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MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 131

**Intrageneric Relationships Among Colubrid  
Snakes of the Genus *Geophis* Wagler**

BY

FLOYD LESLIE DOWNS  
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ANN ARBOR  
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN  
JULY 26, 1967

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## INTRODUCTION

SMALL, SECRETIVE colubrid snakes pose special problems to systematists. Owing to their small size and secretive habits, they are generally collected only sporadically and in small numbers, and consequently are poorly represented in museum collections. Some of these snakes possess characteristics which make them, at least superficially, unique; these are often treated as monotypic genera. At the opposite extreme are the large, polytypic genera such as the oriental *Calamaria*, the South American *Atractus*, and the Central American *Geophis*. Within these groups, gene flow between populations is apparently rather restricted. The resulting populational differences have led to the description of numerous nominal forms, including some 80 in *Calamaria* and *Atractus* and about half that number in *Geophis*. Unfortunately, the rather constant increase in the number of described forms was not accompanied by syntheses at the generic level. Only recently have these syntheses been attempted. Marx and Inger (1955) discussed the range of variation and the evolutionary trends in *Calamaria*, and Savage (1960), as well as defining species groups, did the same for Ecuadorian *Atractus*.

The genus *Geophis* has been in particular need of a study of a revisionary nature. Unlike *Calamaria* and *Atractus*, which despite the large number of included forms are relatively homogeneous groups, *Geophis* includes a highly diverse array of snakes. This diversity has left *Geophis* systematics in a chaotic state; this study was prompted by that chaos, and dedicated to reducing it. My principle aims have been three: (1) an analysis of intraspecific and intrageneric variation; (2) the establishment of species groups within *Geophis* which can be meaningfully compared with one another and with other genera; and (3) the synthesis of current knowledge of the genus into a single volume.

## ACKNOWLEDGMENTS

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My wife Joanne deserves special thanks. Her many hours of typing, combined with her interest and encouragement, aided materially in the completion of the study.

My committee has allowed me to develop this study in my own way, while at the same time remaining available for advice and consultation. For this I am deeply appreciative. I am in special debt to Charles F. Walker, who at my request examined type material in several European collections, who throughout the study has been a constant source of advice, and who, at a time of maximal demand on his energies, generously agreed to assume the chairmanship of my committee.

This investigation was begun, and in large part completed, under the direction of the late Norman Hartweg. His advice and probing questions were invaluable assets to the study; to him I am deeply grateful.



## MATERIALS AND METHODS

This study is based on the examination of some 1610 specimens of *Geophis*. Thirty-one of these have been examined by others at my request; the remainder I have examined personally. Among the latter have been type materials (holotype and/or paratypes) of 26 nominal forms, and among the former types of an additional 12 forms. I have placed no reliance on literature records unless the specimen has been checked in my behalf.

The standard counts and measurements of ophidian systematics have been utilized in this study. Measurements of tail and total length were taken to the nearest millimeter, using a meter rule. Head scales were measured with the aid of an ocular micrometer in a dissecting microscope and were recorded to the nearest micrometer unit (9 units = one millimeter). Skeletal material is not available for a large majority of the forms. The few available skulls were supplemented by material cleared in KOH and stained with alizarin red, and by radiographs of all available species. Maxillaries, and their ectopterygoidal articulations, have been examined after removal from the skull and cleansing in a dilute solution of commercial Chlorox. Sexing was accomplished by dissection.

An extended period has elapsed since the last summary of the genus appeared. I have found it advisable therefore to dwell in some length on the variation, both intrageneric and intraspecific, that occurs in the various features of these snakes. Details of how particular counts were made, or along which axis various measurements were taken, are included under the appropriate headings.

The systematic part of the report is arranged by species groups, alphabetically, and the included species alphabetically within them. The discussion of each group includes its characterization, the intragroup relationships, and the accounts of the included species. The figures showing the head scutellation were traced from projected 35-mm transparencies. Known locality records were plotted using several sources, but primarily from the American Geographical Society's Map of Hispanic America (1:1,000,000) and from the more recent maps of the Comision Intersecretarial Coordinadora del Levantamiento de la Carta Geografica de la Republica Mexicana (1:500,000).

The synonymy of each form includes the original description, the names of synonymous forms, the various combinations by which authors have referred to the species and its synonyms, and the nomenclature used in certain important papers and checklists (e.g., Boulenger, 1894; Smith and Taylor, 1945).

A list of the specimens examined and their respective localities is provided at the end of each species account. Countries are arranged geogra-

phically from north to south; hence Mexican localities are given first, Colombian last. States (provinces, departments) are listed alphabetically within countries, localities alphabetically within states, and museum abbreviations alphabetically within localities. The following system of abbreviations is used:

American Museum of Natural History (AMNH); Academy of Natural Sciences of Philadelphia (ANSP); British Museum (Natural History) (BMNH); California Academy of Sciences (CAS); Chicago Natural History Museum (CNHM); University of Southern California, Costa Rican Expedition (CRE); Douglas C. Robinson (DCR); Frederick Medem (FM); James R. Dixon (JRD); Louisiana State University (LSU); Museum of Comparative Zoology, Harvard University (MCZ); Museum National d'Histoire Naturelle, Paris (MNHN); Museum of Vertebrate Zoology, University of California (MVZ); Museo Zoológica de Tuxtla Gutierrez, Chiapas, México (MZTG); Naturhistorischen Museums Wien (NHMW); Senckenbergische Natur-Museum, Frankfurt (SNM); Stanford University Natural History Museum (SU); Texas Cooperative Wildlife Collection, Agricultural and Mechanical College of Texas (TCWC); University of California at Los Angeles (UCLA); University of Illinois Museum of Natural History (UI); University of Kansas Museum of Natural History (UK); University of Michigan Museum of Zoology (UMMZ); United States National Museum (USNM); Zoologisches Museum, Berlin (ZMB).

## CHARACTER ANALYSIS

### SCUTELLATION

The following discussion deals with both intraspecific and intrageneric variation in the number, size, and shape of the various head scales. I have tried to indicate which conditions are generalized and which are specialized. Wherever possible, evolutionary pathways from generalized to specialized conditions have been suggested. Since different levels of, and different pathways to, specialization help characterize the various species groups, the discussion may be supplemented by reference to the figures of the dorsal and lateral head scutellation of the members of the respective species groups (Figs. 3, 5, 7, 9, 11, 12, 16, 19).

**DORSAL SURFACE OF THE HEAD.**—Most species of *Geophis* have a “generalized” colubrid complement of head scales, including a rostral, paired internasals, paired prefrontals, a frontal, paired supraoculars, and paired parietals (Fig. 1). The absence of supraoculars in some species is discussed in the section on the ocular region.

The rostral, which because of its position acts as a primary foil against the environment, is a fairly accurate indicator of the degree of specialization toward a fossorial existence. The proportions of the eye and snout in the *omiltemanus* group are of a type common to many colubrid genera, suggesting a generalized condition; in this group, the rostral is not prominent and is scarcely visible from above. At the other extreme are species (e.g., *G. championi*) in which the small eye and pointed, wedge-like snout are surely

burrowing adaptations; the rostral of such forms dominates the anterodorsal aspect of the snout, and projects posteriorly between the internasals to almost contact (or to contact) the prefrontals. The actual contact of the rostral with the prefrontal is typical only of those species without internasals, but the contact does occur in a few specimens of other species.

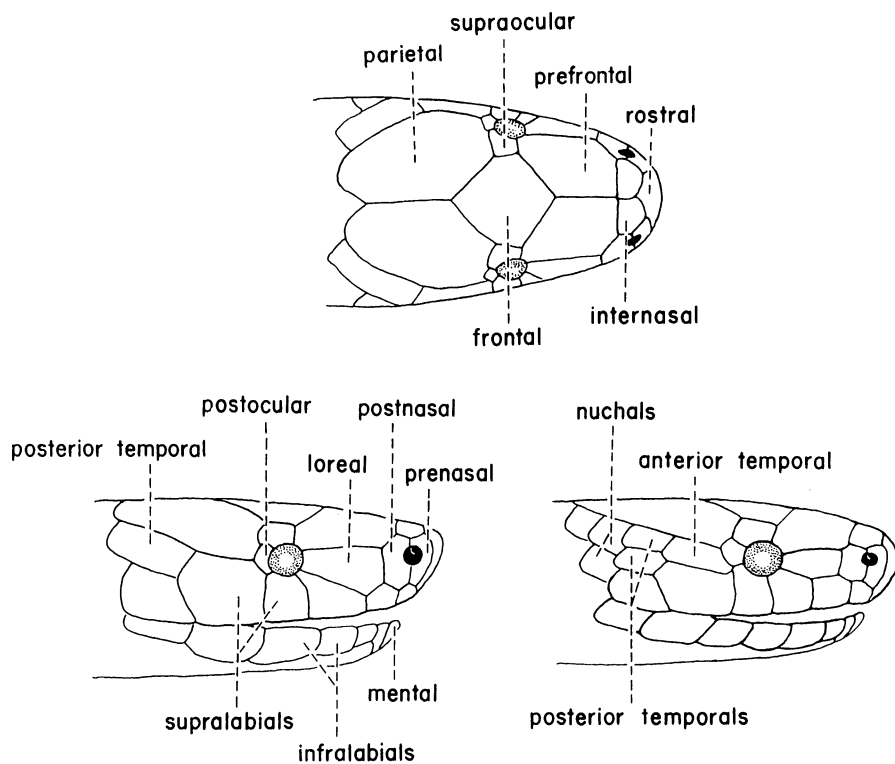


FIG. 1. Terminology used for the head scutellation in members of the genus *Geophis*.

There is some instability in the internasal-prefrontal region of *Geophis*. In 31 specimens, representing seven species, the internasal is fused (or partially fused) with the prefrontal on one or both sides of the head. This failure of the internasal-prefrontal suture to develop is apparently characteristic of two species, *dubius* and *cancellatus*. Of 15 specimens of *dubius*, nine exhibit no internasal, two an internasal on one side, and four an internasal on each side. In *cancellatus*, neither of the two known specimens has internasals. *G. semidoliatus*, the closest relative of *cancellatus*, normally possesses internasals, but 11 of the 691 specimens of *semidoliatus* examined show the internasal-prefrontal fusion. Other species which occasionally show some

degree of internasal loss are *hoffmanni*, *sallaei*, *petersi*, *omiltemanus*, and *dugesi*. Except for the latter two species, these are all specialized forms. One specimen each of *omiltemanus* and *dugesi* shows a partial fusion of the internasal and prefrontal. In each the medial parts of the internasal and prefrontal are continuous, but the lateral parts are separated by a partially developed suture. This condition prevails on both sides of the specimen of *omiltemanus*, but only on the right side of the specimen of *dugesi*.

Those exhibiting some tendency for the fusion of the internasal with the prefrontal represent several species groups. The fusion appears to represent a minor change in the developmental process, and should not be considered an important indicator of relationship.

In spite of the difficulties caused by intraspecific variation and the rather large number of species involved, the relative sizes of the internasal and the prefrontal are useful for distinguishing some of the species groups. This is particularly true of the groups characterized by long snouts. The elongation of the snout appears to have taken place in the internasal region of some species and in the prefrontal region of others. The result is that the former have long internasals and short prefrontals and the latter have short internasals and long prefrontals. Because of the tendency of the rostral to project posteriorly between the internasals, the internasal suture is an inadequate indicator of the size of the internasal; the greatest length of the internasal must be used. The median suture between the paired prefrontals, although not a measure of their maximum length, is an adequate indicator of their relative length. *G. championi* and its relatives are exemplary of the large internasal-short prefrontal condition, and the *sieboldi* group shows the contrasting condition. This difference in the region of elongation is also determinable on the lateral surface of the snout, where the relative sizes of the postnasal and the loreal are correlated with the sizes of the internasal and the prefrontal. In *championi*, for example, the elongation of the internasal region has resulted in an elongate postnasal and a relatively short loreal. In *sieboldi*, the postnasal is not strongly enlarged, but the loreal is quite long (see below).

The frontal may have four, five, or six sides. Two of the sides, representing the frontal-parietal suture on each side, are subject to little variation, extending posteromedially from the orbital region to meet at a distinct angle at the midline. The lateral edges of the frontal are responsible for most of the variation in the shape of that scale, and this variation can be correlated with the size of the supraocular. Since the lateral margin of the frontal corresponds to the suture between the frontal and supraocular, its length varies directly with the length of the latter scale. In a form with a large supraocular (e.g., *tarascae*), the correspondingly long lateral margins of the frontal give that

scale the shape of a shield. As the supraocular decreases in size (correlated with a displacement posteriorly) the frontal becomes progressively less shield-shaped until the logical extreme is reached in *G. godmani*. Since *godmani* has no supraocular (the parietal and prefrontal meet above the middle of the eye) the frontal has no lateral edge; the four margins of such a frontal, comprising the prefrontal-frontal and parietal-frontal sutures, outline a diamond-shaped scale.

The anterior margin of the frontal may form a single transverse edge or extend obliquely forward on each side to meet at an angle at the posterior end of the prefrontal suture. It is obvious that much of this variation is directly related to the supraocular condition. The anterior margin, or margins, of the frontal correspond to the sutures between the frontal and the two prefrontals; these sutures are contiguous with, and basically extensions of, the sutures between the prefrontals and the supraoculars. In forms with large supraoculars the prefrontal-supraocular suture extends medially from the anterior edge of the eye; its extension, the prefrontal-frontal suture, continues toward the midline in a basically transverse orientation; the sutures from the left and right meet imperceptibly or at a slight angle. In forms with small supraoculars, the prefrontal-supraocular suture originates in a more posterior position, above the middle of the eye; the prefrontal-frontal sutures extend obliquely forward and medially, meeting at the midline at a distinct angle.

The only example of fusion involving the frontal in *Geophis* occurs in *G. rhodogaster*. In this species the frontal is fused with the supraoculars, and thus forms the dorsal margin of the orbit. In all other species the frontal is excluded from the orbit by the supraocular, prefrontal, and, in some instances, the parietal.

Except for a partial fusion (at the posterior ends) in the type of *G. semiannulatus*, the parietals are always paired. They are large scales, prone to further enlargement by fusion with smaller scales around them. In several of the more highly modified forms, the irregular posterior margins of the parietals indicate the incorporation of one or more nuchals into the parietals. The parietal also tends to encroach on the scales bordering the eye, in some instances incorporating the supraocular and postocular within its boundaries. In several specimens of *G. hoffmanni*, the oculars are present, but separated by a projection of the parietal, which enters the orbit.

The length of the parietals (measured along their common suture) is limited in its usefulness by the same factors which restrict the value of the other head scales. The parietal suture is about equal to the length of the snout in the short-snouted forms, and only half that in some of the long-snouted species. The parietals can, therefore, be used to distinguish the

extreme types. The magnitude of the interspecific variation is not great enough, however, to separate clearly all of the species groups into two or three mutually exclusive categories based on parietal length.

The apparent differences in parietal length noted above are not simply a reflection of the comparison to snouts of different lengths. The length of the parietals varies in absolute terms as well. In generalized forms, such as the members of the *chalybeus* group, the parietals are long and narrow; their median suture is about 35 per cent of the head length. In specialized forms, as members of the *championi* group, the parietals are short and broad, their median suture occupying little more than 20 per cent of the head length.

**PREOCULAR REGION.**—The single scale separating the postnasal from the orbit is usually considerably longer than high, and I, therefore, follow other recent authors in referring to this scale as a loreal, rather than as a preocular. The preocular is normally absent, although occasionally the loreal may be divided into two scales, one of which might then be called a preocular. In the holotype of *G. aquilonaris*, for example, the left loreal is divided by a vertical suture near the orbit, resulting in a small, squarish "preocular." A contrasting aberration is present in three specimens of *G. semidoliatus*; in these the suture dividing the loreal is near the anterior end of the normal loreal, creating a small, squarish "loreal" and a larger, elongate "preocular." In both instances the area occupied by the two scales coincides with the area normally occupied by the single loreal. Günther, in his description of *G. omiltemanus* (1893), stated that there are two preoculars. One of these is the scale herein called a loreal, and the other is a small scale representing that part of the third supralabial that normally borders the orbit. This small scale, separating the third labial from the orbit, is found in only one of Günther's three syntypes, and because of its position might better be called a presubocular.

The preocular region of *G. latifrontalis* is so variable that the "normal" condition cannot be determined. None of the close relatives of *latifrontalis* (*mutitorques*, *semiannulatus*, and *blanchardi*) has a preocular; the elongate loreal forms the anterior border of the orbit. In the 20 known specimens of *latifrontalis*, only 17 of the 40 sides conform to the preocular-loreal condition of its close relatives. An additional three sides lack a preocular, but in these the loreal is excluded from the orbit by the prefrontal and the third supralabial (a condition found in one specimen of *G. mutitorques*). The remaining 20 sides of the head have at least one preocular each, which is of variable shape and position. On one side of one specimen there are two preoculars, one of which is a small squarish scale separating the loreal from the orbit, much like the scale on the type of *G. aquilonaris* noted previously. The second one is a more standard colubrid preocular, separating the prefrontal

from the orbit. It is difficult to determine whether the two-preocular condition is primitive for the group, but it seems apparent that at least the dorsal preocular represents that of the "generalized" colubrid condition, which has not yet been completely lost in *latifrontalis*. Those specimens having one preocular may have the dorsal one (12 sides) or the lower one (7 sides). In one of the specimens with the dorsal preocular, it is partially fused with the prefrontal. The dorsal preocular may be in contact with the third supralabial (10 sides, but in several the contact is at a point) or be separated from the labial series by the loreal (two sides). The lower preocular, when present, always separates the loreal from the orbit, but its size is reduced to a narrow, triangular sliver on both sides of two specimens. Some of the variations found in the preocular region of *G. latifrontalis* are illustrated in Fig. 11.

**SUPRAOCULARS.**—The size and shape of the single supraocular, characteristic of most species, are correlated with the degree of specialization for a burrowing existence. Since with increased specialization the supraocular decreases in size and occupies less and less of the dorsal margin of the orbit, it is convenient to use orbital exposure as an indicator of the degree of specialization.

The least specialized forms (e.g., *tarascae*) have a large, quadrangular supraocular that forms almost the entire dorsal margin of the orbit. The supraocular in these forms is as long or considerable longer than the loreal. At the other extreme are species such as *dubius* and *hoffmanni* in which the length of the supraocular is only 40 per cent of that of the loreal. In these species, the supraocular is displaced from the anterior part of the dorsal border of the orbit by the prefrontal until the supraocular-prefrontal suture lies above the middle of the eye. The displaced supraocular often extends ventrally along the posterior edge of the eye, the curving border of the orbit forming one side of the almost triangular supraocular. Because of small size and posterior position this scale is similar to an upper postocular; since I am convinced it represents a displaced supraocular, I will refer to it as such.

The supraocular has been lost completely in two forms. In *G. rhodogaster* it is fused with the frontal, which is in contact with the orbit. The second method by which the supraocular has been lost is by fusion with (or displacement by) the parietal. This appears to be a relatively simple modification, derived from those forms having a small, triangular supraocular. The supraocular-parietal fusion is characteristic of *G. godmani*; in about half of the known specimens, the postocular is also fused with the parietal. The fusion is also found on the type of *G. anocularis*, but here I am convinced that it is individual variation, and have synonymized *anocularis* with *G. dubius*. The holotype of *dubius* is itself aberrant in the supraocular condition; the

ocular is distinct on the right side of the head, but partially fused with the parietal on the left. It is obvious that the loss of the supraocular requires no drastic genetic modification.

POSTOCULARS.—The presence of two postoculars appears to represent the least specialized condition. Two postoculars are characteristic of *bicolor*, *omiltemanus*, *isthmicus*, and of more than half of the specimens of *incomptus*. All of these forms are judged to be rather unspecialized for other reasons, such as the presence of a relatively short snout, large eye, and an anterior temporal (only as an unusual condition in *bicolor*). In *G. incomptus*, which has apparently been derived from an *omiltemanus*-like form, each of eight specimens has two postoculars, one has two on one side and one on the other, and six have one on each side; the single persistent postocular corresponds to the upper postocular of *omiltemanus*. This conclusion is based not only on the size, shape, and dorsal position of the ocular, but also on the shape of the fourth labial. Where the second postocular is absent, the fourth supra-labial extends dorsally along the posterior margin of the orbit. There is little doubt that this extension is the result of the fusion of the lower postocular and the labial. Similarly, the relatives of *G. bicolor*, which have a single postocular, have lost the lower postocular of *bicolor* by fusion with the labial. The postocular of members of the other more specialized species groups is more difficult to assess. Its position is somewhat ventral (but overlapping) to that of the upper postocular in the generalized forms. This may represent a displacement by the supraocular; in the specialized forms, the supraocular is displaced posteriorly and curves along the eye to form the upper part of the posterior margin of the orbit.

There is no postocular in one specimen of *G. dubius* (the type of *G. anocularis*) nor in about one-half of the specimens of *G. godmani*. In these specimens both the postocular and the supraocular are incorporated into the parietal, or, as in some of the specimens of *godmani*, the postocular is fused with a supralabial. The postocular may also be lost as a separate element by fusion with the supraocular, as occurs in some specimens of *semi-doliatus* and *hoffmanni*.

Variation in the number of postoculars is presented in Table 1.

NASAL-LOREAL REGION.—The loreal is normally the only scale separating the nasals from the orbit. Occasionally the loreal is excluded from the orbit by a preocular (see above) or by contact of the prefrontal with the third supralabial. The latter condition is found in two specimens of *latifrontalis*, one *mutitorques*, seven *hoffmanni*, and four *brachycephalus*. In these specimens the posterior part of the loreal tapers to a point, formed by the intersection of the downward-curving loreo-prefrontal suture and the upward-curving loreo-labial suture.



TABLE 1  
VARIATION IN THE NUMBER OF POSTOCULARS IN *Geophis*

Species	0-0	0-1	1-1	1-2	2-2	2-3
<i>aquilonaris</i>			9			
<i>bicolor</i>					8	
<i>blanchardi</i>			17	1		
<i>brachycephalus</i>		2	228	1		1
<i>cancellatus</i>			2			
<i>carinosus</i>			5			
<i>chalybeus</i>			3			
<i>championi</i>			2			
<i>dubius</i>	1		14			
<i>dugesi</i>			7			
<i>dunni</i>			1			
<i>fulvoguttatus</i>			2			
<i>godmani</i>	5		6			
<i>hoffmanni</i>	2	2	62	4		
<i>immaculatus</i>			2			
<i>incomptus</i>			6	1	8	
<i>isthmicus</i>					1	
<i>laticinctus</i>			1			
<i>latifrontalis</i>			14	4	2	
<i>maculiferus</i>			1			
<i>mutitorques</i>		1	51	1	1	
<i>nasalis</i>	1	2	316	2	1	
<i>nigrocinctus</i>			3			
<i>omiltemanus</i>					9	
<i>petersi</i>			10			
<i>rhodogaster</i>		1	29			
<i>ruthveni</i>		1	5			
<i>sallaei</i>	1		5			
<i>semiannulatus</i>			17			
<i>semidoliatus</i>	7	5	658	4	1	
<i>sieboldi</i>			6		1	
<i>tarascae</i>			3			
<i>zeledoni</i>			16	1		

The length of the loreal is usually correlated with the length of the snout (the distance from the tip of the snout to the anterior border of the orbit). Species with short, rounded snouts have relatively short loreals (e.g., *chalybeus* group), those with long snouts (e.g., *sieboldi* group) relatively long ones. In both of the above groups, the prenasal and postnasal are approximately equal in length. In the *chalybeus* group, the short loreal is about as long as the combined length of the pre- and postnasal; in the *sieboldi* group, the elongate loreal is much longer than the nasals. A third extreme occurs in two other groups with long pointed snouts; in the *championi* and *dubius*

groups, the elongate nature of the snout is associated with a greatly enlarged postnasal rather than with an elongate loreal. The *latifrontalis* and *semi-doliatus* groups also have rather long snouts, but the elongation is not noticeably associated with any one scale; rather, the loreal, prenasal, and postnasal are all moderately elongate.

In addition to the variation in size of the postnasal noted above, there is some variation in shape that is not dependent on size alone. In species or individuals that have no internasal (or, more correctly, in which the internasals are fused with the prefrontals) the dorsomedial projection of the postnasal has been rounded off. This projection normally separates the posterolateral part of the internasal from the anterolateral part of the prefrontal. The cause and effect relationship between the prefrontal-internasal fusion and the rounding off of the postnasal is particularly evident in two specimens of *G. dubius* that have the fusion on only one side of the head. On the side with a distinct internasal, the projection of the postnasal is present, but on the fusion side it is not. The rounded postnasal is thus of no significance except when viewed as a correlate of the fusion of the internasals and prefrontals.

TEMPORAL REGION.—The temporals, and in particular the presence or absence of an anterior temporal, have played an important role in the systematic history of *Geophis* (see *History of the Use of the Name Geophis*). Boulenger's (1894) action in removing from *Geophis* all forms possessing an anterior temporal has been effectively refuted by Dunn (1928a) and Smith (1941b). The anterior temporal does, however, retain some measure of importance in the separation of species groups. The only clear exception is in the *latifrontalis* group, in which the temporal is present in three of the species but absent in the fourth (*blanchardi*). The anterior temporal is also present in the *omiltemanus* group but absent in all others.

There is little intraspecific variation in the presence or absence of the anterior temporal. One of the eight specimens of *bicolor* possesses an anterior temporal; Günther (1893) referred to this scale as a detached part of the fifth labial, but it may represent the original temporal. Similarly, one specimen of *aquilonaris* has an anterior temporal (followed by two posterior temporals); it is long and narrow, much like the condition in the *latifrontalis* group. An individual of *brachycephalus*, in contrast, has a very small temporal, quite unlike that of any of the species in which that element is normally present.

In two individuals of *G. mutitorques*, which possesses an anterior temporal, the scale is fused with the upper posterior temporal, creating a long, narrow scale adjacent to the lateral edge of the parietal. In a third specimen of this species, the anterior temporal is almost completely fused with the parietal, although its position is indicated by partially developed sutures.

Unfortunately, the aberrant specimens noted above do not clearly establish the developmental pathway involved in the evolutionary loss of the temporal. The partial fusion of the parietal and temporal is suggestive of one possibility, but I regard this as a doubtful one. My doubts are based primarily on the lateral extent of the parietal; if the temporal were included in the parietal, the lateral edge of the latter would extend toward the ventral part of the eye. Although broader in some species than in others, the parietal does not extend far enough onto the lateral aspect of the head to support the idea of inclusion of the temporal.

A second possibility is the fusion of the temporal with the fifth labial. The fifth labial in *blanchardi*, which has no anterior temporal, occupies the area covered by the fifth labial and the temporal in the other members of the *latifrontalis* group. The anterior temporal in this group is a long, narrow scale paralleling, and lying immediately above, the fifth labial. A simple fusion of the fifth labial and temporal could account for the loss of the temporal in *blanchardi*. The aberrant specimen of *aquilonaris* mentioned above supports this interpretation, since its temporal is of the *latifrontalis* type.

In the other group of species possessing an anterior temporal (*omiltemanus*, *isthmicus*, *incomptus*, *maculiferus*), the relative positions of the temporal and fifth labial are quite different from those of the *latifrontalis* group. In these forms the fifth labial is anterior and ventral to the temporal, although still in contact with it. The temporal is in contact with the postocular and fifth supralabial anteriorly, but the greater part of its length is in contact with the sixth labial. In *G. incomptus*, the fifth labial is normally separated from the parietal by a narrow contact of the postocular and temporal. In three specimens, however, the fifth labial projects between the ocular and temporal to contact the parietal. In addition, *G. omiltemanus*, *G. maculiferus*, and *G. incomptus* form a graded series in the positions and sizes of the fifth labial and temporal. In *G. omiltemanus*, the fifth labial is quite small, and separated from the parietal by a broad contact between the temporal and postocular; *G. maculiferus* is intermediate; in *G. incomptus* the fifth labial is large and narrowly separated from the parietal. If this trend were to continue (as in the three specimens of *incomptus* noted above), the enlarging fifth labial would gradually displace the anterior temporal posteriorly, leaving the fifth labial in contact with the parietal.

There is indirect evidence to support the contention that the loss of the anterior temporal has involved fusion with the fifth labial in some species, and displacement posteriorly in others. The length of the contact between the fifth labial and the parietal is one line of evidence. Judged from the condition in *incomptus*, this contact would be expected to be relatively short if the temporal were displaced posteriorly; similarly judged, the

posterior edge of the fifth labial, since the dorsal margin of the labial (the labial-parietal suture) would be much shorter than its maximum length, would be expected to slant posteroventrally from its contact with the parietal. These expectations describe the condition found in all but one of the members of the *chalybeus* group; the exception is *G. aquilonaris*, the least typical member of the group.

If, from a *latifrontalis*-like condition, the anterior temporal were lost by direct fusion with the fifth labial, the composite labial would share a long suture with the parietal. Since the temporal in the *latifrontalis* group is as long as the fifth labial, the posterior margin of such a labial would not slant posteriorly; the length of its dorsal margin would approximate the greatest length of the labial. The large, rectangular labial (the fifth in *cancellatus* and *laticinctus*, the fourth in *semidoliatus*) found in the members of the *semidoliatus* group matches these criteria. The method of temporal loss in the members of the *championi*, *dubius*, and *sieboldi* groups cannot be clearly surmised from the labial-parietal condition.

In all species without an anterior temporal, a single posterior temporal separates the last labial from the parietal. This posterior temporal could represent the displaced anterior temporal of a form such as *G. incomptus*. The *latifrontalis* group (except *blanchardi*) has one anterior and two posterior temporals. If the anterior temporal were lost by fusion with the fifth labial, the two posterior temporals would also have to fuse to account for the single posterior temporal of most of the species of *Geophis*. This double fusion has apparently taken place in at least some species, since (1) *blanchardi*, a member of the *latifrontalis* group, has no anterior and a single posterior temporal, and, (2) the aberrant specimen of *G. aquilonaris*, which normally has no anterior and one posterior temporal, has a *latifrontalis*-like anterior temporal and two posterior temporals. It is reasonable to conclude that among the diverse forms included in the genus the temporal area has undergone a reduction in the number of elements by more than one developmental process.

The posterior temporal (or temporals) is considerably more variable than the anterior. The most frequent variation is a fusion of the posterior temporal and one or more of the nuchal scales posterior to it. The result of this fusion is a large scute curving along the lateral and posterior margins of the parietal. The fusion tends to occur more frequently in members of specialized groups than in generalized forms, but intraspecific variation is so great that the character is of little use for systematic purposes. As noted above, the posterior temporal is fused with the anterior temporal in two specimens of *mutitorques*; it is fused with the fifth labial on one side of a specimen of *semiannulatus*. The latter species is the most variable in the number of posterior temporals; the basic condition of two posterior tem-

porals is reduced to one in a large percentage of the specimens from the Gomez Farias region of Tamaulipas, Mexico.

**SUPRALABIALS.**—The supralabial series, like the head scales in general, exhibits a trend toward a reduction in the number of elements. The modal number of supralabials in most species is six, with the third and fourth forming the ventral margin of the orbit. Among these species, 31 of 773 specimens have the number of supralabials reduced to five on at least one side of the head. In contrast, on only one side of one individual is there an increase to seven labials; in this one instance, the first labial is divided into two small scales. Reduction in the number of labials is the result of a failure of the suture to develop between two labials, as is clearly demonstrated by the several examples of partial development of the suture. Of the 31 specimens showing the labial reduction, three are lacking the suture between the first and second labials, three between the second and third, nineteen between the third and fourth, and six between the fifth and sixth. Only the suture between the fourth and fifth labials seems immune to this abnormal condition.

In most forms having six supralabials the fifth is the largest, both in area and in exposure along the lip. In those forms without an anterior temporal, the fifth labial contacts the parietal. In *G. omiltemanus*, however, the fifth labial is rather small, and the sixth is very large. This enlarged sixth labial is apparently the result of the fusion of two or more scales (the sixth and seventh labials, with perhaps a lower posterior temporal included) of some ancestral form. The only species with seven supralabials currently placed in *Geophis* is *G. isthmicus* (Boulenger), originally proposed as a substitute name for *Rabdosome zebrinum* Bocourt. The type (the only known specimen) was well illustrated by Bocourt (1883), but until a detailed re-examination of the specimen is accomplished, its allocation to *Geophis* must be regarded as tentative.

Two species (*semidoliatus*, *hoffmanni*) characteristically have five supralabials, but the arrangement of the five is different in each. The reduction in *semidoliatus* is clearly the result of the fusion of the original third and fourth labials, with the composite scale then forming the entire ventral margin of the orbit. The closely related *G. cancellatus* has six labials, with the third and fourth in the orbit. Although derived from a form with six labials, *semidoliatus* apparently does not regress to the six-labial condition; of 677 specimens on which labials were counted, none has six labials while 46 showed a further reduction to four (7 by fusion of the first and second, 39 by fusion of the fourth and fifth).

The second species having five supralabials, *G. hoffmanni*, also appears to have been derived from a form with six labials. In this instance, however,

the reduction is not the result of scale fusion, but rather is an indirect result of the overall shortening of the jaw and corresponding narrowing of the gape. In *hoffmanni* the third and fourth labials border the orbit as in most other species of the genus, but posterior to the eye there is but one labial instead of the usual two. Judging from the size of this fifth labial, and the difficulty of determining in some specimens whether the fifth is indeed the last, it appears that the angle of the jaw has moved anteriorly until the original sixth labial no longer borders the lip; in this instance it has become a lateral nuchal scale.

Occasionally the suture between two labials forms in a peculiar position; in such examples, the number of labials may be normal for the species, but their relative sizes and shapes may not. For example, in one individual of *G. zeledoni* (UK 63823) only the posterior part of the third labial is fused with the fourth; the anterior part remains as a small, separate scale. The labial count is a normal six, but only the composite fourth labial borders the orbit. Variation in the number of supralabials is presented in Table 2.

CHIN REGION.—The shape of the chin region is correlated with the shape of the snout. The chin is broad and rounded in species with blunt, rounded snouts, and tapers to a point in species with narrow, pointed snouts. The mental scale itself follows the same pattern. Its anterior margin is rounded in generalized forms, but pointed in specialized ones. In the former the mental is much broader than long, but in the latter the width and length are about equal. In both situations, the mental is occasionally in contact with the anterior chinshields; this condition is common only in *G. dubius*. About one-half of the specimens of *dubius* have the mental-chinshield contact. In all other species the mental is normally separated from the chinshields by a median suture formed by the first pair of infralabials. One specimen each of *aquilonaris* and *semidoliatus* has an azygous scale behind the mental.

The number of chinshields has been used by Savage (1960) to distinguish the species of *Atractus* which occur sympatrically with *Geophis*. The species of *Atractus* have one pair of chinshields, and the relevant species of *Geophis* have two pairs. Bocourt also utilized this feature to separate *Geophis* from *Rabdosoma* (= *Atractus*) in 1883. Stating that *Geophis* possesses two pairs of chinshields is unfortunately an over-simplification. Many forms clearly have a posterior pair as well as the anterior pair, but in other species (or individuals) the scales corresponding to the posterior chinshields are little differentiated from the adjacent gular scales. Often these "posterior chinshields" are completely separated from one another by a median gular, which may be as large as the supposed chinshields. It is questionable whether these scales would be labelled chinshields by an investigator free from the

TABLE 2  
 VARIATION IN THE NUMBER OF SUPRALABIALS IN *Geophis*

Species	4-4	4-5	5-5	5-6	6-6	6-7	7-7
<i>aquilonaris</i>			1	1	7		
<i>bicolor</i>					8		
<i>blanchardi</i>				1	17		
<i>brachycephalus</i>			3	7	221	1	
<i>cancellatus</i>					2		
<i>carinosus</i>			1?	1	5		
<i>chalybeus</i>					3		
<i>championi</i>					2		
<i>dubius</i>					15		
<i>dugesi</i>			1		5		
<i>dummi</i>					1		
<i>fulvoguttatus</i>					2		
<i>godmani</i>			1	1	9		
<i>hoffmanni</i>	1	1	70				
<i>immaculatus</i>					2		
<i>incomptus</i>			1	1	13		
<i>isthmicus</i>							1
<i>laticinctus</i>					1		
<i>latifrontalis</i>					20		
<i>maculiferus</i>					1		
<i>multitorques</i>			1		53		
<i>nasalis</i>				1	322		
<i>nigrocinctus</i>			1		2		
<i>omiltemanus</i>					9		
<i>petersi</i>				1	9		
<i>rhodogaster</i>			1		29		
<i>ruthveni</i>					6		
<i>sallaei</i>			1		7		
<i>semiammulatus</i>				1	16		
<i>semidoliatus</i>	17	29	631				
<i>sieboldi</i>					7		
<i>tarascae</i>					3		
<i>zeledoni</i>			3	3	11		

bias of prior knowledge that *Geophis* is "supposed" to have two pairs. The absence of the posterior chinshields, such as in *Atractus*, appears to be a specialization, derived through intermediate conditions and eventual loss of identity. These intermediate conditions are exemplified by the arrangement of the scales of the chinshield region in the species of *Geophis* in which the determination of the presence or absence of the posterior pair involve purely subjective decisions.

Many of the early descriptions of species, before and immediately after the turn of the 20th century, reported the number of infralabials in contact

with the anterior chinshields, but not the total number of infralabials. The two features are correlated, but not strongly. Forms with seven infralabials usually have four in contact with the anterior chinshields (the fourth is also in contact with the posterior pair). The reduction to six infralabials usually involves the fusion of two labials in the anterior part of the infralabial series, leaving only three pairs in contact with the chinshields. This generalization is subject to extensive inter- and intraspecific variation. Often the suture between the third and fourth infralabials is located immediately adjacent to the posterior end of the anterior pair of chinshields. A very minor change in the position of this suture determines the number of labials in contact with the chinshields; it is not uncommon for this character to differ on each side of the head, limiting its usefulness.

**INFRALABIALS.**—The number of infralabials is both intra- and interspecifically more variable than the number of supralabials. For this reason the infralabials are not an important taxonomic character, even though various populations are different in the statistical sense. The clear trend toward a reduction in the number of supralabials is not evident in the infralabial series. Variation may include numbers above, below, or on both sides of the mode. An example of the first type of variation occurs in *G. rhodogaster*, in which each of 21 specimens has six infralabials, 5 have seven each, and 5 have six on one side and seven on the other. The second type is illustrated by *G. mutitorques*, with 52 specimens having seven infralabials each, one has six, and two have the six-seven condition. *G. nasalis* is exemplary of the third type, with the mode of seven infralabials (225 specimens) reduced to six in each of 13 specimens and increased to eight in 45 specimens.

In some species, e.g., *G. sallaci* and *G. ruthveni*, the number of infralabials is so variable among the few specimens available that the usual number for the species (if in fact there is a "usual" number) cannot yet be ascertained (Table 3).

**DORSAL SCALE ROWS.**—Members of the genus *Geophis* have either 15 or 17 rows of dorsal scales; there is no reduction in number on the posterior part of the body. The number of scale rows is an important systematic character at the specific level, but less important at the species group level.

Intraspecifically, there is virtually no variation in the number of rows. Only two specimens are known to be aberrant in this character, both showing irregular counts along the body. One of the syntypes of *R. guttulatum* (= *G. chalybeus*) has 15 rows of dorsals throughout much of its length. At various points on the body, however, the number of rows increases to 16 or 17. Where 15 rows are present, the paravertebral row on each side is enlarged; 16 and 17 rows result when the enlarged paravertebral splits into two smaller scales on one or both sides of the body, respectively. In the other



TABLE 3  
 VARIATION IN THE NUMBER OF INFRALABIALS IN *Geophis*

Species	5-5	5-6	6-6	6-7	7-7	7-8	8-8	other
<i>aquilonaris</i>			9					
<i>bicolor</i>				1	7			
<i>blanchardi</i>				3	13			
<i>brachycephalus</i>		2	141	43	41	1	2	
<i>cancellatus</i>				1				1 (6-8)
<i>carinosus</i>		1?	4	1				
<i>chalybeus</i>					3			
<i>championi</i>			2					
<i>dubius</i>			12		2			
<i>dugesi</i>		1	5					
<i>dummi</i>							1	
<i>fulvoguttatus</i>			1					
<i>godmani</i>			8	2				1 (5-7)
<i>hoffmanni</i>		3	68	1				
<i>immaculatus</i>			2					
<i>incomptus</i>			4	2	9			
<i>isthmicus</i>			1					
<i>laticinctus</i>					1			
<i>latifrontalis</i>			5	3	11			
<i>maculiferus</i>	1							
<i>mutitorques</i>			1	2	51			
<i>nasalis</i>			8	5	255	26	19	
<i>nigrocinctus</i>			3					
<i>omiltemanus</i>				1	8			
<i>petersi</i>		1	8					
<i>rhodogaster</i>			21	5	5			
<i>ruthveni</i>	1	3	1		1			
<i>sallaei</i>			1	3	1	1	2	
<i>semiamulatus</i>					17			
<i>semidoliatus</i>	4	10	654	4				1 (4-5)
<i>sieboldi</i>			2			2	1	2 (8-9)
<i>tarascae</i>		1	2					
<i>zeledoni</i>		2	14	1				

two syntypes, the paravertebrals are not enlarged and the scales are in 17 rows throughout, obviously the normal condition.

The second individual with an inconsistent scale row count is UMMZ 104698, referred to *G. nasalis* by J. A. Peters (1954:22) and to *G. petersi* by Duellman (1959:6; 1961:98). This specimen, from Coalcoman, Michoacan, shows scale fusions in the paravertebral region which reduce the number of rows from 17 to 16 to 15. The size of the paravertebrals indicates that the rows are normally 17. I refer this specimen to *G. sieboldi*, rather than to the closely related *G. nasalis* (see accounts of species).

The number of scale rows is not consistent within some species groups; the *chalybeus*, *omiltemanus*, and *sieboldi* groups contain some species with 17 rows and others with 15. In contrast, all members of the *championi* and *semidoliatus* groups have 15 rows, and the *latifrontalis* and *dubius* groups have 17. Both within a single group, and between different groups, species with 15 scale rows appear to have been derived from forms with 17 rows. The aberrant syntype of *R. guttulatum* and the Coalcoman specimen of *G. sieboldi* belong to species groups in which 15 and 17 scale rows occur. It is not improbable that the phylogenetic reduction of scale rows has taken place in much the same way as exemplified by the aberrant specimens; i.e., by the fusion of two rows in the paravertebral region.

SCALE ORNAMENTATION.—Secondary sexual scale ornaments include tubercles on the chin scales of adult males and on the dorsal scales immediately above the vent in adults of one or both sexes. The latter structures have been called anal ridges when they occur in smooth-scaled species and knobbed anal keels in keeled-scaled forms (Blanchard, 1931:95).

Neither of these sexual ornaments is easily dealt with when inadequate series of specimens are studied; hence, a thorough study of these ornaments in the genus *Geophis* is not possible at this time. Certain species (e.g., *tarascae*) appear not to have chin tubercles, but the discovery of larger males may reveal their presence. Smith (1942:176), for example, stated that the snakes of the genus *Adelphicos* do not develop chin tubercles, but these structures are present on a male of *A. veraepacis nigrilatus* examined by me. Although their absence is questionable, the chin tubercles do vary in prominence. In some groups they are large and easily visible to the naked eye (e.g., *sieboldi* group) and in others small and inconspicuous (*omiltemanus* group). The tubercles often occur on the lateral scales of the snout as well as on the various scales of the chin region.

The tubercles above the vent region are found in adults of both sexes in some species (e.g., *incomptus*), but are usually more conspicuous and more widely distributed in adult males. In other species, such as *G. nasalis*, the tubercles are absent in females. In keeled-scaled forms the tubercle is usually located at the anterior tip of the keel. In *dugesii*, a smooth-scaled species, the tubercle is rather elongate, like a thick keel, and suggests possible homology between tubercle and keel. However, tubercles are not always restricted to the midline of the scale, nor are they limited to one per scale. A specimen of *brachycephalus* (UK 63801), for example, has at least one tubercle on virtually every dorsal scale. Anteriorly and dorsally each scale has a tubercle near its midline; posteriorly and laterally, several tubercles are distributed randomly over each scale. Tubercles may also occur on the anterior and lateral edges of the ventrals on the anterior part of the body.

The presence or absence of keeling on the dorsal scales is not sex-dependent and is subject to little intraspecific variation. Only three species (*dubius*, *incomptus*, *semidoliatus*) are known to include keeled and smooth-scaled individuals. When present, the keeling in these three species is faint and restricted to the tail base.

Two species groups (*chalybeus*, *latifrontalis*) are composed of only smooth-scaled species. All species in the *sieboldi* group have distinct keels; although they are restricted to the tail base in some species, in most of the species the keeled scales occupy the posterior two-thirds or one-half of the body and at least the anterior half of the tail. The keeling is usually weak or absent on the lateral rows of scales.

Within the *omiltemanus* group, *omiltemanus* has faint posterior keeling; *isthmicus*, and perhaps *maculiferus*, have smooth scales; and *incomptus* has faint keeling in some specimens and smooth scales in others. Smooth-scaled and keeled-scaled forms are also found in the *dubius* and *championi* groups; in the *semidoliatus* group, in which *semidoliatus* is the only species known from more than two specimens, variation in keeling seems to be individual. In most of the keeled members of these latter groups, the keeling is faint and restricted to the tail base. The determination of the presence or absence of keeling in juvenile specimens of such species is often difficult; the difficulty is probably the direct result of the small size of the scales rather than of ontogenetic changes in the intensity of the keeling.

The absence of keeling is not directly correlated with specialization to a fossorial existence. The strongest keeling is found in some of the most specialized forms, such as *G. nasalis*. *G. ruthveni* and *G. championi* are very similar, specialized forms, but the former is strongly keeled and the latter is smooth-scaled.

When viewed by transmitted light, the body scales of all species appear to have at least faint longitudinal striations. The striations are scarcely discernible in many of the smooth-scaled species, but distinct in strongly keeled forms. Like the keels, the striations are usually most distinct on the posterior part of the body.

As recently as 1954, Taylor described *G. bakeri* from Costa Rica on essentially the sole basis of paired apical pits. Taylor (1954:691) stated, "The presence of the scale pits has not [,] to my knowledge, been reported in a typical *Geophis* previously and it might be well to re-examine members now recognized as belonging to the genus. Usually the character has been regarded as having a generic significance." By mounting scales from various parts of the body on glass slides, and using transmitted rather than reflected light, I found that a majority of the species of *Geophis* possess paired apical pits. In some species (particularly if the snake was about to shed when preserved) the pits are visible without magnification; in others they were dis-

covered only after repeated viewings and manipulations of the intensity and direction of the light source. Consequently, I am extremely reluctant to accept any statement in the literature that scale pits are absent in a particular species or group. Scale pits were said to be absent in *Tropidodipsas* and *Chersodromus* (as well as in *Geophis*) by Dunn (1928b), but I have found them in at least one species (*T. fasciata*) of the former and on the anterior scales of the latter.

I am equally reluctant to accept my own conclusion that apical pits are absent in some *Geophis*. The distinctness of these pits (to the observer at least) depends on the distinctness of the striations; they stand out as clear areas surrounded by striated parts of the scale, and are most obvious on strongly keeled species, which characteristically also have strong striations. The pits are least obvious on smooth-scaled forms, and unfortunately it is just these species that apparently have none. Nonetheless, the fact that the forms without the apical pits generally make up particular species groups, and the fact that the pits have been seen on some smooth-scaled species (which have keeled relatives with pits) indicates that the pits are absent in the *chalybeus*, *omiltemanus*, and *latifrontalis* groups.

The pits have not been discovered in *G. godmani* or *G. petersi*; the relationships of these species are with forms having scale pits. The apparent absence of pits may be the result of insufficient material for examination. Although several specimens of both *godmani* and *petersi* are available, none has loosened scutes which can be readily lifted from the underlying epidermis for slide-mounting.

SEGMENTAL COUNTS.—The numbers of ventral and subcaudal scales are important features in distinguishing between populations of *Geophis*. These counts are sexually dimorphic, and therefore most effective when the sexes are considered separately. In all adequately known species, the counts for the two sexes overlap widely; in general, however, males average five to ten fewer ventrals and five to ten more subcaudals than females of the same species. This dimorphism itself is subject to interspecific variation. In members of the *latifrontalis* group, for example, males average at least ten fewer ventrals than females; in other species (e.g., *nasalis*) the difference is of the order of two or three ventrals. Unfortunately, too few species are sufficiently well known to evaluate these differences at the species group level.

A high number of ventrals is not necessarily correlated with a high number of caudals, thus enhancing the usefulness of the counts. For example, the known females of both *aquilonaris* and *cancellatus* have more than 170 ventrals, but they are different in subcaudal counts (55–63, 21–23, respectively). Similarly, *petersi* and *sallaei* have comparable caudal counts, but differ markedly in ventral counts.

The total range in the number of ventrals in the genus is from 115 (in *nasalis*) to 185 (*semiannulatus*). A single species, *G. semidoliatus*, spans a large part of this range (131–179), but most species have a range of about twenty ventrals.

Insufficient locality records prevent a study of geographic variation in most forms; the few exceptions (e.g., *semidoliatus*, *mutitorques*, *nasalis*, *brachycephalus*) are dealt with in the species accounts. No south-north nor altitudinal clines are evident intraspecifically, although within the genus as a whole the species with high ventral counts are concentrated in the northern half of the geographic range. It is also true that the species occupying the northern limits of the distribution of the genus (*aquilonaris* in northwestern Mexico, *semiannulatus* in northeastern Mexico) have higher ventral counts than any other species.

Local variation in the number of ventrals is striking in *G. semidoliatus*; populations of this form within a few miles of each other may have quite different average ventral counts (see Fig. 18). The extent of this type of variation in other species is unknown, but the implication that gene flow is sometimes severely restricted even between essentially adjacent local populations indicates that overemphasis of modest differences in segmental counts should be avoided.

The number of subcaudals in the genus varies from 19 pairs in some specimens of *semidoliatus* to 66 pairs in *aquilonaris*. The greatest range in a single species is 28–49 in *semiannulatus*. Species with relatively short tails (e.g., *semidoliatus*) tend to have fewer subcaudals than species with long tails (e.g., *aquilonaris*); however, there are many exceptions to this generalization.

The effect of sexual dimorphism in segmental counts can be largely eliminated by a summation of the ventral and subcaudal counts. Accordingly, the range of this sum is included in each of the species accounts. Such a practice is often desirable when considering literature records in which the sex is not designated or in samples in which one or both sexes are poorly represented.

The ventrals were counted from the first scale clearly twice as broad as long up to, but not including, the anal plate; this system does not follow the suggestion of Dowling (1951), but in practice is identical or nearly identical with it. The number of subcaudals was counted from the first pair to reach the midline behind the anal plate up to, but not including, the terminal spine. The number of subcaudals indicated throughout the text refers to the number of pairs. There are a few specimens of various species in which transverse fusion occurs between the members of a subcaudal pair; this may involve several pairs, but is not known to occur in all of the subcaudals of a single individual. Since my counts involve only one member of

each pair, the fusion does not alter the count. In the accounts of the various species, the range in the number of ventrals and subcaudals for each sex is followed parenthetically by the mean. If no mean is given the sample is not homogeneous, and a detailed explanation is included in the discussion of variation.

The number of ventrals and subcaudals in members of the genus, with the mean and associated parameters, is not presented in tabular form because (1) the majority of the species are known from too few specimens (each of eleven is known from 3 specimens or less); and (2) several of the adequately known species show geographic variation in the segmental counts, and therefore require individual analysis.

#### SKULL AND DENTITION

Unfortunately, skeletal material representing species of *Geophis* is almost completely lacking; to overcome this dearth of material, I have made cleared and stained preparations of the heads of a few of the species, and have radiographed specimens of all species available to me. Both techniques are severely limited in their usefulness, primarily because of the small size of the snakes. My observations have been limited primarily to the dorsal surface of the skull. Aside from the skull proportions, which parallel the external measurements (e.g., relative snout length), two characteristics have been noted to have some systematic significance.

The first of these features is the condition of the postorbital bone, which is absent in a large number of species; unfortunately, its presence or absence is not consistent within certain species groups. In the *omiltemanus* group, the bone is absent except in *G. maculiferus* (and perhaps *isthmicus*, which has not been examined); in the *chalybeus* group the bone is present except in some specimens of *G. dugesi*. The postorbital is absent in all members of the *dubius* and *semidoliatus* groups, and present in the *latifrontalis*, *championi*, and *sieboldi* groups. In the *latifrontalis* group it is large and robust; in the *sieboldi*, *championi*, and relevant members of the *chalybeus* groups, it is slender. The loss of the postorbital bone apparently has little adaptive significance, since it is absent in generalized (*omiltemanus* group) as well as specialized (*dubius* group) forms.

The second skull feature of interest is the anterior edge of the parietal bone. This edge tends to be transverse in some groups (e.g., *chalybeus* group) and concave in others (e.g., *semidoliatus* group), but is too variable to be an important systematic character. In the *latifrontalis* group, however, the anterior edge of the parietal, although still variable, is distinctive in an interesting way; the anterolateral edge extends forward along the dorsal margin of the eye socket, sometimes excluding the frontal bone from the

socket. The possible significance of this feature is that it is one of several characters in which members of the *latifrontalis* group resemble members of the genera *Atractus* and *Adelphicos*.

Teeth are borne on the maxilla, palatine, pterygoid, and dentary; in this study only the maxilla and the associated anterior end of the ectopterygoid have been utilized. The difficulties encountered in the removal of the maxillae (some of which are less than 2 mm long) without undue damage to the bone and to the head precluded any attempt at removal of the entire maxillo-palato-ptyerygoid arch and the dentary.

With few exceptions, the maxilla and ectopterygoid are useful taxonomic characters, particularly at the species group level. Among the pertinent characteristics of the maxilla are the anterior extension (in relation to supra-labial level), the relative stoutness, presence or absence of dorsoventral compression, and presence or absence of a laterally compressed flange at the posterior end. The maxillary teeth vary in the position of the first tooth (in the *sieboldi* group the anterior tip of the maxilla is toothless), the number and curvature of the teeth, and the relative length of each tooth in the series. The number of teeth given in the descriptions includes empty sockets. The curvature varies from the shallowly curved, needle-like teeth of *G. tarascae* to the shorter, strongly curved teeth of forms such as *nasalis*; in the latter, the distal half of the tooth almost parallels the main axis of the maxilla. The relative lengths of the individual teeth in the maxillary series are usually categorized as subequal, increasing or decreasing posteriorly. All of these categories are found within the genus, but with the following qualification: in almost all cases the first and the last two or three teeth are somewhat shorter than the others; the posterior shortening compensates for the downward curvature of the posterior part of the maxilla. The teeth are herein considered to be subequal even if the last few are noticeably shorter than the others (see, for example, *G. incomptus* in Fig. 2). The teeth are considered to decrease in length posteriorly only if this decrease takes place throughout the row (again, the first tooth may be slightly shorter than the second). In a few species the tooth length gradually increases posteriorly, including the last few teeth.

The shape of the posterior end of the maxilla affords one of the most distinctive differences between certain species groups. Correlated with these are differences in the shape of the anterior end of the ectopterygoid, which articulates with the maxilla. The posterior end of the maxilla may be greatly expanded into a laterally compressed flange, modestly expanded, or simply tapered to a blunt point. The ectopterygoid may be single or bifurcate; if bifurcate, the branches may be subequal or quite different in length, and cylindrical or flattened and expanded in shape. For example, a bifurcate ectopterygoid with one branch long and expanded and the second branch

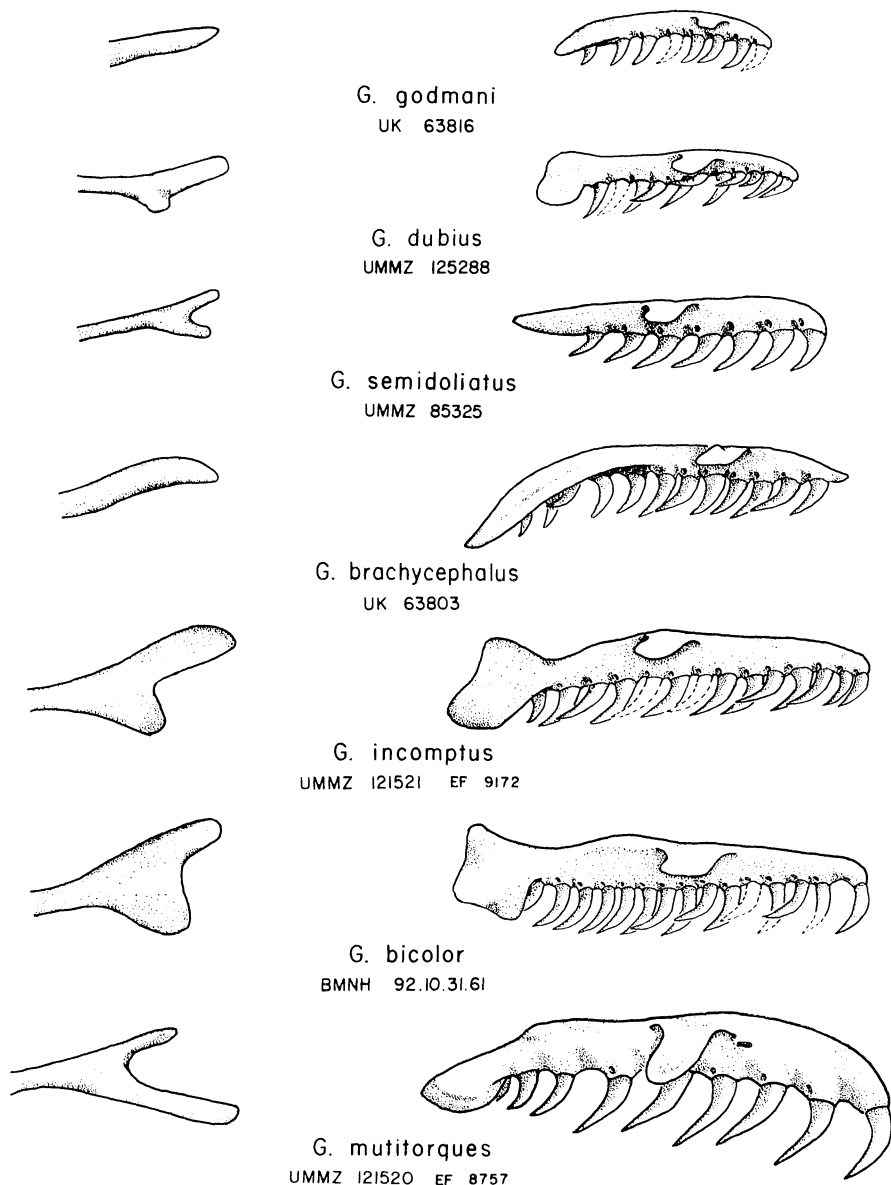


FIG. 2. Representative maxillaries and ectopterygoids of the species groups of *Geophis*. All are shown about 14 times natural size. The snout-vent length of the individual and the species groups represented are: *G. godmani*, 287 mm (*championi* group); *G. dubius*, 211 mm (*dubius* group); *G. semidoliatus*, 257 mm (*semidoliatus* group); *G. brachycephalus*, 333 mm (*sieboldi* group); *G. incomptus*, 312 mm (*omiltemanus* group); *G. bicolor*, 250 mm (*chalybeus* group); and *G. mutitorques*, 330 mm (*latifrontalis* group).



short and not expanded has the general shape of a mitten; one which is single, flattened, but not expanded has the shape of a blade.

The general features of the maxilla and ectopterygoid of the various groups are shown in Figure 2. The number of maxillary teeth is recorded for each species in Table 4.

HEMIPENIS

Unless otherwise noted, the descriptions of the hemipenes in the systematic section are based on organs in the retracted position. Unfortunately, males

TABLE 4  
VARIATION IN THE NUMBER OF MAXILLARY TEETH IN SPECIES OF *Geophis*

Species	Number of Maxillary Teeth											
	6	7	8	9	10	11	12	13	14	15	16	17
<i>aquilonaris</i>						1	2					
<i>bicolor</i>								1		1		
<i>blanchardi</i>						1	2					
<i>brachycephalus</i>						3	3	8	8	4		
<i>cancellatus</i>		1										
<i>carinosus</i>					1	1	1	2				
<i>chalybeus</i>								2				
<i>championi</i>			1									
<i>dubius</i>					4	1	1					
<i>dugesi</i>				2								
<i>dummi</i>							1					
<i>fulvoguttatus</i>						1						
<i>godmani</i>		1	2	1								
<i>hoffmanni</i>			2	3	1							
<i>immaculatus</i>								1				
<i>incomptus</i>							1	3	2			
<i>isthmicus</i>												
<i>laticinctus</i>	1											
<i>latifrontalis</i>					2	1	1					
<i>maculiferus</i>												1
<i>mutitorques</i>			2	3	1							
<i>nasalis</i>						3	3	3				
<i>nigrocinctus</i>						2						
<i>omillemanus</i>								1	2			
<i>petersi</i>	3											
<i>rhodogaster</i>									1	1	2	1
<i>ruthveni</i>		1	1									
<i>sallaei</i>							1	1				
<i>semiannulatus</i>					1	3						
<i>semidoliatus</i>		9	2									
<i>sieboldi</i>						1	2		1			
<i>tarascae</i>					1							
<i>zeledoni</i>								2	1			

are not available in several species, and in others only the everted organ has been available. Where applicable, the nomenclature suggested by Dowling and Savage (1960) has been followed.

