

Not so rare snakes: a revision of the *Geophis sieboldi* group (Colubridae: Dipsadinae) in lower Central America and Colombia

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The *Geophis sieboldi* species group is composed of 16 currently recognized species distributed from Mexico to Colombia. Within this group, snakes of populations referred to the *Geophis brachycephalus* complex of lower Central America and Colombia display a remarkable polychromatism and the systematic status of these and other populations is problematic. The present study provides an analysis, including multivariate techniques, of variation in scalation, coloration, relative tail length and hemipenes to clarify the specific allocation of the populations belonging to this clade. Our results confirm the validity of three previously described taxa, namely *G. brachycephalus*, *G. nigroalbus* and *G. talamancae*, with reassignments of several populations previously referred to *G. brachycephalus*. In addition we recognize as a new species a suite of western Panama *Geophis* previously of uncertain status. We further provide a review of all other members of the *G. sieboldi* group in lower Central America and Colombia based on material obtained since the last revision of the group. Basic synonymies, diagnostics and known distributions are included for the treated taxa. Dietary guild, possible venomous coral snake mimicry and distributional anomalies for the group are discussed. © 2008 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2008, 153, 561–599.

ADDITIONAL KEYWORDS: analysis of similarity – Costa Rica – distribution – goo-eaters – mimicry – Nicaragua – polychromatism – reptiles – scalation – systematics.

INTRODUCTION

Among the most common semifossorial, leaf-litter snakes found on the premontane and lower montane slopes of Costa Rica and western Panama are those currently assigned to *Geophis brachycephalus* (Cope, 1871). Wilson, McCranie & Williams (1998) regarded this species as one of 15 taxa comprising the *Geophis sieboldi* group *sensu* Downs (1967). Other included species are: *G. laticollaris* Smith, Lynch & Altig, 1965, *G. petersii* Boulenger, 1894, *G. pyburni* Campbell & Murphy, 1977, *G. russatus* Smith & Williams, 1966,

G. sallei Boulenger, 1894 and *G. sieboldi* (Jan, 1862) from Mexico, *G. nasalis* (Cope, 1868) from Mexico and Guatemala, *G. damiani* Wilson *et al.*, 1998 from Honduras, *G. hoffmanni* Peters, 1859 from Honduras to Colombia, *G. dunni* Schmidt, 1932 from Nicaragua, *G. talamancae* Lips & Savage, 1994 and *G. zeledoni* Taylor, 1954 from Costa Rica, and *G. betaniensis* Restrepo & Wright, 1987 and the putative valid species *G. nigroalbus* Boulenger, 1894 from Colombia. Recently, Myers (2003) added a 16th species, *Geophis bellus*, from east-central Panama to the group and reported the occurrence of *G. brachycephalus* from east of the Panama Canal area. He also raised questions regarding a possible unrecognized sibling species included within nominal *G. brachycephalus* in western Panama and the validity of the southern Costa Rican *G. talamancae* as distinct from *G. brachycephalus*. He did continue to recognize

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G. nigroalbus Boulenger, 1908, placed as a synonym of *G. brachycephalus* by Downs (1967), as a valid Colombian form.

The present study was initiated in an attempt to address the questions raised by Myers (2003) in light of the availability of extensive previously unreported material of snakes of the *G. sieboldi* group from Costa Rica and Colombia. The primary focus of this study is to describe variation within and among populations of *G. brachycephalus* (*sensu* Downs, 1967) and its close allies, the nominal species *G. nigroalbus* and *G. talamancae*, in lower Central America and Colombia. Although not directly involved in the problem of the status of several populations in this complex, we have included information for the related forms, *G. hoffmanni* and *G. zeledoni*, based on material accumulated since the publication of Downs' opus. We also present a diagnosis of *G. betaniensis* of Colombia for comparative purposes. We further take this opportunity to provide additional information on recently discovered material (Appendix 1) of the poorly known Costa Rican species *G. downsi* Savage, 1981 and *G. ruthveni* Werner, 1925, although they are members of the *Geophis championi* species group (Downs, 1967).

Geophis brachycephalus, as presently understood, displays remarkable polychromatism in dorsal coloration. Individual snakes may be uniformly dark, as in the holotype (BMNH 1946.1.6.53) of *Geophis moestus* Günther, 1872, and the holotype (KU 31983) of *Geophis bakeri* Taylor, 1954 from Costa Rica: Cartago: Cartago and Costa Rica: Heredia: Isla Bonita, respectively (see locality explanation below); have bright red longitudinal stripes on a darker ground colour, as in the holotype (ANSP 3337) of *Colobognathus brachycephalus* (Cope (1871) from Costa Rica: San José: San José; or have red lateral blotches and/or cross bands on a darker ground colour, as in the holotype (ANSP 3306) of *Colobognathus dolichocephalus* (Cope (1871) from Costa Rica: San José: near San José. As pointed out by Downs (1967) and emphasized by Savage (2002) all three of these colour patterns may occur in individuals from the same locality.

Myers (2003) recognized that uniform and red-blotched variants were found together in the same population samples from sites in upland western Panama. He further noted that a series of seven specimens with uniform black dorsa from western Panama differed from the large dichromatic, upland sample (Slevin, 1942) from Panama: Chiriquí: Boquete, in having higher ventral counts. Comparison of a single male from each of these groups also showed differences in details of hemipenial morphology. Myers (2003) presumed that the snakes in question were from a population in which there was no dichromatism, and placed them as *Geophis, species*

inquirenda. He further commented that other upland dichromatic samples from western Panama had high ventral counts and that those from central Costa Rica resembled the uniform Panama snakes in this feature. Myers also questioned the status of *Geophis talamancae* Lips & Savage, 1994 (LACM 147196) from Costa Rica: Puntarenas: Las Tablas: Finca Jaguar, but reached no conclusion as to its possible synonymy with *G. brachycephalus* or *G. nigroalbus*.

MATERIAL AND METHODS

MATERIAL EXAMINED

Downs (1967) examined 232 snakes that he referred to *Geophis brachycephalus*. This included two of the seven specimens of Myers' *Geophis, species inquirenda*, two large series from upland Panama, one of which was Slevin's Boquete sample ($N = 58$) and the second from Chiriquí: Finca Lérica ($N = 37$), and four examples from Colombia. He also had available for study the unique holotype of *G. dunni*, 72 *G. hoffmanni* and 17 *G. zeledoni*. The senior author re-examined most of these, except for some in European museums, during preparation of his book on the Costa Rica herpetofauna (Savage, 2002) but we only list those that we examined for the purposes of the present study (Appendix 2). Reference to individual specimens follows the abbreviations in Leviton *et al.* (1985) with the additions indicated below.

Since the appearance of Downs' revision in 1967, additional material has accumulated from Costa Rica, principally contained in the Museo de Zoología, Universidad de Costa Rica (UCR) ($N = 64$) and the Natural History Museum of Los Angeles County (LACM) ($N = 21$). Additional material, mostly from western Panama and located in the Circulo Herpetológico de Panamá (CHP), includes nine snakes that appear referable to Myers' concept of *Geophis, species inquirenda*. Several smaller samples at other institutions as identified in the acknowledgements have yielded critical information. We have also been fortunate in obtaining data on a fine series of putative *G. nigroalbus* from Colombia housed at the Museo de Zoología, Universidad de Valle (UVC) ($N = 34$). We have not examined one snake from the Gorgas Memorial Laboratory, Panama (GML), but have relied on the complete description and figure in Myers (2003).

METHODS OF STUDY

Standard length (tip of snout to vent) and tail length were determined by moderately stretching preserved specimens alongside a metric rule. We follow Downs (1967) in considering snakes 201 mm or more in total length to be adults. We use the term 'smaller' snakes for individuals having a standard length of 200 mm or

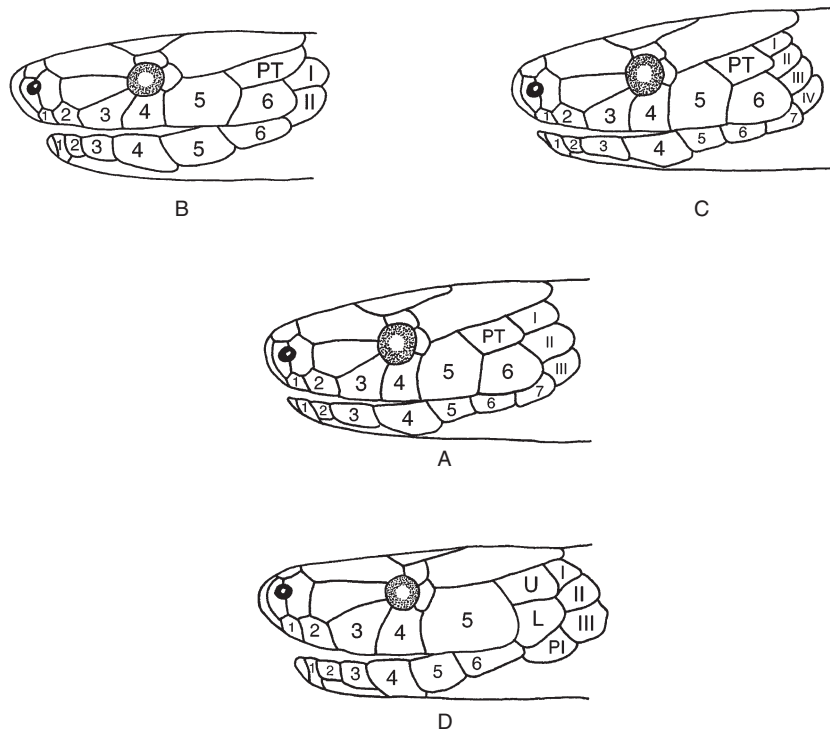


Figure 1. Lateral head scalation in *Geophis*: A, pattern typical of *G. zeledoni*; B, pattern typical of *G. brachycephalus* complex; C, variant pattern; D, pattern typical of *G. hoffmanni*. PT, posterior temporal; U, upper postsupralabial; L, lower postsupralabial; PI, postinfralabial; number of supra-labials and infra-labials indicated by Arabic numerals; number of jubals indicated by Roman numerals.

less in order to make inclusive comparisons among juvenile and small adults having complete or incomplete tails. Standard terminology for the head plates generally follows Peters (1964). However, we utilize the term jubals for the series of scales just posterior to the posterior temporal and the last supra- and infra-labial or the posterior temporal, postsupralabials and postinfralabial (Fig. 1). Ventral and subcaudal scutes were counted as described in detail in the section on Characters below. Where quantitative features are expressed by a three-number notation (e.g. 30–42.2 ± 1.1–43), the values are for the lower limit of the range, the mean and standard deviation, and the upper range limit, respectively. Examination of dentition utilized the technique described by Myers (1974). Hemipenes were prepared using the methods recommended by Myers & Cadle (2003). Descriptions of the hemipenes follow the terminology of Dowling & Savage (1960), as modified by Myers & Campbell (1981) and Zaher (1999).

We have only provided minimalist synonymies citing original descriptions of available names, different generic combinations, and the most recent treatments in Savage (2002), Myers (2003) and Solórzano (2004).

Terminology for describing broad habitats follows the senior author's modifications (Savage, 2002) of the Holdridge (1967) system. Data for localities are based on the 1:50 000 topographic maps from the Instituto Geográfico Nacional de Costa Rica, the Instituto Geográfico 'Tommy Guardia' de Panamá and Paynter (1997) and Restrepo & Wright (1987) for Colombia. All specimens reported here were collected before Geographical Positioning System (GPS) technology was available to and/or used by field biologists. Where localities are mentioned in the text they are cited, for example, as Panama: Chiriquí: Boquete, with the country listed first, followed by the department or province and then more specific localities. Localities for specimens not analysed or examined for this study are represented by open symbols on the maps; solid symbols indicate localities for specimens used in this analysis.

CHARACTERS

The exemplary study of *Geophis* by Downs (1967) reviewed the character states and variation in systematic features, especially scutellation, dentition, hemipenes, proportions and coloration for the genus.

In the section below we emphasize those characters found to be useful in distinguishing among the treated populations within the *Geophis sieboldi* group. Some redundancy with Downs' account is required, however, to describe interspecific versus intraspecific variation fully.

SCUTELLATION

Lateral head scalation: Four principal patterns occur in the arrangement of these plates in the species under consideration:

- A. six supralabials, two posterior to the eye, 0 + 1 short posterior temporal (PT) and three jubals bordering the posterior temporal and last supralabial (Fig. 1A).
- B. six supralabials, two posterior to the eye, 0 + 1 elongate posterior temporal (PT) and two jubals bordering the posterior temporal and last supralabial (Fig. 1B).
- C. as in B but four jubals bordering the posterior temporal (PT) and last supralabial (Fig. 1C).
- D. five supralabials, the last one large and posterior to the eye; no posterior temporal but an upper (U) and lower (L) postsupralabial and a postinfra-labial (PI) which are bordered posteriorly by three jubals (Fig. 1D).

Rare variants produced by fusion of two supralabials may reduce their number to five (A, B, C) or four (D) but the number of supralabials posterior to the orbit and the relationship to the postlabials (when present) and jubals to one another is unchanged.

Scale ornamentation: The upper surface of the dorsal and caudal scales may be variously embellished by striae, a median keel or a knobbed keel. In those species having smooth scales, weak striae may be noted under high magnification ($\times 250$) or transmitted light. Striae are more pronounced in forms having median keels on the scales. The keels are best developed on the upper seven to nine rows of dorsal scales, on those above the vent, and on the anterior caudal scales. Supracloacal scales may have median keels (ridges in Downs, 1967) in otherwise smooth-scaled species. These keels are usually raised into a knob at the anterior tip in forms having keels on the dorsal scales. Both kinds of supracloacal modifications tend to show sexual dimorphism either in occurrence (only in adult males) or degree of development, being more strongly and/or more widely distributed in adult males.

Keels on the dorsal and caudal scales have been denoted as distinct (Downs, 1967) or strong (Savage, 1981; Lips & Savage, 1994), moderate (Myers, 2003) or light (Downs, 1967). Downs recognized four pat-

terns of keeling in the *Geophis sieboldi* group: (1) distinctly keeled except on neck; (2) distinctly keeled on the posterior half of the body and anterior portion of the tail; (3) keeled on the posterior one-fifth of the body and lightly keeled above the vent and on the base of the tail; and (4) smooth except above the vent.

Conditions 2–4 seem clear enough. There is, however, some ambiguity involving the definition of condition 1. In snake taxa lacking hypapophyses on the posterior trunk vertebrae, as in *Geophis*, the neck is usually defined as the region where the anterior vertebrae have hypapophyses. These vertebrae make up the first 15–33% of the postcranial vertebrae (Kellicott, 1898; Hoffstetter & Gasc, 1969; in Gans, Bellairs & Parsons, 1969). However, Savage (1981) and Lips & Savage (1994) considered the neck as being a short region immediately posterior to the head. Downs (1967), by contrast, seems to have used the term for the anterior one-quarter to one-third of the body.

It now appears that strictly speaking snakes lack a neck entirely. This is evidenced by the presence of ribs on the anterior vertebrae, the presence of hypaxial muscles associated with them, and the forward extension of the peritoneal cavity all the way to the base of the head (Cundall & Greene, 2000 in Schwenk, 2000). Confirmation of this interpretation is provided by expression of the *Hox-6* gene, which specifies the boundary between cervical and thoracic regions, and the *Hox-8* gene, which usually specifies an area in the posterior thoracic region. Both are expressed directly behind the head in all snakes studied to date (Cohn & Tickle, 1999). In light of this evidence it seems best to use terms such as 'head not distinct from body' and 'head distinct from body' rather than mentioning a neck in describing conditions in snakes. The 'nuchal' region also might better be referred to as the postoc-cipital region.

In uniformly coloured or striped snakes, determination of the first keeled dorsal scale row in species of *Geophis* is complicated by scale iridescence and striation. Reflected light from the shiny scales or the low middle ridge on striated scales can easily be misinterpreted. Thus, there is some subjectivity in determining where keeling first appears on a snake's body. Repeated counts on the same individuals suggest a level of error of 5–10% between the lowest and highest records. Another problem is created by specimens that were poorly fixed or were preserved after they had died. Areas where nearly all the epidermis has been sloughed in some examples and/or there is a section of the body that is decayed make it impossible to determine if keels were present. Unless median scale keels are present on scales anterior to the sloughed areas, specimens with these kinds of damage were not used in the analysis of the extent of scale keeling.

To avoid ambiguity regarding the extent of keeling on the body we record the proportion (as a percentage) of the body length having keeled scales. In this system the value of 100% indicates that keels are present for the entire length of the body and a value of 75% indicates that the posterior three-quarters of the body has keeled scales, and so on. A similar scheme applies to keeling of the caudal scales.

The putative difference, along with the differences in ventral counts, between *Geophis talamancae* and *G. brachycephalus* was thought to be in the extent of dorsal scale keeling (Lips & Savage, 1994). The holotype (LACM 147196) and several other specimens subsequently referred to the former have about the posterior 33% of the body with keeled scales. *Geophis brachycephalus* was said to have all dorsals keeled 'except on the neck' (Downs, 1967). Myers (2003) suggested that the extent of keeling probably did not distinguish the two nominal forms. As the specimens of putative *G. talamancae* are subadults or juveniles it seemed possible that the extent of keeling of the dorsal scales might have an ontogenetic component with older (larger) snakes having more of the body covered with keeled scales than younger (smaller) ones. Consequently, we have included an analysis of the relationship between extent of keeling versus standard length for the Costa Rica, Boquete, Panama and Colombia populations. The condition of the snakes in the large Lérída, Panama, sample precludes determination of keeling in most examples, but we have included those where the keeling is determinable.

Segmental counts: The ventral and subcaudal scute counts are presumed to have a one to one relationship to the number of dorsal and caudal vertebrae, respectively, excluding the axis-atlas, the vertebrae in the cloacal region and the last caudal vertebra. The enlarged subcloacal scute ('anal plate') is not included in any of the counts defined below.

Ventrals: Myers (2003) discussed several methods used by various authors for counting ventral scutes. The protocol followed here is that used by Downs (1967) where the first scute posterior to the genials (chin shields) that is clearly twice as broad as long is regarded as the first ventral (Fig. 2B). In *Geophis* there are between one and three enlarged preventrals (postgenials) anterior to the first ventral defined by this method. The midgular scale(s) lying between the posterior genials and the preventrals are not included in the ventral count. This mode of counting averages about the same count as the Dowling (1951) method and usually two less than the classic method (Schmidt & Davis, 1941) followed by Slevin (1942).

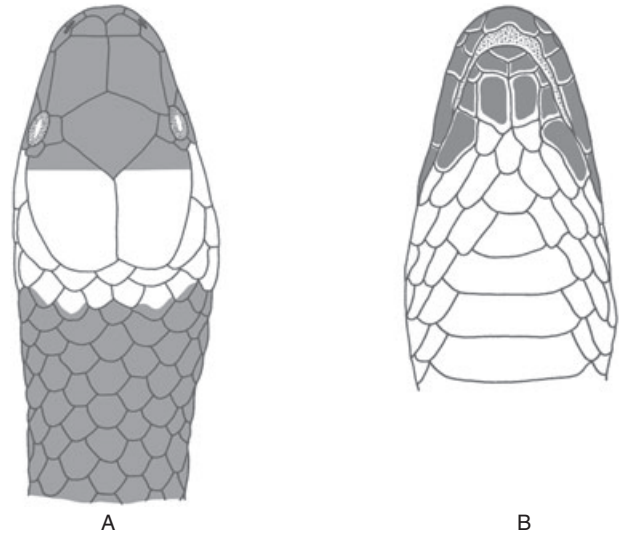


Figure 2. Head plates and coloration in *Geophis*: A, dorsal view showing light head band; B, ventral view; note two preventrals (postgenials) between midgular and first ventral.

Subcaudals: Counts of the paired subcaudals were made following Peters (1964) where the count begins at the first pair of scutes in contact across the midline of the tail and continues to the last pair. The terminal spine is not included in the count.

Total segmentals: There is definite sexual dimorphism in the number of ventrals (higher in females) and subcaudals (higher in males) in most *Geophis*. However, there is usually not a significant difference between the sexes in most samples in total segmental counts, the number of ventrals plus the number of subcaudals (Downs, 1967).

COLORATION

Dorsal and caudal: The lateral and upper surfaces of the body and tail exhibit considerable colour variation. In most populations, the dark ground colour is uniform glossy black in life or it appears greyish approaching the shedding process. The ground colour usually fades to brown in preservative. The light pattern elements found on many examples are red or red-orange in life but may fade to pink or cream in preservative. The following are the principal variants: Uniform: uniform

Red spots: paired small lateral spots that are often offset (Fig. 3A)

Red blotches: paired but usually offset irregular lateral blotches (Fig. 3C)

Red bands: transverse bands (Fig. 3C) that do not extend laterally to the 1st scale row

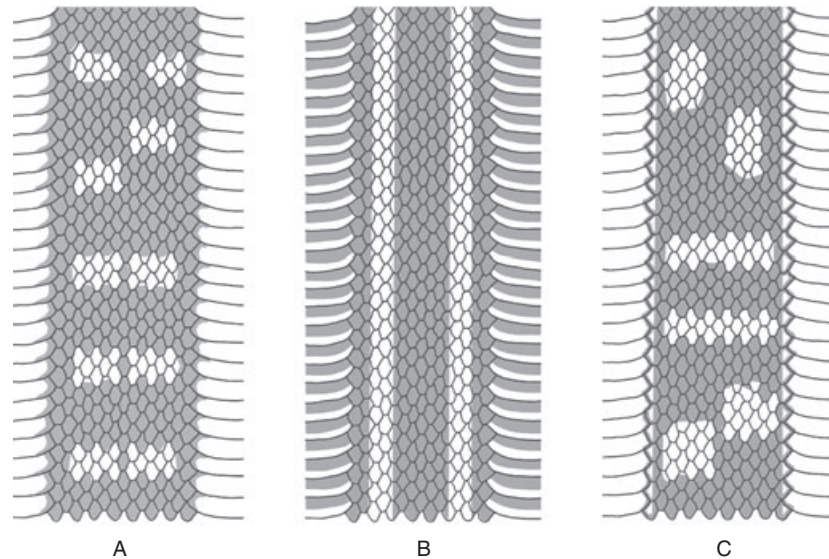


Figure 3. Dorsal patterns in *Geophis*: A, light spots, typical of snakes from western Panama; B, longitudinal lateral light stripes found in many Costa Rican snakes; C, light blotches and transverse bands, typical of many snakes from Costa Rica.

