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A new species of *Ninia* (Serpentes: Dipsadidae) from Chocó-Magdalena biogeographical province, western Colombia

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Abstract

We describe a new species of the genus *Ninia* from the Chocó-Magdalena biogeographic province, which was previously reported as a distinct population of *N. maculata* or as *N. atrata* from the western slopes of the Cordillera Occidental of Colombia. The new species is similar to *N. atrata*, *N. celata*, *N. espinali*, *N. franciscoi*, and *N. maculata*. It shares the following characteristics with the species mentioned above: 19 dorsal scale rows without reductions; dorsal ground color black or dark brown; white or cream occipital nuchal collar. However, it is easily distinguished from all other congeners because it has a non-regular color pattern in the ventral surfaces of the head and body, subcaudal surface homogeneously black or dark brown, two nasal scales, and one lateral projection ornamented with a large basal hook-shaped spine that is larger than any other spine on the hemipenial body. The presence of a lateral projection on the hemipenial body makes the new species the only member of the genus from South America that shares this feature with its Central American congeners. This feature suggests a closer relationship with this lineage. Finally, our results indicate that proper and careful revision of the *Ninia atrata* species complex will help to understand and clarify the taxonomic composition of the genus.

Key words: External morphology, Biogeography of the Colombian Pacific lowlands, Hemipenis, *Ninia atrata*, *Ninia maculata*, taxonomy

Resumen

Describimos una nueva especie del género *Ninia* de la provincia biogeográfica Chocó-Magdalena, la cual fue reportada anteriormente como una población disyunta de *N. maculata*, así como de *N. atrata* sobre las vertiente occidental del Cordillera Occidental de Colombia. La nueva especie es similar a *N. atrata*, *N. celata*, *N. espinali*, *N. franciscoi*, and *N. maculata* al presentar 19 hileras de escamas dorsales sin reducciones, dorso negro o café oscuro, collar nuchal crema o blanco. No obstante, ésta se diferencia fácilmente de todos sus congéneres por presentar machas negras irregulares sobre la superficie ventral de la cabeza y el cuerpo sin un patrón definido, superficie subcaudal homogéneamente negra o café oscuro, dos escamas nasales, y una proyección lateral que sobresale del cuerpo del hemipene ornamentada con una larga espina en forma de garfio. La presencia de una proyección lateral sobre el cuerpo del hemipene hace de ésta la única especie Suramericana, conocida hasta el momento, que comparte este carácter con sus congéneres Centroamericanos, sugiriendo una relación cercana con este linaje. Finalmente, nuestros resultados indican que una revisión cuidadosa del complejo especies *N. atrata* permitirá comprender y clarificar la composición taxonómica del género.

Palabra clave: Biogeografía de las tierras bajas del Pacífico colombiano, Hemipenes, Morfología externa, *Ninia atrata*, *Ninia maculata*, taxonomía

Introduction

The genus *Ninia* currently comprises eleven nominal species that primarily inhabit leaf litter in most of habitats from southern Mexico to northern Peru at altitudes between sea level and 1800 m above sea level [hereafter asl]

(Savage, 2002; Angarita-Sierra 2014): *Ninia atrata* Hallowell 1845, *N. celata* McCrane & Wilson 1995, *N. espinali* McCrane & Wilson 1995, *N. diademata* Baird & Girard 1853, *N. franciscoi* Angarita-Sierra 2014, *N. hudsoni* Parker 1940, *N. labiosa* Bocourt 1883, *N. maculata* Peters 1861, *N. pavimentata* Bocourt 1883, *N. psephota* Cope 1875, and *N. sebae* Dumeril, Bribon & Dumeril 1854. Since Dunn's (1935) early efforts to clarify the taxonomy of *Ninia* in Central America, only a few herpetologists had reviewed specimens of *N. atrata*-like snakes. McCrane and Wilson (1995) were the first to attempt a comprehensive taxonomic assessment of specimens of *N. atrata* and found that populations from South America could be distinguished at the species level from those from Costa Rica, western Panama (posteriorly described as *N. celata*), Honduras and El Salvador (posteriorly described as *N. espinali*). Likewise, Angarita-Sierra (2009, 2014) evaluated the geographic variation of *N. atrata* in Colombia as well as the hemipenial morphology from throughout its geographic range of distribution. Angarita-Sierra's findings show that the genus *Ninia* in Trinidad is represented by two sympatric species, the previously recognized species *Ninia atrata* (Dunn 1935; Murphy 1997; Boos 2001) and an undescribed species (described there as *Ninia franciscoi*). These authors agreed, therefore, that *N. atrata* as currently understood represent a species complex that requires revision.

Ninia atrata is the most widely distributed species of the genus in South America. It ranges from western Panama, Colombia, Ecuador, Venezuela and Trinidad and Tobago with disjunct populations inhabiting in the trans-Andean Magdalena Valley, on the western slopes of the Cordillera Occidental and Chocóan rainforest (Colombia and Ecuador), as well as the Caribbean coast reaching the northern slopes of the Cordillera de Merida (Venezuela) to Trinidad and Tobago, and Orinoquia and Amazon basins (McCrane & Wilson 1995; Ingrasci 2011; Rivas *et al.* 2012; Angarita-Sierra 2009, 2014, 2015; Mesa-Joya 2015; Medina-Rangel 2015).

After the comprehensive characterization of the *Ninia maculata* populations from Costa Rica and western Panamá made by Savage & Lahanas (1991), Castaño-M, *et al.* (2004) reported the presence of *N. maculata* populations in South America based on a single specimen (ICN 6906) from corregimiento of Santa Cecilia, municipality of Pueblo Rico, department of Risaralda, Colombia, on the western slopes of the Cordillera Occidental (biogeographical-Chocó region; Poveda-M, *et al.* 2004). In addition, these authors reported three specimens of *N. atrata* for the biogeographical-Chocó region, showing the sympatry among these species. However, their diversity analysis and reptile checklist of the biogeographical-Chocó region did not consider the direct examination of the specimens cited. The studies only made a literature review and a records compilation based on database available from major Colombian biological collections and natural history museums. Therefore, the accuracy of the taxonomic identifications was not considered.

