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Systematics of Snakes Referred to *Dipsas variegata* in Panama and Western South America, with Revalidation of Two Species and Notes on Defensive Behaviors in the Dipsadini (Colubridae)

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Fig. 1. *Dipsas nicholsi* (Dunn), a snail-eater endemic to central Panama. **Top:** A specimen (not collected) photographed in 1974 in the Madden Forest Preserve, by Harry W. Greene. **Bottom:** Another specimen from Madden Forest, this one in a final stage of defense posturing (see figs. 20–21), photographed in 1966 by C.W. Myers.

ABSTRACT

The name *Dipsas variegata* (Duméril, Bibron, and Duméril) has been applied to snakes disjunctively distributed in northeastern South America and in Panama and western South America. The specific name *variegata* is here restricted to populations occurring from Venezuela to Trinidad and French Guiana, and seemingly to the mouth of the Amazon in Brazil. Records from Colombia are unsubstantiated.

The name *Dipsas nicholsi* (Dunn) is revalidated for a Central American endemic with an exceptionally small range in central Panama. Specimens from western Ecuador previously assigned to ''*Dipsas variegata nicholsi*'' represent a different species—*Dipsas andiana* (Boulenger), which is resurrected from the synonymy of *Dipsas oreas* (Cope). Other records of *Dipsas variegata* from western Ecuador and southeastern Peru are based on misidentifications of species well known from those areas.

Dipsas nicholsi and *D. andiana* differ in some scutellation, hemipenial, and color pattern characters. The two species share an unusual head pattern, but data are insufficient to conclude that they are sister species, although their disjunct distribution pattern (Panama and Chocoan South America) is one shared by many other organisms thought to be phylogenetically related.

Hemipenes of *Dipsas nicholsi* and *D. andiana* are slightly bilobed and fully capitate; the sulcus spermaticus divides within the capitulum and has centrolineal branches. The capitulum is ornamented with papillate calyces. A battery of enlarged spines encircles the organ below the capitulum (with more spines in *nicholsi* than in *andiana*). There is an elongated basal nude pocket positioned laterally on the organ. Overall hemipenial morphology is similar to other species of the tribe Dipsadini (*Dipsas, Sibon*, *Sibynomorphus*, *Tropidodipsas*) for which organs have been described.

The Dipsadini are docile snakes that, in the authors' experience, never defend themselves by biting or even striking with mouth closed. Defensive positional deportment is nonetheless widespread and varied, most commonly including acquisition of a triangular head shape in at least three genera of Dipsadini (and other snakes as well), which is brought about by dorsolateral spreading of the quadratomandibular articulations. Either asymmetrical or symmetrical coiling and head-hiding also occur in diverse species; there is evident individual variability in some species, whereas others possibly lack specialized behavior. A specimen of *Dipsas nicholsi* did not show the common head triangulation, but repeatedly exhibited stereotypic stages of defensive positioning that resulted in it taking the shape of a raised spiral coil.

RESUMEN

El nombre *Dipsas variegata* (Duméril, Bibron, y Duméril) ha sido utilizado para serpientes distribuidas disyuntivamente en el noreste de América del Sur y en Panamá y la parte occidental de América del Sur. En este trabajo se limita el nombre específico *variegata* a las poblaciones que ocurren desde Venezuela hasta Trinidad y la Guayana Francesa, y aparentemente a la boca del Río Amazonas en Brasil. Registros para Colombia quedan sin fundamento.

Se revalida el nombre *Dipsas nicholsi* (Dunn) para una especie centroamericana endémica con un rango excepcionalmente pequeño en Panamá central. Especímenes del Ecuador occidental asignados anteriormente a ''*Dipsas variegata nicholsi*'' representan una especie distinta—*Dipsas andiana* (Boulenger), que resucitamos de la sinonimia de *Dipsas oreas* (Cope). Otros registros para *Dipsas variegata* del Ecuador occidental y del sureste del Perú se basan en especímenes mal identificados, y representan especies bien conocidas de esas áreas.

Dipsas nicholsi y *D. andiana* son diferentes en algunos caracteres de la escamación, los hemipenes, y los patrones de coloración. Aunque estas dos especies tienen un patrón raro sobre la cabeza, los datos son insuficientes para concluir que sean especies hermanas. Sin embargo, su patrón de distribución disyuntiva (Panamá y la región Chocó de América del Sur) es común a bastantes otros organismos que se consideran relacionados filogenéticamentes.

Los hemipenes de *Dipsas nicholsi* y *D. andiana* son ligeramente bilobulados y completamente capitatos; el surco espermático se divide dentro del capítulo y tiene ramas centrolineales. El capítulo es ornamentado con cálices que llevan papilas. Proximal al capítulo hay una serie de espinas agrandadas que rodean el órgano (con más espinas en *nicholsi* que *andiana*). Un bolsillo desnudo basal se encuentra en la superficie lateral del órgano. Esta morfología es similar a otras especies del tribo Dipsadini (*Dipsas*, *Sibon*, *Sibynomorphus*, y *Tropidodipsas*) para las cuales existen descripciones de los hemipenes.

En la experiencia de los autores, los Dipsadini son culebras dóciles cuyo comportamiento defensivo nunca incluye intentos de morder o aun de lanzarse con la boca cerrada. Sin embargo, conducta defensiva posicional es general y variada, y comunmente incluye la adquisición de una forma triangular de la cabeza al menos en tres géneros de Dipsadini (y otras culebras también); esto se produce por extender dorsolateralmente las articulaciones cuadradomandibulares. Diversas especies se enroscan asimétricamente, mientras que otras se enroscan simétricamente; diversas especies se enroscan con la cabeza escondido; hay variabilidad individual evidente en algunas especies, mientras otras posiblemente carecen de comportamientos especializados. Un ejemplar de *Dipsas nicholsi* no demostró el comportamiento común de ensancharse la cabeza, pero reiteradamente demostró etapas estereotípicas de tomar una posición defensa en la cual adoptó la forma de un anillo espiral elevado.

INTRODUCTION

Snakes of the Neotropical colubrid genus *Dipsas* are in need of further systematic revision. Although Peters (1960a) reviewed much of the material then available, he was unable to examine type specimens of some nominal taxa. In the interim, new collections have permitted a deeper understanding of distributions and geographic variation of many species.

Species of *Dipsas* are notoriously variable in many standard scale and coloration characters typically used in colubrid systematics. The extreme variability has made it difficult to infer species limits and interpret patterns of geographic variation, especially when few specimens are spread across a broad geographic area. This report had its genesis in attempts by Cadle to clarify the identity of specimens of *Dipsas* and the related genus *Sibynomorphus* from western Ecuador and Peru. Many of these were identified in their respective collections as *Dipsas variegata* (Duméril, Bibron, and Duméril, 1854), with the type locality ‘‘Surinam’’. Peters (1960a: 132–141) viewed *D. variegata* as a species with a broad, but apparently disjunct, distribution: central Panama; Venezuela, Guyana, Surinam, and Trinidad; western Ecuador; and southeastern Peru. Subsequently, the name *D. variegata* has appeared in checklists and other literature on the herpetology of Panama, Colombia, Ecuador, and Peru (e.g., Hoogmoed, 1979: 274; Miyata, 1981; Pérez-Santos and Moreno, 1988, 1991; Ibáñez and Solís, ‘‘1991’’ [1993]; Carrillo de Espinoza and Icochea, 1995). It became clear that there was a general confusion about the identity of many specimens referred to *D. variegata*, and that the status of two other nominal taxa, *D. nicholsi* (Dunn) and *D. andiana* (Boulenger), with type localities in Panama and Ecuador, respectively, needed to be reexamined. Myers had also earlier recognized the distinctiveness of *D. nicholsi*, and we here document our conclusions that both *D. nicholsi* and *D. andiana* are valid species. In addition, we show that *D. variegata* is not definitely known outside Venezuela, the Guayanan Region, and the island of Trinidad. We provide systematic and biological summaries for *D. nicholsi* and *D. andiana*. The status and distribution of some other species of *Dipsas* and *Sibynomorphus* in western Ecuador and Peru will be addressed in a separate report (Cadle, MS).

Our methods follow those previously outlined (e.g., Myers, 1974; Cadle, 1996, 1999). Coordinates and other geographic data for central Panama were referenced mainly from the map *Canal Zone and Vicinity 1:100,000* (1957 edition, U.S. Army Map Service, Washington, D.C.). Coordinates for South American localities (and elevations if not reported by collectors) were obtained from the Ornithological Gazetteers of the Neotropics (Stephens and Traylor, 1983; Paynter, 1993, 1997), Lynch and Duellman (1997: appendix II), and the online versions of the gazetteers of the U.S. Board on Geographic Names at the GEOnet Names Server: http://164.214.2.59/gns/html/index.html. Bracketed data in localities are inferences from these sources. Sample means for scale counts were compared statistically using Student’s *t*-test for small samples after first testing for homogeneity of variances (Sokal and Rohlf, 1981:

226–231). For reasons outlined later, statistical comparisons involving *Dipsas variegata* and *D. oreas* included data only for the nominotypical forms of those species (tables 1 and 3). Institutional abbreviations are given at the beginning of the appendix.

NOMENCLATURAL HISTORY OF *DIPSAS VARIEGATA* (DUMÉRIL, BIBRON, AND DUMÉRIL)

According to current taxonomy (Peters, 1960a, 1964; Peters and Orejas-Miranda, 1970), there are three geographic races of *Dipsas variegata*:

Dipsas variegata variegata (Duméril, Bibron, and Duméril, 1854; type locality: Surinam), distributed from northwestern and western Venezuela (Test et al., 1966; Markezich, 2002) to French Guiana (Gasc and Rodrigues, 1980; Chippaux, 1986), thence southward to the mouth of the Amazon River in the state of Pará, Brazil (Cunha and Nascimento, 1993)—with records also for Colombia, western Ecuador, and southeastern Peru.[3]

Dipsas variegata trinitatis Parker (1926), from Trinidad.

Dipsas variegata nicholsi (Dunn) (1933; type locality: Chagres River and Pequeni River, Panama), occurring in central Panama and in western Ecuador (see also *D. v. variegata* above).

Dipsas ''*variegata*'' *nicholsi* was originally described as *Sibynomorphus nicholsi* (Dunn, 1933) and later transferred to *Sibon* (Dunn, 1940) and *Dipsas* (Smith, 1958). Peters (1960a) recognized it as a subspecies of *D. variegata* and, in addition to central Panamanian specimens, identified several specimens from western Ecuador as *D. v. nicholsi*. ''*Dipsas variegata nicholsi*'' (or simply *Dipsas variegata*) has subsequently appeared in checklists of the snake fauna of Panama and Ecuador. But it has remained peculiarly unknown from the intervening region of eastern Panama and western Colombia, although Peters and Orejas-Miranda (1970: 90) extrapolated its distribution as ''Atlantic side of Panama to northwestern Ecuador''.

Parker (1926) described *Dipsas trinitatis* from a single specimen but recognized its close relationship to *D. variegata*, which occurs on the adjacent mainland. He distinguished the two species on the basis of characters now known to vary considerably within species of *Dipsas* (e.g., preocular presence/absence, number of upper labials, minor differences in color pattern; see tables 1 and 2 and Peters, 1960a: 141). Peters (1960a) recognized *trinitatis* as a subspecies of *D. variegata* based solely on perceived color differences from the nominotypical form. We have not undertaken a detailed comparison of *D. v. variegata* and *D. v. trinitatis*, but the two forms are similar in scutellation (table 1) and color pattern. Thus, for comparisons in this paper we accept Peters' (1960a) conclusion that *D. trinitatis* and *D. variegata* are conspecific. However, Murphy (1997: 171) indicated that *D. v. trinitatis* ''may deserve full species status'', and we note that *D. v. trinitatis* has a smaller head in relation to the body and fewer maxillary teeth than does *D. v. variegata* (fig. 3 and table 1).

In contrast, we do not concur with the synonymy of *Dipsas nicholsi* with *D. variegata* as proposed by Peters (1960a). In documenting that conclusion we clarify several interrelated issues pertaining to the systematics of *Dipsas* in Panama and western South America. First, we show that records of *D. v. variegata* from Ecuador and Peru are based on misidentifications. We then present evidence that *D. nicholsi* is not conspecific with *D. variegata* and that records of ''*D. variegata nicholsi*'' from Ecuador represent a distinct species, *D. andiana* (Boulenger, 1896; type locality: ''Quito, Ecuador''), which Peters (1960a) had considered a synonym of *D. oreas* (Cope). An earlier record of ''*D. variegata*'' in western Ecuador (Steindachner, 1902) probably also pertains

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[3] The Ecuadorian and Peruvian records will be considered herein, but there appear to be no actual specimens from Colombia, although that country is sometimes given or suggested as part of the distribution of *D. variegata* (Nicéforo María, 1942; Daniel, 1949; Roze, 1966: 115; Pérez-Santos and Moreno, 1988: 150). All the subsequent citations seem to be based on Nicéforo María (1942), who followed Amaral (1929) in referring the type of *Leptognathus nigriceps* Werner (type locality ''Cañon de Tolima'', northwest of Ibague, upper Río Magdalena valley, Tolima Department) to the synonymy of *D. variegata*. However, this name is currently considered a synonym of *Dipsas pratti* (Peters, 1960a: 136). Unless new material becomes available, we suggest removal of Colombia from the known distribution of *D. variegata*.

TABLE 1

Comparisons of Size (in mm) and Standard Characters in *Dipsas variegata* and *D. nicholsi*[a]

	Dipsas variegata Guyana, Venezuela	*Dipsas variegata* Trinidad[b]	*Dipsas nicholsi* Panama
Total length (and SVL) of largest ♂ and ♀	♂ 570+ (468) ♀ 822 (616)	♂ 707 (517) ♀ 643 (478)	♂ 861 (646) ♀ 798 (607)
Tail length/total length	3♂ 0.24–0.26 0.25 ± 0.01 4♀ 0.23–0.26 0.25 ± 0.01	11♂ 0.25–0.28 0.26 ± 0.01 7♀ 0.25–0.26 0.26 ± 0.025	3♂ 0.25 1♀ 0.24
Maxillary teeth	9 (N = 2) 10 (N = 2) 11 (N = 3)	6 (N = 2) 7 (N = 3) 8 (N = 3)	11 (N = 1) 12 (N = 1) 13 (N = 2) 14 (N = 1)
Dorsal scales	15-15-15 17-15-15 (N = 1)	15-15-15	15-15-15
Ventrals	5♂ 176–191 180.4 ± 6.19 4♀ 171–182 176.8 ± 4.79	12♂ 178–187 182.2 ± 2.76 6♀ 172–189 179.7 ± 5.50	5♂ 198–208 202.4 ± 3.78 1♀ 200
Subcaudals	3♂ 85–92 89.0 ± 3.61 5♀ 74–86 80.2 ± 4.76	11♂ 81–96 90.5 ± 4.18 7♀ 79–91 84.4 ± 3.8	4♂ 92–98 96.0 ± 2.71 1♀ 95 (N = 1)
Anal scale	single	single	single
Postoculars	1 (N = 2) 2 (N = 15) 3 (N = 3)	1 (N = 2) 2 (N = 33) 3 (N = 1)	2 (N = 12)
Primary temporals[c]	1 (N = 4) 2 (N = 5) 3 (N = 3)	1 (N = 13) 2 (N = 22) 3 (N = 1)	1 (N = 6) 2 (N = 6)
Secondary temporals[c]	1 (N = 2) 2 (N = 7) 3 (N = 5)	2 (N = 23) 3 (N = 17)	2 (N = 3) 3 (N = 7) 4 (N = 2)
Supralabials (touching eye)	7 (3–4) N = 2 8 (3–5) N = 5 8 (4–5) N = 1 9 (3–5) N = 8 10 (3–5) N = 1 10 (4–6) N = 1	7 (3–5) N = 1 7 (3–4) N = 7 7 (4–5) N = 1 8 (3–5) N = 8 8 (4–5) N = 13 9 (3–5) N = 3 9 (4–5) N = 1 9 (3–4) N = 1 10 (5–6) N = 1	7 (3–4) N = 3 7 (4–5) N = 1 8 (3–5) N = 2 8 (4–5) N = 3 8 (5–6) N = 1 9 (4–5) N = 1 9 (5–6) N = 1
Infralabials	11 (N = 3) 12 (N = 7) 13 (N = 3)	9 (N = 1) 10 (N = 8) 11 (N = 16) 12 (N = 2)	10 (N = 1) 11 (N = 4) 12 (N = 5) 13 (N = 2)
No. dorsal blotches on body	5♂ 25–34 4♀ 19–24	12♂ 18–24 4♀ 20–24	5♂ 17–21 1♀ 22

[a] Means ± SD are given for segmental counts. For bilateral head-scale counts, each side of each specimen was treated as an independent observation since these are often asymmetrical within a specimen; for these counts, the frequency of each observation is given to emphasize the considerable variation. N = sample size.

[b] Data presented by Murphy (1997) for specimens from Trinidad do not significantly extend the variation in our sample (e.g., only one or two scales for ventral and subcaudal counts). His data are not included since males and females were not treated separately.

[c] Peters (1960: 26–27) indicated that scales of the temporal region varied more than any others within *Dipsas*. We agree and found patterns of fragmentation and fusion so extensive that accurate delineation of primary, secondary, and tertiary temporals was not always easy. Hence, we report counts only for the first two, but we excluded many specimens because of the difficulties.

to *D. andiana*. Finally, we consider the relationship between *D. nicholsi* and *D. andiana*.

In following our discussion of *Dipsas nicholsi* it is helpful to keep in mind that Peters' (1960a) account of ''*D. variegata nicholsi*'' was based almost entirely on Ecuadorian specimens that we refer to *D. andiana*. All Panamanian specimens available to him, including the type, were ''head only'' specimens collected during the Panama snake census by H.C. Clark of the Gorgas Memorial Laboratory (summarized in Dunn, 1949a). Thus, the only complete specimens of ''*Dipsas variegata nicholsi*'' that Peters studied were actually of a different, albeit very similar, South American species. This especially affected Peters' assessment of variation in segmental counts for *Dipsas nicholsi* in comparison to *D. variegata* and other species.

ERRONEOUS RECORDS OF *DIPSAS VARIEGATA* IN ECUADOR AND PERU

Peters (1960a: map 9, p. 132) conceived of *Dipsas variegata* as a species ranging over a large portion of northern South America, including west of the Andes in Ecuador, and in central Panama. However, several aspects of the distributions of the subspecies of *D. variegata* portrayed by Peters are puzzling. First, very few reptile or amphibian species or vicariant species pairs have disjunct distributions both in the Guayanan Region of South America and in lower Central America–northwestern South America (see, e.g., the distributional summaries by Dixon, 1979; Hoogmoed, 1979; Lynch, 1979; and Duellman, 1999). Moreover, Peters (1960a, 1964) and Peters and Orejas-Miranda (1970) reported that the distribution of nominotypical *variegata* included not only the Guayanan Region, but also southwestern Ecuador and southeastern Peru. Thus, Peters (1960a: map 9) showed the presence of both *D. v. variegata* and *D. v. nicholsi* in western Ecuador, and his record of *D. v. variegata* from southeastern Peru is far removed from any other reported locality for the species.[4] All these records of *D. v. variegata* in Ecuador and Peru are based on misidentifications and have confused the literature on these species.

Peters' Ecuadorian and Peruvian records for *Dipsas v. variegata* included, respectively, USNM 98923 (Catamayo Valley [Loja Province], Ecuador), USNM 237040 (0.5 km E Loja [Loja Province]; = JAP 2378 cited in Peters, 1964), and USNM 60718 (Puquiura [Cuzco Department], Peru; = Pucyura of Barbour and Noble, 1920) (Peters, 1960a, 1964). We examined the three specimens and conclude that the correct identifications are as follows: USNM 98923 = *Dipsas oreas*; USNM 237040 = *Sibynomorphus petersi*; and USNM 60718 = *Dipsas peruana*, which Barbour and Noble (1920) also had recognized much earlier. These reidentifications remove the distributional anomalies for *D. variegata variegata*, which is documented only for Venezuela and the Guayanan Region (Guyana, Surinam, French Guiana; Beebe, 1946; Chippaux, 1986) and Pará, Brazil (Cunha and Nascimento, 1993). USNM 98923 and a few other specimens (e.g., the holotype of *Leptognathus andrei* Sauvage; see Kofron, 1982a) document the southernmost Ecuadorian records of *D. oreas*, although that species is now known also from western Peru (Cadle, MS). *Sibynomorphus petersi* is known from several

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[4] Peters (1960a: 135–136) discussed other possible records of *Dipsas variegata* outside the Guayanan Region and Venezuela/Trinidad based on descriptions in the literature. We consider all of these doubtful until the specimens are reexamined. Peters was forced to rely on segmental counts and a few aspects of color pattern for making species determinations based on literature descriptions, characters which are difficult to use in *Dipsas* without direct comparisons of specimens. With respect to *D. variegata*, Peters (1960a) and Peters and Orejas-Miranda (1970) also placed *Leptognathus robusta* L. Müller (1923) (type locality: eastern Ecuador) in the synonymy of *Dipsas variegata variegata*. Peters (1960a: 136) was tentative in this synonymy, but indicated that ''there is no character given for *robusta* that is not duplicated by specimens of *variegata*''. However, we note that the type specimen of *L. robusta*, a female, is much larger (918 mm total length) than any other specimen of *D. variegata* reported by Peters (1960a) or examined by us (table 1). Also, the relative tail length of the holotype of *L. robusta* (21% of total length), based on measurements reported by Müller (1923), is much less than in any specimen of *D. variegata* we examined (25–28%). We doubt the synonymy of *L. robusta* with *D. variegata* and suggest that the type should be reexamined to correctly place this name.

localities in southern Ecuador, including the vicinity of Loja, as documented by USNM 237040 and other specimens (Orcés and Almendáriz, 1987; Cadle, MS). USNM 60718 is from within the known range of *Dipsas peruana* (type locality: Santa Ana, Cuzco Department), a species with which Cadle has had some field experience.

With the above removal of erroneous records of *Dipsas variegata variegata* from western Ecuador and eastern Peru, the only other taxon of that complex of concern in Ecuador is ‘‘*D. variegata nicholsi*’’, which is reported from central Panama to western Ecuador (Peters and Orejas-Miranda, 1970), notwithstanding the apparent absence of specimens from eastern Panama and Colombia. The earliest record of *Dipsas variegata* in western Ecuador seems to be that of Steindachner (1902: 108), who referred a specimen from Babahoyo [Los Ríos Province] to ‘‘*Leptognathus variegata* Duméril and Bibron’’. Peters (1960a: 139) concluded that this specimen was the form ‘‘*D. variegata nicholsi*’’ based solely on Steindachner’s detailed description. However, Steindachner gave no reasons for considering his western Ecuadorian specimen conspecific with *D. variegata*. Peters (1960a: 139) may have been simply following Steindachner’s lead, but offered these comments:

> That *nicholsi* is a direct derivative of *variegata* through a comparatively minor change in color pattern can hardly be questioned. Although *variegata* usually lacks a distinct head pattern, certain specimens show strong indications of the steps necessary to form an inverted U on the parietals and frontal [characteristic of *nicholsi*; see fig. 4]. As to scutellation, there is no character expressed in the specimens of *nicholsi* examined that is not included within the variation of the subspecies *variegata*.

