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On the Uniquely Fragmented Distribution of a Rare Panamanian Snake, *Dipsas nicholsi* (Colubridae: Dipsadinae)

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ABSTRACT

Dipsas nicholsi has been known from a handful of specimens collected during the final three-quarters of the 20th century. All came from a restricted lowland area (60–150 m) in central Panama, in the upper drainage of the Río Chagres.

A recently identified specimen, the first known juvenile and only the second female, was found in 1997 in the Darién highlands (Serranía de Jingurudó, 855 m) of extreme eastern Panama, about 250 km from the clustered lowland localities in central Panama. It differs from central Panamanian specimens in some scutellation characters and especially in details of dorsal color pattern. The species' rarity makes it impossible to determine whether differences reflect geographic isolation or unknown aspects of ontogenetic, sexual, or individual variation.

Distributional disruptions are commonplace in the Panamanian herpetofauna, although difficult to verify in the case of rare species. However, in the absence of a present-day habitat corridor, the Darién specimen of *Dipsas nicholsi* clearly represents a population widely separated and discontinuous from the one in central Panama. The Serranía de Jingurudó population, apparently a distributional relict, slightly closes the wide geographic gap between *Dipsas nicholsi* and its likely sister species, *D. andiana,* of western Ecuador.

Commentary is provided on the cartographic names of several eastern Panamanian highlands. The Serranía de Jingurudó takes its name from a river, as shown by the Emberá suffix *-dó*. This highland was known for nearly half a century as the Sierra or Serranía de "Jungurudó", probably a confused combination of a still-older map name (Sierra de "Jungururo") and the Río Jingurudó.

RESUMEN

Dipsas nicholsi ha sido conocida a partir de unos pocos especímenes recolectados durante los tres-cuartos finales del siglo XX. Todos provinieron de una área restringida en las tierras bajas (60–150 m) de Panamá central, en la cuenca superior del Río Chagres.

Un espécimen identificado recientemente, el primer juvenil conocido y sólo la segunda hembra, fue encontrado en 1997 en las tierras altas de Darién (Serranía de Jingurudó, 855 m) del extremo este de Panamá, aproximadamente a 250 km de distancia de las localidades agrupadas en Panamá central. Éste difiere de los especímenes de Panamá central en algunas características de la escutelación y, especialmente, en detalles del patrón dorsal de color. La rareza de la especie hace imposible juzgar si estas diferencias reflejan aislamiento geográfico o aspectos desconocidos de variación ontogenética, sexual, o individual.

Discontinuidades en la distribución son comunes en la herpetofauna panameña; no obstante, a menudo son difíciles de verificar, especialmente en el caso de las especies raras. Sin embargo, en ausencia de un corredor de hábitat actual, el espécimen de Darién de *Dipsas nicholsi* representa claramente a una población separada ampliamente y discontinua de la conocida en Panamá central. La población de la Serranía de Jingurudó, aparentemente un relicto en la distribución, cierra levemente la amplia brecha geográfica entre *Dipsas nicholsi* y su probable especie hermana, *D. andiana*, del oeste de Ecuador.

Se proveen comentarios sobre nombres cartográficos de varios lugares de tierras altas del este de Panamá. La Serranía de Jingurudó se le nombra por un río, como lo muestra el sufijo Emberá *-dó*. Esta serranía fue conocida por cerca de la mitad de un siglo como Sierra o Serranía de "Jungurudó", probablemente debido a una combinación confusa de un nombre en un mapa aún más antiguo (Sierra de "Jungururo") y el Río Jingurudó.

INTRODUCTION

The Isthmus of Panama supports a rich snake fauna, with a current total of about 132 named species.[4] This fauna includes species whose ranges traverse the isthmus, as well as southern and northern snakes whose respective distributions (wide-ranging or not) terminate either in eastern or western Panama. About 12% of the total fauna (16 named

[4]This number is based on Ibáñez et al. ("1995a" [1997]) and Solís et al. (1996), with the inclusion of *Leptophis nebulosus* (see Jaramillo and Ibáñez, 2003) and the several species recently described by Myers (2003), as well as two species not yet formally documented. The last include *Leptodeira rubricata* (USNM 166170, determined by Myers, unpubl.) and *Trimetopon pliolepis* (Myers, MS.)—the sources for Savage's (2002) mention of Panama in the ranges. Still unnamed species are not counted.

species) appears endemic to the isthmus. The endemic snakes are either relatively or absolutely rare in collections, with half a dozen species known to science from only one or two specimens. The majority of the endemics are members of the large Neotropical clade Dipsadinae, which is the predominant component of the Central American snake fauna (Cadle, 1984; Zaher, 1999).

One of the "least rare" of the endemics is *Dipsas nicholsi* (Dunn), whose taxonomic status, endemicity, and behavior were recently documented by Cadle and Myers (2003). This snake was discovered in lowland central Panama in 1933 and, up until the 1960s, was known only from about five heads (including the holotype). All this early material was obtained by the 1929–1953 Panama Snake Census, which was conducted by H.C. Clark, director of the old Gorgas Memorial Laboratory.[5] Nine whole specimens were obtained subsequently.[6] Cadle and Myers (2003: 15) described the distribution in this way:

> *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 … 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.

Although small ranges are not uncommon in the Dipsadinae (Cadle, 1985), *Dipsas nicholsi* appeared to have an exceptionally confined distribution in a moderately well-known region of lowland forest. Some confidence in the limits of this distribution was imparted by the absence of *D. nicholsi* on nearby Barro Colorado Island, which has one of the world's best-known tropical herpetofaunas (Myers and Rand, 1969; Rand and Myers, 1990), and equally by the continued lack of specimens from other lowland areas around the Panama Canal (Ibáñez et al., "1995a" [1997]). Also noteworthy, albeit less convincing, was the continued failure by collectors (see especially Ibáñez et al., "1994" [1995]) to find *D. nicholsi* in the low uplands around the upper parts of the Río Chagres drainage.

The above picture has now been expanded (see map 1), owing to the collection by Ibáñez of a single juvenile *Dipsas* from a remote locality in the Darién uplands, approximately 250 km SE of the known localities of *D. nicholsi* in central Panama. Despite some differences from previous material, we conclude that the specimen is referable to *D. nicholsi*.

We here document this conclusion through comparisons of the new specimen with central Panamanian *Dipsas nicholsi* and with the only similar species, *Dipsas andiana* of Ecuador, followed by comments on biogeographic significance of the new record.

