RELATIONSHIPS AMONG MONTANE POPULATIONS OF *CROTALUS LEPIDUS* AND *CROTALUS TRISERIATUS*

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ABSTRACT: The systematics of montane Mexican rattlesnakes has been in considerable debate for many years. Within this group, the taxonomic status of *Crotalus triseriatus aquilus* has been especially questionable. Klauber (1952) expressed the belief that *Crotalus triseriatus triseriatus* and *Crotalus triseriatus aquilus* might some day be shown to represent two distinct species. Campbell and Lamar (1989) noted that *Crotalus triseriatus aquilus* should probably be considered a subspecies of *Crotalus lepidus* or a full species.

In this study fifty different characters were examined including those of lepidosis, color pattern, body proportions, hemipenes, and the skeleton. Twenty-seven of these characters were subsequently found to be informative and analyzed cladistically.

Several phylogenies were produced in which *Crotalus triseriatus aquilus* and *Crotalus lepidus* consistently formed a monophyletic group differing from *Crotalus triseriatus* by several derived characters. I propose that *Crotalus aquilus* Klauber, therefore, be assigned full species status.

INTRODUCTION

There are a number of species of relatively small, montane rattlesnakes that range from the southern United States to central Mexico. Because of inaccessible terrain, isolated populations, or inadequate collecting, the systematics of these rattlesnakes has only recently begun to be more fully understood. Ten species of rattlesnakes may be assigned to this group including *Crotalus stejnegeri*, *C. lannomi*, *C. polystictus*, *C. triseriatus*, *C. intermedius*, *C. transversus*, *C. pusillus*, *C. lepidus*, *C. pricei* and *C. willardi* (Klauber, 1972). Some of these species such as *C. stejnegeri*, *C. lannomi*, *C. polystictus* and *C. pusillus* are considered primitive (Klauber, 1972). Other species, such as *C. willardi*, possess a number of characters which are considered derived (Klauber, 1972).

Earlier in this century only six species of montane rattlesnake were recognized. Subsequently, *C. willardi* Meek (1905), *C. transversus* Taylor (1944), *C. pusillus* Klauber (1952), and *C. lannomi* Tanner (1966) were described. Gloyd's (1940) monograph on rattlesnakes was the first study to thoroughly examine the relationships of all rattlesnake species. Gloyd considered all taxa of montane rattlesnakes (excluding *C. polystictus*, *C. stejnegeri* and *C. willardi*) to belong to two species, *C. triseriatus* (Wagler, 1830) and *C. lepidus* (Kennicott, 1861). Gloyd considered these two closely related species to constitute the *Triseriatus* group. Gloyd recognized several taxa, which are currently considered to be full species, as geographic races of *C. triseriatus*, including *C. intermedius*, *C. pricei*, and *C. triseriatus*. Gloyd was the first to recognize two subspecies of *C. triseriatus*, *C. t. triseriatus*, the northern form, and *C. t. anahuacus*, the southern form.

Shortly after the appearance of Gloyd's monograph, many changes occurred in the taxonomy and composition of the *Triseriatus* group. Taylor (1944) described two new species, *C. transversus* and *C. semicornutus*. Smith (1946) recognized *C. pricei* as a distinct species and suggested that *C. triseriatus* and *C. lepidus* were each other's closest relatives. He separated *C. gloydi*, *C. omiltemanus*, (both later recognized as subspecies of *C. intermedius*, *fide* Klauber, 1952) and *C. transversus* from *C. triseriatus*. Smith also recognized *C. semicornutus* and stated that it might represent an example of the ancestral *C. lepidus* stock.

The species recognized by Smith as members of the *Triseriatus* group were divided into two distinct groups by Klauber (1952): the *Intermedius* group and the *Triseriatus* group. *Crotalus intermedius* and *C. transversus* comprised the *Intermedius* group, while *C. triseriatus* and *C. pusillus*, made up the *Triseriatus* group. However, Klauber stated that the closest relative of *C. lepidus* is *C. triseriatus*, evinced by the frequent occurrence of a divided upper preocular and other uniquely derived scale peculiarities shared by the two species. Contradictory to this statement, Klauber (1952) did not recognize *C. lepidus* as a member of the *Triseriatus* group. *Crotalus pricei* was also not included in the *Triseriatus* group. Klauber (1952) recognized the southern form of *C. triseriatus* as the race represented by the type specimen used in Wagler's original description and therefore designated it as *C. t. triseriatus* instead of *C. t. anahuacus*, and named the northern subspecies *C. t. aquilus*. *Crotalus t. triseriatus*, *C. t. aquilus*, and *C. lepidus* range from the southwestern United States to the Transverse Volcanic Cordillera in central Mexico (Fig. 1). *Crotalus semicornutus* was relegated to synonymy of *C. lepidus klauberi* by Klauber (1952) who also described a new subspecies of *C. lepidus*, *C. l. morulus*, from the mountains northwest of Gómez Farias, Tamaulipas.

Two decades later, Klauber (1972) constructed a phylogeny of rattlesnakes that agreed with his previous conclusions (Klauber, 1952). In this phylogeny, *C. stejnegeri* was considered to be most closely related to the larger rattlesnakes such as *C. durissus*, *C. atrox* and *C. viridis*. All other montane rattlesnakes were considered to comprise a monophyletic group. Klauber (1972) stated that *C. lepidus* is most closely related to *C. triseriatus*. However, the phylogeny constructed by Klauber excludes *C. lepidus* from the monophyletic group including *C. intermedius*, *C. transversus*, *C. triseriatus*, *C. pusillus* and *C. pricei*.

Tanner et al. (1972) described a new subspecies of *C. lepidus*, *C. l. maculosus*, from near the junction of the states of Durango, Sinaloa and Nayarit. They suggested that this new subspecies is more closely related to *C. l. lepidus* than to *C. l. klauberi*, with which it is closest geographically. Tanner et al. (1972) also hypothesized that the existence of *C. l. maculosus* suggested that *C. l. lepidus* is the more primitive of the subspecies and that its former range was divided by the dispersal of *C. l. klauberi* which left a remnent population on the Pacific versant of the Sierra Madre Occidental. It is

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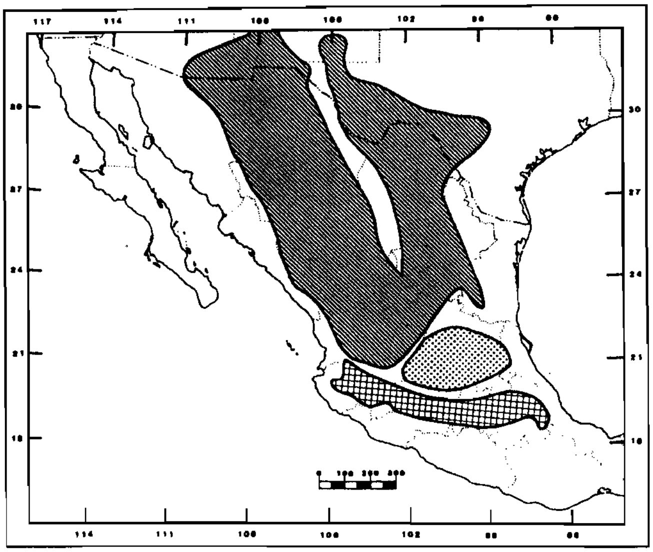

Fig. 1. Range map of *Crotalus lepidus* (diagonals), *C. triseriatus* (crosshatch), and *C. aquilus* (stipple).

difficult to consider this hypothesis plausible because of the complicated events that would have to occur. A simpler hypothesis, supported by historical climatology and geologic studies, will be presented in this paper. One of the last major additions to the taxonomy of montane rattlesnakes was the description of C. *triseriatus armstrongi* from Jalisco (Campbell, 1979).

Throughout the literature there are references to the close relationship of *C. lepidus* and *C. triseriatus* (Gloyd, 1940; Smith, 1946; Klauber, 1952 and 1972; Armstrong and Murphy, 1979; Campbell and Lamar, 1989). The common occurrence of a vertically divided upper preocular, the unique posterior projection of the prenasal under the postnasal, the presence of several subloreals (prefoveals), the numerous supralabials and the numerous (23) midthoracic scale rows (Smith, 1946) indicate a close relationship between *C. lepidus* and *C. triseriatus.*

For some time there have been questions regarding the proper taxonomic status of *Crotalus triseriatus aquilus.* Gloyd (1940), was the first to separate *C. triseriatus* into northern and southern populations. He noted that, although the northern and southern races of *C. triseriatus* appear to resemble each other structurally, there were no specimens known which could be considered intergrades. Smith (1946) stated that the two forms were clearly subspecies, but discussed only two major differences between them: the number of body blotches and the number of ventrals. Klauber (1952) stated, in the description of *C. t. aquilus,* that the subspecific relationship of the two populations is based upon general similarity rather than any specimens which could be considered intergrades. Armstrong and Murphy (1979) expressed the need for a review of the relationships of *C. triseriatus* and *C. lepidus,* especially regarding the proper taxonomic placement of *C. t. aquilus.* Campbell and Lamar (1989) state that they suspect a thorough review of the systematics of this group would reveal that *C. t. aquilus* should be considered a subspecies of *C. lepidus* or a full species.

In anticipation of future systematic studies, Harris and Simmons (1978) recognized *C. t. aquilus* as a full species (= *C. aquilus*) but offered no data supporting this change. They also resurrected *C. t. anahuacus* and described a new subspecies, *C. t. quadrangularis.* Harris and Simmons purportedly reviewed all rattlesnake species and made several other taxonomic changes, all without proper justification. Harris and Simmons' paper was critically reviewed and the majority of its conclusions rejected shortly after its publication (McCranie and Wilson, 1979).

In this paper I examine and analyze specimens representing all taxa of *C. triseriatus* and *C. lepidus.* Conclusions are reached regarding the taxonomic status of *C. t. aquilus* and a hypothesis is proposed to explain the biogeography of the *Triseriatus* group.

MATERIALS AND METHODS

Characters of lepidosis, color pattern, body proportions, hemipenial, and skeletal characters were analyzed in this study. For purposes of discussion, each character is numbered.