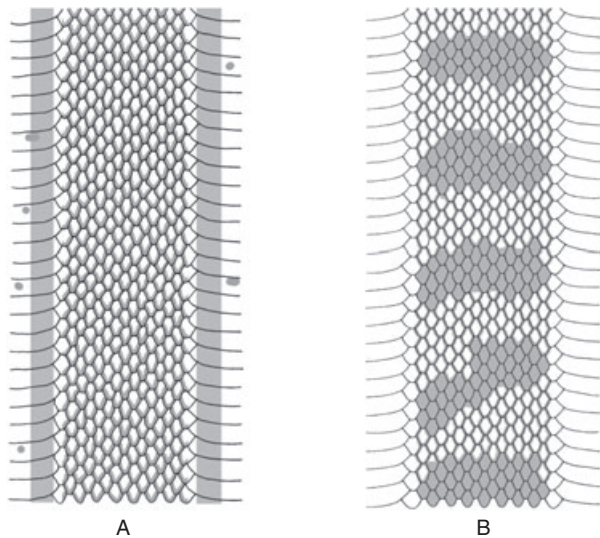


Figure 4. Dorsal patterns in *Geophis*: A, dorsal pattern of *G. betaniensis*; B, dark transverse bands typical of *Geophis dunni*.

Red stripes: paired longitudinal light stripes that may be continuous or broken into several interrupted segments (Fig. 3B)

Dark bands: transverse bands (Fig. 4A) that do not extend laterally to the ventrals.

Red blotches and transverse bands often are found as pattern elements on the same snake (Fig. 3C). Downs (1967) and Myers (2003) refer to the transverse bands as half rings and dorsal rings, respectively.

Head band: A white head band involving the parietal plates and extending a short distance onto the body is present in many, but not all, juveniles (Fig. 2A). It may be complete but tends to be invaded by dark pigment through the course of ontogeny. Frequently, the band is broken by dark pigment along the midline and then spreads laterally. In intermediate-sized individuals, the band is evident but suffused with dark pigment, except laterally. The suffusion becomes more concentrated in some examples so there is no contrast with the head or body colour although light lateral remnants of the band are present. In some fairly large snakes (220–250 mm in total length), the band is completely obscured by dark pigment but appears reddish-brown in preservative and contrasts with the head and body colour. The smallest juvenile with a complete head band is 135 mm in total length. A complete head band is only present in juveniles under 200 mm in total length. It occurs in uniform, red-banded and red-striped individuals. Other juveniles in this size range have the band variously suffused with dark pigment but some lack any indication of the band. Several larger snakes (222–247 mm in total length) have the band completely suffused by darker pigment (dark reddish-brown in preservative) that contrasts with the darker dorsum. The band is white in uniform and red-striped individuals and red in spotted and blotch/banded ones. The white head band is retained in adult *Geophis bellus*.

Chin: The chin and anterior infralabials are usually heavily marked with dark pigment (Fig. 2B).

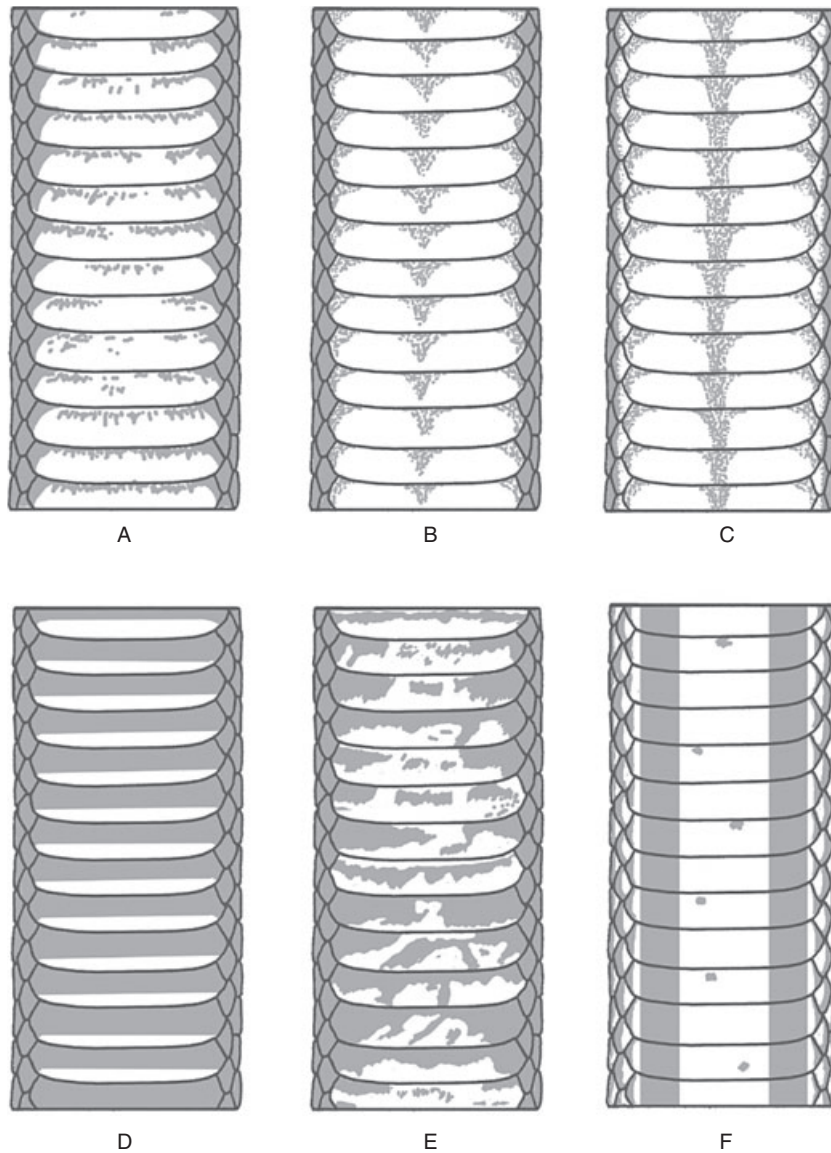


Figure 5. Ventral patterns in *Geophis*: A, speckled; B, spotted; C, lined; D, banded; E, variegated, typical of *Geophis zeledoni*; F, longitudinal ventrolateral dark stripes, typical of *Geophis betaniensis*.

Ventral: Snakes in this group may have the venter white over most of its length in life, but varying from white to cream in preservative, or variously marked with dark pigment. The tips of the ventrals are marked with dark pigment (Figs 3A, B, 5) in most examples. In a few juveniles and intermediate-sized individuals having immaculate venters, the first scale row on each side is bordered or marked anteriorly with dark pigment (Fig. 3C).

The following are the principal ventral pattern types. In most cases when present, the heaviest dark pigment is concentrated along the anterior margin of each ventral scute as seen through the overlapping posterior margin of the preceding one.

Immaculate: white

Speckled: scattered small dark areas (Fig. 5A)

Spotted: speckles concentrated along the midline to form spots (Fig. 5B)

Lined: concentrations of dark pigment along midline form an irregular midventral stripe (Fig. 5C)

Banded: an anterior band of dark pigment on each ventral contrasting with the light posterior margin (Fig. 5D)

Variegated: extensive irregular dark markings covering most of each ventral (Fig. 5E)

Striped: paired broad dark ventrolateral stripes present (Fig. 5F)

Uniform: black.

Table 1. Sexually dimorphic and ontogenetic variation in tail length as a percentage of total length in four population samples of the *Geophis brachycephalus* complex

	Juvenile males	Juvenile females	Adult males	Adult females
Costa Rica	<i>N</i> = 9 15.0–17.1 ± 1.8–20.0	<i>N</i> = 5 11.8–13.5 ± 1.2–15.0	<i>N</i> = 45 15.9–18.0 ± 1.4–21.8	<i>N</i> = 32 12.2–15.0 ± 1.1–16.8
Lérida	<i>N</i> = 7 10.2–16.4 ± 2.7–19.4	<i>N</i> = 6 13.4–15.8 ± 2.3–20.0	<i>N</i> = 1 16.2	<i>N</i> = 4 16.0–17.7 ± 1.1–18.5
Boquete	<i>N</i> = 14 15.4–16.9 ± 1.1–19.1	<i>N</i> = 6 14.7–16.5 ± 1.8–19.9	<i>N</i> = 17 17.0–18.5 ± 0.8–19.8	<i>N</i> = 21 15.1–16.4 ± 0.8–19.0
Colombia	<i>N</i> = 1 17.9	<i>N</i> = 1 17.2	<i>N</i> = 22 16.0–19.5 ± 1.8–21.9	<i>N</i> = 8 15.0–16.1 ± 0.6–16.8

The extent and intensity of the dark pigmentation increase with age. In smaller specimens it may be expressed only on the posterior ventrals. In larger examples it usually shows an increase in concentration from anterior to posterior ventrals.

Subcaudal: The subcaudals may be nearly immaculate (white to cream in preservative), but even the smallest juveniles have some dark flecking. The amount of dark pigment increases with age. In most cases the coloration resembles that of the ventrals but the dark pigment tends to be more extensive and intense than on the ventrals of the same snake. In some adult specimens the subcaudals are nearly uniform black with only a small light area or are completely black.

RELATIVE TAIL LENGTH

This variable is expressed as a percentage of total length. Males have relatively longer tails than females and juveniles have relatively shorter tails than adults of the same sex. For this reason, ranges and means are given separately for juveniles (under 201 mm in total length) and adults (Table 1). For ease of interpretation, statistical tests of sexual dimorphism in relative tail length include pooled data for juveniles (when sex is known) and adults.

MAXILLO-PALATO-PTERYGOID ARCH

Most members of the *Geophis sieboldi* group have the maxilla extending slightly anterior to the suture between the second and third supralabial; its anterior extension about equal to that of the palatine; posterior one-third curving ventrally in lateral view; bearing 8–15 rather stout, subequal teeth; anterior tip pointed and toothless; posterior end depressed and tapering to a blunt point; anterior tip of ectopterygoid single, not expanded. Two species differ from other members of the group in having a tooth at the anterior tip of the maxilla or the first tooth preceded by a

short toothless area and in one of these the maxilla is not dorsoventrally depressed.

HEMIPENES

The hemipenes of lower Central American and Colombian snakes of the *Geophis sieboldi* group share the following features. The organ is capitate with a biramous (dividing within the capitulum) sulcus spermaticus. The pedicel is covered with spinules or spicules and two to four large spines distally. The truncus is covered by spines and small hooks. A large naked pocket is present basally on the sulcate side. Differences exist among populations in the size and number of spines on the pedicel and truncus. Most species have a centrolineal sulcus spermaticus but one has a modified centrifugal sulcus. The capitulum may be calyculate or mostly covered with small spines. Differences also exist in the shape and relative length of the capitulum and whether the hemipenis is single, slightly bilobed or definitely bilobed.

COMPARISONS OF POPULATIONS CURRENTLY REFERRED TO *G.*

BRACHYCEPHALUS AND *G. NIGROALBUS*

Before turning to an analysis of the status of *Geophis talamancae* Lips & Savage, 1994 and the snakes assigned to *Geophis*, *species inquirenda* by Myers (2003) it is necessary to clarify the situation for populations placed in *Geophis brachycephalus* and *G. nigroalbus*. In this section, comparisons among four major population samples will be detailed. This analysis forms the basis for evaluating the status of these populations, specimens from outlying localities, and the equivocal *G. talamancae* and *G. species inquirenda*. Throughout this and subsequent sections in our analysis, the snakes of these four populations and individuals [e.g. *G. talamancae* and *G. species inquirenda sensu* Myers (2003)] resembling them

in the characteristics listed below are termed the *Geophis brachycephalus* complex.

The four populations share the following features (Fig. 1B) that will distinguish them from other species in the *G. sieboldi* group except for the nominal species *Geophis talamancae* and *G., species inquirenda*: (1) usually six supralabials, rarely five or seven; (2) two supralabials lie posterior to the orbit; (3) no anterior temporal or postlabials; (4) last supralabial usually separated from the parietal by the elongate posterior temporal; (5) usually two jubal scales posterior to posterior temporal and last supralabial and upper jubal separated from contact with the parietal by the elongate posterior temporal; (6) dorsal scales in 15–15–15 rows; (7) caudal scales strongly keeled except in juveniles; (8) maxilla curving ventro-posteriorly; anterior tip pointed, toothless; posterior end depressed.

VARIATION IN THE COSTA RICA SAMPLE

Downs (1967) examined or obtained data on 124 snakes (54 males and 70 females) from this population. He noted that there seemed to be no geographical trends within his sample. The sample used in the present analysis includes 14 specimens available to Downs and additional material to total 47 males over 200 mm in standard length, nine smaller males, 34 females over 200 mm in standard length, nine smaller females and four juveniles of indeterminate sex 112–193 mm in standard length. The holotype of *Geophis talamancae* (LACM 147196) was not included in this analysis and will be treated separately later in this paper. The largest male is 357 mm in standard length but has an incomplete tail. The largest male with a complete tail is 354 mm in standard length with a tail length of 73 mm (17.2% of total length); total length 427 mm. The largest female is 438 mm in standard length with a tail length of 69 mm (13.3% of total length); total length 496 mm. Relative tail lengths as percentages of total length are 15–17.1 ± 1.8–20% in juvenile males ($N = 9$), 15.9–18.0 ± 1.4–21.8% in adult males ($N = 45$), 11.8–13.5 ± 1.2–15.0% in juvenile females ($N = 5$) and 12.2–15.0 ± 1.1–16.8% in adult females ($N = 32$). Note that when summarizing characters by age–sex classes, totals do not necessarily add up to the total N for each population because not all individuals could be scored for all characters.

Scutellation (head scalation): Thirteen examples have a short posterior temporal and three jubals on one side of the head; six have this condition on both sides. One of the latter (UCR 1434) has the upper jubal on the right side forming an elongate scale through fusion with the next posterior scale bordering the parietal. One specimen (LACM 15492) has a single

large jubal (fusion of the usual two) on the left side and two on the right. All have 0–0 preoculars and 1–1 postoculars. Supralabials, including Costa Rican specimens in Downs (1967), have counts of 5–5 ($N = 2$), 5–6 ($N = 9$), 6–6 ($N = 212$) and 6–7 ($N = 3$). One example (LACM 151271) has five supralabials on the left side with supralabial 3 formed by fusion of supralabials 3 and 4. In this specimen, also on the left side of the head, an azygous triangular scale borders the loreal and is wedged between portions of supralabials 2 and 3. Most snakes have supralabials 3 and 4 bordering the orbit, but 2–3, 3–3, 3–4–5 and 4–5 occur on one side in one example each. Infralabials, including Costa Rican specimens in Downs (1967), have counts of 5–5 ($N = 1$), 5–6 ($N = 4$), 6–6 ($N = 116$), 6–7 ($N = 49$), 7–7 ($N = 47$), 7–8 ($N = 1$) and 8–8 ($N = 3$); infralabials bordering genials (no separate values in Downs, 1967): 3–4 ($N = 3$), 4–4 ($N = 40$), 4–5 ($N = 15$), 5–5 ($N = 17$) or 5–6 ($N = 1$). One snake (UCR 15492) has the first infralabials separated from contact with each other by the mental and the forward-projecting left genial. Other variants reported by Downs (1967) include: loreal excluded from the orbit by contact between supralabial 3 and the prefrontal (UMMZ 123195; KU 57103); one to two postoculars and small anterior temporal split off from supralabial 5 (KU 63810); two to three postoculars (MCZ 15321).

Dorsal and caudal scale keeling: One small juvenile (142 mm in total length) has the keels on the body restricted to the area above and just anterior to the vent. Variation in individuals with definite keels is 22–59.6 ± 16.0–99.0% of the dorsal scale rows. The tail has strong keels over most of its length (50–90%) except in one juvenile (190 mm in total length) with relatively weak keels.

Segmental counts: Ventrals are 129–140.1 ± 4.2–149 in males and 136–141.9 ± 2.5–147 in females. Subcaudals are 35–39.5 ± 3.3–48 in males and 29–33.4 ± 2.2–39 in females. Ventrals plus subcaudals for all individuals are 168–177 ± 4.5–190. These values are similar to those recorded by Downs (1967) for his Costa Rica sample with 131–138.5–148 in males, 135–140.7–145 in females; subcaudals 36–40.2–48 in males and 30–33.5–39 in females. Males with high subcaudal counts, in the range 44–48, occur at scattered localities. High numbers of subcaudals in females are not consistently from these same sites. Downs (1967) did not give values for ventrals plus subcaudals for Costa Rican specimens, but for all snakes included in his concept of *G. brachycephalus*.

Coloration: Fifty-seven snakes, 28 males, 28 females and one of indeterminate sex 199–438 mm in standard length, have a uniform dorsum. The ventrals

and subcaudals are banded (Fig. 5D) in most individuals but small juveniles may have the ventrals immaculate or with some dark speckling (Fig. 5A), usually posteriorly if present. The subcaudals in large adults and some juveniles are mostly to entirely black. In a few juveniles the subcaudals have only some dark speckling.

Thirty-two individuals, 18 males, 12 females, and two of indeterminate sex ranging between 126 and 370 mm in standard length, have a striped pattern (Fig. 3B). Eleven of these have even-edged stripes located on scale rows 2–3–4–5 (1/2–1–1–1/2) or 2–3–4 running the length of the body and occasionally onto the tail. Thirteen have stripes evident but invaded by dark pigment. In some of these the stripes are irregular or wavy in form because each scale in the stripe is marked with black. In a few the black marks are expanded to suffuse the stripe wholly and render it obscure. In others the black pigment obliterates parts of the stripe to break it up into disjunct sections with the anterior elements consisting of small blotches or crescents with the upper margin convex. All of these snakes have the ventrals banded with dark pigment (Fig. 5D) and their subcaudals are mostly black.

In three of the males, the stripes are fragmented into a series of very small and suffused light spots. These pattern elements are much smaller than the blotches found in specimens having a blotched and/or banded pattern (Fig. 3A, B). The spotted individuals also have the banded ventral pattern and mostly black subcaudals. These three specimens were scored as being 'striped' for the analysis of pattern variation.

Fourteen snakes, ten males, three females, and one of indeterminate sex ranging in size between 112 and 334 mm in standard length, exhibit a pattern of light blotches and/or bands (Fig. 4C). The number of blotch and band positions, counting each pair of blotches and each band as one, is $16\text{--}20.9 \pm 4.1\text{--}29$. Of these, 0–10 are complete transverse bands, 0–14 are offset bands interrupted on the midline and 0–15 are blotches that are usually offset. There is no consistent sequence of bands and other pattern elements. The tail is marked by 1–6 bands or blotches, the last one or two usually reduced to small spots. One male (KU 31988) has 24 blotch/band positions but on the left side of the body three oblong blotches have been formed by fusion of six, six and eight blotches. The venter in all of these snakes is immaculate with some speckling on the most posterior few ventrals in large individuals and the subcaudals are banded.

Sixteen snakes 200 mm or less in total length include four (three uniform, one banded) lacking a light head band. In others in this size range the head bands are complete (one uniform, one striped, two banded), broken (one striped), suffused (four uniform,

one striped) or obscure (two uniform). One of the blotched and banded snakes (UCR 11721) 163 mm in total length has a complete red head band. Three examples with uniform dorsa 222–247 mm in total length have obscure head bands and one large uniform adult (UCR 1054) has remnants of the head band laterally.

Hemipenes: Description based on everted organs (UCR 779, 5357, 14915, 16034). Organ slightly bilobed. Short pedicel covered with spicules basally and bearing two large spines distally. Short truncus covered with 20–30 medium spines and hooks. Capitulum moderately long but slender, about 2.5 times as long as short truncus on asulcate side, and covered with spinulate calyces.

VARIATION IN THE LÉRIDA, PANAMA, SAMPLE

Finca Lérída lies on the eastern slope of Volcán Barú at c. 1600 m in the Distrito de Boquete, Provincia de Chiriquí. We have re-examined all 37 specimens listed by Downs (1967) in his material examined. These include those listed as being from 'Panama Sabanas' but which are actually from Finca Lérída (see Appendix 3). However, Downs mentions only a total of 35 specimens in his description. The Lérída sample consists of three males over 200 mm in standard length, 11 smaller males, 11 females over 200 mm in standard length, 11 smaller females and one juvenile of indeterminate sex.

Most of these specimens appear to have been preserved in concentrated formalin and are shrunken and very brittle. In all but a few, the body and tail are convoluted and distorted, making measurement difficult or impossible. The head plates and dorsal scales are wrinkled in most examples, making it impossible to evaluate the degree of keeling in the latter. Keels on the caudal scales are strong and evident on most snakes. The 'Panama Sabanas' examples are in better condition.

The largest male is 269 mm in standard length with a tail length of 52 mm (16.2% of total length); total length 321 mm. The largest female is 290 mm in standard length but has an incomplete tail. The largest female with a complete tail is 254 mm in standard length with a tail length of 56 mm (18.1% of total length); total length 310 mm. Relative tail lengths as percentages of total length are $10.2\text{--}16.4 \pm 2.7\text{--}19.4\%$ in juvenile males ($N = 7$), 16.2% in the adult male, $13.4\text{--}15.8 \pm 2.3\text{--}20.0$ in juvenile females ($N = 6$) and $16.0\text{--}17.7 \pm 1.1\text{--}18.5\%$ in adult females ($N = 4$).

