

SYSTEMATICS OF THE NEOTROPICAL SNAKE *DENDROPHIDION PERCARINATUM* (SERPENTES: COLUBRIDAE), WITH DESCRIPTIONS OF TWO NEW SPECIES FROM WESTERN COLOMBIA AND ECUADOR AND SUPPLEMENTARY DATA ON *D. BRUNNEUM*

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ABSTRACT. *Dendrophidion percarinatum* (Cope) is redefined on the basis of standard and new characters to distinguish it from two new South American species with which it has previously been confused. The redefined *D. percarinatum* is distributed from Honduras through Central America to western Colombia, with a seemingly outlying locality in extreme western Venezuela. One new species, *D. prolixum*, is sympatric with *D. percarinatum* at a few localities in central western Colombia and the distribution of the new species continues southward into northwestern Ecuador. A second new species, *D. graciliverpa*, occurs throughout western Ecuador, where its distribution extensively overlaps that of *D. brunneum* (Günther). Hemipenes of the two new species are unusually long and slender (gracile morphotype), a morphology distinct from other described *Dendrophidion* hemipenes, which are shorter and more robust (robust morphotype). Additionally, the new species differ from *D. percarinatum* in color patterns but not in standard scutellation characters such as segmental counts. Similarly, the two new species differ from one another in coloration but not in scutellation or hemipenial morphology. Hemipenes of *D. percarinatum* and the new species are described in detail. The holotype of *D. brunneum* is redescribed to ensure the proper application of that name. New specimens document the widespread occurrence of *D. brunneum* in the lowlands of western Ecuador and apparent extensive pattern polymorphism, including unicolor, striped, crossbanded, and punctate forms; more data on coloration in life are needed. Some previous records of “*D. percarinatum*” from interandean valleys of the Río Cauca/Magdalena system are from mistaken identities. However, several specimens from the Río Magdalena resemble *D. percarinatum* in scutellation but differ in color pattern; their status needs further study.

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Key words: Colombia, Ecuador, systematics, Chocó, Central America, South America, *Dendrophidion*, snakes, new species, hemipenis, morphology

RESUMEN. *Dendrophidion percarinatum* (Cope) se redefine sobre la base de caracteres estandarizados y nuevos para distinguirlo de dos nuevas especies sudamericanas con que se confundieron anteriormente. El redefinido *D. percarinatum* se encuentra desde Honduras por América Central hasta el oeste de Colombia, con una localidad aparentemente alejada en el extremo occidental de Venezuela. Una nueva especie, *D. prolixum*, es simpátrica con *D. percarinatum* a pocas localidades en el centro-occidental de Colombia; la distribución de la nueva especie continua hacia el sur hasta el noroeste de Ecuador. Una segunda nueva especie, *D. graciliverpa*, ocurre en todo del Ecuador occidental, donde su distribución traslapa la distribución de *D. brunneum* (Günther). Los hemipenes de ambas nuevas especies son excepcionalmente alargados y delgados (morfofoto esbelto). Es una morfología distinta de los otros hemipenes de *Dendrophidion*, que son más corto y robusto (morfofoto robusto). Además, las nuevas especies se distinguen de *D. percarinatum* por la coloración pero no se distinguen en caracteres estandarizados de escutellación como cuentas segmentales. De modo parecido, las dos nuevas especies se distinguen por coloración pero no por la escutellación ni la morfología de los hemipenes. Se describen los hemipenes de *D. percarinatum* y las nuevas especies. Para asegurar la aplicación apropiada del nombre *D. brunneum* se redescubre el holotipo de esta especie. Nuevas especímenes documentan la ocurrencia amplia de *D. brunneum* en las tierras bajas del Ecuador occidental y también polimorfismo extenso de patrones, incluyendo patrones unicolor, rayado, con bandas, y con manchas; se necesitan más datos sobre la coloración de vida. Algunos registros anteriores de "*D. percarinatum*" desde los valles interandinos de la sistema Ríos Cauca/Magdalena son de identidades equivocadas. Sin embargo, existen especímenes del Río Magdalena que son parecidos a *D. percarinatum* en la escutellación pero son distintos en coloración; su estatus merece más estudio.

INTRODUCTION

At the time of his death in 1972, James A. Peters had been accumulating data in preparation for a revision of the Neotropical snake genus *Dendrophidion* Fitzinger and he indicated that the account given by Peters and Orejas-Miranda (1970: 79) would "be rather thoroughly changed upon completion of the review." Forty years hence there still has been no comprehensive review of *Dendrophidion*, although various workers have chipped away at particular geographic or taxonomic segments of the genus. Lieb (1988), working in part from Peters' unpublished data, resurrected *D.*

nuchale (W. Peters) from the synonymy of *D. dendrophis* (Schlegel), stabilized the application of the last name by designating a lectotype for it, and clarified the application of other names in the much-confused literature on these snakes. Lieb (1988) also briefly summarized characters and distributions for the nine species of *Dendrophidion* he recognized and apportioned eight of them between two species groups. McCranie (2011) resurrected the name *D. clarkii* Dunn for application to Central American members of the complex including *clarkii* and *nuchale*. Cadle (2010) reviewed the systematics, natural history, and hemipenial morphology of *D. brunneum* based on new material and field observations, and Cadle (2012) partitioned *D. vinitor* by describing two new cryptic species previously confused with it. Freire et al. (2010) described another new species of the *D. dendrophis* group from northeastern Brazil. Other taxonomic issues still need resolution.

This paper focuses on *Dendrophidion percarinatum*, which according to current taxonomy is distributed from Honduras to Ecuador and Venezuela. During my review of *D. brunneum* (Cadle, 2010), I had examined material referred to "*D. percarinatum*" from western Colombia and Ecuador and indicated that revision of *D. percarinatum* appeared necessary (Cadle, 2010: 2, 24). Further investigation has confirmed that suggestion and has caused me to revise some of my earlier assessments concerning *D. brunneum*. In particular, I came to realize that most specimens previously referred to "*D. percarinatum*" in western Colombia and Ecuador were, in fact, distinct species. *Dendrophidion percarinatum* is widespread in Central America, but other than a few localities around the Golfo de Urabá in northern Colombia, it is definitely known from only a handful of localities in the Chocó region and one in extreme western Venezuela.

In this paper I review the systematics of *Dendrophidion percarinatum* with special reference to populations in western Colombia and Ecuador. Two species previously

confused with *D. percarinatum* from the last two areas are described as new. Hemipenes of the three species are described. The review of western Ecuadorian specimens of *Dendrophidion* also resulted in the discovery that the distribution of *D. brunneum* includes previously unrecognized lowland localities and broadly overlaps the distribution of one of the new species in western Ecuador. The holotype and new material of *D. brunneum* are reviewed to supplement the earlier account (Cadle, 2010) and to ensure proper application of this name.

MATERIALS AND METHODS

Methods follow procedures described in Cadle (2005, 2007, 2012). Methods for scoring dorsocaudal reductions, dorsal keeling, aspects of color pattern, and statistical methods are described by Cadle (2012) for other *Dendrophidion*. Additional comments on characters especially relevant to *D. percarinatum* and the new species described herein are detailed below. Measurements (in mm) of hemipenes and for a loreal scale character in the section on *Dendrophidion brunneum* were made with Helios dial calipers to the nearest 0.01 mm under a dissecting microscope. For purposes of analyzing intraspecific differences in mean SVL of adult males and females, specimens >400 mm snout to vent length (SVL) were considered adults because sexual maturation occurs at 400–500 mm SVL (Goldberg, 2003; Stafford, 2003). Similarly, because relative tail length increases proportionally with SVL, the range of adult relative tail length (RTL) was assessed for individuals with SVL > 300 mm because RTL approaches an asymptote at approximately this size. Methods of hemipenial study are covered in the introduction to that section.

My sampling of *Dendrophidion percarinatum* has not been even from throughout the range. Sample sizes of *D. percarinatum* as redefined here from throughout the range are as follows (number of males, number of females): Honduras (10, 12),

Nicaragua (3, 3), Costa Rica (29, 26), Panama (56, 37), Colombia (7, 4). I also examined the lectotype of *D. percarinatum* and the holotype and additional specimens of *D. brunneum*. Hemipenial morphology offered some early insights into the systematics of these species, and I examined everted hemipenes from throughout the range of *D. percarinatum* and the internal morphology of retracted organs of selected specimens. I also examined all available everted hemipenes of the two new species and the internal morphology of other retracted organs.

Except where specifically qualified (e.g., “*Dendrophidion percarinatum sensu Lieb 1988*”), I use the name *Dendrophidion percarinatum* to refer to this snake as redefined herein, which excludes certain populations in western Colombia and Ecuador that have been included in other literature (e.g., Lieb, 1988, 1996; Savage, 2002; Stafford, 2003; Cadle, 2010). I refer to *D. percarinatum* plus the two new species described herein as the “*Dendrophidion percarinatum* complex” with no assumption that the complex is monophyletic within *Dendrophidion*. These species plus *D. brunneum* and *D. paucicarinatum* comprise the *D. percarinatum* species group of Lieb (1988). Unresolved systematic issues pertain to other species names within *Dendrophidion*, and I use the name “*D. nuchale auctorum*” for the complex of species represented by this name, as explained in Cadle (2012: 188; see also Savage, 2002: 655; McCranie, 2011: 106–107).

Appendix 1 lists specimens examined of *Dendrophidion percarinatum*, *D. brunneum* (Ecuadorian specimens identified subsequent to Cadle [2010] only), and several specimens of uncertain status (*D. species inquirendum*). Specimens of the new species are listed in the text. The accounts of new species include some specimens listed as “other referred specimens” rather than paratypes. These specimens are all juvenile or adult females, which are sometimes difficult to identify from preserved specimens (depending on state of preservation

and/or characters of individual specimens). These difficulties are discussed in the species accounts. Scutellation data from the referred specimens were included in the data summaries except as noted (e.g., Table 1). Appendix 2 contains coordinates and notes on the localities for the new species. Coordinates, some elevations, and other information on localities were derived primarily from Brown (1941; Ecuador), Fairchild and Handley (1966; Panama), Paynter (1993, 1997; Ecuador and Colombia), Lynch and Duellman (1997; Ecuador), McCranie (2011; Honduras), and the National Geospatial-Intelligence Agency (NGA, 2010-2012) online gazetteer (GEO-net). There have been changes in Ecuadorian administrative divisions associated with some well-known localities in western Ecuador (e.g., Santo Domingo de los Colorados). Two new provinces, Santo Domingo de los Tsáchilas and Santa Elena, were created in 2007 from portions of Pichincha and Guayás provinces, respectively. I record both provinces for these localities to prevent confusion when cross-referencing with other taxonomic literature on this area.

Table 1 presents summary taxonomic and morphological data for species of the *Dendrophidion percarinatum* complex. Data summarized therein for *D. percarinatum* are for specimens from throughout the geographic range of this species (Honduras to western Colombia). Geographic variation for some characters of *D. percarinatum* is discussed in the species account (see also Tables 2 and 3). Hemipenial characters are discussed in the section devoted to them after the species accounts.

TAXONOMIC CHARACTERS OF SPECIAL RELEVANCE TO THE *DENDROPHIDION PERCARINATUM* COMPLEX

At the outset it is appropriate to discuss the primary character systems used in my assessments of species boundaries within the *Dendrophidion percarinatum* complex.

Although many of the same character systems relevant to the systematics of the *D. vinitor* complex (Cadle, 2012) are pertinent to *D. percarinatum*, the informative aspects of variation are sometimes a bit different. For example, color patterns are relevant to differentiating species in both groups, but the aspects of coloration of particular value in each group differ. The following sections discuss variation in several character systems as they pertain to the *D. percarinatum* complex.

Color Pattern. *Dendrophidion percarinatum* as conceived in previous works is highly variable in coloration and pattern (Lieb, 1988, 1996; Savage, 2002). However, little attention has been given to the relationship of this variation to geography or its potential systematic implications. During my review it became clear that, although pattern variation within *D. percarinatum* in Central America is comparatively minor, in northern South America several distinct color patterns were present. Further consideration suggested that these distinct color patterns had both geographic integrity (i.e., discrete geographic distributions) and were correlated in some cases with other characters (e.g., hemipenial morphology) suggestive of systematic distinction. Thus, color pattern variation played a significant role in my assessment of species boundaries within the *D. percarinatum* complex, particularly in the absence of strong differentiation using standard scale characters (Lieb, 1988; Cadle, 2010, 2012; documented herein). Unfortunately, coloration in life is available for relatively few specimens. Changes induced by preservation and perhaps differences in preservation techniques make it impossible to correlate preserved coloration to colors in life with any ease. Some pattern elements seemingly become more prominent upon preservation (e.g., pale crossbands) even as others become more obscure. Other factors, such as the integrity of the stratum corneum on a given specimen, also affect the appearance of preserved specimens.

Narrow pale crossbands are expressed in some individuals of all species of the

TABLE 1. TAXONOMIC DATA FOR *DENDROPHIDION PERCARINATUM* (RANGEWIDE SUMMARY) AND TWO NEW SPECIES. BODY PROPORTIONS, SEGMENTAL COUNTS, SCALE REDUCTIONS, MAXILLARY TEETH, AND NUMBER OF PALE BANDS ARE GIVEN AS RANGE FOLLOWED BY MEAN ± SD. BILATERAL COUNTS ARE SEPARATED BY A SLASH (/). FOR TEMPORALS AND LABIAL SCALES, EACH SIDE OF A SPECIMEN WAS COUNTED AS AN INDEPENDENT OBSERVATION. SAMPLE SIZES IN PARENTHESES. ASTERISKS INDICATE STATISTICAL SIGNIFICANCE OF INTRASPECIFIC DIFFERENCES BETWEEN MEANS OF MALE AND FEMALE SIZE, PROPORTIONS, OR MERISTIC COUNTS (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$); NO ASTERISK INDICATES NONSIGNIFICANCE.

	<i>Dendrophidion percarinatum</i> (Cope) Rangewide Summary	<i>Dendrophidion prolixum</i> New Species	<i>Dendrophidion graciliverpa</i> New Species
Largest specimens: total length, SVL (mm)			
Male	1,358+, 852 [1,236, 747] [†]	1,003+, 650 [1,037, 642] [†]	1,054+, 676 [964, 605] [†]
Female	1,300, 778	976+, 675 [1,116, 662] [†]	922+, 663 [1,027, 631] [†]
Mean adult SVL (mm)			
Male	401–852 577.3 ± 93.18 (73)	455–650 582.6 ± 61.95 (10)	409–605 517.5 ± 58.30 (16) ^{***}
Female	437–778 604.4 ± 74.63 (51)	425–675 604.3 ± 76.15 (15)	543–663 615.5 ± 37.92 (11)
Tail length/total length			
Male	0.38–0.45 0.42 ± 0.019 (52) ^{**}	0.38–0.40 0.39 ± 0.009 (5)	0.37–0.42 0.39 ± 0.0002 (9) ^{**}
Female	0.37–0.43 0.40 ± 0.014 (24)	0.38–0.41 0.40 ± 0.012 (6)	0.36–0.39 0.37 ± 0.014 (6)
Tail length/SVL			
Male	0.62–0.82 0.72 ± 0.054 (52) ^{***}	0.62–0.67 0.65 ± 0.021 (5)	0.59–0.72 0.65 ± 0.038 (9) ^{**}
Female	0.59–0.75 0.68 ± 0.039 (24)	0.63–0.69 0.66 ± 0.026 (6)	0.56–0.64 0.59 ± 0.035 (6)
Maxillary teeth	33–42 37.1 ± 1.84 (59)	36–42 38.5 ± 1.65 (22)	33–44 38.8 ± 2.40 (23)
Dorsal scales	17–17–15 (180) other patterns (4)	17–17–15 (37)	17–17–15 (27) 17–19–17 (1)
Ventrals			
Male	147–170 155.8 ± 3.51 (103) ^{***}	150–164 157.7 ± 4.63 (17) [*]	153–163 157.5 ± 2.15 (22) ^{***}
Female	156–167 160.2 ± 2.42 (80)	152–164 160.9 ± 3.42 (17)	152–166 160.7 ± 3.37 (23)
Subcaudals			
Male	137–163 150.7 ± 6.32 (71) ^{***}	134–150 140.5 ± 5.15 (11)	132–153 142.3 ± 6.41 (12) ^{**}
Female	133–157 145.6 ± 5.26 (46)	133–150 143.3 ± 5.07 (9)	120–143 133.5 ± 7.32 (13)
Total segmental counts (ventrals + subcaudals)			
Male	293–323 306.6 ± 6.19 (72)	284–310 297.3 ± 8.49 (11)	290–309 299.3 ± 7.01 (12)
Female	293–321 305.9 ± 5.60 (46)	285–313 303.4 ± 7.89 (9)	275–304 293.0 ± 9.42 (12)
Dorsocaudal reduction, 8 to 6 (subcaudal number)			
Male	8–26 16.0 ± 3.60 (103) ^{***}	16–26 19.8 ± 3.05 (17) ^{***}	12–27 20.3 ± 3.69 (21) ^{***}
Female	5–24 10.4 ± 3.02 (81)	8–24 12.4 ± 4.50 (17)	7–19 12.0 ± 3.53 (23)
Dorsal scales, posterior reduction (ventral number)			
Male	84–102 92.6 ± 3.85 (88) ^{***}	84–99 92.9 ± 4.27 (32) ^{***}	78–95 90.8 ± 3.73 (30) ^{***}
Female	91–106 96.8 ± 3.30 (54)	91–110 98.7 ± 3.93 (32)	90–101 94.9 ± 9.59 (24)

TABLE 1. CONTINUED.

	<i>Dendrohidion percarinatum</i> (Cope) Rangewide Summary	<i>Dendrohidion prolixum</i> New Species	<i>Dendrohidion graciliverpa</i> New Species
Preoculars	1/1 (186) 1/2 (2)	1/1 (34)	1/1 (43)
Postoculars	1/1 (1) 1/2 (2) 2/2 (182) 2/3 (2) 3/3 (1)	2/2 (32) 2/3 (2)	2/2 (37) 2/3 (2) 3/3 (4)
Primary temporals	1 (2) 2 (370)	1 (1) 2 (61) 3 (1)	2 (84) 3 (2)
Secondary temporals	1 (1) 2 (362) 3 (3)	2 (61) 3 (2)	2 (85) 1 (1)
Supralabials, supralabials touching eye	8, 3–5 (1) 8, 4–5 (1) 8, 4–6 (2) 9, 4–6 (363) 10, 5–7 (9)	9, 4–6 (67) 10, 4–7 (1)	8, 3–5 (5) 8, 4–5 (1) 9, 4–5 (2) 9, 4–6 (76)
Infralabials	8 (1) 9 (17) 10 (321) 11 (32) 12 (2)	8 (3) 9 (16) 10 (28) 11 (20) 12 (1)	8 (3) 9 (13) 10 (54) 11 (12) 12 (1)
Supralabial/ temporal pattern	G, 6.8% P, 82.8% irregular/ambiguous, 10.4% (221)	G, 76% P, 4.5% irregular/ambiguous, 19.4% (67)	G, 66.7% P, 2.9% irregular/ambiguous, 30.4% (69)
No. of pale bands on body	71–96 81.2 ± 6.87 (45)	49–57 53.0 ± 2.59 (12)	57–87 70.5 ± 8.81 (26)
Hemipenial characters	robust morphotype < 40 enlarged spines	gracile morphotype > 60 enlarged spines	gracile morphotype > 60 enlarged spines

† The largest specimens in these cases had incomplete tails. Measurements of the largest specimens with complete tails in brackets.

Dendrohidion percarinatum complex. Juveniles have more distinct crossbands than adults, in which the bands may be either distinct or indistinct. The number of pale crossbands on the body (neck to vent) is useful in distinguishing one of the new species described herein compared with the other two members of the complex. However, because crossbands are not always evident over the entire body in some specimens of all three species, this character cannot always be scored. The width of the pale bands is not useful for distinguishing the two new species from one another or from *D. percarinatum* (the bands are typically one dorsal row or less in width in all three species), but the number of scale rows separating pale bands on the neck is

helpful when the bands are evident on the neck. In these cases, the counts were made as described in Cadle (2012) for scoring the width of pale bands in the *D. vinitor* complex (except that rows between bands, rather than rows encompassed by bands, were counted). Neck bands can sometimes be discerned under magnification and good lighting even on excessively darkened preserved specimens (the dark borders to the bands are often better clues than the pale band itself); such observations are best made with the specimen submerged in alcohol. These comments apply to preserved museum specimens, but a caveat is that observations presented herein for the two new species suggest that the appearance of pale crossbands can be enhanced in

preserved specimens compared with the live snakes.

Other elements of pattern are highly variable within and between species. The venter of the two new species in the *Dendrophidion percarinatum* complex develops narrow dark transverse lines across the anterior edge of each ventral scale (a character also found in some other species of *Dendrophidion*). There is seemingly an ontogenetic component to this variation: larger individuals typically have more fully developed lines in those species in which they occur. Nonetheless, some juveniles have ventral lines, and considerable variation in the prominence of the lines exists in adults as well. These lines seem to develop first on the posterior venter and eventually can encompass nearly all the ventral scutes. Superficially, these lines might appear to be on the posterior edges of the ventral scutes, but close examination shows that they are on the anterior edges of the scales and merely show through the nearly transparent posterior edge of the adjacent anterior scute.

I also examined other aspects of color pattern, such as the dark dorsal longitudinal stripes in the dorsolateral region and flanks seen in many specimens of *Dendrophidion percarinatum*. There is considerable variation in these features, and I did not find them useful for discriminating the three species of the *D. percarinatum* complex. I refer to some other coloration features, particularly with reference to *D. brunneum*.

Supralabial/Temporal Pattern. The arrangement of scales on the lateral surfaces of the head behind the eye is a useful aid in distinguishing species of the *Dendrophidion percarinatum* complex (perhaps more broadly within *Dendrophidion*, but this needs further study). I stress *useful aid* because it is not an infallible character. Some cases are ambiguous because the configuration of these scales is influenced by irregularities such as scale fusions, divisions, or other anomalous patterns. In other cases the patterns are downright misleading (i.e., some specimens have the

atypical arrangement for the taxon to which I refer them). For this reason I do not include the supralabial patterns in the list of characters at the beginning of the diagnoses, although I do use them for comparative purposes when they seem useful.

The relevant scales are the lower primary and secondary temporals and their relationship to the penultimate and ultimate supralabials. I distinguish two basic configurations (Fig. 1), which were scored on both sides of a sampling of each species. Frequencies of the patterns are given in Table 1. Early in my work on the *percarinatum* complex I designated these patterns as *P* and *G* for *D. percarinatum* and *D. graciliverpa*, the first pair of species that I distinguished by this character. Atypical or ambiguous configurations were coded separately from the basic configurations.

P-Pattern or *percarinatum Pattern* (Fig. 1A). (As a mnemonic, *P* could also refer to the pentagonal shape of the penultimate supralabial in this pattern.) Penultimate supralabial (nearly always the eighth) broadly contacts the lower secondary temporal, separating the lower primary temporal from the ultimate (ninth) supralabial. The penultimate supralabial is relatively tall and usually in the shape of an irregular pentagon, with the vertical dimension of the posterior part greater than that of the anterior part. The posterior border of the penultimate supralabial is usually even with, or posterior to, the posterior border of the lower primary temporal.

G-Pattern or *graciliverpa Pattern* (Fig. 1B). (As a mnemonic, the first "r" in *graciliverpa* could also refer to the rectangular shape of the penultimate supralabial in this pattern.) Penultimate supralabial (nearly always the eighth) separated from the lower secondary temporal by contact between the lower primary temporal and the ultimate (ninth) supralabial. The penultimate supralabial is usually relatively narrow and homogeneous in vertical dimension and in the shape of an elongate rectangle (sometimes squarish). The posterior border of the penultimate

supralabial is usually anterior to the posterior border of the lower primary temporal.

Hemipenial Characters. Detailed descriptions of hemipenes of the species described herein are presented in a separate section at the end. However, hemipenial characters play a fundamental role in the recognition of the new species described here and in the application of the name *Dendrophidion brunneum* (Günther) discussed later. Thus, a few comments on hemipenial length and overall shape are pertinent here. Cadle (2012: 217–220) provided a general overview of *Dendrophidion* hemipenes. Detailed descriptions and discussion of morphological variation of hemipenes in other species are in Cadle (2010: 14–20; 2012: 220–228).

Most *Dendrophidion* hemipenes are of what may be termed the “robust (or compact) morphotype” (Fig. 2). Hemipenes of this form are relatively short. The narrow proximal portion of the hemipenial body bearing minute spines is short, and the distal section bearing enlarged spines, calyces and/or flounces, and other apical ornamentation is greatly expanded. The distal bulbous section comprises half or more of the length of everted organs.

In contrast, the two new species described herein are characterized a hemipenial morphology that may be called “gracile morphotype” (Fig. 2). Compared with hemipenes of other species of *Dendrophidion* with the possible exception of *D. bivittatum*, gracile hemipenes are exceptionally long. A long, slender proximal section of the hemipenial body bears minute spines, distal to which is a moderately bulbous region bearing enlarged spines, calyces and/or flounces, and other apical ornamentation. The bulbous region of gracile hemipenes is not expanded to the extent that it is in robust organs, and it comprises much less than half of the total length of everted organs. *Dendrophidion bivittatum* seemingly has gracile hemipenial morphology, but I have seen only one somewhat desiccated everted organ of this species; its proportions in retracted organs is similar to the gracile hemipenes described here, though perhaps not quite as

long as in the two species described herein (see Stuart, 1932: pl. I, fig. 2 for an illustration of a retracted organ of *D. bivittatum*).

The compact and gracile morphologies are easily discerned in everted organs (Fig. 2). However, in retracted hemipenes, the overall length of the organ (number of subcaudals subtended) is a reliable indicator of the morphology, even when the internal morphology is not examined and despite some variation in the length of retracted organs (detailed in the section on hemipenial morphology). “Robust” organs generally subtend fewer than 10 subcaudals, whereas “gracile” organs usually subtend 10 or more subcaudals (up to 15 in the specimens I examined). If the internal morphology of retracted hemipenes is examined, the relative proportions of the relatively unadorned base compared with the distal section differentiate the two morphotypes (Fig. 3). For this purpose the distal section comprises the section of enlarged spines (using the most proximal sulcate enlarged spine as a landmark) + flounces/calyces + apical region. The bulbous distal section comprises a much greater proportion of the length of retracted robust organs compared with gracile organs.

REDEFINITION AND DESCRIPTION OF *DENDROPHIDION* *PERCARINATUM* (COPE)

Figures 1A, 1C, 2, 4–8, 12A, 13A, 19, 38–41

Drymobius percarinatus Cope “1893” (1894): 344 (two syntypes from Boruca and Buenos Ayres, Costa Rica); “1894” [1895]: 427; 1895: 205.

Drymobius dendrophis: Boulenger, 1894: 16 (part). Günther, 1885–1902: 127 (? part; Nicaragua, Costa Rica). Amaral “1929” [1930]: 154 (part). Dunn and Emlen, 1932: 31 (Honduras; ANSP 20817). Schmidt “1933” [1935]: 15 (Panama; USNM 54080).

Cacocalyx percarinatus: Cope “1894” (1895): 427; 1895: 205 + pl. 19, fig. 2; 1900: 778, 781 + pl. 17, fig. 2.

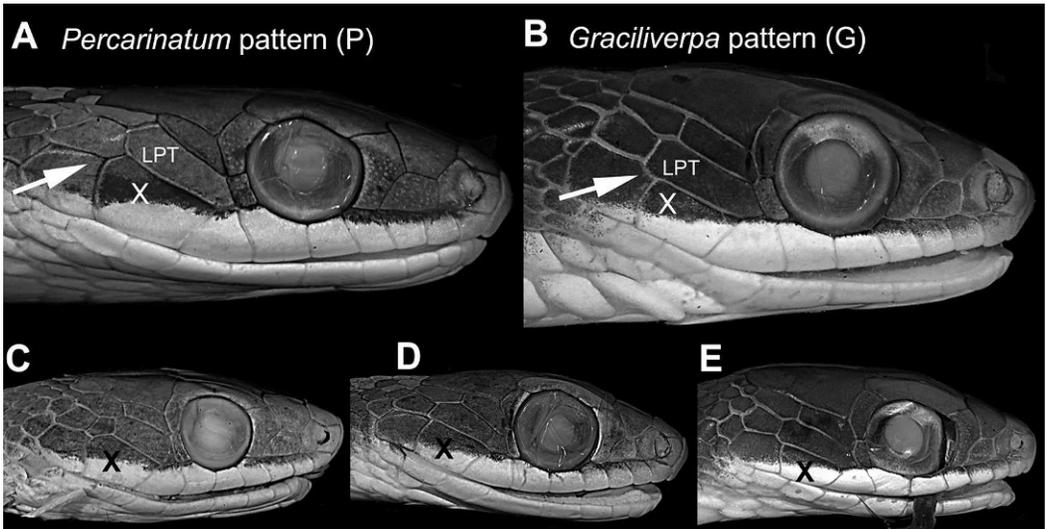


Figure 1. Contrasting configurations of scales in the posterior supralabial and lower temporal regions in the *Dendrophidion percarinatum* complex. (A) Stereotypical *percarinatum* (*P*) configuration (*D. percarinatum*, LACM 148558); (B) Stereotypical *graciliverpa* (*G*) configuration (*D. graciliverpa*, AMNH R-110585). Bottom panel shows other representations of the typical patterns: (C) *D. percarinatum*, AMNH R-17374, *P* pattern with lower secondary temporal divided vertically; (D) *D. prolixum*, AMNH R-109724, *G* pattern; (E) *D. graciliverpa*, UIMNH 92244, *G* pattern. Panels C, D, and E are left sides reversed. *Abbreviations and symbols*: X, penultimate supralabial (nearly always the eighth); LPT, lower primary temporal. *Arrows* indicate the lack of contact between the lower primary temporal and ultimate supralabial in the *P* pattern, and contact between these two scales in the *G* pattern (arrows lie diagonally across the ultimate labials). Note contrasting shapes of the penultimate supralabial in the *P* (pentagonal) and *G* (rectangular) patterns. See text for further discussion and variation.

Dendrophidion dendrophis: Gaige et al., 1937: 12 (part). Nicéforo María, 1942: 87 (part; ?specimen from Sasaima; see comments under Distribution). Taylor, 1951: 92 (Costa Rica). ?Pérez-Santos and Moreno, 1988: 134 (part; Pacific lowlands of Colombia); 1991b: 135 (part; “lower Central America and northern South America”).

Dendrophidion percarinatus. Stuart, 1932: 6. Smith, 1941; 1958: 223. Taylor, 1954: 727 (lectotype designated: “the adult specimen from Boruca” [= AMNH R-17366]). Smith and Grant, 1958: 210. Sexton and Heatwole, 1965: 41. Peters and Orejas-Miranda, 1970: 80. Pérez-Santos and Moreno, 1988: 135 (Colombia).

Dendrophidion percarinatum Dunn, 1944: 477 (? part). Savage, 1973: 14; 1980: 92; 2002: 657 + pl. 418 (part). Wilson and Meyer, 1985: 41. Scott et al., 1983: 372. Savage and Villa, 1986: 148, 169. Villa et al., 1988: 63. Lieb, 1988: 172 (part); 1996:

636.1 (part). Pérez-Santos and Moreno, 1988: 135 (part); 1989: 3 (part); 1991a: 138 (part). Rand and Myers, 1990: 395. Ibáñez and Solís, “1991” [1993]: 30, 33. Pérez-Santos et al., 1993: 116. Auth, 1994: 16. Guyer, 1994: 382. Ibáñez et al., “1994” [1995]: 26. Pérez-Santos, 1999: 99, 102. Nicholson et al., 2000: 29. McCranie et al., 2002: 27; 2006: 147, 229, 237 (part). Goldberg, 2003. Köhler, 2003: 200; 2008: 215. Stafford, 2003 (part). Solórzano, 2004: 234–236 + fig. 59 (part). Guyer and Donnelly, 2005: 184 (part). McCranie and Castañeda, 2005: 8 (part). McDiarmid and Savage, 2005: 391, 421 (part). Wilson and Townsend, 2006: 96, 106; 2007: 136, 139. Rojas-Runjaic and Rivero, 2008. Santos-Barrera et al., 2008: 766. Laurencio and Malone, 2009: 126. McCranie, 2009: 12; 2011: 108. Savage and Bolaños, 2009: 14. Bolaños et al., 2010. Cadle, 2010 (part).

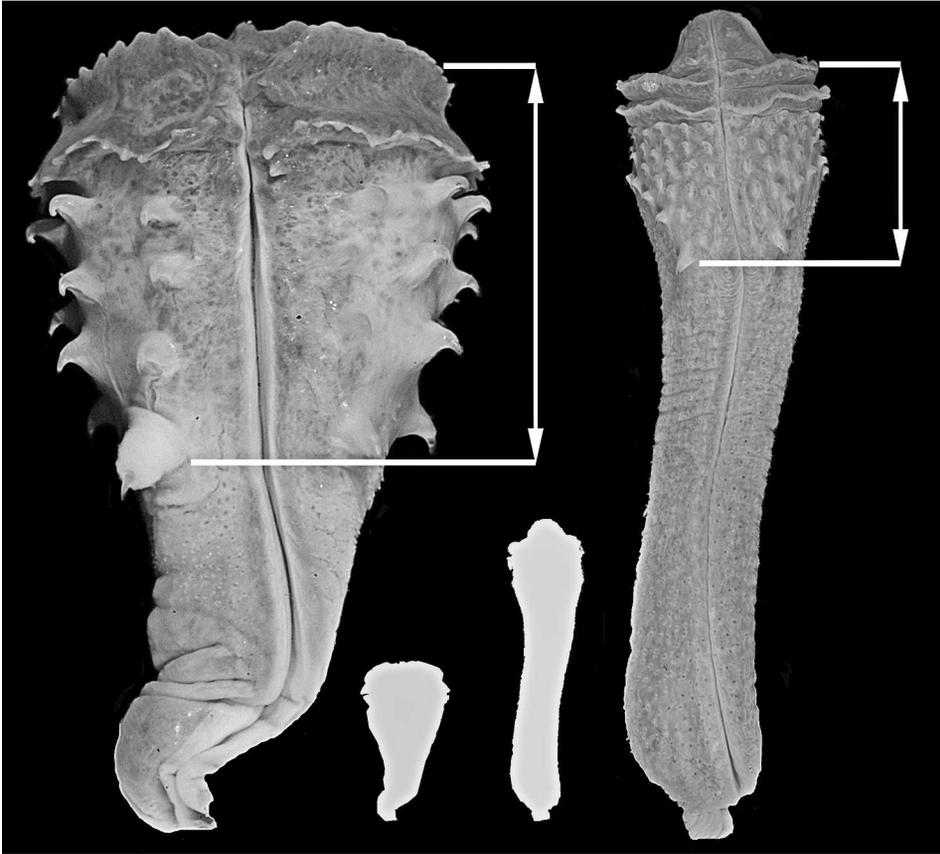


Figure 2. Comparison showing proportional differences between the “robust” (left) and “gracile” (right) hemipenis morphotypes within *Dendrophidion*. The robust hemipenis photograph was scaled to the same length as the gracile organ. Horizontal lines are placed at the level of the proximal enlarged sulcate spine and the distal flounce in each organ (assumed to be homologous morphological markers). The apical region so delimited is a much greater proportion of the hemipenial body and relatively broader in the robust hemipenis than in the gracile one. Reverse silhouettes at bottom center show actual sizes of the organs. The representative hemipenes are *D. percarinatum* (robust, USNM 559611) and *D. graciliverpa* (gracile, AMNH R-110584 [holotype]).

Lectotype of Dendrophidion percarinatum (Figs. 4–6). Cope (“1893” [1894]) described *Drymobius percarinatus* from two Costa Rican specimens, an adult from “Boruca” collected 13 December 1891 (now AMNH R-17366; Figs. 4–5) and a young specimen from “Buenos Ayres” (originally AMNH R-9561 but now apparently missing). Both were sent to Cope by George K. Cherrie, a resident of San José who worked for a time for the national museum of Costa Rica. Myers (1982: 23) explained the history of these collections and their acquisition by the American Museum of Natural History. Recent liter-

ature (e.g., Lieb, 1996; McCranie, 2011) continues to refer to “syntypes” of *D. percarinatus* but Taylor (1954: 727) had designated AMNH R-17366 as the lectotype by referring to this specimen as “the type,” in accordance with requirements for lectotype designations before 2000 (International Commission on Zoological Nomenclature, 1999: Article 74.5). The type locality, Boruca, is a small town in the foothills of the Fila Costeña on the north side of the Río Grande de Térraba where that river divides the coast range in southern Puntarenas Province (southwestern Pacific versant of Costa Rica).

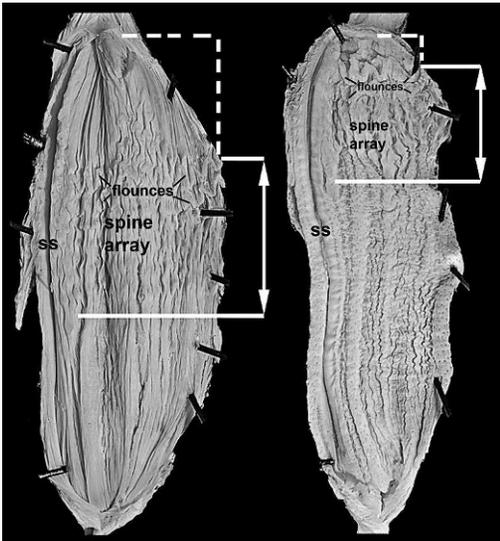


Figure 3. "Robust" (left) and "gracile" (right) hemipenial morphotypes as they appear in retracted organs (scaled to the same length, distal toward the top). Horizontal solid lines placed as in Figure 2. Dashed lines delimit the extent of apical tissue distal to the flounces. The hemipenes are *Dendrophidion brunneum* (robust, USNM 237060) and *D. graciliverpa* (gracile, UIMNH 77347). Abbreviations and labels: ss, sulcus spermaticus; spine array, compact tissue bearing the enlarged spines. The flounces appear as zigzag transverse lines of tissue distal to the spine array. *Dendrophidion brunneum* has an extensive area of nude apical tissue in the everted hemipenis, which accounts for the large area of pleated apical tissue in the retracted organ (left; Cadle [2010] illustrated the everted hemipenis of this species).

AMNH R-17366 is an adult male in good condition; the tail tip is missing and approximately the distal one-third of the remaining tail is broken off and tied to the specimen (Fig. 4). There is a midventral incision in the base of the tail. Total length 834+ mm; tail length 363+ mm; SVL 471 mm. 154 ventrals (2 preventrals); 143+ subcaudals; anal plate divided; 37 maxillary teeth with the last 3 somewhat enlarged; dorsocaudal reduction from 8 to 6 at subcaudal 23; dorsal scale reduction from 17 to 15 at ventral 93; 9/9 supralabials (2–4 touching the loreal; 4–6 touching the eye); 2/2 postoculars; 2+2 temporals; 10/10 infralabials. The supralabial/temporal pattern is the *P* pattern on both sides, as described above (Fig. 5A).

Narrow (<1 scale row wide) pale crossbands over the entire body (less distinct on

the neck) narrowly bordered by dark brown flecks, which often tend to invest the pale portion of the bands. Dorsal crossbands peter out on the anterior portion of the tail. Narrow dark brown lateral stripe along the suture line of dorsal rows 2–3 on the posterior half of body (Fig. 5B). Ventrolateral tail stripe at the dorsocaudal/subcaudal junction (Fig. 5C) + dusky median four rows of dorsocaudals on the anterior part of the tail (dusky continues onto posterior body, where the three paravertebral rows on each side are dusky). Venter immaculate except for narrow triangular encroachment of dorsal pigment onto lateral edges of ventral scutes. Head cap extends down to top of supralabials except the last (covers two-thirds of this scale) and the penultimate (covers somewhat less than half of this scale).

