

The systematic status of Guatemalan populations of snakes allied with *Ninia maculata* (Reptilia: Colubridae)

Brian E. Smith and Jonathan A. Campbell

Department of Biology, University of Texas at Arlington, Arlington, Texas 76019-0498, U.S.A.
(Current address for BES) U.S. National Biological Service, Northern Prairie Science Center,
8711 37th St. SE, Jamestown, North Dakota 58401-7317, U.S.A.

Abstract.—The Guatemalan colubrid snake, formerly recognized as *Ninia maculata pavimentata*, is elevated to a full species. This species is closely related to *N. maculata* of southern Central America, but differs in segmental counts, relative tail length, various measures of head shape, and ventral coloration. Three recently collected specimens of *N. pavimentata* represent significant range extensions of this snake in Guatemala. *Ninia pavimentata* is re-described and ecological notes are provided.

Resumen.—El colúbrido guatemalteco conocido como *Ninia maculata pavimentata* es elevado al nivel de especie. Esta especie se encuentra cercanamente relacionada a *Ninia maculata*, del sur de Centro America, pero difiere de esta en número de segmentos, largo relativo de la cola, medidas cefálicas y coloración ventral. Tres especímenes de *Ninia pavimentata* recientemente colectados representan extenciones de rango significativas para esta serpiente en Guatemala. Se redescrive *Ninia pavimentata* y se provee datos ecológicos.

The apparent distribution of the colubrid snake known as *Ninia maculata* has been an enigma to biogeographers. Peters (1861) originally described *N. maculata* from a single specimen taken in Costa Rica. Bo-court (1883) noted similarities between four specimens from Alta Verapaz, Guatemala, and snakes from Costa Rica, and described the Guatemalan specimens as a new sub-species, *N. maculata pavimentata*. In his revision of the genus, Dunn (1935) did not consider the taxonomic position of this sub-species, and apparently never examined the types. Stuart (1948) noted the large hiatus between the provenance of *N. maculata pavimentata* in Alta Verapaz and the northernmost record of *N. m. maculata*, given by Dunn (1935) as Jinotega, Nicaragua. Stuart (1948) predicted that intergrades would eventually be collected in the intervening area. Savage & Lahanas (1991) noted that no such specimens had been forthcoming, and they anticipated that *N. m. pavimentata*

would eventually be elevated to full specific status.

The senior author, as part of an ongoing study of the genus *Ninia*, has examined 14 specimens of *N. m. pavimentata* housed in collections, including several specimens from Guatemala collected far from the type-locality. It has become clear that these specimens share certain unique similarities with each other, but differ from the more southern populations, indicating that the northern population deserves full species status.

Materials and Methods

Material from the Museum National d'Histoire Naturelle (MNHN), Carnegie Museum (CM), Los Angeles County Museum (LACM), Museum of Vertebrate Zoology (MVZ), University of Michigan Museum of Zoology (UMMZ), Florida State Museum (UF), the University of Texas at Arlington (UTA), and the Universidad del Valle of Guatemala (UVG) was examined.

Standard scale counts and measurements of the head and body were taken on all specimens. Counts of paired characters were made on both sides of the body. The following counts were made: number of dorsal scale rows one head-length behind the angle of the jaw, at mid-body, and one head length anterior to the anal plate; number of ventrals (method of Dowling 1951); number of subcaudals (counted on the left side, beginning with the first subcaudal in contact with an opposite subcaudal, the "best" method of Peters 1964); the number and position of supralabials, infralabials, supraoculars, loreals, preoculars, postoculars, anterior temporals, posterior temporals, chin tubercles (males only); and dark bands on the left side of the body. Ventral color pattern was scored using the categories of Savage & Lahanas (1991:43, their figure 4). Several measurements of the head were made to the nearest 0.1 mm using a vernier caliper, and the following variables were normally distributed: head length from the front face of the rostral to the angle of the jaw on the left side of the head, head width at the level of the angle of the jaw, snout length from the tip of the snout to the anterior margin of the orbit, head width at the widest point (immediately behind the orbit), length of the prefrontal suture, length of the parietal suture, and length and width of the frontal scale. Three juvenile *Ninia pavimentata* were used in the species description, but were not used in statistical analyses. Other head scale measurements used in the description of head scale shape included rostral height-width and loreal length-height. Measurements of paired cephalic scales were taken on the left side of the head only. Measurements of snout-vent length and tail length were made with a standard metric ruler to the nearest 1 mm.