Consideration of the New Specimen

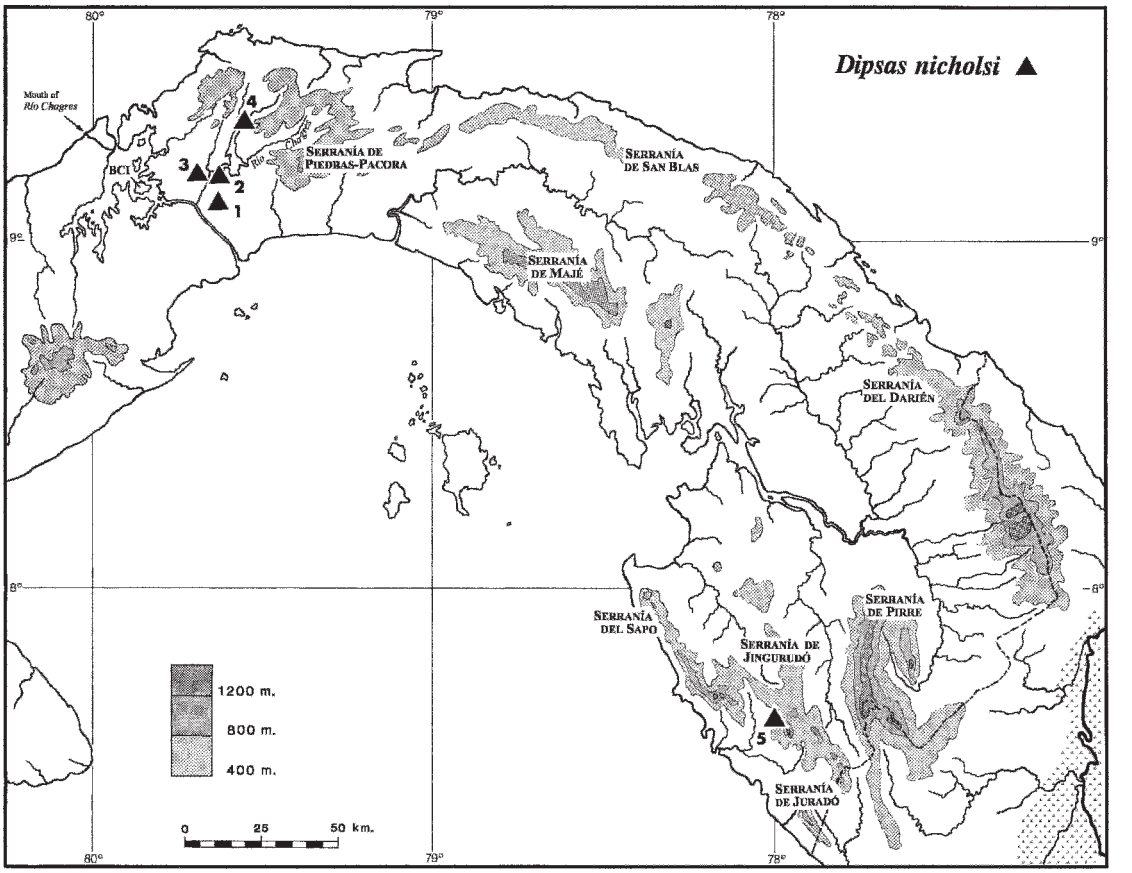
The specimen (fig. 1) was collected on August 13, 1997 by Ibáñez, in the Serranía de Jingurudó, Province of Darién, eastern Panama, at an elevation of 855 m (7°38′N, 78°01′W). See locality no. 5 in map 1. It is cataloged as MVUP-1856 in the Museo de Vertebrados de la Universidad de Panamá (originally CH-4660, Círculo Herpetológico de Panamá).

Standard Taxonomic Data: Descriptive data for MVUP-1856 are presented here. As

[5]The history and the significance of Clark's Panama Snake Census were discussed by Myers (2003: 4–5). The related discovery of *Dipsas nicholsi* was given in detail by Cadle and Myers (2003: 15–18).

[6]The count of nine whole specimens includes five males and one female studied by Cadle and Myers (2003), and three additional males subsequently examined by Ibáñez at the Smithsonian Tropical Research Institute in Panama. The last three were collected by A. Stanley Rand, one in 1969 (Madden Forest Preserve) and two in 1987 (5 km SE Gamboa; 10 km E Gamboa). The localities (approximated by locality no. 1 in map 1) fall within the southern part of the area discussed in Cadle and Myers (2003: 15–18).

The additional specimens (STRI 0301–0303) are adult males, with ventral/subcaudal counts of 198/104, 198/93, and 206/110, respectively, and snout-vent/total lengths of 658/882 mm, 694/943 mm, and 610/829 mm, respectively. Ventrals fall within the previously known range, but the maximum subcaudal count is increased from 98 to 110. Two specimens exceed the previous known total length of 861 mm for males (the only known female measured 798 mm total length). Color patterns closely resemble specimens previously reported from central Panama.



Map 1. Eastern Panama, showing locality records for *Dipsas nicholsi* (Dunn). Specimen localities: **(1)** Madden Forest; **(2)** "Chagres Villages"; **(3)** Agua Clara; **(4)** mouth of Río Pequení near head of Madden Lake. **(5)** Serranía de Jingurudó.

Localities **1–4** are in lowland wet forest in the upper drainage of the Río Chagres, which ultimately discharges into the Caribbean. *Dipsas nicholsi* does not occur in the well-known fauna of Barro Colorado Island (BCI), a former hilltop in Gatun Lake, which was formed by damming of the Río Chagres during construction of the Panama Canal. Locality **5** is a montane cloud forest site in the Pacific drainage of Darién Province.

will be apparent shortly, most characters ally the specimen with the rare *Dipsas nicholsi* as currently understood. In the following description, the variational ranges for characters of central Panamanian *D. nicholsi* are given parenthetically after the characteristics of MVUP-1856. Character data for six central Panamanian *D. nicholsi* (5♂, 1♀) are taken from Cadle and Myers (2003), with inclusion of segmental counts for three additional males from the same population (data in footnote 6). For a few characters of exceptionally high variability (e.g., temporal and supralabial patterns) only the characteristics of MVUP-1856 are given, but the same character states nonetheless occur also in the previously studied sample of *D. nicholsi*. Bilateral counts are separated by a solidus (left/right).

