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Hemipenial Morphology in the Semifossorial Snakes of the Genus *Ninia* and a New Species from Trinidad, West Indies (Serpentes: Dipsadidae)

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Abstract. The hemipenial morphology of nine species in *Ninia* is described for the first time. A total of 65 hemipenes of all recognized species of *Ninia* were examined. As a result of the evaluation of the hemipenial and caudal morphology, *Ninia diademata labiosa* is elevated to full species status and a new species is described from 240 m above sea level in the Northern Range of Trinidad. The new species exhibits several diagnostic features, including (1) a primary temporal scale that is extremely long and contacts the upper labial scales 5–7; (2) a temporal scale formula 1 + 2, with the primary temporal scale three times longer than the lower posterior temporal; and (3) forked hemipenes. The male genitalia of *Ninia* are excellent indicators of species limits and an effective tool to clarify the identity of cryptic species in the genus.

Keywords. Male genitalia; Reproduction; Squamata; Taxonomy.

Resumen. Este trabajo presenta por primera vez la descripción de la morfología hemipenial de nueve especies de *Ninia*. Se revisaron 65 hemipenes de todas las especies conocidas del género. Como resultados de la evaluación de la morfología hemipenial y caudal, se eleva a *Ninia diademata labiosa* al nivel de especie formal. Adicionalmente, se describe una nueva especie para el género *Ninia* que habita la isla de Trinidad y se diagnostica por los siguientes caracteres: (1) escama temporal anterior extremadamente larga y en contacto con 5ª, 6ª, y 7ª escama supralabial; (2) fórmula temporal 1 + 2, en la cual la escama temporal anterior es tres veces más larga que la escama temporal posterior inferior; y (3) hemipenes bilobulados y divididos. Se concluye que la morfología hemipenial en el género *Ninia* es un excelente indicador de especies y es una herramienta taxonómica muy útil para dilucidar la identidad de las especies crípticas en el género.

INTRODUCTION

Ninia is a widespread Neotropical genus of semifossorial snakes composed of nine species that occur from southern Mexico to northern Peru. These snakes are an important and locally abundant component of the leaf-litter herpetofauna (Savage and Lahanas, 1991). Nonetheless, this taxon has been poorly studied, and several aspects of its biology remain unknown (see Dunn, 1935; Stuart, 1948; Taylor, 1951; Schmidt and Rand, 1957; and Peters and Orejas-Miranda, 1970). In the last two decades, some herpetologists suggested that the genus requires revision. Savage and Lahanas (1991) were the first in recent decades to attempt to solve some of the systematic problems of named subspecies of *Ninia*, focusing on taxa in Costa Rica and Panamá. McCranie and Wilson (1995) showed that two different and new entities *N. celata* and *N. espinali*, were hidden in the *Ninia atrata* complex from El Salvador and Honduras. Smith (1996) found geographic variation in *N. sebae* and *N. diademata* throughout their broad distribution in Central America. Additionally, he showed the relevance of studying intraspecific variation for the comprehension of the phenotypic plasticity in the genus for characters such as pigmentation, color pattern, body size, segmentation and cephalic morphology.

Likewise, Smith and Campbell (1996), after evaluating 14 specimens from Guatemala, concluded that *Ninia maculata pavimentata* deserved full species status. Savage (2002) detailed the taxonomic status, morphology, geographic distribution, and natural history of the four species that occur in Costa Rica, and Angarita-Sierra (2009) reported on the geographic variation of *N. atrata* in Colombia.

Hemipenial morphology can be a useful marker of snake relationships at many taxonomic levels (Keogh, 1999). Several herpetologists have used male genitalia as a phylogenetic and taxonomic tool to resolve snake relationships (Cope, 1893, 1895; McCann, 1946; Inger and Marx, 1962; Dowling, 1967, 2002; Myers and Campbell 1981; Branch, 1986; Campbell and Smith, 1998; Zaher, 1999; Myers and Cadle, 2003; Jadin *et al.* 2010; Cadle 2012). Zaher (1999) and Zaher and Prudente (2003) used hemipenial morphology of various suprageneric colubroid clades to describe and compare the variation within the colubroid radiation and assess their bearing on the higher level phylogeny of colubroids. Similarly, Passos *et al.* (2009, 2010, 2012) used hemipenial characters to describe new species and test species boundaries in *Atractus*. Likewise, Harvey and Embert (2008), Passos *et al.* (2004, 2005), MacCulloch and Lathrop (2004), and Cadle and Myers (2003) have attempted to solve the taxonomic

and phylogenetic problems of *Dipsas* by including hemipenial features as a part of their datasets. Despite all these contributions, no one has attempted a comprehensive taxonomic and systematic assessment of the species throughout *Ninia* since Dunn's (1935) early efforts. For this reason, the aim of this study is to provide new evidence to clarify the identity of the species of *Ninia* that are poorly described and describe hemipenial morphology as an effective tool to clarify the identity of cryptic species in genus.

