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The Variations and Affinities of the Dwarf Boas of the Genus *Ungaliophis*

By Charles M. Bogert[1]

Since the small boa that became the holotype of *Ungaliophis continentalis* was discovered in Guatemala well over 90 years ago, only six additional snakes of the genus have been reported. These few records leave no doubt that dwarf boas of the group inhabit portions of Colombia, Panama, Nicaragua, Honduras, Guatemala, and Mexico. Additional populations will surely be discovered, but it is improbable that members of the genus are continuously distributed throughout Central America. These dwarf boas tolerate environments ranging from the lowland rain forest of southeastern Nicaragua to those of the pine woodland of eastern Chiapas, where Conant (1966) discovered one at an elevation of approximately 2100 meters. Reptiles regarded as relicts seldom tolerate such a wide range of environmental conditions. In other respects, however, the distribution now known for *Ungaliophis* is much like that of several reptiles surviving in Central America as isolated remnants of populations once more widely and uniformly distributed.

If populations of *Ungaliophis* are discovered in the future at the same rate they have been discovered in the past, one or two centuries may elapse before the distribution of the group can be mapped in any detail. With the meager information now available, it would be presumptuous to attempt to indicate the extent of the fragmentation that has occurred

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in the range. Nevertheless at least one hiatus in the distribution of these dwarf boas must have occurred at an early stage in the evolution of the genus. This examination of specimens and review of the literature were prompted by the need for information concerning the affinities of a boa remotely resembling *Ungaliophis* that was discovered in a cloud forest in Mexico in 1967. When an effort was made to compare the genera of dwarf boas, however, it became evident that *Ungaliophis* warranted attention in a separate account of the genus.

The account that follows is concerned primarily with the variation and differentiation within the genus, and hence also with the names that have been proposed since Müller supplied a name for the genus. Stuart (1954) has shown beyond any reasonable doubt that *Ungaliophis continentalis* Müller (1882) is the valid name for the small boa from Retalhuleu, Guatemala, that Müller (1878) had described four years earlier. *Ungaliophis* Müller, therefore, stands as the valid name of the genus.

SUMMARY OF THE LITERATURE

The boa from Guatemala that became known as *Ungaliophis continentalis* in 1882 has since been redescribed, mentioned, or listed in various catalogues, faunal reports, or check lists. Those published prior to 1921, however, added little or nothing to the information contained in the original description. Werner (1921), who reported the first specimen from Mexico, indicated that it had been taken west of the type locality, near Tapachula, in the state of Chiapas. Two boas of the genus subsequently reported were designated as holotypes and hence described in detail, but others were incompletely described or merely cited as specimens preserved and catalogued. Authors who have indicated range extensions sometimes failed to document their statements.

Thus Amaral (1929) added Panama to the range of *U. continentalis,* presumably because he was aware of a specimen in the United States National Museum that E. A. Goldman had obtained on Cerro Brujo in 1911. The source of this record was not apparent until four years later when this snake was described as *Ungaliophis panamensis* by Schmidt (1933), who pointed out that it differed in several respects from the Guatemalan boa that Müller had described. The name Schmidt proposed was, however, omitted from the check list of the members of the family Boidae that Stull (1935) prepared. Stull also overlooked Werner's record for *U. continentalis* in Mexico, although she indicated that the range of this species extended into Nicaragua. This record remained undocumented until Dunn and Bailey (1939) referred to a

specimen in the United States National Museum from the Río Misterioso, 10 miles from San Juan del Norte ("Greytown"), Nicaragua. It is uncertain whether Dunn and Bailey had examined the specimen, but they considered it to be conspecific with the boa that Schmidt had described as *U. panamensis*. A second record of *U. panamensis* from the Canal Zone (Nemuras, 1967) proves to have been based on a juvenile of *Corallus hortulana* (*fide* C. W. Myers, *in litt.*).

Schmidt's description of the boa in Panama had apparently not been seen by Prado (1940) when he proposed the name *Ungaliophis danieli* for a juvenile male that had been taken in the Andes of Colombia, "*sudoeste de Antioquia.*" Prado's description and his figures of the holotype reveal that it closely resembles Schmidt's *Ungaliophis panamensis*.

A moderately large specimen (a female, A.M.N.H. No. 76303) of uncertain origin that had reached the United States in a shipment of bananas was depicted by Oliver (1956). After noting the scarcity of *Ungaliophis* in collections, and the variations reported in the few specimens described, Oliver suggested that the genus might prove to consist of one species widely distributed throughout Central America, perhaps represented by three incompletely differentiated populations. Conant (1966), who reported his discovery of the second specimen from Mexico, and the first record of the genus in Honduras, was inclined to agree with Oliver. Conant pointed out, however, that the pattern on the snakes from Mexico and Honduras consists of paravertebral rows of isolated dark ovoid spots, whereas the spots on the snake depicted by Oliver had angular borders and were virtually unseparated. Through the kindness of Dr. James A. Oliver and the New York Zoological Society the photograph illustrating Dr. Oliver's report is reproduced as figure 4 of this account.

Several years earlier, in a discussion of the fauna of Costa Rica, Taylor (1951) called attention to the absence of records for *Ungaliophis continentalis* "south of Nicaragua." He failed to note that Dunn and Bailey (*supra cit.*) had assigned the Nicaraguan specimen to *U. panamensis*, which is, therefore, the species to be expected in Costa Rica. Evidence to be discussed below points to the probability that gene exchange was interrupted in the area between Honduras and southeastern Nicaragua at an early stage in the evolution and differentiation of the boas now placed in the genus *Ungaliophis*.

DATA AVAILABLE

The data summarized below were derived from 12 specimens, three of which I have not examined. Through the courtesy of Dr. James A.

Peters of the United States National Museum of the Smithsonian Institution (U.S.N.M.), I have seen the holotype of *Ungaliophis panamensis* and the specimen from Nicaragua mentioned by Dunn and Bailey (*supra cit.*). I have not examined the specimen from Mexico in the Zoologisches Museum, Hamburg, Germany (Z.M.H.), that Werner (*supra cit.*) mentioned. Nor have I seen the holotype of *U. continentalis* in the Naturhistorisches Museum, Basel (N.M.B.), or the holotype of *Ungaliophis danieli* described by Prado (*supra cit.*), who reported the specimen as being a juvenile male in the museum of the Colegio de San José (M.C.S.J.) in Medellin, Colombia. Five of the specimens examined are in the American Museum of Natural History (A.M.N.H.). These include the two previously reported by Conant (*supra cit.*), from Mexico and Honduras, respectively, and three that were discovered in bananas believed to have been shipped to the United States from Central America. Two additional specimens of uncertain origin have also been examined, one in the collection of the Los Angeles County Museum of Natural History (L.A.C.M.) lent through the courtesy of Dr. John W. Wright, and one in the Museum of Comparative Zoology (M.C.Z.) helpfully made available by Dr. Ernest E. Williams.