The specimen is a juvenile female, with a total length of 350 mm, including 76 mm tail length. Tail as a percentage of total length = 22% (1♀ 24%, 6♂ 25–26%). Maxillary teeth 11 (11–14). Body strongly compressed. Vertebral row nearly twice the width of the paravertebral rows. Dorsals in 15-15-15 rows. Preventrals 2 + 206 ventrals (198–208♂, 200♀). Subcaudals 87 (92–110♂, 95♀). Anal plate undivided. Postoculars 2/2 (2).

Fig. 1. *Dipsas nicholsi* (Dunn), a rarely collected Panamanian snail-eater (MVUP-1856, about ×2.6 life size). This specimen, the first known juvenile, provides evidence of a fragmented distribution on the Isthmus of Panama. (From a transparency by Marcos A. Guerra)

Temporals 2 + 3 + 4/2 + 4 + 4. Supralabials 8/7 with 4–5/3–4 touching eye. Infralabials 12/11 (10–13). The genials, 2/3 (2–3), are unpaired, with the two on the left asymmetrically positioned against the three on the right. Two pairs of infralabials in contact behind mental (one or two pairs in contact, or one infralabial in contact with an opposite pair). Loreal and prefrontal bordering anterior edge of eye on right. On the left side, the prefrontal borders the eye dorsally, but the loreal is divided by a small suture cutting off a small triangular corner posteroventrally; the larger portion of the left loreal touches the eye at a single point between the prefrontal and the small triangular scale (similar to loreal pattern 5 in Cadle [2005: fig. 1], except for the narrower contact between the loreal and eye in the present specimen).

Dorsal body blotches (including an elongate blotch on each side of the neck): 17 along left side, 19 along right (17–22); 7 additional blotches on tail.

COLOR PATTERN: In life (fig. 1), MVUP-1856 was pale orangish brown with contrasting black markings on the dorsum and head; the venter was grayish cream; the iris was grayish. In preservative (fig. 2), the colors are similar but somewhat duller. The dorsal ground color is pale brown, turning duller grayish on the lower sides, and the markings are dark brown to milk chocolate (not blackish).

The form of the dorsal blotches and head markings are critical to comparison of the

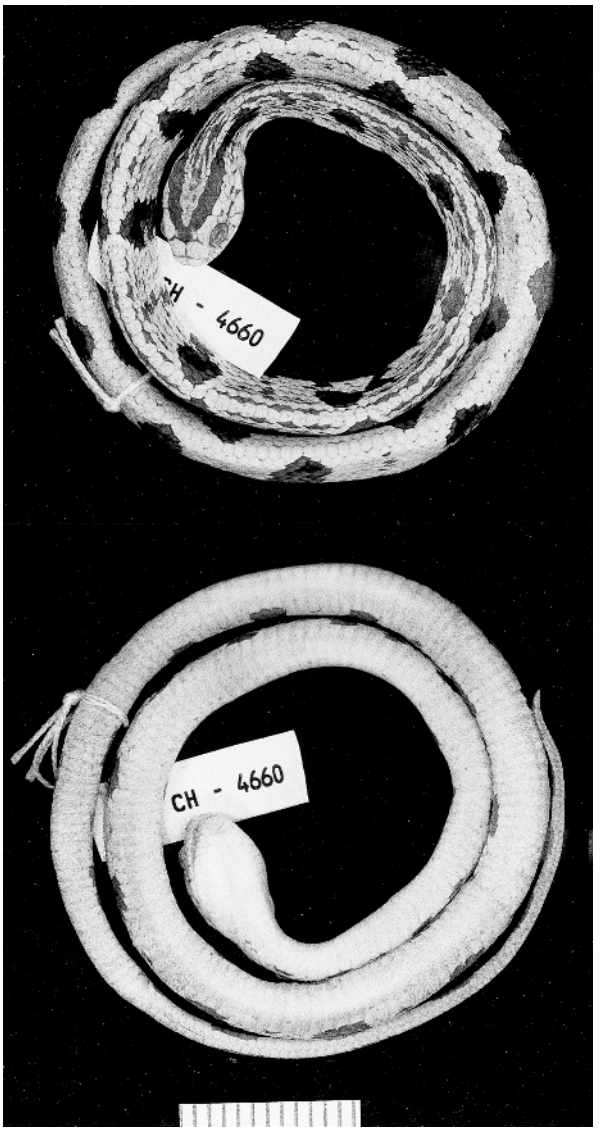


Fig. 2. Juvenile specimen (MVUP-1856) of *Dipsas nicholsi* in dorsal and ventral view, ×1.8 (scale divisions = mm).

specimen with *Dipsas nicholsi* from central Panama, and are described here in detail.

The top of the head bears a prominent ∩-shaped marking whose apex is at the frontal/prefrontal suture and whose branches diverge across the parietal scales. Posteriorly the branches of this marking are confluent with an elongate blotch on each side of the neck. The branches of the ∩ are broadly divergent and there are 4 to 5 scales between branches of the head marking at the level of the mouth commissure. The head mark is narrowly edged by a whitish line. Apart from the conspicuous head marking, a few head scales are edged with dark brown, especially in the temporal region and on the supralabials. Otherwise, the head (including gular region) is unmarked.

As mentioned above, the two elongate blotches behind the head are confluent with the branches of the ∩. These are followed

posteriorly by a series of lateral blotches, each of which extends dorsally to the outer edge of the vertebral scale row. The four anterior blotches behind the neck blotches are separated from the ventral plates by 1–2.5 lower dorsal rows, whereas the other dorsal blotches extend to the outer edges of the ventral plates. On the anterior third of the body, ventrolateral spots are positioned at the conjunction of the ventral plates and lower dorsal rows, and positioned more or less ventral to the lateral body blotches. The ventrolateral spots gradually enlarge posteriorly to become fused with their corresponding lateral blotches. This fusion of ventrolateral and lateral blotches is responsible for the more posterior blotches extending down to the ventral plates, whereas the anterior body blotches terminate on scale rows 1–3. Each dorsal blotch (including the neck blotches) has a narrow whitish margin.