Scutellation (head scalation): Five examples have a short posterior temporal (Fig. 1A) on one side of the head; one has this condition on both sides. Preoculars

0–0; postoculars 1–1. Supralabials 5–5 ($N = 1$), 6–6 ($N = 36$); supralabial 4 bordering orbit ($N = 1$), supralabials 3–4 bordering orbit ($N = 36$). Infralabials 6–6 ($N = 21$), 6–7 ($N = 11$), 7–7 ($N = 5$); infralabials contacting genials: 4–4 ($N = 21$), 4–5 ($N = 11$) or 5–5 ($N = 5$).

Dorsal and caudal keeling: Downs (1967) examined this series and indicated that they all had keeled dorsal scales, except on the neck and extensive and strong keeling on the tail. In one large female, 80% of the dorsal scale rows are keeled. Only 10–24% of the rows are keeled in small individuals (under 178 mm in total length) and moderate-sized specimens had 29–90% of the rows with keels. Variation in the percentage of dorsal scale rows with keels is (all individuals): $10\text{--}34.1 \pm 22.5\text{--}80.0\%$. The caudal scales are heavily keeled for 80–90% of the length of the tail, except in the smallest snakes, which have keels on the basal one-third of the tail.

Segmental counts: 124–129.1 \pm 2.1–132 ventrals in males, 125–131.7 \pm 3.3–139 in females; subcaudals 35–37.8 \pm 1.4–40 in males, 30–32.9 \pm 2.1–37 in females; ventrals plus subcaudals 158–165.4 \pm 3.1–171.

Coloration: Twenty-seven snakes, ten males and 17 females, ranging between 111 and 290 mm in standard length have a uniform dorsum and upper tail. The venter is immaculate in smaller snakes in this group. In several snakes the anterior venter is immaculate followed posteriorly by speckling ($N = 5$) or the lined condition ($N = 3$). Anterior speckling followed posteriorly by banded ventrals occurs in one individual, two individuals have the lined state and 13 the banded condition for the entire length of the venter. The subcaudals are banded to mostly black in all specimens.

Five males and five females have the anterior one-quarter to one-third of the body uniform black followed by 6–10.8 \pm 3.47–18 paired, usually offset, red spots and the upper surface of the tail uniform black. There are no red transverse bands or longitudinal stripes in the patterns of this series. In one male (ANSP 24767), 133 mm in standard length, the 11 pairs of spots are nearly obliterated by dark pigment. One example has some speckling on the posterior ventrals but in all others the ventrals are immaculate. The subcaudals are mostly or entirely black.

VARIATION IN THE BOQUETE, PANAMA, SAMPLE

These snakes were collected at or in the vicinity of Boquete, Distrito de Boquete, Provincia de Chiriquí, Panama (c. 1200 m), an area about 7 km south-east of

Finca Lériida. This population is represented by material in the California Academy of Sciences referred to *G. brachycephalus* by Slevin (1942) that had been collected by him in 1939, with the exceptions noted below, and three snakes from other collections (ANSP 22422; UMMZ 57957–59758). As pointed out by Downs (1967), the California Academy series included representatives of two other species of *Geophis*, the second known specimen (CAS 78977, an adult female) of *Geophis championi* Boulenger, 1894 and two examples (CAS 78976, an adult female; CAS 79033, a juvenile) of *G. hoffmanni* (Peters, 1859). We have re-examined all of the Boquete snakes and confirm Downs' identifications for CAS 78976–78977 and 79033. In our analysis of variation we have added CAS 78943, which was not included in Slevin's (1942) summary of scutellation. In addition, two problematic snakes (CAS 78979 and 78983, both males) with exceptionally high ventral counts included in *G. brachycephalus* by Slevin (1942), Downs (1967) and Myers (2003) agree in characteristics with Myers' *G.*, *species inquirenda* and will not be included in this analysis. They will be treated separately in a later section.

There is a discrepancy in Downs (1967) regarding the number of specimens from this locality. In the specimens examined he lists: CAS 78940–78975, 78977–79001 and the three specimens in other museums for a total of 64. However, as pointed out above, CAS 98977 is a specimen of *G. championi*, which means the actual number referred to *G. brachycephalus* would be 63. Earlier Downs cites a total of 58 snakes from Boquete. He then indicates that there are 34 males and 28 females, a total of 62 examples of this species from that locality. In a later section, he states there are 18 snakes with uniform coloured dorsa and 41 with a light blotched pattern, for a total of 59 from Boquete. Our reanalysis of the Boquete series agrees with the total count of 58 for CAS specimens following Slevin (1942), excluding the three specimens not conspecific with the rest of the species in the series and two tentatively referred to *G. species inquirenda*. If the three Boquete specimens in other museums are included, the total is 61. We cannot explain the discrepancies in Downs' totals unless the specimen of *G. championi* (CAS 78977) is added to Downs' numbers ($62 + 1 = 63$) in one case, but this would not account for the other totals of 58 and 59.

This population is represented by 14 males over 200 mm in standard length, 19 smaller males, 21 females over 200 mm in standard length and seven smaller females. The largest male is 282 mm in standard length but has an incomplete tail. The largest male with a complete tail is 280 mm in standard length with a tail length of 65 mm (18.8% of total

length); total length 345 mm. The largest female is 292 mm in standard length with a tail length of 59 mm (16.8% of total length); total length 351 mm. Relative tail lengths as percentages of total length are 15.4–16.9 ± 1.1–19.1 in juvenile males ($N = 14$), 17–18.5 ± 0.8–19.8 in adult males ($N = 17$), 14.7–16.5 ± 1.8–19.9 in juvenile females ($N = 6$) and 15.1–16.4 ± 0.8–19.0% in adult females ($N = 21$).

Scutellation (head scalation): One example has a short posterior temporal and three jubbals on the left side of the head; two have this condition on both sides. All have preoculars 0–0; postoculars 1–1; supralabials 6–6 with 3–4 bordering the orbit ($N = 61$). Infralabials 6–6 ($N = 36$), 6–7 ($N = 10$), 7–7 ($N = 13$); infralabials contacting: genials 4–4 ($N = 34$), 4–5 ($N = 10$), 5–5 ($N = 13$).

Dorsal and caudal scale keeling: Keels on the dorsal scales are absent, weak or restricted to the area above the vent in most small juveniles (119–143 mm in total length). The statistics for individuals with more extensive keeling, including several small juveniles (199–133 mm in total length), are 10.0–53.1 ± 16.0–88.0% of the dorsal scale rows with keels. The caudal scales are strongly keeled for most of the tail length (66–90%), except for two small snakes (123–204 mm in total length) with strong keels only on the base of the tail and several juveniles (92–119 mm in total length) that have no caudal keels.

Segmental counts: 118–122.9 ± 2.3–128 ventrals in males, 121–125.7 ± 2.5–130 in females; subcaudals 36–38.3 ± 1.3–41 in males, 33–34.3 ± 1.2–38 in females; ventrals plus subcaudals 154–160.6 ± 3.0–166.

Coloration: Slevin (1942) notes that in life these snakes are uniform black or black with red markings above and the ventral ground colour is white. Twenty-one specimens, 11 males and 10 females, have a uniform dorsum and upper surfaces of the tail. The venter is immaculate in small examples under 150 mm in total length and some larger ones in the range 243–302 mm. Most examples over 200 mm in total length have some dark markings on the venter, two with speckling, one with midventral spots, two with the lined condition, two immaculate anteriorly and banded posteriorly, and two with midventral marks anteriorly and banded ventrals posteriorly. As a high proportion of snakes in the sample are juveniles it seems likely that all adults will have some kind of dark markings on the venter. The subcaudals in all but the very smallest individuals are mostly black.

Forty snakes, 22 males and 18 females, have the anterior one-third to one-half of the body uniform

black followed by pairs of usually offset red spots that are rarely expanded into oblong blotches. There are 7–13.2 ± 3.42–19 spot positions counting each pair of spots as one. There are no transverse red bands in the dorsal pattern. The tail is uniform black above in these snakes. The most anterior and posterior spots tend to be suffused with dark pigment. In some individuals the spots are obscured by dark pigment throughout. In one female (CAS 78994) 275 mm in total length, the red markings are reduced to barely discernible spots by expansion of dark pigment. In one male (CAS 78944) 242 mm in total length, several of the lateral spots have fused with an adjacent one to produce oblong blotches. These may be paired or asymmetrical on the two sides of the body. On the right side there are two spots + two fused into a blotch + three spots + an elongate blotch + two spots; on the left side, three spots + four spots fused into a blotch + two spots (= ten and nine spot positions). The upper margins of the oblong blotches have a slight bulge in their outline. In one male (CAS 78941) 290 mm in total length there are two pairs of spots + seven spots fused into a longitudinal stripe with a wavy upper margin on scales rows 2–3 + one pair of spots (= ten spot positions). On the left side there is one spot + eight spots fused into a stripe with an irregular upper margin (= nine spot positions). These two specimens are those that Slevin (1942) evidently considered to have short stripes. However, these elongate markings do not appear to be homologous to the longitudinal stripes found in Costa Rica material but correspond to fused spots.

The majority of patterned individuals have immaculate venters ($N = 22$). In one of these snakes the venter is immaculate anteriorly but with heavy dark pigment on the last several ventrals. Speckling is present in two small specimens and one has midventral spots. Nine examples have the lined pattern throughout the length of the venter. In four snakes the lined condition is present on the anterior venter but is replaced by dark bands on the last several ventrals.

The subcaudals tend to be banded with dark pigment in most individuals having uniform black dorsa. In patterned snakes the subcaudals are usually mostly to entirely black with less pigmentation in smaller individuals.

Snakes less than 200 mm in total length include six without light head bands (two uniform, four spotted). In others the head band ranges from complete (one uniform), through partially broken (one uniform, one spotted), broken (two uniform, four spotted), to remnant (six spotted). No large individuals with a uniform dorsum have any indication of a head band. Among spotted snakes two males, 244 and 325 mm in total length, and four females, 234–304 mm in total

length, have the head band obscured by dark pigment. One large male (CAS 78958), 248 mm in total length, has only a remnant of the head band.

Hemipenes: Based on an everted hemipenis (UMMZ 57958). Organ slightly bilobed. Pedicel covered with spicules basally and bearing two or three large spines distally. Short truncus bearing 20–30 medium spines and hooks. Capitulum, robust and relatively short, about twice as long as truncus on asulcate side and covered with spinulate calyces.

Remarks: As mentioned above, Slevin (1942) included CAS 79077, the second known specimen (a female) of *Geophis championi* and CAS 98976, an adult female, and CAS 97033 an unsexed juvenile, *G. hoffmanni* from Boquete in his listing of scale counts for Boquete *G. brachycephalus*. Myers (2003) inadvertently included the counts for the two females in his comparisons of the Boquete sample with his *Geophis, species inquirenda*. Removal of the data for these two specimens affects the ventral and subcaudal counts and their means for females in Myers' Table 3. The numbers used by Myers are from Slevin (1942), who used the classic method of counting ventrals. These corrections change the values from 118–127.4–132 ventrals to 123–127.7–132 and 26–33.6–38 subcaudals to 33–34.2–38 for the 22 females in Slevin's list. These compare with the values of 123–127.1–132 ventrals in Downs (1967), who used the same method of counting ventrals as we have in the present paper. Downs based his counts on 28 females from Boquete including four juvenile CAS females not sexed by Slevin. However, we suspect that he used Slevin's original counts for the adult females from Boquete. Our recounts of these snakes, which do not include the prefrontals, are lower for the maximum (130) and minimum (121) than those reported by Downs as 132 and 123. The latter two numbers are identical to those in Slevin (1942). The listed ranges in males, not including CAS 38979 or 78983, tentatively assigned here to *G. species inquirenda*, are as follows: Slevin (1942) 121–129 ($N = 16$) and Downs (1967) 119–128 ($N = 32$). Our counts are 118–128 ($N = 33$).

VARIATION IN THE COLOMBIA SAMPLE

Geophis nigroalbus was described by Boulenger (1908) from Colombia: Valle del Cauca: Pavas (1350 m) on the western slope of the Cordillera Occidental. Downs (1967) placed this form in the synonymy of *Geophis brachycephalus*. Restrepo & Wright (1987) regarded *G. nigroalbus* as valid based on a large series from Colombia: Valle del Cauca: Bolivar: Betania (1680 m) on the eastern slope of the Cordillera Occidental. One of these was deposited in LACM

(136675). Myers (2003) examined five of the six specimens listed by Downs from Colombia, including the holotype (BMNH 1946.1.6.50) of *G. nigroalbus* and the LACM specimen. He was reluctant to conclude that a single species was represented based on this small sample. Fortunately, Dr Fernando Castro of the Universidad de Valle kindly arranged to have data recorded and sent to us for the Betania series that clarify the status of the Colombia snakes. C. W. Myers also aided our analysis by providing data for the Colombia specimens he examined for his 2003 paper.

Comparison of the characteristics of the Betania series and the holotype of *G. nigroalbus* indicates they represent the same taxon. The segmental counts for the type (137 ventrals, 45 subcaudals for a total count of 182) fall well within the range for the Betania sample as do all other features. The complete white head band considered distinctive and illustrated by Myers (2003) also occurs in several small *Geophis* from Betania. Three other Colombian snakes, one juvenile (BMNH 98.10.27.3) from Colombia: Antioquia: Santa Rita, and two adults from 'Colombia' in the Field Museum of Natural History, also show features encompassed by the variation in the Betania snakes. Neither Myers nor we could locate or examine the specimen (Fred Medem 91) from the Cordillera Oriental: Santander: Landazuri (900 m) cited by Downs (1967). It seems likely that the latter may represent an undescribed species belonging to the *G. sieboldi* group.

The Colombian sample consists of 39 snakes, 22 males over 200 mm in standard length, two smaller males, six females over 200 mm in standard length, three smaller females and six juveniles of indeterminate sex. The largest male is 315 mm in standard length with a tail length of 85 mm (21.3% of total length); total length 400 mm. The largest female is 316 mm in standard length with a tail length of 60 mm (16.0% of total length); total length 376 mm. Relative tail lengths as percentages of total length are 17.9% in the juvenile male holotype ($N = 1$), 16.0–19.5–1.8–21.9% in adult males ($N = 22$), 17.2% in the juvenile female and 15.0–16.1–0.6–16.8% in adult females ($N = 8$).

Scutellation (head scalation): Four examples have the supraocular and postocular separated from contact on both sides of the head by a narrow projection of the parietal shield. One snake (FMNH 54882) has the upper jubal fused with the posterior temporal and two jubals on both sides of the head; two have a short posterior temporal and three jubals on one side; another has a short posterior temporal and four jubals on one side (Fig. 1C). Seven have a short posterior temporal on both sides of the head; one of these has four jubals on both sides, and the others have

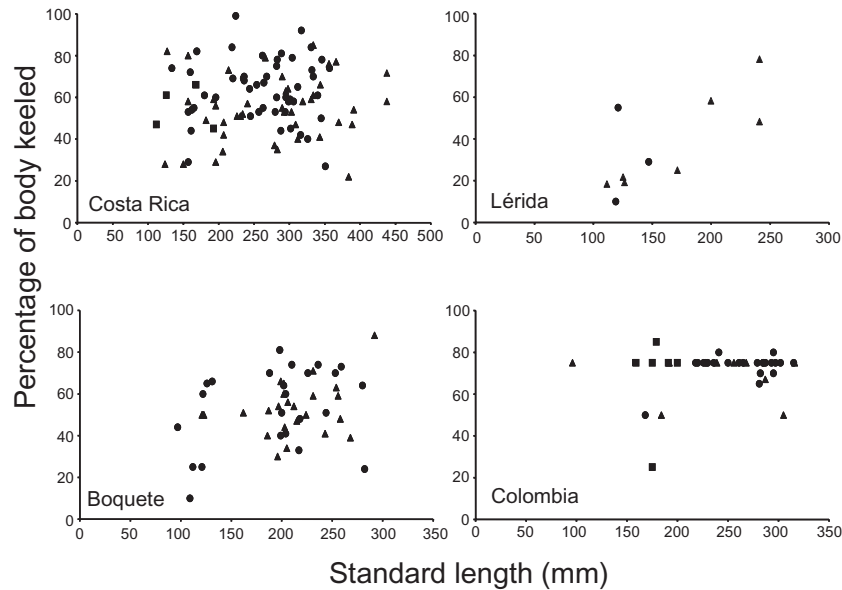


Figure 6. Extent of keeling on dorsal scales versus standard length in four population samples of the *Geophis brachycephalus* complex. Circles indicate males, triangles females, squares juveniles.

three jugals on both sides. All have 0–0 preoculars and 1–1 postoculars. Supralabials 6–6 ($N = 38$), 6–7 ($N = 1$). Infralabials 5–5 ($N = 1$), 6–7 ($N = 2$), 7–7 ($N = 32$), 7–8 ($N = 2$), 8–8 ($N = 2$), 4–4 ($N = 28$); infralabials usually bordering genials but sometimes 3–3 ($N = 1$), 3–4 (2), 4–5 (2) or 5–5 (4).

Dorsal and caudal scale keeling: Keels on the dorsal scales are present only on the posterior one-quarter of the body in two small juveniles (134–200 mm in total length). For the larger Betania sample, our Colombian colleagues provided only approximate estimates of the amount of dorsal scale keeling, accounting for the anomalous concentration of values at 75% (Fig. 6). Most specimens have strong keeling over 25–71.5 ± 10.7–85% of the body. The caudal scales are strongly keeled over most of the length of the tail.

Segmental counts: Ventrals 134–143.5 ± 3.8–149 in males, 141–148.0 ± 5.2–157 in females; subcaudals 42–46.3 ± 2.1–51 in males, 37–41.3 ± 2.8–46 in females; ventral plus subcaudals 180–189.9 ± 5.3–206.

Coloration: The dorsum and upper surface of the tail is uniform dark brown (probably black in life). The venter is probably white in life but is cream in preservative. In five examples (116–230 mm in total length) the venter and subcaudal area are immaculate. All other specimens have banded ventrals and the subcaudals mostly black.

A complete light head band is present in eight examples 226 mm in total length or smaller, including the holotype. A faint band broken on the midline occurs in one snake (BMNH 98.10.27.3) 116 mm in total length. Two examples in the range 211–219 mm total length have the head band suffused with dark pigment.

Hemipenes: Based on an everted hemipenis (FMNH 43727). Organ slightly bilobed. Pedicel covered with spinules. Short truncus covered with 20–30 medium spines and hooks. Capitulum long and slender about three times length of truncus on asulcate side and covered by spinulate calyces.

ANALYSIS OF VARIATION

Relative tail length: (Table 1) Males had relatively longer tails than females in the Costa Rica, Boquete and Colombia populations ($t = -10.358$, d.f. = 89, $P < 0.001$; $t = -3.24$, d.f. = 45, $P = 0.002$; and $t = -6.801$, d.f. = 36, $P < 0.001$, respectively). There was no sexual dimorphism in relative tail length in Lérída specimens ($t = 0.146$, d.f. = 16, $P = 0.886$). We are inclined to believe that the lack of sexual dimorphism in relative tail length in Lérída specimens is a reflection of small sample sizes, particularly of adult males, rather than a truly non-significant difference in relative tail length.

Dorsal scale keeling: (Table 2; Figs 6, 7) We excluded data from the Lérída sample because of small sample size and poor condition of the specimens. For the

Table 2. Variation in the extent of dorsal scale keeling as a percentage of body length in four populations of the *Geophis brachycephalus* complex

	Males	Females	Juveniles	All individuals
Costa Rica	<i>N</i> = 52 27–64.1 ± 15.4–99	<i>N</i> = 41 22–54.3 ± 15.8–85	<i>N</i> = 4 45–54.7 ± 10.3–66	<i>N</i> = 98 22–59.6 ± 16.0–99
Lérida	<i>N</i> = 3 10–31.3 ± 22.6–55	<i>N</i> = 8 10–34.7 ± 23.9–80		<i>N</i> = 11 10–33.8 ± 22.6–80
Boquete	<i>N</i> = 24 10–53.5 ± 19.0–81	<i>N</i> = 25 30–52.8 ± 12.4–88		<i>N</i> = 49 10–53.1 ± 16.0–88
Colombia	<i>N</i> = 23 50–73.5 ± 5.9–80	<i>N</i> = 9 50–68.6 ± 10.8–75	<i>N</i> = 6 25–68.3 ± 21.6–85	<i>N</i> = 38 25–71.5 ± 10.7–85

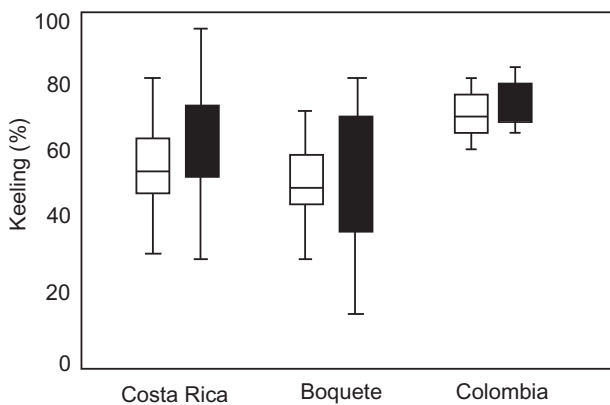


Figure 7. Sexual dimorphism in extent of keeling on dorsal scales in three population samples of the *Geophis brachycephalus* complex.

remaining three sites, there was significant sexual dimorphism in the degree of body keeling in Costa Rica ($t = -3.045$, d.f. = 92, $P = 0.003$; Table 2, Fig. 6), but not in Boquete ($t = -0.134$, d.f. = 47, $P = 0.894$) or Colombia ($t = -1.657$, d.f. = 30, $P = 0.108$). Although the sexually dimorphic difference in body keeling for the Costa Rican population was statistically significant, there was a large amount of overlap between males and females with only a 10% difference in percentage body keeling between the sexes (Table 2). Similarly, there was so much overlap in the percentage of body keeling among populations that we consider the degree of body keeling a marginal character for the purpose of differentiating populations/species, and make no further reference to it in this treatment.