We do not find Peters’ argument compelling. Apart from questioning whether a particular color change can be considered ‘‘minor’’, the head pattern of *Dipsas nicholsi* is unusual and consistently present in all specimens. Furthermore, several species of *Dipsas* can have a pattern of blotches that might suggest ‘‘steps necessary to form an inverted U’’. However, we have seen none that approach the regular condition observed in *D. nicholsi* except *D. andiana*, which is considered subsequently in this paper. Moreover, as alluded to in our introduction, species of *Dipsas* often overlap in standard scutellation characters. So the fact that *D. variegata* and *D. nicholsi* might do so is inconsequential, but we note that Peters’ perception of overlap in ventral counts was entirely due to his inclusion of specimens of *D. andiana* (which has lower counts than *D. nicholsi*) in his concept of *D. variegata nicholsi* (tables 1, 2). Average segmental counts for *D. nicholsi* are significantly greater than for *D. variegata* (table 1), and the ranges of ventral counts in the two species scarcely overlap, even when comparisons use the greater range reported in the literature for *variegata* (see footnote 5).

We suggest that the characters reported by Steindachner (1902) for the specimen from Babahoyo, Ecuador, are more consistent with *Dipsas andiana* (Boulenger) than with *D. variegata*. Steindachner’s data are given in table 2. His specimen has more ventrals and subcaudals (201 and 98, respectively) than our specimens of *D. variegata* (table 1), as well as a distinct color pattern. In these respects, as well as distribution, Steindachner’s specimen is similar to others we refer to *D. andiana*; we conclude that it probably is a member of that species and provide details in the subsequent section on *D. andiana*.

We next discuss the characters distinguishing *D. variegata* and *D. nicholsi* and conclude that no specimens known to us from Panama or western South America are attributable to the former species.

RESURRECTION OF *DIPSAS NICHOLSI* FROM THE SYNONYMY OF *DIPSAS VARIEGATA*

The type of *Dipsas nicholsi* (MCZ 37884) consists of a head and neck only. Dunn (1933) used primarily color pattern to diagnose *D. nicholsi* from other species in Panama and Colombia, pointing out that coloration often seemed to be more constant in species of this group (i.e., *Dipsas*, *Sibon*, and *Sibynomorphus*) than did standard scale counts and head scale patterns (Dunn, 1933, 1940). This is certainly true, but coloration is equally variable in some species and is sometimes highly polymorphic within species (see, e.g., Rossman and Kizirian, 1993). Problems with identifications are exacerbated because many species have broadly overlapping standard scale counts, so these are often unreliable as exclusive characters for identifying specimens. We think this is what led Peters to misidentify specimens of *D. peruana* and *D. oreas* as *D. v. variegata*. Nonetheless, the combination of characters of scutellation, color pattern, and body form which we document here distinguishes *D. nicholsi* from *D. variegata*. The two species also differ in hemipenial morphology (see Hemipenis under the following species account for *Dipsas nicholsi*).

Variation in standard scale characters of *Dipsas variegata* (segregated by Trinidad and mainland localities) and *D. nicholsi* is shown in table 1. For most characters the range of variation in these characters exhibited by *D. nicholsi* overlaps that of *D. variegata*. However, *D. nicholsi* has significantly higher ventral and subcaudal scale counts than does *D. variegata* for both sexes[5]:

Ventrals:
  males, $t = 6.17$, df = 8, $p < 0.01$
  females, $t = 3.74$, df = 3, $p < 0.05$
Subcaudals:
  males, $t = 2.62$, df = 5, $p < 0.05$
  females, $t = 2.84$, df = 4, $p < 0.05$

Furthermore, *Dipsas nicholsi* seems to have a consistent color pattern different than that of *D. variegata*—in fact, color pattern seems to be far more consistent than many scale characters in *D. nicholsi* (see comments by Dunn, 1940). We present herein the first photographs of living and preserved *D. nicholsi* (Peters' [1960a: pl. 5c] photograph of ''*Dipsas variegata nicholsi*'' is of an Ecuadorian specimen of *D. andiana*). The ∩-shaped marking on the head of *D. nicholsi* (fig. 4) was mentioned by Dunn and Peters and seems to be a universal character, with little variation among the specimens we examined. In contrast, we have seen no specimens of *D. variegata* that approach this condition any more than other species of *Dipsas* with spots or blotches on the head (e.g., *D. oreas*). Many specimens of *D. variegata* show no distinct pattern on the top of the head (fig. 2). In addition, rounded body blotches separated by broader light interspaces also are a constant feature in *D. nicholsi*. This pattern is very different from that of *D. variegata*, which has a series of irregularly rounded blotches or narrow vertical bars with irregular edges, with a tendency toward light centers (fig. 3; Peters, 1960a: pl. 5e; Lancini, 1979: fig. 39; Murphy, 1997: pl. 125; Cunha and Nascimento, 1993: fig. 28). Finally, we note that *D. nicholsi* has a rather large, rounded head in proportion to the body, whereas *D. variegata* has a relatively small head (compare figs. 3 and 5). *Dipsas nicholsi* perhaps attains a larger body size than does *D. variegata* (table 1).

Apart from the morphological and color-pattern differences between *Dipsas variegata* and *D. nicholsi*, the geographic disjunction also bears explanation. Not only are the ranges of these two taxa separated by several high chains of the Andes and inter-Andean valleys, but no specimens attributed to either taxon have been reported from west of the states of Aragua and Portuguesa in Venezuela, or in Colombia (see footnote 3). Peters (1960a) incorporated geographic distributions into his concepts of species boundaries, and we suspect he was misled by his conclusion that *D. v. variegata* occurred in western Ecuador, based on the misidentified specimens cited earlier. Although he does not explicitly articulate this, an indication of his concept of the relationship between geography and species limits is given in his discussion of *D. viguieri* (eastern Panama) and *D. gracilis* (western Ecuador): ''If the ranges of *viguieri* and *gracilis* were contiguous there would be reason to consider them only subspecifically distinct'' (Peters, 1960a: 52). Thus, had Peters (1960a, 1964) not misidentified western Ecuadorian specimens as *D. v. variegata*, and had not also assigned specimens from western Ecuador to *D. v. nicholsi*, he probably would not have viewed *D. ni-*

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[5] Data reported for *Dipsas variegata* from Venezuela and the Guayanan region indicate broader ranges for some scale counts than represented in our sample. For example, Roze (1966) and Lancini (1979) reported up to 107 subcaudals for Venezuelan specimens. Chippaux (1986) reported 191–196 ventrals and 89–100 subcaudals for three specimens from French Guiana, and Cunha and Nascimento (1993) reported similar counts for seven specimens from Pará, Brazil (191–198 ventrals and 89–92 subcaudals). Nonetheless, even ignoring the scale differences apparent in our comparisons of *D. nicholsi* and *D. variegata*, the body form, head shape, and color pattern provide substantial diagnostic differences between these species.

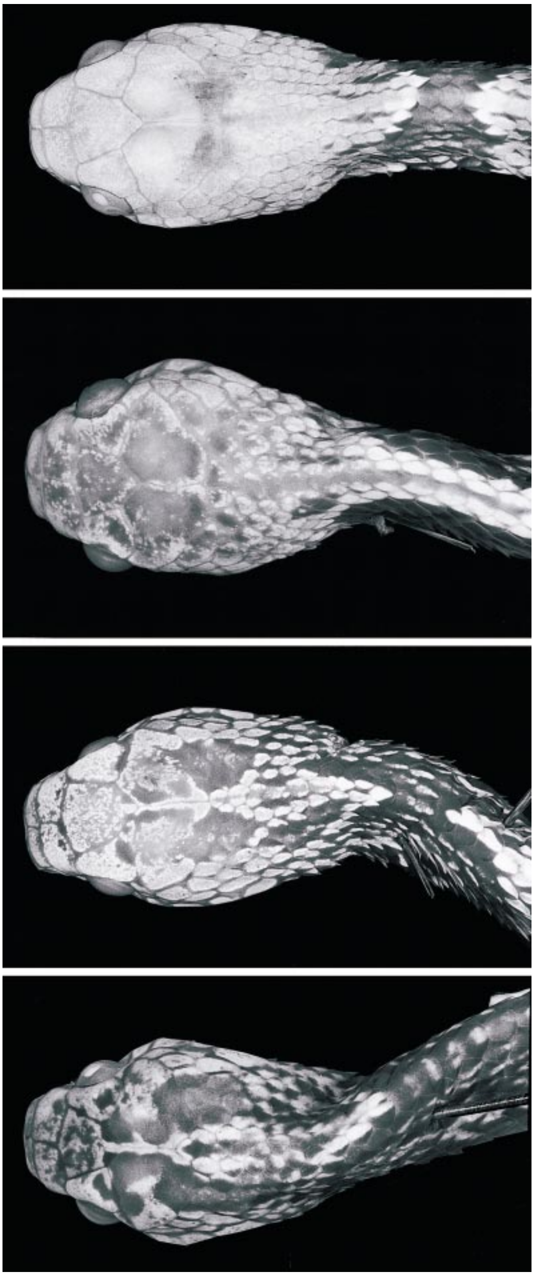

Fig. 2. Variation in dorsal head patterns of *Dipsas variegata* (Duméril, Bibron, and Duméril). From top to bottom: AMNH 111075 (Bolívar, Venezuela), AMNH 137584 (Trinidad), AMNH 21275 (Guyana), AMNH 114769 (Bolívar, Venezuela). The cephalic color pattern of *Dipsas variegata*, which varies from indistinct to blotched, lacks the distinctive ∩-shaped marking that characterizes *D. nicholsi* and *D. andiana* (cf. figs. 4, 8).

cholsi as a subspecies of *D. variegata*. Steindachner's (1902) earlier referral of a western Ecuadorian specimen to *D. variegata* also may have influenced Peters.

In conclusion, we see no reason to maintain Peters' idea that *Dipsas nicholsi* and *D. variegata* are conspecific. The two taxa differ significantly in the number of ventral scales, body form, and color patterns, and their distributions are disjunct in a manner that would be unusual for a species of Neotropical snake. Thus, we resurrect *Dipsas nicholsi* (Dunn, 1933) as a species distinct from *D. variegata*.

Dipsas nicholsi (Dunn)

Figures 1, 4–6, 20–21; maps 1, 3

Sibynomorphus nicholsi Dunn, 1933: 193. Type locality: ''Mid-basin of Chagres River and mouth of Pequeni River, Panamá'', obtained by H.C. Clark in early 1933 (locality clarified herein as junction of Río Pequení with Río Boquerón [since 1936 = approximately mouth of Río Pequení at head of Madden Lake], in upper drainage of Río Chagres at 9°21′N, 79°33′W).

Sibon nicholsi: Dunn, 1940: 117.

Dipsas nicholsi: Smith, 1958: 223.

Dipsas variegata nicholsi, part (records from Ecuador are referred herein to *Dipsas andiana*): Peters, 1960a: 137; 1960b: 517. Myers and Rand, 1969: 5. Peters and Orejas-Miranda, 1970: 90. Pérez-Santos et al., 1993: 116. Köhler, 2001: 37.

Dipsas variegata: Villa et al., 1988: 64. Rand and Myers, 1990: 395. Ibáñez and Solís, ''1991'' [1993]: 30. Auth, 1994: 16.

DIAGNOSIS: *Dipsas nicholsi* is a pale brown snake with distinctive contrasting patterns on the head and dorsum. The head is relatively unmarked except for a bold blackish brown ∩-shaped marking extending from the anterior edge of the frontal or frontal/prefrontal sutures to the neck, where the branches are confluent with a pair of elongate dorsolateral blotches (figs. 4, 5). Apart from the dorsal head marking and occasional narrowly darkened sutures, the head is unmarked. The blotches on the dorsum are black or blackish brown, strongly elliptical or oval and much broader than tall, and have a variably distinct narrow pale border. The interspaces are slightly broader than the blotches for the length of the body. Additional blackish streaks or

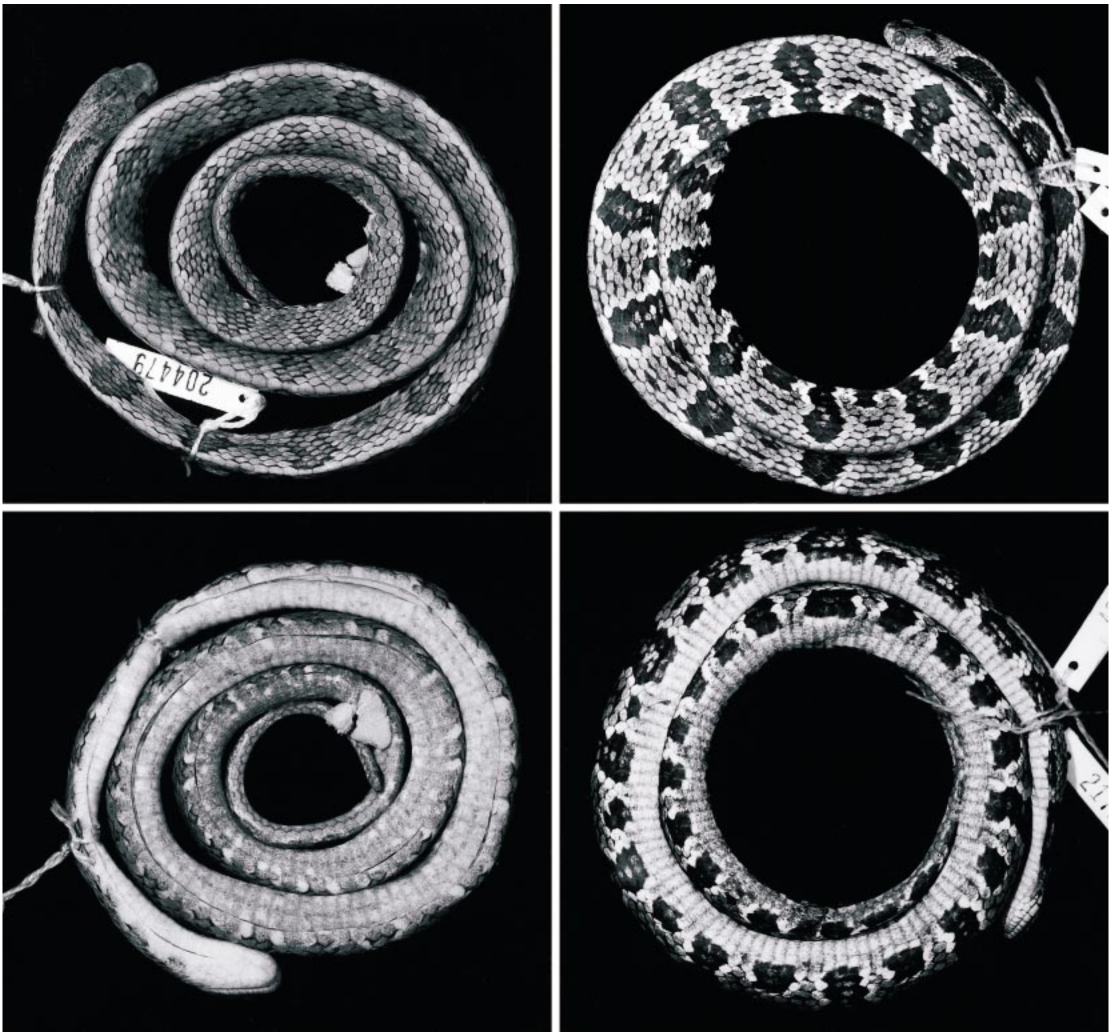

Fig. 3. *Dipsas variegata* (Duméril, Bibron, and Duméril). Representative specimens in dorsal and ventral view. **Left:** *D. v. variegata* from Rancho Grande, Venezuela (FMNH 204479, 468 mm SVL). **Right:** *D. v. trinitatis* from near Asa Wright Nature Center, Trinidad (FMNH 217217, 419 mm SVL).

irregular spots are sometimes present between the blotches. These pattern characteristics, particularly the form of the dorsal head marking and the dorsal blotches (including pale border), are constant in all specimens of *D. nicholsi* we have examined.

Dipsas nicholsi has a relatively high number of ventrals (males 198–208, one female 200) and subcaudals (males 92–98, one female 95) (table 1). However, scale characters overlap greatly among species of *Dipsas* and should not be used exclusively for identifications. The color pattern seems to be the most constant and readily diagnostic feature, as noted by Dunn (1933). No other known species of *Dipsas* from Panama or western Colombia and Ecuador, with the exception of *D. andiana*, has the distinctive head marking present in *D. nicholsi*.

Dipsas nicholsi is very similar in color pattern and scutellation to *D. andiana* from western Ecuador. These two species are compared

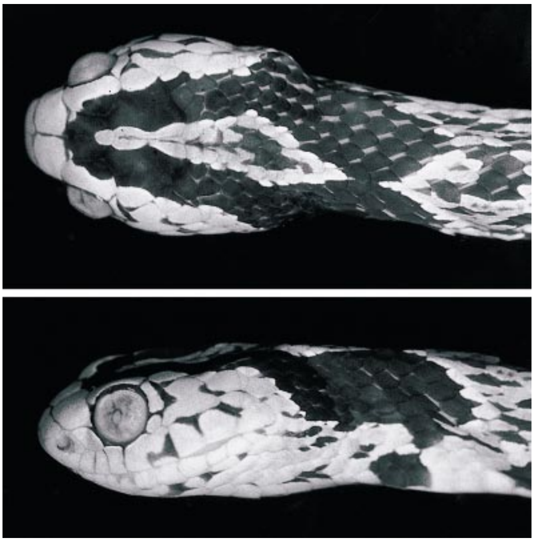

Fig. 4. *Dipsas nicholsi* (Dunn). Dorsal and lateral views of the head (KU 110312).

in detail at the end of this paper, following the species account for *Dipsas andiana*.

Description

Size and Scutellation: Largest specimen a male 861 mm total length, 646 mm SVL; one female 798 mm total length, 607 mm SVL. Tail 24–25% of total length. Body strongly compressed. Dorsal scales in 15–15–15 rows. Vertebral scale row slightly wider than, up to about 1.5×, the width of paravertebral rows. Ventrals 198–208, averaging 202 in males, 200 in one female (table 1). Anal single. Subcaudals 92–98, averaging 96 in males, 95 in one female. Loreal and prefrontal bordering the anterior edge of the eye. Head scales highly variable: postoculars 2, primary temporals 1–2, secondary temporals 2–4, supralabials 7–9 (usually 3–4 or 4–5 bordering the eye), infralabials usually 11 or 12 (range 10–13). Either one or two pairs of infralabials in contact behind the mental, with the following frequencies in our sample: first infralabials in contact (2), first two in contact (1), one infralabial in contact with two on the opposite side (3). Maxillary teeth 11–14 (N = 5).

Color in Life: There is a degree of intrapopulational variation in dorsal and ventral ground colors, as indicated by Myers' notes on three specimens from Madden Forest (KU 110311–110313). The dorsal ground color of head and body varied from light gray to light brown; the supralabials were noted as yellowish brown in one specimen, but otherwise were the same hue as the head and body. The dark dorsal markings (described below) were described as dark blackish brown in all, but the blotches appear black in color photographs (fig. 1). The chin and anterior ventral surface were pale yellowish or light yellow, turning either grayish brown or yellowish tan posteriorly, and light brown under the tail; two were noted as having dark grayish brown ventral spots, either scattered or arranged in a double row. The iris was some shade of gray in all three specimens, variously described as light gray, brownish gray, or bluish gray. The tongue of one specimen was pale brown, turning white at the tips of the fork.

Color and Pattern in Preservative: Dorsal ground color of head and body pale grayish brown to tan. Head with a distinctive dark brown or blackish ∩-shaped marking beginning at the prefrontal/frontal suture and extending to the neck, where it is confluent with the first pair of body blotches (figs. 1, 4–5). Apart from the dorsal figure, the head usually bears few other markings; dark sutures and scale edges are present, usually on the postoculars, temporals, and posterior supralabials, and the posterior infralabials often have gray stippling.