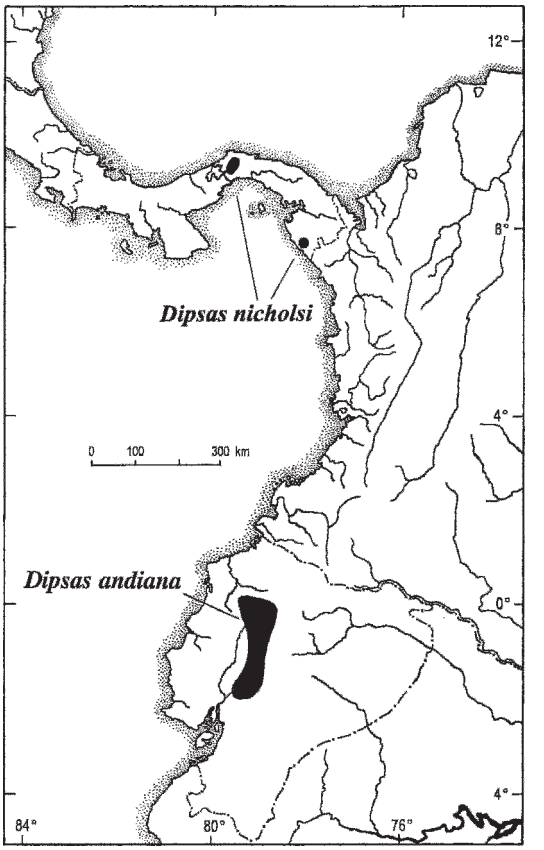
In no case do opposite blotches fuse dorsally. Anterior blotches are slightly offset from one another, whereas posteriorly the blotches tend to alternate. Blotches have a maximum width of 4–5 scales; interspaces are usually 6–8 scales wide (in a range of 5–11). Blotches are higher than wide, with a rather pointed apex dorsally and a base that is somewhat narrowed (to 3–5 scales across) from the midpoint of the blotch. The blotches are about twice the width of the interspaces anteriorly, and nearly twice the width posteriorly.

The spaces between the blotches on the anterior half of the body bear numerous longitudinal streaks formed by dark pigment along the upper and lower edges of the dorsal scales. The anterior two-thirds of the body has virtually continuous dark pigment running along the adjacent edges of the vertebral and paravertebral scale rows.

The ventral surfaces have scattered, diffuse dusky punctations (visible only with magnification) concentrated toward the outer edges of the ventral plates. The dorsal blotches on the posterior two-thirds of the body encroach onto the outer edge of the ventral plates. Otherwise, the venter is unmarked.

Comparisons with *D. nicholsi* and *D. andiana*

The morphology and collection locality of MVUP-1856 clearly associate the specimen with two similar species previously known either from the lowlands (60–150 m) of central Panama (*Dipsas nicholsi*) or from the lowlands and Pacific slopes (5–1140 m) of western Ecuador (*D. andiana*). The similarities between these species include a well-defined ∩-shaped (or ∧-shaped) marking atop the head. MVUP-1856 comes from a locality intermediate between the known distributions of *D. nicholsi* and *D. andiana* (map 2), for which reason we compare the specimen in detail with both species. Cadle and Myers (2003) summarized the taxonomy and biology of *D. nicholsi* and *D. andiana* and concluded that no other species of *Dipsas* approaches these two in substantive systematic characters; a sister-group relationship seems likely but needs corroboration.



Map 2. The widely separated distributions of *Dipsas nicholsi* in eastern Panama and its possible sister species, *Dipsas andiana*, in western Ecuador.

Dipsas nicholsi (Dunn): Comparison is problematic because *Dipsas nicholsi* previously was known only from six complete museum specimens; a photograph of a seventh specimen, not preserved, provided additional data on color pattern (Cadle and Myers, 2003: fig. 1, top).[7] Only one of the previous museum specimens is a female, and all are much larger than the present juvenile female. Thus, the extent of variation especially in female *D. nicholsi* is unknown, and there are no data on ontogenetic variation.

All body proportions and standard scutellation characteristics of MVUP-1856 are close to previously reported data for *Dipsas nicholsi* (as shown by parenthetical values in the description above). Species of *Dipsas* are notoriously variable in some standard scutellational features such as temporal and other head scale patterns, and the differences between MVUP-1856 and specimens of *D. nicholsi* are unremarkable in this regard. Two scutellation characteristics and the relative tail length of MVUP-1856 are worthy of comment. First, the segmental counts (ventrals and subcaudals) of the new specimen combined with those of the previously known female provide a minimal range of variation in these characters for females (ventrals 200–206, subcaudals 87–95). The subcaudal count of MVUP-1856 also slightly extends the range downward for females and males combined (87–110). Second, the divided loreal on the left side of MVUP-1856 is a variation not observed among the complete specimens of *D. nicholsi* studied by Cadle and Myers (2003). However, one of the new specimens mentioned in footnote 6 also has a divided loreal on both sides, with the posteroventral fragment looking like a "small preocular" as in MVUP-1856. Several of the "head only" specimens examined by Dunn (1933, 1940a), including the holotype, have a "small preocular" (in Dunn's terminology) below or above the loreal on one or both sides, so the region of loreal-eye contact is variable. (Scales in the loreal/preocular region of *Dipsas* frequently vary by fusions or divisions [e.g., see Cadle, 2005: 71–73, fig. 1].) The proportional tail length of MVUP-1856 (22% of total length) is shorter than other specimens examined by Cadle and Myers (2003), who reported 24% for the single female they examined. However, the difference seems trivial.

In contrast to seemingly minor differences in scutellation and body proportions, the major differences between MVUP-1856 and other specimens of *Dipsas nicholsi* are in details of color pattern. Nonetheless, we stress that the diagnostic head marking connected to lateral neck blotches is fully formed in MVUP-1856 and very similar to the configuration in other known specimens of *D. nicholsi* (e.g., Cadle and Myers, 2003: figs. 1, 4–5). This detail is discussed below where its differences from the pattern in *D. andiana* are emphasized. Similarly, the longitudinal blackish streaks in the interspaces of the dorsal pattern in MVUP-1856 are characteristic of other known specimens of *D. nicholsi*.

The form of the dorsal blotches is the major difference between MVUP-1856 and other specimens of *Dipsas nicholsi*. In MVUP-1856 the dorsal blotches are narrowed at the top and bottom (pointed at top) and are maximally 4–5 scales wide; each blotch is higher than wide (see comparisons with *D. andiana* below). In contrast, in previously known specimens (including those in footnote 6) of *D. nicholsi* the blotches are rounded dorsally, only very slightly narrowed ventrally (more or less truncated on ventral side), and wider (4–8 scales); blotches are invariably wider (often much wider) than high, round or elliptical, and about as wide as the interspaces between them. On the other hand, the dorsal blotches of *D. nicholsi* are of similar width throughout the body (a difference between this species and *D. andiana*), and in this respect MVUP-1856 is like *D. nicholsi*.