MATERIALS AND METHODS

A total of 65 hemipenes of all the recognized species of *Ninia* specimens (Appendix) representing nine species of the genus (Savage, 2002) was examined from seven natural history collections. Frequently, fully or partial everted hemipenes were badly preserved or damaged, and their taxonomic value was limited. In this case, only the unaffected characters such as the hook-shaped basal spines, the bifurcation point of the *sulcus spermaticus*, and the spine rows were scored. The sub-caudal counts used the method of Peters (1964), and the ventral counts used to describe the new species from Trinidad follow Dowling (1951). The vertebral insertion point of the muscle *retractor penis magnus*, hemipenis forking point, and hemipenial length were measured following Dowling and Savage (1960). Tail length (TL) and snout–vent length (SVL) measurements were made to the nearest 0.5 mm using a metric ruler. Hemipenial length was measured to the nearest 0.02 mm using a Vernier caliper with the help of a dissection microscope. This measurement was only used to calculate the degree of apical differentiation and classify hemipenes into one of the four categories described by Keogh (1999): simple (S), shallowly forked (SF), forked (F), and deeply forked (DF). Institutional acronyms follow Sabaj Perez (2010).

Hemipenial preparation procedures of Myers and Cadle (2003), Zaher and Prudente (2003), and Smith and Ferrari-Castro (2008) were followed, with the addition of (1) complete cut and dissection of the *muscle retractor penis magnus* in the attachment point between the muscle and the hemipenial lobes, and (2) a water bath (37.7°C) for 15 or 20 min to accelerate the staining process (Jadin and Smith, 2010). Terminology for hemipenial morphology follows Dowling and Savage (1960), Myers (1974), Myers and Campbell (1981), Keogh (1999), and Zaher (1999).

RESULTS

The copulatory organ in *Ninia* is conservative and all species share the following general morphology:

hemipenes extending from caudal base to 6th–14th sub-caudal scales, shallowly forked or forked; *sulcus spermaticus* centrifugal or centrolineal, bifurcate, each branch lying on the surface of the everted hemipenis and running longitudinally toward the apex of the lobes; the bifurcation point of the *sulcus spermaticus* located at mid-point of hemipenial body (except in *N. espinali*, *N. hudsoni*, *N. psephota*); hemipenial body slender or robust, with basal projections ornamented with hooks and spinules on the sulcate and asulcate sides, or lacking projections; asulcate side with only one medial projection ornamented with rows of spines arranged in an inverted “V” (except in *N. espinali*); lobules globular or slender and with a biculcate condition; vertebral insertion of *muscle retractor penis magus* at different levels of sub-caudal counts (24, 25, 26, 27, 28, 29, 30, 31, 32, 33, or 34). Nevertheless, taxonomic groups can be distinguished unambiguously, and each species has diagnostic hemipenial morphology.

Through this morphological survey, I discovered a new cryptic species in the *Ninia atrata* complex from the Northern Range of Trinidad that can be distinguished from all congeners by hemipenial and cephalic morphology. Likewise, the hemipenial morphology of the *Ninia didemata* provides evidence to elevate a subspecies within this group to species level. The following descriptions of the species belonging to *Ninia* were based on hemipenial morphology and caudal characters (Table 1).

