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A New Genus and Species of Colubrid Snake from the Mexican State of Oaxaca

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In the summer of 1962 Mr. Boone Hallberg gave the American Museum of Natural History a small collection of snakes that he had obtained at Yelagago, a Zapotec Indian village in northeastern Oaxaca. It was evident to the senior author that one of the specimens could not be readily assigned to any genus previously known from Mexico. The specimen was shown to Dr. Herndon G. Dowling, who recalled that the junior author also had showed him a snake from Oaxaca that did not fit existing descriptions. Correspondence between us left little doubt that our specimens were conspecific. Accordingly we have combined our efforts in diagnosing and describing the species as the type of a new genus.

Similarities in size, habitus, pattern, vertebrae, and the mode of scale-row reduction suggest that these two snakes from Oaxaca have affinities with snakes of the genera *Leptodeira* and *Tantalophis*. Several peculiarities preclude their inclusion in either of these genera, however, or in any other nominal genus of Neotropical snakes. In allusion to the cool cloud-forest habitat of these snakes in Oaxaca, the genus is herewith given a name derived from the Greek *kryos*, cold.

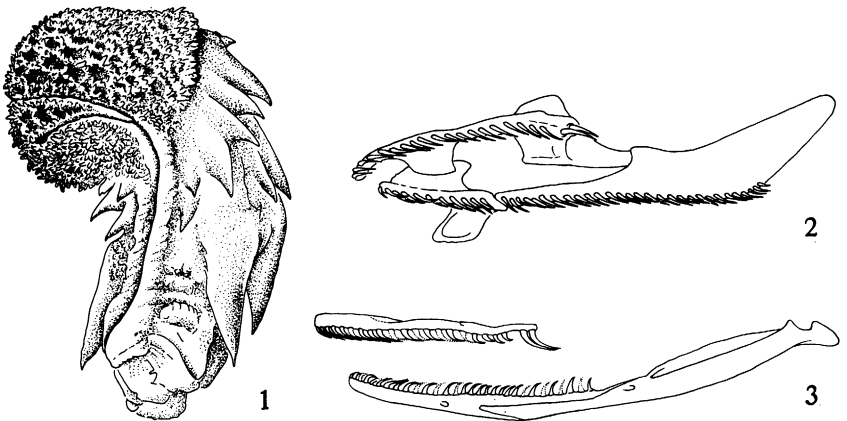
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CRYOPHIS, NEW GENUS

TYPE SPECIES: *Cryophis hallbergi*.

DEFINITION: The genus is characterized by the following combination of characters: The vertebrae on the posterior portion of the body lack hypapophyses. The hemipenis is single; distally the enlarged basal spines are followed by smaller spines and finally by calyces on the capitulum. The sulcus extends to the depression at the terminus, bifurcating after passing beyond the edge of the capitulum (fig. 1). Keels are present, but there are no apical pits on the dorsal scales, which are arranged in 23



FIGS. 1-3. *Cryophis hallbergi*. 1. Left hemipenis of holotype. $\times 5$. 2. Ventral view of left maxilla and palatamaxillary arch of paratype, A.M.N.H. No. 89594. $\times 2$. 3. Lateral view of maxilla and mandible of paratype, A.M.N.H. No. 89594. $\times 2$.

rows at midbody; posteriorly the paravertebral rows terminate, thereby diminishing the number of scale rows, first to 21 and finally to 19 anterior to the vent. The plates on the head resemble those of many other colubrids, but the nasal is single, three supralabials normally extend to the loreal, and the rostral is concave and tilted forward. The anal is divided, and the subcaudals are paired. The tail comprises approximately one-fifth of the total length.

On the maxilla (figs. 2, 3) there are from 19 to 22 teeth, followed by a diastema and two enlarged, slender teeth that lack grooves. The teeth anterior to the diastema become progressively shorter, stouter, and less strongly recurved from front to rear. The eye is moderately large, its diameter being one-third greater than its distance from the mouth; the pupil is oval or feebly elliptical.