Dorsum with 17–22 round to slightly elliptical lateral blotches, each with a narrow pale brown border, which is sometimes only marginally distinct from the dorsal ground color. Longitudinal width of blotches anteriorly (after the first neck blotch) 5–7 scales, at midbody 4–6 scales, and posteriorly (just anterior to vent) 5–7.5 scales; thus, there is little variation along the length of the body in overall size of the blotches. The blotches immediately behind the head (with which the head marking is confluent) are often elongate and have a more irregular shape than the other body blotches. Interspaces approximately equal to, or slightly greater than, the width of the blotches the length of the body. Especially on the anterior half to two-thirds of the body, the interspaces have a variable number of black streaks or spots

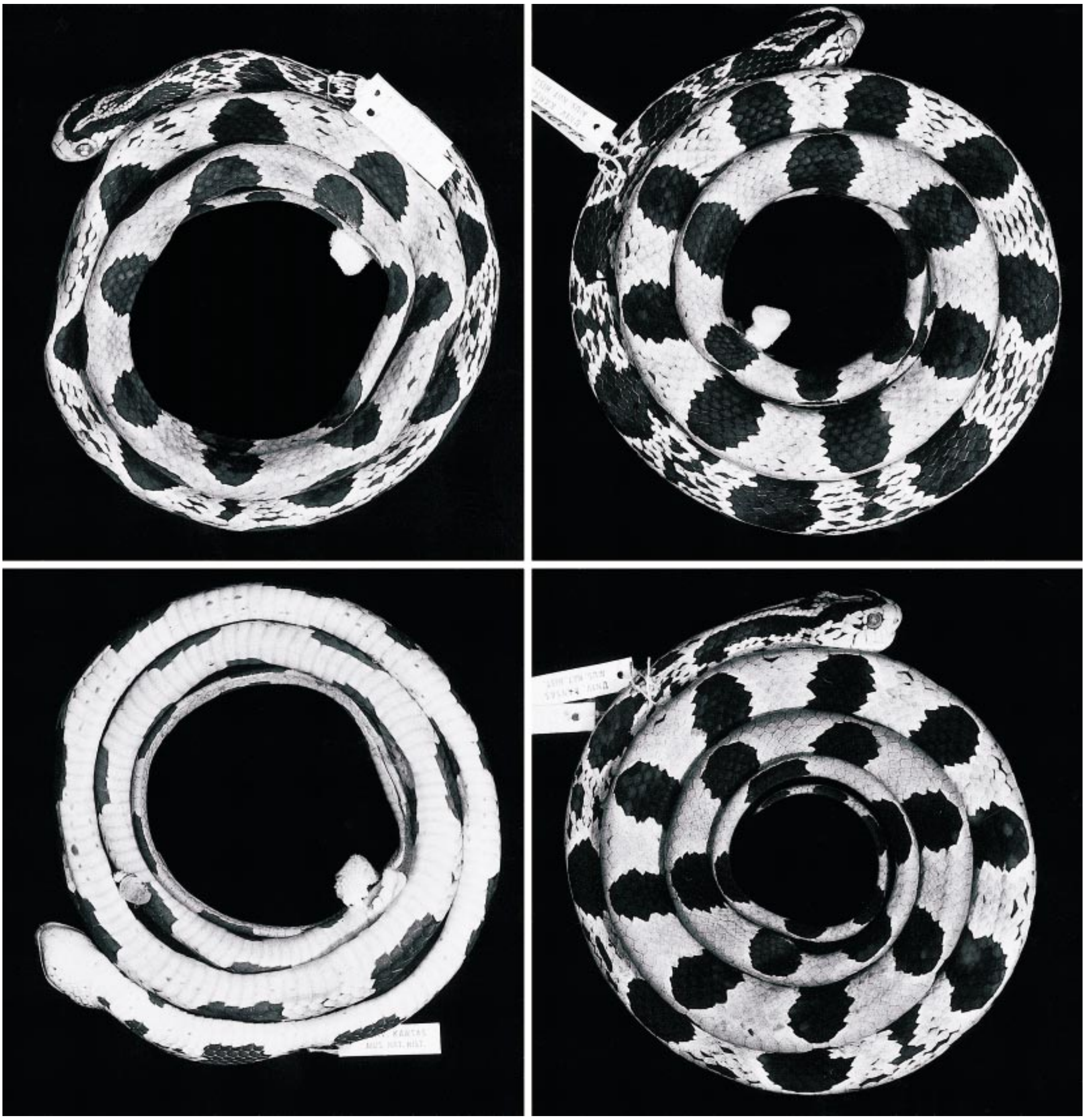

Fig. 5. *Dipsas nicholsi* (Dunn) from Madden Forest, central Panama. **Left:** KU 110311 in dorsal and ventral view. **Right:** KU 110312, above; KU 110313, below.

(fig. 5), which sometimes fuse into somewhat larger irregular blotches (fig. 5, upper right).

Venter pale grayish brown, either without distinct markings or with a variable amount of dark streaking or spotting. Occasionally an undulating line of dark smudged spots down the outer edges of the ventrals; such a line may be more distinct anteriorly than posteriorly, or it may be more or less complete for the length of the body. Tail patterned similar to body.

HEMIPENIS

The hemipenes of KU 110311–110312 and 110314 are fully everted and were examined in situ, with one later being removed for illustration (fig. 6). The hemipenis is slightly bilobed at the tip and fully capitate.

The sulcus spermaticus divides just within the capitulum, with the branches going to the periphery of the tips of each lobe in centrolineal orientation. The capitulum is entirely calyculate, and the calyces are densely ornamented with fleshy papillae.

Just proximal to the capitulum is a battery of large, hooked spines encircling the organ in a band 3–4 spines wide. Below this the organ is ornamented with spinules (minute spines not evident in fig. 6) all around.

There are 2–4 (the number varies among specimens) large, hooked spines in an irregular transverse row on the basal half of the asulcate side of the organ, well below the encircling battery of spines; these spines are somewhat larger than those in the battery above. There is a large, elongate, laterally positioned nude pocket, which curves toward the middle of the asulcate side to terminate at the level between the battery of spines and the aforesaid transverse row (fig. 6, bottom). The pocket has thickened edges and a somewhat pronounced lobe along one side.

The hemipenis of *Dipsas nicholsi* is similar to that of other species of *Dipsas* and the related genera *Sibon*, *Sibynomorphus*, and *Tropidodipsas* for which the organs are known. These include 12 Central American and one South American species described previously (Kofron, 1982b; 1985a, 1985b; 1987, 1988; Porto and Fernandes, 1996; Savage and McDiarmid, 1992),[6] and our observations of everted organs of the following Central and South American species: *Dipsas andiana* (KU 132503), *D. oreas* (ANSP 31778–31781, 31783, 31785–31786), *D. variegata* (FMNH 204479), *Sibon argus* (AMNH 115927), *S. dimidiatus* (FMNH 20351), *Sibon nebulatus* (FMNH 204481), and *Sibynomorphus petersi* (KU 121309, 142804). All these species have a fully capitate organ in which the capitulum is ornamented with papillate calyces, and a battery of enlarged spines of varying width

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[6] Species reported in the published descriptions are *Dipsas brevifacies, D. gaigeae, D. neivai, Sibon anthracops, S. argus, S. carri, S. dimidiatus, S. longifrenis, Tropidodipsas annulifera, T. fasciata, T. fischeri, T. philippii*, and *T. sartorii*. Kofron (1985b) and Wallach (1995) discussed alternative views concerning recognition of *Tropidodipsas*.

encircling the organ proximal to the capitulum. The hemipenis of *D. nicholsi* is less bilobed than that illustrated by Porto and Fernandes (1996) for *D. neivai*, but more bilobed than described and illustrated for *D. brevifacies*, *D. gaigeae*, *Sibon carri*, *T. fischeri*, or *T. fasciatus* (Kofron, 1982b; 1985a, 1985b).

A basal nude pocket is present in all species we examined, and is mentioned in all descriptions except *Dipsas neivai* (Porto and Fernandes, 1996), *Tropidodipsas philippii* (Kofron, 1987), and three species examined by Savage and McDiarmid (1992): *Sibon argus*, *S. dimidiatus*, and *S. longifrenis*. Descriptions for the last three were very brief and the pocket probably was overlooked, as suggested by our observation of prominent pockets in the hemipenes of a specimen each of *S. argus* (AMNH 115927) from Panama and *S. dimidiatus* (FMNH 20351) from Guatemala.[7] The nude pocket in all hemipenes we examined is exceptionally long, extending from the base to, or nearly to, the battery of enlarged spines encircling the organ (pockets 3–5.5 mm long in organs of 9–15 mm total length). There is variation in the position of the pocket in different species. The pocket in *D. variegata* and *S. nebulatus* is on the asulcate side of the hemipenis, more or less opposite the fork of the sulcus spermaticus. However, in all other species we examined, the pocket is on the ''lateral'' side of the organ, as shown for *Dipsas nicholsi* in figure 6.

The hemipenes of *Dipsas nicholsi* and *D. variegata* differ in relatively minor ways that distinguish the hemipenes of *Dipsas* for which we have data. The principal differences concern the encircling battery of enlarged hooked spines and the position of the nude pocket. In *D. variegata* the battery is 4 to 5 rows across adjacent to the sulcus spermaticus, and broadens to 7 or 8 rows on the asulcate side; enlarged spines on the asulcate side fill the area between the capitulum and the distal end of the nude pocket. In *D. nicholsi* the battery is only 3 or 4 rows across. The nude pocket in *D. nicholsi* is on the ''lateral'' side of the organ (fig. 6), whereas the pocket in *D. variegata* is on the asulcate surface. These differences corroborate the other characters indicating that *D. nicholsi* and *D. variegata* are not conspecific (see Resurrection of *Dipsas nicholsi* above).

DISTRIBUTION AND NATURAL HISTORY

DISTRIBUTION: *Dipsas nicholsi* appears to be endemic to a small area lying mainly (if not entirely) in the upper Río Chagres drainage in central Panama, in lowland forest approximately 60–150 m above sea level (map 1). There is a distance of only 33 km between the southernmost and the northernmost parts of its known range—from the southern edge of Madden Forest Preserve to the mouth of Río Pequení near the head of Madden Lake (see below). This statement of distribution needs amplification, inasmuch as the basin of the Río Chagres has been drastically altered by dredging and other construction activity associated with the interoceanic Panama Canal.

The Río Chagres rises in the low mountainous region of east-central Panama (northeast of the Canal), flowing first southwestward and then northwestward to empty into the Caribbean Sea. Damming of the Río Chagres in 1912 flooded the lower part of the Chagres Basin, creating Gatun Lake and isolating the hilltop now known as Barro Colorado Island (map 1). Ocean-going ships are raised and lowered to and from Gatun Lake by a series of locks at either end of the Canal, resulting in some loss of water with each passage. In order to provide another reservoir

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Fig. 6. Hemipenis of *Dipsas nicholsi* (Dunn). Right everted organ of KU 110312 shown (from top to bottom) in sulcate, asulcate, and apical-lateral view. Scale divisions in mm. The lowermost view shows the very elongated ''basal'' nude pocket (4 mm long) extending distad up from the base of the hemipenis. This organ is completely everted; the internal insertions of the divided retractor muscle show through the tissue as pale areas obscurring the overlying calyces.

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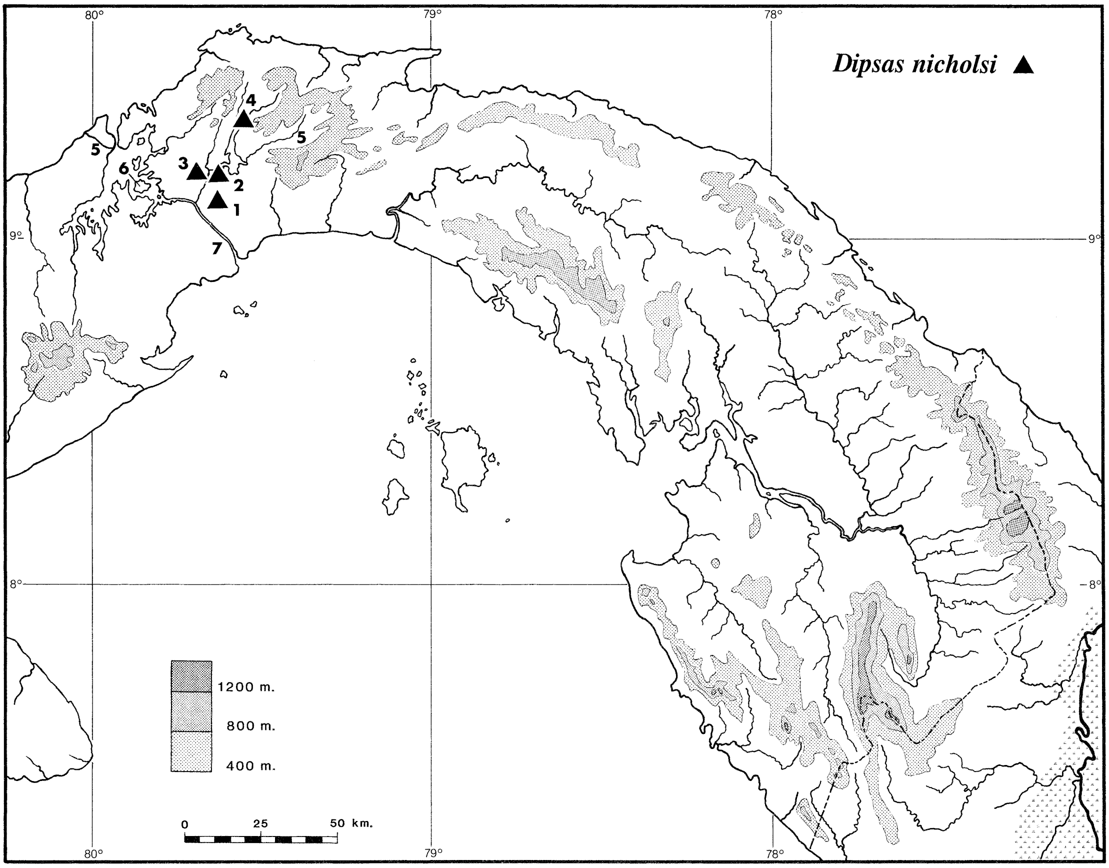
[7] The basal nude pocket is often obscured among folds at the base of the hemipenis, which must be carefully separated to demonstrate the pocket. It is especially difficult to see when the base of the hemipenis has been tied off with thread, in which case severing the thread is usually required.



Map 1. Eastern Panama, showing locality records for *Dipsas nicholsi* (Dunn), which appears endemic to a small area of lowland forest on the central part of the isthmus. Specimen localities: **(1)** Madden Forest; **(2)** ‘‘Chagres Villages’’ (see footnote 9); **(3)** Agua Clara (see footnote 10); **(4)** mouth of Río Pequení near head of Madden Lake. Other geographic features mentioned in text: **(5)** upper and lower Río Chagres; **(6)** Barro Colorado Island in Gatun Lake; **(7)** Panama Canal. See also map 3.

to compensate for such loss during the dry season, an additional dam was constructed higher on the Río Chagres, flooding part of the upper drainage and creating Madden Lake (= Lago Alajuela of recent maps). The Madden Dam was completed in 1936—three years after the first specimen of *Dipsas nicholsi* was acquired.

As summarized in Dunn (1949a: table 7), five head-and-neck specimens of *Dipsas nicholsi*, all part of the ‘‘Chagres Collection’’, were purchased from local inhabitants during the old Panamanian snake census conducted by H.C. Clark, Director of the Gorgas Memorial Laboratory.[8] The first specimen (the holotype) was collected in early 1933 at the mouth of the Río Pequení (Dunn, 1933; see Clarification of Type Locality below); the other four specimens were obtained in 1938 and 1939 (Dunn, 1940: 117).

The holotype and the other four partial specimens of *Dipsas nicholsi* came from

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[8] A total of 13,745 snakes were logged by the census during 1929–1953 (Wright, 1970: 39), but probably no more than a few hundred of the heads were placed in museum collections. Dunn’s (1949a) paper is the most complete and easily accessible report of census results (see also Clark, 1942; Dunn, 1942, 1949b). A brief history of the census and Dunn’s role is given by Myers (2003).

three generalized localities ‘‘in the Chagres valley between the normal Canal Zone boundary and the head of Madden Lake’’—i.e., the ‘‘Madden Lake area’’ (the holotype), ‘‘Chagres villages’’[9], and ‘‘Agua Clara’’[10] (Dunn, 1940: 117; 1949a: 48–49). According to Clark (1937: 15; see also Dunn, 1949a: 48), the Chagres Collection came

> almost entirely from the mid-basin of the valley of the Chagres River in the rocky, forested portion. During the census the bottom of Madden Lake areas was deforested and this accounted for the increased number of tree vipers and made a more general catch of all species possible.

Four of the five *D. nicholsi* heads were obtained after completion of Madden Dam. Three came from the Chagres villages, but only one from ‘‘Agua Clara’’, which yielded 47 species of snakes from 1937 to 1945 (Dunn, 1949a: table 3). The five heads were dispersed to different institutions, with the first one (MCZ 37884) having been designated as holotype by Dunn (1933).

CLARIFICATION OF TYPE LOCALITY: Dunn (1933) gave the type locality as ‘‘Mid-basin of Chagres River and mouth of Pequeni River’’. We interpret this rather inexplicit wording to mean *the junction of the Río Pequení with the Río Boquerón in the ‘‘mid-basin’’*[11] *[= upper drainage] of the Río Chagres at approximately 9°21′N, 79°33′W*—this location being about 20 km NNE of the present-day Madden Dam. The holotype was obtained in 1933, three years prior to the filling of Madden Lake, the waters of which reached to the type locality.

The Río Pequení enters the northern end of Madden Lake to the southeast of another tributary, the Río Boquerón. A 1:62,500 map of the Madden Lake Watershed[12], with the original courses of rivers indicated below lake level, shows the Río Pequení entering Madden Lake approximately 3500 ft (about 1 km) upstream from the original junction of the Pequení and Boquerón, which was flooded by the rising lake. The lower part of the Río Boquerón was submerged farther upstream to form the northernmost head of Madden Lake at an elevation (fide Dunn, 1949a: 48) of about 260 ft (79 m). The upper Río Chagres enters Madden Lake farther south, about 6 km ENE of Madden Dam.

MADDEN FOREST: Until the 1960s, *Dipsas nicholsi* was known only from the heads obtained by the Panama snake census and reported on by Dunn (1933, 1940, 1949a [other records are considered erroneous; see below]). The several subsequent specimens known to us are all from the Madden Forest Preserve, including four snakes (KU 110311–110314) collected by Myers in 1965 and 1966.

The Madden Forest Preserve (formerly in the Canal Zone, now in Prov. Panamá) straddles Madden Road, a paved highway between Summit and Madden Dam. The roughly rectangular Preserve, about 3 × 5 km, lies across the very low continental divide, which swings close to the Pacific coast and seldom exceeds 200 m above sea level on this part of the isthmus. The northerly (Atlantic) drainage via the upper Río Chilibre system flows into the Chagres below Madden Dam; the southerly (Pacific) drainage adds to the Canal waters via the Río Pedro Miguel. The vegetation is lowland monsoon rain forest.

ERRONEOUS LOCALITIES: Peters (1960) repeated the names of the several localities published by Dunn, but also indicated that two heads of *Dipsas nicholsi* came from Barro Colorado Island. This misinformation

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[9] According to Dunn (1940: 117), the ‘‘Chagres villages’’, not shown on maps, were in the vicinity of Juan Mina, a settlement situated on the old Canal Zone border at 9°10′N, 79°39′W. Dunn (1949a: 48) later added that the Chagres Villages were situated ‘‘between Zone border and Madden Dam’’. These villages were new settlements made by clearing forest due to an ‘‘exodus from the Canal Zone as a result of the decision not to renew leases’’ (Dunn, 1949a: 48).

[10] According to Dunn (1949a: 48) ‘‘Agua Clara lies about two miles from the [Chagres] river, just outside the Zone border, and almost directly north of Gamboa.’’ Agua Clara evidently was named after the Quebrada Agua Clara that edges and then crosses the old Canal Zone border at about 9°11′N, 79°41′W.

[11] The part of the basin in question extends well into the upper part of the Chagres drainage system. ‘‘Mid-basin’’ of the Chagres, as used in connection with the Panama snake census, makes sense only if the present-day Río Chagres is arbitrarily considered to end at the Panama Canal, after which the river and its lower tributaries are subsumed in Gatun Lake. The Chagres regains a short course to the Caribbean Sea northwest of the Gatun Locks and Dam, at the Atlantic side of the Canal. See map 1.

[12] Produced for limited official use in blueprint format January 19, 1937, based on 1936 survey.

came from Dunn, presumably based on faulty memory. After examining the evidence, Myers and Rand (1969: 5 [also Rand and Myers, 1990: 395]) excluded the species from the well-known fauna of Barro Colorado Island:

> *Dipsas variegata nicholsi* (Dunn): This snake was reported by Peters (1960, pp. 138–139) on the basis of information supplied by E. R. Dunn on two specimens. One of these (no. 7157, a head) is in the Barro Colorado laboratory in a jar of mixed species labelled ‘‘not known from B.C.I.’’ Both specimens are from the old Panamanian snake census . . . Furthermore, as a wildlife preserve, Barro Colorado was not included in the scope of the census and Dunn (1949a, table 7), who reported on the census, did not denote the species (by asterisk) among those which he knew to occur on the island.

Myers and Rand (loc. cit.) thought it to be curious that no species of Dipsadini has ever been found on Barro Colorado Island, but that

> it would not be surprising if *D. variegata* eventually reached Barro Colorado, as it does occur in the Chagres drainage and is not uncommon in lowland Madden Forest Preserve, about 24 km to the southeastward.

Despite the proximity of Barro Colorado to known localities a bit higher in the same (Chagres) drainage, we now think it unlikely that *Dipsas nicholsi* will ever be found on the island. This is only partly due to the fact that only a single snake (*Erythrolamprus*) was added to the BCI fauna between 1969 and 1990 (Rand and Myers, 1990: 389); mainly it is because we now suspect that *D. nicholsi* is not as widespread as might be anticipated for a lowland forest snake (see later comments under Comparison of *Dipsas nicholsi* and *Dipsas andiana*).

Pérez-Santos and Moreno (1988: 151) mentioned the possibility of *Dipsas variegata nicholsi* occurring on the Pacific side of Colombia, but there are no Colombian specimens (see also footnote 3). *Dipsas variegata nicholsi* has been reported from western Ecuador by Peters (1960a) and others (e.g., Pérez-Santos and Moreno, 1991), but we refer all those specimens to *Dipsas andiana* (Boulenger), which is resurrected and illustrated later in this paper.

In a presumed *lapsus memoriae*, Villa et al. (1988: 64) implied mistakenly that Peters (1960a) had confused a Panamanian specimen of ‘‘*variegata*’’ with *Dipsas tenuissima*.

NATURAL HISTORY: Four specimens were collected by Myers in Madden Forest in the months of June, July, and September 1965–1966. One specimen was dead on the highway and two others were crossing the road at night (one at 2 AM). The fourth specimen (KU 110313) was found in the open on the ground at night, in forest close to the highway; a specimen of *Dipsas viguieri* (KU 110317) was found in the forest nearby, about 2.4 m aboveground in a small tree.

The remains of a snail or slug were forced from the stomach of one *Dipsas nicholsi*. These snakes were docile, with no evidence of defensive behavior when handled. However, one specimen was kept alive for a few days and exhibited remarkable posturing whenever it was placed on a flat surface and touched or prodded (see figs. 1, 20–21 and description under Defensive Behaviors in the Dipsadini).

RESURRECTION OF *DIPSAS ANDIANA* (BOULENGER) FROM THE SYNONYMY OF *DIPSAS OREAS* (COPE)

With correction of the erroneous records of *Dipsas variegata variegata* from Ecuador and Peru, and proper differentiation of *D. nicholsi* from *D. variegata*, one further point concerning this complex in western South America remains to be clarified: the identity of specimens from western Ecuador that Peters (1960a) assigned to ‘‘*D. variegata nicholsi*’’. We suggest that these specimens are properly identified as *D. andiana* (Boulenger), a name that Peters (1960a) relegated to the synonymy of *D. oreas* (Cope).

Boulenger (1896: 452, pl. 23, fig. 2a–c) described *Leptognathus andiana* based on a specimen from ‘‘Quito, Ecuador’’, and provided excellent figures of the type. Peters (1960a: 92), without examining the type specimen, placed *L. andiana* in the synonymy of *Dipsas oreas*. He explained away some color pattern differences between *L. andiana* and typical *D. oreas* because the type specimen of *L. andiana* is a juvenile (Peters, 1960a: 93–94). Peters was also perhaps misled because Boulenger, either through a counting error or misprint, gave an erroneous count of 184 ventrals for the type, a count at the upper extreme for *D. oreas* (table 3). However, the corrected count of 191 ventrals far exceeds the range we have observed for *D. oreas*. We compared the holotype of *Leptognathus andiana* directly with other similar specimens from western Ecuador, including those that Peters had assigned to ''*D. variegata nicholsi*'', with specimens of *Dipsas oreas* from Ecuador and Peru, and with *D. nicholsi* from Panama. These comparisons showed that *Leptognathus andiana* is not a synonym of *D. oreas*, but that it is a valid species of western Ecuador.