The two holotypes I have not examined have been figured, as well as described, but ventral and subcaudal counts are the only data Werner (*supra cit.*) provided for the specimen from Mexico in the museum in Hamburg. These specimens, along with those examined, are listed by museum numbers, and arranged geographically in the list that follows:

A.M.N.H. No. 93813, Mexico, Chiapas, 12.8 kilometers (via road) east-southeast of Teopisca, in pine woodland at an elevation of approximately 2100 meters, on the Atlantic drainage.

Z.M.H. No. 3151, Mexico, Chiapas, La Joya, 5 kilometers south of Tapachula, at an elevation of 100 meters, 27 kilometers inland from the Pacific coast.

N.M.B. No. 426, Guatemala, [vicinity of] Retalhuleu, at an elevation of 200 meters, roughly 35 kilometers inland from the Pacific coast. (Holotype of *U. continentalis* Müller.)

A.M.N.H. No. 70205, Honduras, Departamento Francisco Morazán, La Montañita, at an approximate elevation of 1600 meters, on the Pacific drainage.

U.S.N.M. No. 29215, Nicaragua, Río Misterioso, 17 kilometers inland from San Juan del Norte ("Greytown") on the Atlantic coast.

U.S.N.M. No. 54059, Panamá, at an elevation of *ca.* 870 meters on Cerro Brujo, in the Serranía del Brujo, northeast of Colon, near the Caribbean coast. (Holotype of *U. panamensis* Schmidt.)

M.C.S.J. No. 189, Colombia, Province of Antioquia, *"Andes a sudoeste de Antioquia."* (Holotype of *U. danieli* Prado.)

A.M.N.H. Nos. 58845, 62639, 76365, M.C.Z. No. 56051, L.A.C.M. No. 2535 (without locality data).

INACCURACIES IN DIAGNOSES AND DESCRIPTIONS

Virtually every diagnosis, definition, and description of boas assigned to the genus *Ungaliophis* thus far published contain errors traceable directly to Müller's careless examination of the holotype of *U. continentalis.* Although I have not examined this holotype, it becomes evident from an examination of nine specimens, including females from Chiapas and Honduras closely resembling the holotype, that members of the genus do not have the nostril situated *"zwischen 3 Schildern,"* as described and depicted by Müller (1878). Bocourt (1882), who repeated the statement, corrected it only to the extent of noting that the three shields were the internasal and two nasals. Bocourt's illustrations, as do those of Müller, erroneously show the nostril emerging on a suture. Boulenger (1893) perpetuated the error by stating in his definition of the genus that the nostril was "between three shields." Without the aid of a dissecting microscope, anyone might be similarly misled, but, when the plates on the snout are viewed under magnification, the nostril invariably proves to be situated in the anterior nasal.[1]

When Schmidt (1933) described *Ungaliophis danieli* he added to the confusion by referring to the posterior nasal as the "anterior loreal." In a brief discussion following the description, he noted that the plate behind the nasal of *U. panamensis* "apparently corresponds with the posterior nasal of *continentalis,*" thus invalidating the statement in the diagnosis that *U. panamensis* differs in having two "elongate loreals," and an undivided nasal. Schmidt correctly observed that the Panamanian boa differed from *U. continentalis* in having the rostral and prefrontal separated by internasals, but he omitted this information from his diagnosis.

The boa from Colombia described by Prado (1940) as *U. danieli* closely resembles *U. panamensis,* from which it differs in having nine instead of eight supralabials, and 19 rather than 21 dorsal scales at midbody. The illustrations of *U. danieli* show the internasals meeting behind the rostral, widely separating it from the azygous prefrontal, as they do on the holotype of *U. panamensis.* The internasals are not mentioned in the description of *U. danieli,* however, wherein Prado, following the precedent set by earlier authors, merely described the nasal as being *"tripartida."* Prado's otherwise excellent illustrations show the nostril as though the opening were bordered by the inter-

[1] Dr. E. Kramer, who examined the holotype of *U. continentalis* in February, 1968, reports that the nostril is in the anterior nasal.

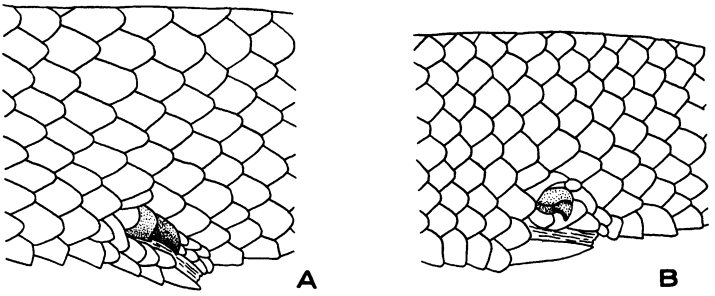

FIG. 1. Spurs on male dwarf boas, as viewed from left side of anal region. A. *Ungaliophis panamensis,* M.C.Z. No. 56051. B. *Tropidophis feicki,* A.M.N.H. No. 81130.

nasal, although the nostril is doubtless in the anterior nasal, as it is in the holotype of *U. panamensis.* The rostral is presumably wider than high in *U. danieli,* as Prado noted, in contrast to *U. continentalis* on which the width of the rostral more closely approximates the height. *Ungaliophis danieli* does not differ from *U. panamensis* in this respect, but, as noted above, Prado was evidently unaware of Schmidt's description of the species from Panama. Although the holotype of *U. danieli* has fewer rows of dorsal scales than any other member of the genus examined or reported, the other characters that Prado cited in his diagnosis fall within the range of variations observed in specimens that have the internasals meeting behind the rostral.

Prado reported the holotype of *U. danieli* to be a juvenile male. Neither Müller nor Schmidt mentioned the sex of the holotypes in their respective descriptions, but the holotype of *U. panamensis* proves to be a female. If Bocourt (1882) correctly reported that no vestiges of limbs were present on *U. continentalis,* it seems probable that the specimen Müller described was also a female. Only one of the nine specimens examined, M.C.Z. No. 56051, is a male. The external vestiges of limbs are extraordinarily well developed on this individual, on which the paired spurs are appreciably larger than they are on males of the genus *Tropidophis,* as shown in figure 1. Until additional males of *Ungaliophis* are discovered, uncertainties remain, but it is a reasonable assumption that spurs will prove to be restricted to males of the genus, as they are on all species of *Tropidophis* that retain external vestiges of the limbs. If spurs are present on the holotype of *U. danieli,* however, Prado failed to mention them, or he may have been misled in his efforts to ascertain the sex of the specimen.

