

CRYPTIC SPECIES WITHIN THE *DENDROPHIDION VINITOR* COMPLEX IN MIDDLE AMERICA (SERPENTES: COLUBRIDAE)

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ABSTRACT. Snakes previously referred to *Dendrophidion vinitor* from southern Mexico to eastern Panama comprise three sibling species primarily distinguishable by substantial differences in hemipenial morphology and some subtle aspects of color pattern. *Dendrophidion vinitor* Smith is here restricted to populations from southern Mexico to Belize. *Dendrophidion apharocybe* new species is distributed from Honduras to Panama, primarily on the Atlantic versant. *Dendrophidion crybelum* new species is known from middle elevations of the Río Coto Brus valley in southwestern Costa Rica (Pacific versant). Hemipenes of *D. vinitor* and *D. apharocybe* are similar in overall shape (short, bulbous) but the former has a highly ornate apex with

membranous ridges and an unusual apical boss, whereas *D. apharocybe* has a largely nude apex strongly inclined toward the sulcate side. *Dendrophidion crybelum* has an elongate cylindrical hemipenis with a large number of spines. In general, these species are not distinguishable by standard scutellation characters. Hemipenial and other characters suggest that these species are a monophyletic group within *Dendrophidion* and have the following relationships: (*vinitor* (*apharocybe*, *crybelum*)). Some aspects of the systematics and biogeography of *Dendrophidion* are discussed. Divergence among the three species is associated with two geological features important to speciation in Middle America, the northern Motagua–Polochic fault zone (Guatemala–Belize) and the southern Cordillera Talamanca (Costa Rica–Panama).

Key words: Snakes, New Species, Central America, Mexico, Systematics, Costa Rica, Hemipenis, Morphology

RESUMEN. Las serpientes anteriormente referidas a *Dendrophidion vinitor* desde el sur de México hasta Panamá oriental se componen tres especies hermanas que se distinguen por diferencias importantes en la morfología de los hemipenes y aspectos sutiles de coloración. *Dendrophidion vinitor* Smith se limita a las poblaciones del sur de México, Guatemala, y Belice. *Dendrophidion apharocybe*, nueva especie, se encuentra desde Honduras hasta Panamá primariamente en la vertiente Atlántica. *Dendrophidion crybelum*, nueva especie, se conoce solamente de elevaciones medias del valle del Río Coto Brus en el suroeste de Costa Rica (vertiente Pacífica). Los hemipenes de *D. vinitor* y *D. apharocybe* son similares en forma (corte, bulboso) pero el primero tiene un ápice muy ornamentado con crestas membranosas y una protuberancia apical, mientras *D. apharocybe* tiene un ápice mayormente nudo y fuertemente inclinado al lado sulcado. *Dendrophidion crybelum* tiene un hemipene alargado y cilíndrico con muchas espinas. Generalmente, estas especies no se distinguen por caracteres estandarizados de escutelación. Los característicos de los hemipenes y otros caracteres sugieren que estas especies se componen un grupo monofilético dentro *Dendrophidion* con las relaciones siguientes: (*vinitor*

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(*apharocybe, crybelum*). Se discuten algunos aspectos de la sistemática y biogeografía de *Dendrophidion*. La divergencia entre las tres especies es asociada con dos rasgos geológicos importantes para la especiación en América Central, la falla Motagua–Polochnic (Guatemala–Belice) en el norte y la Cordillera Talamanca (Costa Rica–Panamá) en el sur.

INTRODUCTION

The Neotropical snake genus *Dendrophidion* Schlegel currently comprises eight or nine recognized species (Lieb, 1988; McCranie, 2011). Despite considerable progress in clarifying the taxonomy and species limits over the last three-quarters of a century (Smith, 1941; Peters and Orejas-Miranda, 1970; Lieb, 1988; Savage, 2002), it is clear that additional work is needed. Smith (1941) described *D. vinitor* (type locality: Piedras Negras, Guatemala) to accommodate a Mexican and Middle American species with a single anal plate, a relatively low number of subcaudals, and strongly keeled scales. His primary objective was to distinguish this species from the catch-all earlier name *D. dendrophis* (Duméril, Bibron, and Duméril) (type locality: Cayenne, French Guiana), which had been widely applied to Middle American forms of *Dendrophidion* with an undivided anal plate. In doing so, Smith helped clarify the presence and characters of four species of *Dendrophidion* in Central America: *D. clarkii* Dunn, *D. paucicarinatum* (Cope), *D. percarinatum* (Cope), and *D. vinitor*. Lieb (1988) synonymized *D. clarkii* with *D. nuchale* (W. Peters; type locality: Caracas, Venezuela). However, McCranie (2011) resurrected the name *clarkii* (type locality: El Valle de Antón, Panama) for application to Middle American and western Colombian/Ecuadorian populations of this group based on patterns of geographic variation described by Lieb (1988). Nonetheless, further revision of *D. nuchale/clarkii* is necessary (see comments on name usage in Materials and Methods). Apart from continuing ambiguity concerning *D. nuchale/clarkii*, the taxonomy of Central American species has been stable since Smith's (1941) revisions.

Smith (1941) had referred specimens from southern Mexico to central Panama to *D. vinitor* and thought that the distribution was continuous throughout this area. However, Lieb (1988, 1991) thought the distribution was highly fragmented, with disjunct segments in southern Veracruz, Mexico; Oaxaca, Mexico, to northern Guatemala; Nicaragua to western Panama on the Atlantic versant; southwestern Costa Rica; and Darién, Panama, to northwestern Colombia. Researchers since have considered *D. vinitor* a widespread, if discontinuously distributed, species of the Central American herpetofauna. Lieb (1988) considered *D. vinitor* a member of his "*Dendrophidion dendrophis* species group," which is defined on the basis of hemipenial characters, strong keeling on the dorsal scales, and the point of reduction of the dorsocaudal scales.

During my examination of Costa Rican material referred to *D. vinitor*, it was apparent that specimens from the Atlantic and Pacific versants differed substantially in hemipenial morphology. Furthermore, both of the hemipenial morphs of the Costa Rican specimens were quite distinct from hemipenes of specimens from the northern part of the range of *D. vinitor* (Mexico). Further study indicated that "*Dendrophidion vinitor*" comprised three very similar species distinguishable primarily by strong differences in hemipenial morphology and by a few subtle external characters. The three species occupy geographically discrete distributions, with no contiguity or overlap currently known. The purpose of this paper is to redefine and diagnose *D. vinitor* and to describe the two new species within this complex. Available data on the natural history of these species are summarized, and detailed descriptions of their hemipenes are presented.

MATERIALS AND METHODS

General methodology and methods of recording meristic data and measurements follow procedures previously described (e.g., Cadle, 2005, 2007), but I here amplify

some of the characters particularly useful for the three species covered in this paper. Dorsocaudal reductions were recorded as the subcaudal at which the reduction from eight to six dorsal scale rows on the tail occurred (Lieb, 1988). The point of posterior reduction of the dorsal scales was scored on each side of selected specimens as the ventral scute number at which the reduction occurred and the dorsal rows involved. For purposes of analyzing intraspecific differences in mean snout-vent length (SVL) of adult males and females, specimens with SVL > 450 mm were considered adults (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 analyses showed that RTL approaches an asymptote at approximately this size. When measurements or meristic data for particular specimens are referred to in the text, these data are based on my examinations (data encountered in the literature sometimes differ).

Intraspecific mean differences between male and female sizes and scale counts were tested for significance using *t* tests after testing for homogeneity of variances. *P*-values reported for intraspecific comparisons are two-tailed pairwise comparisons; in the few cases in which there was a priori expectation for one sex or the other to have a greater value for a character (e.g., males having a longer tail or more subcaudals than females), *p*-values for one-tailed tests did not differ from the two-tailed comparison. Similar procedures and two-tailed tests were used for interspecific comparisons, which were analyzed separately for each sex except in cases in which intraspecific sexual differences were nonsignificant (sexes pooled in these cases). Means, standard deviations, and results of intraspecific statistical comparisons for most meristic counts are presented in Table 1, and only summaries are given in the text.

For determining tail breakage frequencies, I counted as "broken" only tails with a

clearly healed cap on the stump; thus, I record the frequency of "broken/healed" tails. In my survey of literature, it was apparent that some authors included any specimens with a tail fracture in their tail breakage frequency calculations (e.g., at least one paper recorded multiple fracture points in a high percentage of specimens). However, this method artificially inflates estimates of tail breakage frequencies because of the inclusion of snakes whose tails were broken during or after capture, or even subsequent to storage in a museum jar. Although these specimens may offer clues as to the fragility of the tail in a particular species, they are not especially useful for comparative purposes.

I scored the number of keeled dorsal scale rows on the neck, at midbody, and just anterior to the vent. Keels in all species of *Dendrophidion* are best developed (i.e., encompassing more dorsal rows) on the posterior body, but the number of keeled rows on the neck or at midbody often show interspecific differences that provide discriminating characters. The three species covered in this paper are similar in their patterns of keeling. The basic pattern of temporal scales in *D. vinitor* and the new species here described is 2+2 (two primary, two secondary). However, temporal scales were often divided by a vertical suture (usually dividing the scale asymmetrically), or, less commonly, two temporal scales were fused or a temporal was fused with a supralabial. I recorded these divisions or fusions separately from the basic pattern. For example, a specimen might be recorded as having 2+2 temporals but with the upper primary and upper secondary fused on one side. Because of frequent asymmetry, temporal scales and supra- and infralabials were scored on each side of a specimen, and each side was treated as an independent observation; the total count of observations for these scale characters (Table 1) is thus about twice the number of specimens examined (damage sometimes prevented scoring on one or both sides of a given specimen).

TABLE 1. SCALE COUNTS, MEASUREMENTS, AND OTHER DATA FOR THE THREE SPECIES OF THE *DENDROPHIDION VINITOR* COMPLEX. BODY PROPORTIONS, VENTRAL AND SUBCAUDAL COUNTS, AND NUMBER OF PALE BANDS ARE GIVEN AS RANGE FOLLOWED BY MEAN \pm SD. BILATERAL COUNTS ARE SEPARATED BY A SLASH (/). FOR PRIMARY AND SECONDARY TEMPORALS AND SUPRA- AND INFRALABIAL SCALES, EACH SIDE OF EACH SPECIMEN WAS COUNTED AS AN INDEPENDENT OBSERVATION. SVL, SNOUT-VENT LENGTH; MEASUREMENTS IN MILLIMETERS. 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 vinitor</i> Smith, 1941	<i>Dendrophidion apharocybe</i> New Species	<i>Dendrophidion crybelum</i> New Species
Largest specimens: total length, SVL	997, 636 ♂ 847+, 595 ♀	1040, 653 ♂ 1045, 672 ♀	985, 625 ♂ 893+, 631 ♀
Tail length/total length	0.35–0.37 ♂ 0.36 \pm 0.006 (8) **	0.35–0.38 ♂ 0.37 \pm 0.008 (15) ***	0.34–0.36 ♂ 0.35 \pm 0.0007 (7) *
Tail length/SVL	0.33–0.36 ♀ 0.34 \pm 0.012 (8) 0.53–0.59 ♂ 0.56 \pm 0.019 (8) **	0.33–0.36 ♀ 0.35 \pm 0.010 (21) 0.53–0.61 ♂ 0.57 \pm 0.021 (15) ***	0.34–0.35 ♀ 0.34 \pm 0.003 (3) 0.51–0.58 ♂ 0.55 \pm 0.021 (7) *
Maxillary teeth	0.49–0.56 ♀ 0.53 \pm 0.025 (8)	0.49–0.57 ♀ 0.54 \pm 0.025 (21)	0.50–0.54 ♀ 0.52 \pm 0.02 (3)
Dorsal scales	38–45 40.8 \pm 1.96 (13)	33–44 39.1 \pm 2.39 (29)	38–44 40.8 \pm 1.91 (8)
Ventrals	17–17–15 (29)	17–17–15 (60)	17–17–15 (16)
Subcaudals	147–156 ♂ 152.0 \pm 3.09 (12) ***	149–160 ♂ 153.9 \pm 2.84 (31) ***	150–153 ♂ 151.6 \pm 0.92 (8) ***
Dorsocaudal reduction, 8 to 6 (subcaudal number)	153–162 ♀ 158.1 \pm 2.93 (17) 112–125 ♂ 118.6 \pm 3.53 (11) 109–122 ♀ 116.8 \pm 3.58 (13)	152–168 ♀ 160.8 \pm 3.79 (34) 115–127 ♂ 121.1 \pm 3.79 (23) 111–129 ♀ 119.9 \pm 4.47 (29)	156–162 ♀ 160.0 \pm 2.27 (8) 112–119 ♂ 116.9 \pm 2.29 (8) 115–119 ♀ 117.2 \pm 1.85 (6)
Dorsal scales, posterior reduction (ventral number)	40–65 ♂ 52.6 \pm 7.49 (12) **	32–63 ♂ 47.8 \pm 7.35 (29) ***	43–58 ♂ 49.0 \pm 4.69 (8) ***
Preoculars	34–59 ♀ 45.3 \pm 5.61 (17)	26–52 ♀ 41.5 \pm 7.43 (31)	42–56 ♀ 48.6 \pm 5.53 (8)
Postoculars	85–96 ♂ 92.8 \pm 2.75 (18) ***	85–102 ♂ 94.6 \pm 3.89 (36) ***	93–99 ♂ 96.0 \pm 1.65 (12) ***
Primary temporals	93–106 ♀ 99.0 \pm 3.64 (24)	93–105 ♀ 99.3 \pm 3.83 (36)	99–104 ♀ 102.1 \pm 1.96 (9)
Secondary temporals	1/1 (28)	1/1 (65)	1/1 (16)
Supralabials, supralabials touching eye	2/2 (28)	2/2 (63) 2/3 (2)	2/2 (16)
	2 (58)	1 (5) 2 (125)	2 (32)
	2 (58)	1 (5) 2 (125)	2 (32)
	8, 3–5 (2) 9, 4–6 (54) 10, 5–7 (2)	8, 3–5 (2) 8, 4–6 (2) 9, 4–6 (119) 9, 5–6 (1) 9, 5–7 (1) 10, 4–7 (3) 10, 5–7 (2)	8, 3–5 (1) 9, 4–6 (31)

TABLE 1. CONTINUED.

	<i>Dendrophidion</i> <i>vinitor</i> Smith, 1941	<i>Dendrophidion</i> <i>apharocybe</i> New Species	<i>Dendrophidion</i> <i>crybelum</i> New Species
Infralabials	9 (52) 10 (3) 11 (1)	7 (1) 8 (7) 9 (116) 10 (5)	9 (32)
No. of pale bands on body	51–70 60.3 ± 4.69 (28)	46–69 54.4 ± 4.48 (54)	36–62 48.2 ± 7.53 (13)

The width of the pale neck bands has been important in distinguishing “*Dendrophidion vinitor*” auctorum from other species. However, neck bands, particularly the first two behind the head (which are often broader than other bands), can be very irregular in outline. Bands on the posterior two-thirds of the body are more uniform and narrower than the anterior bands (and less easily discriminate species). Thus, in scoring the width of neck bands, I used the third and fourth band behind the head as references and counted the scales or fractions thereof encompassed by the pale portion of the band (not including the dark bordering stipple) in the dorsolateral region at the level of dorsal scale rows 6 and 7. I counted scales in a horizontal line, not along the diagonal, as is often counted while doing dorsal scale counts; this was to minimize the effect of irregularities in band shape (e.g., zigzag or not) on scoring width. Thus, my summaries of band widths are somewhat less than some of those encountered in the literature. For example, Costa Rican “*D. vinitor*” are sometimes said to have pale bands 2–3 scale rows wide (Savage, 2002: 655), whereas in my scorings, most specimens have bands 1–2.5 rows wide.

Maxillary dentition is similar in the three species covered in this paper. Teeth gradually enlarge anterior to posterior, but typically, four posterior teeth are abruptly enlarged (and nongrooved). The enlarged teeth are not offset, and a diastema is absent (e.g., see Fig. 8). However, there is some variation within all three species in the abruptness with which the enlarged posterior teeth transition to the smaller anterior

series. I assessed some specimens as having either three or five posterior enlarged teeth (recognizing some subjectivity as to what constitutes an “enlarged” tooth). My impression is that posterior teeth in *D. vinitor*, as redefined herein, are not enlarged to the same degree or as abruptly as in the new species, *D. aphaocybe* and *D. crybelum*. However, this is a subjective impression only—something that is difficult to quantify with wet preparations given the apparent variation. I have not attempted to assess this more fully, although I comment on some of the noticeable variation in the species accounts. Tooth counts are the total number of maxillary teeth, including empty tooth sockets and the enlarged posterior teeth.

Everted hemipenes described in detail and illustrated herein were fully everted in the field at the time of collection. For detailed study they were removed from the specimen and inflated with colored jelly (Myers and Cadle, 2003); manual eversion was used for a few specimens for comparative purposes. Retracted hemipenes were slit midventrally and pinned flat for study. In addition to the hemipenes described in detail, I made reference to others that were everted to varying degrees and studied in situ. Hemipenial measurements were taken with dial vernier calipers to the nearest 0.1 mm. In the species accounts, I give brief characterizations of the hemipenes, emphasizing salient features only. For ease of comparison, detailed descriptions of everted and retracted organs of all three species are deferred to a separate section at the end. However, because these species are most notably distinguished by

details of hemipenial morphology, the detailed descriptions should be considered integral parts of the species accounts. Hemipenial terminology is explained in the detailed accounts.

"*Dendrophidion vinitor*" is discussed in many regional faunistic works for Central America, some of which are cited in the synonymies in the species accounts. However, with few exceptions, the variational data (e.g., scale count ranges or color notes) in these works seem to derive from other sources (e.g., Lieb, 1988). Thus, it is usually not clear whether a particular account is based on specimens from the focal region. For example, Taylor (1954: 729–730) gave data on size, meristics, and color in life "taken from field notes" for "*D. vinitor*" in his account of Costa Rican snakes. However, the color notes he quoted are those for the holotype, which is from Guatemala (Smith, 1941) and the Costa Rican form is a different species described herein. The size and meristic data of Taylor (1954) are a summary from throughout the range given in Smith (1941; Mexico to Panama), with no indication that that is the case. Unless it seems clear that descriptive comments apply to a specific geographic area, I do not cite them here because three species have been confused in previous literature. Similar caveats apply to some natural history data.

Despite progress in understanding the systematics of *Dendrophidion* reviewed in the introduction, my own preliminary study makes it clear that further revisions are necessary. For purposes of this work, some taxonomic conventions, which will ultimately be modified as revisionary work proceeds, are necessary. For convenience in the diagnoses, I use the two species groups of *Dendrophidion* recognized by Lieb (1988): the *D. percarinatum* group comprising *D. bivittatum*, *D. brunneum*, *D. paucicarinatum*, and *D. percarinatum*; and the *D. dendrophis* group comprising *D. dendrophis*, "*D. nuchale/clarkii*," and *D. vinitor* (and by extension, the two new species described here). Lieb did not assign the

Colombian endemic *D. boshelli* to a species group. Species in the *D. percarinatum* group differ from those in the *D. dendrophis* group in having a dorsocaudal reduction from 8 to 6 anterior to subcaudal 25 (posterior to subcaudal 25 in the *D. dendrophis* group, further refined for three species herein), by less strongly keeled dorsal scales, and often by smaller hemipenial spines, among other characters (Lieb, 1988). In addition, I recognize as the "*Dendrophidion vinitor* complex" the two new species described herein along with *D. vinitor* as restricted here. McCranie (2011) resurrected the name *D. clarkii* for part of "*D. nuchale*" *sensu* Lieb (1988), but further revision will be necessary before the application of names in this complex becomes clear; see comments in Savage (2002: 655) and McCranie (2011: 106–107). Thus, in this paper, I refer to the complex of species represented by the names *D. nuchale* and *D. clarkii* as "*D. nuchale* auctorum." Additional comments on taxonomy and character distributions are given in the discussion.

Specimens of *D. vinitor* as restricted herein are listed in Appendix 1, which also includes museum abbreviations used throughout this paper. Specimens of the new species are listed in their species accounts since this material comprises the type series. Notes on the localities and coordinates for specimens examined and for selected localities from literature are in Appendix 2.

Redescription of *Dendrophidion vinitor* Smith, 1941

Figures 1, 2A, 3–4, 6, 18–19

Drymobius dendrophis. Günther, 1885–1902: 127 (part; Guatemala); Boulenger, 1894: 15–16 (part; specimens *b*, *d*, *f* from "Vera Paz" and "Guatemala"). See discussion of historical records under Distribution.

Dendrophidion dendrophis. Duméril et al., 1870–1909: 730–732 (part; specimens from "Peten" and "Vera Paz"). The

“Peten” specimen (MNHN 7353), illustrated by Lieb (1988: fig. 1), is a syntype of *Herpetodryas poitei* Duméril, Bibron, and Duméril, 1854. See discussion of historical records under Distribution.

Dendrophidium dendrophis. Dugés, 1892: 100–101 + pl. (Motzorongo [Veracruz], Mexico). See Smith (1943: 416) and discussion of historical records under Distribution herein.

Dendrophidion vinitor. Smith, 1941: 74–75 (type locality: Piedras Negras, Guatemala) (part; holotype and paratypes from Guatemala and Mexico). Smith, 1943: 415–416 + fig. 13. Taylor, 1944: 184 (EHT-HMS 27496–98). Smith and Taylor, 1945: 46. Stuart, 1948: 63. Smith and Taylor, 1950: 318 (holotype). Stuart, 1950: 23. Darling and Smith, 1954: 191 (UIMNH 33862). Taylor, 1954: 729–730 (part; color description of holotype and some meristic data quoted from Smith, 1941). Cochran, 1961: 172 (part; holotype and paratypes, USNM 110662, 7099, 46589). Duellman, 1963: 246. Stuart, 1963: 94 (part; Mexico and Guatemala). Peters and Orejas-Miranda, 1970: 79 (part). Alvarez del Toro, 1972: 142, 144. Johnson et al. “1976” [1977]: 134, 136–137. Perez-Higareda, 1978: 69, 72. Alvarez del Toro, 1982: 190–191. Pérez-Higareda et al., 1987: 16. Smith, 1987: xxvii (part; based on Günther’s “*Drymobius dendrophis*”). Flores and Gerez, 1988: 218–219, 261. Lieb, 1988: 171 (part). Villa et al., 1988: 63 (part). Campbell and Vannini, 1989: 11. Johnson, 1989: 64. Lieb, 1991: 522.1–522.2 (part). Pérez-Higareda and Smith, 1991: 31, pl. 4. Flores-Villela, 1993: 30. Lee, 1996: 310–311 (Yucatan, base). Campbell, 1998: 207, fig. 127 (part; specimen from Veracruz, Mexico). Lee, 2000: 282–283, fig. 315 (part; Belize). Stafford and Meyer, 2000: 199–200 (Belize). Savage, 2002: 655–656 (part). Köhler, 2003: 200 (part). Meerman

and Lee, 2003: 67, 70. Stafford, 2003: 111 (part; specimens from Mexico, Guatemala). Guyer and Donnelly, 2005: 185 (part). McCranie et al., 2006: 147–148 (part). Köhler, 2008: 215 (part). Savage and Bolaños, 2009: 14 (part). McCranie, 2011: 111 (part).

Holotype (Fig. 1). USNM 110662, from Piedras Negras [El Petén], Guatemala. Collected 21 May 1939 by Hobart M. Smith and Rozella B. Smith (field number 7280) as part of collections assembled during tenure of the Walter Rathbone Bacon Traveling Scholarship (Smith, 1943: 416). The holotype is presently in fair condition. I did not examine it directly but inspected dorsal and ventral photographs provided by USNM and had selected characters verified by USNM personnel. According to Smith (1941), it is a subadult female 510+ mm total length, 169+ mm incomplete tail length (341 mm SVL). The holotype has several irregular longitudinal ventral incisions from the anterior body nearly to the vent and on the anterior ventral part of the tail. The tail tip is missing. Smith (1941) described the holotype in detail, but one character in his description is apparently in error: “nine supralabials, 3rd, 4th and 5th entering orbit”—a character found in no other specimen (Table 1). Both sides of the holotype in fact have nine supralabials but it is the 4th, 5th, and 6th that touch the eye on both sides (verified by Steve Gotte, March 2011), which is the near-universal condition in the specimens I examined (Table 1).

Etymology. The specific name *vinitor* is a Latin noun meaning “vine cultivator” or “vine dresser.” Latin lexicons show that the word is derived from the noun *vinum* (wine). The complete derivation therefore is the stem *vin-* + connective *-i-* + the suffix *-tor*. The termination is a classic noun suffix meaning an agent or doer of something (vine care and pruning in this case). The name was not a good choice for a forest-dwelling snake.