REDESCRIPTION OF *LEPTOGNATHUS ANDIANA* HOLOTYPE: British Museum ledgers indicate that the type specimen of *Leptognathus andiana* (BMNH 1946.1.20.12) was purchased from a ''Mr. Higgens'' and that the only associated locality is ''Quito'' (Colin J. McCarthy, personal commun.). The original catalog number, BMNH 72.2.26.10, indicates that the specimen was cataloged early in 1872, although Boulenger did not describe the species until nearly 25 years later. The clearly incorrect type locality must have been only a shipping point (possibly the base or residence of Mr. Higgens).

Data on the holotype of *Leptognathus andiana* are presented in table 2. The specimen is a juvenile female in good condition (fig. 7). Boulenger's illustrations (1896: pl. 23, fig. 2a–c) and description are accurate except for the incorrect ventral count mentioned previously. After 130 years in preservative, the specimen seems to have changed little in coloration since its description. The dorsum is light grayish brown with chocolate brown lateral blotches; each blotch is outlined with a narrow white border. The blotches are much higher than wide for the length of the body except for the pair just behind the head. Anterior blotches are 4.5–5 scales wide, whereas those from midbody back are 3 scales wide. The anterior four blotches are bilaterally paired. The remaining ones are offset from the corresponding blotch on the opposite side (i.e., they alternate). The interspaces between blotches are about 2.5× the width of the blotches. The anterior half of the body has elongate chocolate brown streaks in the vertebral and paravertebral region. There is a small chocolate brown irregular spot (sometimes no more than a small fleck) between each blotch at the border between the dorsal and ventral scales; this marking encroaches onto the edges of the ventrals. The ventrals are pale dirty brown and unpatterned. The top of the head has a broad ∩-shaped chocolate brown mark (fig. 8) that is similar in form to specimens of *Dipsas nicholsi* from Panama (compare figs. 4, 8). In addition, the top and sides of the head bear other scattered dark streaks and spots. The gular region is immaculate.

The vertebral row is greatly expanded, with each scale being approximately twice the width of the paravertebrals. However, on the anterior quarter of the body and for a short stretch at midbody, many vertebral scales are longitudinally divided into more or less equal scales; occasional vertebrals on other parts of the body are also divided. The specimen has two pairs of chin shields followed by two preventrals. Only the first pair of infralabials is in contact behind the mental.

Distinctive characteristics of the type of *Dipsas andiana* suggesting that it is a valid taxon distinct from *D. oreas* include the peculiar head marking, dark dorsal blotches with a pale border, and high number of ventrals and subcaudals. We include in our concept of this species several other museum specimens with these characters (appendix) and three literature records. We briefly discuss these specimens before providing a formal diagnosis.

ADDITIONAL SPECIMENS AND VARIATION: Comparison of the holotype of *Dipsas andiana* with other specimens of *Dipsas* from western Ecuador shows that the name applies to those that Peters (1960a) referred to *D. variegata nicholsi* (AMNH 35949, 35955). We have seen few others (appendix) and there seem to be few specimens in collections, despite considerable fieldwork conducted by herpetologists in western Ecuador. Indeed, the wholesale destruction of tropical forests in western Ecuador (Dodson and Gentry, 1991) may have brought the species to the brink of extinction. Data on specimens examined are summarized in table 2.

Steindacher (1902) assigned one specimen to *Dipsas variegata*, but details he presented suggest to us that the specimen is *D. andi-*

Fig. 7. *Dipsas andiana* (Boulenger). Dorsal and ventral views of the holotype (BMNH 1946.1.20.12) from an unknown locality in Ecuador.

ana. Steindachner's description is repeated here, in part, emphasizing those characters suggesting that his specimen is *D. andiana* (see also table 2):

> 25 large round reddish brown spots on the back, 14 on the tail. The dorsal spots end on the ascending portion of the belly scales . . . Among the anterior five spots are some isolated small spots, which never reach down to the lateral edge of the belly. All body spots with bright yellow border. Ventral side dirty yellowish, unmarked. Head sulfur-yellow, on the top with a horseshoe shaped curved mark from the front toward the back of the head.

Characters matching *Dipsas andiana* in Steindachner's description include the high number of ventrals and subcaudals (201 + 98; table 2), round spots on the dorsum with a bright yellow border, a curved horseshoe-shaped mark atop the head, and an unmarked venter. The high number of subcaudals indicates that Steindachner's specimen was a male.

Two other literature references are not accompanied by detailed descriptions. The color photograph of a specimen in Pérez-Santos

Fig. 8. *Dipsas andiana* (Boulenger). Close-up of head of holotype. The characteristic ∩-shaped pattern differentiates *andiana* from *Dipsas oreas* and hints at a possible relationship with Panamanian *Dipsas nicholsi*.

and Moreno (1991: photo 74, ''*Dipsas* sp.'') has the following characteristics suggestive of *Dipsas andiana*: ∩-shaped head marking (and head otherwise relatively unmarked), head shape, the form of the dorsal blotches (elliptical and with a narrow light border), and the anterior interspaces much broader than the blotches. These characters seem sufficiently diagnostic to refer the photograph to *D. andiana*. Despax (1911) attributed three specimens in the Muséum National d'Histoire Naturelle (Paris) from ''Santo Domingo'' (here assumed to be Santo Domingo de los Colorados) to ''*Leptognathus andiana*'', but he did not provide sufficient data for corroboration of the identification (the locality is plotted in map 2, but note in the appendix that *Dipsas* ''*oreas*'' *elegans* is also known from this locality).

Fowler (1913) attributed two specimens to ''*Leptognathus andianus*'', but these are here identified as *Dipsas oreas* (see footnote 17 and appendix).

COMPARISON WITH *DIPSAS OREAS* (COPE)

Peters (1960a: 92) synonymized *Leptognathus andiana* with *Dipsas oreas* (Cope, 1868), which, according to current taxonomy (Orcés and Almendáriz, 1987), comprises several rather distinct forms: *D. o. oreas* (Cope), *D. o. elegans* (Boulenger), and *D. o. ellipsifera* (Boulenger). Explicit comparisons with ''*Dipsas oreas*'' herein refer only to the nominotypical form.[13] Several characters of the holotype and other specimens of *D. andiana* distinguish this species from *D. oreas*.

The most obvious differences between the two species are aspects of color pattern and body form. *Dipsas oreas* (figs. 9–11) generally is a distinctly banded snake, at least anteriorly; i.e., the anterior dark markings on each side are continuous middorsally and only occasionally are significantly constricted in that area. The posterior bands in *D. oreas* are usually reduced and may be broken into an alternating series of lateral blotches. In contrast, *D. andiana* has lateral blotches on each side that usually do not meet middorsally and hence do not form distinct bands (figs. 7, 13–15); when opposite blotches do meet, the contact is limited and a definite constriction at the vertebral row is present. In other words, most *D. oreas* can easily

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[13] Photographs of the types of *Dipsas elegans*, *D. ellipsifera*, and *D. oreas*, as well as of *Leptognathus andrei* Sauvage (currently a synonym of *D. o. oreas*), were presented by Kofron (1982a). We leave open the question of the relationship of *elegans* and *ellipsifera* to *D. oreas*, but these names do not bear on the identity of *Leptognathus andiana*.

The elements of color pattern that we describe for *Dipsas oreas* are subject to some variation, which is at least partly geographic (Cadle, MS). Some of the major pattern variants of *Dipsas oreas* include specimens in which the bands tend to be interrupted middorsally such that the pattern might be more appropriately described as blotched. Even in these cases, usually one or more anterior bands will be completely formed (e.g., fig. 10). Specimens from southern Ecuador and Peru appear to have more extensive and completely formed bands than those from central Ecuador. All adult specimens we have seen (and, e.g., photographs such as those in Kofron, 1982a) show a lightening of the centers of the bands or blotches (figs. 9–10). However, this characteristic seems correlated with size—larger specimens have increasingly light centers. In hatchlings and small juveniles the blotches are solid (fig. 11). The lightening may not be evident in poorly preserved or excessively darkened specimens, and may require close examination of individual scales under a microscope. In some specimens with extensive lightening only the periphery of the blotches is evident as irregular ellipses of dark pigmentation. Some specimens of *D. oreas* apparently have essentially unmarked venters as seen, for example, in the holotype of *Leptognathus andrei* illustrated by Kofron (1982a). Most of the specimens we have seen have heavily marked venters.

TABLE 2

Variation in Mensural and Meristic Characters in *Dipsas andiana* (Boulenger)[a]

(Data for holotype and Steindachner's [1902] specimen [see text] are given separately.)

	Dipsas andiana ♀ holotype	"*Dipsas variegata*" fide Steindachner Presumed ♂	*Dipsas andiana* Summary
Total length (and SVL) of largest ♂ and ♀	♀ 260 (198)	♂? 675 (—)	♂ 648+ (488) ♀ 843+ (673)
Tail length /total length		—	5♂ 0.23–0.26 0.25 ± 0.01
	♀ 0.24		4♀ 0.23–0.25 0.24 ± 0.008
Maxillary teeth	13	—	12 (N = 5) 13 (N = 4)
Dorsal scales	15-15-15	15	15-15-15
Ventrals	♀ 191	♂? 201	6♂ 185–196 192.7 ± 4.03
			5♀ 185–191 187.8 ± 2.39
Subcaudals		♂? 98	5♂ 91–106 95.0 ± 6.28
	♀ 83		4♀ 82–83 82.8 ± 0.50
Anal scale	single	single	single
Postoculars	3–3	2	1 (N = 3) 2 (N = 9) 3 (N = 8)
Primary temporals[b]	2–3	—	1 (N = 5) 2 (N = 12) 3 (N = 3)
Secondary temporals[b]	3–5	—	2 (N = 3) 3 (N = 14) 4 (N = 3) 5 (N = 1)
Supralabials (touching eye)	8–8 (3–4)	10 (4–6)/8 (4–5)[c]	8 (3–4) N = 2 8 (4–5) N = 6 8 (3–5) N = 1 9 (3–5) N = 7 9 (4–5) N = 4 10 (4–5) N = 1 10 (4–6) N = 1
Infralabials	9–9	—	9 (N = 2) 10 (N = 7) 11 (N = 10) 12 (N = 3)
No. dorsal blotches on body	18	25	18–25 (N = 11) 22.1 ± 2.63

[a] For bilateral head-scale counts, each side of each specimen was treated as an independent observation since these are often asymmetrical within a specimen; for these counts, the frequency of each observation is given to emphasize the considerable variation. N = sample size. The summaries in the third column include data from the holotype but not from Steindachner's (1902) specimen.

[b] See footnote c, table 1.

[c] Variation left/right sides.

Fig. 9. *Dipsas oreas* (Cope). A typically banded specimen from northern Peru (ANSP 31778). The snake is in a defensive posture (see under Defensive Behaviors in the Dipsadini).

be described as banded snakes, at least anteriorly, whereas *D. andiana* is laterally blotched.

However, occasional specimens of *Dipsas oreas* have a more blotched than banded pattern anteriorly (e.g., fig. 10), which results from the markings on each side being offset from one another; even in such cases, however, at least one broad band on the neck is usually present. Similarly, some specimens of *D. andiana* have one or more complete bands. For example, KU 132504 has two complete bands behind the head, and in KU 164211 (fig. 14 top) dorsal blotches 2–8 are fused across the midline; in such cases of fusion there is a middorsal constriction and the bands would be hourglass-shaped if flattened out.

Other aspects of color pattern also distinguish *Dipsas andiana* from *D. oreas*. Generally, the anterior blotches in *D. andiana* are rounded or irregular in shape, and taller than broad; posterior blotches are more elliptical (3–4 scales wide at midpoint, tapering dorsally and ventrally). The blotches in *D. andiana* usually have curved or irregular borders and lack any lightening of their central portions; furthermore, the blotches in *D. andiana* are narrowly bordered by a distinct pale line. In KU 164211, which has more blotches fused across the midline than in other specimens of *andiana*, the blotches appear more or less as vertical bands with straight edges; however, the pale border is especially evident and diagnostic in such cases.

In contrast, anterior blotches in *Dipsas oreas* are squarish or with jagged edges, and longer than tall; posterior blotches are much taller than broad, with straight vertical or slightly irregular borders. The dorsal blotches in adult *D. oreas* characteristically have light centers and usually lack a pale border (figs. 9, 10; footnote 13). The lightening of the centers of blotches is sometimes so extensive as to suggest that the blotches in adult *D. oreas* have a darkened border, a pattern not observed in *D. andiana*.

The interspaces are broader than the blotches in *Dipsas andiana*, sometimes much broader, whereas the anterior blotches are much broader than the interspaces in *D. oreas* (posterior blotches in *D. oreas* tend to be narrow, often reduced to vertical bars, and are therefore much narrower than the interspaces).

Most specimens of *Dipsas oreas* have a strongly patterned venter consisting of dark and/or light spots or checkerboard pattern on a brown ground color (fig. 10; but see footnote 13). The venter in most specimens of *D. andiana* is relatively unpatterned (figs. 7, 13).

The distinctive ∩-shaped marking on the head of *Dipsas andiana* is constant and well

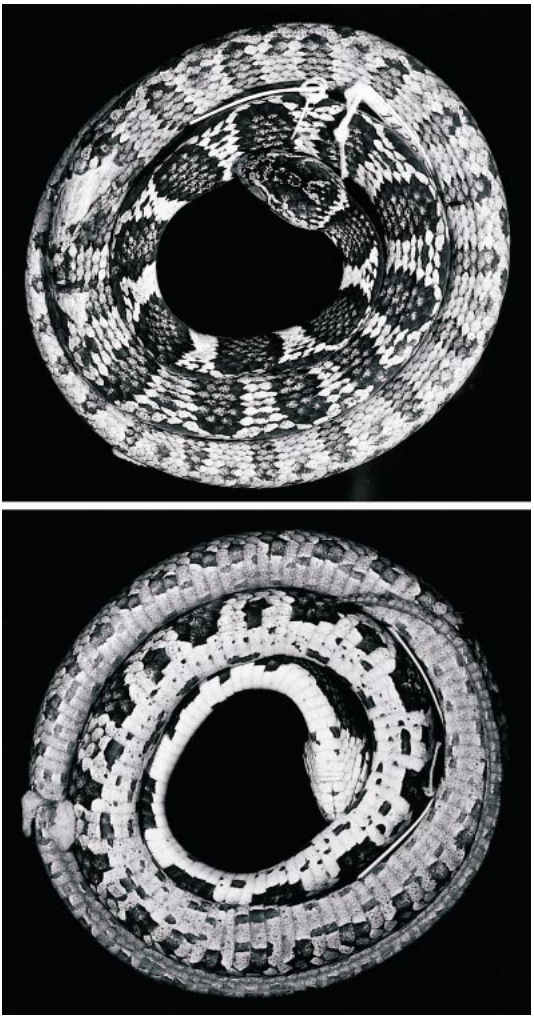

Fig. 10. *Dipsas oreas* (Cope). Dorsal and ventral views of a specimen (KU 142803) from Pichincha Province, Ecuador. Except for the neck band, the anterior bands of this specimen are broken middorsally, resulting in a blotched appearance (vs. banded as in fig. 9). Note the heavily pigmented dorsal surface of the head, the lightening of the central portions of the dorsal blotches, the anterior interspaces narrower than the bands, and heavy speckling on the venter. All these are characteristic of *D. oreas*, but not of *D. andiana*.

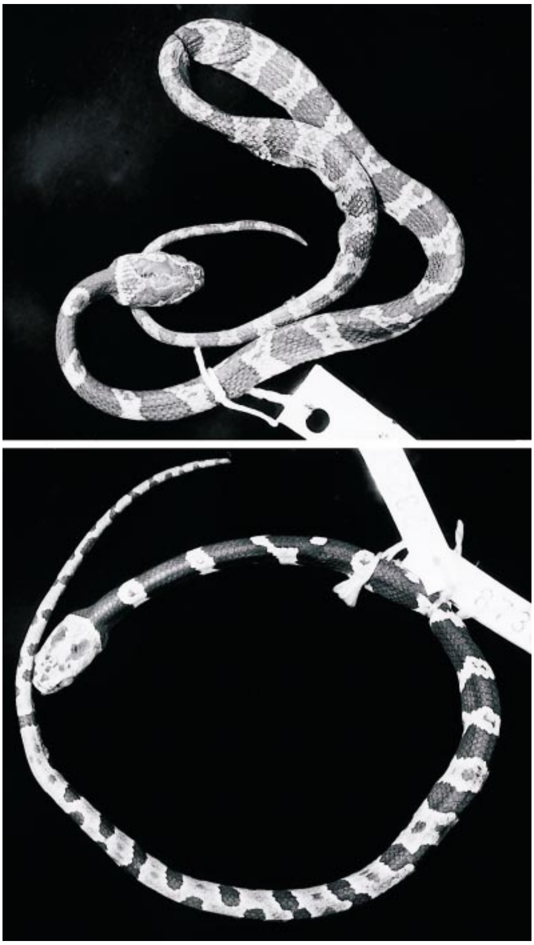

Fig. 11. *Dipsas oreas* (Cope). Two juveniles. **Top:** ANSP 18120, Ecuador. **Bottom:** FMNH 232572, Peru.

formed in juveniles and adults (figs. 8, 12 top). There are few other head markings; the labial scales are uniform pale brown or gray, but a few sutures are sometimes darkened. In contrast, *D. oreas* usually has many obscure irregular flecks and spots on the head, including extensive speckling on the top and sides, and on the labial scales. Many specimens of *D. oreas* have a large, irregular (sometimes elongate) blotch centered on each parietal scale (figs. 9, 10, 12 bottom); these rarely converge and fuse anteriorly (fig. 11 top), forming a single marking similar to but much thicker than in *D. andiana* (see also footnote 17).

Thus, in contrast to some species of *Dipsas*, *D. andiana*, like *D. nicholsi*, seems to have a distinct, relatively conservative color pattern that distinguishes it from other species.

In addition to differences in color pattern, *Dipsas andiana* differs significantly from *D. oreas* in the number of ventrals and subcaudals when specimens are segregated by sex (tables 2, 3).

Ventrals:
  males, $t = 7.213$, df = 10, $p \ll 0.01$
  females, $t = 5.552$, df = 9, $p \ll$; 0.01
Subcaudals:
  males, $t = 4.127$, df = 8, $p \ll 0.01$
  females, $t = 3.237$, df = 7, $p < 0.05$

These tests are conservative in that we have used only Ecuadorian specimens of *Dipsas oreas* (table 3), because they are the most relevant for comparison with *D. andiana*. In all cases except male subcaudals, inclusion of Peruvian *D. oreas* would tend to increase the significance of the tests since mean values for the Peruvian population are more removed from *D. andiana* means than are the mean values for Ecuadorian *D. oreas* (table 3).

We note one final difference between *Dipsas andiana* and *D. oreas*, namely a subjective, but striking difference in head shape (fig. 12). *Dipsas andiana* has a relatively small, foreshortened, rounded head with rounded canthal and temporal regions. In contrast, the head of *D. oreas* is elongate and blocky with angular canthal and temporal regions. Most of the difference in head shape and size between the two species is due to the much longer postocular region of *D. oreas* compared to *D. andiana*, as seen especially when two specimens of equivalent size are compared side by side with the posterior borders of their eyes aligned (e.g., fig. 12). When viewed from above in that alignment, the tips of the snouts are at the same level, but the head (including the parietal scales) of *D. oreas* extends farther posteriorly. The eyes of *D. oreas* are also somewhat larger in comparable-sized specimens (fig. 12).

Juvenile specimens of *Dipsas andiana* in particular might be confused with juveniles of *D. oreas* because of similar color patterns (cf. figs. 11, 14 top). In both species juvenile patterns are more contrasting than in adults, with black or very dark brown markings on a grayish ground color. Juveniles of *D. oreas* often lack the distinctive lightening of the center of the bands characteristic of larger individuals. However, head shape, constant ∩-shaped head marking, and very wide interspaces between dorsal blotches will distinguish *D. andiana* from *D. oreas*.

Based on relatively consistent color pattern differences, significant differences in segmental counts, and differences in head shape, we conclude that *Dipsas andiana* is a valid species and hereby resurrect the name from the current synonymy of *D. oreas* (Peters, 1960a; Peters and Orejas-Miranda, 1970). The name *D. andiana* also is the proper name for specimens from western Ecuador previously referred to *Dipsas variegata nicholsi* Dunn (Peters, 1960a; Peters and Orejas-Miranda, 1970; Miyata, 1981). *Dipsas nicholsi* and *D. andiana* are very similar species, which are compared in detail following the diagnosis and description of *D. andiana*.

Dipsas andiana (Boulenger)

Figures 7–8, 12 top, 13–15; maps 2, 3

Leptognathus andiana Boulenger, 1896: 452, pl. 23, fig. 2a–c. Type locality: ‘‘Quito, Ecuador’’ [probably a shipping point]. Holotype, BMNH 1946.1.20.12. Despax, 1911: 36. Werner, 1923: 197.

Leptognathus variegata: Steindachner, 1902: 108 (misidentification; specimen = *Dipsas andiana* based on details given).

Leptognathus andianus: Fowler, 1913: 169 (misidentifications; see footnote 17).

Sibynomorphus andiana: Parker, 1926: 206.

Sibynomorphus andianus: Amaral, 1929: 195.

[genus?] *andiana*: Dunn, 1933: 194 (compared with the new species *Sibynomorphus nicholsi* Dunn).

Dipsas variegata nicholsi, part (Ecuadorian specimens only): Oliver, 1955: 70–71, photo (usage probably derived from Peters’ 1952 Ph.D. dissertation [= Peters, 1960a]). Peters, 1960a: 137; 1960b: 517. Peters and Orejas-Miranda, 1970: 90. Miyata, 1981: 16. Pérez-Santos and Moreno, 1991: 161.

Dipsas oreas, part: Peters, 1960a: 92; 1960b: 517. Peters and Orejas-Miranda, 1970: 88. *Leptognathus andiana* listed as a synonym.

