

American Museum Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N. Y. 10024

NUMBER 2277

DECEMBER 19, 1966

The Differential Characteristics of the Mexican Snakes Related to *Geophis dubius* (Peters)

BY CHARLES M. BOGERT¹ AND ANN P. PORTER²

INTRODUCTION

Several species of small fossorial snakes currently assigned to the colubrid genus *Geophis* Wagler are represented in collections by extremely small samples, in some instances only by the holotype. Authors dealing with the Mexican species have found it difficult, therefore, to evaluate differences. Investigations of the assemblage have been further hampered by indefinite or erroneous type localities and incomplete or inaccurate descriptions. Statements concerning the sex of specimens have commonly been omitted from descriptions, and few authors have availed themselves of the information that can be derived from examinations of the teeth and hemipenes.

Geophis dubius has been confused with *Geophis rostralis* since 1894, when Boulenger essayed to redefine the two species on the basis of five specimens, only one of which (the holotype of *G. fuscus* Fischer, 1886) was accompanied by locality data. Smith (1959), who obtained a specimen from San Andrés Lovené [more often mapped as "Lovené (San Andrés)," also "Loveni"] in southern Oaxaca, reviewed the literature dealing with both species in an effort to appraise the differences be-

¹ Curator, Department of Herpetology, the American Museum of Natural History.

² Scientific Assistant, Department of Herpetology, the American Museum of Natural History.

tween them. Because he found it difficult to decide whether the Oaxacan specimen should be assigned to one species or the other, Smith concluded that *Geophis rostralis* should be relegated to the synonymy of *G. dubius*. Nevertheless, he noted the extraordinarily wide range in ventral counts that resulted. Our examination of small series from two localities in Oaxaca showed that they differed from the specimen reported by Smith, whereas they conformed closely to the holotype of *Geophis dubius*. Furthermore, analysis of the data obtained from our series indicated that the characters Boulenger employed to distinguish the species were more variable than those Bocourt (1883) had used a decade earlier. It seemed worth while, therefore, to extend our investigation.

REVIEW OF THE LITERATURE

The systematic status of the two species has remained obscure largely because of the absence of information concerning the sex or the source of either of the holotypes. Jan (1864) did not state where he obtained the specimen he depicted as *E [lapoides] rostralis*, and apparently it was not examined by Bocourt or by Boulenger. Peters (1861) provided a reasonably complete description of the holotype (now No. 4064 in the Zoologisches Museum Berlin, according to Stuart, 1963) of the snake he called *Geophidium dubium*, though he mentioned only one specimen and stated explicitly that its source was unknown ("Fundort unbekannt"). It is incomprehensible, therefore, to find that Bocourt (*supra cit.*) had referred to two types, "provenant de Tehuantepec qui nous ont été communiqués par M. le professeur W. Peters." Perhaps Bocourt assumed that the two specimens received from Peters were types of *dubius*, but it is possible that he referred one of them to *Geophis rostralis*, for Bocourt also noted that Peters sent him a specimen of *rostralis* from "Mexique" and that the species was otherwise known only from the figures supplied by Jan.

Bocourt provided measurements for only two specimens in his series of *G. dubius*. The data for one of these, listed as the "type ♂," indicate a total length of 270 mm. and a tail length of 56 mm.; the other was a female with an over-all length of 385 mm. Peters had clearly indicated in the original description that the tail of the holotype was incomplete ("Subcaudalia 20 + ?"). Though he stated that the total length was 260 mm., and the tail 26 mm., Peters inserted a plus sign in front of the figure given for the tail length. Bocourt could scarcely have measured the specimen with an incomplete tail that Peters described, for the tail-to-total-length ratios calculated from Bocourt's figures are

0.21 for the male and 0.14 for the female; these closely approximate those of specimens of the same sex recently obtained. It is questionable, therefore, whether either of the specimens sent by Peters was actually the holotype of *dubius*, and improbable that seven specimens from "Mexique" and one allegedly from "western Guatemala" were "identical" with them, as Bocourt stated. He indicated ranges of 136 to 151 for ventrals, and 36 to 48 for subcaudals in the 10 specimens he examined.

Although Bocourt failed to mention other variations or sexual dimorphism, his concept of the species and the characters that distinguish it from *G. rostralis* were reasonably accurate. He correctly noted that *dubius* differed from *rostralis* in lacking internasals, and that *rostralis* had keels on the posterior dorsal scales, whereas the dorsal scales were smooth on *dubius*. The paired internasals of *rostralis* are shown in Bocourt's figure as Jan had depicted them, separated by the rostral, which extends to an apex in contact with both prefrontals. Bocourt described and depicted both species as having the first pair of infra-labials separated by the mental, which extends between them to form a broad contact with the first pair of chin shields.

Boulenger (1894), in his accounts of the two species, listed only four specimens, three of which were from "Mexico." The fourth, a specimen from "Jalapa," was the holotype of *Geophis fuscus* Fischer, 1886, which Boulenger correctly placed in the synonymy of *G. dubius*, insofar as one can judge from Fischer's description. It is doubtful whether Boulenger had sound reasons for assigning one of the other specimens from "Mexico" to *dubius*, or for referring one that lacked internasals to *G. rostralis*. In his description of *rostralis* Boulenger wrote that the internasals may be fused with the prefrontals, "as in the specimen in the Collection." Plainly he realized that it differed in this respect from the holotype depicted by Jan.