Previously recognized species

Ninia atrata (Hallowell, 1845)

Hemipenes extend from the caudal base to 9th–14th sub-caudal scale; shallowly forked; capitate only on the asulcate side; *sulcus spermaticus* centrifugal, bifurcate, the point of bifurcation always at mid-point of the hemipenis body and up to the 4th–7th sub-caudal scale. Each branch of the *sulcus spermaticus* runs longitudinally to the tip of the lobes in which it inserts laterally (Fig. 1A). The intrasulcar region is covered with calyces ornamented with spinulate edges. The walls of the *sulcus spermaticus* are robust and well defined with edges ornamented with numerous spinules, which decrease gradually in length toward the apex of each lobe. In sulcate view, basally the hemipenis is covered with small hook-shaped spines. Laterally, it possesses two oblique rows on each side of the hemipenis body with large hook-shaped spines that gradually decrease in length. The first basal spine of the first row is larger than any other spine that ornaments the hemipenis. The lobes are globular, clearly differentiated from the body, which is slender or robust, without lateral or basal projections. Each lobe is ornamented homogeneously with large calyces with spinulate edges. In asulcate view, basally the hemipenis has two conspicuous, long, hook-shaped

Table 1. Hemipenial meristic characters evaluated in the genus *Ninia*. Hemipenial length, *sulcus spermaticus* bifurcation point, and vertebral insertion point are measured in subcaudals. TL = tail length.

Species	Hemipenial length	<i>Sulcus spermaticus</i> bifurcation point	Vertebral insertion point	No. subcaudals	TL (mm)	SVL (mm)	Tail Proportion %
<i>Ninia atrata</i>	9, 14 (n = 10)	6, 7	29, 32	55–67 (\bar{X} = 61.5)	72–95 (\bar{X} = 81.5)	221–315 (\bar{X} = 273)	28.2–30.2 (\bar{X} = 30)
<i>Ninia diademata</i>	8, 9 (n = 4)	4, 5	29	89–93 (\bar{X} = 91)	100–114 (\bar{X} = 107)	214–250 (\bar{X} = 232)	40–57.23 (\bar{X} = 48.61)
<i>Ninia espinali</i>	10 (n = 3)	3	31, 32	55–66 (\bar{X} = 62.3)	80–89 (\bar{X} = 84.5)	270–299 (\bar{X} = 284.5)	29.77–34.78 (\bar{X} = 32.27)
<i>Ninia franciscoi</i> sp. nov.	8, 9 (n = 1)	4, 5	33	57	69	250	27.6
<i>Ninia hudsoni</i>	9, 12 (n = 3)	5, 6	26, 30, 31	60–72 (\bar{X} = 66)	65–127 (\bar{X} = 103.3)	210–372 (\bar{X} = 316.6)	30.95–32.07 (\bar{X} = 32, 4)
<i>Ninia labiosa</i>	7, 8, 9 (n = 13)	3, 4, 5	27, 28, 29, 30, 31	98–119 (\bar{X} = 102)	89–128 (\bar{X} = 109)	175–241 (\bar{X} = 215)	37.3–55.9 (\bar{X} = 47.6)
<i>Ninia maculata</i>	7, 8 (n = 2)	4, 5	28	58–62 (\bar{X} = 60)	69–73 (\bar{X} = 71)	220–250 (\bar{X} = 235)	31.4–33.2 (\bar{X} = 32.9)
<i>Ninia pavimentata</i>	7, 10 (n = 7)	4, 5	25, 27, 30, 31	58–70 (\bar{X} = 64)	73–83 (\bar{X} = 82)	176–220 (\bar{X} = 205)	46.6–55.9 (\bar{X} = 51.7)
<i>Ninia psephota</i>	7, 8, 11 (n = 3)	5, 6	27, 28, 29	73–77 (\bar{X} = 75)	84–134 (\bar{X} = 118)	230–365 (\bar{X} = 306)	36.5–41.1 (\bar{X} = 38.4)
<i>Ninia sebae</i>	6, 7, 8, 9, 13 (n = 19)	2, 3, 4, 5, 6	24, 25, 26, 27, 28, 29, 30, 31, 32	53–68 (\bar{X} = 62)	64–94 (\bar{X} = 75)	191–285 (\bar{X} = 227)	30.0–38.6 (\bar{X} = 33.9)