Hemipenis of the Lectotype. Because of the critical importance of hemipenial characters to the systematics of *Dendrophidion*, the left hemipenis of the lectotype of *D. percarinatum* was manually everted using methods of Myers and Cadle (2003) (the right hemipenis had been damaged by a previous incision into the tail base). The manual eversion was successful (Fig. 6), although, as is typical in many manually everted hemipenes, it is not maximally expanded (Myers and Cadle, 2003). In particular, the apex is much narrower than in everted organs described later herein, resulting in a different shape from field-everted organs. Nonetheless, the ornamentation of the entire everted organ except for the very tip of the apex can be studied. Before excision, the retracted left hemipenis extended to the proximal portion of subcaudal 7. The *retractor penis magnus* was proximally undivided.

Approximate measurements of the manually everted organ: total length, 15.3 mm. Length from base to the right enlarged sulcate spine, 6.8 mm. Length of apex (spinose part to tip), 8.5–9 mm. Sulcus spermaticus simple, centrolineal. Just distal to the distal flounce is a single calyx on each side of the sulcus (distal flounce forms proximal border of each calyx). Sulcus continues to center of apex; could not really

determine well whether the tip of the sulcus was expanded (flared) or not.

Hemipenis with narrow base, distally expanded (but shape is not as bulbous as field-everted organs). One pair of spines at proximal edge of spine array (one on each side of sulcus, right one somewhat more proximal than the left one), each somewhat larger than other spines in the array. Spine array three rows across adjacent to sulcus and on the asulcate side, narrowing slightly to two to three rows on lateral sides in between. Thirty-two spines in the array including the two enlarged sulcate spines. Individual spines are of typical form (see later hemipenial section for relevance), strongly mineralized, hooked at the tip. A narrow circumferential section of the hemipenial body immediately proximal to the spine array is ornamented with minute spines/spinules; hemipenial body proximal to minute spines is nude.

Distal to the spine array the hemipenis is encircled by two flounces having scalloped edges, between which are a few low longitudinal ridges (more concentrated on the asulcate side). On the asulcate side distal to the distalmost flounce and extending toward the apical tip are several calyces in about two rows (transverse walls of these calyces are more strongly developed than the longitudinal walls); from these calyces a raised triangular area extends to the center of the apical tip. The tip of the apex is not fully everted, and I did not attempt full eversion because of the fragility of the specimen. Apart from the sulcus and its associated pair of calyces, and the asulcate triangular extension of raised tissue, the apex is nude.

Diagnosis. *Dendrophidion percarinatum* is characterized by (1) dorsocaudal reduction from 8 to 6 occurring anterior to subcaudal 27 (range, 5–26); (2) divided anal plate; (3) subcaudal counts >130 in males and females; (4) subadults with narrow pale bands or transverse rows of ocelli (<1 dorsal row wide throughout the body) separated by fewer than three dorsal rows on the neck (bands retained or become obscure in adults, often heavily invested

with dark pigment); total number of pale bands on the body >70 (range, 71–96); (5) ventrals immaculate except for lateral dark blotches or mottling; (6) in life, dorsal coloration various shades of brown or gray and usually including dark-bordered pale crossbands anteriorly (sometimes indistinct) and dark brown or blackish stripes posteriorly (often a broader pair of paravertebral stripes and a narrow lateral stripe on dorsal rows 2 and/or 3); venter without extensive dark spots or transverse lines (scattered small spots may be present), and (7) everted hemipenis of the “robust” morphology, with a relatively short, narrow hemipenial body proximal to a bulbous region bearing spines, calyces, and other apical ornamentation (retracted hemipenis usually extending to between subcaudals 6 to 9, rarely reaching subcaudal 10); total number of enlarged spines on hemipenis <45 (range, 26–40).

Dendrophidion percarinatum differs from species of the *D. dendrophis* species group (*D. dendrophis*, *D. atlantica*, *D. nuchale* auctorum, *D. apharocybe*, *D. crybelum*, *D. vinitor*) in having a more proximal reduction in the dorsocaudal scales (nearly always >30 in the *D. dendrophis* group). A high number of subcaudals and divided anal plate will distinguish it from *D. apharocybe*, *D. crybelum*, and *D. vinitor* (<130 subcaudals and anal plate nearly always single in these species). *Dendrophidion dendrophis*, *D. atlantica*, and *D. nuchale* auctorum have different color patterns (often with extensive dark ventral spots and flecks; see Duellman, 1978: 236–237, 2005: pl. 175; Savage, 2002: 654–655, fig. 11.39c, pls. 413–415), attain greater sizes than *D. percarinatum*, and have several enormously enlarged hemipenial spines (not so enlarged in *D. percarinatum*). *Dendrophidion percarinatum* differs from *D. boshelli* in having 17 midbody scale rows (15 in *D. boshelli*).

Dendrophidion percarinatum differs from *D. paucicarinatum* in having pale dorsal crossbands (variably distinct), often has dark longitudinal stripes on the posterior body, and has an immaculate venter. *Dendrophidion paucicarinatum* usually has

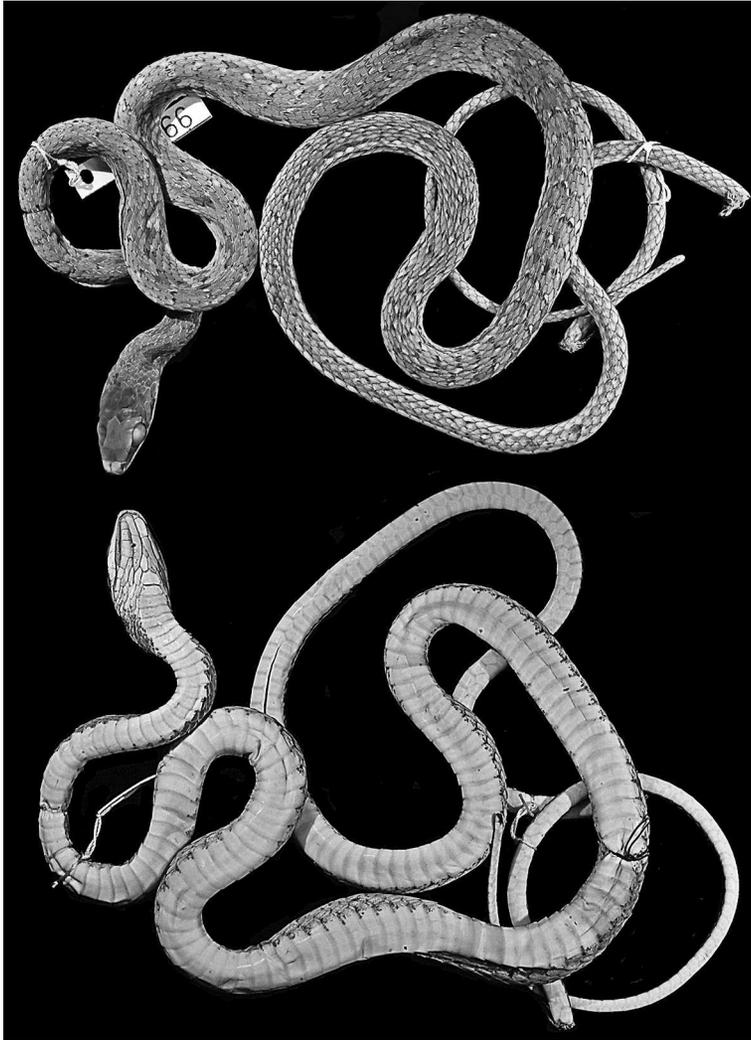


Figure 4. Lectotype of *Dendrophidion percarinatum* (Cope), AMNH R-17366, from Boruca, Puntarenas Province, Costa Rica.

a more uniformly colored dorsum lacking distinct pale crossbands, has narrow dark lines across the venter in adults and many juveniles, and has a higher number of ventrals (>175) than *D. percarinatum* (nearly always <170 except occasional individuals from Panama and Colombia; see discussion of geographic variation). *Dendrophidion paucicarinatum* may have either a single or divided anal plate.

Dendrophidion bivittatum differs from *D. percarinatum* in having a color pattern

consisting of prominent blackish dorsal stripes on the posterior body and a greenish dorsal ground color. *Dendrophidion bivittatum* also has a shorter tail and fewer subcaudals (<60% of SVL and usually <130, respectively) than *D. percarinatum*. *Dendrophidion brunneum* has a greenish to brownish dorsum generally without pale crossbands in adults (often with dark stripes or paravertebral punctations and often with dark transverse lines and other markings on the venter).

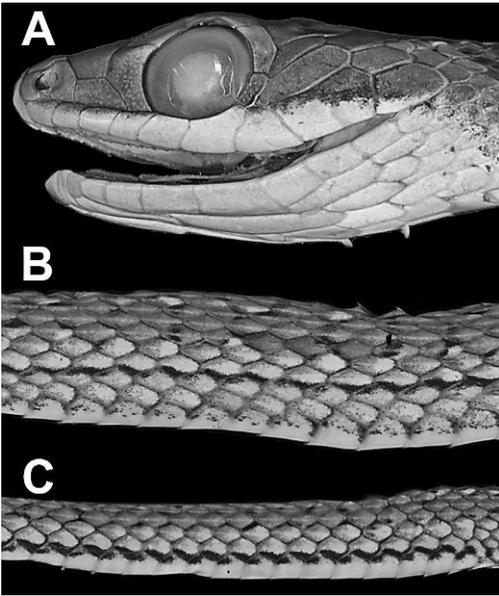


Figure 5. Lectotype of *Dendrophidion percarinatum* (Cope), AMNH R-17366. (A) Head, left side. Note the typical P pattern of the supralabials/temporals (see Fig. 1). (B) Posterior lateral stripe on dorsal rows 2–3. (C) Ventrolateral tail stripe.



Figure 6. Manually everted hemipenis of the lectotype of *Dendrophidion percarinatum*, AMNH R-17366, in sulcate and asulcate views. The spinose region and apex are not fully inflated even though the hemipenis is virtually fully everted.

Dendrophidion percarinatum differs from the two new species described herein (*D. prolixum* and *D. graciliverpa*) in having a “robust” hemipenial morphotype as characterized herein (“gracile” in the last two species). *Dendrophidion percarinatum* also differs from these species in coloration. *Dendrophidion prolixum* and *D. graciliverpa* are green on the anterior body (sometimes restricted to the head) and often have narrow dark transverse lines on the anterior edges of ventral scutes, especially on posterior body. Additional differentiating characters and comparisons are given in the diagnoses for the new species.

Description (104 males, 85 females). Table 1 summarizes size, body proportions, and meristic data for *Dendrophidion percarinatum* throughout its geographic range; geographic variation and sexual dimorphism in some characters are summarized in the next sections. Largest specimen (AMNH R-119376 from Panama) a male 1,358+ mm total length, 852 mm SVL (largest male with a complete tail, 1,236 mm total length,

747 mm SVL). Largest female (MCZ R-20552 from Panama) 1,300 mm total length, 778 mm SVL. Tail 38–45% of total length (62–82% of SVL) in males; 37–43% of total length (59–75% of SVL) in females. Dorsal scales in 17–17–15 scale rows, the posterior reduction usually by fusion of rows 2 + 3 ($N = 92$), 3 + 4 ($N = 19$), or loss of row 3 ($N = 11$) at the level of ventrals 84–106. Ventrals 147–170 (averaging 155.8) in males, 156–167 (averaging 160.2) in females; usually 2 preventrals anterior to ventrals (about 9% of specimens have 1 preventral; rarely, 3 preventrals were present). Anal plate divided. Subcaudals 137–163 (averaging 150.7) in males, 133–157 (averaging 145.6) in females. Dorsocaudal reduction at subcaudals 8–26 in males (mean 16.0), 5–24 in females (mean 10.4). Preoculars 1, postoculars 2, primary temporals 2, secondary temporals 2, supralabials usually 9 with 4–6 bordering the eye (occasionally 8 with 3–5 bordering

the eye or 10 with 5–7 bordering the eye), infralabials usually 9 (low frequency of 10 or 11). Maxillary teeth 33–42 (averaging 37), typically with 3 or 4 posterior teeth enlarged (occasionally only 2 teeth or up to 5 posterior teeth were enlarged). Enlarged teeth are ungrooved, not offset, and there is no diastema.

Two apical pits present on dorsal scales. About 39% of specimens have keels only on the vertebral or vertebral + 1 or 2 paravertebral dorsal rows on the neck (usually at least 4–6 rows lack keels on the neck and occasionally keels are absent). At midbody, 52% of specimens lack keels only on dorsal row 1; another 38% lack keels on rows 1 and 2, and the remainder lack keels on the first 3 or 4 dorsal rows. On the posterior body, 91% of specimens lack keels only on row 1 (sometimes weak on row 2); the remainder lack keels on rows 1 and 2. Fusions or divisions of temporal scales were moderately common, with the following frequencies (counting each side separately): upper or lower primary or secondary divided (30%), irregular fusions or divisions or fragmentation (8.7%), other divisions or fusions (0.8%). Eighty-three percent of scorings for the supralabial/temporal pattern were *P*, whereas only 6.8% were *G* (the remaining were ambiguous or irregular).

Hemipenis unilobed with a bulbous apex; overall morphology “robust” as characterized herein. Spinose region followed distally by two flounces and poorly developed calyces. Apex delimited by the distal flounce. The apex has an asulcate roughly triangular raised area bearing calyces on the asulcate side, and a thick pad of raised tissue on each side of the distal portion of the sulcus spermaticus; lateral to the raised sulcate and asulcate areas the apex is nude. Sulcus spermaticus simple, centrolineal, extending to the center of the apex, and having a slightly flared tip in everted organs. There is considerable variation in the development of the calycular structures (from fully formed to much more rudimentary) and spines (see details in the hemipenial descriptions). Retracted hemipenis

usually extending to subcaudals 7–9 and only rarely extending to subcaudal 10 or beyond.

Sexual Dimorphism, Geographic Differentiation, and Other Variation. Tails are proportionally shorter in small individuals. Specimens <300 mm SVL have tail lengths 36–42% of total length, 57–74% of SVL ($N = 43$, males and females combined). Rare individuals have 15, 16, or 18 dorsal scale rows on the neck (one individual each), and one specimen had 15 dorsal rows at midbody.

Considering the rangewide sample, males and females differ significantly in relative tail lengths (male longer), ventral counts (female greater), subcaudal counts (male greater), the point of dorsocaudal reduction (male more distal), and the point of dorsal scale reduction (female more posterior) (Table 1). The sexes do not differ in adult body size. These are common patterns in other species of *Dendrophidion* (Cadle, 2012) and are found widely among other snakes. These patterns hold when samples are analyzed by geographic origin, except that samples from Panama-Colombia are not significantly dimorphic in relative tail lengths (Table 2). This nonsignificance is due to the fact that males from Panama-Colombia average much shorter relative tail lengths than males farther north; females from throughout the range are similar in relative tail lengths.

There is minor geographic variation in size, body proportions, and segmental counts in *Dendrophidion percarinatum* (Table 2). Mean body size increases from north to south in both males and females, whereas relative tail length and subcaudal counts decrease in the same pattern. The point of dorsocaudal reduction in males from Panama and Colombia is more proximal than in specimens from north of Panama. For most characters the greatest quantitative change in mean character values occurs between Costa Rica and Panama-Colombia rather than farther north (e.g., between Honduras-Nicaragua compared with Costa Rican specimens). For

TABLE 2. GEOGRAPHIC VARIATION IN SELECTED CHARACTERS OF *DENDROPHIDION PERCARINATUM*. DATA PRESENTATION FOLLOWS THE FORMAT IN TABLE 1.

	Honduras-Nicaragua, 13 Males, 15 Females	Costa Rica, 29 Males, 26 Females	Panama-Colombia, 62 Males, 41 Females
Adult body size (mm, SVL)			
Male	407–595 511.7 ± 52.15 (13)	401–652 549.5 ± 65.91 (20)*	419–852 613.5 ± 100.95 (39)
Female	437–635 553.0 ± 65.37 (9)	457–695 599.7 ± 61.58 (21)	465–778 631.0 ± 80.40 (21)
Tail/total length			
Male	0.42–0.45 0.44 ± 0.008 (10)***	0.42–0.44 0.44 ± 0.002 (12)***	0.38–0.43 0.40 ± 0.011 (30)
Female	0.41 0.41 ± 0.0 (3)	0.39–0.43 0.41 ± 0.014 (8)	0.37–0.43 0.40 ± 0.015 (13)
Tail/SVL			
Male	0.74–0.82 0.78 ± 0.024 (10)***	0.72–0.80 0.77 ± 0.025 (12)***	0.62–0.77 0.68 ± 0.031 (30)
Female	0.69–0.71 0.70 ± 0.010 (3)	0.64–0.75 0.70 ± 0.039 (8)	0.59–0.75 0.67 ± 0.040 (13)
Ventrals			
Male	151–156 153.7 ± 1.60 (13)***	147–158 153.4 ± 2.95 (28)***	152–170 157.4 ± 3.14 (62)***
Female	157–160 158.8 ± 1.31 (14)	157–164 159.8 ± 2.06 (26)	156–167 160.9 ± 2.70 (40)
Subcaudals			
Male	153–163 157.4 ± 2.76 (10)***	148–161 155.2 ± 3.34 (15)***	137–160 147.8 ± 5.66 (46)*
Female	143–151 147.8 ± 2.76 (8)	133–157 147.4 ± 7.27 (11)	135–156 144.3 ± 4.57 (27)
Dorsocaudal reduction			
Male	14–22 17.0 ± 2.74 (13)***	10–26 18.9 ± 3.24 (27)***	8–22 14.5 ± 3.09 (62)***
Female	5–15 9.7 ± 2.87 (15)	7–24 11.2 ± 3.50 (25)	6–17 10.2 ± 2.71 (41)

example, for both sexes, mean RTL of Honduran-Nicaraguan specimens is similar to that of Costa Rican specimens, but mean RTL for Panamanian-Colombian specimens is less. In general, males show stronger geographic differentiation than females for the same character.

Ventral and subcaudal counts and relative tail lengths reported by Rojas-Runjaic and Rivero (2008) for the male from western Venezuela are similar to Panama-Colombian males (Table 2): 157 ventrals, 146 subcaudals (ventrals + subcaudals, 303), and relative tail length 41% of total length, 69% of SVL. This specimen has several uncommon scutellation features (1/2 pre-

oculars, 2+3 temporals, and 9 supralabials with only supralabials 5 and 6 touching the eye); its dorsocaudal reduction at subcaudals 24–26 is greater than the range I observed in specimens from Panama-Colombia (Table 2).

The Cordillera de Talamanca of Costa Rica and western Panama is a strong biogeographic barrier to many groups of organisms and separates differentiated populations or closely related species on the Atlantic and Pacific versants in lower Middle America (Daza et al., 2010; Chan et al., 2011). Within *Dendrophidion*, this mountain range separates sibling species within the *D. vinitor* complex and presum-

TABLE 3. GEOGRAPHIC DIFFERENCES IN SELECTED CHARACTERS OF ATLANTIC VS. PACIFIC POPULATIONS OF *DENDROPHIDION PERCARINATUM* IN COSTA RICA. DATA PRESENTATION FOLLOWS THE FORMAT IN TABLE 1. NONE OF THE ATLANTIC/PACIFIC CHARACTER DIFFERENCES WERE SIGNIFICANT IN COMPARISONS BY SEX.

	Atlantic Versant, (10 Males, 8 Females)	Pacific Versant, (19 Males, 18 Females)
Adult body size, SVL (mm)		
Male	531–596 556.8 ± 21.38 (8)	401–652 534.3 ± 80.14 (12)
Female	567–670 607.9 ± 33.88 (8)	457–695 594.7 ± 74.70 (13)
Tail/total length		
Male	0.43–0.44 0.44 ± 0.006 (3)	0.42–0.44 0.44 ± 0.007 (10)
Female	0.41 0.41 ± 0.0 (3)	0.39–0.43 0.41 ± 0.019 (5)
Tail/SVL		
Male	0.75–0.80 0.78 ± 0.029 (3)	0.72–0.80 0.77 ± 0.022 (10)
Female	0.69–0.71 0.70 ± 0.011 (3)	0.64–0.75 0.69 ± 0.050 (5)
Ventrals		
Male	149–156 152.3 ± 2.45 (10)	147–158 154.3 ± 2.93 (19)
Female	157–162 159.6 ± 1.71 (8)	157–164 159.9 ± 2.22 (18)
Subcaudals		
Male	152–158 154.0 ± 2.83 (4)	148–161 156.2 ± 3.56 (13)
Female	143–153 147.7 ± 5.03 (3)	133–157 147.3 ± 8.26 (8)
Dorsocaudal reduction		
Male	10–21 18.2 ± 3.29 (10)	14–26 19.2 ± 3.49 (19)
Female	7–15 10.6 ± 2.72 (8)	8–24 11.4 ± 3.86 (17)

ably played a role in their speciation (Cadle, 2012). Thus, it was of interest to compare character differentiation between populations of *D. percarinatum* inhabiting the Atlantic and Pacific versants in Costa Rica (Table 3). In contrast to the *D. vinitor* complex, in which sibling species are differentiated by color pattern and hemipenial morphology but not scutellation (Cadle, 2012), no such differentiation is apparent in *D. percarinatum*. None of the standard scutellation characters are significantly different between snakes of the Atlantic and Pacific versants, and I detected no consis-

tent differences in coloration or hemipenial morphology between these population segments. Thus, at least as reflected by standard external characters, Atlantic and Pacific populations of *D. percarinatum* in lower Middle America show no population divergence, even though the southwestern Costa Rican populations may be isolated from the Atlantic versant populations (see Distribution).

Coloration in Life. A sampling of color photographs of *Dendrophidion percarinatum* from Costa Rica includes Savage (2002: pl. 418), Solórzano (2004: 236, pl. 59), and Köhler, 2008 (fig. 582). Photographs of



Figure 7. *Dendrophidion percarinatum* in life. LACM 114102 from Finca Las Cruces, Puntarenas province, Costa Rica. From a color slide by Roy W. McDiarmid.

Honduran specimens include Köhler (2003: fig. 480), McCranie et al. (2006, pl. 119), and McCranie (2011, pls. 6B, C). Guyer and Donnelly (2005) identified their plate 148 as *D. percarinatum* (“Brown Forest Racer”), but I identify this photograph as *D. nuchale* auctorum based on its color pattern (the specimen was photographed and released at the La Selva Biological Station, Costa Rica; Craig Guyer, personal communication). Black and white photographs of *D. percarinatum* from Costa Rica are in Taylor (1954: 728) and Lieb (1996). A color photograph of a specimen from southwestern Costa Rica (near the type locality) is shown in Figure 7.

Specimens from Honduras and Costa Rica are brown to yellowish brown or grayish brown with narrow dark-bordered pale brown crossbands anteriorly grading to dark crossbands posteriorly and often dark stripes or alternating dark and pale stripes posteriorly and on the tail (Savage, 2002: 658; Solórzano, 2004: 234; Guyer and Donnelly, 2005: 184; McCranie, 2011: 109). The venter is immaculate, except for lateral dark pigment common to all *Dendrophidion*, and white or with a yellowish to orange wash. Some specimens apparently have a more uniformly colored dorsum (see also Coloration in Preservative). Overwhelmingly, the predominant dorsal colors of *Dendrophidion percarinatum* are shades

of brown and with a general absence of extensive green colors (compare the two new species described herein). Color notes for specimens from the southern part of the range (given below) are similar to that just described. For many specimens it appears that the dark borders to the pale crossbands are more prominent than the pale portions of the bands, which are sometimes not mentioned in individual descriptions.

The following color notes are extracted from the field notes of Charles W. Myers for specimens from Panama and Colombia (AMNH R-108468 only). Specimens are listed roughly in order of increasing SVL:

AMNH R-109643 (female, 199 mm SVL): Lateral light bars pale yellow on neck, pale grayish brown on body. Venter white, with a yellowish tinge on throat. Iris pale tan upper quarter sector, dark brown below. Tongue black with an orangish tinge near base of fork.

AMNH R-129757 (male, 213 mm SVL): Upper quarter sector of iris tan, lower three quarters dark brown. Tongue dark brown with black fork.

KU 107656 (male, 229 mm SVL): Color like [KU 107652], except venter white instead of yellow, light dorsal spots pale brown rather than gray, and yellow of scale bases is light, not bright.

KU 107647 (male, 236 mm SVL): Brown above with tan light areas. Venter white. Iris pale bronze with red-brown half moons either side of pupil.

KU 107645 (male, 258 mm SVL): Anterior part of body with pink cast to the brown background. Trace of yellow on supralabials and on neck along lower scales and first 6 ventrals. Venter immaculate white. Iris pale tan with red brown half moons.

KU 107659 (male, 329 mm SVL): Brown with yellowish dark-bordered crossbars anteriorly and black crossbars posteriorly, where there are also lateral dark lines and a vertebral light yellowish area. A yellow tinge in neck region followed by an orangish cast to entire dorsum (brown) to a bit past midbody. Labials and anterior venter white except for a yellow tinge on venter, turning pale grayish near anus and under tail. Iris

rich brown, except upper one-third, which is pale orangish tan. Tongue orangish brown with gray tips.

KU 107651 (female, 536 mm SVL): Reddish brown above, turning gray-brown on posterior one-third of body and tail; scales on anterior two-thirds of body with bright yellow anterior margins (tip of base has a small black spot). Entire body with black and lighter brown crossbanding of an odd pattern. Labials and chin white, turning yellow-green on ventrals and yellow on subcaudals. Upper one-fifth of iris light tan; lower parts brown.

KU 107650 (male, 604 mm SVL): Brown above, white below.

KU 75678 (female, 641 mm SVL): Dorsum brown with transverse black markings; bases of scales on anterior two-thirds of body yellow. Labials and underside of head white, changing to greenish white on anterior three-fourths of belly and to pale yellow on posterior one-fourth. Subcaudals bright yellow. Iris tan above, brown below.

KU 107652 (female, 651 mm SVL): Brown with grayish spotting and black crossbars. Anterior bases of scales bright yellow on anterior two-thirds of body, especially noticeable on neck where the skin does not have to be stretched to show a yellow cast. There seems to be no special behavioral display associated with this hidden color. Labials and ventrals greenish white, turning light yellow on posterior one-third of body and bright orange-yellow under tail. Upper quarter section of iris light brown and lower part dark brown. No dark stripes, even on tail.

KU 107654–55 (male and female, 543 and 720 mm SVL): Color like [KU 107652] except stripes are present and greenish white of anterior ventrals not extending under head and on labials, which are white. Tongue red with black tips in -54 [?], all black in other.

KU 107653 (male, 703 mm SVL): Color much like [KU 107652] except the dorsal ground is darker and conspicuous stripes are present posteriorly.

AMNH R-119376 (male, 852 mm SVL): Head greenish gray, neck yellowish brown

(anterolateral scale bases bright yellow), turning brown on body. Underside of head and most of belly white, turning pale yellow toward tail and yellow under tail. Iris brown except that upper quarter sector is pale tan. Tongue deep red with black fork.

AMNH R-108468 (Colombia; male 615 mm SVL): Dull brown with indistinct black stripes. Anterior bases of scales are yellow in the neck region and then pale green to slightly past midbody, after which the scale bases are not differently colored. Supralabials and underside of head white; first 20 ventrals are yellow, then venter turns greenish white and, on last few dozen ventrals and on subcaudals, yellowish orange. Tongue dark. Iris pale brown on top quarter sector, dark brown on lower three-quarters.

Coloration in Preservative. Generally, the color pattern described above for living specimens is maintained in well-preserved specimens, but color tones become dull brown, olive, or gray. There is considerable variability in the distinctness of the pale crossbands and their dark edging (from virtually absent to very distinct) (Fig. 8). The extent to which this reflects color pattern in life or differences in preservation is unknown. The vertebral scale row is often distinctly paler than paravertebral rows, especially on the posterior body. In some specimens this results in the appearance of longitudinal paravertebral stripes. There is usually a lateral dark brown stripe posteriorly on dorsal rows 2 and/or 3; this varies from very prominent to indistinct. Occasional specimens from Costa Rica and Panama (and perhaps other parts of the range) have a very subdued pattern in preservative (Fig. 8B) and presumably in life as well. In these individuals pale anterior bands are absent, and the dark stripes on the body and tail nearly match the dorsal ground color, rendering a pale grayish or grayish brown dorsum with obscure dark lines. These individuals are otherwise typical of *Dendrophidion percarinatum* in other characters (two examples I have seen are females), and I assume they represent color variants within the species.

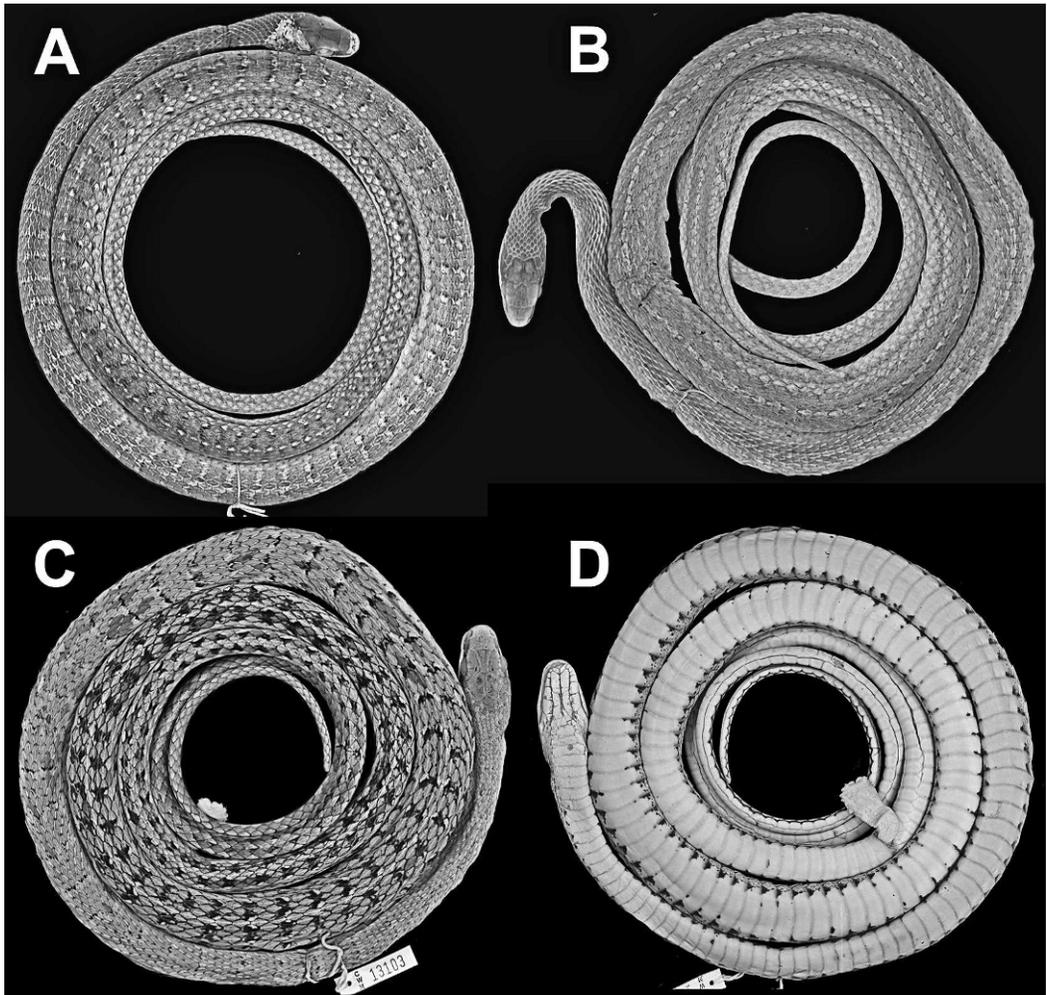


Figure 8. Representative specimens of *Dendrophidion percarinatum*. (A) UMMZ 79764 (Nicaragua). (B) UMMZ 63762 (Panama). (C) and (D) AMNH R-119376, dorsal and ventral (Panama).

The venter sometimes has scattered small dark spots.

Distribution. Northern Honduras (Atlántida Province; McCranie, 2011) eastward and south throughout Central America to northern Colombia and northwestern Venezuela (Rojas-Runjaic and Rivero, 2008), and western Colombia (Chocóan region) to the vicinity of the Bahía de Buenaventura. *Dendrophidion percarinatum* occurs on the Pacific versant only in Costa Rica, Panama, and Colombia. Most localities are <1,000 m elevation but *D. percarinatum* occurs up to 1,200 m in

southwestern Costa Rica (Río Coto Brus valley). In Honduras the maximum elevation attained is 685 m (McCranie, 2011: 110), and other elevational records derived from specimens I examined are 930 m (Panama), 520 m (Nicaragua), and 200 m (Colombia; but see below for a potentially much higher record). McCranie (2011: 109) and Savage (2002: 657) mapped localities for Honduras and Costa Rica, respectively. Lieb (1996) mapped the rangewide distribution, but the localities and range he gave for *D. percarinatum* in South America need correcting with the taxonomic

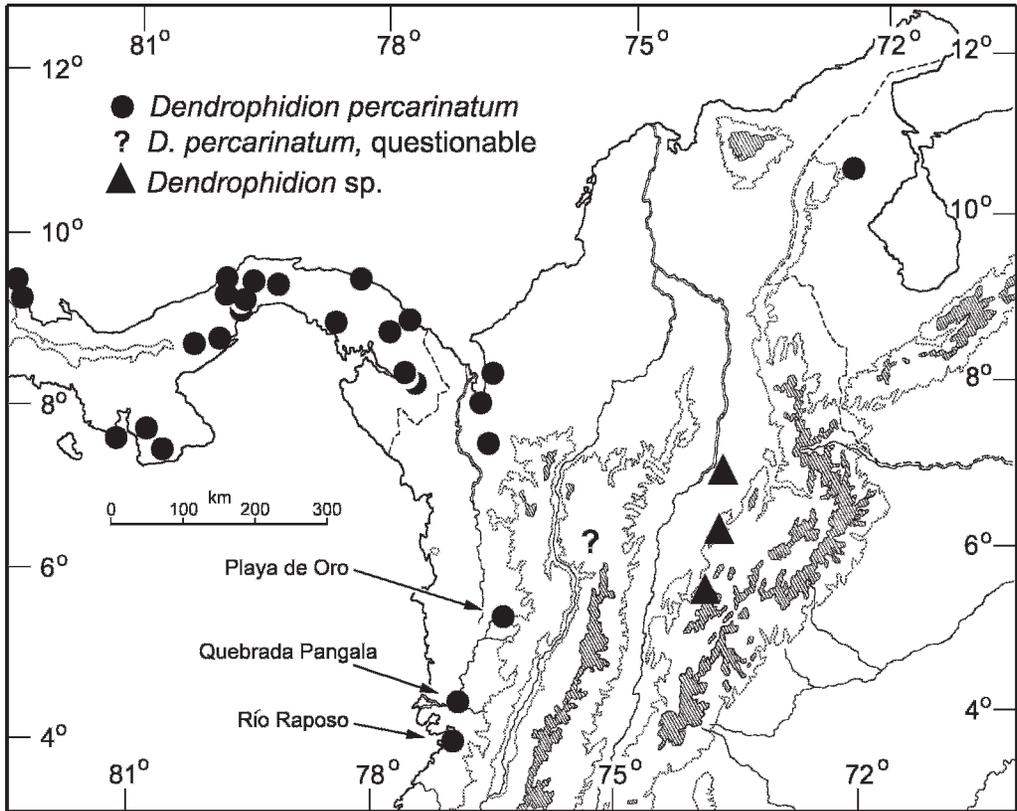


Figure 9. Distribution of *Dendrophidion percarinatum* in Panama and northwestern South America. All known South American localities are plotted. Three labeled localities in western Colombia (arrows) are sites where *D. percarinatum* is sympatric with *D. prolixum*. Locality in western Venezuela (about 10°40'N, 72°30'W) is from Rojas-Runjaic and Rivero (2008). ? in the Río Cauca valley is Medellín, a questioned locality for *D. percarinatum* (see text). Triangles in central Colombia (Río Magdalena valley) are localities for specimens similar to *D. percarinatum* in segmental counts, but which may represent differentiated populations or a distinct species; see *Distribution* in the *D. percarinatum* account and Appendix 1 (*Dendrophidion* species inquirendum).

revisions herein, about which more is said shortly. Figure 9 shows the distribution of *D. percarinatum* in Panama and South America as I presently understand it.

The southernmost specimen in western Colombia that I refer to *Dendrophidion percarinatum* is USNM 151658, a juvenile from the vicinity of the Bahía de Buenaventura (approximately 3°45'N; see Figs. 12A, 13A, and discussion in the account for *D. prolixum*). However, few specimens of any species of *Dendrophidion* in U.S. collections seem to have been collected between this point and the Ecuadorian frontier. Some difficulties in distinguishing juveniles of *D. percarinatum* and

the two new species are discussed in the account for *D. prolixum*.

Sympatry between *Dendrophidion percarinatum* and the new species *D. prolixum* is documented at three localities in western Colombia (Fig. 9): Playa de Oro, Quebrada Pangala, and the Río Raposo just south of Buenaventura. At each locality the specimens documenting each species have the distinctive color pattern characters of each; exemplars are illustrated in the account for *D. prolixum* (see *Distribution*). At Playa de Oro the documenting specimens are both males with everted hemipenes, which are described and illustrated later (see Figs. 39A, 42).

Populations of *Dendrophidion percarinatum* in southwestern Costa Rica (Río Coto Brus valley and Golfo Dulce/Osa Peninsula, including the type locality) are seemingly isolated from populations of the Atlantic versant and uplands of northwestern Costa Rica (Savage, 2002: 657). Carara National Park is the only documented lowland locality on the Pacific versant north of the Osa Peninsula region. Despite this apparent disjunction, Atlantic and Pacific populations in Costa Rica do not differ substantively in standard external morphological characters (see above discussion of geographic variation). Similarly, *D. percarinatum* seemingly has a somewhat spotty distribution in Panama, a not-infrequent pattern for Panamanian snakes (Myers, 2003; Myers et al., 2007: 12–14). The identities of *D. percarinatum* and *D. prolixum* have previously been confused in western Colombia (see discussion in the next section), where their distributions overlap. Areas of sympatry of these two species are discussed in the species account for *D. prolixum*.

Previous Records of Dendrophidion percarinatum in Colombia and Venezuela. Because of the confused identity of South American specimens previously referred to *Dendrophidion percarinatum*, I briefly comment on a few South American references to this species (Ecuadorian specimens are referred to in the species account for *D. graciliverpa*). Lieb (1988: 166) correctly inferred that records for “*D. percarinatum*” reported by Alemán (1953; “*D. dendrophis*”) from western Venezuela and by Roze (1966) from the Cordillera de la Costa of northern Venezuela were misidentified specimens of *D. nuchale* auctorum. Many specimens of *D. nuchale* auctorum are available from the Cordillera de la Costa. The four specimens reported by Alemán (cited by Roze) are from Zulia state in western Venezuela near the recently reported “first record” of *D. percarinatum* from Venezuela (Rojas-Runjaic and Rivero, 2008). The last authors did not mention the specimens listed by Alemán (1953), who reported segmental counts and body pro-

portions consistent with either *D. percarinatum* or *D. nuchale* auctorum. These four specimens were apparently examined, and their identity confirmed as the last species, by James R. Dixon in 1981 (Fernando Rojas-Runjaic, personal communication).

The scalation data and color details given by Rojas-Runjaic and Rivero (2008) for the “first valid record” of *D. percarinatum* from western Venezuela are consistent with that species as redefined herein, even though some of the reported head scutellation is rare in my sample (see above section on variation). These authors also described the anterior dorsum of the specimen as “grayish green uniform,” which is seemingly unlike most descriptions of Central American specimens (brown, yellowish brown, reddish brown; see *Coloration in Life*). The specimen is a male with everted hemipenes according to the authors, and hemipenial characters could confirm its identity. Other Venezuelan records of “*D. percarinatum*” (e.g., Test et al., 1966; Lancini, 1979) undoubtedly refer to *D. nuchale* auctorum, as recognized by Lieb (1988).