For purposes of orientation, the hemipenis has been divided into three regions, which I have termed basal, central, and distal. In most species this division has a clear anatomical basis, but in others it is largely arbitrary. The basal region shows little variation; it bears numerous minute spinules, a few large spines, and a naked pocket. The large spines are generally in the distal half of the basal region, and could be included in the central region; however, they are separated from the spines of the central region by a more or less distinct gap, and for convenience are considered to be basal spines. The naked pocket persists in the everted position, flanked by raised, flaccid ridges, which tend to form a roof over the pocket, and by the large basal spines; the function of this pocket is unknown.

The central part of the hemipenis bears a variable number of large or medium-sized spines and hooks, arranged as a collar around the organ; the spines are largest immediately lateral to the sulcus, and smallest on the antisulcus side. The central spines are sharply demarcated from the small spinules of the distal region in some species, but merge gradually with the distal spinules in others; the latter condition is associated with a non-capitate, or but weakly capitate, hemipenis.

The distal region of the hemipenis is responsible for most of the hemipenial variation between species groups. It is distinctly capitate in the *chalybeus*, *omiltemanus*, *sieboldi*, and *semidoliatus* groups; in these the capitulum has an obvious free edge demarcating its proximal limit. In the *latifrontalis* and *dubius* groups, this free edge is reduced, but still present, and the spinules in the proximal part of the capitulum are scarcely smaller than the spines of the central part of the hemipenis; the capitation in these forms is obscure. In the *championi* group, the capitate nature of the distal region has apparently been lost completely.

The spinules and papillae in the distal region are usually borne on calyces, but the latter are often poorly developed and sometimes discernible only at the apex of the organ. In many species the density of spinules in the proximal part of the capitulum prevents a clear determination of the hemipenial surface underlying the spinules.

The apex of the hemipenis is highly variable within the genus. Most commonly, the apex is slightly bilobed, but not enough to be evident in the everted position; this type is found in the *chalybeus*, *omiltemanus*, *sieboldi*, and *semidoliatus* groups. In the *dubius* group the bilobation extends for two or three subcaudal lengths, and is evident when the organ is everted. The apex is single in the *latifrontalis* and *championi* groups. Associated with these different apices are differences in the *M. retractor penis magnus*.

This muscle has its origin on the vertebral column in the posterior part of the tail, and extends anteriorly to insert on the apex of the hemipenis. In forms with an undivided apex, the muscle is single throughout its length. Where the apex is bilobed, the muscle bifurcates into two slips just before reaching the hemipenis; one slip attaches to each lobe of the apex.

The *sulcus spermaticus* is bifurcate in all members of the genus; both branches usually reach the apex. In the *latifrontalis* group, however, one of the branches fails to reach the apex; it fades out among the calyces about midway between the point of bifurcation and the tip of the apex. The lateral walls of this shortened branch are lower than those of the normal branch, and it appears that in this group the sulcus is functionally single.

Inger and Marx (1962) have cautioned that hemipenial variation, even intraspecific variation, can be extensive. The wide variation they found in *Calamaria lumbricoidea* has no apparent parallel among the species of *Geophis*. Within species groups, however, variation is evident in the length of the organ, the number of the central spines, the distinctness of the capitulation, and the conspicuousness of the calyces. This variation is particularly evident in the *sieboldi* group, but appears to some degree in all groups.

The hemipenis does not seem to be a reliable indicator of intergroup relationships. The variation in capitulation and bilobation of the organ does not correlate with the differences in non-hemipenial features. The most common, and perhaps primitive, hemipenial type is capitate and slightly bilobed. The two groups in which the apex is single have little else in common, indicating that the condition has developed independently in the two groups. The relationships of the *dubius* group, in which the hemipenis is distinctly bilobed and weakly capitate, appear to be with groups having both single and slightly bilobed hemipenes. These inconsistencies indicate that hemipenial differentiation has occurred independently in the various groups, in several directions and at various rates. For this reason I have not placed great reliance on hemipenial similarities or dissimilarities in the determination of affinities among the groups, and in some instances, among species.

#### PROPORTIONS

**EYE SIZE.**—The relative size of the eye appears to be an excellent indicator of the degree of specialization toward a fossorial existence. Intrageneric variation is extensive, and in general negatively correlated with the length of the snout. In specialized forms, such as members of the *championi* group, the eye diameter is only two-thirds to three-fourths its distance from the lip; at the other extreme, in the *chalybeus* group, the eye diameter may be more than half-again its distance from the lip. In the latter, the snout is about twice as long as the eye diameter; in the former it may be four times as long.

The eye size in relation to its distance from the lip is subject to ontogenetic change resulting from allometric growth patterns; the distance from the eye to the lip increases faster than the size of the eye. The eye is, therefore, relatively larger in juveniles than in adults, a fact that should be considered when comparing single specimens of one species with another. In the descriptions of species the eye size presented is based whenever possible on the adult condition.

**SNOUT LENGTH.**—The snout length has been measured as the distance from the tip of the snout to the anterior border of the orbit. It constitutes about 35 per cent of the head length (tip of snout to end of parietal suture) in members of the *chalybeus* group, and almost 50 per cent in some of the specialized forms. Although this percentage is useful only in distinguishing the extremes within the genus, the several species groups comprised of species with long snouts can be further subdivided by the relative lengths of the various scales on the snout. Snout elongation in the *latifrontalis* and *semidoliatus* groups is associated with an increase in the length of the snout scales in general; in the *dubius* and *championi* groups the elongation has primarily involved the internasal-postnasal region, and in the *sieboldi* group the prefrontal-loreal region. These differences have been described in more detail in the discussion of the relevant head scales.

**TAIL LENGTH.**—Total length was measured from the tip of the snout to the end of the tail, tail length from the posterior end of the anal plate to the end of the tail. The length of the largest specimen of each sex is included in the description of each species, but, since most species are known from small samples, and since the maximum length does not appear to vary widely among the various species, no attempt has been made to use this feature in a diagnostic way. The relative tail length is useful in describing many forms, particularly at the species group level. The relative tail length has been calculated as the ratio of tail length to total length, and expressed as a percentage.

Males have relatively longer tails than females and adults have relatively longer tails than juveniles. These relationships are summarized for two species in tabular form (Table 5). In order to eliminate other variables, such as length of time in preservation, data for *G. brachycephalus* was obtained from a single series of specimens from Boquete, Panama, and for *G. nasalis* from two series of specimens, collected in 1924 and 1926, from Volcan Zunil, Guatemala. In species with very short tails, such as *G. semidoliatus*, both the sexual and ontogenetic differences are less pronounced than in the species shown in Table 5.

All members of the genus have relatively short tails, but the tail length varies enough between some species groups to make it a useful systematic

character. The relative tail length in the species with the longest tail (*aquilonaris*) is about twice that in the short-tailed forms (e.g., *semidoliatus*). The tabular presentation of the tail length in the various species includes only the number of specimens and the range of variation (Table 6). In small samples, the calculated mean of a character showing allometric variation would reflect the size distribution of the few available specimens rather than a parameter of the natural population.

TABLE 5

SEXUALLY DIMORPHIC AND ONTOGENETIC VARIATION IN RELATIVE TAIL LENGTH IN TWO SPECIES OF *Geophis*. THE TAIL LENGTH IS GIVEN AS A PERCENTAGE OF THE TOTAL LENGTH; THE OBSERVED RANGE IS GIVEN PARENTHETICALLY BENEATH THE MEAN. JUVENILES ARE SPECIMENS WITH A TOTAL LENGTH UP TO AND INCLUDING 200 MM; ADULTS ARE SPECIMENS MORE THAN 200 MM IN TOTAL LENGTH.

Species	Juveniles		Adults	
	N	Tail/Total	N	Tail/Total
<i>G. brachycephalus</i>	Females	5 15.4 (14.9-15.7)	20	15.9 (14.6-17.5)
	Males	16 16.8 (16.0-18.4)	16	18.5 (17.1-20.1)
<i>G. nasalis</i>	Females	37 12.9 (11.0-14.9)	52	13.6 (12.5-15.3)
	Males	47 15.4 (13.9-17.5)	67	17.3 (15.9-19.2)

COLORATION

In the systematic section, coloration is described on the basis of preserved material; available information on the coloration in living material is included under the heading *Remarks*.

The color pattern is an important systematic character for distinguishing one species from another within certain species groups (e.g., the *latifrontalis* group). However, intraspecific variation is extensive in some of the better known forms, and presumed differences in the coloration of species currently known from small samples may be judged invalid when additional specimens are available. Variation may be individual, ontogenetic, and presumably geographic, although conclusions regarding the latter must await additional specimens. Individual variation of the dorsal pattern is most pronounced in *G. brachycephalus*, but is known to occur in other species (e.g., *dugesii*) as well. The venter may be strongly banded or not in specimens of *godmani*, *brachycephalus*, and *incomptus*, and may be immaculate or not in *semi-*

TABLE 6  
TAIL LENGTH AS A PERCENTAGE OF THE TOTAL LENGTH IN SPECIES OF *Geophis*

Species	Females		Males	
	N	Tail/Total	N	Tail/Total
<i>aquilonaris</i>	4	19.5-22.1	5	19.7-23.2
<i>bicolor</i>	5	15.4-17.2	3	18.8-22.4
<i>blanchardi</i>	11	11.9-13.8	4	15.7-17.2
<i>brachycephalus</i>	50	13.0-17.6	80	15.8-21.2
<i>cancellatus</i>	2	07.7-08.0		
<i>carinosus</i>	4	18.4-19.5	2	22.9-23.9
<i>chalybeus</i>	3	15.8-16.9		
<i>championi</i>	1	12.2	1	16.0
<i>dubius</i>	5	14.3-18.1	10	16.0-21.6
<i>dugesi</i>	2	15.1-17.3	5	16.5-19.1
<i>dunni</i>	1	15.5		
<i>fulvoguttatus</i>			1	16.1
<i>godmani</i>	5	11.5-13.8	2	16.4-17.1
<i>hoffmanni</i>	33	12.5-15.1	29	14.1-18.5
<i>immaculatus</i>	2	13.6-14.4		
<i>incomptus</i>	9	11.7-15.6	6	14.5-17.7
<i>isthmicus</i>	1	11.6		
<i>laticinctus</i>	1	10.9		
<i>latifrontalis</i>	12	10.3-12.7	8	14.8-15.8
<i>maculiferus</i>			1	13.2
<i>multitorques</i>	28	09.9-13.5	24	12.1-17.1
<i>nasalis</i>	140	11.0-16.1	168	13.7-19.2
<i>nigrocinctus</i>	1	17.7	1	21.3
<i>omillemanus</i>	4	14.9-17.4	4	18.3-21.2
<i>petersi</i>	4	12.5-15.4	5	13.2-15.9
<i>rhodogaster</i>	15	13.5-16.7	12	18.7-22.2
<i>ruthveni</i>	1	13.5	6	16.8-19.8
<i>sallaei</i>	3	13.8-16.2	4	17.0-18.3
<i>semiannulatus</i>	13	10.2-14.9	4	13.9-17.1
<i>semidoliatus</i>	104	07.4-10.3	91	09.5-12.2
<i>sieboldi</i>	2	13.8-16.2	5	16.1-17.7
<i>tarascae</i>	1	17.5	2	18.8-20.5
<i>zeledoni</i>	7	15.4-18.5	8	17.5-20.2

*doliatus* and other forms. A light juvenile collar is obliterated in the adults of several species, as are the dorsal and ventral patterns in some.

Extensive intragroup variation in color pattern prevents the application of color differences at the species group level. Several groups include both species with dorsal crossbands and those with a unicolor dorsum, species with an immaculate venter and those with a blotched or banded venter. Despite this intragroup variability, the color patterns found in any one group can be derived from one another without difficulty. The direction of

the derivation (e.g., from unicolor to blotched or from blotched to unicolor) can usually, but not always, be surmised from the distribution of other characteristics; i.e., from the establishment of generalized and specialized forms.

#### SUMMARY OF SYSTEMATIC CHARACTERS

Among the various characteristics analyzed, the most useful in the establishment of the species groups have been (1) the characteristics of the maxilla; (2) the relative snout length, eye size, and tail length; (3) the presence or absence of an anterior temporal; (4) in forms with elongated snouts, the head scales affected by the elongation; and, to a lesser extent, the characteristics of the hemipenis, the relative numbers of ventrals and caudals, the presence or absence of scale pits, and the presence or absence of the postorbital bone.

Characters whose application is justified only at the specific level include (1) the loss (by fusion) of head scales such as the internasals, supraoculars, or members of the labial series; (2) the number of dorsal scale rows; (3) the presence or absence of keels; (4) minor differences in segmental counts; and (5) coloration.

These two groupings of characteristics are by no means mutually exclusive. Some species groups contain only smooth-scaled species, for example, and that character is a useful part of the diagnosis of the group. The two categories are meant only as a general guide to the reliability of various features at the two levels of distinction. In all instances, the characteristics must be applied in combination.

#### SYSTEMATIC SECTION

##### HISTORY OF THE USE OF THE NAME *Geophis*

In 1830 Wagler erected the genus *Catostoma* to accommodate a new species of colubrid snake, which he called *Catostoma chalybeum*. Later in the same paper, to avoid confusion with the piscine genus *Catostomus* Lesueur, Wagler proposed the name *Geophis* as a substitute name for *Catostoma*. The species *chalybeum* became the type species of *Geophis* by monotypy. The spelling was changed to *chalybeus* to conform with the masculine gender of the new generic name.

Duméril erected the genus *Rabdosoma* in 1853, and Duméril, Bibron, and Duméril (1854) included the species *semidoliatum*, *badium*, *torquatum*, *crassicaudatum*, *lineatum*, and *longicaudatum* under that name. W. Peters (1859) synonymized *Rabdosoma* with *Geophis*, and included both *chalybeus* and *semidoliatus* under the name *Geophis*. He reported briefly on several specimens of *chalybeus* in the Berlin collection, but since he gave no notice

of his having seen the type of *chalybeus*, his inclusion of the Berlin specimens, and of *semidoliatus*, under the name *Geophis* was apparently based upon the nebulous description of the genus given by Wagler. In this same paper, Peters described *Colobognathus hoffmanni*, new genus and species, as being similar to *Geophis* but with very short maxillary and palatine bones, leaving the anterior part of the mouth toothless.

Cope (1860) was apparently unaware of Wagler's substitution of *Geophis* for *Catostoma*, and credited the name *Geophis* to Fitzinger (1843), even though Fitzinger himself gave Wagler credit for the name. Cope accepted the congeneric relationship of *chalybeus* and *semidoliatus*, but working under the misconception that *Geophis* was an 1843 Fitzinger name, he included the two species under the name *Catostoma*. Peters (1861) pointed out Cope's error in a footnote to the description of yet another new genus and species, *Geophidium dubium*, which he recognized as being similar to *Geophis* and *Colobognathus*, but differing by having the internasals fused with the prefrontals.

Jan (1862) regarded *Geophis* and *Colobognathus* as subdivisions of *Elapoides* Boie 1827, the type species of which is *Elapoides fuscus* of Java. Jan placed his new species, *E. sieboldi*, with *semidoliatus* in the *Geophis* group and retained the subdivision *Colobognathus* for *E. hoffmanni*. In the *Iconographie Generale des Ophidiens* (1865), Jan continued this arrangement, adding a new species, *E. rostralis*. In both of these works Jan utilized *Rabdosoma* as a genus distinct from *Elapoides*, even though he placed *R. semidoliatum* Duméril, Bibron, and Duméril in the genus *Elapoides*.

In 1868, Cope described two new species, *Catostoma nasale* and *Colophrys rhodogaster*. He erected the genus *Colophrys* on the basis of the absence of a supraocular in *rhodogaster*. Both species, however, were compared with *Catostoma chalybeum* Wagler. The wording of this comparison implies that Cope had a very definite concept of the identity of *chalybeum*, but the source of his concept is unknown. The only published accounts of *chalybeum* at the time were the type description and Peters' footnote in 1859. The information given by Cope exceeds that of the type description and does not agree with that given by Peters (Peters stated eight infralabials, Cope six). Furthermore, Cope did not specifically acknowledge having seen any specimens of *chalybeum*. Günther also described two new species in 1868, *latifrons* and *bicolor*, but followed Fitzinger and Peters in using the generic name *Geophis*.

Cope (1871), reporting on specimens received from Costa Rica, added two new species to the genus *Colobognathus*, *C. dolichocephalus* and *C. brachycephalus*. He also transferred his *Catostoma nasale* to *Colobognathus*, while retaining *semidoliatum* under *Catostoma* and *rhodogaster* under *Colophrys*. Günther (1872) further confused the matter by describing a new



species as *Geophis moestus* and then, despite the strict synonymy of *Geophis* and *Catostoma*, presenting notes on specimens he called *Catostoma chalybeum*. The source of Günther's concept of *chalybeum* is unknown, but his concept differed from those of Peters (1859) and Cope (1868).

Garman became the first American worker to use the name *Geophis* when he described *G. latifrontalis* in 1883. In the same year, Bocourt greatly expanded the limits of the genus by including under *Geophis* the genera *Colobognathus* Peters, *Geophidium* Peters, *Colophrys* Cope, and the New World forms placed by Jan in the genus *Elapoides* Boie. Following Jan, Bocourt placed South American species (plus *zebrinum*, from "Tehuantepec," Mexico) in the genus *Rabdosoma*.

Cope (1885*b*) erroneously stated that Bocourt had listed a divided anal plate as characteristic of *Rabdosoma*, and concluded that Bocourt's *Rabdosoma* was not synonymous with the original *Rabdosoma* of Duméril, Bibron, and Duméril. Cope, therefore, transferred *zebrinum*, placed by Bocourt under *Rabdosoma*, to *Rhegnops* Cope, a genus characterized by a divided anal plate. Cope further stated that *Rabdosoma* and *Geophis* were synonyms of *Catostoma*. Actually, Bocourt had indicated quite clearly that the anal plate was single in both *Geophis* and *Rabdosoma*. He apparently separated the two genera by the number of pairs of chinshields; two pairs in the former, one pair in the latter. Thus, Cope's transfer of *zebrinum* to *Rhegnops* was ill-founded and unnecessary. Later in 1885, Cope (1885*a*) reversed his classification and decided that *Geophis* and *Catostoma* were synonyms of *Elapoides*, but that *Rabdosoma* was a distinct genus. Cope distinguished the two genera by the presence of keeled scales in *Elapoides* and smooth scales in *Rabdosoma*. Nonetheless, two of the species he placed in *Elapoides* (*chalybeus*, *dugesi*) have smooth scales, and two he placed in *Rabdosoma* (*rostrale*, *nasale*) have keeled scales. Cope continued this usage of *Elapoides* and *Rabdosoma* in 1887, and also recognized three monotypic genera, *Colophrys rhodogaster*, *Geophidium dubium*, and *Colobognathus hoffmanni*. This marked the last usage of any of these five generic names for the snakes currently included in the genus *Geophis*. Cope did use the name *Rabdosoma* in 1896, but applied it to South American forms now placed in *Atractus*.

The species distributed among five genera by Cope were all included in the genus *Geophis* by Günther (1893). Günther also synonymized several forms, the most noteworthy of which involved the species *chalybeus*, which Cope had placed in *Elapoides*. Günther not only rejected Cope's use of *Elapoides* for *chalybeus*, but also relegated to the synonymy of *chalybeus* all three of the monotypic genera recognized by Cope. Günther's concept of *chalybeus* was so unwieldly that Boulenger (1894) sorted Günther's specimens into no less than nine species. Some of these Boulenger

simply removed from Günther's synonymy, but others were described as new species (*sallaei*, *godmani*, *petersi*, *championi*). Boulenger also transferred three Mexican species possessing an anterior temporal scute to the genus *Atractus*. Four other species were grouped by Boulenger into a new genus which he called *Dirosema*. Thus Boulenger used *Geophis*, *Atractus*, and *Dirosema* for the species Cope (1887) had placed in *Elapoides*, *Rabdosoma*, *Colobognathus*, *Geophidium*, and *Colophrys*. Species of the South American *Rabdosoma* were placed by Boulenger in the genus *Atractus* Wagler.

Mocquard (1908) followed Boulenger's use of *Dirosema*, but Dunn (1928a) placed three of its species (*bicolor*, *omiltemanum*, and *brachycephalum*) back in *Geophis* and transferred the fourth species (*psephotum*) to the genus *Ninia*. Dunn also tentatively returned the three Mexican "*Atractus*" (*isthmicus*, *latifrontalis*, *longiceps*) to *Geophis*. Amaral (1929) accepted Dunn's treatment of *Dirosema*, but used the name *Catostoma* rather than *Geophis*. Amaral followed Boulenger's use of *Atractus* for South American forms.

The basic disagreement between Boulenger and Dunn involved the significance of the anterior temporal. Boulenger included in *Geophis* only those forms which did not possess the anterior temporal, and thus had the parietal in contact with the supralabial series. Dunn felt that the presence of the anterior temporal was not sufficient evidence for exclusion from *Geophis*. Dunn's arrangement has been generally accepted for the past twenty years, mostly because of the supporting evidence provided by Smith (1941b). Smith pointed out that *blanchardi*, which has no anterior temporal, appeared to be very closely related to *latifrontalis*, which has that scale. Similarly, the relationships of *dugesii* appeared to be with *omiltemanum* rather than with *blanchardi*, even though *dugesii* and *blanchardi* do not have the temporal and *omiltemanum* has it. Smith concluded that the importance Boulenger placed on the temporal character was not justified, and he therefore rejected Boulenger's classification in favor of Dunn's. Smith's paper represents the last re-evaluation of the limits of the genus *Geophis*, although since 1941 fifteen new species have been added to the genus. The limits proposed by Dunn and Smith have been utilized by authors comparing other genera with *Geophis*, such as *Adelphicos* (Smith, 1942), *Schmidtophis* (Taylor, 1949), *Chersodromus* (Zweifel, 1954b), and *Atractus* (Savage, 1960).

#### THE IDENTITY OF THE TYPE SPECIES, *Geophis chalybeus* (WAGLER)

The inadequate nature of the type description of *Geophis chalybeus* is evident from the fact that even such basic information as the number of dorsal scale rows, ventrals, and subcaudals was omitted. At present, as

throughout the history of *Geophis* systematics, any small Central American snake without an anterior temporal is almost automatically allocated to *Geophis*, yet this "key" characteristic is not mentioned in the description of the type species of the genus. Many of the characteristics listed by Wagler are given in subjective terms; the interpretation of such features is therefore dependent on one's basis for comparison.

There is no evidence that the type specimen of *chalybeus* has ever been knowingly re-examined. I have made a serious effort to locate the type, but have been unable to do so. Menico Torchio of the museum in Milan stated (pers. com.) that the type was destroyed during the war, but it is not clear that this statement is based on concrete evidence establishing the presence of the type in the Milan collection prior to the war. It seems equally likely that the type is at present masquerading under another name, perhaps as the type specimen of a subsequently described species. This conjecture is based on the theory that the type of *chalybeus* was lost (at least figuratively) or overlooked shortly after the description of the species. Although included by Fitzinger (1843) in his classification of the snakes, *chalybeus* and its type specimen are not mentioned (except in a reproduction of Fitzinger's earlier classification) in the comprehensive works of Duméril and Bibron (1844), Duméril, Bibron, and Duméril (1854), or Jan and Sordelli (1865). Until the fate of the type specimen is clearly established the identity of *chalybeus* must be ascertained from the description provided by Wagler.

Rather surprisingly, the combination of the few features given by Wagler, such as the absence of a preocular, the presence of one postocular, the smoothness of the dorsal scales, and the color pattern of dark above and light below, cannot be applied to any Mexican snake currently placed in a genus other than *Geophis*. Within the genus *Geophis*, however, the name *chalybeus* has been applied to two distinct forms. The first specimens, other than the type (or types), to be allocated to *chalybeus* were reported in a footnote by W. Peters in 1859. Bocourt (1883) borrowed one of Peters' specimens, and by publishing a more detailed description of it established the first clear concept of the form. This concept was temporarily interrupted by Günther's unwieldy concept of *chalybeus*, but Boulenger (1894) quickly re-established Bocourt's use of the name. This usage remained unaltered until 1941, when Smith rejected it.

Smith (1941*b*) listed six characteristics of *chalybeus*, and concluded, through a process of elimination, that the only known form which possessed all six of these features was *Rhabdosoma guttulatum* Cope. Smith, therefore, considered *guttulatum* a synonym of *chalybeus*, a concept which has been accepted to the present. Smith's rejection of Bocourt's concept was prompted by the fact that *chalybeus*, as used by Bocourt, was a form with keeled dorsal scales, whereas Wagler's original description stated that the

scales were smooth. Ironically, both Bocourt and Smith assumed that the specimens reported on by Peters (1859) were the types of *chalybeus*. Bocourt borrowed one of the specimens and formed his concept from it. Smith, thinking that Wagler's original description and Peters' footnote were based on the same specimens, concluded that Peters' specimens had smooth scales since (1) Wagler had stated that the scales were smooth, and (2) Peters had not mentioned keeling in his brief report.

I find little justification for considering Peters' specimens the types of *chalybeus*. Peters' footnote begins, "*Geophis* Wagler ist übereinstimmend mit *Rhabdosoma* D. B. Sein *Geophis chalybeus* aus Mexico befindet sich in mehreren Exemplaren, von Deppe in Mexico gesammelt, in dem zoologischen Museum unter dem Namen *Elaps chalybeus*. Ich habe seiner Beschreibung nur hinzuzufügen, das . . ." This statement does not claim that the specimens collected by Deppe are the types of *chalybeus*, nor that Peters had ever seen the types. He apparently allocated the specimens to *chalybeus* on the basis of the type description of the species. On the other hand, there is indirect evidence that Wagler had access to the Deppe specimens. Deppe's collections were made (1824–1829) shortly prior to the publication of Wagler's description (1830), and it is known that Wagler studied Deppe's ornithological collections (Stresemann, 1954).

Of the six characteristics of *chalybeus* listed by Smith, only four were derived from Wagler's type description. These were: the presence of one supraocular, of one postocular, of smooth scales, and of a color pattern of dark above and light below. The other two features, the presence of 17 dorsal scale rows and of 6 supralabials with the fifth in contact with the parietal, were gleaned from Peters' footnote, and therefore cannot properly be assumed characteristic of *chalybeus*. Smith utilized these last two features to eliminate eight species from consideration, but the seriousness of this error is mitigated by the fact that these eight species can be eliminated by other means, such as coloration or the presence of keeled scales. Thus, despite his apparently erroneous assumption in regard to the types of *chalybeus*, Smith still might well have concluded that *R. guttulatum* Cope agreed with the type description of *chalybeus* better than any other Mexican *Geophis*.

I have examined the three syntypes of *guttulatum* and the series of specimens reported on by Peters. The latter do have keels on the posterior part of the body, and appear to be conspecific with the poorly known *Geophis sieboldi* (Jan), a species closely related, perhaps subspecifically, to *G. nasalis* (Cope). Bocourt (1883) was aware of this, and synonymized *sieboldi* and *nasalis* under the name *chalybeus*. In the following few paragraphs I shall refer to Peters' specimens (collected by Deppe) as *sieboldi*. *R. guttulatum* Cope represents a species group different from the above forms, and is most

closely related to *Geophis bicolor* Günther. At least one other known species of *Geophis* may have been the basis for the description of *chalybeus*. This third possibility is *G. dubius* (Peters). Most specimens of *dubius* have the internasals fused with the prefrontals, and would not fit the description of *chalybeus*. Some individuals of *dubius*, however, have the fusion on one side only, and in others the internasals are distinct on both sides. Among the latter is the type of *Elapoides rostralis* Jan, a synonym of *dubius*, but which I shall refer to as *rostralis* in the following discussion.

The subjective features listed by Wagler in the description of the genus *Geophis* indicate a rather highly specialized fossorial, or semi-fossorial, form. The head is indistinct from the neck, the rostrum is a depressed wedge, the mouth is inferior (hence the original name, *Catostoma*), the supraocular is small and triangular, the eye is minute, and the scales are smooth. Of the three forms under consideration, *rostralis* is the most specialized for a burrowing existence, *sieboldi* is intermediate, and *guttulatum* is the least modified. It is therefore not surprising that, of the three, *rostralis* has the least distinct head, a produced rostrum, an inferior mouth, the smallest supraocular, and the smallest eye; *sieboldi* is intermediate in most of these characteristics, although it is not out-ranked by *rostralis* in the produced nature of the rostrum and the inferior position of the mouth. In all of these features of the head, *guttulatum* is the least modified. It must be emphasized, however, that Wagler was not comparing these three forms with one another when he wrote his description.

*R. guttulatum* fares considerably better when the dorsal scales are considered. The smooth scales listed by Wagler apply to *guttulatum*, but would seem to eliminate *sieboldi* from consideration since its scales, even to the naked eye, are distinctly keeled. An intermediate condition exists in *rostralis*, which has smooth scales over most of the body, but faintly keeled scales above the vent region. These faint keels could easily be overlooked, particularly without adequate magnification and illumination. Furthermore, some specimens herein considered conspecific with the type of *rostralis* have completely smooth scales. Even when present the keeling in *rostralis* is too faint and too restricted to eliminate the species from consideration.

These comparisons indicate that *R. guttulatum*, at least in hindsight, does not convincingly fit the type description of *chalybeus*. This conclusion is strengthened by a closer comparison of *guttulatum* with Wagler's description. For example, it seems unlikely that Wagler would have described the eye of *guttulatum* as minute, since the eye diameter is as much as 1.4 times the distance from the eye to the lip (nearly the maximum for the genus). In contrast, the type of *rostralis* has an eye diameter 0.8 times the eye-to-lip distance. The supraocular in *guttulatum* is rather large and quadrangular

instead of small and triangular. Even acknowledging the subjective nature of Wagler's description, it is difficult to reconcile these differences.

Hopefully, the future rediscovery of Wagler's type will clearly establish the identity of *G. chalybeus*. At present our concept of *chalybeus* must be chosen from three alternatives: (1) the concept of Peters and Bocourt, based on the specimens collected by Deppe; (2) a *rostralis*-like form, which in hindsight fits the original description reasonably well; and (3) the currently accepted concept based on *guttulatum*. Despite the evidence that Deppe's specimens may have passed through Wagler's hands, the first concept is unacceptable because of the clear conflict between the specimens and the description regarding the presence or absence of keeling. The second alternative, although seemingly the most reasonable, is nonetheless based strictly on conjecture. I see no advantage in discarding one tentative concept in favor of a second, equally tentative. Since Smith's concept has been in use since 1941, I shall continue in this paper to consider *R. guttulatum* Cope a synonym of *G. chalybeus* (Wagler).

#### DEFINITION AND COMPOSITION OF THE GENUS

As currently recognized, the genus *Geophis* includes a wide diversity of forms, necessitating rather broad generic limits. The fusion of particular scales in a small minority of species adds to the difficulty of defining the genus concisely. In such instances, the character is stated as exemplified by the vast majority of species, with exceptions noted parenthetically. There are specimens which, because of individual variation, are not entirely consistent with the definition.

The following attempt to define the genus is not meant to be exhaustive. It is, rather, a collection of features of some diagnostic value in distinguishing *Geophis* from the genera with which it is most likely to be confused. Since the primary aim of this study has been the establishment of meaningful intrageneric units, the generic definition is supplemented by a characterization of each species group under the appropriate heading in the *Species Accounts*.

#### GENUS *Geophis* WAGLER

*Catostoma* Wagler, 1830:194 (Type species: *Catostoma chalybeum* Wagler, 1830, by monotypy).

*Geophis* Wagler, 1830:342 (Substitute name for *Catostoma* Wagler, 1830, to prevent confusion with *Catostomus* Lesueur, 1817, a fish; the type species is therefore *Catostoma chalybeum* Wagler).

*Rabdosoma* Duméril, 1853:440 (Type species: *Rabdosoma semidoliatum* Duméril, Bibron, and Duméril, 1854, *vide* Smith and Taylor, 1945:65).

*Colobognathus* Peters, 1859:275 (Type species: *Colobognathus hoffmanni* Peters, 1859, by monotypy).

*Geophidium* Peters, 1861:923 (Type species: *Geophidium dubium* Peters, 1861, by monotypy).

*Colophrys* Cope, 1868:130 (Type species: *Colophrys rhodogaster* Cope, 1868, by monotypy).

*Parageophis* Bocourt, 1883:435 (Type species: *Rabdosoma semidoliatum* Duméril, Bibron, and Duméril, 1854, by monotypy; proposed as a subgenus).

*Dirosema* Boulenger, 1894:298 (Type species: *Geophis bicolor* Günther, 1868, by subsequent designation of Dunn, 1928a:2).

Small neotropical colubrid snakes (maximum total length about 400 mm) with short or moderate tail lengths (less than one-fourth of total length); posterior vertebrae without hypapophyses; maxilla, palatine, pterygoid, and dentary toothed; 6–17 maxillary teeth, roughly equally spaced; dorsal scales in 15 or 17 rows; no reduction in number of dorsal scale rows on posterior part of body; dorsal scales smooth or keeled, with or without paired apical pits; ventrals 115–185; anal undivided; subcaudals in 19–66 pairs.

Dorsum of head with rostral, 2 internasals (fused with prefrontals in *cancellatus* and some *dubius*), 2 prefrontals entering orbit, frontal, 2 supraoculars (fused with frontal in *rhodogaster*, with parietals in *godmani*), and 2 parietals; nostril between 2 nasals; loreal more or less elongate, enters orbit; no preocular; 1 postocular (2 in *isthmicus*, *bicolor*, and *omiltemanus*); anterior temporal present or absent; supralabials 5–7, usually 6; one labial, usually fifth, markedly larger than others (except in *isthmicus*).

*Sulcus spermaticus* bifurcate; hemipenis simple or bilobed; a basal naked pocket; central part of organ spinous; distal part capitate or not, spinulate or papillate, calyculate at least apically.

The geographic range of the genus is from Tamaulipas and Chihuahua, Mexico, to northwestern Colombia.

Some 58 nominal forms have been proposed in the genus *Geophis*, some by original description and others by subsequent transfer from other genera. Many of these have since been relegated to other genera or to the synonymy of other forms within *Geophis*. I have found it necessary to add a single new form to the list. Of the available names, I recognize 33 as representing valid species of *Geophis*. The proposed names, and their status as recognized in this report, are given below.

Original Description	Present Status
<i>Geophis acutirostris</i> Taylor	<i>G. hoffmanni</i>
<i>Geophis albonuchalis</i> Günther	<i>Agrophis albonuchalis</i>
<i>Geophis annulatus</i> Peters	<i>Tropidodipsas sartori annulatus</i>
<i>Geophis anocularis</i> Dunn	<i>G. dubius</i>
<i>Geophis aquilonaris</i> Legler	<i>G. aquilonaris</i>
<i>Geophis bakeri</i> Taylor	<i>G. brachycephalus</i>
<i>Geophis bartholomewi</i> Brattstrom and Howell	<i>G. hoffmanni</i>
<i>Geophis bicolor</i> Günther	<i>G. bicolor</i>
<i>Geophis blanchardi</i> Taylor and Smith	<i>G. blanchardi</i>

<i>Colobognathus brachycephalus</i> Cope	<i>G. brachycephalus</i>
<i>Geophis cancellatus</i> Smith	<i>G. cancellatus</i>
<i>Geophis carinosus</i> Stuart	<i>G. carinosus</i>
<i>Catostoma chalybeus</i> Wagler	<i>G. chalybeus</i>
<i>Geophis chalybeus</i> var. <i>quadrangularis</i> Günther	<i>G. brachycephalus</i>
<i>Geophis championi</i> Boulenger	<i>G. championi</i>
<i>Geophis diplozeugus</i> Schmidt and Walker	<i>Atractus elaps</i>
<i>Colobognathus dolichocephalus</i> Cope	<i>G. brachycephalus</i>
<i>Geophidium dubium</i> Peters	<i>G. dubius</i>
<i>Geophis dugesii</i> Bocourt	<i>G. dugesi</i>
<i>Geophis dunni</i> Schmidt	<i>G. dunni</i>
<i>Geophis emmeli</i> Boettger	<i>Atractus emmeli</i>
<i>Geophis fulvoguttatus</i> Mertens	<i>G. fulvoguttatus</i>
<i>Geophis fuscus</i> Fischer	<i>G. dubius</i>
<i>Geophis godmani</i> Boulenger	<i>G. godmani</i>
<i>Geophis guentheri</i> Wucherer	<i>Atractus guentheri</i>
<i>Rhabdosoma guttulatum</i> Cope	<i>G. chalybeus</i>
<i>Colobognathus hoffmanni</i> Peters	<i>G. hoffmanni</i>
<i>Geophis immaculatus</i> , sp. nov.	<i>G. immaculatus</i>
<i>Geophis incomptus</i> Duellman	<i>G. incomptus</i>
<i>Atractus isthmicus</i> Boulenger	<i>G. isthmicus</i>
<i>Geophis laticinctus</i> Smith and Williams	<i>G. laticinctus</i>
<i>Geophis latifrons</i> Günther	<i>Atractus latifrons</i>
<i>Geophis latifrontalis</i> Garman	<i>G. latifrontalis</i>
<i>Rhabdosoma longiceps</i> Cope	<i>G. mutitorques</i>
<i>Geophis maculiferus</i> Taylor	<i>G. maculiferus</i>
<i>Geophis moestus</i> Günther	<i>G. brachycephalus</i>
<i>Rhabdosoma mutitorques</i> Cope	<i>G. mutitorques</i>
<i>Geophis mutitorques yucatanicus</i> Cole and Barbour	<i>Stenorrhina freminvilli apiata</i>
<i>Catostoma nasale</i> Cope	<i>G. nasalis</i>
<i>Geophis nigroalbus</i> Boulenger	<i>G. brachycephalus</i>
<i>Geophis nigrocinctus</i> Duellman	<i>G. nigrocinctus</i>
<i>Geophis omiltemana</i> Günther	<i>G. omiltemanus</i>
<i>Geophis petersii</i> Boulenger	<i>G. petersi</i>
<i>Catostoma psephotum</i> Cope	<i>Ninia psephota</i>
<i>Geophis reticulatus</i> Boulenger	<i>Atractus reticulatus</i>
<i>Colophrys rhodogaster</i> Cope	<i>G. rhodogaster</i>
<i>Elapoides rostralis</i> Jan	<i>G. dubius</i>
<i>Geophis ruthveni</i> Werner	<i>G. ruthveni</i>
<i>Geophis sallaei</i> Boulenger	<i>Oxyrhabdium modestum</i>
<i>Geophis schadenbergi</i> Fischer	<i>G. sallaei</i>
<i>Elapoides sieboldi</i> Jan	<i>G. sieboldi</i>
<i>Geophis semiannulatus</i> Smith	<i>G. semiannulatus</i>
<i>Rhabdosoma semidoliatum</i> Duméril, Bibron, and Duméril	<i>G. semidoliatus</i>
<i>Geophis stenorhynchus</i> Günther	<i>Xilophus stenorhynchus</i>
<i>Geophis tarascae</i> Hartweg	<i>G. tarascae</i>
<i>Geophis tecpanecus</i> Dugés	<i>Geatractus tecpanecus</i>
<i>Geophis unicolor</i> Fischer	<i>Enulius unicolor</i>
<i>Geophis zeledoni</i> Taylor	<i>G. zeledoni</i>



TABLE 7  
SELECTED FEATURES OF THE MAXILLA, ECTOPTERYGOID, AND HEMIPENIS IN THE  
SPECIES GROUPS OF *Geophis*

Species Group	Maxilla					Hemipenis	
	Anterior extension (supralabial level)	Number of teeth	Relative size of teeth	Posterior end	Anterior end of ectopterygoid	Apex	Capitation
<i>chalybeus</i>	suture of 1 and 2	9 to 15	subequal	large flange	bifurcate, compressed	slightly bilobed	strong
<i>championi</i>	suture of 2 and 3	7 to 9	subequal	acuminose	single, acuminose	single	absent
<i>dtubius</i>	suture of 1 and 2	10 to 17	increasing posteriorly	moderate flange	bifurcate, one arm knob-like, other long, blade-like	distinctly bilobed	weak
<i>latifrontalis</i>	supralabial 1	8 to 12	decreasing posteriorly	moderate flange	bifurcate, not compressed	single	weak
<i>omiltemanus</i>	suture of 1 and 2	12 to 17	subequal	large flange	bifurcate, compressed	slightly bilobed	strong
<i>semidoliatus</i>	supralabial 1	6 to 8	decreasing posteriorly	acuminose	bifurcate, not compressed	slightly bilobed	strong
<i>sieboldi</i>	suture of 2 and 3	7 to 15 (anterior tip toothless)	subequal	acuminose	single, acuminose	slightly bilobed	strong

TABLE 8  
SELECTED FEATURES OF THE SCUTELLATION AND HEAD FORM IN THE SPECIES GROUPS OF *Geophis*

Species Group	Ventrals		Subcaudals		Snout (into head length)	Anterior temporal	Head Scale Ratios		
	Males	Females	Males	Females			Internasal: Prefrontal	Supraocular: Loreal	Parietal: Head
<i>chalybeus</i>	149-185	154-183	41-66	37-63	0.32-0.40	absent	0.50-0.88 <sup>1</sup>	6.88-1.40 <sup>1</sup>	0.31-0.42
<i>championi</i>	123-143	130-145	33-41	26-32	0.44-0.49	absent	0.67-1.00	0.42-0.50	0.19-0.24
<i>dubius</i>	120-143	126-147	34-49	27-43	0.40-0.50	absent	0.55-1.00	0.33-0.64	0.22-0.30
<i>latifrontalis</i>	149-169	159-185	28-49	24-38	0.36-0.44	present (except in <i>blanchardi</i> )	0.45-0.60	0.50-0.75	0.24-0.38
<i>omiltemanus</i>	142-158	146-166	31-51	26-42	0.33-0.39	present	0.38-0.67	0.67-0.85	0.33-0.40
<i>semidoliatus</i>	131-160	141-179	22-30	19-33	0.37-0.44	absent	0.47-0.60	0.50-0.67	0.27-0.35
<i>sieboldi</i>	118-151	118-154	28-51	23-43	0.38-0.51	absent	0.33-0.62 <sup>2</sup>	0.33-0.67	0.22-0.34

<sup>1</sup> Does not include the atypical *G. aquilonaris* (see text).

<sup>2</sup> Does not include the atypical *G. petersi* (see text).

I have arranged the 33 recognized forms into 7 species groups, based primarily on characteristics of the maxilla, scalation, and body form. The unifying features of each group are given in the *Species Accounts*, and some of these features are summarized in Tables 7 and 8.

The following key is offered to facilitate the identification of the various species of *Geophis*. Certain useful "key" characteristics, such as the number of dorsal scale rows or the fusion of adjacent scales, are not characteristic of all members of a given species group. Such features tend to widely separate closely related forms within the body of the key. The proximity of related forms is entirely incidental, and the key does not necessarily indicate relationships.

KEY TO THE SPECIES OF *Geophis*

1.	Anterior temporal present .....	2
1 <sup>1</sup> .	Anterior temporal absent .....	8
2 (1).	Dorsal scales in 15 rows .....	3
2 <sup>1</sup> .	Dorsal scales in 17 rows .....	4
3 (2).	Internasals dark; infralabials 6 or 7; anterior edges of ventrals dark.....	
	..... <i>G. incomptus</i> (p. 118)	
3 <sup>1</sup> .	Internasals whitish; infralabials 5; ventrals immaculate whitish.....	
	..... <i>G. maculiferus</i> (p. 122)	
4 (2 <sup>1</sup> ).	Two postoculars; anterior temporal in contact with supralabials 5 and 6..	5
4 <sup>1</sup> .	One postocular; anterior temporal in contact with supralabial 5, not with supralabial 6 .....	6
5 (4).	Supralabials 6, the sixth much the largest; faint keeling on posterior dorsals; narrow light crossbands on a dark dorsum .... <i>G. omiltemanus</i> (p. 124)	
5 <sup>1</sup> .	Supralabials 7, none notably enlarged; dorsal scales smooth; dark blotches on a light dorsum .....	<i>G. isthmicus</i> (p. 121)
6 (4 <sup>1</sup> ).	Dorsum uniformly brownish or blackish (a light collar may be present in juveniles) .....	7
6 <sup>1</sup> .	Dorsum light with dark crossbands, often complete across venter .....	
	..... <i>G. semiannulatus</i> (p. 109)	
7 (6).	Chin creamish; ventrals light, mottled with dark; dorsum unicolor in all age groups .....	<i>G. latifrontalis</i> (p. 101)
7 <sup>1</sup> .	Chin blackish; venter checkered (uniformly blackish in large adults); light juvenile collar present .....	<i>G. mutitorques</i> (p. 104)
8 (1 <sup>1</sup> ).	Dorsal scales in 17 rows .....	9
8 <sup>1</sup> .	Dorsal scales in 15 rows .....	19
9 (8).	Dorsal scales distinctly keeled on at last posterior half of body .....	10
9 <sup>1</sup> .	Dorsal scales smooth, or keeled only above the vent region .....	13
10 (9).	Dorsum unicolor brownish to blackish .....	11
10 <sup>1</sup> .	Dorsum light with dark blotches or saddles .....	<i>G. dumni</i> (p. 153)
11 (10).	Loreal distinctly longer than combined nasals; greatest internasal length less than half as long as prefrontal suture; venter predominantly light, not banded .....	12
11 <sup>1</sup> .	Loreal shorter than combined nasals; greatest internasal length three-fourths as long as prefrontal suture; venter distinctly banded .....	
	..... <i>G. carinosus</i> (p. 81)	

12 (11).	Sum of ventrals and caudals, 171-191; dorsals moderately keeled on posterior half of body; scales of first dorsal row light-centered . . . . .	<i>G. sieboldi</i> (p. 171)	
12 <sup>1</sup> .	Sum of ventrals and caudals, 142-172; dorsals keeled on posterior two-thirds of body; scales of first dorsal row not distinctly light-centered . . . . .	<i>G. nasalis</i> (p. 160)	
13 (9 <sup>1</sup> ).	Supraocular distinct, frontal not in orbit . . . . .		14
13 <sup>1</sup> .	Supraocular absent, frontal enters orbit . . . . .	<i>G. rhodogaster</i> (p. 92)	
14 (13).	Head distinct from neck; eye diameter as long as loreal; snout not projecting beyond lower jaw . . . . .		15
14 <sup>1</sup> .	Head not, or scarcely, distinct from neck; eye diameter distinctly shorter than loreal; snout projecting well beyond lower jaw . . . . .		16
15 (14).	One postocular; sum of ventrals and caudals, 192-196 . . . . .	<i>G. chalybeus</i> (p. 57)	
15 <sup>1</sup> .	Two postoculars; sum of ventrals and caudals, 195-209 . . . . .	<i>G. bicolor</i> (p. 55)	
16 (14 <sup>1</sup> ).	Venter light; frontal half-again to twice as long as parietal suture; infralabials 6 . . . . .		17
16 <sup>1</sup> .	Venter checkered; frontal slightly longer than parietal suture; infralabials 7 . . . . .	<i>G. blanchardi</i> (p. 99)	
17 (16).	Dorsum unicolor . . . . .		18
17 <sup>1</sup> .	Dorsum with light lateral blotches on dark ground-color . . . . .	<i>G. fulvoguttatus</i> (p. 88)	
18 (17).	Internasals distinct; dorsal scales smooth; lip exposure of fifth supralabial nearly twice that of fourth . . . . .	<i>G. immaculatus</i> (p. 90)	
18 <sup>1</sup> .	Internasals often fused with prefrontals; dorsal scales usually keeled above vent region; lip exposure of fifth supralabial only slightly greater than that of fourth . . . . .	<i>G. dubius</i> (p. 84)	
19 (8 <sup>1</sup> ).	Supraocular distinct; color of rostral and prenasals similar to adjacent scales . . . . .		20
19 <sup>1</sup> .	Supraocular absent, parietal enters orbit; rostral and prenasal whitish, contrasting with adjacent head scales . . . . .	<i>G. godmani</i> (p. 72)	
20 (19).	Five supralabials, venter mostly light . . . . .		21
20 <sup>1</sup> .	Six supralabials; venter light or not . . . . .		22
21 (20).	Two supralabials behind eye; dorsum light with dark saddles . . . . .	<i>G. semidoliatus</i> (p. 133)	
21 <sup>1</sup> .	One supralabial behind eye; dorsum uniformly dark (light collar in young) . . . . .	<i>G. hoffmanni</i> (p. 155)	
22 (20 <sup>1</sup> ).	Internasals fused with prefrontals; dark dorsal saddles separated by narrow light interspaces; ventrals light and immaculate . . . . .	<i>G. cancellatus</i> (p. 129)	
22 <sup>1</sup> .	Internasals distinct; coloration not as above . . . . .		23
23 (22 <sup>1</sup> ).	Sum of ventrals and caudals less than 225; body without complete dark and light rings . . . . .		24
23 <sup>1</sup> .	Sum of ventrals and caudals more than 225; body with alternating dark and light rings . . . . .	<i>G. aquilonaris</i> (p. 52)	
24 (23).	Combination of black dorsum with narrow light crossbars and black venter with few light blotches . . . . .	<i>G. laticinctus</i> (p. 131)	
24 <sup>1</sup> .	Combination of dorsal and ventral coloration not as above . . . . .		25
25 (24 <sup>1</sup> ).	Head distinct from neck; eye contained twice in snout length; supraocular as long or longer than loreal . . . . .		26
25 <sup>1</sup> .	Head not or scarcely distinct from neck; eye contained thrice or more in snout; supraocular distinctly shorter than loreal . . . . .		28
26 (25).	Venter whitish, spotted with black; dorsum with dark crossbands or irregular markings . . . . .		27

26 <sup>1</sup> .	Venter immaculate whitish; dorsum blackish, with 0-7 narrow white crossbands on anterior third of body . . . . .	<i>G. dugesi</i> (p. 59)
27 (26).	Irregular blackish markings on neck, disappearing on posterior part of body . . . . .	<i>G. tarascae</i> (p. 65)
27 <sup>1</sup> .	Numerous narrow dark crossbands throughout length of body and tail . . . . .	<i>G. nigrocinctus</i> (p. 63)
28 (25 <sup>1</sup> ).	Dorsal scales smooth, or faintly keeled above the vent region . . . . .	29
28 <sup>1</sup> .	Dorsal scales keeled on at least the posterior half of body . . . . .	31
29 (28).	Sum of ventrals and caudals more than 170; dorsal scales keeled above the vent region; snout bluntly rounded from above . . . . .	30
29 <sup>1</sup> .	Sum of ventrals and caudals less than 170; dorsal scales smooth throughout length; snout acuminate from above . . . . .	<i>G. championi</i> (p. 70)
30 (29).	Venter predominantly blackish; rostral length less than one-third its distance from frontal . . . . .	<i>G. zeledoni</i> (p. 174)
30 <sup>1</sup> .	Venter whitish; rostral length more than half its distance from frontal . . . . .	<i>G. petersi</i> (p. 164)
31 (28 <sup>1</sup> ).	Loreal longer than combined nasals; greatest internasal length less than half as long as prefrontal suture; frontal a third longer than parietal suture . . . . .	32
31 <sup>1</sup> .	Loreal shorter than combined nasals; greatest internasal length as long as prefrontal suture; frontal twice as long as parietal suture . . . . .	<i>G. ruthveni</i> (p. 75)
32 (31).	Prefrontal suture more than three-fourths as long as parietal suture; dorsum grayish-brown, scales of first row with light centers; venter whitish . . . . .	<i>G. sallaei</i> (p. 168)
32 <sup>1</sup> .	Prefrontal suture less than three-fourths as long as parietal suture; dorsum unicolor, blotched, or with lateral stripe; scales of first row dark; dark pigment usually present along anterior edges of at least some ventrals . . . . .	<i>G. brachycephalus</i> (p. 146)

SPECIES ACCOUNTS

THE *chalybeus* GROUP

Dorsal scales in 15 or 17 rows, smooth throughout length; no apical pits. Head distinct from neck; snout short, bluntly rounded from above; eye large; rostral short, not produced posteriorly between internasals; pre- and postnasals subequal in length; internasals and prefrontals moderate; frontal forms long suture with supraocular; parietals long; supraocular large, forms almost entire dorsal margin of orbit; no anterior temporal. Ventrals 149-185 in males, 154-183 in females. Subcaudals 41-66 in males, 37-63 in females. Percentage tail of total length 16.5-23.2 in males, 15.1-22.1 in females.

Maxilla extends anteriorly to suture between first and second supralabials; anterior extension greater than that of palatine; maxilla slender to moderately stout, straight in lateral view; 9-15 long, slender maxillary teeth, subequal in length; first tooth at anterior tip of maxilla; posterior end of maxilla laterally compressed, forms large flange. Anterior end of ectopterygoid expanded into mitten-like flange. Postorbital bone present (absent in some *dugesi*).

Hemipenis (condition unknown in *chalybeus*) slightly bilobed at tip; *sulcus spermaticus* bifurcate; naked basal pocket poorly developed; large spines in central part of organ; distal part capitate, weakly calyculate, spinulate; M. retractor penis magnus divides into two slips at apex of hemipenis.

I include six forms in this group (Fig. 3): *G. aquilonaris*, *G. bicolor*, *G. chalybeus*, *G. dugesi*, *G. nigrocinctus*, and *G. tarascae*. Geographically, the group ranges from Chihuahua southward in the Sierra Madre Occidental to

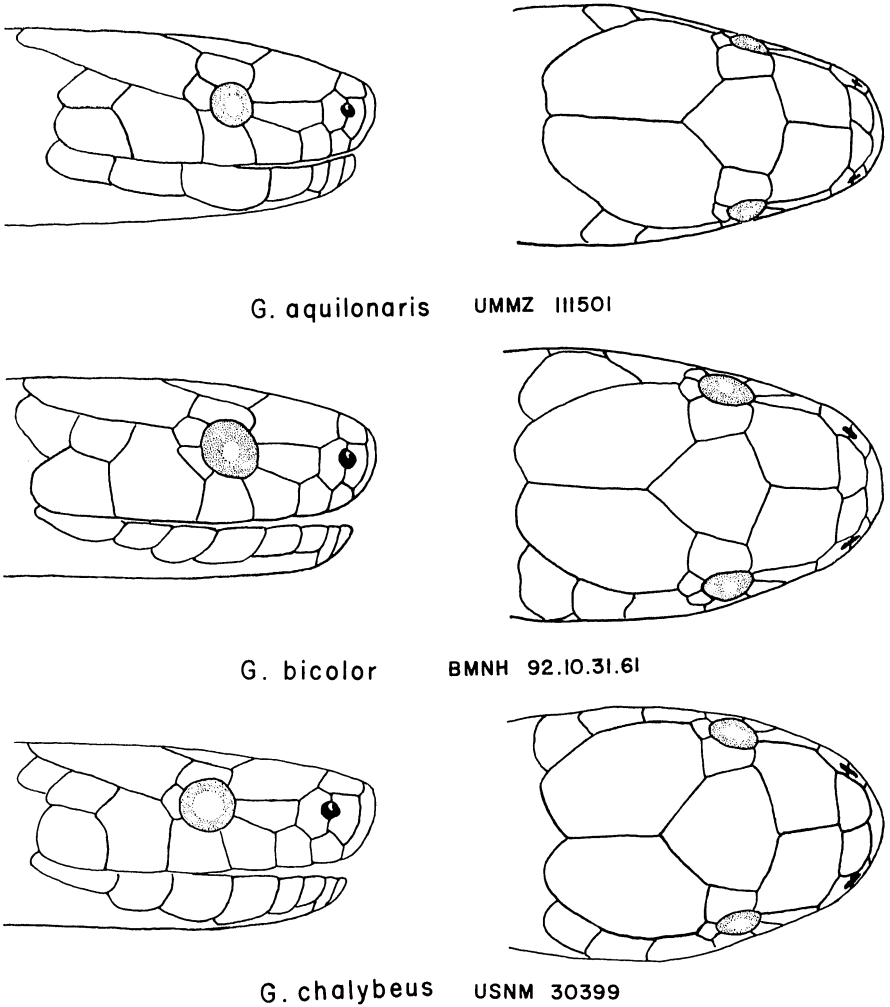


FIG. 3. Dorsal and lateral head scutellation in members of the *chalybeus* group. Scale: *G. aquilonaris*, about 5×; *G. bicolor*, about 5×; *G. chalybeus*, about 4.5×.

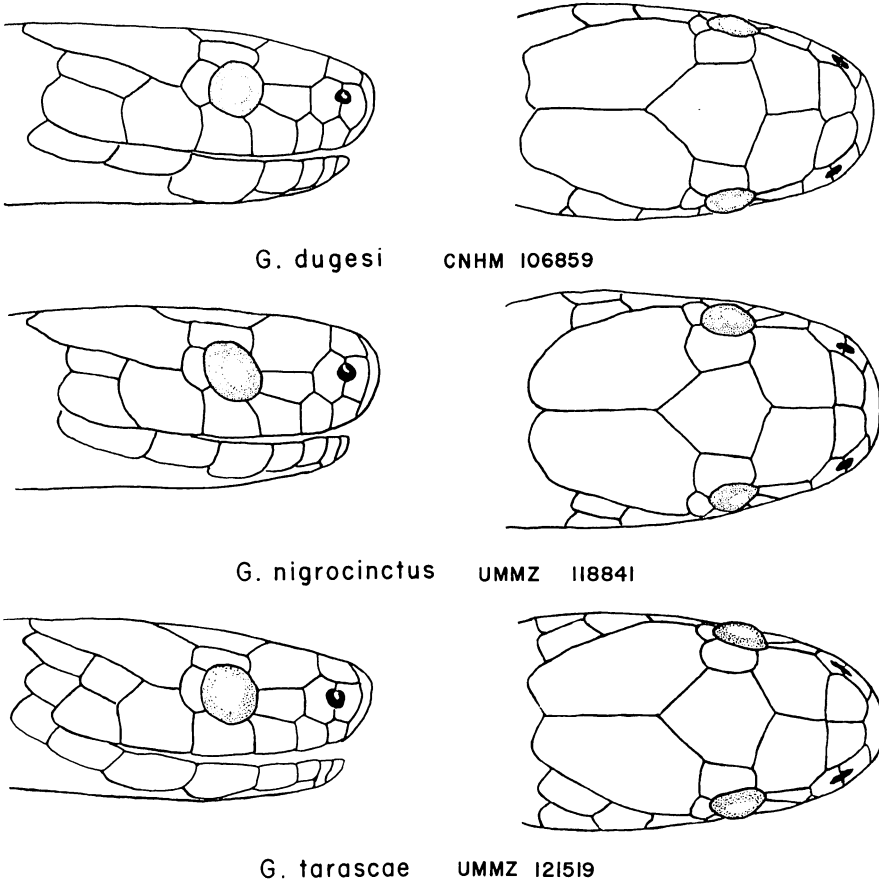


FIG. 3 (Cont.). Scale. *G. dugesi*, about 5.5 ×; *G. nigrocinctus*, about 5 ×; *G. tarascae*, about 5 ×.

the highlands of Jalisco, the Sierra de Coalcoman and Cordillera Volcanica of Michoacan, and eastward along the southern edge of the Mexican Plateau to Veracruz (Fig. 4).

The most distinctive member of the group, *G. aquilonaris*, occupies the northern extreme of the geographic range. Like *dugesi*, *nigrocinctus*, and *tarascae*, *G. aquilonaris* has 15 dorsal scale rows. In all other respects, however, the first three species are closer to the species with 17 scale rows (*bicolor*, *chalybeus*) than to *aquilonaris*. Compared with its relatives to the south, *aquilonaris* has a smaller eye, a distinctive color pattern of alternating dark and light rings, a higher number of ventrals and subcaudals, shorter internasals and nasals, and longer prefrontals and loreals.

Among the other members of the group, *G. bicolor* and *G. chalybeus* are distinguished by the presence of 17 dorsal scale rows. These two nominal forms differ in minor respects, and although I retain the currently accepted nomenclature, it is important to note that three, not two, populations are involved. In the population from Mirador, Veracruz (*chalybeus*), there is one postocular, an immaculate venter, and perhaps a slightly lower number of ventrals; the syntypes of *bicolor*, from the vicinity of Mexico City, have two postoculars and an immaculate venter; specimens from Jalisco referred to *bicolor* (initially by Boulenger, 1894) have two postoculars and a spotted venter. In all other features these populations are similar. It is reasonable to anticipate that a single, polytypic species will be indicated as specimens from intervening localities become available.

Of the remaining three species, all of which have 15 rows of dorsal scales, *G. nigrocinctus* and *G. tarascae* are closely related. The most impressive evidence for this affinity is the presence in both forms of long, needle-like teeth, borne on a delicate maxilla. Although the maxillary teeth in the other members of this species group are long and slender, none attain the needle-like quality of those in *nigrocinctus* and *tarascae*. Externally, the two are distinguished primarily by coloration. *G. nigrocinctus* has a series of narrow dark crossbands that tend to become less conspicuous on the posterior part of the body; in *tarascae*, the dorsum has irregular dark markings on the neck, but is blackish posteriorly. Both forms have dark mottling on the dorsal surface of the head, but the dark blotches are fewer and larger (coalesced) in *nigrocinctus*; the venter is spotted with black in both forms, but the spots are larger in *nigrocinctus*. The two nominal forms are known only from their respective type localities in the highlands of Michoacan; these localities are separated by the arid Tepalcatepec Valley. Their differences may eventually be considered subspecific.