Hobart Smith gave no etymological information in the original description, but

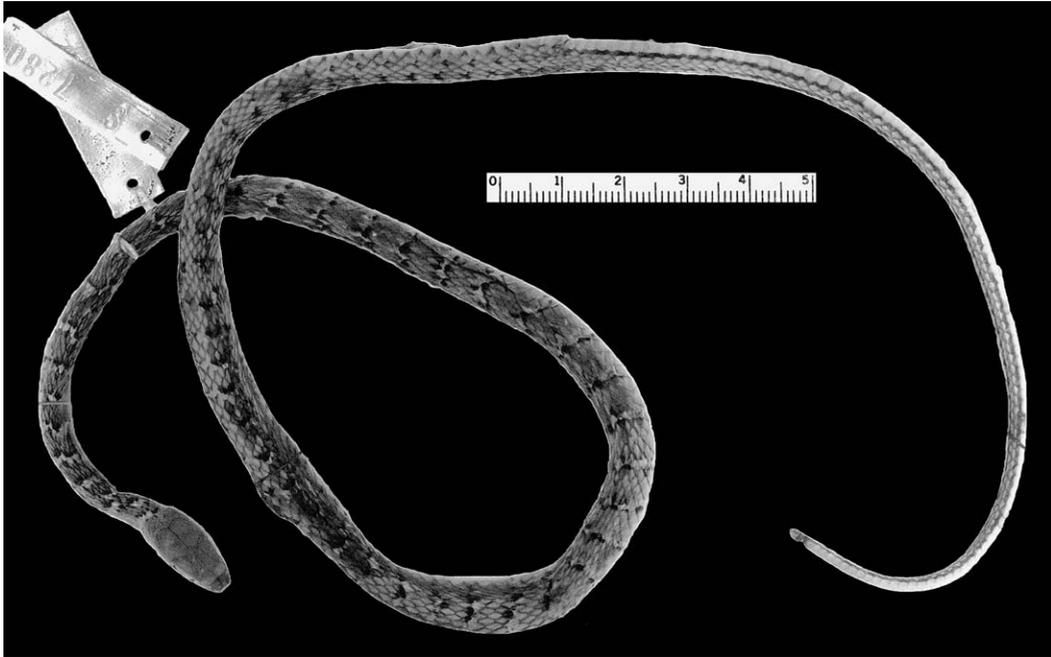


Figure 1. Holotype of *Dendrophidion vinitor* Smith (USNM 110662) from Piedras Negras, Guatemala (Petén Department). Scale = 5 cm.

provided different intended meanings to other taxonomists: Lee (1996: 311) quoted Smith as stating that the name means “a dweller in vines”; McCranie (2011: 113) quoted Smith as stating that he could not know for sure what he had in mind but that he had intended “vine-climber.” In any case, Lee (1996: 311) was incorrect in stating that *vinitor* is derived from “*vinea*,” which is both an adjective pertaining to wine and a substantive meaning vineyard or vines.

Diagnosis. *Dendrophidion vinitor* is characterized by (1) Dorsocaudal reduction from 8 to 6 occurring posterior to subcaudal 30 (range, 34–65); (2) single anal plate (rarely divided); (3) relatively low subcaudal counts (<130 in males and females); (4) pale dorsal crossbands usually less than one dorsal row wide and bordered posteriorly (often anteriorly as well) by dark brown or black; (5) immaculate ventrals and subcaudals except for lateral dark pigment common to all species of *Dendrophidion*; and

(6) a bulbous hemipenis with a highly ornate apex, including: asulcate flounces; a series of free-standing membranous ridges, the median one of which is taller than others and bisects the apex; and a raised rounded boss or protuberance on the sulcate edge of the apex (the sulcus spermaticus ends beneath its free edge). The combination of few subcaudals and (in most individuals) a single anal plate will distinguish *D. vinitor* from all other species of *Dendrophidion* except *D. apharocybe*, *D. crybelum*, and *D. paucicarinatum*.

Dendrophidion vinitor differs from the four species of the *D. percarinatum* group in having the dorsocaudal reduction from 8 to 6 posterior to subcaudal 30 and more strongly keeled dorsal scales, and from all species of the *D. percarinatum* group except some individuals of *D. paucicarinatum* in having a single anal scale. *Dendrophidion paucicarinatum* usually has a more uniformly colored dorsum lacking distinct pale crossbands, has narrow dark lines across

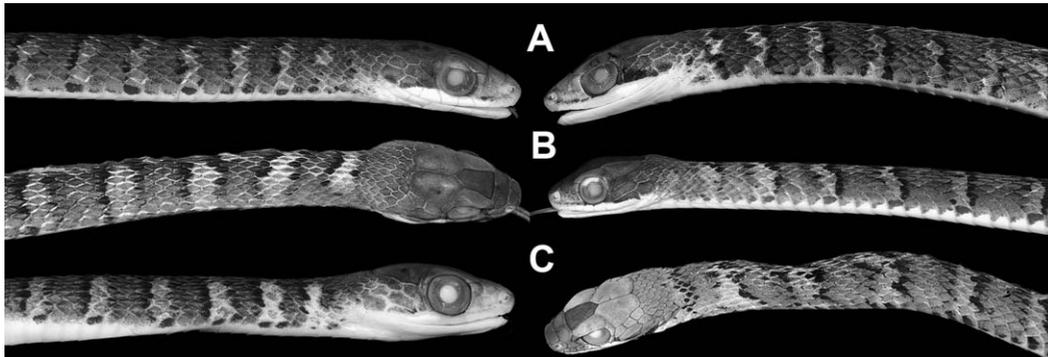


Figure 2. Comparison of pale bands on the anterior body of representative specimens of the *Dendrophidion vinitor* complex. Each pair (left, right) representative of one species. (A) *Dendrophidion vinitor* as restricted herein (UMMZ 121145, UMMZ 122767; both Veracruz, Mexico). (B) *Dendrophidion apharocybe* new species (KU 112974, Nicaragua; LACM 148593, Costa Rica [holotype]). (C) *Dendrophidion crybelum* new species (LACM 114108, LACM 148599 [holotype]; both Costa Rica).

the venter in adults and many juveniles, and has a higher number of ventrals (>175 compared with <170 in *D. vinitor*). *Dendrophidion vinitor* differs from *D. boshelli* in having 17 midbody scale rows (15 in *D. boshelli*). *Dendrophidion vinitor* has fewer subcaudals (<130) and usually a shorter adult relative tail length ($<60\%$ of SVL) than *D. nuchale* auctorum and *D. dendrophis* (>130 and usually $>60\%$ of SVL, respectively); the anal plate may be either single or divided in these last two species.

Dendrophidion vinitor differs from the new species described herein, *D. apharocybe* and *D. crybelum*, in having narrower pale bands on the neck/anterior body (Fig. 2). Although “*Dendrophidion vinitor*” is often stated to have broader bands than other congeners, such as *D. percarinatum* (e.g., Savage, 2002: 655), those statements are based on a comparison of the two new species described herein, *D. apharocybe* and/or *D. crybelum*, with other species. *Dendrophidion vinitor* as redefined here has narrow pale crossbands, generally one scale row or less in width (as pointed out by Smith [1941] for the holotype), compared with crossbands more than one row wide in *D. apharocybe* and *D. crybelum* (Fig. 2). In *D. vinitor*, the crossbands become indistinct posteriorly or restricted to the dorsolateral/vertebral region, whereas in *D. apharocybe* and *D. crybelum*, the posterior crossbands

usually become invested with dark pigment so that each crossband appears as a transverse dark band with embedded pale ocelli. These patterns of *D. apharocybe* and *D. crybelum* are easily seen in the color plates of Savage (2002: pl. 416), Solórzano (2004, fig. 60), Figure 9 herein for *D. apharocybe*, and Figures 15 and 16 herein for *D. crybelum*. *Dendrophidion vinitor* has a significantly greater mean number of pale bands on the body than either *D. apharocybe* ($p < 0.001$) or *D. crybelum* ($p < 0.001$), although the ranges of band numbers overlap broadly among the three species (Table 1).

Additionally, *Dendrophidion vinitor* differs from *D. apharocybe* and *D. crybelum* in hemipenial morphology (see detailed descriptions). The everted hemipenis of *D. vinitor* is rather short and stout and has a highly ornate bulbous apex ornamented with largely nonanastomosing (free-standing) membranous ridges (reduced remnants of calyces primitively present). The apex has a prominent rounded protuberance, or *apical boss*, on the sulcate side; the centrolateral sulcus spermaticus ends underneath its free edge. One of the free-standing ridges bisects the apex in a line from the front edge of the apical boss directly across the apex to the asulcate side. The other ridges extend obliquely outward toward the asulcate side from this median ridge.

Dendrophidion aphaerocybe has a hemipenis similar in shape to that of *D. vinitor*, but the apex is strongly inclined toward the sulcate side, lacks an apical boss, and, in contrast to *D. vinitor*, is nude except for low rounded ridges. *Dendrophidion crybelum* has a relatively long cylindrical hemipenis with a small, nonbulbous apex bearing short ridges, and a large number of enlarged spines (≥ 70) on the hemipenial body compared with < 50 in *D. vinitor*.

Description (12 males, 17 females). Table 1 summarizes size, body proportions, and meristic data for *D. vinitor*. Largest specimen (UIMNH 37165) a male 997 mm total length, 636 mm SVL. Largest female (UIMNH 35546) 847+ mm total length, 595 mm SVL. Tail 35–37% of total length (53–59% of SVL) in males; 33–36% of total length (49–56% of SVL) in females. Dorsal scales in 17–17–15 scale rows, the posterior reduction usually by fusion of rows 2+3 at the level of ventrals 85–106 (see sexual dimorphism below). Ventrals 147–156 (averaging 152) in males, 153–162 (averaging 158.1) in females; usually one preventral anterior to ventrals (about 33% of specimens have two preventrals; rarely, preventrals were absent). Anal plate nearly always single (divided in two of 29 specimens). Subcaudals 112–125 (averaging 118.6) in males, 109–122 (averaging 116.8) in females. Dorsocaudal reduction at subcaudals 40–65 in males (mean 52.6), 34–59 in females (mean 45.3). 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 38–45 (averaging 41), typically with four posterior teeth abruptly enlarged; sometimes the enlargement appears more gradual and with three or five somewhat enlarged. Smith (1943: 416) illustrated head scalation for EHT-HMS 27496 (now UIMNH 17632).

Two apical pits present on dorsal scales. About 85% of specimens have keels on all dorsal rows of the neck except row 1; the

others lack keels on row 2 additionally. Virtually all specimens have all dorsal rows except row 1 keeled at mid- and posterior body; an exception is a small juvenile female (294 mm SVL) in which all rows are keeled at mid- and posterior body (keels very weak on row 1 in both positions). Fusions or divisions of temporal scales were moderately common, with the following frequencies: upper primary divided (10), upper secondary divided (10), upper or lower primary + secondary fused (3), lower primary divided (2), lower secondary fused with ultimate supralabial (1), upper + lower secondary fused (1, partial fusion).

Hemipenis unilobed with a somewhat bulbous apex; spinose region followed distally by flounces, poorly developed calyces, and a highly ornate apex, including free-standing spinulate ridges and an apical boss on the sulcate side. Sulcus spermaticus simple, centrolineal, with a slightly flared tip in everted organs.

Geographic and Other Variation. Tails are proportionally shorter in small individuals. Specimens less than 300 mm SVL have tail lengths 29–34% of total length, 40–51% of SVL ($N = 8$, males and females combined). No strong geographic trends were evident among the characters examined. Johnson et al. "1976" [1977] reported a male from near Ocozocuatla (Chiapas, Mexico) with 157 ventrals and 127 subcaudals, which are slightly greater than counts for specimens I examined (Table 1). The posterior reduction of the dorsal scales always involves lateral rows, but in addition to the rows most commonly involved (2+3), reduction occasionally occurs by fusion of rows 3+4 and rarely by loss of row 3 or fusion of rows 1+2.

Two specimens from Guatemala (UTACV 22155, 22755), both from the same general locality, have divided anal plates and are the only specimens examined having this condition (the only known specimen from nearby in Belize, KU 300784, has a single anal plate). Ordinarily, a divided anal plate in northern specimens of *Dendrophidion* suggests an identity with *D. nuchale* auc-

torum but the color pattern and low subcaudal counts (115–116) of these specimens confirms their identity as *D. vinitor*. Whether this is a peculiarity of this population or whether divided anal plates occur with low frequency in others is unknown (but see comments on historical records in Distribution). No other characteristic of these specimens is particularly unusual, although in UTACV 22755, the last ventral plate is also divided. At least three other species of *Dendrophidion* (*D. dendrophis*, *D. nuchale* auctorum, *D. paucicarinatum*) are variable in the single/divided nature of the anal plate.

Sexual Dimorphism. A few characters showed significant sexual dimorphism (Table 1). Although the largest specimen is a male, mean sizes of adult males (542 mm SVL) and females (535 mm SVL) are not significantly different (with the caveat that sample sizes are small and sample variances high). Females have significantly greater ventral counts than males and the posterior reduction of the dorsal scales occurs farther posteriorly in females (mean ventral 99.0, $N = 24$) than in males (mean ventral 92.8, $N = 18$; $p < 0.001$). In males, the dorsocaudal reduction (8 to 6) occurs at a significantly more posterior position than in females. Males also have a proportionally longer tail than females, but males and females do not differ in subcaudal counts.

Coloration in Life. Color photographs of *D. vinitor* from Veracruz, Mexico, were published by Pérez-Higareda and Smith (1991, pl. 4) and Campbell (1998, fig. 127) and from Belize by Lee (2000, fig. 315; = KU 300784 fide Julian C. Lee, personal communication). Alvarez del Toro (1972, fig. 133; 1982, fig. 143) illustrated a specimen from Chiapas, Mexico, in black and white, and Dugés (1892) provided a somewhat stylized colorized drawing of a specimen from Veracruz.

Smith (1941) gave detailed color notes for the holotype in life (repeated virtually verbatim by Taylor [1954: 729–730]), here paraphrased: Head and temporal region down to upper edges of two postocular

labials and all of the last labial brownish gray, the sutures darker and with a slightly reddish tinge (lower edge of head cap dark brown, mixed with dull brownish brick-red); upper parts of anterior supralabials with a reddish tinge; supralabials below the head cap pure white; 59 bands on body, 54 on tail; bands on neck covering one scale length, brownish gray laterally, yellow dorsally and bordered anteriorly, posteriorly, or both by narrow irregular areas of black; size of yellow dorsal area in light bands decreasing and eventually disappearing posteriorly; light bands gradually disappearing posteriorly; tail bands and those on posterior part of body black; black borders of light bands interspersed or themselves bordered by brick-red, this color especially prominent medially; central ground color between bands brownish gray anteriorly, becoming light brown tinged with red on middle and posterior body; tail with a stripe of dark brown (black) interspersed with brick-red, involving edges of subcaudals and lower half of first dorsocaudal row; gular region white; belly yellow; subcaudals yellow, paler posteriorly.

Alvarez del Toro (1972: 144) described a specimen from Chiapas, Mexico: “general coloration reddish brown, a little grayish toward the sides. On the neck are three yellow bands, and an additional 62 yellowish ones on the body; all the bands or bars bordered posteriorly by narrow black bands. The lips and throat are white, the venter yellow orange” (description repeated by Alvarez del Toro [1982: 191] except the neck bands are said to be orange).

Coloration in Preservative. Dorsal ground color of preserved specimens yellowish brown, brown, or gray (smaller specimens usually paler than larger ones). Pale crossbands yellowish brown to gray. In adults, posterior pale crossbands become indistinct, marked only by dark transverse stippling with occasional pale flecks dorsolaterally and indistinct or absent on the flanks (Fig. 3). The number of pale bands/ocelli on the body ranged from 51 to 70 with a mean and median of 60 and a mode of 59

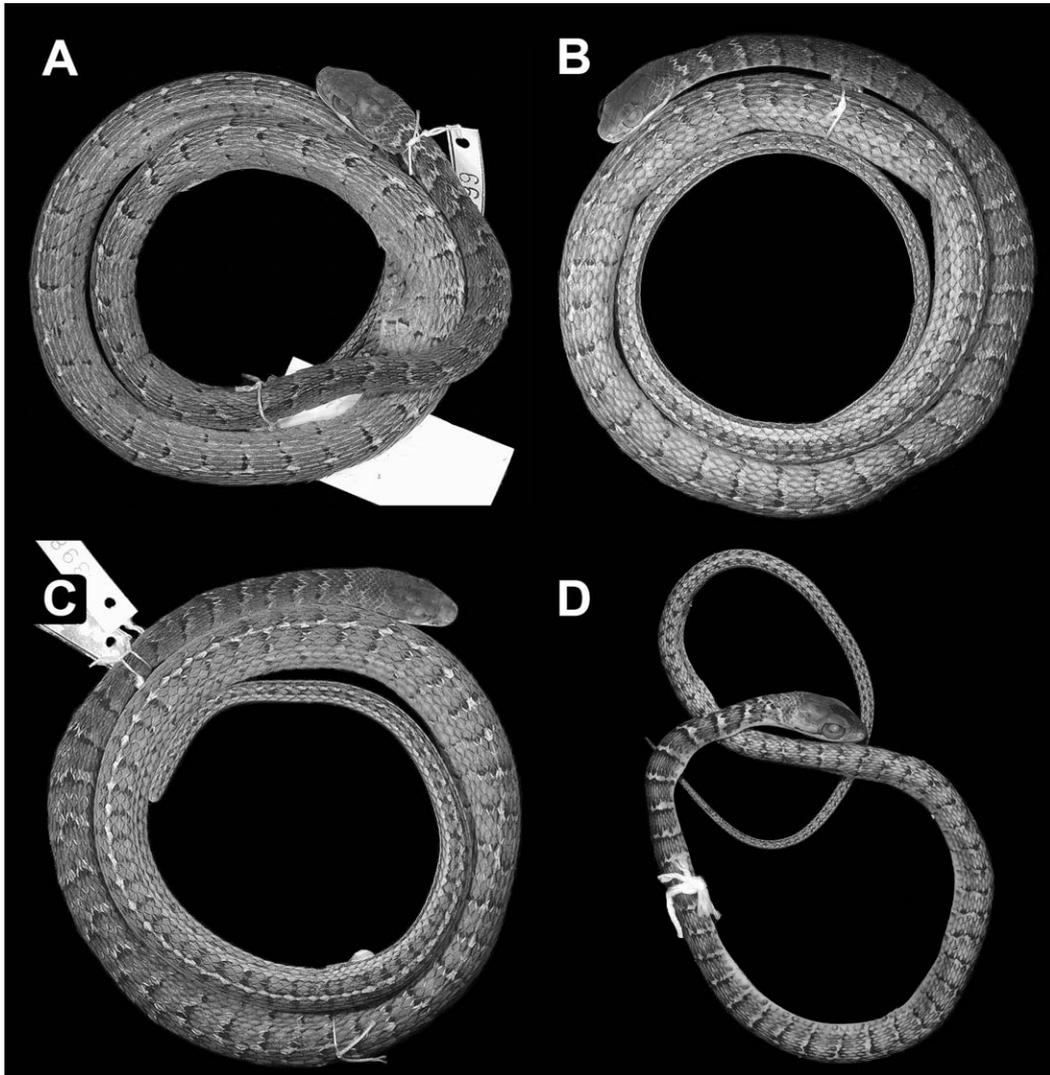


Figure 3. Representative specimens of *Dendrophidion vinitor* from Mexico. (A) AMNH R-66845 (Oaxaca). (B) UMMZ 122767 (Veracruz). (C) UMMZ 121145 (Veracruz). (D) UCM 39912 (Oaxaca; juvenile, 218 mm SVL).

(posterior indistinct bands included; no significant difference between males and females). In about 85% of the specimens neck bands were one scale row or less in width; in the remainder, the neck bands were 1–1.5 rows wide. Vertebral region usually retains whitish spots that sometimes form a more or less continuous vertebral streak punctuated by larger irregular pale spots (like beads on a string) at the position

of crossbands (Figs. 3B, 3C, 4). The dark ventrolateral tail stripe mentioned by Smith (1941; see Fig. 1) varies from distinct to indistinct. On the posterior body most specimens have a series of small, widely spaced dark spots on scale row 2 or the suture line between rows 2–3 (occasionally forming a more or less broken line). This line is often highlighted by paler scales in rows 3–4 on the posterior body (e.g.,

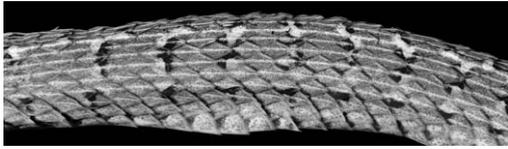


Figure 4. A typical posterior body pattern of *Dendrophidion vinitor* (AMNH R-66845). Section is from the posterior third of the body. The vertebral row is marked by a whitish line punctuated with larger blotches at the position of pale crossbands which, on the posterior body, are mainly restricted to a dorsolateral position and heavily invested with dark pigment.

Fig. 3B). Venter yellowish to whitish and immaculate except for lateral dark pigment. Most juveniles have more distinct pale crossbands on the posterior body than do adults, and in general, their patterns are more contrasting than those in adults (Fig. 3D).

Distribution (Fig. 5). Central Veracruz state, Mexico, eastward to southeastern Guatemala and southern Belize. *Dendrophidion vinitor* occurs on the Atlantic and Pacific versants of the Isthmus of Tehuantepec but otherwise appears to be restricted to the Atlantic versant. The northernmost record is from Las Minas, Veracruz (Pérez-Higareda and Smith, 1991), assuming I have identified the locality correctly. Recorded elevations for specimens I examined are

lowland (<100 m) to about 800 m on the slopes of Volcán San Martín in southern Veracruz (most localities 400–600 m), with the single Belize specimen from slightly higher, between 940 and 1,035 m (see Appendix 2, Little Quartz Ridge).

Several historical records of *D. vinitor* deserve comment because they document localities from which no recent specimens are available. Dugés (1892; “*Dendrophidium dendrophis*”) gave a detailed description and color illustration of a specimen from Motzorongo, Veracruz, which leaves little doubt about its identity as *D. vinitor*. Specimens from Guatemala are scarce, and I am aware of only two specimens obtained since the holotype was collected in 1939 (Appendix 1), despite considerable biological inventory of that country (e.g., Duellman, 1963; Stuart, 1963; Campbell, 1998). There has been controversy about the origin and identity of several specimens obtained in Guatemala during the 19th century (see synonymy under the names *Drymobius dendrophis* and *Dendrophidion dendrophis*).

Duméril et al. (1870–1909: 730–732) reported a specimen obtained by Arthur Morelet from “Peten” and two others (“seen alive,” collector not indicated) from “Vera

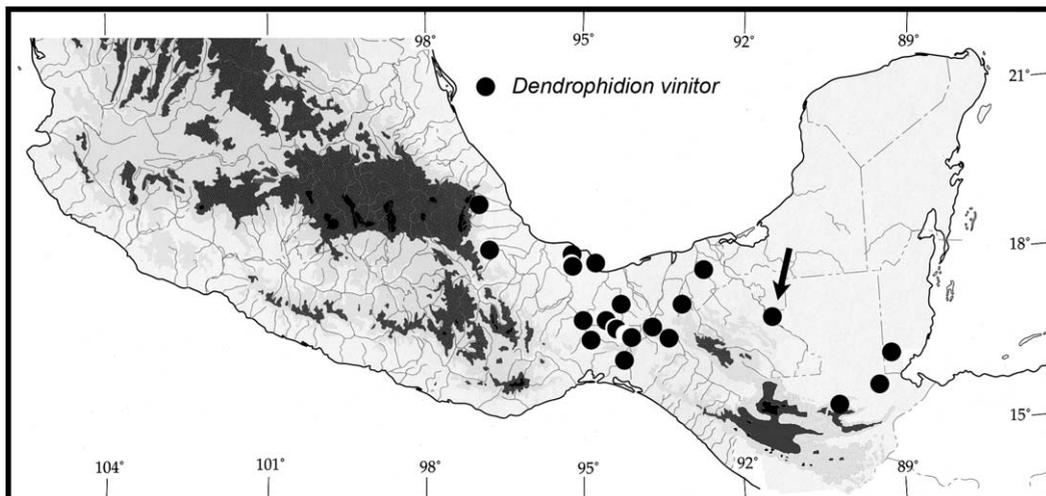


Figure 5. Distribution of *Dendrophidion vinitor* in southern Mexico, Guatemala, and Belize. A few symbols represent multiple contiguous localities. Arrow indicates the type locality.

Paz”; their composite “*Dendrophidion dendrophis*” also included specimens from northern South America. Some details in their account (e.g., single anal plate and low subcaudal counts [119–127]), suggest *D. vinitor*, although Lieb (1988: 164–165) pointed out some confusion in their subcaudal counts and tail lengths. The “Peten” specimen is one of three syntypes of *H. poitei* Duméril et al. (1854: 208), a name that Lieb (1988: 165) made an objective junior synonym of *D. dendrophis* (Schlegel) by designating MNHN 41 from French Guiana as the lectotype of both names, thus preserving Smith’s name *D. vinitor* for the Central American species. Lieb (1988, fig. 1) illustrated the “Peten” syntype of *H. poitei*, whose banding pattern is consistent with *D. vinitor* (pale bands becoming restricted dorsolaterally on the posterior body).

Lieb (1991: 522.1) thought the Petén specimen of Duméril et al. (1870–1909) “almost certainly originated from ... Flores [Guatemala], where [Morelet’s] collectors were most active.” I think it’s far from certain that Morelet’s specimen came from Flores, although he spent a long sojourn there. Morelet traveled extensively in the Mexican states of Tabasco and northern Chiapas, ascending the Río Usumacinta to near the present Guatemalan border (all within the known range of *D. vinitor*) before traveling overland to Flores (Morelet, 1871). The specimen could have come from anywhere along this route, and I discount the “Flores” locality based on this historical material. Owing to its accessibility and location along a major route, perhaps more biologists have passed through Flores than any other part of Petén. Duellman (1963: 246) listed *D. vinitor* as “hypothetical” in southern Petén but obtained no material during a 2-week survey of rainforests there, nor did Stuart (1934, 1935, 1958) working in the same region. Thus, apart from western Petén along the Río Usumacinta (type locality), the presence of *D. vinitor* in Petén is unsubstantiated.