Lieb (1996) included as part of the distribution of *Dendrophidion percarinatum* two localities in the interandean valleys of the Río Cauca and Río Magdalena of northern Colombia, stating some equivocation as to their identity: “Isolated populations tentatively referred to [*D. percarinatum*] occur in the Departments of Antioquia and Cundinamarca in north-central Colombia; these snakes are somewhat divergent in the anterior body color pattern from *D. percarinatum* in other parts of the range” (Lieb, 1996: 636.1–636.2). These records are apparently based in part on MCZ R-21984 (Sonsón, Antioquia department) and MCZ R-42185 (Villeta, Cundinamarca department), which Lieb (1988: 174) cited as specimens of *D. percarinatum*; he indicated at least the first locality (Sonsón) on an accompanying map (Lieb, 1988: fig. 5). However, both of these specimens are unequivocally *D. bivittatum* (personal observations of both specimens, and Stuart [1932] for MCZ R-21984).

I am aware of only one specimen of *Dendrophidion percarinatum* potentially from the deeper interandean portion of the Río Cauca: BMNH 1897.11.12.10, collected by A. E. Pratt and said to be from “Medellín.” If the locality is the well-known Andean city of that name, and is truly the point of origin of the specimen (rather than a shipping point), then this would be an elevational record for the species (1,440–1,540 m). As a cautionary note, the NGA (2010–2012) online gazetteer (GEONet) lists six other place names “Medellín” in the northern Colombian departments of Córdoba, Sucre, Magdalena, and Bolívar—any of which are at lower elevations and would bridge the lowland distributional “gap” between the northern Colombian localities for *D. percarinatum* around the Golfo de Urabá (about 8°N) and the westernmost Venezuelan locality (Fig. 9). In the absence of other documented specimens from this area, I am hesitant to include the interandean city “Medellín” as a documented locality for *D. percarinatum*.

Several specimens with segmental counts similar to *Dendrophidion percarinatum* are known from 150–1,242 m elevation in the Río Magdalena valley (Fig. 9; Appendix 1, “*Dendrophidion* species inquirendum”; see also Dunn, 1944: 477). Lieb (1988) had examined one of these, MCZ R-42186, from Boyacá department in central Colombia but, perhaps as a lapsus, did not include Boyacá in his above-cited quotation. A specimen reported as “*D. dendrophis*” (Niséforo María, 1942: 87) from Sasaima (approximately 1,100–1,200 m, upper Río Magdalena) may also pertain to this group (or to *D. nuchale* auctorum). The three specimens I have seen from the Río Magdalena do have somewhat peculiar color patterns compared with typical *D. percarinatum* and, although their scale counts are similar to *D. percarinatum*, segmental counts by themselves often are unhelpful in distinguishing species of *Dendrophidion* (Cadle, 2012; this paper). Unfortunately, the only male among the three is a small

juvenile (217 mm SVL) with retracted hemipenes previously exposed by a somewhat mangled dissection. Some aspects of their morphology (e.g., a proportionally short spinose + apical region) seem unlike other *D. percarinatum* hemipenes I have examined but better preparations would be needed for confirmation. Study of additional specimens from this area will be needed to resolve the taxonomic status of these populations, but the available specimens are, in any case, seemingly geographically isolated from other known populations referable to *D. percarinatum* (Fig. 9).

A summary of the Colombian specimens referred to *Dendrophidion percarinatum* by Lieb (1988) and my re-assessments of their identities are as follows: MCZ R-21984, R-42185 (= *D. bivittatum*); FMNH 54949, FMNH 54958–64, FMNH 54965, LACM 36782, LACM 45443, USNM 151659 (= *D. prolixum*); and MCZ R-42186 (= *species inquirendum*). I concur with the identity of the other Colombian specimens cited by Lieb (1988) as *D. percarinatum* as redefined here: FMNH 63761, FMNH 63772–73, FMNH 78118, USNM 151658. Stafford (2003: 111) referred LACM 45443 from Chocó department to *D. vinitor* but there are no documented occurrences of that species complex in Colombia (Cadle, 2012: 206–207), and I refer LACM 45443 to *D. prolixum*.

Natural History. General overviews of the natural history of *Dendrophidion percarinatum* include Guyer and Donnelly (1990, 2005), Savage (2002: 657–658), Solórzano (2004: 234–236), and McCranie (2011: 108–111). Diet and reproductive parameters are summarized by Goldberg (2003), Stafford (2003), and Sexton and Heatwole (1965). *Dendrophidion percarinatum* is a diurnal, terrestrial to semiarborescent snake of lowland and premontane moist tropical forests. At night it has been found sleeping on low vegetation. The diet consists primarily of terrestrial leaf-litter frogs (e.g., *Pristimantis*, *Craugastor*), with a lesser component comprising lizards (*Anolis*, *Cnemidophorus*; Stafford, 2003). *Dendrophidion percarinatum* is oviparous with recorded

clutch sizes of three to six and perhaps with multiple clutches per year in the southern portion of the range (Goldberg, 2003; Stafford, 2003).

Brief field notes recorded for Panamanian specimens by Charles W. Myers include the following (observations by day except where indicated). Six specimens were on the forest floor (AMNH R-129757; KU 107647, 107651–53, 107656). Four were associated with water courses: on a riverbank, along a forest stream, in leaves of a dry stream bed, in a river (AMNH R-119376, 109643; KU 107650, 107659). One was in an open grassy situation (KU 107645), and two were sleeping at night on a palm leaf 3 ft. (~0.9 m) above a stream bank and in a *Heliconia* 5 ft. (~1.5 m) above ground (KU 107654–55). Myers' notes indicate that a light quickly awakens sleeping snakes, which "then behave as if flying snakes." One specimen encountered by day remained motionless rather than fleeing (KU 107652). Myers forced the hind legs of a large *Craugastor* (*C. fitzingeri* group) from either KU 107654 or 107655 (adults, 543 and 720 mm SVL, respectively).

Dendrophidion percarinatum is sympatric with several other species of *Dendrophidion* within its range. The range of *D. percarinatum* overlaps with *D. apharocybe* and/or *D. nuchale* auctorum from Honduras to Panama, and all three occur together at some localities (e.g., La Selva Biological Station, Costa Rica). At the Las Cruces Biological Station in southwestern Costa Rica *D. percarinatum* is sympatric with three other species—*D. crybelum*, *D. nuchale* auctorum, and *D. paucicarinatum*—yielding perhaps the highest species density of *Dendrophidion* anywhere. In western Colombia the distributions of *D. percarinatum*, *D. prolixum*, and *D. nuchale* auctorum overlap broadly, with two of the three documented sympatrically at several localities; it would be unsurprising to find the three species occurring together.

TWO NEW SPECIES FROM WESTERN COLOMBIA AND ECUADOR

Dendrophidion percarinatum as redefined here is relatively homogeneous in color pattern and hemipenial morphology from eastern Honduras to northwestern Colombia. However, in western Colombia and Ecuador are snakes similar to *D. percarinatum* in standard scutellation characters and body proportions, but they differ strongly from that species in coloration and hemipenial morphology. Lieb (1988, 1996) included these snakes in his concept of *D. percarinatum*, and his concept was followed by others (e.g., Savage, 2002; Stafford, 2003; Cadle, 2010). However, they comprise diagnosable units that I consider two distinct new species. Both new species have an exceptionally long, slender hemipenis (gracile morphology) and color patterns different from *D. percarinatum*. The taxonomic distinction of the new species is also supported by the fact that the distributions of *D. percarinatum* and the first of the new species to be described overlap in western Colombia, including the three localities of documented sympatry mentioned above. In the area of distributional overlap, specimens of *D. percarinatum* maintain the typical color pattern and hemipenial morphology expressed throughout the rest of its geographic range, whereas the sympatric new species is distinctive in both features. The situation in western Ecuador proved more confusing because not only do the two new species occur there but *D. brunneum* does as well. Preserved specimens of the three species can be a challenge to distinguish, and in fact, I was unsuccessful in allocating some specimens to any of the three with certainty.

Dendrophidion prolixum New Species

Figures 1D, 10–11, 12B, 13B, 14–17, 19, 42, 43A

Drymobius dendrophis. Boulenger, 1913: 1034 (specimen from Peña Lisa, Colombia; = BMNH 1913.11.12.40).

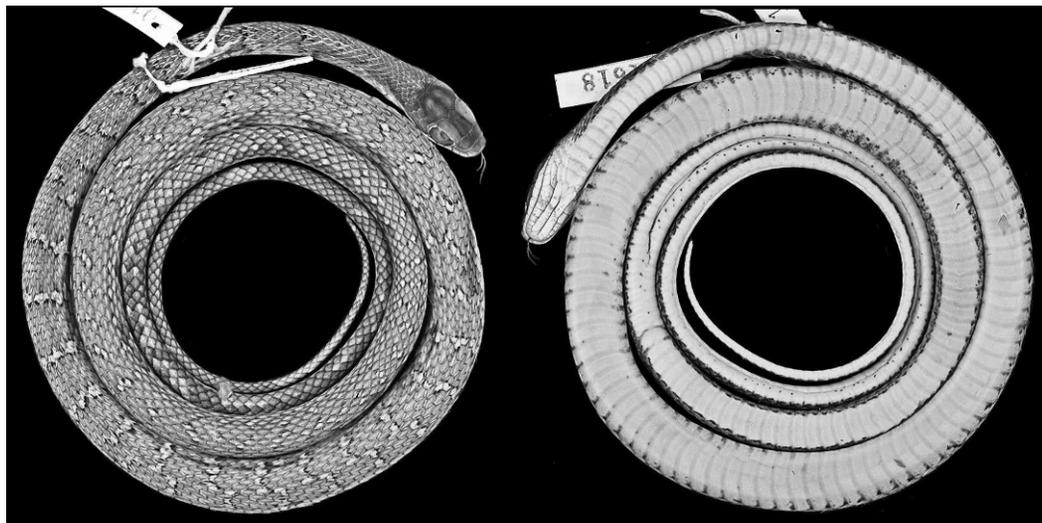


Figure 10. Holotype of *Dendrophidion prolixum* (AMNH R-109721). Male from Quebrada Guanguí, Chocó department, Colombia.

?*Dendrophidion dendrophis* (part). Peters and Orejas-Miranda, 1970: 80 (“southern part of Central America and northern South America”). Pérez-Santos and Moreno, 1988: 134 (Pacific lowlands of Colombia).

Dendrophidion percarinatum (part). Dunn, 1944: 477 (? part). Savage and Villa, 1986: 148, 169. Lieb, 1988: 172; 1996: 636.1. Pérez-Santos and Moreno, 1991b: 138. Savage, 2002: 657–658. Stafford, 2003: 111 (BMNH 1913.11.12.40). Solórzano, 2004: 234–236. Guyer and Donnelly, 2005. McCranie and Castañeda, 2005: 8. McDiarmid and Savage, 2005: 391, 421. Cadle, 2010: 24.

Holotype (Figs. 10–11). AMNH R-109721 from Quebrada Guanguí, 0.5 km above Río Patia (upper Saija drainage), 100–200 m, Cauca department, Colombia [about 02°50'N, 77°25'W; Myers, 1991: 8]. Collected 9 February 1973 by Charles W. Myers and John W. Daly (field number C. W. Myers 11618).

The holotype is a male, presumed adult, 754 mm total length, 307 mm tail length (447 mm SVL); relative tail length 41% of

total length, 67% of SVL; dorsocaudal reduction from 8 to 6 at the level of subcaudal 27; 153 ventrals, 2 preventrals, 142 subcaudals; 12 left and 11 right infralabials. An unusual temporal scale configuration: 2+3+2 on each side (Fig. 11A). Supralabial/temporal pattern G (irregular because of divisions in temporal scales). Other head scales are typical of the species (Table 1 and description below). Both hemipenes are retracted but exposed by a ventral incision in the tail base; the right hemipenis extends to the middle of subcaudal 13, the left to the middle of subcaudal 15. The retractor penis magnus is slightly divided proximally. The type retains elements of the juvenile color pattern: approximately 51 pale crossbands on the body (tending to form ocelli and somewhat indistinct posteriorly; Fig. 11B), an indistinct broken line on the suture line of dorsal rows 2 and 3 posteriorly (Fig. 11C), and a venter with only scattered small dark spots in addition to dark transverse lines indicated only at the lateral edges of the ventral scutes.

Paratypes. Colombia: Cauca: Quebrada Guanguí, 0.5 km above Río Patia (upper Saija drainage), 100–200 m, AMNH R-109722–28

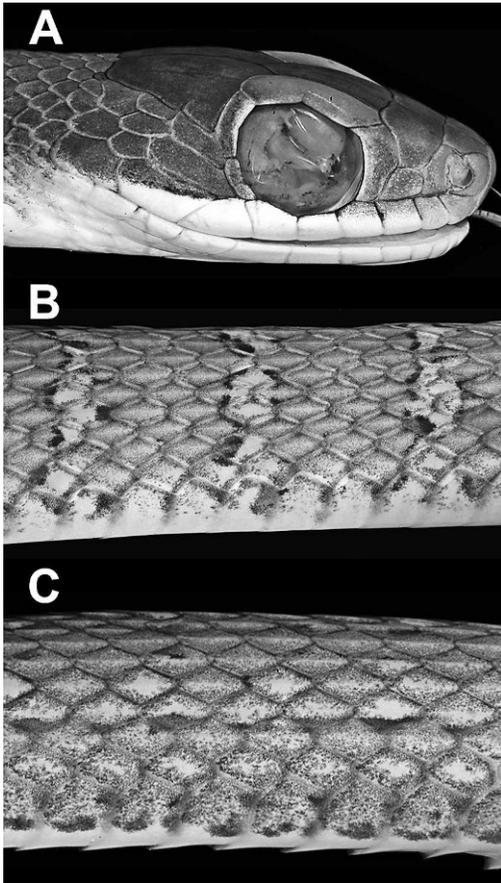


Figure 11. Holotype of *Dendrophidion prolixum* (AMNH R-109721). (A) Head, right side. (B) Midbody pattern, lateral view. (C) Posterior lateral pattern.

(topotypes). **Chocó:** Peña Lisa, Condoto, 300 ft. [90 m], BMNH 1913.11.12.40. Playa de Oro, Río San Juan, 400 m, FMNH 54965, AMNH 108469. Quebrada Bochoramá, Loma de Encarnación on right bank, LACM 45443. Quebrada Docordó, middle Río San Juan (about 17 km airline SSW Noanamá), AMNH R-123749–51. Quebrada Pangala, lower Río San Juan (about 17 km airline NE Palestina), AMNH R-123746. Quebrada Taparal, lower Río San Juan (about 7 km airline NE Palestina), AMNH R-123744, R-123753. Upper Río Buey, 110–160 m, LACM 36782. Sierra [Serranía] de Baudó, 3,000 ft. [915 m], Pacific side, ANSP 25609. Serranía de Baudó, north slope of Alto del

Buey, 900 m, AMNH R-119801. **Risaralda:** [Between] Pueblo Rico [and] Santa Cecilia, Pacific side, 800 m, FMNH 54949, 54958–64. **Valle del Cauca:** Río Raposo, Virology Field Station near Buenaventura, USNM 151659.

Referred Specimens. Colombia: **Chocó:** Quebrada Pangala, lower Río San Juan (about 17 km airline NE Palestina), AMNH R-123747. **Nariño:** Riquarte [= Ricaurte], 3,900 ft. [1,189 m], Pacific side, ANSP 25608. **Ecuador:** **Esmeraldas:** Immediate environs of Cachaví, 20 m, USNM 237064. Río Cachaví, USNM 237065. **Imbabura:** Paramba, northwestern Ecuador [= Hacienda Paramba; 800–1,000 m], FMNH 4055, 4056(?) (the last two specimens not included in data summaries). The referred specimens are small juveniles except FMNH 4056 (adult female in fair condition).

Etymology. The species name is the neuter form of the Latin adjective *prolixus* meaning “stretched far out” or “long,” used especially in reference to parts of the body. The reference is to the unusually long hemipenis of this species compared with most other *Dendrophidion*.

Diagnosis. *Dendrophidion prolixum* is characterized by (1) dorsocaudal reduction from 8 to 6 occurring anterior to subcaudal 27 (range, 8–26); (2) divided anal plate; (3) subcaudal counts >130 in males and females and adult tail length >60% of SVL; (4) subadults with narrow pale crossbands or transverse rows of ocelli separated by >3 dorsal rows on the neck (adults retain bands or become predominantly brown or green without distinct pale bands); total number of pale bands on the body fewer than 60 (range, 49–57) when they are distinct; (5) ventrals immaculate or (in some adults) with narrow transverse dark lines across the anterior border of each ventral plate; (6) in life, head reddish brown and dorsum mainly green (brownish green in juveniles); and (7) everted hemipenis of “gracile” morphology, with an exceptionally long, slender hemipenial body proximal to an expanded tip bearing spines, calyces, and other apical ornamentation (retracted hemipenis nearly always to subcaudal 10 or

greater); total number of enlarged spines on the hemipenis >60 (65–89 in four organs studied).

“Gracile” hemipenial morphology will distinguish *D. prolixum* from all other species of *Dendrophidion* except *D. graciliverpa* described herein and perhaps *D. bivittatum* (see above comments where the gracile morphology is described). *Dendrophidion bivittatum* has a different color pattern (greenish dorsum with prominent blackish longitudinal stripes), a tail <60% of SVL, and fewer than 130 subcaudals.

Dendrophidion prolixum differs from species of the *D. dendrophis* species group (*D. dendrophis*, *D. atlantica*, *D. nuchale* auctorum, *D. apharocybe*, *D. crybelum*, *D. vinitor*) in having a reduction in the dorsocaudal scales anterior to subcaudal 30 (posterior to subcaudal 30 in the *D. dendrophis* group except occasional females). A high number of subcaudals and divided anal plate will distinguish it from *D. apharocybe*, *D. crybelum*, and *D. vinitor* (<130 subcaudals and anal plate nearly always single in these species). *Dendrophidion dendrophis* and *D. nuchale* auctorum may have either single or divided anal plates, but these species have different color patterns, usually involving numerous narrow pale bands and/or ocelli (see Savage, 2002: 654–655, for discussion of *D. nuchale*), attain greater body sizes, and have different hemipenial morphologies (robust morphology and enormously enlarged spines in *D. dendrophis* and *D. nuchale*). *Dendrophidion prolixum* differs from *D. boshelli* in having 17 midbody scale rows (15 in *D. boshelli*).

Dendrophidion paucicarinatum lacks distinct pale crossbands and has a higher number of ventrals than *D. prolixum* (>175 compared with <165 in *D. prolixum*). *Dendrophidion paucicarinatum* may have either a single or divided anal plate. *Dendrophidion prolixum* differs from *D. brunneum* in color pattern (adult *D. brunneum* generally lack pale bands) and in hemipenial morphology (robust in *D. brunneum*; see Fig. 3 and Cadle, 2010).

Dendrophidion prolixum is distinguished from *D. graciliverpa* by the wide spacing of the pale dorsal bands on the neck (bands generally separated by >3 dorsal scale rows in *D. prolixum*, <3 dorsal rows in *D. graciliverpa*). Consequently, *D. prolixum* has fewer pale bands on the body when these can be discerned: 49–57 in *D. prolixum* compared with 57–87 in *D. graciliverpa*. In life *D. prolixum* has a reddish brown head and greenish body, compared with a green head and brown to gray body in *D. graciliverpa*. These two species are exceedingly similar in most characteristics (Table 1), and I discovered no consistent differences in hemipenial morphology between them in the few everted hemipenes examined when intra-specific variation is considered. Preserved specimens without discernible pale crossbands are problematic to identify, and several specimens from the borderlands of northern Ecuador and southern Colombia are of questionable referral to either *D. prolixum* or *D. graciliverpa*.

Dendrophidion prolixum has previously been confused with *D. percarinatum*, and these species cannot be distinguished by traditional scutellation features other than a few mean character differences (Table 1). These two species differ in (1) color pattern: reddish brown head with a greenish brown to green body, and venter either immaculate or with dark transverse lines (*D. prolixum*) vs. head and body primarily browns to grays, and venter immaculate (*D. percarinatum*); (2) number of pale crossbands on the body: 49–57 and separated by ≥ 3 dorsal scale rows on the neck (*prolixum*) vs. 71–96 and separated by <3 dorsal scale rows on the neck (*percarinatum*) (pale crossbands can be indistinct in either species, but especially adult *D. prolixum*); (3) relationship between the posterior supralabials and temporals (see Materials and Methods and Table 1): G pattern most commonly (*D. prolixum*) vs. P pattern most commonly (*D. percarinatum*); (4) hemipenial morphology: gracile (*prolixum*) vs. robust (*percarinatum*); retracted hemipenes of *D. percarinatum*

TABLE 4. COMPARISON OF PRESERVED SPECIMENS OF THREE SPECIES OF THE *PERCARINATUM* COMPLEX IN WESTERN COLOMBIA AND ECUADOR. PATTERN ELEMENTS ARE BASED ON JUVENILES WITH DISTINCT BANDING PATTERNS, WHICH ARE RETAINED ONLY IN SOME ADULTS OF EACH OF THE THREE SPECIES.

	<i>D. percarinatum</i> , Figures 12A, 13A	<i>D. prolixum</i> , Figures 12B, 13B	<i>D. graciliverpa</i> , Figures 12C, 13C
Supralabial/temporal pattern	usually <i>P</i>	usually <i>G</i>	usually <i>G</i>
No. of dorsal rows separating neck bands	< 3	3–4	< 3
No. of pale bands on the body	71–96	49–57	57–87
Head cap	brown	brown	dark gray
Form of the neck bands	usually bandlike	usually ocellate (rounded pale spots surrounded by dark pigment); often heavily invested with dark pigment	bandlike (usually) or ocellate
Distinctness of neck bands	usually distinct	usually distinct	often obscured by gray head cap extending onto the neck
Contact between neck bands and ventral pale coloration	pale portion of bands usually confluent with pale ventral color	pale portion of bands usually cut off from pale ventral color by two or three dorsal rows; often a distinct dark brown lower border on neck ocelli	pale portion of bands confluent or not (extension of dark gray head color often interrupts bands on lower dorsal rows)

rarely extend to subcaudal 10, whereas retracted organs of *D. prolixum* nearly always extend beyond subcaudal 10. The strong differences between *D. prolixum* and *D. percarinatum* in color pattern and hemipenial morphology are maintained in the area of western Colombia where their geographic ranges overlap, including several localities of sympatry discussed later.

Distinguishing Juvenile Preserved Specimens of the D. percarinatum Complex. Preserved juveniles of *Dendrophidion prolixum*, *D. percarinatum*, and *D. graciliverpa* present some challenges to identify, which is relevant not only to proper species recognition but also to discerning distributions, range overlap, and sympatry of the three species. The pattern of pale crossbands on the neck and a few other characters offer differentiating, if subtle, characters (Table 4, Figs. 12–13), although no single character will necessarily be decisive for a given specimen. These characters will also work with those adults that retain distinct bands. These characters

were instrumental in identifying the southernmost specimen of *D. percarinatum* in my sample (Figs. 12A; 13A, left) and in demonstrating sympatry between *D. percarinatum* and *D. prolixum* in western Colombia discussed later in this species account. There is also potential confusion of juvenile *D. graciliverpa* and *D. brunneum* in western Ecuador, but I have seen too few of the last species to be confident of differentiating juvenile characters; this problem is discussed in the later section on *D. brunneum*.

The two most consistent characters (Table 4) are the total number of pale crossbands on the body and their separation on the neck. These two in combination will usually easily separate *D. prolixum* (Figs. 12B, 13B) from the other two species (pale bands are distinct in juveniles of all three species, unlike in adults). *Dendrophidion percarinatum* and *D. graciliverpa* have a greater total number of bands, which are more narrowly separated on the neck. Side by side comparison of either of these with *D. prolixum* immediately shows a greater

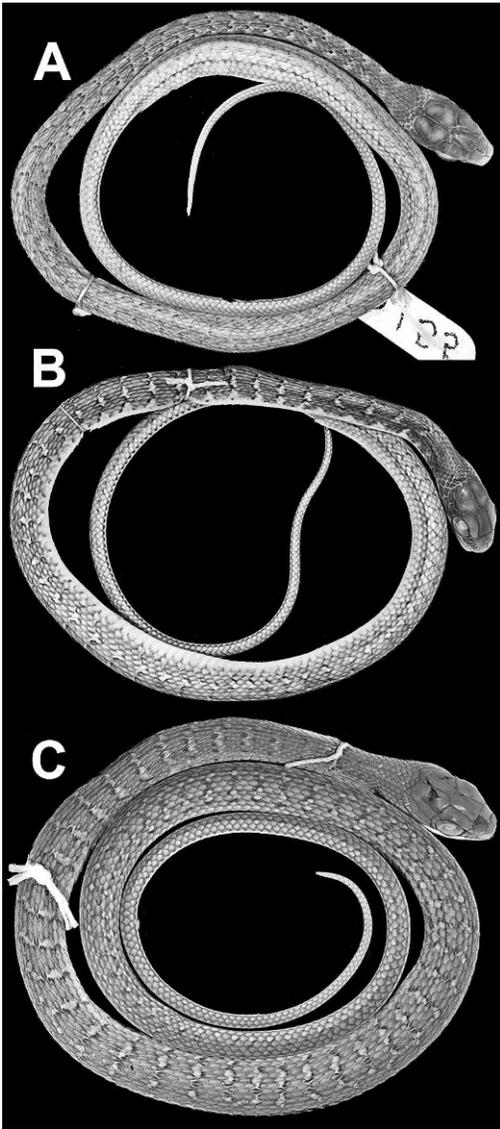


Figure 12. Juvenile specimens of (A) *Dendrophidion percarinatum* (USNM 151658, Chocó department, Colombia). (B) *D. prolixum* (USNM 237065, Esmeraldas province, Ecuador). (C) *D. graciliverpa* (KU 179501, Pichincha province, Ecuador).

band density on the neck in the first two compared with *D. prolixum* (Fig. 13).

Most of the other characters in Table 4 are subject to some intraspecific variation (supralabial/temporal pattern) or to conditions of preservation interacting with the color pattern of a given specimen. None-

theless, careful comparisons usually make it possible to identify preserved specimens confidently (coloration in life would prove diagnostic, if available). For example, in *Dendrophidion prolixum* the neck bands are distinctly ocellate, having the form of pale spots that are usually at least partly surrounded by dark pigment and are not confluent with the pale ventral color (Fig. 13B). Neck bands in *D. percarinatum* and *D. graciliverpa* are usually more band-like (narrow, relatively straight) and usually confluent with the pale ventral color. This pattern can be disrupted if the bands are disrupted on the side of the neck, as occurs with some frequency in *D. graciliverpa* (e.g., Fig. 13C, right side). In these cases the upper portions of the crossbands can appear as ocelli, but they are not generally set off by dark pigment as in *D. prolixum* (Fig. 13B). In a few specimens of *D. graciliverpa* the neck bands are distinctly more ocellate, and other characters must be used.

Clearly, preserved juveniles of *Dendrophidion percarinatum* and *D. graciliverpa* will cause the most difficulty because these two can have similar total number of bands (Table 1). Three features in combination usually permit separation: the supralabial/temporal pattern (*P* vs. *G*, subject to intraspecific variation documented in Table 1); the shading of the head cap (usually brown and similar to the rest of the dorsum in well-preserved *D. percarinatum* vs. dark gray in *D. graciliverpa*, which presumably reflects the green coloration of the head/neck in life); and the distinctness of the anterior three or four pale crossbands on the neck (distinct in *D. percarinatum* vs. obscured by dark gray [green in life] extension of the head cap coloration onto the neck in *D. graciliverpa*; compare Figs. 13A, C). In *D. graciliverpa* the dark gray extension onto the neck sometimes (seemingly mostly in smaller juveniles) occurs only on the lower dorsal scale rows. This obscures the ventral portions of the neck bands, resulting in the appearance of ocelli in this species. This potentially creates some confusion with *D. prolixum*, but

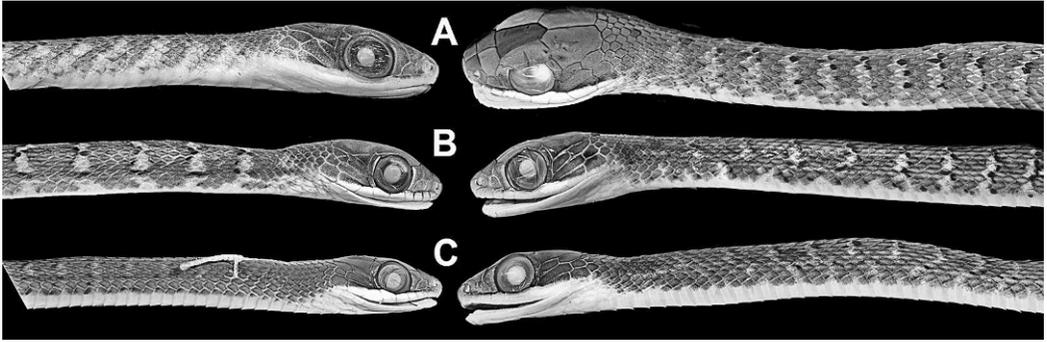


Figure 13. Comparison of pale bands on the anterior body of juvenile specimens. Each pair (left, right) representative of one species: (A) *Dendrophidion percarinatum* (USNM 151658, 191 mm SVL and AMNH R-123748, 272 mm SVL; both Colombia). (B) *D. prolixum* (AMNH R-109725, 208 mm SVL, Colombia; USNM 237065, 210 mm SVL, Ecuador). (C) *D. gracilliverpa* (KU 179501, 231 mm SVL and KU 291237, 265 mm SVL; both Ecuador).

distinct dark brown flecks or spots generally edge the ocelli in the last species.

Description (17 males, 17 females). Table 1 summarizes size, body proportions, and meristic data for *Dendrophidion prolixum*. Largest specimen (ANSP 25609) a female 675 mm SVL (total length 966+ mm, tail incomplete); the largest female with complete tail (USNM 151659) was 662 mm SVL, 1,116 mm total length. Largest male (AMNH R-123750) 650 mm SVL (1,003+ mm total length, tail incomplete); largest male with complete tail (AMNH R-123751) 642 mm SVL, 1,037 mm total length. Tail 38–40% of total length (62–67% of SVL) in males; 38–42% of total length (63–72% of SVL) in females.

Dorsal scales in 17–17–15 scale rows, the posterior reduction by fusion of rows 2+3 ($N = 25$) or 3+4 ($N = 35$) or by loss of row 3 ($N = 8$) at the level of ventrals 84–110 (sexual dimorphism discussed below). Ventrals 150–163 (averaging 157.4) in males, 152–164 (averaging 160.9) in females; ventrals preceded by 2 preventrals in about 70% of specimens (24% have only 1 preventral and rarely 3 preventrals were present or pre-ventrals were absent). Anal plate divided. Subcaudals 134–150 (averaging 140.5) in males, 133–150 (averaging 142.9) in females. Preoculars 1, postoculars 2 (rarely 3), primary temporals usually 2 (rarely 1 or 3), secondary temporals 2 (rarely 3), supralabials usually 9 with 4–6 bordering the eye (rarely

10 with 4–7 bordering the eye), infralabials usually 10 (range 8–12 with high frequencies of 9 and 11). Dorsocaudal reduction from 8 to 6 occurs at subcaudals 16–26 in males, 8–24 in females. Maxillary teeth 36–42 (averaging 38), usually with 3 or 4 posterior teeth enlarged and ungrooved; rarely, only 2 or as many as 5 teeth were enlarged. Enlarged teeth are not offset and there is no diastema.

Two apical pits present on dorsal scales. Most specimens lack keels on the lower 4, 5, or 6 dorsal scale rows on the neck (occasionally lacking on higher rows); nearly all specimens lack keels only on row 1 at midbody (sometimes keels are weak on row 2 and one specimen lacked keels on row 2); on the posterior body keels are almost always present on all except dorsal row 1 (one specimen lacked keels on rows 1–2, and another had weak or partial keels on some scales in row 1). Fusions or divisions of temporal scales occurred with the following frequencies: upper or lower temporal divided vertically (4), upper temporal divided horizontally (1), upper primary + secondary temporal fused (2), upper + lower primary fused (1, partial fusion). Seventy-six percent of scorings of the supralabial/temporal pattern were *G*, whereas only 4.5% were the *P* pattern; the remaining were irregular or ambiguous patterns.

Hemipenis unilobed, with an exceptionally long hemipenial body proximal to a

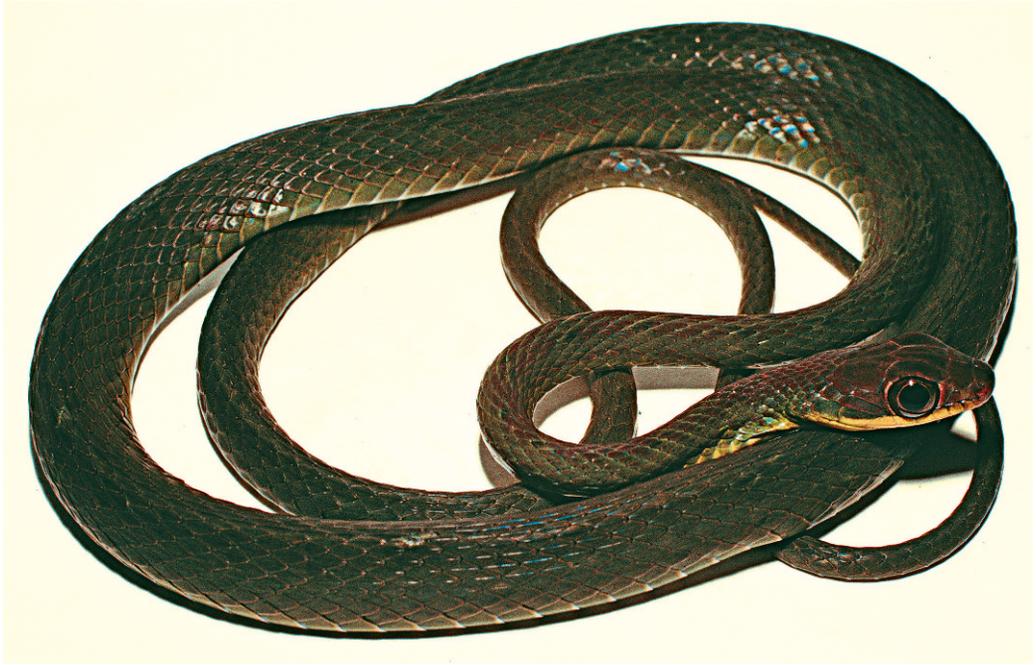


Figure 14. *Dendrophidion prolixum* in life from the type locality (AMNH R-109726). Adult male, 628 mm SVL. From a color slide by Charles W. Myers.

somewhat bulbous apex. Overall morphology “gracile.” Spinose region followed distally by 2 frounces and poorly developed calyces. Enlarged spines >60. Apex nude except for poorly developed calyxlike structures on the asulcate side and thickened tissue immediately adjacent to the tip of the sulcus spermaticus. Sulcus spermaticus simple, centrolinal, with a slightly flared tip in everted organs. Retracted hemipenis nearly always to subcaudal 10 or greater (to 15 or more).

Variation and Sexual Dimorphism. Tails are proportionally shorter in small individuals. Specimens <300 mm SVL have tail lengths 35–39% of total length, 53–64% of SVL ($N = 9$, males and females combined). No strong geographic trends were evident among the characters examined. Males and females differ significantly in ventral counts (female greater), the point of dorsocaudal reduction (male more distal), and the point of dorsal scale reduction (female more

posterior) (Table 1). The sexes do not differ in adult body size, relative tail lengths, or subcaudal counts. These are common patterns in other species of *Dendrophidion* (Cadle, 2012) and are found widely among other snakes.

Coloration in Life. The following color description for *Dendrophidion prolixum* is extracted from color notes of Charles W. Myers for specimens from western Colombia: the type locality (two juveniles, four adults), Serranía de Baudó (one juvenile), and Playa de Oro (one adult). Notes for individual specimens are presented after the summary. A color photograph of a specimen from the type locality is in Figure 14 (AMNH R-109726).

The color pattern changes ontogenetically from banded juveniles to (usually) more uniformly patterned adults (see variation below). Three juveniles have pale brown or tan crossbands (pale blue on the neck in one specimen) on a brown to grayish brown

dorsum. Adults are seemingly polymorphic in dorsal ground color (greenish to brownish or reddish brown); the largest adults for which color descriptions are available (>550 mm SVL) are green to dark green but may have a brown or reddish brown suffusion. The head of adults is reddish brown, contrasting with the general dorsal coloration; reddish brown dorsolateral and lateral stripes may be present on the anterior half of the body. The venter is white to grayish white anteriorly in juveniles and adults, and there may be a yellowish wash on the posterior venter and tail. The venter in small juveniles is immaculate, but larger individuals develop indistinct to prominent transverse grayish lines across the anterior edges of the ventral scales (superficially, the lines seem to be on the posterior edges of the scutes, but that is an illusion caused by the lines showing through the nearly-transparent posterior edge of the next anterior ventral scute).

Although Myers' notes do not indicate pale dorsal bands in individuals >447 mm SVL (see below), most preserved specimens retain some trace of bands (appearing as scattered whitish dorsal flecks or transverse rows of pale spots); one large adult female is strongly banded (see below) so retention of distinct crossbands may vary. The following notes on coloration in life from field notes of Charles W. Myers are arranged in order of increasing SVL so as to highlight the relation of color pattern to size (starting with AMNH R-109721 and following are considered adults):

AMNH R-119801 (juvenile, Serranía de Baudó, 211 mm SVL): Body grayish brown with pale blue lateral spots on neck, these turning pale brown on rest of body. Reddish brown lateral stripe. Underside of head white, turning grayish white over rest of ventral surfaces. Upper one-fifth of iris tan, lower four-fifths reddish brown. Tongue black.

AMNH R-109722–23 (juveniles, Quebrada Guanguí, 235 mm and 283 mm SVL): Tan interspaces on brown dorsum. Venter white anteriorly, grading to yellowish posteriorly. Iris tan in upper quarter, brown below. Tongue black.

AMNH R-109721 (holotype, Quebrada Guanguí; male, 447 mm SVL): Reddish brown with gray interspaces; touch of green on lower sides of neck. Underside of head and anterior venter white with some blotches of yellow on throat and supralabials, turning light yellow on posterior belly and under tail. Iris brown, tongue black.

AMNH R-109727 (Quebrada Guanguí; male, 564 mm SVL): Top and sides of head red-brown, body green. Labials and most of under-head bright yellow with only a few small white areas. Color otherwise like [AMNH R-109726, below].

AMNH R-109724 (Quebrada Guanguí; female, 594 mm SVL): Head red-brown; body overall dark green, with some dark reddish suffusions anteriorly. Supra- and infralabials bright golden yellow. Venter whitish anteriorly, turning golden yellow (like labials) under posterior belly and tail. Iris red-brown, palest in upper quarter sector. Tongue black.

AMNH R-109726 (Quebrada Guanguí; male, 628 mm SVL; Fig. 14): Green on snout, turning red-brown atop most of head, with the red color extending caudad on neck in the form of vague dorsal and lateral stripes. Supra- and infralabials bright golden yellow, genials mostly white. Venter grayish white with gray crosslines, turning light yellow under tail. Iris brown. Tongue black.

AMNH R-108469 (Playa de Oro; male, 644 mm SVL): Green above and on outer quarters of ventrals, being brightest on lower sides and ventral tips. Head deep red-brown, this color extending on body as a pair of vague dorsolateral stripes (parts of scale rows 6–8) and as a vague lateral stripe (rows 2–3). These stripes disappear at midbody, and posteriorly the dorsum acquires a slight brownish suffusion in the green. Labials and middle of venter white, turning pale yellow under tail. Iris red-brown, turning tan in upper quarter. Tongue blackish gray.

A color photograph of the head and neck of a snake from northwestern Ecuador (Ortega-Andrade et al., 2010: appendix 3, “*Dendrophidion brunneus*”) may be a photograph of *Dendrophidion prolixum*.