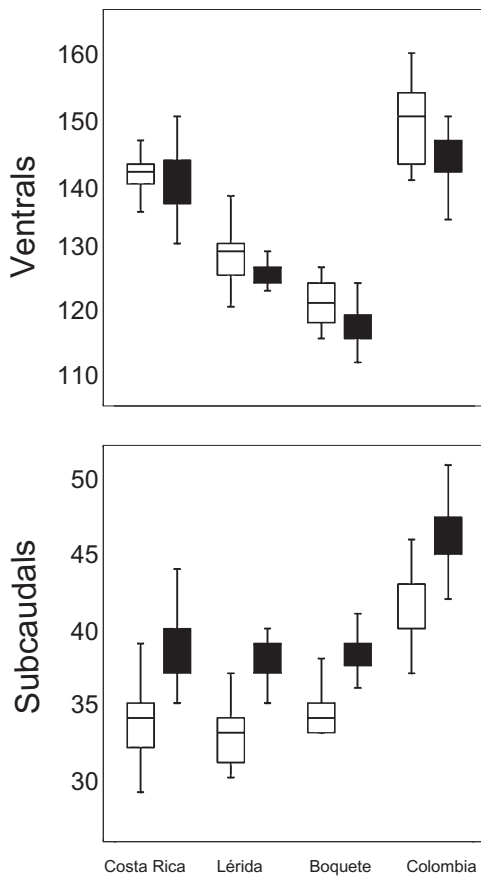
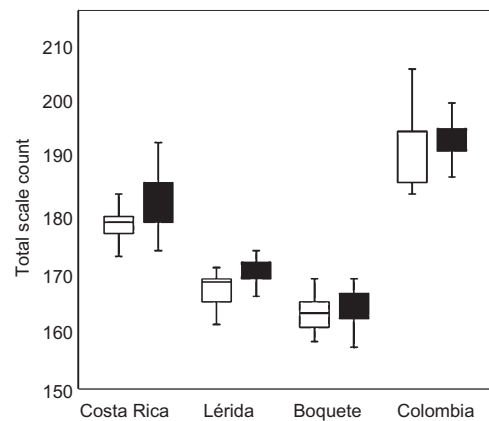
Segmental counts: (Table 3, Figs 8, 9) There was significant sexual dimorphism in scale counts across all sites (for ventrals $F_{1,224} = 31.90$, $P < 0.001$; for subcaudals $F_{1,206} = 244.07$, $P < 0.001$; for ventrals + subcaudals $F_{1,206} = 25.51$, $P < 0.001$). Within sites, there was significant sexual dimorphism in both ventral scales counts (for Costa Rica $t = -2.634$,

d.f. = 97, $P = 0.01$; for Lérida $t = -2.59$, d.f. = 34, $P = 0.014$; for Boquete $t = 4.64$, d.f. = 59, $P < 0.001$; for Colombia $t = 2.78$, d.f. = 31, $P = 0.009$) and subcaudal counts (for Costa Rica $t = 9.778$, d.f. = 89, $P < 0.001$; for Lérida $t = 7.32$, d.f. = 28, $P < 0.001$; for Boquete $t = 11.91$, d.f. = 59, $P < 0.001$; for Colombia $t = 5.54$, d.f. = 30, $P < 0.001$). Total scale counts (ventrals + subcaudals) showed sexual dimorphism in Costa Rica ($t = 5.130$, d.f. = 89, $P < 0.001$) and Lérida ($t = 2.80$, d.f. = 28, $P = 0.008$), but not in Boquete or Colombia ($t = 1.64$, d.f. = 56, $P = 0.107$ and $t = 0.254$, d.f. = 30, $P = 0.805$, respectively). We ascribe the sexual dimorphism in total scale counts in the Costa Rica and Lérida populations to a greater difference in subcaudal counts than in the other two populations; when sexual dimorphism in subcaudal counts is expressed as a percentage of the mean male subcaudal count for each population, the difference is greater in the Costa Rica population and Lérida (male subcaudal count – female subcaudal count/male subcaudal count = 0.15 for the Costa Rica population, and 0.13 for Lérida) than in Boquete (0.10) or Colombia (0.11).

Coloration: Downs (1967) discussed at length colour pattern as the most perplexing variable in snakes that he referred to *Geophis brachycephalus*. The additional material now at hand allows for a fuller understanding of this variation and clarifies the significance of ontogenetic and geographical trends. In the Costa Rica sample, the predominant pattern for dorsal and caudal regions is uniform black in both juveniles and adults. Small juveniles having this pattern may have an immaculate venter or there is some dark pigment on the posterior ventrals. During ontogeny the ventrals become increasingly marked with dark pigment and develop the banded ventral pattern. The striped and blotched/banded dorsal/caudal patterns only occur in the Costa Rica sample. All adults with the striped pattern have banded venters. Downs (1967) implies that stripes are produced by a fusion of light lateral spots, presumably

Table 3. Variation in segmental counts in four population samples of the *Geophis brachycephalus* complex

	Males	Females	All individuals
Costa Rica	<i>N</i> = 56	<i>N</i> = 43	<i>N</i> = 99
Ventrals	129–140.1 ± 4.2–149	136–141.9 ± 2.5–147	129–140.8 ± 3.7–149
Subcaudals	35–39.5 ± 3.3–48	29–33.4 ± 2.2–39	29–36.8 ± 4.0–48
Ventrals + Subcaudals	171–179.3 ± 4.5–190	169–175.4 ± 3.3–181	168–177.5 ± 4.5–190
Lérida	<i>N</i> = 14	<i>N</i> = 22	<i>N</i> = 36
Ventrals	124–129.1 ± 2.1–132	125–131.7 ± 3.3–139	124–130.7 ± 3.1–139
Subcaudals	35–37.8 ± 1.4–40	30–32.9 ± 2.1–37	30–35.2 ± 3.1–40
Ventrals + Subcaudals	161–167.0 ± 2.7–171	158–164.0 ± 2.9–168	158–165.4 ± 3.1–171
Boquete	<i>N</i> = 33	<i>N</i> = 28	<i>N</i> = 61
Ventrals	118–122.9 ± 2.3–128	121–125.7 ± 2.5–130	118–124.2 ± 2.7–130
Subcaudals	36–38.3 ± 1.3–41	33–34.3 ± 1.2–38	33–36.4 ± 2.4–41
Ventrals + Subcaudals	154–161.2 ± 2.8–166	155–160.0 ± 3.1–166	154–160.6 ± 3.0–166
Colombia	<i>N</i> = 24	<i>N</i> = 9	<i>N</i> = 33
Ventrals	134–143.5 ± 3.8–149	141–148 ± 5.2–157	134–144.9 ± 4.8–159
Subcaudals	42–46.3 ± 2.1–51	37–41.3 ± 2.8–46	37–44.8 ± 3.3–51
Ventrals + Subcaudals	180–190 ± 3.6–197	181–189.3 ± 7.5–203	180–189.9 ± 5.3–206

**Figure 8.** Sexual dimorphism in ventral and subcaudal scutellation in four population samples of the *Geophis brachycephalus* complex.**Figure 9.** Comparison of variation in total segmental counts in four population samples of the *Geophis brachycephalus* complex.

ontogenetically. However, the converse seems to be the case as dark pigment invades the stripes to a greater or lesser degree during ontogeny. Well-developed stripes are present in snakes as small as 187 mm and as large as 412 mm in total length but in examples of intermediate size the stripes may be variously interrupted or obscured by dark pigment. In some large specimens (up to 405 mm in total length) the stripes are fragmented and reduced to a series of small, light spots heavily suffused with dark pigment. These spotted snakes all have banded ventrals. It does not appear that any uniform adults are the result of complete suffusion of stripes by black pigment during ontogeny.

Blotched/banded dorsal/caudal patterned snakes differ from uniform, striped and spotted ones in

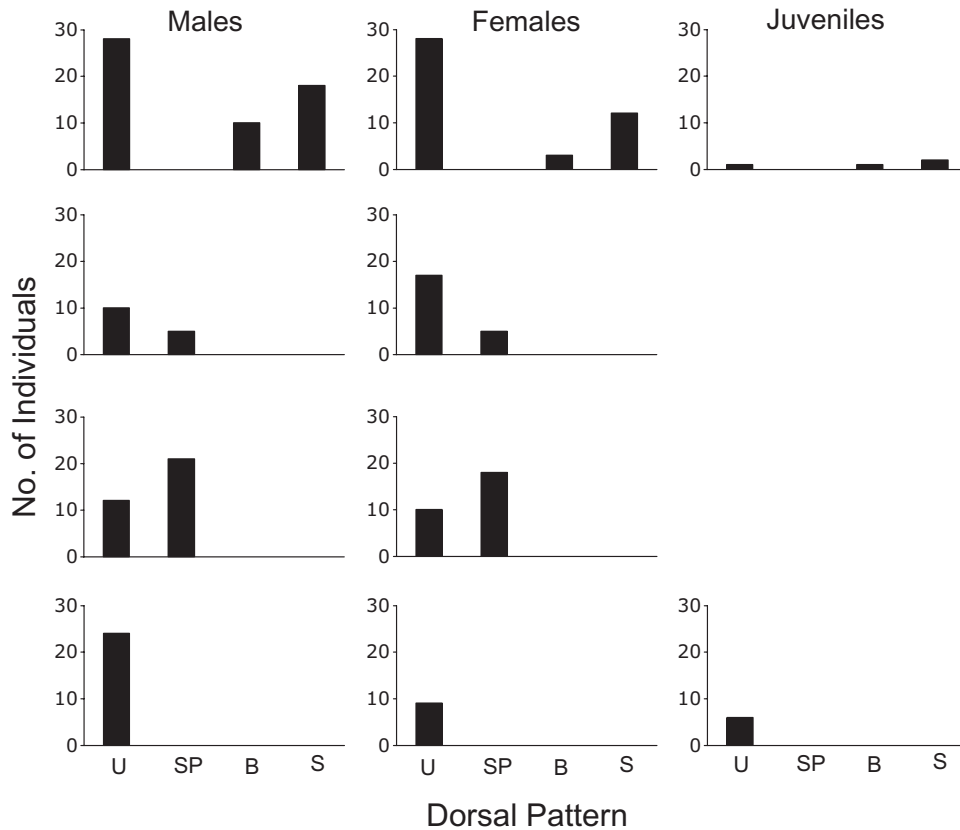


Figure 10. Polychromatism in four populations of the *Geophis brachycephalus* complex; U, uniform; SP, spots; B, blotched/banded; S, striped. Rows indicate (from top) Costa Rica, Lérída, Boquete and Colombia.

having immaculate venters at all stages. In large specimens with this pattern the last few ventrals may have some dark speckling. Costa Rican blotched/banded snakes differ from patterned snakes from the two large Panama series in usually having light markings for most of the length of the body and one or more light blotches on the tail.

In the two large Panama samples, both uniform and spotted patterns are found. The venter in small, uniform juveniles is immaculate. Most adults with this pattern have some dark markings on the ventrals with the banded condition the most frequent. As a large proportion of these snakes are juveniles, it seems probable that most adults in these populations having the uniform pattern will have banded ventrals.

The spotted dorsal pattern in the Panama samples differs from the blotched/banded variants in Costa Rica in that the anterior one-third to one-half of the body is solid black, the light markings are relatively small spots and the tail is uniform black above. The venter is immaculate in these individuals or there are some dark markings midventrally (Fig. 5A–C).

Hemipenes: The principal differences among the three samples (there are no hemipenes available for Lérída snakes) are in the shape and relative length of the capitulum. All of the everted hemipenes are slightly bilobed. In the Costa Rica sample the capitulum is moderately long and slender and about 2.5 times the length of the truncus on the asulcate side. In the Boquete example the capitulum is short, robust and about twice the length of the truncus. In the Colombia specimen the capitulum is long, slender and about three times the length of the truncus.

MULTIVARIATE ANALYSIS

To determine whether the four populations could be distinguished on the basis of tail length/total length ratios (Table 1), scale counts (ventral and subcaudal, Table 2) and dorsal colour pattern (Fig. 10), we analysed the multivariate data using analysis of similarity (ANOSIM) and visualized the data using non-metric multidimensional scaling (nMDS) using the program PRIMER (Clarke & Warwick, 2001). For the ANOSIM, we tested for significant differences in factor levels (site) based on comparisons of multivari-

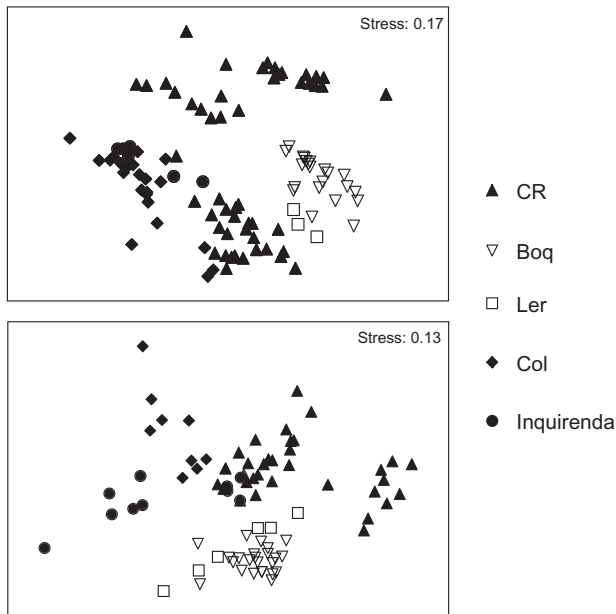


Figure 11. Multivariate nMDS plot of four populations of the *Geophis brachycephalus* complex; upper for males, lower for females. 'Stress' is a measure of structure in a nMDS plot, with values < 0.2 indicating a meaningful ordination. 'Inquirenda' indicates the position of specimens we refer to *Geophis, species inquirenda* with respect to individuals from the other four populations (CR, Costa Rica; Boq, Boquete; Ler, L rida; Col, Colombia). Characters included in analysis were tail length/total length ratios, scale counts (ventral and subcaudal) and dorsal colour pattern.

ate data using Euclidian distance (Clarke & Warwick, 2001). The ANOSIM produces a test statistic (Global R) and a P -value based on 500 randomizations of the dissimilarity matrix. These data are presented graphically in an nMDS plot, in which the axes are undefined, but the separation among points in the plot is proportional to their compositional similarity. We included four characters that varied among populations and were available for most specimens: ventral scale count, subcaudal scale count, tail length/total length ratio and dorsal colour pattern. For both females and males, the four populations were distinguishable based on the four morphological characteristics (Global $R = 0.504$, $P < 0.001$, and Global $R = 0.464$, $P < 0.001$ for females and males, respectively), and all pairs of sites differed significantly from one another (Fig. 11).

SUMMARY OF POPULATION VARIATION

The extent of keeling of the dorsal scales along the body does not provide a basis for distinguishing among the four population samples. The caudal scales

are heavily keeled throughout the length of the tail except in a few small juveniles where the scales are only keeled on the base of the tail. The four populations differ significantly from one another in ventral counts for both sexes (Fig. 8), with Costa Rica and Colombia samples having higher numbers than seen in the two Panama samples. The Colombia sample differs significantly from the other three in having higher numbers of subcaudals in both sexes (Fig. 8). All samples differ significantly from one another in total segmental counts (Fig. 9).

All Colombia snakes had the upper surfaces of the body and tail uniformly dark (probably black in life). The ventrals and subcaudals are immaculate in small juveniles but banded (ventrals) and mostly dark (subcaudals) in larger individuals. A light head band is variably present but most common in juveniles.

The Costa Rica sample exhibits the greatest degree of polychromatism, and this can be seen in the separation of Costa Rican specimens into two groups in the nMDS plot (Fig. 11). The majority of specimens have the upper surfaces of the body and tail uniformly dark (usually black in life). The ventrals in these snakes are usually banded and the subcaudals are mostly dark. Small juveniles with this dorsal pattern have immaculate venters that are increasingly marked with dark pigment with age. A similar ontogenetic change is seen in the coloration of the subcaudals. The second pattern class consists of a pair of dorsolateral longitudinal red stripes (Fig. 5B) on a black ground colour on the body and sometimes extending onto the tail. The stripes may be even edged or variously invaded by darker pigment to produce wavy margins or to interrupt the stripe and fragment it into segments. In a few extreme cases the stripes are broken up into a series of small spots. In snakes having the striped or fragmented pattern the ventrals are banded with dark pigment, and the subcaudals show a progression of increasing amounts of dark pigment with age. The third pattern consists of red bands and/or red blotches (Fig. 3C) over all but the anterior most section of the dorsum. Usually there are several of these pattern elements on the caudal surface and at least one is always present on the base of the tail. Snakes having this pattern have immaculate venters except that the posteriormost one or two ventrals may be marked with dark pigment. The subcaudals are usually banded but in smaller specimens there are little or no darker markings.

In the two Panama samples the upper surface of the body and tail may be uniformly dark (probably black in life) with the ventrals usually banded and the subcaudals mostly black. Small juveniles with this pattern may have the venter and subcaudal areas immaculate but dark pigmentation increases with age. Individuals in these samples have the

dorsum, for at least the anterior one-third of the body, and upper surface of the tail uniform dark. The remainder of the dorsum is marked with a series of red spots (Fig. 3A) that are sometimes fused into one or more elongate blotches. The venters of these snakes are immaculate or there may be a series of darker markings along the midventer (Fig. 5A–C). The subcaudals are mostly dark in larger individuals having this dorsal pattern.

The differences among the samples in hemipenes are suggestive, but too few everted organs are available to be conclusive. Data in Downs (1967) indicates that hemipenial length tends to be positively correlated with relative tail length and the number of subcaudals within different *Geophis* species groups. This seems to be reflected in a general way in members of the *G. brachycephalus* complex. The Colombia sample averages the highest numbers of subcaudals in males and the hemipenis is characterized by a long slender capitulum. The Boquete population has low numbers of subcaudals and the available hemipenis has a relatively short, robust capitulum. Costa Rica males also have relatively high numbers of subcaudals but a slender and moderately long capitulum.

TAXONOMIC CONCLUSIONS

The Colombia series is most obviously different from the other three samples in having a significantly higher number of ventrals and subcaudals, which is reflected in its high values for total segmentals (Table 3). The difference in hemipenial morphology (e.g. long, slender capitulum) also seems to differentiate it from other samples for which hemipenes are available.

The Costa Rica sample also has a high number of ventrals (Table 3) and two of its polychromes, striped and blotched/banded (Fig. 3A, B), are not present in the Panama populations. The moderately long, slender capitulum appears further to differentiate it from Colombia and Boquete populations.

The Lérída and Boquete, Panama, samples have lower ventral counts than the other two samples. They differ significantly from one another in ventral counts and this also produces a significant difference between them in total segmentals. However, there is extensive overlap: Lérída males: ventrals 124–132; females: ventrals 125–139; total segmentals 158–171 versus Boquete males: ventrals 118–128; females: ventrals 121–130; total segmentals 154–168.

The two populations further agree in having a high proportion of the spotted polychrome and in lacking red markings on the tail. Because the geographical areas from which these two samples were accumulated are only about 7 km apart and the differences

between them are slight we consider them to represent the same taxon. We think that the differences in segmental counts may have been influenced by the large number of small juveniles in the Lérída sample. In many snakes, hatchlings or neonates exhibit extremes in variation in ventrals and subcaudals that frequently are selected against early in life and are not found in the adult breeding population (Klauber, 1956). The available everted hemipenis from the Boquete sample differs most obviously from those in snakes from Costa Rica and Colombia in having a short, robust capitulum instead of a slender capitulum.

On the basis of our analyses we conclude that there are three taxa represented by the four samples: (1) a species represented by the Costa Rica sample for which the earliest available name is *Geophis brachycephalus* (Cope, 1871); (2) a species represented by the Colombia snakes for which the name *Geophis nigroalbus* Boulenger, 1908 is available; and (3) a species represented by the Lérída and Boquete, Panama, samples. Resolution of the taxonomy for the two Panama samples is contingent upon analysis of the status of the nominal species *Geophis talamancae* Lips & Savage, 1994 and *Geophis, species inquirenda* (*sensu* Myers, 2003) as detailed in the following section.

SYSTEMATIC ALLOCATIONS FOR OTHER SPECIMENS OF THE *G. BRACHYCEPHALUS* COMPLEX FROM COSTA RICA AND PANAMA

Lips & Savage (1994) described *Geophis talamancae* from Costa Rica: Puntarenas: Zona Protectora Las Tablas, Finca Jaguar (1800 m) near the western boundary of Chiriquí Province, Panama. This locality is about 29 km north-west of Lérída on the Pacific slope of the Cordillera Talamanca-Barú. The holotype is an immature female, uniform black above with keels on the posterior 20% of the dorsal scales and on the caudal scales throughout the length of the tail. The segmental counts are: ventrals 134, subcaudals 32 and total 166, using the methods of counting adopted for this paper. In these counts (see Table 2) and all other features the holotype closely resembles unicolour representatives of the *G. brachycephalus* complex from Lérída. As pointed out above, we regard the Lérída–Boquete samples as conspecific with one another and constituting a species distinct from both *G. brachycephalus* and *G. nigroalbus* in having low ventral counts. As *G. talamancae* is clearly based on a representative of this low ventral count taxon, it becomes the valid name for that species.