Günther (1885–1902) reported four specimens from “Vera Paz, between Cobán and Lanquín” (in present-day Alta Verapaz

province) and another from “Guatemala” collected by Osbert Salvin. Their identity has been questioned mainly on the basis of scale counts and a divided anal plate reported by Günther. It should be noted that Boulenger (1894: 16, specimens *b–f*) gave ventral and subcaudal counts for the same specimens, in some cases substantially different from Günther’s. Based on Boulenger’s subcaudal counts, it seems likely that only specimens *b*, *d*, and *f* (subcaudals 113, 116, 119, respectively) are *D. vinitor* because it is the only *Dendrophidion* from that area with such low subcaudal counts (counts of the other two specimens are consistent with *D. nuchale* auctorum, which is known from the region). The only character seeming to disallow the identity of the three Salvin specimens as *D. vinitor* is the divided anal plate reported by Günther (not recorded by Boulenger). However, the only two recently collected Guatemalan specimens of *D. vinitor* are from near Salvin’s Alta Verapaz locale and have divided anal plates (see above Description), so this character is no longer an obstacle. Thus, I accept this locality and include it in Figure 5. I am aware of only one published reference based on a re-examination of Salvin’s material (Stafford, 2003; see Appendix 1), but Stafford cited only one of the specimens in his study.

I confirmed several erroneous reports of “*Dendrophidion vinitor*” from Belize and the outer Yucatán Peninsula first pointed out by Lieb (1991): Wilson (1966; based on LSUMZ 8901–03; = *D. nuchale* auctorum); McCoy (1970; UCM 25708, 25794, 25805–06, 25846–47, 25874; = *D. nuchale* auctorum); and Lee (1980: 34, 65; UCM 28122; = *Mastigodryas melanolomus*). However, a recently collected specimen documents *D. vinitor* in southern Belize (KU 300784; Fig. 6). KU 300784 is a female, and its identification as *D. vinitor* is based on the narrow pale crossbands on the neck and other features of coloration, 119 subcaudals, and dorsocaudal reduction at subcaudal 47. This specimen is the basis for the record reported as a personal communication by

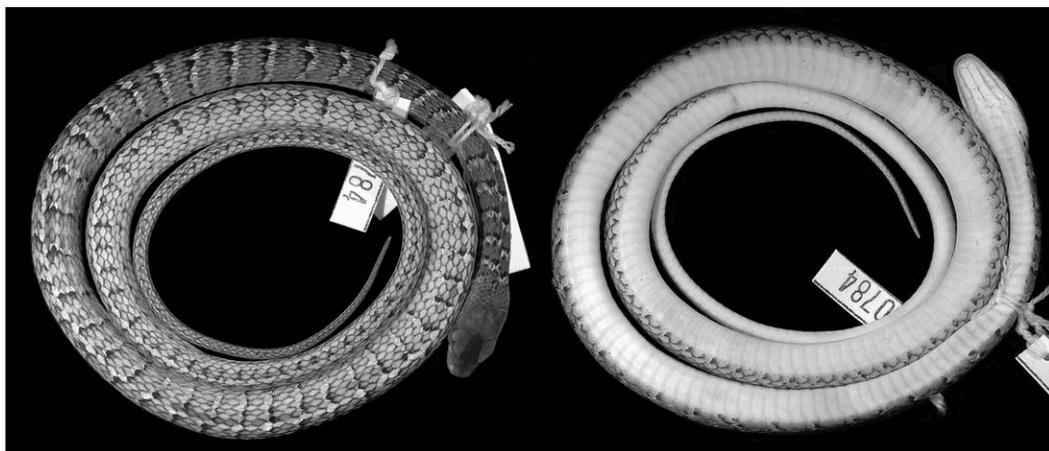


Figure 6. *Dendrophidion vinitor* (KU 300784), the only known specimen from Belize. A color photograph of this specimen in life is in Lee (2000: fig. 315).

Stafford and Meyer (2000: 200) and for the color photograph in Lee (2000, fig. 315; Julian C. Lee, personal communication, January 2011); see Meerman and Lee (2003).

Natural History. The few specimens of *D. vinitor* accompanied by habitat information suggest that it inhabits relatively intact forests, variously described as “rainforest” or “lower montane rainforest” (e.g., Duellman, 1960: 34, for Donají, Oaxaca; Johnson, 1989: 64, for Chiapas). Goodwin (1969: 259) gave brief habitat notes on Oaxacan localities for specimens collected by Thomas MacDougall, as follows: La Gloria (coffee plantations, milpas, rainforest; elevation about 1,500 ft.); Cerro Azul (“cloud forest,” high north-facing slopes swept by gale-force winds, elevation of peaks to about 8,000 ft., collections from 4,000 to 7,000 ft.); Cerro Atravesado (open pine stands, grass and rocks, patches of “cloud forest” at north end, some ranches on lower slopes. Elevation about 4,750 ft.).

Few natural history or behavioral data seem to have been recorded for *D. vinitor*. Darling and Smith (1954: 191) found a juvenile coiled by a trail during the day on Volcán San Martín, Veracruz, Mexico. Two specimens (FMNH 126554–55) are accompanied by notes indicating they were “in heavy shade, in daytime, on ground.” Johnson et al. “1976” [1977] reported a male from

near Ocozocuatla (Chiapas, Mexico) actively foraging on the forest floor at 3:30 p.m. on 28 December 1974. Alvarez del Toro (1972, 1982) reported *D. vinitor* as “relatively common” in the hills surrounding Presa Malpaso, a large hydroelectric reservoir in the Río Grijalva basin of northern Chiapas, Mexico; he stated that it inhabits the shady parts of the forest and rapidly hides in the leaf litter upon disturbance. At Los Tuxtlas Biological Station Perez-Higareda (1978) encountered *D. vinitor* much more frequently in the dry season and first half of the rainy season (April–October), with a peak encounter rate in October, than in the period of more consistent heavier rains (November–March). Stomach contents of two specimens I examined (576 and 248 mm SVL) each comprised a single small frog (*Pristimantis* or *Craugastor*; 20 and 15 mm SVL, respectively). In contrast to some species of *Dendrophidion*, the frequency of broken/healed tails in *D. vinitor* is relatively low—13.7% of the specimens examined compared with 30% or more in some species (Stafford, 2003; Cadle, 2010); this may indicate a less easily pseud-autotomic tail than other species or differential predation intensities.

Stafford (2003) included specimens of *D. vinitor* as redefined herein in a study of morphology, diet, and reproduction of

Dendrophidion spp., but most of his specimens actually are the two new species described in this paper. Among specimens I examined, a gravid female from Veracruz (491 mm SVL; KU 27564) was collected 30 March 1949. UCM 41162 from Oaxaca (567 mm SVL) had vitellogenic ova 3–5 mm in length and was collected 5 May 1967. UTACV 22755 from Guatemala (427 mm SVL), a female (? adult) with thin, nonconvoluted oviducts, was collected 16 October 1987. The two smallest individuals were 199 mm SVL (Veracruz; collected 19 September 1965) and 218 mm SVL (Oaxaca; collected July to September 1968).

Vernacular names for *D. vinitor* given in various regional works include *zumbadora aquillada de barras* (Guatemala), *culebra barrada* (Guatemala and Mexico), *kuyunkan* (Lacandón Maya), and *sabanerita* (Belize) (Alvarez del Toro, 1972; Lee, 1996: 310; Campbell, 1998: 207; Stafford and Meyer, 2000).

Dendrophidion apharocybe **New Species**

Figures 2B, 7–10, 13B, 13D, 14C, 14D, 20, 21

Dendrophidion dendrophis (part). Gaige et al., 1937: 12 (UMMZ 79765–66). Dunn and Bailey, 1939: 15 (two specimens from Pequení–Esperanza ridge = MCZ R-42782–83).

Dendrophidion vinitor. Smith, 1941: 74–75 (part; paratypes from Nicaragua, Costa Rica, Panama). Barbour and Loveridge, 1946: 99–100 (paratypes from Nicaragua, Costa Rica, Panama). Peters, 1952: 43 (paratypes from Nicaragua). Taylor, 1954: 729–730 (part; Costa Rica). Smith, 1958: 223 (Panama). Cochran, 1961: 172 (part; paratypes from Nicaragua). Peters and Orejas-Miranda, 1970: 79 (part). Savage, 1973: 14 (part), 1980: 92 (part). Scott et al., 1983: 372 (part; “La Selva”). Kluge, 1984: 54 (Nicaragua: UMMZ 79766). Wilson and Meyer, 1985: 41 (key). Savage and Villa, 1986: 17,

148, 169 (part). Lieb, 1988: 171 (part). Villa et al., 1988: 63 (part). Pérez-Santos and Moreno, 1989: 4 (part; Colombia listed but no details given). Ibáñez and Solís, “1991” [1993]: 30, 33 (Panama). Lieb, 1991: 522.1–522.2 (part). Pérez-Santos et al., 1993: 116. Guyer, 1994: 382 (Costa Rica). Auth, 1994: 16 (part). Ibáñez et al., “1994” [1995]: 26 (Panama). Lee, 1996: 310–311 (part). Campbell, 1998: 207 (part). Stafford, 1998: 16–17. Lee, 2000: 282–283 (part). Stafford and Meyer, 2000 (part; specimen from Costa Rica), pl. 113. Savage, 2002 (part): 655–656, pl. 416. Goldberg, 2003: 298–300 (part). Köhler, 2003: 200, figs. 478 (Panama) and 479 (Costa Rica) (part). Stafford, 2003: 111 (part; specimens from Nicaragua, Costa Rica, Panama). Wilson et al., 2003: 18. Solórzano, 2004: 236–239, fig. 60 (part). Guyer and Donnelly, 2005: 185, pl. 149 (part). McCranie et al., 2006: 147–148 (part). Wilson and Townsend, 2006, tables 1, 3. Köhler, 2008: 215, figs. 580–581 (Panama, Nicaragua) (part). McCranie, 2009: 12. Savage and Bolaños, 2009: 14 (part). Bolaños et al., 2010: 12 (part). McCranie, 2011: 111 (part).

Holotype (Figs. 2B, 7, 14C). LACM 148593, an adult male from Finca La Selva, 40 m elevation, Heredia Province, Costa Rica. Collected 9 December 1974 by C. Dock, Carl Lieb, and Catherine Toft. Formerly CRE (Costa Rica Expeditions) 8598. The holotype is 908 mm total length; 574 mm SVL; 334 mm tail length (complete). It has 152 ventrals and 123 subcaudals. The left hemipenis is nearly fully everted (small portion of apex un-everted); right hemipenis everted to the base of the apex just beyond the flounces. Most of the stratum corneum is missing from the dorsal scales. The middle half of the venter has a long midventral slit exposing the viscera; a shorter irregular slit (about 100 mm long) begins about 35 mm in front of the vent.

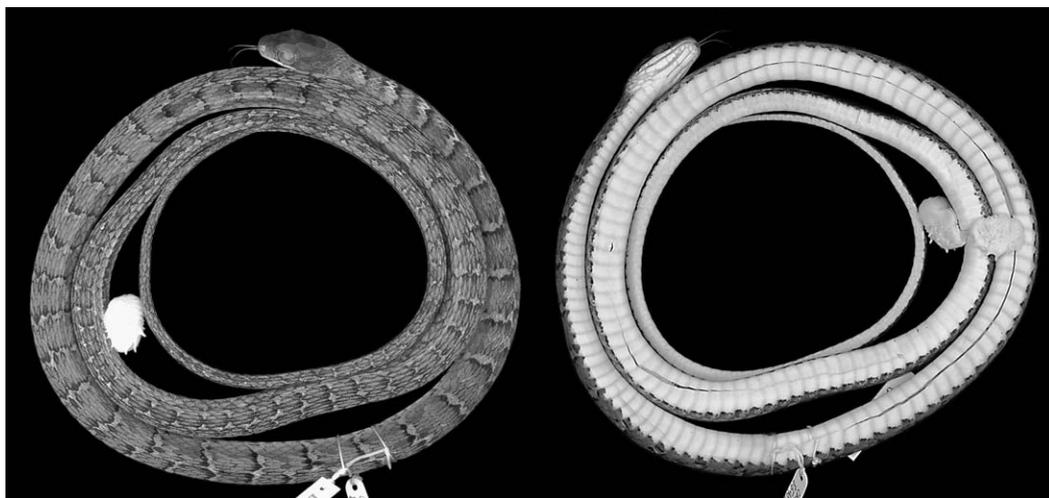


Figure 7. Holotype of *Dendrophidion apharocybe* (LACM 148593) from La Selva, Costa Rica (Heredia Province).

Paratopotypes. LACM 148591, 148595, 148597–98, 148603–05, 148609–11, 148616, 148619, 148621; CM 53948.

Other Paratypes. **Honduras:** *Gracias a Dios:* Bodega de Río Tapalwás, 190 m, USNM 559615, 561032. Caño Awalwás (camp), 100 m, USNM 559616. Crique Ibantara, 70 m, USNM 559617. Warunta Tingni Kiam, 150 m, USNM 561920. Hiltara Kiam, 150 m, USNM 562874. Sachin Tingni, 150 m, USNM 562875. Near Crique Wahatingni, USNM 562876. Near Crique Yulpruan, 140 m, USNM 563303. **Olancho:** Planes de San Esteban, 1,100 m, USNM 565534. **Nicaragua:** Eastern Nicaragua, ANSP 22863–64 (paratypes of *D. vinitor* Smith). [*Atlántico Norte*]: Musawas, Waspuc River, AMNH R-75223. [*Atlántico Sur*]: Cara de Mono, KU 112974. Recreo, Río Mico, UMMZ 79766 (paratype of *D. vinitor* Smith; see Appendix 2 for locality clarification). Río Mico, 10 mi above Recreo, UMMZ 79765 (see Appendix 2 for locality clarification). **Matagalpa:** Hacienda La Cumplida, 19 km N of Matagalpa, 2,500 ft. [762 m], UMMZ 115259. Matagalpa, MCZ R-9561 (paratype of *D. vinitor* Smith), UMMZ 90670 (paratype of *D. vinitor* Smith, formerly MCZ R-17117). **Costa Rica:** *Alajuela:* Poco Sol de La Tigre,

540 m, LACM 148601. *Cartago:* ca. 2.5 km N Pavones, 700 m, LACM 148594. Pavones, near Turrialba, KU 140055. *Guanacaste:* Cacao Biological Station, 729–1,528 m, LACM 148589. Silencio, 10 km SES [? SSE] from La Casa, 875–940 m, LACM 148607. *Heredia:* Río Puerto Viejo near junction with Río Sarapiquí, KU 35639. 10 km WSW Puerto Viejo de Sarapiquí, MVZ 217610. Zona Protectora, La Selva, trail from 1,000-m camp to 1,500-m camp, 990 m, LACM 148600. *Limón:* Pandora, 50 m, LACM 148618. Suretka, MCZ R-19342 (paratype of *D. vinitor* Smith). Near Suretka, Mt. Mirador, KU 35638. **Panama:** *Bocas del Toro:* Almirante, 10 m, KU 80223. 11 km NW Almirante, 600 ft. [183 m], FMNH 153653, 154038–39. South end of Isla Popa, 1 km E of Sumwood Channel, USNM 347352. La Loma, W. Panama, MCZ R-19344 (paratype of *D. vinitor* Smith). Peninsula Valiente, Bluefields, 70 m, KU 107646. Peninsula Valiente, Quebrada Hido, USNM 338624. *Coclé:* Continental divide N El Copé, 600–700 m, AMNH R-115922. *Darién:* North slope of Cerro Malí, 700–1,200 m elev., AMNH R-119377. Laguna, 820 m, KU 75680. [*Panamá*]: Pequení–Esperanza ridge, near head of Río Pequení, 2,000 ft. [610 m], MCZ

R-42782 (paratype of *D. vinitor* Smith). Pequení-Esperanza ridge, junction main divide, 1,200 ft. [366 m], MCZ R-42783 (paratype of *D. vinitor* Smith). **Panamá:** Cerro Azul region, Río Piedra, AMNH R-119878. Cerro Campana, 3,000 ft. [915 m], UMMZ 155745. S slope of Cerro Campana, 900–950 m, AMNH R-108693. **San Blas:** Border of Darién, summit site, 320 m, 08°55'N, 77°51'W, FMNH 170138. **Vera-guas:** Cerro Delgadito, 2–4 mi. W Santa Fe, AMNH R-147806–07. Cerro Arizona above Alto de Piedra, North of Santa Fe, 4,700 ft. [1,433 m], UMMZ 155725.

Other Referred Specimens and Locality Records from Literature (specimens not seen except LACM 148622). **Costa Rica:** **Heredia:** Finca La Selva (type locality), LACM 148622 (fragmentary skin), LACM 163285–87 (skeletons). **Limón:** Guápiles, UCR 6327 (Lieb, 1988). 7 km NW Peshurst, San Clemente, UCR 7545 (Lieb, 1988). **Honduras:** *Gracias a Dios:* Las Marías (McCranie, 2011: 114). **Nicaragua:** No specific locality, USNM 14215 (paratype of *D. vinitor* Smith) (another paratype of *D. vinitor* from an unspecified locality in Nicaragua, USNM 14220, was reidentified as “*D. nuchale*” by Stafford [2002, 2003], but that identity seems not to have been independently verified). [*Chontales*]: Santo Domingo, Chontales Mines, 2,000 ft. [610 m], BMNH 94.10.1.19–20 (Stafford, 2003). [*Río San Juan*]: Río San Juan (Köhler, 2008, fig. 581). **Panama:** *Bocas del Toro:* South end of Isla Popa, 1 km E Sumwood Channel, USNM 319234 (skin + skeleton). Savage (2002: 656) plotted additional Costa Rican localities for *D. apharocybe* based on specimens that I did not see (mainly at UCR), but see comments under Distribution on two erroneous lowland Pacific localities indicated by Savage.

Etymology. The species name is a feminine noun in apposition derived from the Greek words *aphares* (ἀφάρης), meaning naked or unclad, and *kybe* (κύβη), meaning head. The “naked head” refers to the distinctive unadorned apex of the hemipenis of *D. apharocybe* compared with its sibling species.

Diagnosis. *Dendrophidion apharocybe* is characterized by (1) dorsocaudal reduction from 8 to 6 occurring posterior to subcaudal 25 (range, 26–63); (2) single anal plate; (3) relatively low subcaudal counts (<130 in males and females); (4) black-edged pale crossbands on the neck nearly always more than one scale row wide; (5) immaculate ventrals and subcaudals except for lateral dark pigment; (6) a relatively short hemipenis with a bulbous apex strongly inclined toward the sulcate side (asulcate edge of apex higher than sulcate edge) and largely devoid of ornamentation (apex nude). The combination of few subcaudals and a single anal plate will distinguish *D. apharocybe* from all other species of *Dendrophidion* except *D. vinitor*, *D. crybelum*, and *D. paucicarinatum*.

Dendrophidion apharocybe differs from species of the *D. percarinatum* group (*D. bivittatum*, *D. brunneum*, *D. paucicarinatum*, *D. percarinatum*) in having the dorso-caudal reduction from 8 to 6 usually posterior to subcaudal 30 (26–30 in some specimens from Costa Rica and Panama; see Sexual Dimorphism and Geographic Trends). A single anal plate will distinguish *D. apharocybe* from all of these except some individuals of *D. paucicarinatum* (anal plate variable in this species). *Dendrophidion paucicarinatum* usually has a more uniformly colored dorsum lacking distinct crossbands, has narrow dark lines across the venter in adults and many juveniles, has a higher number of ventrals (>175 compared with <170 in *D. apharocybe*), and has more weakly keeled dorsal scales. *Dendrophidion apharocybe* differs from *D. boshelli* in having 17 midbody scale rows (15 in *D. boshelli*). *Dendrophidion apharocybe* has fewer subcaudals (<130) and usually a shorter adult relative tail length (<60% of SVL) than *D. nuchale* auctorum and *D. dendrophis* (>130 and usually >60% of SVL, respectively); the anal plate may be either single or divided in these last two species, and their venters are often heavily marked with dark pigment (immaculate in *D. apharocybe*).

Dendrophidion aphaocybe previously has been confused with another new species, *D. crybelum*, and with *D. vinitor* as redefined herein. *Dendrophidion aphaocybe* differs from *D. crybelum* (characters in parentheses) in the following hemipenial characters: hemipenis rather short and with a bulbous apex comprising well over one-third the length of the organ (longer and cylindrical, without a distinctly expanded apex that comprises one-fourth or less the length of the hemipenis); apex strongly inclined toward the sulcate side and nude (not inclined and ornamented with many free-standing membranous ridges having embedded spinules); hemipenis with relatively few moderately enlarged spines, total enlarged spines <45 (many greatly enlarged spines, total enlarged spines >70). *Dendrophidion aphaocybe* and *D. crybelum* are very similar in color patterns, but *D. aphaocybe* has immaculate ventrals and subcaudals, whereas adult *D. crybelum* have small dark spots on the posterior ventrals and the subcaudals (juveniles sometimes have only dark suffusion on the subcaudals); see species account for *D. crybelum* for details. *Dendrophidion aphaocybe* averages more pale body bands (Table 1) than *D. crybelum* ($p < 0.001$) and fewer than *D. vinitor* ($p < 0.001$), but the ranges overlap greatly in each case.

Hemipenes of *D. aphaocybe* and *D. vinitor* are similar in overall shape, but the apex of the former is nude and strongly inclined toward the sulcate side, and it lacks an apical boss. The hemipenis of *D. vinitor* has a highly ornate apex, including an apical boss, and it is not strongly inclined (see detailed hemipenial descriptions). Additionally, these two species differ in aspects of color pattern (see species account for *D. vinitor*).

Description (31 males, 34 females). Table 1 summarizes size, body proportions, and meristic data for *D. aphaocybe*; McCranie (2011) summarized data for 10 Honduran specimens, most of which are also included in this summary. Largest specimen (KU 35638) a female 1,045 mm

total length, 672 mm SVL. Largest male (KU 80223) 1,040 mm total length, 653 mm SVL (another male, LACM 148601, was also 653 mm SVL but had an incomplete tail). Tail 35–38% of total length (53–61% of SVL) in males; 33–36% of total length (49–57% of SVL) in females. Dorsal scales in 17–17–15 scale rows, the posterior reduction by fusion of rows 2+3 (40%) or 3+4 (54%) or loss of row 3 (6%) at the level of ventrals 85–105 (see Sexual Dimorphism below). Ventrals 149–160 (averaging 153.9) in males, 152–168 (averaging 160.8) in females; 1 or 2 preentrals anterior to ventrals (preentrals rarely absent). Anal plate single. Subcaudals 115–127 (averaging 121.1) in males, 111–129 (averaging 119.9) in females. Dorsocaudal reduction at subcaudals 32–63 in males (mean 47.8), 26–52 in females (mean 41.5). Preoculars 1, postoculars nearly always 2 (rarely 3), primary temporals usually 2 (rarely 1), secondary temporals usually 2 (rarely 1), supralabials usually 9 with 4–6 bordering the eye (range 8–10 with other combinations bordering the eye; Table 1), infralabials usually 9 (range 7–10). Maxillary teeth 33–44 (averaging 39), typically with four posterior teeth abruptly enlarged; sometimes the enlargement appeared more gradual and with three or five somewhat enlarged (Fig. 8).

Two apical pits present on dorsal scales. Nearly 60% of specimens have all dorsal rows except row 1 keeled on the neck (in about half of those, keels on row 2 were scored as weak); another 34% of specimens lacked keels on rows 1 and 2 on the neck (in one-quarter of those keels were weak on row 3); the remaining specimens lacked keels on rows 1–3 on the neck (these proportions differ from *D. crybelum*; see species account). In all except five specimens, keels were present on all dorsal rows except row 1 at mid- and posterior body; in the five exceptions (four from Panama, one from Costa Rica) keels were present additionally on scale row 1 posteriorly (sometimes weak). Fusions or divisions of temporal scales were common, with the following



Figure 8. Maxillary dentition of *Dendrophidion apharocybe*. Right maxilla of LACM 148597 showing four enlarged posterior teeth (anterior to the right). The gap anterior to the enlarged posterior teeth is an empty tooth position, not a diastema.

frequencies: upper primary divided (5), upper secondary divided (5), upper primary + secondary fused (5), lower primary divided (2), lower secondary fused with the last supralabial (4), upper + lower secondary fused (2), upper + lower primary fused (2), lower secondary divided (1). On eight sides, a dorsal projection of the lower primary temporal extended between the upper primary and secondary temporals, separating them and contacting the parietal scale. In one specimen supralabials 6–8 were fused on one side. In LACM 148616 subcaudals 3–16 are entire or only partially divided.

Hemipenis unilobed with a bulbous apex. Sulcus spermaticus simple, centrolinal, with a distinctly flared tip. Central part of hemipenis ornamented with spines, distal to which is a series of flounces (about four on the sulcate side to about seven on the asulcate side). The broad apex is strongly inclined toward the sulcate side and entirely nude except for some low rounded ridges (noticeable only with magnification).

Geographic Variation, Ontogenetic Variation, and Sexual Dimorphism. No strong geographic trends were evident except in the point of dorsocaudal reduction, which is more distal in northern compared with southern specimens. The mean subcaudal number at the point of reduction for Honduran–Nicaraguan specimens is 45.4 and 50.8 (females and males, respectively). In Panamanian specimens these means are 35.6 and 43.8 (the means for all non-Panamanian specimens combined are 43.5 and 49.3 for females and males, respectively). Dorsocaudal reductions anterior to subcaudal 30 occurred only in females from Panama and Costa Rica (uni- or bilateral

reductions at subcaudals 26–29 in five specimens). Relative tail length increases with body size in subadults. Specimens <300 mm SVL have tail lengths 30–35% of total length, 44–53% of SVL ($N = 15$, males and females combined); see Table 1 for adult proportions.

Patterns of sexual dimorphism in *D. apharocybe* are similar to those in *D. vinitor* (Table 1). Mean sizes of adult males (571 mm SVL) and females (575 mm SVL) are not significantly different ($N = 19$ males, 23 females). Females have a significantly greater ventral count than males and the posterior reduction of the dorsal scales occurs farther posteriorly in females (mean ventral 99.3) than in males (mean ventral 94.6; $p < 0.001$). The dorsocaudal reduction occurs at a significantly more posterior position in males than in females. Males have a proportionally longer tail than females but the sexes do not differ in subcaudal counts.