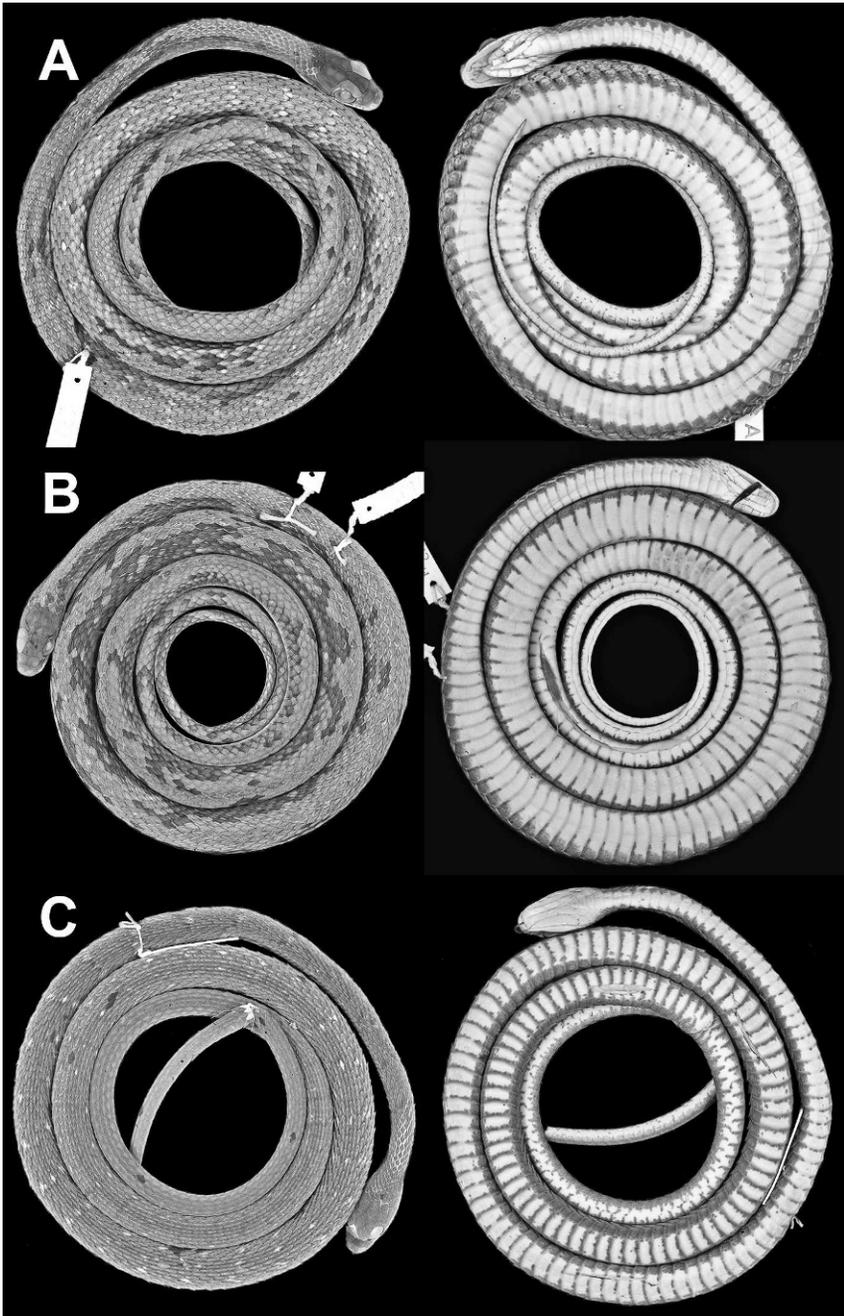


Figure 15. *Dendrophidion prolixum* adult dorsal and ventral patterns. (A) AMNH R-123746 (532 mm SVL; Quebrada Pangala). (B) AMNH R-109727 (564 mm SVL; Quebrada Guanguí). (C) AMNH R-123753 (598 mm SVL; Quebrada Taparal).

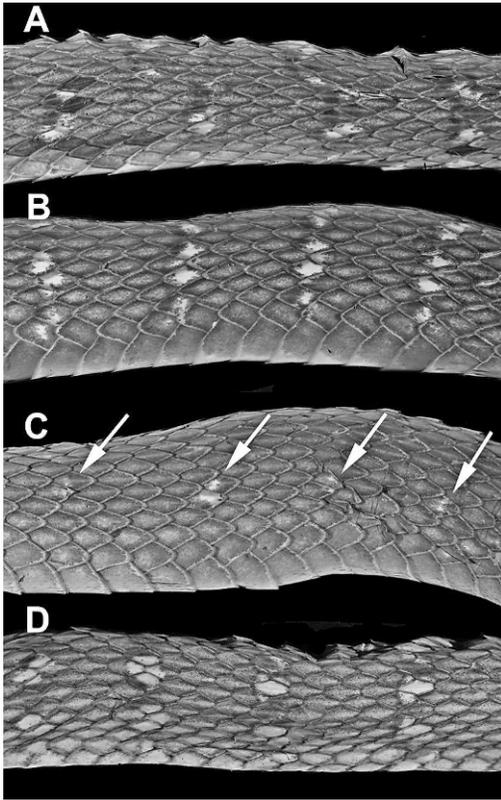


Figure 16. Variation in expression of transverse rows of pale spots/ocelli at midbody in preserved adults of *Dendrophidion prolixum*. (A) FMNH 54960 (587 mm SVL). (B) FMNH 54958 (648 mm SVL). (C) FMNH 54964 (661 mm SVL). (D) USNM 151659 (662 mm SVL). Arrows in panel C indicate traces of ocelli reduced to small pale flecks; compare panel D, which is of similar size.

The photo shows the top of the head brown or reddish brown, extending onto neck with a narrow brownish lateral stripe on rows 2–3, a dorsolateral stripe on rows 6–7 or more; remainder of neck scales bright green; upper labials and visible portions of gular/anterior ventrals bright yellow. The color pattern is similar to several of the above-described specimens (compare especially AMNH R-109726, R-108469). This photograph potentially documents one Ecuadorian locality for *D. prolixum* (see later discussion of problematic localities).

Coloration in Preservative. Ground color of adults brown, grayish brown, or dark gray, usually with some indication of pale (cream to

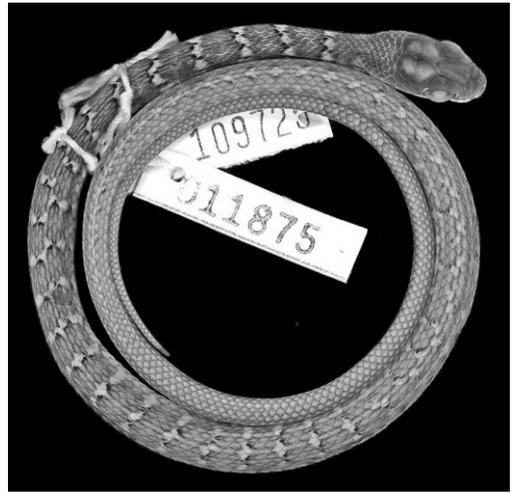


Figure 17. *Dendrophidion prolixum* juvenile. AMNH R-109725 (Chocó department, Colombia; 208 mm SVL).

whitish) crossbands or transverse rows of spots (Figs. 15–16). The variation in dorsal ground colors is perhaps due to preservation differences. Pale crossbands are more prominent in smaller individuals (Fig. 17) than larger ones; crossbands in the largest specimens are sometimes so reduced that only a trace is evident (Fig. 16C); these specimens appear dark blue gray, sometimes blackish (Figs. 15B, C). The venter is immaculate in juveniles, but most adults have indistinct to prominent transverse narrow dark gray or blackish lines across the anterior edges of the ventral scutes (sometimes more continuous or prominent posteriorly than anteriorly) (Fig. 15). The whole range of color patterns in preserved specimens is seen in a series from the type locality (AMNH R-109721-28).

Distribution (Fig. 18). Lowlands and premontane foothills of western Colombia (Chocó, Risaralda, Valle del Cauca, and Nariño departments) and northwestern Ecuador (Esmeraldas province). Latitudinal range from about 6°6'N south nearly to the equator (Fig. 18). Elevational distribution from about 100 m up to 930 m in the Serranía de Baudó (Chocó department, Colombia) and 1,189 m (Ricaurte, Nariño department, Colombia). The distribution in southern Colombia and northwestern

Ecuador presents some interpretive problems taken up in the next section.

Sympatry between *Dendrophidion prolixum* and *D. percarinatum* is documented at three localities in western Colombia: two in the Río San Juan drainage (Playa de Oro and Quebrada Pangala) and another at the Río Raposo just south of Buenaventura (Fig. 9). At these localities the two species maintain their distinguishing characteristics as given in the above diagnoses and in Table 4. Documentation for these localities is provided by the following specimens: Playa de Oro (AMNH R-108468, *percarinatum*; AMNH R-108469, *prolixum*), Quebrada Pangala (AMNH R-123745 and R-123748, *percarinatum*; AMNH R-123746–47, *prolixum*), and the Río Raposo just south of Buenaventura (USNM 151658, *percarinatum*; USNM 151659, *prolixum*). Two examples are presented in Figure 19. At Playa de Oro the documenting specimens are both males with everted hemipenes (Fig. 19A), which are described and illustrated later (see Figs. 39, 42).

Interpretive Problems Associated with the Southern Portion of the Distribution of Dendrophidion prolixum. The southern portion of the distribution of *Dendrophidion prolixum* (localities 1–4 in Fig. 18) and its overlap with that of *D. graciliverpa* described later is problematic in several respects. The documentation for these localities is entirely based on small juveniles that I refer to *D. prolixum* (and one of the records is based on the identification of a photograph in the literature). The only adult from the four localities cannot with any certainty be attributed to any species. Moreover, a few adult specimens from other parts of northwestern Ecuador could be referred to either *D. prolixum* or *D. graciliverpa*. These interpretive problems are discussed in the following paragraphs, beginning with numbered localities in Figure 18 for which concrete evidence for the occurrence of *D. prolixum* exists. Reference to the above discussion on the identification of juveniles (see Diagnosis and Table 4) is pertinent here.

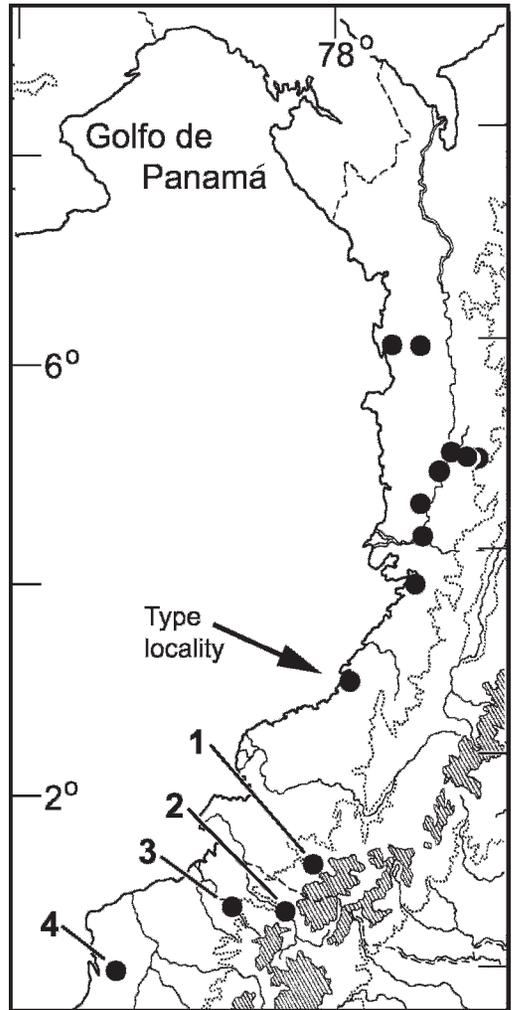


Figure 18. Distribution of *Dendrophidion prolixum*. Arrow indicates the type locality. Numbered localities are the following discussed in the text: 1, Ricaurte (Nariño department, Colombia). 2, Paramba (Imbabura province, Ecuador). 3, Río Cachaví (Esmeraldas province, Ecuador). 4, Bilsa Biological Station (Esmeraldas province, Ecuador).

Localities 1 and 3 (Fig. 18; Ricaurte, Colombia and Río Cachaví, Ecuador). These localities are documented by three juvenile specimens: ANSP 25608 (Ricaurte) and USNM 237064–65 (Río Cachaví; Fig. 12B). Diagnostic characters of the three specimens are the wide separation, distinctness, and somewhat ocellate form of the pale bands on the neck, low number of pale body bands (52, 49, and 57,

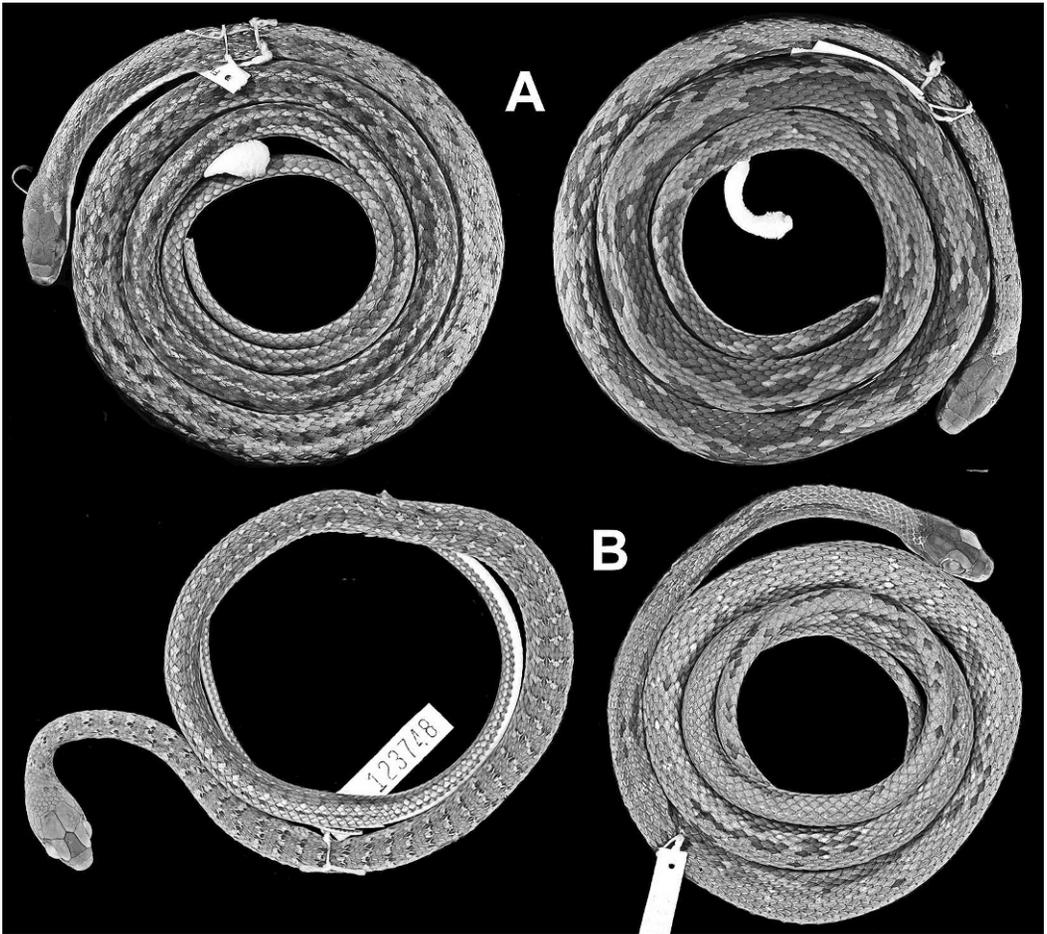


Figure 19. Examples of sympatry between *Dendrophidion percarinatum* and *D. prolixum* in western Colombia. Specimens on the left are *D. percarinatum*; on the right are specimens of *D. prolixum* from the same localities: (A) Playa de Oro (AMNH R-108468 and AMNH R-108469, respectively); (B) Quebrada Pangala (AMNH R-123748 and AMNH R-123746, respectively). See Figure 9 for locations. Everted hemipenes of the specimens in panel A are illustrated in Figures 39A and 42, respectively.

respectively), and brownish head/neck ground color. These characters are considered diagnostic of *D. prolixum*, so the identity of these specimens is reasonably secure.

Locality 2 (Paramba, Ecuador). Two females are available from this locality (FMNH 4055–56). FMNH 4055 is a small juvenile (234 mm SVL) with an incomplete tail, 158 ventrals, a dorsocaudal reduction at subcaudal 11, and supralabial/temporal pattern *G* on both sides. Its scale counts and the *G* supralabial/temporal pattern are consistent with either *D. prolixum*, *D.*

graciliverpa, or *D. brunneum*, the three species known from the region. The supralabial/temporal pattern makes one of the first two more likely than *D. brunneum* simply based on frequency of occurrence (71.6% of *brunneum* scores were *P*, only 4% *G*). The pattern of FMNH 4055 is suggestive of *D. prolixum* (dark brown ground color with somewhat ocellate pale spots on the neck, wide spacing of the neck spots (2.5–4 dorsal rows), and 59 total bands on the body. FMNH 4056 is an adult (517 mm SVL) with 161 ventrals, 144 subcaudals, dorsocaudal reduction at subcaudal 9, a

relative tail length of 42% of total length (72% of SVL), and supralabial/temporal pattern G on both sides. The specimen is overall very dark gray, almost blackish, with no discernible dorsal pattern and an immaculate venter. All of these characters are consistent with *D. prolixum*, *D. graciliverpa*, or *D. brunneum* (with the last less likely based on the supralabial/temporal pattern). Based on FMNH 4055, I include locality 2 as a documented locality for *D. prolixum*; either of the other two species could be represented by FMNH 4056.

Locality 4 (Bilsa Biological Reserve). I have seen two juveniles from this locality, USNM 541964 and KU 291237 (Fig. 13C, right), which I refer to the new species *D. graciliverpa* based on color pattern and scutellation characteristics (Table 4). Both have the G supralabial/temporal pattern, and the retracted hemipenis of KU 291237 extends to the middle of subcaudal 10 (not examined for USNM 541964). A herpetofaunal survey report illustrates in color three species of *Dendrophidion* from Bilsa Biological Reserve (Ortega-Andrade et al., 2010: 148). One photograph is correctly identified as “*D. nuchale*” (auctorum). A second, “*D. percarinatus*,” appears to be the species here described as *D. graciliverpa*. The third species, “*D. brunneus*,” has a color pattern very similar to one described above for *D. prolixum*: a reddish brown head with the brown color extending onto the neck as dorsolateral and lateral stripes on a green ground color; labials, throat, and anterior ventrals yellow. Thus, I tentatively include locality 4 in the distribution of *D. prolixum*, but it needs verification. The photographs of “*D. percarinatus*” and “*D. brunneus*” in Ortega-Andrade et al. (2010) appear to be juveniles. If I have identified the photograph correctly, it would corroborate the only documented sympatry between *D. prolixum* and *D. graciliverpa*.

The fact that all of the southern records of *Dendrophidion prolixum* are based on juveniles and the lack of adults from this region is disconcerting. Moreover, several adults from other localities in western

Ecuador are without discernible pattern elements and are dark gray or brownish, similar to some adult *D. prolixum*. I refer these to *D. graciliverpa* but that is based mainly on the fact that the only specimens from the same or nearby localities are referable to that species based on color pattern characters visible in preserved specimens—certainly a less than desirable situation. Additional data on coloration in life would help resolve these problems because *D. prolixum* and *D. graciliverpa* are otherwise quite similar in characters observable on preserved specimens, including hemipenial morphology discussed later.

Natural History. The type locality of *Dendrophidion prolixum* is also the type locality of *Phyllobates terribilis* and *Colostethus lacrimosus* (Myers et al., 1978, Myers, 1991). Myers et al. (1978: 321–324, figs. 4–5) described and illustrated the area as of 9–21 February 1973, when Myers and Daly collected the topotypic series of *D. prolixum*. The following is quoted from their account (references to figures and notes omitted):

[Quebrada Guanguí is set] in rough hilly country at the western foot of a northerly inclined spur of the Cordillera Occidental. ... Slopes are more often steep than gentle, and perpendicular surfaces are not uncommon. Hillside soils are gravelly in places. Drainage is by clear-water streams flowing over rock, gravel, and sand. The principal stream, a tributary of the Río Saija, is the Río Patia, which originates along the western base of Cerro Tambor. The Quebrada Guanguí is a southward flowing tributary that empties into the Río Patia at an elevation of about 90 m. above sea level. Hilltops in the immediate vicinity are about 200 m. above sea level.

The region has a decidedly tropical wet climate (*Af* in the Köppen system [Köppen, 1931]) [and] receives a yearly rainfall probably in excess of 5 m. ... It seems certain that relative humidity is always very high, especially inside the forest.

There is no undisturbed forest along the larger streams, where small terraces and adjacent hillsides are either under cultivation ... or in dense second growth. Inland, the native lowland rain forest is relatively undisturbed but only of moderate height, probably due to the precipitous slopes. There are occasional tall emergents that break the uniformity of the forest canopy. Most of the larger trees have buttressed roots, and tall palms with stilt roots are common. Tree-trunk moss is sparse. Small bromeliads commonly grow low on the trunks, but the bromeliad population is not dense and they rarely occur on the ground. The understory and ground vegetation of saplings and treelets, small palms, and herbaceous plants and ferns, varies from dense to moderately open. The forest tends to be most open on gravelly slopes, some of which are quite wet due to seepage. Leaf litter is sparse. (Myers et al., 1978: 321–322)

Three specimens are accompanied by notes indicating they were active by day on the forest floor (AMNH R-119801; juvenile), on a stream bank (AMNH R-109727; adult), or on the ground in a brushy part of a ridge top forest (but with large trees, shaded at ground level) (AMNH R-109726; adult).

In addition to sympatry between *Dendrophidion prolixum* and *D. percarinatum* discussed above, *D. prolixum* is broadly sympatric with *D. nuchale* auctorum throughout western Colombia; sympatry is documented at the type locality (AMNH R-109718-20) and Quebrada Docordó (CAS 119591, 119604; AMNH R-123752). The distributions of *D. prolixum* and *D. graciliverpa* seemingly overlap in northwestern Ecuador and documentation of actual sympatry is poor, but may occur at the Bilsa Biological Station (Esmeraldas province); see above discussion.

Dendrophidion graciliverpa **New Species**

Figures 1B, 1E, 2, 3, 12C, 13C, 20–26, 35B, 43B, 44–46

?*Herpetodryas dendrophis* (part). Jan 1863: 81 (Cayenne, Popayán, Guayaquil, Ecu-

dor). Jan and Sordelli, 1869: Livr. 31, pl. 3, fig. 2 (young individual from “Équateur”). The young specimen illustrated by Jan and Sordelli has a pattern and head scalation consistent with *D. graciliverpa*; the adult (their fig. 1), a blotched snake, appears to be *Drymobius rhombifer* (a conclusion reached independently by Savage and McDiarmid; personal communication from Jay M. Savage).

Drymobius dendrophis (part). Boulenger, 1894: 16 (a male from western Ecuador collected by Louis Fraser, BMNH 1860.6.16.59)

?*Dendrophidion dendrophis* (part). Pérez-Santos and Moreno, 1988: 134 (Pacific lowlands of Colombia). Pérez-Santos and Moreno, 1991b: 135 (“southern part of Central America and northern South America”).

Dendrophidion percarinatum (part; western Ecuador included implicitly or explicitly as part of the distribution). Dunn, 1944: 477 (? part). Savage and Villa, 1986: 148, 169. Lieb, 1988: 172; 1996: 636.1. Almendáriz, 1991: 143. Pérez-Santos and Moreno, 1991a: 134. Savage, 2002: 657. Köhler, 2003: 200; 2008: 215. Solórzano, 2004: 234–236. Guyer and Donnelly, 2005. McCranie and Castañeda, 2005: 8. McDiarmid and Savage, 2005: 391, 421. Rojas-Runjaic and Rivero, 2008: 129. Cadle, 2010: 24.

Dendrophidion percarinatus. Ortega-Andrade et al., 2010: 148.

Holotype (Figs. 20, 21, 23, 26A). AMNH R-110584 from 3 km E Pasaje, 30 m elevation, El Oro province, Ecuador [03°20'S, 79°49'W]. Collected 11 February 1974 by Charles W. Myers and John W. Daly (field number C. W. Myers 12250).

The holotype is an adult male, 964 mm total length, 359 mm tail length (605 mm SVL); relative tail length 37% of total length, 59% of SVL; dorsocaudal reduction from 8 to 6 at the level of subcaudals 26–27; 157 ventrals, 2 preventrals, 137 subcaudals. Head scales are typical of the species

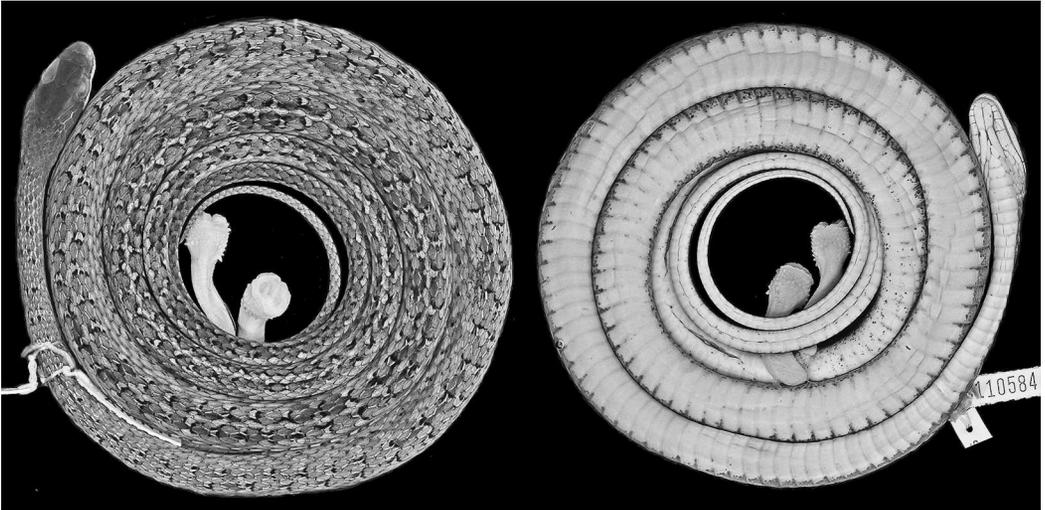


Figure 20. Holotype of *Dendrophidion graciliverpa* (AMNH R-110584). Adult male from near Pasaje, El Oro province, Ecuador.

(Table 1 and description below) except that three postoculars are present on each side; supralabial/temporal pattern G (Fig. 21). Both hemipenes are fully everted. The right hemipenis was fully inflated for illustration and description but was not removed from the specimen; at full inflation it is about 38.6 mm in length (Fig. 44). The preserved type has pale crossbands (87 on the body) and a pale vertebral line (Fig. 26A); the venter has dense gray pigment laterally, indistinct narrow grayish lines on the anterior edges of the ventral scutes (more prominent posteriorly), and irregular small dark spots on the posterior ventrals. The head and neck are dark gray. In life the head was bright green and the dorsum brown to orangish brown but without distinct crossbands (detailed color notes below; see Fig. 23).

Paratopotypes. AMNH R-110585–86, AMNH R-119835. *Other Paratypes:* “Peru,” no specific locality [probably Ecuador; see Cadle, 1989: 422–423], ANSP 5519. **Ecuador:** “western Ecuador,” no other data, BMNH 1860.6.16.59.² [*Chimborazo*]: Chaguarapata, 2,000 ft., AMNH R-23032. *El Oro*: Hualtaco, USNM 237085. Rosa Delia Plantation, USNM 60523. *Esmeraldas*: Bilsa Biological Reserve, KU 291237. [*Guayas*]:

Guayaquil, USNM 12268. Río Pescado [about 488 m], AMNH R-23438. [*Guayas*?]: Headwaters of the Río Congo, USNM 237063. *Imbabura*: Lita, USNM 237084. *Los Ríos*: Finca Playa Grande [53 m], UIMNH 77347. Playas de Montalvo, 15 m, UMMZ 83949. [*Los Ríos*]: Centro Científico Río Palenque, 47 km S. Santo Domingo de los Colorados on rd to Quevedo [220 m], MCR R-156328–29, R-156955. [*Loja*]: Alamor, AMNH 22232. *Pichincha*: Puerto Quito, MCZ R-166539. [*Santo Domingo de los Tsáchilas*] [ex *Pichincha*]: Canoas near Santo Domingo de Los Colorados, USNM 237067. Finca La Esperanza near Santo Domingo de los Colorados, USNM 237072. Joe Ramsey Farm, km 19 on Chone Road, 18 km W of Santo Domingo de los Colorados, USNM 237069. Meme, km 96 on road to Saloya at crossing of Río Toachi,

²I arbitrarily assigned this BMNH catalogue number to one specimen of a series of four (see footnote 3, Appendix 1, for details). By this scheme, BMNH 1860.6.16.59 is a male with an incomplete tail, and the largest specimen of the series (1,054+ mm total length, 676 mm SVL). These details should enable the identification of the correct specimen if the catalogue numbers ultimately become dissociated. The other three specimens of the series are *Dendrophidion brunneum*.



Figure 21. Holotype of *Dendrophidion graciliverpa* (AMNH R-110584), head in lateral view.

USNM 237074–75. Mulaute, on tributary of Río Blanco, USNM 237073. Rancho Santa Teresita, km 25 on route to Chone from Santo Domingo de Los Colorados, USNM 283531–32. Río Baba, 24 km S Santo Domingo de los Colorados, UIMNH 77345, 92243. Río Baba, 19 km S and 5 km E Santo Domingo de los Colorados, UIMNH 92244. Santo Domingo de los Colorados, 550–660 m, KU 179500–01; USNM 237068. 2 km E of Santo Domingo de Los Colorados, USNM 237070. 5 km W of Santo Domingo de Los Colorados, USNM 237071.

Other Referred Specimens (Ecuador). *Cotopaxi*: Las Pampas [1,750 m], MCZ R-163968–69. *Esmeraldas*: Quininde [about 100 m], USNM 237066. 41 km WSW of Quininde, Bilsa Biological Reserve, Black Trail, 300 m, USNM 541964. [*Los Ríos*]: 1 km N Buena Fe, MCZ R-156327. [*Santo Domingo de los Tsáchilas*] [ex *Pichincha*]: below Río Toachi, USNM 237076.

Etymology. The specific name is a feminine noun in apposition derived from the Latin words *gracilis* (slender or gracile) + *verpa* (penis). The name refers to the long, slender hemipenis of this species in comparison specifically to *Dendrophidion percarinatum*, with which it has been confused, but also more generally to hemipenes of most other species of *Dendrophidion*.

Diagnosis. *Dendrophidion graciliverpa* is characterized by (1) dorsocaudal reduction from 8 to 6 occurring anterior to subcaudal 28 (range, 7–27); (2) divided anal plate; (3) subcaudal counts ≥ 120 in males and females; (4) subadults with narrow pale bands (<1 dorsal scale width on the neck)

or transverse rows of ocelli; adults retain bands or become predominantly brown or green (pale bands usually separated by fewer than three dorsal scale rows on the neck; total number of pale bands on the body >55); (5) ventrals immaculate or with narrow transverse dark lines across the anterior border of each ventral plate; (6) in life, head greenish brown to green and body brownish, olive, or grayish; and (7) everted hemipenis of the “gracile” morphology, with an exceptionally long, slender hemipenial body proximal to an expanded distal portion, which bears spines, calyces, and other apical ornamentation (retracted hemipenis nearly always to subcaudal 10 or greater); total number of enlarged spines on hemipenis >80 (81, 84, and 116 in three studied organs).

“Gracile” hemipenial morphology will distinguish *D. graciliverpa* from all other species of *Dendrophidion* except *D. prolixum* described herein and perhaps *D. bivittatum* (see above comments where the gracile morphology is described). *Dendrophidion bivittatum* has a different color pattern (greenish dorsum with blackish longitudinal stripes).

Dendrophidion graciliverpa differs from species of the *D. dendrophis* species group (*D. dendrophis*, *D. atlantica*, *D. nuchale* auctorum, *D. apharocybe*, *D. crybelum*, *D. vinitor*) in having a reduction in the dorsocaudal scales anterior to subcaudal 30 (posterior to subcaudal 30 in the *D. dendrophis* group except occasional females). A divided anal plate will distinguish it from *D. apharocybe*, *D. crybelum*, and *D. vinitor* (anal plate nearly always single in these species). *Dendrophidion dendrophis* and *D. nuchale* auctorum may have either single or divided anal plates but have different color patterns (see Duellman, 1978: 236–237, 2005: pl. 175; Savage, 2002: 654, pls. 413–415), attain greater body sizes, and have different hemipenial morphologies (robust morphology and enormously enlarged spines in *D. dendrophis* and *D. nuchale*). *Dendrophidion graciliverpa* differs from *D. boshelli* in having 17 midbody scale rows (15 in *D. boshelli*).

Dendrophidion graciliverpa has previously been confused with *D. percarinatum*, and these species cannot be distinguished by traditional scutellation features other than a few mean character differences (Table 1). These two species differ in (1) color pattern: greenish head and anterior body, and venter either immaculate or with dark transverse lines (*D. graciliverpa*) vs. head and body primarily browns to grays, and venter immaculate (*D. percarinatum*); (2) hemipenial morphology: gracile (*graciliverpa*) vs. robust (*percarinatum*); retracted hemipenis nearly always to subcaudal 10 or greater (*D. graciliverpa*) vs. <10 subcaudals (*D. percarinatum*); total number of enlarged spines on the hemipenis >80 (*D. graciliverpa*) vs. fewer than 45 (*D. percarinatum*); (3) relationship between the posterior supralabials and temporals as discussed above: G pattern most commonly (*D. graciliverpa*) vs. P pattern most commonly (*D. percarinatum*). *Dendrophidion graciliverpa* has a greater number of pale bands on the body and different overall coloration than *D. prolixum* (see account for the last species and Table 4 for details).

Description (22 males, 21 females). Table 1 summarizes size, body proportions, and meristic data for *Dendrophidion graciliverpa*. Largest specimen (BMNH 1860.6.16.59) a male 676 mm SVL (1,054+ mm total length, tail incomplete; largest male with a complete tail (AMNH R-110584) 605 mm SVL (964 mm total length). Largest female (KU 179500) 663 mm SVL (922+ mm total length, tail incomplete); largest female with complete tail (USNM 237085) 631 mm SVL, 1,027 mm total length. Tail 37–42% of total length (59–72% of SVL) in males; 36–39% of total length (56–64% of SVL) in females. Dorsal scales in 17–17–15 scale rows, the posterior reduction by fusion of rows 2+3 ($N = 13$), 3+4 ($N = 34$), or loss of row 3 ($N = 7$) at the level of ventrals 78–101 (see sexual dimorphism below). Ventrals 153–163 (averaging 157.5) in males, 152–166 (averaging 160.7) in females; ventrals preceded by 2 (rarely 1 or 3) preentrals. Anal plate divided. Subcaudals 132–153

(averaging 142.3) in males, 120–143 (averaging 133.5) in females. Preoculars 1, postoculars 2 (occasionally 3), primary temporals usually 2 (rarely 3), secondary temporals 2 (rarely 1), supralabials usually 9 with 4–6 bordering the eye (rarely 8 and with other combinations bordering the eye), infralabials usually 10 (range 8–12 with high frequencies of 9 and 11). Dorsocaudal reduction from 8 to 6 occurs at subcaudals 12–27 in males, 7–19 in females. Maxillary teeth 33–44 (averaging 39), usually with the 3 or 4 posterior teeth enlarged, ungrooved, and not offset; rarely, 5 teeth were enlarged. Maxillary diastema absent.

Two apical pits present on dorsal scales. Usually the lower 5–7 dorsal rows on the neck lack keels; keels are usually lacking on the lower 2 rows at midbody (or row 1 only but with weak keels on row 2); all except the first dorsal row are keeled on the posterior body (keels sometimes weak or absent on row 2 as well). Nearly 67% of scorings for the supralabial/temporal pattern were G, and only about 3% were P (the remainder ambiguous or irregular). Fusions or divisions of temporal scales were moderately common, with the following frequencies: upper or lower primary or secondary divided vertically (5.8%), upper primary divided horizontally (1%), upper or lower primary + secondary fused (1%). One specimen had 17–19–17 dorsal scale rows. Tails are proportionally shorter in small individuals. Specimens <300 mm SVL have tail lengths 34–38% of total length, 52–62% of SVL ($N = 11$, males and females combined). No strong geographic trends were evident among the characters examined.

Hemipenis unilobed and of the gracile morphotype. Proximal portion of hemipenial body exceptionally long, slender, and ornamented with minute spines. Distal region slightly bulbous, containing a spinose region followed distally by 2 flounces and a largely nude apex. Usually an exceptionally large irregular calyx, and sometimes additional poorly developed calyces, on the asulcate side of the apex. Sulcus spermaticus simple, centrolinal, with the appearance of a terminal division in everted organs

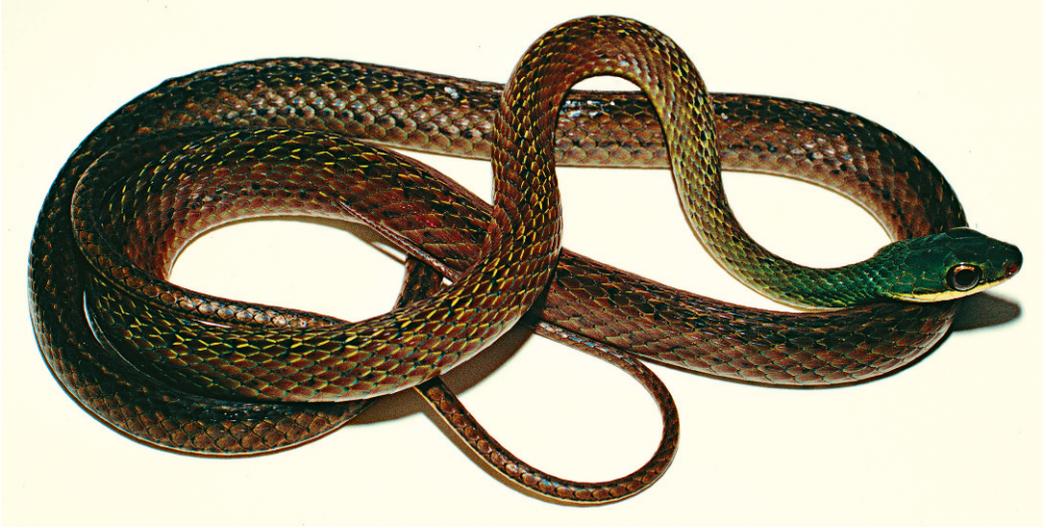


Figure 22. Holotype of *Dendrophidion graciliverpa* in life (AMNH R-110584). Adult male, 605 mm SVL. From a color slide by Charles W. Myers.

(divergent sulcus lips separated by a triangular tissue wedge).

Sexual Dimorphism. Females average a significantly greater mean adult body size and ventral counts and a more posterior point of dorsal scale reduction than males, whereas males have a greater mean relative tail length and subcaudal counts and a more posterior point of dorsocaudal reduction than females (Table 1).

Coloration in Life. Color notes for four specimens from the type locality (field notes of Charles W. Myers for AMNH R-110584-86, R-119835) indicate that the head and neck are greenish brown in juveniles to bright green in adults. Ground color of the rest of the dorsum is brown to orangish brown or olive. Concealed anterolateral edges of the dorsal scales are bright yellow, especially on the anterior body. Supralabials yellowish white to golden yellow. Gular region white. Venter pale green to bright golden yellow.