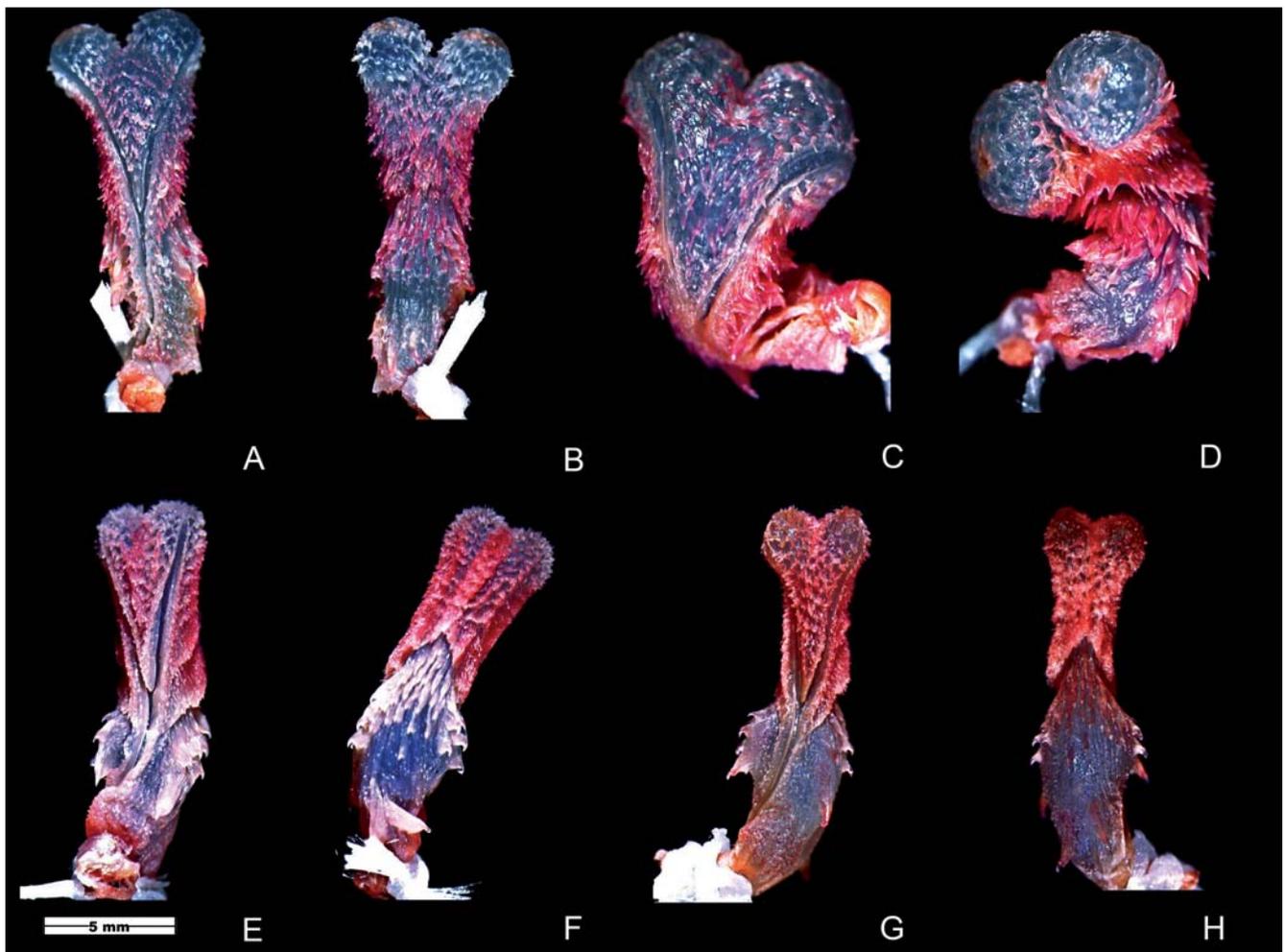


Figure 1. Hemipenial architecture in *Ninia*. (A–B) *N. atrata* (AMNH 123767). (C–D) *N. espinali* (KU 183928). (E–F) *N. diademata* (AMNH 162268). (G–H) Sulcate side of *N. labiosa* (UTA-R 1237).

spines surrounded by small spines. The basal spiny region is followed by a weakly ornamented or totally nude region (Fig. 1B). Medially, the hemipenis body possesses a globular projection ornamented with 3–4 rows of spines organized as an inverted “V”. The spines that ornament the medial projection increase gradually in length from the base to the apex. The plane of capitation coincides with the point at which the medial projection protrudes. The plane of capitation is located just distal to the bifurcation point of the *sulcus spermaticus* (sulcate side). The region between the capitation plane and the forked point of the lobes possesses numerous dense rows of spines organized in an inverted “V”.