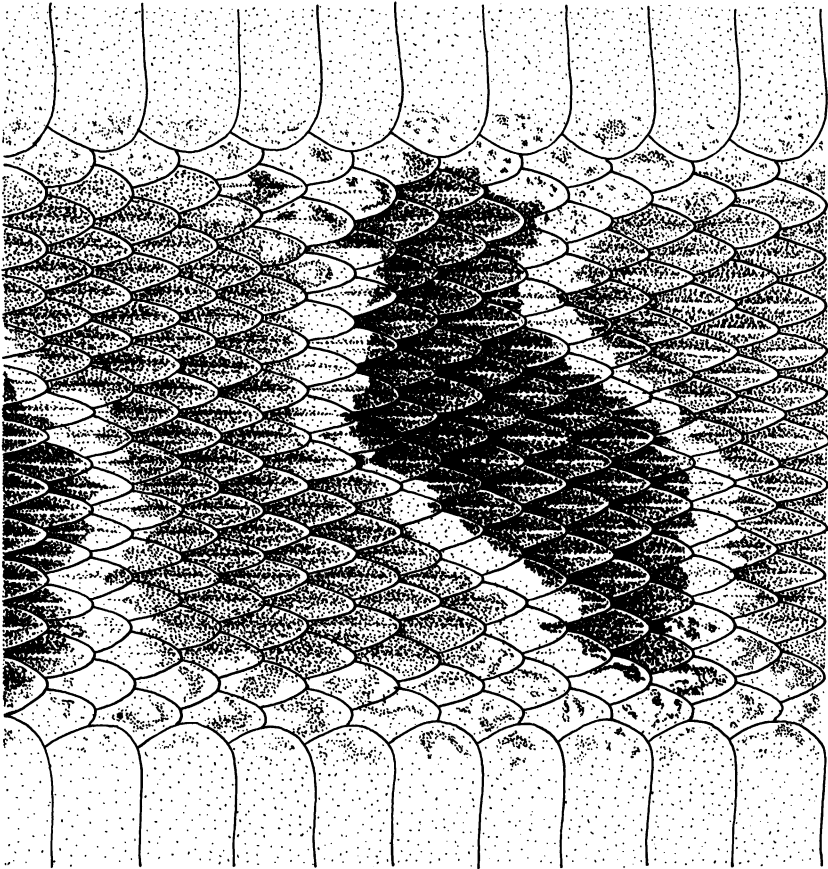


FIG. 4. Midbody pattern and scutellation of *Cryophis hallbergi*, semidiagrammatic, from holotype.

DIAGNOSIS: (1) The bifurcated sulcus, (2) the keeled dorsal scales (fig. 4) without pits, (3) 19 or more maxillary teeth that are progressively shorter and stouter toward the rear of the bone where a diastema separates them from two enlarged but (4) ungrooved teeth, and (5) a feebly elliptical pupil readily distinguish snakes of the genus *Cryophis* from all members of the genus *Leptodeira* Fitzinger, 1843, in which (1) the sulcus is undivided, (2) paired apical pits are present on the smooth dorsal scales, (3) there are 18 or fewer maxillary teeth, subequal or progressively larger toward the rear of the bone where the diastema separates them from a pair of enlarged (4) grooved fangs, and (5) the pupil is strongly elliptical.

Cryophis may be as closely related to *Tantalophis* Duellman (1958b)

which it resembles in having the sulcus bifurcated, posterior maxillary teeth lacking grooves, and a feebly elliptical pupil. The hemipenis is appreciably longer and bilobed in *Tantalophis*, however, and the single species in this genus has fewer maxillary teeth (12 to 16+2), the smallest of which are at the front of the bone, fewer rows of dorsal scales (21-19-17), and fewer supralabials (seven to eight versus nine). The mode of scale-row reduction is the same in both genera, but *Tantalophis* more closely resembles *Leptodeira* in having smooth scales with paired apical pits. *Cryophis* (figs. 4, 5) has a pattern similar to but somewhat more complex than that of *Tantalophis*. In view of the variations of the pattern within the genus *Leptodeira* (Duellman, 1958a), this character is of little assistance in defining the affinities of the three genera.