Dipsas andiana (Boulenger): Cadle and Myers (2003) resurrected and re-described *Dipsas andiana* (Boulenger) and pointed out the previous confusion of that species with *D. nicholsi*.[8] Because *D. andiana* is the only other species of *Dipsas* with a stereotypical ∩-shaped head marking resembling that of *D. nicholsi*, and because the species are otherwise

[7] *Dipsas nicholsi* is known from five additional "head only" specimens collected as part of the Panama Snake Census (Cadle and Myers, 2003: 15–17), and the three additional specimens mentioned in footnote 6.

[8] Peters (1960) had synonymized the name *Leptognathus andiana* Boulenger with *Dipsas oreas* (Cope), but had applied the name "*Dipsas variegata nicholsi*" to Ecuadorian specimens of *Dipsas andiana*.

similar (Cadle and Myers 2003), a passing comparison of MVUP-1856 with *D. andiana* is warranted.

With regard to scutellation, MVUP-1856 differs significantly from the previously reported sample of 11 specimens (including 5♀) of *Dipsas andiana* in ventral and subcaudal counts (206 and 87 compared with 185–191 and 82–83 for *D. andiana*).[9] The supralabial pattern of 7 (3–4 touching eye) in MVUP-1856 was not found in our previous sample of *D. andiana*, but labial scale patterns are highly variable within *Dipsas* (e.g., see data for *D. andiana*, *D. nicholsi*, *D. oreas*, and *D. variegata* in Cadle and Myers 2003).

Dipsas andiana differs from *D. nicholsi* in average segmental counts and in some more subtle aspects of color pattern, including the configuration of the ∩-shaped head mark and the form of the dorsal blotches. In *D. andiana* the branches of the head marking are more parallel than in *D. nicholsi* and are almost universally detached from the neck blotches. Cadle and Myers (2003: 33) quantified the divergence between the branches by scoring the number of scales between them at the level of the mouth commissure: 4–5 scales in *D. nicholsi* versus 2–4 in *D. andiana*. In these respects MVUP-1856 conforms to *D. nicholsi* more precisely than to *D. andiana* by having the branches of the head marking divergent and attached to the neck blotches. MVUP-1856 has 4–5 scales between the branches of the ∩ at the mouth commissure, actually comprising three complete medial scales and about 2/3 of each adjacent lateral scale—again a similarity to *D. nicholsi*.

On the other hand, the configuration of the dorsal blotches of MVUP-1856 is at first glance more similar to *Dipsas andiana* (blotches higher than wide, distinctly narrower than interspaces) than to *D. nicholsi* (wider than high, about equivalent width to interspaces). However, dorsal blotches in *D. andiana* are more variable in shape than those in *D. nicholsi*, with posterior blotches narrower than anterior ones. In this respect MVUP-1856 is more similar to the pattern in *D. nicholsi* in having blotches of similar width throughout the body.

[9]Results of t-tests for comparison of a single sample with a sample mean (in this case, all females reported by Cadle and Myers, 2003) are: Ventrals, t = 6.95, df = 4. Subcaudals, t = 7.50, df = 3. Both tests are highly significant ($P < 0.01$).

Systematic Conclusion

The scutellation, color pattern, and other features of MVUP-1856 are consistent with its identification as *Dipsas nicholsi*, whereas all characters except width of the body blotches are unlike *D. andiana*. The somewhat low subcaudal count of MVUP-1856 compared with other *D. nicholsi* might be attributed either to unknown geographic variation or simply to uncharacterized sexual dimorphism, given that only a single female of this species is available for comparison. It is a minor difference that gives no reason to question the assignment of MVUP-1856 to *D. nicholsi*.

It cannot be determined at this time whether differences in the form of the dorsal blotches between MVUP-1856 and other specimens are attributable to geographic, ontogenetic, or simply individual variation. However, given the uniformity in color pattern of specimens of *D. nicholsi* from the Río Chagres basin, it seems most likely that the differences reflect geographic variation.

Habitat and Distribution

A few previous observations indicated that *Dipsas nicholsi* is nocturnal, although there was no documentation of suspected arboreal inclinations (species of *Dipsas* are nocturnal and largely arboreal). The new specimen, found by Ibáñez at night, was active in low vegetation in cloud forest at an elevation of 855 m above sea level.

The lowland (< 150 m) rain forest habitat of *Dipsas nicholsi* in the Río Chagres drainage of central Panama is physiognomically very different from the montane cloud forest in the Serranía de Jingurudó (figs. 3, 4). Myers (1969b: 18–21, under "Jaqué-Imamadó Divide") described this cloud forest, in an elevational range of 800–960 m, as less dense and with less fog than the higher-elevation cloud forest of the neighboring Serranía de Pirre to the northeast and the Serranía del Sapo to the northwest (map 1)—but nonetheless with frequent rain and fog, and with the

Fig. 3. Diverse habitats of *Dipsas nicholsi*. **Top:** Cloud forest (855 m) in the Serranía de Jingurudó, Darién, extreme eastern Panama. (Photograph by Bill Hatcher, August 1997) **Bottom:** Lowland forest along Camino de Cruces in the former Madden Forest Preserve, in upper Río Chagres drainage of central Panama. (Photograph by Roberto Ibáñez, November 20, 2004)

Fig. 4. Camp in tall cloud forest on the Jaqué-Imamadó divide (part of the Serranía de Jingurudó), 800 m elevation, perhaps 8 km distant from the upper scene in figure 3. Trees are unusually tall for a ridge-top forest in eastern Panama. (Photograph by C. W. Myers, April 22, 1967)

annual dry season being much less evident than in the adjacent hot lowlands. Myers made his expedition in late April, 1967, and established a week-long base camp (fig. 4) at 800 m elevation, only about 8 km SE of the locality collected by Ibáñez and colleagues 30 years later.[10]

The herpetofauna of this cloud forest (as represented by the several dozen species collected by the two parties) is comprised primarily of well-known animals having a fairly wide elevational tolerance. Notable exceptions include a few mainly cloud-forest species such as the frog *Gastrotheca nicefori* and the lizard *Ptychoglossus myersi*. The only snakes found in addition to *Dipsas nicholsi* were the terrestrial *Nothopsis rugosus* and the arboreal *Dipsas temporalis*, *Imantodes cenchoa*, and *Oxybelis brevirostris*.

Dipsas nicholsi is the most unexpected component of the Serranía de Jingurudó collections. Its occurrence in cloud forest above 800 m proves that it is not as strictly a lowland animal as supposed. This rare snake might therefore be expected above 150 m immediately to the east of known records, in the headwater drainage of the upper Río Chagres (see map 1).