In addition to the specimens mentioned above we have examined one male (CHP 4106) and two females

Table 4. Variation in selected characters in *Geophis tectus* sp. nov. from Panama

	Males	Females	All individuals
TL-TOT	17.0–20.2 ± 1.7–21.6	16.7–19.0 ± 1.6–21.8	
Body Keeling	47–73.6 ± 20.8–95	19–63.2 ± 24.4–81	
Ventrals	137–138.7 ± 1.0–140	137–138.7 ± 1.2–140	137–138.7 ± 1.1–140
Subcaudals	44–46.0 ± 1.8–49	41–42.7 ± 1.4–44	41–44.3 ± 2.3–49
Ventrals + Subcaudals	183–184.7 ± 1.2–186	180–181.3 ± 1.4–184	180–183.0 ± 2.1–186

(KU 75695, USNM 129382) from Panama: Chiriquí: El Hato del Volcán (often called simply El Volcán, 1200 m), that may be referred to *G. talamancae*. This locality is c. 17 km south-east of Las Tablas, Costa Rica and c. 16 km south-west of Lérída. These snakes have the anterior third of the body uniform black followed by a series of mostly offset red spots, the upper surface of the tail is uniform black and the venters are immaculate. Counts are: male 132 ventrals, 39 subcaudals and total 171; females 132–133 ventrals and 32 subcaudals and total 165 (in specimens with a complete tail). Another specimen (CHP 3360) from ‘Panama’ without additional locality data is a small female with 136 ventrals, 32 subcaudals and 168 total segmentals. It has the characteristic dorsal pattern of red spots found in most *G. talamancae*. We consider this snake also to be a representative of *G. talamancae*.

Myers (2003), in his review of Panama members of the *Geophis brachycephalus* complex, followed Downs (1967) in assigning the upland Lérída and Boquete snakes (*G. talamancae*) to *G. brachycephalus*. He allocated nine others with uniform dorsums and white venters from western Panama that seemed to differ from the upland samples, to *G.*, *species inquirenda* primarily because they had higher segmental counts. He also noted that the everted hemipenis of one male (MCZ 19326) differed from that in the Boquete male (UMMZ 57958) in being single (not slightly bilobed) and in having a moderately long and slender (not short and robust) capitulum. He suggested that these snakes represented a different taxon than other western Panama snakes of the complex in which polychromatism was found. However, he left its definitive determination to subsequent researchers.

In our preliminary survey of Panama material, we identified nine additional specimens that generally conform to Myers’ characterization of *G.*, *species inquirenda*. However, on the basis of segmental counts it soon became obvious to us that two entities were represented in the combined sample of 18 snakes. The first of these consists of one male (FMNH 130969) from Bocas del Toro: Río Changena, three females, reported by Myers (2003) from Chiriquí: Fortuna Dam site area (1000 m) on the upper Río

Chiriquí (AMNH 114317–114319) and two females (CHP 4603, 4612) from *quebradas* (c. 1100 m) now draining into the impoundment behind the finished dam. Myers was tentative in his inclusion of the AMNH examples in *G.*, *species inquirenda* but did so because they had higher segmental counts than found in the Lérída–Boquete series (here referred to *G. talamancae*). The combined counts for the five females are: 137–140.0–142 ventrals, 34–34.5–35 subcaudals and 171–174.5–176 ventrals plus subcaudals (in four specimens with complete tails). The counts for the male are 134 ventrals, 45 subcaudals and 179 total segmentals. These values are well within the limits of variation for Costa Rica *Geophis brachycephalus* (Table 3, Fig. 8) with which the five agree in all other features. Consequently, we conclude that they should be referred to that species.

The remaining ‘*species inquirenda*’ include six males and six females differing from Lérída–Boquete *G. talamancae* in having higher ventral, subcaudal and total segmental counts and from *Geophis brachycephalus* in having lower ventral, and higher subcaudal and total segmental counts. Values for males are: ventrals 137–138.7–140, subcaudals 44–46–49, ventrals plus subcaudals 183–184.7–186; females: 137–138.7–140 ventrals, 41–42.7–44 subcaudals, ventrals plus subcaudals 180–181.3–184 (Table 4, Fig. 12); thus approaching *G. brachycephalus* in ventral number and *G. nigroalbus* in subcaudal counts. It is noteworthy that this sample shows no sexual dimorphism in ventral counts and that females have high subcaudal counts as compared with female *G. brachycephalus* and *G. talamancae*.

One female (AMNH 12015) assigned to this entity is from Quebrada Arena (1120 m), which drains into the Fortuna Dam impoundment. It has 138 ventrals, 43 subcaudals and 181 total segmentals. This contrasts with the counts of 140 ventrals, 35 subcaudals and 175 total segmentals for a virtually sympatric female *G. brachycephalus* (CHP 4603). Two males (CAS 78979, 78983) from the Boquete area have 139 and 140 ventrals, 44 and 46 subcaudals, and 183 and 186 total segmentals, respectively. This compares with 118–128 ventrals, 36–41 subcaudals and 154–166 total segmentals in the virtually sympatric snakes of the

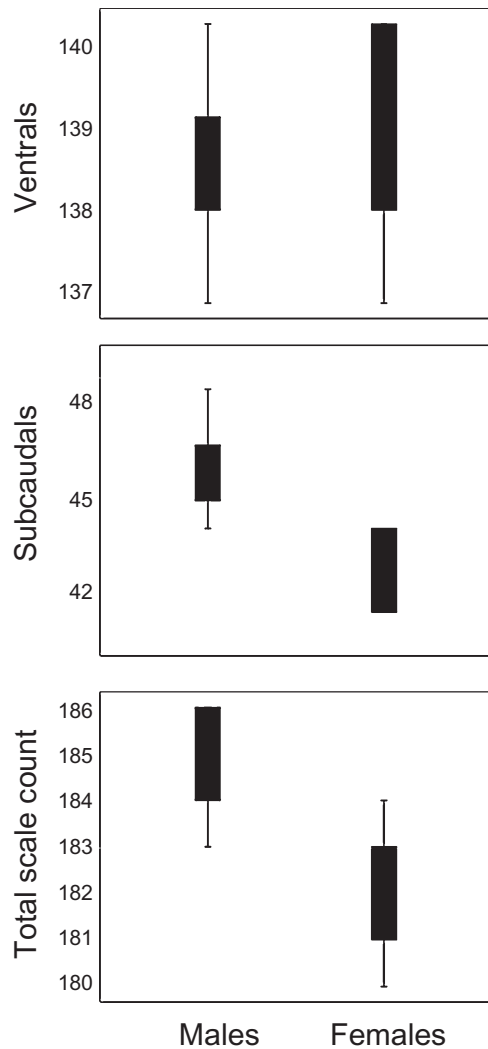


Figure 12. Variation in segmental counts in *Geophis tectus* sp. nov. from Panama.

Lérida–Boquete populations of *G. talamancae*. The differences in segmental counts combined with the distinctive features of the hemipenis, a single organ with a moderately slender capitulum that is about 2.5 times the length of the truncus (Myers, 2003), and the apparent sympatry with other species supports the distinctiveness of this population. As no name is available for this form we provide one below.

Myers (2003) reported the occurrence of *Geophis brachycephalus* from east-central Panama on the basis of a juvenile male (GML) from Panamá: the Piedras-Pacora Ridge: Cerro Azul (= Cerro Jefe). This snake has the anterior one-third of the dorsum uniformly black followed by a series of paired and mostly light, dorsal blotches (mostly off-set) and bands (3bl + 2Bd + 1spot + 2Bd + 3bl) with four light bands on the tail. These markings were probably red

in life as are the light dorsal and caudal markings in other populations in this complex. The venter is immaculate except there is some dark mottling on the last seven to eight ventrals and the subcaudals are mostly black. The dorsal pattern is similar to that of patterned *Geophis talamancae* in having the anterior one-third of the body uniform black but resembles the blotched/banded polychrome of *Geophis brachycephalus* in the size of the blotches and in having light markings on the tail. Scale counts are: 138 ventrals, 50 subcaudals and 188 total segmentals. The ventral and correlated total segmental counts are well within the limits for both the distinctive unicolor population of this complex from western Panama and those of the Colombian *G. nigroalbus*.

In the western Panama form, the subcaudals for males show a geographical trend from west to east. Males from Bocas del Toro and Chiriquí provinces have 44–46 subcaudals and those from further east in Coclé: N El Copé have 45–49. The latter locality is 153 km south-west of the locality at Cerro Azul where the patterned specimen in question, which has 50 subcaudals, was collected. The males from the El Copé area (CHP 0355 and 0983) have 49 subcaudals and 137 ventrals (total 186) and 45 subcaudals and 139 ventrals (184 total), respectively, and closely approach the values for the GML specimen. The nearest record of *G. nigroalbus* to the eastern Panama site is from c. 450 km south-east in north-western Colombia and is a female with 183 total segmentals. The male holotype of *G. nigroalbus* is from c. 400 km further south in south-western Colombia and has 137 ventrals, 45 subcaudals and 182 total segmentals. All of the Colombia snakes ($N = 51$) placed in *G. nigroalbus* have uniform dorsal coloration as do the western Panama snakes. As may be seen in Table 3 the Cerro Azul specimen could be placed in either *G. nigroalbus* or the western Panama taxon based on segmental counts, although its ventral counts are closer to the mean for ventrals in the latter form. We did consider the possibility that the Cerro Azul snake, based solely on its coloration, might represent a species different from both of the unicolor taxa. We are reluctant to follow that course as patterned and unicolor specimens are variants in two other species of the *G. brachycephalus* complex. Consequently, we tentatively assign the eastern Panama snake to the new species based on its similarity in segmental counts to the geographically nearest members of the new form from Coclé Province.

MULTIVARIATE COMPARISONS

We used the same multivariate analyses presented previously (ANOSIM and nMDS; see 'Analysis of variation' above) to test our assignment of individuals

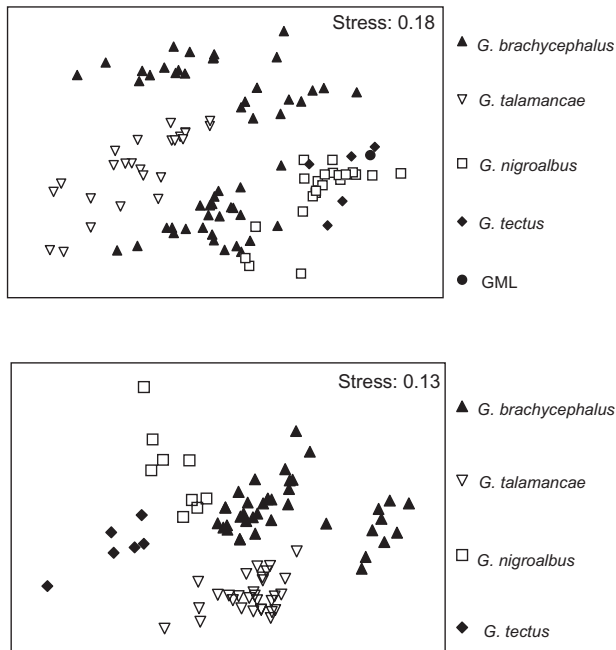


Figure 13. Multivariate analysis for the five species of the *Geophis brachycephalus* complex; upper, males; lower, females. GML, Gorgas Memorial Laboratory specimen referred to *Geophis tectus* sp. nov.

to the four species outlined above (*G. brachycephalus*, *G. talamancae*, *G. nigroalbus*, or the new taxon). We included several specimens previously considered *G.*, *species inquirenda* as *G. brachycephalus*, while the rest of the *G.*, *species inquirenda* were assigned to the new taxon. Overall results for both males and females (Fig. 13) were significant (Global $R = 0.595$, $P < 0.001$ and Global $R = 0.496$, $P < 0.001$ for females and males, respectively). For females, all pairwise comparisons were significantly different whereas males of *G. nigroalbus* and the new taxon cannot be differentiated statistically in our analyses. Whereas females of all species and males of most species may be distinguished from each other by the combination of dorsal colour pattern, ventral and subcaudal scale counts, and tail length/total length ratios, male *G. nigroalbus* and the new taxon must be differentiated by a combination of scale counts and other diagnostic characters not included in our multivariate analyses (see below).

TAXONOMIC CONCLUSIONS

GEOPHIS SIEBOLDI GROUP:

GEOPHIS BRACHYCEPHALUS COMPLEX

GEOPHIS BRACHYCEPHALUS (COPE, 1871)

Colobognathus brachycephalus Cope, 1871: 211 (Type Locality: Costa Rica: San José: San José, 1160 m; Holotype: ANSP 3337, a juvenile male).

Colobognathus dolichocephalus Cope, 1871: 211 (Type locality: Costa Rica: San José: nr San José, c. 1160 m; Holotype: ANSP 3306).

Geophis moestus Günther, 1872: 15 (Type Locality: Costa Rica: Cartago: Cartago, 1435 m; Holotype: BMNH 1946.1.6.53).

Catastoma chalybeum Günther, 1872: 16.

Elapoidis brachycephalus Cope, 1885: 386.

Elapoidis dolichocephalus Günther, 1893: 87.

Geophis chalybaea var. *quadrangularis* Günther, 1893: 89, pl. 33, fig. B (Type Locality: Costa Rica: Cartago: Cartago, 1435 m; Holotype: BMNH).

Catastoma brachycephalum Cope, 1875: 147.

Catastoma dolichocephalum Cope, 1875: 147.

Dirosema brachycephalum Boulenger, 1894: 299.

Rhabdosoma moestum Cope, 1887: 85.

Geophis hoffmanni Boulenger, 1894: 319 (in part).

Geophis brachycephalus Slevin, 1942: 474 (in part); Dunn, 1942: 4 (in part); as first reviser Dunn selected *Colobognathus brachycephalus* over *Colobognathus dolichocephalus* both of Cope, 1871; Downs, 1967: 146, fig. 19 (in part); Savage, 2002: 602, pls 369–70 (in part); Myers, 2003: 39; Campbell & Lamar, 2004, pl. 119; Solórzano, 2004: 276, figs 75, 76 (in part).

Geophis bakeri Taylor, 1954: 689 (Type Locality: Costa Rica: Alajuela: Sarapiquí: Isla Bonita, 1200 m; Holotype: KU 31983, an adult female).

Geophis nigroalbus Downs, 1967: 146.

Geophis, species inquirenda Myers, 2003: 38, fig. 19 (in part).

Diagnostics: This species is characterized by having the following combination of features: (1) ventrals in males $129\text{--}140.0 \pm 4.2\text{--}149$, in females $136\text{--}141.7 \pm 2.5\text{--}147$; subcaudals in males $35\text{--}39.6 \pm 3.4\text{--}48$, in females $29\text{--}33.5 \pm 2.2\text{--}39$; ventrals plus subcaudals in males $171\text{--}179.6 \pm 4.5\text{--}190$, in females $169\text{--}175.3 \pm 3.2\text{--}181$; (2) uniform black dorsum and upper surface of tail or with red longitudinal stripes that may be fragmented by suffusions of dark pigment or with a blotched/banded pattern on at least the posterior three-quarters of the body that continues onto the upper surface of the tail; (3) hemipenes slightly bilobed, capitulum moderately long but slender, about 2.5 times length of truncus on asulcate side.

Remarks: The geographical distribution of the three colour patterns in this species was commented on by Downs (1967). The additional material requires some revisions to his discussion. Only uniform coloured snakes are known from the Cordillera de Tilarán, Volcán Poás, the passes between Volcán Poás and Volcán Barva and Volcán Barva and Volcán Irazú, and on the Atlantic slope of the Cordillera Central. Only specimens with the blotched/banded pattern are

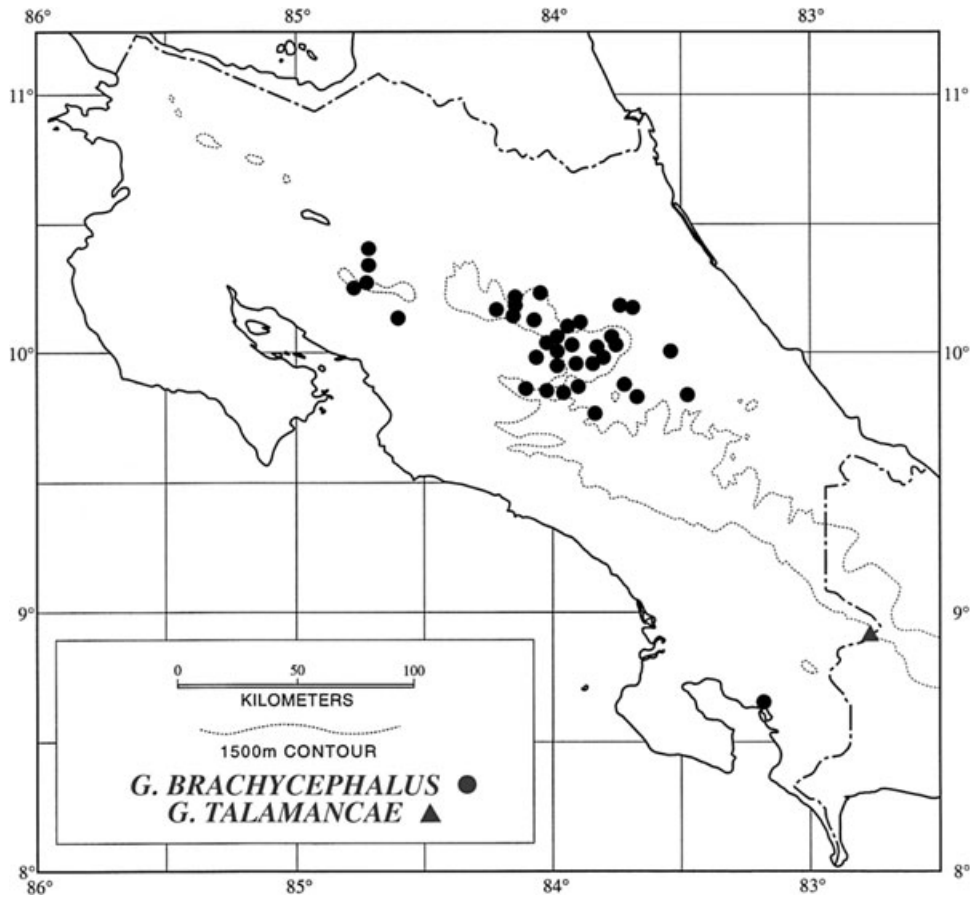


Figure 14. Geographical distribution of two species of *Geophis* in Costa Rica.

known from along the Atlantic slope at Alajuela: Fortuna (250 m), Limón: La Emilia, near Guápiles (260 m), Alto Guayacán (750 m), and El Tigre (680 m). Uniform and blotched/banded snakes co-occur on the Atlantic slope of the Cordillera de Tilarán at Alajuela: Reserva San Ramón (660 m) and Cordillera de Talamanca at Cartago: Moravia de Chirripó (1116 m). The striped pattern predominates on the Mesata Central and the Pacific slope of Volcán Barva and co-occurs with uniform patterned snakes on the slopes of Volcán Turrialba and in the area south-west of Cartago at: Cangreja (1680 m) and Palo Verde (1590 m). The striped pattern co-occurs with the banded/blotched pattern at San José: San José (1190 m), and Cartago: Turrialba (640 m) area. The striped pattern also occurs in one specimen from the Pacific lowland locality of Puntarenas: Golfito (13 m). Apparently all three patterns co-occur at Cartago: Cartago (1453 m). The pattern in which the stripes are suffused by black pigment and reduced to a series of small 'spots' is known from one specimen from the lowland locality of Limón: Guápiles (262 m) and two from higher elevations at Cartago: Cervantes (1441 m) and San José: Granadilla (1410 m).

We have some reservations regarding the record of the striped female (UF 55309) from Puntarenas: Golfito (c. 13 m) in the Pacific lowlands. This site is many kilometres from any upland locality (Fig. 14) for the species. As this is a semifossorial form it seems possible that the snake might have been transported in soil from upland Costa Rica to the lowlands. Such a thought has also crossed our minds regarding snakes of this taxon from the Atlantic lowlands in the area of Limón: Guápiles, 260 m, which have a blotched/banded pattern (ANSP 21401) or the stripes reduced to small spots (UCR 11139). Alternatively, these animals may have been washed down from higher elevations during the wet season.

Distribution: Found in a broad elevational range in areas currently or originally covered by tropical lowland wet forest and premontane and lower montane moist and wet forests and rainforest in Costa Rica; also in the tropical premontane rainforest of western Panama, 13–2115 m (Figs 14, 15).