Specimens were provided by the American Museum of Natural History (AMNH), the Field Museum of Natural History (FMNH), Louisiana State University (LSU), the Texas Cooperative Wildlife Collection (TCWC), the United States National Museum (USNM), the University of Illinois Natural History Museum (UINHM), the University of Kansas (KU), the University of Michigan Museum of Zoology (UMMZ), and the University of Texas at Arlington (UTA). A total of 216 specimens was examined (Appendix I).

Lepidosis

The number and arrangement of scales have traditionally been employed as important characters for distinguishing species of snakes. Squamation differentiates most species of snakes, more often than the variable colors and patterns that may provide an unreliable basis for identification. In this study, scale characters were examined to ascertain similarities and differences among the different taxa being considered. A total of 19 scale characters was examined. Paired scales were counted on each side of the head and noted as right/left (e.g. 8/9 supralabials). Definitions for lepidotic characters (Fig. 2) are as follows:

1. *Loreal.* Any scale that lies at least 50% below a line extending from the uppermost contact of the prenasal with the postnasal and the lowermost anterior projection of the supraocular. The loreal is situated between the preoculars and the nasals.

2. *Preocular.* Any scale in contact with and situated directly anterior to the eye (Klauber, 1972). The upper preocular is sometimes divided vertically in rattlesnakes. The presence or absence of this vertical suture was also noted.

3. *Subocular.* Any scale in contact with and situated directly below the eye but not bordering the margin of the upper lip (Klauber, 1972).

4. *Postocular.* Any scale in contact with and situated directly posterior to the eye (Klauber, 1972).

5. *Interoculabials.* Any scale situated directly below the eye between the suboculars and the supralabials. The number of

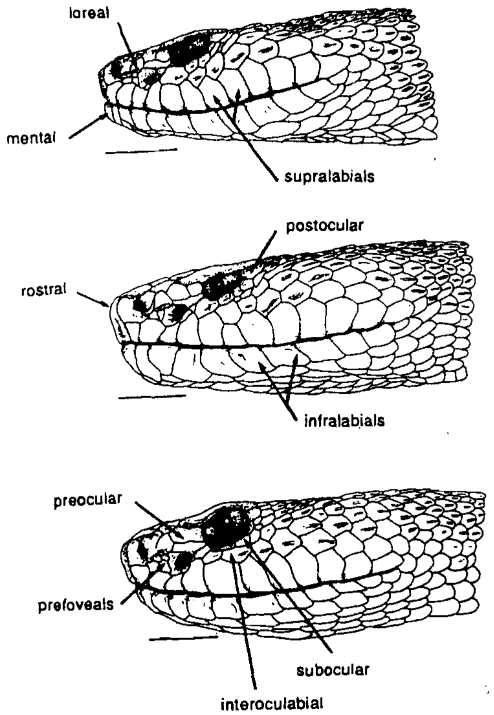

Fig. 2. Lateral view of heads of *Crotalus lepidus* (UTACV R-17832) (top), *C. aquilus* (UTACV R-12968) (center), and *C. t. triseriatus* (UTACV R-12600) (bottom). Note the relative eye size and presence or absence of a divided upper preocular. Bar = 5 mm.

interoculabials was counted along a vertical line passing through the center of the eye.

6. *Prefoveals.* The scales situated anterior to the lacunals (the scales bordering the pit) and are surrounded by the loreal, nasals, and supraoculars (Klauber, 1972).

7. *Supralabials.* The scales situated along the margin of the upper lip between the rostral and the angle of the mouth (Klauber, 1972).

8. *Infralabials.* The scales situated along the margin of the lower lip between the mental and the angle of the mouth (Klauber, 1972).

9. *Internasals.* The scales that extend between the nasals across the top of the head and remain in contact with the rostral.

10. *Canthals.* The scales along the canthus rostralis, between the internasals and the supraoculars (Klauber, 1972).

11. *Intercanthals.* The scales situated on top of the head between the canthal scales.The lowest number of scales between the canthals on opposite sides of the head serves to characterize the relative size and arrangement of the intercanthal scales.

12. *Prefrontals.* Scales in the prefrontal area on top of the snakes head were counted. The prefrontal area was delineated as that area on top of the head anterior to an imaginary line drawn between the most anterior portion of the supraoculars. Internasals, canthals and intercanthals were included in this count.

13. *Ventrals.* The large scutes on the venter of the snake. The first ventral is usually distinguished by its position directly under the atlas and its contact on each side with the paraventral row of dorsal scales; the last ventral is situated just anterior to the anal (Dowling, 1951). There is sexual dimorphism in the number of ventrals; therefore samples were segregated by sex for analysis.

14. *Subcaudals.* The scales on the ventral surface of the tail beginning with the first scale posterior to the cloaca and ending just anterior to, but not including, the rattle-fringe scales that surround the proximal rattle segment (Klauber, 1972). There is sexual dimorphism in the number of subcaudals, and males and females were analyzed separately.

15. *Rattle-fringe scales.* The most distal scales on the tail which surround the anterior edge of the proximal rattle segment (Klauber, 1972).

16. *Dorsal scale rows.* The small, imbricate scales that cover the dorsum and sides of the body; included are the paraventral and all rows situated dorsally. The dorsal scale rows were counted on the neck at a level one head-length behind the head, at midbody, and on the posterior part of the body at a level one head-length anterior to the vent.

17. *Rostral.* The large scale covering the tip of the snout (Fig. 3). The height and width of the rostral were measured to the nearest 0.1 mm; a ratio was calculated by dividing the height by the width.

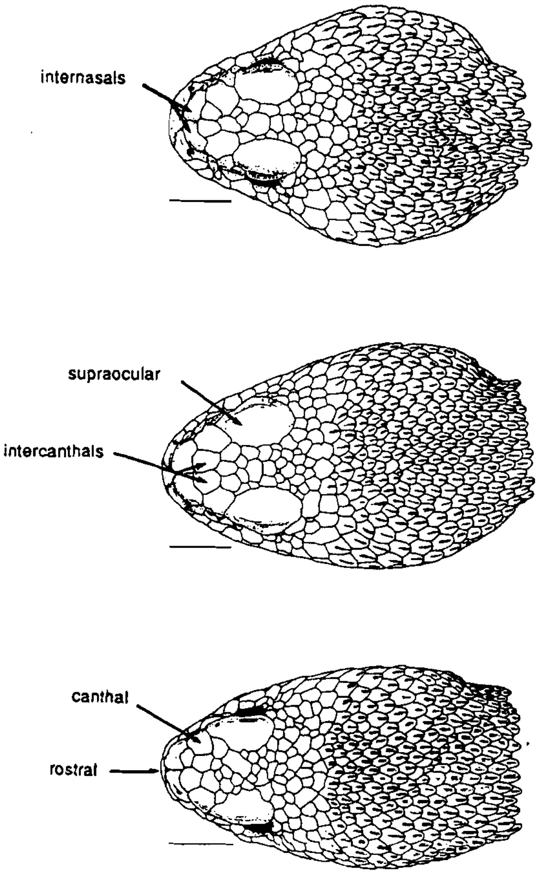

Fig. 3. Dorsal view of heads of *Crotalus lepidus* (UTACV R-17832) (top), *C. aquilus* (UTACV R-12968) (center), and *C. t. triseriatus* (UTACV R-12600) (bottom). Note differences in relative head shape. Bar = 5 mm.

18. *Mental.* The triangular-shaped scale at the anterior tip of the lower jaw. The height and width of the mental were measured to the nearest 0.1 mm; a ratio was calculated by dividing the height by the width.

19. *Prenasal shape.* The scale situated just anterior to the nostril and forming the anterior border of the nostril (Klauber, 1972). In some species of rattlesnake the prenasal extends sharply under the postnasal. The presence or absence of this extension was noted on each snake examined.

Color Pattern Characteristics

Although often variable, some aspects of body pattern appear to be useful systematically. The characters examined are:

20. *Body-blotches.* The number of dorsal body-blotches was counted on each snake, including the nuchal blotch, if present. This count did not include blotches present on the tail.

21. *Tail-markings.* Tail-markings in preserved specimens of *C. lepidus* and *C. triseriatus* sometimes tend to fade distally. Nevertheless, it was usually possible to obtain an accurate tail-blotch count for most specimens.

22. *Sexual dimorphism in ground color.* In some rattlesnake populations there is a pronounced sexual dimorphism in the ground color of individuals. When the snakes are preserved, the colors tend to be altered dramatically, but differences in ground color are still discernable, especially when the specimens are examined in conjunction with photographs of live snakes.

23. *Postocular stripe.* The presence or absence of a postocular stripe was noted for each specimen examined.

24. *Ventral mottling.* The degree of mottling on the venter of each snake was subjectively determined to be either heavy, medium or slight.

Body Proportions and Ratios

Differences in body proportions differentiate taxa of rattlesnakes. However, morphological proportions must be considered with care owing to ontogenic variation. Because most populations of montane rattlesnakes in the *Triseriatus* group are considered adults when 300 mm long, no snake with a total length of less than 300 mm was used in making proportional comparisons among taxa. Most snakes also exhibit sexual dimorphism for certain features, such as tail length. As a result of these phenomena, males and females were considered separately for statistical analysis. Head and scale measurements were made using vernier calipers and taken to the nearest 0.1 mm, unless otherwise specified. Other measurements, such as total and tail length, were taken to the nearest mm using a standard meter stick. The proportions examined are as follows:

25. *Eye/upper lip.* The vertical distance between the lower edge of the supraocular and edge of the upper lip was divided by the vertical diameter of the eye.

26. *Snout/eye diameter.* The distance between the front edge of the eye and the tip of the rostral scale was divided by the horizontal diameter of the eye.

27. *Head width/head length.* The width of the head was measured at a point about equal to the posterior edge of the supralabials and divided by the length of the head. The length of the head was measured from the tip of the rostral to the most posterior extension of the mandible. Snakes with badly distorted or damaged heads were not measured.

28. *Head length/total length.* Head length was measured from the tip of the snout to the posterior end of the mandible. This measurement was then divided by the total length of the snake. The total length of the snake was measured as the distance between the tip of the rostral scale and the posterior edge of the rattle-fringe scales. Head length was also divided by the body (snout to vent) length.