During the study of the role of African oil palm plantations in the conservation of snakes in Colombia, we found six specimens of the genus *Ninia* from the municipality of Tumaco, department of Nariño, Colombia (biogeographical-Chocó region; Poveda-M, *et al.* 2004), that share certain unique similarities traits with each other, but differ from the more northern populations (from Costa Rica and Panamá) of *N. maculata* stated by Savage & Lahanas (1991) and Auth (1994), or sympatric populations of *N. atrata* reported by Angarita-Sierra (2009, 2014). Also, we made a direct examination of the specimens cited by Castaño-M, *et al.* (2004) as *N. maculata* and *N. atrata*, finding that these specimens do not match with the previous descriptions of the taxa or any recognized species of the genus (Hallowell 1845; Peters 1861; Dunn 1935; Savage & Lahanas 1991; Smith & Campbell 1996; Savage 2002; Köhler 2008; Angarita-Sierra 2009, 2014), but they shared unique similarities with the specimens collected at the municipality of Tumaco. Hence, it has become clear that these specimens were previously confused with *N. maculata* as well as with *N. atrata* by Castaño-M *et al.* (2004) and represent an undescribed species. Therefore, the aim of this paper is to describe this new species and discuss its unique morphology and distribution pattern.

Materials and methods

Fieldwork was carried out in the palm oil plantations of Santa Helena S.A. and Santa Fé S.A. in the municipality of Tumaco, department of Nariño, Colombia. The plantations are located on the floodplains of the Mataje and Caunapi Rivers. Searches for snakes were conducted from 8:00 to 11:30 am with a sampling effort of 270h in April 2010. Individuals were immediately put into cloth bags to general procedures of measurement and identification. Additionally, for comparative purposes, we examined preserved specimens housed in the following collections:

Instituto de Ciencias Naturales, Universidad Nacional de Colombia (ICN); Museo de Historia Natural, Universidad de Antioquia (MHUA); Museo de la Universidad La Salle (MLS); American Museum of Natural History (AMNH); Field Museum of Natural History (FNMH); University of Kansas, Biodiversity Institute (KU); National Museum of Natural History, Smithsonian Institution (USNM); and Amphibian and Reptile Diversity Research Center, University of Texas at Arlington (UTA).

Hemipenial preparation procedures follow Pesantes (1994). Also, we follow the adjustments to the Pesante's method made by Myers and Cadle (2003), Zaher and Prudente (2003) and Smith and Ferrari-Castro (2008). The staining process follows Jadin and Smith (2010) and Angarita-Sierra (2014). Terminology for hemipenial morphology follows, Zaher (1999) and Myers and McDowell (2014). Variation in meristic, color pattern, morphometric and hemipenial characters was evaluated for 70 specimens of *Ninia atrata* from northern South America. General terminology and morphometric characters of the cephalic shields follows McCranie & Wilson (1995) and Angarita-Sierra (2009). Measurements of the following variables were made with a vernier caliper to the nearest 0.1 mm: head length (HL); head width (HW), parietal length (PL), parietal width (PW), frontal length (FL), frontal width (FW), prefrontal length (PFL), prefrontal width (PFW), internasal length (INL), internasal width (INW), supraocular length (SPL), supraocular height (SPH), loreal height (LH), loreal length (LL), internasal suture (INS) prefrontal suture length (PFS), parietal suture length (PS). Tail length (TL) and snout-vent length (SVL) measurements were made to the nearest 0.5 mm using a metric ruler (Table 1). Ventral and subcaudal scale counts follow Dowling (1951) and Peters (1964).

We performed a multidimensional scaling test (MDS) to test whether the cephalic morphometry distinguishes the Chocoan specimens from the remaining *Ninia atrata* populations. The MDS is a statistical technique that allows depicting the morphometric similarities (or distances) between points in a high dimensional space into a lower dimensional space, providing a visual indication of the similarity (or dissimilarity) (Ren & Frymier 2003; Guisande *et al.* 2014). Also, this statistical technique allow to condense the information contained in a large number of original variables into a smaller set of new composite dimensions, while making no a priori assumptions about groupings in the data (Guisande *et al.* 2014). Further, the MDS allows identify whether one cluster of items is dimensionally distinct from another through of the variables that have the highest variability and discrimination degree without linearity assumptions (Kruskal & Wish 1978). The goodness of fit between the fitted and observed distances was measured by a stress test "Kruskal's stress" (S) (Kruskal & Wish 1978; Fox *et al.* 2014) which is an average of the deviations between the end and the initial spatial distances normalized to take values between 0 and 1. Values near 1 indicate the worst fit, and values near 0 indicate the best fit. However, values between 0.025–0.05 are considered good values, < 0.025 are excellent, and values equal 0 are perfect (Guisande *et al.* 2014). To avoid allometric effects during statistical inference, each morphometric parameter were divided by snout-vent length (SVL). Therefore, only the quotients were employed to perform MDS. The sexual dimorphism among morphometric characters were investigated through multivariate analysis of variance (MANOVA). All statistical approaches were carried out using the software R wizard version 1.2 (Guisande *et al.* 2014) and the MDS function of the vegan package (Oksanen *et al.* 2013). The function "scatterplot" of the car package was used to generate the biplot graphic (Fox *et al.* 2014).

Results

The morphometric features used in our MDS and the qualitative differences in traits as pigmentation, hemipenial morphology and nasal scales suggest the independent evolution of Chocoan population from the remaining *Ninia atrata* populations. Chocoan specimens can be distinguished in function LH/SVL, PFW/SVL, and PW/SVL ratios, whereas that *N. atrata* is distinguished in function of LL/SVL, PFW/SVL, and INW/SVL ratios. The MDS goodness of fit between the fitted and observed distances shows a good stress value (S) = 0.048 which indicate that there is an underlying structure based on the set of measures used that allow clearly differentiate two groups (Fig. 1). Also, the MANOVA test support that these differences are not product of sexual dimorphism (Pillai = 0.223, F(1, 17) = 0.907, p = 0.567). Likewise, the color pattern of the ventral surfaces of head and body and the presence of a lateral projection on the hemipenial body (see below) fully supports that the Chocoan population represent a new taxon described as follow.