As noted above, Bocourt mentioned the keels on the dorsal scales near the base of the tail of *rostralis*. Strong keels are present on one of the two specimens with internasals that we have examined, whereas keels are barely discernible on the lateral rows above the anal region of adult specimens of *dubius*. Boulenger, having confused the two forms by centering his attention on the presence or absence of the contact between the mental and the anterior chin shields, defined both as having feebly keeled scales above the anal plate. He thereby ignored Bocourt's interpretations and descriptions, which were more nearly correct. Contrary to Smith (1959), Bocourt did not state that the chin shields were separated from the mental; he described both species as

having the first pair of chin shields separated from each other medially. Thus his descriptions agree with his illustrations of *dubius* and *rostralis*, which show the mental to be in contact with the chin shields. This condition is perhaps more prevalent in *rostralis* than in *dubius*, but, as Smith observed, the character is too variable to be diagnostic.

Though Smith listed references to *rostralis* in the synonymy he provided for *Geophis dubius*, he did not mention the report by Webb and Fugler (1957), who assigned a specimen from Puebla to *Geophis rostralis*. Through the kindness of Dr. William E. Duellman we have examined this individual, U.K. No. 39642, which proves to be a male on which the tail is incomplete, though it terminates in a thickened spine. The specimen resembles *rostralis*, as portrayed by Jan, in having internasals, as well as keels on the dorsal scales of the anal region. The specimen differs from the holotype in not having the under side of the tail darker than the venter, whereas the snake from Lovené, Oaxaca, more nearly resembles the specimen that Jan illustrated. The status of the population represented by the specimen from Puebla will remain uncertain until more specimens become available from areas between southern Oaxaca and Puebla.

The only other specimens with locality data that have been mentioned since *dubius* and *rostralis* were described over a century ago, therefore, are the male from Lovené, and the holotype of *Geophis fuscus*. Most of the specimens previously available were either from "Mexico," from "Western Guatemala," or their source was unknown. Authors have assumed that "Jalapa," the locality given by Fischer (1886) as the source of the specimen described as *Geophis fuscus*, refers to the well-known city in Veracruz. Such an assumption may be gratuitous, for Fischer did not specify the state, and there are at least a dozen other localities with the same name in Mexico, including two in the state of Oaxaca. It is also possible that the snake Fischer described had been mailed or shipped to him from Jalapa, Veracruz, though it had been obtained elsewhere. *Geophis dubius* may not be restricted to habitats as far above sea level as those of the mountains in Oaxaca where our specimens were found. Nevertheless, without better evidence to substantiate the occurrence of the species in the lowlands, it is questionable whether Jalapa should be included in the range. It is even more doubtful that *dubius* will be found at elevations as low as Tehuantepec, though Smith and Taylor (1950), evidently following Bocourt, restricted the type locality to this city "and its environs."

ACKNOWLEDGMENTS

We have not attempted to assemble all the specimens that may be available in collections, though we have examined the few specimens with locality data that have been mentioned in the literature. Dr. Charles F. Walker of the Museum of Zoology, University of Michigan (U.M.M.Z.), generously lent one specimen that had not been reported. Dr. Hobart Smith of the University of Illinois Museum of Natural History (U.I.M.N.H.) and Dr. William E. Duellman of the University of Kansas Museum of Natural History (U.K.) permitted us to examine material in the collections in their charge. We are grateful to those who lent us material, as well as to Dr. Rodolfo Hernández Corzo, Director General of the Departamento de Conservación de la Fauna Silvestre, Secretaría de Agricultura y Ganadería, in Mexico, who courteously issued us the permits that enabled us to obtain many of the specimens that led to this investigation.

MATERIAL EXAMINED

In addition to the male of uncertain status from Puebla, we have examined nine specimens (table 1) from the state of Oaxaca. One series of four was taken in the vicinity of Ixtlán de Juárez. A smaller series was obtained approximately 4 kilometers west of San Vicente Lachixío. Ixtlán de Juárez is situated on the southern slope of the Sierra de Ixtlán at an elevation of 2100 meters. Most of the specimens from the area were found at the Vivero Rancho Teja near the ridge approximately 2 kilometers to the east, and 100 to 150 meters above the town. The area is drained by tributaries of the Río Grande, which flows into the Río Papaloápan and empties into the Atlantic. San Vicente Lachixío is on the Pacific side of the Continental Divide, roughly 100 kilometers to the southwest of Ixtlán de Juárez, and at almost the same elevation. Both localities are in pine-oak woodland, with manzanita and madroño.¹

The internasals are fused with the prefrontals on these three males and four females from the mountains of central Oaxaca, whereas internasals are present on the two specimens taken at lower elevations. Lovené, the source of the specimen reported by Smith (*supra cit.*), is at an elevation slightly exceeding 1500 meters, and scarcely 35 kilometers

¹ An additional female, roughly 330 mm. in over-all length, was found beneath a log 7.5 kilometers north of Jaltianguis, Oaxaca, on July 30, 1966. This site is situated on the western slope of the Sierra de Juárez at an elevation of 2650 meters, appreciably higher than other sources of specimens of *Geophis dubius*.