However, continuity between populations of *Dipsas nicholsi* in central Panama and in Darién can *not* be assumed and is highly unlikely owing to habitat discontinuities. Savanna covers the Pacific lowlands south of the Serranía Piedras-Pacora, and the nearly base-leveled lowlands comprising most of the isthmus to the east of that are occupied by cuipo forest (*Cavanillesia platanifolia* association) and interspersed river-swamp forest (Myers, 1969b: 6–12). The only way to link the populations would be to assume a narrow and tenuous habitat corridor along the low continental divide, which runs eastward close behind the Atlantic coast before swinging south along the Colombian border (map 1). This narrow corridor provides the minimal elevation and slight-to-modest orographic rainfall needed for a reasonable continuity of well-drained, evergreen seasonal forest.

However, as already indicated (see Introduction), results of the long-term Panama Snake Census and the activities of many other collectors indicate that *Dipsas nicholsi* occupies only a very restricted part of available humid lowland forest in central Panama. It may yet be found higher in the Río Chagres drainage, but a much broader continuous distribution can hardly be expected.

Although one hopes that additional populations of this rare snake await discovery, *Dipsas nicholsi* likely was affected by the same climatic-vegetational changes that fragmented the geographic distributions of many other species on the Isthmus of Panama.

Biogeography

The present-day herpetofauna of Panama is comprised of varied historic components superimposed on a small land mass of great climatic and vegetational diversity, and greatly affected by past extinction events (Ibáñez et al., "1995b" [1997]; Myers, 1972; Savage, 2002). There is a great diversity of intracountry range gaps that impart a mosaic pattern to the collective distributions of many isthmian species; that diversity can be highlighted by two examples, a western and an eastern species, respectively: (1) The common highland snake *Geophis brachycephalus* occurs from Costa Rica to Boquete in western Panama, and then is represented by a presumably relict population more than 300 km to the east in the Serranía Piedras-Pacora of

[10]In 1997, Ibáñez' party obtained coordinates of 7°37′30″N, 78°00′34″W (datum NAD 27) by GPS satellite receiver (accuracy, however, can be assumed only to the nearest minute because point-position exactness of civilian GPS devices was limited for military reasons to about 100 m prior to May 2000). For the expedition report, see Angehr et al., 2004.

Myers' estimated coordinates for his 1967 base camp are 7°35′N, 77°57′W, as derived from sheet 12 of the *Mapa General de la República de Panamá 1:250,000* (1st ed., circa 1966–1967, Dirección de Cartografía, Panama City). This plot was made with the aid of field sketches and landscape photos in conjunction with two maps used in the field: a Panama census map (*Distrito de Chepigana* [1:125,000], February 1957) and a 1:500,000 military map (sheet 3 of the USARCARIB Special Map of Republic of Panama map, 1956). Elevations were tracked with a Lufft pocket altimeter having 20-m graduations.

Myers (1969b: 18) found a high point of 960 m, past where there was a rapid drop. Angehr et al. (2004: 53) recorded an elevation of "*c.*1,000 m", but believed that broken terrain and dense vegetation separated them from a slightly higher summit thought to be much lower than shown on an available 1993 map (see footnote 13).

east-central Panama (Myers, 2003). (2) The marsupial frog *Gastrotheca nicefori* is mentioned above as having been found in the Serranía de Jingurudó along with *Dipsas nicholsi*. This frog also occurs in the Serranía de Pirre and Serranía del Darién (see map 1), but its distinctive voice has not been heard in central Panama, and there is a gap of over 400 km between the Darién populations and one in the Serranía de Tabasará of western Panama (Myers and Duellman, 1982: 11). Intervening populations of such species may well be found, but these and many others clearly do not have continuous distributions on the isthmus.

Extinction of populations has been most dramatic on the eastern half of the isthmus, affecting both branches of the broken Panamanian "X" pattern (Dunn, 1940b; Myers, 1972: 202). Thus, relict populations of some amphibians and reptiles in the savannas of Pacific-western Panama are now widely separated from conspecifics or closely related populations in the Atlantic lowlands of northern South America (e.g., the frog *Pleurodema brachyops* and the snake *Liophis lineatus*). Similarly, some species in western and/or central Panama are widely separated from close relatives in Pacific lowlands of western Colombia—good examples being frogs of the genus *Phyllobates* and of the monophyletic *histrionicus* species group of *Dendrobates* (Myers et al., 1984: 19). Thus, the existence of a "Darién Gap"[11] in the distribution of some species or monophyletic groups can scarcely be denied.

Not unexpectedly, eastern Panama also is a region of endemic species and relict populations. Some snakes of the region illustrate this point well, and also demonstrate the difficulty of drawing microgeographic conclusions based on limited collections of rare species.

It is particularly hard to generalize on the distributions of endemic species whose known distributions are single map-points based on one or two type specimens! For example, one may generalize that most species of the genus *Atractus* occur only on the eastern half of the isthmus; there is, however, no way of reliably predicting whether any of the five named species of eastern Panamanian *Atractus* occur very far from their type localities (Myers, 2003, map 1).

The blunt-headed vine snakes of the genus *Imantodes* are slow-moving, slender serpents of strongly nocturnal habits, tending to be common where they occur. The genus is comprised mainly of widely distributed species, with a major exception being *Imantodes phantasma*, which is known only from cloud forest of the Serranía de Pirre (Myers, 1982). The arboreal forest species of *Imantodes* are easily collected in low vegetation at night, as was the case with the type specimens of *I. phantasma*. This snake so far has not been found during night collecting in seemingly suitable habitat in nearby highland areas of eastern Panama and adjacent Colombia, and on that basis is considered endemic to the Serranía de Pirre (map 1).

A small terrestrial snake, *Coniophanes joanae*, also was discovered and named from the Serranía de Pirre cloud forest. And it also would be considered a Pirre endemic—except for its fortuitous collection in the Serranía Piedras-Pacora (map 1), about 235 km northwest of the type locality (Myers, 1969a). *Coniophanes joanae* remains known from only two specimens; Myers' (2003: 5) recent assumption of a third specimen was an unwarranted error.

It is easy to conclude the existence of range disjunctions and/or endemism of montane species such as the above, but it is harder in the case of lowland species. Thus, the small terrestrial snakes *Urotheca fulviceps* and *Trimetopon barbouri* are central Panamanian lowland species that also are known from specimens in Darién (Myers, 1974, map 14; Myers, MS.). Possibly these are range disjunctions, although one could also hypothesize a narrow but continuous lowland distribution adjacent to the continental divide—i.e., the habitat corridor that we discussed above as being improbable in the case of *Dipsas nicholsi*.