29. *Tail length/total length.* The tail length was measured from the posterior edge of the anal scute to the posterior edge of the rattle-fringe scales. It was then divided by the total length. Because tail length in rattlesnakes is sexually dimorphic, data for males and females were analyzed separately.

30. *Proximal rattle width.* The dorsoventral width of the proximal rattle segment was taken, and this measurement was then divided by the head length.

Hemipenes

Hemipenes were prepared for study by everting the organ and filling the blood sinuses with paraffin wax (Dowling and Savage, 1960). Care was taken not to damage the organ while removing it from the snake or subsequent filling of the sinuses with wax would be made difficult. The organ was deflated by gently squeezing to remove any excess fluid from the sinuses. A syringe filled with melted paraffin was used to inflate the organ while the hemipenis and needle were immersed in hot (approximately 65°C) water, which kept the paraffin in a liquid state. The syringe used had a large-bore needle (18 gauge) with the sharp tip removed. A cotton string was used to tie off the base of the hemipenis and to tie a tag onto the organ. The tissue of the organ was usually white, but by dyeing the paraffin before injecting it into the organ, the different structures on the surface of the organ became more easily distinguishable. Simply melting a portion of a crayon into the paraffin made this an easy task. After the organs were prepared and tagged, they were stored in 70% ethanol. To facilitate comparisons the right organ was used whenever possible.

The hemipenes of *Crotalus* are deeply divided with a bifurcate sulcus that terminates on each tip of the organ (Fig. 4). The basal area of the organ is covered with many spines and the lobes are generally covered with calyces, or ridges, which tend to become reticulate on the tips of the organ. The calyces also are ornamented with various sizes of spines and/or papillae. The tips of each lobe may be bulbous or cylindrical (Campbell and Lamar, 1989). Ten different hemipenial characters were examined. They are as follows:

31. *Subcaudal length.* Subcaudal length was measured by placing a hemipenis against the ventral side of the tail in the same position the organ would be when naturally everted. Length was determined by using the number of subcaudal scales as the point of reference. Only fully everted hemipenes were measured.

32. *Lobe shape.* Distal end shape was ascertained by examining fully everted hemipenes viewed from the sulcus side and was determined to be subcylindrical, cylindrical,

slightly bulbous, bulbous, or very bulbous.

33. *Crotch shape.* The crotch of a hemipenis is the medial part of the organ where the two lobes meet (Fig. 4). The crotch of the organ was examined and determined to be either "U" or "V" shaped.

34. *Basal spine length.* Basal spines are located below the first calyx on the basal area of the organ (Fig. 4). Basal spines were determined to be either short, medium, long, or very long.

35. *Basal spine shape.* Basal spines were determined to be either obtuse, slightly sharp, or sharp.

36. *Microornamentation.* Microornamentation was determined only from the medial lobe of the organ. The microornamentation was examined on both the mesial and lateral surfaces, and on the distal and proximal regions of the lobe. Microornamentation was determined to be slightly papillate, papillate, slightly spinulate, spinulate or very spinulate in each of these four regions.

37. *Total number of basal spines.* The total number of spines was counted in the basal area below the first calyx (Fig. 4). This count included the large basal hooks (character # 38) located in this region.

38. *Total number of large basal hooks.* The total number of large basal hooks was counted in the basal area below the first calyx (Fig. 4).

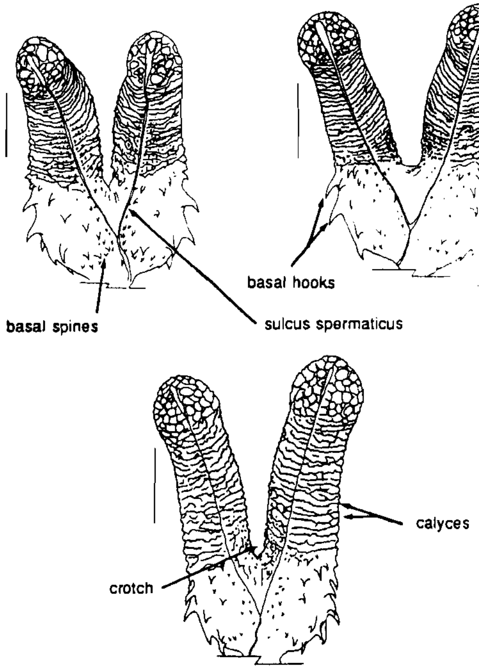

Fig. 4. Sulcate view of hemipenes of *Crotalus lepidus* (UTACV R-17835) (top, left), *C. aquilus* (UTACV R-12969) (top, right), and *C. t. triseriatus* (UTACV R-8142) (bottom). Note relative overall shape and length. Bar = 5 mm.

39. *Number of calyces.* The number of calyces was determined to be the number of ridges that terminate along the lateral edge of the sulcus on the medial lobe of the hemipenis (Fig. 4).

40. *Width and length of medial lobe.* The length of the inner lobe of the organ was measured from the point of bifurcation of the sulcus to the tip of the lobe. Inner lobe length was divided by the width of the lobe measured midway between the crotch and the tip. Both measurements were taken to the nearest 0.1 mm.

Osteology

Skeletal characters usually tend to be more conservative among individuals of a population than other kinds of characters such as lepidosis and body pattern (Klauber, 1972). Therefore, skeletal characters, depending on the level of analysis, may be especially useful in determining systematic relationships. Skeletal material of many species of montane rattlesnakes is difficult to obtain and also difficult to prepare; because of this, only 15 skulls were available for study, including 4 *C. lepidus*, 4 *C. triseriatus aquilus*, 4 *C. t. triseriatus*, and 3 *C. t. armstrongi*. Skulls were prepared for study in one of two ways. One method was to skin the snake before preservation and place the skull in a colony of dermestid beetles, *Dermestes maculatus*. This method was the simplest but has three disadvantages. First, only snakes that have not been preserved can be used. Second, the beetles tend to leave traces of uric acid on the bone which can obscure sutures and other osteological details. Third, the beetles sometimes will actually eat parts of the bone if it is left in the colony too long. The other method can be done after preservation and involves skinning the snake as before and then manually removing muscle tissue. This is tedious work and care must be taken not to break small bones.

A dissecting scope was used to make most of the osteological observations and measurements. The following characters were examined:

41. *Squamosal length.* The squamosal is the bone connecting the pro-otic to the quadrate (Fig. 6). The relative length of the squamosal was determined to be long or short.

42. *Quadrate length.* The quadrate is the bone connecting the posterior end of the squamosal to the posterior end of the pterygoid. The relative length of the quadrate was determined to be long or short.

43. *Prearticular crest height.* The prearticular crest is the laterally flattened flange of the posterior end of the mandible (Fig. 5).The relative height of the prearticular crest was determined to be low or high.

44. *Prearticular crest length.* The relative length of the prearticular crest was determined to be long or short (Fig. 5).

45. *Maxillary foramen size.* The size of the foramen in the maxillary was determined to be either small or large for each specimen examined.

46. *Parietal/supraoccipital contact.* The posterior edge of the parietal may or may not reach the most posterior edge of the supraoccipital (Fig. 6). Each skull was examined and the parietal was determined to be in contact with the posterior edge of the supraoccipital or not.

47. *Mandible curvature.* The mandible may be curved or it may be relatively straight (Fig. 5).

48. *Neural spine height.* The height of the neural spine of a mid-thoracic vertebra was determined to be either high or low.

49. *Postzygapophysis length.* The relative length of the postzygapophysis of a mid-thoracic vertebra was determined to be either long or short for each specimen examined.

50. *Neural arch width.* The relative width of the neural

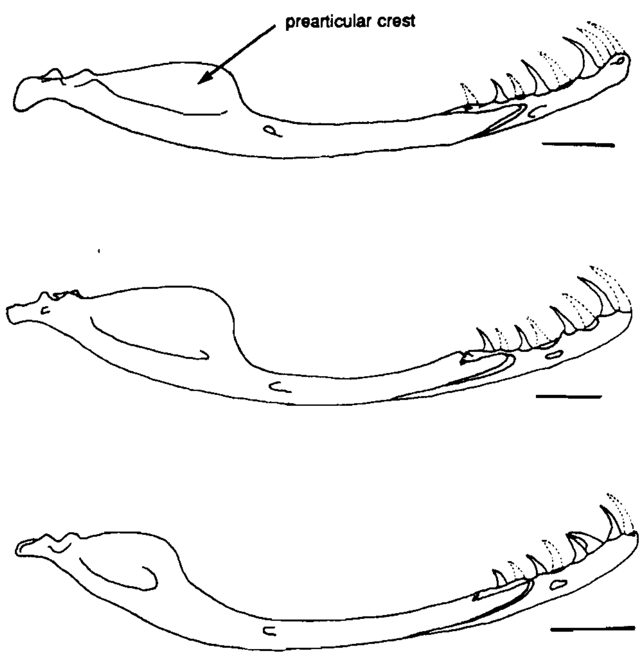

Fig. 5. Mandibles of *Crotalus lepidus* (UTACV R-22519) (top), *C. aquilus* (UTACV R-4540) (center), and *C. t. triseriatus* (UTACV R-7286) (bottom). Note the relative size of prearticular crest and curvature of mandible. Bar = 3 mm.

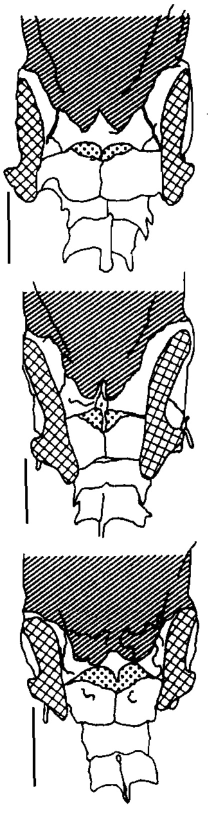

Fig. 6. Base of skulls of *Crotalus lepidus* (UTACV R-22519) (top), *C. aquilus* (UTACV R-4540) (center), and *C. t. triseriatus* (UTACV R-7286) (bottom). Note presence or absence of contact between the parietal (diagonals) and supraoccipital (stipples). Note also the relative size and shape of the squamosal (crosshatch). Bar = 3 mm.

arch of a mid-thoracic vertebra was determined to be either wide or narrow for each specimen examined.