***Ninia celata* McCranie and Wilson, 1995**

Only one male of *Ninia celata* was available for the current study (KU 35526). The hemipenis of this specimen was badly preserved, damaged, and dissected from the snake's body. Its taxonomic value is limited, and I could not examine the morphological characters in full eversion because the hemipenes were totally broken. Hence, the description is based on the observations of the sulcate side. The hemipenis is shallowly forked, bicaliculate, *sulcus spermaticus* centrifugal and bifurcate; the point of bifurcation is at mid-point of the hemipenis body. Each branch of the *sulcus spermaticus* runs longitudinally to the tip of the lobes in which it inserts laterally. The intra-sulcar region is covered with numerous spinules and has calyces near the forked point of the lobes. The walls of the *sulcus spermaticus* are robust and well defined with edges ornamented with numerous spinules that decrease gradually in length toward the apex of each lobe. Basally, the hemipenis is covered with hook-shaped spines organized in longitudinal ridges. Laterally, it has two oblique rows on each side of the hemipenis body with large hook-shaped spines that decrease gradually in length.

***Ninia espinali* McCranie and Wilson, 1995**

The hemipenial morphology of this species was described by McCranie and Wilson (1995) on the basis of one of their paratypes. The following description adds three specimens from new localities in Honduras and El Salvador (Appendix). Hemipenes extend from the caudal base to the 9th–10th sub-caudal scales; shallowly forked; capitate only on the asulcate side; *sulcus spermaticus* centrifugal, bifurcate, the bifurcation point always proximal to mid-point of hemipenis body and to 3rd sub-caudal scale (Fig. 1C). Each branch of the *sulcus spermaticus* runs longitudinally to the tip of the lobes in which it inserts laterally. The intra-sulcar region is covered with a few (< 60) spinules. The walls of the *sulcus spermaticus* are robust and well defined with edges ornamented with numerous spinules that decrease gradually in length toward

the apex of each lobe. In sulcate view, basally the hemipenis is covered with small hook-shaped spines. Laterally, it possesses 3–4 oblique rows on each side of the hemipenis body with large, hook-shaped spines, which decrease gradually in length. The first basal spine of the first row is larger than any other spine that ornaments the hemipenis. The lobes are globular, clearly differentiated from the body, which is slender, without lateral or basal projections. Each lobe is ornamented homogeneously with large calyces with spinulate edges with five or six spinules. From the asulcate view, basally the hemipenis has two conspicuous and long hook-shaped spines, surrounded by small spines that ornament the small basal projection (Fig. 1D). The basal region of spines is followed by a shallowly ornamented or totally nude region. Medially, the hemipenis body possesses a globular projection ornamented with 3–4 rows of spines organized in a horizontal linear pattern. The spines that ornament the medial projection decrease gradually in length from the base to the apex. The plane of capitation coincides with the point in which the medial projection protrudes. The plane of capitation is located distal to the bifurcation point of the *sulcus spermaticus* (sulcate side) and up to the 4th sub-caudal scale. The region between the capitation plane and the forked point of the lobes possesses 8–10 rows of spines organized in a parallel line.

***Ninia diademata* Baird and Girard, 1853**

Conspicuous differences exist among populations of this species in the hemipenial architecture, which provides evidence to recognize two geographical sub-groups: (1) the *N. d. labiosa* sub-group, distributed at moderate elevations of the Pacific slopes from Oaxaca, Mexico, to Guatemala, and (2) the *N. d. diademata* sub-group (combining the subspecies *N. d. diademata*, *N. d. nietoi* and *N. d. plorator*), distributed on the Caribbean slopes from Puebla and Veracruz, Mexico, to Honduras. The names of the units were taken from Burger and Werler (1954) and Peters and Orejas-Miranda (1970), who noted the same populations as sub-specific taxa from *Ninia diademata*.

***Ninia diademata nietoi* sub-group.** Hemipenes extend from the caudal base to the 8th–9th sub-caudal level; capitate only on asulcate side; *sulcus spermaticus* centrolateral, bifurcate, the point of bifurcation always at mid-point of the hemipenis body and up to sub-caudal scale 4–5 (Fig. 1E). Each branch of the *sulcus spermaticus* runs longitudinally to the tip of the lobe in which it inserts orbitally. The intra-sulcar region is covered with numerous calyces with strongly spinulate edges that decrease gradually in length toward the apex of each lobe. In sulcate view, basally the hemipenis is covered with small hook-shaped spines. Laterally, it possesses two globular projections on each side of the hemipenis body, which is