DIAGNOSIS: *Dipsas andiana* is a pale brown or grayish snake with a distinctive contrasting pattern on the head and dorsum. The head is relatively unmarked except for a bold blackish brown ∩-shaped or inverted V-shaped marking extending from the anterior edge of the frontal to the neck (fig. 8). Dorsal markings consist of a series of large round, elliptical, or irregular dark blotches on each

TABLE 3

Measurements (in mm) and Standard Characters in *Dipsas oreas*[a]

	Ecuador[b]	Peru (Río Zaña)
Total length (and SVL) of largest ♂ and ♀	♂ 691 (509) ♀ 659 (502)	♂ 758 (543) ♀ 721 (548)
Tail length/total length	6♂ 0.25–0.26 0.26 ± 0.004	7♂ 0.24–0.28 0.27 ± 0.01
	5♀ 0.23–0.24 0.24 ± 0.005	2♀ 0.24 0.24 ± 0.0
Maxillary teeth	12–13 (N = 4)	13–14 (N = 8)
Dorsal scales	15-15-15	15-15-15
Ventrals	7♂ 173–184 178.7 ± 3.06	8♂ 168–180 174.1 ± 4.58
	7♀ 171–180 177.5 ± 3.51	2♀ 167–175 171.0 ± 5.66
Subcaudals	6♂ 82–87 85.3 ± 2.23	7♂ 83–91 88.1 ± 2.85
	6♀ 74–83 76.3 ± 3.44	2♀ 74–77 75.5 ± 2.12
Anal scale	single	single
Postoculars	2 (N = 14) 3 (N = 10) 4 (N = 2)	1 (N = 3) 2 (N = 13) 3 (N = 18)
Primary temporals[c]	1 (N = 5) 2 (N = 19) 3 (N = 2)	1 (N = 2) 2 (N = 18) 3 (N = 13) 4 (N = 1)
Secondary temporals[c]	2 (N = 3) 3 (N = 18) 4 (N = 4)	2 (N = 1) 3 (N = 19) 4 (N = 14)
Supralabials (touching eye)	7 (3–5) N = 2 7 (4–5) N = 5 8 (3–5) N = 4 8 (4–5) N = 1 8 (4–6) N = 12 9 (4–6) N = 1 9 (4–7) N = 1	6 (3–4) N = 1 7 (3–4) N = 1 7 (3–5) N = 9 7 (4–5) N = 8 8 (3–4) N = 1 8 (3–5) N = 2 8 (4–5) N = 8 8 (4–6) N = 3
Infralabials	10 N = 1 11 N = 12 12 N = 12 13 N = 2	10 N = 1 11 N = 3 12 N = 12 13 N = 12

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[a] For bilateral head-scale counts, each side of each specimen was treated as an independent observation since these are often asymmetrical within a specimen; for these counts, the frequency of each observation is given to emphasize the considerable variation. N = sample size.

[b] The Ecuador sample includes only specimens referable to the nominotypical form (*D. o. oreas*) sensu Orcés and Almendáriz (1987); the forms *ellipsifera* and *elegans* are excluded.

[c] See footnote c, table 1.

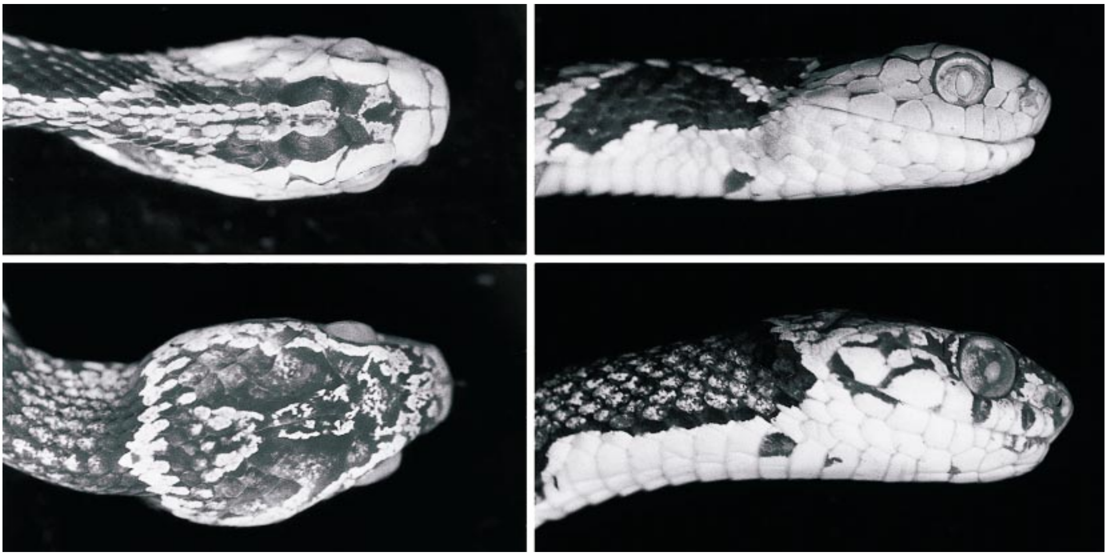


Fig. 12. Comparison of head shapes and color patterns in *Dipsas andiana* and *Dipsas oreas* at equivalent magnifications. **Top:** *D. andiana* (KU 132503, 622 mm total length). **Bottom:** *D. oreas* (KU 142803, 629 mm total length). *Dipsas andiana* has a stereotypical ∩-shaped pattern on the dorsal surface and is relatively unmarked otherwise, whereas *D. oreas* has irregularly and heavily pigmented dorsal and lateral surfaces of the head. *Dipsas oreas* also has angular canthal and supratemporal regions and a relatively longer postorbital region than does *D. andiana*.

side, each with a narrow pale border. Corresponding blotches from each side occasionally meet middorsally, in which case there is a definite constriction at the vertebral scale row. Anteriorly, blotches tend to be opposite one another, whereas posteriorly they tend to alternate. Interspaces between the blotches are broader than the blotches (in some specimens 2–2½×) for the entire length of the body; anteriorly, the interspaces tend to be narrower than posteriorly. *Dipsas andiana* has a high number of ventrals (185–201) and subcaudals (5♂, 91–106; 4♀, 82–83). See table 2 for character summary of specimens examined.

Other species of *Dipsas* in western Ecuador include *D. gracilis, D. oreas* auctorum (including *D. ellipsifera* and *D. elegans*; see Orcés and Almendáriz, 1987), and *D. temporalis*. These species lack the distinctive head marking of *D. andiana*, although they usually have extensive dark markings on the head. *Dipsas gracilis* and *D. temporalis* are similar to *D. andiana* in having high numbers of ventrals and subcaudals; however, these are distinctly banded snakes in which the bands are much broader than the interspaces, are not round or elliptical, and lack distinct pale borders. The bands in *D. gracilis* extend across the venter, whereas the blotches in *D. andiana* end on the lateral edges of the ventrals. *Dipsas ellipsifera* and *D. elegans* have narrow rectangular blotches or bands with light centers and straight edges (Peters, 1960a: pl. 4a; Kofron, 1982a: fig. 1). Characters distinguishing *D. andiana* and *D. oreas* s.s. are given above, where these two species are compared in more detail.

DESCRIPTION

Largest male 648+ mm total length (tail incomplete), 488 mm SVL; largest female 843+ mm total length (tail incomplete), 673 mm SVL. Body strongly compressed. Tail 23–26% of total length. Dorsal scales in 15–15–15 rows. Width of vertebral scale row slightly greater than that of paravertebral row in adults, much greater in juveniles. Ventrals 185–196 with broad overlap between the sexes (table 2; the range extends to 201 for males if we have correctly inferred the identity and sex of Steindachner's [1902] specimen). Anal single. Subcaudals 83–106, av-

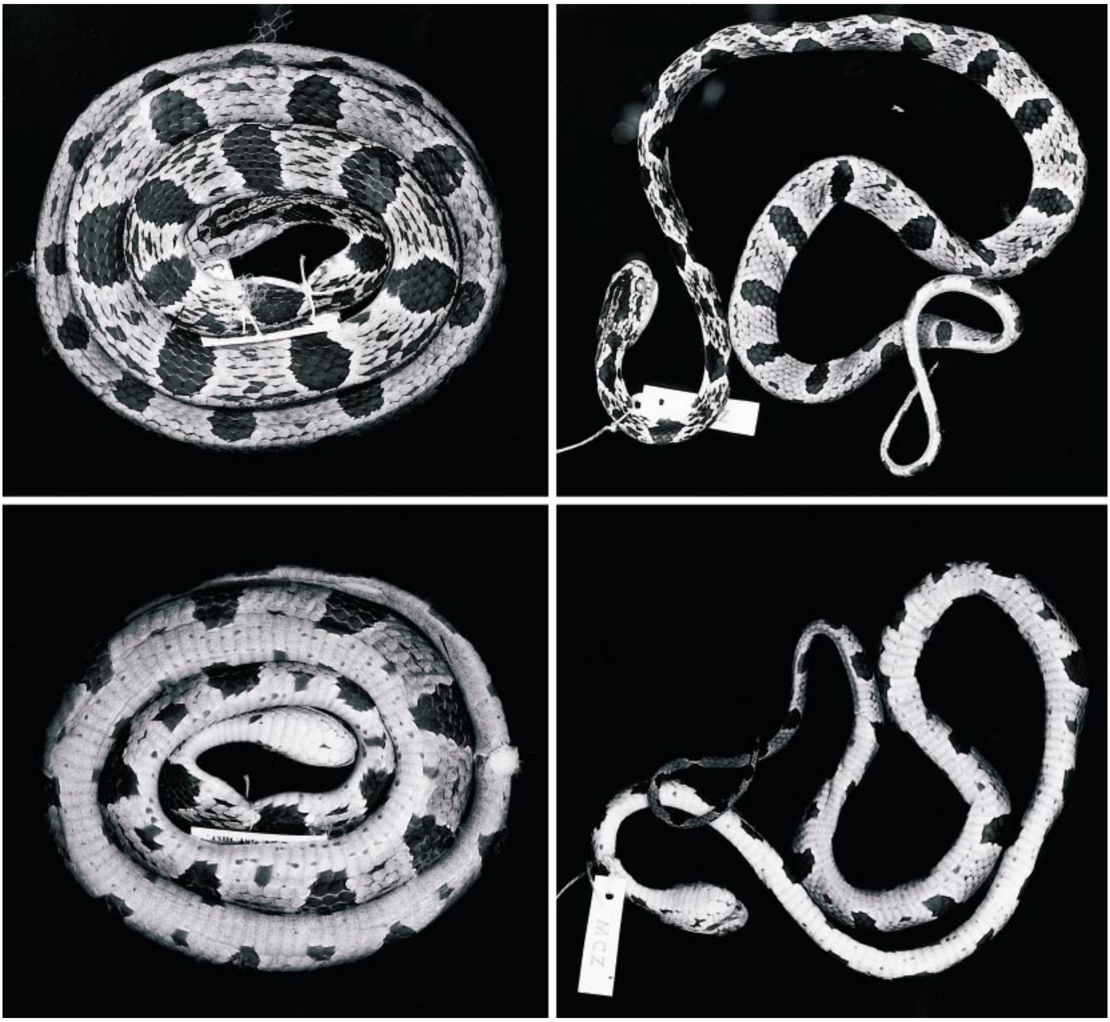


Fig. 13. *Dipsas andiana* (Boulenger) in dorsal and ventral view. **Left:** Specimen from Bolívar Province, Ecuador (KU 132503). **Right:** Specimen from Pichincha province, Ecuador (MCZ 166543).

eraging 95 in males, 83 in females. Loreal and prefrontal bordering the anterior edge of eye. Head scales highly variable: postoculars 1–3, primary temporals 1–3, secondary temporals 2–5, supralabials 8–10 (usually 4–5 or 3–5 bordering the eye), infralabials usually 10 or 11 (range 9–12). Either one or two pairs of infralabials in contact behind the mental, with the following frequencies in our sample: first infralabials in contact (N = 1), first two in contact (7), one infralabial contacts two on the opposite side (2). Maxillary teeth 12–13 (N = 9); dentary teeth 20 in one specimen (KU 110312).

COLOR IN LIFE: We have not seen living specimens of *Dipsas andiana*. A color photograph of a specimen we refer to *D. andiana* (Pérez-Santos and Moreno, 1991: photo 74 of ‘‘*Dipsas* sp.’’) shows the dorsal ground color of the head and body as being pale brown (almost tan). The head marking and dorsal blotches are black, with narrow borders of white to pale brown. Steindachner (1902) described his specimen of ‘‘*Leptognathus variegata*’’ as having reddish brown dorsal blotches with bright yellow borders, a sulfur-yellow ground color on the head, and a dirty yellowish venter.

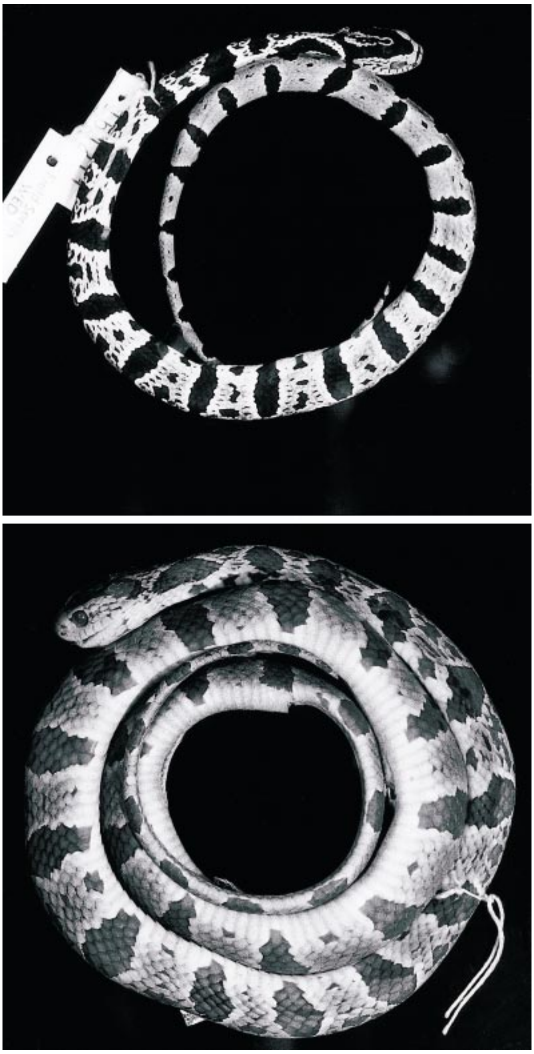


Fig. 14. *Dipsas andiana* (Boulenger). **Top:** Juvenile specimen from Pichincha province, Ecuador (KU 164211); compare with the juvenile holotype in figure 7. **Bottom:** Adult specimen from an unknown locality (AMNH 58204).

Color notes are associated with several specimens we examined (from field catalogs of John D. Lynch and William E. Duellman):

> KU 132503 (JDL 6612): Dorsum dull brown with dark brown saddles edged by very pale brown; the edging of the saddles takes on a yellow cast near the ventrals anteriorly; iris gray; venter yellow brown becoming pale brown-gray toward tail; throat creamy yellow.
>
> KU 132504 (JDL 7813): Ground color brown (more grayish posteriorly); spots dark brown, edges of spots outlined with very pale yellow; iris graywhite; top of head brown with very dark brown markings; venter pale yellow anteriorly becoming nearly gray posteriorly; dark brown flecking on venter.
>
> KU 164210–164211 (WED 48442–48443): Dorsum pale brown with black blotches narrowly outlined by cream. Throat and anterior part of venter creamy white. Rest of venter grayish white with black spots. Iris grayish tan. Tongue black with cream tip.

COLOR AND PATTERN IN PRESERVATIVE: Dorsal ground color of head and body light brown to grayish. Top of head with blackish ∩-shaped marking from prefrontal/frontal border to the neck. Head generally with few distinct markings apart from the ∩-shaped mark; sutures and scale edges may be outlined with black (apparently more prominent in juveniles than in adults). The head marking normally is not connected to the first pair of neck blotches (compare *D. nicholsi*), except for AMNH 79013, in which the marking is broadly confluent with the neck blotch on the right side (similar to the pattern in *D. nicholsi*) and very narrowly connected on the left side (fig. 15); the color pattern and scutellation of AMNH 79013 are otherwise characteristic of *andiana*.

Dorsum with 18–25 elliptical lateral blotches, each taller than wide and with a narrow pale border. Width of blotches anteriorly (first pair after the neck blotches) 3.5–5 scales, at midbody 3–4 scales, and just anterior to vent 2.5–3.5 scales. The interspaces are as broad to much broader (2–2.5×) than the dorsal blotches for the entire length of the body. Often, but not universally, the first pair of blotches on the neck is elongate. Blotches vary from rather round to more irregular or vertical (figs. 13–14). Dorsal blotches extend only to the outer edges of the ventral scales. Elongate blackish streaks and/or small irregular spots frequently occur between the dorsal blotches (e.g., figs. 7, 13) and are more prominent on the anterior half of the body than posteriorly. Pale borders to the dorsal blotches are obvious in nearly all specimens, but are obscure in some, especially posteriorly, possibly a preservation artifact.

The venter is often without distinct markings, but may have a variable amount of dark streaking or spotting (fig. 13). The venter is relatively unmarked in the holotype, KU 132503, AMNH 35955, and MCZ 166543, but is streaked or partly checkered with dark brown in KU 164211 and AMNH 35949. These variations do not seem correlated with size. The tail is patterned similar to the body dorsally and ventrally.

In juveniles the blotches and head marking are dark chocolate brown, whereas the ground color is light grayish brown; this is a more contrasting pattern than in adults. In larger specimens the markings tend to be dark (but not chocolate) brown, whereas the interspaces are medium brown. Juvenile specimens also seem to have more dark suture lines and markings on the head than do adults. However, this is not universal. For example, MCZ 166543 (total length 505 mm and presumed to be adult) has many dark suture lines, whereas these markings are much reduced in KU 132503 (total length 622).

HEMIPENIS

The hemipenes of KU 132503 were only partially everted when the specimen was preserved. Using a modification of the technique of Pesantes (1994; Cadle, 1996), the left organ was removed, fully everted, and inflated with colored jelly. Although the eversion was successful, the overall inflation of the organ is probably somewhat less than in a fully inflated organ. Nonetheless, a complete description is possible.

The hemipenis is slightly bilobed distally and fully capitate. The major retractor muscle is divided for about 5 mm at its insertion (the length of the division probably varies depending on the extent of eversion of the organ). The sulcus spermaticus divides just within the capitulum, with the branches going to the periphery of the tips of each lobe in centrolineal orientation.

The capitulum is entirely calyculate and the calyces are densely ornamented with fleshy papillae. The calyces between the branches of the sulcus spermaticus are more weakly developed than those on the rest of the capitulum (i.e., the ridges forming the calyces are lower); however, the papillae in this area are as well developed as elsewhere on the capitulum.

Just proximal to the capitulum is a single transverse row of large, more or less straight, hooked spines encircling the entire organ. Between these spines and the groove delimiting the capitulum on the asulcate side of the organ is a partial row of smaller, straight, hooked spines. The entire organ proximal to the enlarged spines is ornamented with spinules all around.

The sulcate side of the organ below the encircling row of enlarged spines bears additional ornamentation. A patch of curved, hooked spines is present on each side of the distal end of the undivided portion of the sulcus spermaticus (i.e., just proximal to the encircling hooked spines); the patch comprises four spines on one side, seven on the other. Tapering away from each patch toward the asulcate side of the organ are several similar spines in an irregular row.

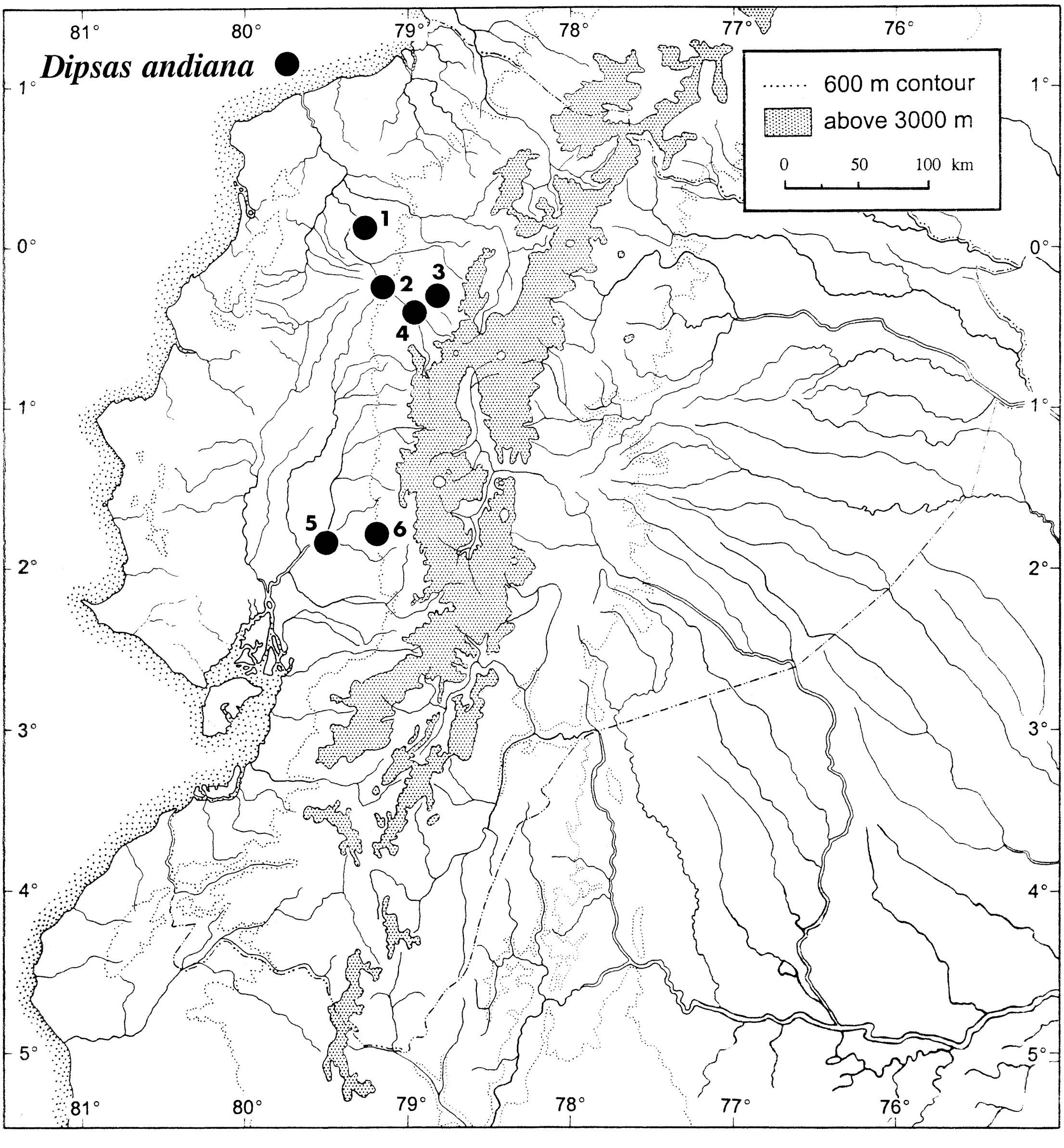
There is a laterally positioned, elongate nude pocket below the capitulum (similar to the position in *Dipsas nicholsi* in fig. 6, bottom); the middle of the pocket is bordered on each side by rounded lobes. The pocket curves slightly mediad onto the asulcate surface distally, terminating below a pair of enlarged, hooked spines. There is another pair of enlarged hooked spines lying towards the asulcate side of the organ, adjacent to the lobe bordering the elongate pocket (these spines seemingly corresponding to the irregular row of enlarged spines on the asulcate side in *D. nicholsi*).