Analysis and Polarization of Characters

When appropriate, one-way anovas were performed to determine significance of the various quantitative characters examined. Out of a total of 50 characters, 27 were found to vary significantly and therefore to be useful in cladistical analysis. The other 23 characters did not show significant difference among the taxa being studied and were not used in the analyses. Significance between specific taxa was determined using comparisons among means tests (Sokal and Rohlf, 1981). The characters were polarized and coded as being either primitive (0) or derived (1 or 2) and then cladistically analyzed using the Phylogenetic Analysis Using Parsimony (PAUP) 2.4.1 computer program (Swofford, 1985). Polarization was determined using other rattlesnakes and other pitvipers as outgroups. In some analyses, (1) *Crotalus pricei* and (2) *C. atrox* were used to root the tree. In a third analysis, a (3) hypothetical ancestor in which all characters were coded as primitive was used to root the tree. Five different analyses were performed using each of the three ancestors to root the tree. The first analyisis used hemipenial characters; the second skeletal characters; the third consisted of hemipenial and skeletal characters combined; the fourth anayalized lepidosis, body pattern and body proportions; and the fifth analyzed all 27 characters combined. The following is a list of the 27 characters which proved useful in cladistical analysis with a brief explanation of how they were polarized.

2. *Frequency of a divided upper preocular.* A divided upper preocular is rarely found in rattlesnakes and other vipers in general, it• was considered to be the derived state. An undivided upper preocular was considered primitive.

12. *Prefrontal scales.* Rattlesnakes of the genus *Sistrurus* have few scales in the prefrontal area (usually four). Most montane rattlesnakes tend to have relatively few scales in the prefrontal area when compared to other rattlesnakes and Neotropical pitvipers. Few scales in the prefrontal area was considered to be the primitive state and a high number of scales was considered derived. The number of scales in the prefrontal area was also found to be highly significant (ANOVA $p<0.001$) among taxa examined.

13. *Ventral number.* Ventral number is a sexually dimorphic character and therefore anovas were performed separately on each sex. Both proved to be highly significant (ANOVA $p<0.001$). Since a short, stocky body is probably the primitive state among snakes (Cadle, 1988), a low number of ventrals was considered to be primitive and a high number derived.

14. *Subcaudal number.* Subcaudal number is also a sexually dimorphic character and therefore two anovas were performed. Both of these proved to be highly significant (ANOVA $p<0.001$). Comparing the examined taxa to other rattlesnakes and pitvipers in general, it was presumed that a long tail is a primitive condition. A short tail and therefore fewer subcaudals was considered derived.

15. *Rattle-fringe scale number.* A large rattle is obviously derived and, correspondingly, many rattle-fringe scales were considered derived and few rattle-fringe scales primi-

tive. Differences among taxa examined were found to be highly significant (ANOVA p<0.001).

17. *Size and shape of rostral.* Since primitive rattlesnakes such as *Sistrurus* tend to have a high rostral, this was considered to be the primitive state, whereas a relatively low rostral was considered derived. This character also showed high significance (ANOVA p<0.001).

19. *Prenasal shape.* The prenasal rarely extends under the postnasal in rattlesnakes or other vipers, this was considered to be the derived condition. The absence of this extension was regarded as primitive.

20. *Body-blotch number.* Most primitive rattlesnakes and other Neotropical pitvipers tend to have a high number of body-blotches. Therefore a relatively high number was considered to be the primitive state, and low number of body-blotches was considered derived. Differences in body-blotch number were highly significant (ANOVA p<0.001).

21. *Number of tail markings.* A high number of tail markings is present in primitive rattlesnakes (e.g. *Sistrurus*) and other Neotropical pitvipers and therefore was considered primitive, whereas a low number was considered derived. When analyzed statistically this character proved highly significant (ANOVA p<0.001).

22. *Sexual dimorphism in ground color.* Sexual dimorphism is not found in primitive rattlesnakes and other Neotropical pitvipers and was considered a derived characteristic. The absence of sexual dimorphism in ground color was considered primitive.

26. *Snout/eye diameter.* Vipers in general are nocturnal and therefore have a small eye. Hence, a small eye was considered to be the primitive state. A large eye was considered derived. This character was also found to be highly significant (ANOVA p<0.001).

28. *Head length/total length.* A short, stocky head is a derived character shared by many species of pitvipers. A long head was considered primitive. This was also found to be significant (ANOVA p<0.001).

29. *Tail length/total length.* A relatively long tail was considered the primitive state and a short tail derived. Tail length is a character that shows sexual dimorphism with males having longer tails than females. Therefore separate analyses were performed and both showed high significance (ANOVA p<0.001).

30. *Proximal rattle width.* The rattle is a derived character, and a large rattle was considered more derived than a small rattle. Proximal rattle width was found to be a highly significant character when analyzed statistically (ANOVA p<0.001).

33. *Crotch shape of hemipenis.* In primitive rattlesnakes such as *Sistrurus* the hemipenes have a U-shaped crotch. Therefore, a U-shaped crotch was considered to be the primitive state and a V-shaped crotch was considered derived.

36. *Microornamentation of the lateral distal lobe of the hemipenis.* In primitive rattlesnakes and other pitvipers the hemipenes tend to be heavily microornamented (spinulate). Heavy microornamentation was considered to be the primitive state. Reduced microornamentation (papillate) was considered derived.

38. *Number of large basal hooks.* A high number of large basal hooks is characteristic of primitive rattlesnakes. A small number of basal hooks was regarded as primitive and a high number as derived. When analyzed statistically this character proved to be highly significant (ANOVA p<0.001).

39. *Number of calyces.* Primitive rattlesnakes tend to have short hemipenes with fewer calyces. This was considered to be the primitive state. Snakes with hemipenes that have many calyces were considered derived. This was found to be highly significant (ANOVA p<0.001)

40. *Length of hemipene lobes. Sistrurus,* a primitive rattlesnake, tends to have short, stubby hemipenes, and this was considered to be the primitive state. Long, thin lobes were considered derived. This character was found to be highly significant (ANOVA p<0.001).

41. *Squamosal length.* A long squamosal is associated with a long head and was considered primitive. A short squamosal was considered derived.

42. *Quadrate length.* A long quadrate is associated with a long head and was considered primitive. A short quadrate was considered derived.

43. *Prearticular crest height.* Primitive rattlesnakes and other pitvipers have large, robust jaw muscles. Large jaw muscles are usually associated with large attachment sites on bones. Because of this, a high prearticular crest of the compound bone was considered primitive and a low one derived.

44. *Prearticular crest width.* For the same reasons associated with prearticular crest height, a wide prearticular crest was considered primitive and a narrow one derived.

45. *Maxillary foramen size.* Primitive rattlesnakes and other pitvipers in general have a small foramen in the maxillary bone, consequently this was considered to be the primitive state. A relatively large foramen was considered derived.

46. *Parietal/supraoccipital contact.* The parietal does not reach the posterior edge of the supraoccipital in primitive rattlesnakes and other pitvipers. This condition was therefore considered primitive. The derived condition is a contact between the parietal and edge of the supraoccipital.

47. *Mandible curvature.* Primitive rattlesnakes and other pitvipers have a relatively straight mandible; a curved mandible was considered derived.

50. *Neural arch width.* Primitive rattlesnakes and other pitvipers in general have a relatively wide neural arch; a narrow neural arch was considered derived.

RESULTS

Crotalus t. triseriatus tends to be a relatively slender rattlesnake with a long, slender tail, a large eye and long head. *Crotalus l. lepidus* and *C. l. klauberi* tend to be stocky snakes with short tails, small eyes and proportionately shorter heads. *Crotalus t. aquilus* does not resemble *C. t. triseriatus,* but more closely resembles *C. lepidus. Crotalus t. aquilus* has a relatively short head, a small eye, and a tail intermediate in length between *C. t. triseriatus* and *C. lepidus.* In fact, *C. t. aquilus* has many characters intermediate between *C. t. triseriatus* and *C. lepidus* (Tables 1-4).

When subjected to statistical analysis using one-way anovas, differences were noted among several characters.

Table 1. Lepidotic characters of *Crotalus lepidus* and *C. triseriatus*. Parentheses indicate mode in all characters except 14, 15, 17 and 18 where they indicate mean.