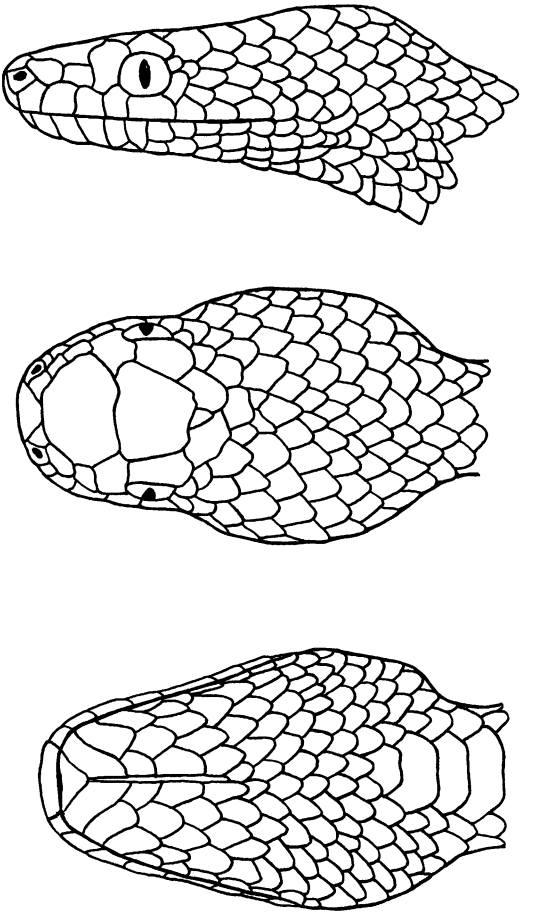

FIG. 2. *Ungaliophis continentalis,* lateral, dorsal, and ventral views of head, A.M.N.H. No. 70205, female from La Montañita, Honduras.

To clarify the ensuing discussion the illustrations provided by Prado (1940) have been redrawn to show the nostril correctly and reproduced (fig. 2) along with figures showing the arrangement of the plates and the position of the nostril on A.M.N.H. No. 70205, from Honduras (fig. 3), which conforms in most details to the specimen from Chiapas, A.M.N.H. No. 93813. It is pertinent to note that the modified figures of *U. danieli,* copied from those accompanying Prado's description, might well illustrate the holotype of *U. panamensis,* except for the presence of an additional supralabial on the snake from Colombia. The fourth,

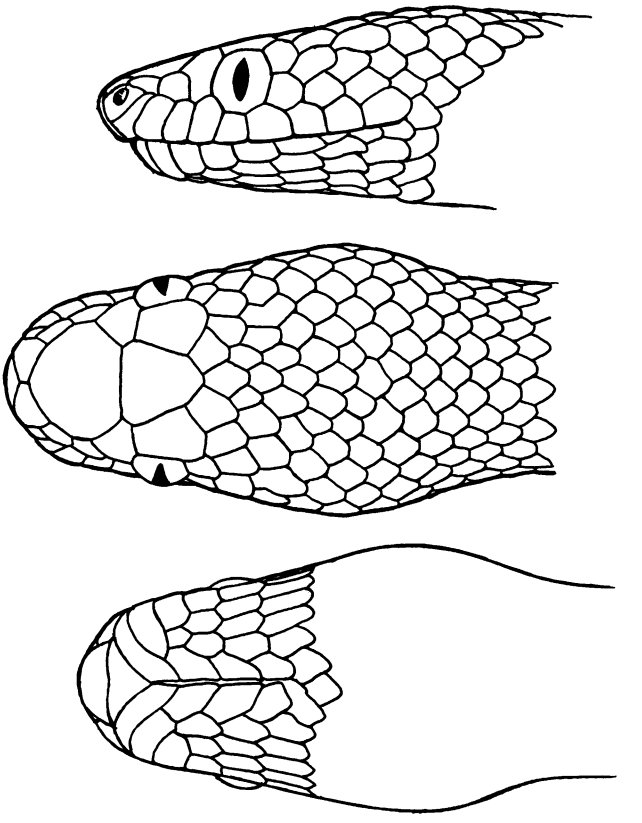

FIG. 3. *Ungaliophis panamensis,* lateral, dorsal, and ventral views of the head, showing the cephalic scutellation as depicted for the holotype of *U. danieli* by Prado (1940), slightly modified to show position of nostril in anterior nasal.

fifth, and sixth supralabials reach the orbit, and the loreal is situated above the suture between the second and third supralabials on *U. panamensis,* as shown by Prado for *U. danieli.*

ANALYSIS OF DATA

To facilitate comparison, the meager data obtainable from the literature for three specimens have been combined in table 1 with the data derived from an examination of nine specimens. Detailed locality data (provided above) are omitted from the table, which is restricted to characters subject to individual variation. All specimens examined have two nasals, one loreal, and one preocular. I have made no effort to deal

TABLE 1

VARIATIONS OBSERVED OR REPORTED IN SPECIMENS OF *Ungaliophis*

Specimen Number	Sex	Source	Shape of Paravertebral Spots	Middorsal Scale Rows	Post-oculars	Supra-labials	Supra-labials Reaching Orbit	Ventrals	Subcaudals	Maxillary Teeth
A.M.N.H. No. 93813	♀	Mexico	Ovoid	25	2-2	9- 9	4,5-4,5	204	39	12-12
Z.M.H. No. 3151	?	Mexico	Ovoid	25	—	—	—	239	46	—
N.M.B. No. 426	?♀	Guatemala	Ovoid	25	2-2	10-10	4,5-4,5	258	47	—
A.M.N.H. No. 70205	♀	Honduras	Ovoid	25	3-2	10- 9	5,6-4,5	230	46	12-12
U.S.N.M. No. 29215	♀	Nicaragua	Triangular	23	3-3	8- 8	4,5-4,5	250	46	13-13
U.S.N.M. No. 54029	♀	Panama	Triangular	21	2-2	8- 8	4,5,6-4,5,6	236	[a]	14-14
M.C.S.J. No. 189	"♂"	Colombia	Triangular	19	2-2	9- 9	4,5,6-4,5,6	226	41	—
L.A.C.M. No. 2535	♀	No data	Triangular	25	3-3	9- 8	4,5-4,5	239	45	14-14
A.M.N.H. No. 58845	♀	No data	Triangular	23	3-3	9- 9	4,5-4,5	237	[a]	13-15
A.M.N.H. No. 62639	♀	No data	Triangular	23	3-2	8- 8	3,4,5-3,4,5	231	45	14?
A.M.N.H. No. 76305	♀	No data	Triangular	23	3-3	8- 8	4,5-4,5	247	46	13-14
M.C.Z. No. 56051	♂	No data	Triangular	23	3-3	9- 9	4,5-4,5	245	43	—

[a] Incomplete.