Coloration in Life. Color photographs of *D. apharocybe* from the type locality are published in Savage (2002, pl. 416), Solórzano (2004, fig. 60), and Guyer and Donnelly (2005, pl. 149); from other Costa Rican localities in Stafford and Meyer (2000, pl. 113) and Köhler (2003, fig. 479); from Honduras in Wilson et al. (2003, fig. 4; same photograph but with distinctly red/orange tones in McCranie et al. [2006, pl. 120]) and McCranie (2011, pl. 6D); from Nicaragua in Köhler (2008, fig. 581); and from Panama in Köhler (2003, fig. 478; 2008, fig. 580). A black and white photograph of the head/neck (La Selva, Costa Rica) is in Lieb (1991).

Salient characteristics of adult coloration in life, as described by Stafford (1998),



Figure 9. *Dendrophidion aphaerocybe* in life. AMNH R-115922 from continental divide N of El Copé, Panama (Coclé Province). Adult female, 666 mm SVL. From color slide by Charles W. Myers. A reverse image of the same photo was published in Köhler (2003: fig. 478, 2008: fig. 580).

Savage (2002: 656), Guyer and Donnelly (2005: 185), McCranie et al. (2006: 148), McCranie (2011: 112), and Charles W. Myers (field notes for KU 107646; AMNH R-108693, R-115922, R-119377) include a gray to brown dorsum with a series of dark-edged pale grayish to pale brown crossbands (ground color or crossbands often with reddish or orange tones, especially on head, anterior and midbody). Posteriorly, pale bands tend to become invested with dark pigment, forming transverse series of pale ocelli set within darker pigment. Posterior ocelli are not mentioned in all color descriptions, but they are visible in virtually every published photo from throughout the range. Often a pale vertebral line posteriorly. Usually a narrow lateral dark line on dorsal rows 2 and/or 3 on the posterior body (sometimes indistinct) and a similar dark line at the subcaudal/dorsocaudal border. Skin between the anterior dorsal scales pale blue or bluish white. Top of head brown, sometimes invested with reddish or greenish tones. Supralabials and throat pale to bright yellow. Venter in adults whitish to yellow, often with an orangish or greenish

wash. Juveniles similar to adults but reddish or orange tones in dorsal ground color reduced or absent; venter usually whitish, greenish white, or orange/yellow.

Guyer and Donnelly (2005: 185) described specimens from the type locality as follows: Dorsum gray brown anteriorly, shading to brown posteriorly. Crossbands pale grayish tan bordered by dark. Anterior-most interspace between pale bands rusty red, the rest gray brown. Skin between the anterior dorsal scales pale blue, creating a bluish tint to the light bands or, when the lung is expanded, a blue band. Posterior body middorsal tan stripe interrupted by thin, dark bands that shade to gray laterally. Venter immaculate white to light yellow. Head gray brown. Supralabials brownish anteriorly, white to pale yellow posteriorly.

Figure 9 illustrates an adult female *D. aphaerocybe* from Panama, whose coloration in life was described thus (Charles W. Myers, field notes): Head brown, turning gray-brown on neck and then greenish brown over rest of body. Pale crossbands gray anteriorly, pale orange at midbody, pale brown posteriorly. Skin within cross-

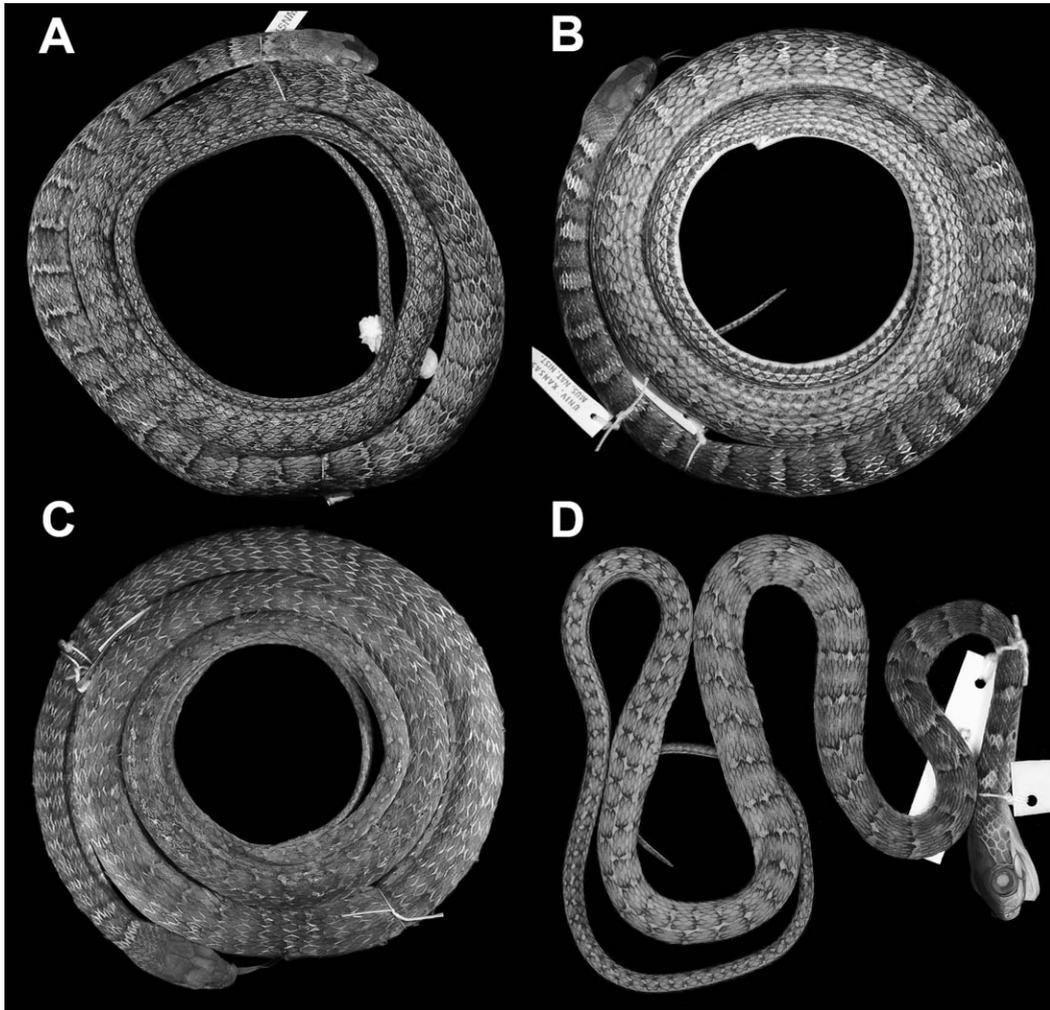


Figure 10. Representative specimens of *Dendrophidion apharocybe*. (A) USNM 562874 (Honduras). (B) KU 112974 (Nicaragua). (C) UMMZ 115259 (Nicaragua; primary banding pattern obscured by formation of secondary bands). (D) FMNH 153653 (Panama; juvenile, 275 mm SVL).

bands bright yellow except on anterior one-third of body, where it is orange for a short distance just behind the head and bluish white thereafter. Labials, underside of head, and neck golden yellow, turning golden orange over rest of venter. Upper one-fourth of iris tan, lower three-quarters gray brown with a few darker brown spots. Tongue, including fork, black.

Coloration in Preservative. Dorsum gray to brown with pale gray or brown cross-

bands (sometimes offset), broader on the neck than more posteriorly (specimens with intact stratum corneum tend to be brown, those without, gray) (Fig. 10). Each cross-band bordered posteriorly by narrow irregular blackish border; a less distinct border on anterior edge. The number of pale bands/ocelli on the body ranged from 46 to 69 with a mean and median of 54 and a mode of 53. Neck bands in about 80% of the specimens were 1 to 1.5 scale rows in width;

in another 18% the bands were up to 2.5 rows wide; in one specimen, the neck bands were three rows wide and in another they were less than one row wide. In some preserved specimens (e.g., Fig. 10C) the pale dorsal bands are indistinct posteriorly, seemingly because of secondary lightening of the interspaces between the pale bands.

Crossbands extend down to lateral edges of ventrals and merge with dark pigment on the lateral edges of the ventral scales. Posterior crossbands become invested with dark pigment so that each crossband is broken into a transverse series of vertebral and lateral pale spots (ocelli) separated by dark pigment (lateral ocelli on dorsal rows 3–5 and comprising adjacent parts of three or four scales). Narrow broken blackish lateral stripe on suture line between dorsal rows 2–3 on posterior third or more of body; distinctness and extent of interruption of this stripe varies. Ventrolateral blackish tail stripe on suture between subcaudals and dorsocaudal row 1. The dark posterolateral and tail stripes are indistinct in some specimens.

Top of head uniform brown or gray down to upper edges of supralabials. Ill-defined postocular stripe extending across top edge of penultimate supralabial. Rest of supralabials and gular region immaculate whitish. Venter immaculate except for fairly pale brown/gray speckling (often containing some larger dark spots) on extreme lateral edges. Subcaudals immaculate; no investing dark pigment or spots on subcaudals or posterior ventrals (compare *D. crybelum*). One specimen from Costa Rica (KU 35638) has an unusual ventral pattern: in addition to lateral dark blotches, the anterior third of the body has short dark lateral lines across the anterior edges of the ventral plates. These lines are never complete (as in some other *Dendrophidion*, e.g., *D. paucicarinatum*), the extensions occupying only the lateral portions of the plates.

Juveniles are similar to adults but color tones are lighter. Anterior ground color medium to pale brown (unlike juvenile *D. crybelum*). Ocelli on the posterior body are

poorly defined because the investment of pale bands with dark pigment is much less in small juveniles than in adults.

Distribution (Fig. 11). Atlantic versant of Central America from extreme eastern Honduras to eastern Panama at the Colombia border; upland Pacific drainages in northwestern Costa Rica (Cordillera de Tilarán and Cordillera de Guanacaste) and in Panama. The elevational range derived from data associated with specimens is 10 to 1,433 m (most records <200 m). Records from the Pacific lowlands of Costa Rica (Savage, 2002: 656; Laurencio and Malone, 2009) are erroneous, as discussed below. The distributions of *D. vinitor* and *D. apharocybe* are separated by about 400 km at their closest localities in Guatemala/Belize and Honduras, respectively (Fig. 11).

Savage (2002: 656, map 11.79) indicated two lowland localities of “*Dendrophidion vinitor*” on the Pacific side of Costa Rica (denoted by “X” in Fig. 17). I conclude that both are based on mistaken identities (I am indebted to Jay M. Savage for pointing me toward the source of the records and to Gerardo Cháves for information and photographs of UCR specimens). The first, due east of the tip of the Nicoya Peninsula (Savage, 2002: 656, map 11.79), is based on UCR 14406 and 14620, which were obtained during a survey of Carara National Park (Laurencio and Malone, 2009; David Laurencio, personal communication, March 2011). These specimens were initially identified as “*D. vinitor*,” but both have divided anal plates and pattern characters of *D. percarinatum* rather than “*D. vinitor*” (characters confirmed from photos provided by Gerardo Cháves, who also examined the specimens at my request, May 2011). The second erroneous record is from the Pacific lowlands due north of the Osa Peninsula (Savage, 2002: 656, map 11.79), purportedly based on UCR 7235 cited by Lieb (1988) from Cajón (north bank of the Río Térraba, about 80 m, Puntarenas Province). However, that UCR number is seemingly in error, and the UCR collection currently has no specimens of “*D. vinitor*” from Puntarenas

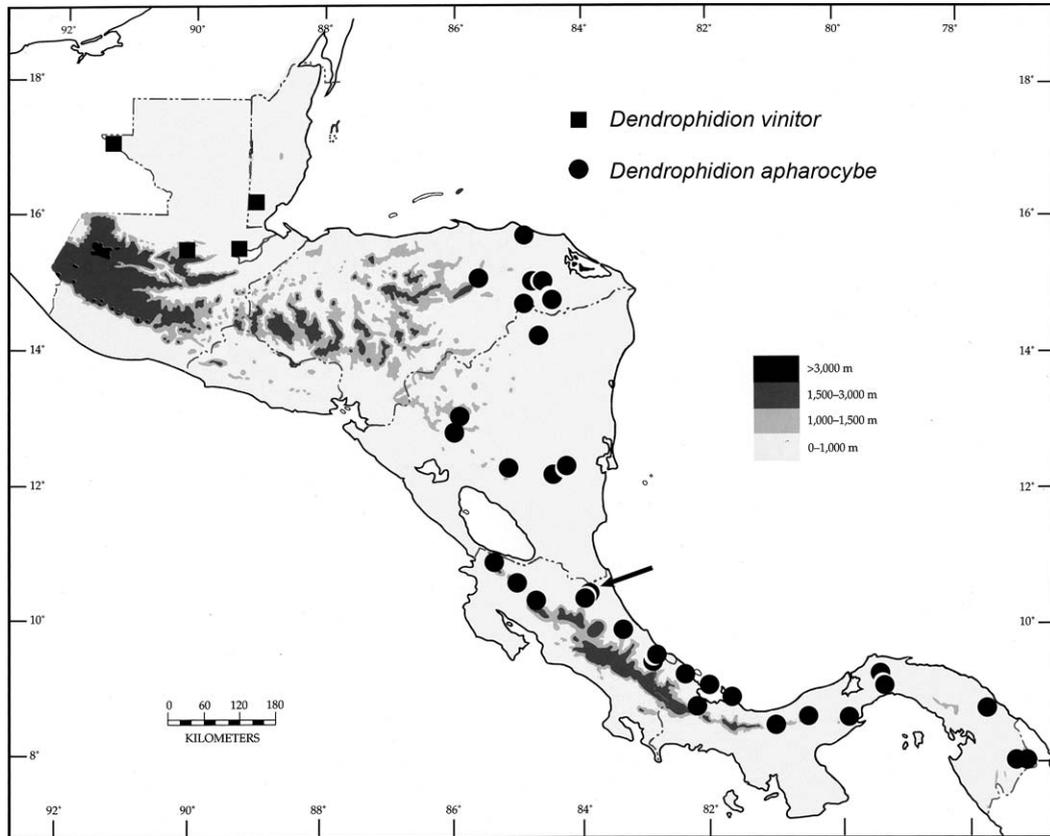


Figure 11. Distribution of *Dendrophidion aphaocybe*, with adjacent localities for *D. vinitor* in Guatemala and Belize shown (see Fig. 5 for complete distribution of *D. vinitor*). A few symbols represent multiple contiguous localities. A detail of the distribution of *D. aphaocybe* in Costa Rica is shown in Figure 17 for comparison with that of *D. crybelum*. Arrow indicates the type locality of *D. aphaocybe*.

Province other than the above-cited misidentified specimens from Carara National Park. Another specimen from a locality near Cajón, LACM 148592, was previously identified as *D. vinitor* in the LACM catalogs, but I identify this specimen as *D. percarinatum* (again based on a divided anal plate, pattern characters, and a more proximal dorsocaudal reduction). Thus, there are no confirmed records of “*D. vinitor*” from the Pacific lowlands of Costa Rica.

Dendrophidion aphaocybe undoubtedly occurs in northwestern Colombia (Chocóan region) given the proximity of definite Panamanian localities (Fig. 11). However, I have been unable to document a definitive

Colombian record, although several authors have listed the species for Colombia (as “*D. vinitor*”). Pérez-Santos and Moreno (1989) included it in “addenda and corrigenda” to Pérez-Santos and Moreno (1988) but listed its distribution in Colombia as “desconocida.” Lieb (1988) included Colombia as part of the distribution but listed no Colombian material; he later (Lieb, 1991) plotted a locality well into western Colombia on a distribution map for “*D. vinitor*” but queries to identify the source of the record went unanswered. Stafford (2003: 111) identified LACM 45443 (from Chocó, Colombia) as “*D. vinitor*,” but this specimen is a member of the *D. percarinatum*

group (personal observation). Several other works have cited Colombia as part of the distribution apparently based on these sources. Likewise, Lieb (1991) indicated a locality on the tip of the Azuero Peninsula (Cerro Hoya area) on the Pacific side of western Panama, which is far from any locality from which I have seen specimens (Fig. 11). According to Jay M. Savage (personal communication, March 2011), this locality is based on a misidentified specimen.

Natural History. *Dendrophidion aphaerocybe* is a diurnal snake found in humid forests (lowland to montane rainforests, cloud forests) and is the best known species of the *D. vinitor* complex owing to incidental or focused attention by students of the Costa Rican herpetofauna. Most natural history data for *D. aphaerocybe* come from the relatively well-studied La Selva Biological Station, the type locality, operated by the Organization for Tropical Studies (all literature references to "*D. vinitor*"); the La Selva ecosystem is described in McDade et al. (1994) and Holdridge et al. (1971, under the name "Sarapiquí"). Guyer (1994: 382) and Guyer and Donnelly (2005) reported *D. aphaerocybe* as common and semi-arboreal, and Guyer and Donnelly (1990) summarized data on size, mass, and body proportions for this population. Guyer and Donnelly (2005: 185) further observed that *D. aphaerocybe* is "typically observed crossing trails in primary and secondary forest. It is wary ... usually races away when approached ... [and is] an adept climber... found at night coiled in understory shrubs and trees. At La Selva this snake consumes ... [*Craugastor*] *bransfordii* and ... [*Dendropsophus*] *ebraccata*."

In the Cordillera de Guanacaste, Costa Rica (750–850 m elevation), Stafford (1998) found two juveniles (about 250 mm total length) active at 10:00 a.m. and "late morning" on sunny June days after rain. Stafford reported that *D. aphaerocybe* is wary and swift and, when alarmed, raises the head and forebody high off the ground (as shown by photographs in Stafford and

Meyer [2000, pl. 113] and Köhler [2003, fig. 479]).

Goldberg (2003) reported reproductive data for "*Dendrophidion vinitor*" in Costa Rica based on a mix of specimens of *D. aphaerocybe* and *D. crybelum*. Because he reported data for individual specimens, it is possible to extract data for *D. aphaerocybe*, all of which are from the type locality. A gravid female (LACM 148598, 567 mm SVL) collected 11 December 1974 had a clutch size of five estimated from yolked ovarian follicles >12 mm length. A female (LACM 148609, 657 mm SVL) collected in June 1983, although "not undergoing yolk deposition" (Goldberg, 2003), has swollen convoluted oviducts (personal observation), suggesting that it had perhaps recently laid a clutch. Males undergoing spermiogenesis were collected in April, May, November, and December ($N = 4$); the smallest actively spermiogenic male, collected in May, was 420 mm SVL but a smaller individual (402 mm SVL) also showed some evidence of spermatid transformation. Goldberg (2003) inferred that sperm production may proceed year-round. Stafford (2003) included specimens of *D. aphaerocybe* in an ecological study of *Dendrophidion* spp. but presented summary data only, making it impossible to disentangle data specific to *D. aphaerocybe* from the other two species of this complex. Other natural history data for *D. aphaerocybe* and *D. crybelum* combined were summarized by Savage (2002) and Solórzano (2004).

I made incidental observations of reproductive condition in several other specimens (eggs not counted unless previous incisions in a given specimen permitted thorough study): a female with enlarged (20 mm) oviductal eggs collected 21 June 1967 (KU 140055, Costa Rica; 612 mm SVL); a female with three large shelled oviductal eggs collected 23 February–6 March 1967 (FMNH 170138, Panama; 583 mm SVL); a female with five large nonoviductal eggs about 25 mm long collected in June 1963 (KU 75680, Panama; 534 mm SVL). The smallest individual of *D. aphaerocybe* (from

Panama) was 172 mm SVL and collected 4 April 1980; two others from Panama were 200 mm SVL (collected 23 January 1953 and 24 January 1975), and one individual was 204 mm SVL (collected 4 April 1980). The smallest specimens from La Selva, Costa Rica, 209–219 mm SVL, were collected between 30 June and 26 August. The smallest specimen from the northern part of the range (Honduras) was 228 mm SVL, collected in February 2006.

Reports from other parts of the range give portraits of *D. aphaocybe* similar to Costa Rican populations. In Honduras this species is infrequently encountered from 30 to 1,100 m elevation in Lowland Moist and Premontane Wet forests (Wilson et al., 2003: 18; McCranie et al., 2006: 148; Wilson and Townsend, 2006, tables 1, 3; McCranie, 2011: 113). Honduran habitats are discussed and illustrated by McCranie (2011: 22–25, pl. IA–B). Two specimens were active about midday and late afternoon on forest floor; two others were sleeping at night on understory vegetation in forest. Two specimens inflated the anterior body when disturbed, exposing the pale blue skin between the dorsal scales (McCranie, 2011: 113).

Ibáñez et al. (“1994” [1995]: 26) reported *Dendrophidion aphaocybe* as “infrequent, unpredictable” in eastern Panama, and it has not been recorded for the well-known herpetofauna of Barro Colorado Island, Panama (Rand and Myers, 1990). A juvenile from Cerro Campana (AMNH R-108693, 203 mm SVL) regurgitated the remains of an adult *Eleutherodactylus* [now *Diasporus*] *diastema* (Charles W. Myers, field notes). Myers (1969: 24–25; see also Anthony [1916: 358–363]) described the environment at Cerro Malí (Darién Province, Panama), from which he obtained a specimen of *D. aphaocybe* (AMNH R-119377): “Cerro Malí is high (about 1,410 meters [AMNH R-119377 from 700 to 1,200 m]) and wet, but is affected by the dry season and much of its forest is possibly no more than transition to cloud forest. ... the forest contains many small trees, including palms,

reaching heights of ± 12 meters. Larger trees up to ± 30 meters are scattered through the forest. There is an understory of bushes and ferns. Most of the trees have a thin covering of moss on the trunks. There is a thick mulch layer on the ground and many rotting logs. Many bromeliads and a few orchids present; few tree ferns.”

Like the other species of the *D. vinitor* complex (see species accounts), snakes with broken/healed tails in *D. aphaocybe* were of low frequency (13.3%) compared with some other species of *Dendrophidion* (>30%, e.g., Stafford, 2003; Cadle, 2010). *Dendrophidion aphaocybe* is sympatric with at least two other species of *Dendrophidion* in some parts of its range. The distributions of *D. aphaocybe* and *D. percarinatum* broadly overlap from Honduras through Panama, and both species occur at some localities (e.g., near Recreo, Nicaragua, and La Selva, Costa Rica). *Dendrophidion aphaocybe* is also broadly sympatric with *D. nuchale* auctorum in Costa Rica and Panama, and both species have been collected together at some localities (e.g., Laguna, Darién, Panama, and La Selva, Costa Rica, where both occur with *D. percarinatum*). *Dendrophidion nuchale* auctorum has not been formally reported from La Selva (Guyer, 1994; Guyer and Donnelly, 2005), but I identify as this species a color photograph in Guyer and Donnelly (2005, pl. 148, “Brown Forest Racer” = *D. percarinatum* according to the authors); the specimen was photographed and released at La Selva (Craig Guyer, personal communication, December 2010). Solórzano (2004) used the vernacular name *corredora quillada* for *D. aphaocybe* in Costa Rica.

Because its diet comprises small terrestrial frogs almost exclusively (e.g., Stafford, 2003), populations of *D. aphaocybe* in Costa Rica and Panama are undoubtedly affected to some extent by well-documented declines in amphibian populations in lower Central America. For example, populations of prey species of frogs at La Selva, the type locality, collectively have declined by about

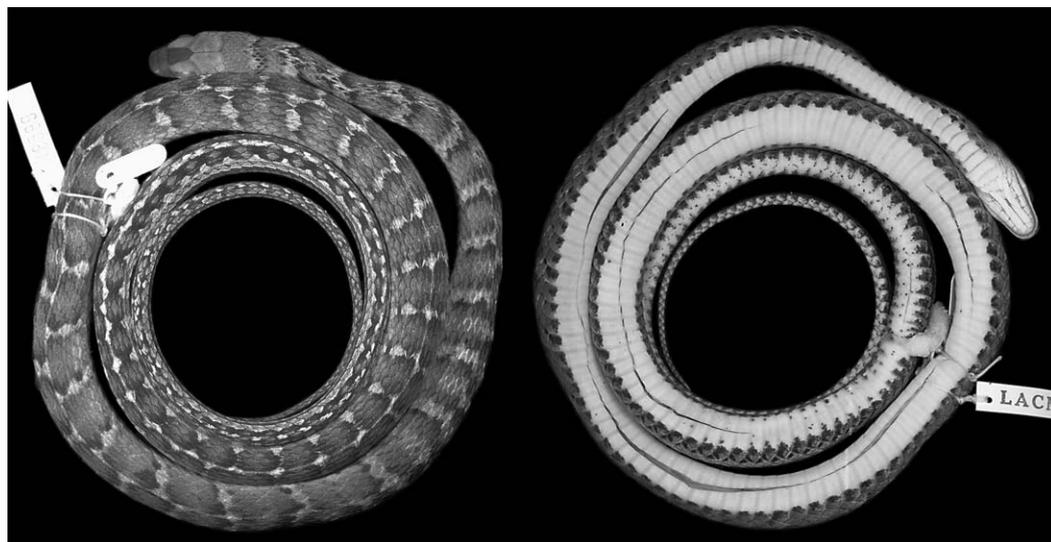


Figure 12. Holotype of *Dendrophidion crybelum* (LACM 148599) from Finca Las Cruces, Costa Rica (Puntarenas Province).

75% since 1970, probably due to climate-driven changes in the amount of surface leaf litter (Whitfield et al., 2007). Several localities in western Panama from which *D. aphaerocybe* is documented (e.g., El Copé and Santa Fe) have experienced precipitous declines in amphibian populations due to disease. Lips et al. (2006) documented >90% decline in abundance and >60% decline in amphibian species richness at El Copé. All of these declines involved species of *Pristimantis*, *Craugastor*, and *Diasporus*, which are the predominant prey for *Dendrophidion* (Stafford, 2003). These prey declines and associated climate changes have unknown effects on snake predators such as *D. aphaerocybe*, but they deserve study.