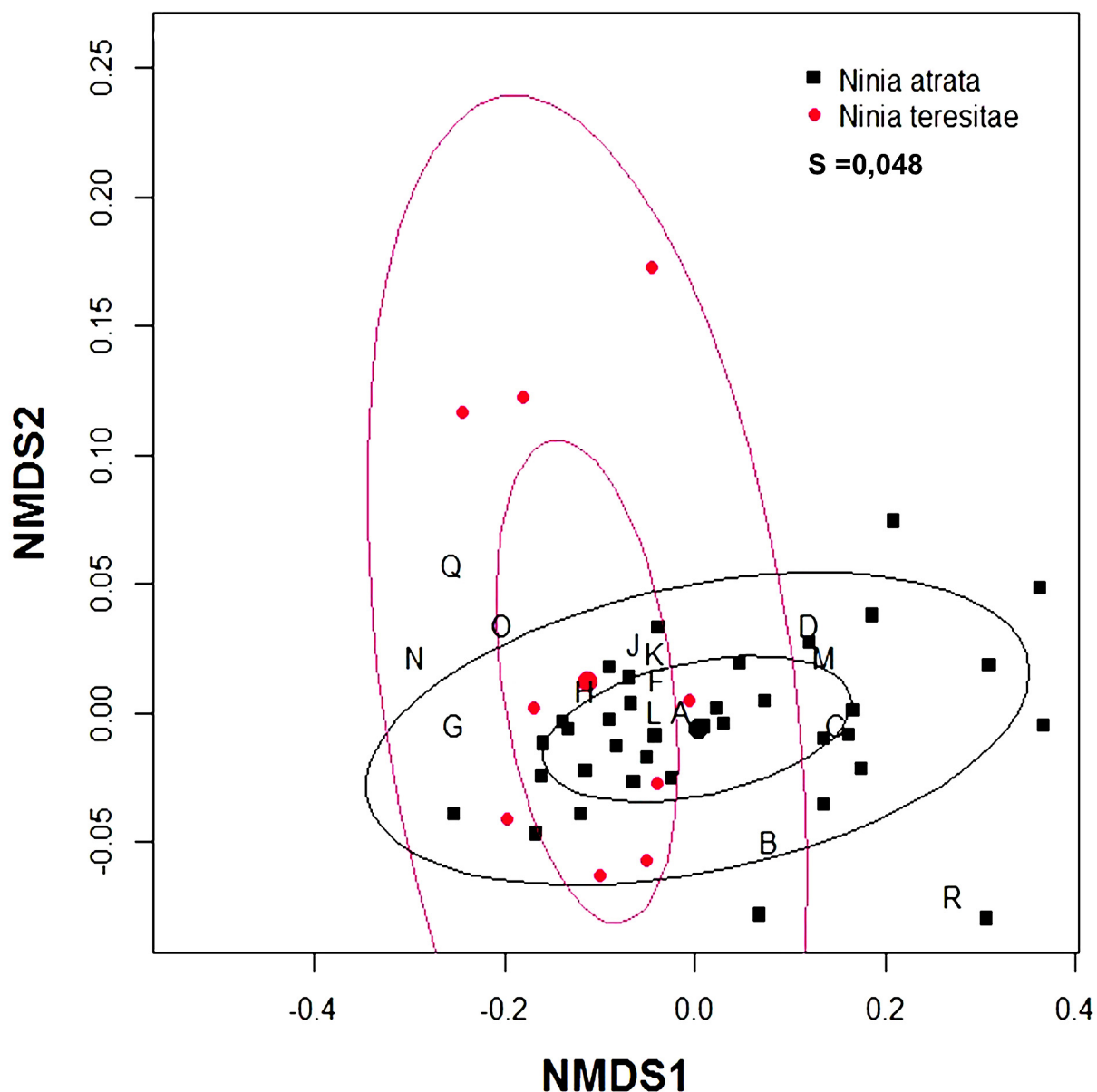


FIGURE 1. Multidimensional scaling test of the cephalic morphometry among *Ninia atrata* (black squares) and *N. teresita* (pink dots): Inner ellipse represents 0.5 of significance; outer ellipse represents 0.95 of significance. Cephalic measurements: (A) head length; (B) head width; (C) parietal length; (D) parietal width; (F) frontal length; (G) frontal width; (H) prefrontal length; (I) prefrontal width; (J) internasal length; (K) internasal width; (L) supraocular length; (M) supraocular height; (N) loreal height (O) loreal length; (P) internasal suture length; (Q) prefrontal suture length; (R) parietal suture length.

***Ninia teresitae* sp. nov.**

Fig. 2

Cresonyms. *Ninia atrata* (ICN 10661) and *Ninia maculata* (ICN 6906): Castaño-M, O. V., Cardenas-A, G., Hernández-R, E. & Castro, F, 2004, *Reptiles en el Chocó biogeográfico-catálogo*, p. 613,619. In: Rangel-Ch, J. O. (Ed.), 2004.

Holotype. Adult male, ICN 12527, collected by Lucas Barrientos on April 9 2010 at Santa Helena oil palm plantation (01°37'30"N, 78°44'20"W; 20 m asl), municipality of Tumaco, Km 28 of the Tumaco–Llorente road, 1 km S of Tumaco, department of Nariño, Colombia.



FIGURE 2. General view of the holotype (ICN 12527) of *Ninia teresitae* sp. nov, in life (A), dorsal (B) and ventral (C) views after its preservation.

Paratypes. Nine specimens: adult female (ICN 10661) collected at La Cabaña (6°3'7.82"N, 76°15'4.7"W; 1404m asl), near Calles River, Parque Natural Nacional Las Orquideas, municipality of Urrao and adult female

(MHUA 14860) collected at the Hydroelectric dam San Carlos (06°12'39.00"N, 74°50'26.00"W; 740 m asl), vereda Juarez, municipality of San Carlos, both of department of Antioquia; adult male (ICN 7927) collected between vereda La Cristalina and Dosquebradas near the Police station of Puerto Romero (05°54'41.83"N, 74°21'8.65"W; 704 m asl), municipality of Puerto Boyacá, department of Boyacá; five specimens all from the municipality of Tumaco, department of Nariño, male (ICN 12528) same provenance as the holotype, females (ICN 12523–25) and male (ICN 12526) collected at Santa Fé oil palm plantation (1°24'8.5"N; 78°33'30" W; 105 m), Km 63 of the road Tumaco–Llorente, 4 km west near Llorente; and adult female (ICN 6906) from corregimiento de Santa Cecilia (5°11'25.22"N, 76°24'16.41"W), municipality of Pueblo Rico, department of Risaralda.

Diagnosis. *Ninia teresitae* can be distinguished from all congeners by the following combination of characters: ventral surfaces of head and body spotted without regular pattern (Fig. 3), subcaudal surface homogeneously black or dark brown; two nasal scales; bilobed hemipenis (50–74% respect to hemipenial body); centrifugal, bifurcation of the sulcus spermaticus proximal to midpoint of the hemipenial body; lateral projection ornamented with a large basal hooked spine that is larger than any other spine on the hemipenial body.