DESCRIPTION OF THE TYPE SPECIES

The capture and preservation of the first specimen available for study can be attributed to Mr. Boone Hallberg's broad interest in the fauna and flora of Mexico. In recognition of this and Mr. Hallberg's generous cooperation in securing other specimens of herpetological interest, the snake may appropriately be called

***Cryophis hallbergi*, new species**

HOLOTYPE: No. 70901 in the collection of the Museum of Natural History, University of Kansas, taken 6 kilometers south of Campamento Vista Hermosa, at an elevation of 1865 meters, at the northern periphery of the Sierra de Juárez, Distrito de Ixtlán, Oaxaca, Mexico, by William E. Duellman on June 27, 1962. Campamento Vista Hermosa, shown on few maps, is situated near latitude 17° 50' N., longitude 96° 20' W., on the drainage of the Río San Cristobal, to the southwest of Valle Nacional.

DIAGNOSIS: The nearest relatives of *Cryophis hallbergi* are assigned to the genera *Leptodeira* and *Tantalophis*. Consequently the characters listed above in the diagnosis of the genus serve equally well to distinguish the species. In some keys to the snakes of Mexico, *Cryophis* might be confused with *Natrix* if keeled dorsal scales are employed to differentiate snakes of the latter genus from those having smooth dorsal scales. Paired apical pits, usually but not always present on snakes currently referred to *Natrix*, would otherwise distinguish them from *Cryophis*. Scale-row reductions on the trunk of *Natrix* ordinarily result from the loss or fusion of lateral rows, in contrast to *Cryophis* on which the paravertebral rows are lost. The carinate scales of *Natrix* and *Cryophis* are not indicative of close rela-

tionships; despite the superficial similarities of snakes in these genera, numerous osteological characters point to separate lineages.

DESCRIPTION OF THE HOLOTYPE: The preserved specimen, an adult male (fig. 4) has a head length of 20.5 mm., a body length of 519 mm., and a tail length of 131 mm. that comprises 20.2 per cent of the over-all length of 650 mm. The body is relatively slender, not exceeding 12 mm. at the greatest width, and tapers to 7 mm. at the constriction immediately behind the head, the width of which approximates the maximum width of the body. At the base of the tail the body is 6 mm. in width. The body and tail are somewhat triangular in cross section, with the flanks of the body forming a blunt apex above the vertebral column.

The head shields (fig. 6) are essentially similar to those of the least-specialized colubrids. The rostral is less than twice as broad as high, slightly concave in front, and tilted ventrally so that only the upper margin is visible from above. Paired indentations on the rostral at the middle of the lower margin seemingly provide for the extrusion of the forked tongue. The lateral edges of the rostral are in broad contact with the first supralabial on each side. The paired internasals are slightly wider than long; the curved lateral margin of each forms a broad suture with a nasal. The paired prefrontals are slightly wider than long and curve down and over the canthus, where they are in broad contact with the loreal. Posteriorly the prefrontals form a common suture with the flat anterior edge of a frontal that is as long as broad and bordered by supraoculars that are subtriangular in shape. A median groove extends nearly halfway to the apex of the frontal, where it projects between the anterior ends of the paired parietals. The parietals meet along a common suture that is slightly shorter than the maximum width of the individual parietals, each of which extends laterally to an angle projecting between the upper postocular and the anterior temporal. An irregular, suture-like groove extends across the common suture of the parietals, producing, in effect, a small scale on the right intercalated between the two shields, with a similar, but incompletely separated, scale attached to the left parietal.

The nasal is one-third longer than high and best construed as being undivided, though a faint groove extends from the nostril to the common suture of the first and second supralabials. The loreal, roughly twice as long as high, is in contact with the second, third, and fourth supralabials on the left, but the second supralabial fails to reach the loreal on the right. There are three preoculars; the upper one is much larger than the others, and extends to the frontal on the left, but not on the right. The lower preocular consists of a small scale situated above the suture of the fourth and fifth supralabials. The diameter of the eye is one-third greater than

its distance from the mouth. The pupil is slightly elliptical. There are two postoculars, the larger of which reaches the parietal. The temporals are 2+2+3. There are nine supralabials, of which the fifth and sixth reach the orbit, and the seventh is the largest.