Among the rare snakes of eastern Panama, *Dipsas nicholsi* provides an unusual example of one that is known to have both a lowland and a highland component to its distribution. Another, even more striking example is

[11]This term originally applied to a broad break in the Pan-American Highway, but it is equally and perhaps more permanently useful as a biogeographic descriptor.

Urotheca decipiens, which occurs in known elevational ranges of 15–1500 m in Costa Rica (Savage, 2002: 641–642) and 850–1620 m in western Panama (Myers, 1974: 175; Montgomery et al., 2006; E.J. Griffith Rodríguez, personal commun.). *Urotheca decipiens* is then unknown throughout most of Panama, but it has been reported at an elevation of 1050 m in the Serranía de Sapo of Darién and 2740 m in the Cordillera Occidental of northern Colombia (Myers, 1974). An additional specimen has since been found in the Serranía del Darién (AMNH 119390, Cerro Malí, 1400 m).

The examples given above well illustrate the difficulty of generalizing present-day distribution patterns on the Isthmus of Panama. Some fragmented distributions show little congruence and that of *Dipsas nicholsi* appears to be unique among Panamanian reptiles and amphibians.

Geographic Notes: Names of the Eastern Highlands

The eastern Panamanian highlands are interesting areas of endemism clearly in need of much further study. We show names of the principal montane areas in map 1. Three of these names, however, are not well established cartographically and deserve comment. It should be realized that, whereas there are well-known local names for individual peaks and ridges (some not on any map or in any gazetteer), names for the diverse mountain ranges and ridge complexes are mostly cartographic inventions.

Serranía de Piedras-Pacora: It seems very odd that the low highlands northeast of Panama City have never received a widely accepted map name (usually no name is given, although "Sierra Maestra" has been shown for part of the uplift). This is a zoogeographically important region that has been most studied along the Continental Divide in the southern part of the uplift. Dunn and Bailey (1939) and Myers (2003) designated this area the "Piedras-Pacora Ridge", and Ibáñez et al. ("1994" [1995]) called it the "Serranía Piedras-Pacora". We use the latter in map 1, but point out that this name is really descriptive only of the southern part of the uplift, which "may be a premontane forest refuge for some small part of the fauna that is barely surviving the climatic-vegetational vicissitudes of the Pleistocene" (Myers, 2003: 5).

Serranía de Majé: Modern maps show this as being a replacement for what used to be generally shown as the Serranía de Cañazas, although the name Cañazas sometimes is retained for the eastern part of the range. Myers (1969b: 27) thought that this highland "almost certainly bears limited areas of good ridge-top cloud forest". This was confirmed by Angehr and Christian (2000), who found cloud forest above 1150 m on Cerro Chucantí.

Sierra de Jingurudó: Most Panama maps prior to the 1960s either left this highland unnamed or implied that it was a northern continuation of the "Sierra" or "Cordillera" Juradó. For his 1967 collections, Myers (1969b: 18) used the term "Jaqué-Imamadó Divide", which he described as "a ridge … in the Cordillera de Juradó". Inhabitants along the upper Río Jaqué seemed to have no special name for this highland, which lacks cartographic and structural definition, as it is contiguous with the Cordillera de Juradó to the south and the Serranía del Sapo to the northwest.

In the last half of the 20th and early 21st centuries, the name *Sierra* (or *Serranía*) *de* "*Jungurudó*" appeared regularly on both official and privately published maps, as well as in major gazetteers (U.S. Board on Geographic Names, 1969: 145; 1990: 230; Universidad de Panamá, 2001: 418). Despite this recognition and occasional use in scientific papers, the appellation "Jungurudó" was an enigma—appearing to be a spelling variant or combination of *Jungururo* and *Jingurudó*. It was termed *Sierra de Jungururo* in the old American Geographic Society millionth series (1945, sheet N.B-18, Bogota, Provisional Edition, 1:1,000,000). The subsequent spelling "Jungurudó" indicates that it is named after a river,[12] but we are unaware of a "Río Jungurudó" as factually distinct from the *Río Jingurudó*.

[12]The word *dó*—the Emberá word for *river*—is seen as a suffix in the names of numerous streams from the Pacific lowlands of northwestern Colombia into extreme southeastern Panama (some tributaries of the Río Jaqué and Río Sambú). It is also rendered orthographically by linguists as *to* (Mortensen, 1999) and *dhó* (Sara, 2001).

The Río Jingurudó empties into the Río Sambú to the north of this serranía, and is shown on various maps and in gazetteers. A populated place at the mouth of the Río Jingurudó is shown on maps either as "Jingurudó" or usually as "Boca de Jingurudó" at 7°53′N, 78°05′W. Although not on all government maps, this place appears even on commercial road and tourist maps of Panama (e.g., Esso Standard Oil S.A. Ltd., 1964; and ITMB Publishing, Vancouver, circa 2000–2001), as well as on the Panama census and U.S. military maps referenced in footnote 10. However, a place name "Jungurudó" is shown alongside the name Boca de Jingurudó on error-prone reissuances of one experimental map.[13]

The place name "Jungurudó" recently appeared also in the online USBGN database (accessed in 2004), although a river of that name was not listed. However, the latest edition of the *Diccionario Geográfico de Panamá* gives both a Río "Jingurudo" *and* a Río "Jungurudo" (but not a place name Jungurudó)—but the descriptions are very similar and may represent the same river (Universidad de Panamá, 2001: 409, 418).[14]

[13]The original version of this map—the *Darien Province Special Map Sheet*—was prepared by the Raytheon Corporation based on 1967 radar data and issued in July 1968 by the U.S. Army Engineer Topographic Laboratories. The paper map was published along with a striking, equal-sized (56 × 73 cm) *uncontrolled* radar mosaic in an *approximate* scale of 1:250,000. This was a pioneering attempt at producing a map by means of side-looking radar, but it was issued with the warning "Caution, reliability unknown, neither horizontal nor vertical data has been field checked".