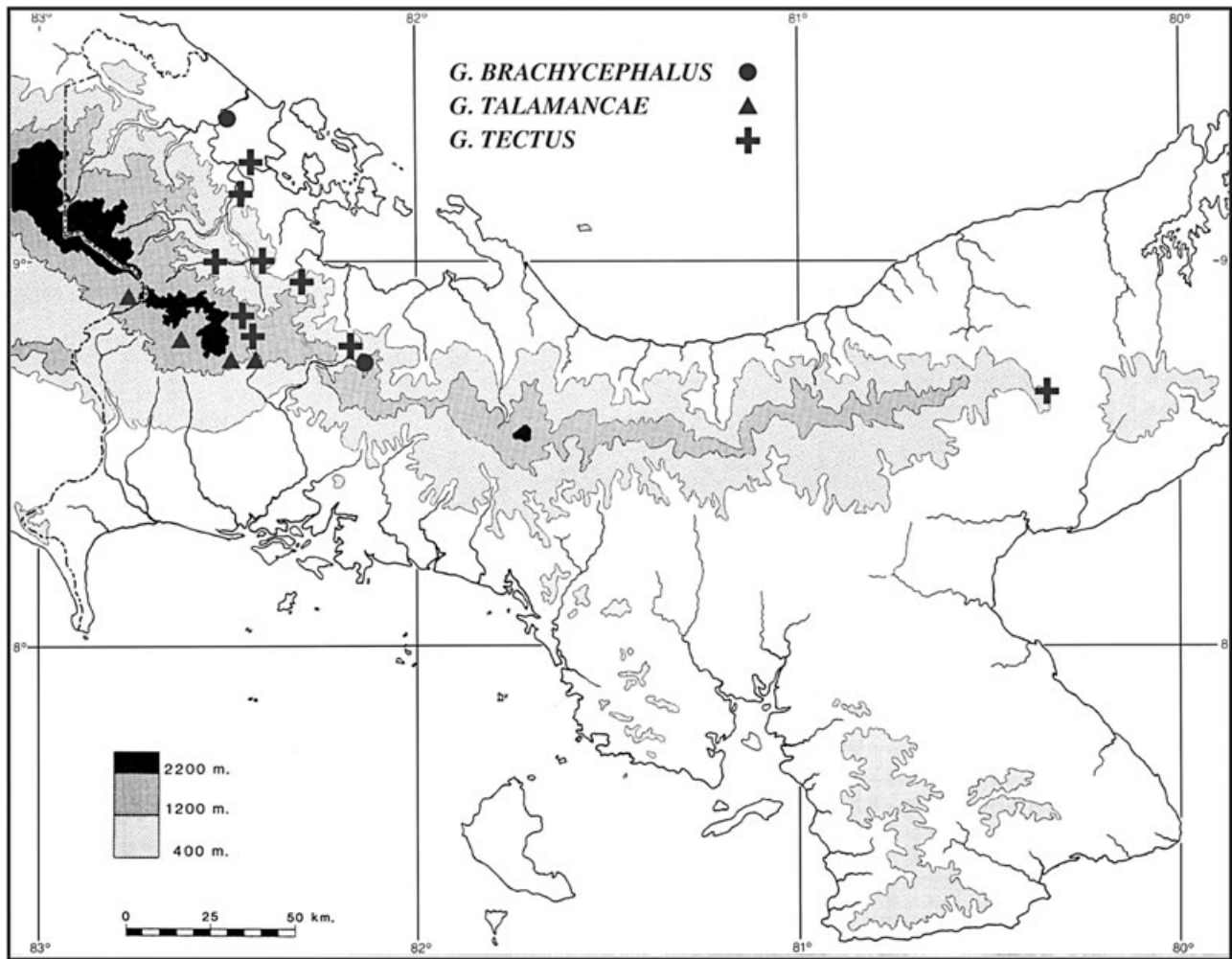


Figure 15. Geographical distribution of three species of *Geophis* in western Panama. *Geophis tectus* sp. nov. is virtually sympatric with *G. brachycephalus* in the upper Río Chirripó drainage and with *G. talamancae* near Boquete.

GEOPHIS NIGROALBUS BOULENGER, 1908

Geophis nigroalbus Boulenger, 1908: 552 (Type locality: Colombia: Valle del Cauca: Pavas, 3°41'N, 76°35'W, 1350 m; Holotype BMNH 1946.1.6.50, a juvenile male); Restrepo & Wright, 1987: 195; Myers, 2003: 33, figs 15–17.

Diagnostics: Distinguished from other species in the *Geophis brachycephalus* complex by the following combination of characters: (1) ventrals 134–143.5 ± 3.8–149 in males, 141–148.0 ± 5.2–157 in females; subcaudals 42–46.3 ± 2.1–51 in males, 37–41.3 ± 2.8–46 in females; total segmentals 180–190.0 ± 3.6–197 in males, 181–189.3 ± 7.5–203 in females; (2) upper surfaces of body and tail uniform black; (3) hemipenis slightly bilobed with a long, slender capitulum about 3 times length of truncus (Myers, 2003).

Distribution: Tropical premontane wet forest sites in the Cordillera Occidental of Colombia, 1350–1680 m (Fig. 16).

GEOPHIS TALAMANCAE LIPS & SAVAGE, 1994

Geophis brachycephalus, Slevin, 1942: 474 (in part); Dunn, 1942: 4 (in part); Downs, 1967: 146 (in part); Savage, 2002: 604 (in part); Myers, 2003: 38 (in part); Solórzano, 2004: 276 (in part).

Geophis talamancae Lips & Savage, 1994: 410, fig. 1 (Type locality: Costa Rica: Puntarenas: Coto Brus, Sitio Las Tablas: Finca Jaguar, 1800 m; Holotype: LACM 147196, a subadult female); Savage, 2002: 602; Solórzano, 2004: 290, fig. 82.

Diagnostics: Unique within the *Geophis brachycephalus* complex in having the following combination of characters: (1) 118–124.9 ± 3.7–132 ventrals in male,

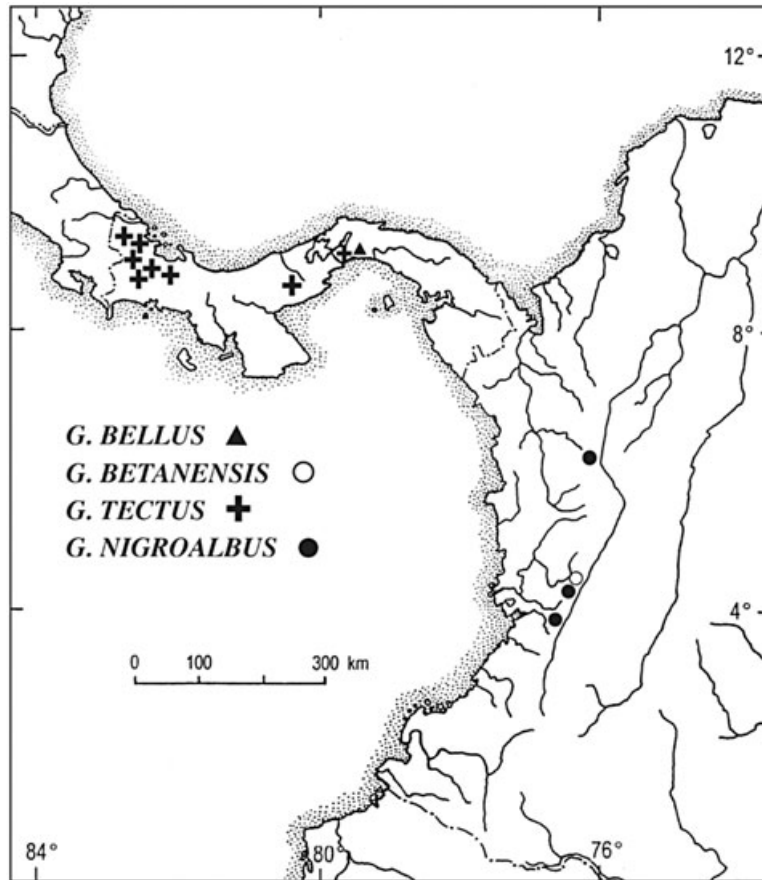


Figure 16. Geographical distribution of four species of *Geophis* in Panama and western Colombia. *G. betanensis* and *G. nigroalbus* are sympatric in Colombia.

121–128.8 ± 4.4–139 in females; 35–38.1 ± 1.4–41 subcaudals in males, 23–33.4 ± 2.3–38 in females; 154–163.2 ± 4.0–171 total segmentals in males, 155–161.7 ± 3.9–171 in females; (2) upper surfaces of body and tail uniform black or anterior body uniform black and rest of body black with pairs of red spots that are usually offset and sometimes fused to form elongate blotches; tail black above; (3) hemipenis slightly bilobed with short, robust capitulum that is about twice length of truncus on asulcate side (Myers, 2003).

Distribution: Tropical premontane wet forest and rainforest and lower montane rainforest on the Pacific slope of the Cordillera Talamanca-Barú in extreme south-western Costa Rica and adjacent western Panama, 1200–1800 m (Figs 14, 15).

***GEOPHIS TECTUS* SP. NOV.**

Geophis brachycephalus, Dunn, 1942: 4 (in part); Downs, 1967: 146 (in part); Savage, 2002: 604 (in part); Myers, 2003: 37, fig. 18 (in part); Solórzano, 2004: 276 (in part).

Geophis, species inquirenda, Myers, 2003: 39, fig 20B (in part).

Holotype: MCZ 19326, an adult male from La Loma (= Buena Vista), Distrito de Chiriquí Grande, Provincia de Bocas del Toro, Panama; c. 8°50'N, 82°13'W (300 m). Collected by E. R. Dunn and Chester B. Duryea, some time in July–August 1923.

Paratypes: All are from Panama. Provincia de Bocas del Toro: BYU 19149, Río Changena, Río Changena camp (732 m), 35 km W Almirante; KU 110702, Río Changena (830 m); KU 110701, 3 km W Almirante (40 m); MCZ 19325, La Loma (Buena Vista), 300 m; Provincia de Chiriquí: CHP 1034–1035 Cerro Horqueta (1707 m, 1676 m, respectively); CAS 78979, 78983, Boquete (c. 1200 m); AMNH 124015, S slope Quebrada Arena (1120 m), tributary to Río Chiriquí nr Prensa Fortuna impoundment; Provincia de Coclé: CHP 0355, 0983, N of El Copé (c. 600–800 m).

Referred specimen: Provincia de Panamá: GML, Piedras-Pacora Ridge: Cerro Azul (= Cerro Jefe) (c. 200–800 m).

Diagnosis: This species differs from other members of the *G. brachycephalus* complex by having high numbers of subcaudals in females and in lacking sexual dimorphism in ventral counts (Table 4). It is characterized by having the following combination of features: (1) 137–138.5 ± 0.9–140 ventrals in males, 138 in the female; 44–47.0 ± 2.4–50 subcaudals in males, 43 in the female; 183–185.5 ± 1.9–188 total segmentals in males, 181 in the female; (2) uniform black dorsum and upper surface of tail or with the light blotched/banded pattern on posterior two-thirds of body and light markings on upper surface of tail (light markings probably red in life); (3) hemipenes simple, capitulum moderately long but slender, about 2.5 times as long as the short truncus on the asulcate side (Myers, 2003).

Description of holotype: A snake 253 mm in standard length with a tail length of 68 mm (21.2% of total length); dorsal scales in 15–15–15 rows, with keels on all rows except the first six; caudal scales heavily keeled; a pre- and postnasal present followed by a long loreal; preoculars 0–0; postoculars 1–1; 0 + 1 elongate temporal followed by two jubals bordering the last supralabial; supralabials 6–6, 3–4 bordering the orbit; 6–6 infralabials, four bordering the chin shields on each side; subcloacal scute single; two preentrals, 138 ventrals, 47 subcaudals and 185 total segmentals; dorsum uniform brown and upper caudal surface brown in preservative; venter cream in preservative; subcaudals banded with dark pigment.

Hemipenes: The hemipenis of the new species resembles that of *G. brachycephalus* but appears to be single, not slightly bilobed. It agrees with the former by having the capitulum moderately long and slender and in relative proportions, with the length of the capitulum about 2.5 times that of the truncus on the asulcate side. Other members of the *G. brachycephalus* complex have either a much longer and more slender capitulum (*G. nigroalbus*) or a shorter and more robust capitulum (*G. talamancae*).

Variation: The paratypes agree with the holotype in most features. The largest male is 287 mm in standard length with a tail length of 76 mm (21.5% of total length). The largest female is 310 mm in standard length with a tail length of 71 mm (18.6% of total length). The proportion of tail length to total length is 17.0% in the juvenile male, 19.6–21.6% in adult males, 16.7% in the juvenile female and 18.4–21.6% in adult females. In one specimen the right loreal is excluded from the orbit by supralabial 3. One example (CAS 78983) has a short second temporal and 4–4 jubals contacting the last supralabial. All specimens have 6–6 supralabials. Infralabials are

usually 6–6 ($N=4$) or 7–7 ($N=5$) but may be 6–5 ($N=1$) or 6–7 ($N=2$). There are usually four or five infralabials in contact with the chin shields but rarely three. The degree of dorsal scale keeling varies in well-preserved adults from 37 to 86% in adults. Caudal scales are strongly keeled in all specimens.

Specimens from western Panama have a uniform dark dorsum and caudal surface. The patterned example (GML) from just east of the Canal Zone area is described in detail above. The venter is usually immaculate or a few examples have a little mottling or speckling of dark pigment. Five adults have definite dark bands on the ventrals. The subcaudals vary from nearly immaculate to heavily banded with dark pigment in seven of the larger snakes. A light head band suffused with dark pigment occurs in three smaller examples (145–226 mm in standard length) and two others (142–151 mm in standard length) have the band obscured or faintly suggested.

Etymology: The specific name is from the Latin *tectus* meaning secret or disguised in allusion to this species being concealed under the name *G. brachycephalus* for over 90 years.

Distribution: From tropical lowland moist forest and premontane rainforest on the Atlantic slopes of the Cordilleras de Talamanca-Barú and Tabasará and tropical premontane and lower montane rainforest on the Pacific slope in western Panama; also in tropical premontane rainforest on the Piedras-Pacora Ridge in east central Panama, 40–1700 m (Figs 15, 16).

A REVIEW OF OTHER MEMBERS OF THE *G. SIEBOLDI* SPECIES GROUP IN LOWER CENTRAL AMERICA AND COLOMBIA

GEOPHIS BELLUS MYERS, 2003

Geophis bellus Myers, 2003: 30, figs 11–14 (Type locality: Panama: Panama: Pacora: east of Cerro Jefe: near Altos de Pacora, 700 m; Holotype: KU 110703, an adult male).

Diagnostics: The single known male specimen is distinguished from other members of the *Geophis sieboldi* species group by the following combination of characters (see Fig. 1B): (1) six supralabials; (2) two supralabials posterior to the orbit; (3) no anterior temporal or postlabials; (4) last supralabial separated from the parietal by an elongate posterior temporal; (5) two jubals posterior to posterior temporal and last supralabial, upper separated from contact with the parietal by the elongate posterior temporal; (6) dorsal scales in 15–15–15 rows; (7) dorsal scales on posterior 50% of body keeled; (8) anterior tip of maxilla pointed

and toothless; posterior end depressed, curving slightly ventrad posteriorly; (9) ventrals 131; subcaudals 33; ventrals plus subcaudals 164; (10) upper surfaces glossy black with a white head band, venter uniform black.

Other features: The holotype is 169 mm in standard length with a tail length of 32 mm (15.9% of total length); total length 201 mm. Preoculars 0–0. Postoculars 2–2. In the holotype, supralabial five on the right side of the head is split with the upper portion (anterior temporal of Myers, 2003) bordering the parietal and posterior temporal and the latter is shorter than its equivalent on the left side. Supralabials 6–6; supralabial 4 bordering the orbit on the right side of the head with 3–4 bordering the orbit on the left side. Infralabials 7–7, 5–5 bordering the chin shields.

Hemipenes: Based on an everted hemipenis (KU 110703). Organ bilobed. Sulcus spermaticus apparently centrifugal. Pedicel covered with spinules and small spines and two larger spines distally. Capitulum about twice as long as the truncus on asulcate side and covered mostly with small spines (Myers, 2003).

Distribution: Known from a tropical premontane wet forest site east of the Panama Canal and a tropical premontane rainforest site west of the Canal in central Panama, 600–800 m (Fig. 16).

GEOPHIS BETANIENSIS RESTREPO & WRIGHT, 1987
(FIG. 4A)

Geophis betaniensis Restrepo & Wright, 1987: 191, figs 1–3 (Type locality: Colombia: eastern slope of the Cordillera Occidental: Valle del Cauca: Bolivar: Corregimiento de Betania, 4°23'N, 76°21'W, 1680 m; Holotype: UVC 7360, an adult female; Lips & Savage, 1994: 414; Myers, 2003: 36.

Diagnostics: A member of the *Geophis sieboldi* species group characterized by the following combination of features (see Fig. 1B): (1) six supralabials; (2) two supralabials posterior to orbit; (3) no anterior temporal or postlabials; (4) last supralabial separated from contact with the parietal by a short posterior temporal; (5) three jupal scales posterior to the posterior temporal and last supralabial with the upper jupal in contact with the parietal; (6) dorsal scales in 15–15–15 scale rows; (7) dorsal and caudal scales smooth; (8) anterior tip of maxilla with first tooth at tip, posterior end of maxilla not depressed, not curving ventrad; (9) 140–143 ventrals in female; 20–28 subcaudals in females; ventrals plus subcaudals 168–173; (10) upper surfaces of body and tail

reddish-brown with posterior margins of each scale black; black longitudinal ventrolateral stripes on tips of ventral from postoccipital region to tip of tail; venter yellow laterally, midventral area greenish-yellow; subcloacal plate red.

Other features: The largest female is 260 mm in standard length with a tail length of 36 mm (12.2% of total length); total length 296 mm. Tail length as a percentage of total length 12.2–12.3%. Preoculars 0–0. Postoculars 2–2. Supralabials 6–6, 3 and 4 bordering orbit. Infralabials 6–6, 4 in contact with genials.

Restrepo & Wright (1987) state that the holotype, and presumably the paratypes, had a pair of black stripes on scale rows 1 and 2 on each side in life. These stripes are not evident in the paratype (LACM 136189) examined by us.

Hemipenes: No information as both known specimens of this species are females.

Distribution: In the tropical premontane wet forest zone of the Cordillera Occidental of Colombia, 1680 m (Fig. 16).

GEOPHIS DUNNI SCHMIDT, 1932 (FIG. 4B)

Geophis dunni Schmidt, 1932: 8 (Type locality: Nicaragua: Matagalpa: Matagalpa, 705 m; Holotype MCZ 31870, an adult female); Downs, 1967: 153, fig. 19.

Diagnostics: The single known female specimen of this species is distinguished from other members of the *Geophis sieboldi* species group by the following combination of characters (see Fig. 1B): (1) six supralabials; (2) two supralabials posterior to orbit; (3) no anterior temporal or postlabials; (4) last supralabial separated from contact with the parietal by the elongate posterior temporal; (5) two jupal scales posterior to the posterior temporal and last supralabial and upper jupal separated from contact with the parietal by the elongate posterior temporal; (6) dorsal scales in 17–17–17 rows; (7) dorsal and caudal scales strongly keeled except on anterior part of body; (8) anterior tip of maxilla pointed, toothless; posterior end of maxilla depressed, curving ventrad; (9) 140 ventrals; 36 subcaudals; ventrals plus subcaudals 176; (10) ground colour of upper surface pale yellowish with most scales edged with brown; 23 and one half dorsal band positions consisting of 13 transverse bands, ten bands offset on the two sides but broadly continuous across the back, two offset but narrowly connected, and one completely offset, plus one blotch; none of the dorsal dark markings extends to the ventrals; seven irregular transverse dark bands

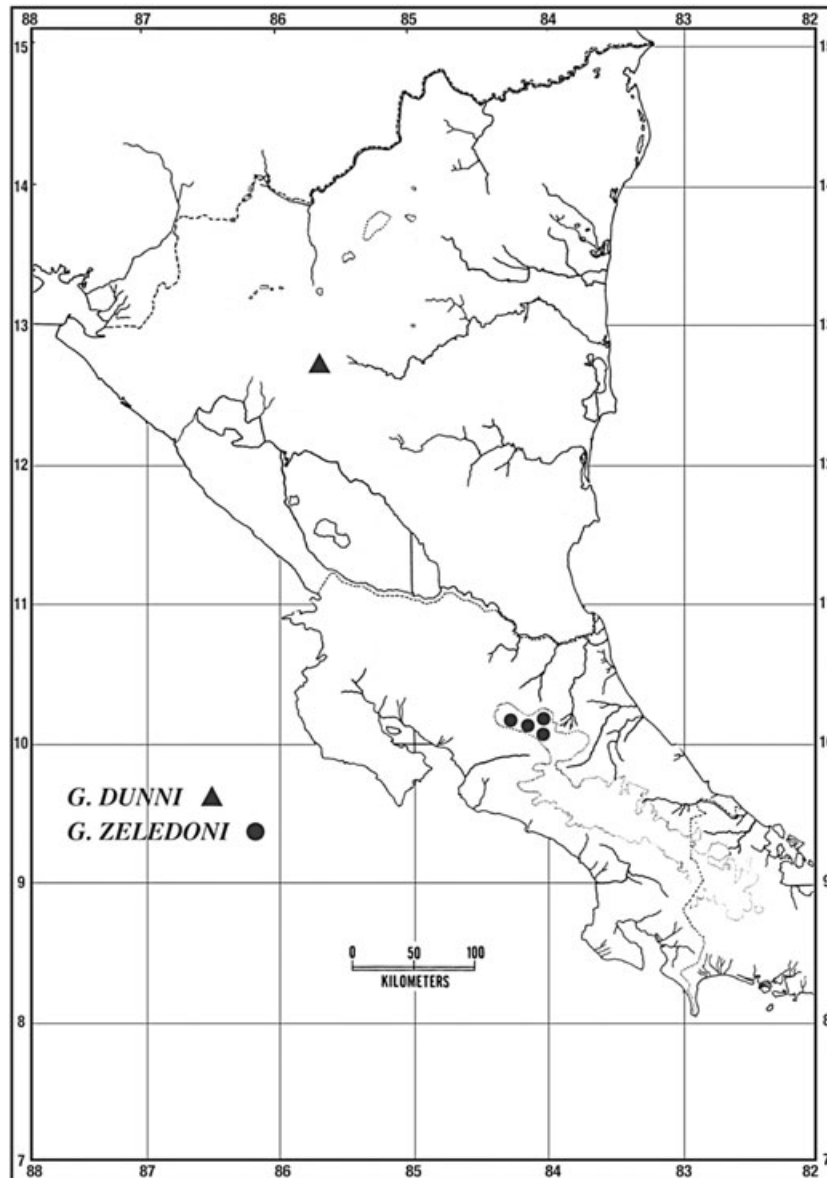


Figure 17. Geographical distribution of two species of *Geophis* in Nicaragua and Costa Rica. Symbols may indicate more than one locality.

on tail and posterior one-third of tail with small dark spots; ventrals and subcaudals immaculate yellow in preservative; a yellowish head band is heavily suffused with dark pigment anteriorly.