The first pair of infralabials meet on a broad suture behind the acute angle formed by the posterior part of the mental and separate the anterior chin-shields for one-third of their length. The posterior chin-shields are longer than the anterior pair and in contact for a third of their length, but separated at the rear by two gular scales, one of which comprises part of two transverse rows of gulars anterior to the first ventral. There are 11 infralabials, of which the fifth and sixth reach the anterior chin-shields; the sixth and seventh are largest, subequal in size and in contact with the posterior chin-shields.

The dorsal scales (fig. 4) are disposed in 25 rows on the nape, but diminish in number to 23 where the second scale row is lost (or coalesced with the third) above the fourth ventral. Posteriorly the number of scale rows is further reduced from 23 to 21, by the loss of the paravertebral rows, and finally to 19 anterior to the base of the tail. The dorsal scale formula is

$$25 \begin{array}{c} -2 \\ -2 \end{array} \begin{array}{c} (4) \\ (4) \end{array} \quad 23 \begin{array}{c} -11 \\ -11 \end{array} \begin{array}{c} (112) \\ (113) \end{array} \quad 21 \begin{array}{c} -11 \\ -11 \end{array} \begin{array}{c} (131) \\ (131) \end{array} \quad 19 \quad (186).$$

With exception of the scales in rows contiguous to the ventrals, the dorsal scales are keeled. The keels are inconspicuous on the scales in the second row but become progressively more strongly keeled in the rows above. Apical pits are not discernible on the scales of the trunk, but pustules are present on some dorsal scales behind the head anterior to the first reduction. There are 186 ventrals, followed by a divided anal plate and 67 pairs of subcaudals (the terminal spine is missing).

The dorsal surface of the head is uniformly dark brown, except for an ill-defined, creamy yellow stripe that extends through the temporals from the angle of the mouth to the upper postocular, where it is visible from above. The brown coloration continues onto the sides of the head, encompassing the nasal, loreal, and postoculars; posteriorly the brown color extends through the lower temporals, the upper parts of the seventh and eighth, and all of the ninth supralabials. The two upper preoculars are pale in the center but margined with brown. The dorsal and lateral edges of the rostral are brown. The first six supralabials, the mental, and the six anterior infralabials have dark brown posterior margins. There are also brown margins on the supralabials bordering the suture between the eighth and ninth on the right, and between the ninth and tenth on the left, where the color extends to one gular scale. There are faint brown dots

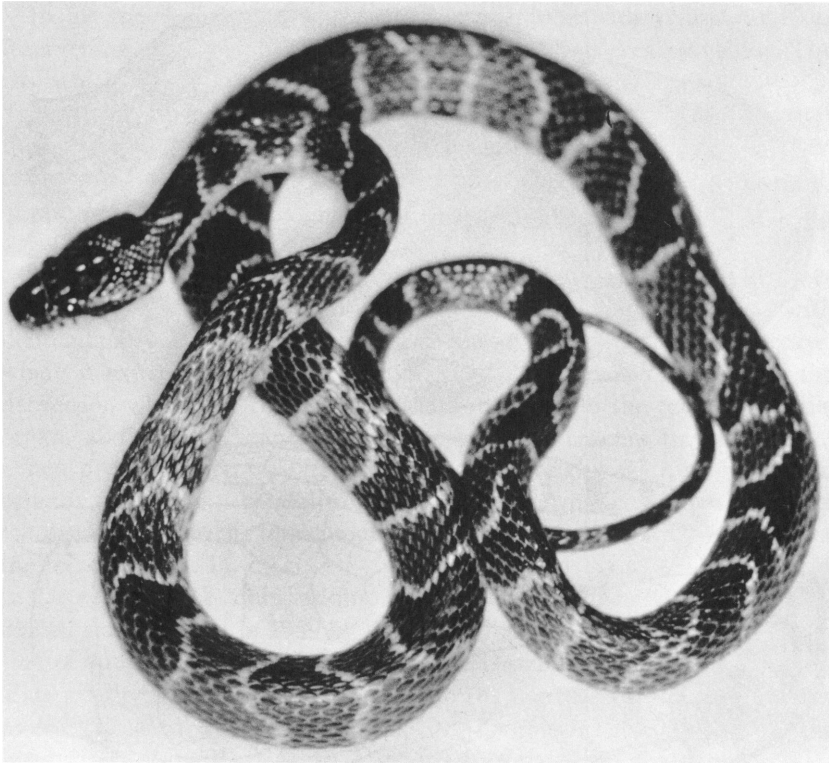


FIG. 5. *Cryophis hallbergi*, holotype, photographed while alive. Approximately $\times 1$.

scattered on the anterior chin-shields and the inner margins of the infralabials. The posterior chin-shields, the gulars, and most of the belly are uniformly dull white, but a few faint dots are present on the posterior ventrals. The under side of the tail is mottled with brown that becomes progressively darker toward the terminus.