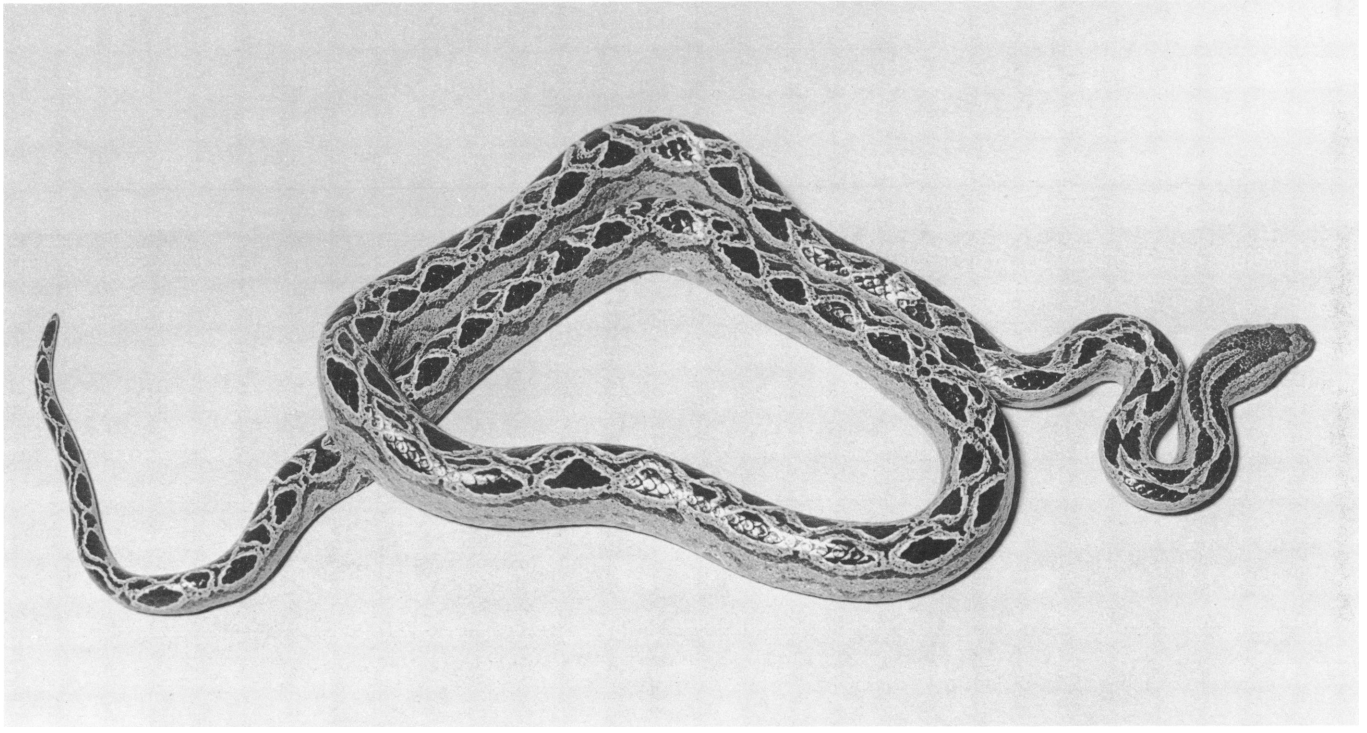

FIG. 4. *Ungaliophis panamensis,* adult female, now A.M.N.H. No. 58845, showing the angular paravertebral blotches, as depicted by Oliver (1956). Reproduced from original photograph through the courtesy of Dr. James A. Oliver and the New York Zoological Society.

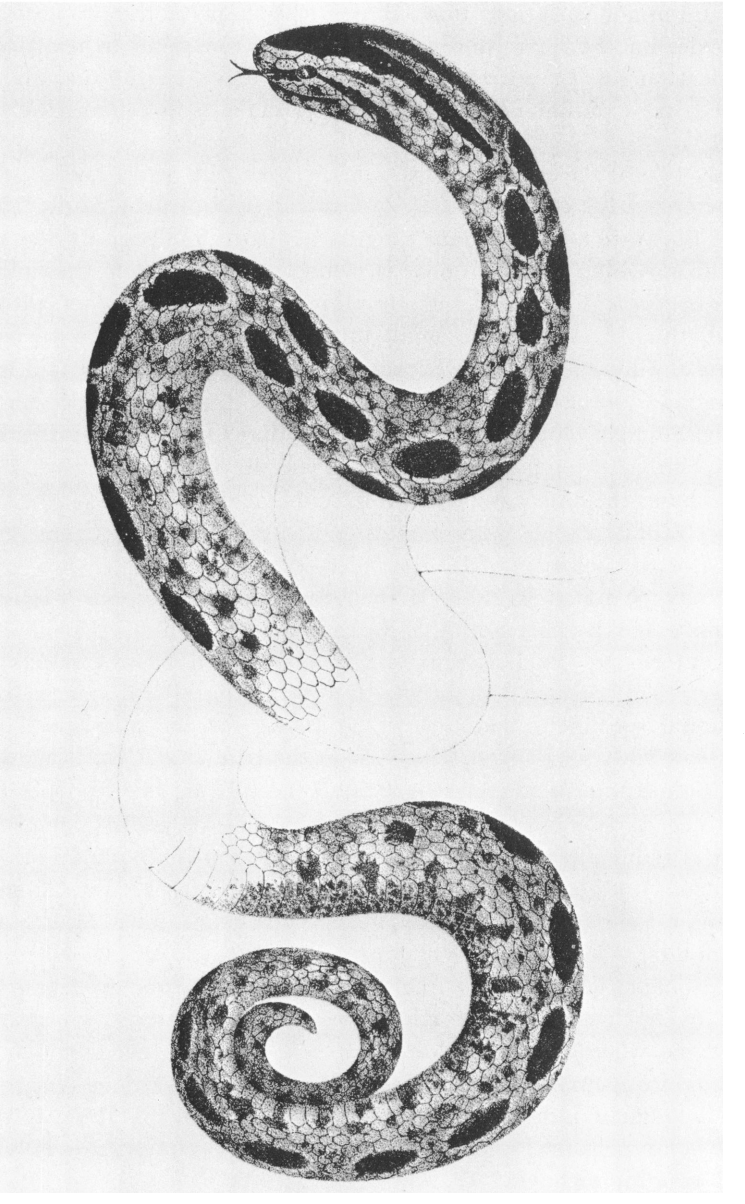

FIG. 5. Holotype of *Ungaliophis continentalis,* showing the ovoid paravertebral blotches characteristic of dwarf boas in Mexico, Guatemala, and Honduras (from Müller, 1878).

with the minor variations that occur in the shape or the proportions of the scales on the head, and the samples are too small to reveal ontogenetic changes. Except for the presence of spurs on the one male examined, no external differences between males and females were detected.

Only two of the specimens examined possess the ovoid markings that characterized the holotype of *U. continentalis,* as shown by Müller (1878) whose illustration is reproduced herein as figure 5. These are the specimens from Chiapas and Honduras, which also conform to the holotype of *U. continentalis* in having the prefrontal in broad contact with the rostral, thus separating the small internasals. All other specimens, including the individual from Nicaragua, those of uncertain origin found in banana shipments, and the holotype of *Ungaliophis panamensis,* possess the angular blotches of the specimen that Oliver (1956) illustrated (fig. 4 herein). Moreover, all of the latter, the male as well as the females, have the internasals in broad contact between the rostral and the prefrontal, closely approximating the condition shown by Prado (1940) for the holotype of *U. danieli.*

As may be noted in table 1, the boas from Mexico and Honduras that have the pattern and the cephalic scutellation of *U. continentalis* also conform to the holotype, and the specimen from Chiapas that Werner (1921) reported, in having 25 rows of dorsal scales at midbody. Additional specimens may reveal variations, for the number of midbody scale rows varies from 19 to 25 on the boas that have the angular blotches and internasals meeting behind the rostral. The few specimens available, however, suggest that there is a cline or a directional trend toward a reduction in the number of scale rows in the populations from Nicaragua southeastward through Central America to the Andes of Colombia. Four of the specimens of uncertain origin have 23 scale rows at midbody, whereas 25 are present on the fifth (L.A.C.M. No. 2535). It is problematical whether the latter specimen came from an area north or northwest of the Río Misterioso, in extreme southeastern Nicaragua, where U.S.N.M. No. 29215 was obtained, even though it is tempting to assume that the cline continues northward in Nicaragua. The Nicaraguan individual has 23 scale rows, whereas 21 are present on the holotype from Panama, and Prado (1940) described the holotype from Colombia as having 19.