*G. dugesi*, although similar to *nigrocinctus* and *tarascae*, is clearly the most distinctive of the three. The maxillary teeth, although relatively long, are not needle-like; the ventrals are immaculate, and the head does not have the mottled appearance of *nigrocinctus* and *tarascae*. The dorsal coloration is variable in *dugesi*. For at least most of the body length, the dorsum is blackish; there is a small whitish spot near the center of each scale in the lateral rows, much as in *bicolor* and *chalybeus*. Most specimens also have several narrow light crossbands on the anterior part of the body. Neither the banded nor unbanded patterns have much in common with the dorsal coloration of *nigrocinctus* and *tarascae*, although in all three the pattern is restricted to, or most pronounced on, the anterior part of the body. Specimens of *dugesi* from Michoacan, in contrast to other members of the group, have no postorbital bone. Two recently acquired specimens from southern Sinaloa, which are tentatively referred to *dugesi*, possess the postorbital. The



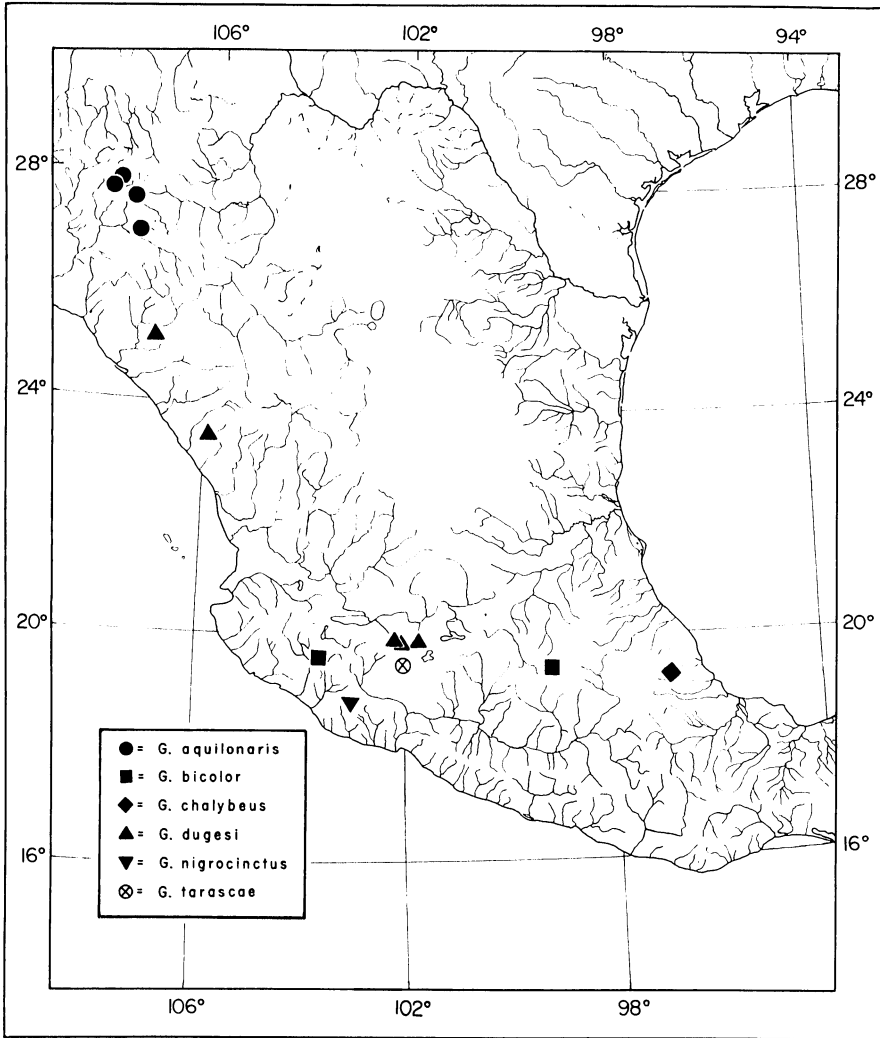


FIG. 4. Locality records for members of the *chalybeus* group. The Sinaloan specimens are only tentatively referred to *G. dugesi*.

latter specimens may represent a distinct species, but at present it seems preferable to admit intraspecific variation in the presence or absence of the postorbital bone.

It is clear that *G. aquilonaris* is unique among the members of the *chalybeus* group, and that its origin preceded that of the other species with 15 scale rows. Judged from its present distribution, the *aquilonaris* stock prob-

ably became isolated to the north of its relatives; available material indicates that its distribution is allopatric to other members of the group.

Of the remaining species, *G. bicolor*, with two postoculars, 17 scale rows, seven infralabials, and a generalized maxilla, appears to be the most generalized. *G. chalybeus*, which has a single postocular, is apparently the result of a relatively recent, *in situ* differentiation from an isolated eastern population of the *bicolor* stock, comparable to the differentiation of *bicolor* itself into two populations with different ventral patterns.

There is little doubt that *G. nigrocinctus*, *G. tarascae*, and *G. dugesi* have been derived from a *bicolor*-like form. This derivation has involved a reduction in the number of dorsal scale rows (from 17 to 15), postoculars (from 2 to 1), and infralabials (from 7 to 6). The number of times that these reductions have taken place is not clear. The reduced number of scale rows, postoculars, and infralabials is characteristic of *dugesi* as well as *nigrocinctus* and *tarascae*, suggesting a common origin and subsequent differentiation of the three. The ventral coloration, however, does not support this suggestion; the spotted venter is shared by *nigrocinctus*, *tarascae*, and specimens of *bicolor* from Jalisco, and the immaculate venter by *dugesi*, *chalybeus*, and specimens of *bicolor* from "Mexico City." Furthermore, the only highland masses connecting the known ranges of *nigrocinctus* (Sierra de Coalcoman of Michoacan) and *tarascae* (Cordillera Volcanica of Michoacan) are to the west, in the mountains of Jalisco. These western highlands represent the probable dispersal center of the ancestral stock of these closely related forms, and are currently occupied by the populations of *bicolor* having spotted venters. The distribution of the forms with immaculate venters is not as suggestive. Whether these similarities in ventral coloration reflect genetic affinity, with the implication that the reduction to 15 scale rows occurred independently in the *dugesi* and *nigrocinctus-tarascae* stocks, or a parallel development in isolated populations cannot be determined at present. Whatever their origin, the distinctive dentition and dorsal coloration of *nigrocinctus* and *tarascae* indicate that they have diverged from the *bicolor* stock to a greater degree than has *dugesi*. The same features indicate a relatively recent differentiation between *nigrocinctus* and *tarascae*.

#### *Geophis aquilonaris* Legler

*Geophis aquilonaris* Legler, 1959:329, figs. 1-2.

HOLOTYPE.—UK 44265, an adult female from 23 miles S and 1.5 miles E of Creel, Chihuahua, Mexico; July 23, 1957; presented by natives to R. H. Pine. There are five paratypes, all from Chihuahua: UK 44266, same date as holotype; UMMZ 117770, Mojarachic; UMMZ 111501-02 and 117771, Maguarachic.

DISTRIBUTION.—Known only from the western slopes of the Sierra Madre Occidental of southwestern Chihuahua, Mexico; 1500–2100 meters above sea level.

DIAGNOSIS.—Distinguished from other members of the genus by the combination of (1) dorsal scales in 15 rows, smooth throughout length; (2) no anterior temporal; (3) a high number of subcaudals (55–66); and (4) color pattern of alternating dark and light rings, usually complete across venter.

DESCRIPTION.—Head moderately distinct from neck; snout short, bluntly rounded from above, scarcely projecting beyond lower jaw; rostral inconspicuous from above, not produced posteriorly between internasals, its length less than one-sixth its distance from frontal; internasals broader than long, slightly less than half as long as prefrontal suture; prefrontal suture two-thirds to three-fourths as long as frontal; frontal as long as broad, slightly angulate anteriorly, forms long suture with supraocular; parietals long, their median suture longer than frontal; supraocular large, quadrangular, slightly shorter than loreal, forms almost entire dorsal margin of orbit; one postocular, higher than long, less than half as large as supraocular.

Nasal divided, pre- and postnasals about equal in length, their combined length slightly less than that of loreal; loreal moderate, contained less than twice in snout length, half-again as long as eye diameter; eye moderate, contained about thrice in snout length, its vertical diameter equal to its distance from lip; supralabials 6, third and fourth in orbit, fifth largest and in contact with parietal; no anterior temporal; one posterior temporal, not fused with nuchal along parietal margin.

Mental broadly rounded, much broader than long, separated from chinshields by first pair of infralabials; infralabials 6, pairs 1–4 contact anterior chinshields; anterior chinshields twice as long as broad; posterior chinshields in broad medial contact, half as large as anterior pair; 2–3 rows of gulars separate chinshields from first ventral.

Dorsal scales in 15 rows, smooth throughout length; no apical pits. Ventrals in five males, 172–185 (177.0); in four females, 173–183 (179.8); anal undivided; subcaudals in five males, 59–66 (62.0); in four females, 55–63 (57.8). Total ventrals plus caudals, 228–246. Total length of largest male, 462 mm; tail, 91 mm (19.7%); largest female, 461 mm; tail, 90 mm (19.5%).

Maxilla extends anteriorly to level of first supralabial; anterior extension greater than that of palatine; 11–12 long, shallowly curved maxillary teeth, subequal in length; first tooth at anterior tip of maxilla; posterior end of maxilla laterally compressed, expanded into large flange; anterior end of ectopterygoid compressed into mitten-like flange. Postorbital bone present, slender.

Hemipenis extends posteriorly to ninth or tenth subcaudal; basal part of

organ bears minute spinules, a naked basal pocket, and 3-4 large spines distally. Central part of organ bears about 35 medium spines. Distal part of hemipenis capitate, calyculate, and spinulate; apex slightly bilobed. *Sulcus spermaticus* bifurcates opposite subcaudal 6; each branch reaches apex. *M. retractor penis magnus* divides into two slips; one slip attaches to each lobe of apex.

Ground color of head grayish- to brownish-black; prefrontals with or without a pair of light spots; a whitish collar, interrupted middorsally in some specimens, occupies the posterior tips of the parietals, the temporals, part of the fifth and all of the sixth supralabials, one or more rows of nuchals, and the posterior parts of the chin; an elongate light spot occupies the medial parts of both parietals, often contiguous with collar. Body with alternating dark (brownish or blackish) and light (whitish) rings; 29-39 light rings on body, 12-17 on tail; each light ring alternately one and two scales long, jagged in outline; light rings lengthen toward venter, occupy 3-4 ventrals, usually complete across venter; dark rings 3-6 scales long mid-dorsally, narrow ventrally. Dorsum and venter of tail similar to body.

VARIATION.—The left side of the holotype, and both sides of UMMZ 117771, have only five supralabials; the fifth and sixth are fused. The type has a small preocular on the left side, representing a detached part of the loreal. An azygous scale separates the first pair of infralabials in UMMZ 117771.

In UMMZ 117770 and BMNH 1911.12.12.31 a small "anterior temporal" separates the posterior part of the fifth labial from the parietal; this scale is followed by a normal, single posterior temporal. In BMNH 1911.12.12.30, the fifth labial is completely separated from the parietal by an elongate anterior temporal, and two posterior temporals surmount the sixth labial. This temporal condition is similar to the temporal region in the *latifrontalis* group.

Variation in coloration involves the number and completeness of the rings; although complete across the venter in most specimens, the majority of the rings in UMMZ 111502 and UMMZ 117771 are incomplete. The dark ground color is blackish except in UMMZ 111501-02; in the latter it is brown.

REMARKS.—The maxillary tooth counts presented here are five or six higher than given in the original description; this discrepancy reflects the inclusion of sockets in my counts. Legler (1959:330) also stated that in the type the last tooth was longest and separated from those preceding it by a diastema (he reported the diastema absent in a paratype); in maxillae examined by me the teeth are evenly spaced and the last tooth is shorter than the others.

SPECIMENS EXAMINED (9).—MEXICO: **Chihuahua**: 23 mi S and 1.5 mi E Creel, UI 44265-66; Maguarachic, UMMZ 111501-02, 117771, 118925; Mojarachic, UMMZ 117770; Joquiro (Yoquivo), Tarahumari Sierra, BMNH 1911.12.12.30-31.

*Geophis bicolor* Günther

*Geophis bicolor* Günther, 1868:416.; Dunn, 1928a:2; Smith and Taylor, 1945:67.

*Geophis chalybeus*, Bocourt (in part), 1883:530.

*Dirosema bicolor*, Boulenger (in part), 1894:298; Mocquard, 1908:878.

*Rhabdosoma bicolor*, Cope (in part), 1885a:385; Cope (in part), 1887:85.

*Catostoma bicolor*, Amaral, 1929:191.

**HOLOTYPE**.—Originally four syntypes, BMNH 1946.1.1.63-66, from the neighborhood of Mexico City, Mexico; Doorman, collector. BMNH 1946.1.1.64 is herein chosen as lectotype.

**DISTRIBUTION**.—Known from the type locality and two localities in Jalisco; the southern edge of the Mexican Plateau between 1800-2600 meters above sea level.

**DESIGNATION OF A LECTOTYPE**.—The original description is based on the four syntypes. The only feature listed that applies to a single specimen is size, which is given for the largest specimen. This specimen is BMNH 1946.1.1.64, which, in addition to being mentioned specifically in the description, has the advantage of being an adult male in a good state of preservation. It is, therefore, selected as lectotype; the specimen has 159 ventrals, 47 subcaudals, and a total length of 372 mm. The paralectotypes, BMNH 1946.1.1.63 and 1946.1.1.65-66, are either in a poor state of preservation (the former) or are juveniles (the latter two).

**DIAGNOSIS**.—Distinguished from other members of the genus by the combination of (1) dorsal scales in 17 rows, smooth throughout length; (2) no anterior temporal; (3) two postoculars; (4) more than 160 ventrals in females; (5) dorsum blackish, scales of lateral rows with white centers; and (6) ventrals whitish, immaculate, or spotted with black.

**DESCRIPTION**.—Head distinct from neck; snout short, rounded from above, scarcely projecting beyond lower jaw; rostral short, not produced posteriorly between internasals, its length less than one-fourth its distance from frontal; internasals broader than long, half as long as prefrontal suture; prefrontal suture half as long as frontal; frontal as long as broad, angulate anteriorly, forms long suture with supraocular; parietals long, their median suture as long as frontal; supraocular large, slightly longer than loreal, forms almost entire dorsal margin of orbit; two postoculars, the upper as high as long and about half as large as supraocular, the lower higher than long.

Nasal divided, pre- and postnasals about equal in length, their combined

length slightly shorter than loreal; loreal contained twice in snout length, about as long as eye diameter; eye large, contained twice in snout length, its vertical diameter one-third longer than its distance from lip; supralabials 6, third and fourth in orbit, fifth largest and in contact with parietal; no anterior temporal; one posterior temporal, not fused with nuchals along parietal margin.

Mental rounded, much broader than long, separated from chinshields by first pair of infralabials; infralabials 7, first four pairs in contact with anterior chinshields; anterior chinshields half-again as long as broad, longer than posterior pair; posterior chinshields in contact anteriorly, separated posteriorly; two rows of gulars separate chinshields from first ventral.

Dorsal scales in 17 rows, smooth throughout length; no apical pits. Ventrals in three males, 149–159 (153.0); in five females, 161–168 (164.8); anal undivided; subcaudals in three males, 46–50 (47.7); in five females, 38–46 (41.4). Ventrals plus caudals, 195–209. Total length of largest male, 402 mm; tail, 90 mm (22.4%); largest female, 390 mm; tail, 67 mm (17.2%).

Maxilla extends anteriorly to suture between first and second supralabials; anterior extension greater than that of palatine; 13–15 long, curved, maxillary teeth, subequal in length; first tooth at anterior tip of maxilla; posterior end of maxilla laterally compressed, expanded into large flange; anterior end of ectopterygoid compressed, expanded into mitten-like flange. Postorbital bone present, slender.

Hemipenis extends posteriorly to level of subcaudal 11; basal part of organ bears numerous minute spinules, a large spine near base, and three large distal spines; naked basal pocket poorly defined. Central part of organ bears about 20 medium spines. Distal part of hemipenis capitate, with obvious free edge; capitulum calyculate, spinulate; apex slightly bilobed. *Sulcus spermaticus* bifurcates opposite eighth subcaudal; each branch reaches apex. *M. retractor penis magnus* bifurcates near apex; one slip attaches to each lobe.

Dorsum of head dark brown or blackish; anterior head scales with small creamish spots; ventral parts of supralabials white or creamish; dorsum of body dark brown or blackish; scales in first four rows (occasionally in other rows) with whitish spot in center; spots usually most prominent in scale rows 1 and 4. Chin region whitish; infralabials spotted with brown or black; lateral edges of ventrals dark brown or black; midventral area whitish, immaculate, or spotted with brown or black; spots form two imperfect longitudinal rows; subcaudals blackish, white along their posterior margins.

VARIATION.—The only significant variation in scutellation occurs in the temporal region. In BMNH 92.9.5.44 a small anterior temporal separates the fifth labial from the parietal; its size and shape do not correspond to the temporals found in the *latifrontalis* and *omiltemanus* groups. A single

short posterior temporal is present in all specimens, but it is followed by one or two scales that are often technically within the temporal region. On the left side of BMNH 92.10.31.61, the posterior temporal is fused with the scales posterior to it.

Variation in color pattern is largely geographic, and involves the ventral surface. In the syntypes, the dark dorsal coloration reaches only the edge of the ventrals; the gross appearance of the venter (excluding the subcaudal surface) is immaculate white. Specimens from Jalisco, however, have extensive blackish or brownish spotting on the ventrals. The spots (excluding the dark anterolateral edges of the ventrals) tend to occur in two longitudinal rows since each ventral tends to have two spots, one on each side of the midline. This arrangement is very imperfect. The spots are larger, and therefore more confluent, in specimens from La Cumbre de los Arrastrados than in the single specimen from the slopes of Nevado de Colima. Unfortunately, the former locality cannot be found on any map, nor in any gazetteer, examined by me.

REMARKS.—The coloration in a recently preserved specimen, UMMZ 125287, is blackish; the lip and chin region are creamish; the light spots on the dorsal scales and the light areas of the venter are white.

Smith and Taylor (1950:329) questioned the accuracy of the type locality. Although "the neighborhood" of Mexico City should perhaps be interpreted loosely, I find no reason to question the occurrence of *bicolor* in that general region of the southern edge of the Mexican Plateau. The syntypes differ from the specimens from Jalisco in ventral coloration, and the closely related *G. chalybeus* is known only from near Mirador, Veracruz. The type locality occupies a logical position in this geographic picture.

SPECIMENS EXAMINED (8).—MEXICO: **Distrito Federal**: neighborhood of Mexico City, BMNH 1946.1.1.63–66. **Jalisco**: La Cumbre de los Arrastrados, BMNH 92.9.5.43–44, 92.10.-31.61; N slope Nevado de Colima, UMMZ 125287.

### *Geophis chalybeus* Wagler

*Catostoma chalybeum* Wagler, 1830:194 (*Geophis* substituted for *Catostoma*, *op. cit.*: 342); Amaral (in part), 1929:191.

*Geophis chalybeus*, Bocourt (in part), 1883:530; Günther (in part), 1893:87; Boulenger (in part), 1894:318; Smith, 1941*b*:3; Smith and Taylor, 1945:67.

*Rhabdosoma guttulatum* Cope, 1885*a*:385 (types, USNM 25024–25, Mirador, Veracruz and USNM 30399, "Veracruz").

*Geophis bicolor*, Günther (in part), 1893:91.

*Dirosema bicolor*, Boulenger (in part), 1894:298.

*Atractus chalybeus*, Cope (in part), 1900:1232.

*Catostoma bicolor*, Amaral (in part), 1929:191.

HOLOTYPE.—Unknown, from "Mexico"; perhaps destroyed (see p. 37).

DISTRIBUTION.—Known only from Mirador, Veracruz, Mexico; about 1150 meters above sea level.

DIAGNOSIS.—Distinguished from other members of the genus by the combination of (1) dorsal scales in 17 rows, smooth throughout length; (2) no anterior temporal; (3) one postocular; (4) fewer than 160 ventrals in females; (5) dorsum brown, scales in lateral rows spotted with cream; and (6) ventrals creamish, immaculate.

DESCRIPTION.—The description is based on the syntypes of *R. guttulatum* Cope. Head distinct from neck; snout short, rounded from above, scarcely projecting beyond lower jaw; rostral short, not produced posteriorly between internasals, its length less than one-fourth its distance from frontal; internasals broader than long, about half as long as prefrontal suture; prefrontal suture one-half as long as frontal; frontal as long as broad, slightly angulate anteriorly, forms long suture with supraocular; parietals long, their median suture as long as frontal; supraocular large, as long as loreal, forms almost entire dorsal margin of orbit; one postocular, higher than long, one-third as large as supraocular.

Nasal divided, pre- and postnasals subequal in length, their combined length as long as or longer than loreal; loreal contained slightly more than twice in snout length, as long as eye diameter; eye large, contained more than twice in snout, its vertical diameter a third greater than its distance from lip; supralabials 6, third and fourth in orbit, fifth largest and in contact with parietal; no anterior temporal; one posterior temporal, not fused with nuchal along parietal margin.

Mental rounded, much broader than long, separated from chinshields by first pair of infralabials; infralabials 7, first four pairs in contact with anterior chinshields; anterior chinshields much longer than broad; posterior chinshields half as large as anterior pair, in contact medially; two rows of gulars separate chinshields from first ventral.

Dorsal scales in 17 rows, smooth throughout length; apical pits absent. Ventrals in three females, 154–155; anal undivided; subcaudals in three females, 38–41. Ventrals plus caudals, 192–196. Total length of largest female, 305 mm; tail, 50 mm (16.4%).

Maxilla extends anteriorly to suture between first and second supralabials; anterior extension greater than that of palatines; 13 long, curved maxillary teeth, subequal in length; first tooth at anterior tip of maxilla; posterior end of maxilla laterally compressed, expanded into large flange; anterior end of ectopterygoid expanded into mitten-like flange. Postorbital bone present.

Hemipenial characteristics unknown.

Dorsum of head and body brownish; lower parts of supralabials yellowish-



cream; dorsal scales of first four rows with creamish spot in center. Venter yellowish-cream, immaculate.

VARIATION.—The three syntypes of *guttulatum* are similar in scutellation and coloration. One of the three is aberrant in the number of dorsal scale rows. In USNM 25024, the number of rows is 15 throughout much of the body length; in these areas, the paravertebral scales are obviously enlarged. At several points along the body, one or both of these enlarged paravertebrals is represented by two scales of normal size, this increasing the number of rows to 16 or 17, respectively. The unusually large size of the paravertebrals where 15 scale rows are present, and the 17 scale rows in the other syntypes, indicate that the normal number of rows in the species is 17.

SPECIMENS EXAMINED (3).—MEXICO: **Veracruz**: Mirador, USNM 25024–25; probably Mirador, USNM 30399.

### *Geophis dugesi* Bocourt

*Geophis dugesi* Bocourt, 1883:573, pl. 37, fig. 1; Günther, 1893:91; Boulenger, 1894:317; Smith and Taylor, 1945:68.

*Elapoides dugesi*, Cope, 1885a:386; Cope, 1887:85.

*Catostoma dugesi*, Amaral, 1929:191.

HOLOTYPE.—MNHN 83–278, a male from Tangancicuaro, Mexico; received from Dugès, collected by O. Navarro.

DISTRIBUTION.—Known from several localities along the southern edge of the Mexican Plateau in Michoacan, between 1750–2050 meters above sea level, and perhaps from southern Sinaloa (see *Remarks*).

DIAGNOSIS.—Distinguished from other members of the genus by the combination of (1) dorsal scales in 15 rows, smooth throughout length; (2) no anterior temporal; (3) supraocular as long as loreal; (4) dorsum brownish or blackish, with 0–7 narrow light crossbands on anterior part of body; and (5) ventrals creamish or white, immaculate.

DESCRIPTION.—Head distinct from neck; snout short, bluntly rounded, scarcely projecting beyond lower jaw; rostral not produced posteriorly between internasals, its length less than one-fourth its distance from frontal; internasals large, broader than long, more than half as long as prefrontal suture; prefrontal suture about one-half as long as frontal; frontal as long as or slightly longer than broad, slightly angulate anteriorly, forms long suture with supraocular; parietals long, their median suture as long as frontal; supraocular large, as long or longer than loreal, forms almost entire dorsal margin of orbit; one postocular, higher than long, smaller than supraocular.

Nasal divided, pre- and postnasals subequal in length, their combined length greater than that of loreal; loreal short, contained more than twice in snout length, about equal to eye diameter; eye large, contained twice in snout, its vertical diameter almost half-again its distance from lip; supralabials 6, third and fourth in orbit, fifth largest and in contact with parietal; no anterior temporal; one posterior temporal, not fused with nuchals along parietal margin.

Mental rounded, much broader than long, separated from chinshields by first pair of infralabials; infralabials 6, pairs 1-4 in contact with anterior chinshields; anterior chinshields nearly twice as long as broad; posterior chinshields in contact medially, smaller than anterior pair; 1-3 rows of gulars separate chinshields from first ventral.

Dorsal scales in 15 rows, smooth throughout length; apical pits absent. Ventrals in five males, 150-162 (154.4); in two females, 160-164; anal undivided; subcaudals in five males, 41-43 (42.0); in two females, 37-39. Ventrals plus caudals, 192-204. Total length of largest male, 325 mm; tail, 62 mm (19.1%); larger female, 318 mm; tail, 55 mm (17.3%).

Maxilla extends anteriorly to suture between first and second supralabials; anterior extension greater than that of palatine; maxilla moderately stout, bears 9-10 long, slender teeth, subequal in length; first tooth at anterior tip of maxilla; posterior end of maxilla laterally compressed, expanded into large flange; anterior end of ectopterygoid expanded into mitten-like flange; no postorbital bone.

Hemipenis extends posteriorly to level of ninth subcaudal; basal part of organ bears numerous spinules, and, distally, two large spines; no well-developed naked pocket. Central part of hemipenis bears about 25 medium spines and hooks. Distal part of organ capitate, weakly calyculate, spinulate; apex slightly bilobed. *Sulcus spermaticus* bifurcates opposite subcaudal 7; each branch reaches apex. *M. retractor penis magnus* divides into two slips at apex of hemipenis; one slip attaches to each lobe.

Ground color of dorsum dark brownish- or bluish-black; anterior head scales often flecked with white or cream; lower parts of supralabials creamish or whitish; 0-7 narrow whitish crossbands on anterior part of body, the first forming a collar behind head; collar often heavily suffused with dark pigment, sometimes scarcely discernible; light crossbands 2-3 scales long, about one-fifth as long as interspaces; scales of interspaces uniformly dark; last light crossband diffuse, barely perceptible; scales in first row mostly light, with dark anterodorsal edges; scales in other rows (except in the interspaces between the light crossbands) dark with a light spot near center; light spots most consistent and most conspicuous in lateral rows, but often present on scales of dorsal rows. Chin creamish, mottled with black along sutures between infralabials and chinshields; ventrals immaculate whitish,

with black lateral edges; subcaudals predominantly whitish, with dark mottling scattered or concentrated in midventral area.

VARIATION.—The prefrontals of UI 17703 are partially fused with one another; the anterior halves are separated by a suture, but the posterior halves are confluent. A transverse suture divides the left supraocular into anterior and posterior parts in SU 4408. SU 4407 has five supralabials, the result of the fusion of the fifth and sixth; the composite scale is in contact with the parietal anteriorly, and separated from that scale posteriorly by a narrow posterior temporal. The same specimen has five infralabials on the right side; the second and third are fused, leaving only three infralabials in contact with the anterior chinshields.

The dorsal color pattern is highly variable. The presence or absence of the light collar is apparently age-dependent; it is most distinct in smaller individuals, such as SU 4407. In larger specimens the collar is obliterated by dark pigment; the oblitative process begins middorsally and proceeds laterally. The variation in the other light crossbands is individual rather than ontogenetic. The light bands may be clearly defined, about two scales long, and composed of entirely whitish scales, or diffuse light areas, usually more than two scales in length, formed by dark-bordered, light-centered scales. BMNH 97.3.10.3 incorporates both types. In this specimen the light collar is obliterated dorsally; following the collar are two distinct and three indistinct light bands, separated by areas of completely dark scales (except in the lateral rows). On the posterior part of BMNH 97.3.10.3 all of the scales, dorsal as well as lateral, have light centers. CNHM 106859 has a collar followed by two distinct bands, but no indistinct ones; in contrast, SU 4408 has a dorsally interrupted collar followed by two indistinct and no distinct bands. UI 17703 has a faint indication of a single indistinct band.

This variability in dorsal coloration is probably of evolutionary significance. The light-centered dorsal scales are characteristic of *G. bicolor* and *G. chalybeus*, the presumed ancestral stock of *G. dugesi*. The light crossbands in *dugesi* have clearly developed by the expansion of the light centers of some scales, and the obliteration of the light pigment on the scales of the interspaces.

Except for the narrow dark area on the lateral edges of each ventral, the ventrals are immaculate in all specimens examined. The subcaudals may be immaculate (CNHM 106859), lightly edged with dark pigment (BMNH 97.3.10.2–3), or bear scattered dark mottling (SU 4407). In all instances, the subcaudal surface is predominantly light.

REMARKS.—Dugès (1884) reported that according to Navarro the light bands are white in living specimens. The same publication, and an error in Bocourt's original description, have resulted in considerable confusion con-

cerning the type specimen. The type, collected by Navarro, was given to Dugès, who in turn sent the specimen to the museum in Paris, where it was described as a new species by Bocourt. Navarro subsequently acquired a second specimen, reported on by Dugès in 1884. In this paper, Dugès presented a translation of Bocourt's original description, and parenthetically added comments about the second specimen he had received from Navarro. The original description stated that the number of ventrals was 176, and at this point in the translation Dugès added that he had counted 154 ventrals on his specimen. Smith (1939:29) assumed that Dugès had counted 154 ventrals on the type specimen before sending it to Bocourt. Smith therefore requested Dr. Angel to re-examine the type, and when Angel reported 156 ventrals Smith's assumption seemed confirmed. Duellman (1961:96) followed Smith by assuming that the specimen illustrated by Dugès was the type. Dugès (1884:360–361) stated, however, "Hasta aqui la descripcion de Bocourt. He puesto entre parentesis las reflexiones que me inspiraba la comparacion con el unico specimen que yo poseo . . . Los dos individuos que debo a la bondad del Dr. Octaviano Navarro provienen de Tangancicuaro (Michoacan)." It is clear that Dugès was comparing a second specimen with the type description, and that his count of 154 ventrals applied to the second specimen, not the type. Although Smith's assumption is invalid, the type specimen does have 156 ventrals, as confirmed for me by Jean Guibé.

The British Museum contains two specimens of *G. dugesi* (BMNH 97.3.10.2–3), both from Tangancicuaro, and both received from Dugès. I believe BMNH 97.3.10.3 is the specimen Dugès compared with the type description; on it I count 153 ventrals.

I have tentatively referred to *dugesi* two specimens recently collected in southern Sinaloa. One of these (UK 78939) agrees with specimens from Michoacan except in the presence of a postorbital bone. It is a female with 154 ventrals, 37 subcaudals, an immaculate venter, and a light spot in the center of each dorsal scale; no light crossbands are evident. The second specimen (UK 75622) is a male with 177 ventrals and 58 subcaudals; both of these counts are difficult to reconcile not only with Michoacan specimens but with the Sinaloan female as well. The color pattern of UK 75622 is also distinctive, although consisting of the same basic elements as in the other specimens. The venter is immaculate, and the lateral scales all have light centers; only certain of the scales in the middorsal rows, however, have light centers. These light-centered scales, particularly on the anterior part of the body, tend to occur in transverse rows; separating these "crossbands" of light spots are uniformly dark areas, usually two or three scales in length. Posteriorly, the tendency toward transverse rows of spots is reduced, but still obvious. From the available specimens, a strong case could be made, based primarily on the segmental counts and the unique dorsal color pattern,

for recognizing the Sinaloan male as a distinct species. The female, however, can be distinguished from specimens of *dugesii* only by the absence of the postorbital bone in the latter. Since the significance (if any) of the loss of the postorbital is poorly understood at present, it seems best to at least temporarily assign the Sinaloan specimens to *dugesii*.

SPECIMENS EXAMINED (9).—MEXICO: **Michoacan:** No locality, SU 4407-08; Tangancicuato, BMNH 97.3.10.2-3, MNHN 83.278; near Zacapu, UI 17703; 4 mi before Uruapan road, CNHM 106859. **Sinaloa:** 5 km SW Palmito, UK 75622; 19.2 km NE Santa Lucia, UK 78939.

*Geophis nigrocinctus* Duellman

*Geophis nigrocinctus* Duellman, 1959:1, fig. 1, pl. 1.

HOLOTYPE.—UMMZ 118841, a male from Dos Aguas, Michoacan, Mexico; June 18, 1958; John Wellman, collector. UMMZ 118842-43, females, are paratopotypes.

DISTRIBUTION.—Known only from the type locality, a lumber camp in the pine-oak zone in the Sierra de Coalcoman; about 2100 meters above sea level.

DIAGNOSIS.—Distinguished from other members of the genus by the combination of (1) dorsal scales in 15 rows, smooth throughout length; (2) no anterior temporal; (3) supraocular as long as loreal; (4) 47-60 narrow dark crossbands on a gray-brown ground color; and (5) ventrals whitish, spotted with black.

DESCRIPTION.—Head distinct from neck; snout short, bluntly rounded, scarcely projecting beyond lower jaw; rostral not produced posteriorly between internasals, its length less than one-fourth its distance from frontal; internasals large, slightly broader than long, about two-thirds as long as prefrontal suture; prefrontal suture half as long as frontal; frontal slightly longer than broad, slightly angulate anteriorly, forms long suture with supraocular; parietals long, their median suture as long as frontal; supraocular large, quadrangular, longer than loreal, forms almost entire dorsal margin of orbit; one postocular, higher than long, smaller than supraocular.

Nasal divided, pre- and postnasals subequal in length, their combined length almost half-again as long as loreal; loreal short, contained more than twice in snout length, shorter than eye diameter; eye large, contained twice in snout, its vertical diameter half-again its distance from lip; supralabials 6, third and fourth in orbit, fifth largest and in contact with parietal; no anterior temporal; one posterior temporal, not fused with nuchals along parietal margin.

Mental rounded, much broader than long, separated from chinshields by first pair of infralabials; infralabials 6, pairs 1-4 in contact with anterior

chinshields; anterior chinshields much longer than broad, half-again as long as posterior pair; posterior chinshields in contact medially, separated from first ventral by one or two rows of gulars.

Dorsal scales in 15 rows, smooth throughout length; apical pits absent. Ventrals in single male, 163; in two females, 161–170; anal undivided; subcaudals in male, 50; in single female, 41. Ventrals plus subcaudals, 202–213. Total length of male, 367 mm; tail, 78 mm (21.3%); total length of undamaged female, 356 mm; tail, 63 mm (17.7%).

Maxilla extends anteriorly to suture between first and second supralabials; anterior extension greater than that of palatine; maxilla slender, delicate, bears 11 long, needle-like teeth; first tooth at anterior tip of maxilla; posterior end of maxilla laterally compressed, expanded into large flange; anterior end of ectopterygoid expanded into mitten-like flange. Postorbital bone present, slender.

Hemipenis (based on everted organ) bears numerous spinules and two large spines in basal region; no well-developed naked basal pocket. Central part of organ bears about 45 medium spines and hooks in oblique rows. Distal part of hemipenis capitate, weakly calyculate, spinulate; apex of organ slightly bilobed. *Sulcus spermaticus* bifurcates, each branch reaches apex. M. retractor penis magnus divides into two slips, one slip attaches to each lobe.

Ground color of dorsum grayish-brown, darkening toward posterior part of body; head mottled with irregular black markings; lower parts of supralabials creamish; 47–60 dark crossbands on body, often reaching lateral edges of ventrals; dark bands decrease in length from neck (3–5 scales long) to posterior part of body (1 scale long); interspaces increase in length from neck (1–2 scales long) to posterior part of body (2–4 scales long); pattern most conspicuous on neck, partially obscured posteriorly by darkened interspaces. Chin creamish, with black mottling concentrated along medial edges of infralabials; ventrals whitish or creamish, spotted with black; subcaudals whitish, spotted with black, spots concentrated or not in midventral area.

VARIATION.—One of the paratypes, UMMZ 118842, has five supralabials, the result of fusion between the fifth and sixth. The same condition occurs in a specimen of *G. dugesi*. The black spots on the ventrals are largest in UMMZ 118843; in this specimen the spots on consecutive ventrals are often confluent, creating longitudinal bars of various lengths, and giving the venter a checkered appearance. In UMMZ 118842 the ventral spots are smaller and not confluent, and the dark pigment on the subcaudal surface is distributed linearly along the midline.

REMARKS.—Duellman's (1959:3) description includes the following information: ground color in life, dull brick-red; dark crossbands black, the

anterior bands narrowly outlined with creamish pigment; belly cream, spotted with black: The type was found in a rotten pine stump, the paratypes beneath logs.

SPECIMENS EXAMINED (3).—MEXICO: **Michoacan:** Dos Aguas, UMMZ 118841-43.

*Geophis tarascae* Hartweg

*Geophis tarascae* Hartweg, 1959:1, pl. 1, fig. 1.

HOLOTYPE.—UMMZ 99151, a male collected in the Parque Nacional, Uruapan, Michoacan; July 18, 1947; N. Hartweg, collector. ANSP 15356, Uruapan, Michoacan, is a paratype.

DISTRIBUTION.—Known only from the vicinity of Uruapan, in the pine-oak zone on the southern slopes of the Cordillera Volcanica of Michoacan, Mexico; about 1600 meters above sea level.

DIAGNOSIS.—Distinguished from other members of the genus by the combination of (1) dorsal scales in 15 rows, smooth throughout length; (2) no anterior temporal; (3) supraocular longer than loreal; (4) irregular dark markings on head and neck, disappearing posteriorly; and (5) ventrals whitish with small black spots.

DESCRIPTION.—Head distinct from neck; snout short, bluntly rounded, scarcely projecting beyond lower jaw; rostral not produced posteriorly between internasals, its length less than one-fourth its distance from frontal; internasals large, slightly broader than long, about two-thirds as long as prefrontal suture; prefrontal suture about half as long as frontal; frontal slightly longer than broad, slightly angulate anteriorly, forms long suture with supraocular; parietals long, their median suture as long as frontal; supraocular large, quadrangular, longer than loreal, forms almost entire dorsal margin of orbit; one postocular, twice as high as long, much smaller than supraocular.

Nasal divided, pre- and postnasals subequal in length, their combined length almost half-again as long as loreal; loreal short, contained twice and a half in snout length, shorter than eye diameter; eye large, contained slightly more than twice in snout, its vertical diameter half-again its distance from lip; supralabials 6, third and fourth in orbit, fifth largest and in contact with parietal; no anterior temporal; one posterior temporal, not fused with nuchals along parietal margin.

Mental rounded, much broader than long, separated from chinshields by first pair of infralabials; infralabials 6, pairs 1-4 in contact with anterior chinshields; anterior chinshields much longer than broad, half-again as long as posterior pair; posterior chinshields usually in contact medially; 1-2 rows of gulars separate chinshields from first ventral.

Dorsal scales in 15 rows, smooth throughout length; no apical pits. Ventrals in two males, 164–165; in female, 179; anal undivided; subcaudals in two males, 46–50; in female, 45. Ventrals plus caudals, 210–224. Total length of larger male, 372 mm; tail, 70 mm (18.8%); total length of female, 382 mm; tail, 67 mm (17.5%).

Maxilla extends anteriorly to suture between first and second supralabials; anterior extension greater than that of palatine; maxilla slender, delicate, bears 9–10 long, needle-like teeth; first tooth at anterior tip of maxilla; posterior end of maxilla laterally compressed, expanded into large flange; anterior end of ectopterygoid expanded into large, mitten-like flange. Post-orbital bone present, slender.

Hemipenis extends posteriorly to level of subcaudal 6; basal part of organ bears numerous small spinules and, distally, two large spines; naked basal pocket poorly developed. Central part of organ bears about 40 medium spines and hooks. Distal part of hemipenis capitate, weakly calyculate, spinulate; apex of organ slightly bilobed. *Sulcus spermaticus* bifurcates opposite subcaudal 4; each branch reaches apex. M. retractor penis magnus divides into two slips at apex of hemipenis.

Head pale brown with numerous small, irregular dark markings; ventral parts of supralabials creamish-white; neck pale brown with irregular dark markings, some of which form short transverse and longitudinal bars; posterior five-sixths of body dark brown or blackish, individual scales often irregularly marked with flecks of light and dark pigment. Chin whitish, mottled with dark; lateral edges of ventrals dark; venter whitish, bears small dark spots; dark spots scattered or linearly arranged along midline; subcaudals white, with blackish margins.

VARIAION.—With the exception of slight differences in the size and shape of individual scales, the only variation in the head scales is the fusion of infralabials 2 and 3 on the left side of the paratype. The details of coloration vary somewhat, but the basic pattern of irregular dark markings on the neck is constant. The dark ventral spots are concentrated near the midline as a linear series in the type; in the other two specimens they are scattered. The posterior part of the dorsum is dark in gross appearance, but the distribution of dark and light pigment on the individual scales is variable. On some scales the dark pigment forms a longitudinal bar along the midline of the scale; more commonly, the scales are mottled or spotted.

REMARKS.—In life, UMMZ 121519 was considerably darker than the long-preserved type and paratype. The ground color of the head and neck was a dark purplish-brown, and the irregular dark markings were discernible only upon close inspection. Similarly, the rest of the dorsum was blackish, with little evidence of a lighter ground color. The venter was white with black



spots, the chin cream-white. Since its preservation, the ground color, particularly on the neck, has lightened to a yellow-brown, exposing the irregular dark markings.

In UMMZ 121519 and the paratype the head is much broader than the neck. In the type specimen the skin is loose in the neck region; because of this, the photographs accompanying the type description do not adequately reflect the distinctness of the head from the neck.

The extremely long, needle-like teeth found in *tarascae* and *nigrocinctus* suggest that these snakes feed on slugs or other soft-bodied prey; this type of dentition is associated with such a diet in *Contia tenuis* (Zweifel, 1954a:299).

SPECIMENS EXAMINED (3).—MEXICO: **Michoacan:** Uruapan, ANSP 15356; Uruapan, Parque Nacional, UMMZ 99151, 121519.

#### THE *championi* GROUP

Dorsal scales in 15 rows, smooth or keeled; paired apical pits present above vent (except perhaps in *godmani*). Head indistinct from neck; snout long and pointed; eye very small; rostral prominent, extends posteriorly between internasals; internasals and postnasals elongate; prefrontals and loreal short; supraocular small or absent (*godmani*); parietals short; no anterior temporal. Ventrals 123–143 in males, 130–145 in females. Subcaudals 33–41 in males, 26–32 in females. Percentage tail of total length 16.0–19.8 in males, 11.5–13.8 in females.

Maxilla short, extends anteriorly to suture of supralabials 2 and 3; anterior extension about equal to that of palatine; maxilla curved in lateral view, highest in center, lowest at ends; posterior end tapers to blunt point; 7–9 maxillary teeth; first tooth at anterior tip of maxilla; teeth subequal in length. Anterior tip of ectopterygoid single, not expanded. Postorbital bone present, slender.

This highly specialized group contains three forms: *G. championi*, *G. godmani*, and *G. ruthveni* (Fig. 5). The group ranges geographically from northern Costa Rica to the Canal Zone of Panama, at elevations between 500–2100 meters above sea level (Fig. 6).

*G. godmani* is the most distinctive member of the group. Compared with the other two forms, it has a higher number of ventrals, no supraocular, a stout, heavy body, and a white rostral and prenasal.

Excepting the presence of a supraocular, the head scutellation of *G. championi* and *G. ruthveni* is similar to that of *godmani*. Despite having smooth scales in common, *godmani* appears to be less closely related to *championi* than is *ruthveni*. The latter two forms are small, terete snakes, virtually identical in scutellation, coloration, and the characteristics of the maxilla;

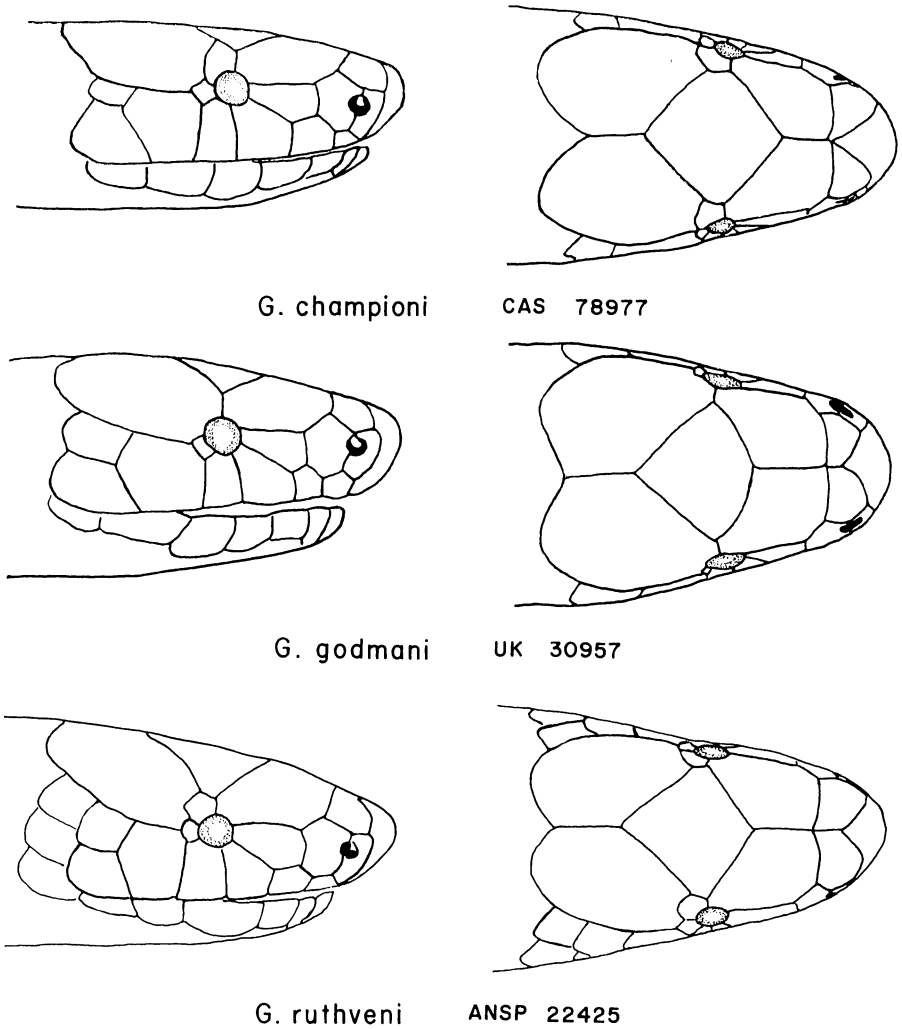


FIG. 5. Dorsal and lateral head scutellation in members of the *championi* group. Scale: *G. championi*, about 7 $\times$ ; *G. godmani*, about 8 $\times$ ; *G. ruthveni*, about 6.5 $\times$ .

The only notable difference observed between the two is the presence of keeled dorsal scales in *ruthveni*. There is no evidence of sympatry or intergradation between the two.

*G. godmani* and *G. championi* are geographically sympatric on the slopes of Volcan Chiriqui in Panama, although *godmani* is known from a higher elevation than the latter. This mountain mass has served as a center of secondary differentiation in species of *Geophis*. *G. hoffmanni* and *G. brachy-*

*cephalus* both have distinctly lower segmental counts on Volcan Chiriqui than in neighboring Costa Rican populations. *G. championi* fits this pattern rather well, since its differentiation from *ruthveni* (namely, the loss of keeling) is relatively minor. The Chiriqui individuals of *godmani* are represented only by the heads and necks; when complete specimens become available, it would not be surprising to find that *godmani* too has undergone local differentiation on Volcan Chiriqui.

Intragroup affinities and distributional data suggest that the ancestral stock of the *championi* group underwent an initial differentiation, probably in the Costa Rican highlands, into a larger, robust form (*godmani*) and a

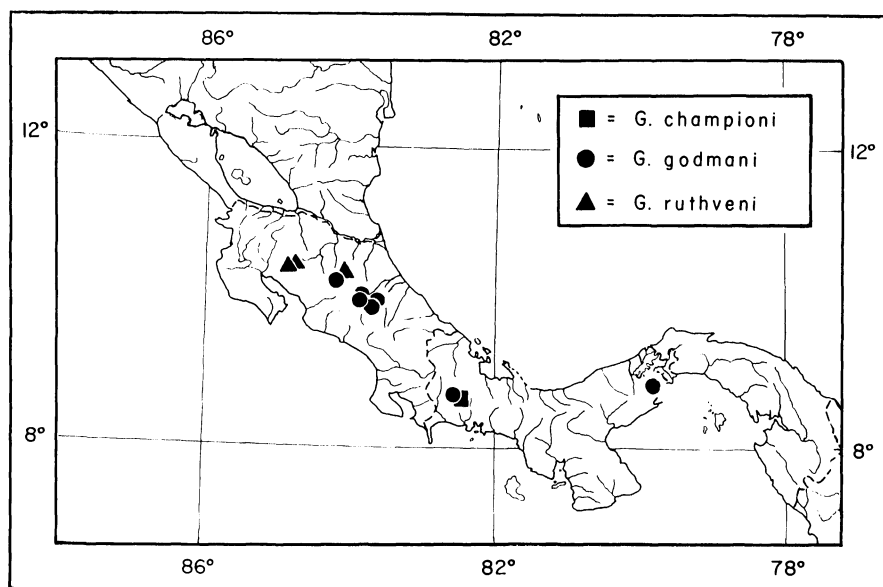


FIG. 6. Locality records for members of the *championi* group

smaller, terete form (*ruthveni-championi*). A southward dispersal of both groups apparently preceded the presumed isolation of Volcan Chiriqui; secondary differentiation of one (resulting in *championi*) and perhaps both groups then proceeded *in situ* in the Chiriqui populations. *G. godmani* occurs at higher elevations than either of the other forms, suggesting that the initial differentiation may have been between highland and lowland populations. An alternate, not necessarily conflicting, possibility is the isolation of the Pacific and Caribbean populations; for example, *godmani* may have developed on the Pacific slopes surrounding the central plateau of Costa Rica, and the second stock at lower elevations on the Caribbean slopes.

*Geophis championi* Boulenger

*Geophis championi* Boulenger, 1894:321, pl. 16, fig. 3.

*Geophis chalybaea*, Günther (in part), 1893:87.

*Calostoma championi*, Amaral 1929:191.

*Geophis brachycephalus*, Dunn (in part), 1942:4.

HOLOTYPE.—BMNH 1946.1.1.77, a male from Chiriqui, Panama; collected by Champion and Godman.

DISTRIBUTION.—Known only from the type locality and Boquete (1370 meters above sea level) on the eastern slopes of Volcan Chiriqui, Chiriqui Prov., Panama.

DIAGNOSIS.—Distinguished from other members of the genus by the combination of (1) dorsal scales in 15 rows, smooth throughout body; (2) no anterior temporal; (3) long, pointed snout with rostral produced posteriorly between internasals; (4) low number of ventrals (125–130); (5) uniform dark dorsal coloration; and (6) venter strongly banded.

DESCRIPTION.—Head not distinct from neck; snout long, pointed, protruding well beyond lower jaw; rostral pronounced, extends posteriorly between internasals, its length three-fourths to equal its distance from frontal; internasals large, rounded anteriorly, about as long as prefrontal suture; prefrontals short, their median suture less than half as long as frontal; frontal as long as broad, anterior edge distinctly angulate; parietals short, their median suture half as long as frontal; supraocular small, broader than long, half as long as loreal, forms posterior half of dorsal margin of orbit, extends behind eye to form part of posterior orbital margin; one postocular, slightly higher than long, smaller than supraocular.

Nasal divided, postnasal twice as long as prenasal, their combined length greater than that of loreal; loreal short, less than half of snout length, almost twice eye diameter; eye very small, contained four times in snout length, its vertical diameter two-thirds or less its distance from lip; supralabials 6, third and fourth enter orbit, fifth in contact with parietal; no anterior temporal; posterior temporal small, directly above sixth labial, not fused with nuchals along parietal margin.

Mental acuminate anteriorly, broader than long, separated from chinshields by first pair of infralabials; infralabials 6, pairs 1–3 in contact with anterior chinshields; anterior chinshields longer than broad; posterior chinshields irregular in shape, or scarcely distinct from gulars; 3 rows of gulars between chinshields and first ventral.

Dorsal scales in 15 rows, completely smooth throughout body and tail; scales above vent faintly striated, with faint paired apical pits. Ventrals in male, 125, in female, 130; anal undivided; subcaudals in male, 33; in

female, 26. Ventrals plus caudals, 156–158. Total length of male, 250 mm; tail, 40 mm (16.0%); total length of female, 255 mm; tail, 31 mm (12.2%).

Maxilla extends anteriorly to suture between second and third supralabials; anterior extension equal to that of palatine; 9 stout maxillary teeth, subequal in length; first tooth at anterior tip of maxilla; shortest distance from tip of longest tooth to maxilla equal to depth of maxilla; maxilla curved in lateral view, the anterior and posterior ends curving ventrally; posterior end of maxilla acuminate, not laterally compressed; anterior end of ectopterygoid not bifurcate, not expanded. Postorbital bone present, slender.

Hemipenial characteristics unknown.

Dorsal coloration of head and body brownish-black, lighter and grayer on head than on body; lateral scale rows lighter than middorsal ones; first scale row mottled, anterior and dorsal parts of each scale dark, posteroventral parts light. Chin region mostly whitish; some dark mottling along medial edges of first pair of infralabials and anterior chinshields; gulars and first few ventrals white; remaining ventrals brown along their anterior edge, white on posterior edge; gross appearance of venter heavily banded; subcaudals dark with light posterior edges; near end of tail, subcaudals entirely dark.

VARIATION.—CAS 78977 differs little from the illustration of the type provided by Boulenger. The rostral does not extend between the internasals as much in the type as in the second specimen; in CAS 78977 the rostral almost comes in contact with the prefrontals. The postocular is higher than long in the type, about as high as long in CAS 78977. The posterior chinshields are symmetrical in the type, and are separated throughout their length by a median gular. In CAS 78977 both the anterior and posterior chinshields are asymmetrical; the anterior pair are not of equal length; the posterior chinshields are irregular in shape, and in contact medially.

REMARKS.—Selander and Vaurie (1962:26) considered Chiriqui, as used in the *Biologia Centrali-Americana*, as referring to the village (ca. 12 km E of David) rather than the district. The itinerary of Champion's travels (Godman, 1915:46–54) indicates that he used Chiriqui to designate the general region, not the specific village. Champion's daily travels, using David as a base of operations, list many specific localities, but not Chiriqui.

The large series of snakes from Boquete, called *G. dolichocephalus* by Slevin (1942:474), includes the second known specimen of *G. championi* and two specimens of *G. hoffmanni*.

SPECIMENS EXAMINED (2).—PANAMA: **Chiriqui**: No specific locality, BMNH 1946:1.1.77; Boquete, CAS 78977.

*Geophis godmani* Boulenger

*Geophis godmani* Boulenger, 1894:322, pl. 16, fig. 4.

*Geophis chalybaea*, Günther (in part), 1893:87.

*Catostoma godmani*, Amaral, 1929:192.

**HOLOTYPE.**—Originally two syntypes, BMNH 1946.1.6.40–41, from Irazu, Costa Rica; O. Salvin and F. D. Godman, collectors. BMNH 1946.1.6.41 is herein designated as lectotype (see below).

**DISTRIBUTION.**—Known from the Caribbean and Pacific slopes of central Costa Rica southward to the Canal Zone of Panama; definite localities for this species are between 1300–2100 meters above sea level.

**DESIGNATION OF A LECTOTYPE.**—In most respects, the original description could apply to either of the syntypes. The two do not differ significantly in scutellation, and the identity of the illustrated specimen is therefore questionable. The description does distinguish between the two in the presentation of size measurements. Boulenger stated the total length as 400 mm, which clearly refers to the larger of the two specimens, BMNH 1946.1.6.41, a female with 145 ventrals and 28 subcaudals. This specimen has been measured for me, and measures 401 mm (the other syntype is 227 mm in total length). Both are females, and differ by only one scale in both ventral and subcaudal counts. I therefore choose the larger specimen, BMNH 1946.1.6.41, as lectotype.

**DIAGNOSIS.**—Distinguished from other members of the genus by the combination of (1) dorsal scales in 15 rows, smooth throughout length; (2) no anterior temporal; (3) supraocular absent, parietal in contact with prefrontal; (4) ground color of head dark, but rostral, prenasal, and occasionally other head scales whitish; and (5) venter light with a few scattered dark markings.

**DESCRIPTION.**—Head not distinct from neck; snout long, pointed, protruding well beyond lower jaw; rostral pronounced, extending posteriorly between internasals, its length from above one-half its distance from frontal; internasals large, rounded anteriorly, two-thirds to as long as prefrontal suture; prefrontals short, their median suture one-half or less the frontal length; frontal as long as broad, four-sided (one suture with each prefrontal and parietal), angulate anteriorly; parietals short, broad, their median suture slightly more than half as long as frontal; parietal in contact with prefrontal above middle of orbit, forms posterior half of dorsal margin and part of posterior margin of orbit; no supraocular; postocular present or absent, when present small, squarish, posteroventral to eye; when absent, fused with parietal or supralabial 5.

Nasal divided, postnasal about twice as long as prenasal, their combined

length equal to or greater than that of loreal; loreal short, less than half of snout length, less than twice the eye diameter; eye small, contained three or more times in snout length, its vertical diameter two-thirds to equal its distance from lip; supralabials 6, third and fourth enter orbit (or, if postocular fused with labial 5, third, fourth and fifth enter orbit), fifth in broad contact with parietal; no anterior, one posterior temporal; temporal directly above sixth labial, usually not fused with nuchals along parietal margin.

Mental acuminate anteriorly, broader than long, separated from chinshields by first pair of infralabials; infralabials 6, pairs 1-3 in contact with anterior chinshields; anterior chinshields as broad as long; posterior chinshields scarcely definable, about as large as anterior pair, separated throughout their length by median gular of almost equal size; 3-4 rows of gulars separate chinshields from first ventral.

Dorsal scales in 15 rows, smooth throughout length, perhaps with faint striations above vent; no paired apical pits discernible. Ventrals in two males, 132-143; in six females, 133-145 (139.2); anal undivided; subcaudals in two males, 34-36; in five females, 26-28 (27.0). Ventrals plus caudals, 162-177. Total length of larger male, 350 mm; tail, 60 mm (17.1%); total length of largest female, 401 mm; tail, 52 mm (13.0%).

Maxilla extends anteriorly to suture between second and third supralabials; anterior extension equal to that of palatine; 7-9 stout maxillary teeth, subequal in length; first tooth at anterior tip of maxilla; shortest distance from tip of longest tooth to maxilla equal to depth of maxilla; maxilla curved in lateral view, the anterior and posterior ends curving ventrally; posterior end of maxilla acuminate, not laterally compressed; anterior end of ectopterygoid not bifurcate, not expanded. Postorbital bone present, slender.

Hemipenis extends posteriorly to level of eighth or ninth subcaudal; basal part of organ bears numerous minute spinules and a short, naked basal pocket; no enlarged spines in distal half of basal region. Central part of organ bears medium spines in longitudinal rows; spines larger in proximal half, progressively smaller in distal half, merging with small spines of distal part of organ. Distal part of organ not capitate; well-developed calyces bear spinules; tip of organ single. *Sulcus spermaticus* bifurcates opposite subcaudal 5; each branch reaches apex. M. retractor penis magnus single throughout its length.

Dorsum of head and body dark brown or brownish-black; rostral, prenasal, supralabial 1, and less frequently other head scales (internasals, postnasals, supralabials) creamish-white; dorsal scales with narrow creamish anterior edges; lateral scale rows not noticeably lighter than dorsal rows, sharply demarcated from ventral coloration. Chin region creamish, not mottled with dark pigment; ventrals creamish-white, with or without scat-

tered brown spots or irregular transverse bands; subcaudals similar to ventrals in color variation.

VARIATION.—The highly variable postocular is present in 6 specimens and absent in 5. Its absence is the result of either of two fusions. In ANSP 22426 the postocular is incorporated into the parietal; the parietal, therefore, excludes the fifth labial from the orbit. In four other specimens the fusion is with the fifth labial, which enters the orbit. No specimens are known in which the postocular is present on one side of the head and absent on the other.

The supralabial series is reduced in two specimens. On the right side of UK 63816 supralabials 1 and 2 are fused. On both sides of CRE 43 the reduction occurs posterior to the eye; there is one large labial behind the eye (similar to normal condition in *G. hoffmanni*), but it is not clear whether this scale represents a fusion of the fifth and sixth labials or an enlarged fifth labial which has crowded the sixth labial from the lip. The infralabials are reduced from 6 to 5 on the left side of ANSP 22910 by fusion of the third and fourth. On the right side of the same specimen, and on one side of two other specimens, there are 7 infralabials; this increase takes place in the anterior part of the infralabial series in ANSP 22910, but in the posterior half in ANSP 22426 and UK 63818. In ANSP 22426 the extra scale is a small detached part of either the fourth or fifth labial; it has a short lip exposure between the two, but is enclosed medially by the larger fourth and fifth labials.