ornamented with 2–3 hook-shaped rows of spines that decrease gradually in length. The lobes are globular and shallowly differentiated from the body, which is as wide as the lateral projections. Each lobe is homogeneously ornamented with large calyces with spinulated edges. In asulcate view, basally the hemipenis has a small ornamented projection with two long hook-shaped spines. The basal projection is followed by a shallowly ornamented or totally nude region. Medially, the hemipenis body possesses a globular ornamented projection with 4–5 hook-shaped rows of spines of equal size arranged in an inverted “V” (Fig. 1F). The plane of capitation coincides with the point in which the medial projection protrudes. The plane of capitation is located at the same level of the bifurcation point of the *sulcus spermaticus* (sulcate side). The region between the capitation plane and the forked point of the lobes possesses numerous, dense spines and calyces. The spines are located just distal to the point where the medial projection protrudes and form an inverted “V”. These spines are followed by dense, homogeneous calyces organized in longitudinal ridges.

***Ninia diademata labiosa* sub-group.** Hemipenes extend from the caudal base to the 7th–11th sub-caudal scale; capitate (sulcate and asulcate sides); *sulcus spermaticus* centrifugal, bifurcate, the point of bifurcation always at mid-point of the hemipenis body and up to the 4th–5th sub-caudal scale and coincides with the plane of capitation (Fig. 1G). Each branch of the *sulcus spermaticus* runs longitudinally to the tip of the lobes in which it inserts laterally. The intra-sulcar region is covered with numerous calyces with strongly spinulate edges. The walls of the *sulcus spermaticus* are well defined with ornamented edges with numerous spinules that decrease gradually in length toward the apex of each lobe. In sulcate view, basally the hemipenis is covered with small hook-shaped spines. Laterally, it possesses two globular projections on each side of the hemipenis body that are ornamented with 2–3 rows of hook-shaped spine that decrease gradually in length. The lobes are globular and clearly differentiated from the slender body. Each lobe is ornamented homogeneously with large calyces with spinulate edges. In asulcate view, basally the hemipenis has a small ornamented projection with two long hook-shaped spines. The basal projection is followed by a shallowly ornamented or totally nude region (Fig. 1H). Medially, the hemipenis body possesses a globular ornamented projection with 3–4 hook-shaped rows of spines of equal size organized in an inverted “V”. The plane of capitation coincides with the point in which the medial projection protrudes. The plane of capitation is located just distal to the bifurcation point of the *sulcus spermaticus* (sulcate side). The region between the capitation plane and the forked point of the lobes possesses numerous, dense rows of spines organized in an inverted “V”.

***Ninia hudsoni* Parker, 1940**

Hemipenes extend from the caudal base to the 9th–12th sub-caudal scale; non-capitate on the sulcate side; shallowly forked; *sulcus spermaticus* centrifugal, bifurcate, the bifurcation point always slightly proximal to the mid-point of the hemipenis body and up to 5th–6th sub-caudal scale. Each branch of the *sulcus spermaticus* runs longitudinally to the tip of the lobes in which it inserts laterally. The intra-sulcar region is covered with numerous spinules and dense calyces with strongly spinulate edges (Fig. 2A). The walls of the *sulcus spermaticus* are robust and well defined with ornamented edges with numerous spinules that decrease gradually in length toward the apex of each lobe. In sulcate view, basally it is covered with a few small spines. The hemipenis does not show basal projections. Laterally, it has 2–3 oblique rows on each side of the hemipenis body with large hook-shaped spines of the same size, and it decreases gradually in length. The first basal spine of the first row is larger than any other spine that ornaments the hemipenis. The lobes are oblong, weakly differentiated from the hemipenis body, and covered homogeneously with dense and numerous calyces with large spinules (6–8 spinules per calycle). In asulcate view, basally the hemipenis possesses a small projection ornamented with a few small hook-shaped spinules and two large and parallel hook-shaped spines. Distal to this basal projection is a band-shaped, shallowly ornamented or totally nude region. This region is followed by a medial globular ornamented projection with 3–4 hook-shaped rows of spines of equal size organized in an inverted “V” (Fig. 2B). The plane of capitation is located just distal to the bifurcation point of the *sulcus spermaticus* (sulcate side). The region between the capitation plane and the forked point of the lobes possesses numerous, dense rows of spines organized in an inverted “V”.