Dendrophidion crybelum New Species

Figures 2C, 12, 13A, 13C, 14A, 14B, 15, 16, 22, 23

? *Drymobius dendrophis*, part. Boulenger, 1894: 15–16 (? specimen *g* from “Chiriqui”). See comments under Distribution.

Dendrophidion vinitor, part (southwestern Costa Rica mentioned explicitly or implicitly as part of the distribution, or listing of specimens in the type series). Savage, 1973: 14. Savage, 1980: 92. Scott et al., 1983: 372 (“Las Cruces”). Savage and Villa, 1986: 17, 148, 169. Lieb, 1988: 171. Villa et al., 1988: 63. Lieb, 1991: 522.1–522.2. Auth, 1994: 16. Lee, 1996, fig. 164 (illustration of head scales of CRE 5099; = LACM 148612). Savage, 2002: 655–656. Goldberg, 2003: 298–300. Stafford, 2003: 111. Solórzano, 2004: 236–239. Guyer and Donnelly, 2005: 185. McCranie et al., 2006: 147–148. Köhler, 2008: 215. Savage and Bolaños, 2009: 14. McCranie, 2011: 111 (part).

Holotype (Figs. 2C, 12, 14B). LACM 148599, an adult male from Finca Las Cruces, near San Vito de Java, 4 km S San Vito, 1,200 m elevation, Puntarenas Province, Costa Rica. Collected in September 1972 by James E. DeWeese and Ron T. Harris. Formerly CRE 3182. The holotype is 850 mm total length, 552 mm SVL,

298 mm tail length (complete), and has fully everted hemipenes (the left one removed for description and illustration). It has 152 ventrals and 115 subcaudals. Supralabial 2 on the left side is partially divided by a suture on its upper edge. The left and right upper primary temporal and the right lower primary temporal are divided by a vertical suture. Three long midventral slits through the body wall (one on anterior body, two posterior to attached collection tags). Most of the stratum corneum is missing from the dorsal scales. A histological study of the reproductive system indicated active spermiogenesis (Goldberg, 2003).

Paratopotypes. LACM 114106–08, 148596, 148602, 148606, 148608, 148613–15, 148617. The stated localities for the topotypes vary somewhat among the specimens according to the LACM catalogues (different collectors over a period of years). All have the basic locality “Finca Las Cruces” with little more specific information. Elevations associated with paratopotypes range from 1,100 to 1,300 m.

Other Paratypes. LACM 148590, 148620 from Finca Loma Linda, 2 km SSW Canas Gordas, 1,170 m, Puntarenas Province, Costa Rica. LACM 148612 from Finca Las Alturas, vicinity of main plaza and surrounding streams and forests, 1,330 m, Puntarenas Province, Costa Rica. UF 16425 from Finca Mellizas, 14 km ENE La Unión, near the Panama border [approximately 1,310 m], Puntarenas Province, Costa Rica.

Etymology. The species name is derived from the Greek adjective *krybelos* (κρύβηλος) meaning “hidden” or “secret.” Transliteration to Latin yields *crybelum* (with neuter gender ending to agree with the neuter generic name). It recognizes the cryptic nature of this species and the fact that it remained unrecognized for so long in a well-studied herpetofauna.

Diagnosis. *Dendrophidion crybelum* is characterized by (1) dorsocaudal reduction from 8 to 6 occurring posterior to subcaudal 40 (range, 42–58); (2) single anal plate; (3) low subcaudal counts (<120 in males and females); (4) black-edged pale crossbands

on the neck nearly always more than one scale row wide; (5) pale crossbands continuing to the vent but posteriorly tending to become invested with dark pigment, forming a lateral and vertebral series of ocelli within dark bands; (6) in adults, a tendency for small dark spots and flecks on subcaudals and posterior ventrals; (7) a relatively long cylindrical hemipenis with a large number of spines (>70) and a short, nonbulbous apex ornamented with free-standing membranous ridges. The combination of few subcaudals and a single anal plate will distinguish *D. crybelum* from all other species of *Dendrophidion* except *D. vinitor*, *D. apharocybe*, and *D. paucicarinatum*.

Additional distinguishing characters and comparisons include the following. *Dendrophidion crybelum* differs from species of the *D. percarinatum* group (*D. bivittatum*, *D. brunneum*, *D. paucicarinatum*, *D. percarinatum*) in having the dorsocaudal reduction from 8 to 6 occurring posterior to subcaudal 40. A single anal plate will distinguish *D. crybelum* from all of these except some individuals of *D. paucicarinatum* (anal plate variable in this species), but *D. paucicarinatum* lacks distinct pale crossbands in adults; has narrow dark lines across the venter; and a large number of ventrals (>175 compared with <165 in *D. crybelum*). In addition to having a divided anal scale, *D. percarinatum* has narrow pale crossbands (<1.5 scale rows wide) on the neck. *Dendrophidion bivittatum* and *D. brunneum* have divided anal scales and different color patterns (posterior blackish dorsolateral and lateral stripes in *D. bivittatum* and uniform greenish or with a combination of paravertebral stripes or spots, or indistinct crossbands in *D. brunneum*; see Cadle, 2010). *Dendrophidion crybelum* differs from *D. boshelli* in having 17 midbody scale rows (15 in *D. boshelli*).

Dendrophidion crybelum differs from two other members of the *D. dendrophis* group, *D. dendrophis* and *D. nuchale* auctorum (characteristics in parentheses), in having fewer subcaudal scales (≥ 130); a

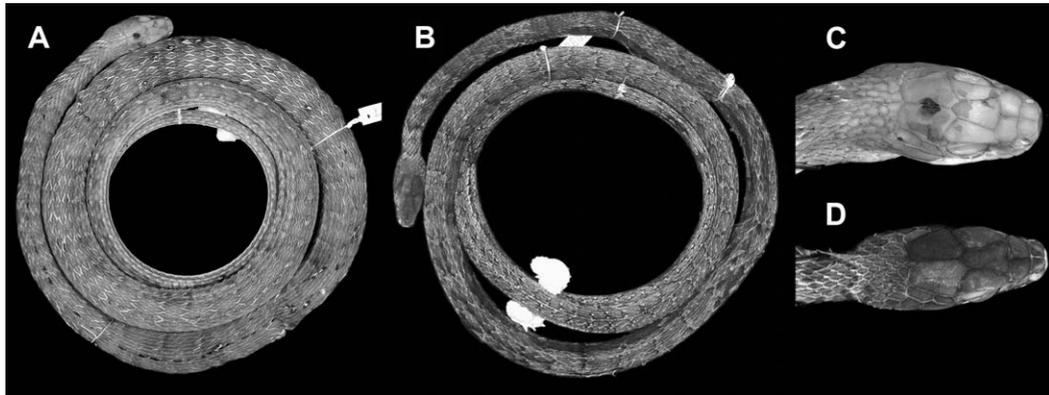


Figure 13. Comparison of closely size-matched males of (A, C) *Dendrophidion crybelum* (LACM 148590, 625 mm SVL) and (B, D) *D. apharocybe* (LACM 148601, 653 mm SVL). (A) and (B) are to the same scale, (C) and (D) to the same scale. Relative to body size, *Dendrophidion crybelum* has a more robust body and a broader head than *D. apharocybe*.

venter without extensive dark pigment, usually only scattered spots on the most posterior ventrals (venter often heavily marked with dark pigment, especially posteriorly); smaller body size (adults commonly more than 1 m in total length); a shorter relative tail length in adults, <60% of SVL (tail usually more than 60% of SVL); and in hemipenial morphology (hemipenes bulbous rather than long and cylindrical; a spinose battery followed distally by several transverse flounce-like structures). In *D. dendrophis* and *D. nuchale* auctorum the anal plate may be either single (as in *D. crybelum*) or divided.

Dendrophidion crybelum differs from *D. apharocybe* and *D. vinitor* most notably in hemipenial morphology, including overall shape (elongate and cylindrical vs. shorter and bulbous in the last two species), number of spines (>70 vs. <45), and apical morphology (narrow and with reduced calycular structures vs. nude and strongly inclined in *D. apharocybe*, or with well developed membranous ridges and an apical boss in *D. vinitor*). See complete descriptions for details.

Other characteristics distinguishing *D. crybelum* from *D. apharocybe* and *D. vinitor* are subtle. *Dendrophidion crybelum* is a more robust animal than either *D. apharocybe* or *D. vinitor*, which is most

easily seen in side-by-side comparisons of individuals of comparable body length, as shown for two males illustrated at the same scale in Figure 13. The body of *D. crybelum* is more massive, and the head is larger and more angular, than similar sized specimens of *D. apharocybe* or *D. vinitor*.

Adults of *D. crybelum* have fine dark speckling on the subcaudal scales, often concentrated along suture lines, and small dark flecks and spots on the posterior ventral plates (Fig. 14). However, these features vary among adults (very distinct and numerous to only scattered flecks), and they appear to develop ontogenetically. Juveniles often have only a fine peppering on the distal subcaudals forming a dark suffusion easily visible only with magnification. On the other hand, apart from lateral dark pigment on the ventrals and subcaudals common to all species of *Dendrophidion*, the ventral plates and subcaudals of *D. apharocybe* and *D. vinitor* are immaculate (Fig. 14; see Fig. 6 for *D. vinitor*). *Dendrophidion crybelum* averages fewer pale bands on the body than *D. apharocybe* or *D. vinitor* (Table 1; $p < 0.01$ and $p < 0.001$, respectively), although the ranges overlap greatly. The pale neck bands in *D. crybelum* are typically broader than those of *D. vinitor* (Fig. 2).

Description (8 males, 8 females). Table 1 presents standard meristic and mensural

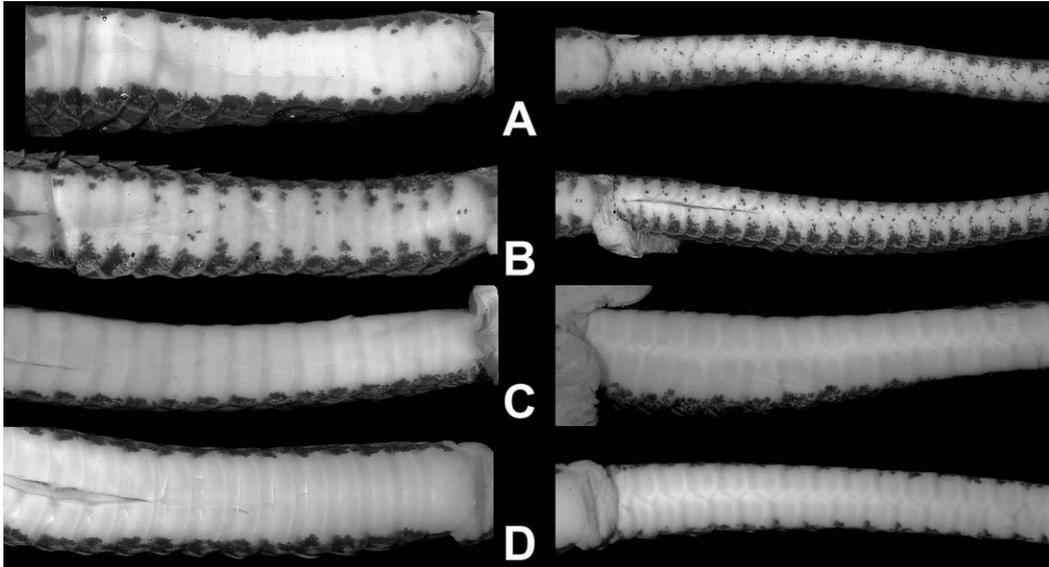


Figure 14. Comparison of posterior ventral and subcaudal patterns of *Dendrophidion crybelum* and *D. aphaocybe*. *Left series*: Ventral plates immediately anterior to the vent. *Right series*: Tail base immediately posterior to the vent. Vent toward the center in each series. (A, B) *D. crybelum* (LACM 114107 and LACM 148599 [holotype], respectively). (C, D) *D. aphaocybe* (LACM 148593 [holotype] and LACM 148609, respectively). Posterior ventrals and subcaudals of *D. crybelum* have fine dark spots and speckling compared with the immaculate ventrals and subcaudals of *D. aphaocybe*. The specimen in panel A is atypical for adult *D. crybelum* in having only a few widely scattered spots on the ventral scutes, but its subcaudals were extensively speckled; the ventral spotting of the specimen in panel B is more typical. *Dendrophidion vinitor* is similar to *D. aphaocybe* in having immaculate posterior ventral and subcaudal patterns (see Fig. 6 for an example).

data for *D. crybelum*. Largest male (LACM 148590) 985 mm total length, 625 mm SVL; largest female (LACM 114107) 631 mm SVL, 893+ mm total length (tail incomplete; a female 621 mm SVL was 956 mm total length). Tail 34–36% of total length (51–58% of SVL) in males; 34–35% of total length (50–54% of SVL) in females. Dorsal scales in 17–17–15 scale rows, the posterior reduction usually by fusion of rows 3+4 (90%; remainder 2+3) at the level of ventrals 93–104 (see Sexual Dimorphism below). Ventrals 150–153 (averaging 151.6) in males, 156–162 (averaging 160) in females; 1 or 2 preentrals anterior to ventrals. Anal plate divided. Subcaudals 112–119 (mean 116.9) in males, 115–119 (mean 117.2) in females. Dorsocaudal reduction at subcaudals 43–58 in males (mean 49), 42–56 in females (mean 48.6). Preoculars 1, postoculars 2, primary temporals 2, secondary temporals 2. Supralabials nearly always 9 with supralabials 4–6

bordering the eye (rarely 8 with 3–5 bordering eye). Infralabials 9. Maxillary teeth 38–44, usually with the last four (occasionally three) enlarged.

Two apical pits present on dorsal scales. In most specimens (including juveniles) all dorsal rows except row 1 are keeled from the neck to the vent. In occasional specimens (juveniles and adults) all rows are keeled at midbody and posteriorly (in these cases scales in row 1 usually have very weak keels and sometimes not every scale in row 1 has a detectable keel); one adult lacked keels on rows 1–3 on the neck only. Divisions (but no fusions) of temporal scales were recorded as follows: upper primary divided (5), upper secondary divided (6), lower primary divided (4).

Hemipenis cylindrical, much longer than wide, lacking a bulbous apex. Sulcus spermaticus simple, centrolineal, and with a flared tip. Hemipenial body dominated by a great number of enlarged spines. Spines



Figure 15. *Dendrophidion crybelum* in life from the type locality (paratypes). (A) LACM 114107 (adult female, 631 mm SVL). (B) LACM 114108 (juvenile female, 298 mm SVL). From color slides by Roy W. McDiarmid.

followed distally by a very short apex ornamented with a crowded series of flounces, calyces, and (on the apex proper) free-standing ridges. Small apical region essentially covered with these ornaments (i.e., nude areas very small).

Sexual Dimorphism and Ontogenetic Variation. Small sample sizes hamper a full exploration of sexual dimorphism, and the only statistically significant standard scale count differences are the greater number of ventrals in females compared with males ($p \ll 0.001$; Table 1) and a different point of dorsal scale reduction (mean ventral numbers 96 and 102.1 for males and females, respectively; $p < 0.001$). Males and females do not differ significantly in mean adult SVL (581 mm and 574 mm SVL, respectively), subcaudal number, or the point of dorso-caudal reduction. The difference between male and female relative tail lengths is marginally significant ($p = 0.045$). The

mean points of dorso-caudal reduction in male and female *D. crybelum* differ by less than one scale, and this character presents a departure from the pattern of sexual dimorphism in *D. vinitor* and *D. apharocybe*, which are sexually dimorphic for this character (Table 1). Specimens <300 mm SVL have relatively shorter tails (31–34% of total length, 46–52% of SVL; $N = 4$, males and females combined) than larger specimens (Table 1).

Coloration In Life. I am unaware of previously published photographs of *D. crybelum*. Figure 15 presents photographs of *D. crybelum* in life from color slides by Roy W. McDiarmid. An adult female (LACM 114107, Fig. 15A; the same specimen is illustrated in Fig. 16A) has a deep chocolate brown ground color; pale bands washed with orange on the neck and the posterior two-thirds of the body, grayish in between, and invested irregularly with black (tendency for the bands to form transverse series of ocelli posteriorly); a pale vertebral line washed with orange; and whitish lips. The juvenile (LACM 114108, Fig. 15B) is patterned similarly but has a pale brown ground color (somewhat tan); pale bands/ocelli and pale vertebral line grayish anteriorly, invested with yellowish brown posteriorly and on the first two or three bands on the neck. McDiarmid's slide collection also has a photo of LACM 114106 in life, an adult female with clouded eyes (preparing to shed). Its coloration appears similar to that of LACM 114107 except perhaps a paler brown ground color (not as pale as the juvenile described above) and more orangish wash in the pale bands. The venter of LACM 148614 (339 mm SVL) was described as "yellowish" (Roy W. McDiarmid, field note).

Coloration in Preservative. Overall dorsal coloration predominantly grays and browns (tendency for brown with stratum corneum intact, grays without). A series of pale gray to pale brown crossbands (sometimes offset) on the body from the neck to the vent, continuing onto the tail as a variably distinct series of pale dorsolateral spots (Fig. 16).

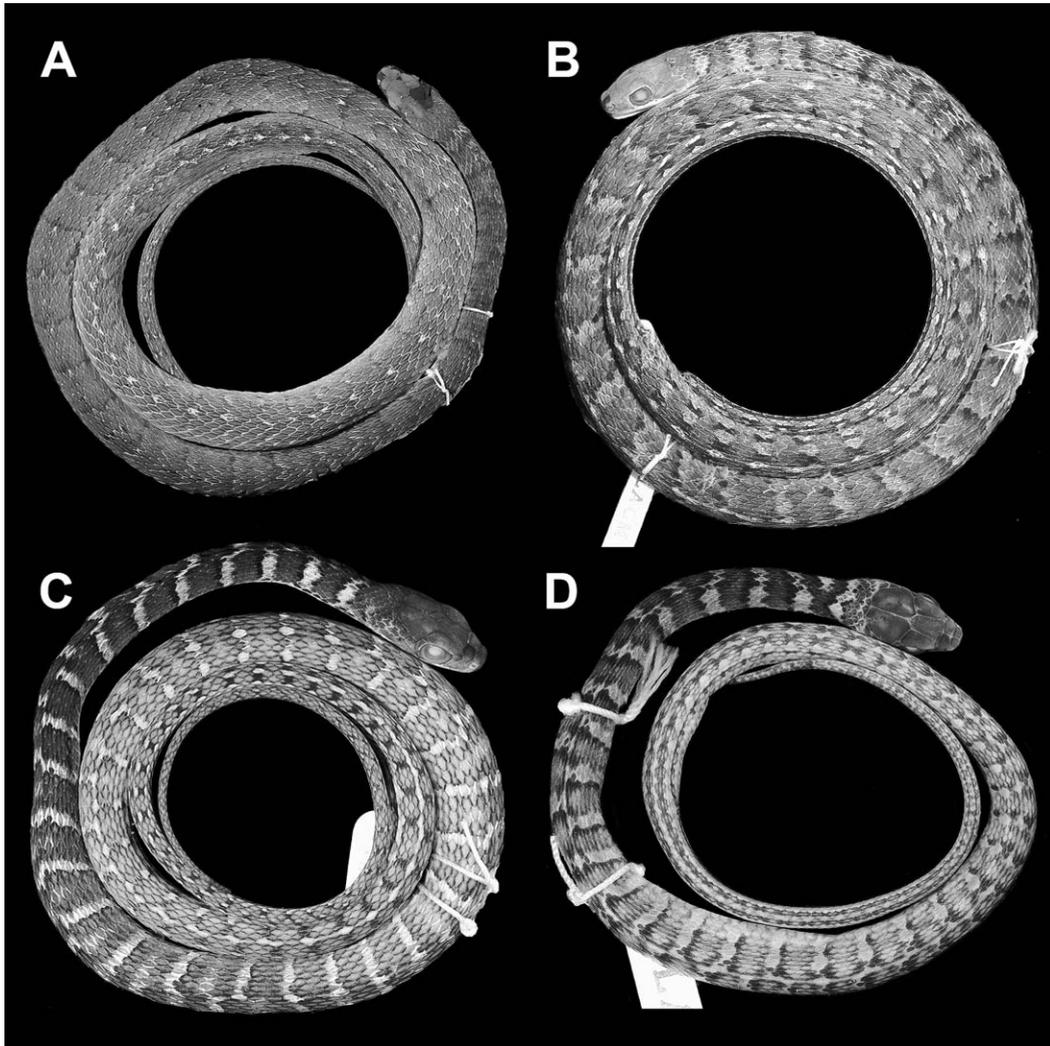


Figure 16. Representative specimens of *Dendrophidion crybelum*. (A) LACM 114107 (primary banding pattern obscured partly by formation of secondary bands and darkening of primary bands during preservation; compare Fig. 15A). (B) LACM 148596. (C) LACM 148613 (juvenile, 304 mm SVL). (D) LACM 148620 (juvenile, 185 mm SVL).

The number of pale bands/ocelli on the body ranged from 36 to 62 (mean 48.2). In about 58% of the specimens neck bands were 1.5–2 scale rows in width; in another 25% the bands were 1–1.5 rows wide; in the remainder, the neck bands were more than two scale rows wide or less than one row wide.

Crossbands bordered anteriorly and posteriorly by irregular black pigment forming

narrow jagged border (usually better developed on posterior edges). Posterior crossbands become invested with greater amount of dark pigment, usually becoming fragmented into a lateral and vertebral series of ocelli (lateral ocelli occupy parts of four adjacent scales on rows 3–5); less distinct ventrolateral ocelli sometimes on row 1. Crossbands extend to lateral edges of ventrals, which are marked with dark gray

and brown or black irregular spots. The first few bands on the neck and anterior body are broader than more posterior bands. Narrow broken blackish lateral stripe (or series of dashes/spots) occurs on the suture line between rows 2 and 3 on the posterior one-third of body. Black ventrolateral tail stripe on suture line between subcaudals and dorsocaudal row 1 extends to tail tip.

Two specimens (LACM 148596, 148599) have more vivid banding pattern than others; these two also tend to be grayer than others, which are browner. Crossbands obscure in other preserved adults (LACM 148590, 114106–07) seemingly because they are invested with brown pigment (except for neck bands) nearly the same color as the ground color and the crossband borders are not distinctly marked with pigment darker than ground color. Specimens with a dark brown ground color and contrasting pale bands in life may have obscure bands when preserved (compare Figs. 15A and 16A).

Top of head more or less uniform gray or brown down to superior edge of supralabials (last two supralabials mostly gray or brown). Faint blackish postocular stripe extends diagonally down across penultimate supralabial. Gular region immaculate.

Lateral portions of ventrals with dense grayish black pigment, within which are darker irregular spots. Remainder of most ventrals immaculate. However, posterior ventrals (up to about the 20th ventral anterior to the vent) have small scattered irregular black spots that vary in number from relatively many (LACM 148596, 148599) to almost none (LACM 114106–07) (Fig. 14). Subcaudals with ventrolateral stripe (described above) and generally with dense blackish/gray pigment investing subcaudals, especially along suture lines, and scattered irregular small round black spots on many subcaudals (Fig. 14).

Juveniles similar to adults but pale bands/ocelli are much better defined. Spotting or stippling on posterior ventrals and proximal subcaudals very faint, but even relatively small specimens have fine speckling of dark pigment on posterior portion of tail (e.g.,

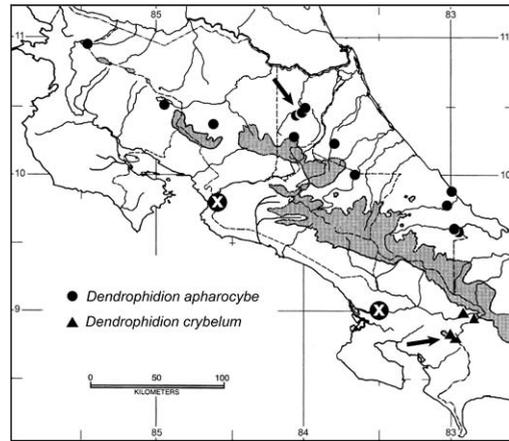


Figure 17. Distribution of *Dendrophidion crybelum* and of *D. apharocybe* in Costa Rica; see Savage (2002) for a more complete representation of localities. Arrows indicate type localities. A few symbols represent multiple contiguous localities. Two localities indicated by "X" within dots in western (Pacific) Costa Rica are erroneous localities for "*D. vinitor*" indicated by Savage (2002: 656); see species account for *D. apharocybe*.

LACM 114108, 298 mm SVL), especially on suture lines and laterally. Anterior ground color dark brown to blackish (contrasting greatly with pale crossbands), becoming lighter posteriorly (pale brown to tan on posterior half to two-thirds of body). Posterior lateral stripe broken; tail stripe quite distinct. Secondary pale bands between the primary crossbands already evident in LACM 148613–14. Width of pale dorsal bands in LACM 148614, 148617 is no more than about one scale wide. Juvenile *Dendrophidion crybelum* have a more contrasting pattern and well-developed ocelli on the posterior body compared with juvenile *D. apharocybe*.

Distribution (Fig. 17). Definitely known only from middle elevations (1,100–1,330 m) at the eastern end of the Fila Costeña and the south slope of the Cordillera Talamanca in southwestern Costa Rica. All known localities are in the uplands of the upper Río Coto Brus, separated from the lowlands of the Osa Peninsula–Golfo Dulce by the Fila Costeña. Despite relatively intensive surveys, "*D. vinitor*" has not been recorded

from lowland sites on the Osa Peninsula (Scott et al., 1983; McDiarmid and Savage, 2005). See the species account for *D. aphaerocybe* for discussion of two lowland Pacific localities erroneously attributed to “*D. vinitor*.”