TABLE 1
VARIATIONS IN SPECIMENS OF *Geophis dubius* AND *Geophis rostralis* IN SAMPLES FROM THE STATE OF OAXACA
(Those with internasals are referred to *rostralis*.)

| Museum Number | Locality | Sex | Inter-nasals | Mental Reaching Chin Shields | Ventrals | Caudals | Total Length (in Mm.) | Tail Length (in Mm.) | Ratio, Tail/Total Length |
|----------------------|-------------------------------|-----|--------------|------------------------------|----------|---------|-----------------------|----------------------|--------------------------|
| A.M.N.H. No. 65888 | Ixtlán de Juárez | ♂ | Absent | No | 142 | 49 | 244 | 49 | 0.20 |
| A.M.N.H. No. 94713 | Ixtlán de Juárez | ♂ | Absent | Yes | 138 | 43 | 261 | 51 | 0.20 |
| A.M.N.H. No. 91066 | San Vicente Lachixío | ♂ | Absent | No | 142 | 37 + | 231 + | 32 + | Inc. |
| A.M.N.H. No. 89345 | Ixtlán de Juárez | ♀ | Absent | No | 144 | 36 | 333 | 53 | 0.16 |
| A.M.N.H. No. 93229 | Ixtlán de Juárez | ♀ | Absent | No | 156 | 38 | 156 | 25 | 0.16 |
| A.M.N.H. No. 91067 | San Vicente Lachixío | ♀ | Absent | Yes | 147 | 31 + | 343 + | 50 + | Inc. |
| A.M.N.H. No. 91068 | San Vicente Lachixío | ♀ | Absent | No | 151 | 34 + | 347 + | 47 + | Inc. |
| U.I.M.N.H. No. 46710 | Lovené (San Andrés) | ♂ | Present | Yes | 126 | 42 | 292 | 62 | 0.21 |
| U.M.M.Z. No. 125288 | North of San Gabriel Mixtepec | ♂ | Present | Yes | 132 | 43 + | 266 + | 54 + | 0.20 + |

inland from the coast of southern Oaxaca, on a tributary of the Río Copalito. A second specimen, U.M.M.Z. No. 125288, was taken farther west on the Pacific slope of the mountains of southern Oaxaca, 25 miles via road north of San Gabriel (Mixtepec). The locality is approximately 140 kilometers west of Lovené, at an elevation of 1700 meters. Both specimens are males, and the internasals are in contact on both specimens, rather than separated by the apex of the rostral, as they were on the holotype of *rostralis* depicted by Jan, which closely resembles the individual Bocourt illustrated. There are supra-anal keels on the lower rows of the San Gabriel specimen, but on the male from Lovené there are keels on the dorsal scales of all rows at the base of the tail and the posterior portion of the body, as Jan indicated. The keels are also faintly discernible on the specimens that lack internasals; hence such structures are of little use in distinguishing the two forms.

If the sexes are considered separately, snakes that lack internasals also prove to have higher ventral counts. The variations in the number of subcaudals detract from the value of this character, as may be seen in the following tabulation of the data obtained from the nine specimens, with means followed by extremes in parentheses.

| | INTERNASALS PRESENT | INTERNASALS ABSENT | |
|------------|---------------------|--------------------|-----------------|
| | Males | Males | Females |
| Ventrals | 129 (126–132) | 140.6 (138–142) | 147.0 (144–151) |
| Subcaudals | 42.5 + (42–43 +) | 46.0 (43–49) | 34.5 (31–38) |

The mental is in broad contact with the chin shields on both specimens with internasals, but on those without internasals it is separated from the chin shields on five of the seven specimens. The first infralabials meet to form a broad contact behind the mental of one specimen, but on four the posterior apex of the mental is barely separated from the chin shields, which are partly fused with the first infralabial on one individual. There is no broad contact of the mental and chin shields, such as that seen on specimens with internasals, and as Jan shows in the holotype of *rostralis*. The mental does reach the chin shields, however, on a male from Ixtlán de Juárez and on a female from San Vicente Lachixió. Five supralabials are present on one side of the San Gabriel specimen, but all other specimens examined possess six supralabials, of which the third and fourth reach the orbit. The infralabials are normally six, but five are present on one side of two specimens. Three or, less commonly, four infralabials are in contact with the anterior chin shields. A relatively large postocular is invariably present, though it is fused with the small supraocular on one side on a male from near San Vicente Lachixió,

and a small postocular is present below the normal one on one side of another. On all specimens except one, from Ixtlán de Juárez, the supraoculars are smaller than the postoculars. The nasal is invariably divided, and the loreal (presumably fused with the preocular) extends to the eye. The fifth labial is broadly in contact with the parietal, and the posterior temporal, which is the only one present. The dorsal scales are disposed in 17 rows throughout the length of the trunk; those in contact with the ventrals are widest, but they become progressively narrower toward the median row, which is the narrowest. Keels, though absent on small specimens lacking internasals, are discernible on the scales of the lateral rows above the vent of adults of both sexes. Strongly keeled scales are present on all rows at the base of the tail of but one of the two specimens that retain internasals, as noted above.

All specimens are uniformly gray above, and the color extends onto the outer margins of the ventrals. The smallest specimens are the darkest, and large females, the lightest in color, have pale margins on the dorsal scales. The venter of small specimens is whitish, but faintly yellow on large individuals of both sexes. The subcaudals, particularly those near the end of the tail, are slightly darker than the ventrals on some specimens lacking internasals. The entire under side of the tail is as dark as the dorsum on the specimen from Lovené, but ventrals and subcaudals are equally pale on the other male that retains internasals.