The dorsum is reddish brown, with 26 irregular dark brown blotches narrowly separated from the ground color by dull white margins (figs. 4, 5). The dark blotches are from there to seven scales in length at the vertebral row, where they usually are separated by three or four scales of pale brown and the intervening white margins, which usually are less than one-half scale in length. In effect the pattern is comprised of dark brown, white-margined blotches that alternate with pale brown blotches; both the pale and dark blotches extend onto the edges of the ventrals. There is little uniformity in the shape of the blotches, but the dark brown

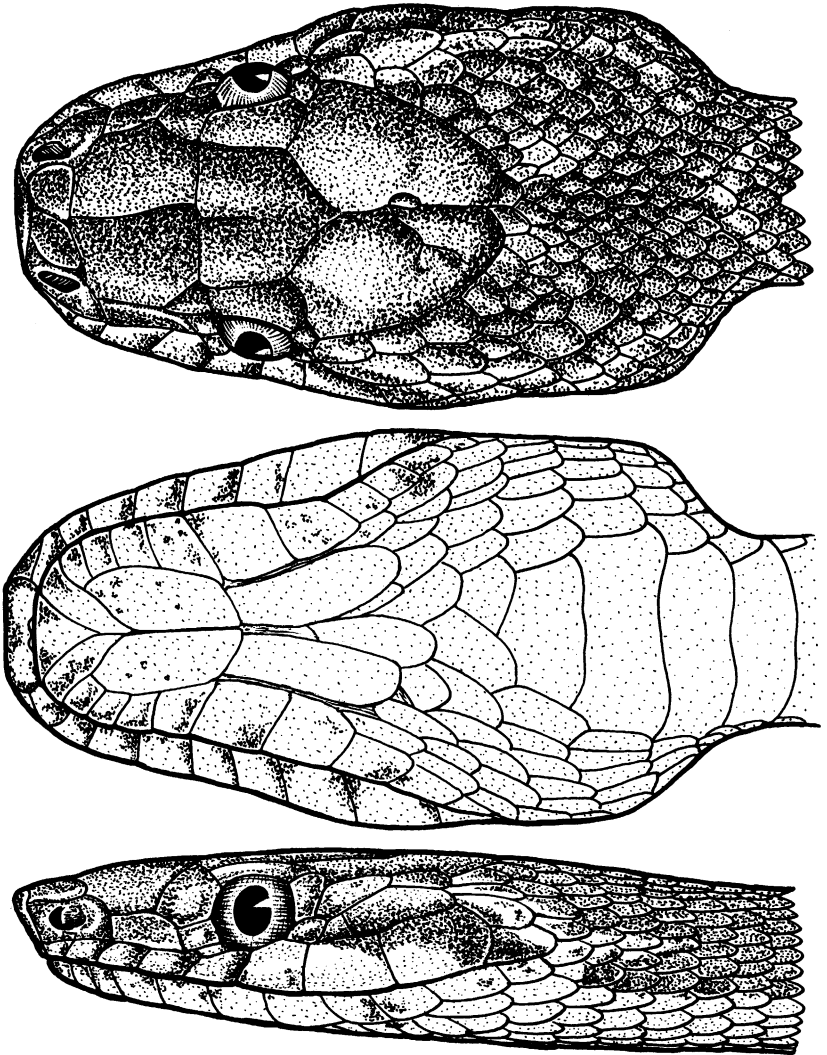


FIG. 6. Dorsal, ventral, and lateral views of *Cryophis hallbergi*, holotype. $\times 4$.

blotches tend to become narrower on the flanks of the body, with a corresponding expansion of the pale brown blotches. Irregular dark areas, intercalary blotches, are present in the pale brown areas along the edges of the belly. The pattern continues onto the tail, where there are 13 dark blotches, including vestiges, as the white margins become progressively fainter toward the tip.