The hemipenis of *Dipsas andiana* is similar in overall morphology to that of *D. nicholsi* and the other species of Dipsadini discussed previously (see description of *D. nicholsi* hemipenis). There are minor differences between the organs of *D. nicholsi* and *D. andiana* (see below under Comparison of *Dipsas andiana* and *Dipsas nicholsi*).

DISTRIBUTION AND NATURAL HISTORY

Dipsas andiana occurs along the Pacific versant of western Ecuador—approximately from the equator to latitude 2° South—in a known elevational range of 5–1140 m (maps 2, 3).

Little is known of the natural history of this species. Field notes by John D. Lynch (for KU 132503–132504) and William E. Duellman (KU 164210–164211) include the following comments: KU 132503 was ‘‘coiled up in *Costus* [Costaceae: Zingiberales] leaves in open area by river about 1 m



Map 2. Locality records for *Dipsas andiana* in western Ecuador. Localities: **(1)** Puerto Quito; **(2)** Santo Domingo de los Colorados (Despax, 1911); **(3)** Dos Ríos; **(4)** Las Palmas; **(5)** Babahoyo (Steindachner, 1902); **(6)** Balsapamba. See also map 3.

off the ground.'' KU 132504 was ''sleeping (?) by night on fern frond along side of road.'' KU 164210 and 164211 were ''coiled in branch of trees ca. 2.5 m above ground at night.'' The KU specimens were collected in April, July, and August in the early to mid-1970s; MCZ 166543 was collected in September 1983.

See also Lynch's note on *Dipsas andiana* under *Dipsas nicholsi,* in Defensive Behaviors in the Dipsadini.

Oliver (1955) gave a sense of the diverse Central American and South American reptiles that once made their way to the banana terminal in New York Harbor and even to local grocery stores. Widespread adoption of

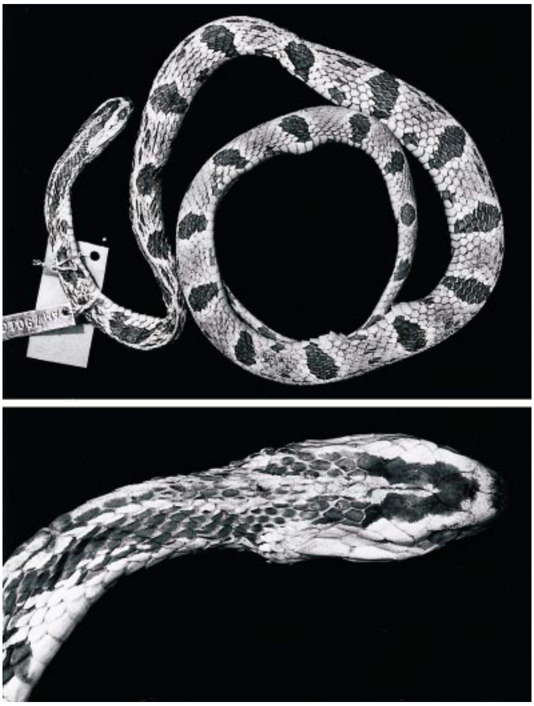


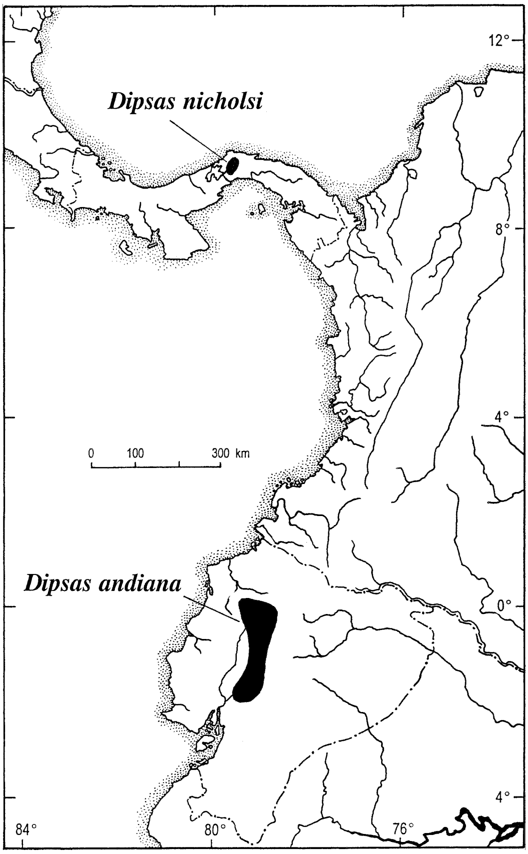
Fig. 15. *Dipsas andiana* (Boulenger). A specimen of unknown locality (AMNH 79013) with an atypical head pattern. See text.

modern methods of spraying, packing, and shipping bananas has drastically curtailed such traffic. But at least five specimens of *Dipsas andiana* found their way to New York in the period 1939–1958. AMNH catalog localities (‘‘Guatemala’’, ‘‘NW Colombia’’) for a few specimens were conjectures, and we suspect that all derived from banana shipments out of Ecuador.

A banana stowaway (AMNH 79013) received from the Bronx Zoo contains two intact pulmonate gastropods (minus shells) that had been fed to the snake in captivity. Oliver (1955: 70–71, under the name *D. v. nicholsi*) noted that banana stowaways acquired by the Bronx Zoo learned to prefer snails that had been removed from their shells, showing ‘‘a marked disdain for those still in the shell’’. Neither of the two Bronx Zoo *Dipsas andiana* shown in a photograph made their way into the AMNH collection, but one of them resembles AMNH 79013 in having an ‘‘atypical’’ head pattern in which the cephalic marking is confluent with the neck blotch on the right side (compare fig. 15 with Oliver, 1955: 71, photo lower right).

COMPARISON OF *DIPSAS ANDIANA* AND *DIPSAS NICHOLSI*

As currently understood, *Dipsas andiana* and *D. nicholsi* are definitely known only from western Ecuador and central Panama, respectively (map 3). Our recognition of *D. andiana* as the proper name of Ecuadorian specimens previously referred to *D. variegata nicholsi* requires us to compare these two species in greater detail. In fact, Dunn had recognized the similarity between *D. nicholsi* and *D. andiana* when he described the former: ‘‘The nearest approach in color [to *D. nicholsi*] seems to be *andiana*, which has one lower labial pair in contact behind men-



Map 3. The widely separated distributions of *Dipsas nicholsi* in central Panama and *Dipsas andiana* in western Ecuador. Based on locality records in maps 1 and 2.

tal and whose locality is quite remote'' (Dunn, 1933: 194).

DIAGNOSTIC DIFFERENCES: Distinctive characters shared by the two species include (figs. 5, 13): (1) unusual ∩-shaped marking on the head; (2) similar dorsal patterns, including uniform light brown ground color and dark round or elliptical blotches with narrow pale borders; (3) relatively unmarked venters (variable in *D. andiana*); (4) relatively high numbers of ventrals and subcaudals (tables 1, 2); and (5) similar overall body form and size, although tables 1 and 2 indicate that *D. nicholsi* may attain a somewhat larger size than *D. andiana*. We now know that the differentially diagnostic character of the infralabial scales mentioned by Dunn (1933) is variable within both species (see descriptions), as recognized later by Dunn for *D. nicholsi* (1940: 117). Nonetheless, several scutellation, coloration, and hemipenial characters distinguish *D. nicholsi* and *D. andiana*.

Male *Dipsas nicholsi* have significantly higher ventral counts (tables 1, 2) than male *D. andiana* ($t = 4.09$, df = 9, $p \ll 0.01$; male subcaudal counts not significantly different). The ventral and subcaudal counts of the single female of *D. nicholsi* are significantly different ($p \ll 0.01$ in each comparison) from the female sample of *D. andiana* (ventrals: $t = 7.38$, df = 4; subcaudals: $t = 15.4$, df = 3). In addition, several subtle aspects of color pattern distinguish the two species (characters following are given for *D. nicholsi* first, *D. andiana* second; see figs. 4–5 vs. 13–14): (1) All dorsal blotches wider than tall vs. blotches taller than wide. (2) Blotches broader vs. narrower. This is most easily seen at midbody and just anterior to the vent, where blotches are 4.5–6 and 5–7 scales wide, respectively, in *D. nicholsi* vs. 3–4 and 2.5–3.5 in *D. andiana*. This difference corresponds to a tendency toward greater relative width of the interspaces (compared to the blotches) in *D. andiana*, whereas in *D. nicholsi* the interspaces and blotches are more nearly the same. The difference is most easily seen by comparing patterns on the posterior body in the two species. (3) Branches of the ∩-shaped marking on the head continue onto the neck as broad, elongate streaks fused to the first pair of neck blotches vs. marking ends on the head and usually not connected to neck blotches (cf. figs. 4, 8; but see fig. 15 for one exception in *D. andiana*). (4) Branches of the head marking continually diverging vs. more or less parallel (compare figs. 4, 8, especially the orientation of the inner margins of the markings on the posterior part of the head). The difference in configuration results in a different scale count between the branches of the marking at the level of the mouth commissure: the branches in *D. nicholsi* are separated by 4–5 scales at this level, whereas those in *D. andiana* are separated by only 2–4 scales.

A few more subtle aspects of color pattern and body form distinguish these species. *Dipsas andiana* has a more variable dorsal pattern than *D. nicholsi*, at least in the small samples available. For example, the shape of the blotches and the width of the interspaces vary more in our series of *D. andiana* than in *D. nicholsi* (compare figs. 13–15 with fig. 5). In general, the blotches in *D. nicholsi* are more rounded than those in *D. andiana*. The relative width of the interspaces varies along the length of the body in *D. andiana*: posterior interspaces are broader relative to the blotches than are the anterior ones. In contrast, the blotches and interspaces are more similar along the length of the body in *D. nicholsi*. In part, this difference corresponds to the generally narrower posterior blotches (compared to anterior ones) in *D. andiana*, whereas blotches are a more uniform shape and size the entire length of the body in *D. nicholsi*. Adult *Dipsas nicholsi* have a more foreshortened and rounded head than *D. andiana* (head longer and narrower; compare fig. 4 with figs. 12 top and 15 bottom), and *D. andiana* has a rather more compressed body than *D. nicholsi*.

Dipsas andiana and *D. nicholsi* also differ in hemipenial morphology, with the caveat that we have examined only a single organ of *D. andiana* and cannot exclude the possibility of some variation. The enlarged spines encircling the organ are straighter and more slender in *D. andiana* than in *D. nicholsi*, and the battery comprises only a single row across on most of the organ in *D. andiana*, compared with 3–4 rows in *D. nicholsi*. The reduced calyces observed between the branches of the sulcus spermaticus in *D. andiana* were not observed in *D. nicholsi*, which has well-developed calyces in this area. *Dipsas andiana* has more distinct lobes on each side of the nude pocket than does *D. nicholsi*. Otherwise, the hemipenes of these two species are similar to one another and to other Dipsadini (references cited under *D. nicholsi*).

BIOGEOGRAPHY: The above differences in scutellation, color pattern, body form, and hemipenes justify the recognition of *Dipsas nicholsi* and *D. andiana* as separate species. The two are widely allopatric, appearing to be absent in the intervening area of western Colombia and eastern Panama (map 3). The distribution of *Dipsas nicholsi* appears exceptionally small for a lowland forest snake, but there are several other endemic snakes at low and moderate elevations in central Panama (Myers, 2003).

Because of strong similarities in body form and color pattern, especially the peculiar head marking, it is tempting to suggest that *Dipsas nicholsi* and *D. andiana* might be sister species. The unusual head marking seems uniquely shared by the two species and is a potential synapomorphy. However, in the absence of other corroborating characters or a more explicit phylogenetic analysis of *Dipsas*, we are not overly confident about this interpretation. The hemipenes of *D. andiana* and *D. nicholsi*, although similar, are also in many respects comparable with those of other Dipsadini (see above discussions of hemipenial morphology); they provide no unambiguous synapomorphies exclusive to *D. andiana* and *D. nicholsi*.

We are intrigued by the conjunction of unusual characters shared by *Dipsas nicholsi* and *D. andiana*, and by their geographical distribution. Many taxa of amphibians and reptiles reputed to comprise groups of closely related species, if not sister species pairs, are distributed in patterns roughly similar to that of *D. nicholsi* and *D. andiana*—with a separating gap in eastern Panama and/or western Colombia.

A few examples include frogs of the the *Dendrobates histrionicus* group (Myers et al. 1984), the genus *Phyllobates* (Maxson and Myers, 1985), the *Eleutherodactylus fitzingeri* group (Lynch and Myers, 1983), and *E. bufoniformis* and *E. necerus* (Lynch and Duellman, 1997); and snakes of the *Coniophanes dromiciformis* group (Cadle, 1989), and *Dipsas viguieri* and *D. gracilis* (Peters, 1960a: 48). The pattern is not restricted to amphibians and reptiles, as shown by examples from birds (Brumfield and Capparella, 1996), fish (Vari, 1988), and plants (Gentry, 1982). Apart from specific clades, a proportion approaching 90% of the amphibians and reptiles shared by rain forests of eastern Panama and northwestern South America is endemic (Lynch, 1979; Duellman, 1999). However, isthmian distributions reflect a complicated history, and, unlike *Dipsas nicholsi*, some other snakes endemic to central Panama lack such apparent close relatives in northwestern South America (Myers, 2003).

Because of their unusual shared characteristics and a disjunct distribution common to diverse faunal elements, we suspect that *D. nicholsi* and *D. andiana* may be sister species. Corroboration must await more explicit phylogenies than currently exist.

DEFENSIVE BEHAVIORS IN THE DIPSADINI

In our experience, the Dipsadini are docile snakes when handled and never attempt to defend themselves by biting, nor have we ever seen one feign a strike with either open or closed mouth.[14] Nevertheless, many species acquire a defensive head shape and some have stylized defensive posturing. Until recently, the literature has been curiously silent on defensive behavior in the Dipsadini. Greene's (1988) important review of antipredator mechanisms in reptiles includes an extensive taxonomic index (his appendix D) that led us only to Mole's (1924) brief report for *Sibon nebulatus*. Prof. Greene (personal commun.) subsequently has flagged three new references pertaining to species of *Dipsas* and *Sibynomorphus* (Sazima, 1992; Martins and Oliveira, 1998; Marques et al.,

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[14] We stress ‘‘in our experience’’, not only because we have no familiarity with many species, but also because snakes are sometimes crafty and unpredictable. For example, the rear-fanged, cat-eyed snakes of the colubrid genus *Leptodeira* also can normally be handled without expectation of being bitten. In San Blas, Panama, however, Myers encountered two uncharacteristically ferocious specimens, one of which succeeded in biting its captor (KU 110621, *L. septentrionalis*).

2001); the four literature references are incorporated below.

Unless otherwise referenced, the following commentaries are extracted from Myers' field catalogs. Obvious defensive behavior was often recorded, but usually there was no actual attempt to evoke a behavioral response from a captive that was headed for the preserving tray. Eventually, however, it was realized that some dipsadinine behaviors exist that are never manifest in a hand-held snake, and that interesting results are sometimes obtained if a newly caught snake is placed on a substrate and deliberately provoked by a prodding finger. Thus, many snakes were poked and harassed, but many more were not, and some potential behaviors may well have been overlooked.

Furthermore, casual notes suggest that some species may show individual variation in their responses (see *Sibon nebulatus* below), and some species perhaps lack defensive behavior altogether. One possibility of the latter might be *Sibon annulatus*, for which specialized defensive behavior was not noted in five observations in Panama; fieldnotes for a specimen (KU 112472) from the mouth of the Río Concepción, Veraguas, explicitly stated ''No special defense behavior except coiling passively but then taking off rapidly once it is induced to move''. Finally, since many or most newly caught, hand-held colubrid snakes defensively void fecal material and/or anal gland secretions, this behavior usually was not recorded and is not considered further.

CHANGE IN HEAD SHAPE

The acquiring of a more-or-less triangular head shape is the most common and widespread performance by newly caught Dipsadini (and various other snakes), even when being held in hand. It makes the rear of the head much wider than the neck, which is exceptionally slender in some species (fig. 16). So widespread is this behavior among the Dipsadini that we suppose occasional predators must be deterred by it.

The process of behavioral widening or ''triangulation'' of the head for defense involves the raising and lateral spreading of the quadratomandibular articulations—a secondary use of the highly kinetic feeding mechanism of serpents. Since it is an easy thing for a snake to do, it is not surprising that head triangulation is practiced by a variety of snakes, including other species living together with some of the Dipsadini (e.g., see note under *Dipsas* sp. below). The biomechanics has been little studied except by Young et al. (1999), who demonstrated differences in the musculoskeletal mechanisms of defensive head triangulation in two not-closely related colubrids (not discussed is the

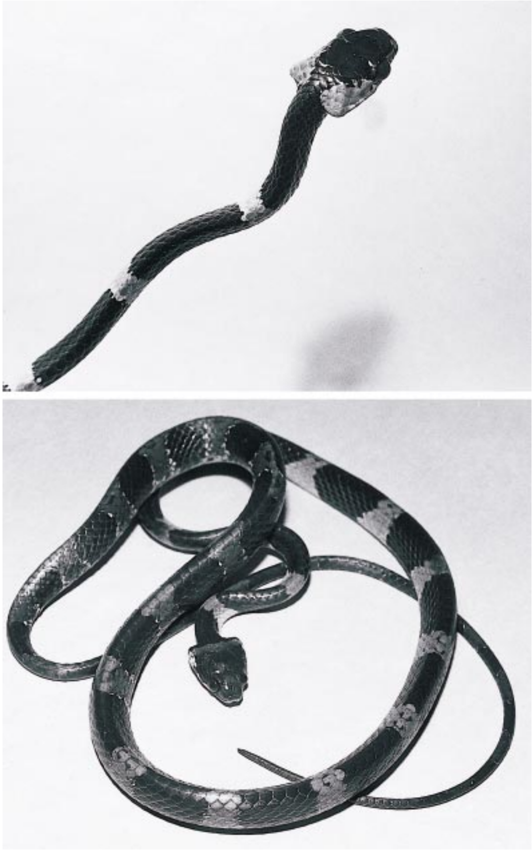

Fig. 16. Head widening (triangulation)—the temporary acquisition of triangular head shape by spreading the jaw articulations—a common defensive trait among the Dipsadini and some other snakes. This behavior can also be seen in figures 9 and 17–19. **Top:** *Dipsas viguieri* from lowland Madden Forest, central Panama (KU 110317). **Bottom:** *Dipsas temporalis* from cloud forest on ridge between Río Jaqué and Río Imamadó, 800–890 m, Darién, Panama (specimen one of KU 110294–110297).

possibility that adaptations for very different foods [toads vs. bird eggs] might influence the details of triangulation).

Head triangulation such as that shown in figure 16 is now known for the following species in three of the four genera of Dipsadini (we have no experience with *Tropidodipsas*); head triangulation sometimes was accompanied by a false striking position, sometimes by an attempt to flee. An asterisk (*) before the name denotes additional behaviors that are discussed in subsequent paragraphs.

**Dipsas albifrons*: Head triangulation is shown in photographs in Marques et al. (2001: 33, 125).

Dipsas catesbyi: Myers photographed a specimen (MZUSP 8730) showing head triangulation at Santa Cruz da Serra, in Rondônia, Brazil. Cadle observed several specimens from Pando, Bolivia, that also exhibited the behavior, and one of these also flattened most of its body.

**Dipsas indica*: Head triangulation occurs as part of more complex behavior (see below).

Dipsas oreas: Cadle photographed several individuals from two localities in northwestern Peru in which head triangulation was accompanied by raising the anterior part of the body and bringing the head back into an S-shaped loop (fig. 9); occasionally an additional bend was added to the loop. The posterior body was usually ‘‘anchored’’ with a loose coil. As in a *D. viguieri* described below, individuals would crawl while holding this position, and striking behavior could not be induced.

**Dipsas pavonina*: Head triangulation is part of a defensive display (see below).

Dipsas temporalis: This is a relatively common Panamanian species usually found active in low vegetation at night. Several were found by day in bromeliads on sides of trees about 1.2–3 m aboveground in a Darién cloud forest (Myers, 1969: fig. 11). They were tightly but variably coiled, apparently sized to fit available crevices in the bromeliads. They remained in their original passive coils when first picked up—except for spreading the rear angles of the jaws. When handled more roughly they attempted to escape while still keeping the triangulated head shape. When placed on a flat surface (fig. 16 bottom) they would respond to a light touch by ‘‘an abrupt reflexive jerk’’; the head would be raised from the ground when they then attempted to flee.

Dipsas viguieri: Head triangulation was noted in a specimen from lowland Madden Forest (fig. 16 top) and in another (KU 110316) from the upper Río Tuira in Darién, Panama. Myers' field notes for the last specimen stated that

> This snake has a threat display: the anterior part of the body is raised and the head brought back into a short S-shaped loop and the rear of the head expanded; the loop is held close and short, giving considerably more emphasis to what is otherwise a slight anterior. The snake would crawl [while holding] this position (including anterior part of body raised); it couldn't be induced to strike.

Dipsas sp: A distinctively colored, but still-unidentified specimen (AMNH 14685), from the continental divide north of El Copé, 600 m, Coclé, Panama, widened its head as its ‘‘only defense’’. A specimen (AMNH 115924) of *Leptodeira annulata* from the same locality also spread its ‘‘rear jaw articulations noticeably’’, as did a sympatric specimen of *Sibon argus*.

**Sibon argus*: The aforementioned specimen of *S. argus* (AMNH 115927) widened its head (fig. 17 top) as part of more complex behavior. See below.

**Sibon nebulatus*: At least some specimens of this common species exhibit head triangulation, sometimes with body coiling and head hiding. See below.

**Sibynomorphus mikanii*: Head triangulation was part of a more elaborate display of body inflation, coiling, and head hiding, as discussed below.

Sibynomorphus neuwiedi: Sazima (1992: 211, fig. 18f) considered *S. neuwiedi* a probable mimic of *Bothrops jararaca* in southeastern Brazil. His photograph shows a specimen with triangulated head ‘‘in cocked posture’’ (but not facing the camera). The defensive displays were said to ‘‘approach those described here for *Dipsas* [*indica*]’’, suggesting possibly a different pattern from that described below for a specimen of *Sibynomorphus mikanii*.