		lepidus (n=31)	*klauberi* (n=49)	*morulus* (n=2)	*maculosus* (n=4)	*aquilus* (n=54)	*armstrongi* (n=19)	*triseriatus* (n=57)
1.	Loreal	1-2 (1)	1-2 (1)	1	1	1-2 (1)	1	1-2 (1)
2.	Preocular	2	2	2	2	2	2	2
2.a	Divided upper preocular %	94.4	79.0	0	0	37.3	5.3	14.6
3.	Suboculars	2-5 (3)	2-4 (3)	3-4 (4)	3	2-5 (3)	2-3 (3)	2-4 (3)
4.	Postoculars	1-3 (2)	2-3 (2)	2	2-3 (2)	1-4 (2)	1-3 (2)	2-3 (2)
5.	Interoculabials	0-2 (1)	1-2 (1)	1	1	1	1-2 (1)	0-1 (1)
6.	Prefoveals	1-7 (2)	0-6 (3)	3	1-3 (2)	1-6 (3)	1-6 (3)	1-7 (3)
7.	Supralabials	10-14 (12)	11-14 (12)	12-13 (13)	12-13 (12)	10-14 (12)	11-13 (12)	10-14 (12)
8.	Infralabials	10-13 (11)	10-13 (11)	12-13 (13)	10-13 (12)	9-13 (11)	10-14 (12)	9-13 (11,12)
9.	Internasals	2	1-2 (2)	2	2	2-3 (2)	2-3 (2)	2-3 (2)
10.	Canthals	1-2 (2)	1	1	1-2 (1)	1-2 (1)	1	1-2 (1)
11.	Intercanthals	1-3 (2)	1-2	1-2	2	0-2 (2)	1-3 (2)	1-3 (2)
12.	Prefrontals	6-12 (8)	5-11 (8)	7	6-8 (8)	5-10 (7)	6-8 (6)	6-9 (6)
13.	Ventrals (male)	150-170 (160.5)	149-168 (158.1)	165	160-164 (162.7)	140-158 (149.6)	130-154 (141.6)	125-151 (140.2)
	Ventrals (female)	155-173 (163.5)	149-170 (159.3)	161	162	138-156 (148.1)	138-152 (143.0)	137-150 (144.3)
14.	Subcaudals (male)	20-27 (24.3)	21-29 (25.2)	27	27	22-31 (26.5)	24-32 (28.3)	27-33 (29.1)
	Subcaudals (female)	17-21 (19.5)	17-21 (19.2)	20	20	19-24 (21.0)	19-28 (21.5)	20-28 (24.4)
15.	Rattle-fringe scales	10-14 (12)	8-12 (10)	10,12	10	8-11 (10)	8-10 (8)	8-10 (8)
16.	Dorsal scale rows neck	21-26 (23,25)	21-26 (23,25)	27,30	25-26 (25)	21-27 (25)	23-27 (25)	23-28 (25)
	mid-thoracic	20-24 (23)	21-25 (23)	23	23	20-25 (23)	21-24 (23)	21-25 (23)
	posterior	14-19 (17)	16-19 (17)	17	17-18 (17)	15-19 (17)	17-19 (17)	15-19 (17)
17.	Rostral H/W %	57.5-87.5 (66.4)	52.3-85.2 (66.6)	58.1-63.9 (61.0)	60.5-87.5 (70.5)	46.2-100.0 (69.5)	61.7-111.5 (77.2)	61.0-97.4 (76.0)
18.	Mental H/W %	52.0-85.7 (68.8)	37.9-87.5 (60.8)	71.9-76.9 (74.4)	56.8-77.8 (66.5)	50.0-78.3 (76.6)	52.2-81.1 (62.6)	43.8-82.5 (57.9)
19.	Prenasal shape	curves under postnasal	curves under postnasal	N/A	curves under postnasal	curves under postnasal	does not curve under postnasal	does not curve under postnasal

Table 2. Color pattern and body proportions of *Crotalus lepidus* and *C. triseriatus*. Parentheses indicate mean except in character 21 where they indicate mode.

	lepidus (n=31)	*klauberi* (n=49)	*morulus* (n=2)	*maculosus* (n=4)	*aquilus* (n=54)	*armstrongi* (n=19)	*triseriatus* (n=58)
20. Body-blotch #	16-23 (19)	14-31 (17)	31,33	29-37 (33)	21-41 (31)	32-54 (43)	30-53 (42)
21. Tail-marking #	1-4 (3)	1-4 (2,3)	3,4	2-5 (3)	3-8 (5)	5-9 (6)	3-10 (7)
22. Sexual dimorphism in ground color	present	present	present	present	present	present	absent
23. Postocular stripe	distinct	indistinct	variable	distinct	present	present	present
24. Venter mottling	variable	variable	variable	heavy	variable	heavy	heavy

	lepidus (n=28)	*klauberi* (n=44)	*morulus* (n=2)	*maculosus* (n=3)	*aquilus* (n=31)	*armstrongi* (n=17)	*triseriatus* (n=38)
25. Eye/upper lip	0.85-2.23 (1.50)	0.85-2.58 (1.37)	0.96-1.38 (1.17)	0.94-1.79 (1.25)	0.93-2.76 (1.43)	1.16-2.05 (1.52)	0.87-2.04 (1.42)
26. Snout/eye diameter	1.53-3.37 (2.43)	1.83-3.47 (2.42)	2.14-2.33 (2.24)	2.52-2.89 (2.68)	1.65-3.17 (2.21)	1.47-2.27 (1.91)	1.51-3.16 (2.07)
27. Head width/ head length	50.2-74.7 (67.1)	47.9-77.6 (66.7)	59.2-69.2 (64.2)	66.4-75.0 (70.1)	60.9-83.5 (66.6)	60.8-79.9 (70.2)	56.9-72.8 (66.3)
28. Head length/ total length	3.9-5.3 (4.6)	4.1-6.0 (4.8)	4.6-4.7 (4.6)	4.3-4.6 (4.5)	4.5-5.4 (5.0)	4.9-5.9 (5.5)	4.6-6.4 (5.5)
29. Tail length/ total length (male)	6.9-9.3 (8.0)	6.5-10.4 (8.5)	8.7	7.7-9.1 (8.5)	7.9-10.2 (9.1)	9.1-11.1 (10.1)	7.9-12.1 (10.1)
29. Tail length/ total length (female)	6.4-8.4 (7.0)	5.4-7.8 (7.0)	7.6	7.4	5.9-7.9 (7.0)	5.7-11.0 (8.2)	7.1-11.0 (8.3)
30. Proximal rattle width	25.1-36.8 (31.2)	19.6-37.1 (29.4)	20.6-28.4 (24.5)	17.8-20.8 (18.8)	18.4-26.2 (22.8)	12.5-16.7 (14.3)	11.6-18.0 (14.6)

Table 3. Hemipenial data for *Crotalus lepidus* and *C. triseriatus*. Parentheses indicate mean.

	lepidus (n=5)	*klauberi* (n=23)	*maculosus* (n=2)	*aquilus* (n=14)	*armstrongi* (n=4)	*triseriatus* (n=7)
31. Subcaudal length	8	7-11 (9)	7	7-10 (8)	9-11 (10)	9-10 (9)
32. Lobe shape	cylindrical	bulbous	bulbous	bulbous	variable	bulbous
33. Crotch shape	U	U	V	U	V	V
34. Basal spine length	medium	medium	medium	medium	short	long
35. Basal spine shape	sharp	sharp	sharp	sharp	slightly sharp	sharp
36. Microornamentation mesial/distal	papillate	papillate	papillate	papillate	papillate	papillate
mesial/proximal	very spinulate	spinulate	spinulate	spinulate	spinulate	spinulate
lateral/distal	slightly papillate	slightly papillate	slightly papillate	slightly papillate	papillate	papillate
lateral/proximal	slightly spinulate	slightly spinulate	slightly spinulate	slightly spinulate	papillate	slightly papillate
37. Basal spine #	35-54 (44)	30-54 (43)	36	37-58 (47)	40-54 (47)	33-57 (47)
38. Large basal hook #	16-25 (21)	16-27 (22)	20	20-30 (25)	16-19 (18)	14-20 (16)
39. Calyx #	21-24 (23)	20-26 (22)	25	21-28 (24)	23-25 (24)	24-27 (25)
40. Medial lobe L/W	2.7	2.4-3.0 (2.7)	2.8	2.4-3.7 (3.0)	2.3-2.7 (2.5)	2.8-3.7 (3.3)

Table 4. Skeletal characters in *Crotalus lepidus* and *C. triseriatus*.

	lepidus (n=2)	*klauberi* (n=2)	*aquilus* (n=4)	*armstrongi* (n=3)	*triseriatus* (n=4)
41. Squamosal length	long	long	long	short	short
42. Quadrate length	long	long	long	short	short
43. Prearticular crest height	high	high	high	low	low
44. Prearticular crest length	long	long	long	short	short
45. Maxillary foramen size	small	small	small	large	large
46. Parietal/supraoccipital contact	no contact	no contact	no contact	contact	contact
47. Mandible curvature	straight	straight	straight	curved	curved
48. Neural spine height	low	low	low	high	low
49. Postzygapophysis length	long	long	long	long	short
50. Neural arch width	wide	wide	wide	narrow	narrow

Table 5. Polarized characters used in phylogenetic analyses of *Crotalus lepidus* and *C. triseriatus*. 0 is primitive and 1 and 2 are derived; 9 is unknown.

	lepidus	*klauberi*	*morulus*	*maculosus*	*aquilus*	*armstrongi*	*triseriatus*
2a. Divided upper preocular %	2	2	2	2	1	0	0
12. Prefrontals	1	1	1	1	0	0	0
13. Ventrals	0	0	0	0	1	2	2
14. Subcaudals	2	2	1	1	1	0	0
15. Rattle-fringe scales	2	1	2	1	1	0	0
17. Rostral H/W %	1	1	1	1	1	0	0
19. Prenasal shape	1	1	1	1	1	0	0
20. Body-blotch #	2	2	0	0	1	0	0
21. Tail marking #	2	2	2	2	1	0	0
22. Sexual dimorphism in ground color	1	1	1	1	1	1	0
26. Snout/eye diameter	0	0	0	0	0	1	1
28. Head length/ total length	2	1	2	2	1	0	0
29. Tail length/ total length	2	2	1	2	1	0	0
30. Proximal rattle width	2	2	1	1	1	0	0
33. Crotch shape	0	0	9	1	0	1	1
36. Microornamentation lateral/distal	1	1	9	1	1	0	0
38. Large basal hook #	1	1	9	1	1	0	0
39. Calyx #	0	0	9	1	1	1	1
40. Medial lobe L/W	0	0	9	1	1	0	1
41. Squamosal length	0	0	9	9	0	1	1
42. Quadrate length	0	0	9	9	0	1	1
43. Prearticular crest height	0	0	9	9	0	1	1
44. Prearticular crest length	0	0	9	9	0	1	1
45. Maxillary foramen size	0	0	9	9	0	1	1
46. Parietal/ supraoccipital contact	0	0	9	9	0	1	1
47. Mandible curvature	0	0	9	9	0	1	1
50. Neural arch width	0	0	9	9	0	1	1

These informative characters were coded as being primitive (0) or derived (1 or 2) (Table 5). When characters were subjected to cladistic analysis using the PAUP program, several different, equally parsimonious phylogenetic trees were produced for most analyses. However, most of the trees placed the various taxa in consistent groups; in other words certain commonalities were apparent in most analyses. A maximum of ten equally parsimonious cladograms for each of the analyses was incorporated into the program. But, the maximum number of trees produced by any specific analysis was only five. Because only two specimens of *C. l. morulus* were available for study, this subspecies was only used in analyses involving the combination of lepidosis, body pattern, and body proportions. *Crotalus l. maculosus* was not used in any of the analyses in which only skeletal characters were used because no skeletal material was available for this species.