Myers' coloration notes on individual specimens are here quoted in full:

AMNH R-110584-86 (holotype and two topotypes; Fig. 22): Head and neck greenish brown in smallest specimen [AMNH R-

110586; 409 mm SVL], bright green in [AMNH R-110584-85; 605 and 453 mm SVL, respectively]. Body color brown to orangish brown with concealed (anterolateral) scale edges bright yellow, especially on anterior body. Supralabials yellowish white (two smaller specimens) to light golden yellow (largest; holotype). Under head white; slight yellowish tinge under neck; anterior venter pale green, turning bright golden yellow under posterior body and tail. Upper one-third of iris tan, lower two-thirds dark brown. Tongue black, including tips.

AMNH R-119835 (topotype, 565 mm SVL): Head and front of neck region bright green, turning olive with grayish black markings on body. Genial plates white, but labials and entire venter bright golden yellow. Top quarter-sector of iris tan, lower three-quarters dark brown. Tongue, including tips, black.

Color notes for specimens from Pichincha province are the following:

KU 179501 (231 mm SVL; field notes of John D. Lynch): Brown above with creamy brown bars edged with black (neck and head with green wash). Lips and throat lemon yellow. Venter somewhat dirty



Figure 23. *Dendrophidion graciliverpa* in life (MCZ R-156328, a juvenile, 308 mm SVL, from Pichincha province). From a color slide by Kenneth Miyata (courtesy of MCZ Department of Herpetology).

yellow. Upper edge of iris pale copper. Most of iris reddish brown.

MCZ 156328 (308 mm SVL; notes from a color slide by Kenneth Miyata reproduced here as Fig. 23): Similar to the above-described AMNH specimens in having a greenish brown head and neck, with the rest of the dorsum various shades of brown, including pale brown crossbands or dorsolateral ocelli on a medium brown ground color; on the posterior half to two-thirds of the body, a narrow dusky to dark brown lateral line along the suture line of dorsal rows 2 and 3, ending at the vent; and a dark brown line along the subcaudal/dorsocaudal border the entire length of the tail. The labials, throat, and visible portions of the anterior ventrals are pale yellow.

KU 179500 (663 mm SVL; field notes of John D. Lynch): Brown above with pea green on skin between scales. Lips, throat, and anterior venter lemon yellow. Middle one-third of venter dull gray-green with some yellow. Posterior belly and underside of tail yellow. Iris brown.

Based on these descriptions it appears that the green coloration of the head and neck may be less intense or greenish brown in smaller specimens, becoming bright green in adults, at least in El Oro province. The presence of green on the head was not mentioned for KU 179500, an adult female, but was present in a juvenile from the same locality (KU 179501) and in MCZ 156328 (Fig. 23) from a nearby locality. This may indicate some variation in the presence of anterior green coloration. Oddly, the prominent pale crossbands and vertebral line in the preserved holotype (Fig. 20) are not

evident in the live specimen (Fig. 22). Indistinct indications of crossbands can be discerned by subtle transverse alignment of dark pigment middorsally but this would not be clear except by comparison of the photos of the live and preserved specimens. In fact, Myers' notes mention no pale bands on any of the four specimens from the type locality and yet all of them have distinct pale bands in preserved specimens (Fig. 24D shows another example). This surely gives one pause in the interpretation of the considerable variation in pattern evident among the preserved specimens referred to this species. The possibility that more than one taxon is represented should be reevaluated as material with associated color notes becomes available.

A photograph of a specimen from Esmeraldas province (Ortega-Andrade et al., 2010: 148, "*Dendrophidion percarinatus*") may be *D. graciliverpa*. Its head is greenish gray anteriorly, more greenish posteriorly. Supralabials whitish. Anterior dorsal ground color pale green. The pale bands on the neck are more ocellate (invested with blackish pigment tending to form round yellow spots partly surrounded with black) than is typical in *D. graciliverpa*, but their spacing appears too close for *D. prolixum*. Anterior ventrals pale yellow with whitish patches.

The disparity in appearance between pale-banded preserved specimens of *Dendrophidion graciliverpa* compared with more uniformly colored live specimens (Figs. 20, 22) is considerable, but there is precedent in other snakes for similar alterations in color pattern due to preservation. Smith (1955) reported a situation in which transverse series of *pale* spots appeared in preserved specimens of *Thamnophis rufipunctatus* in the positions occupied by *dark* spots in life. The difference in spotting resulted in dramatically different appearances of the preserved vs. live specimens. Smith attributed the coloration differences, in part, to the differential solubility of various skin pigments in alcohol. Realization of these preservational

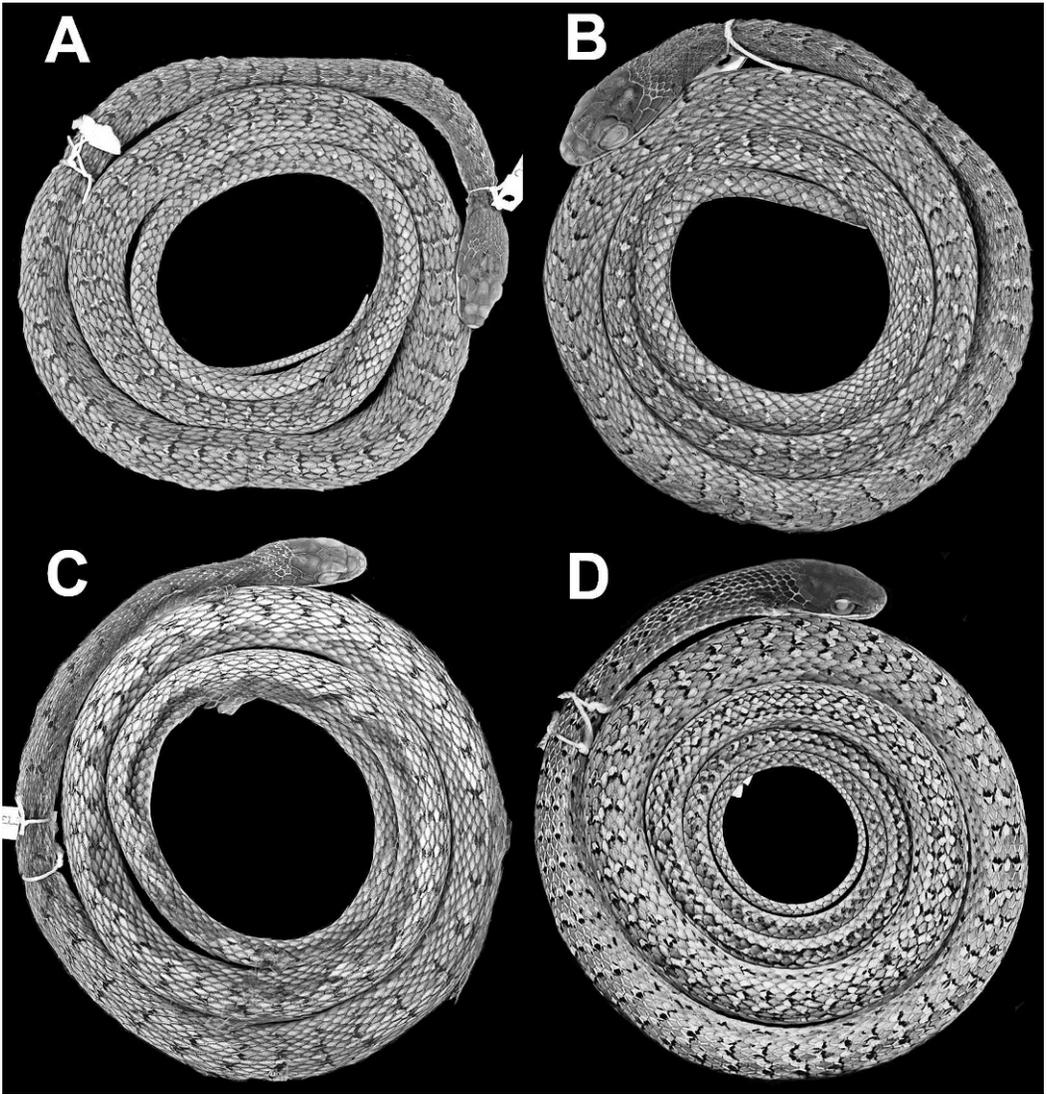


Figure 24. Representative preserved specimens of *Dendrophidion graciliverpa* with prominent bands. (A) AMNH R-23438 (Guayas province). (B) AMNH R-22232 (Loja province). (C) UIMNH 77347 (Los Ríos province). (D) AMNH R-110585 (El Oro province, topotype).

effects on color pattern helped Smith resolve some nomenclatural issues related to original descriptions of color pattern in this group of *Thamnophis*. What remains unclear is why some preserved specimens I refer to *D. graciliverpa* have prominent pale bands in preservative whereas others do not (see the next section). The differences among preserved specimens suggest some-

thing more than simple differential solubility of pigments. This will probably only be resolved when more data on coloration in life and preservative for individual specimens are available.

Coloration in Preservative. Preserved adult specimens exhibit two basic patterns, one with pale crossbands (similar to the juvenile pattern) and the other more

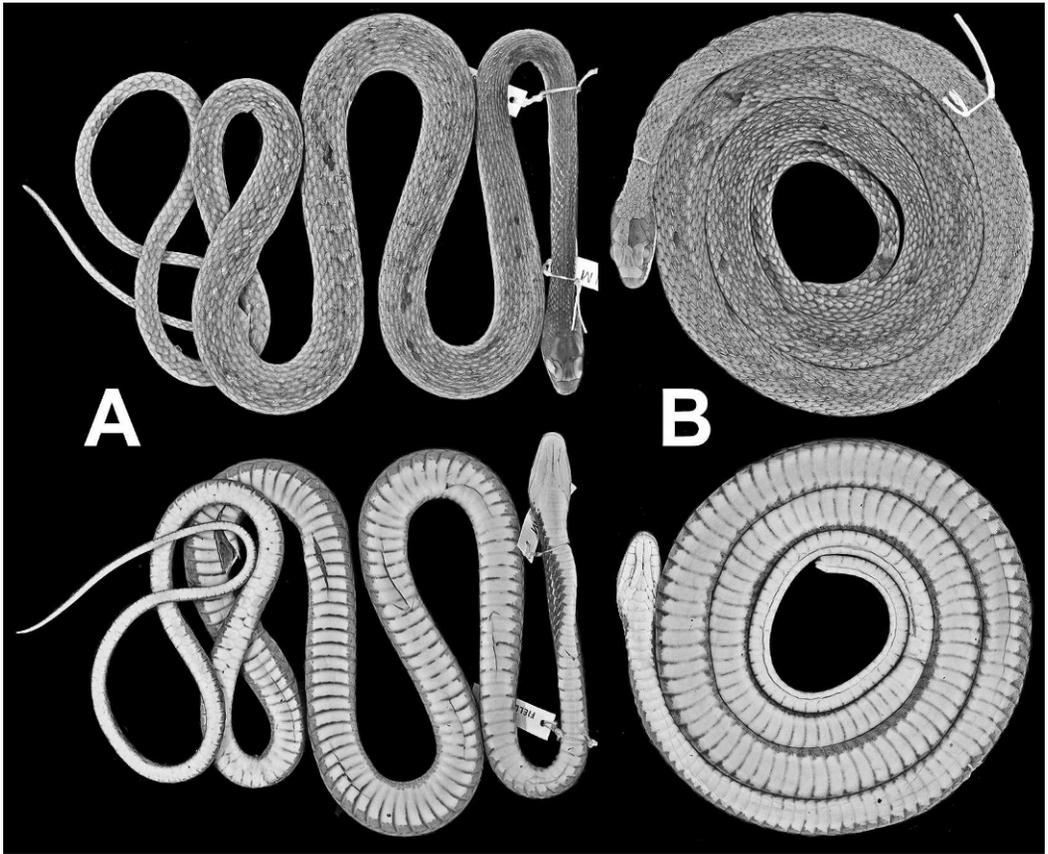


Figure 25. Representative preserved specimens of *Dendrophidion graciliverpa* without strongly banded patterns (dorsal and ventral). (A) USNM 283532. (B) KU 179500. Both specimens from Pichincha province.

unicolor or with indistinct crossbands (Figs. 24–26). The extent of gradation between these pattern forms is unclear, although there is considerable variation in the expression of distinct bands. The two forms are described separately here.

Crossbanded pattern (Figs. 24, 26A–C, F): Dorsal ground color brown, grayish brown, reddish brown, or gray. Individual scales finely peppered with blackish/dark brown, often more concentrated on posterior scale edges (keels often paler than rest of scale). Head and neck often darker (often dark gray) than remainder of dorsum. Many specimens have narrow pale crossbands (one dorsal scale or less) bordered with irregular black or dark brown flecks on anterior and posterior edges; these are

present the entire body length and usually become indistinct on the proximal portion of the tail. Crossbands often less distinct on neck of adults (more evident in juveniles overall), restricted middorsally (lower sides of neck dark gray or gray). Vertebral row often paler or of contrasting color (e.g., gray compared with brown) than adjacent dorsal rows. On the posterior one-third of the body, dorsal rows 3 and 4 or just row 3 often with pale centers or paler overall than adjacent scale rows. Venter immaculate in small juveniles. Larger individuals (some juveniles but mostly adults) have varying expression of narrow dark transverse lines across anterior edges of ventral scales (expression varies from fine peppering of dark pigment across scales to dense

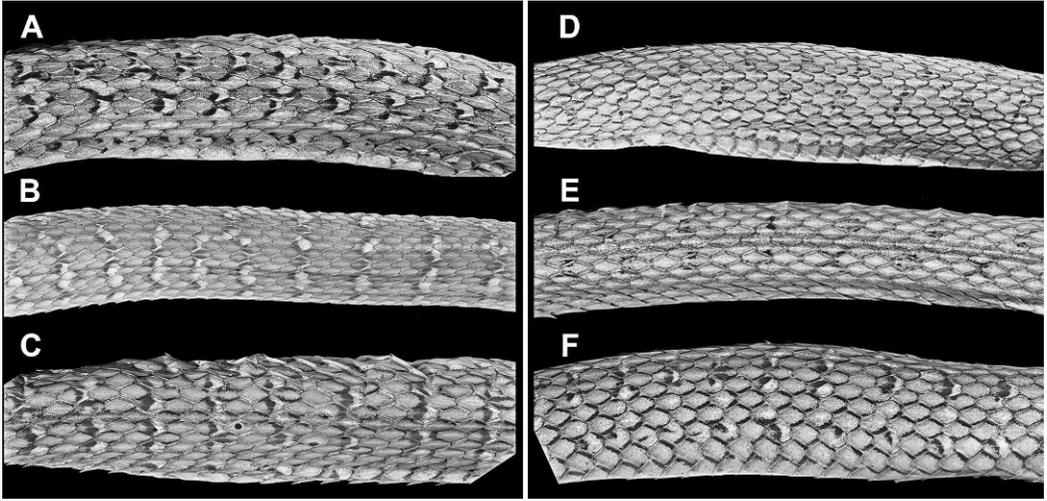


Figure 26. Variation in dorsal patterns of preserved specimens of *Dendrophidion graciliverpa*. Dorsal views at approximately midbody except (F) (lateral view); adults except (B) (juvenile). (A) AMNH R-110584 (holotype, El Oro province). (B) KU 179501 (juvenile, Pichincha province). (C) AMNH R-23438 (Guayas province). (D) USNM 237070 (Pichincha province). (E) USNM 237085 (El Oro province). (F) AMNH R-23438 lateral view (Guayas province).

complete lines). These lines are often more distinct on posterior venter than anteriorly, where they are often incomplete across the middle of the scales. Subcaudal suture lines often bordered similarly. In addition to transverse lines, the venter may have scattered dark spots or speckling, especially posteriorly (but nowhere dense), sometimes giving the venter a “dirty” white appearance. Sometimes a poorly defined ventrolateral dark brown stripe on the anterior part of the tail at the subcaudal/caudodorsal border.

Unicolor form (Figs. 25, 26D–E): Dorsum generally gray to dark gray (sometimes more brownish with stratum corneum intact). Crossbands nowhere distinct (sometimes a middorsal indication, such as USNM 283532, in which they are indicated on posterior half of body as pale punctuations along vertebral line and dark flecking indicating the dark borders for a greater portion of the body (Fig. 25A). Dark transverse ventral lines similar to the crossbanded form, with similar variable expression in larger individuals.

Comments on Referral of Specimens. *Dendrophidion graciliverpa* as here con-

ceived is highly variable in the color patterns of preserved specimens. Specimens with prominent crossbands (Fig. 24) in preserved adults are mainly from the southern portion of the distribution (southern Guayas, El Oro, and Loja provinces). Preserved specimens from the north (Pichincha, Chimborazo, and Imbabura provinces) generally lack prominent crossbands in adults (indistinct indications of bands are usually present) (Fig. 25). But there are exceptions to this generalization. For example, USNM 237085, a specimen from southern Ecuador near the type locality and where nearly all other specimens have distinct pale crossbands, has only transversely oriented middorsal irregular brown spots or stipple indicating bands. Unfortunately, the extent of color variation in life is not known and pale crossbands seemingly can be enhanced upon preservation, since several specimens with color notes or photographs in life do not mention prominent pale crossbands. This is particularly well shown by photographs of the holotype in life and preserved (Figs. 20, 22, 26A). Nonetheless, a color photograph of a juvenile from the northern populations

(Fig. 23) is very similar to the life colors of the holotype. I detected no scutellation differences among northern vs. southern specimens, although scale differences often seem not to be good predictors of species limits within *Dendrophidion*.

Hemipenial morphology discussed later likewise suggests no cryptic species within my concept of *Dendrophidion graciliverpa*. However, I have examined relatively few hemipenes from different parts of the range, and some hemipenial variation seems not to correlate well with geography (see account of hemipenial morphology). The only everted organ available from northern Ecuador (USNM 237069 described and illustrated later) is virtually identical to the everted hemipenis of the holotype from southern Ecuador, despite strong differences in preserved color pattern between the two specimens. Until more thorough data are available on geographic differences in coloration, subdivision of *D. graciliverpa* is unwarranted.

There is the added complication that *Dendrophidion prolixum* also occurs in northwestern Ecuador if several juveniles are correctly referred to that taxon (see account for that species). Resolving the extent of distributional overlap and sympatry of *D. graciliverpa* and *D. prolixum* in this area will require more specimens than have been available. As suggested above, the two species seemingly occur together at the Bilsa Biological Station, but a few adult specimens without distinct patterns (dorsum uniformly dark gray or brown) could be referred to either species. The referral of these Ecuadorian specimens to *D. graciliverpa* is based to a great extent on the fact that other specimens (especially juveniles) with distinctive *graciliverpa*-like patterns have been collected at proximate localities, but no specimens with *prolixum*-like patterns are known from Ecuador except the few juveniles cited earlier. More definitive evidence is certainly desirable.

Distribution (Fig. 27). *Dendrophidion graciliverpa* occurs in the lowlands of western Ecuador from Esmeraldas and

Imbabura provinces in the north to Loja province in the south. The upper elevational record, 1,750 m, is based on a juvenile male and female from Cotopaxi province (MCZ 163968–69, referred specimens). These specimens have typical *graciliverpa* banding patterns, and the retracted hemipenis of the male extends to the proximal suture of subcaudal 15 (potential confusion with *D. brunneum* is possible in this area, but gracile hemipenial morphology is decisive for identification).

Natural History. The holotype and three topotypes were collected while active in the late afternoon in dry leaf litter in a cacao plantation. AMNH R-119835 ate an *Epipedobates anthonyi* from the same site kept in a common collecting bag and later ate another from a nearby population about 1,000 m higher. Myers and Daly saw five specimens of *D. graciliverpa* during four man-hours on two visits to the type locality (one escaped after its tail broke off while pinned down under a boot). KU 179500–01 were collected by day in banana groves; the tail of the first broke during capture (John D. Lynch, field notes at KU). Despite its wide distribution in western Ecuador, virtually nothing has been reported concerning the natural history of this species. The specimens I refer to *D. graciliverpa* seemingly occupy several distinct forest types in western Ecuador (Dodson and Gentry, 1978), but detailed habitat data are needed because of microgeographic variation in the habitat mosaic of this area. The distribution of *D. graciliverpa* narrowly overlaps those of *D. nuchale auctorum* and *D. prolixum* in northwestern Ecuador and more broadly overlaps that of *D. brunneum*.

APPLICATION OF THE NAME *DENDROPHIDION BRUNNEUM* (GÜNTHER) AND NEW DATA FROM WESTERN ECUADOR

When I began work on the *Dendrophidion percarinatum* group in western Colombia and Ecuador it quickly became apparent that at least four species-group

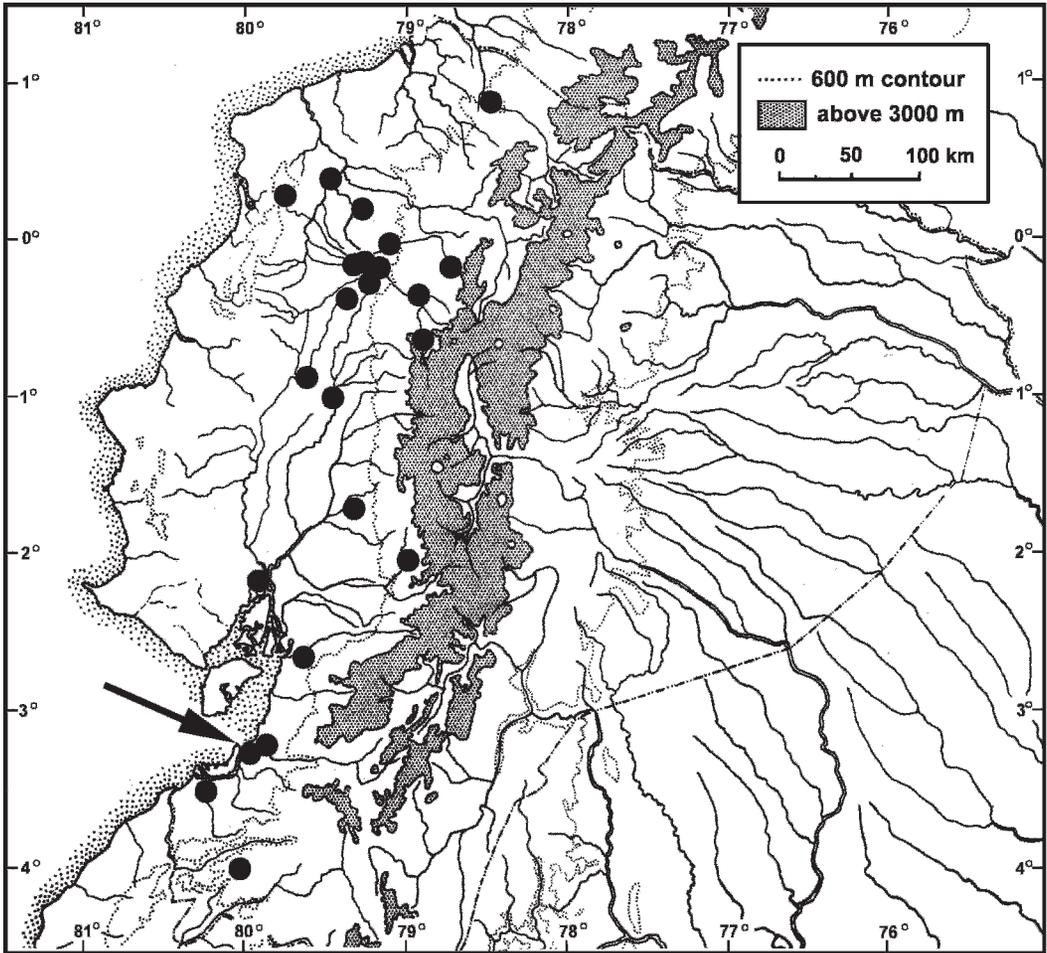


Figure 27. Distribution of *Dendrophidion graciliverpa*. Arrow indicates the type locality.

taxa of the *percarinatum* group are present in this area (*D. nuchale* auctorum of the *dendrophis* group also occurs there, but it is easily distinguished from species of the *percarinatum* group; see Lieb, 1988; Savage, 2002). Two are the previously named taxa *D. percarinatum* (Cope), as redefined herein, and *D. brunneum* (Günther, 1858), an Ecuadorian and Peruvian species for which Lieb (1988) and Cadle (2010) summarized taxonomic and natural history data. *Dendrophidion percarinatum* and *D. brunneum* (*sensu* Lieb, 1988; Cadle, 2010; hereafter *D. brunneum sensu* Lieb/Cadle) have hemipenes of the “robust” morphology

characterized herein. The other two taxa in western Colombia and Ecuador are characterized by long, slender hemipenes (gracile morphotype) and aspects of coloration. These are the two new taxa described herein: *D. prolixum* and *D. graciliverpa*. All four western South American taxa of the *percarinatum* group are exceedingly similar in standard taxonomic characters (e.g., scale counts and body proportions) and are most easily distinguished by color patterns and hemipenial morphology. However, color patterns can be difficult to interpret in some preserved specimens and some specimens of all four species appear uncannily

similar. The situation is not helped by the fact that color patterns within *D. brunneum* and *D. graciliverpa* vary considerably as judged by preserved specimens. At least *D. brunneum* as presently understood is polymorphic in life colors (Cadle, 2010; data herein).

Cadle (2010) had followed Lieb (1988) in recognizing *Dendrophidion brunneum* as a species primarily of the uplands in Ecuador and Peru, with the lowland type locality (Guayaquil, Ecuador) assumed to be a shipping point for the holotype. Cadle (2010: 10–11) concluded that no lowland records of *D. brunneum* from Ecuador could be confirmed, although several from northern Peru seemed valid. That assertion is overturned by some reinterpretations and the new material uncovered in this study. Lieb (1988) had examined only three specimens of *D. brunneum* but summarized data on other specimens from the notes of James A. Peters. Cadle (2010) examined the three specimens seen by Lieb and many others of the same taxon, primarily from Peru. However, neither Cadle (2010) nor Lieb (1988) had examined the holotype of *D. brunneum* (BMNH 1946.1.12.98).

My continued study of specimens from western Ecuador (mainly labeled “*D. percarinatum*” or “*D. dendrophis*” in their respective collections) led to the realization that *D. brunneum sensu Lieb/Cadle* was much more widely distributed in western Ecuador than previously recognized. Moreover, it occurs broadly in the lowlands, where its distribution overlaps that of *D. graciliverpa*. Both species occur at Guayaquil, if the locality as a point of origin is to be believed, and have been taken at some other closely contiguous localities. Thus, two species, one with a robust hemipenis (putative *D. brunneum*) and the other with a gracile hemipenis (*D. graciliverpa*), have been confused. (*D. prolixum* seemingly occurs only in far northwestern Ecuador and seems to pose no problem concerning the name *D. brunneum*.) It was only through examination of hemipenial morphology (mainly of retracted organs, as few

everted hemipenes were available) that the species were sorted out. Preserved females, juveniles, and poorly preserved specimens of these taxa can be difficult to distinguish—scutellation is of little help, and subtle aspects of dorsal pattern sometimes provide the best clues.

The existence of two easily confused taxa in western Ecuador made it imperative to determine to which taxon—the robust or gracile hemipenis form—the name *Dendrophidion brunneum* (Günther) applies. This presented a problem inasmuch as the holotype is a female with an incomplete tail, and few coloration or pattern characters are discernible on the 150+ year old specimen. Nonetheless, a detailed consideration of the holotype suggests that Lieb (1988) and Cadle (2010) applied the name correctly to the taxon having a hemipenis of the robust morphotype. To make this case, I redescribe the holotype of *D. brunneum* and then compare it to specimens of *D. brunneum sensu Lieb/Cadle* and to *D. graciliverpa* in greater detail. I then summarize my current understanding of the apparent considerable color pattern polymorphism in *D. brunneum* and its distribution in Ecuador.

Redescription of the Holotype of Dendrophidion brunneum. The holotype of *Dendrophidion brunneum* (BMNH 1946.1.12.98; Figs. 28–29) is an adult female said to be from Guayaquil. It is in fair condition, somewhat soft, and with most of the stratum corneum missing. There is a long midventral slit in the base of the tail. Total length 867+ mm; tail length 224+ mm (with a healed cap on the stump); SVL 643 mm. Ventrals 154 (2 preventrals); 62+ subcaudals; anal plate divided; dorsocaudal reduction from 8 to 6 at subcaudal 10; Dorsals in 17–17–15 rows, the posterior reduction at ventrals 91/93 by fusion of rows 3 + 4 (left) and 2 + 3 (right); 9/9 supralabials (2–3 touching the loreal; 4–6 touching the eye); 2/2 postoculars; 2 + 2 temporals each side (upper primary temporal divided vertically on both sides); 10/10 infralabials; 34/36 maxillary teeth (left/right) with 4 or 5

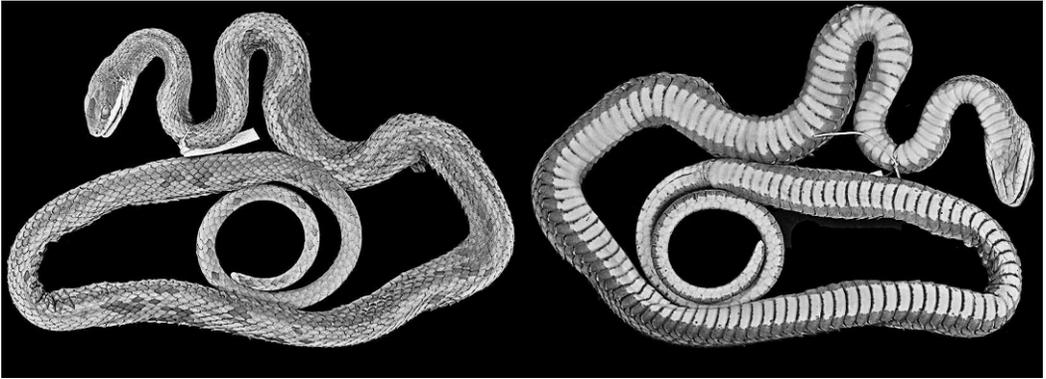


Figure 28. Holotype of *Dendrophidion brunneum* (Günther) (BMNH 1946.1.12.98) in dorsal and ventral views.

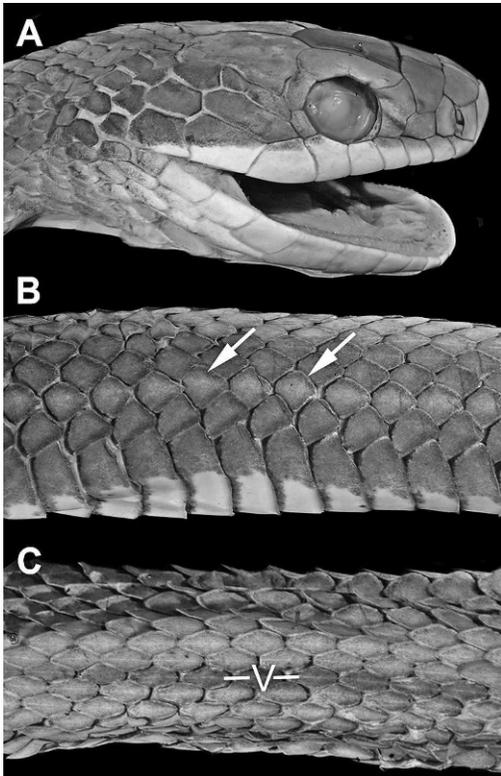


Figure 29. Holotype of *Dendrophidion brunneum* (Günther) (BMNH 1946.1.12.98). (A) Head, right side, showing the *P* pattern of supralabial/temporal relationship (left side virtually identical). (B) Posterior body in lateral view showing subtle paling of centers of dorsal scales in row 2 (arrows). (C) Approximately midbody, middorsal view showing three pale paravertebral rows. V indicates the vertebral row.

posterior teeth enlarged, ungrooved, not offset, and without a diastema. The supra-labial/temporal pattern, as described in the section on systematic characters, is the *P* pattern on both sides (Fig. 29A).

It should be noted that Günther's (1858) measurements of the holotype—"length of tail 12"; total length 39"—are not in modern inches, as the symbol " (double prime) is interpreted nowadays and as I thought before examining the specimen (Cadle, 2010: 4). Either his measurements are in error or, more likely, are in an archaic measure of inch or some other unit. I have not thoroughly investigated this detail, which seems unimportant for present purposes; the length of an inch has varied through its many centuries of use.³ In modern inches the holotype is about 34.25 inches total length, 8.75 inches incomplete tail length. Günther (1858) did not mention the incomplete tail, although Boulenger (1894) and Parker (1938) did. Other specimens of *D. brunneum* have 4 or 5 enlarged posterior maxillary teeth like the

³In a nearly contemporaneous paper Cope (1863) also used the double prime symbol for measurements of several specimens. Myers and Cadle (1994: 25) concluded that Cope's symbol did not denote inches but perhaps represented the metric system (cm), which seemed to be the case for the holotype of *Taeniophallus poecilopogon*. However, metric units make no more sense than inches for the type of *Dendrophidion brunneum* using Günther's numbers.



Figure 30. Maxillary dentition of *Dendrophidion brunneum*, UF 66199.

holotype, which is illustrated by another specimen (Fig. 30). The posterior teeth in *D. brunneum* are relatively more robust and not enlarged to the same extent (compared with more anterior teeth) as in some other *Dendrophidion* species (e.g., *D. apharocybe*) (Cadle, 2012: fig. 8).

The dorsum of the holotype is blue gray without stratum corneum, olive brown in patches where the stratum corneum is intact. On the posterior half of the body, scales in dorsal row 2 have somewhat pale centers (Fig. 29B). In a few places the 3 paravertebral rows appear paler compared with a darker vertebral row and lower flanks (Fig. 29C), but this is very subtle. Venter marked laterally with blue gray patches similar to the dorsum. Beginning about one-quarter of the body length behind the head are dark gray ventral lines extending across the anterior edges of each ventral scute. These are at first restricted laterally and little more than dense stippling, but by one-third the body length they are complete across the venter; they become more solid and dense posteriorly, tending to refragment a short distance anterior to the vent. Lateral subcaudal sutures lined with dark gray, and a few scattered subcaudal spots, but otherwise the subcaudals are immaculate.

Application of the Name *Dendrophidion brunneum*. The conclusion that Lieb (1988) and Cadle (2010) applied the name *brunneum* correctly to the robust-hemipenis taxon of western Ecuador is suggested mainly by two characters of the holotype. First, the holotype has the *P* supralabial/temporal pattern on both sides (Fig. 29A). This is by far the most prevalent pattern in *D. brunneum sensu* Lieb/Cadle; 71.6% of scorings have the *P* pattern compared with

4% with the *G* pattern ($N = 74$). In *D. graciliverpa* the *G* pattern is predominant (66.7% of scorings *G* compared with only 2.9% *P*; Table 1).

Second, the shape of the loreal in the holotype is more consistent with its shape and size in *Dendrophidion brunneum sensu* Lieb/Cadle than with *D. graciliverpa*. Cadle (2010: 4) indicated that the shape of the loreal seemed useful in distinguishing *Dendrophidion brunneum* from "*D. percarinatum*" (= *D. graciliverpa* described here): rectangular and longer than tall in *D. brunneum*, an irregular polygon as tall as or taller than long in *D. graciliverpa*. I quantified this character by measuring the loreal length (along the base at the supralabial border) and height (greatest height, usually at the posterior prefrontal suture) for a sample of *D. brunneum sensu* Lieb/Cadle and *D. graciliverpa* (both loreal scales were measured for each specimen in the sample). The results (Fig. 31) show that the subjective impression of loreal shape difference is substantially true—in *D. brunneum* the loreal scales are longer than tall, in contrast to *D. graciliverpa*, whose loreal height for a given length is nearly always greater than that of *D. brunneum*. Furthermore, loreals in *D. graciliverpa* do not attain the lengths, even in large specimens, as the loreals of *D. brunneum* (the longest measured loreal of *D. graciliverpa*, 2.34 mm, was in a specimen 658 mm SVL, just shy of the maximum recorded length of 676 mm SVL). The holotype of *D. brunneum* (asterisks indicated by arrows in Fig. 31) clearly falls in line with the specimens of *D. brunneum sensu* Lieb/Cadle.

Based on the supralabial/temporal pattern and the shape of the loreal, the female

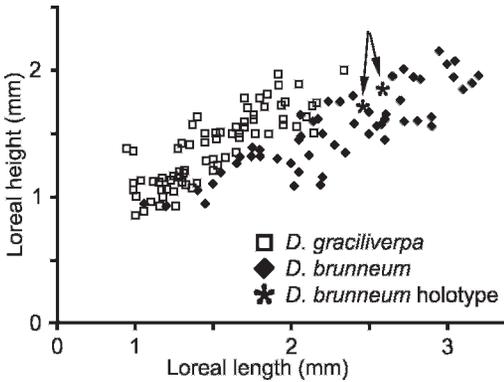


Figure 31. Bivariate plot of loreal length vs. loreal height in a sample of *Dendrophidion brunneum* and *D. graciliverpa*. The points for the holotype of *D. brunneum* (BMNH 1946.1.12.98) are shown by asterisks indicated by the arrows.

holotype of *Dendrophidion brunneum* is reliably associated with the snakes of “robust” hemipenial morphology in western Ecuador. Apart from these two characters, virtually all other characters of the holotype are consistent with either *D. brunneum* or *D. graciliverpa*. A few pattern characters are similar to other specimens referred to *D. brunneum* (e.g., pale centers on dorsal scales of row 2 and indistinct pale paravertebral rows; see Figs. 29B, 34B and Cadle, 2010: 7–8), but these are subtle and with substantial interpretation in the old holotype. Both species can have dark transverse lines on the venter, as in BMNH 1946.1.12.98 (e.g., Figs. 25, 32). Moreover, the specimens newly referred to *D. brunneum* in this paper significantly broaden my concept of color pattern variation in this species. In the following sections I address the color polymorphism and new distributional data.

Color Pattern Polymorphism in Adult Dendrophidion brunneum. Cadle (2010: 6–8) discussed polymorphism in dorsal coloration in life within a Peruvian population of *Dendrophidion brunneum*. This polymorphism involved mainly transitions between a primarily greenish to more brownish, olive, or coppery coloration, and some individual specimens showed anterior to posterior transitions in this shading.

Nonetheless, significant variation in dorsal pattern was suggested by two preserved Ecuadorian specimens with dorsolateral and lateral stripes and a Peruvian specimen that had indistinct pale anterior crossbands (Cadle, 2010: 7–8). Other specimens had dark paravertebral spots usually more prevalent on the posterior body.

The new specimens show that these color variants are more common and widespread among Ecuadorian populations. With a few notable exceptions, specimens from southern Ecuador and (especially) northern Peru appear more uniform in color pattern. The emerging picture is that *D. brunneum* (assuming only one taxon is involved) exhibits substantial color polymorphism, such as that documented for many other snake species; see Wolf and Werner (1994) for a brief review and Brodie (1990, 1992) for an elegant analysis of a case of extensive polymorphism in *Thamnophis*. Major pattern characteristics of adults are taken in turn in the following paragraphs (juvenile patterns are discussed separately below). Except for the first two color morphs, my interpretations are based entirely on preserved specimens (with the same caveats about translating preserved color patterns to life colors or vice versa mentioned in connection with *D. graciliverpa*).