The largest individuals in the series are females. The over-all length of one from Ixtlán de Juárez is 333 mm., slightly exceeded by two from San Vicente Lachixío, one of which is 343 mm. in length, and the largest is 347 mm. The smallest snake in the series, a female, 156 mm. in length, is from Ixtlán de Juárez. The largest male, also from the latter locality, has over-all dimensions of 231 mm., but the tail lacks the terminal spine as well as a few subcaudals. The lengths of two other males from Ixtlán de Juárez are, respectively, 244 and 261 mm. The male from Lovené is 292 mm. in length, and the male from above San Gabriel is smaller, 266 mm. in over-all length, but the tail is not quite complete. The presence of fewer subcaudals on females lacking internasals is correlated with their proportionately shorter tails. The tail comprises 20 to 21 per cent of the total length of males, but only 16 per cent of the length of females. Two females and one male from San Vicente Lachixío have slightly shorter tails, but they lack the terminal spine, and probably a few subcaudals as well.

Hemipenes, examined on two males from Ixtlán de Juárez, extend to the level of the fourteenth (on the smaller of the two) or fifteenth subcaudals. The organ bifurcates at the eleventh subcaudal, and the sulcus

bifurcates at the seventh. Relatively straight spines flank the sulcus from the level of the third to the eighth pair of subcaudals. Distally the spines first increase and then diminish in size as they are gradually replaced on each lobe by calyces with strongly crenulated edges. The hemipenis of the male from Lovené extends to the eleventh subcaudal and bifurcates at the tenth. The sulcus bifurcates at the seventh subcaudal, however, as it does in the other specimens examined. The hemipenes of the other snake that retains internasals had been partly everted, but they appear to be somewhat shorter. Otherwise, the hemipenes of the snakes with and without internasals are similar. Essentially the same sort of hemipenis is present on a Guatemalan specimen of *Geophis nasalis*, A.M.N.H. No. 63376. The organ on this individual extends to the twelfth subcaudal, bifurcating at the eighth, whereas the sulcus bifurcates at the sixth. Enlarged spines on the proximal portion are replaced by strongly crenulated calyces on the lobes. (On the snake of uncertain status from Puebla, the hemipenis extends to the eleventh subcaudal, and bifurcates at the seventh, but the sulcus bifurcates at the fourth, and the spines are much smaller.)

Relatively little information concerning the dentition of *Geophis* has been published, though Boulenger defined the genus as having from seven to 12 maxillary teeth. On the maxilla of specimens from the mountains of central Oaxaca we find 11 stout, recurved teeth that are progressively but very slightly larger posteriorly. All teeth are deeply buried in tissue. The sharp snout is evidently supported by other bones, for the maxilla and the palatine extend barely as far forward as the posterior margin of the second labial. The dentary contains eight or nine teeth that are similar in size to those in the maxilla. The snake from above San Gabriel has 11 teeth on the maxilla.

DISCUSSION

The meager information derived from nine specimens representing four localities does not provide answers to all the questions raised. *Geophis dubius* and *G. rostralis* are undoubtedly closely related, but it is also evident that the snakes have become differentiated to the extent that those with internasals also have fewer ventrals than those lacking internasals. Insofar as can be ascertained, therefore, the snakes with internasals conform to Jan's figure of the holotype of *rostralis*, even though the source and sex of the specimen remain unknown. If the tail is accurately illustrated, the holotype had 43 subcaudals. One of the males ("spec. a") with internasals that Boulenger (1894) referred to *dubius* had 134 ventrals and 48 subcaudals. Thus it is evidently closer to *rostralis*, whereas

there are uncertainties concerning the individual that Bocourt (1883) referred to the species. The measurements Bocourt provided indicate that it was a male, for the ratio of tail length to total length is 0.20, but it is apparently the individual described as having 138 ventrals and 47 subcaudals.

Peters' (1861) description of the holotype of *Geophis dubius*, despite the incomplete tail, leaves fewer uncertainties concerning the identity of the specimens obtained in the mountains of central Oaxaca. All characters mentioned by Peters fall within the variations tabulated, and the holotype was probably a female, as indicated by the ventral count of 144. A female with 146 ventrals and 40 subcaudals that lacked internasals was assigned by Boulenger (1894) to *rostralis*, but plainly it should have been referred to *dubius*. Boulenger appears to have identified correctly as *dubius* the female with 146 ventrals and 43 subcaudals on which the internasal was fused with the prefrontal on the left side, but present on the right side. The ventral count is within the range of that of females assigned to *dubius*, but the number of subcaudals is somewhat beyond the range of the few females with complete tails that we have examined.

The other male that Boulenger referred to *dubius* is the holotype of *fuscus* that Fischer (1886) described as having 142 ventrals and 49 subcaudals. Boulenger indicated that it had 141 ventrals and 48 subcaudals, but such minor discrepancies are to be expected. Fischer did not mention the sex of the specimen, but he gave the total length as 200 mm., and the tail length as 32 mm. The tail comprises 16 per cent of the length, indicating the proportions of a female, whereas the ventral and subcaudal counts suggest that Boulenger had correctly identified it as a male. As we have already noted, it is problematical whether the specimen was actually taken in or near Jalapa, Veracruz, which is less than 300 meters above sea level. It is improbable but possible that an isolated population comprised of individuals with shorter tails occurs in Veracruz. But the snake was perhaps an abnormal individual, or it may have been carelessly measured. The specimen had a small scale below the normal postocular, but this is duplicated on one side of a specimen from Ixtlán de Juárez, and in other respects the holotype conforms to *dubius*.