To avoid overwhelming the reader, I have included only seven of the twenty-eight different cladograms produced in the analyses. Included are four examples of cladograms rooted with *C. atrox* and using hemipenial characters, skeletal characters, hemipenial and skeletal characters combined, and lepidosis, body proportions and color pattern combined. I have also included three cladograms developed using all twenty-seven characters and rooted with *C. atrox, C. pricei* and a hypothetical ancestor. The first analysis was done using *C. atrox* to root the tree. Because *C. atrox* appears to be more highly derived than the montane rattlesnakes, it might be expected that an analysis rooted with *C. atrox* would show more homoplasies (reversals or convergences) than an analysis rooted with a more closely related species such as *C. pricei* or a hypothetical ancestor in which all characters are coded as primitive. Ten homoplasies were present in the first analysis, which used *C. atrox* to root the tree and all characters combined. But when analyzed using *C. pricei* or the previously mentioned hypothetical ancestor, eight and seven homoplasies were produced, respectively.

When analyzed using only hemipenial characters and *C. atrox* to root the tree, two equally parsimonious trees were produced. In the first of these trees, the subspecies of *C. lepidus* were grouped with *C. t. aquilus* (Fig. 7). In the second tree, *C. t. aquilus* was grouped with *C. t. triseriatus* as was *C. l. maculosus.* Only five characters were used to form this tree. In the first tree there were two convergences. One involved crotch shape and the other involved the length of the hemipenial lobes. In the second tree two reversals were present. The first of these involved the microornamentation of the lateral distal end of the organ and the second involved the length of the hemipenial lobes.

The second analysis using *C. atrox* to root the tree used only skeletal characters. This resulted in the production of only one tree (Fig. 8). This tree showed *C. t. aquilus* sharing a common ancestor with *C. lepidus.* All eight skeletal characters exhibited the primitive state in *C. lepidus* and *C. t. aquilus* and the derived state in *C. t. triseriatus* and *C. t. armstrongi.* No convergences or reversals were present in this tree.

The third analysis using *C. atrox* to root the tree was performed using skeletal and hemipenial characters combined. Only one tree was produced and it placed *C. t. aquilus* with *C. lepidus* (Fig. 9). Only two convergences were present and they involved hemipenial crotch shape and the length of the hemipenial lobes.

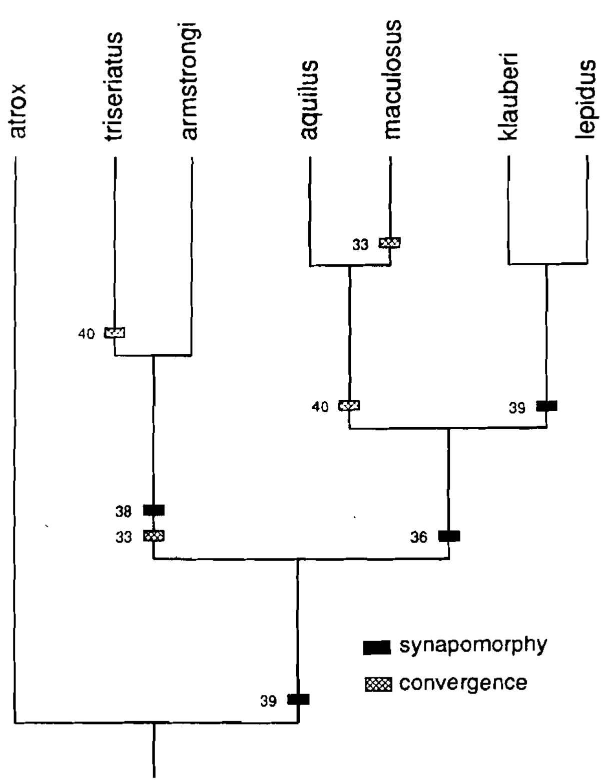

Fig. 7. Cladogram constructed using hemipenial data and rooted with *Crotalus atrox.*

When rooted with *C. atrox* and analyzed using lepidosis, body proportions, and body pattern combined, only one tree was produced (Fig. 10). This tree placed *C. t. aquilus* in a monophyletic group with *C. lepidus.* Many reversals were present in this tree, probably most as a result of using *C. atrox* to root the tree.

Finally, when analyzed using all twenty-seven characters, only one tree was produced (Fig. 11). This tree placed *C. lepidus* and *C. t. aquilus* into a monophyletic group united by twelve synapomorphies. Five reversals and three convergences were present in this tree.

When cladistically analyzed using *C. pricei* to root the tree similar results were obtained. The first analysis was done using only hemipenial characteristics. Only five hemipenial characters were shown to be useful in determining the group's relationships. Four equally parsimonious trees were produced, and they tend to vary considerably. Three of the trees placed *C. t. aquilus* in a monophyletic group with *C. lepidus.* But one of the trees produced a trichotomy with *C. lepidus, C. triseriatus,* and *C. t. aquilus,* leaving their relationships unresolved.

The second analysis was done using skeletal data. This analysis produced only one tree. In this tree *C. t. triseriatus* and *C. t. armstrongi* were united by all eight skeletal characters. This tree leaves the relationships between *C. t. aquilus,* the other subspecies of *C. triseriatus,* and the subspecies of *C. lepidus* unresolved.

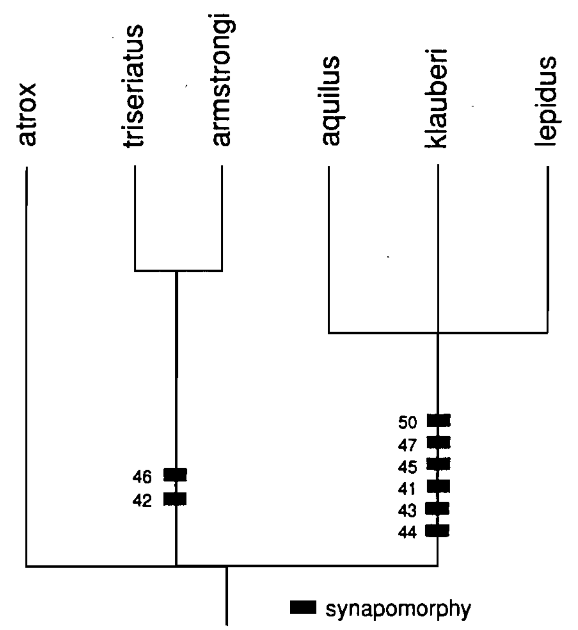

Fig. 8. Cladogram constructed using skeletal data and rooted with *Crotalus atrox.*

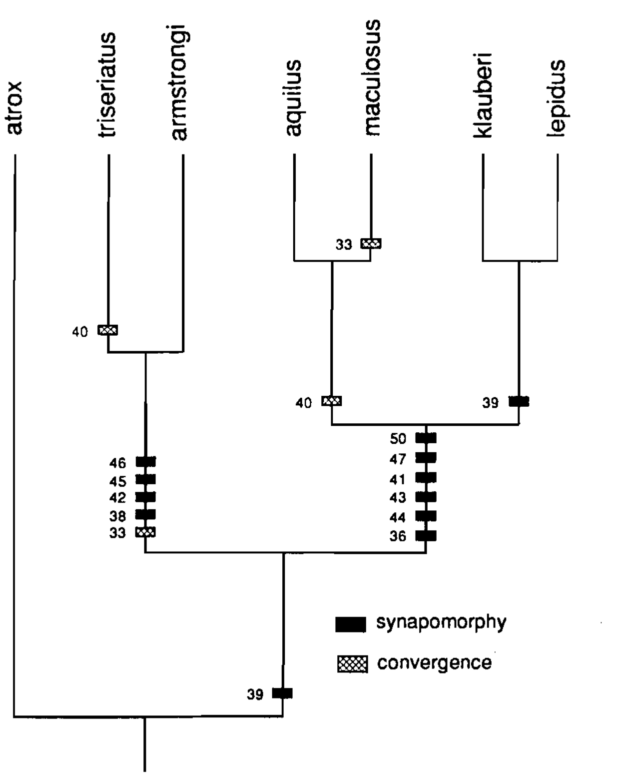

Fig. 9. Cladogram constructed using hemipenial and skeletal data combined and rooted with *Crotalus atrox.*

When analyzed using *C. pricei* to root the tree and using skeletal and hemipenial characters combined, three equally parsimonious trees were produced. Two of the trees placed *C. t. aquilus* in a monophyletic group with *C. lepidus.* However, in the third tree there exists an unresolved trichotomy between the subspecies of *C. lepidus, C. t. aquilus,* and the subspecies of *C. triseriatus.* In all three trees two homoplasies were present in varying combinations.

When analyzed using lepidosis, body pattern and body proportions with *C. pricei* to root the tree, only one tree was produced. In this tree *C. t. aquilus* shares a common ancestor with the subspecies of *C. lepidus.* Five reversals and two convergences are present in this tree.

When analyzed using all twenty-seven available characters, with *C. pricei* as the root, only one tree was produced (Fig. 12). This tree was remarkably similar to the tree rooted with *C. atrox* (Fig. 11). *Crotalus t. aquilus* was placed with *C. lepidus* in a monophyletic group which is united by ten characters. Seven reversals and two convergences exist in this tree.

The third taxon used to root the tree was a hypothetical ancestor in which all characters were coded as primitive. It was believed that this might give the best indication of the proper systematic relationships among the taxa being studied. When other "real life" species are used to root the tree the results are often clouded because the root species themselves may have derived characters. By using a hypothetical ancestor with all primitive characters this can be avoided.