Aside from having fewer rows of dorsal scales at midbody, no other character adequately distinguishes *Ungaliophis danieli* Prado (1940) from *Ungaliophis panamensis* Schmidt (1933), or the specimens with 23 or 25 middorsal scale rows that closely resemble *U. panamensis* in other features

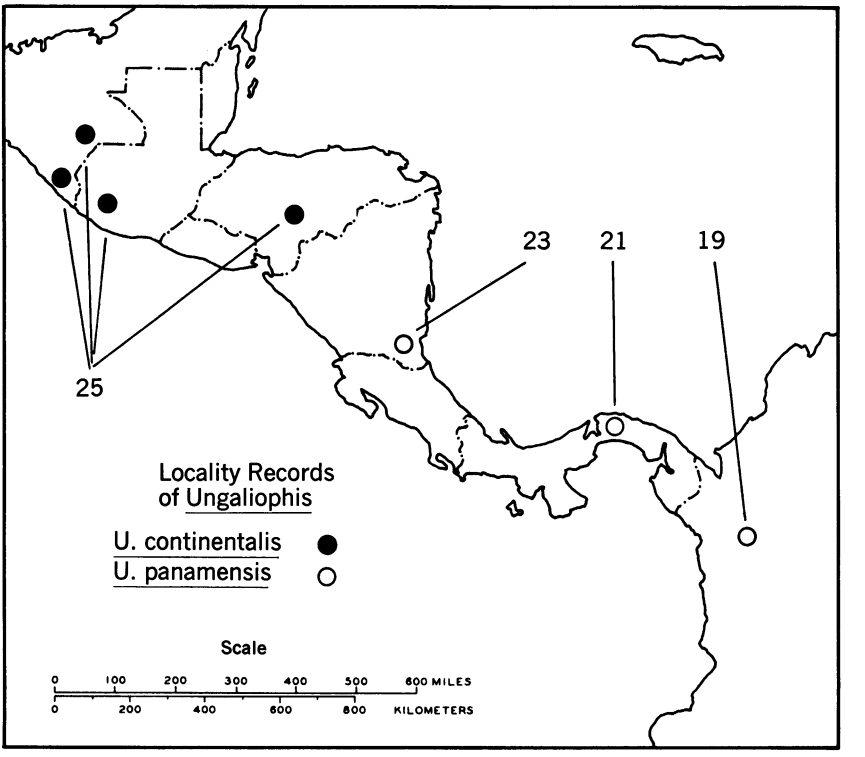

FIG. 6. Map showing localities in southeastern Mexico, Central America, and Colombia where the two species of *Ungaliophis* are known to occur. The figures indicate the number of middorsal scale rows on snakes from each locality.

of their scutellation and pattern. The specimens that have the internasals meeting behind the rostral share a few other characteristics that aid in distinguishing them from *U. continentalis,* including the proportionately broad rostral noted by Prado. Members of the genus from Honduras, Guatemala, and Mexico also tend to have fewer postoculars, and more supralabials, but the supralabials vary too extensively to be employed in diagnoses.

The holotype of *U. continentalis* has more ventrals (258) than any other member of the genus examined, and the specimen that Conant obtained in the mountains of Chiapas has the fewest (204). Counts for all other specimens of the genus that have been seen or reported fall between these extremes. The individuals with the fewest ventrals also have the

fewest subcaudals, and those with high ventral counts tend to have more subcaudals. Members of the genus with the internasals meeting behind the rostral that have 23 or 25 rows of dorsal scales tend to have more ventrals than those with 21 or 19 scale rows. The holotype of *U. danieli* with the fewest rows of dorsal scales also has fewer ventrals and subcaudals than the specimens it most closely resembles.

No one has described the dentition of these boas, although Müller noted that the teeth at the front of the jaws were stouter and longer than the others. There are 12 maxillary teeth on the snakes from Mexico and Honduras, whereas the snakes with internasals meeting behind the rostral have from 13 to 15 (nine maxillae examined). The difference appears to be of taxonomic significance, although larger samples may reveal an overlap in tooth counts. On all maxillae the anterior four or five teeth are set off by a short diastema from smaller, more slender teeth, subequal in size. The teeth on the dentary vary from 13 to 15; on the palatine, from five to eight; and on the pterygoid, from 11 to 15.

TAXONOMIC IMPLICATIONS

Despite the variations noted in some characters, an analysis of the data obtained from descriptions and an examination of nine specimens show that the genus *Ungaliophis* contains two well-differentiated species. The name *Ungaliophis continentalis* Müller (1878) is applicable to the populations in Mexico, Guatemala, and Honduras (fig. 6, map). The specimens from Nicaragua, Panama, and Colombia, as well as the five individuals lacking locality data, must all be referred to *Ungaliophis panamensis* Schmidt (1933). Before the characters that distinguish the two species are discussed, it is necessary to consider the status of *U. danieli.*

As noted above, most of the characters employed by Prado (1940) to distinguish *U. danieli* from *U. continentalis* fall within the range of variation of the specimens with internasals meeting behind the rostral. The holotype of *U. danieli* differs from the holotype of *U. panamensis* in having fewer rows of dorsal scales, fewer ventrals, and perhaps fewer subcaudals (the macerated condition of the incomplete tail on the specimen from Panama precludes comparison of the latter character). It may be noted (table 1), however, that the individual from extreme southwestern Nicaragua (U.S.N.M. No. 29215) differs from the Panamanian holotype in having two additional rows of dorsal scales as well as more ventrals. Where directional trends in characters occur, in this instance along a cline that extends from Nicaragua through Panama to Colombia, no useful purpose is served by applying names to popula-

TABLE 2

DIFFERENTIAL CHARACTERS OF THE SPECIES OF *Ungaliophis*

Character	*U. continentalis*	*U. panamensis*
Internasals	Widely separated by broad contact of rostral and azygous prefrontal	Meet on suture behind rostral, separating it from prefrontal
Maxillary teeth	12	13–15
Markings on dorsum	Dark brown ovoid spots, with light margins well separated (fig. 5)	Dark brown triangular spots with light margins narrowly separated (fig. 4)
Middorsal scale rows	25	19–23, rarely 25
Postoculars	Normally 2, rarely 3	Normally 3, occasionally 2

tions distributed along the cline. It would be illogical to recognize *U. danieli,* even as a subspecies, without also proposing a name for the population in Nicaragua. A more reasonable alternative consists in placing *Ungaliophis danieli* Prado (1940) in the synonymy of *Ungaliophis panamensis* Schmidt (1933).