The head is peculiarly variable in coloration. The rostral, prenasal, and first supralabial are consistently creamish-white; on some specimens other head scales are also whitish. In UK 63816, for example, the right fifth supralabial and the left fifth and six labials are light; in CRE 43 the internasals, postnasals, second supralabial, and lower parts of supralabials 3 and 4 are whitish.

The venter is virtually immaculate in UK 63816 and 63818, although a few scattered small dark spots are present. CRE 43, in contrast, has a large amount of dark pigment on the venter; the posterior edge of many of the ventrals is dark brown for at least part of its width. The dark-banded ventrals tend to occur in groups, separated by series of immaculate ventrals.

Unfortunately, the three Panamanian individuals I have seen are represented by only the heads and necks. Geographic variation in the number of ventrals and caudals is therefore unknown; other species known from Costa Rica and the Chiriqui area of Panama (*hoffmanni*, *brachycephalus*) have fewer ventrals and subcaudals in the Chiriqui region.

REMARKS.—Field notes supplied by W. E. Duellman suggest that the ventral coloration may change ontogenetically. Two females obtained near



Las Nubes, Costa Rica, have total lengths of 145 and 324 mm (tail slightly incomplete in larger specimen); the ventral coloration of the juvenile was white in life, that of the adult yellow. The dorsal coloration was black. Taylor (1954:687) reported that UK 30957, a female 156 mm in total length, was black above and creamish-white below; the light head scales, in this case most of rostral, internasals, and supralabials 1 and 6, were creamish.

The specimen reported by Taylor was found under a rock at the edge of a patch of forest; UK 63816 and 63818 were discovered beneath logs, the former in a pasture, the latter not specified.

In addition to the specimens listed below, Dunn (1942:4) listed one from Tierra Blanca, Costa Rica. I have not seen this specimen, but the locality is within the known range of the species. The species apparently has a wide altitudinal range, as it occurs above 2000 meters on the slopes of Volcan Turrialba in Costa Rica and, assuming the locality is correct, close to sea level at "Panama Sabanas." According to Dunn (1949:39) the latter locality refers to the Province of Panama and the Pacific side of the Canal Zone.

**SPECIMENS EXAMINED (11).**—**COSTA RICA:** No locality, ANSP 22426. **Alajuela:** 8.1 km beyond Vara Blanca on rd to crater of Volcan Poas, UMMZ 125570. **Cartago:** Pacayas, UK 30957; Volcan Turrialba, 4.9 mi SE Lecheria Central, CRE 43. **San Jose:** Escazu, BMNH 1913.7.19.144; Irazu, BMNH 1946.1.6.40-41; 2 km N Las Nubes, UK 63816; 2.6 km N Las Nubes, UK 63818. **PANAMA:** **Chiriqui:** Volcan Chiriqui, Finca Lerida, ANSP 22910, 24756. **Panama:** "Panama Sabanas," ANSP 24722.

### *Geophis ruthveni* Werner

*Geophis ruthveni* Werner, 1925:60.

*Catostoma ruthveni*, Amaral, 1929:193.

**HOLOTYPE.**—NHMW 16508, a male supposedly from Sarapiquí, Brasilien, but almost certainly in error; probably from Sarapiquí, Heredia Prov., Costa Rica (see *Remarks* below).

**DISTRIBUTION.**—Known in Costa Rica from the Caribbean slopes of the western end of the Cordillera Central and the Pacific versant of the Cordillera de Guanacaste; 550-1600 meters above sea level.

**DIAGNOSIS.**—Distinguished from other members of the genus by the combination of (1) dorsal scales in 15 rows, strongly keeled on posterior body and tail; (2) anterior temporal absent; (3) snout pointed, rostral produced posteriorly between internasals; (4) dorsum unicolor, dark (light collar in juveniles); and (5) venter strongly banded.

**DESCRIPTION.**—Head not distinct from neck; snout long, pointed, protruding well beyond lower jaw, rostral pronounced, extends posteriorly between internasals, its length from above more than one-half its distance from

frontal; internasals large, rounded anteriorly, as long as prefrontal suture; prefrontals short, their median suture one-third to one-half as long as frontal; frontal as long as broad, anterior edge angulate; parietals short, broad, their median suture half as long as frontal; supraocular small, broader than long, half as long as loreal, forms posterior half of dorsal margin of orbit, extends behind eye to form part of posterior orbital margin; one postocular, higher than long, slightly smaller than supraocular.

Nasal divided, postnasal twice as long as prenasal, their combined length greater than that of loreal; loreal short, less than half of snout length, almost twice the eye diameter; eye very small, contained four times in snout length, its vertical diameter three-fourths or less its distance from lip; supralabials 6, third and fourth in orbit, fifth in contact with parietal; no anterior, one posterior temporal; temporal directly above sixth labial, not fused with nuchals along parietal margin.

Mental acuminate anteriorly, slightly broader than long, separated from chinshields by first pair of infralabials; infralabials variable, 5-7; first three or four pairs in contact with anterior chinshields; anterior chinshields almost as broad as long, slightly longer than posterior ones; posterior chinshields short, in contact anteriorly, diverging posteriorly; 3-4 rows of gulars separate chinshields from first ventral.

Dorsal scales in 15 rows, strongly keeled on posterior part of body and on tail; posterior scales striated, with paired apical pits. Ventrals in six males, 123-126 (125.5); in single female, 135; anal undivided; subcaudals in six males, 37-41 (39.5); in female, 32. Ventrals plus caudals, 163-167. Total length of largest male, 238 mm; tail, 42 mm (17.6%); total length of female, 260 mm; tail, 35 mm (13.5%).

Maxilla extends anteriorly to suture between second and third supralabials; anterior extension equal to that of palatine; 7-8 stout maxillary teeth, subequal in length; first tooth at anterior tip of maxilla; shortest distance from tip of longest tooth to maxilla equal to depth of maxilla; maxilla curved in lateral view, the anterior and posterior ends curving ventrally; posterior end of maxilla acuminate, not laterally compressed; anterior end of ectopterygoid not bifurcate, not expanded. Postorbital bone present, slender.

Hemipenis extends posteriorly to level of eighth to tenth subcaudal; basal part of organ bears minute spinules and a short naked basal pocket; no enlarged spines in distal part of basal region. Central part of organ with medium spines in longitudinal rows; spines larger in proximal half, progressively small in distal half, merging with spinules of distal part of organ. Distal part of hemipenis not capitate, bears spinules on well-developed calyces; apex of organ single. *Sulcus spermaticus* bifurcates opposite sub-

caudal 5; each branch reaches apex. *M. retractor penis magnus* undivided throughout its length.

Dorsum of head and body dark brown or bluish-black; sides of head paler; a light collar in juveniles involves supralabial 6, posterior parts of parietals, and first 3–4 rows of nuchals; collar obliterated by dark pigment in adults; scales of first dorsal row dark at base, otherwise whitish; second scale row with or without light mottling; scales of remaining rows uniformly dark or with slightly paler posterior edges. Mental, anterior chinshields, and lateral parts of infralabials mottled; remainder of chin creamish-white; anterior edge of each ventral dark brown or black, posterior edge whitish; dark band narrow laterally, expanded midventrally; expanded midventral parts of consecutive bands confluent on posterior part of body; subcaudals mostly dark with light posterior edges, or solidly dark.

VARIATION.—The head scutellation is quite constant in the seven known specimens. The major exception is the infralabial series, in which the number of infralabials is too variable to designate a “normal” condition. One specimen has 5 infralabials on each side, one 6–6, one 7–7, and three 5–6; the fusion or splitting of labials occurs in both anterior and posterior halves of the row. When 5 or 6 labials are present, three are in contact with the anterior chinshields; when 7 are present, four are in contact.

The postocular is absent on the right side of ANSP 22425, the result of fusion with the fourth supralabial. On the left, the postocular is small and squarish. In other specimens it is larger, and higher than long.

The variation in coloration is partly ontogenetic, partly individual. The light collar is most evident in the smallest specimen (UK 35881), although even in this specimen (total length, 107 mm) it is extensively mottled with dark pigment. UK 35892 (total length, 168 mm) shows trace of the light collar; the other specimens lack it completely. The first and second supralabials are whitish on the right side of UK 35895, a condition reminiscent of the color variation in *G. godmani*. The venter is banded throughout the length of ANSP 22425. In other specimens the dark pigment dominates the posterior part of the venter so completely that the gross effect is one of solid darkness. The same is true of the subcaudal surface.

The difference noted in the dorsal ground color appears to reflect length of time in preservative. The bluish-black coloration of the specimens collected in 1954 (UK specimens) probably is similar to the color in life. The brown coloration of ANSP 22425 is presumably the result of fading.

REMARKS.—The type description states that the type locality is Sarapigui, Brasil. This locality has been subject to question on two counts: (1) the only other *Geophis* reaching South America extends only into northwestern

Colombia, and (2) Sarapigui is found on no map or gazetteer of Brazil, but Sarapiqui is a well-known river, district, and town in Costa Rica. Dunn (*in litt.*) first suggested that the type locality was in error, and his suggestion was followed by Savage (1960:31), who considered *G. ruthveni* a non-South American form. This conclusion was reached without the benefit of additional specimens.

The recently collected specimens herein referred to the species *ruthveni* clearly support Dunn's suggestion that the type locality is in error. Josef Eiselt of the Vienna museum has compared the type with a drawing of the head scales of one of the additional specimens, and confirms the close similarity of the two. Two of the additional specimens were collected at Cinchona, Costa Rica, which is located along the Rio Sarapiqui at 1600 meters above sea level. Selander and Vaurie (1962:56) placed the town of Sarapiqui as a village along the river of the same name at about 1220 meters above sea level. Although the type locality may not refer specifically to the village, it appears certain that it refers to this general area in Costa Rica.

**SPECIMENS EXAMINED (7).**—**COSTA RICA:** No locality, ANSP 22425. **Alajuela:** La Cinchona, UK 35881, 35892. **Guanacaste:** Tilaran, UK 35893–94; 4 km NE Tilaran, UK 35895. **BRASIL** (probably in error), Sarapigui (probably Sarapiqui, Costa Rica), NHMW 16508.

#### THE *dubius* GROUP

Dorsal scales in 17 rows, smooth or keeled; scales above vent bear paired apical pits (except in *rhodogaster?*). Head not or scarcely distinct from neck; snout long, bluntly pointed; rostral prominent, its visible length one-third or more its distance from frontal; internasals large, rounded anteriorly; prefrontals short; anterior edge of frontal sharply angulate; parietals short; supraocular small, triangular (absent in *rhodogaster*); eye small; post-nasal enlarged; loreal short; no anterior temporal. Ventrals 120–143 in males, 126–147 in females. Subcaudals 34–49 in males, 27–43 in females. Percentage tail of total length 16.0–23.9 in males, 13.6–19.5 in females.

Maxilla extends anteriorly to suture between first and second supralabials (second and third in *dubius*); anterior extension greater than that of palatine; maxilla straight or slightly curved in lateral view, slenderest anteriorly; 9–17 maxillary teeth, longest in posterior part of row; first tooth at anterior tip of maxilla; posterior end of maxilla laterally compressed into moderate flange; anterior end of ectopterygoid bifurcate, one branch short and blunt, second long, compressed, blade-like. No postorbital bone.

Hemipenis (condition unknown in *immaculatus*) bilobed for length of 2–3 subcaudals; *sulcus spermaticus* bifurcate, each branch reaches apex of one lobe; a naked basal pocket; central part of organ with numerous long slender spines in oblique rows; distal part weakly capitate, calyculate,

spinulate; *M. retractor* penis magnus divides into two slips near apex of hemipenis.

I recognize five species (*G. carinosus*, *G. dubius*, *G. fulvoguttatus*, *G. immaculatus*, *G. rhodogaster*) in this group (Fig. 7). Geographically, the group ranges from Puebla and Oaxaca, Mexico, southeastward through Guatemala to El Salvador (Fig. 8).

*G. dubius* appears to be the most specialized member of the group; it has the longest snout, most prominent rostral, and the greatest tendency toward reduction in the number of head scales. *G. carinosus* is basically very similar to the other members of the group, but is distinctive in being the smallest, most terete species and the only member of the group with widely distributed, distinct keeling of the dorsal scales. *G. rhodogaster* has no supraocular (fused with, or displaced by, the frontal); it has a distinctive maxilla that bears a greater number of teeth than are present in the other forms. The smooth scales and body shape suggest that *rhodogaster* is closer to the Pacific versant forms (*immaculatus*, *fulvoguttatus*) than to the Caribbean form (*carinosus*). *G. immaculatus* and *G. fulvoguttatus* differ in the details of coloration and scutellation, but appear to be closely related.

The center of differentiation in this group appears to have been the Guatemalan and adjacent uplands. Three, and probably four, of the species occur in Guatemala; the fourth, *fulvoguttatus*, is known only from the Metapan mountains of El Salvador, but almost certainly occurs in the adjacent highlands of Guatemala.

Members of this species group are associated with, and characteristic of, several of the biotic areas proposed (and elaborated on) by Stuart (1943: 1950: 1951: 1954) for Guatemala. *G. carinosus* is known in Guatemala only from the Sierra de los Cuchumatanes (Cuchumatan Biotic Area); *G. rhodogaster* is widely distributed in the Southwestern Highlands (Chimaltenangan Biotic Area) and the higher parts of the Southeastern Highlands (Esquipulan Biotic Area); *G. immaculatus* is known only from the Pacific escarpment (Fuegan Biotic Area).

The ancestral stock of this group appears to have been split into a highland element, a Caribbean versant element, and a Pacific versant element, possibly by the well known orogeny during the Pliocene. The Caribbean versant element (*G. carinosus*) apparently dispersed into Mexico only recently, since it is found in essentially unmodified form in the isolated Los Tuxtlas range of Veracruz and in only slightly modified form in Puebla; presumably this dispersal took place during the late Pleistocene. The highland element (*G. rhodogaster*) apparently developed *in situ* on the Guatemalan Plateau; it probably utilized the downward vertical displacement of the pine-oak zone during glacial periods to spread through the southeastern highlands of Guatemala into El Salvador; *G. rhodogaster* is

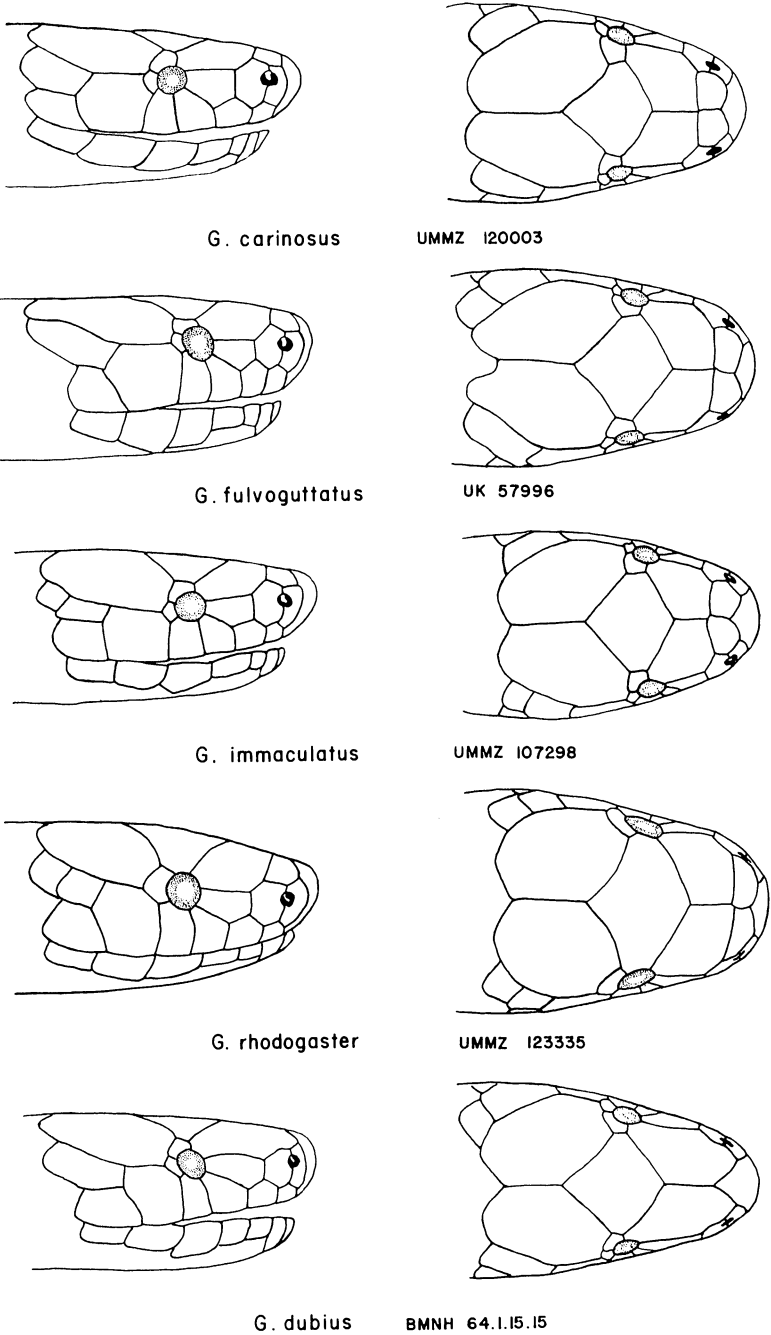


FIG. 7. Dorsal and lateral head scutellation in members of the *dubius* group. Scale: *G. carinosus*, about 5 ×; *G. fulvoguttatus*, about 4 ×; *G. immaculatus* (paratype), about 5 ×; *G. rhodogaster*, about 5 ×; *G. dubius*, about 4.5 ×.

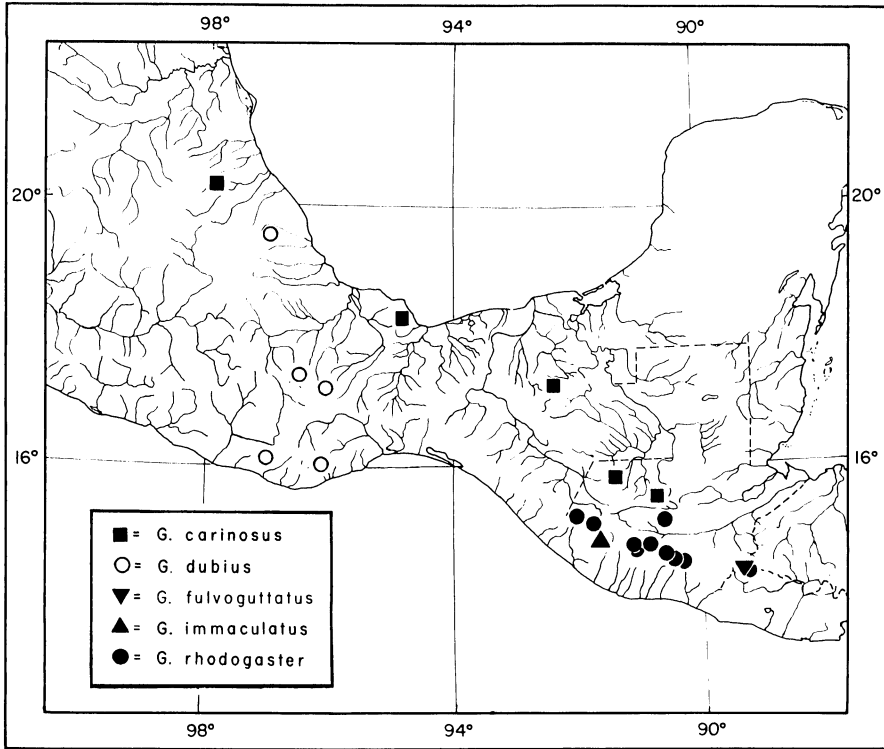


FIG. 8. Locality records for members of the *dubius* group

sympatric with *G. fulvoguttatus* in El Salvador. The Pacific versant element has apparently differentiated into three forms. Of the three, *G. dubius* is the most distinctive; its dispersal across the Isthmus of Tehuantepec presumably preceded that of *G. carinosus*, which is but feebly differentiated west of the Isthmus. Subsequent to the splitting off of the *dubius* stock, the Pacific element underwent a secondary differentiation into *G. immaculatus* and *G. fulvoguttatus*.

Available specimens and known localities are too few to characterize the habitats of these species accurately. From what little evidence is available, *G. dubius* and *G. rhodogaster* appear to inhabit the pine-oak zone; *G. carinosus*, *G. immaculatus*, and *G. fulvoguttatus* are apparently distributed in cloud forest.

*Geophis carinosus* Stuart

*Geophis carinosus* Stuart, 1941:3.

HOLOTYPE.—UMMZ 89082, an adult male from Finca San Francisco, 27 km NE of Nebaj, El Quiché, Guatemala; August 2, 1940; L. C. Stuart, collector.

**DISTRIBUTION.**—Known from the Sierra de los Cuchumatanes of Guatemala, the adjacent Caribbean slopes of Chiapas, the Sierra de los Tuxtles of Veracruz, and the Sierra Madre Oriental of Puebla; generally between 1000–1500 meters above sea level.

**DIAGNOSIS.**—Distinguished from other members of the genus by the combination of (1) dorsal scales in 17 rows, distinctly keeled on posterior part of body; (2) no anterior temporal; (3) total nasal length greater than that of loreal; (4) dorsum grayish- or brownish-black; and (5) each ventral brownish-black anteriorly, yellowish-white posteriorly.

**DESCRIPTION.**—Head indistinct from neck; snout long, bluntly pointed, projecting well beyond lower jaw; rostral prominent, one-third to one-half as long as its distance from frontal; internasals large, rounded anteriorly, three-fourths as long as prefrontal suture; prefrontals short, their common suture half as long as frontal; frontal broader than long, anterior margin distinctly angulate; parietals short, broad, their median suture four-fifths as long as frontal; supraocular small, half as long as loreal, forms little more than posterior half of dorsal margin of orbit; one postocular, higher than long, slightly smaller than supraocular.

Nasal divided, postnasal half-again as long as prenasal, their combined length greater than that of loreal; loreal short, contained twice and a half in snout length, half-again as long as eye diameter; dorsal edge of loreal straight; eye small, contained four times in snout length, its vertical diameter three-fourths its distance from lip; supralabials 6, third and fourth enter orbit, fifth largest and in contact with parietal, fourth higher than long; no anterior temporal; one posterior temporal, usually fused with nuchal along parietal margin.

Mental broader than long, acuminate anteriorly, separated from chinshields by first pair of infralabials; infralabials 6, first three or four pairs in contact with anterior chinshields; anterior chinshields broad, twice as long as posterior pair; posterior chinshields in contact anteriorly, separated posteriorly by median gular; 2–3 gulars separate chinshields from first ventral.

Dorsal scales in 17 rows, smooth on neck, distinctly keeled on posterior two-thirds of body and on tail; paired apical pits present. Ventrals in two males, 120–123; in four females, 126–134 (131.0); anal undivided; subcaudals in two males, 44–48; in four females, 41–44 (42.5). Ventrals plus caudals, 164–178. Total length of larger male, 276 mm; tail, 66 mm (23.9%); largest female, 273 mm; tail, 52 mm (19.1%).

Maxilla extends anteriorly to anterior part of second supralabial; anterior extension greater than that of palatine; maxilla straight in lateral view, slenderest anteriorly; 10–13 maxillary teeth, increasing in length posteriorly; first tooth at anterior tip of maxilla; posterior end of maxilla laterally



compressed into moderate flange; anterior end of ectopterygoid bifurcate, one branch short and blunt, second branch long, compressed, blade-like; no postorbital bone.

Hemipenis (everted) extends to sixth subcaudal; basal part of organ bears numerous minute spinules and one enlarged spine; a basal naked pocket on antisulcus side, flanked by elevated, inflated ridges. Central part of hemipenis bears about 40 medium spines in oblique rows. Distal part of organ capitate, spinulate; capitation obscured by gradation between spines of central part of organ and those of proximal edge of capitulum; capitulum bears weak calyces near apex; apex distinctly bilobed. *Sulcus spermaticus* bifurcate, each branch reaches apex of one lobe. M. retractor penis magnus divides into two slips near apex of hemipenis.

Dorsum of head and body dark brownish- or grayish-black; posterior edges of scales in lateral rows slightly paler; lateral parts of head not noticeably paler than dorsal parts. Chin region brownish; each ventral whitish with a narrow dark anterior margin; lateral edges of ventrals mottled with brown; anterior half of each subcaudal dark brownish-black; posterior half pale yellowish-brown.

**VARIATION.**—In the above scale counts, I have not included a juvenile male from ten miles southwest of Villa Juarez, Puebla, Mexico. This specimen, UK 39642, was referred to *G. rostralis* (= *G. dubius*) by Webb and Fugler (1957:35); unfortunately, the illustrations provided by them bear little resemblance to UK 39642. The heavy keeling, prominent scale pits, straight dorsal margin of the loreal, and general head scutellation of UK 39642 all indicate a conspecific relationship with *G. carinosus*. The Puebla specimen has 132 ventrals and 35 subcaudals, the former about ten greater and the latter about ten fewer than the comparable counts in the other two males of *carinosus*. This suggests the possibility of differences between populations north of the Isthmus of Tehuantepec and those to the south. Specimens from Veracruz, Chiapas, and Guatemala, however, show no evidence of significantly different segmental counts. The paucity of specimens prohibits definite conclusions regarding any of these populations.

The third and fourth supralabials are fused on one side of UK 39642, and the number of infralabials is increased to seven on one side of UMMZ 120004. There is little variation in the other head scales. The ventral banding is indicated, but not as strongly developed, in UK 39642 and UK 57995.

**REMARKS.**—In life, UK 57995 was metallic gray above and grayish-white below (field notes of W. E. Duellman).

**SPECIMENS EXAMINED (7).**—**MEXICO:** **Chiapas:** Yajalon, MZTG 530. **Puebla:** 10 mi SW Villa Juarez, UK 39642. **Veracruz:** Sierra de los Tuxtles, Volcan San Martin, DCR uncataloged, UK 57995. **GUATEMALA:** **El Quiche:** Finca San Francisco, UMMZ 89082. **Huehuetenango:** 1 km S Barillas, UMMZ 120003; 2 km E Barillas, UMMZ 120004.

*Geophis dubius* (Peters)

*Gophidium dubium* Peters, 1861:923; Cope, 1887:86.

*Geophis dubius*, Bocourt, 1883:532; Boulenger, 1894:322; Smith and Taylor, 1945:67; Smith, 1959:265.

*Atractus dubius*, Cope, 1900:1230.

*Catostoma dubium*, Amaral, 1929:191:

*Elapoides rostralis* Jan (in Jan and Sordelli), 1865: livr. 12, pl. 2, fig. 2 (type, ZMB 6407; Mexico).

*Geophis rostralis*, Bocourt, 1883:533; Günther, 1893:89; Boulenger, 1894:323; Smith and Taylor, 1945:69.

*Rhabdosoma rostrale*, Cope, 1885a:385; Cope, 1887:85.

*Catostoma rostrale*, Amaral, 1929:192.

*Geophis fuscus* Fischer, 1886:11, pl. 2, fig. 5 (type, BMNH 1946.1.6.48; Jalapa, Mexico; Kienast, collector).

*Geophis chalybaea*, Günther (in part), 1893:87.

*Geophis anocularis* Dunn, 1920:127 (type, USNM 46556; Totontepec, Oaxaca, Mexico; Nelson and Goldman, collectors).

HOLOTYPE.—ZMB 4064, an adult female with an incomplete tail; type locality unknown (see *Remarks*).

DISTRIBUTION.—Known from Jalapa, Veracruz, and several localities in the highlands of Oaxaca, Mexico; 1420–2260 meters above sea level.

DIAGNOSIS.—Distinguished from other members of the genus by the combination of (1) dorsal scales in 17 rows, smooth throughout body or faintly keeled above vent; (2) no anterior temporal; (3) internasals fused with prefrontals or, when distinct, nearly as long as broad; (4) snout long, pointed, one-half the head length; (5) loreal slightly longer than combined pre- and postnasal length; (6) lip exposure of fourth supralabial nearly as long as that of fifth; and (7) dorsum brownish or blackish, venter whitish and usually immaculate.

DESCRIPTION.—Head indistinct from neck; snout long, pointed; projecting well beyond lower jaw; rostral prominent, produced posteriorly between internasals (or between fused internasals and prefrontals), its length from above one-third to equal its distance from frontal; internasals usually fused with prefrontals; if distinct, internasals large, rounded anteriorly, nearly as long as broad, more than half as long as prefrontal suture; if distinct, prefrontals short, their median suture slightly more than one-third as long as frontal; frontal as long as broad, sharply angulate anteriorly, forms short suture with supraocular; parietals short, broad, their median suture two-thirds or less as long as frontal; supraocular small, triangular, less than half as long as loreal, forms posterior half of dorsal margin of orbit; supraocular occasionally fused with or partially displaced by parietal; one postocular, higher than long, often larger than supraocular.

Nasal divided, postnasal almost twice as long as prenasal, their combined length slightly less than that of loreal; loreal moderate, contained slightly more than twice in snout length, half-again as long as eye diameter; dorsal margin of loreal often convex; eye small, contained three or four times in snout, its vertical diameter three-fourths its distance from lip; supralabials 6, third and fourth enter orbit, fifth largest and in contact with parietal; posterior margin of fifth labial angles anteroventrally to lip; lip exposure of fifth labial slightly greater than that of fourth; lip exposure of third supralabial distinctly longer than that of second; no anterior temporal; sixth supralabial separated from parietal by one posterior temporal; temporal usually fused with nuchal along parietal margin.

Mental acuminate anteriorly, as long as broad, usually in contact with anterior chinshields; infralabials 6, three or four pairs in contact with anterior chinshields; anterior chinshields long, broad, much larger than posterior pair; posterior chinshields in contact anteriorly, often separated posteriorly by median gular; 2-3 gulars separate chinshields from first ventral.

Dorsal scales in 17 rows, smooth throughout length or weakly keeled above vent; paired apical pits present above vent. Ventrals in ten males, 124-143 (see *Variation*); in five females, 144-147 (145.4); anal undivided; subcaudals in ten males, 35-49 (see *Variation*); in four females, 36-43 (39.8). Ventrals plus caudals, 159-191. Total length of largest male, 311 mm; tail, 67 mm (21.5%); largest female, 342 mm; tail, 62 mm (18.1%).

Maxilla extends anteriorly to suture between second and third supralabials; anterior extension about equal to that of palatines; maxilla straight in lateral view, narrowest anteriorly; 10-12 maxillary teeth, increasing slightly in length toward posterior part of row; first tooth at anterior tip of maxilla; last tooth longest; posterior end of maxilla laterally compressed into moderate flange; anterior end of ectopterygoid bifurcate, one branch short and blunt, other long, compressed, blade-like; no postorbital bone.

Hemipenis long and slender, extends posteriorly to level of subcaudal 12-14; basal part of organ bears numerous spinules and, in distal part, 2-3 larger spines; a naked pocket on antisulcus side. Central part of organ bears 35-40 long, slender spines in oblique rows. Distal part of organ capitate; capitulation obscured by gradation between spines of proximal edge of capitulum and those of central part of organ; capitulum calyculate, spinulate; apex bilobed for 2-3 subcaudal lengths. *Sulcus spermaticus* bifurcates opposite sixth to eighth subcaudal; each branch reaches apex. *M. retractor penis magnus* divides into two slips near apex of hemipenis; one slip attaches to each lobe.

Dorsum brownish or slate-black, paler on lateral scale rows and lateral aspect of head; scales of first few scale rows usually distinctly darker along

anterior edge. Chin region whitish, immaculate, or with pale brown mottling on infralabials; ventrals whitish, usually with brownish lateral edges on posterior part of body, occasionally immaculate throughout length; subcaudals whitish with brown or grayish anterior edges.

VARIATION.—The head scutellation in this specialized species is highly variable, and shows a distinct tendency toward a reduction in the number of scales. In nine specimens, both internasals are fused with the prefrontals; USNM 31352 lacks only the right internasal; the left internasal is partially fused with the prefrontal in BMNH 64.1.15.14, but the right internasal is distinct; both internasals are distinct in four specimens. The dorsal margin of the postnasal extends as a wedge between the lateral margins of the internasals and prefrontals. Where the latter scales are fused, the dorsal margin of the postnasal is rounded off and the margin of the internasal-prefrontal scale forms a smooth curve.

The rostral is a dominant part of the snout in all specimens, but its length and extension between the internasals (or prefrontals) is quite variable. In the type and USNM 46556 its visible length from above is one-third its distance from the frontal; in USNM 31351, ZMB 6407, and several others the rostral is as long as its distance from the frontal; other specimens are intermediate.

The oculars vary greatly in size and shape, generally as a result of displacement by the parietal. The supraocular and postocular are fused with the parietal in USNM 46556; in ZMB 4064 the supraocular and parietal are partially fused on the right side; on the left side of USNM 31352 the supraocular and postocular are fused. In other specimens the supraocular is distinct, but reduced in size because of displacement by the parietal; in AMNH 65888 this displacement reduces the supraocular to a thin sliver, much smaller than the postocular.

The first pair of infralabials separates the mental from the chinshields in five specimens; in eight others the mental extends between the infralabials to touch the chinshields. In specimens with 6 infralabials, three or four pairs are in contact with the anterior chinshields. Two specimens, BMNH 1946.1.6.48 and ZMB 6407, have seven infralabials, with four in contact with the anterior chinshields; the extra labial is a small scale in the anterior part of the row.

Unfortunately, many of the available specimens of *dubius* are from indefinite localities. The numbers of ventrals and subcaudals in these specimens are similar to the same counts in specimens from near Ixtlan de Juarez, Oaxaca, a locality in the highlands northeast of the city of Oaxaca. The range in ventrals and subcaudals in seven male specimens from indefinite localities, Ixtlan, Oaxaca, and Jalapa, Veracruz, is 134–143 (mean,

138.9) and 43–49 (mean, 47.3), respectively. In USNM 46556, from Totontepec, Oaxaca, there are 124 ventrals and 35 subcaudals; Totontepec is separated from Ixtlan by the valley of the Rio Cajones. Two males from the Sierra Madre del Sur of Oaxaca have 126 and 132 ventrals and 42 and 43 subcaudals, respectively. Only additional specimens can clarify these differences; at present I interpret them as differences between local populations of a single species.

There is little variation in coloration, except that reflecting the length of time in preservative. The older specimens are brown, in contrast to the grayish-black or brownish-black of those recently obtained. UMMZ 125288 is the only specimen with extensive brownish mottling on the ventrals; the diffuse brown pigment is most conspicuous on the anterolateral part of each ventral. All other specimens have a predominantly whitish venter, with the ventrals often immaculate.

REMARKS.—Two specimens of *G. dubius* from "Tehuantepec" have been erroneously considered the types of the species by recent authors (Smith and Taylor, 1945; Smith, 1959; Stuart, 1963). This misconception was established by Bocourt (1883:533) when he stated that his specimens were identical with the two types from Tehuantepec sent to him by Peters. The type description, however, clearly states that the name is based on a single specimen of unknown origin. This specimen, the type, is ZMB 4064; the two specimens from Tehuantepec are ZMB 7221.

Until recently, *G. dubius* and *G. rostralis* have been regarded as distinct species, based primarily on the presence of internasals and keeling above the vent in *rostralis* and the absence of these features in *dubius*. Smith (1959:265) recently synonymized the two forms, partly on the basis of UI 46710, from San Andres Lovene, Oaxaca. I have examined the types of both forms, and concur with Smith's relegation of *rostralis* to the synonymy of *dubius*. Both types have faint keeling above the vent (although some specimens referred to *dubius* do not); the presence of internasals in the type of *rostralis* is not significant since in two specimens the internasal is distinct on one side of the head and partially or completely fused with the prefrontal on the other. The mental is in contact with the chinshields in the type of *rostralis*, and separated from the latter in the type of *dubius*. The contact occurs in seven other specimens, and shows no correlation with the absence or presence of internasals. There is no apparent justification for the recognition of *rostralis* as a distinct species.

Dunn (1920:127) distinguished *G. anocularis* from *dubius* and *rostralis* by the presence in the former of fewer ventrals, four instead of three infra-labials in contact with the anterior chinshields, a less produced rostral, and the absence of a supraocular and postocular. Although always prominent,

the rostral in *G. dubius* varies considerably in the degree to which it is produced posteriorly between the internasals; in some specimens, notably the type, the rostral length is only one-third its distance from the frontal; in others it is as long as its distance from the frontal. This range of variation encompasses the rostral condition in the type of *anocularis*. The apparent difference in the number of infralabials in contact with the anterior chinshields is also invalid, since several specimens of *dubius* have four pairs in contact. As pointed out in the above discussion of variation in the species, the type of *anocularis*, UI 46710, and UMMZ 125288 have fewer ventrals and subcaudals (and hence of their sum) than other specimens of *dubius*. Like *dubius*, and unlike the type of *anocularis*, UI 46710 and UMMZ 125288 have distinct supraoculars and postoculars. I regard the absence of oculars as unimportant, since the supraocular is partially fused with the parietal on one side of the type of *dubius* and is reduced to a narrow sliver by encroachment of the parietal in several others. The lower number of ventrals and subcaudals, the only remaining difference, is in my judgment (particularly since the difference is relatively minor) not sufficient to warrant the retention of the name *anocularis* for USNM 46556, UI 46710, and UMMZ 125288. It seems more reasonable to assume that local populations of a single species of *G. dubius* differ in these segmental counts.

SPECIMENS EXAMINED (14).—No locality: ZMB 4064. MEXICO: No locality: BMNH 64.1.15.14–15, USNM 31351–52, ZMB 6407. Oaxaca: Ixtlan de Juarez, AMNH 65888; 1 mi E Ixtlan de Juarez, AMNH 89345; San Andres Lovene, UI 46710; 23 mi N San Gabriel, UMMZ 125288; Totontepec, USNM 46556; "Tehuantepec." ZMB 7221 (2). Veracruz: Jalapa, BMNH 1946.1.6.48.

### *Geophis fulvoguttatus* Mertens

*Geophis fulvoguttatus* Mertens, 1952b:134; 1952a:65, pl. 14, fig. 82.

HOLOTYPE.—SNM 43248; Hacienda Monte Cristo, Gebirge von Metapan, Dept. Santa Ana, El Salvador; August, 1951; A. Zilch, collector.

DISTRIBUTION.—Known only from the type locality; Mertens (1952a:15) characterized this area as cloud forest at 2200 meters above sea level.

DIAGNOSIS.—Distinguished from other members of the genus by the combination of (1) dorsal scales in 17 rows, smooth throughout body length; (2) no anterior temporal; (3) total nasal length greater than that of loreal; (4) dorsum dark, with 17–22 irregular light blotches; and (5) ventrals whitish, lateral edges mottled with dark pigment.

DESCRIPTION.—Head indistinct from neck; snout long, not strongly tapered, projecting well beyond lower jaw; rostral prominent, its visible length one-third its distance from frontal; internasals large, rounded anteriorly, about three-fourths as long as prefrontal suture; prefrontals short, their median

suture one-third the frontal length; frontal broader than long, anterior margin distinctly angulate; parietals short, broad, their median suture two-thirds as long as frontal; supraocular small, slightly more than half as long as loreal, forms little more than posterior half of dorsal margin of orbit; one postocular, higher than long, smaller than supraocular.

Nasal divided, postnasal half-again as long as prenasal, their combined length exceeds that of loreal; loreal short, contained twice and one-half in snout length, slightly longer than eye diameter; eye small, contained thrice in snout length, its vertical diameter four-fifths its distance from lip; supra-labials 6, third and fourth in orbit, fifth largest and in contact with parietal; lip exposure of fifth labial half-again as long as that of fourth; no anterior temporal; one posterior temporal, fused with nuchal along parietal margin.

Mental broader than long, acuminate anteriorly, separated from chinshields by first pair of infralabials; infralabials 6, first three pairs in contact with anterior chinshields; anterior chinshields less than twice as long as broad, longer than posterior pair; posterior chinshields in narrow contact anteriorly, separated posteriorly by median gular; three rows of gulars separate chinshields from first ventral.

Dorsal scales in 17 rows, smooth throughout body length; scales above vent bear paired apical pits. Ventrals in single undamaged male, 137; anal undivided; subcaudals in two males, 34-36. Ventrals plus caudals, 171. Total length of male, 335 mm; tail, 54 mm (16.1%).

Maxilla extends anteriorly to suture between first and second supra-labials; anterior extension greater than that of palatine; maxilla curved in lateral view, slenderest anteriorly; 10 maxillary teeth, increasing in length posteriorly; first tooth at anterior tip of maxilla; posterior end of maxilla laterally compressed into moderate flange; anterior end of ectopterygoid bifurcate, one branch short and blunt, second branch long, compressed, blade-like; no postorbital bone.

Basal part of everted hemipenis bears numerous spinules and one large spine; a basal naked pocket on antisulcus side, flanked by raised, inflated ridges. Central part of organ bears about 35 long, slender spines in oblique rows. Distal part of organ capitate; capitation obscured by gradation between spines of central part of organ and those of proximal edge of capitulum; capitulum spinulate; calyces discernible at apex only; apex distinctly bilobed. *Sulcus spermaticus* bifurcate, each branch reaches apex of one lobe. *M. retractor penis magnus* divides into two slips near apex of organ.

Ground color of head and anterior part of body grayish, becoming darker brownish-black toward posterior end of body; posterior parts of scales in first row mottled with yellowish-white; anterior fourth of body uniformly dark; 17-22 irregular yellowish-brown to reddish blotches on posterior part of body; first few blotches suffused with dark pigment; remaining blotches

not sharply demarcated, mottled along their edges; light blotches either single and middorsal or divided into paired lateral blotches; 3–4 irregular light blotches on basal half of tail; terminal half of tail unmarked. Dorsum of head grayish; lateral parts paler; most of fourth, fifth, and sixth supralabials yellowish. Chin region yellowish; mental and infralabials lightly mottled with brown; ventrals yellow-white, lateral edges mottled with grayish-brown; a few dark mottlings in midventral area on posterior part of body; subcaudals gray-brown; anterior subcaudals with pale posterior margins.

VARIATION.—I have not examined the type. It is a juvenile male (total length, 130 mm) with 17 light blotches on the body. In the type only the fifth and sixth supralabials are light; in UK 57996 the fourth is also light. The type is damaged ventrally; the number of ventrals was estimated to be between 145 and 150 by Mertens. The posterior edges of the parietals are peculiarly shaped in UK 57996, the result of fusion with a nuchal.

REMARKS.—In life, the coloration is grayish-black with reddish blotches; the venter is dirty white (D. L. Hoyt, pers. com.).

SPECIMEN EXAMINED (1).—EL SALVADOR: Santa Ana: Metapan Mountains, Hacienda Monte Cristo, UK 57996.

### *Geophis immaculatus*; new species

*Geophis dubius*, Stuart (in part), 1963:99.

HOLOTYPE.—UMMZ 107297, an adult female; Guatemala, Quetzaltenango, Finca Lorena; L. C. Stuart, collector. UMMZ 107298 is a paratopotype.

DISTRIBUTION.—Known only from the type locality, on the Pacific versant of Guatemala; about 1700 meters above sea level (Stuart, 1951:44).

DIAGNOSIS.—Distinguished from other members of the genus by the combination of (1) dorsal scales in 17 rows, smooth throughout length; (2) no anterior temporal; (3) anterior tip of each dorsal brownish-black, central parts brown, lateral edges yellowish-white; (4) anterior edges of ventrals pale brownish, posterior edges yellowish-white; (5) total nasal length greater than that of loreal; and (6) lip exposure of fifth labial nearly twice that of fourth labial.

DESCRIPTION OF HOLOTYPE.—Head indistinct from neck; snout long, bluntly pointed from above, projecting well beyond lower jaw; rostral moderate, half as long as its distance from frontal; internasals slightly broader than long, rounded anteriorly, their greatest length nearly as long as prefrontal suture; prefrontals short, their median suture about one-third as long as



frontal; frontal broader than long, angulate anteriorly, forms short suture with supraocular; parietals short, broad, their median suture two-thirds as long as frontal; supraocular small, triangular, half as long as loreal, forms posterior half of dorsal margin of orbit; one postocular, higher than long, slightly smaller than supraocular.

Nasal divided, postnasal half-again as long as prenasal, their combined length greater than that of loreal; loreal short, contained twice and a half in snout length, half-again as long as eye diameter; dorsal margin of loreal straight; eye small, contained four times in snout length, its vertical diameter two-thirds its distance from lip; supralabials 6, third and fourth in orbit, fifth largest and in contact with parietal; lip exposure of fifth supralabial nearly twice that of fourth; lip exposure of third supralabial about equal to that of second; no anterior temporal; one posterior temporal separates sixth labial and parietal; temporal fused with nuchal along parietal margin.

Mental slightly broader than long, acuminate anteriorly, separated from chinshields by first pair of infralabials; infralabials 6, pairs 1-3 in contact with anterior chinshields; anterior chinshields less than twice as long as broad, half-again as large as posterior pair; posterior chinshields in narrow contact anteriorly, separated for most of length by median gular; four series of irregular gulars separate chinshields from first ventral.

Dorsal scales in 17 rows, smooth throughout length; paired apical pits present on scales above vent; 130 ventrals; anal undivided; 29 subcaudals. Total ventrals plus caudals, 159. Total length, 305 mm; tail, 44 mm (14.4%).

Maxilla extends anteriorly to suture between first and second supralabials; anterior extension greater than that of palatine; maxilla curved in lateral view, slender anteriorly, thicker posteriorly; 12 maxillary teeth, increasing slightly in length toward posterior end of row; first tooth at anterior tip of maxilla; posterior end of maxilla laterally compressed into moderate flange; anterior end of ectopterygoid bifurcate, one branch short and blunt, other long, blade-like.

Dorsum of head dark grayish-brown; sides of head slightly paler; ground color of dorsum brownish; scales of first two rows darkest at anterior tip, brownish centrally, pale yellowish-brown on posterior parts; scales of other rows with a dark brownish-black spot at anterior tip, dark brown centrally, with yellowish lateral edges; dorsal rows appear outlined by yellow pigment; dorsal scales of tail uniformly brownish-black, notably darker than body, somewhat paler laterally. Chin region pale brownish-yellow; anterior ventrals yellowish, mottled with brown along lateral edges; posterior ventrals lightly banded, each scale with brown pigment along anterior and lateral edges, yellowish along posterior edge; subcaudals dark brown along anterior edges, yellowish along posterior edges.

VARIATION.—The paratype is similar to the type; it is a female with a total length of 213 mm, and a tail length of 29 mm (13.6%). There are 134 ventrals and 27 subcaudals; the posterior temporal is not fused with a nuchal along the parietal margin on the right side; the mental extends as a narrow wedge between the first pair of infralabials to touch the anterior chinshields. The coloration is similar to that of the type, but the tail is less noticeably darker than the body, and the brownish edges of the posterior ventrals and subcaudals are considerably paler than in the type.

REMARKS.—This species is most closely related to *G. fulvoguttatus*, known only from the highlands of El Salvador. *G. immaculatus* can be readily distinguished from *G. fulvoguttatus* by the absence of the lateral reddish spots found in the latter form (hence the name, *immaculatus*), and by the fewer ventral scales.

*G. immaculatus* is difficult to distinguish from certain individuals of *G. dubius* from the Sierra Madre del Sur of Oaxaca, Mexico. These specimens, UI 46710 and UMMZ 125288, are both males, and have lower ventral counts than most males of *dubius*; although their ventral counts cannot be compared directly with those of the female specimens of *immaculatus*, the sums of the ventrals and caudals (effectively eliminating sexual differences) are similar to those of *immaculatus*. UI 46710 and UMMZ 125288 also have distinct internasals (absent in most *dubius*), adding to the similarities between these specimens and *immaculatus*. Several minor differences in head proportions, head scutellation, and the characteristics of the maxilla between the individuals from the Sierra Madre del Sur and those of *immaculatus* convince me that the Oaxacan specimens are conspecific with *dubius* and distinct from *immaculatus*. In contrast to UI 46710, UMMZ 125288, and other specimens of *dubius*, *G. immaculatus* has a relatively shorter, less pointed snout, a shorter loreal, longer parietals, longer lip exposures of the second and fifth supralabials, and a maxilla that is curved in lateral view and extends farther anterior than in *dubius*. With the exception of the lip exposure of the second supralabial, which is about equal to that of the third labial in *immaculatus* and much shorter than the third in *dubius*, these characteristics of *immaculatus* are shared by *G. fulvoguttatus*.

SPECIMENS EXAMINED (2).—GUATEMALA: **Quetzaltenango**: Finca Lorena, UMMZ 107297–98.

### *Geophis rhodogaster* (Cope)

*Colophrys rhodogaster* Cope, 1868:130, fig.; Cope, 1887:86.

*Geophis rhodogaster*, Bocourt, 1883:531; Boulenger, 1894:317; Stuart, 1963:100.

*Geophis chalybaea*, Günther (in part), 1893:87.

*Catostoma rhodogaster*, Amaral, 1929:192.

**HOLOTYPE.**—Originally three syntypes, collected from “the elevated country in the neighborhood of the city of Guatemala,” by Van Patten; two of the three are ANSP 3316–17, and the third almost certainly is USNM 12425. ANSP 3317, an adult female, is herein designated as lectotype (see below).

**DISTRIBUTION.**—Known from the western part of the Guatemalan Plateau, eastward through the southeastern highlands of Guatemala into adjacent El Salvador; generally from oak-pine associations between 1500 and 2500 meters above sea level.

**DESIGNATION OF A LECTOTYPE.**—Although mentioning that three specimens had been received from Van Patten, the original description apparently was based primarily on a single specimen. Cope’s description (1868:131) stated, “Gastrosteges 144, urosteges 30; in a second specimen 140–41. Length of largest specimen 12 inches; tail 2 in. 1.5 lines.” Although I cannot duplicate Cope’s counts precisely, his “second specimen” clearly refers to a male, presumably ANSP 3316, but possibly USNM 12425. The counts of his “first” specimen, and the linear measurements of the largest specimen, clearly refer to ANSP 3317, an adult female on which I count 142 ventrals and 29 subcaudals. The figure of the head scales presented by Cope can be applied to any of the three. The evidence clearly indicates that a large female was being described, and I therefore designate ANSP 3317 as lectotype.

Barbour and Loveridge (1929:243) listed three specimens (MCZ 5828) in the Museum of Comparative Zoology as cotypes of this species. This claim was apparently based on the fact that Van Patten had collected the specimens, but can be dismissed since (1) there are actually four specimens under MCZ 5828; and (2) the largest of the four is only slightly more than half as long as the specimen specified by Cope.

**DIAGNOSIS.**—Distinguished from other members of the genus by the combination of (1) dorsal scales in 17 rows, completely smooth throughout length; (2) no anterior temporal; (3) no supraocular, frontal enters orbit; and (4) venter immaculate yellowish-white.

**DESCRIPTION.**—Head scarcely distinct from neck; snout moderate, bluntly rounded from above, moderately projecting beyond lower jaw; rostral not strongly produced posteriorly between internasals, its length one-third to one-half its distance from frontal; internasals large, broader than long, their greatest length three-fourths as long as prefrontal suture; prefrontals short and broad, their median suture less than half as long as frontal; frontal much broader than long, enters orbit; parietals short, their median suture three-fifths as long as frontal; supraocular absent (fused with, or displaced by, frontal); one postocular, much higher than long, separates parietal from orbit.

Nasal divided, postnasal half-again as long as prenasal, their combined length greater than that of loreal; loreal less than twice as long as high, slightly longer than eye diameter; vertical diameter of eye three-fourths to equal its distance from lip; supralabials 6, third and fourth enter orbit, fifth largest and in broad contact with parietal; no anterior temporal; one posterior temporal, separates sixth labial from parietal, not fused with nuchals along parietal margin.

Mental bluntly pointed anteriorly, broader than long, separated from chinshields by first pair of infralabials; infralabials 6 (7), pairs 1-3 (1-4) in contact with anterior chinshields; anterior chinshields short, broad, larger than posterior pair; posterior chinshields in contact anteriorly, separated by median gular posteriorly; 2-3 rows of gulars separate chinshields from first ventral.

Dorsal scales in 17 rows, smooth throughout length; paired apical pits apparently absent. Ventrals in fourteen males, 131-138 (134.8); in sixteen females, 136-147 (141.9); anal undivided; subcaudals in fourteen males, 39-44 (41.6); in sixteen females, 29-35 (32.6). Ventrals plus caudals, 169-182. Total length of largest male, 324 mm; tail, 71 mm (21.9%); largest female, 377 mm; tail, 63 mm (16.7%).

Maxilla extends anteriorly to suture between supralabials one and two; anterior extension greater than that of palatine; maxilla narrow anteriorly, thicker posteriorly; 14-17 maxillary teeth, increasing in length posteriorly; first tooth at anterior tip of maxilla, last few on ventrolateral surface of posterior flange; posterior end of maxilla compressed and expanded into moderate, almost horizontal, flange; anterior end of ectopterygoid bifurcate, one branch short and blunt, the other long, blade-like; no postorbital bone.

Hemipenis long and slender, extends posteriorly to subcaudals 11-13; basal part of organ bears many minute spines and, in distal parts, 2-3 larger spines; a basal naked pocket present on antisulcus side. Central part of organ bears about 35 medium spines and hooks. Distal part of organ capitate; capitation obscured by gradation between spines of proximal edge of capitulum and central part of organ; capitulum calyculate and papillate near apex, spinulate proximally; apex strongly bilobed, each lobe two subcaudals in length. *Sulcus spermaticus* bifurcates at subcaudal 8-9. *M. retractor penis magnus* divides into two slips, one attaches to each lobe of hemipenis.

Ground color of dorsum grayish to reddish-brown; supralabials 1-2, most of labials 3-4, and lower halves of labials 5-6 immaculate yellow; ventral parts of rostral, nasals, and loreal mottled with yellow and gray-brown; scales in anterior part of first scale row yellow, those in posterior parts yellow except for dark anterior edge; scales in second row yellow with dark

edges, forming a row of spots along most of body length; scales in other rows with dark anterior edges. Chin region and ventrals yellowish, immaculate; subcaudals yellow, edges lightly mottled with grayish-brown.

**VARIATION.**—None of the specimens show any trace of a supraocular. The postocular is absent as well in UK 58000; on the left it is completely fused with the parietal, and on the right only a partial suture separates the two. Reduction in the number of supralabials occurs in but one individual, UMMZ 98310; in that specimen the third and fourth labials are fused, reducing the number to five. The infralabials, however, are more variable; 21 specimens have 6–6 infralabials, five 6–7, and five 7–7. Most of this infralabial variation occurs in specimens from the central part of the range, near the eastern limits of the Guatemalan Plateau; for example, in the three original syntypes from near the city of Guatemala, five of the six sides have seven labials. Individuals from the western part of the Plateau, and from El Salvador, consistently have six labials. There is no indication of geographic variation in the number of ventrals or caudals.

Variation in color is largely restricted to the lateral scale rows; the light ventral coloration occasionally (e.g., UK 57997) extends laterally to the third scale row as well as the first two rows. This extension is most evident on the anterior part of the body.

**REMARKS.**—The dorsum in life is apparently iridescent slate-brown, the light area reddish-orange (Cope, 1868:131).

The occurrence of *G. rhodogaster* at various localities within its range is apparently determined by the availability of cover, rather than the more general aspects of the environment; Stuart (1951:20) reported finding *rhodogaster* under debris in such diverse habitats as moist, forested river flood plains, cultivated hillsides, and dry grassy slopes of pine parklands.

Günther (1893:88) and Boulenger (1894:317) included Yucatan and Costa Rica within the range of *rhodogaster*; Günther listed specimens (not by catalog number) in the Smithsonian Institution as the basis for this apparent range. There are no such specimens in that collection at present. The Yucatan record can be discounted on the basis of environmental conditions. I also concur with Taylor (1951:39) that the Costa Rican record is doubtful; no other species in the genus occurs in both Guatemala and Costa Rica.

**SPECIMENS EXAMINED (28).**—**GUATEMALA:** No locality: MCZ 5828 (4), USNM 12425, ZMB 10196. **Baja Verapaz:** Rio Chisoy, below Cubulco, BMNH 69.2.22.5–6. **Chimaltenango:** Chichavac, CAS 67010–15. **Guatemala:** Finca Santa Lucia, UMMZ 106552; near Guatemala City, ANSP 3316–17; Las Nubes, 11 km E San Jose Pinula, UMMZ 100515. **San Marcos:** Rio Achute flood plain below Tacana, UMMZ 98308; near Tacana, UMMZ 98309; 3 km E Tejutla, UMMZ 98310. **Solola:** Lake Atitlan, near Hotel Tzanjuyu, UMMZ 120445–46; Panajachel, MCZ 22441, UMMZ 123334–35. **EL SALVADOR:** **Santa Ana:** Metapan Mountains, Hac. Monte Cristo, UK 57997–58000.

THE *latifrontalis* GROUP

Dorsal scales in 17 rows, smooth throughout length; no paired apical pits. Head indistinct from neck; snout moderate, rounded from above; eye small; rostral not prominent from above; scales of snout moderate, neither internasals and postnasals nor prefrontals and loreal particularly elongate; supraocular moderate, forms posterior two-thirds of dorsal margin of orbit; parietals long; anterior temporal present, long and narrow (absent in *blanchardi*); one or two posterior temporals. Ventrals 149–169 in males, 159–185 in females. Subcaudals 28–49 in males, 24–38 in females. Percentage tail of total length 12.1–17.2 in males, 9.9–14.9 in females.

Maxilla extends anteriorly at least to middle of first supralabial; anterior extension greater than that of palatine; maxilla large, stout, curved in lateral view; 8–12 long maxillary teeth, decreasing in length posteriorly; first tooth at anterior tip of maxilla; posterior end of maxilla flattened, not expanded, deflected ventromedially from major axis of maxilla. Anterior end of ectopterygoid bifurcate, branches subequal in length, not expanded. Postorbital bone present, stout; parietal bones extend anteriorly along orbits, often exclude frontal from orbit.

Apex of hemipenis single; *sulcus spermaticus* bifurcate; one branch of sulcus obsolescent, fails to reach apex; a naked basal pocket opposite sulcus; large spines of central part of organ grade into smaller spines of capitulum; distal part of organ weakly capitate; capitulum calyculate, spinulate proximally, papillate distally; M. retractor penis magnus single throughout length.

I include four forms (*G. blanchardi*, *G. latifrontalis*, *G. mutitorques*, *G. semiannulatus*) in this group (Fig. 9). Geographically, the group is distributed along the Sierra Madre Oriental and adjacent part of the Mexican Plateau from Tamaulipas and San Luis Potosi southward to Veracruz (Fig. 10). The species occupy humid montane forests between 1000 and 2600 meters above sea level.

Within the group, *G. blanchardi* is unique in the absence of the anterior temporal. In many respects it is similar to *mutitorques*, and is presumably most closely related to that species. Both forms have a checkered venter and unicolor dorsum; the venter is dominated by the light checkers in *blanchardi*, by the dark in *mutitorques*. The dorsum in *blanchardi* is bluish-gray, that in *mutitorques* bluish-black; the light collar of juvenile *mutitorques* is absent in all age classes of *blanchardi*, and the ventral pattern is not obliterated with dark pigment in adult *blanchardi*. The two posterior temporals of *mutitorques* are reduced to a single scale in *blanchardi*. *G. blanchardi* has a lower number of ventrals than any other member of the group. Geographically, the eastern edge of the transverse neovolcanic plateau inter-

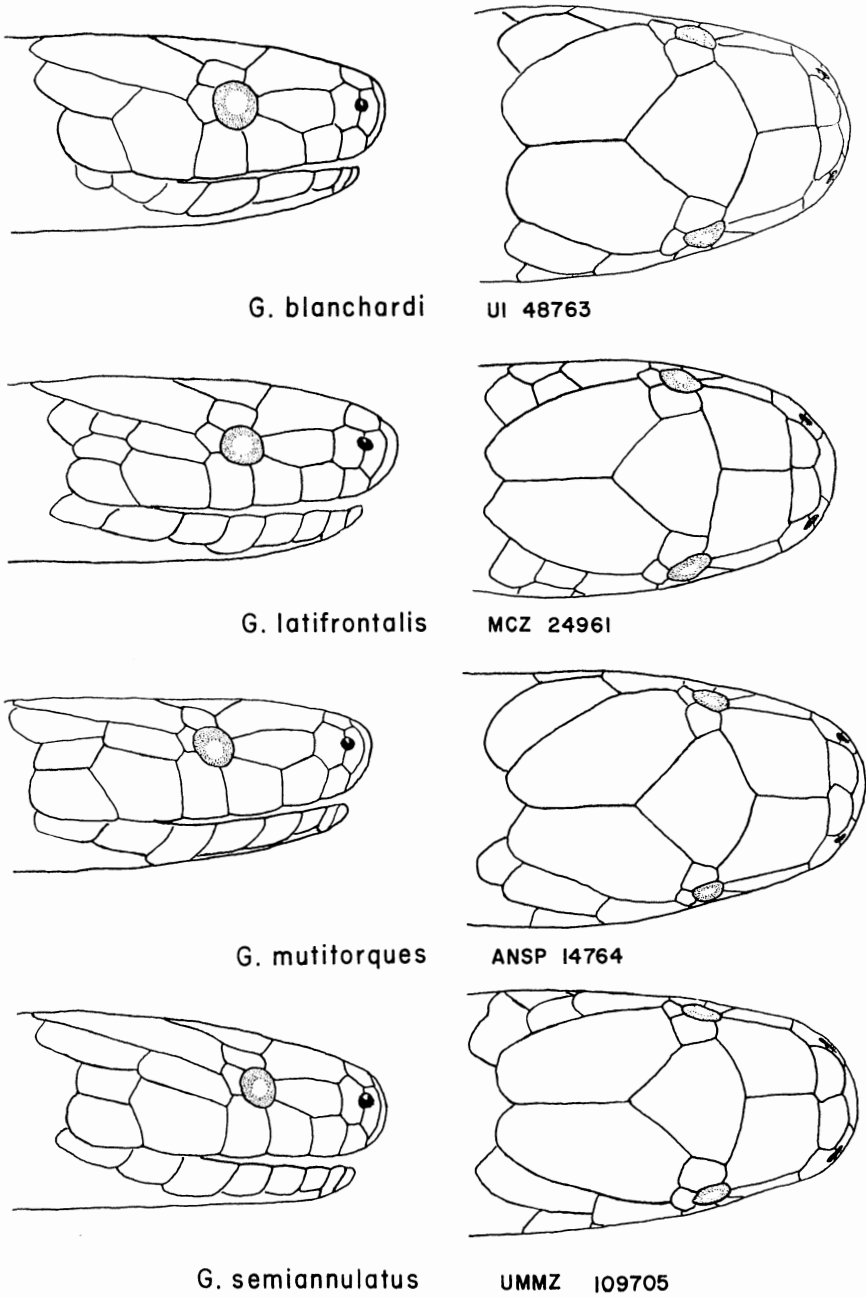


FIG. 9. Dorsal and lateral head scutellation in members of the *latifrontalis* group. Scale: *G. blanchardi*, about 5.5 ×; *G. latifrontalis*, about 6.5 ×; *G. mutitorques*, about 5 ×; *G. s. miannulatus*, about 6 ×.