Other features: The holotype is 310 mm in standard length with a tail length of 57 mm (15.5% of total length); total length 367 mm. Preoculars 0–0. Postoculars 1–1. Supralabials 6–6, 3–4 bordering orbit. Infralabials 8–8, 5 in contact with genials.

Hemipenes: No information as the only known specimen of this species is a female.

Distribution: From a tropical premontane moist forest area in north-central Nicaragua, 705 m (Fig. 17).

GEOPHIS HOFFMANNI (PETERS, 1859) (FIG. 1D)

Colobognathus hoffmanni Peters, 1859: 276, fig. 2 [Type locality: Costa Rica; Lectotype: ZMB 4003, an adult female by action of Downs (1967)].

Elapoides hoffmanni, Jan, 1862: 22.

Geophis hoffmanni, Bocourt, 1883 in A. Duméril, Bocourt & Mocquard, 1883: 529, pl. 31, figs 8, 8a–c; Downs, 1967: 155, fig. 19; Savage, 2002: 603, pls 371–72; Myers, 2003: 40; Solórzano, 2004: 284, fig. 79.

Rhabdosoma bicolor, Cope, 1885: 529 (in part).

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

Catastoma hoffmanni, do Amaral, 1929: 192.

Geophis bartholomewi, Brattstrom & Howell, 1954: 120, fig. 1 (Type locality: Honduras: El Paraíso: Los Arenales, 380 m = Nicaragua: Nueva Segovia: Arenal of original description; Holotype: CAS 91202, an adult female).

Geophis acutirostris, Taylor, 1954: 691, fig. 3 (Type Locality: Costa Rica: Cartago: Oreomuno: Cot, 1817 m; Holotype: KU 34760).

Diagnostics: One of the most distinctive species of *Geophis* differing from all others in the following combination of characters: (1) usually five supralabials, rarely four; (2) one supralabial lies posterior to orbit; (3) no anterior or posterior temporal but post-supralabials present; (4) very large last supralabial in broad contact with the parietal; (5) two large post-supralabials posterior to last supralabial and upper in contact with the parietal; (6) dorsal scale in 15–15 rows; (7) dorsal and caudal scales smooth, except for a few above vent; (8) anterior tip of maxilla pointed, toothless; posterior end of maxilla depressed and curving ventrad; (9) ventrals 117–124.5–130 in males ($N = 33$), 122–131.2–135 in females ($N = 42$); subcaudals 28–32.1.9–37 in males ($N = 31$), 23–27.9–32 in females ($N = 38$); ventral plus subcaudals 147–168 ($N = 60$); ventrals 128, subcaudals 27 in one juvenile of indeterminate sex; (10) upper surfaces of body and tail black; venter immaculate in juveniles, banded in larger snakes; light head band present in most juveniles, obliterated in larger specimens.

Variation: This summary includes data on this common species from Downs's (1967) account: the largest male is 197 mm in standard length with a tail length of 36 mm (15.5% of total length); total length 233 mm. The largest female is 260 mm in standard length with a tail length of 40 mm (13.3% of total length); total length 300 mm.

The loreal is excluded from the orbit by contact between the prefrontal and third supralabial in seven snakes; the shape of the supralabials indicates that this condition involves fusion of the supralabial with the posterior portion of the loreal. Preoculars 0–0. Postoculars 0–0 ($N = 2$), 0–1 ($N = 2$), 1–1 ($N = 70$), 1–2 ($N = 4$); postocular reduced and separated from supraocular by an extension of the parietal ($N = 10$). In one snake a narrow extension of the upper post-supralabial separates the fifth supralabial from contact with the parietal (Savage, 2002). Supralabials 4–4 ($N = 1$), 4–5 ($N = 1$), 5–5 ($N = 70$). The four-supralabial condition results from a fusion of supralabials 3 and 4; supralabials 3 and 4 usually border the orbit but only the third supralabial when only four

supralabials are present. Infralabials 5–6 ($N = 3$), 6–6 ($N = 74$), 6–7 ($N = 1$); usually four ($N = 75$) and rarely two or five infralabials contact the genials. See Appendix 4 for notes on the type series.

Hemipenes: Based on a retracted hemipenis (Downs, 1967). Organ slightly bilobed. Pedicel covered with spicules and 2–3 medium spines in the distal region. Truncus bears numerous spines. Capitulum covered with spinulate calyces.

Remarks: Myers (2003) extended the known range of this species in Panama from Downs' easternmost record at Coclé: Valle de Antón to two sites east of the Panama Canal, Panamá: Madden Forest, c. 100 m (AMNH 113561) and Panamá: Piedras-Pacora Ridge: Cerro La Victoria, 670 m (FMNH 152047). He also recorded *G. hoffmanni* (AMNH 108373) for the first time from Colombia (no specific locality). Additional Panama records include two females (CHP 605 and 4343) from Panamá: Parque Nacional de Altos Campana and one juvenile (FMNH 216258) from Panama: around Panama City. All three have 15–15 rows of dorsal scales, supralabials 5–5, with three and four bordering the orbit, no temporals and 6–6 infralabials (four bordering the genials). CHP 605 is 183 mm in standard length with a tail length of 24 mm (11.6% of total length) and has 133 ventrals, 26 subcaudals and ventrals plus subcaudals number 159. CHP 3243 is 156 mm in standard length with a tail length of 19 mm (11.0% of total length); total length 175 mm; 127 ventrals, 23 subcaudals and the ventrals plus subcaudals equal 150. FMNH 216258 is 146 mm in standard length with a tail length of 20 mm (12.0% of total length); total length 166 mm; ventrals 128, subcaudals 27 and ventrals plus subcaudals equal 155.

Downs (1967) and Myers (2003) both pointed out that the reduction to five supralabials in this species is not due to fusion of two supralabials. Rather, it is caused by a shortening of the gape and jaw (Fig. 1D). The upper post-supralabial is clearly homologous to the posterior temporal and the lower post-supralabial to supralabial 6 of other species treated here. The postinfralabial seems to be homologous to infralabial 7 or 7 fused with jubal IV. These features indicate that the shortening of the jaws was from the posterior end.

Distribution: Found in areas that currently or formerly were covered by a variety of forest vegetation, including tropical lowland moist and wet forests, tropical premontane moist and wet forests and rain-

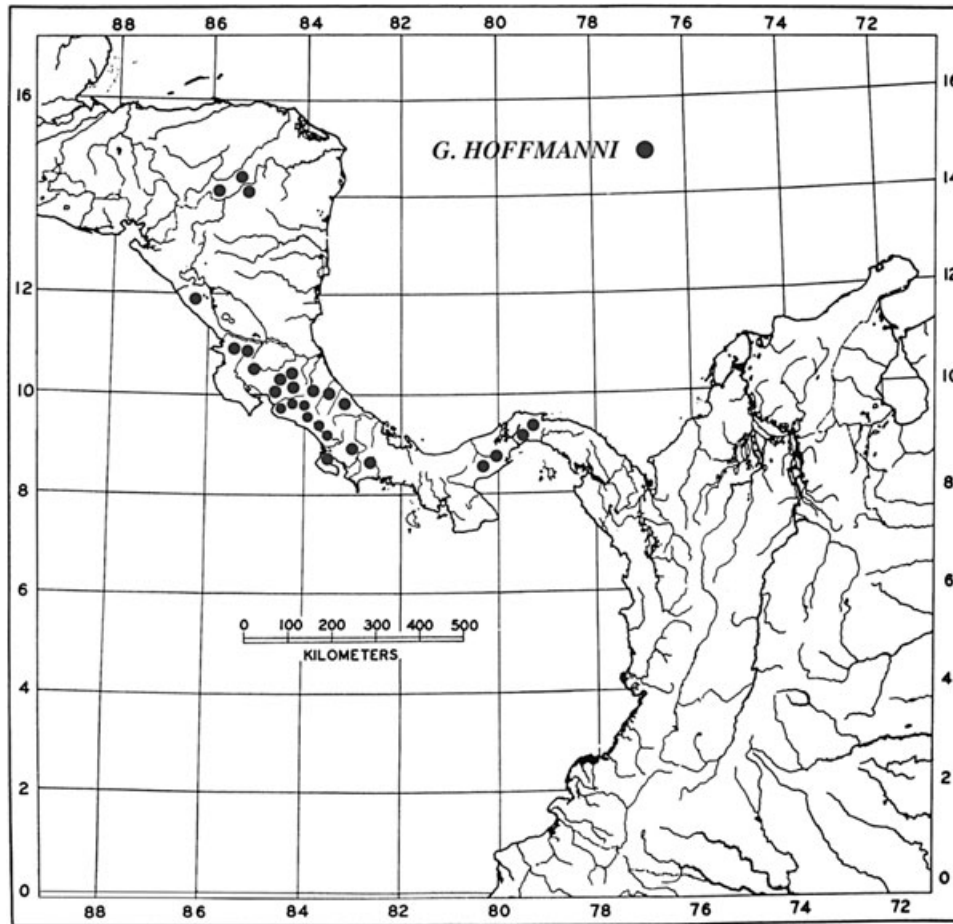


Figure 18. Geographical distribution of *Geophis hoffmanni*. This species is also known also from 'Colombia' without further locality data. Symbols may indicate more than one locality.

forest, and tropical lower montane wet forest, from eastern Honduras to Colombia, 18–1670 m (Fig. 18).

GEOPHIS ZELEDONI TAYLOR, 1954 (FIG. 1A)

Geophis zeledoni Taylor, 1954: 693, fig. 4 (Type locality: Costa Rica: Alajuela: between Volcán Barva and Volcán Poás: Finca Zeledón, c. 1829 m; Holotype: KU31992, an adult female); Downs, 1967: 174, fig. 19; Savage, 2002: 604 (in part); Solórzano, 2004: 292, figs 83, 84 (in part).

Diagnostics: This species is distinctive within the *Geophis sieboldi* species group in the following combination of features: (1) usually six supralabials, often five; (2) two supralabials lie posterior to orbit; (3) no anterior temporal or postlabials; (4) last supralabial usually separated from the parietal by a short posterior temporal; (5) usually three jubbals posterior to the posterior temporal and last supralabial and the upper juba in contact with the parietal; (6) dorsal scales in

15–15–15 rows; (7) caudal scales weakly keeled to smooth; (8) first tooth at tip of maxilla or preceded by a short toothless area; posterior half of maxilla depressed, curving ventrad posteriorly; (9) ventrals 139–143.7–149 in males ($N = 15$), 141–144.8–150 in females ($N = 14$); subcaudals 37–43.1–46 in males ($N = 13$), 36–39.3–43 in females ($N = 12$); ventrals plus subcaudals 178–184.4–191 ($N = 12$); (10) dorsum and upper surface of tail uniform black; no light head band in juveniles; venter banded or variegated; subcaudals mostly to entirely black.

Variation: Twelve additional specimens, five males and seven females, referable to this species bring the total to 29 known examples, 15 males and 14 females. The largest male is 379 mm in standard length, has a slightly incomplete tail but measures 417 mm overall; the largest male with a complete tail is 311 mm in standard length with a tail length of 64 mm (17.1% of total length); total length 375 mm. The largest female is 377 mm in standard length but with an incomplete

tail (74 mm). The largest female with a complete tail is 344 mm in standard length with a tail length of 74 mm (17.7% of total length); total length 418 mm. Relative tail lengths as percentages of total length, including data for five specimens seen by Downs (1967), are 16.0–16.5–17.0% in juvenile males ($N = 2$), 17.1–19.6–22% in adult males ($N = 5$), 17.2% in a juvenile female and 16.9–18.1–21.0% in adult females ($N = 5$).

One juvenile female (LACM 150741) has a moderately elongate posterior temporal and two jubals on the right side of the head. Examination of the maxilla confirms that this specimen is a *G. zeledoni*. One snake (UCR 3953) has the upper jubal split into two scales on both sides of the head (Fig. 1C). Preoculars 0–0; postoculars 1–1 ($N = 28$), 1–2 ($N = 1$); the second postocular is apparently split off from supralabial 4. Supralabials 5–5 ($N = 7$), 5–6 ($N = 3$), 6–6 ($N = 19$). The five-supralabial condition usually involves the fusion of supralabials 5 and 6; in one specimen (LACM 150742) this state involves fusion of supralabials 2 and 3 on one side; supralabials 3 and 4 usually border the orbit ($N = 21$); 2 and 3 border the orbit on one side ($N = 1$) and 3 on both sides ($N = 7$). Infralabials 4–6 ($N = 1$), 5–6 ($N = 5$), 6–6 ($N = 22$), 6–7 ($N = 1$); four infralabials are the result of fusion of 4–6 and five through fusion of 5–6; 2–4 ($N = 1$), 3–3 ($N = 1$), 3–4 ($N = 3$) and 4–4 ($N = 24$) contact the genials.

Hemipenes: Based on a retracted (Downs, 1967) and an everted hemipenis (UCR 3953). Organ slightly bilobed. Pedicel covered with minute spines and bearing 3–4 large spines. Truncus covered with 35–40 medium spines. Capitulum covered with spinulate calyces.

Remarks: The reference by Savage (2002) to a striped specimen (UF 10438) of this species from Volcán Irazú in the Cordillera Central of Costa Rica is in error. This snake is a representative of *G. brachycephalus* with sloughing skin that does not show keeling on the dorsal scales. The caudal scales are strongly keeled. Examination of the maxilla confirms the re-identification. Among the snakes examined in the course of this study is a single male (USNM 297710) from Panama: Bocas del Toro-Chiriquí: Cerro Bollo: 3.5 km E Escopeta Camp. It is a male 241 mm in standard length with a tail length of 61 mm (tail length/total length, 20.2%) and 141 ventrals, 43 subcaudals for a total segmental count of 184. It agrees with other members of the group in lower Central America in having 1–1 supraoculars and 0 + 1 temporals. The first tooth on the maxilla is at the tip and the posterior portion of the bone is somewhat flattened and deflected ventrally. Other features are 6–6

supralabials (3 and 4 bordering the orbit), 0–0 preoculars, 1–1 postoculars, a short posterior temporal and 3–3 jubals in contact with the temporal and last supralabial. It is not possible to determine the number and relationship to other scales for the infralabials as this area is damaged and the condition of the snake suggests that it may have died before preservation. There are 15–15–15 dorsal scale rows with weak keels on the last 13% of the rows and on the base of the tail. The upper surfaces are uniform brownish (probably black in life), the venter is white and the subcaudals mostly white with some dark pigment on the anterior lateral margins. Surprisingly, all these features fall within the range of variation for *Geophis zeledoni*, a species that otherwise appears to be endemic to Volcanes Poás and Barva in the Cordillera Central or Volcanica of Costa Rica, 250 km to the north-west. Only the collection of additional material from this portion of the Serranía de Tabasará near Cerro Santiago will resolve the status of this specimen and the population that it represents.

Distribution: Restricted to tropical lower montane wet forest and tropical lower montane rainforest on the slopes of Volcán Barva and Volcán Poás in the Cordillera Central of Costa Rica, 1830–2100 m (Fig. 17).

DISCUSSION

Geophis belongs to a clade and ecomorphological guild within the Diapsidinae comprising fossorial and cryptozoic snakes that specialize on soft-bodied prey, primarily earthworms, that is represented by goo in stomach contents (Cadle & Greene, 1993). Member genera of ‘goo-eaters’ are, in addition to *Geophis*, *Adelphicos*, *Atractus* and *Ninia*. These genera are considered to be part of the autochthonous Middle American Element of the herpetofauna (*sensu* Savage, 2002) that evolved *in situ* in Mesoamerica through most of the Cenozoic but invaded South America over the last 3 Myr across the uplifted Panama Isthmus.

In addition to being ‘goo-eaters’ a number of *Geophis* are considered putative mimics of venomous coral snakes (Elapidae) (Savage & Slowinski, 1992; Campbell & Lamar, 2004). Within other species groups of *Geophis* a number of taxa are characterized by red bands on a black ground colour (*G. cancellatus*, *G. laticinctus*, *G. semidoliatus*) or black bands on red (*G. duellmani*). In the *sieboldi* group, one species (*G. damiani*, from Honduras) has red bands on a black ground colour and another (*G. russatus* of Mexico) has black bands on red. We suspect that *G. dunnii* may have had a pattern similar to that of *G. russatus* in life. Three species of the *sieboldi* group (*G. brachycephalus*, *G. talamancae*, *G. tectus*)

A KEY TO THE SPECIES OF THE LOWER CENTRAL AMERICA AND COLOMBIA
G. SIEBOLDI GROUP

- 1a. Dorsal scales in 17 rows at midbody; dorsal pattern of dark blotches on light background (Fig. 4B) *Geophis dunni*
- 1b. Dorsal scales in 15 rows at midbody; dorsum without dark blotches on light background, usually uniform or with light markings 2
- 2a (1b). One supralabial posterior to orbit; five or fewer supralabials; no anterior or posterior temporal, two postsupralabials present (Fig. 1D) *Geophis hoffmanni*
- 2b. Two supralabials posterior to orbit; a posterior temporal but no postsupralabials 3
- 3a (2b). Venter uniform black *Geophis bellus*
- 3b. Venter immaculate, with black ventrolateral stripes or ventrals variously marked with dark pigment (Fig. 5A–F) 4
- 4a (3b). A pair of ventrolateral dark stripes (Fig. 5F) *Geophis betaniensis*
- 4b. Venter immaculate or ventrals variously marked with dark pigment (Fig. 5A–E), never with paired ventrolateral dark stripes 5
- 5a (4b). Last supralabial usually separated from parietal by a short posterior temporal; usually three jubals and the upper jubal in contact with the parietal (Fig. 1A); maxilla not pointed, first tooth at tip or preceded by a short toothless area; caudal scales smooth to weakly keeled *Geophis zeledoni*
- 5b. Last supralabial usually separated from parietal by an elongate posterior temporal; usually two jubals, upper separated from parietal (Fig. 1B); anterior tip of maxilla pointed and toothless; caudal scales strongly keeled except in some juveniles 6
- 6a (5b). Relatively low segmental counts: ventrals 118–132 in males, 121–139 in females; subcaudals 35–41 in males, 30–38 in females *Geophis talamancae*
- 6b. Relatively high segmental counts: ventrals 129–149 in males, 136–157 in females; subcaudals 35–51 in males, 29–46 in females 7
- 7a (6b). Number of subcaudals relatively low, usually 43 or fewer in males, 29–39 in females
..... *Geophis brachycephalus*
- 7b. Number of subcaudals relatively high, usually 44 or more in males, usually 40 or more in females 8
- 8a (7b). Number of ventrals relatively high with marked sexual dimorphism: usually more than 140 in males (134–149); 141–157 in females *Geophis nigroalbus*
- 8b. Number of ventrals lower with no sexual dimorphism: usually less than 140 in males (137–140), 137–140 in females *Geophis tectus* sp. nov.

are unique in the genus in having polychromatism with red spotted, blotched or banded polychromes forming at least incipient mimetic patterns. Further study is indicated to determine if predators differentially avoid the red marked snakes given a choice between them and their uniform black conspecifics and possibly to elucidate the initial stages of evolution of mimetic patterns.

Species of the *Geophis sieboldi* group are the only representatives of the genus in Lower Central and South America and are found primarily in upland habitats. Their known distribution appears to be fragmented (Figs 14–18). Within the region, the apparently most derived species in which the maxilla is greatly post-shortened, *G. hoffmanni*, has the broadest range from Honduras to Colombia but with great gaps in its known distribution (Fig. 18). Similarly, the known range of the *G. brachycephalus* complex does not include most of the southern Cordillera de Talamanca in Costa Rica, most of the Serranía de Tabasará in western Panama and most of eastern Panama and north-western Colombia (Figs 14–16, 18). The gap areas are very difficult to access, and the

absence of records may be due to lack of sampling. We anticipate, however, that *G. talamancae* will be found to be wide-ranging on the Pacific slope of the southern Talamanca and that *G. tectus* will occur throughout the Serranía de Tabasará. Especially puzzling are the few specimens of *Geophis* in collections from the rather isolated upland areas just east of the Canal Zone region as noted by Myers (2003). Both *G. bellus* and *G. tectus* are represented from this area by single examples. Several other upland taxa (e.g. *Atractus*, *Coniophanes joanae* and *Ninia atrata*) and some lowland ones (e.g. *Dipsas nicholsi*) are rare denizens of the area of east-central Panama but are present in extreme western Panama too. It seems likely that future collecting will establish the presence of *G. hoffmanni* in the gap between central and western Panama as it is known from Colombia. It also seems likely that a member of the *G. brachycephalus* complex will be found to occur in the area between central and western Panama or disjunctly in extreme western Panama. Whether the species represented is one known from central Panama, *G. nigroalbus*, currently known only from further south in western

Colombia, or an as yet undiscovered taxon, remains to be seen.

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APPENDIX 1

ADDITIONAL RECORDS FOR *G. DOWNSI* AND
G. RUTHVENI

Geophis downsi: Additional material brings the total known specimens of *Geophis downsi* Savage, 1981 to five. Two females referable to this species from near the type locality add to its known variation. They agree with the type series consisting of two males (LACM 130254 and 147210) and one female (USNM 212045) in having 15–15–15 dorsal scale rows that are strongly keeled on the posterior body as are the caudal scales; no anterior temporal; three jugals bordering the posterior margin of the last supralabial and a single posterior temporal; the snout pointed with the rostral produced posteriorly between the internasals; the upper surfaces of the body and tail uniform black and the upper surface of the head more greyish than the body and tail; the venter banded black on their anterior margins and the subcaudals nearly uniform black.