COMPLEX DEFENSIVE BEHAVIORS: HEAD TRIANGULATION, BODY INFLATION, BODY COILING, AND HEAD HIDING

In some species, head triangulation is accompanied by more elaborate body positioning.

Dipsas albifrons: Sazima (1992: 211) stated that Brazilian *D. albifrons* ‘‘from the Atlantic Forest mimics even better [than *D. indica*] the color pattern and defensive movements of *B[othrops] jararaca* (pers. obs.).’’ Marques et al. (2001) indicated by use of symbols that these defensive movements include head triangulation, erratic movements, and striking with the head (presumably with closed mouth). A photograph (Marques et al., 2001: 125) also shows a specimen in a tight, nearly flat, symmetrical coil (probably the end stage of a complex defensive display).

Dipsas indica: Sazima (1992: 211, fig. 18d) observed that in southeastern Brazil:

> When found moving slowly on the ground, an individual of *D. indica* may easily be mistaken for a young or slender *B[othrops] jararaca*. This resemblance is enhanced when the disturbed snake coils, expands its body, cocks and triangulates its head (Fig. 18d), and thrashes the forebody as if delivering false strikes.

Martins and Oliveira (1998: 104) noted that in Amazonia all specimens handled ‘‘thrashed the body, triangulated the head (sometimes exaggeratedly), expelled cloacal gland products, and did not bite.’’

Dipsas pavonina: In Amazonian Brazil, Martins and Oliveira (1998: 105) found that, when approached, *D. pavonina* ‘‘usually becomes immobile and may compress the body dorsoventrally (giving rise to a triangular cross section of the body), enlarge the head, and make subtle thrashes.’’

Sibon argus: Notes and photographs (fig. 17) were obtained for a specimen (AMNH 115927) from 600 m on the continental divide north of El Copé, Coclé, Panama. In addition to head triangulation, there was

> A ‘*coiled spring’ defensive behavior*: When bothered, it started coiling body [counterclockwise] from head (no coiling from tail-end first), forming a raised coil with head concealed in center [fig. 17 bottom]. During this time it also kept rear jaw articulations spread, but made no attempt to strike and kept mouth closed. The coil was maintained even when turned upside down.

Fig. 17. Defensive behavior of *Sibon argus* (AMNH 115927) from 600 m on the continental divide north of El Copé, Coclé, Panama. **Top:** The head is widened when mildly disturbed. **Bottom:** When further harassed, the snake coiled its body into a symmetrically raised spring, keeping its head hidden in the center.

Sibon nebulatus: Most field notes on this common species lack mention of defensive display, but the following brief observations on three specimens from the eastern end of the Isthmus of Panama, Darién, suggest that there is individual variability.

A specimen (AMNH 119391) from 640 m elevation on the Río Pucuro, at the south base of Cerro Tacarcuna, ‘‘when first caught thrashed about and soon coiled into an irregular ball but would not repeat this behavior the following morning’’. (Presence or absence of head triangulation was not noted.)

A specimen (KU 112475) from 540–560 m on the NE slope of Cerro Sapo exhibited more complex behavior:

> When picked up it coiled its body and spread the

Fig. 18. Defensive behavior of *Sibon nebulatus* from the Río, Jaqué, 1.5 km above Río Imamadó, 50 m, Darién, Panama (KU 112474). **Top:** An initial stage with posteriorly widened head. **Middle:** Passive coil with widened head exposed. **Bottom:** An alternative coil with head (still widened) concealed.

> angles of the jaws wide [triangulation]. When disturbed at other times [i.e., during the next day or two before preservation] it would spread the jaws and *either* attempt to hide its head under coils of body, *or* hold the neck in a striking S-shaped curve and sometimes whip the body into a coil.

Variable posturing similar but not quite identical to the above was observed and photographed for a third Darién specimen of *S. nebulatus* (KU 112474), collected at a lowland camp on the Río Jaqué (fig. 18):

> The angle of the jaws are spread widely and the snake assumes a stance with reared-back head in an S-loop much like a *Bothrops*. When further disturbed it forms a close coil, that is however not a symmetrical spring-shape nor done with the jerky movements of *Dipsas nicholsi*. It may hide its head within the coil [fig. 18 bottom] or hang it along side the coil—nose down—with the angles of the jaws still spread [fig. 18 middle]. It would not bite.

The earliest record concerning defensive behavior in any of the Dipsadini seems to be Mole's (1924: 249) comment on *Sibon nebulatus* in Trinidad, given here in full: ''When molested this snake draws back its head in a most threatening manner, and even strikes, *but with closed jaws.*'' We can confirm only the drawing back of the head,[15] since we have never noticed strike-feigning in this or any other species of Dipsadini (but see uncorroborated indication for *Dipsas albifrons* above).

Sibynomorphus mikanii: Observations were made on a specimen (AMNH 114579) lacking data, received at the American Museum in 1973, from the Bronx Zoo. When disturbed (fig. 19 top), this snake raised and widened its head while inflating its body, especially the neck, frequently curling its tail into a flat coil (tail kept dorsal side up). The body inflation resulted in lateral spreading, especially of the neck (fig. 19 top). After continued provoking the snake deflated its body, defecated, and coiled into an irregular ball, concealing its head within or under the ball (fig. 19 middle). There was no apparent consistency in this behavior; figure 19 (bottom) shows an alternative arrangement of the asymmetrical coiling. The snake would not strike or bite.

The lateral neck inflation seemingly approaches the dorsoventral flattening or hood

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[15] It is the essence of snakeness for a serpent to draw back its head for different reasons, including instinctive withdrawal from movement of a strange object such as a camera. Therefore, the reason for an S-shaped posture cannot always be ascertained from a photograph (e.g., the top view in fig. 1). In life, however, there is usually no mistaking the ''threatening manner'' mentioned by Mole.

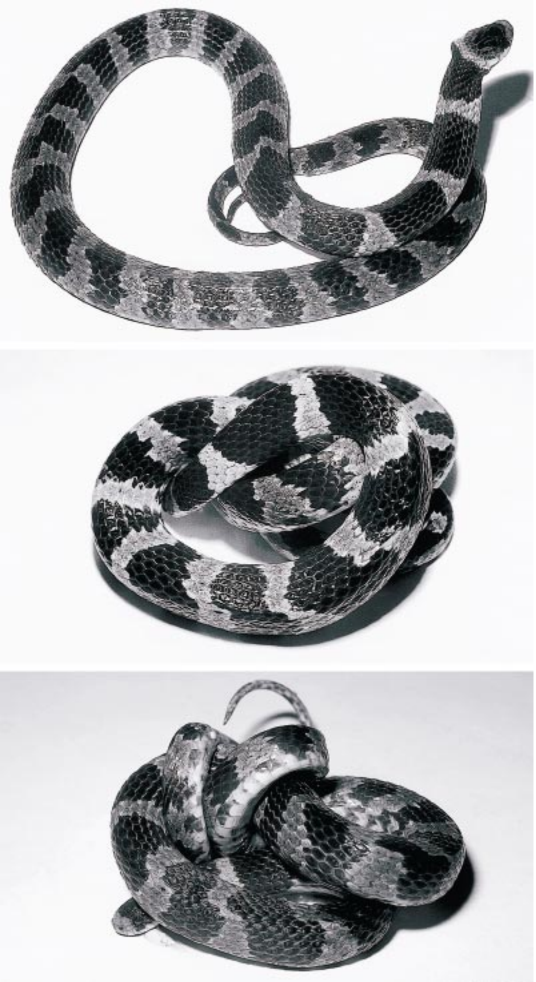

Fig. 19. Complex defensive behavior in *Sibynomorphus mikanii*. **Top:** The head is raised and widened, and the body is inflated, especially obvious at the widened neck (which approaches the dorsoventral hood formation of some snakes). **Middle:** After continued provoking, the snake has deflated the body and arranged itself into a loose asymmetrical coil or ball, with its head hidden. **Bottom:** An alternative coil at another time, with the head almost hidden.

formation of such xenodontine snakes as *Heterodon* and the Xenodontini. The body flattening and head positioning of the snake shown in the top part of figure 19 is also similar to behavior described for the dipsadine *Ninia sebae*, which also hides it head during subsequent parts of a complex display (Greene, 1975: 481). We have not seen neck or body flattening in *Sibon*, but dorsoventral body compression has been noted above for *Dipsas catesbyi* and *D. pavonina*.

STEREOTYPIC COILING BEHAVIOR OF *DIPSAS NICHOLSI*

Not one of the three specimens of *Dipsas nicholsi* collected alive by Myers in central Panama was noted as having displayed head triangulation, although such head widening was recorded for a specimen of *Dipsas viguieri* (fig. 16) found nearby and on the same night as one of the *nicholsi*. The aforesaid specimen of *D. nicholsi* (KU 110313) was kept alive for awhile in Myers' office at the Gorgas Memorial Laboratory in Panama City, where the following observations were made.

The snake was docile when held, but displayed consistent, jerky coiling behavior when it was placed on a flat surface and provoked by touching. There were essentially three stages from the stretched-out snake to the finished coil:

Stage 1: The anterior body was thrown or jerked into a counterclockwise coil, which is shown being initiated in the upper part of figure 20.

Stage 2: If touched again, the posterior body and tail were thrown into a separate coil, as shown in the lower part of figure 20.

Stage 3: When touched a third time, the snake drew itself into the final coil—in the shape of a raised spring, widest at the bottom and with the head always exposed on the top center—as shown in figure 21 (also see fig. 1). It would remain passive in this position for some time (not clocked) before uncoiling and trying to crawl away.

After several days in captivity, stage 2 above was omitted and a different behavioral sequence became evident. The snake would coil its anterior part (stage 1 above), then draw its rear half close to the forward coil, and, while maintaining the anterior coil, suddenly straighten out the rear part in a whipping motion, as though striking. If prodded more, it would go into the stage 3 coil—but it could then be induced to partly uncoil and repeat the whipping motions.

The complete stereotypic coiling sequence of *Dipsas nicholsi*—and its alternative rapid whipping motions while maintaining a for-

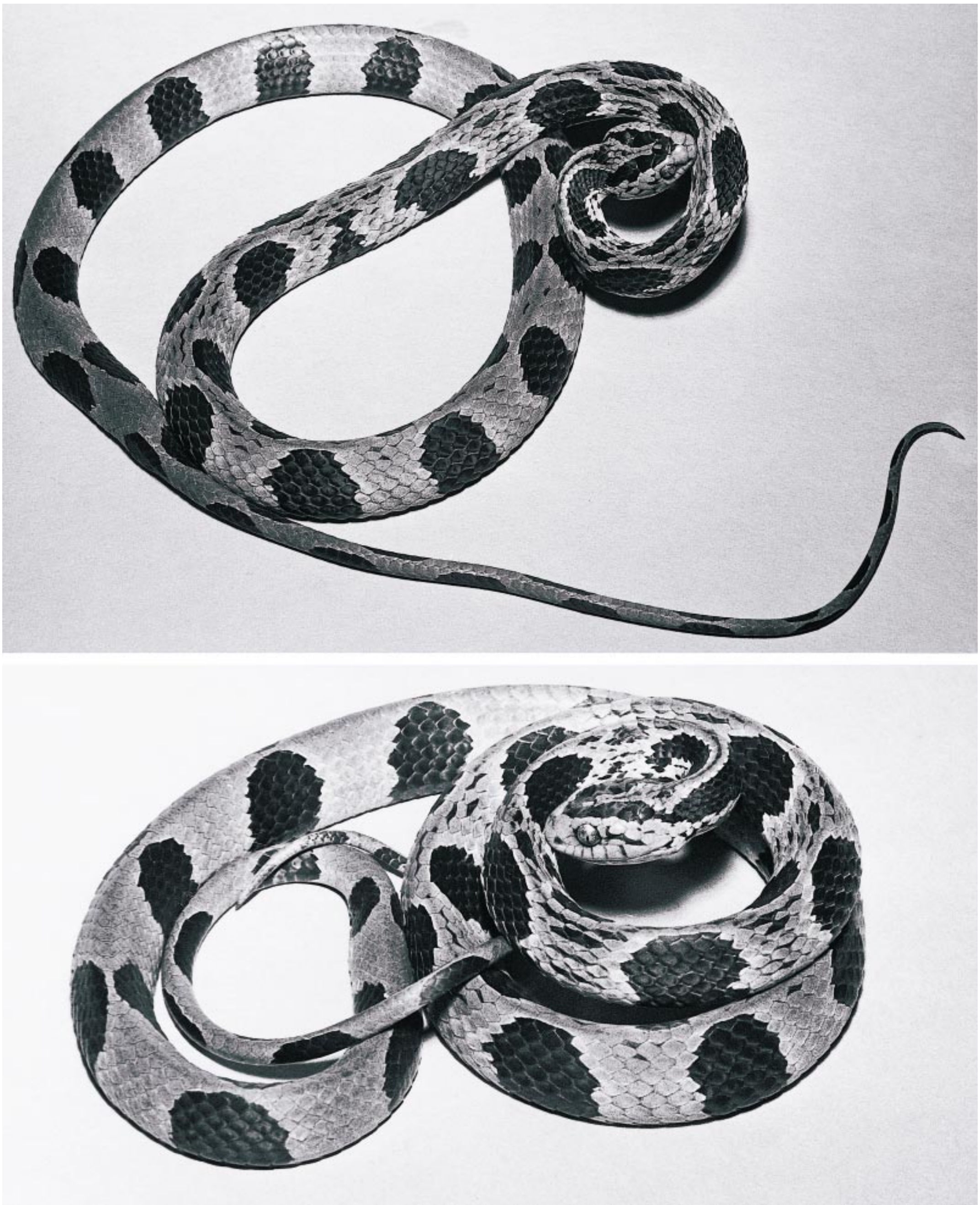

Fig. 20. Initial stages in the defensive coiling of *Dipsas nicholsi* (KU 110313). **Top:** Beginning formation of an anterior coil (stage 1). **Bottom:** Anterior coil complete, posterior coil initiated (stage 2). See text for behavioral sequence in which stage 2 above is replaced by abrupt whipping motions while retaining the forward coil. See figure 21 for stage 3, in which the snake has gathered itself into a single coil.

Fig. 21. The final stage of defensive behavior in *Dipsas nicholsi*—a raised coil narrowest at the top, with the head exposed. Over a period of several days, this snake consistently coiled in the same direction (counterclockwise following the coils from above). See figure 1 for another view of the same specimen.

ward coil—comprise the most elaborate dipsadinine defensive behavior seen by us. The apparent lack of head triangulation in *D. nicholsi* also seems notable, since it is widespread among other species.

It would be interesting to test a specimen of *Dipsas andiana*, conceivably a sister species, for possible behavior comparable to that of *D. nicholsi*. An incidental field note by John D. Lynch stated that one *D. andiana* (KU 132503) reacted to disturbance by ‘‘whipping into a rapid ‘S’ [and its] behavior matches its color similarity to *Bothrops*.’’ The ‘‘whipping’’ movements might be behavioral homologues in *D. andiana* and *D. nicholsi*, but there probably is considerable convergence in such behavior. For example, some colubrid snakes of the African genus *Prosymna* also

> produce a ‘‘watchspring’’ defensive display when disturbed . . . The snake forms a tight and symmetrical flat coil with the head in the centre, then violently uncoils and recoils, making it difficult to comprehend the size of the snake. (Broadley, 1980: 546–547)

The flatter coils and the rapid recoiling are obvious differences from *Dipsas nicholsi*. Direction of coiling might be a difference between *Prosymna* and the Dipsadini. *Prosymna* species appear (always?) to coil in a clockwise direction (see photograph and quote in Broadley, 1980: 546, pl. 4), whereas the above specimen of *Dipsas nicholsi* consistently coiled counterclockwise (following the coils starting at the neck from above), as also seen in photographs of *Sibon argus* and *S. nebulatus* (figs. 17–18) and *Dipsas albifrons* (Marques et al., 2001: 125).

In summary, the not uncommon serpent behavior of head triangulation is widespread but not universal among the Dipsadini, and is sometimes accompanied by drawing back the head in a (false) striking position. Inflating the body while widening and flattening, a less common serpent defensive behavior, has been seen in *Sibynomorphus* and in a few species of *Dipsas*. The occasional elements of jerky or whipping body motions are conceivably distracting to a predator and might be perceived as a snake striking out. Coiling behavior—very asymmetrical in *Sibynomorphus mikanii*, somewhat asymmetrical in *Sibon nebulatus*, but symmetrical in *Sibon argus, Dipsas albifrons* (Marques et al., 2001:

125), and especially in *Dipsas nicholsi*—with or without head-hiding, turns slender snakes into heavier, unpreylike masses.

Owing to coloration and such behavior as head cocking in false striking position, several species of dipsadinines might be mistaken for dangerous vipers, but mimicry seems not to be a driving evolutionary force in the group as a whole. Although members of the Dipsadini cannot inflict damage and doubtless are easy picking for most predators, surely all this defensive posturing cannot always be futile. At least some inexperienced and not overly hungry predators must sometimes be deterred, and any escape that permits a later, successful breeding will have been worth the effort.

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APPENDIX
MUSEUM ABBREVIATIONS AND LOCALITY RECORDS

AMNH	American Museum of Natural History, reptile collection, New York
ANSP	Academy of Natural Sciences of Philadelphia, Philadelphia
BMNH	The Natural History Museum, London
FMNH	Field Museum of Natural History, Chicago
KU	Museum of Natural History, University of Kansas, Lawrence
MCZ	Museum of Comparative Zoology, reptile collection, Harvard University, Cambridge
MUSM	Museo de Historia Natural de San Marcos, Lima
MVZ	Museum of Vertebrate Zoology, University of California, Berkeley
MZUSP	Museu de Zoologia, Universidade da São Paulo, São Paulo
USNM	National Museum of Natural History, Smithsonian Institution, Washington, DC

Dipsas andiana

ECUADOR: ''Quito, Ecuador'' [presumed error], BMNH 1946.1.20.12 (holotype). ''Guatemala'' [error, banana stowaway probably from Ecuador], AMNH 58204. No data [banana stowaway probably from Ecuador], AMNH 75050. ‘‘Colombia?: probably from NW Colombia’’ [presumed error, banana stowaway probably from Ecuador], AMNH 79013. *Bolívar:* Balzapamba (= Balsapamba) [01°47′S, 79°13′W], 800 m, AMNH 35949, 35955; KU 132503. [*Los Ríos*]: Babahoyo [01°49′S, 79°31′W], 5 m (Steindachner, 1902, as ‘‘*Leptognathus variegata*’’). *Pichincha:* Las Palmas, jct. Hwy. 30 and 28, 920 m [00°22′40″S, 78°55′49″W; Lynch and Duellman, 1997: 213], KU 132504. 4 km NE Dos Ríos, 1140 m, [00°19′S, 78°51′W; see Lynch and Duellman, 1997: 209], KU 164210–164211. Puerto Quito [00°08′N, 79°16′W; 280 m], MCZ 166543. Santo Domingo [de los Colorados] [00°15′S, 79°09′W; 600 m] (Despax, 1911).

Dipsas nicholsi

PANAMA: *Colón:* Agua Clara [about 9°11′N, 79°41′W; see footnote 10] (Dunn, 1940, 1949a). *Panamá:* ‘‘Chagres Villages’’ [between Juan Mina and Madden Dam; see footnote 9] (Dunn, 1940, 1949a [1 head not examined for present study = ANSP 21907]). Madden Forest Preserve, 60–150 m [09°06′N, 79°37′W], KU 110310–110314 (including cleared & stained, disarticulated, partially damaged skull of KU 110310). Madden Highway [probably in Madden Forest, see above], FMNH 217310. ‘‘Mid-basin of Chagres River and mouth of Pequeni River’’ [1933 type locality clarified herein as junction of Río Pequení with Río Boquerón (since 1936 = approximately mouth of Río Pequení near head of Madden Lake, about 20 km NNE Madden Dam), in upper drainage of the Río Chagres at 9°21′N, 79°33′W], MCZ 37884 (holotype, head and neck only).

Dipsas oreas

ECUADOR: ‘‘the elevated Valley of Quito’’,[16] ANSP 10115 (holotype). *Chimborazo:* Huigra to Río Chiguancay [02°13′S, 79°03′W], ANSP 18117, 18120, 18123.[17] *Chimborazo/Cañar:* [Río] Chanchan Valley [02°17′S, 79°24′W], MCZ 17083. *Guayas:* Guayaquil [02°10′S, 79°50′W; probably in error because this species does not otherwise seem to occur in the lowlands], USNM 60006, 62797–62802. *Loja:* Catamayo Valley, 9780 ft [2982 m; 03°59′S, 79°21′W], USNM 98923. *Pichincha:* 13 km E Veracruz (20 km NE Catacocha), 2250 m [03°58′S, 79°34′W], KU 142803.

PERU: *Piura:* Immediate vicinity of Ayabaca, approximately 2600 m [04°38′S, 79°43′W], MUSM-JEC 10347.[18] Toronche (town at base of Cerro Aypate), approximately 16 km (airline) SE Ayabaca, 1950 m [04°35′S, 79°32′W], MUSM 16750. 2 km W Porculla [Pass] [05°51′S, 79°31′W], MVZ 119330. *Cajamarca:* vicinity of Monteseco, Río Zaña,[19] 1450–1800 m [06°51′S, 79°06′W], FMNH 232570–232572, MUSM 16751–16752, 5530, 5532–5533, ANSP 31777–31781, 31783–31786.

Dipsas ‘‘oreas’’ elegans

ECUADOR: *Cotopaxi*: Corazón [01°08′S, 79°04′W], USNM 210938–210939. *Pichincha:* [on] way to Mindo [00°02′S, 78°48′W], USNM 210934. Road to Mindo [00°02′S, 78°48′W], USNM 210961. 2.9 km SW Tandayapa on Mindo road [00°01′S, 78°46′W], USNM 285957. Nanegal Grande [00°07′S, 78°46′W], USNM 210936. Below Pacto [00°09′S, 78°45′W], USNM 210937. Santo Domingo de los Colorados [00°15′S, 79°09′W; 600 m], USNM 210935.

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[16] The holotype of *Dipsas oreas*, collected by James Orton and acquired by Cope, is probably from southern Ecuador, as inferred from characters of the specimen. Orton’s locality ‘‘elevated valley of Quito’’ has often been interpreted narrowly as the valley immediately surrounding Quito (e.g., Peters, 1955). However, Orton (1871, 1875) clearly had a much broader region in mind, encompassing the entire Ecuadorian highlands from Colombia to Peru (Cadle, MS).