Given the proximity of Costa Rican localities (Fig. 17), *D. crybelum* undoubtedly occurs on the adjacent Pacific versant of western Panama (Chiriquí province), where similar environments occur. Savage (2002) included “adjacent western [Pacific] Panama” in his distribution summary for *D. vinitor*, the basis being a specimen from “Chiriquí” listed in E. R. Dunn’s notes as having 121 subcaudals and a single anal plate (Jay M. Savage, personal communication, March 2011). This may be the same specimen listed by Boulenger (1894: 16; specimen g collected by Godman in Chiriquí, now BMNH 94.5.17.8), although Boulenger’s subcaudal count is 128. No one seems to have re-examined the specimen recently, so the presence of *D. crybelum* in Panama remains likely, though unsubstantiated. Nonetheless, *D. crybelum* probably has a very restricted distribution in southwestern Costa Rica and adjacent Panama.

Southwestern Costa Rica (Golfo Dulce region) has long been known for both high species diversity and high herpetofaunal endemism (e.g., Duellman, 1966: 712, 716; Savage, 1966: 758, 2002: 85, 813–814). Hence, the presence of a narrowly endemic species of *Dendrophidion* in this region comes as little surprise. In terms of overall species composition (Duellman, 1966) and historical biogeographic origins (Savage, 1966, 2002), the herpetofauna of the Golfo Dulce region shows ties to Atlantic lowland herpetofaunas of Costa Rica and Panama. Many closely related species pairs or conspecific populations of amphibians and reptiles show disjunct distributions in these two areas. Moreover, paleoenvironmental modeling (Chan et al., 2011: 528–531) shows that the Río Coto Brus valley has had a long history of environmental stability. The Pacific populations are isolated by the

presence of subhumid habitats north and south of this area (Savage, 2002). The biogeographic events responsible for these disjunctions are explored in the discussion.

Natural History. Most confirmed specimens of *D. crybelum* come from sites on the north side of the Fila Costeña (separating the Río Coto Brus Valley from the Golfo Dulce) that have been intensively studied by investigators associated with the Organization for Tropical Studies (OTS) and others (e.g., Janzen, 1973; Scott, 1976; Fauth et al., 1989; Santos-Barrera et al., 2008). Other close-by localities are on the southern slope of the Cordillera Talamanca. The type locality (Las Cruces) is classified as Premontane Wet Forest in the Holdridge system; other localities span a range of forest types, including Premontane and Lower Montane Wet Forest and Rainforest (Holdridge, 1967; Holdridge et al. 1971).

Scott (1976: 44, 53, table 1) described the site of quantitative herpetofaunal sampling at Finca Las Cruces (1,200 m) as having a 12-year average rainfall of 4,000 mm/yr, a brief “dry” period January–March, and moderate to steep slopes. Compared with the lowlands, Las Cruces has shorter, smaller trees, more understory, and deeper litter (5–7 cm deep depending on the season). Janzen (1973: 675) added further details: “The overstory canopy is about 30 m high and densely intertwined with vines and heavily laden with epiphytes. ... The understory is rich in palms, Cyclanthaceae, ferns, Marantaceae, and cycads, and appears in general very similar to that of the Osa [Peninsula lowland] primary forest sites except that the [Las Cruces] understory appears to have a much heavier epiphyllae load, the tree trunks have heavy layers of lower plants, and there seems to be a slightly reduced species richness of plants in the 0.3 to 2 m height range. ... *Quercus*, *Prunus*, and *Alnus* are more prominent than in nearby lowland sites.”

The discovery of specimens of *D. crybelum* in Costa Rica came relatively late, the first specimens from the type locality collected by Jay M. Savage and colleagues

in 1964. (A paratype from another locality, UF 16425, was obtained in 1962 and is the earliest known specimen.) Even in the early 1970s Janzen (1973: 675) reported considerable deforestation of lower montane forest in the vicinity of the type locality, which is now a patchwork of severely human-altered habitats (Santos-Barrera et al., 2008). According to Savage (personal communication, March 2011) good primary forest and additional second growth parcels still remain at the type locality (266 ha; now an OTS field station and Wilson Botanical Garden) and nearby indigenous reserves. Forested habitat at Finca Loma Linda is considerably altered, whereas Las Alturas is on the margin of La Amistad Biosphere Reserve, where substantial montane forest still exists (the habitat patchwork of this area is especially well shown on Google Earth).

Unfortunately, the region where *D. crybelum* occurs has also experienced considerable amphibian population declines (Lips, 1998, 1999; Lips et al., 2003, 2006; Santos-Barrera et al., 2008), a fact relevant to sustainability of *Dendrophidion* since leaf litter frogs comprise a major portion of the diet in all species (Stafford, 2003). The declining species documented by Lips and coworkers included species of *Pristimantis*, *Craugastor*, and *Diasporus*, which are major prey for *Dendrophidion*. The effects of extirpation of such prey species on the population biology of their snake predators are, as yet, little understood (Whitfield et al., 2007). In contrast to the population declines at La Selva (see species account for *D. apharocybe*), the amphibian declines at Las Cruces and nearby sites were precipitous and due primarily to the amphibian pathogen *Batrachochytrium*. A recent herpetofaunal inventory of Las Cruces and surrounding areas (Santos-Barrera et al., 2008) recovered two specimens of *D. percarinatum* but none of the three other species of *Dendrophidion* recorded there historically (*D. crybelum*, *D. nuchale* auctorum, and *D. paucicarinatum*; Scott et al., 1983, and personal observations of specimens in LACM). The last specimen of *D.*

crybelum held in U.S. collections was obtained in 1987.

The holotype and most paratypes of *D. crybelum* were included (as "*D. vinitor*") in a study of reproductive cycles in *Dendrophidion* from Costa Rica (Goldberg, 2003) and range-wide, Mexico to Panama (Stafford, 2003; as summary statistics only, along with specimens of *D. vinitor* and *D. apharocybe*). Four males in Goldberg's study (552–625 mm SVL) were undergoing spermiogenesis in April, June, August, and September. Two females (621–631 mm SVL) collected in May and July each had four oviductal eggs. Of the specimens I examined, a female collected 19 June from Las Alturas (LACM 148612, 480 mm SVL), has swollen and convoluted oviducts but no vitellogenic ova, suggesting that it had recently laid a clutch. The two smallest individuals (185 and 206 mm SVL) were collected 6 June and in September, respectively, and their umbilical scars were nearly completely closed. The umbilical scar of the next larger (251 mm SVL) was completely closed, and in two individuals of 304 and 339 mm SVL the umbilical scars were no longer evident. Like the other two species of the *D. vinitor* complex, there is a low frequency of snakes with broken/healed tails in *D. crybelum* (6.7% of the specimens examined).

HEMIPENIAL MORPHOLOGY

An Introduction to *Dendrophidion* Hemipenes

The initial recognition of the new species described herein depended to a great extent on differences in hemipenial morphology. However, *Dendrophidion* hemipenes are peculiar in ways that have never been fully described; thus, it seems pertinent to provide an overview of their general structure and characteristics. I have examined retracted and everted hemipenes of all currently described species of *Dendrophidion* except *D. boshelli*, for which no material has been available. Hemipenes of other species will be described elsewhere. Stuart

(1932) long ago recognized some unusual characteristics of *Dendrophidion* hemipenes, but a detailed description of only one species, *D. brunneum*, is as yet available (Cadle, 2010). Hemipenial terminology follows Dowling and Savage (1960), Myers (1974), Myers and Campbell (1981), Myers and Cadle (1994, 2003), Savage (1997), and Zaher (1999), but the terminology useful in describing certain unusual structures in *Dendrophidion* is further discussed here. Except where noted, these comments apply equally to the *D. dendrophis* and *D. percarinatum* groups (*sensu* Lieb, 1988).

The hemipenis of *Dendrophidion* is either unilobed or slightly bilobed but the overall shape varies considerably among species—from short, bulbous, and cylindrical forms described here to longer, slender and clavate shapes. A short basal nude section (*pedicel* in the terminology of Savage [2002: 539]) is followed by a broader section usually ornamented with minute spines; there are no nude pockets or basal lobes (some organs have round basal bulges when everted). The relatively unadorned base is followed by an array of closely spaced spines that are enlarged to varying degrees and in patterns that are species specific. In general, hemipenial spines in the *D. dendrophis* species group are larger than those in the *D. percarinatum* group. Although hemipenes of the *D. dendrophis* group are sometimes said to have enlarged “basal hooks” or “basal spines” (e.g., Dunn, 1933: 78; Lieb, 1988; Savage, 2002: 654), their enlarged spines are not basal in the same sense as in some snakes, in which enlarged spines are truly positioned at the base of the organ. Rather, they are attached along the central portion of the hemipenial body (*truncus* in the terminology of Savage [2002: 539]). In some species of both the *D. dendrophis* and *D. percarinatum* groups, a pair of spines much larger than any others is positioned near the sulcus spermaticus at the proximal edge of the array of spines (one on each side of the sulcus); this pair is relatively much larger in *D. dendrophis* and *D. nuchale* auctorum than in other species

in which they occur (*D. dendrophis* and *D. nuchale* auctorum also have an additional pair of enlarged spines positioned toward the asulcate side). Species of the *D. vinitor* complex lack such conspicuously enlarged spines.

Distal to the spines are structures that range from more or less definitive calyces (cuplike structures with both longitudinal and transverse walls) to flounces (transverse ridges lacking longitudinal connecting walls), with an array of intermediate structures that are neither definitive calyces nor flounces. For example, the hemipenial apex in two species of the *D. vinitor* complex has long, relatively free-standing ridges that don't conform to strict definitions of either calyces (because they do not form reticulating networks) or flounces (because they are not transverse in orientation). Nonetheless, the morphological similarity among all of these structures is clear and they undoubtedly have similar developmental origins. Further reductions of calyxlike structures result in low fleshy ridges or entirely nude apical areas. Proximal calyces/flounces have broader walls than more distal ones. These descriptors refer to structures visible in everted or retracted hemipenes. In addition, retracted hemipenes may have *pseudocalyces*, which are calyxlike structures visible in retracted organs that disappear upon eversion and full inflation (Myers and Cadle, 1994: 13–14; Cadle, 2010: 19–20). The tip of the apex in *Dendrophidion* has a combination of reduced calyces, free-standing ridges, and/or nude areas in patterns that are species-specific.

Flounces, calyces, and other similar structures are ornamented with mineralized spinules, at least proximally, but spinules are usually reduced or absent in distal calyxlike structures. Most spinules in *Dendrophidion* are atypical in that they lack a tip projecting from atop the calycular walls. Instead, they consist of a mineralized rod completely enclosed by the wall tissue. I refer to these as *embedded spinules* (see also Cadle, 2010: 16 [fig. 6], 19); they are relatively straight and more or less the same thickness throughout.

A general pattern in the arrangement of calyxlike structures seems common to all species of *Dendrophidion*, regardless of the overall pattern in a given species. Calyces are most fully developed on the asulcate side in comparison to the sulcate side, which has few or no full-fledged calyces. On the asulcate side in most species, a calyculate region extends to the tip of the apex, sometimes as far as its midpoint. Additionally, at the proximal edge of the calyculate region, at least one pair of transverse flounces encircles the hemipenis in all species (some species have more than one pair). Transitions between flounces and calyces or calyxlike structures occur abruptly within a single organ.

The sulcus spermaticus in *Dendrophidion* is centrolineal and usually has a slightly flared tip with divergent sulcus lips, but the sulcus is terminally divided in an undescribed species of the *D. percarinatum* group and in *D. dendrophis* (a detailed discussion of this morphology will be presented elsewhere). Savage (2002: 539) introduced the term *semicentripetal* for sulcus conditions such as those *Dendrophidion* with a simple sulcus on a unilobed organ in which the sulcus extends to the tip of the hemipenis with minimal deviation from the midline of the sulcate surface (e.g., hemipenes described herein). This term is unnecessary because it embodies several aspects of hemipenial morphology for which vocabulary already exists, namely the overall hemipenial form (unilobed vs. bilobed), sulcus morphology (simple vs. bifurcate), and sulcus orientation (centrifugal, centrolineal, or centripetal). Because these three aspects of hemipenial morphology can be combined in various ways, I prefer to employ terms that keep the descriptive concepts separate. Thus, I use *centrolineal* to refer to simple or bifurcate sulci that pass distally with little deviation from the middle of the sulcate side of a hemipenis, whether unilobed or bilobed. Other authors (e.g., Zaher [1999] and Myers [2011]) have also used *centrolineal* in this broader sense.

The use of the term *semicentripetal* has other awkward consequences. First, *semi-*

centripetal suggests a relationship to centripetal sulci seen on many bifurcate hemipenes. This relationship is unclear given that simple sulci can be derived in several ways from distinct bifurcate morphologies (centripetal, centrolineal, or centrifugal), and hemipenes in colubrids may have sulci in any of these orientations (Cadle, 2010: 18–19; see also Myers, 2011: 22–24). Secondly, some genera (e.g., *Dendrophidion*, *Leptodeira*, *Taeniophallus*) have species with both divided and simple sulci spermatici on unilobed to slightly bilobed organs; see Schargel et al. (2005, fig. 8) for an example from *Taeniophallus* and Myers (2011: 22–24) for *Leptodeira*. Using *semicentripetal* for those species with a simple sulcus and *centrolineal* for those with a divided sulcus has the undesirable consequence of applying different names to sulcus orientations that are basically the same, the only difference being the simple or divided nature of the sulcus overall. The different terms obscure the clear relation between the simple and divided sulcus conditions within such genera.

The use of *centrolineal* for forked or simple sulci on either bilobed or unilobed hemipenes means that the term applies to a broader array of sulcus topologies than would be the case if it were used exclusively for forked sulci on uni- or bilobed organs (its original definition, used in conjunction with describing the morphology of some dipsadids; Myers and Campbell, 1981: 16). I believe this is a nonissue inasmuch as I use the terms *centrolineal*, *centripetal*, and *centrifugal* to refer *only to the position of the sulcus* on the hemipenis overall, regardless of variations in other aspects of hemipenial morphology such as lobation or whether the sulcus is bifurcate or simple. Other variations, such as deflections of a simple (centrolineal) sulcus to the right (as in Colubridae) or left (in Natricidae) lobe, can simply be described or accommodated by terms already in use (e.g., dextral and sinistral, respectively; Rossman and Eberle, 1977; Myers, 2011: 14). I believe that using terms such as *centrolineal* for discrete

aspects of morphology (in this case *sulcus position only*), rather than combinations of several aspects, is more straightforward and more directly communicates morphological details.

The *retractor penis magnus* in *Dendrophidion* may or may not have a short division at the insertion. In species of the *D. vinitor* complex, some specimens seemed to have a very short separation of muscle fibers at the insertion, but I failed to detect such a separation in others. Whether this reflects true morphological variation or simple difficulty of determination in very short divisions is unclear. On everted hemipenes, two internal points of insertion of the retractor can often be discerned through the apical tissue; the spacing between these points may reflect the degree of division of the muscle.

Dendrophidion vinitor

Everted (UMMZ 121145, Veracruz state, Mexico; Figs. 18, 19). Hemipenis unilobed and with a somewhat bulbous apex. Total length about 17 mm; about 7.5 mm across the widest point (apex). Sulcus spermaticus simple, centrolineal, with a very slightly expanded tip. The tip of the sulcus is near the sulcate side of the apex and entirely hidden beneath the free edge of a raised knob of tissue, the *apical boss* described below.

Short proximal portion of the hemipenial body mostly nude, having only a band of scattered minute spines on the asulcate side and a few adjacent to the sulcus spermaticus just proximal to the array of enlarged spines. Central region of hemipenial body with short, robust, strongly hooked spines arranged in four to five more or less regular transverse rows all around. Total spines in the array 46. Spines are shorter on the sulcate side and longer on the asulcate side but there is little proximal-to-distal size differentiation.

Distal to the spines four or five flounces completely encircle the hemipenis. On the apex, these flounces grade into calyxlike structures and free-standing ridges that are

more fully described below. The flounces have a short, thick, fleshy base and a wider outer membranous portion (within which are embedded spinules). Flounces somewhat wider on the asulcate side than on the sulcate side, and they gradually narrow in width distally. There is an abrupt transition between the array of spines and the flounces, but in some places, particularly adjacent to the sulcus spermaticus, spines in the distalmost row are incorporated into the proximal pair of flounces (most evident in the proximal flounce) and appear as especially robust spinules (Figs. 18A, 19B). These incorporated spines have a more strongly projecting and hooked distal tip compared with other spinules.

On the distal portion of the asulcate side are eight to 10 poorly developed calyces between the distal three flounces (i.e., four to five between the distal two flounces, and another four to five between the penultimate and antepenultimate flounce). Longitudinal walls of calyces much lower than transverse walls (which make up the flounces). Among the proximal three flounces on the asulcate side are a few other poorly developed longitudinal walls, which form very large irregular calyces (obscured by the overhanging flounces in Fig. 18A).

All flounces, calyces, and similar structures (including those on the apex) have embedded spinules. Adjacent to the sulcus spermaticus the spinules have a short projecting tip, but away from the sulcus the spinules are completely embedded. Spinules near the sulcus are also hooked (probably represents transitional structure to spines in the array), but they are relatively straight away from the sulcus.

Tip of the apex with a complex series of free-standing ridges similar to flounces except that they extend mostly obliquely across the apex from a median axis (Figs. 18A, 19A, B). Around the periphery of the apex, especially on the asulcate side, a few poorly developed connections among the apical ridges form rudimentary calyces. One of the apical ridges (the *median bisecting ridge*) is taller than the others

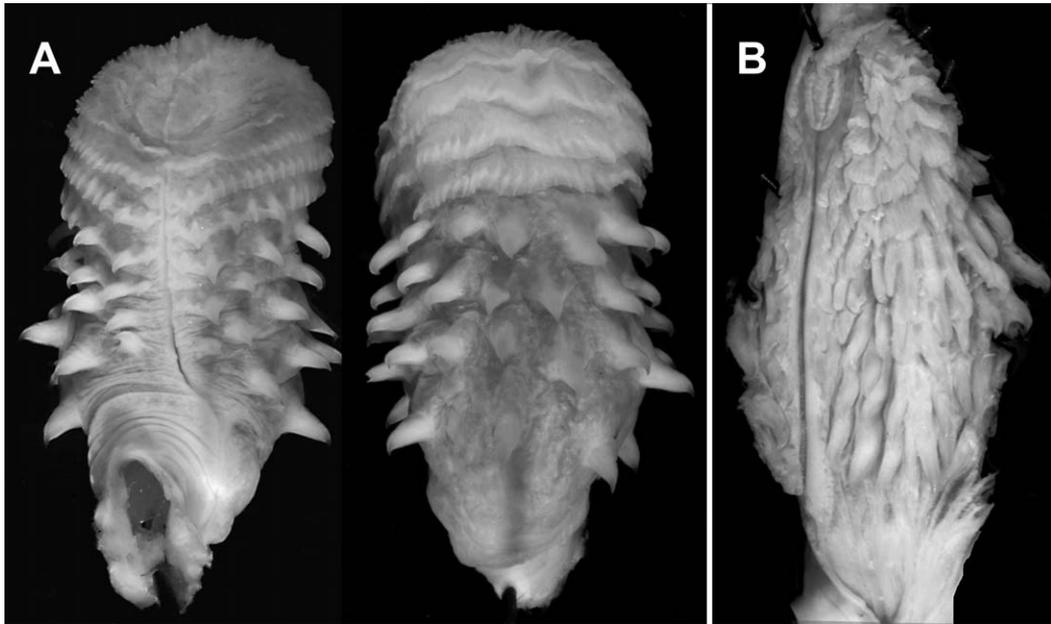


Figure 18. Hemipenes of *Dendrophidion vinitor*. (A) Everted organ in sulcate and asulcate views (UMMZ 121145; Veracruz, Mexico; right hemipenis). (B) Retracted organ slit midventrally and spread flat (UIMNH 35547; Oaxaca, Mexico; left hemipenis). See Figure 19 for details of apical morphology.

and bisects the apex in a line extending from above the tip of the sulcus spermaticus directly across the middle of the apex; it is not straight, but undulates, and has well-developed embedded spinules (Fig. 19B). A series of shorter, lower ridges runs obliquely outward from the median bisecting ridge toward the asulcate side. These also have

embedded spinules but the spinules are less regularly developed than on the median ridge. On its sulcate end the median bisecting ridge continues across a prominent bulbous knob (the *apical boss*), bisecting it as well (seen in Figs. 18A and 19A as a line of denser whitish tissue extending across the middle of the boss). The borders

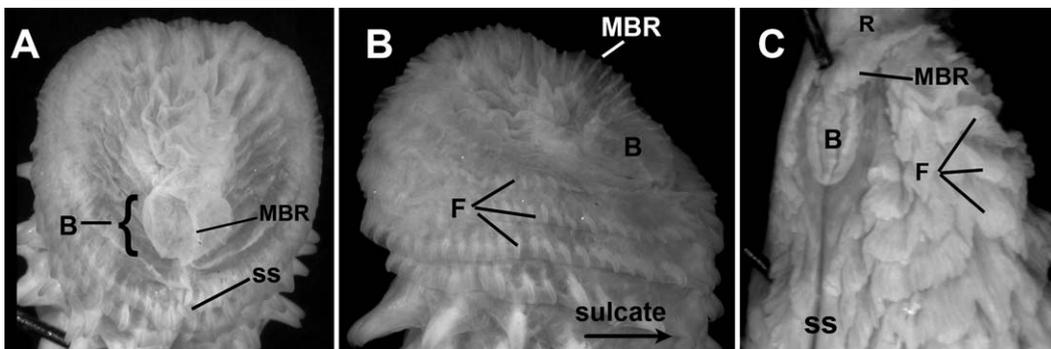


Figure 19. Details of apical morphology of the hemipenis of *Dendrophidion vinitor*. (A) Apical view of UMMZ 121145 (everted, sulcate edge of apex toward bottom). (B) Lateral view of UMMZ 121145 (everted, sulcate side to the right). (C) Apical region of a retracted organ (UIMNH 35547; distal toward the top). *Abbreviations:* B, apical boss; F, flunces; MBR, median bisecting ridge; R, retractor penis magnus; ss, sulcus spermaticus. Compare Figure 18.

of the boss are well-defined and raised. The sulcate edge of the boss is elevated above the apical tissue and the sulcus spermaticus ends beneath it.

Retracted (UIMNH 35547, Oaxaca state, Mexico; Figs. 18B, 19B). Hemipenis extends to the middle of subcaudal 8. There appeared to be a slight separation of muscle fibers at the insertion of the *retractor penis magnus*. Extreme proximal portion of hemipenial body nude, followed by a band of scattered minute spines proximal to the array of enlarged spines (minute spines perhaps a bit denser around the sulcus and on the asulcate side). Ornamentation of the body dominated by an array of enlarged spines (45 total); enlarged spines robust, hooked at the tip, larger proximally and on the asulcate side, gradually decreasing in size distally. Each side of the sulcus spermaticus bordered by a line of seven to nine much smaller spines (small spines one-fourth or one-fifth the size of the enlarged spines in the array).

Three frounces on sulcate side of organ, increasing to five or more on the asulcate side; these grade into the apical freestanding ridges. All frounces/ridges with embedded spinules. Proximal frounces broader than the more distal ones and mainly membranous rather than fleshy. Some low and weak connections extend between adjacent distal frounces, especially on the asulcate side, and form poorly developed calyces.

At the tip of the organ is a prominent tissue ridge (equivalent to the median bisecting ridge and associated oblique ridges in the everted organ) extending from the asulcate side across the apex and bisecting the apical boss, which lies at the tip of the sulcus spermaticus (Fig. 19C). The boss has a prominent ridge delimiting its border but is nude apart from this border and the bisecting ridge; its morphology in the retracted organ is similar to that in the everted state. The bordering ridge has a few crenulations, which seem to have short embedded spinules. A few loose folds (presumably forming the oblique ridges in

the everted organ) lie lateral and distal to the boss and bisecting ridge; tissue mainly lateral and proximal to the boss is nude.

Sulcus spermaticus simple, in the dorso-lateral wall of organ, ending distally beneath the sulcate edge of the apical boss. Tip of the sulcus not expanded, the groove actually appearing to narrow slightly at its terminus. The sulcus lips also do not appear to diverge distally.

There is some variation in the length of retracted hemipenes. Of nine retracted hemipenes examined superficially in situ, four ended between the suture of subcaudals 7/8 and the suture of subcaudals 8/9; four ended between the middle of subcaudal 9 and the middle of subcaudal 10; and one extended to the middle of subcaudal 11. The major retractor muscle appeared undivided in four specimens, but three others appeared to have a slight separation of muscle fibers at the insertion.

Dendrophidion apharocybe

Everted (LACM 148600, Heredia province, Costa Rica; Fig. 20). Hemipenis short, stout, with a slightly bulbous apex having an asulcate indentation, giving a somewhat cordate shape to the apex when viewed from the sulcate side. Total length about 21 mm. Length of base proximal to spine array on sulcate side about 3.5 mm. Length of apex from proximalmost frounce to tip on sulcate side about 13 mm. Maximum width of organ 11.5 mm (across middle of apex). Sulcus spermaticus simple, centrolineal, with a distinctly flared tip.