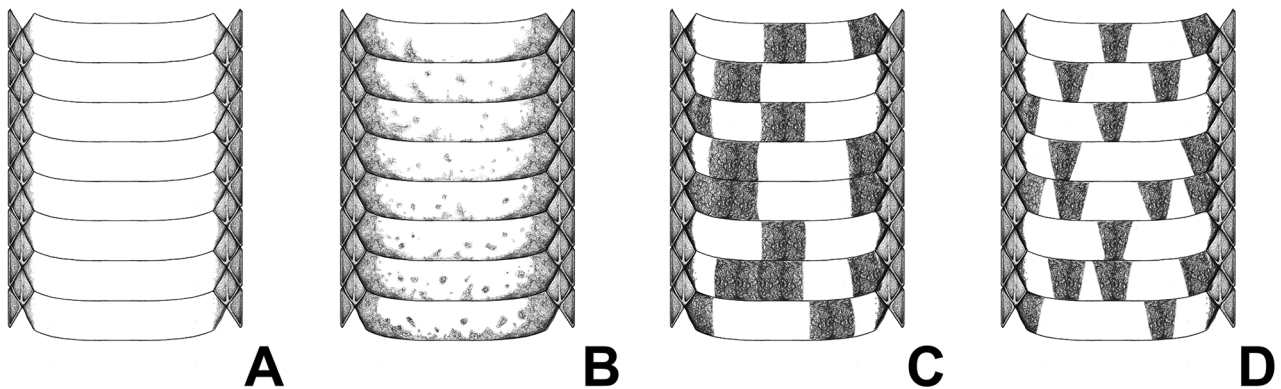


FIGURE 3. Color pattern variation of ventral surface at midbody among similar species of *Ninia*. Ventral pattern homogeneously cream in *Ninia atrata* (ICN 12530 - A), edged of the ventral scales uniformly black or dark brown with ventral scales heavily marked with black pigment in *N. teresitae* (ICN 12527 - B), squarish marking in *Ninia maculata* (UTA-R 5400 - C), and wedge-shaped in *Ninia pavimentata* (UTA-R 39508 - D).

Comparisons. *Ninia teresita* was previously identified as *N. atrata* and *N. maculata* by Castaño-M *et al.* (2004). Nevertheless, conspicuous characters distinguish it from both these species, such as the uniformly black or dark brown dorsal ground color (vs. dark body bands in *N. maculata*), ventral surfaces of head and body spotted without regular pattern, chin surface black or dark brown (vs. ventral surfaces of head and chin homogeneously cream in *N. atrata* or arranged in checkered patterns in *N. maculata*); subcaudal surface homogeneously black or dark brown (vs. subcaudal surface cream in *N. atrata*, or arranged in checkered pattern in *N. maculata*), hemipenis with a lateral projection ornamented with a large basal hook-shaped spine that is larger than any other spine on the hemipenial body (vs. hemipenial body without lateral projection), and two nasal scales (vs. one nasal scale in *N. atrata*) (Table 1).

Description of the holotype. Adult male, 429 mm TL; 105 mm CL; 324 mm SVL; CL/SVL ratio 0.32; head distinct from body; HL 11.72 mm; HW 7.14 mm; rostral wider than high; internasals wider than long (1.64 x 1.12 mm); internasal suture 0.88 mm; prefrontals longer than internasals, longer than wide (3.38 x 2.72 mm; suture 2.68 mm); frontal cordiform and slightly longer than wide (3.64 x 3.4 mm); parietals longer than wide (6.28 x 3.42 mm); interparietal suture 3.44 mm; supraoculars 1/1, each longer than wider (1.78 x 0.88 mm), entering orbit and contacting postocular; nasal scales 2/2 where proximal nasal scale contacts internasal, rostral, first supralabial, and posterior nasal in contact with loreal, prefrontal, internasal, first and second supralabials; loreal single, longer than high (2.16 x 1.8 mm), entering orbit and in contact with 2nd and 3rd supralabials; postoculars 1/1; temporal formulae 1+2, anterior temporal scale two times longer than lower posterior temporal; anterior temporal in contact with 5th and 6th supralabials; supralabials 7/7; 4th and 5th supralabials entering orbit, 5th in contact with postocular; infralabials 8/8, 1–5 in contact with two pairs of chin scales; small tubercles present on mental scale, all infralabials, and chin scales; dorsal scales in 19/19/19 rows, keeled, strongly striated, lacking apical pits; ventrals 145; divided subcaudals 65; cloacal plate undivided.

Dorsal surface uniformly dark brown, without nuchal band; ventral ground color creamish white with ventral scales heavily marked with black pigment; edged of the ventral scales uniformly black or dark brown; ventral surfaces of head and gular region black or dark brown; subcaudal surface homogenously black or dark brown. (Figs. 2, 3B, 4B).