In life the dark brown blotches were margined with yellow, and the intervening areas were reddish brown. The belly was creamy yellow. The iris, which is slate-gray in preservative, was reddish bronze.

There are 22 teeth on the right maxilla and 20 on the left, followed at the posterior extremity of each bone by a diastema and two large, slender, ungrooved teeth. The teeth in the series anterior to the diastema diminish in size from front to back, as they become progressively stouter and not so strongly recurved.

The hemipenis is single and capitate. The organ has large basal spines and a spinous middle part that is sharply delineated from the calyces with denticulated edges on the capitulum. The sulcus spermaticus bifurcates where it extends onto the capitulum; the right branch extends into the depression where the retractor muscle is attached to the terminus of the organ, and the left branch terminates before it reaches the depression. When pressed to the tail, the everted organ, roughly 11 mm. in length, extends to the sixth caudal, and the sulcus spermaticus bifurcates near the suture between the fourth and fifth caudal, approximately 4 mm. from the terminus (fig. 1).

PARATYPE: The only additional specimen known, A.M.N.H. No. 89594, was obtained in 1959 by Boone Hallberg at Yelagago, at an elevation of approximately 1150 meters, in the Distrito de Villa Alta, Oaxaca. This locality is less than 50 kilometers to the southeast of the type locality and is situated at latitude 17° 25' N., longitude 96° 05' W., on the headwaters of the Río Manso, a tributary of the Río Papaloápan.

Though the paratype is a female, externally it differs in few respects from the male holotype. It is somewhat larger, 600 mm. in body length, and the incomplete tail, 125 mm. in length, comprises 20.8 per cent of the over-all length of 725 mm. The shields on the head are similar to those of the male, except for a single postocular, followed by a single anterior temporal. There are no disrupting sutures on the frontal and the parietals, such as those on the holotype, which is probably abnormal in this respect. On the paratype the second, third, and fourth supralabials extend to the loreal on both sides, and an additional infralabial is present on the right side, where six infralabials reach the anterior chin-shield. Like the male, the female has 186 ventrals; in each specimen an additional broad scale is present anterior to the first ventral, which reaches the first scale-row on each side. The anal is divided; owing to the incomplete tail, the caudal count of 61+ is of little value. The dorsal scale formula is

$$25 \frac{-2(5)}{-2(5)} \quad 23 \frac{-11(111)}{-11(111)} \quad 21 \frac{-11(141)}{-11(138)} \quad 19(186).$$

The paratype has almost the same coloration and pattern as the holotype, though the blotches are slightly more irregular. There are 24 or 25 dark brown blotches with white borders on the body; on the tail there are 10 or more darker areas, though blotches with well-defined borders are restricted to the basal part. The upper preocular, the postocular, and the anterior temporal are darker at the margins than medially, much as in the holotype, but the dark margins on the supralabials and infralabials are less conspicuous.

OSTEOLOGICAL COMPARISONS: The skull of the paratype of *Cryophis hallbergi* was compared with skulls of *Leptodeira septentrionalis*, which closely

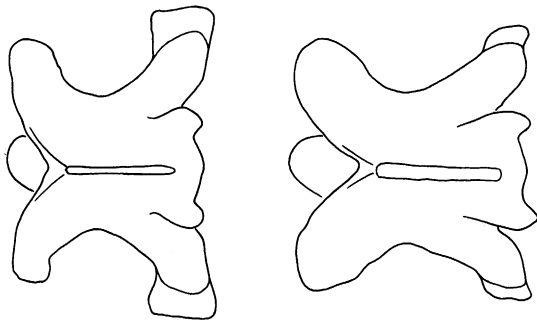


FIG. 7. Dorsal views of vertebrae near the level of the forty-fifth, showing differences between *Leptodeira* (left) and *Cryophis* (right) in the expansions of the prezygapophyses. Based on the paratype of *Cryophis hallbergi*, A.M.N.H. No. 89594, and *Leptodeira septentrionalis*, A.M.N.H. No. 73154. $\times 8$.