Base of organ proximal to the array of enlarged spines very short, ornamented with minute spines. The relatively unornamented base is followed by a central section with enlarged spines. Thirty-six spines form the array and a line of very small spines lies on each side of the sulcus just proximal to the apex. Spines arranged in somewhat irregular oblique rows on the sulcate side but no particular arrangement on the asulcate side (appear scattered, irregular). Spines on the asulcate side are much larger than those on



Figure 20. Everted hemipenis of *Dendrophidion apharocybe* (LACM 148600 from near the type locality, left hemipenis) in sulcate, asulcate, and lateral views. Note flared tip of the sulcus spermaticus and the nude apical tip strongly inclined toward the sulcate side (sulcate to the right in lateral view).

the sulcate side. Some small spines are incorporated into the first flounce on the sulcate side. On the sulcate side all spines are more or less the same size (perhaps slightly larger proximally). On the asulcate side, the distal spines are slightly larger than the more proximal ones.

Four flounces on the sulcate side broaden to about seven on the asulcate side. The proximal flounce on the sulcate side becomes the 3rd flounce on the asulcate side (two proximal flounces added on the asulcate side). Flounces curve distad toward the asulcate side, reflecting the inclination of the apex toward the sulcate side (Fig. 20, lateral view). No distinct calyces except for a couple of irregular ones distally on the right asulcate side (i.e., the right side viewed looking toward the asulcate side; see Fig. 20, asulcate view). These calyces are asymmetrical (no comparable ones on the left side). Several other weak calyces present between the first pair of flounces on the asulcate side (weakly developed longitudinal walls between these two flounc-

es). Flounces have a thick fleshy base and an outer membranous part. All flounces have embedded spinules, the tips of which occupy weak scallops on their edges; spinules occupy mainly the membranous part but enter the fleshy part slightly. Scalloping becomes progressively less distally and medially.

Apex strongly inclined so that its distal surface faces toward the sulcate side (flounces extending distad much farther on the asulcate than the sulcate side). Central part of the apex occupied by a prominent bulge, which slopes gradually to meet the asulcate edge of the apex but drops off sharply on the sulcate side (Fig. 20, lateral view). The sulcus ends near the sulcate side of the organ just beneath the bulge. Apex nude except for low rounded ridges that occupy the central bulge. These ridges have the same general pattern as the membranous ridges on the hemipenis of *D. vinitor* (see above description). That is, they extend obliquely outward toward the asulcate side from a median axis; toward the sulcus the

ridges converge on a point on the bulge distal to the tip of the sulcus. An indication of these ridges can be seen in Figure 20 (sulcate view) as oblique darker streaks alternating with wider whitish streaks just lateral to the central part of the apex. Small areas lateral to the sulcus tip are smooth and without ridges. Toward the asulcate edge of the apex some of the oblique ridges are connected by very low additional ridges, forming a series of indistinct reticulating structures (highly reduced calyces).

Retracted (MVZ 217610, Heredia province, Costa Rica; Fig. 21). Hemipenis extends to about the middle of subcaudal 7. Sulcus spermaticus simple, extending distally in dorsolateral wall of the organ and ending short of the tip. At the tip of the sulcus are fine loose folds of tissue within the sulcus groove that presumably expand upon eversion to form the expanded tip of the sulcus in the everted organ.

Extreme basal portion of hemipenis under subcaudal 1 appears to be nude. About three rows of enlarged spines begin at level of the proximal edge of subcaudal 2 and extend to the distal edge of subcaudal 3. About 34 total spines on the organ, with 10–12 of these very large. These spines have a somewhat unusual flattened form with a tiny point at the tip.

About seven or eight rows of calyces/flouces located primarily on the asulcate side (medial and ventral sides of the retracted organ) begin at the level of the proximal edge of subcaudal 4. Only the proximal three flouces extend all the way to the sulcus spermaticus (more distal flouces stop short of the sulcus). Thus, the asulcate surface of the hemipenis is flounced almost to the tip of the organ, whereas on the sulcate side the flouces stop well short of the tip. Distal to the three proximal flouces adjacent to the medial side of the sulcus, the tissue of the hemipenis is smooth and nude and formed into low longitudinal folds. A few calyces are nestled within the distal longitudinal folds, mostly on the asulcate side. On the lateral side of the sulcus are enlarged spines up to

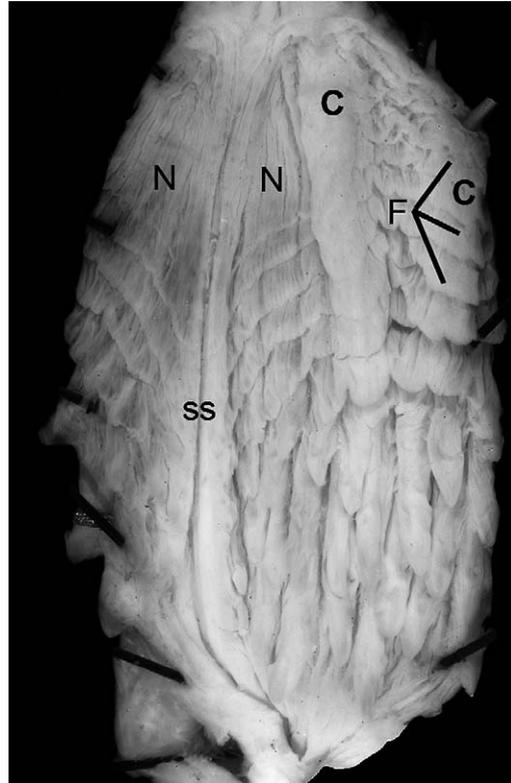


Figure 21. Retracted left hemipenis of *Dendrophidion apharocybe* (MVZ 217610 from near the type locality). Apex toward the top. *Abbreviations*: C, thick cords composed of closely appressed flouces on each side of the apical nude area; F, asulcate flouces; N, expanse of nude tissue on each side of the sulcus spermaticus that forms the nude sulcate face of the apex in the everted organ; ss, sulcus spermaticus. Note the lack of an apical boss and large area of apical nude tissue (compare Figs. 18B, 19C, *D. vinitor*).

about the middle of subcaudal 5, distal to which the hemipenis is nude, smooth, and in low longitudinal folds.

The calyces/flouces are tightly bound, pleated tissue, with adjacent flouces barely overlapping. The flouces are gathered into a pair of thick "cords," one on each side of the apical nude tissue in the intact retracted organ (Fig. 21; in the figure, both cords are on one side of the nude tissue because of the position at which the hemipenis was slit). Between the cords is thinner tissue in which the flouces are individually discrete (the thinner tissue makes up the asulcate

flounces in the everted organ). A few weakly developed longitudinal connections are present between the distal two or three flounces. The flounces seem tightly bound to one another because of sturdy longitudinal connections that occur periodically between adjacent ones. Their free edges are very slightly crenulate and have embedded spinules. The spinules extend to the edge of the flounces but do not seem to extend entirely to their bases. In the most proximal flounce, bunches of four to five spinules are separated by thinner, narrower tissue, such that the edge of this flounce is undulating. The bunches of four or five spinules grade almost imperceptibly into the enlarged spines more proximally.

Variation and Remarks. A consistent and unusual hemipenial morphology is primary evidence that the populations from Honduras to Panama here referred to *D. apharocybe* comprise a single species. Sample sizes from different parts of this range of either fully everted organs or hemipenes everted sufficiently to see the configuration of the apex are 4 (Honduras), 2 (Nicaragua), 7 (Costa Rica), 1 (Panama). In addition, I studied the internal morphology of one retracted organ each from Nicaragua, Costa Rica, and Panama. There is little variation in basic morphology or ornamentation from throughout the range (particularly the distinctive inclination of the apex, asulcate flounces, and large apical nude expanse). The number of enlarged spines in the spine array is variable (23–40) but shows no particular geographic trend. For example, two organs with 23 spines were from Honduras and Panama and two hemipenes with 28 and 40 spines were both from Nicaragua. In large part, the strong consistency of hemipenial morphology throughout the geographic range of *D. apharocybe* lends integrity to the concept of this species as distinct from *D. vinitor* and *D. crybelum*.

Eight retracted hemipenes of *Dendrophidion apharocybe* from Honduras to Panama were superficially examined. Their distal endpoints were between the end of sub-

caudal 6 and the proximal edge of subcaudal 10, with four ending at or proximal to the middle of subcaudal 7. The major retractor muscle appeared undivided in two specimens and with a slight division in two others.

Dendrophidion crybelum

Everted (LACM 148599, holotype, Puntarenas province, Costa Rica; Fig. 22). Hemipenes of the holotype were the only fully everted organs studied in detail. One other was more or less fully everted (LACM 148590); it is essentially identical to the holotype but a few differences are noted. Hemipenis cylindrical, much longer than wide, and lacking a distinctly bulbous apex. Total length about 21.5 mm; width about 6 mm (about 3.6× longer than wide). Sulcus spermaticus, simple, centrolineal, with an expanded tip that broadens and then narrows, forming a tear drop-shaped expanse of nude tissue. The distal narrowing may be an artifact of the field eversion preparation, perhaps slight desiccation (it seems as if some slight folds between the distal lips might expand to form an openly expanded sulcus tip as in other *Dendrophidion* hemipenes). In LACM 148590 the sulcus tip appears to expand in normal fashion and then has a narrow distal nude extension. The distally divergent lips of the sulcus seemingly end short of the nude extension.

Extreme base nude but scattered minute spines occur in a band around the organ proximal to the enlarged spines. A great number of enlarged spines dominate the ornamentation of the hemipenial body (about 90–95 in LACM 148599; about 70–75 spines in LACM 148590). About 12 much smaller spines form a line on each side of the sulcus spermaticus for most of its length. Spines are larger proximally, gradually decreasing in size distally, and somewhat larger on the asulcate compared with the sulcate side.

Distally, spines are followed by a short, nonbulbous apex ornamented with flounces

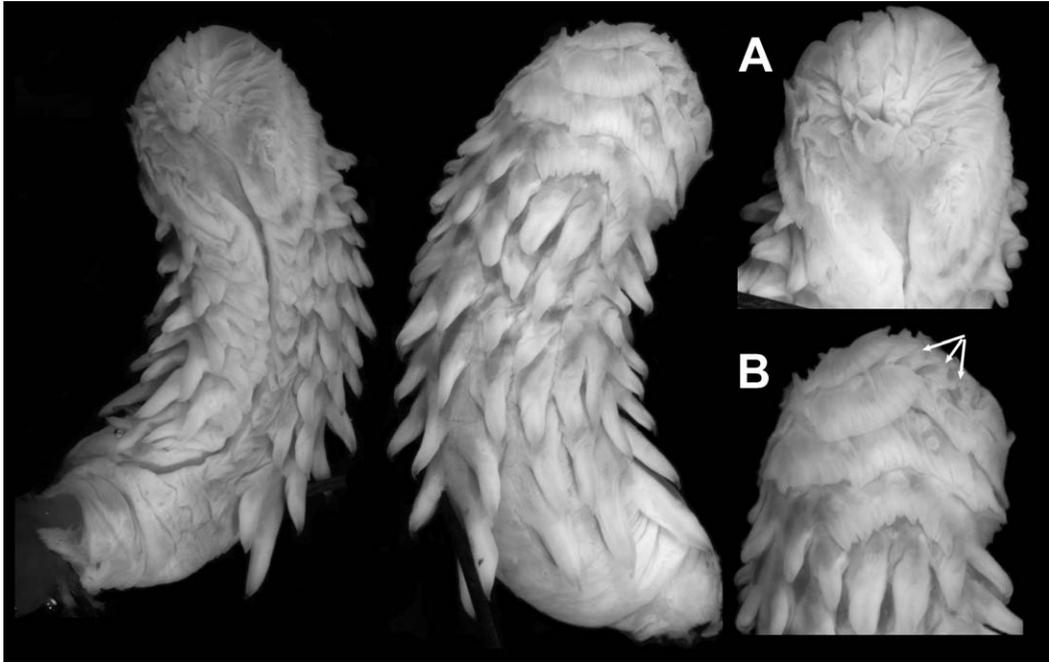


Figure 22. Everted hemipenis of *Dendrophidion crybelum* (LACM 148599, holotype), sulcate and asulcate views. (A) Detail of apical region showing closely packed apical ridges and flared tip of the sulcus spermaticus. (B) Asulcate side of apex showing flounces and rudimentary calyces (arrows).

and calyces. Two flounces adjacent to the sulcus, broadening to four on the asulcate side (the most proximal on asulcate side is short, poorly developed, and asymmetrically placed in about the middle of the asulcate side). The two additional flounces on the asulcate side are proximal to the two on the sulcate side and form from connections among spines in a transverse row (the spines then becoming relatively robust spinules within the flounce). Flounces contain embedded spinules, which span their membranous parts and extend into the outer portion of their fleshy parts (these flounces mostly consist of membranous part, very little fleshy base). On the asulcate side between the distal pair of flounces are several poorly developed calyces with very low, underdeveloped longitudinal walls; these are mostly not visible except by lifting and separating the flounces forming their transverse walls. These calyces are more fully developed on the right side of the apex than the left

(Fig. 22B; similar to the pattern of development in *D. apharocybe*).

Apex with many freestanding ridges containing embedded spinules and very little nude tissue (a small amount on the sulcate side around the tip of the sulcus spermaticus). The ridges generally have the same pattern as the apical ridges in *D. vinitor* (i.e., a median bisecting, somewhat taller ridge from which less prominent ones extend obliquely toward the asulcate side). These ridges are much lower and seem fleshier than the more membranous ridges in *D. vinitor*. They have slightly scalloped edges, and, because the apex is much narrower in *D. crybelum*, the ridges are more tightly packed. Toward the sulcate side, the ridges converge toward a point just distal to the tip of the sulcus spermaticus.

No definitive apical boss such as that in *D. vinitor* is apparent. However, the sulcate tip of the median bisecting ridge has a thickened nodule and, on each side, a short

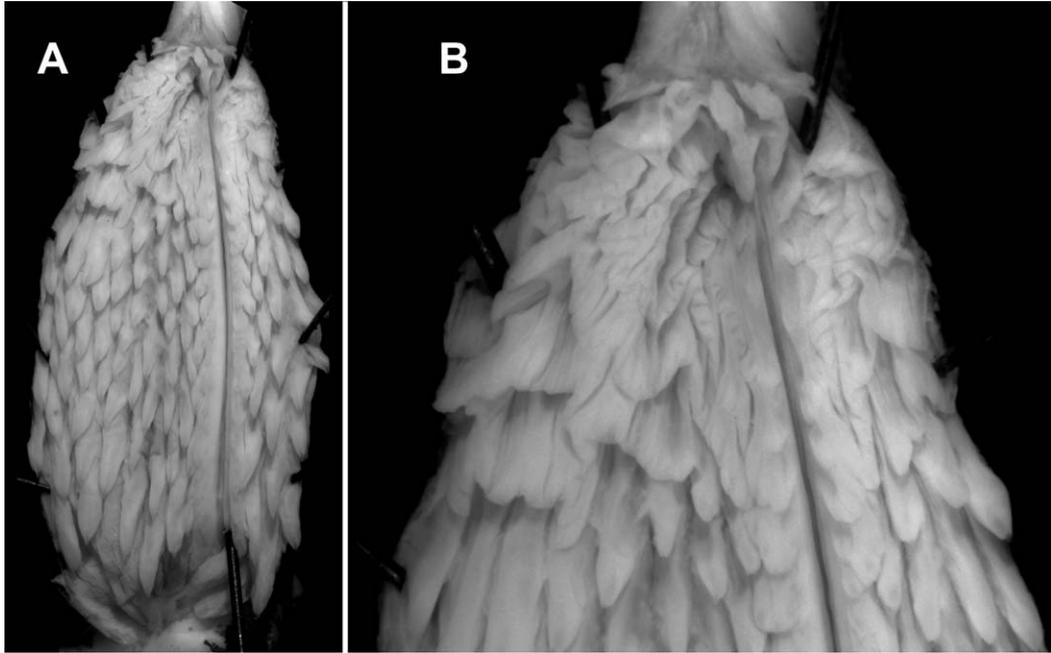


Figure 23. (A) Retracted right hemipenis of *Dendrophidion crybelum* (LACM 148608). (B) Detail of the apex of the same specimen.

segment of calycular tissue with somewhat thickened peripheral edges; the segment on the right side of the sulcus is partially fused with the median bisecting ridge, whereas the one on the left is detached. Toward their asulcate ends, the segments are attached to one of the oblique apical ridges by a constriction in the tissue, which separates them somewhat from the main part of the oblique ridge. The general configuration of this area is reminiscent of the apical boss in *D. vinitor* and may be a less fully developed, but homologous structure. Both hemipenes of *D. crybelum* examined, LACM 148590 and LACM 148599, have similar configurations in this area.

Retracted (LACM 148608, Topotype, Puntarenas province, Costa Rica; Fig. 23). Hemipenis extends to the suture between subcaudals 9 and 10. No division of the major retractor was detected. The base of the organ is nude and followed by a very short region ornamented with minute spines. Hemipenial body dominated by

approximately 92 enlarged spines; a series of much smaller spines lines each side of sulcus spermaticus. Individual spines are robust, very long, with a small hooked spike at tip. The spinose region is followed distally by flounces/calyces; they are more calyxlike on the asulcate side (very deep calyces here), where they extend onto the apical region. All flounces/calyces have embedded spinules.

Sulcus spermaticus simple and in the dorsolateral wall of organ; seemingly not flared at tip, but there is a long very fine ridge of tissue extending along the midline between the sulcus lips at the tip of the organ (may expand upon eversion to form flared tip). Sulcus ends beneath the tips of a pair of membranous ridges (reduced calyx walls) at the sulcate edge of the bisecting apical ridge (the bisecting ridge extends toward the sulcate side and divides, forming a pair of flaps resembling the apical boss in *D. vinitor*; these two flaps are connected by a low transverse ridge extending between

them). The entire sulcus spermaticus between the origin of the enlarged spines and the flounces/calyces is bordered on each side by a line of closely spaced small spines.

Three other retracted hemipenes of *D. crybelum* extended to the middle and end of subcaudal 9 and to the proximal edge of subcaudal 10.

DISCUSSION

Species Groups and Relationships

The recognition of three cryptic species within the *D. vinitor* complex, a detailed understanding of their hemipenial morphology, and comparative data on other species of *Dendrophidion* provide a framework for understanding some aspects of *Dendrophidion* systematics and biogeography. I will elsewhere present detailed hemipenial descriptions of other species of *Dendrophidion* and, for present purposes, mention only a few salient features necessary for understanding hemipenes of the *D. vinitor* complex. Characters suggested here as unifying groups of species are provisional apomorphies pending broader comparative work.

One hemipenial character has been used to define the *D. dendrophis* species group (*D. dendrophis*, *D. nuchale* auctorum, and the three species of the *D. vinitor* complex as defined herein): the presence of “basal spines or elongate hooked villi” or “large basal hooks” (Lieb, 1988; Savage, 2002: 654, 656). As pointed out in the introduction to *Dendrophidion* hemipenes, none of the enlarged spines in *Dendrophidion* hemipenes are truly basal. However, details of hemipenial morphology in the *D. vinitor* complex allow some refinement of hemipenial characterizations of this group. Within the *D. dendrophis* group, only *D. dendrophis* and *D. nuchale* auctorum have a pair of sulcate spines at the proximal edge of the spine array that are enormously enlarged beyond the size of most spines in the array (these two species also have up to two other moderately enlarged spines). These greatly enlarged spines correspond

to the “basal spines” of other authors and are much larger than any other spines on the hemipenis of these two species (unpublished data; see Stuart, 1932).

In contrast, other than a size asymmetry noted below, species of the *D. vinitor* complex have no spines enormously enlarged beyond the majority of “enlarged” spines on the hemipenial body, a detail noted by Smith (1941) in his description of *D. vinitor*. Thus, only part of the *D. dendrophis* species group is characterized by greatly enlarged hemipenial spines. Moreover, although hemipenial spines in the *D. dendrophis* species group are generally larger than those in the *D. percarinatum* group, this generalization does not hold for all species. For example, hemipenial spines in some specimens of *D. percarinatum* are approximately the same relative size as those in *D. vinitor*. While there is great interspecific variation in the absolute sizes of spines in *Dendrophidion*, all species have an array containing “enlarged” spines but the variation in spine size does not clearly distinguish the two species groups. Until more thorough comparative studies of hemipenial morphology within *Dendrophidion* demonstrate consistent differences between the *D. dendrophis* and *D. percarinatum* groups, statements about differences in relative spine enlargement need qualification to account for intragroup variation. The point of dorsocaudal reduction and the prominence of keels on the dorsal scales still provide convenient characters for distinguishing the two species groups of *Dendrophidion*, although whether this convenience reflects phylogeny ultimately should be reexamined.

Is the *D. vinitor* complex monophyletic? Within the *D. dendrophis* group, species of the *D. vinitor* complex share several hemipenial characters compared with *D. dendrophis* and *D. nuchale* auctorum (characters in parentheses): (1) Calyxlike structures reduced to flounces, especially on the asulcate side (Figs. 18, 20, 22) (calyces reduced, but fully formed cuplike structures present on both the sulcate and asulcate

sides); (2) increased number of flounces on the asulcate side compared with the sulcate side (flounces/calyses not increased on asulcate side, perhaps reduced); (3) enlargement of spines within the battery conspicuously asymmetrical, with asulcate spines noticeably larger than sulcate spines, seen especially well in Figure 20, lateral view (no conspicuous general asymmetry in spine enlargement [a pair of enormously enlarged spines on the sulcate side and often another pair toward the asulcate side]); (4) series of freestanding apical ridges with a primarily oblique orientation from a central axis, the median bisecting ridge (freestanding ridges absent; calyses and/or low reticulating ridges may be present). As indicated in the detailed hemipenial descriptions, the freestanding ridges in *D. apharocybe* are reduced to only low rounded ridges, but the pattern of oblique orientation is evident even in such a reduced form (Fig. 20, sulcate view). These characters, plus the absence of several characters uniquely shared by *D. dendrophis* and *D. nuchale* auctorum (e.g., greatly enlarged sulcate spines, a very regular distal row of enlarged spines within the spine array) can be taken as provisional evidence for the monophyly of the *D. vinitor* complex.

Among the three species of the *D. vinitor* complex, the hemipenis of *D. crybelum* stands out because of its unique cylindrical form and great number of enlarged spines. My current assessment is that both of these characters are autapomorphies of *D. crybelum* because the short, bulbous hemipenial form and fewer spines shared by *D. vinitor* and *D. apharocybe* are more widespread within *Dendrophidion*, including the other members of the *D. dendrophis* group, *D. dendrophis* and *D. nuchale* auctorum. On the other hand, *D. apharocybe* and *D. crybelum* share several hemipenial characters relative to *D. vinitor*: (1) reductions in the apical free-standing ridges (more completely reduced in *D. apharocybe* than in *D. crybelum*); (2) poorly developed asulcate calyses that are asymmetrically placed on the right asulcate side; (3) a more strongly

flared tip to the sulcus spermaticus. In addition, *D. apharocybe* and *D. crybelum* are more similar in having wider pale bands that are usually distinct the entire body length and which tend to form pale ocelli on the posterior body. These characters provide evidence suggesting that *D. apharocybe* and *D. crybelum* are more closely related within the *D. vinitor* complex. The apical boss of *D. vinitor* and the nude and strongly inclined apex of *D. apharocybe* are then seen as autapomorphies of these two species.

Apart from hemipenial differences, the three species of the *D. vinitor* complex are exceedingly similar in scutellation and other features generally useful for distinguishing snake species (Table 1). Few of the interspecific comparisons of ventrals, subcaudals, relative tail lengths, maxillary tooth counts, or the point of dorsocaudal reduction were statistically significant. Even in cases in which means were significantly different, the absolute differences were minimal and character ranges overlap substantially, sometimes completely. For example, mean subcaudal number is significantly different between *D. apharocybe* and each of the other two species, but the magnitude of the difference between means in each comparison was only 2.7 or 3.4 (sexes combined). In general, the means for intraspecific differences between males and females were more substantial and of greater statistical significance than interspecific comparisons by sex. The lack of substantive differences in these systematic characters emphasizes the cryptic nature of these species and lends credence to their hypothesized close relationship within *Dendrophidion*.

Biogeography

Considerable progress has been made in understanding biogeographic patterns within Middle America in the last decade. Many of the patterns have been elucidated by comprehensive understanding of phylogeographic patterns shown by Central Ameri-

can snakes, which in many cases have confirmed or refined prior assessments based on patterns of endemism and diversity (reviewed by Daza et al., 2010). Daza et al. (2010) correlated phylogeographic patterns with the history of major tectonic units and concluded that vicariance associated with tectonic events was a predominant agent causing speciation in Middle American snake lineages. Two critical geologic events associated with divergences in snakes are the Motagua–Polochic fault zone (suture of the Maya and Chortis blocks) in present-day Guatemala (3–8 million years ago [MYA]) and the uplift of the Cordillera de Talamanca in Costa Rica and Panama (2.5–3.9 MYA). Other important events are associated with the Isthmus of Tehuantepec, the Nicaraguan Depression, and the primary Middle–South American transition; however, the temporal span of divergences in these areas are broader than the first two, perhaps because geological events in these areas had differential effects in different lineages.

The distributions and relationships of species in the *D. vinitor* complex proposed here fit nicely into this paradigm. *Dendrophidion vinitor*, the proposed sister taxon to *D. apharocybe*–*D. crybelum*, is distributed entirely north of the Motagua–Polochic fault zone, and its isolation there most likely reflects the estimated late Miocene–Pliocene divergence in other snake taxa across this zone (Daza et al., 2010). The more recent divergence between *D. apharocybe* and *D. crybelum* accompanied the vicariance of Atlantic and Pacific slope faunas resulting from elevation of the Cordillera Talamanca in the late Pliocene. Chan et al. (2011: 328–331), in an elegant analysis of relationships among populations of the hylid frog *Dendrosophus ebraccatus* across the Talamanca disjunction in Costa Rica and Panama, found the most strongly supported model to be that suggested here for *D. apharocybe*–*crybelum*. At the level of the species concepts developed here, no differentiation has resulted from the other major Central American tectonic events outlined

by Daza et al. (2010). Nonetheless, finer scale genetic studies could show some intraspecific differentiation due to these last events.