Despite the variations, it is evident that two well-differentiated species have evolved, as indicated in table 2.

AFFINITIES OF *UNGALIOPHIS*

The relatively enormous azygous prefrontal, presumably resulting from the fusion and expansion of the paired prefrontals of a less aberrant ancestor, readily distinguishes *Ungaliophis* from other groups of boas. Unfortunately, few features of the external morphology shed much light on the affinities of the genus. Frazzetta (1959), who reviewed several features of the cranial osteology of boas and pythons, attempted to summarize his observations in a tabular comparison. As outlined by Frazzetta, *Ungaliophis* failed to conform to other boas in three of the 12 characters emphasized in the tabulation. Butner (1963), who restricted his investigation to a few visceral characters, has set forth reasons for grouping *Ungaliophis* with *Tropidophis* and *Trachyboa,* but, contrary to his statement, the kidneys of *Ungaliophis* are lobulated. Brongersma (1951) had suggested earlier that *Trachyboa* and *Tropidophis* warranted recognition as a separate subfamily, the Tropidophinae, but he had not examined *Ungaliophis.* Underwood (1967), in an account confused by his discussion of the Boini under two headings, recognized the group defined by Brongersma as one of four tribes of the subfamily Boinae. Noting that Frazzetta had mentioned only three features of *Ungaliophis* that were not typically "Boine," Underwood, who accepted Butner's statement, added that if the genus "be truly tropidophine then this suggests that the Tropidophini are aberrant boas rather than independently derived from pro-boid stock."

The monotypic genus *Loxocemus,* which Underwood regarded as a "surviving pro-boid," bears little resemblance to *Ungaliophis,* whereas the characters of the latter genus suggest that it is more closely related to *Tropidophis* than to *Trachyboa.* Of the three genera, *Trachyboa* would appear to be the most aberrant, although *Ungaliophis* is probably more specialized than any species of *Tropidophis.* These three genera, as well as a Mexican genus that remains to be diagnosed and described, appear to be remnants of an early dispersal of dwarf boids, presumably from South America. *Trachyboa* is restricted largely to South America,

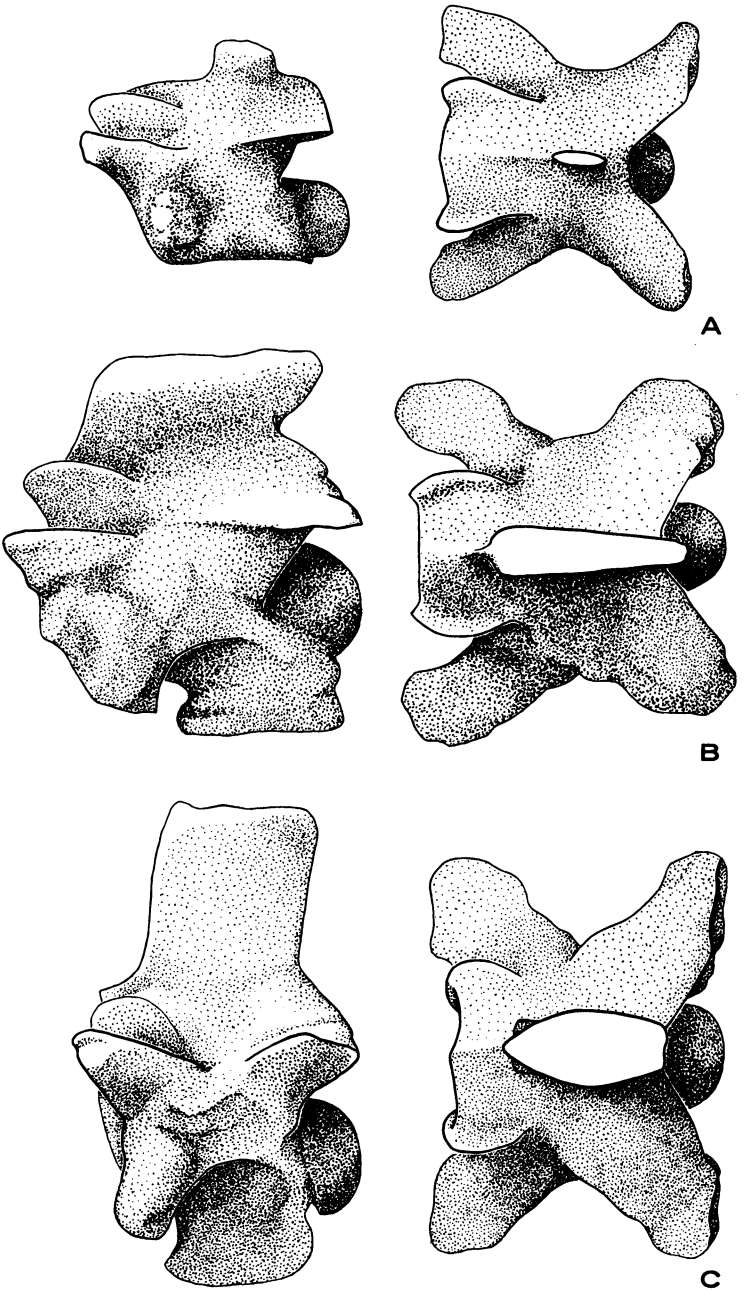

FIG. 7. Lateral and dorsal views of vertebrae from the posterior portion of the trunk of dwarf boas. A. *Ungaliophis panamensis,* juvenile female, A.M.N.H. No. 62639. B. *Tropidophis canus,* adult male, A.M.N.H. No. 73066. C. *Trachyboa gularis,* adult female, A.M.N.H. No. 28982.

although its range extends into Panama. *Tropidophis* is well diversified and widely distributed in the West Indies, but represented by populations in South America, whereas the range of *Ungaliophis,* though largely Central American, also extends into South America.

The adaptive radiation of the boas in South America may have been initiated before the end of the Cretaceous, as suggested by Simpson (1933), who described a gigantic species from Eocene deposits in Patagonia. The smaller, secretive species may not have evolved until much later, but the genera of dwarf boas had perhaps become differentiated as early as the Miocene. Presumably the diversification of *Tropidophis* in the West Indies is a relatively recent phenomenon. The few populations in South America may be regarded as relicts, but they bear no greater resemblance to *Ungaliophis* than some of the species in the West Indies. Despite evidence of affinity, the genera *Trachyboa, Ungaliophis, Tropidophis,* and the genus in Mexico that remains to be described represent four separate and distinct trends in the evolution of dwarf boas in the neotropical region.

The hypapophyses, restricted to the anterior vertebrae of *Ungaliophis,* are slender and pointed as viewed from the side in contrast to those of *Tropidophis pardalis,* which are present throughout the length of the trunk (fig. 7). On other species of *Tropidophis,* however, the hypapophyses are reduced posteriorly, but not lacking as they are on *Ungaliophis.* Hypapophyses are strongly developed throughout the vertebral column of *Trachyboa* (fig. 7).