The first analysis using the hypothetical ancestor to root the tree involved only hemipenial characters. This analysis produced five equally parsimonious trees. In all the trees, *C. t. aquilus* is placed in a close relationship with *C. lepidus maculosus.* Three of these trees placed *C. t. aquilus* in a monophyletic group with *C. lepidus* and its subspecies. The other two placed it in a group with *C. triseriatus.* A total of three homoplasies were present in each tree. These apparent

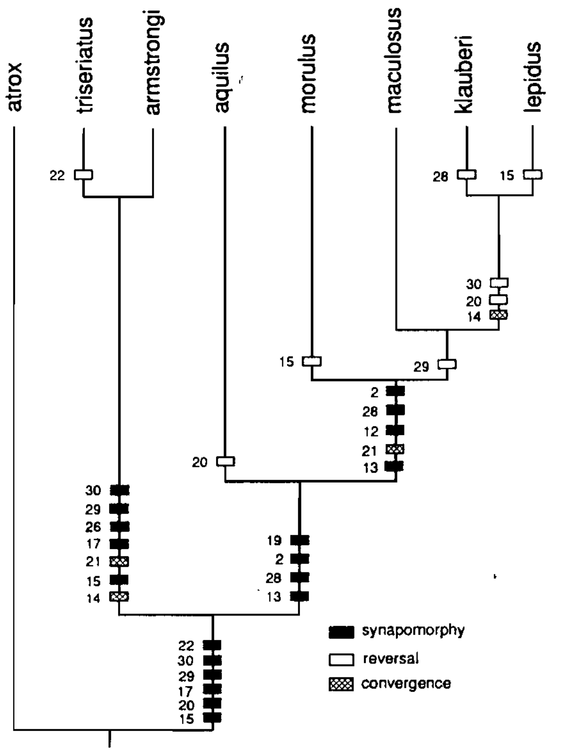

Fig. 10. Cladogram constructed using combined characters of lepidosis, color pattern, and body proportions and rooted with *Crotalus atrox.*

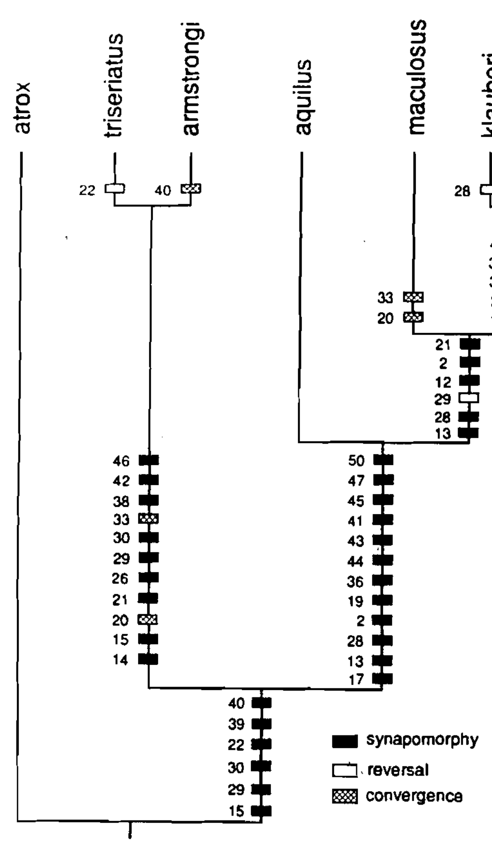

Fig. 11. Cladogram constructed using all data and rooted with *Crotalus atrox*.

inconsistencies can be accounted for by the low number (5) of characters being used in this particular analysis.

The next analysis was performed using only skeletal data and the hypothetical ancestor as the root. This analysis produced only one cladogram. This tree unites *C. t. triseriatus* and *C. t. armstrongi* by eight skeletal characters. It leaves unresolved relationships between the ancestor and the other three taxa.

When the hypothetical ancestor is used to root the tree and skeletal and hemipenial characters are combined, a total of four trees are produced. Two of these trees placed *C. t. aquilus* in a monophyletic group with *C. lepidus.* Two of the trees placed *C. t. aquilus* with *C. triseriatus.* In each tree there are three homoplasies, all of which are hemipenial characters.

When the hypothetical ancestor is used to root the tree and lepidosis, body pattern and body proportion characters are analyzed, only one tree is produced. This tree places *C. t. aquilus* in a monophyletic group with all subspecies of *C. lepidus.* A total of four homoplasies were present (two reversals and two convergences). *Crotalus t. triseriatus* and *C. t. armstrongi* are united by two synapomorphies.

Finally, the last analysis used the hypothetical ancestor as the root and all twenty-seven available characters. This analysis produced only one tree (Fig. 13). This tree placed *C. t. aquilus* in a monophyletic group with the subspecies of *C. lepidus.* The subspecies of *C. lepidus* form the sister group to *C. t. aquilus. Crotalus t. triseriatus* and *C. t. armstrongi* are united by 10 synapomorphies and one convergence; together these two taxa form the sister group to *C. t. aquilus* and *C. lepidus.* Seven reversals and two convergences were present in this analysis.

When analyzed using all twenty-seven characters, regardless of the outgroup used, *C. t. aquilus* appears to share a common ancestor with *C. lepidus,* and the subspecies of *C. lepidus* are united as a monophyletic group.

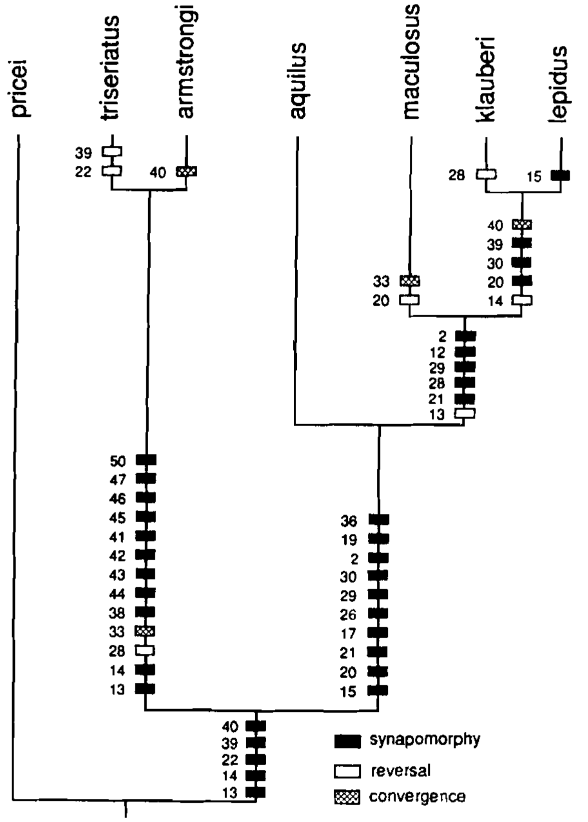

Fig. 12. Cladogram constructed using all characters and rooted with *Crotalus pricei.*

DISCUSSION

Various herpetologists have unraveled much of the misunderstanding regarding the taxonomy of montane Mexican rattlesnakes (Gloyd, 1940; Smith, 1946; Klauber, 1952; 1972). However, the relationships between C. triseriatus and C. lepidus heretofore have remained unclear (Klauber, 1952; 1972; Armstrong and Murphy, 1979; Campbell and Lamar, 1989). Based on morphological data I suggest that *C. triseriatus* and *C. lepidus* are each other's closest relatives, and form a monophyletic group. This close relationship is based on several characters. Smith (1946) noted the presence of several subloreals (prefoveals), numerous supralabials and numerous midthoracic scale rows as characters linking the two species. Both Smith (1946) and Klauber (1952) noted the frequent occurrence of a vertically divided upper preocular as the most remarkable feature linking *C. lepidus* and *C. triseriatus.* I herein define *C. triseriatus* and *C. lepidus* as the *Triseriatus* group, not to be confused with the groups

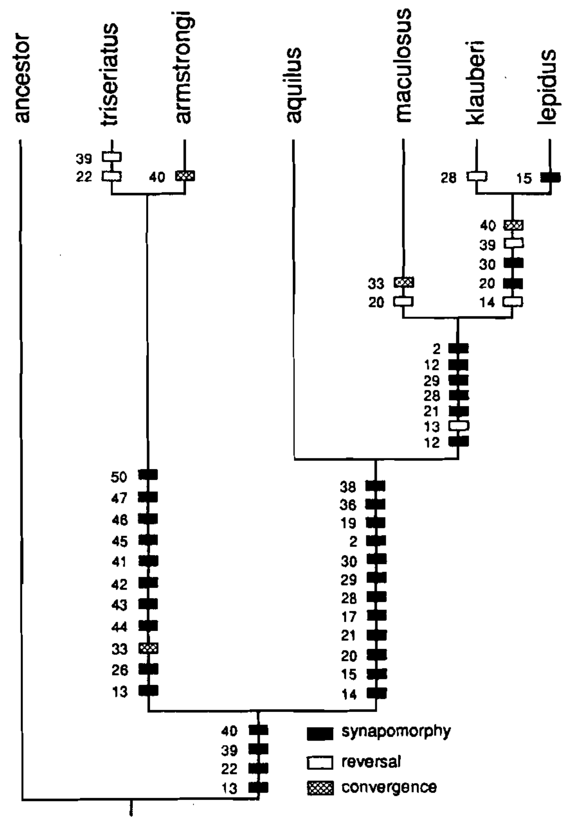

Fig. 13. Cladogram constructed using all characters and rooted with a hypothetical ancestor.

proposed by Gloyd (1940), Smith (1946) or Klauber (1952).

Previously, the main source of confusion has been the taxonomic status of *C. t. aquilus*. It has been suggested that the closest relative of *C. t. aquilus* may be *C. lepidus* rather than the nominate race of *C. triseriatus* (Campbell and Lamar, 1989), the latter being clearly an untenable position. Klauber (1952) hinted at this concept by stating that the subspecific relationship between *C. t. triseriatus* and *C. t. aquilus* is based on general similarity rather than the availability of any specimens that can be called intergrades. Klauber (1952) recognized that *C. t. aquilus* and *C. t. triseriatus* might some day be shown to represent two distinct species. Campbell and Lamar (1989) also suggested that *C. t. aquilus* might be shown to represent a subspecies of *C. lepidus* or a full species.

There are many characters of *C. t. aquilus* that are intermediate between *C. lepidus* and *C. t. triseriatus*. This might be predicted owing to the intermediate geographic position of *C. t. aquilus*. Some of these intermediate characters include: number of ventrals, subcaudals, and rattle-fringe scales; the head length; and the length of the hemipenial lobes. For a list of intermediate characters see Tables 1-4.