Unicolor pattern (green to brown in life without distinct dark stripes, punctations, or pale crossbands; Fig. 32A): Cadle (2010) described and illustrated this color pattern in detail. The dorsum is green to brown, sometimes with yellow, bronze, or coppery highlights. All specimens from northern Peru I have seen in life, including juveniles 277–300 mm SVL, are unicolor. This is the predominant coloration of preserved specimens from both Peru and southern Ecuador, assuming that “green in life” becomes, in preserved specimens, brown with intact stratum corneum or slate blue or dark gray without stratum corneum (a common relationship in snakes). Black or dark brown flecks or spots are present in the paravertebral region of some live and preserved specimens, usually more prevalent on the

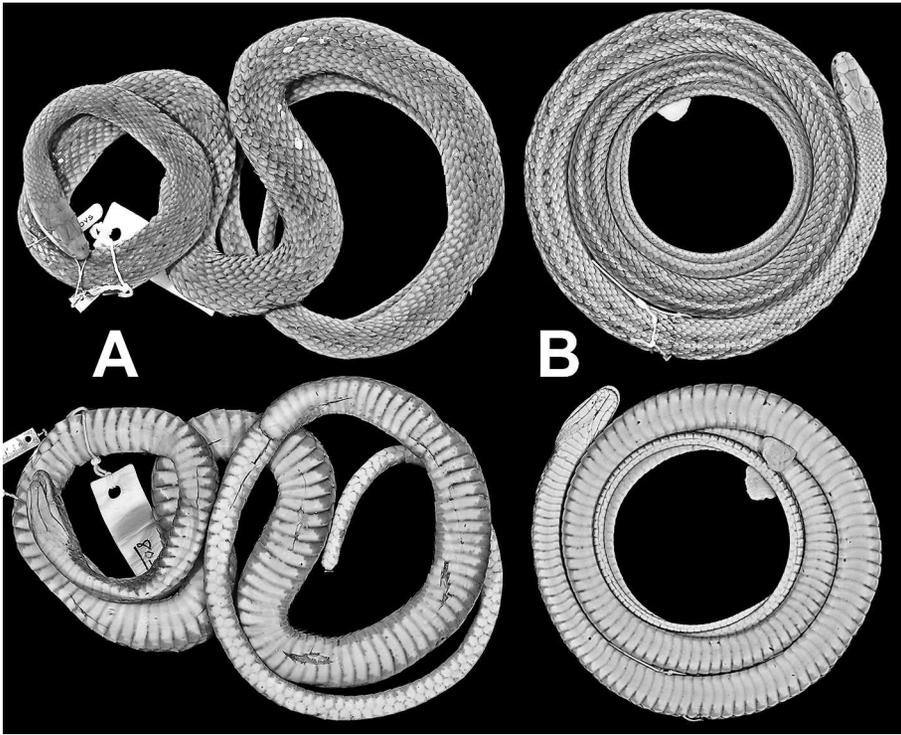


Figure 32. Unicolor and striped color morphs of *Dendrophidion brunneum* from near Loja city in southern Ecuador (their localities are about 30–35 km apart). (A) USNM 237081. (B) KU 142802.

posterior body (Cadle, 2010: 6–7); these are comparable to similar spots in the “punctate” pattern described below but seemingly less prominent. Some specimens from central western Ecuador (e.g., UF 85105 from Los Ríos province) have nearly uniformly brownish dorsums with only hints of paravertebral spots (see punctate pattern below). Whether these are unicolor or appear more punctate in life would be interesting to know.

Striped pattern (dorsal ground color green in life, stripes dark brown to blackish; Figs. 32B, 33A): Snakes with this pattern have broad dark dorsolateral stripes (2–3 paravertebral rows wide) and a narrow dark lateral stripe on dorsal row 2, both usually more distinct on the posterior body. In life the dorsum of KU 142802 (Fig. 32B) was olive green with dark brown stripes; venter creamy white with a tinge of yellow laterally on the neck and faint blue on the anterior

margins of the ventrals; top of head olive brown, iris brown, tongue reddish brown with a black tip (field notes at KU). A color photograph perhaps of this form is in Yáñez-Muñoz et al. (2009: fig. 61, labeled “*Drymoluber* sp.”); this photograph shows a bright green snake (head somewhat darker green) and dark brown stripes that are less distinct on the anterior body. In preserved specimens the stripes are usually rusty reddish brown and can show less contrast with the dorsal ground color than in live specimens; in excessively darkened specimens (ground color dark gray) the rusty stripes appear paler than the background. Some striped specimens have dark paravertebral punctations on some part of the body (e.g., KU 142802, Fig. 34A) and the striped and punctate color morphs may totally grade into one another (see below); colors in life would help interpret these patterns. I suspect that older specimens (e.g., the

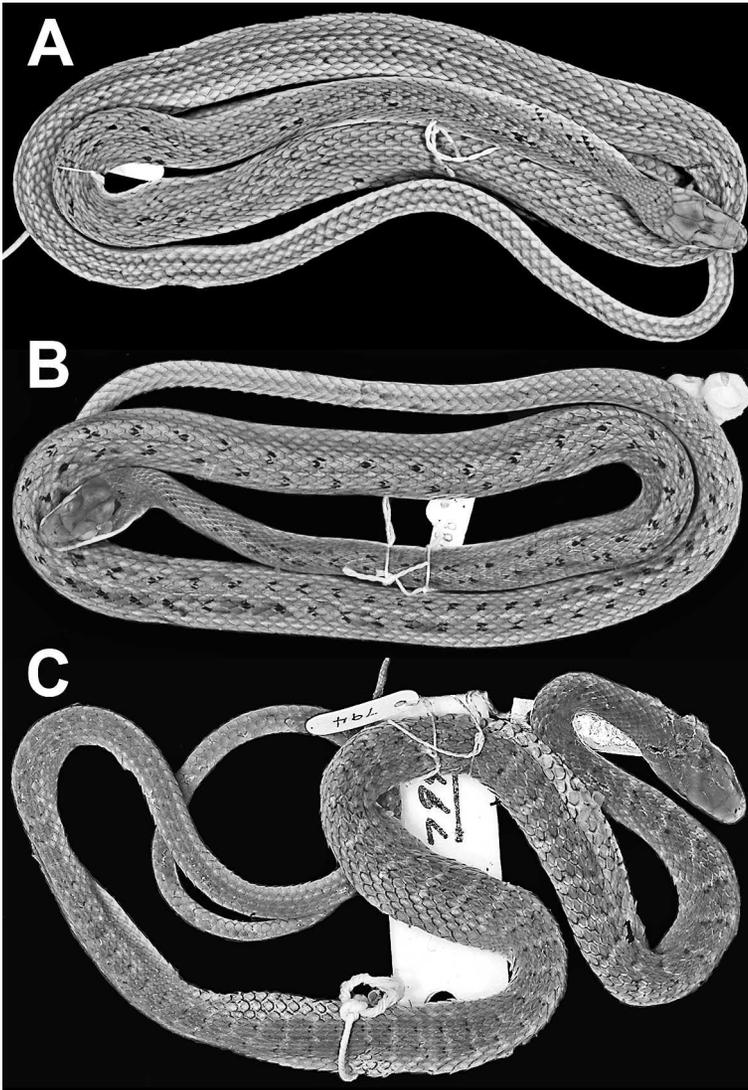


Figure 33. Dorsal pattern polymorphism in *Dendrophidion brunneum*. (A) Striped pattern (UF 87940). (B) Punctate pattern (UF 88467). (C) Banded pattern (USNM 237079).

holotype and MCZ 8393; Figs. 29B, 34B) with pale paravertebral dorsal rows and pale dorsal row 2 on the posterior body may represent the striped morph as it ages in preservative. The striped color morph is known from montane areas in the vicinity of Loja city (KU 142802) and Azuay province (USNM 237042) and from the lowlands farther north in Guayas province (UF 87940

from Daule, Fig. 33A; USNM 237059 from Guayaquil).

Punctate pattern set within dorsolateral rusty or pale brown stripes (colors in life unknown; Figs. 33B, 34B, C): In the lowlands of Guayas province (Río Daule/Babahoyo system) and in northern Ecuador (Imbabura province) are specimens having paravertebral stripes of varying distinctness

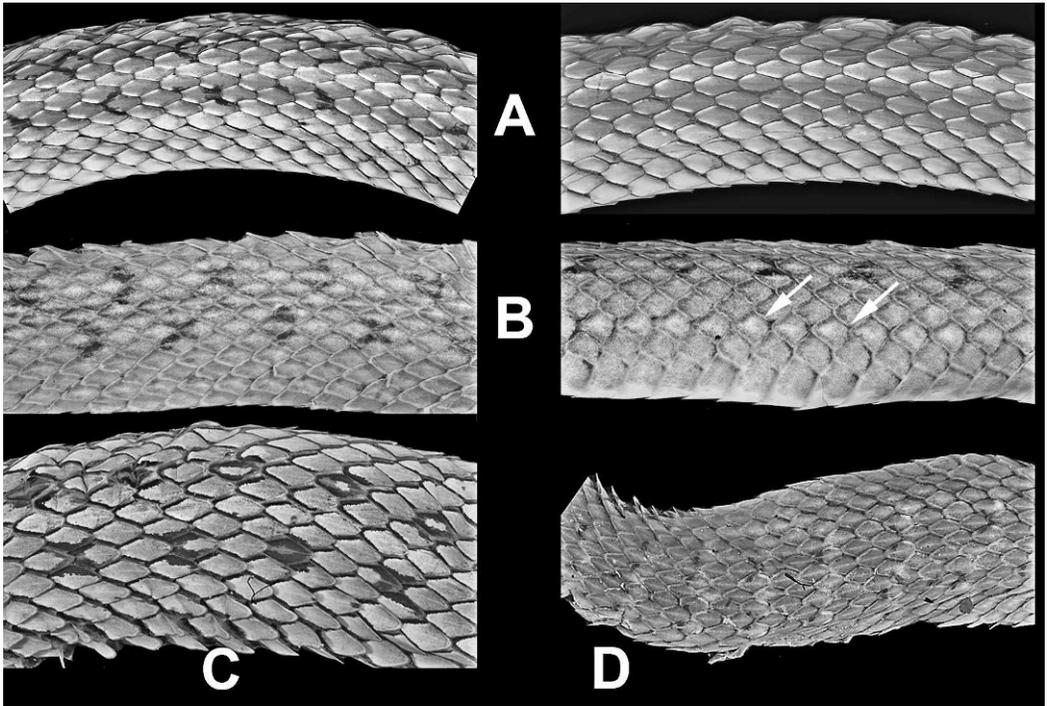


Figure 34. Details of pattern polymorphism in *Dendrophidion brunneum*. (A) Striped pattern. KU 142802 anterior body (left) and midbody (right), dorsal perspectives. (B) Punctate pattern. MCZ R-8393 midbody in dorsal (left) and lateral (right) perspectives. Arrows in lateral perspective indicate the pale centers of dorsal scales in row 2 (compare Fig. 29B). (C) Punctate pattern. BMNH 1860.6.16.58 posterior body in dorsal perspective. (D) Banded pattern. USNM 237079 midbody in dorsal perspective.

(usually rusty red in preserved specimens) but also with extensive dark punctations within the stripes. In different specimens either the punctations or the stripes may have greater prominence, and either element can be quite indistinct. The punctations are often more distinct on one part of the body than another. Examples are UF 66199, 85105, 88466–67 (Fig. 33B); MCZ R-8393 (Fig. 34B); BMNH 1860.6.16.58 (Fig. 34C); USNM 237061 (Fig. 35A), USNM 237083. Note that the punctations are restricted to the paravertebral areas and do not cross the vertebral line to form dark transverse lines. This subtlety is often a clue in distinguishing some preserved specimens of *D. brunneum* from some confusingly similar *D. graciliverpa*. In the last species, dark borders to the pale crossbands superficially have the appearance of the paravertebral spots in *D.*

brunneum, but in *D. graciliverpa* the dark borders tend to cross the vertebral region to form a broken or more continuous middorsal transverse dark line (Fig. 35). However, this difference can be confused when the crossbands are offset, as occurs frequently in *D. graciliverpa*, or when the dark borders to the pale bands are fragmented.

Crossbanded pattern (colors in life unknown; Figs. 33C, 34D): Other than small juveniles discussed below, crossbanded specimens occur together with unicolor specimens in the highlands of Loja province and in northern Peru. Only three examples are known to me: USNM 237078–79 (567 and 328 mm SVL, male and female, respectively; presumed adult and subadult) and FMNH 232578 (adult male, 514 mm SVL; Cadle, 2010: 8). These three are from the region where the unicolor morph

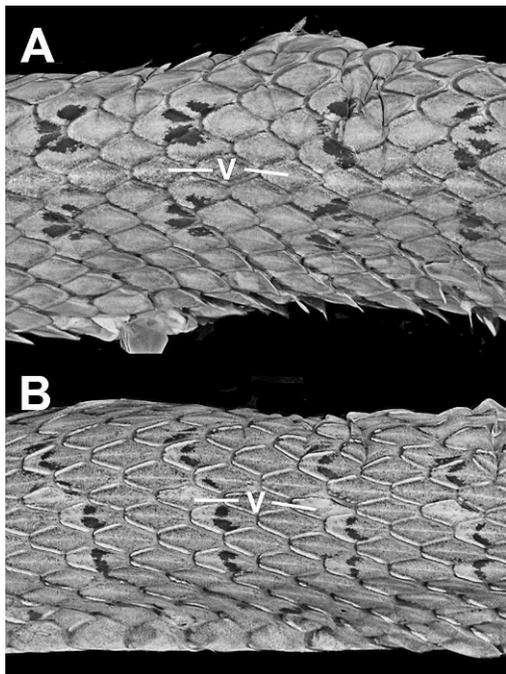


Figure 35. Comparison of midbody pattern details of *Dendrophidion brunneum* and *D. graciliverpa*. (A) *D. brunneum*, punctate pattern (USNM 237061). (B) *D. graciliverpa* (USNM 12268). Both from Guayas province. V indicates the vertebral row. In *D. brunneum* the punctations are paravertebral in position and do not cross the vertebral scale row. In *D. graciliverpa* the dark borders to the pale bands form irregular lines crossing the vertebral scale row. See also Figures 24 and 26.

predominates, and unicolor specimens are known from the same localities as the three crossbanded specimens (unicolor USNM 237077, 237080–81 from the same locality as USNM 237078–79, and many unicolor specimens from the same locality as FMNH 232578; Cadle, 2010). Crossbanded specimens presumably represent individuals that retain the juvenile banded pattern to a greater size than most individuals. The bands on the juvenile (USNM 237079) are much more distinct than those on the adults (USNM 237078, FMNH 232578).

Ventral patterns in *Dendrophidion brunneum* vary from immaculate to having dense dark gray transverse lines across the anterior edges of the ventral scutes (Fig. 32). Additional dark spotting may be present, and in some specimens there is extensive expan-

sion of the lateral dark pigment common to all specimens so that only a central part of each ventral scute is relatively clear (this pattern seems rare). There seems to be little correlation of these patterns with size (most juveniles have immaculate venters but several have well developed transverse lines). Adults with relatively immaculate venters are mainly from the Río Daule/Babahoyo system in central western Ecuador, whereas specimens from southern Ecuador and Peru usually have extensive ventral markings; this parallels the situation in juveniles (see below). But there are exceptions in both regions. For example, the holotype from central western Ecuador has a densely lined venter (Fig. 28).

Juvenile Color Patterns in Dendrophidion brunneum. Cadle (2010) referred only three juveniles (277–300 mm SVL) from northern Peru to *Dendrophidion brunneum*. These specimens had the uniformly green/brown dorsal pattern characteristic of southern populations. The absence of small juveniles attributable to *D. brunneum* was puzzling until it became clearer how to distinguish juveniles of *D. prolixum*, *D. graciliverpa*, and *D. brunneum* brought about by work on the *percarinatum* complex. Consequently, I now believe that Cadle (2010) erred in referring several small specimens from western Ecuador to “*D. percarinatum*” (= *D. graciliverpa*). These specimens are *D. brunneum* having distinctly crossbanded patterns characteristic of juveniles of most species of *Dendrophidion*.

The insight into the identity of these specimens was provided by ANSP 18122 (Chimborazo province; Figs. 36A, B), a male of 194 mm SVL having distinct pale crossbands on the anterior body (present posteriorly as well but there is a general fading on the posterior body); the posterior body has dark paravertebral punctations virtually identical to the above-described adult punctate pattern. Although I had examined the specimen for the 2010 study, I subsequently examined the internal morphology of one of its retracted hemipenes and confirmed that its morphology

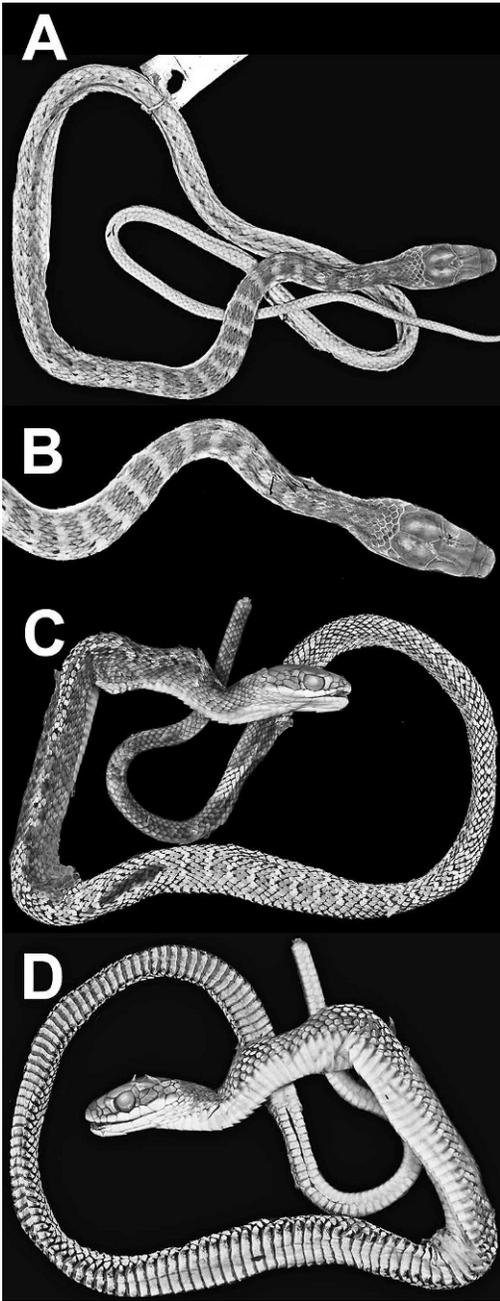


Figure 36. Juveniles of *Dendrophidion brunneum*. (A) and (B) ANSP 18122 dorsal and anterior body detail (Chimborazo province, Ecuador). (C) and (D) BMNH 1930.10.12.22 dorsal and ventral (Loja province, Ecuador).

conforms to other retracted hemipenes of *D. brunneum* (robust morphotype and extensive apical nude area; see Fig. 3). I now believe that two females having similar patterns that I previously identified as “*D. percarinatum*” (= *D. graciliverpa*), ANSP 5709 and FMNH 16942 (317 and 284 mm SVL, respectively; Cadle, 2010: figs. 3A, C), also are juvenile *D. brunneum*.

Two other small banded juveniles that I identify as *D. brunneum* are BMNH 1930.10.12.21–22 (239 and 219 mm SVL, respectively; the first is illustrated in Figs. 36C, D). These were collected along with two adults of the unicolor pattern from the same locality (BMNH 1930.10.12.20, 1931.11.3.10). Bands on the neck extend ventrally to dorsal row 1 or to the edges of the ventrals, but on the posterior body the bands are seemingly restricted to the middorsal area (the posterior dorsum has the appearance of squarish blotches separated by pale interspaces; Fig. 36C). The pale dorsal crossbands of these two specimens are much more distinct in areas without stratum corneum than when the stratum corneum is present (compare anterior and posterior body in Fig. 36C). No typical adult *D. graciliverpa* are known from the highlands of southern Loja province (Fig. 27), whereas *D. brunneum* adults were collected at the same locality as the two juveniles. In BMNH 1930.10.12.21–22 there is the appearance of transverse dark ventral lines (Fig. 36D). In part, this is an illusion because the poor state of preservation of these specimens resulted in clearing along sutures between adjacent ventral plates; the cleared areas appear dark gray, giving the illusion of distinct transverse lines. Nonetheless, on the posterior body these specimens have somewhat heavier dark stippling along the anterior edges of the ventral plates but nowhere distinct crosslines.

The juveniles I refer to *Dendrophidion brunneum* may be distinguishable from juvenile *D. graciliverpa* in having slightly broader pale bands on the neck. In *D. graciliverpa* the neck bands are less than one dorsal scale row wide, whereas in *D.*

brunneum these bands are 1–1.5 rows wide. Larger samples would be needed to confirm whether this apparent difference holds. Similarly, the supralabial/temporal pattern can provide a clue, but this character is ambiguous in some specimens—BMNH 1930.10.12.21–22 and USNM 237079 have the *P* pattern typical of *D. brunneum*, but USNM 237080 has irregular (fragmented) temporals, and ANSP 18122 has the *G* pattern on both sides.

Covariation of Other Characters with Coloration Morphs. Given the apparent color polymorphism in *Dendrophidion brunneum* as I now conceive it, the question of how other characters covary with the patterns should be addressed, something I have not undertaken in any detail. Scutellation and other external characters of the “new” specimens are similar to my previous summary (Cadle, 2010) except that several specimens extend the lower end of the distribution of subcaudal counts: for males to 125 subcaudals from 139 (BMNH 1860.6.16.60 from “western Ecuador”), for females to 118 subcaudals from 135 (BMNH 1860.6.16.58, also “western Ecuador”). Everted hemipenes very similar to those I described earlier for the unicolor morph (Cadle, 2010) are confirmed for the striped morph (KU 142802) and for the punctate morph (UF 88467). The internal morphology of retracted hemipenes (with characteristic extensive apical nude region; Cadle, 2010; Fig. 3) was confirmed in additional specimens, and hemipenial length to verify “robust” morphology was recorded in still others (see Table 5).

Critical to thorough investigation would be more extensive knowledge of color variation in life and whether there is any geographic segregation of the color morphs, as appears to be the case for the unicolor morph. This should also help interpret patterns of specimens already on museum shelves. Of particular interest is the vicinity of Loja city in southern Ecuador where three pattern morphs occur: striped (KU 142802, which also has elements of the punctate morph; see Fig. 34A), unicolor (USNM

237077, 237080–81; BMNH 1930.10.12.20), and banded (USNM 237078–79) (Figs. 32, 33C, 34A, D). The last two color morphs occur together at La Argelia, Loja. A more detailed analysis of color variation in this region should give some insights into whether and how the color morphs intergrade. Since the possibility remains that more than one taxon still resides under the name *brunneum*, the Loja region might provide critical insights into this systematic question. The realization that four species of the *percarinatum* group occur in western Ecuador considerably advances comprehension of the systematics of *Dendrophidion* in this area but is only a first step toward full understanding.

Supplementary Notes on Hemipenial Morphology. Cadle (2010) described everted hemipenes of *Dendrophidion brunneum* in detail. Little can be added to that report, but some minor differences were noted in the hemipenes of specimens examined in this study. Just as in hemipenes of the three species described in detail in the final section of this paper, there is apparent variation in the extent of development of asulcate apical calyces and the distal flounce-like structures in *D. brunneum*. KU 142802 (Loja province) and UF 88467 (Guayas province) have everted hemipenes. In KU 142802 the fully everted, but not maximally inflated, hemipenis shows fairly well developed asulcate apical calyces that extend nearly to the center of the apex; otherwise, the extensive nude apical region is similar to organs previously described (Cadle, 2010). Spine numbers were not reported by Cadle (2010) but KU 142802 has approximately 150–160 spines on each organ. The enlarged sulcate spines are only marginally larger than other spines in the array, which is about five to six rows across on the sulcate and asulcate sides, three to four rows on the lateral sides. The tip of the sulcus spermaticus is slightly expanded in both KU 142802 and UF 88467, but without a distinct tissue ridge separating the divergent lips; the expansion is more difficult to see when the tissue is stretched upon full inflation. Two retracted organs

from Guayaquil (USNM 237059–60) show differential development of the asulcate apical calyces and the third flounce (both more fully developed in USNM 237059). Just as in the hemipenes described later herein, there may be significant variation in the development of ornamentation in *D. brunneum* but more everted hemipenes would be needed to evaluate this possibility. Retracted hemipenes of *D. brunneum* are 8–10 subcaudals long, with most between 8 and 9 subcaudals in length; these data are presented in Table 5 where comparisons with the other species are made.

Distributional Notes and Sympatry of Dendrophidion brunneum and D. graciliverpa. Cadle (2010) found no verifiable lowland (<1,000 m) records of *Dendrophidion brunneum* in Ecuador, although he considered several lowland localities from northern Peru valid. The new specimens (Appendix 1) show that this species as presently conceived is distributed widely in western Ecuador, particularly from the Río Daule/Babahoyo system and southward (Fig. 37). Contrary to what I earlier claimed (Cadle, 2010: 10), I now believe that the type locality “Guayaquil” is a valid locality for *D. brunneum* since other specimens from Guayaquil and nearby can now be documented: two juveniles reidentified above (ANSP 5709, FMNH 16942), MCZ R-8393, and USNM 237059–60. MCZ R-8393 was collected by Edward Whymper and is apparently the specimen reported by Boulenger (1882: 462; 1891: 132), who pointed out the accuracy of Whymper’s localities. Cadle (2010: 11) had pondered the whereabouts of this specimen because it had disappeared from the BMNH by the time Boulenger’s Catalogue appeared (Boulenger, 1894); for years the specimen had been identified in the MCZ as *D. dendrophis*. Likewise, USNM 237059–60 were obtained by Gustavo Orcés-V., and there seems no reason to question the locality. Sympatry of *D. brunneum* and *D. graciliverpa* at Guayaquil is confirmed by three males: USNM 237059–60 (*brunneum*, hemipenes to the middle of subcaudal 8

and the end of subcaudal 9, respectively) and USNM 12268 (*graciliverpa*, hemipenis to the proximal edge of subcaudal 13). In addition to length, the internal hemipenial morphology of these hemipenes was confirmed.

There is a curious gap between the two northern localities of *Dendrophidion brunneum* (Fig. 37) and those farther south. The northern localities are represented by males so that hemipenial morphology could be confirmed (UMMZ 83706, USNM 237083). In between the two northern localities and the next one to the south, many specimens of *D. graciliverpa* have been obtained from the intensely worked region in the vicinity of Santo Domingo de los Colorados and the Río Palenque Science Center (Fig. 27). Yet, *D. brunneum* has not turned up in this area judging by specimens in U.S. collections. The reason for this gap is not obvious, but gaps seem more common in the distributions of some species of *Dendrophidion* than in other codistributed snakes (e.g., *D. clarkii* in Costa Rica and western Ecuador; J. E. Cadle and J. M. Savage, unpublished data).

HEMIPENIAL MORPHOLOGY IN THE *DENDROPHIDION PERCARINATUM* COMPLEX

The distinction between the “robust” and “gracile” hemipenial morphotypes was outlined at the outset. In this section I describe in detail everted and retracted hemipenes of *Dendrophidion percarinatum* (robust morphotype) and *D. prolixum* and *D. graciliverpa* (gracile morphotype). Cadle (2012: 217–220) gave an overview of the structure of *Dendrophidion* hemipenes and terminology as applied here and detailed descriptions of three species in the *D. vinitor* complex. Cadle (2010) described the hemipenis of *D. brunneum*. Hemipenes were studied in both retracted and everted conditions using methods outlined by Myers and Cadle (2003). Descriptions of everted hemipenes are based on organs that were fully everted in the field at the time of preservation. Some mineralized hemipenial structures were visualized by staining with Alizarin Red S (Cadle, 1996: 35).

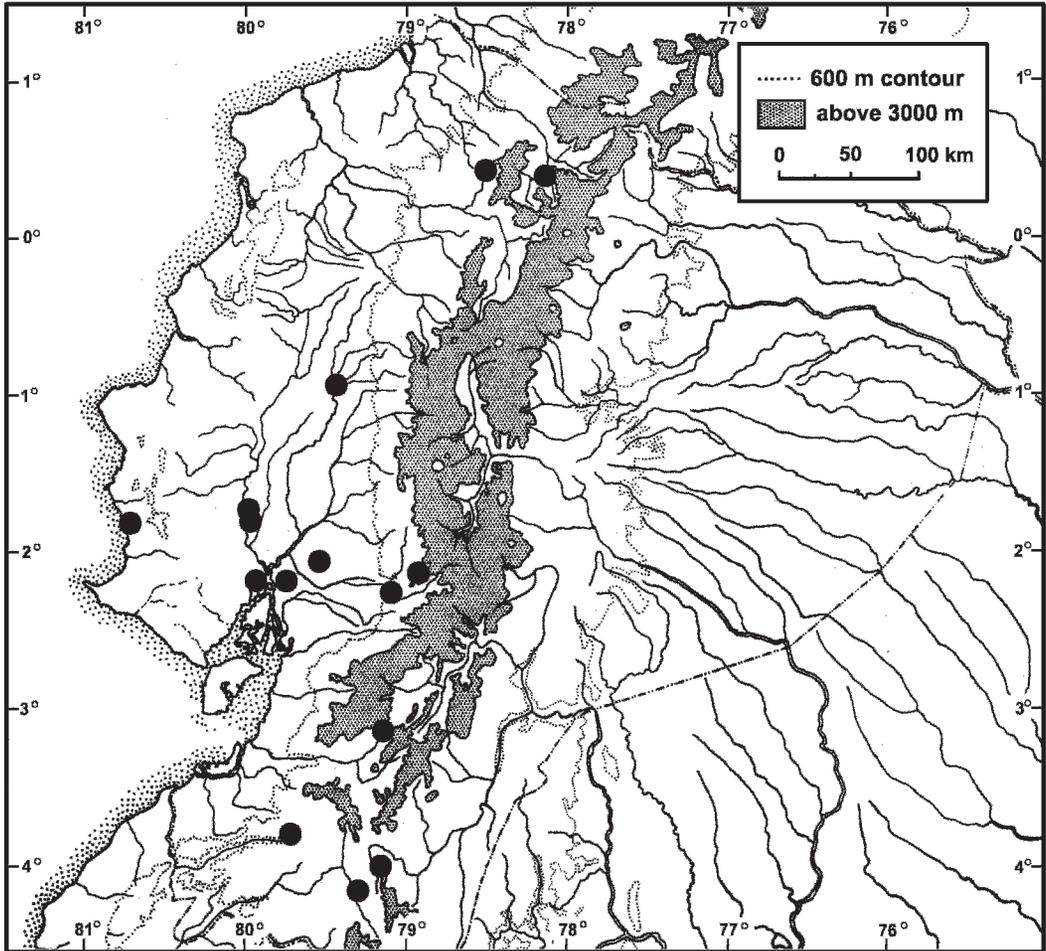


Figure 37. Distribution of *Dendrophidion brunneum* in Ecuador based on the new material examined. Ecuadorian localities referenced by Cadle (2010) are also included.

The length of retracted hemipenes was scored as the number of subcaudals (or fraction) subtended by the organ. Most specimens for which retracted organs were examined were large enough to score fractional subcaudals converted to a number. For example, a hemipenis extending to the suture between subcaudals 7 and 8 was scored “8” (i.e., extending to the proximal suture of subcaudal 8). A hemipenis extending to the middle of subcaudal 8 was scored as “8.5.” Hemipenes extending to points between the proximal suture and midpoint, or between the midpoint

and the distal suture of subcaudal 8, were scored as “8.25” and “8.75,” respectively. This system clearly involves some subjectivity for pliable tissue and is more difficult for small specimens, but the resulting difficulties are ameliorated by the summary score groupings used for comparisons (Table 5). Because I was comparing specimens in some cases of a considerable size range, I was conscious of a possible relationship between snake size and retracted hemipenial length. However, there seemed to be no substantial relationship between size and hemipenial length—

TABLE 5. LENGTH IN SUBCAUDALS OF RETRACTED HEMIPENES OF FOUR SPECIES OF THE *DENDROPHIDION PERCARINATUM* SPECIES GROUP. DATA FOR *D. PERCARINATUM* ARE SORTED BY GEOGRAPHIC ORIGIN. *N* = SAMPLE SIZE.

	<i>N</i>	Length (No. of Subcaudals)						
		5.5–5.75	6.25–7	7.25–8	8.25–9	9.5–10	10.5	
<i>D. percarinatum</i>								
Honduras	2		2					
Nicaragua	3			1	1	1		
Costa Rica	12		1	5	5	1		
Panama	37	2	6	11	14	3	1	
Colombia	4			3	1			
		9–10	10.25–11	11.5–12	12.25–13	13.25–14	14.25–15	15.5
<i>D. prolixum</i>	13	3	4	1	3	1		1
<i>D. graciliverpa</i>	20		4	2	6	4	4	
		8		8.25–9		9.5–9.75		10.25
<i>D. brunneum</i>	17	2		11		3		1

juveniles had hemipenes within the range of adult hemipenial lengths as measured by subcaudals.

Dendrophidion percarinatum

Hemipenes of *Dendrophidion percarinatum* as redefined here are similar in basic structure from Honduras to Colombia (particularly when compared with the two new species described herein). Nonetheless, there is variation in virtually all aspects of hemipenial morphology, including the form of the spines and the degree to which fully formed apical calyces are developed. Despite this variation, hemipenial morphology does not suggest cryptic species within *D. percarinatum*, as was the case in the *D. vinitor* complex (Cadle, 2012). The basic structure of hemipenes of *D. percarinatum* is illustrated in Figure 38 with hemipenes from Honduras and Costa Rica. Some of the variation in structure is shown in Figures 39–40 using specimens from Costa Rica, Panama, and Colombia. However, the structural variation described is not restricted to any particular geographic region, although individual hemipenes may have unique features, as exemplified by the seemingly unique shape of UMMZ 124061 (Barro Colorado Island, Panama; Figs. 39C, 40). Sample sizes for everted hemipenes

examined are: Honduras (9), Nicaragua (1), Costa Rica (14), Panama (6), Colombia (2). The following description is a composite derived from several specimens.

Everted. Typical everted hemipenes from throughout the range of *Dendrophidion percarinatum* have a narrow, relatively short hemipenial body proximally and a bulbous distal section comprising the spinose region and apex (Fig. 38). The hemipenial body proximal to the enlarged spines comprises one half or less of the length of the organ overall; it is ornamented with minute spines in a broad band proximal to the enlarged spines. The base of the hemipenial body is nude. In adults everted hemipenes are about 25 mm or less in length.

Spines are arranged in about three loosely arranged rows all around (perhaps slightly fewer on the lateral sides). The spinose section is followed distally by two closely spaced flouces that completely encircle the organ except where interrupted by the sulcus spermaticus. The proximal flounce is broader than the distal flounce and has a more extensive fleshy base. The distal flounce forms a definitive border around the periphery of the apex. Both flouces have embedded spinules (Cadle, 2010: 19). Between the flouces are a few low, longitudinal connections, which are concen-

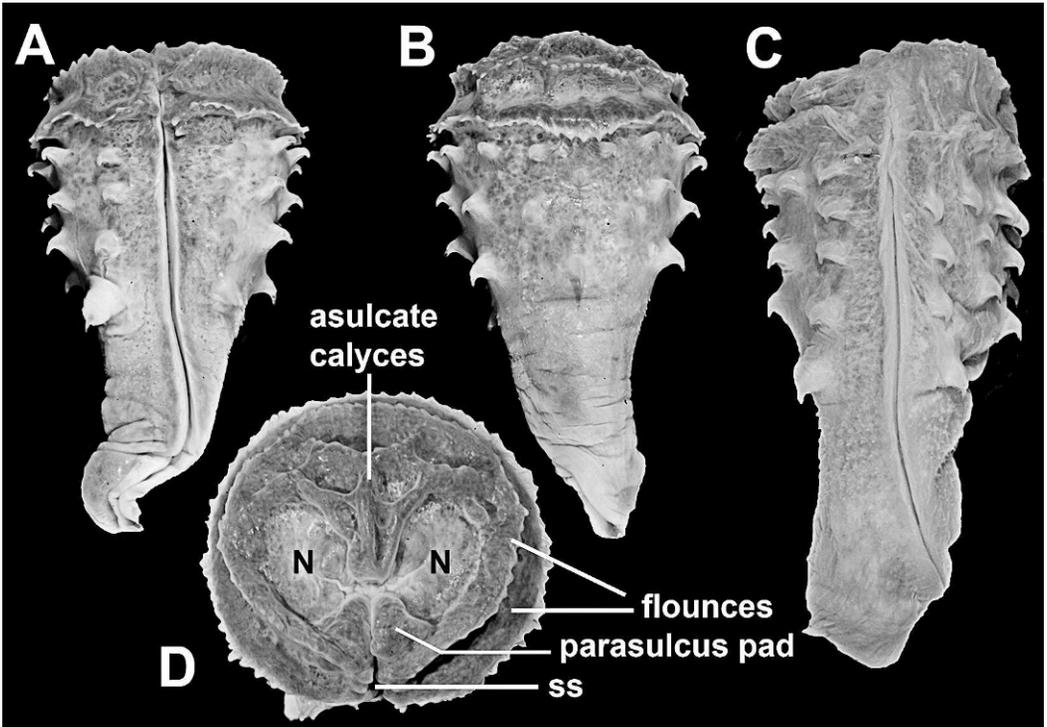


Figure 38. Hemipenial morphology of *Dendrophidion percarinatum*. (A) and (B) Sulcate and asulcate views of USNM 559611 (Honduras). (C) Sulcate view of LSUMZ 34112 (Costa Rica). (D) Apical view of USNM 559611, sulcate edge at bottom. *Abbreviations:* N, nude patches on lateral sides of apex; ss, sulcus spermaticus.

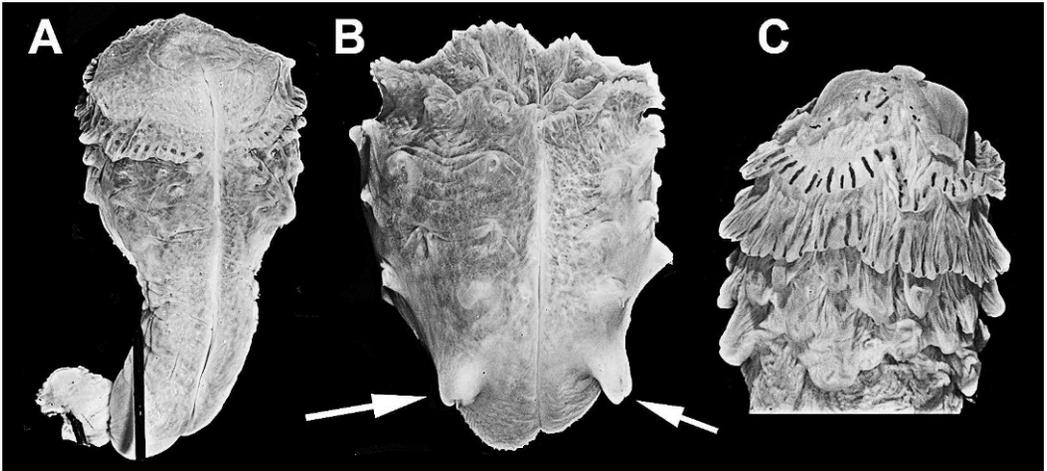


Figure 39. Variations in hemipenial morphology of *Dendrophidion percarinatum*. (A) AMNH R-108468, sulcate view (Colombia). (B) USNM 259130, sulcate view of distal region (spines + incompletely everted apex) (Costa Rica). Arrows indicate sheathed spines. (C) UMMZ 124061, asulcate view, alizarin stained (Panama). All specimens have unusual formations of spines and/or flounces and other ornamentation compared with typical organs (Fig. 38). See text for full explanation.