The counts, presumably based on 10 specimens with both sexes represented, included in Bocourt's description of *dubius* indicate a range of 136 to 151 for ventrals and from 36 to 48 for subcaudals. Except for the low ventral count, these extremes are confirmed by the counts obtained from our series of *dubius* from central Oaxaca. Among the specimens we examined, the snake with the fewest ventrals was a male with 138,

whereas the lowest count for females was 144. It is reasonably certain, therefore, that Bocourt's count of 136 was obtained from a male, and the maximum he gave is also the highest count obtained on the females we examined. He described *rostralis* as having 138 ventrals, and the dimensions provided for the single specimen Bocourt examined show that it had the proportions of a male. The only specimen with both internasals present that Boulenger examined was identified as a male with 134 ventrals.

In the series we examined the sex was ascertained by dissection, but, as we have noted, counts and measurements revealed dichotomous differences between males and females in the number of ventrals and the proportions of the tail. The sexes may not be so readily distinguished by ventral counts or tail proportions in all populations, although the only data that seem to be misleading are the measurements given by Fischer for the holotype of *G. fuscus*. Because it is necessary to consider the sexes separately in any meaningful comparison of these snakes, we have assumed that either ventral counts or proportions, or both, provide reliable clues to the sex of the few specimens that can be singled out in descriptions. The data obtainable from the descriptions supplied by Peters and Bocourt can thus be considered along with those of Boulenger, who designated the sex of individuals for which he supplied counts. The specimens represented in the following tabulation include two males and four females that lack internasals, and two males on which both internasals were present.

| | WITH INTERNASALS | LACKING INTERNASALS | |
|------------|------------------|---------------------|---------|
| | Males | Males | Females |
| Ventrals | 134-138 | 136-142 | 146-151 |
| Subcaudals | 47-48 | 48-49 | 40-43 |

The snakes with internasals that Bocourt and Boulenger described have more ventrals than the specimens we examined. If our inferences concerning the sex of the holotype of *dubius* described by Peters and the specimens represented by counts given by Bocourt are correct, snakes with internasals nevertheless tend to have fewer ventrals than those lacking internasals. These data from the literature extend the range of variation in the number of ventrals for males, but no overlap can be demonstrated in the ventral and subcaudal counts of the males and females that conform most closely to *Geophis dubius*. The four specimens that most closely resemble the holotype of *Geophis rostralis* are males. The two we examined had 126 and 132 ventrals, whereas Boulenger reported 134, and the male Bocourt described had 138. Thus the ven-

trials vary from 126 to 138 in males, and the range for subcaudals is 42 to 48 in males. Such small samples, with only one sex represented, afford only a rough index to variations in the ventral and subcaudal counts of the species; conclusions based on such meager data are necessarily tentative.

Geophis dubius seems to be more specialized than *rostralis*, as suggested by the reduction in sutures resulting from the fusion of the internasals with the prefrontals. *Geophis rostralis* evidently has affinities with *Geophis nasalis*, a species that also retains internasals, though keels are present on most of the dorsal scales except those at the anterior of the trunk. Ventral counts published by Slevin (1939) for 124 males and 90 females, all of them from Finca El Ciprés, which lies at an elevation of approximately 700 meters near Samayak, Guatemala, indicate a range of 116 to 127 and a mean of 120.5 in males, and a somewhat wider range in females, on which ventrals vary from 116 to 130, with a mean of 123.3. Subcaudals range from 23 to 37, mean 32.7, in males, and from 24 to 30, with the mean 26.6, in females. In *nasalis* the difference between the means for males and females in the number of subcaudals is 6.1, whereas there is an extensive overlap in the number of ventrals, and the difference between the means is only 2.7. Only four males of 115 examined by Slevin have fewer than 30 subcaudals, and there was but one female in the series of 84 on which the subcaudal count exceeded 29. The major difference between the sexes of *Geophis nasalis* is in the number of subcaudals rather than in the ventrals, whereas the reverse condition characterizes *G. dubius*.

The retention of the right internasal by one female examined by Boulenger can scarcely be construed as evidence of intergradation with *rostralis*; the ventral count of this individual is near the mean for *dubius* of the same sex and well above that for *rostralis*. *Geophis dubius* was undoubtedly derived from ancestors with internasals, and snakes with the ancestral condition probably occur sporadically in some or all populations. Abnormalities of the sort have been reported for nearly every species of *Geophis* that is moderately well represented in collections.

The distributions would be somewhat perplexing, but, as we have shown, there is nothing to substantiate the statement that the type (or "types") of *dubius* came from Tehuantepec, and the origin of the "Jalapa" specimen is surely uncertain. Bocourt mentioned one individual from "Guatemala occidental," and Stuart (1963) indicated that *Geophis dubius* had been recorded from "intermediate elevations on the Pacific versant of Guatemala." Stuart (*in litt.*) informs us, however, that investigations carried out subsequent to the publication of his check list

revealed that Guatemalan specimens tentatively identified as *dubius* actually represented an undescribed species. Bocourt's record remains unconfirmed, therefore, and there is no reason to believe that *dubius* occurs in Guatemala.