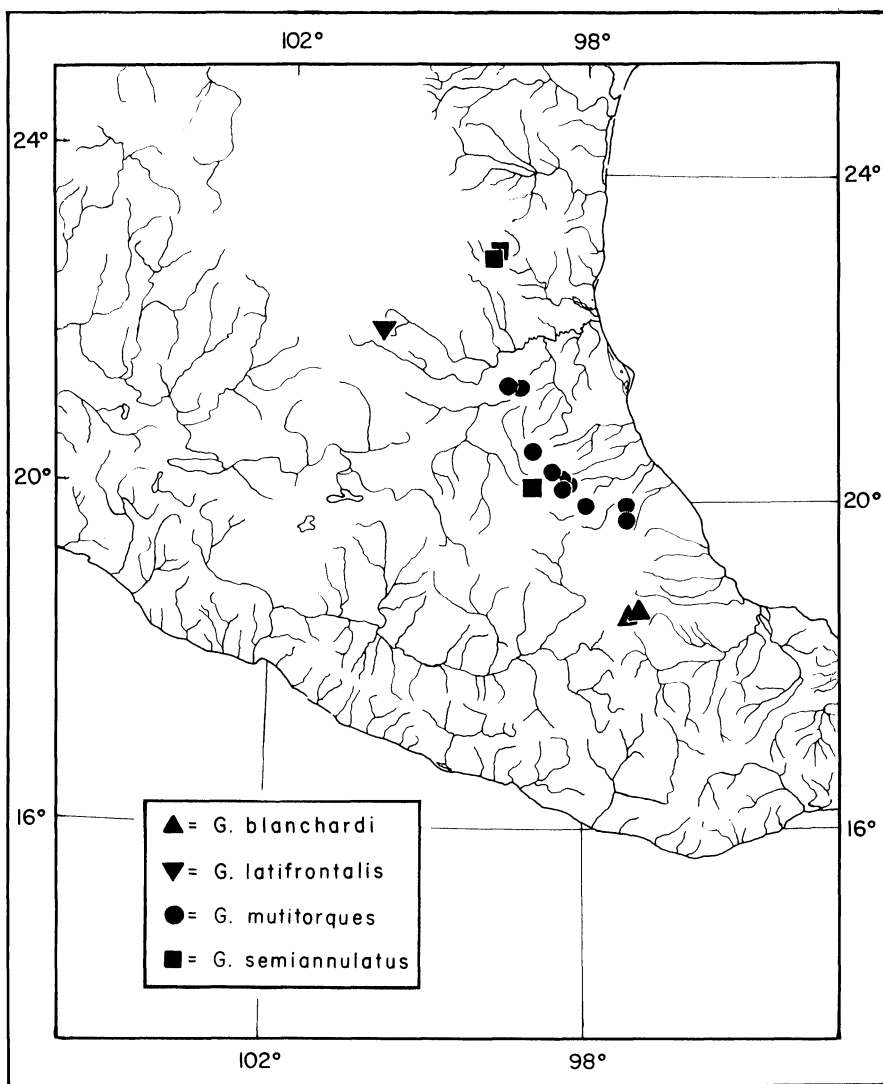


FIG. 10. Locality records for members of the *latifrontalis* group

venes between the range of *blanchardi* and those of the other three forms.

Among the remaining three species, *G. semiannulatus* is the most distinctive. It has a higher number of ventrals than either *latifrontalis* or *mutitorques*, and is the only member of the group with a banded dorsum. The dark dorsal bands usually extend onto the ventral surface, either as alternating blotches or as complete rings; the former pattern is not unlike the checkered venters of *mutitorques* and *blanchardi*. The uniformly dark



dorsum of *mutitorques* can be hypothetically derived from the banded pattern of *semiannulatus* by a simple expansion and coalescence of the black bands; conversely, the banded pattern of *semiannulatus* can be derived from the *mutitorques* condition by an expansion of the light ventral areas onto the dorsal surface. In head scutellation, *semiannulatus* is similar to *mutitorques* and *latifrontalis*; the only notable differences among the three involve the highly variable temporal region of *semiannulatus* and preocular-loreal region of *latifrontalis*.

*G. mutitorques* was placed in the synonymy of *latifrontalis* by Boulenger (1894:304); this arrangement was followed until Smith (1941a:53) reestablished the use of *mutitorques*. Smith's resurrection of *mutitorques*, with which I concur, was based primarily on differences in caudal counts, posterior chinshields, and coloration. Although the ranges in the number of subcaudals in *latifrontalis* and *mutitorques* overlap widely, the mean caudal number is significantly higher in *latifrontalis* than in *mutitorques*; both males and females fit this pattern. The posterior chinshields are usually in contact in *latifrontalis*, and usually separated by a median gular in *mutitorques*. The light collar and checkered venter, characteristic of all but large adult *mutitorques*, are absent in all age groups of *latifrontalis*.

Although they are not known to occur at the same locality, the geographic ranges of *semiannulatus* and *mutitorques* overlap widely; the former is known from as far south as Guerrero, Hidalgo, and the latter from as far north is Xilitla, San Luis Potosi. *G. latifrontalis* is at present isolated in the mountains near Alvarez, San Luis Potosi. These species inhabit humid montane forests, which now occur in isolated patches in the Sierra Madre Oriental. In explaining the present distribution of *G. semiannulatus* and other members of the Northeast Madrean biota, Martin (1958:89) proposed two possible Pleistocene corridors along which dispersion may have occurred; one route follows the escarpment of the Sierra Madre Oriental and the second follows the interior ranges through San Luis Potosi. The known localities of *semiannulatus*, *latifrontalis*, and *mutitorques* are distributed along these routes. Presumably, *G. semiannulatus* spread southward from a northern center during the existence of these corridors; at the same time, *mutitorques* spread northward from a southern center, thus accounting for the overlap between the ranges of these two species. The fragmentation of the corridors, causing disjunction of the humid montane habitat, would account for the presence of *latifrontalis* in the interior ranges.

#### *Geophis blanchardi* Taylor and Smith

*Geophis blanchardi* Taylor and Smith, 1939:245, fig. 2; Taylor, 1940:452; Smith and Taylor, 1945:67.

HOLOTYPE.—CNHM 100037, an adult female collected about 2 miles SW

of Acultzingo, Veracruz; August 14, 1936: E. H. Taylor, collector. CNHM 100337-39, UI 27381, and USNM 139732 are paratopotypes.

**DISTRIBUTION.**—Known only from the Cumbres de Acultzingo region of Veracruz; about 2300 meters above sea level.

**DIAGNOSIS.**—Distinguished from other members of the genus by the combination of (1) dorsal scales in 17 rows, smooth throughout length; (2) no anterior temporal; (3) one postocular; (4) seven infralabials; and (5) dorsum bluish-gray, venter checkered with yellowish-orange and black.

**DESCRIPTION.**—Head scarcely distinct from neck; snout rounded from above, projecting beyond lower jaw; rostral much broader than long, not produced posteriorly between internasals, its length one-fifth to one-fourth its distance from frontal; internasals broader than long, half as long as prefrontal suture; prefrontal suture slightly less than half as long as frontal; frontal as broad as long, subtriangular or with convex anterior margin; parietals long, their median suture slightly shorter than frontal; supraocular two-thirds as long as loreal, forms posterior two-thirds of dorsal margin of orbit; one postocular, slightly smaller than supraocular.

Nasal divided, postnasal slightly larger than prenasal, their combined length three-fourths as long as loreal; loreal moderate, contained less than twice in snout length, less than twice as long as eye; eye small, contained thrice in snout length, its vertical diameter three-fourths its distance from lip; supralabials 6, third and fourth in orbit, fifth largest and in broad contact with parietal; dorsal margin of second labial usually parallel to lip; no anterior temporal; one posterior temporal between sixth labial and parietal, often fused with nuchal along parietal margin.

Mental rounded anteriorly, much broader than long, separated from chinshields by first pair of infralabials; infralabials 7, first three pairs in contact with anterior chinshields; anterior chinshields broad, half-again as long as posterior pair; posterior chinshields in contact medially, separated from first ventral by 3-4 rows of gulars.

Dorsal scales in 17 rows, smooth throughout length; no apical pits. Ventrals in six males, 150-156 (152.3); in 13 females, 159-166 (162.1); anal undivided; subcaudals in six males, 34-40 (37.5); in 12 females, 28-34 (30.8). Ventrals plus caudals, 184-199. Total length of largest male, 325 mm; tail, 55 mm (16.9%); largest female, 404 mm; tail 53 mm (13.1%).

Maxilla extends anteriorly to suture between rostral and first supralabial; anterior extension greater than that of palatine; maxilla large, stout, curved in lateral view; 11-12 curved maxillary teeth, decreasing in length posteriorly; first tooth at anterior tip of maxilla; last 2-3 teeth small, located on ventrolateral aspect of maxillary flange; posterior end of maxilla flattened, not expanded, deflected ventromedially from major axis of maxilla;

anterior end of ectopterygoid bifurcate, branches subequal in length, neither expanded; postorbital bone stout.

Hemipenis extends posteriorly to level of ninth subcaudal; basal part of organ bears numerous spinules and, distally, three large spines; basal naked pocket opposite sulcus. Central part of organ bears numerous long spines, decreasing in length toward apex. Distal part of organ weakly capitate; capitation obscured by gradation between spines of central part of organ and those of proximal edge of capitulum; capitulum calyculate, spinulate proximally, papillate distally; apex of organ undivided. *Sulcus spermaticus* bifurcates opposite seventh caudal; on branch reaches apex; second branch obsolescent, fails to reach apex. M. retractor penis magnus single throughout length.

Dorsum bluish-gray to brownish-black; anterior and lateral head scales grayish; frontal and parietals dark brownish; dorsal scales of lateral rows paler along posterior margins. Chin region yellowish; infralabials mottled with gray; venter checkered with alternating yellowish and blackish blotches; dark blotches usually occupy three ventrals; alternating left and right blotches often share one ventral, form single, jagged blotch across venter; left and right blotches occasionally coincide, form band across venter; yellowish blotches parallel shape of black ones, occupy greater number of ventrals; subcaudal coloration similar to that of ventrals, but black blotches predominate.

VARIATION.—Little variation in scutellation and coloration is evident; CNHM 123384 has two postoculars on one side; the number of supralabials is reduced to five by fusion of the third and fourth labials on one side of UMMZ 88677; the number of infralabials is reduced to six on one side of each of three specimens by a scale fusion in the posterior part of the row; subcaudals 4–11 are undivided in UI 27381. The relative amounts of light and dark ventral pigment varies considerably, but in all cases the light pigment occupies the greater area; in some specimens, e.g., UMMZ 88677, most of the dark blotches are small and fail to reach the midline.

REMARKS.—In recently preserved specimens, the light areas of the venter were orange (Taylor and Smith, 1939:246).

SPECIMENS EXAMINED (19).—MEXICO: **Veracruz**: Acultzingo, UMMZ 88677–79; 2 mi SW Acultzingo, CNHM 100037, 100337–39, UI 27381, USNM 109936–39, 139732; Cumbres de Acultzingo, CNHM 123383–35, UI 27383–84, 48763.

### *Geophis latifrontalis* Garman

*Geophis latifrontalis* Garman, 1883:103; Günther, 1893:93; Dunn (in part), 1928a:1; Smith, 1941a:51; Smith and Taylor, 1945:68.

*Rhabdosoma latifrontale*, Cope, 1887:91.

*Atractus latifrontalis*, Boulenger (in part), 1894:304; Cope, 1896:1023; Cope, 1900:1230; Werner (in part), 1929:155; Amaral (in part), 1929:187.

HOLOTYPE.—MCZ 4538, an adult female from “fifty miles south of San Luis Potosi, Mexico”; E. Palmer, collector.

DISTRIBUTION.—Known only from the vicinity of Alvarez, San Luis Potosi; located on the eastern slope of the mountains southeast of the city of San Luis Potosi, at about 2400 meters above sea level (McVaugh, 1956:137). Humid montane forests persist in this area (Martin, 1958:89).

DIAGNOSIS.—Distinguished from other members of the genus by the combination of (1) dorsal scales in 17 rows, smooth throughout length; (2) one anterior and two posterior temporals; (3) one postocular; (4) dorsum uniformly dark at all ages; and (5) venter yellowish-white, mottled with brown.

DESCRIPTION.—Head indistinct from neck; snout rounded from above, projecting well beyond lower jaw; rostral much broader than long, not produced posteriorly between internasals, its length about one-fifth its distance from frontal; internasals broader than long, half as long as prefrontal suture; prefrontal suture slightly more than half as long as frontal; frontal broader than long, subtriangular or convex anteriorly; parietals long, their median suture slightly shorter than frontal; supraocular about three-fourths as long as loreal, forms posterior two-thirds of dorsal margin of orbit; one postocular, slightly smaller than supraocular.

Nasal divided, postnasal slightly larger than prenasal, their combined length three-fourths that of loreal; preocular sometimes present, variable in size and shape; loreal moderate, contained slightly less than twice in snout length, twice as long as eye; eye small, contained three to four times in snout, its vertical diameter three-fourths its distance from lip; supralabials 6, third and fourth in orbit, fifth largest; dorsal margin of second labial usually parallel to lip; long, narrow anterior temporal separates fifth labial from parietal; two posterior temporals, upper often fused with nuchal along parietal margin.

Mental rounded, much broader than long, separated from chinshields by first pair of infralabials; infralabials 7, first four pairs in contact with anterior chinshields; anterior chinshields longer than broad, twice as long as posterior pair; posterior chinshields usually in contact medially, separated from first ventral by 2–3 rows of gulars.

Dorsal scales in 17 rows, smooth throughout length; apical pits absent. Ventrals in 8 males, 154–163 (158.0); in 12 females, 164–175 (170.8); anal undivided; subcaudals in 8 males, 32–41 (39.5); in 12 females, 27–34 (31.4). Ventrals plus caudals, 192–209. Total length of largest male, 337 mm; tail, 52 mm (15.4%); largest female, 419 mm; tail, 48 mm (11.5%).

Maxilla extends anteriorly to suture between rostral and first supralabial; anterior extension greater than that of palatine; maxilla large, stout, curved in lateral view; 10–12 curved maxillary teeth, decreasing in length pos-

teriorly; first tooth at anterior tip of maxilla; last 2-3 teeth small, located on ventrolateral aspect of maxillary flange; posterior end of maxilla flattened, not expanded, deflected ventromedially from major axis of maxilla; anterior end of ectopterygoid bifurcate, branches subequal in length, not expanded; postorbital bone stout.

Hemipenis extends posteriorly to level of tenth subcaudal; basal part of organ bears numerous spinules and, distally, three large spines; naked basal pocket opposite sulcus. Central part of organ bears numerous long spines, decreasing in length toward apex. Distal part of organ weakly capitate; capitation obscured by gradation between spines of central part of organ and those of proximal edge of capitulum; capitulum calyculate, spinulate proximally, papillate distally; apex of organ undivided. *Sulcus spermaticus* bifurcates opposite eighth subcaudal; one branch reaches apex; second branch obsolescent, fails to reach apex. M. retractor penis magnus undivided throughout length.

Head and dorsum slate-gray to grayish-brown; lateral head scales paler than dorsal ones; dorsal scales of lateral rows with paler posterior margins. Ground color of venter whitish or creamish; chin and anterior ventrals invariably light; posterior ventrals flecked with grayish-brown; dark pigment most prominent along midline and posteriorly; venter of most specimens mostly light; in others, posterior ventrals brownish, with pale posterior margins; subcaudals dark grayish-brown, posterior margins paler.

VARIATION.—The orbital region of *latifrontalis* is extremely variable. One half of the known specimens have one or more preoculars on at least one side of the head; the preoculars are variable in size, shape, and position. This variability has been discussed at length in the character analyses, and is illustrated in Fig. 11. The presence of the preocular usually excludes the loreal from the orbit; in those specimens which have no preocular, the loreal region of *latifrontalis* is similar to those of the other species in the group.

The postoculars are 2-2 in two specimens, 1-2 in four, and 1-1 in fourteen; this variability in postocular number is exceeded only by that in *G. incomptus*. The infralabials are 7-7 in eleven specimens, 6-7 in three, and 6-6 in five; the same conditions occur in the related *G. mutitorques*, but less frequently.

The venter is almost completely dark in the largest specimen; individual variation in the available specimens is too great to conclude that there is an ontogenetic darkening of the ventral surface. In *mutitorques*, the ventral pattern is obliterated ontogenetically by black pigment.

SPECIMENS EXAMINED (20).—MEXICO: San Luis Potosi: Alvarez, ANSP 20066, 20069, MCZ 19044-46, 24961-74; mts. of Alvarez, ca. 50 mi SE San Luis Potosi, MCZ 4538.

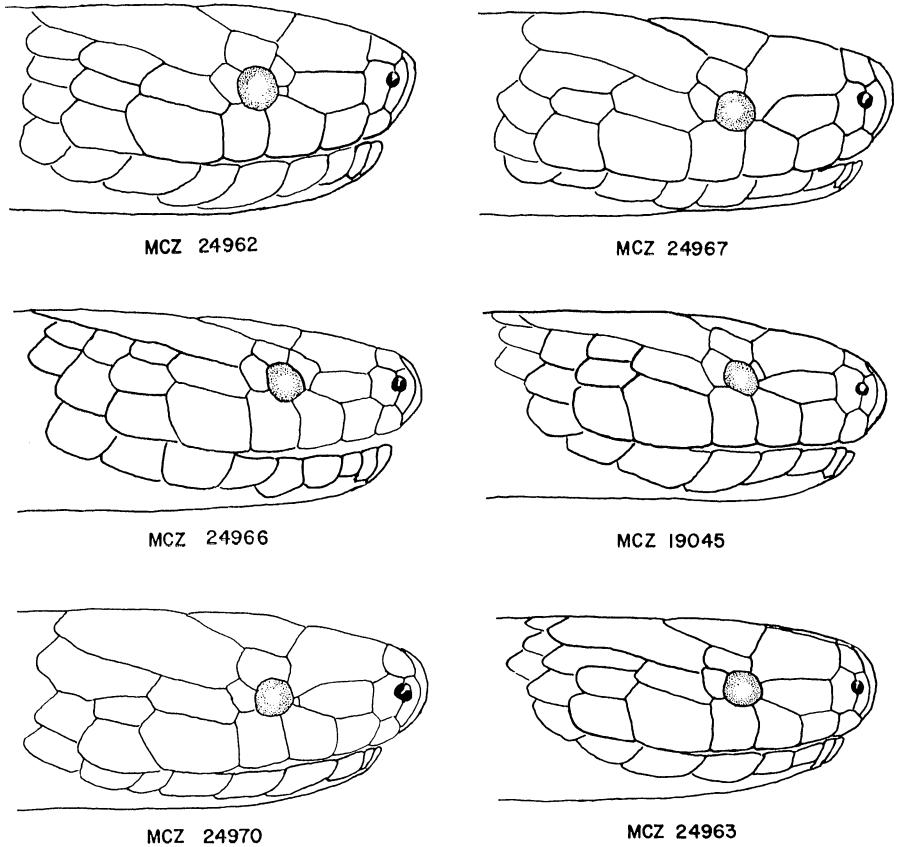


FIG. 11. Variation in the lorcal and preocular regions of *Geophis latifrontalis* from near Alvarez, San Luis Potosi.

### *Geophis mutitorques* (Cope)

*Rhabdosoma mutitorques* Cope, 1885a:384; Cope, 1887:85.

*Rhabdosoma longiceps* Cope, 1886:189 (type, lost; San Jose Acateno, Veracruz, Mexico).

*Geophis mutitorques*, Günther, 1893:93; Smith, 1941a:53; Smith and Taylor, 1945:68.

*Atractus latifrontalis*, Boulenger (in part), 1894:304; Werner (in part), 1929:155; Amaral (in part), 1929:187.

*Atractus longiceps*, Boulenger, 1894:305.

*Geophis latifrontalis*, Dunn (in part), 1928a:1.

*Geophis longiceps*, Dunn, 1928a:1; Smith and Taylor, 1945:68.

*Geophis multitorques* [sic], Taylor, 1949:194.

**HOLOTYPE.**—Cope stated in the original description that he had received six specimens from S. Bernad from the “high land about Zacualtipan.” At present, however, nine specimens (ANSP 11324, 14758–65) in the collections

of the Academy of Natural Sciences of Philadelphia are listed as syntypes. All are from near Zacualtipan. ANSP 14762 is herein designated as lectotype.

**DISTRIBUTION.**—Known from the Sierra Madre Oriental of eastern Mexico; recorded from the highlands of San Luis Potosi, Hidalgo, Puebla, and Veracruz; usually more than 1500 meters above sea level, in humid montane forests.

**DESIGNATION OF A LECTOTYPE.**—Since eight of the nine specimens now listed as syntypes bear consecutive catalog numbers, the three specimens not referred to in the original description were probably in Cope's possession shortly after the description was written. The description is based partly on a single specimen, and partly on the series of syntypes. Segmental counts are given for one specimen, length measurements for two; the description of the coloration implies use of the entire series. The segmental counts (172 ventrals, 24 subcaudals) and the relative tail length of the largest specimen, as recorded by Cope, both indicate a female, and appear to be based on ANSP 11324. The lower, non-consecutive catalog number of this specimen also suggests that ANSP 11324 received special attention from Cope. Unfortunately, the specimen at present is in a poor state of preservation, and would therefore serve inadequately as the lectotype.

The second-largest female among the syntypes is ANSP 14762, with a total length of 337 mm and a tail length of 40 mm. This specimen fits the type description well, with minor differences in segmental counts (169 ventrals, 27 subcaudals). ANSP 14762 is therefore here designated as lectotype; ANSP 11324, 14758–61, and 14763–65 are paralectotypes.

**DIAGNOSIS.**—Distinguished from other members of the genus by the combination of (1) dorsal scales in 17 rows, smooth throughout length; (2) one anterior and two posterior temporals; (3) one postocular; (4) juveniles with a light collar and checkered venter; and (5) large adults uniformly dark above, checkered or black below.

**DESCRIPTION.**—Head indistinct from neck; snout rounded from above, projecting well beyond lower jaw; rostral much broader than long, not produced posteriorly between internasals, its length about one-fifth its distance from frontal; internasals much broader than long, half as long as prefrontal suture; prefrontal suture one-half to two-thirds as long as frontal; frontal slightly broader than long, subtriangular or shallowly angulate anteriorly; parietals long, their median suture as long as frontal; supraocular slightly more than half as long as loreal, forms posterior two-thirds of dorsal margin of orbit; one postocular, higher than long, smaller than supraocular.

Nasal divided, postnasal larger than prenasal, their combined length

about three-fourths as long as loreal; loreal moderate, contained less than twice in snout length, twice as long as eye; eye small, contained thrice in snout, its vertical diameter three-fourths its distance from lip; supralabials 6, third and fourth in orbit, fifth largest; dorsal margin of second labial usually parallel to lip; fifth labial separated from parietal by long, narrow anterior temporal; two posterior temporals, upper often fused with nuchal along parietal margin.

Mental rounded anteriorly, much broader than long, separated from chinshields by first pair of infralabials; infralabials 7, first four pairs in contact with anterior chinshields; anterior chinshields slightly longer than broad, twice as large as posterior pair; posterior chinshields rarely in contact, often scarcely distinguishable from adjacent gulars; 2-3 rows of gulars separate chinshields from first ventral.

Dorsal scales in 17 rows, smooth throughout length; apical pits absent. Ventrals in 25 males, 149-168 (158.2); in 30 females, 160-177 (169.1); anal undivided; subcaudals in 24 males, 28-42 (36.1); in 28 females, 24-33 (28.2). Ventrals plus caudals, 184-207. Total length of largest male, 391 mm; tail, 61 mm (15.6%); largest female, 455 mm; tail, 53 mm (11.6%).

Maxilla extends anteriorly to suture between rostral and first supralabial; anterior extension greater than that of palatine; maxilla large, stout, curved in lateral view; 8-10 maxillary teeth, decreasing in size posteriorly; first tooth at anterior tip of maxilla; last 2-3 teeth small, located on ventrolateral aspect of posterior flange; posterior end of maxilla flattened; not expanded, deflected ventromedially from major axis of maxilla; anterior end of ectopterygoid bifurcate, branches subequal in length, neither expanded; postorbital bone stout.

Hemipenis extends posteriorly to level of ninth subcaudal; basal part of organ bears numerous spinules and, distally, three large spines; naked basal pocket opposite sulcus. Central part of organ bears about fifty long spines, decreasing in length toward apex. Distal part of organ weakly capitate; capitation obscured by gradation between spines of central region and those of proximal edge of capitulum; capitulum calyculate, spinulate proximally, papillate distally; apex of organ undivided. *Sulcus spermaticus* bifurcates opposite seventh subcaudal; one branch reaches apex; second branch obsolescent, fails to reach apex. M. retractor penis magnus undivided throughout length.

Dorsum dark brownish or blackish; scales of lateral rows with pale posterior margins; yellowish collar in small juveniles occupies posterior parts of parietals, posterior temporals, parts of fifth and sixth supralabials, and chin region; collar ontogenetically obliterated by suffusion with dark pigment, absent in large adults. Venter blackish, checkered with yellowish or reddish blotches in juveniles; light areas no more than equal to black ones,



usually distinctly less; light ventral blotches obliterated by black pigment in large adults; black chin scales and ventrals with paler margins; subcaudals black, with paler margins.

**VARIATION.**—A small azygous scale separates the posterior ends of the prefrontals in AMNH 89344. In UI 48779 the loreal is excluded from the orbit by the prefrontal and third supralabial. The anterior temporal enters the orbit below the postocular in USNM 109942; the anterior temporal is fused with the upper posterior temporal on the right side of CNHM 104683 and USNM 109943, and is fused with the parietal in UMMZ 95209. The number of postoculars is increased to two on both sides of UI 48782 and on one side of UMMZ 121520 (EF 8730); the postocular is absent on one side of ANSP 14758. The supralabials are reduced to five in UI 48777 by fusion of supralabials 2 and 3; the infralabials are reduced to six in UMMZ 95209 and on one side of USNM 109942 and UI 17701. The mental is in contact with the anterior chinshields in UMMZ 95209.

Geographic variation may occur in coloration. Smith (1941a:54) stated that the light ventral blotches were usually brick-red in specimens from Pan de Olla, Veracruz. Of 16 specimens from near Huauchinango, Puebla, 13 show at least remnants of the checkered condition; of these 13, the light blotches were yellowish in 11 specimens and reddish in two (data for 7 from J. R. Dixon, pers. com.; for 9 from personal field notes). The dorsum is iridescent bluish-black in life.

Populational differences in subcaudal counts are more pronounced than differences in the number of ventrals. Variation in segmental counts in *G. mutitorques* from three geographic areas is presented in Table 9. The only significant difference in the number of ventrals occurs between males from Zacualtipan and those from near Huauchinango ( $t = 2.7$ ,  $P. = 0.02$ ). The subcaudal counts, however, are different in Zacualtipan and Huauchinango males ( $t = 5.2$ ,  $P.$  less than 0.001), Huauchinango and Pan de Olla males ( $t = 2.9$ ,  $P.$  less than 0.02), Zacualtipan and Huauchinango females ( $t = 2.8$ ,  $P.$  less than 0.02), and Huauchinango and Pan de Olla females ( $t = 3.3$ ,  $P.$  less than 0.01).

The segmental counts (ventrals, 174, 177; caudals 30, 30) of two females from near Xilitla, San Luis Potosi, the northern limit of the known range of the species, suggest that this northern population may have higher counts than any of the above populations (data for LSU 219, Xilitla, San Luis Potosi, from Taylor, 1949:194).

**REMARKS.**—Shortly after describing *R. mutitorques*, Cope (1886) described a specimen from San Jose Acateno, Veracruz, as a new species, *Rhabdosoma longiceps*. Cope described *longiceps* as possessing all of the principle features of *mutitorques*, but with longer head scales, particularly the prefrontals

TABLE 9  
 VARIATION IN THE NUMBER OF VENTRALS AND SUBCAUDALS IN  
*G. mutitorques* FROM THREE REGIONS IN MEXICO

Sex and Character	Vicinity of Zacualtipan, Hidalgo	Vicinity of Huauchinango, Puebla	Vicinity of Pan de Olla, Veracruz
Males			
Ventrals:			
Number	5	8	5
Mean	154.4	159.1	157.6
Range	149-159	155-162	152-163
Subcaudals:			
Number	5	8	5
Mean	33.4	38.8	35.0
Range	32-35	36-42	31-38
Females			
Ventrals:			
Number	4	9	8
Mean	169.5	170.3	167.4
Range	167-172	168-173	160-174
Subcaudals:			
Number	4	9	8
Mean	26.0	29.8	26.5
Range	24-29	27-33	24-29

and supralabials. According to the description, the prefrontals in *longiceps* are five or six times as large as the internasals, supralabial 1 is as high as long, supralabials 2 and 4 are higher than long, supralabial 3 is longer than high, and supralabials 5 and 6 are twice as long as high. Cope's (1885a:384) description of *mutitorques* stated that the prefrontals are four times as large as the internasals, the first four supralabials are higher than long, the fifth is as high as long, and the sixth is longer than high. Unfortunately, direct comparison of the two nominal forms is impossible, since the type (the only known specimen) of *longiceps* is lost. However, variation in the size of the prefrontals (from less than four to more than six times the size of the internasals) and in the relative lengths and heights of the supralabials is so great in a single series of nine specimens of *mutitorques* from near Huauchinango, Puebla, that *longiceps* cannot be retained as a distinct species.

SPECIMENS EXAMINED (53).—MEXICO: No locality: AMNH 19773, UMMZ 100019. **Hidalgo:** Apulca, UMMZ 95209; 10 mi WSW Huauchinango, Puebla, JRD 5247-49, 5318-22; Zacualtipan, ANSP 11324, 14758-65. **Puebla:** Honey. UMMZ 95196; 3.5 mi W Huauchinango, UMMZ 103313; 7.3 mi SW Huauchinango, UMMZ 121520 (9); 12 mi N Huauchinango, UK 39645; Rio Octapa, 2.5 mi NNE Teziutlan, AMNH 88809-10, 89344; Rio

Octapa, 3.2 km NNE Teziutlan, UK 54054; 25 mi N Totalco (San Antonio Limen), CNHM 104683; near Zacatlan (Cecepaco), AMNH 14218, 15251. **San Luis Potosi:** near Xilitla, UK 24002. **Veracruz:** Pan de Olla, MCZ 46869, UI 17701, USNM 109940-43; Toxtlacuaya, UI 48777-83.

*Geophis semiannulatus* Smith

*Geophis semiannulatus* Smith, 1941a:49; Smith and Taylor, 1945:70.

**HOLOTYPE.**—MCZ 11422, a juvenile male, purportedly from Colima, Mexico. This locality is undoubtedly in error, since this species and its relatives are known only from the Sierra Madre Oriental of eastern Mexico.

**DISTRIBUTION.**—Known from cloud forest and pine-oak associations of the Sierra Madre Oriental of Tamaulipas and Hidalgo, Mexico; 1100–2600 meters above sea level.

**DIAGNOSIS.**—Distinguished from other members of the genus by the combination of (1) dorsal scales in 17 rows, smooth throughout length; (2) one anterior and one or two posterior temporals; (3) one postocular; (4) more than 160 ventrals in males, more than 170 in females; (5) 33–50 dark dorsal crossbands; and (6) fifth supralabial largest.

**DESCRIPTION.**—Head indistinct from neck; snout rounded from above, projecting well beyond lower jaw; rostral much broader than long, not produced posteriorly between internasals, its length about one-fifth its distance from frontal; internasals broader than long, half as long as prefrontal suture; prefrontal suture slightly more than half as long as frontal; frontal broader than long, subtriangular or shallowly convex anteriorly; parietals long, their median suture as long as frontal; supraocular two-thirds as long as loreal, forms posterior two-thirds of dorsal margin of orbit; one postocular, higher than long, half or more the size of supraocular.

Nasal divided, postnasal larger than prenasal, their combined length three-fourths that of loreal; loreal moderate, contained twice in snout length, almost twice as long as eye; eye small, contained three to four times in snout, its vertical diameter three-fourths its distance from lip; supralabials 6, third and fourth in orbit, fifth largest; dorsal margin of second labial usually parallel to lip; fifth labial separated from parietal by long, narrow anterior temporal; one or two posterior temporals, variable in size and shape, often fused with nuchal along parietal margin.

Mental rounded anteriorly, much broader than long, separated from chinshields by first pair of infralabials; infralabials 7, first three or four pairs in contact with anterior chinshields; anterior chinshields slightly longer than broad, slightly longer than posterior pair; posterior chinshields distinct, usually in contact medially, separated from first ventral by 2–3 rows of gulars.

Dorsal scales in 17 rows, smooth throughout length; no apical pits. Ventrals in 5 males, 162–169 (165.4); in 12 females, 178–185 (181.0); anal undivided; subcaudals in 5 males, 40–49 (42.6); in 12 females, 28–38 (30.8). Ventrals plus caudals, 202–218. Total length of largest male, 357 mm; tail, 58 mm (16.3%); largest female, 390 mm; tail, 44 mm (11.3%).

Maxilla extends anteriorly to suture between rostral and first supralabial; anterior extension greater than that of palatine; maxilla large, stout, curved in lateral view; 10–11 curved maxillary teeth, decreasing in length posteriorly; first tooth at anterior tip of maxilla; last 2–3 teeth small, located on ventrolateral aspect of posterior flange; posterior end of maxilla flattened, not expanded, deflected ventromedially from major axis of maxilla; anterior end of ectopterygoid bifurcate, branches subequal in length, neither expanded; postorbital bone stout.

Hemipenis extends to level of eleventh subcaudal; basal part of organ bears numerous spinules and, distally, 2–3 large spines; naked basal pocket opposite sulcus. Central part of organ bears numerous long spines, decreasing in length toward apex. Distal part of organ weakly capitate; capitation obscured by gradation between spines of central region and those of proximal edge of capitulum; capitulum calyculate, spinulate proximally, papillate distally; apex of organ undivided. *Sulcus spermaticus* bifurcates opposite seventh subcaudal; one branch reaches apex, second branch obsolescent, fails to reach apex. *M. retractor penis magnus* undivided throughout length.

Dorsum of head dark brown or mottled with white; lateral head scales mottled with brown and white; whitish collar occupies posterior parts of parietals, temporals, and supralabials 5 and 6; dorsum of body with 33–50 dark brown cross bands, broadest (5 or more scale lengths) on neck, narrower (3 scale lengths) on posterior part of body; dark bands usually extend onto ventral surface as alternating blotches, occasionally form complete rings around body; interspaces of dorsum whitish to yellowish, 2–3 scales long, often mottled with brown; dorsum of tail bears 5–11 dark bands. Chin region whitish, infralabials mottled with brown; venter predominantly whitish, with alternating left and right dark blotches; blotches sometimes coincide, form single band across venter; subcaudal surface similar to venter.

VARIATION.—The head scutellation of the holotype is unusual in two respects; a minute “preocular” is present on one side, and the posterior ends of the parietals are confluent as a result of the incompleteness of the parietal suture. The temporals are highly variable in the 17 known specimens. The basic temporal formula appears to be one anterior and two posterior temporals, but a reduction to one posterior temporal is common, and both anterior and posterior are variable in size and shape. The most

bizarre condition is found on the left side of UMMZ 108511; the anterior temporal and sixth supralabial are distinct, but the fifth labial is fused with the posterior temporal (temporals?), resulting in a large, peculiarly shaped scale. The anterior and posterior temporals are fused on the right side of UMMZ 108502; on the left, the anterior temporal is followed by a single posterior temporal. The length of the anterior temporal usually corresponds to the length of the fifth labial, but it is considerably shorter than the labial in some specimens. In UMMZ 109704, for example, the anterior temporal is restricted to the area above the anterior half of the fifth labial, and is followed by a second temporal located above the posterior half of the fifth and anterior half of the sixth; two other temporals surmount the posterior half of the sixth labial. Numerous other variations occur, prohibiting a meaningful statement of the normal temporal formula in the species. The temporal variation is, however, apparently characteristic of only certain populations. Specimens from the Gomez Farias region of Tamaulipas are highly variable, but the three specimens from Guerrero, Hidalgo, all have one anterior and two posterior temporals.

These populations differ also in the number of female subcaudals, and perhaps in the coloration of the subcaudal surface. The number of subcaudals in nine females from Tamaulipas varies from 28 to 33; two females from Hidalgo have 36 and 38 subcaudals, respectively. The subcaudal number in a single male from Hidalgo falls within the range of variation in Tamaulipan males; the two populations show no apparent difference in the number of ventrals. The subcaudal surface in specimens from Hidalgo is predominantly whitish; the dark dorsal bands reach only the lateral edges of the subcaudals. In Tamaulipan specimens, the dark dorsal bands reach the midline of the venter as alternating blotches or as complete rings.

Variation in the number of dorsal bands, extension of the dark bands onto the ventrals, and in the coloration of the head is apparently individual, but ontogenetic changes may be partly responsible for differences in the pigmentation of the light interspaces between the dorsal bands. The interspaces are immaculate or lightly mottled in juveniles; the mottling is more apparent between the posterior bands. In UMMZ 109705, an adult female, and in UMMZ 108512, an adult male, the dark mottling is more pronounced; in the latter the dark pigment of the interspaces tends to form secondary dark crossbands, separated from the primary bands by a single row of nearly immaculate light scales. None of the juveniles approach this condition; some adults, however, also lack the strong mottling (e.g., UMMZ 108513).

The dark crossbands do not extend onto the ventrals in the type; in all other specimens they extend at least onto the lateral edges of the ventrals. In UMMZ 109704, almost all of the dark bands form complete rings; in

other specimens the bands extend asymmetrically to the midline, forming alternating left and right blotches.

The lateral and sometimes dorsal head scales are mottled. In UMMZ 102987 (2 of 3 specimens) the head is predominantly whitish with some pale brown mottling; only the frontal and anterior parts of the parietals are dark brown. The head is uniformly dark in UMMZ 47805. The remaining specimens are intermediate between these extremes; the frontal is the only head scale consistently dark brown. The light collar is incomplete middorsally in UMMZ 67650, and mottled in UMMZ 109795; in all other specimens the collar is complete, although sometimes narrowed middorsally.

REMARKS.—In life, the dark dorsal bands are black; the interspaces are dusky reddish or rosy-pink. Three juveniles (UMMZ 102987) were bone white with black dorsal bands. (Martin, 1955:177–178).

SPECIMENS EXAMINED (17).—MEXICO: "Colima." (undoubtedly in error), MCZ 11422. **Hildago:** Guerrero, UMMZ 47805, 56479, 67650. **Tamaulipas:** 5 mi NW Gomez Farias, Rancho del Cielo, UMMZ 102987 (3), 104310, 108511, 109703, 109706, 112910; 7 mi WNW Gomez Farias, Agua Linda, UMMZ 108512–13, 109704; 1 km NE San Jose, Rancho Viejo, UMMZ 102901, 109705.

#### THE *omiltemanus* GROUP

Dorsal scales in 15 or 17 rows, smooth or faintly keeled on posterior part of body; no paired apical pits. Head moderately distinct from neck; snout short, bluntly rounded; eye moderately large; rostral not produced posteriorly between internasals; internasals, prefrontals, postnasals, and loreal moderate; supraocular moderate, forms posterior two-thirds to three-fourths of dorsal margin of orbit; parietals long; an anterior temporal separates fifth labial from parietal, forms long suture with sixth labial. Ventrals 142–158 in males, 146–166 in females. Subcaudals 31–51 in males, 26–42 in females. Percentage tail of total length 13.2–21.2 in males, 11.6–17.4 in females.

Maxilla extends anteriorly to suture between supralabials 1 and 2; anterior extension greater than that of palatines; maxilla stout, straight in lateral view; 12–17 long, moderately curved teeth; first tooth at anterior tip of maxilla; teeth subequal in length, except first and last few, which are shorter; posterior end of maxilla laterally (or obliquely) compressed, forms expanded flange; last few teeth on labial surface of flange. Anterior tip of ectopterygoid expanded, compressed, mitten-shaped; no postorbital bone (except in *maculiferus*).

Hemipenis (condition unknown in *isthmicus*) slightly bilobed at tip; *sulcus spermaticus* bifurcate; a naked basal pocket opposite sulcus; central part with large spines; distal part capitate, calyculate, spinulate; M. retractor penis magnus divides into two slips at apex of hemipenis.

*G. incomptus*, *G. isthmicus*, *G. maculiferus*, and *G. omiltemanus* are included in this group (Fig. 12).<sup>1</sup> Geographically, the group ranges from the highlands of Michoacan, Mexico, eastward to Oaxaca (Fig. 13); established localities are between 1600–2500 meters above sea level.

Among the four forms, *G. omiltemanus* appears to be intermediate in some respects between *isthmicus* and the forms from Michoacan, *incomptus* and *maculiferus*. In head scutellation, *omiltemanus* is similar to the latter two forms. The relative sizes and shapes of the temporal and fifth and sixth supralabials form a graded series in the three species; in *omiltemanus* the temporal and sixth labial are elongate and the fifth labial is small and widely separated from the parietal; *maculiferus* is intermediate; in *incomptus*, the fifth labial is large and narrowly separated from (or in narrow contact with) the parietal, and the sixth labial and temporal are correspondingly smaller (see Fig. 12). About half the specimens of *incomptus* agree with *omiltemanus* in having two postoculars; the other half are like *maculiferus* in having one. The postorbital bone is present in *maculiferus* and absent in the other two; its loss apparently occurred after the isolation of the three forms. The single specimen of *maculiferus* also lacks the faint keeling of the other forms, but it is a small snake, and large specimens may reveal the presence of keels.

*G. omiltemanus* differs from *maculiferus* and *incomptus* in having 17 scale rows (instead of 15) and a banded dorsum (instead of unicolor). In these respects *omiltemanus* is similar to *G. isthmicus*. The latter species, known only from the type, has dark blotches on a light background. The temporal of *isthmicus* occupies the same position relative to the fifth and sixth labials as in *omiltemanus*, but the temporal and sixth labial are much shorter than in the latter, and followed by a seventh labial and two posterior temporals. Derivation of the *omiltemanus* temporal and labial condition from that of *isthmicus* would require the fusion of the sixth labial, seventh labial, and lower posterior temporal into a single scale, and the fusion of the anterior and upper posterior temporals. I have not seen the type of *isthmicus*, and only tentatively include it in this group (and indeed in the genus). Regard-

<sup>1</sup> Bogert and Porter (1966) indicated a close relationship among *maculiferus*, *incomptus*, and their new form, *Geophis gertschi*. The holotype of *gertschi* (AMNH 94877, from 2 miles south of Tonila, Jalisco, but in the state of Colima, Mexico) is not well preserved, a condition which apparently led to a misinterpretation of the nature of the anal plate. Contrary to the description by Bogert and Porter, the anal is divided. The divided anal, undivided hemipenial sulcus, and absence of a loreal clearly exclude *gertschi* from the genus *Geophis*. These same features, together with extensive agreement in other characteristics of scutellation, coloration, body proportions, and hemipenial structure indicate that *gertschi* is a synonym of, or closely related to, *Tantilla calamarina* Cope. AMNH 94877 differs from the latter principally in having the postoculars fused with the supraoculars; this fusion also characterizes UMMZ 115587, a *T. calamarina* from near Manzanillo, Colima.

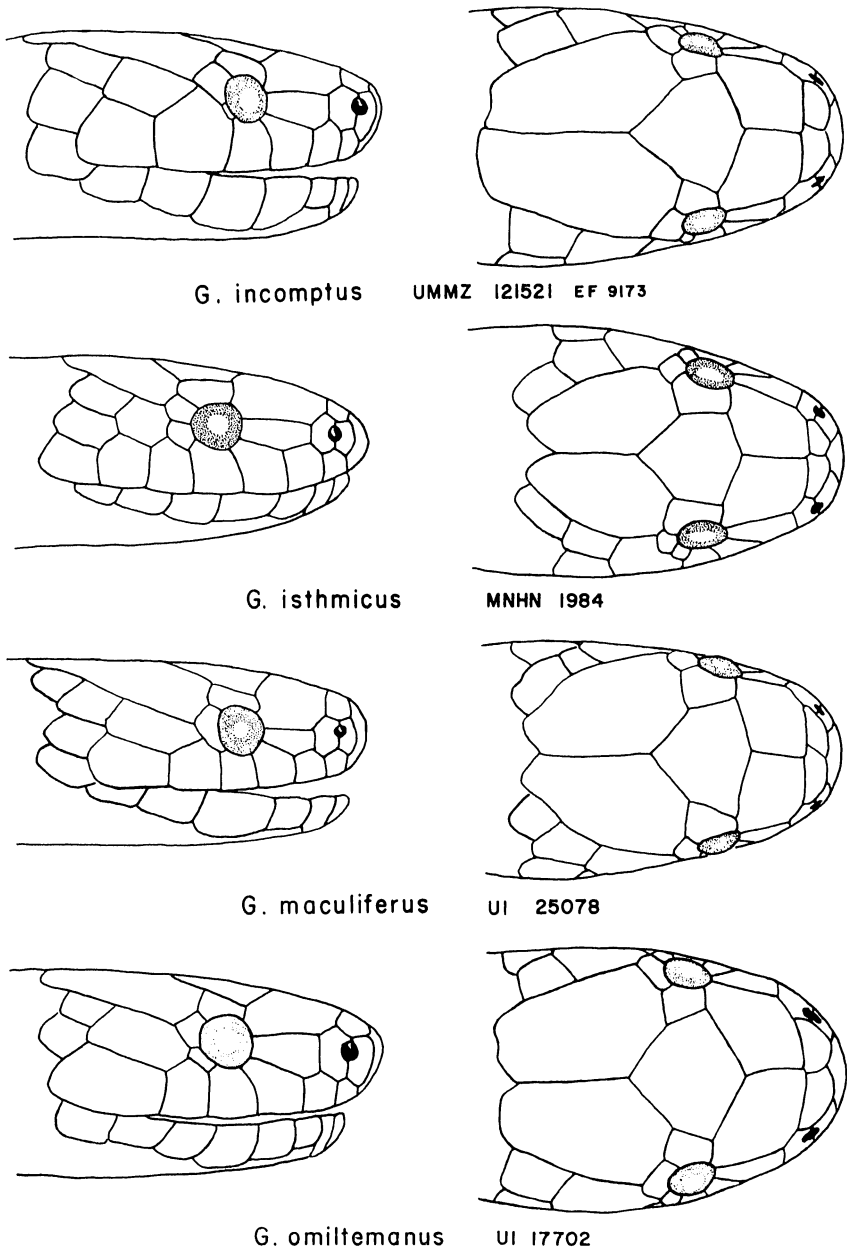


FIG. 12. Dorsal and lateral head scutellation in members of the *omiltemanus* group. Scale: *G. incomptus*, about 5×; *G. isthmicus*, enlarged and reversed from Bocourt, 1883; *G. maculiferus*, about 6.5×; *G. omiltemanus*, about 5.5×.



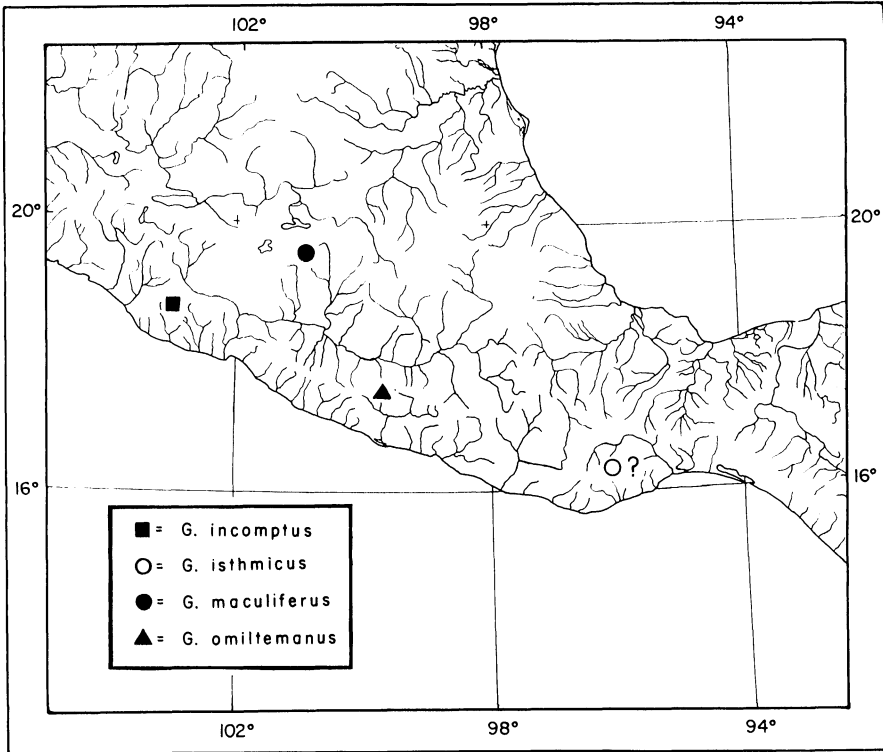


FIG. 13. Locality records for members of the *omiltemanus* group. The questionable locality for *G. isthmicus* is "Tehuantepec," which in this instance probably does not refer to the lowlands.

less of the validity of this inclusion, I believe *isthmicus* is less closely related to *omiltemanus* than are *incomptus* and *maculiferus*.

The latter two forms are apparently very closely related; *incomptus* is known only from Dos Aguas, in the Sierra de Coalcoman, Michoacan, and *maculiferus* from a single locality on the southern slopes of the Cordillera Volcanica of Michoacan. The two localities are separated by the arid Tepelcatepec valley. Duellman's (1959:3) diagnosis of *incomptus* distinguished it from *maculiferus* by the presence in the former of two postoculars instead of one, 6-7 infralabials instead of 5, unicolor snout instead of light internasals and prenasals, and a banded instead of immaculate venter. Additional specimens of *incomptus* have shown the postocular number to be variable; this not only invalidates the generalization that *incomptus* has two postoculars, but also suggests that the number of postoculars may be variable in *maculiferus* as well. The type of *maculiferus* has five infralabials, but this number is possibly atypical of this generalized species; even in

specialized forms, characterized by a reduction in the number of head scales, this number occurs only as an occasional variation. The apparent difference in coloration cannot be assessed, since nothing is known of the variation in *maculiferus*.

The type of *maculiferus* also differs from *incomptus* in having a relatively larger eye, relatively shorter tail, the absence of faint vertebral and paravertebral keels on the posterior part of the body, fewer hemipenial spines,

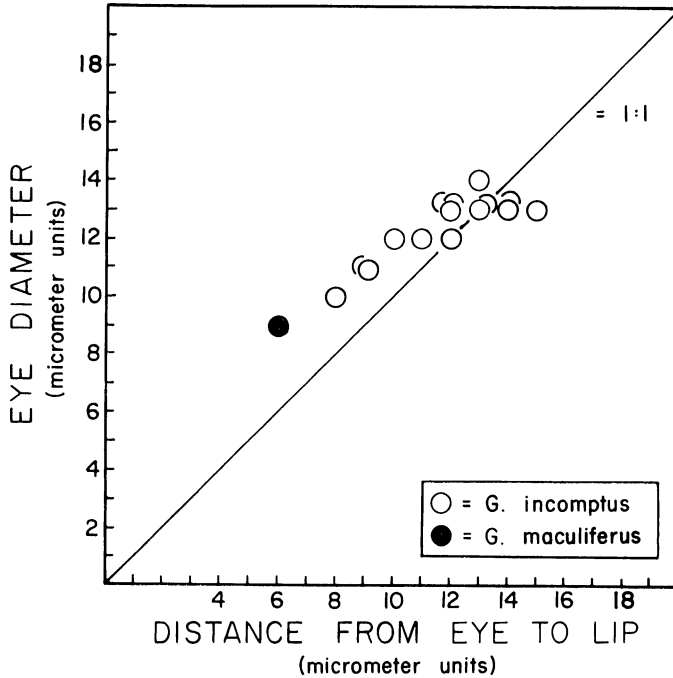


FIG. 14. Scatter diagram of eye diameter against distance from eye to lip in *G. incomptus* and *G. maculiferus*. See text for explanation.

a larger number of maxillary teeth, and the possession of a postorbital bone. The small size of the holotype is directly responsible for some of these apparent differences, and is perhaps indirectly responsible for others. The ratio of eye diameter to distance from eye to lip is 1.5 in *maculiferus*; the average value in *incomptus* is 1.1. This ratio, however, is complicated by allometric growth; with increasing body length, the distance from the eye to the lip (i.e., the height of the fourth supralabial) increases faster than the diameter of the eye. The apparent difference in eye size disappears when eye size and distance to lip are plotted as a regression (Fig. 14). A similar explanation accounts for the relatively shorter tail in the type of *maculi-*

*ferus*; the difference vanishes when tail length and total length are plotted as a regression (Fig. 15).

The absence of keeling in *maculiferus*, and the fewer hemipenial spines, are not convincing differences; they may indicate that these features are not well developed in small juveniles, or may have been misinterpreted owing to the small absolute sizes of the structures involved. The maxillary tooth count (17, compared with 12–14 in *incomptus*) I believe to be accurate, but the count was made *in situ* on an extremely small maxilla. The pres-

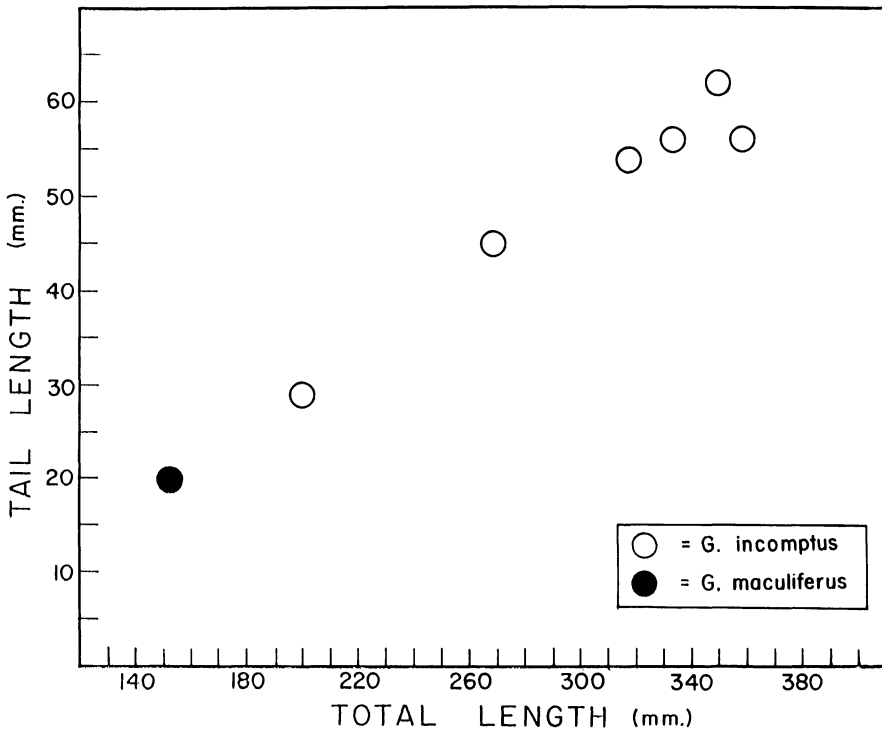


FIG. 15. Scatter diagram of tail length against total length in males of *G. incomptus* and *G. maculiferus*. See text for explanation.

ence (or absence) of the postorbital bone is not known to vary intraspecifically, with the possible exception of *G. dugesi* (the allocation of the specimens with postorbitals to *dugesi* is questionable). The presence of the postorbital in *maculiferus* suggests that the bone has been lost independently in *omiltemanus* and *incomptus*.

The four members of this group are known only from their respective type localities. *G. incomptus*, with its large fifth labial, narrowly separated from or in contact with the parietal, appears to be the most specialized

member of the group; it inhabits the Sierra de Coalcoman in Michoacan, the northwestern limit of the distribution of the group. *G. incomptus* has apparently become distinct from *G. maculiferus* relatively recently; both have 15 scale rows and many other features in common. The latter form occurs on the southern slopes of the Cordillera Volcanica in eastern Michoacan; dispersion along the western part of the Cordillera to the Sierra de Coalcoman could have taken place during a period in which the pine-oak zone was continuous along this route, such as during a Pleistocene depression of montane environments. *G. incomptus* and *maculiferus* share many characteristics with *G. omiltemanus*; the latter form has 17 scale rows and a small fifth labial, and appears to be the most generalized of the three. The ancestral stock of *incomptus* and *maculiferus* and that of *omiltemanus* apparently became distinct from one another on opposite sides of the Balsas Basin; *omiltemanus* is at present known only from the Sierra Madre del Sur of Guerrero. The three above forms are more closely related to each other than to the fourth member of the group, *G. isthmicus*. This poorly known form is the most generalized member of the group; it is known only from "Tehuantepec," which in this instance probably means the Sierra Madre del Sur of Oaxaca, the southeastern limit of the known range of the group. The rather impressive differences in the supralabials and temporals of *omiltemanus* and *isthmicus* indicate that their respective stocks became distinct considerably earlier than the differentiation of the *maculiferus-incomptus* line; geographic isolation was apparently between Guerreran and Oaxacan sections of the Sierra Madre del Sur.

#### *Geophis incomptus* Duellman

*Geophis incomptus* Duellman, 1959:3, fig. 2.

HOLOTYPE.—An adult male, UMMZ 118840, from Dos Aguas, Michoacan, Mexico, collected June 18, 1958, by W. E. Duellman and J. Wellman; UMMZ 118836–39 are paratopotypes.

DISTRIBUTION.—Known only from the type locality, in the pine-oak zone of the Sierra de Coalcoman; about 2100 meters above sea level (Duellman, 1961:97).

DIAGNOSIS.—Distinguished from other members of the genus by the combination of (1) dorsal scales in 15 rows, smooth except scales in vertebral area of posterior part of the body, which are weakly keeled; (2) anterior temporal present, surmounts both fifth and sixth labials; (3) internasals dark; (4) 6 or 7 infralabials; and (5) anterior edge of each ventral brownish-black, posterior edge creamish-white.

DESCRIPTION.—Head moderately distinct from neck; snout short, bluntly

rounded from above, not projecting far beyond lower jaw; rostral not produced posteriorly between internasals, its length about one-third its distance from frontal; internasals broader than long, half as long as prefrontal suture; prefrontals moderate, their common suture half as long as frontal; frontal slightly broader than long, anterior edge angulate; parietals long, their median suture as long as frontal; supraocular large, nearly as long as loreal, forms almost entire dorsal margin of orbit; 1 or 2 postoculars, upper as large or larger than supraocular; lower postocular, when present, small, much higher than long.

Nasal divided, postnasal half-again to twice as long as prenasal, their combined length usually equal to or greater than that of loreal; loreal short, about half of snout length, slightly longer than eye diameter; eye moderate, contained twice and a half in snout length, its vertical diameter equal to its distance from lip; supralabials 6, third and fourth enter orbit, fifth largest and narrowly separated from (occasionally in narrow contact with) parietal by upper postocular and anterior temporal; anterior temporal in broad contact with fifth and sixth labials, major part dorsal to sixth labial; two "posterior temporals," predominantly posterior to sixth labial, but part of each anterior to a line drawn from sixth labial to parietal tip.

Mental broader than long, rounded anteriorly, separated from chinshields by first pair of infralabials; infralabials 6 or 7, first three or four pairs in contact with anterior chinshields; anterior chinshields short, broad, larger than posterior pair; posterior chinshields small, often poorly differentiated from gulars, often separated by median gular of equal size; 2-3 gulars separate chinshields from first ventral.