***Ninia maculata* (Peters, 1861)**

Hemipenes extend from the caudal base to 8th sub-caudal scale; non-capitate (on sulcate and asulcate sides); shallowly forked; *sulcus spermaticus* centrifugal, bifurcate, the point of bifurcation always at the mid-point of the hemipenis body to 5th–6th sub-caudal scale. Each branch of the *sulcus spermaticus* runs longitudinally to the tip of the lobes in which it inserts laterally. The walls of the *sulcus spermaticus* are well defined with ornamented edges with numerous homogeneously sized spinules (Fig. 2C). The intra-sulcar region is covered with large calyces with edges weakly ornamented with long spinules. In sulcate view, basally the hemipenis is weakly covered with small hook-shaped spines. Laterally, it does not show projections; the hemipenis is ornamented only with 3–4 oblique, hook-shaped rows of spines that

decrease gradually in length. The lobes are globular and clearly differentiated from the slender body. Each lobe is homogeneously ornamented with large calyces with spinulate edges. In asulcate view, basally the hemipenis does not have a small projection, but is ornamented with two long hook-shaped spines. The basal spines are followed by a shallowly ornamented or totally nude region (Fig. 2D). Medially, the hemipenis body is ornamented with 4–5 hook-shaped rows of spines of equal size organized in an inverted “V” that ends just distal to the bifurcation point of the *sulcus spermaticus* (sulcate side). The region in between, which corresponds to the bifurcation point of the *sulcus spermaticus* and forked point of the lobes, possesses 4–6 dense rows of spines organized in an inverted “V”.

***Ninia pavimentata* (Bocourt 1883)**

Smith and Campbell (1996) elevated *Ninia maculata pavementata* (Bocourt, 1883; Stuart 1948; Savage and Lahanas, 1991) from the sub-specific level to full species

status based on 14 specimens from several localities in Guatemala based on a Mann-Whitney analysis using segmental counts. I found that the hemipenial architecture of this species has significant differences that support the full species status of *Ninia pavimentata* proposed by Smith and Campbell (1996).

Hemipenes extend from the caudal base to the 7th–10th sub-caudal scale; shallowly forked; capitata (on sulcate and asulcate sides); *sulcus spermaticus* centrifugal, bifurcate, the point of bifurcation always at mid-point of the hemipenis body and up to 4th or 5th sub-caudal scale (Fig. 2E). Each branch of the *sulcus spermaticus* runs longitudinally to the tip of the lobes in which it inserts laterally. The walls of the *sulcus spermaticus* are robust and well defined with ornamented edges with numerous spinules that only extend on the first part of the hemipenial body until the bifurcation point of the *sulcus spermaticus* (rarely just distal to the bifurcation point of the *sulcus spermaticus*). The intra-sulcar region is covered with calices with strongly spinulate edges. Basally, the hemipenis is covered with small, hook-shaped spines. Laterally, it