If *dubius* is restricted to pine-oak habitats in the mountains, as suggested but not necessarily proved by samples from two localities in Oaxaca, it seems probable that its distribution is disjunct. It can scarcely be doubted that it occupies a moderately extensive range. The two snakes most closely resembling the holotype of *rostralis* were both taken on the southern slopes of the mountains bordering the Pacific coast. When the elevations of the four localities are taken into account, and if it be recalled that only four additional snakes (two with imprecise locality data) that appear to be *rostralis* have been reported since Jan depicted the species more than 100 years ago, the distributional situation is not wholly incomprehensible. Annectant or intergrading populations may or may not occur in the area between the populations that differ in ventral counts and the internasal character. Plainly *Geophis rostralis* is an extraordinarily elusive snake, though perhaps no more so than some other members of the genus. Collectors continue to discover new species, and some of those described are known only from holotypes. Now that museums have intensified their efforts to assemble collections from Mexico, perhaps the distributions of some *Geophis* can be more adequately plotted within the next few decades.

Meanwhile, the limited information available strongly suggests that the presence of internasals is correlated with low ventral counts on the snakes that further resemble the holotype of *Geophis rostralis* in having keeled dorsal scales at the base of the tail (though these are present on only one of two specimens examined), and subcaudals that are conspicuously darker than the ventrals. In contrast, the lack of internasals on the snakes that fit the description of *Geophis dubius* is correlated with high ventral counts and smooth dorsal scales, though faint traces of supranal keels are present on adults of both sexes, and some, but not all, of the subcaudals may be darker than the ventrals. In view of the differences in habitat and the nature of some of these characteristics when the sexes are compared separately, we conclude that two moderately well-differentiated species are represented.

HABITS AND HABITAT OF *GEOPHIS DUBIUS*

The three specimens from near San Vicente Lachixío were taken within the same hour on August 16, 1963. One male was discovered on moist soil underneath a relatively large log, and the smaller of two fe-

males was found a few meters from it under a similar log. The largest female was uncovered in a decayed pine stump that was still in the upright position on the slope above the stream. The stump, which was 40 or 50 centimeters in diameter, projected almost a meter above the ground. It was so thoroughly decayed and soaked from recent rains that it was readily hacked apart with a machete. The snake was near the center of the stump, with its head directed upward as though it had

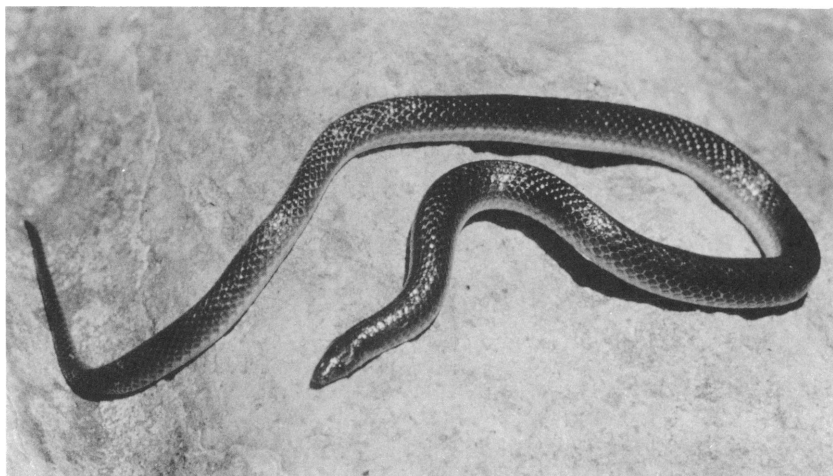


FIG. 1. *Geophis dubius*, an adult female with an over-all length of 333 mm.; taken at the Vivero Rancho Teja, near Ixtlán de Juárez, on the southern slope of the Sierra de Ixtlán in the state of Oaxaca, Mexico.

pushed its way through the decaying wood after entering the stump from the soil below. The snake was at least a third of a meter above the soil. It made no effort to escape when exposed, and the two snakes found beneath logs remained motionless when they were uncovered. Two of the snakes from the Vivero Rancho Teja near Ixtlán de Juárez were found by workmen who were clearing the land. One female (fig. 1) from the same area was found beneath a large flat rock at the edge of the clearing by the senior author on August 27, 1962. The fourth specimen from Ixtlán de Juárez was obtained many years earlier by Mr. T. C. MacDougall, on February 26, 1945.

The largest female, from San Vicente Lachixío, contained eggs approximately 7 mm. in length, two in the right oviduct, and one in the left. One small egg, 2 mm. in length, was present behind the larger eggs in the right oviduct, and an egg similar in size and another that was 5 mm.

in length were present behind the large egg in the left oviduct. A slightly smaller female from the same area contained eggs approximately 7 mm. in length, two in each oviduct. The oviducts of a female taken near Ixtlán de Juárez somewhat later in the same month of the previous year contained small eggs, from 1.0 to 2.5 mm. in length; there were four in the right oviduct and two in the left. Presumably the larger eggs would have been fully developed at the close of the wet season, and laid in September. It is uncertain whether the smaller eggs would have developed.

One specimen kept in a small container of earth and moss readily fed on earthworms, though the actual feeding was never observed. Residents of Ixtlán de Juárez apparently knew that snakes of the species preyed on earthworms, for they referred to the snake as the "*lombricera*" (from the Spanish word for earthworm, *lombriz*). The tongue of *Geophis dubius* is thrust out to an astonishing length, a distance that greatly exceeds the head length. It is of interest to note that the Ceylonese snake *Aspidura trachyprocta*, which distends the tongue well beyond its pointed snout, is also known to subsist largely on earthworms. It also resembles *Geophis dubius* in having the teeth deeply buried. Such similarities are attributable to adaptive convergence, but the association of such specialized feeding habits with the unusually lengthy distention of the tongue remains to be explained.