Dorsal scales in 15 rows, smooth over most of body, faintly keeled in vertebral and paravertebral rows of posterior part of body; no apical pits. Ventrals in six males, 146-153 (149.8); in nine females, 146-154 (151.7); anal undivided; subcaudals in six males, 35-37 (36.0); in nine females, 26-35 (32.0). Ventrals plus caudals, 172-189. Total length of largest male, 358 mm; tail, 56 mm (15.6%); total length of largest female, 391 mm; tail, 53 mm (13.6%).

Maxilla extends anteriorly to suture between first and second supralabials; anterior extension greater than that of palatine; 12-14 curved maxillary teeth, subequal except first and last few, which are shorter; first tooth at anterior tip of maxilla; in lateral view, maxilla gradually increases in depth to middle, then decreases until flange; posterior end of maxilla laterally compressed and expanded into large flange; anterior end of ectopterygoid bifurcate, one branch long and blade-like, the other short and broad; no postorbital bone.

Hemipenis extends posteriorly to level of subcaudal 8; basal part of organ bears minute spinules proximally and 4-5 large spines distally;

naked basal pocket opposite sulcus. Central part of hemipenis bears about fifty medium spines in oblique rows. Distal part of organ strongly capitate; capitulum calyculate, spinulate; apex slightly bilobed. *Sulcus spermaticus* bifurcates opposite subcaudal 4; each branch reaches apex. *M. retractor penis magnus* divides into two slips; each slip attaches to one lobe of apex.

Dorsum of head brown to brownish-black; ventral parts of supralabials yellowish; dorsal scales brown to brownish-black, anterior part of each usually darker than posterior margins; lateral rows not noticeably paler than dorsal ones. Chin region creamish, immaculate; ventrals strongly banded, each scale dark brown or black anteriorly, yellowish or whitish posteriorly; dark ventral bands interrupted midventrally in some specimens; subcaudals blackish; each scale paler along posterior margins.

VARIATION.—The available specimens of *G. incomptus* show considerable variation in the number and relative positions of the various head scales. The postoculars are 2-2 in eight specimens, 1-2 in one, and 1-1 in six; when absent, the lower postocular may be fused with the fourth supralabial (third and fourth labials enter the orbit) or with the fifth (third, fourth, and fifth enter orbit). The number of supralabials is reduced from 6 to 5 in two specimens, the result of fusion between the second and third or third and fourth labials. The fifth labial is narrowly separated from the parietal in twelve specimens, but extends between the temporal and postocular to touch the parietal in three. UMMZ 121521 (EF 9172) has two supraoculars on one side owing to a transverse suture; on the other side the aberrant suture is incomplete and the partially divided supraocular is fused with the prefrontal. The rostral in *incomptus* is generally not strongly developed; in UMMZ 118838, however, it extends between the internasals to touch the prefrontals.

The number of infralabials is 7-7 in nine specimens, 6-7 in two, and 6-6 in four; the reduction usually involves the fusion of the third and fourth infralabials. The posterior chinshields are distinct in some specimens, indistinguishable from the adjacent gulars in others.

REMARKS.—In living specimens, the light pigment of the venter apparently changes ontogenetically. Among ten topotypes (UMMZ 121521) collected by me, the ventral light areas were white in the smallest juvenile, white except for the chin region (pale yellow) in two larger juveniles, and pale to bright yellow in seven adults. The dorsal coloration in life was characterized by Duellman (1959:5) as lavender-brown to bluish-black or bluish-gray. The lip is yellow or yellowish-white.

Although Dos Aguas is in the pine-oak zone, the type series and all save one of the subsequently collected topotypes were collected on or at the base of an extensive limestone outcropping, not in the forest itself. The lone

exception was collected just within the forested area opposite the outcropping. The base of the limestone slope flattens onto a wet, grassy area.

SPECIMENS EXAMINED (15).—MEXICO: **Michoacan:** Dos Aguas, UMMZ 118836–40, 121521 (10).

*Geophis isthmicus* (Boulenger)

*Rhabdosoma zebrinum* Bocourt (not Jan), 1883:539, pl. 34, fig. 1.

*Atractus isthmicus* Boulenger, 1894:307 (substitute name for *R. zebrinum* Bocourt)

*Rhegnops zebrinus*, Cope, 1885b:178.

*Geophis zebrina*, Günther, 1893:94.

*Geophis isthmicus*, Dunn, 1928a:1; Smith and Taylor, 1945:68.

*Atractus zebrinus*, Amaral, 1929:190.

HOLOTYPE.—MNHN 1984, a juvenile female from "Tehuantepec (Mexique occidental)."

DISTRIBUTION.—Known only from the indefinite type locality; "Tehuantepec," judged by the habitats of other species, probably refers to the general region rather than to the lowland environs of the city itself.

DIAGNOSIS.—Distinguished from other members of the genus by the combination of (1) dorsal scales in 17 rows, completely smooth throughout length; (2) one anterior and two posterior temporals; (3) two postoculars; (4) seven supralabials; and (5) venter lightly spotted with brown.

DESCRIPTION.—The following is based partly on the description given by Bocourt (1883) and Boulenger (1894) and partly on the illustration provided by Bocourt. Certain additional information was provided by Jean Guibé.

Head scarcely distinct from neck; snout moderate, rounded from above, not projecting far beyond lower jaw; rostral not produced posteriorly between internasals, its length from above one-fourth its distance from frontal; internasals small, broader than long, less than half as long as prefrontal suture; prefrontals moderate, their median suture two-thirds as long as frontal; frontal slightly longer than broad, shallowly angulate anteriorly; parietals moderate, their median suture three-fourths as long as frontal; supraocular large, nearly as long as loreal, forms almost entire dorsal margin of orbit; two postoculars, subequal in size, half as large as supraocular.

Nasal divided, postnasal longer than prenasal, their combined length less than length of loreal; loreal elongate, more than half of snout length, one-fourth longer than eye diameter; eye moderate, contained twice and a half in snout length, its vertical diameter equal to its distance from lip; supralabials 7, third and fourth enter orbit, fifth small and separated from parietal by postocular and anterior temporal; sixth and seventh labials separated from parietal by part of anterior and two posterior temporals.

Mental much broader than long, rounded anteriorly, separated from

chinshields by first pair of infralabials; infralabials 6, pairs 1-4 in contact with chinshields; a single pair of elongate chinshields, separated from first ventral by three rows of gulars.

Dorsal scales in 17 rows, smooth throughout length of body. Ventrals in single female, 160; anal undivided; subcaudals, 34. Ventrals plus caudals, 194. Total length of female, 155 mm; tail, 18 mm (11.6%).

Characteristics of maxilla and hemipenis unknown.

Dorsal ground color pinkish-yellow; about forty transverse brown spots, irregular in shape. Venter whitish, punctuated liberally with reddish-brown spots.

REMARKS.—The generic allocation of this species remains tentative; it does, however, bear at least superficial resemblances to the members of the *omiltemanus* group.

#### *Geophis maculiferus* Taylor

*Geophis maculiferus* Taylor, 1941:119, fig. 1; Smith and Taylor, 1945:68.

HOLOTYPE.—UI 25078, a juvenile male; type locality given as near "Cicio," Michoacan, but spelling corrected to Tzitzio by Duellman (1961:97); August 14, 1940; E. H. Taylor, collector.

DISTRIBUTION.—Known only from the type locality, which Duellman (1961:97) characterized as a town at 1630 meters above sea level on the southern slopes of the Cordillera Volcanica, at which level an interdigitation of arid tropical scrub forest and pine-oak forest occurs. *G. incomptus* probably occurs in the pine-oak habitat.

DIAGNOSIS.—Distinguished from other members of the genus by the combination of (1) dorsal scales in 15 rows, smooth throughout length; (2) anterior temporal present; (3) five infralabials; (4) internasals and prenasals creamish; and (5) ventrals immaculate, creamish.

DESCRIPTION.—Head moderately distinct from neck; snout short, bluntly rounded, not projecting far beyond lower jaw; rostral not produced posteriorly between internasals, its length from above less than one-fourth its distance from frontal; internasals broader than long, half as long as prefrontal suture; prefrontals short, their median suture half as long as frontal; frontal slightly broader than long, its anterior edge nearly transverse; parietals long, their median suture slightly longer than frontal; supraocular large, as long as loreal, forms almost entire dorsal margin of orbit; one postocular, much higher than long, smaller than supraocular.

Nasal divided, postnasal half-again as long as prenasal, their combined length greater than that of loreal; loreal short, less than half of snout length, slightly shorter than eye diameter; eye large, contained twice in



snout length, its vertical diameter half-again its distance from lip; supralabials 6, third and fourth enter orbit, fifth separated from parietal by postocular and anterior temporal; a long anterior temporal, in broad contact with fifth and sixth labials; two "posterior temporals," predominantly posterior to sixth labial, but part of each anterior to a line drawn from sixth labial to parietal tip.

Mental broader than long, rounded anteriorly, separated from chinshields by first pair of infralabials; infralabials 5, pairs 1-3 in contact with anterior chinshields; anterior chinshields short, nearly as broad as long, slightly larger than posterior pair; posterior chinshields irregular in shape, scarcely differentiated from lateral gulars; posterior chinshields in contact with first ventral.

Dorsal scales in 15 rows, smooth throughout length of body; no apical pits. Ventrals in single male, 142; anal undivided; subcaudals, 30. Ventrals plus caudals, 172. Total length of male, 152 mm; tail, 20 mm (13.2%).

Maxilla extends anteriorly to middle of first supralabial; anterior extension greater than that of palatine; *ca.* 17 maxillary teeth (*in situ*), subequal in length except for first and last few, which are shorter; first tooth at anterior tip of maxilla; last two teeth on labial aspect of flange; posterior end of maxilla laterally compressed and expanded into flange; anterior end of ectopterygoid bifurcate, one branch long and blade-like, the other short and broad; postorbital bone present.

Hemipenis extends posteriorly to level of subcaudal 8; basal part of organ bears minute spinules proximally and 4-5 large spines and hooks distally; a naked basal pocket opposite sulcus. Central part of organ bears about 25 medium spines and hooks in oblique rows. Distal part of hemipenis capitate; capitulum weakly calyculate, spinulate. *Sulcus spermaticus* bifurcate, each branch reaches apex. *M. retractor penis magnus* divides into two slips at apex of hemipenis.

Ground color of head light brown; internasals, prenasals, ventral part of rostral, supralabials 1 and 2, and ventral parts of remaining supralabials creamish; parietal paler than frontal; dorsum of body light brown, lateral scale rows paler than dorsal ones. Chin region and ventrals immaculate, creamish; subcaudals near end of tail lightly mottled with brown.

REMARKS.—Duellman (1961:97) erroneously referred to the type as a female. It was found on a hillside, under a rock (Taylor, 1941:121).

Some of the apparent differences between *maculiferus* and the closely related *G. incomptus* will probably be invalidated when additional, and particularly larger, specimens become available. The implications of the small size of the type of *maculiferus* are discussed in the section on the *omiltemanus* group.

SPECIMEN EXAMINED (1).—MEXICO: Michoacan: near Tzitzio, UI 25078.

*Geophis omiltemanus* Günther

*Geophis omiltemana* Günther, 1893:92, pl. 33, fig. A; Dunn, 1928a:2; Smith and Taylor, 1945:69.

*Diroscema omiltemanum*, Boulenger, 1894:299; Mocquard 1908:879.

*Atractus omiltemanus*, Cope, 1896:1024; Cope, 1900:1232.

*Catostoma omiltemanum*, Amaral, 1929:192.

**HOLOTYPE.**—Originally three syntypes, BMNH 1946.1.6.35–37, collected at Omilteme, Guerrero, Mexico; H. H. Smith, collector. BMNH 1946.1.6.37 is herein designated as lectotype (see below); BMNH 1946.1.6.35–36 are paralectotypes.

**DISTRIBUTION.**—Known only from the vicinity of Omilteme, Guerrero; about 2400 meters above sea level; located in the pine-oak forest on the North-facing slope of the Sierra Madre del Sur (Davis and Dixon, 1959).

**DESIGNATION OF A LECTOTYPE.**—Although Günther did not specify a holotype, the written description and the illustration clearly apply to BMNH 1946.1.6.37. In particular, the following features given by Günther apply only to the above specimen: (1) the presence of a small “preocular” between the third labial and the orbit; (2) 152 ventrals and 52 subcaudals; and (3) a total length of eleven and one-half inches. BMNH 1946.1.6.37 is therefore chosen as lectotype.

**DIAGNOSIS.**—Distinguished from other members of the genus by the combination of (1) dorsal scales in 17 rows, weakly keeled on posterior part of body; (2) a long anterior temporal; (3) two postoculars; (4) dorsum with narrow light crossbands on a reddish-brown ground color; and (5) ventrals immaculate, creamish-white.

**DESCRIPTION.**—Head moderately distinct from neck; snout short, bluntly rounded, not projecting far beyond lower jaw; rostral not produced posteriorly between internasals, its length from above less than one-fourth its distance from frontal; internasals broader than long, about one-half as long as prefrontal suture; prefrontals short, their median suture half as long as frontal; frontal slightly broader than long, anterior edge angulate; parietals long, their median suture as long as frontal; supraocular large, nearly as long as loreal, forms almost entire dorsal margin of orbit; two postoculars, upper as high as long, smaller than supraocular; lower postocular smaller than upper, much higher than long.

Nasal divided, postnasal longer than prenasal, their combined length as great as or greater than that of loreal; loreal short, half or less of snout length, slightly longer than eye diameter; eye moderately large, contained less than thrice in snout length, its vertical diameter about equal to its distance from lip; supralabials 6, third and fourth enter orbit, fifth small and

separated from parietal; sixth labial twice as long as fifth; anterior temporal elongate, forms sutures with posterior half of fifth and entire sixth labials; temporal and postocular separate fifth labial from parietal; two "posterior temporals," predominantly posterior to sixth labial, but part of each anterior to a line drawn from sixth labial to parietal tip.

Mental broader than long, rounded anteriorly, separated from chinshields by first pair of infralabials; infralabials 7, pairs 1-4 in contact with anterior chinshields; anterior chinshields half-again as long as broad, longer than posterior pair; posterior chinshields short and broad, in contact anteriorly or separated throughout length by median gular; one or two rows of gulars between chinshields and first ventral.

Dorsal scales in 17 rows, smooth throughout most of body length; vertebral and paravertebral scales faintly keeled on posterior part of body; no apical pits. Ventrals in five males, 148-158 (152.4); in four females, 156-166 (161.0); anal undivided; subcaudals in four males, 45-52 (48.5); in four females, 38-42 (39.5). Ventrals plus caudals, 193-206. Total length of largest male, 344 mm; tail, 70 mm (20.4%); total length of largest female, 363 mm; tail, 63 mm (17.4%).

Maxilla extends anteriorly to suture between first and second supralabials; anterior extension greater than that of palatines; 13-14 moderately curved maxillary teeth, subequal in length except for last two, which are shorter; first tooth at anterior tip of maxilla, last on labial aspect of flange; in lateral view, maxilla gradually increases in depth to middle, then decreases until flange; posterior end of maxilla laterally compressed and expanded into large flange; anterior end of ectopterygoid bifurcate, one branch long and blade-like, the other short and broad; no postorbital bone.

Hemipenis extends posteriorly to level of subcaudal 10; basal part of organ bears minute spinules proximally, 4-5 large spines distally; a naked basal pocket opposite sulcus. Central part of organ bears about 40 medium spines in oblique rows. Distal part of hemipenis capitate; capitulum bears spinules on weakly developed calyces; apex slightly bilobed. *Sulcus spermaticus* bifurcates opposite subcaudal 6; each branch reaches apex. *M. retractor penis magnus* divides into two slips; each slip attaches to one lobe of apex.

Ground color of dorsum reddish-brown; dorsum of head uniformly dark or with few light spots; ventral parts of supralabials yellowish-white; a narrow yellowish-white collar in juveniles, obliterated in adults; 28-49 narrow yellowish-white crossbands, mottled with brown on posterior part of body; anterior crossbands about two scales long, separated by 8-10 dark scales; posterior crossbands one scale long, occur in pairs, members of each pair widely separated on lateral scale rows but converging (sometimes meeting) middorsally; 4-5 dark scales separate each pair of crossbands mid-

dorsally. Chin region yellowish-white, immaculate or lightly mottled with brown; ventrals immaculate yellowish-white; subcaudals light, immaculate or lightly mottled with brown along anterior edges.

VARIATION.—The lectotype has a small presubocular separating the third labial from the orbit; in all other specimens this scale is incorporated into the third labial. An upper "preocular" separates the prefrontal from the orbit on both sides of CNHM 106785; this scale represents a detached part of the prefrontal, and does not affect the contact between the loreal and the orbit. In TCWC 9496, the internasals are partially fused with the prefrontals; the suture normally separating the two is present laterally, absent medially. BMNH 1946.1.6.36 has only 6 infralabials on one side, the result of fusion in the posterior half of the row; all other specimens have 7 infralabials.

With the exception of the number of light crossbands, there is little variation in coloration. The obliteration of the light color appears to be ontogenetic, but subject to individual variation. The brown mottling on the surface of the chin and subcaudals occurs only in the larger specimens, but evidence for ontogenetic change is inconclusive.

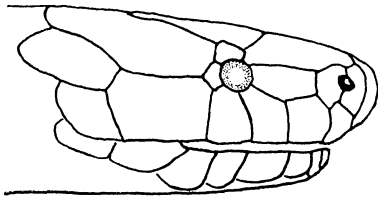
SPECIMENS EXAMINED (9).—MEXICO: **Guerrero**: No specific locality, UI 17702; Omilteme, BMNH 1946.1.6.35–37, CNHM 106785–86, TCWC 9496–97, USNM 109945.

#### THE *semidoliatus* GROUP

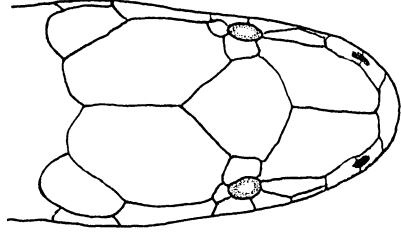
Dorsal scales in 15 rows, smooth on body, smooth or weakly keeled above vent; paired apical pits present on scales above vent. Head indistinct from neck; snout long, rounded from above; eye small; rostral moderate, not produced posteriorly between internasals; scales of snout moderate, neither internasals and postnasals nor prefrontals and loreals greatly enlarged; supraocular moderate, forms posterior two-thirds or more of dorsal margin of orbit; parietals long; anterior temporal absent. Ventrals 131–160 in males, 141–179 in females. Subcaudals 22–30 in males (probably greater in *laticinctus*), 19–33 in females. Percentage tail of total length 9.5–12.2 in males, 7.4–10.9 in females.

Maxilla extends anteriorly to middle of first supralabial; anterior extension greater than that of palatine; maxilla stout anteriorly, tapering posteriorly; 6–8 maxillary teeth, decreasing in size posteriorly; first tooth at anterior tip of maxilla; posterior end of maxilla tapers to blunt point. Anterior tip of ectopterygoid bifurcate; branches subequal in length, not expanded; no postorbital bone.

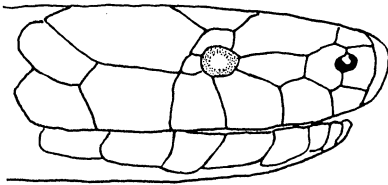
Hemipenis (condition known only in *semidoliatus*) slightly bilobed at apex; bilobation not evident in everted position; a basal naked pocket opposite sulcus; *sulcus spermaticus* bifurcate, each branch reaches apex of



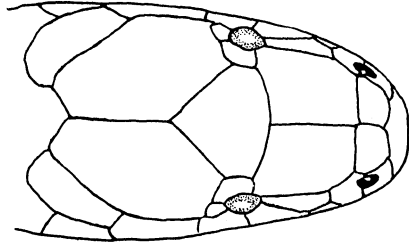
*G. cancellatus*



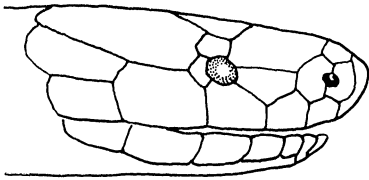
USNM 46441



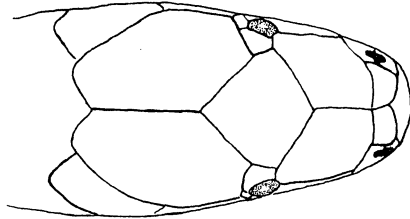
*G. laticinctus*



UI 51352



*G. semidoliatus*



USNM 110073

FIG. 16. Dorsal and lateral head scutellation in members of the *semidoliatus* group. Scale: *G. cancellatus*, about 6×; *G. laticinctus*, about 5.5×; *G. semidoliatus*, about 6×.

hemipenis; central part of organ bears numerous spines in oblique rows; distal part of organ capitate, calyculate, spinulate; M. retractor penis magnus divides into two slips at apex of hemipenis.

This group of short-tailed snakes includes three species (Fig. 16). Geographically the group ranges from central Veracruz (*semidoliatus*) eastward along both the Caribbean (*laticinctus*) and Pacific (*cancellatus*) versants of Chiapas, Mexico (Fig. 17); the latter forms are to be expected in the adjacent regions of Guatemala.

*Geophis laticinctus* is the most generalized member of the group. It is the only species with a complete complement of head scales (excepting the anterior temporal, which is absent in all three species); it also probably has

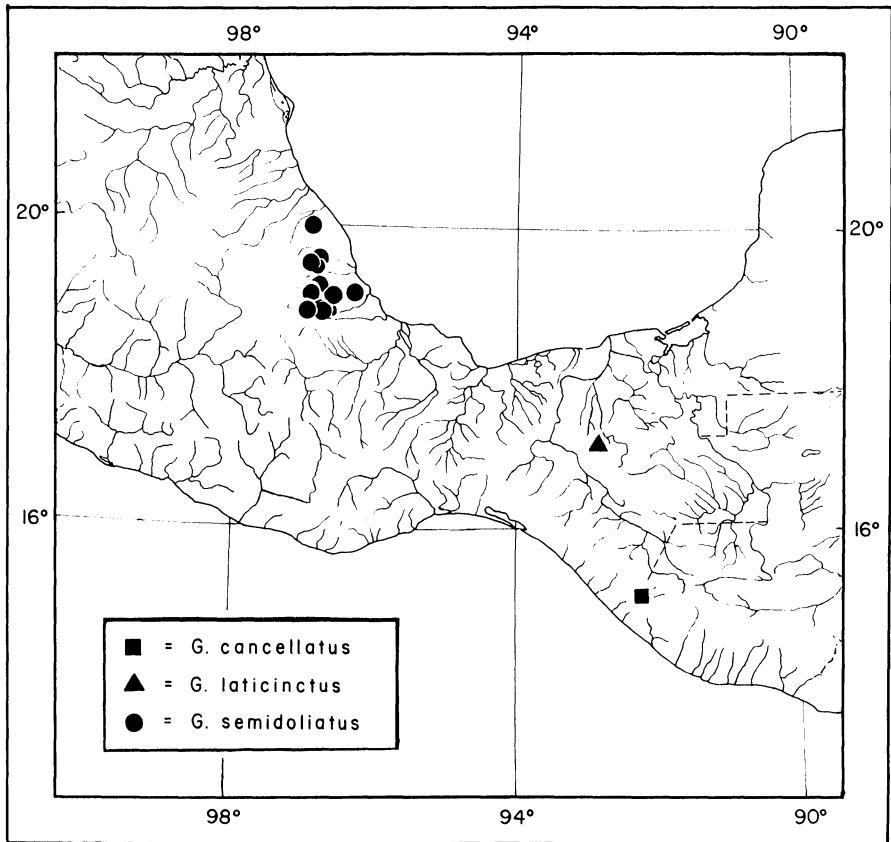


FIG. 17. Locality records for members of the *semidoliatus* group. Only a few of the many recorded localities for *G. semidoliatus* in central Veracruz are included.

the highest number of ventrals and subcaudals, and the relatively longest tail. In *laticinctus* there are six supralabials and the internasals are distinct; in *cancellatus* there are six supralabials, but the internasals are fused with the prefrontals; in *semidoliatus*, the internasals are distinct (occasionally absent) and the number of supralabials is reduced to five. Although *laticinctus* is known from a single female, its relative tail length and subcaudal count are slightly higher than in any female specimen of either of the two other forms; the number of ventrals (175) is four more than the number known for *cancellatus*, and near the upper limit of the range of the number of ventrals in *semidoliatus*.

Since the venter is blackish in *G. laticinctus*, its coloration was described as consisting of narrow light crossbands on a blackish ground color. This apparently contrasts with the dark crossbands or saddles on a light back-

ground characteristic of both *cancellatus* and *semidoliatus*. The only basic difference in coloration, however, is the color of the venter; it is primarily blackish in *laticinctus*, whitish in *cancellatus*, and immaculate or mottled whitish in *semidoliatus*. On the dorsal and lateral surfaces, the distribution of light and dark pigment is similar in the three forms; the head is dark with a light collar and the body has numerous narrow light crossbands alternating with more extensive dark areas. The color patterns of *semidoliatus* and *cancellatus* can easily be derived from the *laticinctus* pattern by a simple reduction of the dark ventral pigment.

*G. semidoliatus* and *G. cancellatus* are clearly more closely related to each other than either is to *G. laticinctus*. The two are so similar that had the types of *cancellatus* been collected sympatrically with *semidoliatus* I am sure their distinctive features would have been accepted as individual variation within the latter species. *G. cancellatus* is at present distinguished from *semidoliatus* by the absence of internasals (fused with prefrontals) and the presence of six supralabials. The fusion of the internasals and prefrontals occurs in 11 specimens of *semidoliatus*, not an impressive percentage of the 691 specimens examined, but sufficient to demonstrate the developmental capacity for this fusion. The third and fourth supralabials in *cancellatus* occupy the approximate area covered by the third labial in *semidoliatus*; the reduction to five labials is clearly the result of the fusion of the original third and fourth members of the series. Only the labial difference distinguishes *cancellatus* from those specimens of *semidoliatus* which do not have internasals. In other characteristics of scutellation, coloration, and dentition, the two forms are similar. Their ranges are separated by the Isthmus of Tehuantepec.

The ancestral stock of this group apparently became divided into Caribbean and Pacific versant elements. The Pacific element apparently underwent a reduction in the pigmentation of the venter, a reduction in the relative tail length, and a reduction in the number of subcaudals (and perhaps the number of ventrals); this stock, relatively recently, traversed the Isthmus of Tehuantepec. Independent reduction in the number of head shields in populations to the north and south of the Isthmus led to the distinguishing features of *semidoliatus* and *cancellatus*, respectively. The Caribbean element (*laticinctus*) is not known to have undergone further specialization.

### *Geophis cancellatus* Smith

*Geophis cancellatus* Smith, 1941b:1; Smith and Taylor, 1945:67.

HOLOTYPE.—USNM 46440, an adult female from Chicharras, Chiapas, Mexico; February, 1896; Nelson and Goldman, collectors. USNM 46441, probably a topotype, is a paratype.

DISTRIBUTION.—Known only from the type locality; about 1035 meters above sea level on the Pacific slopes of Chiapas. Probably ranges westward to the Isthmus of Tehuantepec and eastward into Guatemala.

DIAGNOSIS.—Distinguished from other members of the genus by the combination of (1) dorsal scales in 15 rows, smooth except above the vent; (2) no anterior temporal; (3) six supralabials; (4) internasals fused with prefrontals; (5) 28–32 dark crossbands separated by narrow light interspaces; and (6) ventrals immaculate whitish.

DESCRIPTION.—Head indistinct from neck; snout long, rounded from above, projecting well beyond the lower jaw; rostral much broader than long, not produced posteriorly between prefrontals; internasals fused with prefrontals; prefrontals (and included internasals) very long, their common suture as long as frontal; frontal as broad as long, its anterior margin angulate; parietals long, their median suture slightly shorter than frontal; supraocular moderate, half as long as loreal, forms posterior two-thirds of dorsal margin of orbit; one postocular, higher than long, half as large as supraocular.

Nasal divided, postnasal larger than prenasal, their combined length greater than that of loreal; dorsal margin of postnasal rounded (correlated with internasal-prefrontal fusion); loreal moderate, contained slightly more than twice in snout length, almost twice as long as eye diameter; eye small, contained five times in snout length, its vertical diameter less than three-fourths its distance from lip; supralabials 6, third and fourth in orbit, fifth very large and in broad contact with parietal; no anterior temporal; one posterior temporal, fused with nuchal along parietal margin.

Mental rounded anteriorly, broader than long, separated from chinshields by first pair of infralabials; infralabials variable (6–8), three or four pairs in contact with anterior chinshields; anterior chinshields almost twice as long as posterior pair; posterior chinshields in contact medially; chinshields separated from first ventral by 3 rows of gulars.

Dorsal scales in 15 rows, smooth except above the vent; scales above vent faintly keeled; paired apical pits not discernible. Ventrals in two females, 171; anal undivided; subcaudals, 21–23<sup>2</sup>. Ventrals plus caudals, 192–194. Total length of larger female (type), 410 mm; tail, 32 mm (7.8%).

Maxilla extends anteriorly to middle of first supralabial; anterior exten-

<sup>2</sup> An adult male from the vicinity of Union Juarez, Volcan Tacana, Chiapas, has been recently reported by Landy, Langebartel, Moll, and Smith (1966). The following data are pertinent: Ventrals, 149; subcaudals, 25; total length, 326 mm; tail, 33 mm (10.1%); chin tubercles present; striations, weak keels, and paired apical pits present on scales above the vent. The similarity of the hemipenis to that of *G. semidoliatus*, anticipated on the basis of other similarities, is confirmed by my examination.



sion greater than that of palatine; maxilla stout, tapers posteriorly to blunt point; 7 maxillary teeth, decreasing in size posteriorly; first tooth at anterior tip of maxilla; anterior end of ectopterygoid bifurcate, branches subequal in length, not expanded; no postorbital bone.

Hemipenial characteristics unknown.

Head dark reddish-brown; a yellowish-white collar occupies supralabials 5 and 6, temporal, parietal, and one row of nuchals; brown pigment on medial parts of parietals narrows collar middorsally; dorsum of body with 28–32 broad (3–10 scale lengths) reddish-brown crossbands separated by narrow creamish bands; dark bands reach second scale row, occasionally first row; light bands narrow middorsally (1–2 scale lengths), sometimes interrupted; light bands broaden laterally; first scale row creamish; scales of second row creamish, mottled, or dark; dorsum of tail similar to that of body, with 4–6 dark bands. Anterior parts of chin region dark brownish; posterior chin scales and all ventrals immaculate, creamish; subcaudal surface ringed by dark and light dorsal bands.

VARIATION.—The paratype differs little from the type; the most variable scales are the infralabials, which are 6–8 in the type and 6–7 in the paratype. The increase (or decrease) in number occurs in the posterior half of the infralabial series. The dorsal margin of the second supralabial is horizontal in the paratype, making that scale squarish; in the type the dorsal margin slants posteroventrally. Variation in color pattern is slight; the type has 32 dark bands on the body and 6 on the tail, the paratype 28 and 4, respectively.

REMARKS.—At present it must be assumed that the fusion of the internasals and prefrontals is typical in *cancellatus*. The occurrence of this fusion as an occasional condition in *G. semidoliatus*, which normally has distinct internasals, suggests that the absence of internasals in the two known specimens of *cancellatus* may be atypical of the species as a whole.

SPECIMENS EXAMINED (2).—MEXICO: Chiapas: Chicharras, USNM 46440; probably Chicharras, USNM 46441.

### *Geophis laticinctus* Smith and Williams

*Geophis laticinctus* Smith and Williams, 1963:24, fig. 1 (appeared by typographical error as *G. latinctus*; corrected in *Herpetologica*, 20:144).

HOLOTYPE.—UI 51352, an adult female from Colonia Francisco I. Madero, municipality of Jitotol, Chiapas, Mexico; December 23, 1961; T. MacDougall, collector.

DISTRIBUTION.—Known only from the type locality, about 1800 meters above sea level in the Mesa Central of Chiapas.

**DIAGNOSIS.**—Distinguished from other members of the genus by the combination of (1) dorsal scales in 15 rows, smooth except above the vent; (2) no anterior temporal; (3) 6 supralabials; (4) dorsum blackish with numerous light crossbars; and (5) venter blackish with a few light blotches.

**DESCRIPTION.**—Head indistinct from neck; snout long, rounded from above, projecting well beyond lower jaw; rostral not produced posteriorly between internasals, its length one-fourth its distance from frontal; internasals broader than long, half as long as prefrontal suture; prefrontals moderate, their median suture three-fourths as long as frontal; frontal as broad as long, convex anteriorly; parietals long, their median suture as long as frontal; supraocular moderate, slightly more than half as long as loreal, forms posterior two-thirds of dorsal margin of orbit; one postocular, as long as high, one-third as large as supraocular.

Nasal divided, postnasal one-third longer than prenasal, their combined length as great as that of loreal; loreal moderate, contained slightly more than twice in snout length, twice as long as eye; eye small, contained almost five times in snout, its vertical diameter three-fourths its distance from lip; supralabials 6, third and fourth in orbit, fifth very large and in broad contact with parietal; no anterior temporal; one posterior temporal separates sixth labial from parietal, fused with nuchal along parietal margin.

Mental rounded, much broader than long, separated from chinshields by first pair of infralabials; infralabials 7, first four pairs in contact with anterior chinshields; anterior chinshields twice as long as broad; posterior chinshields in contact medially, three-fifths as long as anterior pair; three rows of gulars separate chinshields from first ventral.

Dorsal scales in 15 rows, smooth except above vent; scales above vent faintly keeled, bear paired apical pits. Ventrals in single female, 175; anal undivided; subcaudals, 33. Ventrals plus caudals, 208. Total length of female, 384 mm; tail, 42 mm (10.9%).

Maxilla extends anteriorly to middle of first supralabial; anterior extension greater than that of palatine; maxilla short, stout, tapers to blunt point posteriorly; 6 maxillary teeth, decreasing in length posteriorly; first tooth at anterior tip of maxilla; anterior end of ectopterygoid bifurcate, branches subequal in length, not expanded.

Hemipenial characteristics unknown.

Head blackish; a pinkish collar occupies posterior half of parietals, temporal, part of fifth and entire sixth labials, and middorsal scale behind parietals; posteromedial parts of each parietal blackish, form dark blotch within collar; collar confluent ventrally with light gular region. Dorsum of body blackish; 28 reddish-yellow crossbars, narrowed middorsally, broader laterally; first few crossbands less than or equal to length of one scale dorsally, about two and one-half scales laterally; bands on posterior body

broader, not noticeably narrowed, but often interrupted middorsally; tail black, with five light crossbars. Anterior parts of chin blackish; infra-labial 7 creamish; gular region and first few ventrals mostly creamish, mottled with black; ventrals and subcaudals blackish, their free edges paler; a few light blotches on venter, some associated with light dorsal bands; subcaudal surface uniformly blackish.

SPECIMEN EXAMINED (1).—MEXICO:Chiapas: Jitotol, Colonia Francisco I. Madero, UI 51352.

*Geophis semidoliatus* (Duméril, Bibron, and Duméril)

*Rhabdosoma semidoliatum* Duméril, Bibron, and Duméril, 1854:93.

*Geophis semidoliatus*, Peters, 1859:276; Bocourt, 1883:534; Günther, 1893:90; Boulenger, 1894:316; Smith and Taylor, 1945:70.

*Catostoma semidoliatum*, Cope, 1860:339; Amaral, 1929:193.

*Elapoides semidoliatus*, Jan, 1862:22; Jan and Sordelli, 1865: livr. 12, pl. II, fig. 1.

*Rhabdosoma semidoliatum*, Cope, 1887:85.

*Atractus semidoliatus*, Cope, 1900:1230.

HOLOTYPE.—Originally five syntypes, from "Mexico"; M. Parduracki, collector. At present, four of the syntypes, MNHN 4522 and 3313 (3), are in the Paris collections; the fate of the fifth syntype is unknown. MNHN 4522 is herein designated as lectotype; the other four specimens are paralectotypes. Smith and Taylor (1950:347) restricted the type locality to Córdoba, Veracruz.

DISTRIBUTION.—Known only from moderate elevations (500–1400 meters above sea level) along the eastern slopes of the neovolcanic plateau from Misantla southward to the Cordoba-Orizaba region of Veracruz, Mexico.

DESIGNATION OF A LECTOTYPE.—The original description concludes with the statement that five specimens had been received from M. Parduracki. The description itself is apparently based on a single specimen. The scale counts (172 ventrals, 24 subcaudals) and the body size and proportions (total length, 310 mm; tail, 27 mm) indicate that the described specimen was an adult female; according to Jean Guibé (pers. com.), MNHN 4522 fits these qualifications, and is therefore designated as lectotype. The three accountable paralectotypes, MNHN 3313, are all juveniles, about 150 mm in total length.

DIAGNOSIS.—Distinguished from other members of the genus by the combination of (1) dorsal scales in 15 rows, smooth throughout length or faintly keeled above vent; (2) no anterior temporal; (3) 5 supralabials, the third in orbit; (4) 17–36 dark dorsal crossbands separated by light interspaces; and (5) venter whitish, immaculate or spotted with brown.

DESCRIPTION.—Head indistinct from neck; snout long, rounded, projecting well beyond lower jaw; rostral not produced posteriorly between internasals, its length from above one-third or less its distance from frontal; internasals broader than long, half as long as prefrontal suture; prefrontal suture slightly more than half as long as frontal; frontal as broad as long, its anterior margin angulate; parietals long, their median suture as long as frontal; supraocular moderate, more than half as long as loreal, forms posterior two-thirds of dorsal margin of orbit; one postocular, higher than long, smaller than supraocular.

Nasal divided, postnasal longer than prenasal, their combined length equals or exceeds that of loreal; loreal contained slightly more than twice in snout length, one-third longer than eye; eye small, contained four to five times in snout, its vertical diameter two-thirds its distance from lip; supralabials 5, third enters orbit, fourth very large and in broad contact with parietal; no anterior temporal; one posterior temporal separates fifth labial from parietal, usually fused with nuchal along parietal margin.

Mental rounded, much broader than long, separated from chinshields by first pair of infralabials; infralabials 6, first four pairs in contact with anterior chinshields; anterior chinshields half-again as long as posterior pair; posterior chinshields usually in contact medially; 2–3 rows of gulars separate chinshields from first ventral.

Dorsal scales in 15 rows, smooth throughout length or faintly keeled above vent; scales above vent bear paired apical pits. Ventrals in 329 males, 131–160; in 348 females, 141–179; anal undivided; subcaudals in 326 males, 22–30; in 343 females, 19–29 (see *Variation* for details). Ventrals plus caudals, 156–201. Total length of second-largest male 327 mm; tail, 37 mm (11.3%); a larger male, with an incomplete tail, is 360 mm long. Total length of largest female, 411 mm; tail, 37 mm (9.0%).

Maxilla extends anteriorly to suture between rostral and first supralabial; anterior extension greater than that of palatine; maxilla short, stout, tapers posteriorly to blunt point; 7–8 maxillary teeth, decreasing in length posteriorly; first tooth at anterior tip of maxilla; anterior end of ectopterygoid bifurcate, branches subequal in length, not expanded; no postorbital bone.

Hemipenis extends to level of eighth subcaudal; basal part of organ bears numerous small spinules and single large spine; basal naked pocket opposite sulcus. Central part of organ bears about 30 medium spines in oblique rows. Distal part of organ capitate, calyculate, spinulate; capitulum slightly bilobed at apex. *Sulcus spermaticus* bifurcates opposite fourth subcaudal; each branch reaches apex of hemipenis. *M. retractor penis magnus* divides into two slips near apex of organ.

Head dark reddish-brown to blackish; a light collar occupies posterior parts of parietals, posterior temporal, fifth supralabial, and posterior parts

of fourth labial; dorsum of body with 17–38 reddish-brown or blackish crossbands, usually, but often not, reaching first scale row; dark bands occupy about 7 scale lengths anteriorly, 4–5 scale lengths posteriorly; adjacent dark bands often confluent middorsally; light interspaces creamish to pinkish-orange, occupy 2–3 scale lengths dorsally, broadened laterally; dorsum of tail similar to that of body, with 3–7 dark bands. Infralabials and chinshields creamish, mottled with brown; remainder of chin creamish; ventrals creamish, usually immaculate or with few scattered dark spots, occasionally heavily spotted with brown; subcaudals brown, with light posterior margins.

**VARIATION.**—Among the almost 700 specimens of *semidoliatus* examined, the most variable head scales are the supralabials. There are six supralabials in both of the other members of the *semidoliatus* group; in *semidoliatus*, which usually has five labials, the third labial occupies the approximate position occupied by the third and fourth labials in *cancellatus* and *laticinctus*, indicating that the reduction to five occurred by a fusion of the latter scales. The labial number is further reduced in about seven per cent of the individuals of *semidoliatus*. This further reduction (to four) is usually the result of fusion between the fourth and fifth labials of the typical condition; in such specimens a single elongate labial occurs posterior to the eye. In some specimens the fusion is between the second and third labials; the labial bordering the orbit is then the second. No specimens with more than five supralabials have been found.

The postocular is fused with the supraocular on at least one side of 12 specimens; it is divided by a suture into two postoculars in five specimens. In three specimens a vertical suture divides the normal loreal into a small, squarish “loreal” and a peculiarly shaped “preocular” which apparently has no evolutionary significance. This condition is further confused in BMNH 1903.9.30.203, in which the small “loreal” is fused with the postnasal.

A particularly pertinent variation in the head scales is the fusion of the internasals and prefrontals, since the absence of distinct internasals is one of the chief characteristics distinguishing *cancellatus* from *semidoliatus*. In the latter species this fusion occurs in eleven specimens.

The number of ventrals and subcaudals is surprisingly variable in *semidoliatus*, particularly since the species occupies a limited geographic area. The remarkable feature of this variation is that populations from within a few miles of one another, such as those from Cuautlapan and the Potrero Viejo region, may have quite different segmental counts; these differences are primarily in the frequency of various counts, rather than in the overall range in the number of ventrals and subcaudals (Fig. 18). There is no apparent correlation between these differences and altitude or latitude.

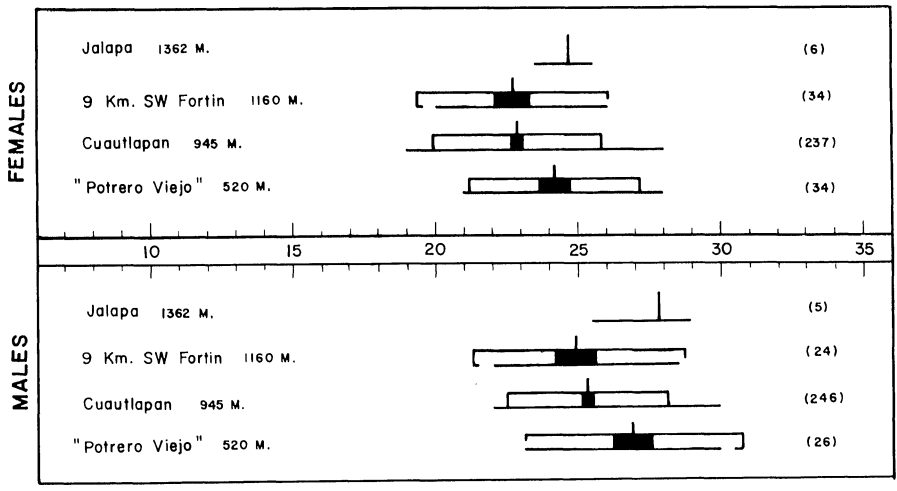
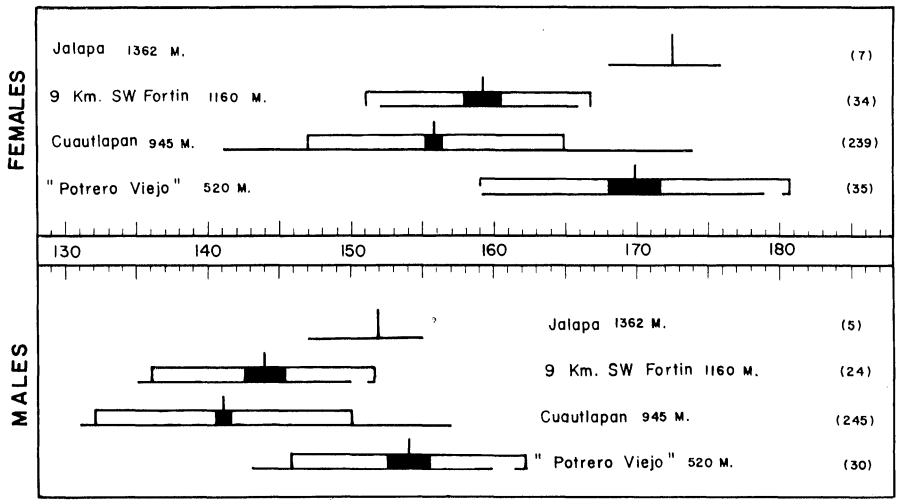


FIG. 18. Variation in segmental counts in *G. semidolius* from several localities in Veracruz, Mexico. Included under "Potrero Viejo" are specimens from Potrero Viejo, Paraje Nuevo, Ojo de Agua, and San Rafael; these localities are in close proximity, and specimens from each show similar variation in segmental counts. Horizontal line, observed range; vertical line, sample mean; large rectangle, twice the standard deviation on each side of the mean; small black rectangle, 95% confidence limits of the mean; the number of individuals is given parenthetically.

The stated range of variation in the number of dorsal crossbands (17–38) is partly a reflection of coalescence between adjacent bands. The dark crossbands usually extend laterally to the first scale row, but in many specimens they extend no farther than the fourth scale row; in a few, the dark bands are reduced to a series of middorsal blotches. The venter is almost always predominantly light, but the amount of dark pigment is highly variable.

REMARKS.—Taylor and Smith (1939:244) noted that in life the dark crossbands are ultramarine in young specimens and dark bluish-black in adults; the light interspaces are pink in juveniles, reddish-orange in adults.

Several large series of this species are available; the largest of these is the collection of 327 specimens (USNM 109968–110294) secured by Smith. These specimens were invariably found under debris in banana patches (Smith, 1943:432).

SPECIMENS EXAMINED (691).—MEXICO: No locality, BMNH 46.3.16.37, MNHN 3313 (3), 4522, USNM 7294, 12090 (3), 12307, 12485 131806, ZMB 1553 (2), 31515 (2). **Distrito Federal:** City of Mexico (probably in error), USNM 12732. **Veracruz:** Cerro, San Cristobal, AMNH 19719; Cordoba, CNHM 38604–05, UI 17705, ZMB 31518; 3.5 mi E Cordoba, AMNH 81961; near Cordoba, Hac. El Potrero, MCZ 45678; Cuautlapan, CNHM 38603, 70744–45, 114030–137, UI 17717–58, UMMZ 105037 (4), 105039 (2), USNM 109968–110294; Djecho, CNHM 56383; 1–2 mi N Fortin, UI 25945–53, 42878, UMMZ 105038; 9 km SW Fortin, UMMZ 95068 (59); Huatusco, BMNH 90.4.24.29, ZMB 3912; Jalapa, BMNH 60.12.18.30–32; 81.10.31.55–56, MCZ 16041–48, UMMZ 56991; 1 mi SE Jalapa, Palo Verde, CNHM 70742; 7 mi SSE Jalapa, El Chico, CNHM 70741, 70743; La Pesca el Potrero, UMMZ 89372; Metlac, MCZ 45690; Mirador, USNM 12114 (5), 25026–28; Misantla, ANSP 11718; Ojo de Agua, UMMZ 85323–26; Orizaba, BMNH 72.4.11.5–6, USNM 12118 (3); Orizaba, above Serritos, BMNH 1903.9.30.-202–04; Paraje Nuevo, UMMZ 88668–69 (16); Potrero Viejo, MCZ 15989, UI 17704, 17711–12, 34930, UK 25758–66, USNM 109946–67; 5 km W Potrero Viejo, UI 17713–16; San Rafael, UMMZ 88667 (3), 88670; Tlilapam, near Cordoba, UI 17706–10; Veracruz, hills W of city, USNM 5315 (3).

THE *sieboldi* GROUP

Dorsal scales in 15 or 17 rows, keeled at least above the vent; paired apical pits present. Head moderately distinct from neck or not; snout long, projecting well beyond lower jaw; eye small to moderate; rostral not produced posteriorly between internasals; internasals and postnasals short; prefrontals and loreals elongate; supraocular forms about posterior half of dorsal margin of orbit; parietals short, broad; no anterior temporal. Ventrals 118–151 in males, 118–154 in females. Subcaudals 28–51 in males, 23–43 in females. Percentage tail of total length 14.1–21.2 in males, 11.0–17.6 in females.

Maxilla extends anteriorly to suture between supralabials 2 and 3; anterior extension about equal to that of palatine; maxilla dorsoventrally compressed; in lateral view, posterior third of maxilla curves ventrally;

anterior tip of maxilla toothless, pointed; 8–15 maxillary teeth, subequal in length; posterior end of maxilla tapers to blunt point. Anterior end of ectopterygoid single, not expanded; postorbital bone narrow.

Hemipenis (condition unknown in *dunni*) slightly bilobed at tip; *sulcus spermaticus* bifurcate; a naked basal pocket; central part of organ with medium to large spines; distal part distinctly capitate, spinulate, calyculate; M. retractor penis magnus divides into two slips at apex of hemipenis.

I include eight forms in this group; *G. brachycephalus*, *G. dunni*, *G. hoffmanni*, *G. nasalis*, *G. petersi*, *G. sallaei*, *G. sieboldi*, and *G. zeledoni* (Fig. 19)<sup>3</sup>. Geographically, the group ranges from Michoacan, Mexico, southward into northwestern Colombia (Figs. 20 and 21).

Partly because of the number of species included, this is the most complex group in the genus. Five of the eight forms, although some have 17 dorsal scale rows and others 15, are basically similar, and form the nucleus of the group. These are *G. brachycephalus*, *G. dunni*, *G. nasalis*, *G. sallaei*, and *G. sieboldi*. Each of the other three species (*hoffmanni*, *petersi*, *zeledoni*) have one or more features which set them apart from the other five, and from each other. All three, however, have certain characteristics consistent with the group as a whole. Recognition of one group of five species and three monotypic groups does not seem warranted or desirable; I therefore include all eight forms in the *sieboldi* group.

The group includes three forms with 17 rows of dorsal scales, and five with 15 rows. The latter group is not homogeneous; the reduction to 15 rows has apparently taken place independently in *petersi*, in *sallaei*, and in the species at the southern end of the group's range (*brachycephalus*, *hoffmanni*, *zeledoni*). In contrast, the three forms with 17 scale rows differ from one another in rather minor details.

Of these three, *G. dunni* is the most distinctive, primarily because it is unique in having dark brown crossbands on a yellowish dorsum. The other two forms, *nasalis* and *sieboldi*, are uniformly dark above. The venter in *dunni* is immaculate yellowish-white; in *nasalis* and *sieboldi* the ventrals have dark pigment along the lateral edges and sometimes, on the posterior

<sup>3</sup>Three individuals with the form and scutellation of *G. sallaei* have recently been collected in the vicinity of Putla, Oaxaca. One of these, the holotype of *G. laticollaris*, I consider a specimen of *G. sallaei*, a form with a unicolor, blackish dorsum (see footnote, p. 168). The other two individuals are the holotype (UI 61409; Oaxaca, La Concepción, near Putla) and a second specimen (UI 68833) of *G. sallaei russatus* Smith and Williams (1966). These two have a reddish dorsum crossed by irregular black bars. In UI 61409, all of the dorsal scales have dark margins; the entire dorsum is therefore rather dark, and the crossbars relatively indistinct. In UI 68833, however, the black crossbars are very prominent against a background of nearly immaculate reddish scales. The occurrence of this distinctive pattern in sympatry with typical *sallaei* suggests that the name *russatus* should be tentatively elevated to specific rank, *Geophis russatus*, new combination.



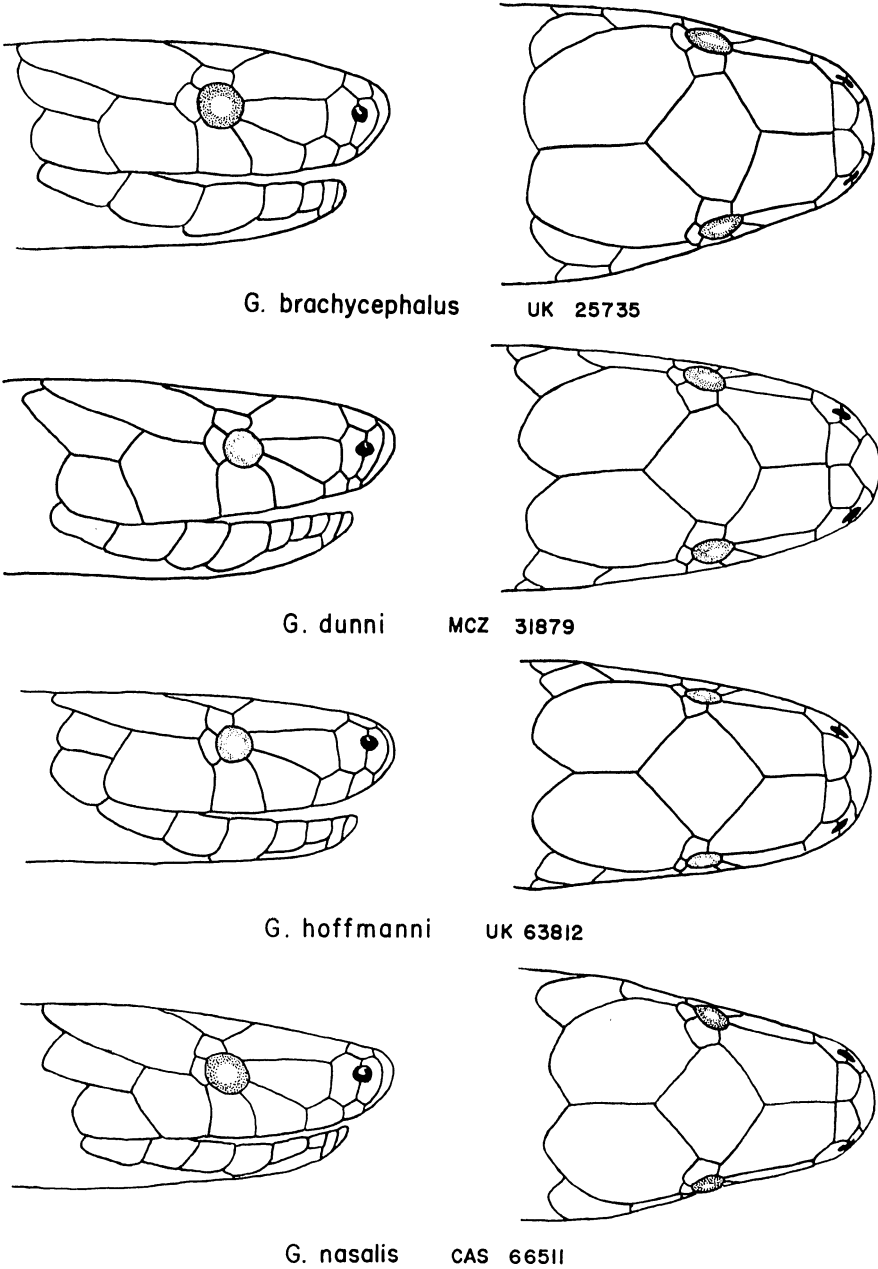
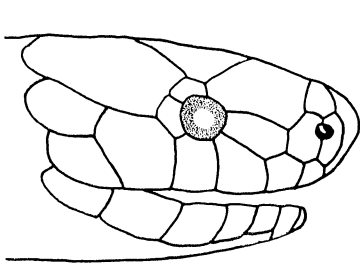
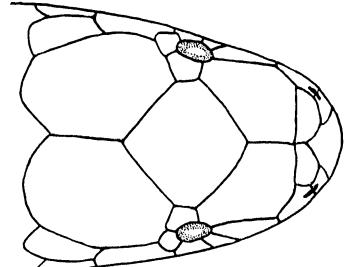
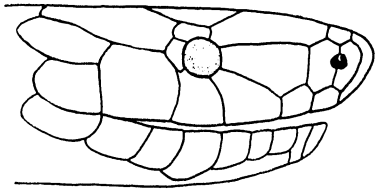
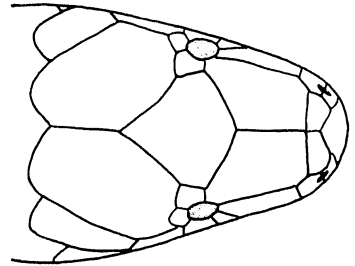


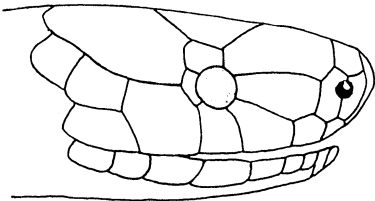
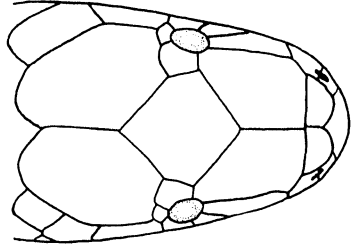
FIG. 19. Dorsal and lateral head scutellation in members of the *sieboldi* group. Scale: *G. brachycephalus*, about 6 ×; *G. dunni*, about 4.5 ×; *G. hoffmanni*, about 6 ×; *G. nasalis*, about 5 ×.

*G. petersi*

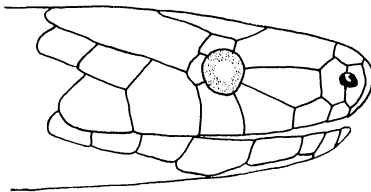
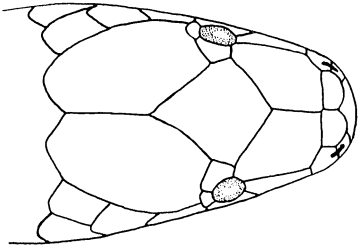
UI 17760

*G. sallaei*

ZMB 3731

*G. sieboldi*

ZMB 1555

*G. zeledoni*

UK 35854

FIG. 19 (cont.) Scale: *G. petersi*, about 7.5 ×; *G. sallaei*, about 5 ×; *G. sieboldi*, about 5 ×; *G. zeledoni*, about 5 ×.

part of the body, on the lateral parts of the anterior edge. In scale features, the three forms are similar. The number of ventrals in the single specimen (female) of *dunni* is lower than the number in female *sieboldi*, and higher than most females of *nasalis*; the count is matched by female *nasalis* from populations in eastern Guatemala, which are geographically closest to the type locality of *dunni*.

*G. nasalis* of Guatemala and adjacent Chiapas, Mexico, and *G. sieboldi* of western Mexico, differ in rather minor details and may eventually be considered only subspecifically distinct. At present the latter form is too imperfectly known to demonstrate intergradation between it and *nasalis*. The two differ primarily in the number of ventrals and subcaudals (both higher in *sieboldi*) and in the strength of the dorsal keeling (stronger in *nasalis*). The two smallest specimens of *sieboldi* also have at least an indication of a light collar, not known to occur in *nasalis*. Finally, *sieboldi* may be a larger form than *nasalis*; although few specimens of *sieboldi* are available, a high percentage of them have total lengths reached by only a small percentage of the large number of available specimens of *nasalis*. One specimen from Guerrero, otherwise referable to *sieboldi*, has a ventral count that is intermediate between those of the remaining *sieboldi* and *nasalis*. No other specimens of either species are known from neighboring localities, and at present I consider the unusual count as individual or populational variation within *sieboldi*. Regardless of whether or not interbreeding occurs between *sieboldi* and *nasalis*, it is clear that the two are closely related, and apparently represent quite recent differentiations between populations presumably isolated on either side of the Isthmus of Tehuantepec. It should be noted that some of the features distinguishing *sieboldi* from *nasalis* are paralleled by differences between certain populations of *nasalis* itself. Specimens of *nasalis* from the Guatemalan Plateau and the Antigua Basin of Guatemala have a greater number of ventrals (although not as great as in *sieboldi*) and weaker keeling than their conspecific relatives from the Pacific versant of Guatemala.