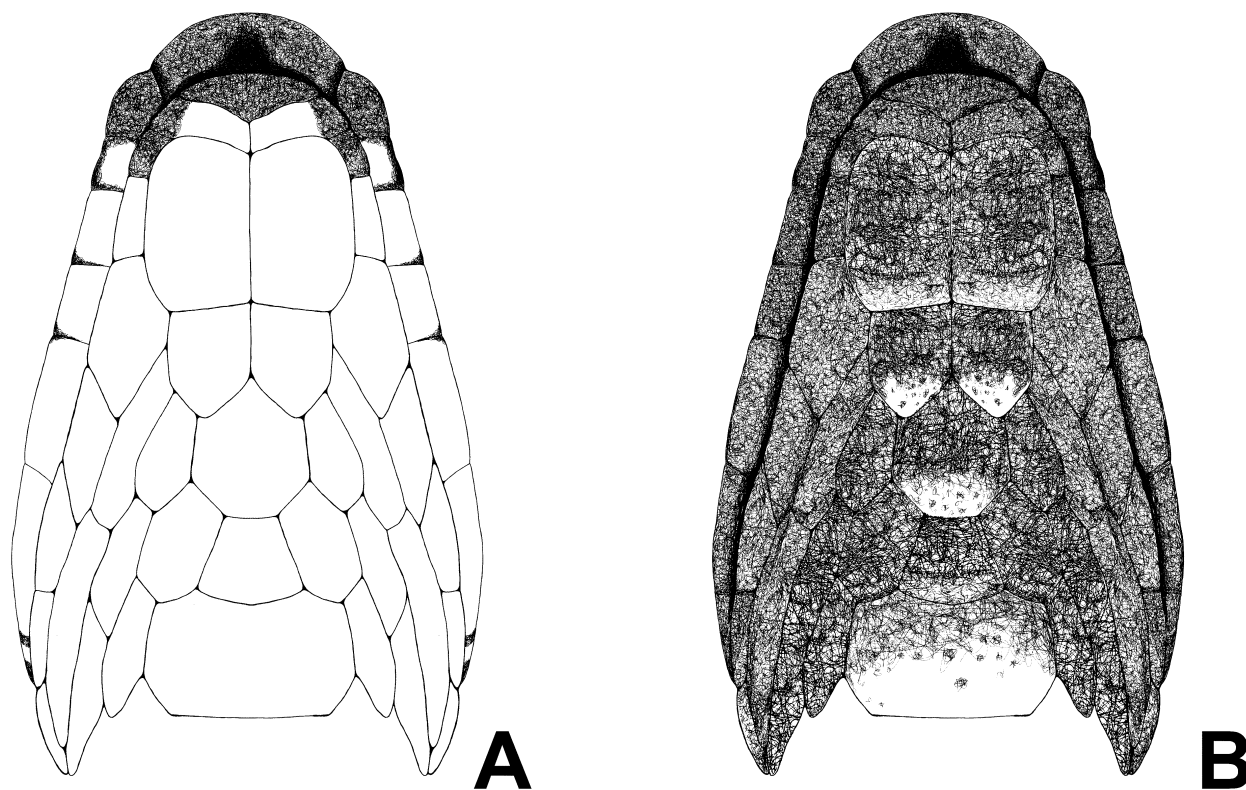


FIGURE 4. Color pattern variation in ventral surfaces of head and gular region of *Ninia atrata* (A) and in *Ninia teresitae* (B).

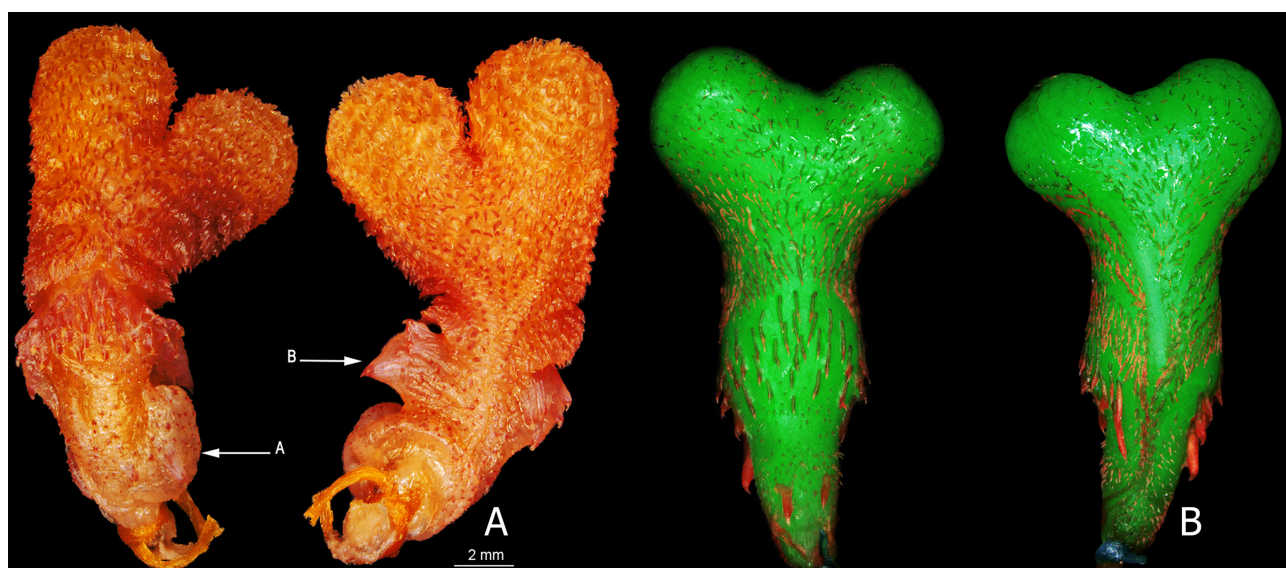


FIGURE 5. Hemipenial morphology of *Ninia teresitae* (ICN 12527—A) from municipality of Tumaco, Km 28 of the Tumaco–Llorente road, 1 km south of Tumaco, department of Nariño, Colombia; and *Ninia atrata* (ICN 12529—B) from municipality of San Martín, Vereda La Castañeda, Palmas del Meta S.A, department of Meta, Colombia. The white arrow represents the pocket-shaped structure, whereas the black arrow represents the lateral projection with a large basal hook-shaped spine.