THE AFFINITIES OF *GEOPHIS*

The few characters shared by all species currently placed in *Geophis* are not so distinctive as those used to define the species. External features common to the assemblage are largely those of small, secretive, semi-fossorial or fossorial colubrids of other genera. One might suspect, therefore, that the similarities of the snakes referred to *Geophis* were due to convergence. Snakes in other continents are superficially similar to those placed in *Geophis*, and comparable modifications have arisen independently in other fossorial colubrids of the Americas.

The species that have been discovered and assigned to *Geophis* since Boulenger attempted to define the genus in 1894 extend the variations beyond those encompassed by his definition. Species now represented in the assemblage include some with 17 rows of dorsal scales, and others with 15. On some species the dorsal scales are smooth, but on others they are keeled, or the scales are smooth on the anterior part of the trunk and keeled posteriorly. The scales that may be more or less consistently present in some species but more often lost or coalesced in others include the internasals, the supraoculars, the lower postocular, and the

anterior temporal. Snakes in the assemblage may be drab or brightly colored, and some species are virtually unicolored; others are characterized by a nuchal collar, by cross bands that are distinct in some, mottled in others. Furthermore, the pattern may consist of ill-defined stripes. Information concerning the dentition and the hemipenes is lacking for many of the species, but the variations in the number of maxillary teeth in those we examined exceed the extremes given by Boulenger. The hemipenis may be strongly bilobed, as it is in *Geophis dubius*, or the lobes may be vestigial. Similarly, the sulcus spermaticus is bifurcated in some species, but it is undivided in others (*maculiferus* and *gertschi*), and the bifurcation of the sulcus appears to be retained by at least two species (*sallaei* and *multitorques*) on which the lobes have all but disappeared.

All species are probably to be regarded as specialized, but not to the same degree or in the same structures. Various lines of evidence suggest that the simple sulcus in various colubrids was derived from one that was bifurcated on the bilobed organ of the ancestor. The bilobed condition, and the bifurcated sulcus, are therefore believed to be primitive. Nevertheless, the sulcus is bifurcated on some (not necessarily all) of the species of *Geophis* on which the cephalic plates have undergone the greatest reduction and which therefore seem to be more highly adapted to subterrestrial environments. Conversely, the sulcus is unbifurcated on the hemipenis of *Geophis maculiferus* and *G. gertschi*, both of which retain the anterior temporal, as well as internasals, and a rounded, relatively unspecialized snout.

Should penial characters prove to be correlated with cranial characters, it may be possible to group the species more satisfactorily. Inferences based solely on external characters, however, are likely to be misleading. Furthermore, statements in print concerning the hemipenes and dentition of the snakes assigned to *Geophis* are not invariably reliable, especially when they are based on one species. The description of the hemipenis of a snake identified by Dunn (1928) as *Geophis longiceps* proves to have been based on a specimen of *Ninia*. Savage (1960) stated that the hemipenis of *Geophis* is not bilobed, but the basis of the statement is obscure. Probably the information was obtained from Dunn, who correctly described the organ of *Geophis sallaei*. The only character of the hemipenis that may serve to distinguish *Geophis* from *Atractus* is the "naked pocket," though it remains to be ascertained whether it is present on "all species," as stated by Savage.

The genus *Contia*, which contains a single species restricted to the Pacific Northwest, is similar to some species of *Geophis*, though it may not be closely related. The hemipenis of *Contia tenuis*, described by Stickel

(1951), is similar to that of *Geophis multitorques*, and the maxillary teeth are similar but longer and more widely spaced than they are in any species of *Geophis* that we have examined. Stickel apparently believed that the wide spaces between the teeth were vacant sockets (described as "weak and shallow, hard to see"). *Contia tenuis* proves to have seven maxillary teeth rather than 11, as described. Zweifel (1954) depicted seven widely spaced teeth in the mandible, without stating how many teeth were normally present, or noting that Stickel had reported at least 14 teeth to be present on the dentary. In having 15 rows of dorsal scales, *Contia* conforms more closely to the less-specialized species of *Geophis*. Such similarities are doubtfully attributable to adaptive convergence, for *Contia* is secretive rather than fossorial. The teeth are somewhat longer but no more strongly recurved in *Contia* than in *Geophis*. Zweifel's belief that *Contia* is specialized as a slug-eating snake may be correct, for the teeth are like those of other slug-eating snakes in being widely spaced. The divided anal scute, the presence of an apical pit on the dorsal scales, and the retention of the loreal, however, readily distinguish *Contia* from any of the species now assigned to *Geophis*.