resemble the skull of *Leptodeira maculata* depicted by Duellman (1958a). As indicated in the diagnosis, *Cryophis* and *Leptodeira* differ in dentition; other differences warrant comment. The dorsal surface of the parietal is flat in *Leptodeira*, whereas in *Cryophis* there are paired convexities where the parietal bulges upward anterior to the attachment of each tabular. The internal process of the maxilla and both the internal and external processes on the dentary are comparatively more slender in *Leptodeira* than they are in *Cryophis* (figs. 2, 3). The teeth, particularly those at the anterior of each series, tend to be more elongate and more strongly recurved in *Cryophis* than in *Leptodeira*. The counts for each series in the paratype of *Cryophis* approximate or exceed the maximums that Duellman (*supra cit.*) reports for *Leptodeira*.

The two ungrooved teeth behind the diastema on the maxilla of the paratype of *Cryophis* are slightly less than twice the size of the nearest

anterior tooth, approximately as in *Leptodeira*. There are 20 teeth anterior to the diastema on the right, 19 on the left. In each palatine there are 11 teeth that resemble those at the front of the maxillae in size and shape; these are followed by 29 teeth, progressively smaller toward the rear on each pterygoid. There are 28 teeth on the right dentary, 30 on the left.

On the paratype the vertebrae posterior to the forty-first lack hypapophyses. The hypapophyses on the anterior vertebrae of *Leptodeira* and *Cryophis* are virtually identical. Similarly, there is no significant difference in the zygosphene or the neural spine when the vertebrae of the two genera are compared. Lateral expansions of the prezygapophyses are more pronounced in *Leptodeira* than in *Cryophis*, as shown in figure 7.

HABITAT

The holotype was taken in a cloud forest at an elevation of 1865 meters on the Atlantic drainage of the rugged Sierra de Juárez. The snake was discovered at night, approximately 4 meters above the ground in a small tree. Dominant trees in the forest include *Liquidambar*, *Acer*, and various species of *Quercus*. Tree ferns, *Cyathea mexicana*, several species of bromeliads, and orchids are plentiful. The region is continually moist, as rain falls in every month of the year. The paratype was taken at a somewhat lower elevation, 1150 meters above sea level, in a similar habitat. Meteorological data recorded by Boone Hallberg at Yelagago during the year 1959, considered to have been a year when normal conditions prevailed, indicate that the annual precipitation is about 6100 mm. During January, the driest and coldest month, the precipitation totaled 126 mm.; the minimum temperature was 8° C., the mean 15.2° C. and the maximum 29.3° C. Yelagago receives 269 mm. of rain during May, the warmest month, when the mean temperature rises to 21.6° C., but temperatures reach a minimum of 14.1° C. and a maximum of 31.6° C.

Few snakes of other species are abroad and active at night at the low temperatures encountered in cloud forests. Possibly *Cryophis* is better adapted and perhaps restricted to the cool, moist conditions that prevail in such environments. Other snakes in the collection from Yelagago, namely, *Pliocercus elapoides*, *Drymobius chloroticus* (not previously reported from Oaxaca), *Tantilla schistosa*, and *Coniophanes imperialis*, have been reported at lower elevations both north and south of the cloud forests of northeastern Oaxaca. If *Cryophis* is both nocturnal and arboreal, as the limited information suggests, it is not astonishing that it escaped the attention of earlier collectors. As a remote possibility, *Cryophis hallbergi* may occur in similar habitats as far north as southern Tamaulipas, or

the same species or closely related forms may be found in Chiapas and Guatemala.

RELATIONSHIPS

The tentative classification of American colubrids that Dunn (1928) devised some years ago emphasized characters of the hemipenis, particularly the presence or absence of a bifurcation in the sulcus spermaticus. Dunn's provocative work aroused wide interest in the hemipenes of snakes and their potential value in systematic studies. As employed by Dunn, in conjunction with osteological characters, the condition of the sulcus provided a promising means of partitioning the Colubridae into subfamilies. Investigations on a broader scale offer little support for Dunn's proposals.