To assess the differences between the Costa Rican and Guatemalan populations, a subset of morphometric measurements were entered into a multivariate analysis of covariance (MANCOVA), using snout-vent length as a covariate. Variables that were

found to be not normally distributed were dropped from this analysis, as noted above. Ventral and subcaudal scale counts are sexually dimorphic in species of *Ninia* (Savage & Lahanas 1991), with slightly higher ventral counts in females, and slightly higher subcaudal counts in males. Ventral and subcaudal counts added together form the segmental count, a variable that was used in a study of Costa Rican *N. maculata* (Savage & Lahanas 1991) as a non-dimorphic measure of vertebral number. In our study, we used segmental counts in a Mann-Whitney U test to compare populations of *Ninia maculata* (sensu lato). Our analysis indicates that *Ninia pavimentata* is distinctive from *N. maculata* and we suggest that these taxa are specifically distinct. Table 1 provides the range of variation for standard scale counts in *N. pavimentata*. Statistical analyses were performed using Statistica version 3.1 (Statsoft, Inc. 1991).

Results and Discussion

Ninia pavimentata is a small colubrid snake from Guatemala (snout-vent length of largest male, 265 mm; largest female, 275 mm). It is characterized by a head slightly distinct from the neck; dorsal scales keeled and heavily striated, in 19 rows throughout; ventrals 142–147 in males, 136–147 in females (except as noted for UVG 382); and subcaudals 68–76 in males, 63–75 in females (except as noted for UVG 382). See Table 1 for standard scale counts. The subcaudals are paired and the anal plate is single. Insufficient data exist to document sexual dimorphism in ventral and subcaudal counts of *N. pavimentata*. The head scalation follows a typical colubrid pattern of nine large, platelike scales. The rostral is 1.35–2 times broader than high, and the internasals are paired, about half the size of the paired prefrontals. The frontal suture is 1.5–1.85 times as long as the prefrontal suture, except for one individual (MVZ 159860) in which the frontal scale is only slightly longer than the prefrontal suture.

Table 1.—Selected features of *Ninia pavimentata* (* tail incomplete, # chinshields dessicated, chin tubercles observed but not counted).

Museum no.	Sex	Snout-vent length (mm)	Tail length (mm)	Ventrals	Subcaudals	Segmental count	Chin tubercles
UTA R-7099	♂	225	83	144	68	214	91
MNHNP 1192	♂	226	82	147	70	217	#
MNHNP 1994.226	♂	209	83	142	74	216	63
MVZ 159860	♂	222	95	143	76	219	79
MVZ 159861	♂	265	103	142	75	217	75
UF 96321	♂	106	40	141	74	215	—
UVG 382	♀	215	62	130	49	179	—
MNHNP 1994.227	♀	275	101*	145	66*	211*	—
MNHNP 1994.228	♀	195	71	144	70	214	—
UMMZ 89083	♀	255	69*	144	49*	193*	—
CM 43954	♀	203	75	147	75	222	—
UTA R-37590	♀	266	81*	136	53*	189*	—
LACM 40055	♀	154	49	142	63	205	—

There is a single frontal, about as long as wide, in all specimens. The suture between the paired parietals is about as long as the frontal scale in all specimens examined. There is a single supraocular, a pre- and postnasal, and the loreal scale is 1.5–2 times as long as high, except for three individuals (LACM 40055, MNHNP 1192, and UMMZ 89083) in which the loreal scale is nearly square. Stuart’s (1948) statement that the loreal is distinctively high and short appears to be relative, based on comparisons with other species with horizontally elongate loreals. There is no preocular (in MVZ 159860, one small scale is present on the left side and two small scales on the right side; on both sides the loreal still contacts the eye), two postoculars (rarely three or, more rarely, one), one anterior temporal, and two posterior temporals. Supralabials and infralabials usually 7 (rarely 6), with supralabials 3 and 4 in contact with the eye except for UF 96321, in which only supralabial 3 contacts the eye on the left side, and only supralabial 4 contacts the eye on the right side. The eye is moderately large, usually just slightly smaller in diameter than the loreal length. The mental is about twice as wide as long, and the first pair of infralabials are in contact, separating the mental and anterior chinshields. The first four infralabials are in contact with anterior

chinshields (except in LACM 40055, in which the third and fourth infralabials are fused on the right side). The fourth infralabial is in contact with the posterior chinshields (except as noted above for LACM 40055). The anterior chin shields are 1.4–1.8 times longer than the posterior chinshields. Males have prominent raised chin tubercles on both chinshields and the first four pairs of infralabials. There are 63–91 chin tubercles on the anterior chinshields and first pair of infralabials.