Errors were introduced in two subsequent Spanish editions, the first one being undated. It most recently was reissued in August 1993 as *Panamá 1:250,000, Darién, Mapa Especial*, by the Instituto Geográfico Nacional "Tommy Guardia". Some names not on the 1968 original were added to the Spanish editions, including the erroneous name "Jungurudó" and the Río Imamadó. The last is badly misplaced, being misapplied to a stream flowing easterly to the Río Jaqué from the northern slopes of the Cordillera de Juradó. As shown on the 1957 census map (*Distrito de Chepigana*, 1:125,000), the Río Imamadó is a higher tributary that drains southwesterly from the southern slopes of the Serranía de Jingurudó (the serranía is unnamed on the census map). The location of the Río Imamadó was verified in the field (Myers, 1969b: 18) by local inhabitants who used the name; there was a large Emberá settlement designated on the census map as *Boca de Imamadó*. *Imamadó* (imaamá-dhó) is Emberá, meaning "river of the tiger [i.e., jaguar]".

A long-held suspicion of cartographic error was bolstered by a recent edition of a widely distributed official map showing the name of the highland area as "SERRANÍA DE J NGURUDÓ", with the letter U having been dropped—suggestive of an unfinished correction from "Jungurudó" to "Jingurudó" (sheet 2 of *República de Panamá, Mapa Físico, 1:500,000*, Instituto Geográfico Nacional "Tommy Guardia", serie E462, edición 14IGNTG, Junio 2000). That this was not a simple typographic error is shown by the subsequent new edition of another map, which for the first time designated this highland as the *Serranía de Jingurudó* (sheet 12 of *Mapa General de la República de Panamá, 1:250,000*, Inst. Geog. Nac. "Tommy Guardia", Agosto 2000[15]).

The correctly spelled map name Serranía de Jingurudó presumably derives from the Río Jingurudó. This river drains north for several kilometers from low foothills at the northern end of the serranía, before changing to a northwesterly and then a final southwesterly course into the Río Sambú. There also is a lesser known *Quebrada Jingurudó* in a different drainage, some 40 km south of the mouth of the Río Jingurudó. The Quebrada Jingurudó drains part of the southern slope of the Serranía de Jingurudó and empties into the upper Río Jaqué, at an airline distance roughly 16 km eastward from the Pacific coastal town of Jaqué. The Quebrada Jingurudó is shown on the 1957 census map (*Distrito de Chepigana*, 1:125,000) and is listed in the *Diccionario Geográfico* (Universidad de Panamá, 2001: 409).

[14]We are aware of no other reference to a "Río Jungurudó", and are unable to verify its existence in the absence of coordinates or a precise map reference. The *Diccionario Geográfico* incorrectly describes the Río Jingurudó as about 10 km long and running west before curving *southeast* ("hacia el Sureste") into the Río Sambú, whereas the "Río Jungurudó" is said to be about 9.5 km long and running northwest before emptying into the Sambú. Maps show the upper Río Jingurudó as having both northwesterly and final southwesterly components. Only the Río Jingurudó is shown on the large (about 0.9 × 1.9 m), name-rich census map (*Distrito de Chepigana*, 1:125,000, 1957).

[15]We were unaware of this edition until completion of the penultimate draft of this manuscript. According to staff at the Instituto Geográfico Nacional "Tommy Guardia", a total of 500 sheets were printed in August 2000, with a subsequent, undated reimpression of 250 sheets.

In summary, the name Serranía de Jingurudó replaces the "Serranía (originally Sierra) de Jungurudó". The latter spelling appears to have been a cartographic error based on confusion between a still-older map name (Sierra de "Jungururo") and the "Río Jingurudó". This has led also to instances of the misspellings "Jungurudó" and "Río Jungurudó" being interpreted as geographically different from the long-established names Jingurudó and Río Jingurudó. It is a not uncommon kind of circularity of confusion between maps and gazetteers. Errors introduced at any point tend to be perpetuated, and correct spellings are especially hard to ascertain when names derive from an indigenous language (Emberá in this case).

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NOTE ADDED IN PROOF

We expressed hope on page 12 that additional populations of this rare snake might be found. We consequently are pleased to announce a recent discovery by Julie Ray and Andrew Hein, who collected the first specimen of *Dipsas nicholsi* in western Panama—at a montane locality about 112 km WSW of the central-lowland population. (The new locality is well off the map on page 4.) Ms. Ray (personal commun.) kindly provided photographs and the following information:

The snake was caught in the Omar Torrijos Herrera National Park (Parque Nacional General de División Omar Torrijos Herrera), at 8°40′N, 80°35′W, elevation 820 m, Coclé Province, on November 11, 2006. It was found after dark, about 1 m aboveground on the branch of a young *Cecropia* tree, in roadside second-growth forest. Ray's photographs show some stages of the curious defensive posturing of *Dipsas nicholsi* (Cadle and Myers, 2003).

The specimen is to be deposited in the Museo de Vertebrados de la Universidad de Panamá (MVUP). It is a female measuring 690 mm SVL, 882 mm total length shortly after preservation (tail 192 mm or 21.8% of total length). There are 24 or 25 dorsal blotches along each side (including tail). Ventrals 192, subcaudals 89, infralabials 10.

The photographs show rounded, slightly elliptical blackish brown markings on a light brown ground color. The diagnostic ∩-shaped marking has its apex slightly anterior to the prefrontal/frontal suture and is posteriorly confluent with the first pair of elongate body blotches. The interspaces between the body blotches are marked with blackish streaks and small spots on the anterior half of the body, but the ground color is virtually immaculate on the posterior body and tail. The overall color pattern is like that of specimens from central Panama.

The new specimen, collected in 2006, comes from an area of wet montane forest about 5 km airline north of the town of El Copé (8°37′N, 80°36′W). Earlier, in October 1977, a new logging road had allowed Myers access to the same area, in cloud forest on the continental divide and upper slopes of the Atlantic versant (600–800 m) north of El Copé; his collection included three species of dipsadinine snakes: *Dipsas* sp. (AMNH R-115923, probably unnamed), *Sibon argus*, and *S. nebulata*. Different species of *Dipsas* occur at other *D. nicholsi* localities on map 1, including *D. viguieri* at locality 1 (Cadle and Myers, 2003: 18), *D. articulata* at locality 4 (Ibáñez et al., 1995a: 115, 129 [their locality 5]), and *D. temporalis* at locality 5 (this paper, p. 12).

In summary, the known geography of *Dipsas nicholsi* lacks commonality with any other isthmian reptile or amphibian that has a fragmented distribution. *Dipsas nicholsi* remains rare, being known from a restricted lowland area in central Panama and from two distant cloud-forest outliers, lying 112 km WSW and 250 km SE from the central population. We thank Julie Ray for her contribution to this update.

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