*G. sallaei*, known from one definite locality in the Sierra del Sur in Oaxaca, Mexico, is clearly a derivative of the *sieboldi-nasalis* stock. Excepting the presence of 15 instead of 17 dorsal scale rows, *sallaei* can scarcely be distinguished from the latter. The number of ventrals in *sallaei* is comparable to the number in most populations of *nasalis*, and contrasts with the higher number in *sieboldi*. *G. sallaei* may have developed on the western side of the Isthmus of Tehuantepec prior to the invasion of *sieboldi*. A second alternative involves the *in situ* differentiation of *sallaei* from a single, widespread stock which also gave rise to *nasalis* and *sieboldi*. From the scant locality data now available, I favor the latter alternative. *G. sallaei* is geographically intermediate between *sieboldi* and *nasalis*, and allopatric

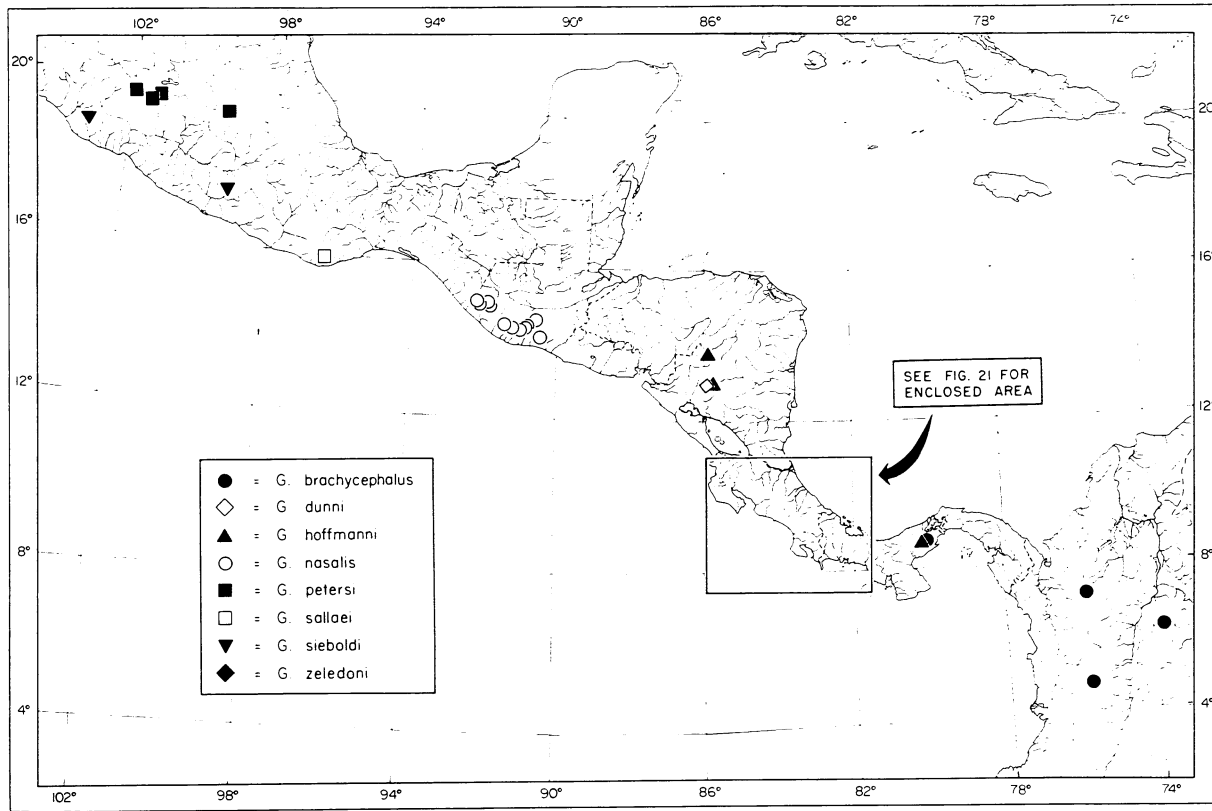


FIG. 20. Locality records for members of the *sieboldi* group. Not included is a specimen of *hoffmanni* from Honduras recently reported by Smith and Smith (1964).

to both. Furthermore, the reduction from 17 to 15 scale rows is not of major significance; a specimen of *sieboldi* from Coalcoman, Michoacan, with 17 scale rows has the number reduced to 15 at several points along the body. If *sallaei* is eventually found to be widespread in western Mexico, and broadly sympatric with *sieboldi*, a re-evaluation of the origin of *sallaei* would be in order.

The third Mexican member of this group, *G. petersi*, is its only representative on the Mexican Plateau. It is the most distinctive member of the group, and therefore the least typical. Although *sallaei* agrees with *petersi* in having 15 scale rows, it is clear that the reduction from 17 rows to 15 has taken place independently in each form. The head scutellation in *petersi* is unique within the *sieboldi* group, and in fact is not dissimilar to that found in members of the *dubius* group. In *petersi* the rostral is prominent, the internasals and postnasals relatively large, and the prefrontals and loreals relatively short. In all other species of the *sieboldi* group, the rostral is moderate, the internasals and postnasals relatively short, and the prefrontals and loreals quite long. On the other hand, the maxilla, the presence of a post-orbital bone, and, for the most part, the hemipenis all indicate that *petersi* should be assigned to the *sieboldi* group and not to the *dubius* group. The maxilla in particular is basically a reduced version of the type found in *sieboldi*, *nasalis*, and the other species in the group, but would be difficult to derive from the type of maxilla found in the *dubius* group. The allocation of *petersi* to the *sieboldi* group perhaps makes this group more inclusive than the other species groups. A similar, but less drastic, situation characterizes the *chalybeus* group, in which the head scutellation of *G. aquilonaris* disagrees with that characterizing the other members of the group. In both instances, I prefer to consider the unique form an early offshoot of the main stock of the group which has evolved in isolation for an extended period of time.

The status of members of the *sieboldi* group in southern Central America is at present highly confused. Taylor (1954) recognized eight nominal forms of *Geophis* in Costa Rica. Seven of the eight are referable to the *sieboldi* group. Of the seven, I recognize three (*brachycephalus*, *hoffmanni*, *zeledoni*). I have placed one of the remaining four forms in the synonymy of *hoffmanni*, and three in that of *brachycephalus*. *G. brachycephalus* (*sensu lato*) may eventually be shown to be composed of more than one species, but at present the various nominal forms appear to be based on the extremes of a highly variable color pattern.

*G. brachycephalus* has 15 dorsal scale rows, but is otherwise very similar to the geographically allopatric *G. dunni* and *G. nasalis*. Of the latter, *G. dunni* appears to be the closer relative since it is geographically nearer and since it and some specimens of *brachycephalus* are the only forms within the group which have dorsal blotches or crossbands. Many specimens of

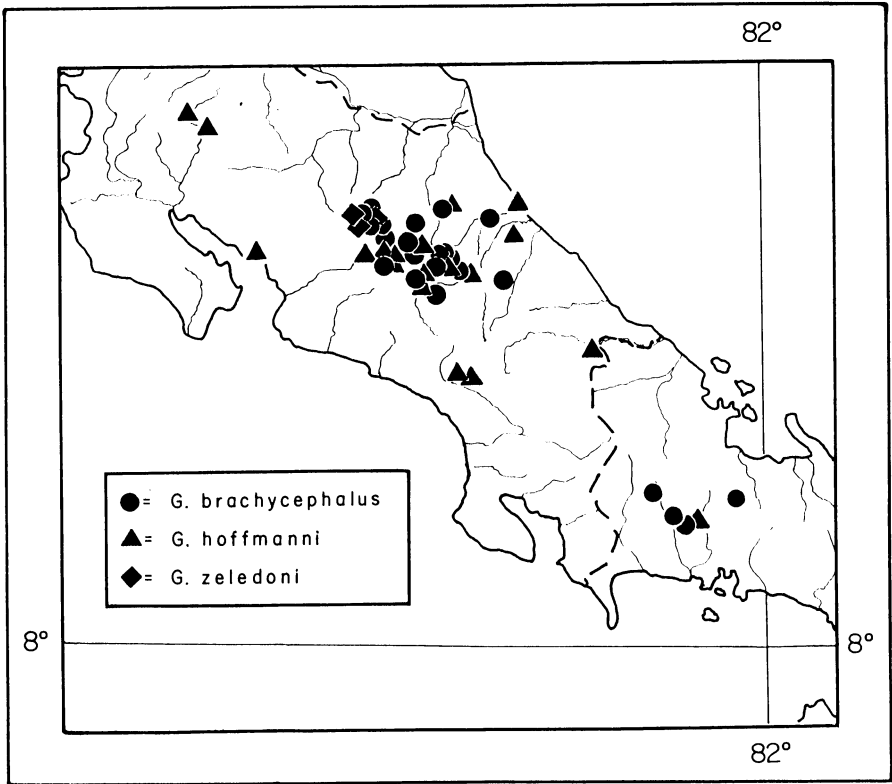


FIG. 21. Locality records for members of the *sieboldi* group in Costa Rica and adjacent Panama. Recorded localities bordering the central plateau of Costa Rica are too numerous to include all. Extralimital localities for *G. hoffmanni* and *G. brachycephalus* appear in Fig. 20.

*brachycephalus* are unicolor above, but the fact that the dorsal pattern is lost ontogenetically in some individuals suggests that the blotched condition is more primitive. Thus *dunni* and *brachycephalus* may have developed from a common ancestor, perhaps on either side of a Nicaraguan portal. At present, *brachycephalus* is known from Volcan Poas, Costa Rica, southward into northwestern Colombia. It is the only *Geophis* known from South America, and its limited distribution there suggests a recent entry into this continent.

*G. zeledoni* is known only from the slopes of Volcan Poas, Costa Rica, where it is sympatric with *brachycephalus*. The two are nearly indistinguishable on scale characters, but *zeledoni* has a distinctive maxilla and hemipenis which set it apart from *brachycephalus* and all other members

of the group. One of the few external features distinguishing *zeledoni* from *brachycephalus* is the keeling of the dorsal scales; in the former the keels are weak and restricted to the region above the vent, and in the latter stronger and more widely distributed. The maxilla of *brachycephalus* and the other members of the group is dorsoventrally compressed throughout its length, and has a pointed, toothless anterior tip. In *zeledoni*, only the posterior half of the maxilla is flattened, and there is no distinct toothless tip. The hemipenis in *zeledoni* is less distinctly bilobed and less distinctly capitate than those of the other members of the group. It is surprising to find these differences between such externally similar forms, but the latter similarities are too pronounced to consider placing *zeledoni* in any other group. I see no alternative to considering *zeledoni* a derivative of the *brachycephalus* stock. Presumably its differentiation proceeded *in situ*, with a later invasion by *brachycephalus* resulting in sympatry.

*G. hoffmanni* also appears to have been derived from a *brachycephalus*-like ancestor. It is the only member of the group with five supralabials, but in other respects its scale features are similar to those of *brachycephalus* and the other related species. The reduction to five labials, only one of which is posterior to the orbit, is the result of an overall shortening of the jaw and narrowing of the gape. The large fifth labial is followed by what appears to be the original sixth labial, which no longer borders the lip. The narrowed gape is one of several features which suggest that *hoffmanni* differs from *brachycephalus* primarily in being more specialized for a burrowing existence. Of the two species, *hoffmanni* has a smaller, more terete body, a less distinct head, a relatively smaller eye, less widely distributed keels, and a shorter maxilla with fewer teeth. The attainment of this different adaptive level by *hoffmanni* implies that its isolation preceded the dichotomy between *brachycephalus* and *zeledoni*. The geographic distribution of the forms supports this implication. The confined distribution of *zeledoni* contrasts sharply with the broad ranges of *hoffmanni* and *brachycephalus*. The latter species overlap widely in Costa Rica and Panama, but *hoffmanni* occurs considerably farther northward than *brachycephalus*, and *brachycephalus* farther southward than *hoffmanni*. The isolation between the two was probably between northern and southern populations, but since *hoffmanni* occurs at generally lower elevation than *brachycephalus* the possibility of altitudinal isolation exists.

*Geophis brachycephalus* (Cope)<sup>4</sup>

- Colobognathus brachycephalus* Cope, 1871:211; Bocourt, 1883:529.  
*Colobognathus dolichocephalus* Cope, 1871:211 (type, ANSP 3306, San Jose, Costa Rica); Bocourt, 1883:529.  
*Geophis moestus* Günther, 1872:15 (type, BMNH 1946.1.6.53, Cartago, Costa Rica); Günther, 1893:90; Taylor, 1951:44.  
*Catostoma chalybeum*, Günther, 1872:16.  
*Elapoidis brachycephalus*, Cope, 1885a:386; Cope, 1887:85.  
*Elapoidis dolichocephalus*, Günther, 1893:87; Boulenger, 1894:320; Taylor, 1951:43.  
*Geophis chalybaea* var. *quadrangularis*, Günther, 1893:89, pl. 33, fig. B.  
*Catostoma brachycephalum*, Cope, 1876:147; Amaral, 1929:191.  
*Catostoma dolichocephalum*, Cope, 1876:147; Amaral, 1929:191.  
*Dirosema brachycephalum*, Boulenger, 1894:299; Mocquard, 1908:880.  
*Rhabdosoma moestum*, Cope, 1887:85.  
*Geophis hoffmanni*, Boulenger (in part), 1894:319.  
*Geophis brachycephalus*, Dunn (in part), 1942:4; Taylor, 1951:46.  
*Geophis bakeri* Taylor, 1954:689 (type, UK 31983, Isla Bonita, Cinchona, Costa Rica).  
*Geophis nigroalbus* Boulenger, 1908:552 (type, BMNH 1946.1.6.50, Pavas, Colombia).

HOLOTYPE.—ANSP 3337, a juvenile male from Costa Rica; Van Patten, collector. Cope did not specify a definite locality in the original description, which was part of a report on specimens collected by Van Patten near San Jose.

DISTRIBUTION.—Known from the Cordillera Central of Costa Rica southward through Panama to Colombia; 250–2000 meters above sea level.

DIAGNOSIS.—Distinguished from other members of the genus by the combination of (1) dorsal scales in 15 rows, distinctly keeled except on neck; (2) no anterior temporal; (3) six supralabials; (4) total nasal length less than that of loreal; (5) prefrontal suture less than three-fourths as long as parietal suture; and (6) anterior half of each ventral, at least on posterior part of body, usually grayish-black, posterior half whitish to grayish (ventrals occasionally immaculate whitish).

DESCRIPTION.—Head scarcely distinct from neck; snout long, bluntly pointed, projecting well beyond lower jaw; rostral moderate, not extending posteriorly between internasals, its length one-third or less than its distance from frontal; internasals small, broader than long, less than half as long as prefrontal suture; prefrontal suture more than half as long as frontal; frontal as long as broad, angulate anteriorly; parietals moderate, their median suture slightly shorter than frontal; supraocular moderate, forms

<sup>4</sup> A cursory look at a specimen recently obtained in eastern Panama by Charles Myers leads me to doubt that my inclusion of *G. nigroalbus* Boulenger in the synonymy of *G. brachycephalus* is justified.



posterior two-thirds of dorsal margin of orbit; one postocular, higher than long, slightly smaller than supraocular.

Nasal divided, postnasal slightly longer than prenasal, their combined length four-fifths that of loreal; loreal long, contained less than twice in snout length, about twice as long as eye; eye moderate, contained thrice or more in snout, its vertical diameter nearly equal to its distance from lip; supralabials 6, third and fourth in orbit, fifth largest and in contact with parietal; no anterior temporal; one posterior temporal, fused with nuchal along parietal margin.

Chin tapered, anterior tip rounded; mental rounded, much broader than long, separated from chinshields by first pair of infralabials; infralabials 6 (7), pairs 1-3 (1-4) in contact with anterior chinshields (variable); anterior chinshields short, broad; posterior chinshields smaller than anterior pair, rounded posteriorly, often separated throughout length by median gular; 2-3 rows of gulars separate chinshields from first ventral.

Dorsal scales in 15 rows, smooth on neck, distinctly keeled on most of body and tail; paired apical pits present. Ventrals in 107 males, 119-148; in 121 females, 123-153; anal undivided; subcaudals in 104 males, 35-51; in 113 females, 30-39 (see *Variation*). Ventrals plus caudals, 154-192. Total length of largest male, 418 mm; tail, 79 mm (18.9%); largest female, 460 mm; tail, 66 mm (14.3%).

Maxilla extends anteriorly to suture between second and third supralabials; anterior extension equal to that of palatine; maxilla dorsoventrally compressed, bears 11-15 subequal teeth; anterior tip of maxilla pointed, toothless; posterior end of maxilla curves ventrally, tapers to blunt point; anterior end of ectopterygoid single, not expanded; post-orbital bone present.

Hemipenis extends posteriorly to level of subcaudals 8-10; basal part of organ bears numerous spinules and, distally, 2 large spines; naked basal pocket present on antisulcus side. Central part of hemipenis bears 20-30 medium spines and hooks in oblique rows. Distal part of organ strongly capitate, calyculate, spinulate; apex slightly bilobed. *Sulcus spermaticus* bifurcates opposite fifth or sixth subcaudal; each branch reaches apex. *M. retractor penis magnus* divides into two slips at apex of hemipenis.

Dorsal ground color brownish, bluish-gray, or blackish; juveniles with or without a light collar; dorsum uniformly dark or with irregular yellowish lateral stripe, or with yellowish lateral blotches; blotches on left and right sometimes confluent middorsally, forming light crossband; stripe and blotches usually obliterated by dark pigment in large specimens. Anterior chinshields blackish; infralabials, mental, and gular region mottled; ventrals yellowish-white, occasionally immaculate, usually banded at least

on posterior part of body; each banded ventral with dark anterior edge, pale posterior edge; subcaudals blackish, with light posterior margins.

VARIATION.—The infralabials are the most variable head scales; the modal number is six, but over one-third of the more than 200 specimens examined have seven infralabials on one or both sides, and a few individuals have five or eight. The supralabials are less variable; the number is reduced from six to five in 10 specimens, and increased to seven on one side of a single specimen. The reduction to five supralabials usually involves the fusion of the third and fourth labials, but may involve the fusion of the first and second, or of the fifth and sixth.

The loreal is excluded from the orbit in UMMZ 123195 and UK 57103; in these specimens the third supralabial is in contact with the prefrontal. In UK 63810 the postocular is divided into two small scales by a horizontal suture on one side of the head; in MCZ 15321 there are two postoculars on one side, and three on the other. UK 63810 has a small anterior temporal, which apparently represents a detached part of the fifth labial.

Several Panamanian populations have markedly lower ventral counts than those from neighboring Costa Rica. The number of ventrals in 28 females from Boquete, Panama, ranges from 123 to 132 (mean, 127.1); in 34 males the range is 119–140 (mean, 124.9). Of the latter, all but two of the 34 specimens have counts between 119 and 128; the exceptional individuals have 139 and 140 ventrals. These two specimens, CAS 78979 and CAS 78983, also have a slightly higher number of subcaudals than the remaining Boquete specimens, but are otherwise indistinguishable from them.

Specimens from Finca Lerida, Panama, have slightly higher ventral counts than the Boquete material, but still considerably lower than Costa Rican specimens. In 13 females from Finca Lerida, the number of ventrals ranges from 128–139 (mean, 131.4); in 10 males, 125–129 (mean, 127.5). Seven females from “Panama Sabanas” have 129–137 ventrals (mean, 131.0); 5 males from the same locality, 123–131 (mean, 125.8). The generalization that Panamanian populations have lower ventral counts does not seem to apply to specimens from La Loma; each of two specimens (MCZ 19325–26), of opposite sexes, has 138 ventrals, and in this respect are similar to Costa Rican specimens.

In Costa Rica, the number of ventrals in 70 females ranges from 135 to 145 (mean, 140.7), and in 54 males from 131 to 148 (mean, 138.5). These total ranges are matched or nearly matched by individual populations from which fairly large numbers of specimens are available (e.g., La Cinchona and the slopes of Volcan Turrialba). Interpopulational differences in ventral counts are not demonstrable from the available Costa Rican material.

The single female *brachycephalus* known from Colombia has 153 ventrals, the highest count known for the species. The range in 4 males is 140 to 142. The male counts, although well within the range of Costa Rican specimens, are all higher than the mean of the Costa Rican counts. Together with the high female count, this suggests that Colombian populations may have generally higher ventral counts than the Central American populations. The few available South American specimens were drawn from at least three different populations, and thus do not represent a homogeneous series.

The marked difference in ventral counts between Panamanian and Costa Rican populations of *brachycephalus* is not paralleled by comparable differences in the numbers of subcaudals. The range in the number of subcaudals in 42 Panamanian females is 30 to 37 (33.1) and in 48 males 35 to 45 (38.0). Not included in these figures are the two specimens from La Loma, which have 43 (female) and 47 (male) subcaudals, respectively. These two stand in contrast to the rather uniform ranges and means of the subcaudal counts found at Boquete, Finca Lerida, and "Panama Sabanas." In Costa Rica, 66 females have a range in the number of subcaudals of 30 to 39 (33.5), and 51 males of 36 to 48 (40.2). In the largest single sample, from La Cinchona, the range is 31 to 38 in 20 females and 38 to 43 in 17 males. Smaller samples from other Costa Rican localities show little variation in the female counts, but do differ in the number of male subcaudals. For example, 8 males from the slopes of Volcan Turrialba have a range of 37 to 40 subcaudals; in contrast, the counts are 43 and 46 in 2 males from La Palma, 43 and 45 in two from Carrillo, and 45 to 48 in three from the lowlands and foothills of eastern Costa Rica. These differences may simply reflect sampling error, particularly since the samples are so small; the discontinuity between the Volcan Turrialba counts and those of the other localities is bridged by 2 males with 39 and 45 subcaudals from Volcan Poas, and by the range of subcaudals shown by the Cinchona population.

The range in the number of subcaudals in 4 males from Colombia is 42 to 51, with a mean of 45.8. Three of the four specimens fall within the range of variation shown by Central American populations, and the mean, because of the small sample, is not significantly different from the mean of the more northern populations. Most of the apparent difference between the Central and South American populations is attributable to the single specimen with 51 subcaudals. The single female from Colombia has 39 subcaudals, which falls in the upper part of the range found in Central American females.

The color pattern is the most perplexing variable in *G. brachycephalus*, and is at least partly responsible for the lengthy synonymy presented above. This variability involves both the dorsal and ventral patterns. The original

description stated that the dorsum is blackish, with a light collar and a series of lateral light spots; the latter are imperfectly fused into a longitudinal stripe, extending from the neck to the tail. The ventrals were described as reddish (not in life) with brown margins. In the same paper, Cope described *Colobognathus dolichocephalus* on the basis of a specimen from San Jose, Costa Rica. The latter form also had a series of light lateral blotches, but instead of being fused longitudinally, some of the blotches were fused across the back to form half rings; the ventrals of *dolichocephalus* did not have the brown margins found in *brachycephalus*. One year later, in 1872, Günther described *Geophis moestus* from Cartago, Costa Rica. His specimen was uniformly dark above, with a light collar; Günther (1893:91) later acknowledged that his species and *brachycephalus* were probably identical.

These three nominal forms, described almost simultaneously, encompass the range of variation in coloration herein attributed to a single species, *G. brachycephalus*. The variation includes the presence or absence of a light collar, the presence or absence of lateral blotches, the direction of fusion of the blotches when present, and the presence or absence of dark margins on the ventrals. If the ventrals have dark margins (lateral and anterior edges) the venter is banded in gross appearance; this appearance is retained even when the entire venter is suffused with dark pigment, since the anterior margins are more densely pigmented than the posterior ones.

Variation in the presence or absence of a light collar is both individual and ontogenetic. The collar is basically a juvenile trait, lost ontogenetically by obliteration with dark pigment. At a given snout-vent length, however, some individuals may still show a trace of a collar while others do not. The large series of specimens from Boquete, Panama, illustrates this variability. All 8 specimens with snout-vent lengths of less than 110 mm have at least a trace of the collar; of 11 specimens with snout-vent lengths between 110 and 130 mm, eight show no trace of the collar; of 39 specimens ranging from 151 mm to 289 mm, only three (154 mm, 187 mm, and 207 mm) have any trace of the collar. The same pattern seems to apply at other localities; the collar is generally lost by the time the individual reaches 150 mm, but occasionally persists in larger specimens. The presence or absence of the collar has no relationship to the presence or absence of blotches or of ventral banding.

Variation in the presence or absence of lateral blotches is individual, ontogenetic, and also populational. In the Boquete series, 18 specimens, some of them small juveniles, have no lateral blotches, and 41 specimens have them. On the slopes of Volcan Turrialba in Costa Rica, individual collections, even at the same elevations, differ. Four individuals from about 6000 feet altitude (UMMZ 117715), ranging in snout-vent length from 174

mm to 280 mm, show no sign of lateral blotches. From the same elevation, 6 specimens (CRE 42) from 6.5 miles southeast of Lecheria Central show evidence of ontogenetic loss of the lateral blotches (in this case fused into a lateral band); the lateral band is distinct in 4 specimens measuring 157 mm to 262 mm, faint in one of 296 mm, and absent in one of 301 mm. This inconsistency characterizes many of the samples from localities in Costa Rica; in some samples all of the specimens, including juveniles, are unicolor above, while in others blotches or lateral stripes may or may not be present. The blotched pattern is not known to occur at any of the localities marking the northwestern limit of the known geographic range (Volcan Poas, La Cinchona, La Concordia, Los Cartagos), nor in South America, at the opposite extreme of the range. Small samples from Cot, Carrillo, and Tapanti in Costa Rica, and La Loma in Panama, are without blotches. At least some specimens have lateral markings in samples from such Costa Rican localities as Volcan Barba, V. Irazu, V. Turrialba, La Palma, Las Nubes, San Jose, Cartago, Cervantes, Pacayas, Moravia de Turrialba, and the eastern lowlands, and at Boquete, Finca Lerida, and "Panama Sabanas" in Panama.

In specimens with lateral blotches, several conditions exist. The blotches may be fused longitudinally to form a lateral band; this band may be well defined and extend for most of the body length, or imperfect in that several short bands are interspersed with distinct blotches, or imperfect in that only the ventral parts of adjacent blotches are involved. The blotches in other specimens are fused across the back to form half-rings (generally only some of the blotches actually meet their counterpart from the opposite side). The transverse type of fusion is known to occur at low elevations in eastern Costa Rica (El Tigre, La Emilia, 4 miles south of Turrialba), at San Jose, and at Cartago; the extent to which the latter localities can be taken literally is open to question.

The correlation of dorsal and ventral color patterns is suggestive, but not without contradictions. In Costa Rica, the specimens characterized by transversely fused blotches have clear, light ventrals (with the exception of the lateral edges, which are dark in all *brachycephalus*). In contrast, nearly all of the specimens showing a tendency toward longitudinal fusion of the blotches have banded ventrals; this may involve ventrals with dark anterior margins and light posterior ones, or generally dark ventrals with the pigment distributed more densely along the anterior margin. There are, however, a few "striped" specimens with nearly immaculate ventrals, and at least one of the specimens with a half-ringed dorsal pattern has dark pigment on the anterior edges of the last few ventrals. Specimens with a uniform dorsum may have a clear light venter, a banded venter, or any one of numerous intermediate conditions; in the latter, the anterior ventrals are clear and the posterior banded, but the relative number of each type varies

considerably. Finally, the correlation between dorsal and ventral color patterns breaks down completely in Panamanian populations. Among the blotched specimens from Boquete, for example, the venter varies from nearly immaculate to heavily banded.

REMARKS.—The synonymy adopted here is basically that of Dunn (1942:4), with the following exceptions: (1) I concur with Smith (1958:223) in considering *G. championi* Boulenger, included in the synonymy of *brachycephalus* by Dunn, as a distinct species; (2) *G. nigroalbus* Boulenger, not dealt with by Dunn, is herein placed in the synonymy of *brachycephalus*; and (3) I include in the synonymy *G. bakeri* Taylor, described subsequent to Dunn's work.

In Cope's original description of *brachycephalus* and *dolichocephalus*, the latter name has line priority. I consider as binding, however, Dunn's (1942:4) selection of *brachycephalus* as the name of the species. Dunn's choice was unfortunate in that the type of *dolichocephalus* is larger than the type of *brachycephalus* and in a much better state of preservation than the latter. Cope's description of the type of *dolichocephalus* stated that the dorsal scales were in 13 rows, and that there were 131 ventrals and 39 subcaudals; in contrast, he described the type of *brachycephalus* as having 15 scale rows, 124 ventrals, and 38 subcaudals. At the request of Boulenger, Cope re-examined the type of *dolichocephalus* and reported that it had 15 dorsal scale rows (Boulenger, 1894:320). My counts on the two types confirm Cope's subcaudal counts, but disagree markedly with his ventral counts; I count 138 ventrals in the type of *dolichocephalus* and 135 in the type of *brachycephalus*. These corrections leave only the color pattern as a major difference between the two, and at present I deem the pattern to be too variable to maintain both names. A specimen from Moravia de Turrialba, Costa Rica, combines the elements of both types of pattern. This specimen, UK 31988, has paired lateral blotches on the anterior part of the body; although not actually fused across the back, some of the pairs are very narrowly separated middorsally. Posteriorly, the blotches are broadly separated dorsally, and irregularly fused into a longitudinal stripe.

*G. moestus* Günther, based on a juvenile with a light collar and a uni-color dorsum, cannot be maintained since the color pattern cannot be correlated with other features. *G. bakeri* Taylor was described primarily on the basis of the presence of scale pits, which were previously not known to occur in the genus. The discovery that scale pits are widespread among forms of *Geophis*, and more particularly among all of the forms of immediate concern, deprives *bakeri* of its distinguishing feature. *G. nigroalbus* Boulenger is apparently based primarily on its South American origin. I have not personally examined the type, but there is nothing in the original

description to distinguish *nigroalbus* from *brachycephalus*; furthermore, the four Colombian specimens seen by me are not distinguishable from Central American populations.

In life, the lateral blotches or stripes are orangish-red to brick red; the dorsum bluish-gray to brownish- or bluish-black; the venter flesh white to grayish, with the anterior edges of banded ventrals a darker shade (Taylor, 1951, 1954; Duellman, pers. com.). Taylor (1951:46) noted that two specimens with reddish lateral stripes were collected from beneath logs also utilized by large black leeches with reddish markings. Both the snakes and leeches were coiled into a ball, each occupying separate depressions beneath the logs.

**SPECIMENS EXAMINED** (234).—**COSTA RICA:** No locality: ANSP 3337, BMNH 1907.6.28.4, 1913.7.19.143. **Alajuela:** La Cinchona, UK 31982-84, 35867-91, 35889-904, 63792-96; Volcan Poas, UMMZ 117716-19, 123195. **Cartago:** Cartago, BMNH 71.11.22.21-22, 1946.1.6.53, MVZ 24223, ZMB 25954, 26229; 6.5 mi SW Cartago, UK 31989; Cervantes, UK 30923-24; Cot, UK 30926-27, 31981, 31990-91; Moravia de Turrialba, UK 31998, 63801; Pacayas, UK 30940; Tapanti, UK 63797-800; 4 mi S Turrialba, UK 25732; Volcan Turrialba, south slope, UMMZ 117715 (4); V. Turrialba, 5 mi SE Lecheria Central, CRE 41 (3); V. Turrialba, 5.2 mi SE Lecheria Central, CRE 46 (2); V. Turrialba, 6.5 mi SE Lecheria Central, CRE 42 (6); V. Turrialba, Santa Cruz, CNHM 101016, 101025, UK 25738, 57103; V. Turrialba, 3 mi above Santa Cruz, UK 25735. **Heredia:** Capilla del Monte La Cruz, UK 31993-95; 2.2 km N La Concordia, UK 63802-06; 5 km S Los Cartagos, UK 63807; Volcan Barba, UK 30925. **Limon:** La Emilia, near Guapiles, ANSP 21401; El Tigre, near Siquirres, CRE 290. **San Jose:** Carrillo, MCZ 15322-23; 2 km N Las Nubes, UK 63808, 63810, 63815; 2.6 km N Las Nubes, UK 63813; La Palma, BMNH 95.7.13.8-9, 98.10.8.25, MCZ 15321, UK 35905, 63814; San Isidro de Coronado, ANSP 22434; San Jose, ANSP 3306, MCZ 28070; Volcan Irazu, AMNH 17300, BMNH 90.4.24.6-9, 90.4.24.28, ZMB 26346 (3). **PANAMA:** **Bocas del Toro:** La Loma, MCZ 19325-26. **Chiriqui:** Boquete, ANSP 22422, CAS 78940-75, 78977-79001, UMMZ 57957-58; El Hato, USNM 129382; Finca Lerida, ANSP 21699, 22922-38, 23877-79, 24766-69. **Panama:** Panama Sabanas, ANSP 24723-34. **COLOMBIA:** No locality: CNHM 43727, 54882. **Antioquia:** Santa Rita, BMNH 98.10.27.3. **Santander:** Landazuri, FM 91. **Valle:** Pavas, BMNH 1946.1.6.50.

### *Geophis dunni* Schmidt

*Geophis dunni* Schmidt, 1932:8.

**HOLOTYPE.**—MCZ 31870, an adult female from Matagalpa, Nicaragua; the specimen was removed from the stomach of a coral snake, *Micrurus n. nigrocinctus*.

**DISTRIBUTION.**—Known only from the type locality; 705 meters above sea level.

**DIAGNOSIS.**—Distinguished from other members of the genus by the combination of (1) dorsal scales in 17 rows, distinctly keeled except on neck; (2) no anterior temporal; (3) dorsum with dark brown crossbands on a yellowish ground color; (4) ventrals immaculate, yellowish.

DESCRIPTION.—Head not distinct from neck; snout long, pointed, projecting well beyond lower jaw; rostral moderate, its length one-third its distance from frontal; internasals small, less than half as long as prefrontal suture; prefrontal suture slightly less than half as long as frontal; frontal as long as broad, angulate anteriorly; parietals short, their median suture two-thirds as long as frontal; supraocular forms posterior two-thirds of dorsal margin of orbit; one postocular, higher than long, smaller than supraocular.

Nasal divided, postnasal slightly longer than prenasal, their combined length three-fourths that of loreal; loreal elongate, contained less than twice in snout length, almost twice as long as eye diameter; eye small, contained thrice and a half in snout, its vertical diameter slightly less than its distance from lip; supralabials 6, third and fourth in orbit, fifth largest and in broad contact with parietal; no anterior temporal; one posterior temporal, fused with nuchal along parietal margin.

Mental rounded anteriorly, broader than long, separated from chinshields by first pair of infralabials; infralabials 8, pairs 1–4 in contact with anterior chinshields; anterior chinshields longer than broad, a third longer than posterior pair; posterior chinshields in contact anteriorly, separated by median gular posteriorly; 2 rows of gulars separate chinshields from first ventral.

Dorsal scales in 17 rows, smooth on nape, distinctly keeled on rest of body; paired apical pits present. Ventrals in single female, 140; anal undivided; subcaudals, 36. Ventrals plus subcaudals, 176. Total length, 367 mm; tail, 57 mm (15.5%).

Maxilla extends anteriorly to level of supralabial 2; anterior extension about equal to that of palatine; maxilla dorsoventrally compressed, bears 12 curved teeth, subequal in length; anterior tip of maxilla pointed, toothless; posterior end of maxilla curves ventrally, tapers to blunt point; anterior end of ectopterygoid single, not expanded; postorbital bone present.

Hemipenial characteristics unknown.

Dorsum of head dark brown; a broad yellowish collar occupies posterior parts of parietals, supralabials 5 and 6, and first 3 or four rows of scales behind head; collar heavily suffused with brown anteriorly; ground color of dorsum pale yellowish, most scales narrowly edged with brown; 24 dark brown saddles on body, not reaching ventrals; 3 additional half-saddles, two of which are narrowly connected to adjacent saddles at midline; dark saddles on tail irregular near tip; first saddle behind head seven scales in length, others 2–4 scale lengths. Mental and infralabials 1–5 mottled with brown; rest of chin and all ventrals immaculate, pale yellowish; subcaudals yellowish; a few small brownish spots near tip of tail.

SPECIMEN EXAMINED (1).—NICARAGUA: *Matagalpa*: Matagalpa, MCZ 31870.



*Geophis hoffmanni* (Peters)

*Colobognathus hoffmanni* Peters, 1859:276, pl., fig. 2.

*Elapoides hoffmanni*, Jan, 1862:22; Jan and Sordelli, 1865: livr. 12, pl. 2, fig. 3.

*Geophis hoffmanni*, Bocourt, 1883:529; Boulenger (in part), 1894:319.

*Rhabdosoma bicolor*, Cope (in part), 1885a:385; Cope (in part) 1887:85.

*Geophis chalybeus*, Günther (in part), 1893:87.

*Catostoma hoffmanni*, Amaral, 1929:192.

*Geophis bartholomewi* Brattstrom and Howell, 1954:120 (type, CAS 91202, Nicaragua, Nueva Segovia Prov., Arenal).

*Geophis acutirostris* Taylor, 1954:691, fig. 3 (type, UK 34670, Costa Rica, Cartago Prov., Cot).

HOLOTYPE.—Eight syntypes, ZMB 1868–70 (5), 4003, 4106 (2) from “Costa Rica,” and one syntype (BMNH 1946.1.6.54) from “Porto Caballo,” Costa Rica. ZMB 1870 is herein designated as lectotype.

DISTRIBUTION.—Known from low and moderate elevations in Honduras (Smith and Smith, 1964:72) and Nicaragua, southward along both Caribbean and Pacific versants of Costa Rica into Panama.

LECTOTYPE DESIGNATION.—The original description of *hoffmanni* is obviously not based on a single individual. None of the syntypes agree with all of the characters listed or shown on the figure accompanying the description. Dunn (1942:4) stated that he had examined the type, which he gave as ZMB 4003. He gave no indication that there was a series of syntypes, and did not state that he was designating a lectotype. ZMB 4003 is objectionable as a lectotype for several reasons. It clearly is not the specimen illustrated by Peters, as it has a peculiar deformation (an azygous scale perforated by a nostril-like opening) between the anterior tips of the prefrontals, and a fusion of the third and fourth supralabials, neither of which is present on the pictured specimen.

Peters' description and illustration provide the following pertinent information: “Ganze Länge,” 245 mm; head, 10 mm; tail, 42 mm; ventrals, 127; subcaudals, 33; supraocular (at least on left) separated from postocular by parietal. If “Ganze Länge” means total length, ZMB 1870 is the closest syntype at 254 mm. However, its tail length is only 35 mm. In describing other new snakes in the same paper, Peters used the term “Totallänge,” and it is therefore likely that “Ganze Länge” was used differently. It also seems likely to me that Peters gave the measurements of the largest syntype, which is ZMB 4003. My measurements of 4003 are: total length of 295 mm, and tail length of 40 mm. When totalled, Peters three measurements equal 297 mm, and probably represent ZMB 4003.

The ventral and subcaudal counts given by Peters clearly are the counts of a male specimen, and cannot be reconciled with the female counts of ZMB 4003 and 1870 (135, 28 and 132, 28, respectively). Three male syn-

types have counts similar to those of Peters, but the largest of the three is only 101 mm in total length, much less than the length given by Peters.

The separation of the supraocular and postocular by the parietal is quite common in the series, but occurs on the left side (the side shown in Peters' illustration) on only three (BMNH 1946.1.6.54, ZMB 1869b, 4003). None of these fits the type description in all essentials. I have examined the eight syntypes in the Berlin collection, and the British Museum syntype has been examined in my behalf. It is clear that the composite description of *hoffmanni* applies to no single specimen, and I therefore feel justified in selecting a lectotype based on considerations other than agreement with the description. I believe the best choice is ZMB 1870, a well-preserved adult female (total length, 254 mm; tail, 35 mm; ventrals, 132; subcaudals, 28) whose features are representative of the species as a whole. The lone unusual condition exhibited by 1870 is the extension of the parietal between the supraocular and postocular, a condition which is not unique to this specimen.

**DIAGNOSIS.**—Distinguished from other members of the genus by the combination of (1) dorsal scales in 15 rows, smooth except above the vent region; (2) five supralabials, the fifth very large; and (3) uniform dark dorsal coloration (a light collar in juveniles).

**DESCRIPTION.**—Head scarcely distinct from neck; snout long, pointed, projecting well beyond lower jaw; rostral moderate, its length one-third or less its distance from frontal; internasals broader than long, about half as long as prefrontal suture; prefrontal suture one-half as long as frontal; frontal slightly broader than long, angulate anteriorly; parietals short, their median suture one-half to two-thirds as long as frontal; supraocular small, forms posterior half of dorsal margin of orbit, curves ventrally along posterior margin; one postocular, smaller than, or as large as, supraocular.

Nasal divided, postnasal slightly longer than prenasal, their combined length less than that of loreal; loreal elongate, contained almost twice in snout length, twice as long as eye; eye small, contained almost four times in snout, its vertical diameter three-fourths its distance from lip; supralabials 5, third and fourth in orbit, fifth very large, in broad contact with parietal; no temporals.

Mental broader than long, acuminate anteriorly, separated from chinshields by first pair of infralabials; infralabials 6, pairs 1–3 in contact with anterior chinshields; anterior chinshields longer than broad; posterior chinshields as long as anterior pair, often separated throughout length by median gular; 2–3 rows of gulars separate chinshields from first ventral.

Dorsal scales in 15 rows, smooth except above vent; scales above vent keeled, bear paired apical pits. Ventrals in 32 males, 117–130 (124.5); in

37 females, 122–135 (131.5); anal undivided; subcaudals in 30 males, 28–37 (32.2); in 34 females, 24–32 (28.2). Ventrals plus subcaudals, 147–168. Total length of largest male, 233 mm; tail, 36 mm (15.5%); largest female, 300 mm; tail, 40 mm (13.3%).

Maxilla extends anteriorly to suture between supralabials 2 and 3; anterior extension about equal to that of palatine; maxilla dorsoventrally compressed, bears 8–10 subequal teeth; anterior tip of maxilla pointed, toothless; posterior end of maxilla curves ventrally, tapers to blunt point; anterior end of ectopterygoid single, not expanded; postorbital bone present.

Hemipenis extends to level of subcaudal 6; basal part of hemipenis bears numerous spicules and, distally, 2–3 moderate spines; basal naked pocket weakly developed. Central part of organ bears numerous spines in oblique rows. Distal part of hemipenis capitate, spinulate, calyculate; apex slightly bilobed. *Sulcus spermaticus* bifurcates opposite subcaudal 4, each branch reaches apex. *M. retractor penis magnus* divides into two slips at apex of hemipenis.

Dorsum of head and body uniformly dark brownish or grayish-black; a yellowish collar present in small juveniles, obliterated ontogenetically by dark pigment; scales of first dorsal row yellowish-white, mottled with brown or gray. Peripheral scales of chin region mottled with dark pigment; ventrals yellowish-white, immaculate or with dark pigment on anterior edges; subcaudals yellowish, edged with brownish-black.

VARIATION.—The scales bordering the orbit are particularly variable in *G. hoffmanni*. The loreal, normally entering the orbit, is excluded from the margin of the orbit by a contact of the prefrontal and supralabial 3 in seven of the 73 specimens examined. Eight specimens vary from the normal condition of one postocular on each side (two have 0–0, two 0–1, and four 1–2). In addition, the postocular is reduced in size and separated from the supraocular by an extension of the parietal in 10 specimens. In the two with the number of supralabials reduced from five to four, the reduction is the result of fusion of the third and fourth labials, leaving only the composite scale forming the ventral margin of the orbit.

The dorsal aspect of the head is less variable, but one of the variations resulted in the description of *Geophis acutirostris* by Taylor in 1954. The type of *acutirostris* is peculiar in several aspects, but I am nonetheless convinced that its peculiarities are merely aberrations, and do not represent specific differentiation. The major features used by Taylor in his diagnosis of *acutirostris* were the absence of internasals and the fusion of the postocular with the supraocular. Taylor suggested that the internasals were fused with the prenasals, since the latter scales extend dorsomedially as a wedge between the rostral and prefrontals. I disagree with this explanation, and believe that the internasals are fused with the prefrontals. The dorso-

medial extension of the prenasal is characteristic of *hoffmanni*, although usually to a lesser extent than on the type of *acutirostris* (UK 34670). The *acutirostris* condition is closely approached by UK 35855, from San Jose, Costa Rica, which has the internasals fused with the prefrontals, and the prenasals extending well toward the midline of the head, but no supra-ocular-postocular fusion. The postocular is absent on other specimens of *hoffmanni* and cannot be assigned diagnostic importance among snakes commonly exhibiting fusion between various head scales. I have examined the type of *acutirostris* and in all other respects it agrees with *hoffmanni*. I conclude that the name *acutirostris* is a synonym of the latter species.

Variation in color pattern occurs ontogenetically and individually. Juvenile specimens have a light collar involving the posterior ends of the parietals and the first few rows of neck scales. The collar is the same color as the venter, but is rather quickly suffused by dark pigment ontogenetically until the uniformly dark dorsum of the adults is attained. The variation in ventral coloration is not associated with age or geographic considerations. The variation involves the amount of dark pigment on the ventral scales. Normally the venter is immaculate, but occasionally the dark dorsal pigment extends onto the lateral edges of the ventrals, forming a narrow bar along the anterior margin of the ventral. This usually is more pronounced on the posterior part of the body. Only rarely does the pigment reach the midline of the ventral surface.

In addition to sex-dependent differences, the number of ventrals and, to a lesser extent, the number of subcaudals show significant geographic variation. The greatest variation occurs at the periphery of the range of the species. Specimens from both the northern (Nicaragua) and southern (Panama) extremes of the range have fewer ventrals and subcaudals than Costa Rican specimens. The range in ventrals of 28 Costa Rican males is 118–130 (mean, 125.4), and in 3 Panamanian males 117–119 (118.3). Ventrals range from 125–138 (131.6) in 36 Costa Rican females, 122–125 (123.7) in 3 Nicaraguan females, and 126 in the single Panamanian female. The subcaudals show a less pronounced, but similar, tendency.

*Geophis bartholomewi* was described on the basis of one of the three Nicaraguan specimens. The authors stated that it differed from *hoffmanni* in the low number of subcaudals (14), the smoothness of all scales, the absence of any dark pigment on the ventrals, and the contact of four (instead of three) infralabials with the chinshields. I have examined the type of *bartholomewi* and found that the tail is obviously incomplete (confirmed by radiograph), thus accounting for the low subcaudal count. The scales above the vent region are lightly keeled as in *hoffmanni*. Immaculate ventrals are the usual condition in *hoffmanni* as well as in the type of *bartholomewi*. Finally the type does have 4 infralabials in contact with

the chinshields, but only 3 in contact with anterior chinshields, just as in *hoffmanni*. There remains the possibility (as suggested by Brattstrom and Howell) that *bartholomewi* is worthy of subspecific status, based on lower ventral and subcaudal counts. However, the number of Nicaraguan specimens now available (3, one with an incomplete tail) is insufficient to clearly demonstrate these differences, and I see no advantage in recognizing these few specimens with a trinomial. The situation in Panama is comparable, with the few available specimens suggesting some degree of differentiation.

Within Costa Rica, there is some evidence that the eastern lowland populations are somewhat different from those of the western lowland. No differences are evident in the few female specimens from these two areas, but in males, the range of ventrals in 4 from the eastern lowland (118–125) does not overlap the range of 3 from the western lowland (126–130). The bulk of the available Costa Rican specimens come from the central plateau and the adjacent slopes of the Cordillera Volcanica. The range of ventrals in males from these regions is 120–130.

REMARKS.—The reduction to five supralabials in this species is not the result of scale fusion, and therefore is not comparable to the condition in *G. semidoliatus*. In *hoffmanni*, the reduction appears to be an indirect result of the narrowing of the gape and corresponding shortening of the jaw. Posterior to the large fifth labial of *hoffmanni* is a scale similar in size and shape to the sixth labial of other species, but this scale no longer borders the free edge of the lip. Between this labial-like scale and the parietal is a scale corresponding to the posterior temporal of other *Geophis*. Only about one-half of this scale lies anterior to a line drawn from the posterior edge of the fifth labial to the posterior tip of the parietal.

In life, the dorsal coloration is bluish-black and the light ventral parts are whitish (Taylor, 1951:42).

Smith and Smith (1964:72) reported a specimen of *G. hoffmanni* from 10 miles east of Dulce Nombre de Culmi, Depto. Olancho, Honduras. Since I have not examined the specimen, this locality is not included in Figure 20. This locality represents the northern extreme of the known range of the species, and is not unexpected, since the species is known from neighboring Nicaragua. The specimen (UI 53021) is an adult female with 122 ventrals and 25 subcaudals.

SPECIMENS EXAMINED (73).—NICARAGUA: **Matagalpa:** Matagalpa, Hacienda La Cumplida, UMMZ 117653. **Nueva Segovia:** Arenal, CAS 91202, UCLA 14784. COSTA RICA: No locality: ANSP 23046, USNM 6358 (2), ZMB 1868–70 (5), 4003, 4106 (2). **Cartago:** Cartago, UK 25737, 35856–58, 35866, USNM 76130; Cot, UK 34670; Monte Redondo, BMNH 95.7.13.10; Navarro, MCZ 15301; Pacayas, UK 30930; Turrialba, CRE 329, MCZ 56100–01, UK 30929; Turrialba, La Hulera, CRE 569. **Guanacaste:** Miravalles, MCZ 15267; Tenorio,

UK 31986. **Heredia:** Santo Domingo, UMMZ 117712-13. **Limon:** Batan, UI 30928; Guapiles, ANSP 22370; La Lola, UMMZ 117714; Suretka, MCZ 19327-28. **Puntarenas:** Puntarenas, MVZ 24229; (?) Porto Caballo, BMNH 1946.1.6.54. **San Jose:** El Cerrito, CRE 514; Guadalupe, UK 63811; Moravia, MCZ 55119, UMMZ 117603; La Palma, MCZ 15271; San Isidro del General, UK 25736, 31985; 2 mi W San Isidro del General, CNHM 101024; 15 km WSW San Isidro del General, UK 35859-63; San Isidro de Perez Zeledon, ANSP 22433; San Jose, ANSP 3305, UK 35855, 35864-65, UMMZ 83176-79, USNM 75034; ca. 5 km NW San Jose, AMNH 89170; San Pedro de Montes de Oca, UK 63812, 63817; Tiribi, CRE 242. **PANAMA:** **Chiriqui:** Boquete, CAS 78976, 79033, UMMZ 57955-56. **Cocle:** El Valle de Anton, AMNH 76016.

*Geophis nasalis* (Cope)

*Catostoma nasale* Cope, 1868:131, fig.

*Elapoides sieboldi*, Müller, 1882:142.

*Geophis chalybeus*, Bocourt (in part), 1883:530; Günther (in part), 1893:87; Boulenger (in part), 1894:318.

*Rhabdosoma nasale*, Cope, 1885a:385; Cope, 1887:85.

*Catostoma chalybeum*, Amaral (in part), 1929:191; Slevin, 1939:404.

*Geophis nasalis*, Smith, 1941b:4; Smith and Taylor, 1945:69; Stuart, 1963:100.

**HOLOTYPE.**—Originally at least four syntypes: ANSP 3319-21, near the city of Guatemala, Guatemala; USNM 12425A, "Guatemala" (but probably also from near the city); Van Patten, collector. ANSP 3320, an adult female, is herein designated as lectotype.

**DISTRIBUTION.**—Known from the Pacific versant of Chiapas, Mexico, and Guatemala, and adjacent parts of the Guatemalan Plateau and South-eastern Highlands in eastern Guatemala; 600-1500 meters above sea level; a snake of the "coffee zone."

**DESIGNATION OF A LECTOTYPE.**—The precise number of specimens in Cope's possession when he wrote the original description of the species is not known. Cope reported "several" specimens received from Van Patten, gave the ventral counts of three, and length measurements of the largest. I cannot duplicate Cope's segmental counts, nor his measurements, on any of the syntypes. Nonetheless, ANSP 3319-21 surely form the basis of at least some of the segmental counts. None of these could be the one from which the measurements were obtained; the tail length recorded by Cope far exceeds that of any of the three. USNM 12425A, with a tail length of 51 mm (Cope said "2 in."), appears to be the largest individual mentioned in the description. The possibility remains that more than four specimens were involved.

Of the four known syntypes, none fits the description or the illustration better than any one of the other three. Inexplicably, the description states that there are 8 supralabials, the illustration shows seven, and the specimens have six; in fact, none of the more than 300 specimens examined has more than 6 supralabials. The syntypes are similar in scutellation; except for

sexual differences in segmental counts, the only variation is the presence of 6 infralabials (instead of 7) in USNM 12425A. Since there is little to recommend any one specimen over the others, I have arbitrarily chosen ANSP 3320 as lectotype. It is an adult female with 135 ventrals, 25 subcaudals a total length of 293 mm, and a tail length of 37 mm. ANSP 3319, ANSP 3321, and USNM 12425A are paralectotypes.

**DIAGNOSIS.**—Distinguished from other members of the genus by the combination of (1) dorsal scales in 17 rows, distinctly keeled except on neck; (2) no anterior temporal; (3) combined length of pre- and postnasal distinctly less than that of loreal; (4) sum of ventrals and subcaudals 142–172; (5) dorsum brown or gray; and (6) ventrals light, not strongly banded.

**DESCRIPTION.**—Head not distinct from neck; snout long, pointed, projecting well beyond lower jaw; rostral moderate, not extending posteriorly between internasals, its length less than one-third its distance from frontal; internasals small, much broader than long, less than half as long as prefrontal suture; prefrontal suture more than half as long as frontal; frontal as long as broad, sharply angulate anteriorly; parietals short, their median suture two-thirds as long as frontal; supraocular moderate, subtriangular, forms slightly more than posterior half of dorsal margin of orbit; one postocular, higher than long, slightly smaller than supraocular.

Nasal divided, postnasal slightly longer than prenasal, their combined length less than three-fourths that of loreal; loreal very long, contained less than twice in snout length, twice as long as eye; eye small, contained four times in snout, its vertical diameter slightly less than its distance from lip; supralabials 6, third and fourth in orbit, fifth largest and in broad contact with parietal; no anterior temporal; one posterior temporal; usually fused with nuchals along parietal margin.

Chin tapered, but not pointed; mental rounded anteriorly, broader than long, separated from chinshields by first pair of infralabials; infralabials 7, pairs 1–3 in contact with anterior chinshields (variable); anterior chinshields short, broad; posterior chinshields smaller than anterior pair, often separated throughout their length; 2–3 rows of gulars separate chinshields from first ventral.

Dorsal scales in 17 rows, smooth on neck, distinctly (usually strongly) keeled on posterior three-fourths of body and basal half of tail; scales striated, bear conspicuous paired apical pits. Ventrals in 175 males, 115–130; in 143 females, 118–142 (see *Variation* for details of ventral counts); anal undivided; subcaudals in 169 males, 29–37 (32.1); in 141 females, 23–33 (26.6). Ventrals plus subcaudals, 142–172. Total length of largest male, 343 mm; tail, 58 mm (16.9%); largest female, 350 mm; tail, 52 mm (14.9%).

Maxilla extends anteriorly to suture between second and third supra-

labials; anterior extension about equal to that of palatine; maxilla dorso-ventrally compressed, bears 11–13 short, curved teeth; teeth subequal in length; anterior tip of maxilla pointed, toothless; posterior end of maxilla curves ventrally, tapers to blunt point; anterior end of ectopterygoid single, not expanded; postorbital bone present.

Hemipenis extends posteriorly to level of subcaudal 9; basal part of organ bears numerous spinules and, distally, two medium spines; naked basal pocket well developed, on antisulcus side. Central part of hemipenis bears about 25 medium spines and hooks. Distal part of organ capitate, weakly calyculate, spinulate; apex slightly bilobed. *Sulcus spermaticus* bifurcates opposite subcaudal 6; each branch reaches apex. *M. retractor penis magnus* divides into two slips at apex of hemipenis.

Dorsum of head and body dark brown or gray, darkest middorsally, paler laterally; individual scales on body darkest along anterior edges; scales in first row pale posteriorly, but gross appearance of row not a series of light spots. Anterior part of chin dark brown, posterior parts yellowish-white; ventrals white or yellowish-white, edged laterally with brown, otherwise immaculate or with faintly brownish anterior edge; subcaudals light, mottled or edged with brown.

VARIATION.—The most variable head scales are the infralabials. The modal number of seven is decreased to six on at least one side of 13 specimens, and is increased to eight in 45 specimens. In contrast, the supralabial number is reduced from six to five in but a single specimen among the 323 examined. The postocular is fused with the supraocular in 3 specimens, and divided into two postoculars in the same number. The prefrontals are partially fused in UMMZ 120447; the normal suture is present anteriorly, but absent posteriorly. UMMZ 89217 has a divided anal plate, the only known example of this condition within the genus. Subcaudals 2–12 are undivided in UMMZ 107022.

Geographic variation occurs in the segmental counts (Fig. 22). The observed range in the number of ventrals in specimens from the eastern part of the geographic range (specifically, from the Antigua Basin, the Guatemalan Plateau, and the southeastern highlands) does not overlap that of specimens from the Pacific versant of western Guatemala and Chiapas. This difference does not apply to the number of subcaudals. Various populations along the Pacific versant from Chicharras, Chiapas, to Yepocapa, Guatemala, show little variation in segmental counts. A notable exception occurs at Finca La Paz, Depto. San Marcos, Guatemala; although the observed ranges overlap widely, the Finca La Paz population averages a higher number of ventrals than other populations along the Pacific slopes.

Specimens from the Antigua Basin are much less strongly keeled than those from the Pacific versant. The syntypes, from the eastern part of the



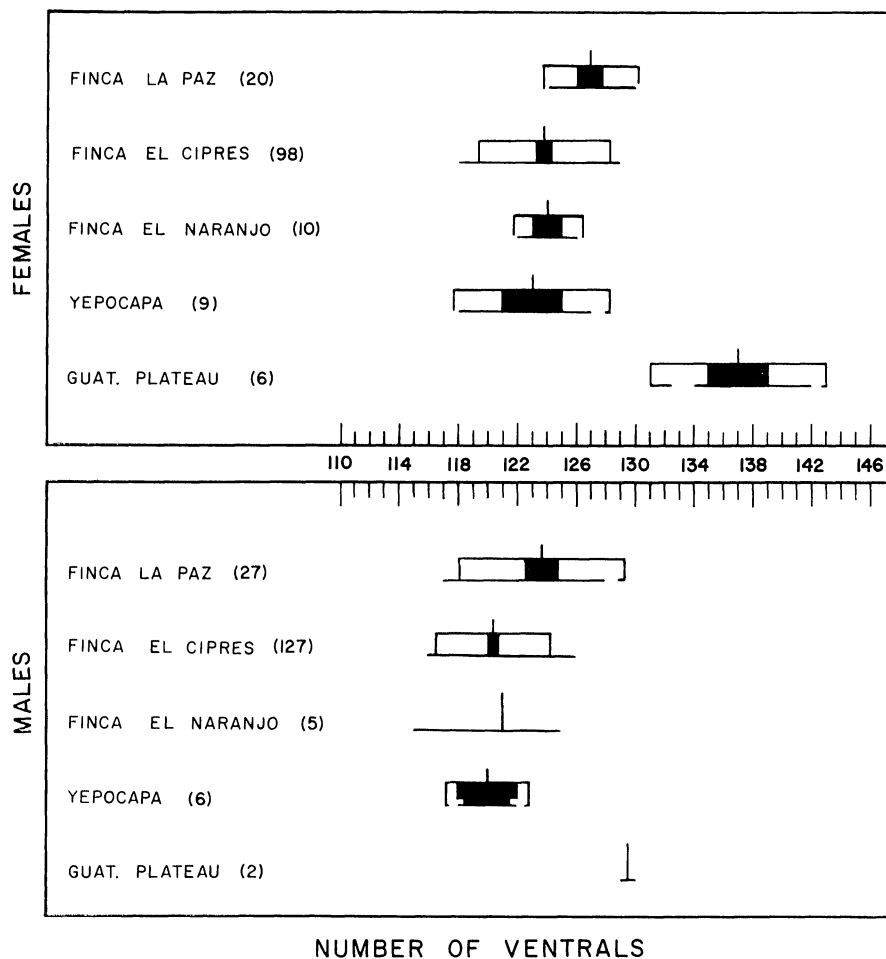


FIG. 22. Variation in the number of ventrals in *G. nasalis* from several localities in Guatemala. The Guatemalan Plateau category includes specimens from the Antigua Basin, the vicinity of Guatemala City, and the southeastern highlands of Guatemala; the other four localities are on the Pacific versant of the southwestern highlands. Horizontal line, observed range; vertical line, sample mean; large rectangle, twice the standard deviation on each side of the mean; black rectangle, 95% confidence limits of the mean.

Guatemalan Plateau, appear to be intermediate. A single specimen from the southeastern highlands of Guatemala, although agreeing with the Antigua Basin and Plateau specimens in having a high number of ventrals, is closer to the Pacific versant populations in the development of the keels.

REMARKS.—*G. nasalis* is apparently quite common in areas with extensive ground litter, such as within coffee plantations. Slevin's (1939:404) series of

217 specimens from Finca El Cipres, at the base of Volcan Zunil in Guatemala, is testimony to the population density reached in such an area. These specimens were collected from piles of debris in the cafetal. Slevin's series of specimens has been utilized by Klauber (1943) in a study of sexual dimorphism, and by Dunn (1947) in a comparison of the ophidian faunas of two geographically separated coffee fincas. The large series is actually composed of material collected during 1924 and 1926. The 1926 specimens were collected between May 25 and July 3; the 1924 collection between July 20 and August 29. The size frequency distribution, when the series is considered as a unit, is bimodal, with peaks at about 150 mm (snout-vent) and 200 mm. More information is obtained, however, by plotting the size distributions of the two collections separately (Fig. 23). The earlier collection (May 25–July 3) shows two disjunct size groups; one centers around 100 mm, and clearly represents the young of the year. In the later collection, which on the average was made two months after the first (although in different years), the size distribution is strongly bimodal, but the disjunct group of small juveniles is absent. It is clear that rapid growth of the young has eliminated the gap noted in the May 25–July 3 collection.

Slevin (1939:404) gave the color of the dorsum in living material as a silvery-gray; some specimens, particularly juveniles, were darker.