In alcohol the dorsal ground color is usually reddish brown, with the exception of UTA R-37590, which is badly formalin-blackened, obfuscating any dark dorsal crossbands. The other specimens we examined have 34–50 well-defined black crossbands. Approximately two-thirds of these crossbands are continuous across the dorsum, others end at the mid-dorsal scale row. The anterior band is always continuous across the dorsum. Immediately in front of this band is a pale nuchal collar, indistinct and narrow, which is usually no wider than one or two scale rows at mid-dorsum, and slightly wider laterally. In seven of 12 snakes this collar is not continuous across the dorsum. The supralabial and infralabial scales are cream colored, with black edges. The distinctive checkerboard ventral pattern is diagnostic for the species. Costa Rican

N. maculata can be similar (see Savage & Lahanas 1991: their fig. 4G and 4H, for illustrations of venters similar to *N. pavementata*), but Guatemalan specimens are much more boldly marked than any Costa Rican specimens that we have examined.

Ninia pavementata can be distinguished from its close relative *N. maculata* by having a broader, blunter, more spatulate head. The upper lips of *N. pavementata* are somewhat flared compared to *N. maculata*, and are easily seen in dorsal view. Additionally, the dorsal pre-orbital surface of the head of *N. pavementata* is distinctively convex, while this surface in *N. maculata* is nearly flat. The snout of *N. pavementata* is fairly blunt, whereas that of *N. maculata* is more angular.

The statistical analyses, while not robust with such small sample sizes, assist in indicating the nature of the differences between the two species. The MANCOVA results separate the species using the following variables: *Ninia pavementata* has a relatively longer tail than *N. maculata* ($f = 29.17$, $P = 0.000039$, $df = 1,18$); *N. pavementata* has a narrower head at the level of the angle of the jaw ($f = 5.55$, $P = 0.030$, $df = 1,18$), probably reflective of the spatulate shape of the head of *N. pavementata*; and *N. pavementata* has relatively larger parietal scales ($f = 4.59$, $P = 0.046$, $df = 1,18$). In addition, *N. pavementata* has a significantly higher segmental count than *N. maculata* ($Z\text{-adj} = -2.97$, $P = 0.0030$). There is little overlap between segmental counts of *N. pavementata* and *N. maculata* (Table 1).

Three snakes warrant special mention. Two of these are significant extensions of the range of *Ninia pavementata*, which had previously been known only from the highlands of Alta Verapaz and adjacent Baja Verapaz. One specimen (UTA R-37590) was recently collected in the province of San Marcos, the first specimen of *N. pavementata* to be collected on the Pacific versant of Guatemala. Examination of this specimen reveals that it is dark (probably

formalin-blackened) but otherwise it agrees with *N. pavementata*. Another specimen (LACM 40055) from near Barillas in the Sierra Cuchumatanes, Huehuetenango, is fairly typical of the species.

Finally, a specimen from near La Francia, Izabal, near the Honduran border (UVG 382) is unusual not only because it is the only *Ninia pavementata* known from the lowlands of Guatemala, but also because it shows a combination of features typical of either *N. maculata* or *N. pavementata*. This snake has a smooth and level surface on the dorsal pre-orbital portion of the head, similar to *N. maculata*, but it has large parietal scales typical of *N. pavementata*. The snout is fairly blunt like *N. pavementata*, but ventral and subcaudal counts are more similar to *N. maculata*. This specimen apparently represents an isolated population restricted to the lowlands of eastern Guatemala and perhaps adjacent Honduras. Despite its morphology, we do not consider it an "intergrade" in the sense of Stuart (1948). This population is separated from the most geographically proximate populations of *N. maculata* in Costa Rica by about 600 km and may have become isolated relatively soon after the vicariant event that separated *N. maculata* and *N. pavementata*. The area in which this specimen was collected is not well known, and further specimens from this area are needed to fully resolve the status of this snake. We tentatively allocate this specimen to *N. pavementata*, but recognize that it may ultimately prove to be distinct.

With respect to the ecology and habits of *Ninia pavementata*, very little is known. Most specimens have come from pine-oak or cloud forest at elevations of 1120 to 1825 meters (Fig. 1). A single lowland specimen was collected below 300 m. *Ninia pavementata* is rarely encountered, either because it is rare or because of secretive behavior. Specimens have been found most frequently in the highlands of Alta Verapaz (with one specimen from nearby Baja Verapaz), but recent specimens collected in the