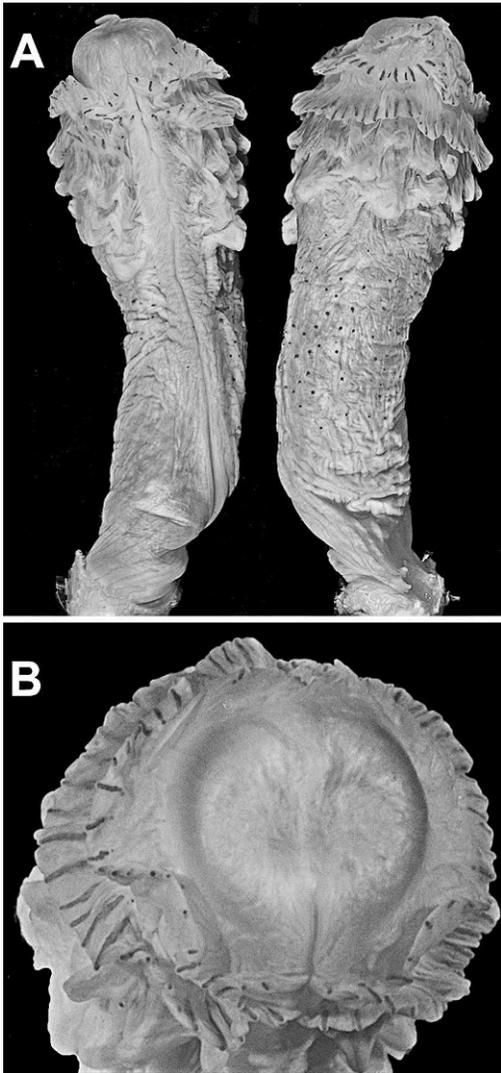


Figure 40. Hemipenis of *Dendrophidion percarinatum* with an unusual morphology. UMMZ 124061 from Barro Colorado Island, Panama. (A) Sulcate and asulcate views. (B) Apical view, sulcate side toward the bottom. Stained with alizarin red so that embedded spinules are visible within the flounces. Apical view shows the near absence of ornamentation. See text for full explanation.

trated on the asulcate side and often incompletely connect the flounces, forming poorly developed calyces. On the asulcate side of the apex directly opposite the tip of the sulcus spermaticus are several calyces distal to the distal flounce. These calyces are within a triangular thickened expanse of

tissue that narrows distally and ends opposite the tip of the sulcus spermaticus just short of the apical center (Fig. 38D). These calyces are subject to some variation in development described below, but when fully developed, there are about three calyces adjacent to the distal flounce, several more distally, and usually a low ridge of tissue bisecting the triangular raised tissue within which the calyces sit. Peripheral to the asulcate triangular calycular tissue and structures associated with the tip of the sulcus spermaticus, the apex is nude.

The sulcus spermaticus is simple and centrolineal and ends with a slightly flared tip just short of the center of the apex; the flared tip can only be seen by parting and lifting the bulbous tissue on each side. After traversing both flounces, the sulcus spermaticus is bordered on each side by a small, roughly triangular pad of raised tissue. Within each pad is usually a single depression just distal to the distal flounce; I interpret these as rudimentary calyces (*parasulcus calyces* or *parasulcus pads* when no distinct calyx is present).

Variation in Hemipenial Morphology of Dendrophidion percarinatum. With a clear exception described below, hemipenes of *Dendrophidion percarinatum* from throughout the range are similar in form. The shape of the distal portion (spines + apical region) is sometimes more elongate, sometimes more rounded, but it is unclear how much of this variation is simply due to differences in the preservation of this pliable tissue. The length of everted hemipenes of *D. percarinatum* is 16.6–25 mm in several adults (compare *D. proluxum* and *D. graciliverpa*). There is minor variation in the number of spines in the array, as shown by these counts from everted hemipenes given as (range, mean, sample size); counts include the two enlarged sulcate spines: Honduras (31–37, 33.4, 9), Nicaragua (34, $N = 1$), Costa Rica (26–40, 32.6, 14), Panama (30–36, 31.8, 6), Colombia (30–36, 33, 2). In most hemipenes the enlarged sulcate spines at the proximal edge of the array (see Cadle,

2012: 218) are distinctly larger than any other spines, but in some organs the size distinction is much more subtle. There is much more variation in the development of apical ornamentation and in the morphology of individual spines.

Figure 38D illustrates a hemipenis with fully developed apical ornamentation (asulcate triangular raised tissue with calyces, and thick pads bordering the apical portion of the sulcus spermaticus). The asulcate calyces have well-developed walls and fully formed cuplike structure. The triangular expanse of tissue within which they sit abuts the distal flounce on the asulcate side of the apex (the distal flounce forms the proximal transverse walls of the most proximal calyces; these proximal calyces are visible at the distal tip of the organ in asulcate view, Fig. 38B). Typically, the asulcate series of calyces comprises three proximal calyces followed by two more distal and then several more irregular calyces toward the center tip of the apex. On the opposite side of the apex each of the sulcate pads has a shallow depression, which I interpret as an incompletely formed calyx; fully formed calyces within these pads were not observed in the hemipenes I examined.

Hemipenes with this fully developed morphology (Fig. 38D) are found throughout the range of *Dendrophidion percarinatum*. However, also throughout the range are hemipenes that vary in the extent to which the ornamentation is developed. In particular, substantial differences in the form of individual spines and the development of the asulcate apical calyces can result in organs that appear strongly differentiated from those with fully developed ornamentation. The strong delimitation of the apical nude areas by raised ridges observed in USNM 559611 (Fig. 38D) is attained in only a few hemipenes I examined, although these nude areas are present in all organs. I resist the temptation to state what is "normal" development in *D. percarinatum* because hemipenes with rudimentary ornamentation were common among the organs I examined.

Some of the variation is illustrated in Figures 39–40 (variation in spine morphology is discussed below). AMNH R-108468 (Fig. 39A) from Colombia shows considerable reduction of the spines to mere nubbins, as well as more subtle reductions in other ornamentation. The asulcate calyces are reduced to irregular calyxlike structures and ridges (only a single definitive asulcate calyx is present, located adjacent to the distal flounce), and its flounces are narrower and less projecting than in many other hemipenes. The only other available everted hemipenis from Colombia (AMNH R-123745) has typical spines and more definitive apical calyces. Other hemipenes show reductions similar to AMNH R-108468; when such reductions occur, the resulting structures are usually more irregular than when the full complement of ornamentation is present. Reduction in one aspect of morphology (e.g., spines) usually entails reductions in others (e.g., calyces). But there are exceptions—USNM 259130 from Costa Rica has reduced spines but unreduced apical calycular structures (Fig. 39B). The most extreme modifications were observed in a single specimen of *Dendrophidion percarinatum* from Panama, whose characteristics are described in detail.

The asulcate apical calycular area can sometimes appear as a third incomplete (noncircumferential) flounce on the asulcate edge of the apex, with a few incomplete longitudinal calycular walls. For example, AMNH R-123745 has a single small median and mostly complete calyx just distal to the circumferential flounces (proximal wall formed by the distal flounce). Distal to the median calyx is an undulating wall (incomplete flounce) centered on the asulcate side and extending about one-third of the distance around the apex. Underneath this incomplete flounce are about four low, incomplete longitudinal walls, partitioning the space between the incomplete flounce and the small median asulcate calyx.

A Most Unusual Hemipenis of Dendrophidion percarinatum. Hemipenes of UMMZ 124061 from Barro Colorado

Island, Panama, were the most peculiar organs I studied, and both are modified similarly (Fig. 40). They have an unusual overall shape (a longer proximal portion of the hemipenial body and less bulbous distal region than is typical), and nearly all aspects of their ornamentation are modified (Figs. 39C, 40). These hemipenes for a time misled me as to what the typical morphology for *Dendrophidion percarinatum* hemipenes actually was—hemipenes of UMMZ 124061 were among the first of this species I studied in detail and I entertained the idea that cryptic species were involved. Examination of other organs convinced me otherwise, and I now view the morphology of UMMZ 124061 as one extreme within a species in which variation in hemipenial morphology seems unusually great. Other specimens from BCI or the adjacent Canal Zone (e.g., CM 6869, KU 80589, UMMZ 297811) have hemipenes more typical in shape and ornamentation than UMMZ 124061, although their ornamentation varies within the limits described above. The unusual shape of UMMZ 124061 does not appear to be due to preservation artifact, which in any case, would not affect the peculiar ornamentation of this specimen.

I stained the right hemipenis of UMMZ 124061 with alizarin red to visualize mineralized structures more fully. Mineralized embedded spinules are seen in Figures 39C and 40 as dark parallel streaks within the flounces and other calycular structures. The mineralized portion of the spines is concealed by thick fleshy tissue. The narrow proximal portion of the hemipenial body has a sparse covering of minute spines on its distal half, extending farther proximally on the asulcate side than on the sulcate side (Fig. 40A; the alizarin-stained minute spines appear as tiny dark spots on the proximal portion). There are about four rows of enlarged spines adjacent to the sulcus spermaticus, narrowing to two rows on the lateral surfaces and continuing in two rows to the asulcate side. The “enlarged” sulcate spines are scarcely larger than other spines in the array. The sulcus spermaticus is

centrolineal and, after transecting the flounces, ends somewhat short of the middle of the apex. Its tip is distinctly flared and even appears somewhat divided by a low wedge of tissue separating the divergent lips.

Individual spines have a very strange structure. Each spine is enveloped by thick fleshy tissue. Close inspection shows that the tissue envelops the tip of the spine like a hood, covering the spine surface toward the apex (i.e., the distal surface) and the hooked tip. The result is that the tips of the spines are not visible except by lifting up the fleshy covering to expose them; without lifting the sheath, this area of the hemipenial body appears to be ornamented with blunt fleshy projections, as they appear in Figures 39C and 40A. The alizarin staining showed that the spines were indeed mineralized underneath and within the fleshy covering (the proximal portion of the spines extended into the fleshy sheath, even though the spine tips were free). This peculiar structure is repeated to a greater or lesser extent in many hemipenes of *Dendrophidion percarinatum* (discussed below).

Distal to the enlarged spines are two circumferential flounces similar to those on other *D. percarinatum* organs. On the asulcate side distal to the flounces is a single very large, asymmetrically positioned calyx (Fig. 39C). Two longitudinal, poorly developed calycular walls further subdivide this calyx. The distal wall of the asulcate calyx forms a sharp angle on the edge of the apex, from which a low fleshy ridge extends nearly to the middle of the apex. On the sulcate side distal to the flounces, the sulcus spermaticus is bordered on each side by a single incomplete calyx with somewhat thickened walls (the wall adjacent to the sulcus is not clearly defined). Alizarin staining showed that poorly formed embedded spinules were present at irregular intervals in both the sulcate and asulcate calyces.

Morphology of Hemipenial Spines in Dendrophidion. The peculiar structure of the spines just described for UMMZ

124061 is not an isolated case either within *D. percarinatum* or more broadly in the genus. In many *Dendrophidion* hemipenes the spines are of the typical morphology seen in most snakes. In *D. percarinatum* and other species of this species group typical spines are relatively short and strongly hooked at the tip (e.g., Fig. 38). However, in other hemipenes the spines are partially or entirely enclosed by a fleshy sheath and, in some cases, seem not only enclosed but also much reduced in size (Fig. 39A). These *sheathed* (or celate, from celatus, Latin for “hidden”) spines have a blunt, fleshy appearance, but a mineralized rod within the fleshy tissue can be demonstrated by probing, by shining a strong light through the translucent tissue, or by staining with alizarin red. In some sheathed spines the mineralized portion does not project at all from the fleshy portion; in others a small point or hook protrudes through the tip (Fig. 39B, left arrow). The enveloping fleshy tissue was, in some cases such as UMMZ 124061 described above, hoodlike, whereas in others it seemed to form a more complete sheath surrounding the entire spine.

Whether spines are typical or sheathed varies intraspecifically in species of both the *Dendrophidion dendrophis* and *D. percarinatum* species groups. *Dendrophidion percarinatum* seems especially prone to this type of variation, but this could be because more everted organs have been available for this species than for any other. I detected no geographic trends in spine morphology (the variation occurs throughout the geographic range of the species). Some hemipenes I examined had a mix of sheathed and typical spines, whereas others were entirely of one type or another. In occasional specimens (e.g., USNM 259130), the spines of one hemipenis were predominantly of typical morphology, whereas the other had celate spines. Considering the entire array of spine morphologies in *Dendrophidion*, there is probably a continual gradation between the celate and typical forms.

What I refer to as celate spines may be equivalent to similar structures reported in

some other snakes, for example “fleshy protuberances ... that form the swollen bases of spines” on some elapid hemipenes (Keogh, 1999: 250). Keogh (1999) scored this as a separate ornamental category than spines for Australian elapids and reported no intraspecific variation (fleshy protuberances were either present or absent for a given species). Smith (1943: 151) stated that the short spines on the hemipenis of *Elaphe taeniura* were “enclosed in a voluminous sheath.” Myers (1974: 33) reported an aberrant specimen of *Rhadinella godmani* in which hemipenial spines were absent, but their locations were indicated by “enlarged tissue bases.” Given the prevalence and seemingly continuous and intraspecific variation between celate and typical spines in *Dendrophidion*, it seems best to recognize celate spines as a common variant of spine morphology, rather than anomalies or an entirely different kind of hemipenial ornamentation for this group of snakes. Possibly, the variable development of spines is related to other reduced aspects of hemipenial morphology in *Dendrophidion*, such as the variable development and manifestation of calyxlike structures. Data for several snake species indicate that spines, calyces, and flounces derive from common anlagen early in development (Clark, 1944).

Retracted Hemipenes of Dendrophidion percarinatum. Retracted hemipenes of *Dendrophidion percarinatum* extend from the middle of subcaudal 5 up to the middle of subcaudal 10 (Table 5), with a clear modal length between 7 and 9 subcaudals. The retractor penis magnus has a very short proximal division. The length of retracted hemipenes observed within *D. percarinatum* (a 5-subcaudal span) is comparable to the span observed in some other snakes (e.g., *Rhadinaea decorata* [9-subcaudal span]; Myers, 1974: 75), *Dipsadoboa unicolor* and *D. weileri* (5-subcaudal spans; Rasmussen, 1993: 146), and *Tantilla* spp. (several species with 5–7-subcaudal spans; Cole and Hardy, 1981: 225–234).

The morphology of the retracted hemipenis corresponds in a straightforward

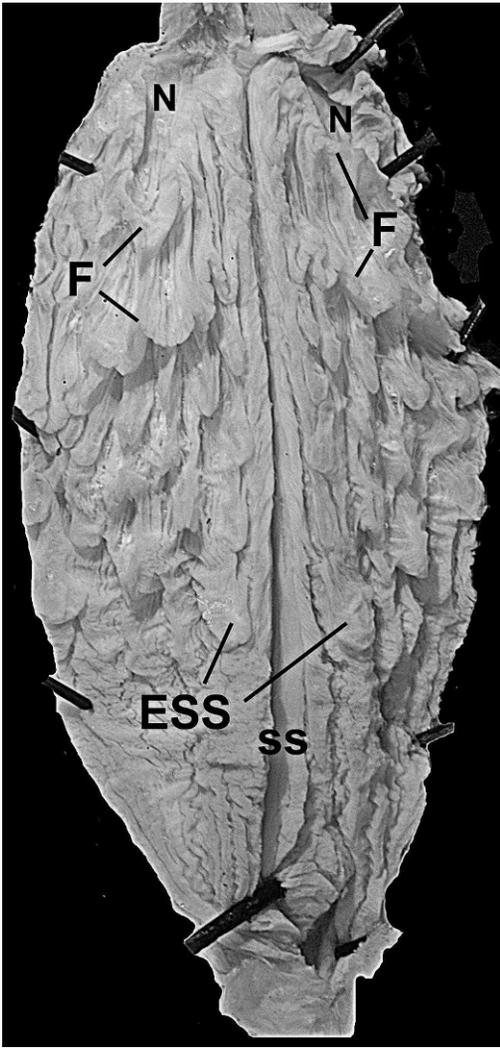


Figure 41. Retracted hemipenis of *Dendrophidion percarinatum* (AMNH R-17374, Costa Rica). Distal toward the top. Abbreviations: ESS, enlarged sulcate spines; F, flocunces; N, nude apical areas; ss, Sulcus spermaticus.

manner to the everted organ (Fig. 41): a proximal portion ornamented with minute spines; a spine array including a pair of spines slightly larger than others adjacent to sulcus spermaticus at the proximal edge of the array (enlarged sulcate spines); two flocunces followed distally by an apex with asulcate calyxlike structures and lateral nude areas; and a simple sulcus spermaticus in its dorsolateral wall, ending with a slightly

flared tip at the distal end of the retracted organ. A few weak longitudinal connections are present between the flocunces.

Dendrophidion prolixum

Everted (AMNH R-108469, Chocó department, Colombia; left hemipenis, Fig. 42). Overall morphology is the "gracile" form. Total length of organ approximately 28–30 mm. Length of the bulbous distal region from the base of the enlarged sulcate spines to the tip of the apex is 8.7 mm (30% of total length). Length from proximal flocunce to apex approximately 4.5 mm. The hemipenis is unilobed, somewhat clavate, and without basal pockets or lobes.

Sulcus spermaticus is centrolineal and ends just short of the center of the apex. The portion of the sulcus distal to the flocunces is bordered by a thick pad of tissue on each side; no depression or other indication of rudimentary calyces were evident within these pads. The tip of the sulcus is slightly expanded and with a narrow wedge of tissue between the divergent lips, resulting in the appearance of a terminal division. The edge of the tissue bordering the short branches of the sulcus is seemingly somewhat thickened (denser white compared with adjacent wedge tissue), perhaps indicative of lip tissue. However, the wedge can be manipulated and flattened unlike in a truly divided sulcus. Each short branch of the "divided" tip is slightly expanded into a teardrop-shape at its tip.

Hemipenial body proximal to the spine array is ornamented with minute spines all around except for a nude patch comprising about the basal one-third of the organ on the left side; otherwise, the minute spines go all the way to the base of the organ and are rather densely arrayed. These minute spines are seemingly somewhat more densely arrayed toward the spine array than more basally.

The enlarged sulcate spines at the proximal edge of the spine array are about two or three times the size of others in the battery (enlarged spine on the right side

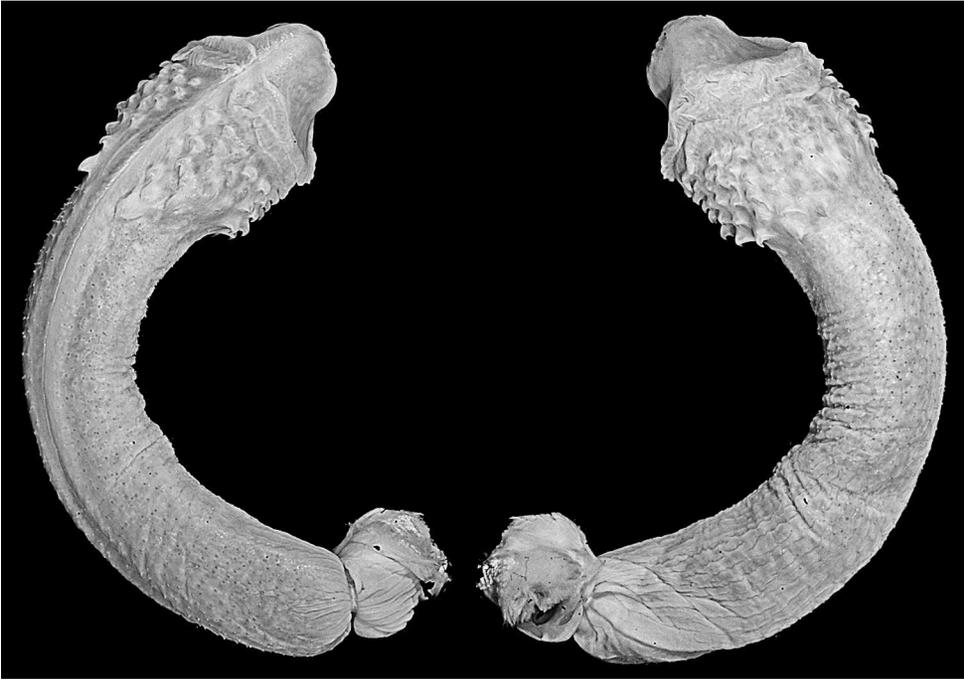


Figure 42. Everted hemipenis of *Dendrophiidion prolixum* (AMNH R-108469) in sulcate and asulcate views.

larger than the one on the left side of the sulcus). Total number of spines in the battery approximately $87+2$ enlarged sulcate spines. Spines are in four to five loosely arranged rows on the sulcate and asulcate sides, three rows on the lateral sides.

Distal to the spines are a pair of circumferential flounces. The proximal flounce is broader than the distal flounce and has an outer more membranous portion and a somewhat fleshy base. The distal flounce has only a very narrow outer membranous portion; most of this flounce is fleshy. Embedded spinules are in the membranous portions of both flounces. The borders of the flounces are smooth (non-crenulate) but somewhat undulating.

On the asulcate side of the apex is a triangular pad of tissue extending toward the center of the apex from the distal flounce (point toward the apex). Within this pad is an irregular, poorly differentiated depression (rudimentary calyx) with fleshy edges. Except for this asulcate pad and

those bordering the distal portion of the sulcus spermaticus, the apex is nude. A pair of shallow dimples, probably the points of internal attachment of the retractor penis magnus, is in the center of the apex.

Retracted (FMNH 54960, Risaralda department, Colombia; Figs. 43A, C). The left hemipenis had been previously slit somewhat irregularly on its ventral/medial surface. Left and right hemipenes extend to middle of subcaudal 11. Retractor penis magnus appears proximally undivided, but there may be some separation of the muscle fibers. Sulcus spermaticus simple, but its tip is flared, and it ends at the tip of the organ. The entire portion of the sulcus distal to the flounces is bordered by a thick pad of tissue on each side; each of these contains a single, very shallow calyx.

The long proximal portion of the hemipenial body has long longitudinal folds and minute spines. On the sulcate side these spines extend nearly to the base of the organ, but toward the asulcate side a long

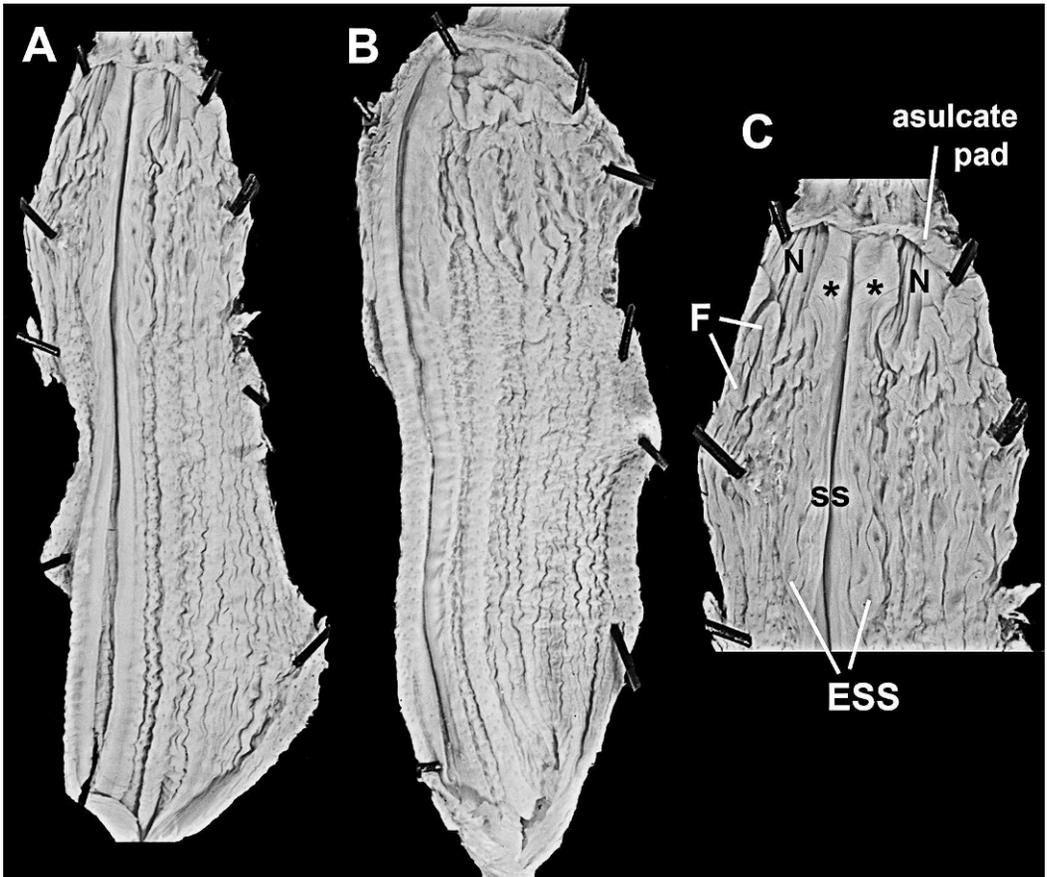


Figure 43. Retracted hemipenes of *Dendrophidion prolixum* and *D. graciliverpa*. Distal toward the top. (A) *D. prolixum* (FMNH 54960; slit medially). (B) *D. graciliverpa* (UIMNH 77347; slit midventrally). (C) Apical region of FMNH 54960 with landmarks indicated. *Abbreviations and labels:* ESS, enlarged sulcate spines; F, flounces; N, apical nude areas; ss, sulcus spermaticus. Asterisks (*), thick pads of apical tissue bordering the distal part of the sulcus. *Asulcate pad*, thickened asulcate apical tissue bearing rudimentary calyces.

section of the organ is nude, and the minute spines are restricted to the distal third to half of the basal section. The array of enlarged spines is broader on the sulcate and asulcate sides (about four to five rows across), and narrower on the intervening sides (lateral sides of the everted organ; about three rows across). A pair of enlarged sulcate spines at the proximal edge of the array is much larger than other spines. The spines are arrayed along the longitudinal folds occupying this area of the organ.

Distal to the spine array are two flounces, which are connected at intervals with poorly developed longitudinal ridges. Each flounce

comprises a basal fleshy portion and an outer membranous portion with embedded spinules. The embedded spinules are short straight splints about the same width throughout. Distal to the flounces is a very short apex, nude except for a thick pad of tissue extending from the distal flounce to the tip of the organ and the pair of pads bordering the sulcus spermaticus. The asulcate apical pad seems to have two or more poorly developed calyces (these are difficult to probe apart).

Variation in Hemipenial Morphology. Everted hemipenes of only four specimens of *Dendrophidion prolixum* were available

(AMNH R-108469, R-123750-51, R-109726). There is little variation in morphology among these except for the asulcate apical calyx and associated structures, the calyx being more definitive in some organs than in others (similar to the variation summarized above for *D. percarinatum* and for *D. graciliverpa* described below). The "enlarged" sulcate spines are sometimes scarcely larger than other spines in array. The approximate number of spines in these organs is as follows: AMNH R-123750, 89+2 (left organ); AMNH R-109726: 65+2 (right), 70 + 2 (left); AMNH R-123751: 87+2 (right and left). The right hemipenis AMNH R-109726 had a total length of 42 mm, and the length from the enlarged sulcate spines to the tip of the apex was 7.9 mm (19% of the total length). Retracted hemipenes vary in length from nine subcaudals (one organ only) to 15.5 subcaudals (Table 5).

Dendrophidion graciliverpa

Everted (AMNH R-110584; holotype, El Oro province, Ecuador; right hemipenis) (Figs. 44–45). Total length about 39 mm. Length of apex from the proximal enlarged sulcate spine to tip of apex, 9.6 mm (distal section about 25% of the length of the organ). Maximum width of expanded apical region, 8.4 mm. Hemipenial body proximal to spines compressed laterally (i.e., broader when viewed from lateral side than when viewed from sulcate or asulcate side). Overall form of "gracile" morphology. The hemipenis is unilobed, with a gradually expanded distal section and without basal pockets or lobes. The long section of the hemipenial body proximal to the enlarged spines is ornamented with minute spines except for a nude basal patch on the right lateral and asulcate sides.

Sulcus spermaticus centrolinal, extending to the center of the apex, terminally divided with equal branches about 1.1 mm long (Fig. 45). The divergent branches are separated by a thick triangular wedge of tissue that may have distal "lip tissue"

(hence, truly divided although this would have to be verified histologically).

The enlarged spine array contains about 116+2 proximal sulcate spines about three times larger than any other spines in array. Spines in about five to six loosely arranged rows on the sulcate and asulcate sides, about three rows on each lateral side. Spines in the array somewhat larger proximally than distally. Spines followed distally by two circumferential flounces bearing embedded spinules, complete except where transected by the sulcus spermaticus; proximal flounce broader than distal one. Flounces have a thick fleshy inner portion and outer membranous portion; the spinules span the width of the membranous portion but barely enter the fleshy portions.

Entire sulcus spermaticus distal to the flounces is bordered by thick triangular pads of tissue (* in Fig. 45). These are broader adjacent to the distal flounce and each has a calyxlike depression. On the asulcate side of the apex, the distal flounce splits to form a large irregular calyx at the sulcate edge of the apical region, the *asulcate calyx* (Fig. 44B); from the distal wall of this calyx an irregular raised triangular area of tissue extends nearly to the center of the apex just opposite the tip of the sulcus spermaticus. On the apical tip lateral to the sulcus and the asulcate triangular tissue, the apex is nude, very smooth, and strongly demarcated peripherally by the distal flounce (Fig. 45).

Variation in Morphology of Everted Hemipenes. Two other everted hemipenes of *Dendrophidion graciliverpa* were studied in detail: AMNH R-119835 (topotype) and USNM 237069 (Pichincha province, Ecuador) (Fig. 46). These hemipenes are similar in basic structure to that of the holotype, but there is some variation in the shape of the apex and calyces. Some features are essentially similar to the holotype: the arrangement and relative sizes of spines, the sulcate pads distal to the flounces, the terminal division of the sulcus, the presence (but not shape) of an irregular asulcate calyx, and apical ornamentation. Basic data on the two organs are:

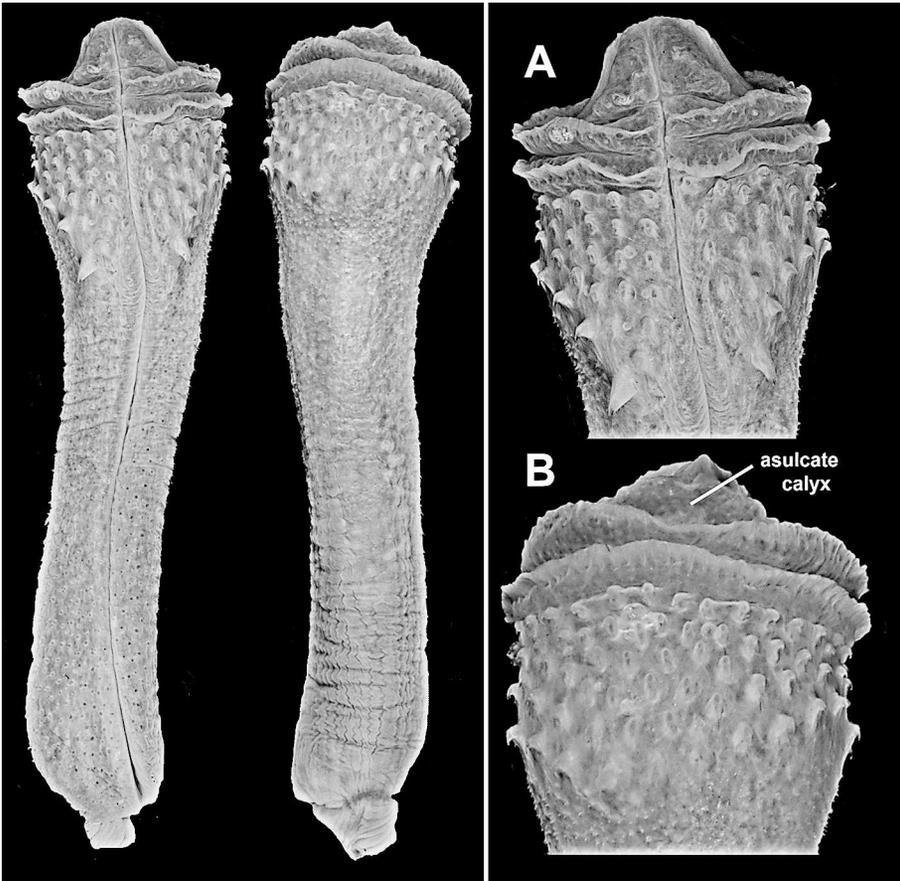


Figure 44. Everted hemipenis of *Dendrophidion graciliverpa* (AMNH R-110584, holotype) in sulcate and asulcate views. (A) and (B) Details of apical region in sulcate and asulcate views, respectively.

USNM 237069 (Figs. 46A, C): Total length approximately 26 mm. Length of apex from the proximal enlarged sulcate spine to the tip of the apex, 7.3 mm (distal section of hemipenis 28% of the total length). Tip of the sulcus spermaticus with divergent lips but not clearly divided as in AMNH R-110584, R-119835. About 84 small spines + 2 enlarged sulcate spines. On the asulcate side of the apex is a thick triangular pad of tissue, within which is a large irregular calyx whose proximal wall is formed by the distal flounce. The large calyx has several small depressions within it (or rudimentary partitions), which makes it appear that the large calyx is formed by

fusion and obliteration of several smaller calyces.

AMNH R-119835 (Figs. 46B, D): Total length 29.4 mm. Length of narrow part of body 21 mm (measured to the base of the pair of enlarged spines at the proximal edge of the apex). Diameter of narrow part 4×5 mm. Length of apex from the proximal enlarged sulcate spine to tip of apex, 8 mm (distal section of hemipenis 27% of the total length). Diameter of globose part 7×7.5 mm. Tip of the sulcus spermaticus seemingly divided about 1 mm because a short ridge separates the divergent lips. About $81 + 2$ enlarged sulcate spines. The asulcate calyx is a large oval formed by

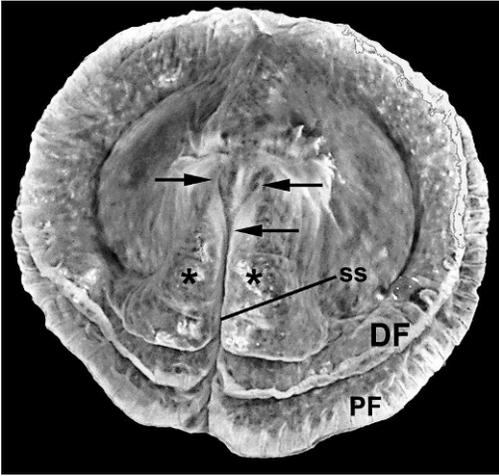


Figure 45. Apical view of the everted hemipenis of *Dendrophidion graciliverpa* (AMNH R-110584, holotype). The contrast is exaggerated so as to emphasize the divided tip of the sulcus spermaticus. *Abbreviations and labels:* Lower arrow, point of division of the sulcus spermaticus; upper arrows, tips of the branches of the divided sulcus; asterisks (*), thick pads of apical tissue bordering the distal part of the sulcus (parasulcus pads); DF, distal flounce; PF, proximal flounce; ss, sulcus spermaticus.

robust, well-defined walls created by division of the distal flounce (Fig. 46D). Within the asulcate calyx are about six pockets, seemingly formed by thinning of tissue of the hemipenial wall; these pockets are irregular in size and position, although most are nestled under the distal fleshy border of the calyx. Immediately distal to the asulcate calyx is a small, deep triangular hole surrounded by thick fleshy ridges (one of which forms part of the distal wall of the asulcate calyx); the ridges surrounding the pore fuse distally, forming a groove that extends distally and ends short of the center of the apex. This hole is presumably a rudimentary calyx.

Although all three everted organs of *Dendrophidion graciliverpa* are basically similar the shapes of their apices differ. The apex and apical ornamentation of AMNH R-110284 (holotype, El Oro province; Fig. 44) are more similar to USNM 237069 (Pichincha province; Figs. 46A, C) than they are to the topotypic specimen (AMNH R-119835; Figs. 46B, D). The apex

of the last is more rounded than in the other two hemipenes, and it has more rudimentary development of the asulcate triangular apical tissue. On the other hand, the large oval asulcate calyx of AMNH R-119835 is a very well defined structure with thick walls (Fig. 46D), whereas in the other two specimens it is a more rudimentary triangular structure without hypertrophied walls (Figs. 44B, C). The strong differences among the few everted hemipenes of *D. graciliverpa* examined suggest that considerable variation in hemipenial morphology might characterize this species, just as suggested above for *D. percarinatum*. However, based on the present small sample it is unclear that this variation is taxonomically significant. It should be noted that hemipenes depicted in Figures 44 and 46B and D are from “crossbanded” specimens of *D. graciliverpa*, whereas Figures 46A and C are from the “unicolor” pattern morph, as discussed in the section on coloration of preserved specimens.

Retracted. I examined the internal morphology of five retracted hemipenes from specimens I refer to *Dendrophidion graciliverpa* (ANSP 5519; BMNH 1860.6.16.59; UIMNH 77347; USNM 12268, 237084). All are very similar to one another and the following description is a composite account. UIMNH 77347 is illustrated in Figure 43B.

These hemipenes extended posteriorly to the suture between subcaudals 10 and 11 up to the proximal portion of subcaudal 14; when hemipenes that were examined only superficially are included, the lengths were 9–15 subcaudals (Table 5). Measured lengths in adults were 27–40.7 mm. The retractor penis magnus appeared distinctly divided in UIMNH 77347 but in other organs the separation was not so distinct. The sulcus spermaticus is simple and centrolateral (in the dorsolateral wall of the organ). It ends just short of the distal tip of the organ and has a flared tip (a couple of the specimens had a low wedge of tissue between the divergent lips but this was most likely a simple fold resulting from the packing of apical tissue in the retracted condition).

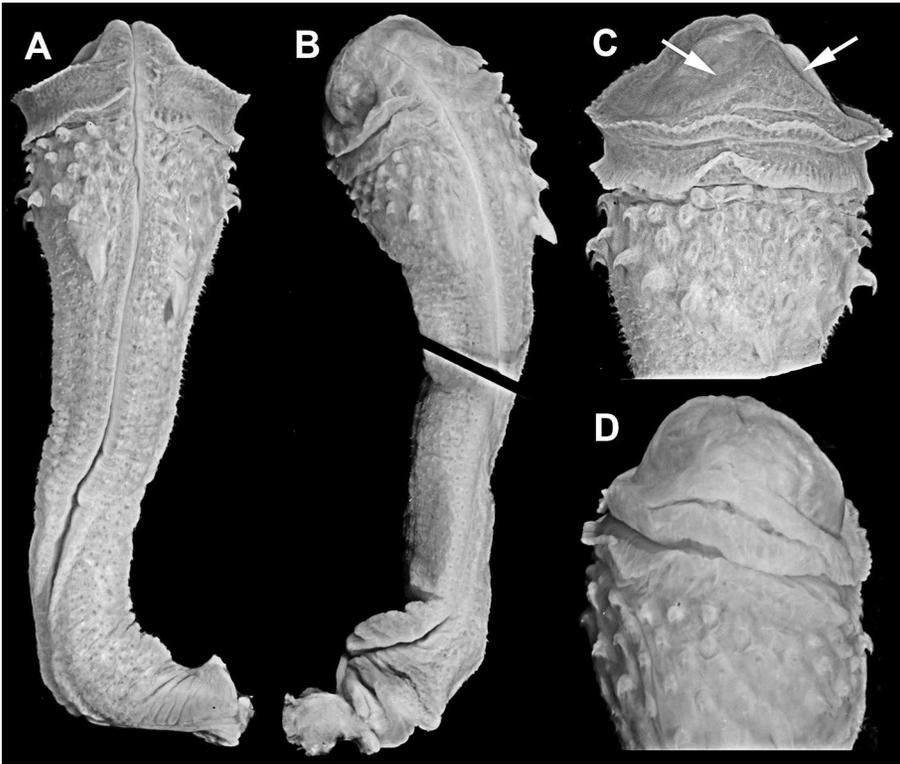


Figure 46. Variation in hemipenial morphology of *Dendrophidion graciliverpa*. (A) USNM 237069 from Pichincha province, Ecuador (sulcate view). (B) AMNH R-119835 from El Oro province, Ecuador (topotype, sulcate view). (C) Detail of apex, USNM 237069, asulcate side. (D) Detail of apex, AMNH R-119835, asulcate side. Arrows in panel C indicate the poorly formed walls of the triangular asulcate calyx; compare panel D, in which the calyx is oval and has prominent walls. The asulcate calyx in the holotype (Fig. 44B) is more similar to that in panel C than to the topotype in panel D.