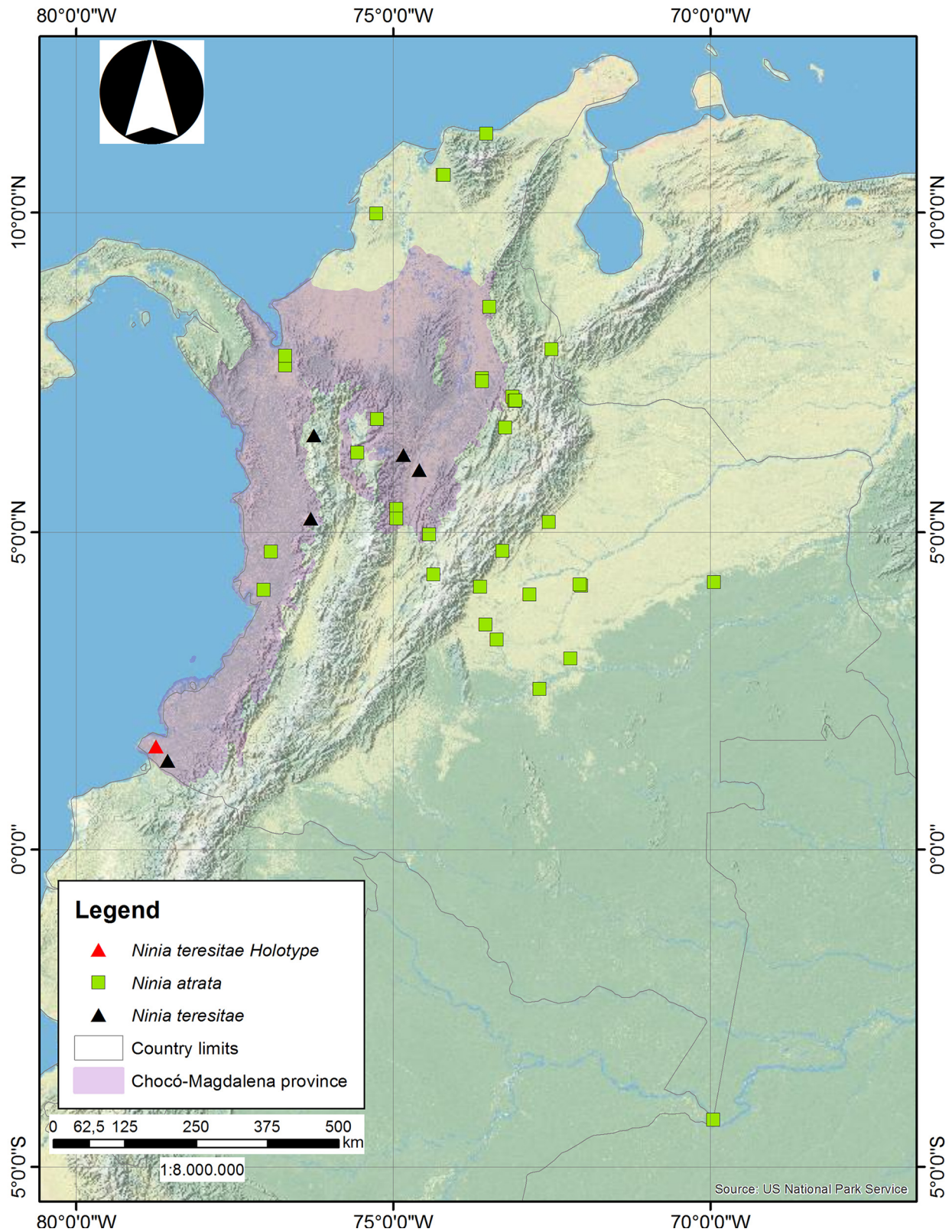


FIGURE 6. Geographical distribution of *Ninia atrata* and *Ninia teresitae* in Colombia.

Color pattern variation. The ventral coloration in some specimens are faintly pigmented with small irregular spots (ICN 7927, 12522–23, 12528); however, other specimens are strongly pigmented with large, irregular, randomly dispersed spots (ICN 6906, 12525, 12528). The nuchal band, when present, resembles the pattern exhibited by trans-Andean *Ninia atrata* populations (ICN 6906, 7927, 12522–23, 12528).

TABLE 1. Lepidosis and comparison of cephalic characters used in the MDS analysis. The abbreviations represent the following variables: SVL=snout ventral length; HL = head length; HW = head width; PL = parietal length; PW = parietal width; FL = frontal length; FW = frontal width; PFL = prefrontal length; PFW = prefrontal width, INL= internasal length; INW = internasal width; SPL = supraocular length; SPH = supraocular height; LH = loreal height; LL = loreal length; INS = internasal suture; PFS = prefrontal suture; PS = parietal suture.

Character	<i>Ninia teresitae</i> sp. nov.	<i>Ninia atrata</i>
Dorsal scales	19/19/19	19/19/19
Ventral scales		
Males	143–151 ($n=4$)	136–158 ($n=31$)
Females	150–160 ($n=5$)	133–169 ($n=30$)
Subcaudals		
Males	63–69 ($n=4$)	36–70 ($n=31$)
Females	53–63 ($n=5$)	41–65 ($n=30$)
Internasal scales	2/2	2/2
Prefrontal scales	2/2	2/2
Parietal scales	1/1	1/1
Temporal formulae	1+2	1+2 (rare 1+3)
Nasal scales	2/2	1/1
Supralabials	7/7	7/7 (occasionally 6 or 8, rare 7)
Infralabials	8/8	8/8 (occasionally 7, rare 9)
SVL (mm)		
Males	273–294 ($\bar{x}=297.75$; $n=4$)	133–370 ($\bar{x}=255.00$; $n=31$)
Females	198–346 ($\bar{x}=296.20$; $n=5$)	102–354 ($\bar{x}=235.48$; $n=30$)
HL (mm)		
Males	10.28–11.72 ($\bar{x}=10.84$; $n=4$)	6.46–12.02 ($\bar{x}=9.33$; $n=31$)
Females	9.32–11.32 ($\bar{x}=10.45$; $n=5$)	6.46–12.10 ($\bar{x}=8.84$; $n=30$)
HW (mm)		
Males	6.20–7.14 ($\bar{x}=6.51$; $n=4$)	4.30–7.52 ($\bar{x}=6.27$; $n=31$)
Females	6.22–7.30 ($\bar{x}=6.72$; $n=5$)	3.75–10.00 ($\bar{x}=5.95$; $n=30$)
PL (mm)		
Males	4.68–6.28 ($\bar{x}=5.16$; $n=4$)	3.10–6.70 ($\bar{x}=4.48$; $n=31$)
Females	4.40–6.10 ($\bar{x}=5.21$; $n=5$)	3.33–6.08 ($\bar{x}=4.25$; $n=30$)
PW(mm)		
Males	2.82–4.90 ($\bar{x}=3.57$; $n=4$)	2.14–3.72 ($\bar{x}=2.82$; $n=31$)
Females	3.00–4.08 ($\bar{x}=3.38$; $n=5$)	1.90–3.92 ($\bar{x}=2.60$; $n=30$)
FL (mm)		
Males	3.10–3.64 ($\bar{x}=3.31$; $n=4$)	2.30–3.62 ($\bar{x}=2.84$; $n=31$)
Females	2.72–3.50 ($\bar{x}=3.10$; $n=5$)	1.75–5.74 ($\bar{x}=2.88$; $n=30$)
FW (mm)		
Males	2.90–3.40 ($\bar{x}=3.10$; $n=4$)	2.12–3.82 ($\bar{x}=3.00$; $n=31$)
Females	3.18–3.56 ($\bar{x}=3.34$; $n=5$)	2.18–4.06 ($\bar{x}=2.83$; $n=30$)
PFL (mm)		
Males	2.68–3.38 ($\bar{x}=3.04$; $n=4$)	1.60–3.50 ($\bar{x}=2.50$; $n=31$)
Females	2.46–3.42 ($\bar{x}=2.95$; $n=5$)	1.20–3.30 ($\bar{x}=2.26$; $n=30$)
PFW(mm)		
Males	2.20–2.72 ($\bar{x}=2.40$; $n=4$)	1.70–3.52 ($\bar{x}=2.34$; $n=31$)
Females	2.14–3.00 ($\bar{x}=2.48$; $n=5$)	1.50–3.40 ($\bar{x}=2.18$; $n=30$)