Cranial characters seem to have been subject to fewer modifications than the cephalic plates, insofar as can be ascertained from an examination of two skulls removed from *Ungaliophis* (A.M.N.H. Nos. 58849 and 62639), and three skulls of two species of *Tropidophis, T. melanurus* (A.M.N.H. No. 46690) and *T. canus* (A.M.N.H. Nos. 45839 and 73066). The skulls of *Ungaliophis* and *Tropidophis* are much alike, although the posterior end of the pterygoid of *Ungaliophis* is more sharply pointed and less robust than it is on any of the three specimens of *Tropidophis* examined. The right Vidian canal is virtually the same size as the left on *Ungaliophis,* and no conspicuous differences between the two were noted on the skulls of *Tropidophis.* The three skulls of the latter genus, however, differ from one another nearly as much as any one of them differs from either skull of *Ungaliophis.*

The anterior maxillary teeth of *Tropidophis* are larger, but no stouter, than those behind them, in contrast to the condition in *Ungaliophis.* Other features of the dentition of *Tropidophis* differ little from those of *Ungaliophis,* particularly *U. panamensis* which tends to have more maxil-

lary teeth than *U. continentalis.* The following variations were noted in the teeth of the three skulls of *Tropidophis:* maxillary teeth, 15 to 17; palatine teeth, six to seven; pterygoid teeth, nine to 12; and 19 to 21 teeth on the dentary. Schwartz (1957) described the holotype of *T. feicki* as having "about 12" maxillary teeth. Actually there are 23 teeth on each side.

Stull (1928) provided counts for several species of *Tropidophis,* and her data indicate the following variations: maxillary teeth, 12 to 19; palatine teeth, four to eight; pterygoid teeth, 10 to 15; dentary, from 15 to 23. Stull's counts conform closely to those obtained from specimens in the American Museum of Natural History. It is noteworthy that the holotype of *T. paucisquamis,* one of the two species restricted to South America, was reported to have 19 maxillary teeth, more than any other species in the genus. A juvenile of the species, A.M.N.H. No. 72426, has 17 teeth in each maxilla, precisely the number found on a specimen of *T. canus curtus* (A.M.N.H. No. 73066) from Bimini Island in the Bahamas.

Tropidophis tends to have a few more teeth on the dentary than *Ungaliophis,* which has stouter teeth at the anterior of the maxilla, but otherwise no dichotomous differences between *Tropidophis* and *Ungaliophis* were noted in the dentition. An examination of the teeth of *Trachyboa gularis* (A.M.N.H. No. 28982 from Ecuador) reveals 19 to 20 teeth on the maxilla, seven on the palatine, 15 on the pterygoid, and 24 to 26 teeth on the dentary. Aside from having a few more teeth on the dentary, *Trachyboa* differs little in dentition, but the skull is more highly modified than that of the other two genera.

Unfortunately the hemipenes were incompletely everted on the only male of *Ungaliophis* known to exist in collections (M.C.Z. No. 56051). Consequently it was impossible to make a wholly satisfactory examination of the copulatory organs. Insofar as could be ascertained, the hemipenis is relatively long, with longitudinal plicae on the basal portion that become interconnected distally as they merge with calyces proximal to the bifurcation of the organ. The smooth-edged calyces are less coarsely reticulated where they extend onto the paired lobes, which are relatively short. The bifurcation of the sulcus spermaticus appears to be hidden in the uneverted portion of the organ examined, but two branches of the sulcus extend into the calyculate area with little divergence. The divergence becomes more pronounced at the base of the paired lobes, but the two branches are not widely separated where, along with the calyces, each branch extends to the end of a lobe. The distal end of each lobe appears to be smooth.

Stull (1928) has depicted hemipenes of *Tropidophis* showing relatively long lobes in proportion to the basal portion. All Stull's figures show the sulcus branching almost at the level of the bifurcation of the organ. Brongersma (1951) has described the hemipenis of *Trachyboa gularis* as extending to the tenth subcaudal, or 10.7 mm. in length, and bifurcating 4.8 mm. from the distal end. He failed to indicate the level of the bifurcation in the sulcus, but noted that there are oblique folds with scalloped borders on the lobes. The organ on a specimen of *Trachyboa boulengeri* from Colombia (A.M.N.H. No. 18238) extends to the ninth subcaudal, bifurcating at the sixth, just beyond the bifurcation in the sulcus. The lobes are covered with crenate flounces that appear to be transverse rather than oblique, and no paired papillae were noted proximal to the bifurcation, as reported by Brongersma for *T. gularis.* In most respects, however, the hemipenes of *Trachyboa* resemble those of *Tropidophis* more closely than those of *Ungaliophis.*

Horny spurs are restricted to males of the three genera (spurs are reported by Stull [1928] to be lacking on both sexes of *Tropidophis semicinctus,* and Amaral [1927], who questioned an earlier statement, failed to consider sexual dimorphism in his account of *Trachyboa*), but those of *Tropidophis* and *Trachyboa* are proportionately smaller and less like claws than the spurs on *Ungaliophis.* Bellairs (1950) has figured and described the spurs of *Trachyboa boulengeri* in detail. Those of *Ungaliophis* and *Tropidophis* are depicted here in figure 1.

The scent glands of the females of both species of *Ungaliophis* are approximately the same size, but staggered in position. The one on the right is situated farther back than the one on the left (fig. 8). A duct leads from the right gland to the posterior wall of the cloaca. The scent glands of *Tropidophis* and *Trachyboa* are adjacent to the vent, but the posterior end of the one on the right extends beyond the extremity of the one on the left. The asymmetrical arrangement of the scent glands seems to be characteristic of boas, but it remains to be ascertained whether other snakes have the right gland as far behind the vent as it is in *Ungaliophis.* (These glands are normally paired, and similar in size in colubrids, which may prove to differ consistently from boids in this respect. More information is needed, however, before any reliable statement can be offered.)

The several species assigned to *Tropidophis* appear to comprise a natural group. A review of the genus more comprehensive than that provided by Stull (1928), or the superficial discussion of affinities provided by Schwartz and Marsh (1960), is needed before the snakes of the group can be satisfactorily compared with those in other genera.

Such variable characters as the numbers of scale rows in *Ungaliophis* fall within the range of variation reported for *Tropidophis.* There are no dichotomous differences between the genera in the number of ventrals and subcaudals, although few species of *Tropidophis* have as many scales in either series as *Ungaliophis.* All species of *Tropidophis* are largely terrestrial, whereas the occurrence of *Ungaliophis panamensis* in banana shipments would suggest that this species is partly arboreal, as indicated by its more slender habitus. However, Dr. Archie Carr, who discovered the specimen of *U. continentalis* in Honduras, noted on the field tag that it was "under bark of pine log."