A survey encompassing a number of African colubrids (Bogert, 1940) showed that distantly related species, only superficially similar, had often been placed in the same genus. Far more acceptable conclusions concerning the relationships of species could be reached when the structures of copulatory organs were taken into account. Though the affinities of a few subterrestrial forms remained obscure, the majority of the species could be grouped in genera on a meaningful basis. Characters of the hemipenis also provided useful clues to the interrelationships of genera, in some instances leaving no doubt concerning affinities. Colubrids of several genera readily defined and diagnosed, and hence sufficiently well differentiated in their dentition, scutellation, or both to warrant their retention, proved to have hemipenes that were virtually identical. Other genera were easily grouped on the basis of similarities in the structure of the hemipenes, though their copulatory organs were not identical.

It became evident that penial characters, though extremely useful in the grouping of the species and genera of snakes in the family Colubridae, had evolved in ways that precluded the use of such characters to define subfamilies. In Dunn's tentative arrangement all colubrids with a bifurcated sulcus were placed in the subfamily Xenodontinae ("Ophiinae," as originally proposed). Dunn thought that members of the subfamily were mainly South American. He doubted whether close relatives existed outside the Americas, and added that "none are known from the Old World." Contrary to the latter assumption, well over 30 per cent of the colubrid genera in Africa proved to have a bifurcated sulcus. Hence they conformed to Dunn's definition of the Xenodontinae. Nevertheless it is questionable whether any African colubrids are closely related to those in the Americas, regardless of the condition of the sulcus. More signifi-

cantly, the evidence derived from this survey of penial characters in African colubrids offers strong support for the belief that the simple sulcus has been derived quite independently from the bifurcated sulcus of ancestral colubrids in widely separated branches of the family.

In view of this evidence, it is not astonishing that species with and without the bifurcation in the sulcus occur among the less distantly related genera of Mexican colubrids. The condition of the sulcus in *Tantalophis*, *Cryophis*, and *Leptodeira* offers further confirmation of the conclusions drawn from the study of African colubrids. Duellman (1958b) has described the bilobed hemipenes of *Tantalophis*, on which the right and left branches of the sulcus extend to the edge of the calyculate area at the terminus of each of the respective lobes, following bifurcation proximal to the crotch. This sort of hemipenis, perhaps somewhat more extensively calyculate toward the base where the sulcus bifurcated, and having each branch continued to the terminus of a lobe, presumably approximates that of the ancestral form from which all three genera evolved. During the evolution of *Cryophis* the lobes of its hemipenis seemingly have become shorter as they coalesced, leaving the bifurcation of the sulcus within the calyculate portion. *Leptodeira* might have dispensed with the lobes in similar fashion, losing the bifurcation later, or the branches of the sulcus were shortened prior to coalescence of the calyculate lobes. The hemipenis of *Tantalophis* has undergone relatively little modification, though each branch of the sulcus may have receded from the calyculate terminus.

Despite similarities in size, habitus, pattern, and coloration, modes of scale-row reduction and vertebral characters that are indicative of their common ancestry, the three genera represent quite separate phyletic lines. *Cryophis* and *Tantalophis* retain the ungrooved teeth at the rear of the maxilla, and neither has advanced far on the trend toward elliptical pupils. *Tantalophis* retains the smooth dorsal scales with apical pits and has proportionately smaller teeth at the anterior of the maxilla, in this respect resembling *Leptodeira*. Following an independent trend, *Cryophis* lost the pits and evolved keels on the dorsal scales and lengthened the anterior maxillary teeth. Grooved fangs, an elliptical pupil, and a simple sulcus evolved only in the line that led to *Leptodeira*, the most diversified, abundant, and widely distributed genus of the three.

It is problematical whether the traits confined to *Leptodeira* account for the greater diversity of this phyletic line. Perhaps this diversification should be attributed to fortuitous circumstances, the endowment of an ancestor with a combination of genes that permitted greater adaptability. Whatever the cause may have been, snakes of this lineage evidently were more successful in their dispersal and their exploitation of habitats. In

contrast, neither *Tantalophis* nor *Cryophis* appears to be abundant or widely distributed. Both genera may be relicts, restricted to montane habitats at the southern periphery of the Mexican Plateau. Equally plausible, early specialization for existence in cool, moist environments could have prevented the dispersal of the ancestral *Cryophis* and *Tantalophis* into the warm lowlands surrounding the area of their origin and descent.

ACKNOWLEDGMENTS

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