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TABLE 1. (Continued)

Character	<i>Ninia teresitae</i> sp. nov.	<i>Ninia atrata</i>
INL (mm)		
Males	1.02–1.12 (\bar{X} =1.08; n =4)	0.75–1.30 (\bar{X} =1.03; n =31)
Females	0.96–1.16 (\bar{X} =1.04; n =5)	0.60–1.7 (\bar{X} =0.98; n =30)
INW (mm)		
Males	1.38–1.64 (\bar{X} =1.50; n =4)	0.96–1.90 (\bar{X} =1.34; n =31)
Females	1.22–1.60 (\bar{X} =1.42; N =5)	0.80–1.92 (\bar{X} =1.21; N =30)
SPL (mm)		
Males	1.28–1.78 (\bar{X} =1.56; n =4)	1.00–2.00 (\bar{X} =1.52 n =31)
Females	1.30–1.70 (\bar{X} =1.46; n =5)	0.13–2.02 (\bar{X} =1.42; n =30)
SPH (mm)		
Males	0.78–1.04 (\bar{X} =0.88; n =4)	0.68–1.63 (\bar{X} =1.02; n =31)
Females	0.82–1.00 (\bar{X} =0.91; n =5)	0.70–2.42 (\bar{X} =1.47; N =30)
LL (mm)		
Males	1.88–2.96 (\bar{X} =1.22; n =4)	0.95–2.10 (\bar{X} =1.53; n =31)
Females	1.66–2.10 (\bar{X} =1.91; n =5)	0.95–2.42 (\bar{X} =1.47; n =30)
LH (mm)		
Males	0.92–1.80 (\bar{X} =1.22; n =4)	0.76–1.38 (\bar{X} =1.07; n =31)
Females	0.98–1.14 (\bar{X} =1.04; N =5)	0.60–1.40 (\bar{X} =1.03; N =30)
INS (mm)		
Males	0.76–0.98 (\bar{X} =0.98; n =4)	0.45–1.20 (\bar{X} =0.84; n =31)
Females	0.68–1.00 (\bar{X} =0.86; n =5)	0.48–1.00 (\bar{X} =0.78; n =30)
PFS (mm)		
Males	2.48–3.32 (\bar{X} =2.74; n =4)	1.50–3.38 (\bar{X} =2.24; n =21)
Females	2.26–2.68 (\bar{X} =2.46; n =5)	1.10–2.98 (\bar{X} =2.02; n =30)
PS (mm)		
Males	2.88–3.44 (\bar{X} =3.21; n =4)	2.00–4.00 (\bar{X} =2.92; n =31)
Females	2.98–3.60 (\bar{X} =3.20; n =5)	2.00–4.00 (\bar{X} =2.77; n =30)

Hemipenial morphology ($n = 3$). Hemipenes in situ extends to the level of 7th or 8th subcaudal; organ bilobed and semicaliculate; sulcus spermaticus centrifugal and bifurcated, bifurcation point always proximal to midpoint of hemipenial body; sulcus spermaticus branch runs to tip of lobes; intrasulcar region densely covered with calyces; capitulation plane just below the bifurcation point; sulcus spermaticus walls robust and well defined; sulcus spermaticus edges ornamented with numerous spinules. In sulcate view, basally, hemipenial body covered with small hook-shaped spines; laterally, ornamented with two oblique rows of hook-shaped spines and only one lateral projection ornate with a large basal hook-shaped spine larger than any other spine on the hemipenial body; globular lobes, conspicuously differentiated from hemipenial body and homogeneously ornamented with calyces. In asulcate view, basally, hemipenial body has a pocket-shaped structure ornate with a small hook-shaped spine in the center and covered by small hook-shaped spines; basal region of spines followed by a region shallowly ornamented or nude. Medially, three or four oblique rows of hook-shaped spines arranged in an inverted “V” pattern; capitulation clotch located just above the bifurcation point of sulcus spermaticus (sulcate side); region between capitulation groove and the forked point of lobes covered with numerous and dense rows of spines organized in an inverted “V” pattern (Fig. 5).

Distribution and natural history. *Ninia teresitae* is known to inhabit in the Chocó-Magdalena biogeographic province of Colombia (Hernández-Camacho *et al.* 1992) between 50–1400 m asl, and occurs in sympatry with *N. atrata* (McCranie & Wilson 1995; Angarita-Sierra 2009, 2014). This province extends from southwestern Ecuador through the Chocóan region to eastern Panamá, including the western margin of the lower Cauca River Basin in Antioquia, the upper San Jorge and Sinu River Basins and reaching the middle Magdalena River Basin (Rangel-Ch & Arellano-P, 2004). During the past twenty years, this region has been deforested for cultivation more than 150,000 hectares of oil palm plantations (Fedepalma 2014). The holotype of *Ninia teresitae* was collected hidden under piles of leaves palm at the Santa Helena oil palm plantation during morning hours (Fig. 6)

Etymology. The specific epithet *teresitae* represent the Latin translation of the nickname from the Spanish “Teresita” and is given in honor to the grandmother of the first author, Maria Teresa Guerrero (1915–2013). “Teresita” was one of the most influential persons in her grandson’s life, who never failed to support him and encouraged his endless passion for snakes.

Discussion

During the Miocene and Pliocene, the continued geological uplift provides many possible scenarios for the diversification and the southward dispersal of the Middle American herpetofauna over an emerging landmass (Savage 2002). Several elements of the Central American herpetofauna extend well into South America and vice-versa, through the completion of the Panamanian Isthmus during the Pliocene. This event allowed the formation of assemblages of Neotropical snakes with members of lineages whose radiations were centered in Central or in South America (Cadle & Greene 1993). As a consequence, biogeographical regions such as the Chocó-Magdalena province of Colombia (Hernández-Camacho *et al.* 1992) and region 12 defined by Cadle (1985) coincide with the snake’s spatial features and generic compositions, in which the dominant elements are the Central American species or species with a closer relationships to them.