LACM 153097 (CRE 4712) is 174.6 mm in standard length with a tail length of 32.4 mm (18.6% of total

length) and has 130 ventral and 37 subcaudal scutes (total 167). It has 5–4 supralabials and no postoculars. The five-supralabial condition appears to be the result of fusion of supralabials 1 and 2 on the right side of the head and the four-supralabial state by fusion of supralabials 3 and 4 on the left side. On the right side supralabials 2 and 3 border the orbit below and supralabial 4 (equivalent to supralabial 5 in snakes having six supralabials) is narrowly separated from the orbit by a posteriodorsal projection of supralabial 3. On the left side the large supralabial 2 borders the orbit below and supralabial 3 (equivalent to supralabial 5 in snakes having six supralabials) narrowly borders the posteroventral border of the orbit. There are 6–6 infralabials, four bordering the genials.

LACM 151261 (CRE 921) is 178.9 mm in standard length with an incomplete tail and has 138 ventral scutes. It has 6–6 supralabials but is unique for the species in having a small postocular on both sides of the head that separates supralabial 5 from the orbit. There are 6–6 infralabials, four bordering the genials. A similar variation (postocular present or absent) is found in the allied *Geophis godmani*. *Geophis downsi* and *G. godmani* are the only members of the genus lacking both an anterior temporal and supraocular scales. They differ most trenchantly as follows:

	<i>G. downsi</i>	<i>G. godmani</i>
Caudal and posterior dorsal scales	Keeled	Smooth
Ventrals		
Males	122–125	132–143
Females	129–133	133–145
Subcaudals		
Males	45–46	34–38
Females	37–41	26–28
Ventrals plus subcaudals	167–174	162–179

Geophis downsi remains known only from the vicinity of the Las Cruces Biological Station, near San Vito de Java, Puntarenas Province, Costa Rica (1100–1200 m). *Geophis godmani* ranges through the Cordillera Central and Cordillera de Talamanca-Barú from central Costa Rica to western Panama (1100–2100 m).

Geophis ruthveni: Three additional specimens of *Geophis ruthveni* Werner, 1925 bring the total known specimens for this rare snake to seven males and three females. They agree with previously recorded examples in having 15–15–15 dorsal scale rows that are keeled on the posterior body and tail; no anterior temporal but three jubbals bordering the last supralabial; a pointed snout with the rostral produced pos-

teriorly between the internasals; the upper surface of the body and tail black with the sides of the head lighter; the ventrals banded black on their anterior margins and the subcaudals mostly or entirely black.

UF 31096 is a juvenile male 182.5 mm in standard length with a tail length of 40.0 mm (18% of total length) and 125 ventrals and 38 subcaudal scutes (total 163). It has 6–6 supralabials, 3 and 4 bordering the orbit; 6–6 infralabials, 4 bordering the genials; 1–1 postoculars. LACM 15759 (CRE 6365) is an adult female 244 mm in standard length with a tail length of 38 mm (13.5% of total length) and 142 ventral and 34 subcaudal scutes (total 176). It has 6–6 supralabials, 3 and 4 bordering the orbit; 5–5 infralabials with 3 bordering the genials; 1–1 postoculars. LACM 151260 (CRE 850) is a juvenile female 147 mm in standard length with a tail length of 24 mm (14.0% of total length) and 130 ventral and 35 subcaudal scutes (total 165). It has 6–6 supralabials, 3 and 4 bordering the orbit; 5–5 infralabials, 3 bordering the genials; 1–1 postoculars. In the females the five-infralabial condition is produced by fusion of infralabials 3–4.

Known variation in segmental counts for this species with these additions is: 123–126 ventrals in males, 130–142 in females; 37–41 subcaudals in males, 32–35 in females; total segmental counts 163–176.

Geophis ruthveni is now known from lowland and premontane slopes on the Atlantic versant of Costa Rica (83–1360 m).

APPENDIX 2

LIST OF EXAMINED AND REFERENCED SPECIMENS

The list is arranged alphabetically by species and within species by country from north to south and east and within country by major political units. Specific localities are clustered roughly by proximity to one another within political units. An asterisk (*) indicates that we have not examined the specimen but have used data from the literature (especially Downs, 1967 and Myers, 2003) or received data on the specimen(s) from a colleague.

Geophis bellus: Panama: *Panamá*: nr Altos de Pacora, 700 m (GML*).

Geophis betaniensis: Colombia: *Valle del Cauca*: Betania, 1680 m (LACM 136189, UVC 7360, holotype*).

Geophis brachycephalus: Costa Rica: *Alajuela*: nr Fortuna, S Volcan Arenal (UF 33387); Valle de Río Peñas Blancas (LACM 151297); Reserva San Ramón, Colonia Palmareña 660 m (UCR 10109–10110, 11721, 11437); 16 km ENE Alajuela, c. 1900 m (UF 115768);

4.9 km N Varablanca, *c.* 1700 m (UF 115769–115770); 1.6 km W, *c.* 1900 m (UCR, 915, 918), 2.3 km W Varablanca Cruce, *c.* 1900 m (UCR4624); Isla Bonita, 1200 m (UCR 674–675); Cinchona, 1360 m (LACM 151275, 151290); Cataracta La Paz Grande, 1380 m (UCR 3330); *Cartago*: Tres Ríos, 1345 m (LACM 151276); Cangreja, 1900 m (UCR 5730–5731, 1713, 7111–7114, 7148); 1.5 km SSE Cangreja, *c.* 1900 m (LACM 151294); vicinity Cangreja, *c.* 1900 m (LACM 151273); Palo Verde, 1590 m (UCR 5482, 7191); Dulce Nombre, 1425 m (UCR 9235); Potrero Cerrado, 2200 m (UCR 4903); 1–2 km SE Santa Teresa, 1600 m (LACM 151281); Cervantes, 1441 m (UCR 11140, 11142); 2 km NW Pastora, 2012 m (LACM 151277, 151293); 1.5 km NW Pastora, 1950 m (LACM 151283); 1 km NW Pastora, 1828 m (LACM 151282, 151284, 151286, 151288, 151291–151292, 151296); Río Orosi Puente, Tapantí, 1203 m (UCR 779, 8290); Tapantí, 1188 m (LACM 150733–150735); CATIE, 601 m (LACM 151274); Morehouse Finca, 600 m (KU25732); Jicotea, 802 m (UCR 11141); Moravia de Chirripó (or Turrialba), 1116 m (KU 31988, 63801); *Heredia*: 20.7 km S Cedal, 1936 m (UCR 8361); N slope Volcan Barva, 1500 m (LACM 151295); Barva, 1177 m (UCR 11138); Cerro Redondo, 1862 m (UCR 7614–7615, 1434); *Limón*: Emilia, 260 m (ANSP 21401) Guápiles, 262 m (UCR 11139); Alto Guayacán 750 m (UCR 14070, 14355, 14579, 14915, 14580, 16034); El Tigre, 680 m (LACM 13567, 151279); *Puntarenas*: Monteverde, 1400–1500 m (LACM 151271–151272, 151280, UCR 1054); Golfito, *c.* 13 m (UF 55309). *San Jose*: 1.1 km W La Hondura, 1128 m (LACM 151287); Bajo Máquina, 1740 m (UCR 7590); Cascajal, 1720 m (UCR 10673); Las Nubes, 1800 m (UCR 8291); 0.5 km S Ipis, 1330 m (UCR 919); San Francisco de Coronado, *c.* 1380 m (UCR 11318); Juncos, 1720 m (UCR 535–558); Hda. La Holanda (UCR 15493); btwn. Finca Lara and Río Blanco, *c.* 1540 m (UCR 3415–3417) Rancho Redondo, 2048 m (UCR 6229, 11143, 15488–15491, 15492); above hydroelectric plant, Volcán Irazú, 1828 m (UF 10438); Granadilla de Curridabat, 1410 m (UCR 3627); Concepción, 1360 m (UCR 14329); 6.4 km NE Tres Ríos, 1524 m (LACM 151278). El Rosario, 1327 m (UCR 6230). Panama: *Bocas del Toro*: Río Changena (FMNH 130969). *Chiriquí*: Prensa Fortuna area, 1000 m (AMNH 114317–114319); Quebrada Arena, *c.* 1100 m (CHP 4603); nr Quebrada Alemán (CHP 4612).

Geophis downsi: Costa Rica: Puntarenas: 2 km S San Vito de Jaba, 1200 m (LACM 151261); Las Cruces Biological Station, 1050 m (LACM 153097).

Geophis dunni: Nicaragua: Matagalpa: Matagalpa, 750 m (MCZ 31870, holotype).

Geophis hoffmanni: Panama: *Panamá*: around Ciudad de Panamá (FMNH 216258); Altos de Campana, *c.* 600 m (CHP 0605, 4343). Colombia: ‘Colombia’ (FMNH 43727).

Geophis nigroalbus: Colombia: ‘Colombia’ (FMNH 43727; 54882). Antioquia: Santa Rita (BMNH 98.10.27.3*). Valle del Cauca: Pavas (BMNH 1946.1.6.50, holotype*); Betania, 1680 m (LACM 2547; UVC 7361–7363*, 7722–7746*, 7749–7753*).

Geophis ruthveni: Costa Rica: ‘Costa Rica’ (ANSP 22425); *Alajuela*: Cinchona, 1360 m (KU 35881, 35892); ‘Sarapigui, Brazil’ = Cariblanco, 853 m (NHMW 16508, holotype*); nr Cariblanco, 853 m (LACM 151259); *Heredia*: Río Frío, 85 m (UF 31096). *Guanacaste*: 4 km NE Tilarán, *c.* 460 m (KU35895); Tilarán, 561 m (KU 35893–35894). *Limón*: 4 km W Guápiles, nr Río Toro Amarillo, 260 m (LACM 151260).

Geophis talamancae: Costa Rica: Puntarenas: Las Tablas: Finca Jaguar (1800) m (LACM 147196, holotype). Panama: ‘Panama’ (CHP 3360). *Chiriquí*: El Hato de Volcán, 1200 m (CHP 4106; KU 75695, USNM 129382); Finca Lérica, *c.* 1321–1615 m (ANSP 21699, 22422, 22922–22938, 23877–23879, 24723–24734, 24766–24769); vic. Boquete, *c.* 1200 m (ANSP 22422; CAS 78940–78976; 78978–79001; UMMZ 57957–57958).

Geophis tectus: (see species description for specimens and localities).

Geophis zeledoni: Costa Rica: *Alajuela*: Poasita, Finca El Tirol, 1980 m (UCR 3900): S slope Volcán Poás (UMMZ 117720); 6.9 km W Varablanca, 1950 m (LACM 150739). *Heredia*: 26.6 km N Heredia (MVZ 110487); Finca Zeledón, btwn. Volcán Barva–Volcán Poás (KU 31951, 31992, holotype); 24 km N Heredia (MVZ 110488); Varablanca (KU 35851–35854); Cruce de Varablanca, 1936 m (LACM 150737, 150741–150742; UCR 395, 638, 676; UMMZ 122640); N slope Volcán Barva, 2050 m (LACM 150736, 150738, 150740); 9 km N Concordia, 1980 m (KU 63819–63823); 1 km N Los Cartagos @ Ruta 127 (UCR 900); Rama Sur, Río Las Vueltas, 2030 m (KU 103884).

APPENDIX 3

PROVENANCE OF *GEOPHIS* AND OTHER SNAKES INCORRECTLY CATALOGED FROM ‘PANAMA SABANAS’

Myers (2003) briefly reviewed the listing in the catalogue of the ANSP for *Geophis brachycephalus* (ANSP

24723–24734), *Geophis godmani* (ANSP 24722), and *Trimetopon slevini* (ANSP 24717–24719) from ‘Panama Sabanas’. As the three species are all upland forms that co-occur in extreme western Panama and all other ‘Sabanás’ material is from lowland central Panama, Myers concluded that their association with that ‘Sabanás’ locality must have been a cataloguing error and that the Academy specimens were part of the Panama Snake Census (PSC) collection from Panama: Chiriquí: Finca Lérica (above Alto Quiel). Here we provide further details from Dunn’s notes regarding the provenance of the specimens in question.

Both the ‘Panama Sabanas’ and the Finca Lérica series are part of Herbert C. Clark’s PSC collections. Clark, then Director of the Gorgas Memorial Laboratory, in Panama City, instituted a survey of Panama snakes beginning in 1929 and continuing through 1953 (see Dunn, 1947, 1949; Myers, 2003). The intent was to assess the relative medical significance of venomous snakes. Bounties were paid for specimens, usually heads, and specimens accumulated at various centres throughout Panama.

In 1949, Emmett Reid Dunn published his classic paper on the distribution and abundance of Panama snakes based primarily on the PSC collections (10 693 specimens) and 1073 snakes from natural history museums. The PSC specimens analysed in that report were from west-central and eastern Panama and grouped by general locality for this purpose as: Coclé-Herrera, Sabanas, Chagres, and Darién. The Sabanas material (3914 snakes) was from a variety of Pacific lowland localities, both east and west of the Panama Canal, between Panama: Panama: Cañita and Capria, respectively. Many of these have specific locality data but others are catalogued from more inclusive sites (e.g. Chorrera to Arraiján) or simply Panama Sabanas (usually Sabanas in Dunn’s notes). These localities all lie in an area having a long dry season (mid-December to April) that originally supported scrub, shrub or savanna vegetation but has been anthropogenically modified to an extreme beginning in preconquest times (Bennett, 1968).

The Lérica PSC collection was not included in Dunn’s (1949) analysis but all Sabanas snakes collected prior to 1946 were. Significantly, *Geophis brachycephalus*, *Geophis godmani* and *Trimetopon* are not referred to anywhere in the 1949 paper. However, Dunn (1947) had published an often overlooked report prescient of the 1949 paper on the snakes of Lérica some 2 years earlier based on PSC material (533 specimens) and seven others in museum collections. This series included 255 *Geophis brachycephalus*, three *Geophis godmani* and 26 *Trimetopon slevini*. The PSC material from Lérica had been accumulated by Tolef B. Mönniche, the owner of the finca, beginning in 1940.

A review of Dunn’s notes accumulated over many years, at least beginning in 1928, and organized as a preliminary synopsis of the ophiofauna of lower Central America, clarifies the source of the Sabanas specimens of questionable locality data. Part of Dunn’s entries for *G. brachycephalus* list the following:

‘Lerida cl 1940 17 + ERD 1
1941 17
1942 35
1943 99
1944 45’

L tot 1947 = 255

In this notation, as throughout Dunn’s notes, cl (= Clark) is used for snakes from the PSC. Year and number of specimens are indicated through 1945. The total of examples from Lérica (L.) through 1947 is also noted and is the same total as listed in Dunn’s 1947 paper. No *G. brachycephalus* from Sabanas or Panama Sabanas are listed among the other 69 cited from Panama. The number is actually 65 as three snakes from Panama: Chiriquí: Boquete, in an extensive series (63 snakes) collected by Joseph R. Slevin (1942) (sl in Dunn’s notes) represent other species of *Geophis* (Downs, 1967) and include the holotype of *G. championi* (BMNH 1946.1.1.77). It seems clear from the above evidence and confirmed below that ANSP 2423–2434 catalogued as being from ‘Panama Sabanas’ are also from Lérica.

Recall that most snakes from the PSC are heads or heads with a short segment of the body and after identification, unfortunately, Dunn did not keep and/or deposit all of them in museums (see Myers, 2003). He did, however, retain rarer forms and smaller complete specimens. The ANSP contains the following *G. brachycephalus* catalogued from Lérica: ANSP 21699, a specimen collected by Dunn in 1939, and the following PSC specimens: 22922–22938, ANSP 23877–23879, ANSP 24766–24769.

The situation for *Geophis godmani* is even more clear-cut. The pertinent material in Dunn’s notes is as follows:

‘Lerida cl 1940 1h, 1941 1h, 1943 1h.’

He makes no mention of other specimens from elsewhere in Panama. The ANSP collections contained only three heads (h in Dunn’s notes) all from the PSC, two from Lérica: ANSP 22910, ANSP 24765, and the putative Sabanas example (ANSP 24722), now lost. Obviously ANSP 24722 is one of the three heads recorded from Lérica by Dunn. Note that typographical errors list ANSP ‘24756’ for one Lérica snake (Downs, 1967) and ANSP ‘24723’ for the ‘Sabanás’ example (Myers, 2003).

The pertinent Dunn notation for *Trimetopon slevini* is:

'Lerida ANS (2) cl. 1941₁–1942₇ 1943₉

The notation 1943₉ apparently refers to the number of specimens collected by the PSC from 1940 to 1943. ANS (2) apparently refers to the two paratypes (ANSP 21700–21701) collected in 1939 prior to when the PSC began obtaining material from the finca or to ANSP 22939–22940. The ANSP catalogue lists four other PSC Lérída specimens: ANSP 23875, ANSP 24770–24772 and three specimens of *T. slevini* (ANSP 24717–24719) are catalogued from 'Panama Sabanas' for a total of 11 Academy specimens of the species. Clearly, the 'Sabanás' specimens are part of the nine collected for the PSC from Lérída. The only other specimen of this species listed in Dunn's notes is the holotype (CAS 78938) from Panama: Chiriquí: near Boquete.

Although not noted by previous authors, another upland snake, *Ninia psephota*, is represented in the Academy collections by a PSC specimen (ANSP 24720) purportedly from 'Panama Sabanas'. Dunn's notes on *N. psephota* state:

'Lerida cl. 1940 31941 31942 13 1944 4 [a line has been drawn through these] Lerida 38'

No mention is made of any members of this species from elsewhere in Panama, except the series of 61 snakes from nearby Boquete reported on by Slevin (1942). The number of snakes of this species listed from Lérída by Dunn (1947) is also 38.

A single specimen of *Liophis epinephelus* (ANSP 24721) listed in the Academy catalogue as being from 'Panama Sabanas' has not been mentioned by previous authors. A typed label in the jar containing this specimen reads 'Finca Lerida, Chiriquí, PSC'. Dunn's notes record 52 (57 in Dunn, 1947) specimens of this species from Lérída and 19 heads from Sabanas. As the Academy specimen is complete and has associated locality data, it must have been collected at Lérída. In an obvious *lapsus* Dunn (1947) lists the number of specimens of this form from Lérída as 31, duplicating the number recorded for *Lampropeltis triangulum*.

Significantly, the catalogue numbers for all the reputed 'Panama Sabanas' PSC specimens that obviously came from Lérída are in a single sequence (ANSP 24717–24734). The previous series, ANSP 24703–24716, are PSC snakes recorded in Dunn's notes and the Academy catalogue as from 'Sabanás'. We can only conclude that there was a cataloguing error where Panama Sabanas was entered as the locality for the next following 18 specimens actually collected from Lérída.

APPENDIX 4

COMPOSITION OF THE TYPE SERIES OF *GEOPHIS HOFFMANNI*

Emmett Reid Dunn examined the type series of this species in Berlin and London during his tour of European museums as a John Simon Guggenheim Fellow in 1928–29. His notes list eight types as follows:

'Bmnh 61-2-10-3
Berl 1868 (2)
'1869 (2)
'1870
'4106
'4003 TYPES'

In 1942 (p. 4) Dunn stated '... I have examined the type (Berlin 4003) ...'. However, as pointed out by Downs under the International Code of Zoological Nomenclature (Art. 72.4.7) this phraseology does not establish ZMB 4003 as the lectotype.

Downs re-examined the Berlin syntypes all from 'Costa Rica' and received data for the syntype in London (new number BMNH 1946.1.6.54) purportedly from 'Porto Caballo, Costa Rica'. He noted that 4106 contained two specimens to bring the total to nine syntypes. Downs (1967) concluded that the original description of this species (Peters, 1859) was a composite of features from several specimens and chose to designate one of the larger syntypes, an adult female (ZMB 1870), as the lectotype. However, it seems likely that the description and illustration in Peters (1859) was based on one of three small male syntypes having the supraocular and postocular separated from contact on the left side of the head by an extension of the parietal. Peters apparently wished to indicate the maximum size of his new form and so the published measurements were for the largest specimen, not the one illustrated and described. Bauer, Gunther & Klipfel (1995) listed the same numbers for the Berlin syntypes as in Dunn's notes and in Downs (1967) but indicated there was only one specimen under number 1869. However, they list a syntype at ZMUC, presumably the missing second specimen of 1869 (but see below). These authors did not realize that Downs had selected ZMB (1870) as the lectotype.

Dr Rainer Günther kindly reviewed the Berlin series for us. He reports that it consists of: ZMB 1866 – two specimens; 1869 – two specimens; 1870 – one specimen; ZMB 4003 – one specimen; ZMB 4106 – two specimens. These are the same numbers and number of specimens reported by Downs (1967). All of these snakes were collected by Carl Hoffmann, who resided in Costa Rica, from 1854 until his premature death in 1859 (Savage, 2002). The specimen in the British Museum is from the type series sent

there as a gift or on exchange shortly after the species description as it was catalogued in 1861. It is unknown how the locality 'Porto Caballo' became associated with this snake, as there is no locality with that name in Costa Rica. There is an Isla Caballo in the Golfo de Nicoya on the Pacific side of Costa Rica. We know of no snakes in collections from this mangrove- surrounded island. *Geophis hoffmanni* is a common and typical snake of upland

Costa Rica and is even today found in vacant lots and gardens on the Meseta Central. As Hoffmann lived and collected for the most part at upland sites it seems more than unlikely that he visited Isla Caballo. Boulenger (1894) and Dunn's notes list it as simply being from Costa Rica, leading to the suspicion that the citation of 'Porto Caballo' was added advertently when this specimen was recatalogued in 1946.