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APPENDIX 1. SPECIMENS EXAMINED AND LITERATURE RECORDS FOR *DENDROPHIDION VINITOR* SMITH

Museum abbreviations used throughout are the following: AMNH—American Museum of Natural History (New York). ANSP—Academy of Natural Sciences of Philadelphia. BMNH—British Museum (Natural History) (London). CM—Carnegie Museum (Pittsburgh). KU—University of Kansas Museum of Natural History (Lawrence). LACM—Natural History Museum of Los Angeles County (California). MCZ—Museum of Comparative Zoology (Cambridge). MNHN—Muséum National d'Histoire Naturelle (Paris). TCWC—Texas Cooperative Wildlife Collection, Texas A&M University (College Station). UAZ—University of Arizona Museum of Natural History (Tucson). UCM—University of Colorado Museum of Natural History (Boulder). UCR—Universidad de Costa Rica Museo de Zoología (San José). 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 of

Texas at Arlington Collection of Vertebrates (Arlington). UTEP—University of Texas at El Paso Centennial Museum (El Paso).

Bracketed data associated with localities here and elsewhere in the text are inferences derived from sources other than the original data associated with specimens as recorded in literature, museum or collectors' catalogues, or specimen labels. Some museum databases (e.g., USNM) unfortunately do not distinguish "original" and "inferred" locality information in this era of databasing and georeferencing, and I have of necessity in most cases taken these sources at face value.

Belize: *Toledo*: Little Quartz Ridge [summit, 940–1,035 m], KU 300784 (Fig. 6). **Guatemala:** "Vera Paz" (Duméril et al. 1870–1909: 732; see comments under Distribution). [*Alta Verapaz*]: between Cobán and Lanquín, BMNH 64.1.26.21 (Stafford, 2003; specimen not seen; see comments under Distribution). *Izabal*: Sierra de Santa Cruz, Semococh, 8 km W Finca Semuc headquarters, UTACV 22155. Sierra de Santa Cruz, Finca Semuc, Serujijá Mountain, 15°37'09"N, 89°22'05"W, 600 m, UTACV 22755. *Petén*: "Peten," no specific locality (Duméril et al. 1854: 208, = MNHN 7353 fide Lieb, 1988: 164, Fig. 1; specimen not seen); Duméril et al. 1870–1909: 732; see comments under Distribution). Piedras Negras, USNM 110662 (holotype; Fig. 1). **Mexico:** No specific locality, USNM 7099 (paratype of *D. vinitor* Smith, specimen not seen; Smith, 1941). *Chiapas*: Presa Malpaso (Alvarez del Toro, 1972: 142, 1982: 191). 26 km N Ocozocuatla (Johnson et al. "1976" [1977], presumably UTEP 6038 cited by Lieb, 1988; specimen not seen). Approximately 8 km S Solosuchiapa, camp on Rio Teapa, ca. 400 ft. [120 m], UAZ 24161. *Oaxaca*: Río Chicapa near El Atravesado, 1,600 ft. [488 m], AMNH R-66845. Donají, Mije [province], UCM 39911–12, 44481. La Gloria (north of Niltepec), 1,500 ft. [457 m], FMNH 126554–55. La Gloria, UIMNH 17632, 35546–47, 37094–95, 37165; TCWC 12797. La Gloria-Cerro Azul, UIMNH 35548. Río Negro (Grijalva), Juchitán [province], UCM 41162. *Tabasco*: Teapa, USNM 46589 (paratype of *D. vinitor* Smith, 1941; specimen not seen). *Veracruz*: Bastonal (8 mi E of Cuatzelapa, Lago Catemaco), CM 41478. Forest at Cascapal, upper Uzpanapa river, Isthmus of Tehuantepec, BMNH 1936.6.6.8 (Stafford, 2003; specimen not seen); see Appendix 2 for comments. Near Coyame, 1,400 ft. [427 m], UMMZ 111450. Coyame, 9–10 mi E Catemaco, UIMNH 39154, 82444. Isla (Perez-Higareda and Smith, 1991: 31). 60 km SE Jesus Carranza, 450 ft. [137 m], KU 23965. 25 km SE Jesus Carranza, 250 ft. [76 m], KU 27564. Las Minas (Perez-Higareda and Smith, 1991: 31). Los Tuxtlas (Perez-Higareda and Smith, 1991: 31). Motzorongo (Dugés 1892). Tesechoacan (Perez-Higareda and Smith, 1991: 31). Uxpanapa (Perez-Higareda and Smith, 1991: 31). SE slope Volcán San Martín, approximately 2,600 ft. [793 m], UMMZ 121145. Volcán San Martín near base, UMMZ 122767. Volcán San Martín, UIMNH 33862. Volcán San Martín, El Tular Station, UIMNH 35472.

APPENDIX 2. GAZETTEER

Except where otherwise stated, coordinates for place names are from the National Geospatial-Intelligence Agency (NGA) online gazetteer (GEOnet Names Server): <http://earth-info.nga.mil/gns/html/>. A few coordinates were taken from Google Earth (GE). Many specimens of *Dendrophidion vinitor* were obtained by Thomas MacDougall, field biologist extraordinaire, whose collections significantly advanced many fields of Mexican zoology and botany (Stix, 1975). Goodwin (1969) reported MacDougall's mammal collections, and I quote from his brief characterizations of various Oaxacan localities before human alteration in the last half century; Goodwin had the opportunity to work directly with MacDougall's notes (Root, 1975). The three northern countries harboring *D. vinitor* are listed first, followed by an alphabetical listing of other Middle American countries with the other two members of the *D. vinitor* complex.

BELIZE AND GUATEMALA (*Dendrophidion vinitor*)

Cobán to Lanquín (Guatemala: Alta Verapaz).

Approximately 15°34'N, 90°09'W (coordinates arbitrarily about midway along the route between the two places). Cobán (approximately 1,320 m elevation) and Lanquín (approximately 335 m) lie about 43 airline kilometers apart in the Río Cahabón basin (north side of the Sierra de Santa Cruz and near Finca Semuc, whence come the only recent Guatemalan records of *D. vinitor*).

Finca Semuc, Serujijá Mountain, Sierra de Santa Cruz, 600 m (Guatemala: Izabal). 15°37'09"N, 89°22'05"W (coordinates from 1:50,000 topographic map, Instituto Geográfico Nacional, Guatemala; provided by the collector of UTACV 22755, Eric N. Smith).

Little Quartz Ridge (Belize: Toledo). 16°24'N, 89°05'W. The single known Belize specimen of *D. vinitor* was collected at the summit of the ridge, given as "940–1035 m elevation" (Meerman and Lee, 2003, table 1). The environment of the area is described in Meerman and Matola (2003).

Piedras Negras (Guatemala: Petén). 17°11'N, 91°15'W. Type locality of *D. vinitor* Smith.

Semococh, 8 km W Finca Semuc headquarters, Sierra de Santa Cruz (Guatemala: Izabal). This locality is seemingly none of several "Semococh" indexed by NGA, most of which are in Alta Verapaz department. Presumably close to coordinates for Finca Semuc listed above.

MEXICO (*Dendrophidion vinitor*)

Bastonal (8 mi E of Cuatzelapa, Lago Catemaco) (Veracruz). 18°19'N, 94°54'W.

Cascapel, upper Uxpanapa river, Isthmus of Tehuantepec (Veracruz). Not located. The spelling "Cascapel" seems clear in BMNH ledgers, as listed by Stafford (2003). This may be a

transcription error for "Cascajal" (or El Cascajal), a village on the upper Río Uxpanapa in extreme southeastern Veracruz near the Oaxaca border (17°37'N, 94°08'W).

Cerro Azul (Oaxaca). See La Gloria.

Coyame, 9–10 mi E Catemaco (Veracruz). 18°26'N, 95°00'W. (and Near Coyame, 1,400 ft. [427 m]).

Donají, Mije [province] (Oaxaca; MacDougall). 17°13'53"N, 95°03'40"W. 90 m elevation in "rainforest" fide Duellman (1960: 34).

El Atravesado (Oaxaca). See Río Chicapa.

El Tular (Veracruz). See Volcán San Martín.

Isla (Veracruz). At least three localities with this name are in Veracruz: 18°36'N, 96°09'W and 18°02'N, 95°31'30"W (NGA); and "La Isla": 17°25'N, 94°01'W (Esparza-Torres, undated).

Jesús Carranza. 60 km SE, 450 ft. [137 m] (KU 23965); and 25 km SE, 250 ft. [76 m] (KU 27564) (both Veracruz). These are localities of Walter W. Dalquest (see Hall and Dalquest, 1963). Original KU catalogue data for the "60 km" locality gave the compass direction as "SW" from Jesús Carranza, which would place the locality in Oaxaca rather than Veracruz. However, according to Robert M. Timm, Dalquest's field catalogue in the Mammal Division at KU has the locality corrected by hand (presumably by Dalquest himself) to "60 km SE Jesús Carranza." According to the itinerary given in Hall and Dalquest (1963: 177), Dalquest worked out of a village (Zapotal) on the Río Coatzacoalcos during the period when KU 23965 was collected. His field notes for mammals collected at the same time indicate that he traveled upriver via the Río Chalchijapa and then Río Solosuchil. Coordinates from the gazetteer of Hall and Dalquest (1963: 184) are: junction of the Río Chalchijapa with the Río Coatzacoalcos (approximately 17°27'N, 94°50'W); junction of the Río Solosuchil with the Río Chalchijapa (approximately 17°23'N, 94°47'W); and "Río Solosuchil" (17°14'N, 94°28'W). Coordinates for the river junctions are quite accurate, as verifiable using Google Earth. The "Río Solosuchil" locale is in southern Veracruz at its headwaters near the Oaxaca border, and close to 60 airline kilometers from Jesús Carranza in an ESE direction (perusal of Hall and Dalquest [1963] suggests they used a fairly loose interpretation of compass directions). This is perhaps the approximate location of KU 23965 (it is not clear whether Dalquest used airline or river distances). In any case, KU 23965 was apparently collected along the Río Solosuchil in southern Veracruz.

La Gloria (north of Niltepec), 1,500 ft. [457 m] (Oaxaca; MacDougall). 16°47'17"N, 94°36'40"W. Located 7 mi S of Santa María Chimalapa in Juchitán district (Goodwin, 1969: 259). Usually stated simply "La Gloria," this is the origin of more specimens of *D. vinitor* in U.S. collections than any other single locality (rivaled only by Volcán San

- Martín in Veracruz). Cerro Azul, associated with La Gloria in one specimen locality, is a local name for high parts of the Sierra Madre of Oaxaca–Chiapas, 25 mi NW of Santo Domingo Zanátpec, also in Juchitán district (Goodwin, 1969: 257); this is not the same “Cerro Azul” indexed by NGA. All of the La Gloria specimens were obtained by Thomas MacDougall. Habitats at La Gloria include “coffee plantations, milpas, rainforest,” whereas Cerro Azul harbors “cloud forest” (Goodwin, 1969: 257).
- Las Minas (Veracruz). 19°42'N, 97°07'W.
- Los Tuxtlas (Veracruz). 18°30'N, 95°10'W.
- Motzorongo (Veracruz) 18°39'N, 96°44'W. Goldman (1951: 277) gives the elevation as 800 ft. (244 m) but in steeply dissected country with hills rising locally to 1,500 ft. (457 m). Goldman (1951: 277–278, 316) briefly describes the vegetation (“fairly uniformly covered with evergreen forest”), which he classified as “Humid Lower Tropical Zone.”
- Ocozocuaula, 26 km N (Chiapas). About 16°55'N, 93°27'W.
- Presa Malpaso (Chiapas). 17°08'N, 93°30'W. Also known as Presa Netzahualcóyotl.
- Río Chicapa near El Atravesado, 1,600 ft. [488 m] (Oaxaca; MacDougall). Pacific drainage. El Atravesado (16°41'N, 94°35'W) is a village near a mountain of the same name. This is an inland locality on the Río Chicapa, not the coastal locality between Unión Hidalgo and the river’s mouth in Laguna Superior indexed by Goodwin (1969: 262). Cerro Atravesado is a “large flat-topped hill 18 mi S of Santa María Chimalapa [with] open pine stands, grass and rocks, patches of “cloud forest” at the north end” (Goodwin, 1969: 257).
- Río Negro (Grijalva), Juchitán [district] (Oaxaca; MacDougall). Atlantic drainage. Goodwin (1969: 262) gives two MacDougall localities with this designation: “[Río Grijalva system at] Junction of Río Negro with Río ‘Porta Monedo’ [sic] near Chiapas border 29 mi north of Tapanatepec,” and 5 mi west of this junction. The “Río Porta Moneda” is in the headwaters of the Río Encajonado system (Goodwin, 1969: 262). Coordinates from NGA: Río Negro, 16°49'36"N, 94°01'25"W; Río Portamonedas, 16°41'15"N, 94°08'22"W. Goodwin (1969) notes “heavy shade of trees in river flat” for the river junction and “many tree ferns ... rainforest [and] tapir trails” for the nearby camp.
- Solosuchiapa, approximately 8 km S; camp on Rio Teapa, ca. 400 ft. [122 m] (Chiapas). 17°24'N, 93°01'W.
- Teapa (Tabasco). 17°33'N, 92°57'W. 800 ft. [244 m] in the Humid Lower Tropical Zone fide Goldman (1951: 257–259).
- Tesechoacan (Veracruz). 18°08'N, 95°40'W.
- Uxpanapa (Veracruz). A name associated with several locations in southeastern Veracruz, including a major river and at least three towns.
- Volcán San Martín (Veracruz). 18°33'N, 95°12'W. A number of localities on the slopes of this volcano (near the base; SE slope, approximately 2,600 ft. [793 m]). The volcano is now part of the Los Tuxtlas Biosphere Reserve. Several places in southern Veracruz have the name El Tular, El Tular station being on the southwestern flank of the Volcán San Martín within the boundaries of the reserve (approximately 18°30'N, 95°13'W, 600 m). Goldman (1951: 283) stated that virgin [rainforest] covered the mountain and that “from the sloping plain the heavy forest, full of small palms, vines, and other undergrowth up to about 4,800 feet changed but little.”

COSTA RICA (*Dendrophidion apharocybe* and *D. crybelum*)

- Cacao Biological Station, 729–1,528 m (Guanacaste). 10°56'N, 85°28'W. Part of the Area de Conservación Guanacaste, the station is on the southwestern slope of Volcán Cacao at about 1,000 m. Montane rainforest to cloud forest on the upper slopes, transitioning to dry forest on the western lower slopes.
- Carara National Park (Puntarenas and San José). 09°46'30"N, 84°36'25"W. Near the Pacific coast in northern Puntarenas and extreme western San José provinces. Origin of two specimens erroneously referred to “*Dendrophidion vinitor*” (Laurencio and Malone, 2009) indicated on the distribution map of Savage (2002: 656). These specimens are *D. percarinatum*. See Distribution in the *D. apharocybe* species account and Figure 17.
- Cajón, N bank of Río Térraba (Puntarenas). 08°56'30"N, 83°20'W, about 80 m. Source of an apparently erroneous lowland Pacific locality for “*D. vinitor*” indicated by Savage (2002: 656). See text discussion under Distribution in species account for *D. apharocybe*.
- Finca La Selva (Heredia). 10°26'N, 83°59'W, 35–137 m (McDade and Hartshorn, 1994). Now the La Selva Biological Station of the Organization for Tropical Studies. Type locality of *D. apharocybe*.
- Finca Las Alturas, 1,330 m (Puntarenas). 08°57'N, 82°50'W. Presently the Las Alturas Biological Station operated by the Organization for Tropical Studies.
- Finca Las Cruces, near San Vito de Java, 4 km S San Vito, 1,200 m (Puntarenas). 08°47'35"N, 82°57'30"W (Wake et al., 2007: 557). Presently the Las Cruces Biological Station operated by the Organization for Tropical Studies. Type locality of *D. crybelum*.
- Finca Mellizas, 14 km ENE La Unión near Panama border (Puntarenas). 08°53'08"N, 82°46'42"W, approximately 1,310 m (GE).
- Finca Loma Linda, 2 km SSW Canas Gordas, 1,170 m (Puntarenas). 08°43.3'N, 82°54.3'W (Wake et al., 2007).

Guápiles (Limón). 10°17'N, 83°46'W.
 La Selva (Heredia). See Finca La Selva.
 Mt. [Cerro] Mirador near Suretka (Limón). 09°36'N, 82°57'W.
 Pandora, 50 m (Limón). 09°44'N, 82°58'W.
 Pavones, ca. 2.5 km N, 700 m (Cartago). Near Turrialba. 09°57'N, 083°37'W.
 Poco Sol de La Tigre, 540 m (Alajuela). 10°22'N, 84°37'W.
 Puerto Viejo de Sarapiquí, 10 km WSW (Heredia). 10°28'N, 84°01'W.
 San Clemente, 7 km NW Penshurst (Limón). 09°50'N, 82°56'W.
 Silencio, 875–940 m (Guanacaste). 10°28'N, 84°54'W.
 Suretka (Limón). 9°34'N, 82°56'W. See also Mt. Mirador.
 Río Puerto Viejo near junction with Río Sarapiquí (Heredia). 10°28'N, 84°02'W.
 Zona Protectora, La Selva, trail from 1,000 m camp to 1,500 m camp, 990 m (Heredia). Approximately 10°17'N, 84°04'W. See Pringle et al. (1984).

HONDURAS (*Dendrophidion aphaocybe*)

Bodega de Río Tapalwás, 190 m (Gracias a Dios). 14°55'39"N, 84°32'02"W. About 20 km NW Rus Rus. Wilson et al. (2003: 18); McCranie et al. (2006: 265).
 Caño Awalwás (camp), 100 m (Gracias a Dios). 14°49'N, 84°52'W. Wilson et al. (2003: 18); McCranie et al. (2006: 261).
 Crique Ibantara, 70 m (Gracias a Dios). 14°47'N, 84°27'W. A tributary of the Río Rus Rus. Wilson et al. (2003: 18); McCranie et al. (2006: 263).
 Crique Wahatingni, near (Gracias a Dios). Tributary of Río Tapalwás, 200 m. McCranie et al. (2006: 265).
 Crique Yulpruan, near; 140 m (Gracias a Dios). 14°54'N, 84°31'W. Tributary of Río Tapalwás, 200 m. McCranie et al. (2006: 266).
 Hilitara Kiamp, 150 m (Gracias a Dios). 14°57'N, 84°40'W. Along the upper portion of the Río Warunta (McCranie, 2011: 615).
 Las Marías, 20 m (Gracias a Dios). 15°40'N, 84°53'W (GE). A village along the Río Plátano (McCranie, 2011: 620). Figures transposed in latitude given by McCranie (2011: 620; 15°04'N).
 Planes de San Esteban, 1,100 m (Olancho). 15°05'N, 85°42'W. Northern slope of the Sierra de Agalta (McCranie, 2011: 609).
 Sachin Tingni, 150 m (Gracias a Dios). 14°57'N, 84°40'W. Tributary of Río Warunta (McCranie, 2011: 633).
 Warunta Tingni Kiamp, 150 m (Gracias a Dios). 14°55'20"N, 84°41'28"W. Campsite along upper portion of Río Warunta (McCranie et al., 2006: 266).

NICARAGUA (*Dendrophidion aphaocybe*)

Cara de Mono (Atlántico Sur), ca. 120 m. 12°07'N, 84°28'W.

Hacienda La Cumplida, 19 km N of Matagalpa, 2,500 ft. [762 m] (Matagalpa). 13°00'N, 85°51'W.
 Matagalpa (Matagalpa). 12°55'N, 85°55'W.
 Musawas, Waspuc River (Atlántico Norte). 14°08'59.6"N, 84°42'18.4"W.

Recero. See Recreo.

Recreo, Río Mico (Atlántico Sur). About 50 m. 12°10'N, 84°19'W. Gaige et al. (1937; see especially pp. 2–3) referred to this place as “Recero” in text and an accompanying map from information provided by Morrow J. Allen, the collector of UMMZ specimens, based in turn on a “U.S. Marine Corps survey map ca. 1930.” The field notebooks of Allen at UMMZ also refer to the place as Recero (Gregory E. Schneider, personal communication, January 2011). No independent sources I have seen refer to the place as “Recero,” which seems to be in the same location as “Recreo” or “El Recreo” in gazetteers and on modern maps (e.g., NGA and Google Earth). “Recero” appears in no geographic reference on Nicaragua that I consulted, including maps and gazetteers contemporary with and earlier than Gaige et al. (1937). However, the place is listed as “Recero” in several other taxonomic works (e.g., Smith [1941: 74, 76], Smith and Taylor [1950: 320], Dunn and Stuart [1951: 58]). All of these seem ultimately to trace back to Allen’s material or to Gaige et al. (1937).

Río Mico, 10 mi above Recreo (Atlántico Sur). Approximately 12°07'N, 84°28'W. See locality notes for Recreo above.

Río San Juan (Río San Juan). River along the frontier between eastern Nicaragua and Costa Rica.

Santo Domingo, Chontales Mines, 2,000 ft. (610 m) (Chontales). 12°16'N, 85°05'W. The locale was made famous by Belt (1874), who described the environment and geology of the area.

PANAMA (*Dendrophidion aphaocybe*)

Almirante, 10 m (Bocas del Toro). 09°18'N, 82°24'W. 11 km NW Almirante, 600 ft. [183 m] (Bocas del Toro); about 09°21'N, 82°28'W.

Cerro Arizona above Alto de Piedra, North of Santa Fe (Veraguas). Not located. Alto de Piedra is a small village about 3 airline kilometers NW (not strictly N as in the original locality data) of the town of Santa Fe (8°31'N, 81°04'W).

Cerro Azul region, Río Piedra (Panamá). 09°13'N, 79°18'W (Fairchild and Handley, 1966).

Cerro Campana, 900–950 m (Panamá). 08°41'N, 79°56'W (Fairchild and Handley, 1966). Myers (1969: 28) described the area, paraphrased here: Small area of cloud forest above 870 m. Forest of moderate height, with few large trees, many small trees, a scattering of tree ferns and small palms, a few stilt palms. Dense cover of bushes, herbs, ferns. Once abundant tree and ground bromeliads and other epiphytes have been reduced. Disturbed vegetation on the top.

- Cerro Delgadito, 2–4 mi W Santa Fe (Veraguas). Approximately 08°30'N, 81°07'W (GE).
- Cerro Malí (Darién). 08°07'N, 77°14'W (Fairchild and Handley, 1966). According to Myers (1969: 25) Cerro Malí is about 1,410 m elevation and southeast of Cerro Tacarcuna and the headwaters of the Río Pucuro (= Río Pucuro; see Myers and Lynch, 1997, figs. 1 and 2). It lies at the southeastern end of the Serranía del Darién, a ridge separating the Pacific-draining Río Tuira system from the Atlantic lowlands of eastern Panama and northern Colombia (the international border follows the continental divide along this ridge). Myers (1969: 24–25) described the general topography and environment. Additional perspectives and details are in Anthony (1916, 1923), Gentry (1983), and Myers and Lynch (1997).
- El Copé, continental divide north of, 600–700 m (Coclé). The village of El Copé is at 08°37'N, 80°35'W (Fairchild and Handley, 1966). El Copé (Omar Torrijos) National Park now encompasses the continental divide.
- Isla Popa, south end of, 1 km E of Sumwood Channel (Bocas del Toro). Approximately 09°09'N, 82°08'W.
- Laguna, 820 m (Darién). 08°04'N, 77°19'W (Fairchild and Handley, 1966). According to Charles W. Myers (personal communication), this locality is on a “ridge south of the Río Tacarcuna (upper tributary of Río Pucuro, Tuira drainage).” Also referred to as “La Laguna,” it is not the village of the same name near the coast in southwestern Darién Province (e.g., as indexed in the NGA), with which it is sometimes confused.
- La Loma, W Panama (Bocas del Toro). 08°50'N, 82°12'W. Also known as Buenavista. 1,200 ft. elevation (366 m) on the Atlantic slope along a trail from Chiriquí Lagoon to David (Dunn, 1942: 478).
- Península Valiente, Bluefields, 70 m (Bocas del Toro). 09°11'N, 81°55'W. Península Valiente delimits the eastern side of the Laguna de Chiriquí.
- Península Valiente, Quebrada Hido (Bocas del Toro). Not located.
- Pequení–Esperanza ridge, near head of Río Pequení, 2,000 ft. [610 m] (Panamá). Approximately 09°29'N, 79°24'W. Now within Parque Nacional Chagres. A ridge northeast of Lago Alajuela (Madden Lake), running roughly northeast to southwest and separating the Chagres–Esperanza river system from the Pequení–Boquerón system (Dunn and Bailey, 1939: 4, 15). Cadle and Myers (2003: 15–17) described some of the geography of the area as altered by damming associated with construction of the Panama Canal. Ibáñez et al. (“1994” [1995], fig. 1) provided an outline map of the major rivers of the region.
- Pequení–Esperanza ridge, junction main divide, 1,200 ft. [366 m] (Panamá). Approximately 09°20'N, 79°20'W. Location not precisely indicated by Dunn and Bailey (1939) but presumably at a lower elevation along the ridge closer to Lago Alajuela than the above-listed locality near the head of the Río Pequení (see above cited references).
- Summit site, border of Darién, 320 m (San Blas). 08°55'N, 77°51'W (coordinates from the collector of FMNH 170138, Michael Duever). Also known as Camp Summit, a canal survey camp in the Serranía del Darién discussed by Myers (1969: 26–27, fig. 1), who gave the elevation as 358 m.

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