The hemipenial morphology of *Ninia* spp. shows clearly an anatomical tendency among Central American and South America species. Angarita-Sierra (2014) found that the presence or absence of lateral projections in basal portion of the organs apparently divides *Ninia* in two groups. The first group lacks lateral projections and is composed of three South American species (*N. atrata*, *N. franciscoi*, and *N. hudsoni*) and two Central American species (*N. espinali* and *N. maculata*). The second group possesses lateral projections and is composed of five Central American species (*N. diademata*, *N. labiosa*, *N. pavimentata*, *N. psephota*, and *N. sebae*). The presence of lateral projections on the hemipenis of *Ninia teresitae* makes it the only member of the genus from South America, so far known, that shares this feature with Nuclear Central American (*sensu* Schuchert 1935) congeners. This putative close relationship showed by *Ninia teresitae*, supported the biogeographic hypothesis of Ingrasci (2011) who stated that the genus *Ninia* has two main areas of diversification, the highlands of Nuclear Central America, and the highlands associated with the Talamanca region of Costa Rica and western Panama. Therefore, *Ninia teresitae* likely derived from the Nuclear Central America lineage following an evolutionary trend and dispersal pattern similar to other immigrant lineages that arrived independently in South America, such as *Coniophanes* (Günther 1858; Cadle 1985), *Rhadineae* (Günther 1865; Myers 1974), *Leptodeira* (Linnaeus 1758, Duellman 1958, Daza *et al.* 2009), and *Urotheca* (Peters, 1863; Myers 1974), among others.

Hernández-Camacho *et al.* (1992) proposed for Colombia and the northern South America ninety-nine biogeographic unities divided hierarchically as territories, massif and provinces (Top), and districts (Bottom). However, these authors never revealed any evidence (diversity patterns, endemism, geological and climate factors, edaphic features, physiognomic vegetation or cladistic criteria) to create these biogeographic units. In addition, they explained that their proposal must be understood as a provisional classification that includes some heuristic or instrumental value, but that needs to be tested and is open to rectification. Despite this, these units have been broadly employed by researchers, planners, and governmental entities to create policies of land use and conservation areas (Henao-Sarmento *et al.* 2008; Latorre *et al.* 2014; Colombia 2012; Ramírez-Chaves *et al.* 2013; Roncancio *et al.* 2011; Solar *et al.* 2013). As Hernández-Camacho *et al.* (1992) points out, these biogeographic units must be tested before employing them. Therefore, a cluster of taxa with restricted distributions and a close relationship with the physical and biotic features of each biogeographic unit must be found. In the case of the Chocó-Magdalena province, species such as *Helicops danieli* (Amaral 1938), *Ninia teresitae*, *Rhinobothryum bovalli* (Andersson 1916), and *Urotheca euryzona* (Cope 1862) are apparently restricted to this unit (Niceforo Maria 1942; Cadle 1985; Rossman 2002; Rojas-Morales 2012). Moreover, *Ninia teresitae*, *Rhinobothryum bovalli*, and *Urotheca euryzona* occurs in the entire range of the Chocó-Magdalena province, making them candidates to characterize this biogeographic unit. Other taxa show the same restricted spatial pattern such as *Agalychnis terranova* (Rivera-Correa *et al.* 2013), *Craugastor raniformis* (Boulenger 1896), *Colostethus inguinalis* (Cope 1866), *Echinosaura palmeri* (Boulenger 1911), and *Leucopternis plumbea* (Salvin 1868), (Fritts *et al.* 2002; Grant 2004; Marquez *et al.* 2005; Rivera-Correa *et al.* 2013; Ospina-Sarria *et al.* 2015). All these evidences corroborate the hypothesis stated by Hernández-Camacho *et al.* (1992) and support that the Chocó-Magdalena province could be consider a full biogeographic unit.

Much of the biological diversity in the Neotropics remains undescribed, with large areas still lacking intensive sampling, especially in northern South America, and particularly in Colombia. Colombia, despite its key geographical position in the historical exchange of faunas between North and South America, remains a 'black box' regarding the systematics of many groups (Pinto-Sanchez *et al.* 2015). In the past twenty-five years, enormous efforts have been made by Colombian and foreign researchers to compile, sample, and elucidate the biological diversity of the country (e.g., Rangel-Ch 1995, 2004, 2009). However, much of this compilation does not consider the direct examination of the specimens cited. Hence, several records were based on specimens erroneously identified. It was the case of *Ninia teresitae*, which was cited as *N. atrata* and *N. maculata* by Castaño-M *et al.* (2004). Often, these misidentifications occur because the researchers of the past decades have employed the key developed by Peters and Orejas-Miranda (1970) as their unique tool to identify specimens. For instance, one of the characters employed by Peters and Orejas-Miranda (1970) to distinguish *N. atrata* from *N. maculata* was the presence or absence of dark markings on ventral surfaces of body. However, dark markings are present on the venter of *N. maculata* and *N. pavimentata*, (Fig. 3), arranged in patterns such as wedge-shaped or squarish shaped, checkered pattern, or dark rectangular markings (Savage & Lahanas 1991). As a result, the irregular spotted patterns seen in specimens of *Ninia teresitae* were allocated to *N. maculata* when individuals were heavily pigmented and to *N. atrata* when it was faint. Finally, our results indicate that proper and careful revision of the *N. atrata* species complex will help to understand and clarify taxonomic composition of the genus.

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APPENDIX. Specimens examined.

- Ninia atrata* (n = 61). COLOMBIA:** ANTIOQUIA: Medellín: (AMNH 35673–74). META: Puerto Lleras: Lomalinda: (UTA-R 3603, 3607, 3641, 3715–16, 3640, 3649), San Martín: Vereda La Castañeda: Palmas del Meta S.A.: (ICN 10756–67, 12529–30); VALLE DEL CAUCA: (USNM 151675). **ECUADOR:** MANABI: Río Cauque: Pedernales-El Carmen road: (UTA-R 23525). **TRINIDAD & TOBAGO:** TRINIDAD: (FNMH 49953, KU112622), St. George: (USNM 146362), Tucker Valley: (AMNH 64472); **TOBAGO:** St. John: (USNM 228096). **VENEZUELA:** ARAGUA: Rancho Grande: (AMNH 98269, FNMH 204475); MIRANDA: Power plant Curupao: (AMNH 59425, 59427).
- Ninia maculata* (n = 2). HONDURAS:** OLANCHO, Sierra de Botaderas Cauca, 5°38'382"N, 86°21'145"W, elevation 895 m, (UTA-R 54000); **PANAMÁ:** DARIÉN: (USNM 50114).
- Ninia pavimentata* (n = 8). GUATEMALA:** BAJA VERAPAZ: Cerro Verde, (UTA-R 7099); SAN MARCOS: San Rafael Pie de la Cuesta, Aldea La fraternidad, elevation 1600m, (UTA-R 39508, 42402, 42405–08, 46560).