[17] Fowler (1913: 169) referred these specimens to *Leptognathus* (= *Dipsas*) *ellipsifera* (ANSP 18117) and *Leptognathus andianus* (ANSP 18120 [fig. 11 top], 18123). All three conform to our concept of *D. oreas* outlined in the text. They have extensive dark markings on the head, heavily pigmented venters, and distinct bands that are broader than the interspaces; none of these is characteristic of *D. andiana*. Head markings consist of thick, elongate, parallel blotches, which are characteristic of *D. oreas* (figs. 9–11, 12 bottom), but in ANSP 18120 the blotches are fused anteriorly (fig. 11 top), a rare condition in *D. oreas* that approaches the pattern in *D. andiana*. In such cases the fusion is incomplete, the mark is much thicker than in *D. andiana*, and it has more irregular edges.

[18] MUSM-JEC numbers refer to Cadle field numbers that are yet to be cataloged into the MUSM collection.

[19] This designation refers to a series of closely contiguous localities along an elevational transect in the upper Río Zaña valley on the western side of the Cordillera Occidental, in the vicinity of Hacienda Monteseco. Specific localities are available for individual specimens. See Cadle (1989, 1991) for discussion.

Dipsas ''oreas'' ellipsifera

ECUADOR: *[Imbabura]:* Ybarra [= Ibarra; 00°21′N, 78°07′W], MCZ 8431.

Dipsas variegata

GUYANA: Kartabo [6°23′N, 58°41′W], AMNH 21275, 81425, 98194. **TRINIDAD:** No specific locality: MCZ 80999, 100072, 100479–100480. Simla [10°41′N, 61°17′W], AMNH 137584. 0.5–3.1 mi S Simla-Quarry Road on Arima-Blanchisseuse Road,[20] FMNH 215834–215837, 217216, 217220. About 0.5 mi S Arima-Blanchisseuse Rd. on Arima Bypass, FMNH 219609. Arima Bypass, FMNH 217221. 1.1 m E Toco Rd. on Valencia Road, FMNH 217222. Bridge B1/4, Arima Blanchisseuse Rd., FMNH 217219. 2.8 mi N Simla-Quarry Rd. on Arima-Blanchisseuse Rd., FMNH 217215. Arima-Blanchisseuse Rd. at Asa Wright Nature Center driveway, FMNH 217217. Arima-Blanchisseuse Rd. 2 mile marker, FMNH 217218. Port- of-Spain [10°39′N, 61°31W], AMNH 73124. **VENEZUELA:** *Aragua:* Choroní, Rd. between cumbre and Maracay, 800 m [10°29′N, 67°36′W], MCZ 112410. Rancho Grande [10°25′N, 67°40′W], AMNH 81423, 98244, FMNH 204479. *Bolívar:* Río Yuruari, upper basin, 300 m [07°07′N, 62°37′W], AMNH 111075. Santa Elena de Uairén, 850 m [4°36′N, 61°05′W], AMNH 114769–114770.[21]

REFERENCES

Amaral, Alfranio do. 1929. Estudos sobre ophidios neotropicos XVIII. Lista remissiva dos ophidios da Região Neotropica. Memorias do Instituto Butantan 4: 127–128 + i–viii + 129–271. [Published in 1930 fide Peters and Orejas-Miranda, 1970: vi]

Auth, David L. 1994. Checklist and bibliography of the amphibians and reptiles of Panama. Smithsonian Herpetological Information Service 98: 1–59. [Commentary by Solís et al., 1996]

Barbour, Thomas, and Gladwyn Kingsley Noble. 1920. Amphibians and reptiles from southern Peru collected by the Peruvian expedition of 1914–1915 under the auspices of Yale University and the National Geographic Society. Proceedings of the United States National Museum 58: 609–620.

Beebe, William. 1946. Field notes on the snakes of Kartabo, British Guiana, and Caripito, Venezuela. Zoologica (New York) 31: 11–52.

Boulenger, George Albert. 1896. Catalogue of the snakes in the British Museum (Natural History). Vol. 3. London: British Museum (Natural History), xiv + 727 pp. + 25 pls.

Broadley, Donald G. 1980. A revision of the African snake genus *Prosymna* Gray (Colubridae). Occasional Papers of the National Museums and Monuments, Series B, Natural Sciences 6(7): 481–556.

Brumfield, Robb T., and Angelo P. Capparella. 1996. Historical diversification of birds in northwestern South America: a molecular perspective on the role of vicariant events. Evolution 50(4): 1607–1624.

Cadle, John E. 1989. A new species of *Coniophanes* (Serpentes: Colubridae) from northwestern Peru. Herpetologica 45(4): 411–424.

Cadle, John E. 1991. Systematics of lizards of the genus *Stenocercus* (Iguania: Tropiduridae) from northern Peru: new species and comments on relationships and distribution patterns. Proceedings of the Academy of Natural Sciences of Philadelphia 143: 1–96.

Cadle, John E. 1996. Snakes of the genus *Liopholidophis* (Colubridae) from eastern Madagascar: new species, revisionary notes, and an estimate of phylogeny. Bulletin of the Museum of Comparative Zoology 154(5): 369–464.

Cadle, John E. 1999. The dentition, systematics, and phylogeny of *Pseudoxyrhopus* and related genera from Madagascar (Serpentes: Colubridae), with descriptions of a new species and a new genus. Bulletin of the Museum of Comparative Zoology 155(8): 381–443.

Cadle, John E. [MS] Systematics of the snakes *Dipsas oreas* and *Sibynomorphus petersi* (Colubridae) in Peru, with other herpetological records and notes from the northern Peruvian Andes.

Carrillo de Espinoza, Nelly, and Javier Icochea. 1995. Lista taxonómica preliminar de los reptiles vivientes del Perú. Publicaciones del Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Serie A Zoología 49: 1–27.

Chippaux, Jean-Phillipe. 1986. Les Serpents de la Guyane Française. Paris: Éditions de l'ORSTOM, 165 pp.

[Clark, Herbert C.] 1937. Progress report on snake census (1929–1936). *In* Annual report of the

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[20] Individual specimens of these series are accompanied by a specific mile indication. All the FMNH specimens from Trinidad that we examined are from within a small area at approximately 10°41′N, 61°00′W.

[21] Specimens obtained in 1974 as a gift from S.J. Gorzula and originally cataloged as *Dipsas* sp. This locality suggests that *Dipsas variegata* probably also occurs on the Brazilian side of the border, in northern Roraima. For locality documentation, see Gorzula and Señaris (1999: 178, 252 [locality U-095]), who treat the same specimens under the name ''*Sibon nebulata*''.

Gorgas Memorial Laboratory, 1936 (75th Congress, 1st session, House Document 46): 15–18.

Clark, Herbert C. 1942. Venomous snakes. Some Central American records. Incidence of snake bite accidents. The American Journal of Tropical Medicine 22(1): 37–49.

Cope, Edward Drinker. 1868. An examination of the reptilia and batrachia obtained by the Orton expedition to Equador and the upper Amazon, with notes on other species. Proceedings of the Academy of Natural Sciences of Philadelphia 20: 96–140.

Cunha, Osvaldo Rodrigues da, and Francisco Paiva do Nascimento. 1993. Ofídios da Amazônia. As cobras da região leste do Pará. Boletim do Museu Paraense Emílio Goeldi, Série Zoologia 9(1): 1–191. (2nd ed. of 1978 ‘‘Ofídios da Amazônia X [etc.]’’, Museu Paraense Emílio Goeldi, Publicações Avulsas 31: 1–218 + foldout map, 41 pls.)

Daniel, Hermano. 1949. Las serpientes en Colombia. Revista de la Facultad Nacional de Agronomía de Medellín 10(36): 301–333.

Despax, Raymond. 1911. Reptiles et batraciens de l'Équateur recueillis par M. le Dr. Rivet. *In* Ministère de l'Instruction Publique (editor), Mission du Service Géographique de l'Armée pour la mesure d'un arc de méridien équatorial en Amérique du Sud sous le contrôle scientifique de l'Académie des Sciences, 1899–1906, tome 9 (Zoologie), fascicule 2 (Reptiles-Poissons-Batraciens): 17–44 + pls. 1–3. Paris: Gauthier-Villars.

Dixon, James R. 1979. Origin and distribution of reptiles in lowland tropical rainforests of South America. *In* W.E. Duellman (editor), The South American herpetofauna: its origin, evolution, and dispersal: 217–240. Lawrence: Museum of Natural History, University of Kansas.

Dodson, Cal H., and Alwyn H. Gentry. 1991. Biological extinction in western Ecuador. Annals of the Missouri Botanical Garden 78(2): 273–295.

Duellman, William E. 1999. Distribution patterns of amphibians in South America. *In* W.E. Duellman (editor), Patterns of distribution of amphibians: a global perspective: 255–328. Baltimore, MD: Johns Hopkins University Press.

Duméril, André Marie Constant, Gabriel Bibron, and Auguste Duméril. 1854. Erpétologie générale ou histoire naturelle complète des reptiles, vol. 7. Paris: Librairie Encyclopédique de Roret, première partie, pp. vii + 4 + xvi + 780; deuxième partie, pp. xii + 780–1536.

Dunn, Emmett Reid. 1933. A new snake from Panama. Copeia 1933(4): 193–194.

Dunn, Emmett Reid. 1940. New and noteworthy herpetological material from Panama. Proceedings of the Academy of Natural Sciences of Philadelphia 92: 105–122.

Dunn, Emmett Reid. 1942. New or noteworthy snakes from Panama. Notulae Naturae of the Academy of Natural Sciences of Philadelphia 108: 1–8.

Dunn, Emmett Reid. 1949a. Relative abundance of some Panamanian snakes. Ecology 30(1): 39–57.

Dunn, Emmett Reid. 1949b. The application of Fisher's formula to collections of Panamanian snakes. Ecology 30(4): 533–536.

Fowler, Henry W. 1913. Amphibians and reptiles from Ecuador, Venezuela, and Yucatan. Proceedings of the Academy of Natural Sciences of Philadelphia 65: 153–173.

Gasc, Jean-Pierre, and Miguel T. Rodrigues. 1980. Liste préliminaire des serpents de la Guyane Française. Bulletin du Muséum National d'Histoire Naturelle, Paris, 4e série, vol. 2, section A, no. 2: 559–598.

Gentry, Alwyn H. 1982. Phytogeographic patterns as evidence for a Chocó refuge. *In* G.T. Prance (editor), Biological diversification in the tropics: 112–136. New York: Columbia University Press.

Gorzula, Stefan, and J. Celsa Señaris. 1999. Contribution to the herpetofauna of the Venezuelan Guayana I. A data base. Scientia Guaianae 8: xviii + 268 pp. + 129 color photos [in 32 end pls.], maps 2–5 in pocket. [‘‘1998’’ on cover, but explicitly January 20, 1999 on reverse of inside title page]

Greene, Harry W. 1975. Ecological observations on the red coffee snake, *Ninia sebae*, in southern Veracruz, Mexico. American Midland Naturalist 93(2): 478–484.

Greene, Harry W. 1988. Antipredator mechanisms in reptiles. *In* C. Gans and R.B. Huey (editors). Biology of the Reptilia, vol. 16B, Defense and life history: 1–152. New York: Alan R. Liss.

Hoogmoed, Marinus S. 1979. The herpetofauna of the Guianan region. *In* W.E. Duellman (editor), The South American herpetofauna: its origin, evolution, and dispersal: 241–280. Lawrence: Museum of Natural History, University of Kansas.

Ibáñez D., Roberto, and F.A. Solís. ‘‘1991’’ [1993]. Las serpientes de Panamá: lista de especies, comentarios taxonómicos y bibliografia. Scientia (Panamá) 6(2): 27–52.

Kofron, Christopher P. 1982a. The identities of some dipsadine snakes: *Dipsas elegans, D. ellipsifera* and *Leptognathus andrei*. Copeia 1982(1): 46–51.

Kofron, Christopher P. 1982b. A review of the

Mexican snail-eating snakes, *Dipsas brevifacies* and *Dipsas gaigeae*. Journal of Herpetology 16(3): 270–286.

Kofron, Christopher P. 1985a. Review of the Central American colubrid snakes, *Sibon fischeri* and *S. carri*. Copeia 1985(1): 164–174.

Kofron, Christopher P. 1985b. Systematics of the Neotropical gastropod-eating snake genera, *Tropidodipsas* and *Sibon*. Journal of Herpetology 19(1): 84–92.

Kofron, Christopher P. 1987. Systematics of Neotropical gastropod-eating snakes: the *fasciata* group of the genus *Sibon*. Journal of Herpetology 21(3): 210–225.

Kofron, Christopher P. 1988. Systematics of Neotropical gastropod-eating snakes: the *sartorii* group of the genus *Sibon*. Amphibia-Reptilia 9: 145–168.

Köhler, Gunther. 2001. Reptilien und Amphibien Mittelamerikas Band 2: Schlangen. Offenbach: Herpeton, Verlag Elke Köhler, 174 pp.

Lancini, Abdem R. 1979. Serpientes de Venezuela. Caracas: Ernesto Armitano, 262 pp.

Lynch, John D. 1979. The amphibians of the lowland tropical forests. *In* W.E. Duellman (editor), The South American herpetofauna: its origin, evolution, and dispersal: 189–216. Lawrence: Museum of Natural History, University of Kansas.

Lynch, John D., and William E. Duellman. 1997. Frogs of the genus *Eleutherodactylus* (Leptodactylidae) in western Ecuador: systematics, ecology, and biogeography. University of Kansas Museum of Natural History Special Publication 23: iv + 1–236.

Lynch, John D., and Charles W. Myers. 1983. Frogs of the *fitzingeri* group of *Eleutherodactylus* in eastern Panama and Chocoan South America (Leptodactylidae). Bulletin of the American Museum of Natural History 175(5): 481–568.

Markezich, Allan L. 2002. New distribution records of reptiles from western Venezuela. Herpetological Review 33(1): 69–74.

Marques, Otavio A.V., André Eterovic, and Ivan Sazima. 2001. Serpentes da Mata Atlântica. Guia ilustrado para a Serra do Mar. São Paulo: Holos Editora, Ribeirão Preto, 184 pp.

Martins, Marcio, and M. Ermelinda Oliveira. 1998. Natural history of snakes in forests of the Manaus region, central Amazonia, Brazil. Herpetological Natural History 6(2): 78–150 + 113 pls. (color photos) on 8 leaves.

Maxson, Linda R., and Charles W. Myers. 1985. Albumin evolution in tropical poison frogs (Dendrobatidae): a preliminary report. Biotropica 17(1): 50–56.

Miyata, Kenneth. 1981. A checklist of the amphibians and reptiles of Ecuador. Smithsonian Herpetological Information Service 54: 1–70.

Mole, R.R. 1924. The Trinidad snakes. Proceedings of the Zoological Society of London 1924(1): 235–278 + 10 pls.

Müller, Lorenz. 1923. Neue oder seltene Reptilien und Batrachier der Zoologischen Sammlung des bayrischen Staates. Zoologischer Anzeiger 57(7/8): 145–156.

Murphy, John C. 1997. Amphibians and reptiles of Trinidad and Tobago. Malabar, FL: Krieger Publishing Company, xiii + 245 pp. + 171 pls. (color photos) on 12 leaves.

Myers, Charles W. 1969. The ecological geography of cloud forest in Panama. American Museum Novitates 2396: 1–52.

Myers, Charles W. 1974. The systematics of *Rhadinaea* (Colubridae), a genus of New World snakes. Bulletin of the American Museum of Natural History 153(1): 1–262.

Myers, Charles W. 2003. Rare snakes—five new species from eastern Panama: reviews of northern *Atractus* and southern *Geophis* (Colubridae: Dipsadinae). American Museum Novitates 3391: 1–47.

Myers, Charles W., and A. Stanley Rand. 1969. Checklist of amphibians and reptiles of Barro Colorado Island, Panama, with comments on faunal change and sampling. Smithsonian Contributions to Zoology 10: 1–11.

Myers, Charles W., John W. Daly, and Victor Martínez. 1984. An arboreal poison frog (*Dendrobates*) from western Panama. American Museum Novitates 2783: 1–20.

Nicéforo María, Hermano. 1942. Los ofidios de Colombia. Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales 5(17): 84–101.

Oliver, James A. 1955. Banana bonanza. Animal Kingdom 58(3): 66–71.

Orcés, Gustavo, and Ana Almendáriz. 1987. Sistemática y distribución de las serpientes dipsadinae del grupo *oreas*. Politécnica 12(4): 135–144.

Orton, James A. 1871. Contributions to the natural history of the valley of Quito.—no. 1. American Naturalist 5(10): 619–626.

Orton, James A. 1875. The Andes and the Amazon; or, across the continent of South America, 3rd ed. New York: Harper, frontisp., 645 pp. + 2 foldout maps.

Parker, Hampton Wildman. 1926. Description of a new snake from Trinidad. Annals and Magazine of Natural History, ser. 9, 18: 205–207.

Paynter, Raymond A., Jr. 1993. Ornithological gazetteer of Ecuador, 2nd ed. Cambridge, MA: Museum of Comparative Zoology, xi + 247 pp.

Paynter, Raymond A., Jr. 1997. Ornithological gazetteer of Colombia. Cambridge, MA: Museum of Comparative Zoology, ix + 537 pp.

Pérez-Santos, Carlos, and Ana G. Moreno. 1988. Ofidios de Colombia. Museo Regionale di Scienze Naturali (Turin), Monografia 6, 517 pp.

Pérez-Santos, Carlos, and Ana G. Moreno. 1991. Serpientes de Ecuador. Museo Regionale di Scienze Naturali (Turin), Monografia 11, 538 pp.

Pérez-Santos, Carlos, Ana G. Moreno, and Angela Gearhart. 1993. Checklist of the snakes of Panama. Revista Española de Herpetologia 7: 113–122. [Commentary by Solís et al., 1996]

Pesantes, Omar S. 1994. A method for preparing the hemipenis of preserved snakes. Journal of Herpetology 28(1): 93–95.

Peters, James A. 1955. Herpetological type localities in Ecuador. Revista Ecuatoriana de Entomología y Parasitología 2: 335–352.

Peters, James A. 1960a. The snakes of the subfamily Dipsadinae. Miscellaneous Publications, Museum of Zoology University of Michigan 114: 1–224.

Peters, James A. 1960b. The snakes of Ecuador, a checklist and key. Bulletin of the Museum of Comparative Zoology 122: 489–541.

Peters, James A. 1964. Supplemental notes on snakes of the subfamily Dipsadinae (Reptilia: Colubridae). Beiträge zur Neotropischen Fauna 4: 45–50.

Peters, James A., and Braulio Orejas-Miranda. 1970. Catalogue of the Neotropical Squamata Part I. Snakes. U.S. National Museum Bulletin 297: viii, 1–347.

Porto, Marcovan, and Ronaldo Fernandes. 1996. Variation and natural history of the snail-eating snake *Dipsas neivai* (Colubridae: Xenodontinae). Journal of Herpetology 30(2): 269–271.

Rand, A. Stanley, and Charles W. Myers. 1990. The herpetofauna of Barro Colorado Island, Panama: an ecological summary. *In* A.H. Gentry (editor), Four Neotropical rainforests: 386–409. New Haven: Yale University Press.

Rossman, Douglas A., and David A. Kizirian. 1993. Variation in the Peruvian dipsadine snakes *Sibynomorphus oneilli* and *S. vagus*. Journal of Herpetology 27(1): 87–90.

Roze, Janis A. 1966. La taxonomía y zoogeografía de los ofidios en Venezuela. Caracas: Universidad Central de Venezuela, 362 pp.

Savage, Jay M., and Roy W. McDiarmid. 1992. Rediscovery of the Central American colubrid snake, *Sibon argus*, with comments on related species from the region. Copeia 1992(2): 421–432.

Sazima, Ivan. 1992. Natural history of the jararaca pitviper, *Bothrops jararaca*, in southeastern Brazil. *In* J.A. Campbell and E.D. Brodie, Jr. (editors), Biology of the pitvipers: 199–216. Tyler, Texas: Selva.

Smith, Hobart M. 1958. Handlist of the snakes of Panama. Herpetologica 14(4): 222–224.

Sokal, Robert R., and F. James Rohlf. 1981. Biometry, the principles and practice of statistics in biological research, 2nd ed. New York: W.H. Freeman, xviii + 859 pp.

Solís, Frank A., Roberto Ibáñez D., and César A. Jaramillo. 1996. Estableciendo una uniformidad sobre las especies de serpientes presentes en Panamá. Revista de Biología Tropical 44(1): 19–22.

Steindachner, Franz. 1902. Herpetologische und ichthyologische Ergebnisse einer Reise nach Südamerika mit einer Einleitung von Therese Prinzessin von Bayern. Denkschriften der Kaiserlichen Akademie der Wissenschaften in Wien (Mathematisch-naturwissenschaftliche Klasse) 72: 89–148 + pls. 1–5.

Stephens, L., and Melvin A. Traylor. 1983. Ornithological gazetteer of Peru. Cambridge, MA: Museum of Comparative Zoology, vi + 271 pp.

Test, Frederick H., Owen J. Sexton, and Harold Heatwole. 1966. Reptiles of Rancho Grande and vicinity, Estado Aragua, Venezuela. Miscellaneous Publications, Museum of Zoology University of Michigan 128: 1–61.

Vari, Richard P. 1988. The Curimatidae, a lowland Neotropical fish family (Pisces: Characiformes); distribution, endemism, and phylogenetic biogeography. *In* P.E. Vanzolini and W.R. Heyer (editors), Proceedings of a workshop on Neotropical distribution patterns held 12–16 January 1987: 343–377. Rio de Janeiro: Academia Brasileira de Ciências.

Villa, Jaime, Larry David Wilson, and Jerry D. Johnson. 1988. Middle American herpetology: a bibliographic checklist. Columbia: University of Missouri Press, xxxvi + 131 pp.

Wallach, Van. 1995. Revalidation of the genus *Tropidodipsas* Günther, with notes on the Dipsadini and Nothopsini (Serpentes: Colubridae). Journal of Herpetology 29(3): 476–481.

Werner, Franz. 1923. Übersicht der Gattungen und Arten der Schlangen der Familie Colubridae. Archiv für Naturgeschichte (Berlin) 8: 138–199.

Wright, Willard H. 1970. 40 years of tropical medicine research. A history of the Gorgas Memorial Institute of Tropical and Preventive Medicine, Inc. and the Gorgas Memorial Laboratory. Washington, D.C.: Gorgas Memorial Institute, xii + 426 pp., frontisp., 18 pls.

Young, B.A., J. Lalor, and J. Solomon. 1999. The comparative biomechanics of an ophidian defensive behaviour: head triangulation in hognose snake (*Heterodon*) and an egg-eating snake (*Dasypeltis*). Journal of Zoology (London) 248(2): 169–177.

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