The proximal part of the hemipenis has many longitudinal ridges or folds, which are ornamented with minute spines except for the extreme base of the organ. A pair of enlarged sulcate spines is positioned at the proximal edge of the spine array, which is about three or four rows across on the sulcate and asulcate sides, slightly fewer in between. The spine array is followed distally by a pair of flounces, between which are some rudimentary longitudinal connections. Distal to the flounces on the asulcate side (ventromedial side of the in situ organ) is a single large irregular calyx, the proximal wall of which is formed by the distal flounce. From this calyx a ridge or pad of tissue extends nearly to the tip of the sulcus spermaticus on the apex. Each side of the

distal portion of the sulcus spermaticus is bordered by a fleshy pad, each with a slight depression. The apex distal to the flounces is very short (about one subcaudal in length) and has thin longitudinal folds (nude tissue in the everted hemipenis), which are largely obscured by the pleats of the flounces covering it from ventral perspective.

COMPARISONS OF HEMIPENIAL MORPHOLOGY OF SPECIES IN THE *DENDROPHIDION PERCARINATUM* COMPLEX

Apart from robust vs. gracile morphology, hemipenes of the three species of the *Dendrophidion percarinatum* complex are similar in basic details: (1) proximal portion of hemipenial body ornamented at least in

part with minute spines; (2) enlarged spine array three to six rows across on the sulcate and asulcate sides and with a somewhat enlarged pair of sulcate spines at its proximal edge; (3) two circumferential frounces with embedded spinules; (4) roughly triangular asulcate apical calycular tissue that varies in morphology, but including at least one large proximal calyx bordering the distal frounce and a more or less defined ridge or other calyces extending nearly to the center of the apex; (5) a fleshy pad (sometimes with a more or less evident calyx within) bordering each side of the apical part of the sulcus spermaticus distal to the frounces; and (6) tip of the sulcus spermaticus terminally flared in everted organs, and sometimes seemingly divided by a tissue wedge in *D. prolixum* and *D. graciliverpa*. Some of these characteristics are more widely distributed within *Dendrophidion* (Cadle, 2012: 217–220). For example, two (and no more) complete circumferential frounces are characteristic of all species in the *D. percarinatum* species group, and enlarged sulcate spines are characteristic of most species of *Dendrophidion*, although details vary among species.

Dendrophidion prolixum and *D. graciliverpa* have nearly identical hemipenes and share several putatively derived hemipenial characters compared with other *Dendrophidion*, especially *D. percarinatum*. Foremost is “gracile” hemipenial morphology, which is unique among known *Dendrophidion* hemipenes, with the possible exception of *D. bivittatum* (see the introductory section on gracile and robust hemipenial morphotypes). Gracile morphology actually comprises several associated, but distinct, characteristics: the hemipenial body proximal to the enlarged spines is exceptionally long relative to the spinose + apical regions; the spinose + apical region is relatively and absolutely less bulbous than in robust hemipenes; and gracile hemipenes are longer in absolute terms than robust organs (measured length or length in subcaudals for retracted organs). Second, *D. prolixum* and *D. graciliverpa* have a large number of

spines (>60 compared with ≤ 40 in *D. percarinatum*). Such a large number of spines is found elsewhere in *Dendrophidion* only in *D. crybelum* (Cadle, 2012: 225), *D. bivittatum* (about 65 spines in the single organ counted), *D. nuchale* auctorum (>85 in one species of the complex; Cadle and Savage, unpublished data), and *D. brunneum*, in which spines are very small and can number upward of 150. Hemipenes of *D. crybelum* and *D. brunneum* are otherwise dissimilar to *D. prolixum* and *D. graciliverpa* apart from characters common to the *D. percarinatum* species group shared by *D. brunneum*, *D. prolixum*, and *D. graciliverpa*. Third, in *D. prolixum* and *D. graciliverpa* the spines are greatly reduced in size and closely packed together (shared with *D. brunneum* and perhaps with *D. bivittatum*). Finally, in everted hemipenes of *D. prolixum* and *D. graciliverpa* the apex is strongly protruding distal to the frounces as a rounded or more angular convexity (compare Figs. 44A, 46C, D). This apical morphology may characterize *D. bivittatum* (the only everted organ examined is problematic to interpret in this regard), but it also appears rarely in *D. percarinatum*, as shown by the peculiar everted hemipenes of UMMZ 124061 (Fig. 40). These unusual and putatively derived hemipenial characters provide strong evidence that *D. prolixum* and *D. graciliverpa* are closely related within *Dendrophidion*. Further study is needed to evaluate the potential relationship of *D. bivittatum* to this pair based on several shared hemipenial characters.

Given the variability that seems to characterize hemipenes of the *Dendrophidion percarinatum* complex, I am hesitant to make much of small differences among the few available everted hemipenial preparations of *D. prolixum* and *D. graciliverpa*. The profound differences evident between two specimens of *D. graciliverpa* from the type locality (Figs. 44, 46B, D) give one pause in making too much of some differences—especially given the greater similarity of one of these (Fig. 44) to a Colombian specimen

of *D. prolixum* (Fig. 42)! Preparations differ in the shape of the apex, the prominence of the asulcate triangular apical tissue, and the shape and definitiveness of the irregular asulcate calyx and the parasulcus calyces. Because of the variability in these organs I fail to find consistent differences in hemipenial morphology between *D. prolixum* and *D. graciliverpa*. The strongly differentiated asulcate calyx of AMNH R-119835 (Fig. 46D) has no equivalent in any other hemipenis of either species. Similarly, a few other differences, including the degree of compression of the long proximal portion of the hemipenial body, the presence and size of nude areas among the minute spines, the width and morphology of the flounces, and so on cannot be ascribed taxonomic significance without additional sampling.

The Sulcus Spermaticus in the Dendrophidion percarinatum Complex. In the three species of the *Dendrophidion percarinatum* complex the sulcus spermaticus in retracted organs ends at the distal tip of the organ, where its lips diverge slightly as the thick parasulcus pads give way to the nude apical tissue (Figs. 41, 43C). This condition is maintained in everted hemipenes of *D. percarinatum*, in which the tip of the sulcus is entirely confluent with the nude apical area and the lateral lips of the sulcus curve sharply around the distal end of the parasulcus pads (Fig. 38D). Everted hemipenes of *Dendrophidion prolixum* and *D. graciliverpa* differ in that a narrow wedge of raised tissue occupies the space between the moderately divergent sulcus lips, resulting in the appearance of a terminal division of the sulcus (Fig. 45). With the small number of preparations of these species available, it is not clear how consistent this apparent division is or whether, in fact, medial “lip” tissue is present on the raised wedge within the divergent lateral lips. In *D. prolixum* the tissue wedge can be easily flattened with manipulation, suggesting that this morphology is not a truly divided sulcus. In two hemipenes of *D. graciliverpa* the sulcus appeared to have a short terminal division, whereas a third seemed to have only

divergent sulcus lips. This suggests that there may be some variation in the expression of this feature. Nearly complete evolutionary loss of the sulcus bifurcation may result in such variation or configurations that are not easily interpreted with respect to a more fully expressed bifurcation; see Myers (2011: 23–24) for possible routes of evolutionary loss of bifurcation of the colubrid sulcus spermaticus.

The apparent terminal division of the sulcus spermaticus in *Dendrophidion prolixum* and *D. graciliverpa* is unusual within *Dendrophidion* but not unique. *Dendrophidion dendrophis* and *D. atlantica* (Freire et al., 2010) have an unambiguously divided sulcus, with fully developed medial and lateral lip tissue along both short branches after the bifurcation. The sulcus is much more deeply forked in *D. dendrophis* than in *D. prolixum* or *D. graciliverpa*. Moreover, the fork is apparent in both the retracted and everted hemipenes in *D. dendrophis* (personal observation), as is typical for divided sulci in general and in contrast to *D. prolixum* and *D. graciliverpa*. Thus, the sulcus spermaticus in *Dendrophidion* shows a variety of conditions: truly bifurcate in *D. dendrophis* and *D. atlantica*, marginally bifurcate or not in *D. prolixum* and *D. graciliverpa*, or with an expanded tip (divergent lips) in the other species.

The terminus of the sulcus spermaticus in the *Dendrophidion percarinatum* complex shows similar ambiguity in interpretation that Myers (2011: 22–24) found in *Leptodeira*. In some species of *Leptodeira* the sulcus is “not clearly forked or divided, [and] terms such as ‘simple’, ‘single’, or ‘unforked’ are not adequate descriptors” of the sulcus condition (Myers, 2011: 23). The situation in the *D. percarinatum* complex is subtly different from what Myers found in *Leptodeira*. In that genus, some species have a truly simple sulcus, but more commonly a small terminal fork is present in retracted hemipenes but lost during eversion, or the terminus presents divergent lips in everted organs. In the *D. percarinatum* complex retracted hemipenes do not

exhibit a bifurcate sulcus, only an expanded sulcus tip, whereas everted organs of two species (*D. prolixum* and *D. graciliverpa*) can have an apparent terminal division to the sulcus.

CONCLUDING REMARKS

My review of two species complexes in *Dendrophidion* shows that speciation within this genus is frequently accompanied by very little differentiation in scutellation characters that typically distinguish snake species (Cadle, 2012; the present work; Table 1). Snake taxonomists rightfully use these characters because of their proven utility in studies of snake systematics, quantitative genetics, and geographic variation, not to mention the ease with which they are scored. However, *Dendrophidion* offers cautionary examples that closely related snake species may not be distinguishable by the usual scale characters. We currently have no measures of how widespread or representative this situation might be among other snakes (a few other examples are well known, e.g., some North American species of *Thamnophis*).

Subtle differences in coloration and rather more profound differences in male genital morphology accompanied speciation within the *D. vinitor* complex (Cadle, 2012), such that distinguishing these species on the basis of external characteristics is problematic (fortunately for nontaxonomists, distributions of those three species are mutually exclusive). A contrasting situation is presented by the *D. percarinatum* complex (this work). Although *D. percarinatum* is distinguished from the other two species in both color pattern characters and hemipenial morphology, *D. prolixum* and *D. graciliverpa* show differences from one another only in coloration. Their hemipenes appear identical when intraspecific variation in hemipenial characters is taken into account, and the two species are not easily distinguished on the basis of scale characters. This scenario of mosaic character evolution or disparate evolutionary rates

among characters is probably more common among snakes than is presently recognized. Close attention to subtle morphological differences among populations offers the best clues to species recognition in these cases. Many putatively widespread snake species may represent complexes of species distinguishable in only subtle ways.

The existence of cryptic species in snakes such as *Dendrophidion* has more than taxonomic interest because it bears on one of the most pressing biodiversity issues of our time: potential declines or extirpations of these snakes in much of their range. Although amphibian biologists have become well attuned to declines of Neotropical frogs and salamanders, reptile biologists have a potentially more difficult job of recognizing declines because absence can be more difficult to detect, especially for snakes (Pounds, 2000: 158–159). Nonetheless, because many tropical forest snakes (including all species of *Dendrophidion*) prey upon anurans, their populations are surely affected by amphibian declines and general environmental degradation. Cadle (2012: 208–209, 216–217) pointed out that populations of two species of the *D. vinitor* complex are probably affected to some degree by widespread amphibian declines and climate-mediated changes in rainforest leaf litter cover (Lips et al., 2006, Whitfield et al., 2007). But there are almost no quantitative or systematic measures of these effects.

Dendrophidion crybelum, known only from a very localized area in southwestern Costa Rica, has not been seen since 1987 despite resurvey of its type locality (Santos-Barrera et al., 2008; Cadle, 2012: 217). At Monteverde, Costa Rica, populations of 11 snake species, including at least one species of *Dendrophidion* (*D. paucicarinatum*), have declined since 1987, and two species are possibly locally extinct (Pounds, 2000). Similarly, *D. prolixum*, described herein, possibly has not been seen since the type series was collected in 1973 (admittedly, few collections have been made from within its known range in the intervening years). The

problem of decline and possible extinction is especially acute when unrecognized cryptic species with restricted ranges exist within what is thought to be a single widespread species, such as the *Dendrophidion* species covered here and in Cadle (2012). Loss of these species, in some cases before their formal descriptions, is cause for heightened awareness among tropical biologists of the potential collapse of populations of snake predators whose biology is intimately tied to declining prey species. Such ramifying ecosystem effects call for redoubled efforts at biodiversity documentation (including systematic studies to reveal cryptic biodiversity) and development of effective methods of ecosystem preservation and restoration.

ACKNOWLEDGMENTS

Many collection personnel offered indispensable assistance and loans during this study: Darrel Frost, David Kizirian, and Charles W. Myers (AMNH); Edward B. Daeschler and Edward (Ned) Gilmore (ANSP); Patrick Campbell, Tracy Heath, and Colin McCarthy (BMNH); Lauren Scheinberg and Jens Vindum (CAS); Stephen P. Rogers (CM); Maureen Kearney, Alan Resetar, Sarah Rieboldt, and Harold K. Voris (FMNH); Rafe Brown, Andrew Campbell, and Linda Trueb (KU); Neftali Camacho, Jeff Seigel, and Christine Thacker (LACM); Christopher Austin, Jeff Boundy, and Alison Hamilton (LSUMZ); James Hanken, Jonathan Losos, and José P. Rosado (MCZ); Christopher Conroy, Michelle Koo, Jimmy McGuire, Carol Spencer, and David B. Wake (MVZ); Toby Hibbitts (TCWC); Michael Granatosky and Kenneth L. Krysko (UF); Christopher Phillips and Dan Wylie (UIMNH); Ronald Nussbaum and Greg E. Schneider (UMMZ); Steve Gotte, Roy W. McDiarmid, James Poindexter, Robert Wilson, and George R. Zug (USNM); and Jonathan Campbell and Carl J. Franklin (UTACV). Charles W. Myers was particularly helpful and generous in sharing his photographs and field notes on *Dendrophidion*; his fine series of *D. pro-*

lixum helped in understanding ontogenetic patterns in that species. Other special assistance was provided by Colin J. McCarthy for preliminary data and photographs of the holotype of *D. brunneum*; José P. Rosado for a scan of a color slide by Kenneth Miyata; Roy W. McDiarmid for his photograph of *D. percarinatum*; Patrick Campbell for photographs of BMNH specimens; Fernando Rojas-Runjaic for information on specimens in the Museo de Historia Natural La Salle; and Neil Duncan and David Kizirian for delving into AMNH archives to help resolve certain Ecuadorian localities. Thanks to Roy W. McDiarmid, Charles W. Myers, and the MCZ Herpetology Department for permission to reproduce their color photographs, and to Darrel Frost for generous permissions to prepare hemipenes from AMNH specimens. For comments and discussions that greatly improved the manuscript, I am deeply indebted especially to Jay M. Savage, Jonathan Losos, and two anonymous reviewers.

APPENDIX 1. SPECIMENS EXAMINED AND LITERATURE RECORDS OF *DENDROPHIDION PERCARINATUM* AND NEW RECORDS OF *D. BRUNNEUM* FROM ECUADOR

Museum abbreviations used throughout are the following: AMNH—American Museum of Natural History (New York). ANSP—Academy of Natural Sciences of Philadelphia. BMNH—The Natural History Museum (London). CM—Carnegie Museum (Pittsburgh). KU—University of Kansas Museum of Natural History (Lawrence). LACM—Natural History Museum of Los Angeles County (Los Angeles). MCZ—Museum of Comparative Zoology (Cambridge). MHNLS—Museo de Historia Natural La Salle (Caracas). TCWC—Texas Cooperative Wildlife Collection, Texas A and M University (College Station). UF—Florida Museum of Natural History, University of Florida (Gainesville). UIMNH—University of Illinois Museum of Natural History (Urbana). UMMZ—University of Michigan Museum of Zoology (Ann Arbor). USNM—National Museum of Natural History, Smithsonian Institution (Washington, DC). UTACV—University Texas at Arlington Collection of Vertebrates (Arlington).

Bracketed data associated with localities here and elsewhere in the text are inferences derived from sources other than original data associated with specimens as recorded in literature, museum or collectors' catalogues, or specimen labels. Countries are listed north to south Honduras to Colombia, followed by Venezuela.

Dendrophidion percarinatum

Honduras: *Atlántida:* CURLA Forestry Station, 120–500 m [15°42'N, 86°51'W fide USNM database], USNM 559613–14. *Lancetilla* [15°42'N, 87°26'W], MCZ R-29677. *Colón:* Los Andes [15°50'N, 85°08'W], ANSP 20817. *Gracias a Dios:* Bodega de Río Tapalwás, 190 m [14°56'N, 84°32'W], USNM 561031, 563301. *Hiltara Kiamp*, 150 m [on the upper Río Warunta; 14°57'N, 84°40'W], USNM 563300, 565532. Between *Hiltara Kiamp* and *Sachin Tingni Kiamp*, 150 m [14°57'N, 84°40'W], USNM 563489. *Kipla Tingni Kiamp*, 160 m [on the upper Río Warunta; 14°56'N, 84°40'W], USNM 565533. *Oscana*, 60 m [14°42'N, 84°27'W], USNM 562872–73. *Rus Rus*, 60 m [14°43'N, 84°27'W], USNM 559612, 561918. *Sachin Tingni*, 150 m [tributary of upper Río Warunta; 14°57'N, 84°40'W], USNM 563302, 563488. *San San Hil Kiamp*, 190 m [hill E of Río Tapalwás; 14°57'N, 84°31'W], USNM 563490, 564078. *Olancho:* Los Chorritos near Campamento, 950 m [14°33'N, 86°39'W; McCranie (2011) gives 685 m as the elevation], USNM 337504. Confluence of Río Wampú and Río Yanguay, 110 m [15°03'N, 85°08'W], USNM 321734. *Quebrada El Guásimo*, 140 m [tributary of Río Patuca; 14°35'N, 85°18'W], USNM 559611. *Warunta Tingni Kiamp*, 150 m [14°55'N, 84°41'W; McCranie, 2011: 639], USNM 561919.

Nicaragua: [*Atlántico Norte*]: *Bonanza*, 850 ft. [260 m; 14°02'N, 84°35'W], KU 86183. *Atlántico Norte:* *Musawas*, *Huaspuc River* [14°09'N, 84°42'W], AMNH R-75428. *Atlántico Sur:* *El Recreo*, 10 mi. W *Rama* [12°10'N, 84°19'W], LACM 74148. Seven miles above *Rama*, *Río Siquia* [approximately 12°10'N, 84°18'W], UMMZ 79767. 10 mi. above *Recero* [= *Recreo*], *Río Siquia Mico* [12°07'N, 84°26'W; see Cadle, 2012: 234], UMMZ 79764. *Boaco:* *Comoapa* [= *Camoapa*; 12°23'N, 85°31'W, about 520 m], MCZ R-9550. *Chontales:* *Santo Domingo*, *Chontales Mines*, 2,000 ft. [610 m; 12°16'N, 85°05'W], BMNH 94.10.1.18 (specimen not seen; Stafford, 2003).

Costa Rica: No additional data, AMNH R-17374, USNM 259130. *Alajuela:* *Venado*, 9 km N *Arenal*, 252 m [10°33'N, 84°45'W], LACM 148580. *Cartago:* *Pavones de Turrialba* [09°54'N, 83°37'W], UTACV 12898. *Turrialba*, 605 m [09°54'N, 83°41'W], LACM 148577, 148579. *Guanacaste:* *Tilarán*, 1,300 ft. [400 m; 10°28'N, 84°58'W], USNM 70663. *Heredia:* *Finca La Selva*, 2.4 km SE *Puerto Viejo* [35–137 m; 10°26'N, 83°59'W; various locations within the *La Selva Biological Station*], KU 305559; LACM 148558, 148560, 148583–86. *Limon:* *Barra del Colorado*, 4 m [10°42'N, 83°36'W], LACM 148587. *Batán* [10°05'N, 83°20'W], KU 30998. Vicinity of *Cahuita*, about 4 m [09°44'N, 82°50'W], LACM 148582. *Los Diamantes* [about 300 m; 10°12'N, 83°47'W; experimental station about 1 km E *Guápiles*], KU 30997. *La Lola*, 39 m [10°06'N, 83°23'W], LACM 148578. *Pandora*, 17 m [09°44'N, 82°58'W], LACM 148581. 2.3 km E *Siquirres*, 280 m [10°06'N, 83°31'W], UMMZ 137389.

Puntarenas: *Boruca* [09°00'N, 83°19'W], AMNH R-17366 (lectotype). *Parque Nacional Carara*, 1.9 rd mi. S *Río Tárcoles* on *Hwy 34* [09°46'N, 84°36'W], TCWC 84024, 84083. *Palmar* [a *Taylor locality* = *Palmar Sur* fide *Jay M. Savage*, personal communication], KU 31948. 15 km E *Palmar Norte*, N *Lagarto* at *Quebrada Yan*, 70 m [08°57'N, 83°23'W], LACM 148574. 2 km S *entrada Palmar Sur*, 15 m [8°58'N, 83°27'W], LACM 148592. Vicinity of *Rincón de Osa* [08°42'N, 83°29'W; various localities within 7.5 km W to SW of the settlement, 5–60 m elevation; see *McDiarmid and Savage*, 2005], ANSP 27900; KU 102505–06; LACM 114100–01, 148561–148563, 148565, 148570–73, 148575–76; LSUMZ 34112–13. *Finca Las Cruces*, about 6 km S *San Vito de Java* [approximately 1,200 m; 08°47'35" N, 82°57'30" W], LACM 114102–04, 148566. *Golfito*, 12 m [08°36'N, 83°09'W], LACM 148568. 0.4 km W of *Motel Bella Vista*, *Golfito*, 15 m [08°36'N, 83°09'W], LACM 148564. 6.3 km S of *Pan American Hwy* on *Golfito Rd.*, 7 m [08°37'N, 83°04'W], LACM 148567. *Gromaco*, at junction of *Río Cotón* and *Río Coto Brus*, 480 m [08°55'N, 93°06'W], LACM 148569. Vicinity of *Río Disciplina*, 80 m [08°58'N, 83°20'W], LACM 148588. *San Luís River* at *footbridge*, about 740 m [10°16'N, 84°49'W], LACM 148559. *San José:* 1.4 mi. N and 0.6 mi. NNE (by road) *Bijagual*; *Montañas Jamaica*, *Parque Nacional Carara* [09°43'N, 84°34'W], TCWC

83370. "Los Cusingos" [09°43'N, 84°34'W; in Quizarrá on the lower slopes of Volcán Chirripó near Santa Elena], Kohler (2008: fig. 582).

Panama: No additional data, FMNH 31214–16 (heads only). "Canal Zone," no additional data, FMNH 6118. *Bocas del Toro:* Almirante, 10 m [09°18'N, 82°24'W], KU 80224, UMMZ 142638. 1.5 mi. W Almirante, Nigua Creek, 10 m [09°17'N, 82°24'W], KU 107644. 4 km W Almirante, 10 m [09°17'N, 82°24'W], KU 107645. Hill above Miramar, 180 m [08°59'N, 82°15'W], KU107647. Torres, western Panama [09°25'N, 82°31'W], MCZ R-19343. [*Chiriquí*]: "Chiriquí," BMNH 94.5.17.8–9 (specimens not seen; Stafford, 2003).

Coclé: El Valle de Anton, 2,000 ft. [610 m; 08°37'N, 80°08'W], AMNH R-71681. *Colón:* Canal Zone, Acliote [= Achiote] Rd., 5.1 km NW Escobal Rd., N of road [approximately 09°15'N, 80°02'W], UMMZ 155740. Agua Clara, Chagres River [09°11'N, 79°41'W], ANSP 25144. Near Buena Vista on Trans-Isthmian Highway, 200 ft. [61 m; 09°16'N, 79°41'W], FMNH 154474. Canal Zone, Buena Vista Peninsula, 1.75 km NNW of Frijoles [09°10'34'N, 79°48'W], USNM 196306. Canal Zone, Camp Chagres, 120 ft [40 m; 09°21'N, 79°57'W], KU 75676. Canal Zone, Fort Randolph [09°23'N, 79°53'W], MCZ R-20552. Canal Zone, Salamanca Hydrographic Station, Río Pequeñí [09°20'N, 79°36'W], MCZ R-39978. Gamboa [09°07'N, 79°42'W], FMNH 154510, USNM 297811. Gatún [09°16'N, 79°55'W], FMNH 16760, USNM 54080. Canal Zone, Atlantic side, Gatún, Fort Davis, [09°17'N, 79°54'W], MCZ R-22255. Cartí Rd. [not located], USNM 266157. *Darién:* Río Tuira, Boca de Cupe, 30 m [08°03'N, 77°35'W], AMNH R-119376. Cana, 2,000 ft. [610 m; 07°47'N, 77°42'W], KU 107651, USNM 50123. [Cerro] Tacarcuna, 550 m [08°10'N, 77°18'W], KU 75677–79. Ortega site, 8°46' 78°00' (30 m), FMNH 170152. Along Río Canclón [= Río Canglón] near mouth of Río Chucunaque [approximately 08°20'N, 77°46'W], UMMZ 124063. Along Río Canclón [= Río Canglón] near crossing of Inter-American Highway [approximately 08°20'20"N, 77°49'50"W], UMMZ 124064. Near mouth of Río Canclón [= Río Canglón; 08°19'N, 77°46'W], UMMZ 124199. Río Tuira at Río Mono, 130 m [07°43'N, 77°33'W], KU 107652–56. Yarrssa [= Yaviza] [08°11'N, 77°41'W], UMMZ 83144. [*Herrera*]: Cerro Mangillo, 2,800 ft., Veragua [854 m; = Cerro Mangillo, 07°34'N, 80°47'W; the Mangillo Massif straddles the border between Veraguas and Herrera province; see Dunn (1943) for a brief recounting of his route], ANSP 22446. *Los Santos:* E slopes of

Cerro Hoya, 930 m [07°19'N, 80°40'W], KU 107659. *Panamá:* Canal Zone, Alhajueta [09°11'N, 79°33'W], UMMZ 76019. Altos de Majé [08°48'N, 78°31'W], AMNH R-109643. Barro Colorado Island: AMNH R-77573, 89971–72; ANSP 22560, 22878; CM S 6869, S 7711; KU 75674–75, 80589–90; MCZ R-18902; UMMZ 63762; 124061–62, 124065–66; USNM 120815. Canal Zone, Chiva Chiva [09°02'N, 79°35'W], MCZ R-24002. Cocolí [08°59'N, 79°35'50"W], USNM 193447. Canal Zone, Contractor's Hill [09°02'N, 79°39'W], CAS 98388. Canal Zone, Curundú [08°59'N, 79°33'W], KU 80255. Canal Zone, Fort Clayton [09°00'N, 79°34'W], KU 107649, 110290, MCZ R-25124. Canal Zone near Fort Clayton, [09°00'N, 79°34'W], UIMNH 41705–19. Fort Clayton, Cardenas River [09°00'N, 79°34'W], KU 110291. Gamboa or Pedro Miguel [approximately 09°03'N, 79°40'W], FMNH 154516. Canal Zone, Juan Mine [09°10'N, 79°39'W], MCZ R-26646. Canal Zone, Madden Forest, Río Pedro Miguel [09°06'N, 79°37'W], KU 107650. Canal Zone, [Madden] Forest Preserve [09°06'N, 79°37'W], AMNH R-89970. Canal Zone, Red Tank [09°00'N, 79°36'W], MCZ R-24000. Cerro Campana, 2,500 ft. [762 m; 08°41'N, 79°56'W], AMNH R-76000. Cerro Campana, 800 m [08°41'N, 79°56'W], AMNH R-129757. Cerro Jefe [09°14'N, 79°21'W], UMMZ 155732. *San Blas:* Armila, Quebrada Venado [08°40'N, 77°28'W], USNM 150139. San Ignacio de Tupile, mainland, 2.5 mi. inland, ca. 250 ft. [75 m; 09°15'N, 78°09'W], USNM 241656. *Veraguas:* Isla Gobernadora [07°33'N, 81°12'W], KU 107648.

Colombia: *Antioquia:* Medellín [06°15'N, 75°35'W], BMNH 1897.11.12.10 (questionable record; see Distribution in the *D. percarinatum* account). Urabá, Río Currulao, 50 m [08°01'N, 76°44'W], FMNH 63772–73. Urabá, Turbo [08°06'N, 76°44'W], FMNH 63761. Villa Arteaga [135 m; 07°22'N, 76°29'W], FMNH 78118, USNM 267273. *Chocó:* Quebrada Pangala, lower Río San Juan (about 17 km airline NE Palestina), 04°15'N, 77°0'W, AMNH R-123745, R-123748. Vicinity of Playa de Oro, upper Río San Juan, ca. 200 m [05°19'N, 76°24'W], AMNH R-108468. Sierra [Serranía] del Darién, Chocó, 600 ft., Pacific side [183 m], ANSP 25606. *Valle del Cauca:* Río Raposo, Virology Field Station near Buenaventura [03°43'N, 77°08'W], USNM 151658.

Venezuela: *Zulia:* Sierra de Perijá, Finca El Progreso, 840 m [10°43'13.30"N, 72°29'16.60"W], MHNLS 17932 (specimen not seen; Rojas-Runjaic and Rivero, 2008).

Dendrophidion brunneum (Ecuador only; see Cadle, 2010: 24 for other records)

Ecuador: No other data, AMNH R-18324. "Western Ecuador," BMNH 1860.6.16.58, 1860.6.16.60, 1860.6.16.67.⁴ *Chimborazo:* Huigra to Río Chiguancay [02°13'S, 79°03'W], ANSP 18122. [*El Oro*]: Portovelo [610 m; 03°42'48"S, 79°36'51"W; Lynch and Duellman, 1997: 215], AMNH 18322. Zaruma [03°41'S, 79°37'W], BMNH 1894.5.29.1. *Guayas:* 5–10 km S Daule [about 01°55'S, 80°00'W], UF 87940, 88466–67. 18 km E Duran [0–50 m; about 02°14'S, 79°38'W], UF 88468. El Milagro [13 m; 02°07'S, 79°36'W], USNM 237061–62. Guayaquil [02°10'S, 79°50'W], BMNH 1946.1.12.98 (holotype); MCZ R-8393; USNM 237059. Near Guayaquil, USNM 237060. 3 km E Olan [?Olón], Crespo Hacienda, 450 ft. [137 m; Olón is on the coast at 01°48'20"S, 8045'28"W; now in the newly created province of Santa Elena], UF 66199. *Imbabura:* Ibarra [about 2,200 m; 00°21'N, 78°07'W], USNM 237083. Intag [about 1,200 m; 00°20'N, 78°32'W], UMMZ 83706. *Loja:* La Argelia, Malacatos, 2,100 m [04°14'S, 79°17'W], USNM 237077–81. *Loja:* Loja [2,200 m; 04°00'S, 79°13'W], BMNH 1930.10.12.20–22, 1931.11.3.10. Masaca (= Hacienda Masaca, near Loja) [03°53'S, 79°14'W], USNM 237082. [*Loja*]: Alamo [1,325 m; 04°02'S, 80°02'W], AMNH 22232. *Los Ríos:* Finca Playa Grande [53 m; 01°01'30"S, 79°27'39"W, 1.6 km N Quevedo; Lynch and Duellman, 1997: 216], UIMNH 77347. 20 mi. NE Quevedo [about 00°53'S, 79°17'W], UF 85105.

Dendrophidion species inquirendum

Colombia: *Boyacá:* Muzo [1,242 m; 05°32'N, 74°06'W], MCZ R-42186. *Santander:* El Centro,

⁴Four specimens were associated with the five BMNH catalog numbers 1860.6.16.58–60, 67–68 when specimens were received on loan. The specimens were not individually tagged with unique catalog numbers but each specimen had previously been individually identified by linen thread tied around the neck: 1, 2, or 3 threads + the smallest of the four with no thread. For purposes of reference and data collection I assigned the three with threads (1, 2, and 3, respectively) to numbers 1860.6.16.58–60, the specimen without thread to 1860.6.16.67 (–68 being therefore unused). Three of the specimens are *Dendrophidion brunneum* (1860.6.16.58, –60, –67). BMNH 1860.6.16.59 is a specimen of *D. graciliverpa* (see footnote 2).

150 m [06°55'N, 73°44'W], USNM 267241. Landazuri, 900 m [06°13'N, 73°49'W], USNM 267272.

APPENDIX 2. GAZETTEER (*DENDROPHIDION PROLIXUM* AND *D. GRACILIVERPA* LOCALITIES)

Dendrophidion prolixum (Colombia except as noted [Ecuador])

Cachaví, 20 m (Esmeraldas [Ecuador]). About 00°58'N, 78°48'W. Also known as Cachabé and San Javier de Cachabé (Paynter, 1993; Duellman and Lynch, 1997: 217).

Lita, Río Mira (Imbabura [Ecuador]). 00°50'24"N, 78°27'18"W; Duellman and Lynch, 1997: 213.

Paramba, northwestern Ecuador (Imbabura). = Hacienda Paramba. 1,067 m. 00°49'N, 78°21'W.

Peña Lisa, Condoto, 300 ft. (Chocó) 90 m; 05°04'N, 76°38'W.

Playa de Oro, Río San Juan, 400 m (Chocó) 05°19'N, 076°24'W.

[Between] Pueblo Rico [and] Santa Cecilia, Pacific side, 800 m (Risarcaldá). Santa Cecilia: 5°20'N, 76°08'W Pueblo Rico: 5°13'N, 76°02'W.

Quebrada Bochoramá, Loma de Encarnación on right bank (Chocó) about 51 km SE of Quibdo at approximately 5°20'N, 76°23'W, about 400 m elevation; Brame and Wake, 1972: 15.

Quebrada Docordó, middle Río San Juan about 17 km airline SSW Noanamá (Chocó). 04°33'N, 77°0'W (coordinates from AMNH database).

Quebrada Guanguí, 0.5 km above Río Patia (upper Saija drainage), 100–200 m, Cauca department, Colombia [about 02°50'N, 77°25'W; Myers, 1991: 8].

Quebrada Pangala, lower Río San Juan about 17 km airline NE Palestina (Chocó). 04°15'N, 77°00'W (coordinates from AMNH database).

Quebrada Taparal, lower Río San Juan about 7 km airline NE Palestina (Chocó). 4°12'N, 77°07'W (coordinates from AMNH database).

Quininde (Esmeraldas). 00°18'50"N, 79°27'40"W About 100 m (Duellman and Lynch, 1997: 216).

Upper Río Buey, 110–160 m (Chocó). Approximately 06°06'N, 77°05'W.

Río Cachaví (Esmeraldas [Ecuador]). 01°03'N, 78°50'W.

Río Raposo, Virology Field Station near Buenaventura (Valle del Cauca). 03°43'00"N, 77°08'00"W.

Riquarte [= Ricaurte], 3,900 ft. [1,189 m], Pacific side (Nariño). 01°13'N, 77°59'W.

Sierra [Serranía] de Baudó, 3,000 ft. [915 m], Pacific side (Chocó). Approximately 06°00'N, 077°05'W.

Serranía de Baudó, N slope of Alto del Buey, 900 m (Chocó). 06°06'N, 077°13'W.

Dendrophidion graciliverpa (Ecuador)

Alamor (Loja). 04°02'S, 80°02'W.

Bilsa Biological Reserve (Esmeraldas). 00°15'N, 79°45'W. Ortega-Andrade et al. (2010: 1) give coordinates: 00°21'33"N, 79°42'02"W; 300–750 m elevation.

Buena Fe, 1 km N of (Los Ríos). 02°16'S, 79°37'W.

Canoas near Santo Domingo De Los Colorados. (Santo Domingo de los Tsáchilas/Pichincha) Not located.

Centro Científico Río Palenque (Los Ríos). 00°35'11"S, 79°22'W, 220 m elevation. Along the road between Santo Domingo de los Colorados and Quevedo. Dodson and Gentry (1978) describe the environment and geography of the area.

Chaguarapata, 2,000 ft. (Chimborazo). Approximately 02°07'S, 78°59'W. This locality goes by several spellings in the literature (mostly ornithological): Chaguarpata (Paynter, 1993), Chaguarpata (Chapman, 1926), Chahuarpata (various). The elevations given are not consistent among sources. AMNH catalogue data for AMNH R-23032 give 2,000 ft., which may be the actual elevation the specimen was collected by G. H. H. Tate. Chapman (1926: 705) gives the elevation of Chaguarpata as 5,800 ft., whereas Tate's typed itinerary in the AMNH mammal department gives 2,300 ft. for the elevation. Chapman (1926: 706) states that Chaguarpata is "in the forest above Cayandede," which is a hacienda north of Bucay in the Río Chimbo basin (see Chapman, 1926: map, pl. 30).

Finca La Esperanza near Santo Domingo de los Colorados. (Santo Domingo de los Tsáchilas/Pichincha). 00°15'S, 79°09'W, 500 m; a farm just NW of Santo Domingo de los Colorados (Lynch and Duellman, 1997: 212).

Finca Playa Grande (Los Ríos). 53 m; 01°01'30"S, 79°27'39"W; near Quevedo; Lynch and Duellman, 1997: 216.

Guayaquil (Guayas). 02°10'S, 79°54'W.

Hualtaco (El Oro). 03°26'S, 80°15'W.

Joe Ramsey Farm, km 19 on Chone Road, 18 km W of Santo Domingo de los Colorados (Santo Domingo de los Tsáchilas/Pichincha). 00°14'S, 79°20'W (USNM electronic database).

Las Pampas (Cotopaxi). 1,750 m; 00°40'S, 78°50'W. Also referred to as San Francisco de las Pampas (Lynch and Duellman, 1997).

Meme, km 96 on road to Saloya at crossing of Río Toachi (Pichincha). 00°06'S, 79°08'W.

Mulaute, on tributary of Río Blanco. (Pichincha). 00°05'S, 79°09'W (USNM electronic database).

Playas De Montalvo 15 m (Los Ríos). 01°48'S, 79°20'W (Paynter, 1993). Also referred to as "Playas" (Chapman, 1926: 732; Brown, 1941: 836).

Puerto Quito (Pichincha). 00°07'N, 79°16'W.

Quininde (Esmeraldas). 00°18'50"N, 79°27'40"W, 40 m elevation (Lynch and Duellman, 1997: 216). Also known as Rosa Zarate.

Rancho Santa Teresita, km 25 on route to Chone from Santo Domingo de Los Colorados (Santo Domingo de los Tsáchilas/Pichincha). 00°15'S, 79°23'W (USNM electronic database).

Río Baba (Santo Domingo de los Tsáchilas/Pichincha). Approximately 00°25'S, 79°17'W, Lynch and Duellman, 1997: 216. Humid tropical. Southward flowing river on Pacific coastal plain; riparian rainforest along river.

Río Congo, headwaters of. USNM database places this locality in Guayas province, which is the location of the main part of the Río Congo. The "headwaters," depending on interpretation, are potentially farther north (Manabí or Los Ríos provinces).

Río Palenque Science Center. See Centro Científico Río Palenque.

Río Pescado (Guayas). About 02°41'S, 79°32'W. This is a collecting site of G. H. H. Tate, a mammalogist who participated in the AMNH ornithological expeditions in the early 1920s (Chapman, 1926). Its location seems to be of some confusion, as various published papers on insects, mammals, and frogs that Tate collected there place the locality in at least four different Ecuadorian provinces (Manabí, Guayas, Azuay, Chimborazo). I am grateful to Neil Duncan of the AMNH mammalogy department

for checking Tate's field notes and a typed summary of the trip in the department archives. He provided the details given here. Tate worked at "Río Pescado" from May 14 to June 3, 1922 (e.g., AMNH R-23438, a specimen of *Dendrophidion graciliverpa*, was collected 19 May 1922). The camp on the Río Pescado was three hours by trail east from Naranjal (02°40'22"S, 79°36'54"W) into the foothills at 1,600 ft [488 m]. The camp was located about 0.5 mi. above the junction of the Río Pescado and the Río Chacayacu and near the Guayas-Azuay provincial border.

Below Río Toachi (Santo Domingo de los Tsáchilas/Pichincha). Lat/Long from USNM database: 00°11'S, 79°11'W (USNM electronic database). Lynch and Duellman (1997: 217) for Río Toachi: 00°23'S, 78°56'W, 800 m elevation.

Rosa Delia Plantation (El Oro). 03°17'S, 79°55'W.

Santo Domingo de los Colorados, 550–660 m (Santo Domingo de los Tsáchilas/Pichincha). 00°15'S, 79°10'W.

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