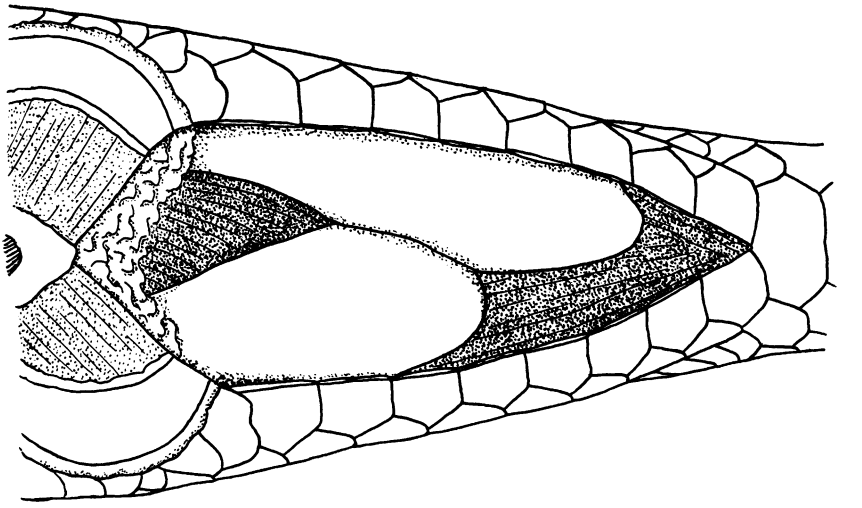

FIG. 8. Ventral aspect of the tail of *Ungaliophis continentalis,* with portions of nine subcaudal plates removed, to show the asymmetrical arrangement of the paired scent glands.

As a rule, arboreal snakes tend to have more vertebrae than their terrestrial relatives, which may be specialized in other respects. Thus *Trachyboa* has evolved as a short, stocky snake, seemingly adapted to forage on the surface, where its brown blotches and extraordinarily rugose skin must blend with the debris of the forest floor. According to Amaral (1927), these dwarf boas live "in humid, very warm, woody and rather low districts," but nothing seems to be recorded concerning their behavior. The extremely short tail is questionably prehensile, as noted by Amaral, and plainly the stout body is ill adapted for rapid locomotion. It may be surmised that both species of *Trachyboa* move

slowly, depending largely on camouflage to escape predators. The skin and plates on the head are devoid of smooth, shiny surfaces that might make the body conspicuous on a debris-covered substratum.

The more diversified genus *Tropidophis* includes species with keeled scales, but no member of the group approaches *Trachyboa* in rugosity. No species of *Tropidophis* is adapted for burrowing, but Schwartz (1957) reported that a paratype of *T. feicki* was discovered crawling into a hole in a limestone cliff. Schwartz's reference to the "clivicolous tendencies" of the species, however, scarcely seems warranted. Snakes of the species superficially resemble some of the smooth-scaled, semi-fossorial colubrids that live in tunnels under rocks, and Schwartz noted that *T. feicki* was also found under a pile of bricks. Other species are perhaps less addicted to rocks, but several of them are known to seek shelter beneath objects lying on the surface.

The cephalic plates have become modified along quite different lines in each of the genera. Paired shields resembling the two pairs of prefrontals characteristic of *Tropidophis* are present on some specimens of *Trachyboa,* but on others the dorsal surface of the head is covered with scales rather than plates. The nostril is in the single nasal retained by *Trachyboa,* as it is in the undescribed genus in Mexico, whereas the nostril is between two nasals in *Tropidophis,* but situated in the anterior nasal of *Ungaliophis.* The rostral is well developed on the other genera, although it is greatly reduced (absent, according to Boulenger, 1893) or fragmented on *Trachyboa.* The paired prefrontals are fused and expanded in *Ungaliophis,* which retains the loreal, whereas *Tropidophis* normally has two pairs of prefrontals, and the loreal has apparently become fused to the lateral margin of the anterior prefrontal. Hence the genus is usually described as lacking a loreal. On some specimens of *Tropidophis* the two pairs of prefrontals have become fused as a single pair. Extensive variations occur in the prefrontals of some species of *Tropidophis.* In a series of *T. feicki* small scales are intercalated between the two pairs or between the prefrontals and the contiguous plates. On one specimen the anterior pair of prefrontals is separated from the frontal by a large, azygous prefrontal. Two pairs of prefrontals are normally present in *Tropidophis,* whereas the prefrontals are consistently fused in *Ungaliophis.*

On the whole the differences between the genera of dwarf boas greatly exceed the similarities. The few peculiarities they share would suggest that their progenitor had evolved during the adaptive radiation of boas in South America. It is conjectural whether boas evolved in Asia, which may nevertheless have been one of the principal centers of dispersal.

If the family Boidae originated in Asia, however, there may have been more than one adaptive radiation of the group on that continent, and more than one group of boas may have reached the Americas. Whatever the history of the family may be, it seems probable that the dwarf boas of the American tropics were derived from a South American ancestor.

More detailed knowledge of the variations in the various boid genera is needed if the members of the family are to be grouped satisfactorily. Little reliance can be placed on classifications based on information derived from one specimen of each genus. Some structures of course are much less variable than others, but variable characters can afford useful clues to relationships if the investigator ascertains the nature and the extent of the variation. Few investigators have devoted much attention to ontogenetic changes and sexual dimorphism, which are often neglected because of the inadequacy of the samples available. Many groups of snakes, including dwarf boas, are still poorly represented in collections.

More comprehensive definitions of genera should facilitate the work entailed in revising families. Knowledge of the genus *Ungaliophis* is far from complete, but the summary that follows will correct errors in earlier accounts, and convey some idea of the variations that have been noted.

SUMMARY OF THE CHARACTERS OF *UNGALIOPHIS*

Relatively small members of the family Boidae known to attain maximum over-all dimensions of 760 mm., with short prehensile tails comprising 0.85 to 0.95 per cent of total length. Trunk and tail slightly compressed, head distinct from neck, spurs restricted to males. Diameter of eye greater than its distance from lip, pupil elliptical. Rostral either wider than high and separated from prefrontal by internasals, or nearly as high as wide and in contact with large, azygous prefrontal. Frontal smaller than prefrontal, bordered on each side by a preocular and a supraocular. Parietals vestigial or indistinguishable from dorsal scales. Two nasals; nostril invariably in anterior nasal. Loreal single; one preocular; two or three postoculars. From eight to 10 supralabials, two or three reaching eye, first two reaching postnasal. Tubercles present on all cephalic shields. Infralabials nine to 11, first pair in broad contact behind a moderately large mental, followed posteriorly by two or three pairs of chin shields.

Dorsal scales smooth, except for minute tubercles; midbody scale rows from 19 to 25, with reductions to 17 or 15 at vent. Addition and

suppression of scale rows occurring between third and eighth rows anteriorly, by loss of paravertebral rows toward base of tail. Ventrals ranging from 204 to 258; anal plate undivided, from 39 to 46 single subcaudals; tail terminating in blunt spine. Hemipenes relatively long, bilobed; plicae on basal portion, calyces lacking crenate edges on lobes; sulcus spermaticus bifurcating near base (?), each branch of sulcus extending through plicate portion and calyces to terminus of lobe.

Premaxilla with an ascending process, without teeth. Maxillary teeth 12 to 15, those at anterior end of bone larger and stouter than those behind them, which are progressively shorter posteriorly; palatine, five to eight; pterygoid teeth, 11 to 15; teeth on dentary, 13 to 15.

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