumosas" [Plomosas], 2500–3000 ft (USNM 46586 [erroneously listed as 46486 in original description]—holotype; USNM 46460—paratype, 2500–3000 ft; UTA R-5926; UTA R-6234); 10–15 mi E Concordia (RS 901 HSH/RSS); 10 mi NE Concordia on Highway 40 (LACM 37718); 2.2 km NE Santa Lucía on Hwy 40, 1156 m (KU 78972).