**SPECIMENS EXAMINED** (326).—**MEXICO: Chiapas:** Cacahuatan, UI 5650; Chicharras, USNM 46611; probably Chicharras, USNM 46613. **GUATEMALA:** No locality; AMNH 63376–77, USNM 12425A. **Chimaltenango:** near Pochute, Finca Santa Emilia, MCZ 31944; Yepocapa, UMMZ 107288–91, 107295, USNM 127963–65; Yepocapa, Aldea Buena Vista, UMMZ 107022; Yepocapa, Finca El Recreo, UMMZ 107019–20, 107292–94; Yepocapa, Rio Pena Blanca, UMMZ 107021; Yepocapa, San Pedro, UMMZ 107018. **Guatemala:** near Guatemala City, ANSP 3319–21. **Sacatepequez:** La Antigua, UMMZ 89217; Duenas, BMNH 64.1.26.150 (2). **San Marcos:** El Porvenir, CNHM 20352–56, 20379; 2 km NW La Reforma, Finca La Paz, UMMZ 98311–13, 106675–79 (34), 107283–87, 120448 (5). **Santa Rosa:** Finca El Progreso, UMMZ 120447. **Solola:** Olas de Moca, CNHM 20422–23; Finca Santo Tomas, UMMZ 107296. **Suchitepequez:** W slope Volcan Santa Clara, Finca El Naranjo, UI 46104–18; Volcan Zunil, Finca El Cipres, CAS 66508–724, 66778, MCZ 22110–16.

### *Geophis petersi* Boulenger

*Geophis petersi* Boulenger, 1894:321, pl. 16, fig. 2; Smith and Taylor, 1945:69.

*Geophis chalybaea*, Günther (in part), 1893:87.

*Catostoma petersi*, Amaral, 1929:192.

**HOLOTYPE.**—Originally two syntypes, BMNH 1946.1.6.31–32, stated to have been collected by Doorman in the City of Mexico, Mexico. The type locality has been restricted to Patzcuaro, Michoacan, Mexico, by Smith and Taylor (1950:335; see *Remarks*). BMNH 1946.1.6.31 is herein designated as lectotype.

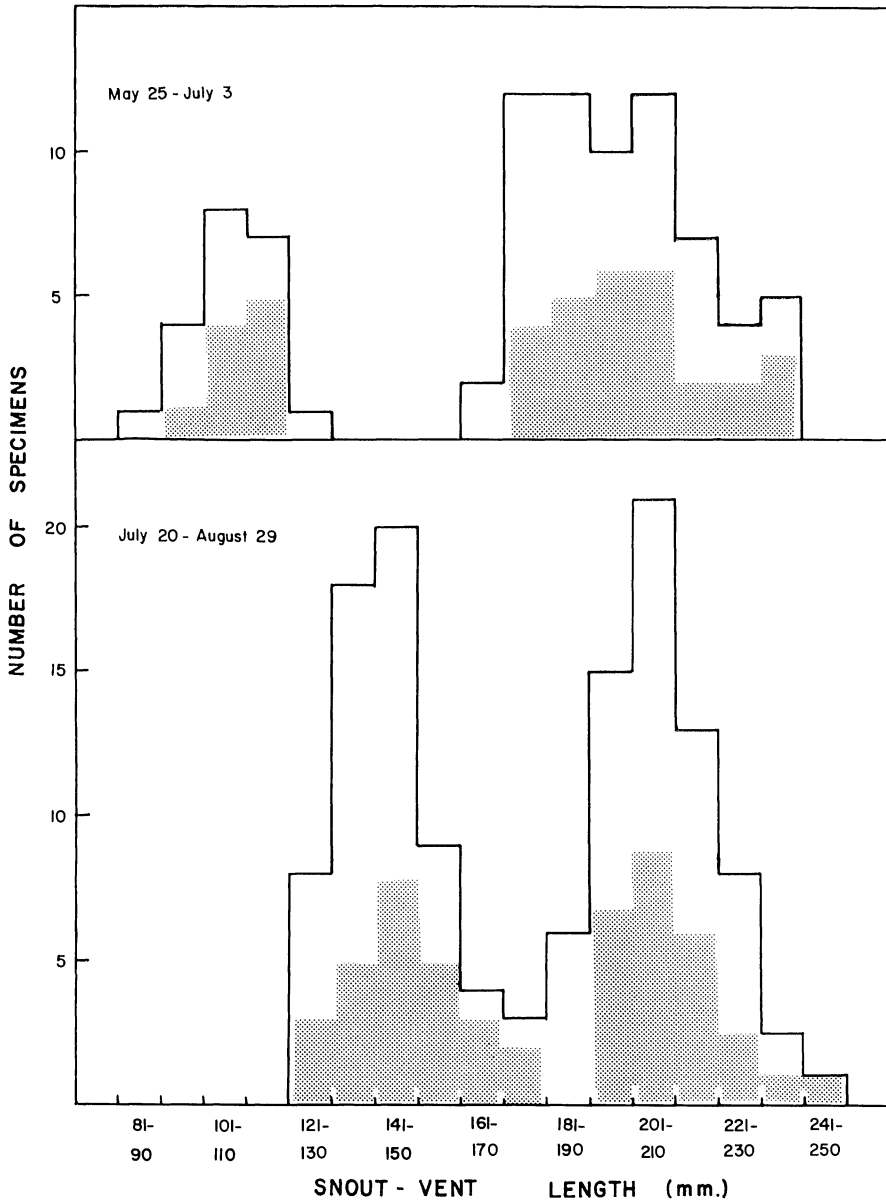


FIG. 23. Size frequency histogram for *G. nasalis* from Finca El Cipres, Volcan Zunil, Guatemala. Histogram based on CAS 66508-724, collected May 25-July 3, 1926, and July 20-August 29, 1924. Stippled areas represent females. See text for explanation.

**DISTRIBUTION.**—Known from the southern edge of the Mexican Plateau in Michoacan, Mexico, and from the questionable type locality (City of Mexico); 1800–2000 meters above sea level, in pine and pine-oak forest.

**DESIGNATION OF A LECTOTYPE.**—The illustrations provided by Boulenger show a specimen in which the anterior chinshields are of unequal size; this feature clearly indicates that BMNH 1946.1.6.31 is the specimen figured. The specimen is a male with 144 ventrals, 36 subcaudals, a total length of 208 mm, and a tail length of 29 mm. The linear measurements are slightly greater than those presented by Boulenger (200 mm, 28 mm, respectively), but are much closer to Boulenger's measurements than are the measurements of the second syntype (total length, 166 mm). BMNH 1946.1.6.31 is therefore designated as lectotype.

**DIAGNOSIS.**—Distinguished from other members of the genus by the combination of (1) dorsal scales in 15 rows, smooth except above the vent region; (2) no anterior temporal; (3) total ventrals and subcaudals more than 175; (4) loreal about equal to length of nasals; (5) six supralabials; and (6) dark above, light below.

**DESCRIPTION.**—Head scarcely distinct from neck; snout long, bluntly pointed from above, projecting well beyond lower jaw, rostral prominent, its length from above one-half or more its distance from frontal; rostral projects posteriorly between anterior parts of internasals; internasals broader than long, rounded anteriorly, their maximum length slightly less than length of prefrontal suture; prefrontals short, their median suture less than half as long as frontal; frontal a little broader than long, distinctly pointed anteriorly; parietals short, broad, their median suture one-half to two-thirds as long as frontal; supraocular small, forms posterior half of dorsal margin of orbit; one postocular, higher than long, as large or larger than supraocular.

Nasal divided, postnasal half again as long as prenasal, their combined length about equal to that of loreal; loreal less than half as long as snout, nearly twice as long as eye diameter; eye small, contained more than thrice in snout, its vertical diameter three-fourths its distance from lip; six supralabials, third and fourth in orbit, fifth largest and in contact with parietal; anterior temporal absent; one posterior temporal, separates sixth labial from parietal.

Mental broader than long, acuminate anteriorly, separated from chinshields by first pair of infralabials; infralabials 6, pairs 1–3 in contact with anterior chinshields; anterior chinshields short, broad; posterior chinshields smaller than anterior pair, separated for most of length by median gular, occasionally scarcely distinguishable from gulars.

Dorsal scales in 15 rows, smooth on most of body, faintly keeled above

vent; no paired apical pits (?). Ventrals in five males, 140–148 (143.8); in four females, 145–148 (146.8); anal single; subcaudals in five males, 34–38 (36.8); in four females, 29–38 (34.5). Total ventrals plus caudals, 177–186. Total length of largest male, 348 mm; tail, 55 mm (15.8%); largest female, 281 mm; tail, 35 mm (12.5%).

Maxilla extends anteriorly to suture between second and third supralabials; anterior extension about equal to that of palatine; maxilla short, dorsoventrally compressed, bears 6 strongly curved teeth, decreasing in length posteriorly; anterior fifth of maxilla toothless; posterior end of maxilla tapers to blunt point, not laterally compressed; anterior end of ectopterygoid single, not expanded; postorbital bone present.

Hemipenis extends posteriorly to level of subcaudals 6–8; basal part of organ bears minute spines, a naked pocket on antisulcus side, and four larger spines distally. Central part of organ bears more than fifty medium spines. Distal part of hemipenis capitate, calyculate, papillate; capitulum slightly bilobed at tip. *Sulcus spermaticus* bifurcates opposite caudals 4–5. *M. retractor penis magnus* divides into two slips at apex of hemipenis.

Dorsal coloration brownish, darkest on middorsal parts of head and body; lateral parts of head and lateral rows of dorsals pale yellowish-brown; posterior edges of dorsals darker than anterior parts. Chin whitish, immaculate or faintly mottled with brown; ventrals and subcaudals immaculate whitish.

VARIATION.—Hartweg (1959:4) has remarked on the variability of the head scales in this species, noting particularly the variation in the number of gular rows (1–4) separating the chinshields from the first ventral and the variation in the presence or absence of contact between the posterior chinshields. In addition, the number of supralabials is reduced to five on the left side of UMMZ 114493 as the result of a rather complex fusion; the anterior part of the normal third labial is fused with the second labial, which is therefore much longer than usual; the posterior part of the normal third labial is fused with the fourth labial, which becomes the third labial and is the only labial in the orbit; this condition requires not only the failure of the sutures between the second and third and between the third and fourth labials to develop, but also the appearance of a new suture near the middle of the third labial. The fifth and sixth labials are partially fused on the left side of CNMH 105714; the same specimen has the internasals partially fused with the prefrontals. In CNHM 105713 the posterior temporal is absent; both the fifth and sixth labials are in contact with the parietal.

REMARKS.—Although *G. petersi* has not been rediscovered in the vicinity of Mexico City, I see little justification in the restriction of the type locality

to Patzcuaro, Michoacan, by Smith and Taylor (1950:335). The species is still too poorly known to deny its presence along the edge of the Mexican Plateau beyond the limits of Michoacan. *Diadophis dugesi*, which probably is similar in habits to *G. petersi*, and occurs in the same type of habitat, is known from near Mexico City and is sympatric with *petersi* in Michoacan. It seems reasonable at least to admit that *petersi* may have the same distributional pattern. As long as this admission remains reasonable, the arbitrary designation of a new type locality is unwarranted.

Duellman (1961:98) incorrectly included a specimen from Coalcoman, Michoacan, under the name *petersi*. This specimen, UMMZ 104698, was previously referred to *G. nasalis* by J. A. Peters (1954:22), who noted several differences between the Coalcoman specimen and Guatemalan *nasalis*, and suggested possible subspecific relationships. The poorly known Mexican form, *G. sieboldi*, is similar to *nasalis*, perhaps only subspecifically distinct; I refer the Coalcoman specimen to *sieboldi*, which is basically in agreement with Peters' arrangement. The specimen (and *sieboldi*) differs from *petersi* in having a longer head, longer loreal, less pronounced rostral, greater number of maxillary teeth, fewer hemipenial spines, and other minor details. The difference in the number of scale rows (17 in *sieboldi*, 15 in *petersi*) is bridged by UMMZ 104698, which has 17 rows on most of the body, but 15 rows in some areas; however, where 15 rows are present, the scales of the paravertebral rows are clearly fused with the vertebral row. The fusion results in scales much larger than the other dorsals, indicating that the normal number of scale rows is 17.

SPECIMENS EXAMINED (10).—MEXICO: **Distrito Federal:** City of Mexico, BMNH 1946.1.-6.31-32. **Michoacan:** 7.4 mi WNW Cheran, UMMZ 114493; 15 km W Morelia, UI 17759; near Patzcuaro, CNHM 105725; 4 mi E Patzcuaro, CNHM 105713-14; near Lake Patzcuaro, UI 17760-61; 5 mi E Lake Patzcuaro, CNHM 106916.

#### *Geophis sallaei* Boulenger<sup>5</sup>

*Geophis sallaei* Boulenger, 1894:318, pl. 16, fig. 1; Smith and Taylor, 1945:69.

*Geophis chalybeus*, Günther (in part), 1893:87.

*Catostoma sallaei*, Amaral, 1929:193.

**HOLOTYPE.**—Originally three syntypes (BMNH 1946.1.6.26-27, 1946.1.6.49) from "Mexico," M. Sallé, collector. BMNH 1946.1.6.27 is herein designated as lectotype.

<sup>5</sup> I consider *Geophis laticollaris*, recently described by Smith, Lynch, and Altig (1965), a synonym of *G. sallaei*. The holotype of *laticollaris*, a juvenile female (total length, 139 mm) from 3 miles south of Putla, Oaxaca, is distinguished only by the presence of a light collar and by a relatively larger eye. A light collar is typical of juveniles of several members of the *sieboldi* group; its presence in juvenile *sallaei* is therefore not surprising. Allometry results in an ontogenetic decrease in relative eye size; hence I view the relatively larger eye of the type of *laticollaris* as a juvenile trait. I have examined the type.

**DISTRIBUTION.**—Known only from “Mexico,” “Oaxaca,” and near Pluma Hidalgo, Oaxaca. Smith and Taylor (1950:339) restricted the type locality to Pluma Hidalgo, which is about 1400 meters above sea level. The specimens collected near Pluma Hidalgo were found in a cafetal.

**DESIGNATION OF A LECTOTYPE.**—In the original description, Boulenger presented the total length and tail length of the largest specimen, but otherwise did not distinguish one syntype from another. The largest specimen is not suitable as a lectotype because it is not the specimen illustrated by Boulenger, and because it is not as well preserved as the other syntypes. Boulenger's illustration shows three infralabials in contact with the anterior chinshields on the left, and four in contact on the right. Among the syntypes, this labial condition can apply only to BMNH 1946.1.6.27, which I, therefore, designate as lectotype. The specimen is a female with a total length of 232 mm (tail, 32 mm), 131 ventrals, and 30 subcaudals.

**DIAGNOSIS.**—Distinguished from other members of the genus by the combination of (1) dorsal scales in 15 rows, distinctly keeled except on the neck; (2) no anterior temporal; (3) sum of ventrals and subcaudals, 156–170; (4) prefrontal suture more than three-fourths as long as parietal suture; (5) dorsum grayish-brown to brownish-black, scales of first row with light centers; and (6) ventrals yellowish-white, usually immaculate.

**DESCRIPTION.**—Head scarcely distinct from neck; snout long, pointed, projecting well beyond lower jaw; rostral moderate, not strongly produced posteriorly between internasals, its length one-third or less its distance from frontal; internasals small, much broader than long, less than half as long as prefrontal suture; prefrontals long, their median suture about two-thirds as long as frontal, more than three-fourths as long as parietal suture; frontal as broad or broader than long, angulate anteriorly; parietals short, broad, their median suture three-fourths as long as frontal; supraocular small, forms scarcely more than half of dorsal margin of orbit; one postocular, much higher than long, smaller than supraocular.

Nasal divided, postnasal slightly longer than prenasal, their combined length less than three-fourths that of loreal; loreal elongate, contained less than twice in snout length, more than twice as long as eye diameter; eye small, contained about four times in snout, its vertical diameter three-fourths its distance from lip; supralabials 6, third and fourth in orbit, fifth largest and in broad contact with parietal; no anterior temporal; one posterior temporal, fused with nuchal along parietal margin.

Chin tapered, anterior tip rounded; mental much broader than long, rounded anteriorly, separated from chinshields by first pair of infralabials; infralabials variable, 6–8, the first three or four pairs in contact with anterior chinshields which are longer than broad, and slightly longer than

posterior ones; posterior chinshields in contact at anterior ends, separated by median gular posteriorly; 2-3 gulars separate chinshields from first ventral.

Dorsal scales in 15 rows, distinctly keeled except on neck; paired apical pits present. Ventrals in five males, 118-129(124.2); in three females, 127-133 (130.3); anal undivided; subcaudals in four males, 33-41 (36.3); in three females, 26-36 (31.7). Ventrals plus caudals, 156-170. Total length of largest male, 335 mm; tail, 61 mm (18.2%); largest female, 301 mm; tail, 48 mm (16.0%).

Maxilla extends anteriorly to suture between supralabials 1 and 2; anterior extension slightly greater than that of palatine; maxilla dorsoventrally compressed, bears 12-13 subequal teeth; anterior tip of maxilla pointed, toothless; posterior end of maxilla curves ventrally, tapers to blunt point; anterior end of ectopterygoid single, not expanded; postorbital bone present.

Hemipenis extends posteriorly to level of subcaudal 7; basal part of hemipenis bears numerous spinules and, distally, two large spines; naked basal pocket present. Central part of organ bears about 20 moderate spines, circling hemipenis. Distal part of organ distinctly capitate, spinulate, calyculate; apex of organ slightly bilobed. *Sulcus spermaticus* bifurcates opposite fifth subcaudal. M. retractor penis magnus divides into two slips at apex of hemipenis.

Dorsum grayish-brown to brownish-black, paler laterally; scales in first row edged with brown, light yellowish in center. Mental, infralabials, and anterior chinshields brownish; ventrals yellowish-white, usually immaculate; some posterior ventrals may have brownish pigment along anterior margins; subcaudals yellowish, with dark brown anterior edges.

VARIATION.—The internasals are fused with the prefrontals in AMNH 19630; correlated with this fusion is the rounded dorsal margin of the postnasal. The same specimen may have the postocular fused with the supraocular, but the shrivelled condition of the specimen makes this decision questionable. The first and second supralabials in AMNH 19633 are fused, leaving five labials with the second and third in the orbit. The infralabial number is highly variable; the infralabials are 6-6 in one specimen, 6-7 in three, 7-7 in one, 7-8 in one, and 8-8 in two. This variation involves the fusion (or division) of labials in both the anterior and posterior parts of the series.

Most specimens have immaculate yellowish ventrals; in ZMB 3731 the posterior ventrals have a darker anterior margin, but the dark pigment rarely reaches the midline.

REMARKS.—Some specimens of *G. brachycephalus* are similar to *G. sallaei*. The former species usually has a higher ventral count, and often a blotched



or striped dorsum. Many specimens (and apparently some populations) of *brachycephalus* are unicolor dorsally, and populations of *brachycephalus* in Panama have ventral counts comparable to those of *sallaei*. Unicolor *brachycephalus* from Panama are therefore quite difficult to distinguish from *sallaei*, except on the basis of locality. The head scutellation of the two is similar, but at least most individuals can be distinguished by the relative length of the prefrontal and parietal sutures. In *sallaei*, the prefrontal suture is nearly as long as the parietal suture; in *brachycephalus* the prefrontal suture is less than three-fourths as long as the parietal suture. Secondly, the first dorsal scale row in *sallaei* is composed of light-centered scales; in gross appearance, these result in a series of light spots along the sides of the snake. In *brachycephalus* this row of small light spots is absent.

SPECIMENS EXAMINED (8).—MEXICO: No locality: BMNH 1946.1.6.26–27, 1946.1.6.49. Oaxaca: No locality, ZMB 3731; Cafetal Alemania, near Pluma Hidalgo, AMNH 19630–33.

*Geophis sieboldi* (Jan)

*Elapoides sieboldi* Jan, 1862:21, pl. 17; Jan and Sordelli, 1865: livr. 12, pl. 1, fig. 4.

*Geophis chalybeus*, Peters (in part), 1859:275; Bocourt (in part), 1883:530; Boulenger (in part), 1894:318; Smith (in part), 1941b:3.

*Catostoma sieboldi*, Cope, 1868:131.

*Elapoides chalybeus*, Cope (in part), 1885a:386; Cope (in part), 1887:84.

*Ninia sieboldi*, Garman, 1883:96.

*Catostoma chalybeum*, Amaral (in part), 1929:191.

*Geophis sieboldi*, Smith, 1941b:4; Smith and Taylor, 1945:70.

HOLOTYPE.—Originally four syntypes (two from "Mexico," one from "Guadalupa," and one unspecified) distributed among the museum collections at Vienna, Milano (2), and Monaco (= Munich). At least some of the syntypes were destroyed during World War II, and none is definitely known to be extant.

DISTRIBUTION.—Uncertain; a specimen from Amula (= Almolonga), Guerrero, and one from Coalcoman, Michoacan, are referred to this species, but each is atypical in some respects. The closely related *G. nasalis* is distributed at moderate elevations along the Pacific versant of Chiapas, Mexico, and Guatemala; it seems likely that *sieboldi* occurs in similar areas west of the Isthmus of Tehuantepec.

DIAGNOSIS.—Distinguished from other members of the genus by the combination of (1) dorsal scales in 17 rows, keeled on posterior half of body; (2) no anterior temporal; (3) combined pre- and postnasal length distinctly less than that of loreal; (4) sum of ventrals and subcaudals, 171–191; (5) dorsum brownish, scales of first row with yellowish centers; and (6) ventrals yellowish-white.

DESCRIPTION.—Head scarcely distinct from neck; snout long, pointed, projecting well beyond lower jaw; rostral moderate, not produced posteriorly between internasals, its length one-third or less its distance from frontal; internasals small, much broader than long, half as long as prefrontal suture; prefrontal suture more than half as long as frontal; frontal as long as broad, angulate anteriorly; parietals short, their median suture about two-thirds as long as frontal; supraocular subtriangular, forms slightly more than posterior half of dorsal margin of orbit; one postocular, higher than long, smaller than supraocular.

Nasal divided, postnasal slightly longer than prenasal, their combined length three-fourths that of loreal; loreal elongate, contained less than twice in snout length, about twice as long as eye diameter; eye small, contained thrice in snout, its vertical diameter slightly less than its distance from lip; supralabials 6, third and fourth in orbit, fifth largest and in broad contact with parietal; no anterior temporal; one posterior temporal, usually fused with nuchal along parietal margin.

Mental broader than long, acuminate anteriorly, separated from anterior chinshields by first pair of infralabials; infralabials variable (6–9), first 3 or 4 pairs in contact with anterior chinshields; anterior chinshields little longer than broad, larger than posterior pair; posterior chinshields separated throughout most or all of length, scarcely distinguishable from gulars; 2–3 rows of gulars separate chinshields from first ventral.

Dorsal scales in 17 rows, distinctly, but not strongly, keeled on posterior half of body and anterior part of tail; scales striated, bear paired apical pits. Ventrals in 5 males, 132–147 (142.0); in 2 females, 147–153; anal undivided; subcaudals in 5 males, 37–42 (39.0); in 2 females, 35–36. Total ventrals plus subcaudals, 171–188. Total length of largest male, 397 mm; tail, 67 mm (16.9%); the larger female, 185 mm; tail, 28 mm (15.1%).

Maxilla extends anteriorly to suture between second and third supralabials; anterior extension about equal to that of palatine; maxilla dorsoventrally compressed, bears 11–14 short, curved teeth; teeth subequal in length; anterior tip of maxilla pointed, toothless; posterior end of maxilla curves ventrally, tapers to blunt point; anterior end of ectopterygoid single, not expanded; postorbital bone present.

Hemipenis extends posteriorly to level of subcaudal 7; basal part of organ bears numerous spinules and, distally, two large spines; naked basal pocket present. Central part of organ bears about 20 medium spines and hooks. Distal part of hemipenis capitata, calyculate, spinulate; apex slightly bilobed. *Sulcus spermaticus* bifurcates opposite subcaudal 6; each branch reaches apex. M. retractor penis magnus divides into two slips at apex of hemipenis.

Dorsum of head and body dark gray or brown; at least some juveniles

with light yellowish collar on posterior part of head and adjacent neck scales; dorsum darkest middorsally, palest laterally; scales of first dorsal row with yellowish centers, brown edges; first scale row spotted in gross appearance. Chin yellowish or whitish, usually mottled laterally with brown; ventrals white or yellowish-white, with brown lateral edges; subcaudals whitish, immaculate, or with dark medial edges which form a jagged dark line mid-ventrally.

VARIATION.—The infralabials are too variable to designate a "normal" condition. Within a single series of 5 specimens (ZMB 1555–1559), the infralabials are 6–6 in one, 7–8 in two, and 8–9 in two. The latter represent the highest number of infralabials recorded in the genus. In the closely related *G. nasalis*, the modal number is seven, but this figure is frequently increased to eight.

BMNH 90.4.24.12 from Amula, Guerrero, has a distinct light collar involving the posterior part of the parietals, supralabials 5 and 6, and the first 2 rows of scales behind the head. The specimen is a juvenile with a snout-vent length of 136 mm. ZMB 1557, 142 mm in snout-vent length, has no distinct collar, but shows faint traces of one; a slightly larger specimen (146 mm) and all of the adults show no indication of a collar. A collar was not mentioned in the original description of the species, even though the smallest syntype had a snout-vent length of 126 mm. Whether this represents populational variation in the presence or absence of a juvenile collar, or simply individual variation in the presence of, or rapidity of loss of, the collar is not clear.

The scale counts of the syntypes are not included in the description of the species presented above. Jan (1862:22) gave the number of ventrals and subcaudals as 146, 151, 153, 154, and 38, 37, 38, 34, respectively. The first two sets of counts probably represent males, since the tail lengths of the two specimens represent 18.1 and 18.7 per cent of the respective total lengths; conversely, the shorter tails (15.9 and 14.7 per cent, respectively) of the latter two specimens indicate that the counts were obtained from females. These counts modify the ranges in the number of ventrals and subcaudals presented above, but the modification is minor. Only one specimen, BMNH 90.4.24.12, has segmental counts which contrast with those of the remaining specimens. It is a male with 132 ventrals and 39 subcaudals; the ventral count is 11 lower than that of any other male, and the sum of the ventrals and caudals (171) is 10 lower than that of any other specimen of either sex.

UMMZ 104698, from Coalcoman, Michoacan, Mexico, has an irregular number of dorsal scale rows. On most of the body there are 17 scale rows, but the number is reduced to 15 at several points along its length. In the areas of reduction, the paravertebral scales are fused with the vertebral row.

REMARKS.—The illustration of *sieboldi* in Jan and Sordelli (1865: livr. 12, pl. 1, fig. 4) shows the keeling of the dorsal scales ending directly above the vent. This feature has been utilized as a distinctive characteristic of *sieboldi* (e.g., Smith, 1941b:4). There are species of *Geophis* in which the keeling is restricted to the region above the vent, but in species with more widespread keeling the keels continue onto at least the basal third of the tail. Such is the case in the specimens herein referred to *sieboldi*, and I believe also in the syntypes; Jan's (1862:21) original description stated, "le carene pero scompaiono alla parte estrema della coda."

SPECIMENS EXAMINED (7).—MEXICO: No locality: ZMB 1555–59. Guerrero: Amula, BMNH 90.4.24.12. Michoacan: Coalcoman, UMMZ 104698.

### *Geophis zeledoni* Taylor

*Geophis zeledoni* Taylor, 1954:693, fig. 4.

HOLOTYPE.—UK 31992, an adult female from Finca Zeledon, between Volcan Barba and Volcan Poas, Costa Rica; July 24, 1952; E. H. Taylor, collector. UK 31951 is a paratopotype.

DISTRIBUTION.—Known only from the slopes of Volcan Poas, 1600–2000 meters above sea level, in the Cordillera Central of Costa Rica.

DIAGNOSIS.—Distinguished from other members of the genus by the combination of (1) dorsal scales in 15 rows, smooth on most of body, lightly keeled above vent; (2) no anterior temporal; (3) six supralabials; (4) dorsum uniformly grayish-black; and (5) chin and venter mostly blackish, with scattered irregular light markings.

DESCRIPTION.—Head scarcely distinct from neck; snout long, bluntly rounded from above, projecting well beyond lower jaw; rostral moderate, its length from above less than one-third its distance from frontal; rostral not produced posteriorly between internasals; internasals much broader than long, their maximum length less than half as long as prefrontal suture; prefrontals moderate, their median suture half as long as frontal; frontal as long or longer than broad, angulate anteriorly; parietals moderate, their median suture two-thirds to three-fourths as long as frontal; supraocular forms posterior two-thirds of dorsal orbital margin; one postocular, much higher than long, smaller than supraocular.

Nasal divided, postnasal half-again as long as prenasal; their combined length less than that of loreal; loreal more than half as long as snout, half-again as long as eye diameter; eye moderate, contained almost thrice in snout, its vertical diameter equal to its distance from lip; supralabials 6, third and fourth in orbit, fifth largest and in contact with parietal; anterior

temporal absent; one posterior temporal, not fused with nuchals along parietal margin.

Mental broader than long, bluntly rounded anteriorly, separated from chinshields by first pair of infralabials; infralabials 6, pairs 1-3 in contact with anterior chinshields; anterior chinshields short, scarcely longer than broad; posterior chinshields small, scarcely distinct from gulars, often separated throughout length by median gular of equal size.

Dorsal scales in 15 rows, smooth and without striations on most of body; scales on posterior fifth of body and on base of tail lightly keeled; paired apical pits present. Ventrals in ten males, 141-146 (144.0); in seven females, 143-150 (145.1); anal single; subcaudals in eight males, 39-46 (43.4); in seven females, 37-43 (39.9). Total ventrals plus caudals, 180-191. Total length of largest male (a male 417 mm long has a slightly incomplete tail), 379 mm; tail, 76 mm (20.1%); largest female, 397 mm; tail, 70 mm (17.6%).

Maxilla extends anteriorly to level of suture between second and third labials; anterior extension about equal to that of palatine; in lateral view, posterior end of maxilla curves ventrally; in ventral view, posterior half of maxilla dorsoventrally flattened, much broader than anterior half; 13-14 maxillary teeth, subequal in length; first tooth at anterior tip of maxilla or preceded by only a short toothless area; anterior end of ectopterygoid single, slightly flattened; postorbital bone present.

Hemipenis extends to level of subcaudals 8-9; basal part of organ bears minute spines, a naked basal pocket on antisulcus side, and 3-4 large spines distally. Central part of organ bears 35-40 medium spines. Distal part of organ capitate, calyculate, spinulate; capitation obscured by gradation between spines of capitulum and those of central part of organ; apex of capitulum scarcely bilobed. *Sulcus spermaticus* bifurcates opposite subcaudal 4-5. *M. retractor penis magnus* bifurcates into two slips, each slip attaches to apex.

Dorsal coloration grayish to brownish-black; lateral parts of head and body not notably paler than middorsal parts. Chin region dark, each scale dark centrally, paler along margins; anterior chinshields darker than other chin scales; ventrals predominantly blackish; light ventral pigment confined to scattered, irregular blotches or diffuse mottled areas; subcaudals blackish, with grayish margins.

**VARIATION.**—The number of supralabials is reduced to five on both sides of three specimens and one side of three others. In all cases the reduction is the result of the fusion of the third and fourth labials; in an additional specimen these scales are partially fused on one side. When five labials are present, only the composite third labial enters the orbit. The infralabials are less variable; reduction from six to five occurs on one side of two specimens and an increase to seven on one side of one individual. A second

postocular is present on the right side of UMMZ 122640; this small scale occupies an area normally included in the fourth supralabial. In the paratype the mental is in contact with the anterior chinshields; in all other specimens this contact is prevented by the intervention of the first pair of infralabials.

In life, the dorsal and ventral coloration of UK63819–23 varied from dull gray to dark brown (Duellman, pers. com.). In most specimens (e.g., the type), the light ventral pigment is concentrated in a few distinct blotches; in UMMZ 122640, the light pigment is more generally distributed, particularly on the anterior ventrals. In no case is the gross appearance of the venter banded.

REMARKS.—The original description is marred by inconsistencies, apparently the result of a confusion between the characteristics of the holotype and paratype. Taylor stated (1954:693), for example, “five supralabials, in the following ascending order of size: 1, 2, 4, 3, 6, 5, the third and fourth entering eye. (In paratype third and fourth fused together.)” The illustration of the head scales presented by Taylor was stated to represent the holotype, but the fusion of the third and fourth labials, and the contact between mental and anterior chinshields, clearly indicates that the drawings are of the paratype (UK 31951).

SPECIMENS EXAMINED (17).—COSTA RICA: **Alajuela:** S slope Volcan Poas, UMMZ 117720. **Heredia:** 9 km N la Concordia, UK 63819–23; Vara Blanca (Alajuela Prov.?), UK 35851–54, 35898, CRE 77 (3), UMMZ 122640; between Volcan Barba and Volcan Poas (Alajuela Prov. ?), UK 31951, 31992.

## EVOLUTIONARY TRENDS AND INTERGROUP RELATIONSHIPS

The principle evolutionary trend in the genus *Geophis* has been toward specialization for a secretive, fossorial existence. This trend is not equally developed among the seven species groups, nor among the species within each group. One group, including *G. chalybeus* and its relatives, has departed from the general trend of the genus as a whole.

The morphological adaptations which reflect the specialization for burrowing are similar to those found in other ophidian cryptophiles. These include a reduction in the width of the head until it is no wider than the neck, an elongation of the snout, a decrease in eye size, a reduction in the number of head scales and in the number of dorsal scale rows, a shortening of the tail, and the development of an inferior mouth with a narrow gape. In *Geophis*, the last feature is associated with a decrease in the size of the maxilla and in the number of maxillary teeth. Although scarcely any of the head scales of the “generalized” colubrid complement have escaped modification

(by fusion with, or displacement by, adjacent scales) in some species or individuals in the genus, the most consistently absent are the preoculars and the anterior temporals. The absence of the former is rather common among neotropical colubrids, but the absence of the temporal has been associated historically with the genus *Geophis*. In spite of this association, the anterior temporal is present in the members (with one exception) of two of the seven species groups. These, the *omiltemanus* and *latifrontalis* groups, are assumed to be generalized (primitive) with respect to the temporal condition.

The *omiltemanus* group appears to be the least specialized in the genus. Within the group, *G. isthmicus* is probably the most generalized, but the species is so poorly known that its allocation to this group, and to the genus itself, must be regarded as tentative. Assuming its allocation is correct, *G. isthmicus* is the only member of the genus with seven supralabials, and with none of the labials notably enlarged. The relatively well-known *G. omiltemanus* is similar to *isthmicus* in most respects, and can serve equally well as an example of the generalized condition. The chief difference between the two is that the position of the sixth and seventh labials in *isthmicus* is occupied by a single, elongate labial in *omiltemanus*. *G. omiltemanus* shows the following features which appear to represent a generalized condition, and from which more specialized conditions were derived: (1) a relatively broad head, moderately distinct from the neck; (2) a rather short, blunt snout; (3) upper and lower jaws approximately equal in length; (4) a moderately large eye; (5) two postoculars; (6) an anterior temporal; (7) a small fifth supralabial, broadly separated from the parietal; (8) 17 rows of dorsal scales; (9) a moderately long tail; (10) a large maxilla, bearing numerous teeth and with an expanded posterior flange; and, (11) a bifurcate, expanded ectopterygoid.

From the generalized condition found in the *omiltemaus* group, two lines of differentiation appear to have developed. In each the anterior temporal has been lost, but in other respects these lines are very different from one another. One of the lines has been characterized by progressively greater specialization toward a burrowing form, and has given rise to the *dubius* and *championi* groups.

The *dubius* group is in many respects intermediate between the generalized *omiltemanus* group and the highly specialized *championi* group, and occupies an intermediate geographic position. In this series, the distinctness of the head from the neck is lost, the snout elongates and becomes acuminose, the body becomes terete, the dorsal scale rows decrease from 17 to 15, the mouth becomes inferior, the maxilla shortens and loses its posterior flange, the number of maxillary teeth decreases, and the anterior end of the ectopterygoid becomes single and acuminose. More specifically, various changes in the individual head scales can be followed. The rostral increases

in prominence until it is a distinct wedge. The internasals, postnasals, and frontal enlarge; the anterior margin of the latter changes from slightly to acutely angulate. The parietals become shorter and broader, and the supraoculars become smaller, triangular instead of quadrangular, and displaced posteriorly. The number of postoculars decreases from two to one, and the anterior temporal is lost, leaving the enlarged fifth labial in contact with the parietal.

Some of the above changes are evident within a single group. In the *omiltemanus* group, for example, the number of postoculars is reduced to one in the single specimen of *G. maculiferus* and in several specimens of *G. incomptus*. The latter species also includes individuals in which the fifth labial narrowly touches the parietal, displacing the anterior temporal (the presumed method by which the anterior temporal has been "lost" in these groups). Within the *dubius* group, the most specialized form (*G. dubius*) is in most respects as specialized as the members of the *championi* group. In general, the members of the *dubius* group show an intermediate level of specialization in the features listed above. The suggested relationship between the *dubius* and *championi* groups is moreover supported by the fact that in both the elongation of the snout is associated with an increase in the lengths of the internasals and postnasals. The affinity between the *omiltemanus* and *dubius* groups is suggested by the basic similarity between members of the former and the least specialized members of the latter. *G. rhodogaster* and *G. fulvoguttatus* in particular bear strong resemblances to members of the *omiltemanus* group.

The *chalybeus* group also appears to have been derived from the *omiltemanus* stock, quite independently from the *dubius-championi* line. The *chalybeus* and *championi* groups represent, in fact, the opposite extremes in body form found within the genus. Whereas the *championi* group epitomizes the narrow pointed head, elongate snout, inferior mouth, and small eye associated with the burrowing habit, the *chalybeus* group has the broadest head, the shortest, bluntest snout, the least inferior mouth, and the largest eye. In this sense, the *chalybeus* group is the most generalized in the genus. Phylogenetically, however, the distinctive features of the *chalybeus* group appear to have been derived from the less extreme conditions of the *omiltemanus* group. The two groups are quite similar in form, scutellation, and characteristics of the maxilla and ectopterygoid. Both include species with 17 dorsal scale rows and two postoculars (presumed to represent the primitive condition in each) and forms with 15 dorsal scale rows and one postocular. In the members of the *chalybeus* group the anterior temporal is absent; the large fifth supralabial is in contact with the parietal. In the *omiltemanus* group, the fifth labial is separated from the parietal by an



anterior temporal. The detailed arrangement of these three scales varies within the group, and this variation provides a clue to the development of the condition found in the *chalybeus* group. In *G. omiltemanus*, the fifth labial is small and broadly separated from the parietal; in *G. maculiferus* it is larger, and in *G. incomptus* larger still. In the latter, the labial is but narrowly separated from the parietal, and in some individuals extends in front of the temporal to touch the parietal. The arrangement in the *chalybeus* group, in which the contact between the fifth labial and the parietal is relatively short, would seem to be the end result of the trend toward an enlarged fifth labial discernible within the *omiltemanus* group. If this proposed direction of derivation is correct, the *chalybeus* group has differentiated in a direction contrary to the principle evolutionary trend of the genus as a whole.

The *latifrontalis* and *semidoliatus* groups also appear to have close phylogenetic affinities. Members of both groups are relatively specialized burrowing forms with elongate (but not pointed) snouts, relatively small eyes, and short tails. The latter feature is particularly pronounced. Elongation has apparently occurred uniformly along the length of the snout; all of the snout scales are moderately long. This contrasts with the long internasal-postnasal and short prefrontal-loreal regions of the *championi* group, and the short internasal-postnasal and long prefrontal-loreal regions of the *sieboldi* group.

The *latifrontalis* group appears to be the more primitive of the two. Three of its four members have an anterior temporal immediately above an elongate fifth labial. The fourth member, *G. blanchardi*, has the fifth labial in broad contact with the parietal; the temporal has almost certainly been lost as the result of direct fusion with the fifth labial. The long contact between the fifth labial and the parietal in the *semidoliatus* group suggests that the absence of the temporal in that group is a result of a similar fusion. This is in contrast to the apparent means by which the temporal has been lost in the forms derived from the *omiltemanus* stock. In addition to the presence of the temporal, the rather frequent occurrence of a preocular (variable in shape and position) in *G. latifrontalis* may represent a primitive condition.

The *semidoliatus* group has apparently been derived from the *latifrontalis* stock, a differentiation characterized by increased specialization toward a burrowing form. Of the two, the former group has the longer snout, smaller eye, shorter tail, and more terete form. The 17 rows of dorsal scales in the *latifrontalis* group are reduced to 15 in the *semidoliatus* group. In addition to the fusion of the anterior temporal with the fifth labial, two members of the *semidoliatus* group show a further reduction in the number of head scales; the third and fourth supralabials are fused in *semidoliatus*, and the

internasals are fused with the prefrontals in *cancellatus*. The maxillaries and ectopterygoids of the two groups are similar, but in the *semidoliatus* group the maxilla is more slender, bears slightly fewer teeth, and does not have the moderate posterior flange. These differences presumably reflect a reduction from the *latifrontalis* condition.

The *sieboldi* group is comprised of rather specialized forms in which the elongation of the snout has resulted in long prefrontals and loreals. The edentulous nature of the anterior tip of the maxilla also distinguishes the group. This group apparently represents an ancient unit within the genus. This supposition is supported by its extensive geographic range, which includes nearly the entire range of the genus, and by the fact that the relationship of the *sieboldi* group to the others is obscure. I have pointed out above that the *sieboldi* group is somewhat more inclusive than the others, and that secondary differentiation within the group has led to a Mexican element, a northern Central American element, and a southern Central American element. These secondary differentiations within the rather inclusive *sieboldi* group probably partly correspond, in degree and time, to the differentiation between some of the less inclusive groups.

I, thus, view the genus as being composed of three ancient stocks: 1. The *latifrontalis* stock, which at present consists of the primitive *latifrontalis* group in eastern Mexico, and the derived *semidoliatus* group, which presumably differentiated to the east of a barrier across the Isthmus of Tehuantepec; 2. The *omiltemanus* stock, in which the primitive forms persist in western Mexico, and from which the *chalybeus* group differentiated in the Sierra Madre Occidental of Mexico, the *dubius* group in northern Central America, and the *championi* group in southern Central America; 3. The *sieboldi* stock, in which intragroup differentiation has taken place in Mexico, northern Central America, and southern Central America (the primitive forms appear to be those in northern Central America).

Unfortunately, the relationships of these three lines, one to the other, are obscure. *G. aquilonaris* does seem to combine some features of the *chalybeus* group with some of the *latifrontalis* group, and *G. petersi* some of the *sieboldi* group with others of the *dubius* group. Both of these species, however, appear to represent end products of differentiation during extended isolation from the other members of their respective groups, rather than primitive forms intermediate between separate groups. The difficulty of tying the three lines together may simply reflect the length of time that the lines have been distinct. In as diverse a group as *Geophis*, it may also indicate that the genus does not represent a natural assemblage. The final answer to this problem must await vastly greater numbers of specimens than are now available.

## GENERIC RELATIONSHIPS

Different authors have associated *Geophis* with a surprisingly diverse array of genera. Boulenger (1894) said that his new genus *Dirosema* connected *Tropidodipsas* with *Geophis*; three of the four species he placed in *Dirosema* are now included within *Geophis*, the fourth in *Ninia*. Dunn (1928a) presented data on what he considered the related genera *Carphophis*, *Geophis*, *Atractus*, and *Adelphicos*, but in the same year (1928b) placed *Adelphicos* in a different subfamily from the others (a dichotomy based on the single or bifurcate nature of the *sulcus spermaticus*). In his study of the genus *Ninia*, Dunn (1935) stated that "The least modified members of *Geophis* (leading to the allied genera *Atractus*, *Carphophis*, *Farancia*, and *Abacura*) are manifestly allied to *Ninia*." Smith (1942), in a revision of *Adelphicos*, considered *Geophis* intermediate between *Atractus* and *Adelphicos*. In 1944, Dunn found affinities among *Ninia*, *Geophis*, *Atractus*, *Tropidodipsas*, and *Dipsas*. Taylor (1949), in erecting the new genus *Schmidtophis*, concluded that its relationships were with *Chersodromus* and *Geophis*. Most recently, Savage's (1960) study of Ecuadorian species of *Atractus* led him to believe that *Atractus* was more closely related to *Geophis* than to any other genus.

The association of a single genus with genera as different as *Adelphicos* and *Ninia* suggests that individual authors have held different concepts of *Geophis*, presumably stemming from the great diversity of forms relegated to the genus. The principle aim of this study has been to organize this diversity into smaller, more homogeneous units that can be meaningfully compared with other groups. My approach has been to try to determine the relationships among the species currently included under the name *Geophis*. This approach has not included an intensive study of other neotropical genera. Nonetheless, I have examined representatives of the genera most commonly associated with *Geophis*, and believe that their relationships to *Geophis* can now be more accurately assessed.

The genera mentioned by the above authors fall into two basic categories. Some, such as *Ninia* and *Tropidodipsas*, are rather generalized forms from which *Geophis* may have been derived (or with which *Geophis* may have shared a common ancestor). Others, such as *Atractus* and *Adelphicos*, are specialized burrowing forms which may have been derived from *Geophis* (or from a common stock). This difference is nicely shown by Dunn's (1935) bold, and I think largely accurate, attempt to relate these diverse genera. Dunn placed *Ninia* in a central, generalized position, leading to a burrowing line through *Geophis* to *Atractus* and other genera, and to an arboreal line through *Tropidodipsas* to *Sibon* and related forms. He also noted the similarity between *Ninia* and *Chersodromus*. Dunn's arrangement was based

on similarities in hemipenial features, dentition, pupil shape, and scalation.

The similarities do not apply very well when *Ninia* is compared with certain species of *Geophis*. Dunn (1935:9) was careful to note, however, that he was referring to the "least modified" species in the genus. These species are the members of the *omiltemanus* group, and do in fact share many features with *Ninia*. Many of the same features are shared by *Tropidodipsas* as well. The maxillaries of these three groups bear comparable numbers of teeth and have an expanded posterior flange; the ectopterygoid is also expanded. The hemipenis in each is capitate, calyculate, slightly bilobed, and bears a divided sulcus. The general arrangement of head scales is similar in the three groups, although most species of *Tropidodipsas* differ from the other two groups in having one or more preoculars. The loss of the preoculars in certain *Tropidodipsas*, e.g., *T. fischeri* and *T. annulifera*, has apparently been independent of the same loss in *Ninia* and *Geophis*. *Ninia* is distinctive among the three groups in the presence of hypapophyses on the posterior vertebrae and in the strongly developed keels and striations on the dorsal scales. The precise relationship of these groups cannot yet be stated with confidence; for the present, Dunn's arrangement, with *Ninia* in a central position, is reasonably convincing.

Neither *Tropidodipsas* nor *Geophis* appears to be as closely related to *Ninia* as are two other neotropical forms. The latter, *Chersodromus liebmanni* and *Schmidtophis rubriventris*, agree with *Ninia* in the presence of posterior hypapophyses and in general form and scutellation. Although such scale features as the fused prefrontals can be used to distinguish *Chersodromus* from *Ninia*, the major distinguishing feature is the maxilla; in the former genus, the anterior part of the maxilla is edentulous (but quite different from the edentulous tip of the maxilla in the *sieboldi* group of *Geophis*). The condition of the maxilla in *Schmidtophis* has not been determined with certainty, but appears to be of the type found in *Chersodromus*. The only known specimen of *Schmidtophis* has but one remaining maxilla; analysis was therefore limited to *in situ* and radiographical examination, neither of which proved thoroughly convincing. *Schmidtophis* agrees with *Chersodromus* in the fusion of the prefrontals, the moderately strong dorsal keeling, the presence of paired apical pits in the neck region, and in form and coloration. It differs from *Chersodromus* primarily in having 15 instead of 17 dorsal scale rows and in having no anterior temporal; in *Schmidtophis* the large fifth labial is in contact with the parietal. It was presumably the latter feature that prompted Taylor (1949) to relate *Schmidtophis* to *Geophis* (as well as to *Chersodromus*). I consider the loss of the temporal to have occurred independently in *Geophis* and *Schmidtophis*. The latter and *Chersodromus* appear to be derivatives of the *Ninia* stock, and neither appears to be any closer to *Geophis* than is *Ninia* itself.

Several snakes with short, blunt snouts and color patterns of dark and light rings have been described from western Mexico. These poorly known forms include *Exelencophis nelsoni* (Slevin), *Geatractus tecpanecus* (Dugès), *Chersodromus annulatus* Zweifel, and *Tropidodipsas malacodryas* Shannon and Humphrey. Although each has been placed in a different genus, the similarities between them have been recognized. Shannon and Humphrey (1959:219) considered the possibility that *malacodryas* was a mainland form of *Exelencophis*, but then decided it was more closely related to *Tropidodipsas annulifera* Boulenger. Zweifel (1954b:18-19) considered his allocation of *annulatus* to *Chersodromus* tentative; he compared the species with *Chersodromus*, *Schmidtophis*, *Geophis omiltemanus*, and *Geatractus*. *Geatractus tecpanecus* was itself described originally as a *Geophis* by Dugès (1896:455-56) who later erected *Geatractus* to contain the single species *tecpanecus*. Norman Scott (pers. com.) has recently concluded that *E. nelsoni*, *C. annulatus*, *T. malacodryas*, and *G. tecpanecus* all belong in the synonymy of *Tropidodipsas annulifera* Boulenger. Although it seems very likely that some of these forms are synonymous, it is unlikely that all are conspecific. Among these forms, I have examined a single, damaged specimen of *Geatractus*; my knowledge of the other nominal forms is based on information taken from the literature. In Scott's arrangement, *T. annulifera* would include individuals with 15 or 17 scale rows, keeled or smooth scales, and an incredible range in the number of subcaudals. The male holotype of *C. annulatus* has 41 subcaudals (Zweifel, 1954b:17); that of *T. malacodryas* was stated to have 96 subcaudals (Shannon and Humphrey, 1959:218). The latter figure may be in error; in the same paragraph, Shannon and Humphrey gave the total length as 195 mm, the tail length as 96 mm, and the percentage tail of total as 19.4. The latter figures are obviously inconsistent with one another, and since the figure 96 appears both as the tail length and as the number of subcaudals, doubt is cast upon both. Regardless of the correct number of species involved, I see no special relationship of these forms with *Geophis* other than that already expressed for *Tropidodipsas*.

*Geophis* has been more frequently associated with *Atractus* than with any other genus. Attempts to define either group to the exclusion of the other have proven difficult and unsatisfactory. Boulenger (1894) placed forms with an anterior temporal in *Atractus* and those without the temporal in *Geophis*, thus including in the former several Mexican species currently placed in the latter. Similarly, two nominal South American forms (*Rhabdosoma poeppigi* Jan and *Geophis diplozeugus* Schmidt and Walker) came to be placed in *Geophis* because of the absence of the temporal; Savage (1960) recently recognized *poeppigi* and *diplozeugus* as individual variants of *Atractus elaps*. The inadequacy of the temporal formula in distinguishing *Geophis* and *Atractus* was pointed out by Dunn (1928a), Smith (1941b), and,

most recently, Savage (1960). Savage noted that in areas where members of the two genera occur sympatrically they may be distinguished by the number of chinshields (2 pairs in *Geophis*, one in *Atractus*). He recognized that this feature would not serve to distinguish all members of *Geophis* from all members of *Atractus*. Savage (1960:30) proposed that the hemipenis be used to distinguish the two; specifically, he noted that the hemipenis in *Geophis* was single (bilobed in *Atractus*), had no lateral naked pocket (present in *Atractus*), and frequently bore calyces near the tip (absent in *Atractus*). Unfortunately, Savage's characterization of the hemipenis in *Geophis* does not apply to all of the species currently placed in the genus, and thus presents the same problems raised by the use of the number of chinshields or the temporal formula.

Different combinations of maxillary, hemipenial, and scale characteristics led Savage (1960) to recognize three species groups within *Atractus*. The most distinctive of these is the *elaps* group, which has compressed, blade-like teeth, a short, blunt head, and correspondingly short snout scales. The *badius* and *trilineatus* groups, which resemble each other in features of the maxillary and scalation, are distinguishable by hemipenial characteristics. The same combinations of characters easily distinguish most of the species groups of *Geophis* from those of *Atractus*. The *latifrontalis* group, however, shows many similarities to the *badius* and *trilineatus* groups of *Atractus*; its members were placed in the latter genus by Boulenger (1894). Although Boulenger's arrangement was based primarily on the presence of an anterior temporal, the most impressive similarities between the *latifrontalis* group and *Atractus* involve the skull and dentition. The maxillaries in particular are almost identical in shape and in the size and disposition of the teeth they bear. The posterior margin of the frontal bones is strongly convex and bordered laterally by anterior extensions of the parietals. Although some differences exist, the head scutellation is basically comparable in the two groups. Members of the *latifrontalis* group, and many forms of *Atractus*, have short, blunt tails.

The most distinctive difference between the *latifrontalis* group and *Atractus* is the character of the hemipenis, which is single and calyculate in the former and bilobed and non-calyculate in the latter. The sulcus is bifurcate in both, but in the *latifrontalis* group one of the branches fails to reach the apex of the organ. Members of *Atractus* usually have 7 supralabials, 2 postoculars, a single pair of chinshields, and a very narrow loreal; the anterior temporal is located above and between the fifth and sixth labials. In the *latifrontalis* group there are 6 supralabials (with the anterior temporal directly above the enlarged fifth), one postocular, 2 pairs of chinshields, and a moderately high loreal. These differences are not great; the labial-temporal arrangement in the *latifrontalis* group can be hypothetically derived from

the *Atractus* condition by a fusion of the fifth and sixth labials of the latter. The reduction from 2 postoculars to one (by fusion of the lower postocular with a labial) has occurred within at least two groups of *Geophis* and within *Atractus* as well.

Many of the features shared by *Atractus* and the *latifrontalis* group of *Geophis* are also characteristic of the members of the genus *Adelphicos*. The skull, maxillary, body form, and scutellation of *Adelphicos* strongly resemble those of the former groups. In the number of postoculars, labials, and chinshields, and in the shape of the loreal, *Adelphicos* agrees with *Atractus*. Within *Adelphicos*, a marked trend toward enlargement of the single pair of chinshields is evident; in one species, the chinshields reach the lip. *Adelphicos* differs from both *Atractus* and the *latifrontalis* group in having a divided anal plate and an unforked *sulcus spermaticus*. The latter feature prompted Dunn (1928b) to place *Adelphicos* in a different subfamily from *Atractus* and *Geophis*. Smith (1942) objected to Dunn's arrangement, and considered *Geophis* intermediate between *Atractus* and *Adelphicos*. Smith (1942:187) referred to continuous northward gradients from *Atractus* through *Geophis* to *Adelphicos* in coalescence of the bifurcate hemipenial elements, reduction in the head scutellation, and in body size. None of the geographically intermediate species of *Geophis* show particularly close affinities with *Atractus* or *Adelphicos*. The *latifrontalis* group, which shows these affinities, is the northernmost of the three groups. Furthermore, it appears to be intermediate between *Atractus* and *Adelphicos* in but one feature; the sulcus, although bifurcate, appears to be functionally single (one of the two branches is obsolescent). In other respects the *latifrontalis* group appears to represent the least differentiated condition (e.g., the chinshields), or the most differentiated condition (e.g., the number of supralabials and postoculars, and the loss of the temporal in one species).

Although *Geophis*, and specifically the *latifrontalis* group, does not appear to represent an intermediate stage of differentiation between *Atractus* and *Adelphicos*, Smith's emphasis of the numerous similarities among the three groups is justified. These similarities do indeed appear to outweigh the difference in the nature of the hemipenial sulcus relied on so strongly by Dunn. The geographic distributions of the *latifrontalis* group, *Adelphicos*, and *Atractus* suggest that they may have differentiated from isolated populations of a common ancestral stock in Mexico, northern Central America, and South America, respectively. Such an ancestral stock might very well have been a generalized, *Ninia*-like form. The major differences in head scutellation distinguishing *Ninia* from *Adelphicos* and *Atractus* reflect the difference in snout shape: the snout is relatively short and blunt in *Ninia*, longer and more pointed in *Adelphicos* and *Atractus*. Except for this adaptive difference, the number and positions of the various scales are similar in

the three groups. Savage (1960:20) has concluded that the presence of seven supralabials represents the primitive condition in *Atractus*. The same number characterizes *Adelphicos* and most species of *Ninia*. In all three, the anterior temporal is located above and between the fifth and sixth labials, and two postoculars are usually present. The combination of these three features characterizes only one member of the genus *Geophis*, the poorly known, and perhaps erroneously allocated, *G. isthmicus*. The remaining *Geophis* have six (or five) supralabials. In the two groups of *Geophis* which have an anterior temporal, the temporal is located either above and between the fifth and an elongate sixth labial (*omiltemanus* group) or directly above an elongate fifth labial (*latifrontalis* group). From a seven-labial condition, the labial and temporal arrangements of the *omiltemanus* and *latifrontalis* groups could have been derived by the fusion of the sixth and seventh labials in the former, and of the fifth and sixth labials in the latter.

There is no doubt that the generalized *omiltemanus* group of *Geophis* resembles *Ninia* much more than does the *latifrontalis* group—*Atractus-Adelphicos* assemblage. The similarities in the maxillaries, hemipenes, and body form of the *omiltemanus* group and *Ninia* are much greater than those between the latter and the other, more specialized, groups. The fact that the *latifrontalis* group, *Atractus*, and *Adelphicos* can be credibly associated with *Ninia* on the basis of scutellation enhances Dunn's suggestion that *Ninia* represents a central, generalized condition from which the specialized forms have been derived.

The relationships of the specialized *sieboldi* group of *Geophis* are not clarified by comparison with other genera. Although its intrageneric affinities are obscure, the *sieboldi* group is clearly more closely related to the other groups of *Geophis* than to the members of any other genus.

#### SUMMARY

As currently recognized, the genus *Geophis* consists of a rather diverse array of small secretive snakes. Although the known geographic ranges of the various species are small, the genus as a whole ranges from Chihuahua and Tamaulipas, Mexico, southward to northwestern Colombia. Most of the 33 recognized species are poorly represented in museum collections. The accumulation of additional material will surely indicate that some of these forms are no more than subspecifically distinct.

The principle evolutionary trend within the genus has been toward a fossorial existence. At its maximum development, this trend has resulted in a narrow, terete head and body, a short tail, a long, pointed snout, a narrow gape (associated with a reduced maxillary), and a reduced number of head scales. These features are well developed in some members of the genus, but



scarcely evident in others. On the basis of these different levels of specialization, and of differing details in the manner that specialization has proceeded, the 33 forms have been arranged in seven species groups. The seven groups appear to represent three ancient stocks within the genus.

The *omiltemanus* group is the most generalized, and represents the base of one of the three major lines of affinity. The group includes four species distributed in the highlands of Michoacan, Guerrero, and Oaxaca, Mexico, at elevations between 1600 and 2500 meters above sea level. Members of this group have retained such generalized features as the presence of an anterior temporal, a short, blunt snout, a relatively large eye, and a head that is broader than the neck.

The *dubius* and *championi* groups appear to represent progressively more specialized offshoots of the *omiltemanus* stock. The *dubius* group is intermediate in many respects between the generalized *omiltemanus* group and the highly specialized *championi* group. The latter is the most specialized in the genus, and exemplifies the fossorial adaptations noted above. I recognize five forms in the *dubius* group, and three in the *championi* group. Members of the former occupy highlands from Puebla and Oaxaca, Mexico, eastward to El Salvador. The *championi* group is found in the highlands of Costa Rica and adjacent Panama.

The *chalybeus* group, with six forms, also appears to be a derivative of the *omiltemanus* stock. It differs from the latter in the absence of the anterior temporal and in other details, and is unique in the genus in that its differentiation has not involved the fossorial adaptations common to the other groups. Members of the *chalybeus* group are distributed in the western highlands of Mexico, from Chihuahua to Michoacan, and eastward along the southern edge of the Mexican Plateau to Veracruz.

The *latifrontalis* group represents the base of a second major stock within the genus. Like those of the *omiltemanus* group, the members of this group, with one exception, possess an anterior temporal. In other respects, the *latifrontalis* group is more specialized than the *omiltemanus* group, and shows no close resemblance to it. The four species of the *latifrontalis* group occupy pine and cloud-forest situations in the Sierra Madre Oriental of Mexico.

Three species are included in the *semidoliatus* group; they are found along the Pacific and Atlantic versants of southern Mexico from Veracruz to Chiapas. The group represents a specialized derivative of the *latifrontalis* group, differing from the latter primarily in the absence of the anterior temporal, the shorter tail, the lower number of dorsal scale rows, and the reduced nature of the maxilla.

The *sieboldi* group has no obviously close relationship to any of the other groups, and appears to represent a third major stock within the genus.

With eight included species, this is the largest and perhaps least homogeneous group. Its members are characterized primarily by long prefrontals and loreals, and by the edentulous nature of the anterior tip of the maxilla. The geographic range of the *sieboldi* group is nearly that of the genus, extending from Michoacan, Mexico, to northwestern Colombia; it is the only group that has managed to reach South America.

The genus as a whole has probably been derived from a *Ninia*-like stock. The *omiltemanus* group in particular shows many resemblances to the *Ninia* condition. The *latifrontalis* group, representing the base of a second major line of divergence within *Geophis*, is quite similar to members of the genus *Atractus*, but it is likely that both were initially derived from the *Ninia* stock. The *sieboldi* group, although its precise relationship to the other groups of *Geophis* is obscure, does not show any closer affinities to other genera; it, therefore, neither supports nor contradicts the proposed origin of the genus.

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