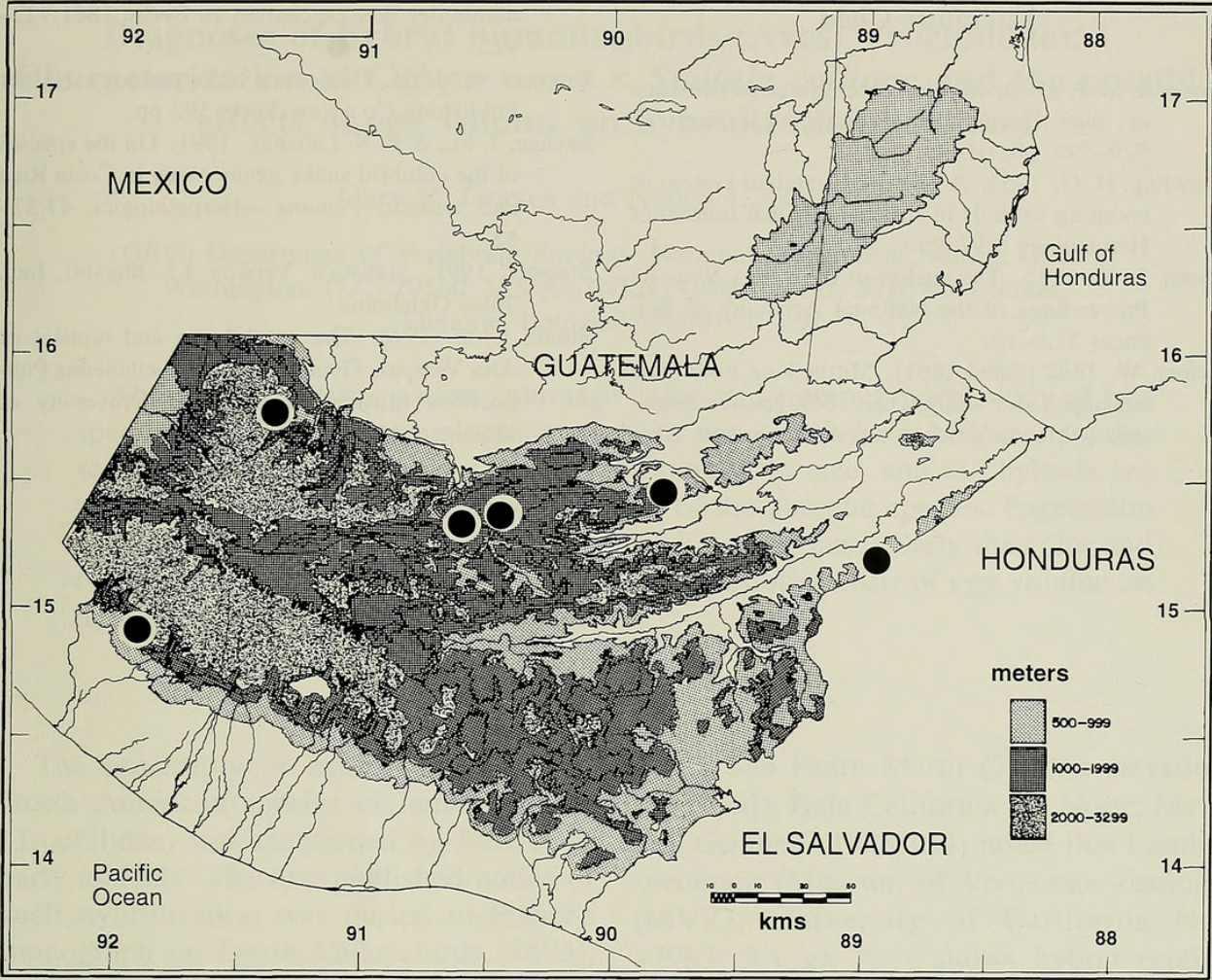


Fig. 1. Localities for *Ninia pavimentata* in Guatemala.

departments of San Marcos and Huehuetenango indicate that this species ranges more widely throughout the Guatemalan highlands than previously thought.

Material examined of Ninia pavimentata.—Guatemala: Alta Verapaz: Municipio de San Cristóbal Verapaz, Baleu, 1350 m (CM 43954); 11 km W San Cristóbal Verapaz, 1120 m (UF 96321); Finca Chichén, 1410 m (UMMZ 89083); Finca Volcán, 25 km by road NW Senahú, 1300 m (MVZ 159860, 159861); no specific locality (MNHNP 1192, 1994.226, 1994.227, and 1994.228—syntypes). Baja Verapaz: Cerro Verde, ca. 1500 m (UTA R-7099). Huehuetenango: Sierra de los Cuchumatanes, Barrillas, 1700 m (LACM 40055). Izabal: Finca Santa Isabel, near La Francia (UVG 382). San Marcos: Aldea La Fraternidad,

Finca La Esperanza, 1825 m (UTA R-37590).

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