Pits are rarely present on the dorsal scales of fossorial snakes, but the anal plate may be either single or divided. Data assembled by Inger and Marx (1965) for blunt-headed, burrowing colubrids in the tropics of Asia and Africa show that an undivided anal is characteristic of nearly all the Asiatic genera, but the anal plate is divided on six of the 10 genera from Africa included in their tabulation. It would be inferred, therefore, that fossorial species tend to retain the condition of the anal plate that was characteristic of their terrestrial progenitors. A divided anal is present on snakes of the majority of the American colubrid genera, including fossorial, terrestrial, and arboreal forms. In a few genera species with the anal entire are grouped with those on which it is divided. The character is unstable in some species but subject to little variation in most populations. Evidence of any correlation with habits, behavior, or environment is lacking. The presence of an undivided anal on all species of *Geophis* is unlikely to be due to convergence, though characters of the sort are seldom important in determining relationships. In this instance it is noteworthy that the anal is divided in nearly all the small, secretive, or fossorial snakes in Mexico, whereas an undivided anal is characteristic of the South American snakes assigned to *Atractus*. The populations of *Geophis* in Central America point to the probability that *Geophis* and *Atractus* share a common ancestry, regardless of whether they have diverged sufficiently to be regarded as separate genera.

Snakes of the Mexican and Central American genus *Adelphicos* have been reviewed by Smith (1942), who suggested that the affinities of the group were with *Geophis*. In external features and dentition the snakes assigned to *Adelphicos* resemble *Geophis*, but the anal is divided, and the anterior chin shields are greatly enlarged. Also, the infralabials are extraordinarily small or, in some populations, the normal series is interrupted by the anterior chin shields, which extend to the margin of the lip. Smith noted that the sulcus spermaticus was undivided on the hemipenis of *Adelphicos*, and the character was cited as evidence that the genus had diverged from *Geophis*. In view of the unstable nature of the sulcus in *Geophis*, as revealed by the few species we have examined, this feature of the hemipenis would not serve to separate the genera unless the species with the undivided sulcus are removed from *Geophis*. As we have noted, however, the sulcus is bifurcated on the most specialized representatives of *Geophis*, and these are the species that most closely resemble those of *Adelphicos*. The snakes of the latter genus, if they share the ancestry of *Geophis*, have evolved a distinctive array of characters, including the divided anal. There appear to be valid reasons, therefore, for retaining the genus *Adelphicos*.

Detailed comparisons of skulls may remove many of the uncertainties that now prevail. Until such studies are carried out, the divergence in scutellation, dentition, and penial characters noted in the species of *Geophis* is not necessarily to be construed as evidence that the genus is polyphyletic. Perhaps some peculiar array of traits in the assemblage will account for the fragmentation of distributions that seemingly preceded widespread isolations of populations, and thereby permitted each of them to evolve independently of the others.

LITERATURE CITED

BOCOURT, MARIE-FIRMIN

1883. Mission scientifique au Mexique et dans l'Amerique Centrale. Études sur les reptiles. Paris, livr. 9.

BOULENGER, G. A.

1894. Catalogue of the snakes in the collection of the British Museum. London, British Museum, vol. 2.

DUNN, E. R.

1928. New Central American snakes in the American Museum of Natural History. Amer. Mus. Novitates, no. 314, pp. 1-4.

FISCHER, J. G.

1886. Herpetologische Notizen. Abhandl. Gebiete Naturwiss., vol. 9, pp. 51-67, pls. 1-2.

INGER, R. F., AND HYMEN MARX

1965. The systematics and evolution of the Oriental colubrid snakes of the

genus *Calamaria*. Fieldiana: Zool., vol. 49, pp. 1-304, figs. 1-73, tables 1-64.

JAN, GEORGES

1864. Iconographie générale des ophiidiens. Milan, vol. 1, livr. 12.

PETERS, W.

1861. [Eine Mittheilung über neue Schlangen des Königl. zoologischen Museums: *Typhlops striolatus*, *Geophidium dubium*, *Streptophorus (Ninia) maculatus*, *Elaps hippocrepis*.] Monatsber. K. Preussischen Akad. Wiss. Berlin, pp. 922-925.

SAVAGE, JAY M.

1960. A revision of the Ecuadorian snakes of the colubrid genus *Atractus*. Misc. Publ. Mus. Zool., Univ. Michigan, no. 112, pp. 1-86, figs. 1-11, tables 1-8.

SLEVIN, J. R.

1939. Notes on a collection of reptiles and amphibians from Guatemala. I. Snakes. Proc. California Acad. Sci., ser. 4, vol. 23, pp. 393-414, pls. 37-38.

SMITH, H. M.

1942. A review of the snake genus *Adelphicos*. Proc. Rochester Acad. Sci., vol. 8, pp. 175-195, figs. 1-6, tables 1-6.

1959. New and noteworthy reptiles from Oaxaca, Mexico. Trans. Kansas Acad. Sci., vol. 62, pp. 265-272, pls. 1-2.

SMITH, H. M., AND E. H. TAYLOR

1950. Type localities of Mexican reptiles and amphibians. Univ. Kansas Sci. Bull., vol. 33, pp. 313-380.

STICKEL, W. H.

1951. Distinctions between the snake genera *Contia* and *Eirenis*. Herpetologica, vol. 7, pp. 125-131.

STUART, L. C.

1963. A checklist of the herpetofauna of Guatemala. Misc. Publ. Mus. Zool., Univ. Michigan, no. 122, pp. 1-150, frontispiece, 1 map.

WEBB, R. G., AND C. M. FUGLER

1957. Selected comments on amphibians and reptiles from the Mexican state of Puebla. Herpetologica, vol. 13, pp. 33-36, fig. 1, pl. 1.

ZWEIFEL, R. G.

1954. Adaptation to feeding in the snake *Contia tenuis*. Copeia, pp. 299-300, fig. 1.