The majority of the characters that suggest a close relationship between *C. t. aquilus* and *C. lepidus* are skeletal. The skeletal characters examined in this study show *C. t. aquilus* and *C. lepidus* to form one monophyletic group separate from *C. triseriatus*. In other words, *C. triseriatus* is paraphyletic as currently recognized.

If *C. t. aquilus* and *C. lepidus* form a monophyletic group, as my data suggest, the question arises whether *C. t. aquilus* should be considered a subspecies of *C. lepidus* or a sister species of *C. lepidus*, both tenable positions. Because of the numerous lepidotic, hemipenial, body proportion and body pattern characters separating *C. lepidus* from *C. t. aquilus*, I recommend that *C. t. aquilus* be recognized as a full species, *Crotalus aquilus* Klauber (1952). For a list of the characters that distinguish *C. lepidus* from *C. aquilus* see Tables 1-4.

Crotalus l. lepidus and *C. l. klauberi* are united by six derived characters in this cladistic analysis. These two subspecies apparently intergrade in the southern portion of their range and appear to be most distinct from each other in the northern portion of their range (Klauber, 1952). This intergradation pattern may be the result of barrier formation in a north-to-south direction during the Pleistocene.

The relationships of *C. l. morulus* and *C. l. maculosus* are more difficult to ascertain. These two subspecies occupy a relatively similar habitat consisting of humid pine-oak forests (Armstrong and Murphy, 1979). *Crotalus l. maculosus* occurs on the Pacific versant of the Sierra Madre Occidental and *C. l. morulus* is found in the northern portions of the Sierra Madre Oriental in the states of Tamaulipas, Nuevo León and Coahuila. Little is known regarding the ecology and relationships of these subspecies, but *C. l. morulus* is known to intergrade with *C. l. lepidus* and *C. l. maculosus* is suspected to intergrade with *C. l. klauberi* in the vicinity of El Salto, Durango (Armstrong and Murphy, 1979).

Crotalus t. armstrongi differed from the nominate race in only two characters (sexual dimorphism in ground color and the length of the hemipenial lobes) and is hypothesized to be most closely related to *C. t. triseriatus*. Its geographic position (in the western portion of the Transverse Volcanic Axis in Jalisco) supports its close relationship to the nominate race.

An attempt to correlate geologic and climatic factors with the phylogeny of this group is offered below to help explain the present day distributions of the species.

The Pleistocene was a time of milder, more humid environments than are found presently in Mexico. Evidence for this is found in packrat (genus *Neotoma*) middens in the deserts of Mexico and the southern United States (Wells, 1976). The climatic history of North America during the Pleistocene was one affected primarily by the ice sheets which covered much of North America on four different occasions (Levin, 1983). During each ice age, the climate of the southern United States and Mexico was milder, being cooler in the summers and warmer in the winters. The present day Chihuahuan, Sonoran and Mojave deserts had more rainfall and were covered by woodland habitat consisting of pine, oak and juniper (Van Devender, 1976). During the three interglacial periods, the temperature was warmer than today and woodland habitat was restricted to the cooler, wet regions. This oscillation between glacial and interglacial periods left a situation in which pine-oak forests were restricted to higher elevations. These forests not only receive more rainfall, but offer cooler temperatures as well (Dorf, 1959).

Two different models are often used to explain distribution.

Dispersal biogeography assumes that the organisms are able to disperse across barriers and inhabit environments similar to the original habitat. Once the organisms are established in the new area, the organisms evolve to enable themselves to better survive in their new habitat (Brown and Gibson, 1983). Vicariance biogeography assumes that barriers form which cause fragmentation of a once continuous range. The phylogenetic distance between two organisms corresponds directly to the time since the fragmentation (Brown and Gibson, 1983).

Dispersal models are difficult to negate, and because they allow for any number of dispersions and extinctions to occur, they usually offer an inadequate biogeographical explanation. Vicariance models are easier to falsify because they make specific assumptions about historical connections among areas. When compared with the geologic and climatic history of the area, the hypothesis may be rejected or supported (Brown and Gibson, 1983). However, accepting vicariance biogeography as a logical approach does not imply that dispersion of organisms from one geographic area to another does not occur. Because the past climate and geologic history of Mexico is becoming better understood, the current distribution of Mexican montane rattlesnakes is most easily explained by a vicariance model.

During the relatively mild climate of Pleistocene, the common ancestor of *C. triseriatus*, *C. aquilus*, and *C. lepidus* ranged across parts of the southwestern United States and the Mexican Plateau (Smith, 1946). The Transverse Volcanic Axis formed during the upper Pliocene (Maldonado-Koerdell, 1964) and created new habitat which the *Triseriatus* group ancestor invaded. The first vicariance event resulted in two lineages, that for *C. t. triseriatus/armstrongi* and that for *C. aquilus/lepidus.*

Oscillations between glacial and interglacial periods during the Pleistocene restricted montane rattlesnakes to higher elevations where suitable climates prevailed. Populations inhabiting the Northern portions of the Mexican Plateau were consequently isolated giving rise to *C. aquilus* and *C. lepidus.*

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APPENDIX I.

Specimens Examined

Crotalus l. lepidus. Coahuila: TCWC-60527; Nuevo Leon: UTACV R-8324, UTACV R-8328, UTACV R-8344, UTACV R-8345, UTACV R-8344, UTACV R-9015, UTACV R-11002; San Luis Potosi: LSU-2438, LSU-4882; Texas: UTACV R-2103, UTACV R-2132, UTACV R-2435, UTACV R-6720, UTACV R-6723, UTACV R-6754, UTACV R-6780, UTACV R-6782, UTACV R-7425, UTACV R-7433, UTACV R-7434, UTACV R-8136, UTACV R-8691, UTACV R-9307, UTACV R-9414, UTACV R-10044, UTACV R-11001, UTACV R-12788, UTACV R-15662, UTACV R-17925, UTACV R-17926.

Crotalus l. klauberi. Aguascalientes: UTACV R-8343, UTACV R-8364, UTACV R-18342, UTACV R-18343, UTACV R-18344, UTACV R-18345, UTACV R-18346; Arizona: UTACV R-6746, UTACV R-7186, UTACV R-10341, UTACV R-16282; Chihuahua: UTACV R-8331, UTACV R-12790, UTACV R-15661, UTACV R-17835, UTACV R-18347, UTACV R-18348, UTACV R-18349; Durango: UTACV R-5847, UTACV R-8257, UTACV R-8327, UTACV R-8330, UTACV R-8338, UTACV R-12789, UTACV R-18350, UTACV R-18351; Nayarit: TCWC-61717; New Mexico: UTACV R-8326, UTACV R-8329, UTACV R-11003, UTACV R-16285, UTACV R-17323, UTACV R-17324, UTACV R-17325, UTACV R-18355, UTACV R-18356; Sonora: UTACV R-17830, UTACV R-17831, UTACV R-17832, UTACV R-17833, UTACV R-17834; Zacatecas: UTACV R-8332, UTACV R-8337, UTACV R-8342, UTACV R-8346, UTACV R-8409, UTACV R-11278, UTACV R-18353, UTACV R-18354.

Crotalus l. morulus. Coahuila: UTACV R-6123; Tamaulipas: UTACV R-8339.

Crotalus l. maculosus. Sinaloa: UTACV R-7228, UTACV R-8408, UTACV R-13020, UTACV R-17836.

Crotalus aquilus. Guanajuato: TCWC-58506; Hidalgo: TCWC-60764, USNM-140070, UTACV R-4540, UTACV R-4675, UTACV R-6115, UTACV R-6941, UTACV R-12592, UTACV R-12593, UTACV R-12594, UTACV R-12595, UTACV R-12596, UTACV R-12967, UTACV R-12968, UTACV R-12969, UTACV R-17904; Michoacan: FMNH-103991, FMNH-111063, FMNH-126508, FMNH-126509, FMNH-126511, FMNH-126512, UINHM-26224, USNM-110597, USNM-110925, UTACV R-6178, UTACV R-6179, UTACV R-6180, UTACV R-12597; Queretaro: TCWC-29473, TCWC-29474, TCWC-29475, TCWC-29476, TCWC-29477, TCWC-29478, TCWC-29479, TCWC-29480, TCWC-29481, TCWC-29482, TCWC-29483, TCWC-29484, TCWC-29485, TCWC-32988, TCWC-36013, TCWC-41554, TCWC-41553, TCWC-45567, TCWC-45568, UTACV R-8322, UTACV R-8323, UTACV R-8335, UTACV R-12598, UTACV R-18341; San Luis Potosi: UTACV R-9094.

Crotalus t. armstrongi. Jalisco: KU-73649, KU-73650, KU-106290, USNM-46465, UTACV R-4909, UTACV R-5893, UTACV R-6257, UTACV R-6258, UTACV R-6259, UTACV R-6260, UTACV R-7232, UTACV R-7739, UTACV R-7937, UTACV R-9357, UTACV R-12589, UTACV R-12590, UTACV R-12591, UTACV R-16352, UTACV R-16353.

Crotalus t. triseriatus. Mexico: FMNH-37038, FMNH-37040, FMNH-37041, FMNH-39099, FMNH-39100, FMNH-39101, FMNH-39104, FMNH-39105, FMNH-39107, FMNH-39122, FMNH-39123, FMNH-39125, FMNH-39126, FMNH-40822, LSU-11014, LSU-28557, UMMZ-98941, UMMZ-121523, UTACV R-7286, UTACV R-7398, UTACV R-8142, UTACV R-8197, UTACV R-8708, UTACV R-9095; Michoacan: AMNH-98846, FMNH-37043, FMNH-37044, FMNH-37045, FMNH-37047, FMNH-39096, FMNH-39098, FMNH-39102, FMNH-39106, FMNH-39108, FMNH-39110, FMNH-39111, FMNH-39114, FMNH-39116, FMNH-39118, FMNH-39119, FMNH-39124, FMNH-40817, FMNH-40820, FMNH-40821, FMNH-40823, UINHM-26225; Morelos: UTACV R-12599, UTACV R-12600, UTACV R-12601, UTACV R-12602, UTACV R-12603, UTACV R-12604, UTACV R-14516, UTACV R-14517, UTACV R-14518, UTACV R-14519; Veracruz: TCWC-820.