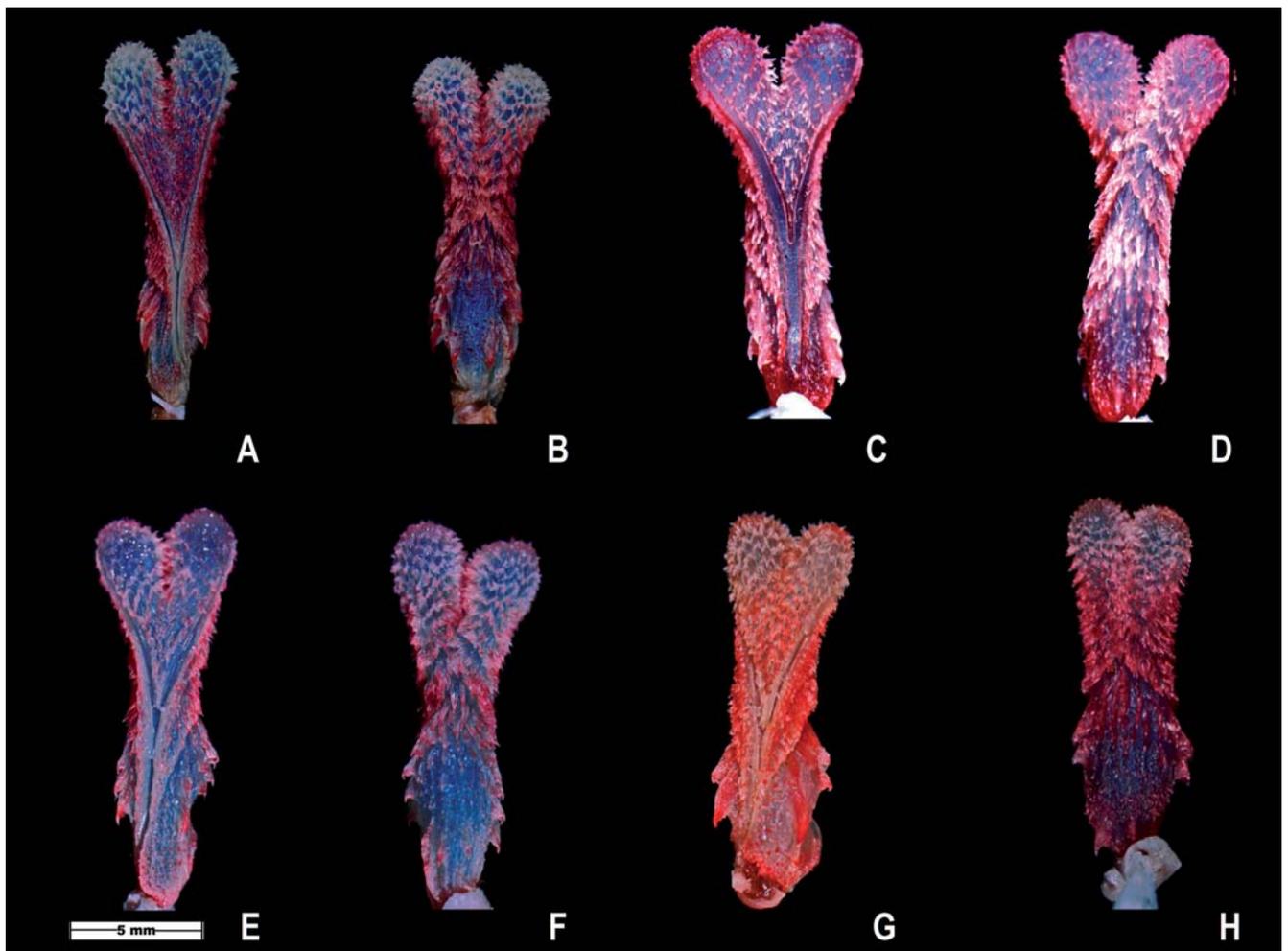


Figure 2. Hemipenial architecture in the genus *Ninia*. (A–B) *N. hudsoni* (USMN 232967). (C–D) *N. maculata* (UTA-R 54000). (E–F) *N. pavimentata* (UTA-R 7099). (G–H) *N. sebae* (UTA-R 21626).

possesses two poorly developed projections ornamented with 2–3 hook-shaped rows of spines of equal size. The lobes are globular, clearly differentiated from the slender body. Each lobe is homogeneously ornamented with large calyces with spinulate edges. In asulcate view, basally the hemipenis is weakly ornamented with small hook-shaped spines that surround two large hook-shaped spines. The basal complex of spines is followed by a shallowly ornamented or totally nude region. Medially, the hemipenis body possesses a globular, ornamented projection with 3–4 hook-shaped rows of spines of equal size organized in an inverted “V” (Fig. 2F). The plane of capitation coincides with the point in which the medial projection protrudes. The plane of capitation is located just distal to the bifurcation point of the *sulcus spermaticus* (sulcate side). The region between the capitation plane and the forked point of the lobes possesses ≥ 5 rows of spines organized in an inverted “V”.

***Ninia psephota* (Cope, 1875)**

Only three specimens were available for the description of this species (UF 84192; KU 35601, 102523), and all the hemipenes were badly preserved. The following description is based on only UF 84192 and KU 102523. To examine the hemipenis of KU 102523, re-hydration and fixation in ETOH 70% was required for 2 days. I could not examine the morphological characters in full eversion of this specimen because the hemipenis was totally broken. Consequently, the taxonomic value of this hemipenis was limited and only the sulcate side could be described. The hemipenis of UF 84192 was also badly preserved and had holes in it, but it allowed more-or-less full eversion and showed sulcate and asulcate ornamentation clearly. However, it was impossible to establish if the hemipenis has lateral or basal projections on the sulcate side because its deformation caused by poor preservation its shape from being determined accurately.

The hemipenis extends from the caudal base to the 9th sub-caudal scale; shallowly forked, capitate on asulcate side, *sulcus spermaticus* centrolateral, bifurcate, the point of bifurcation lying just distal to the mid-point of the hemipenis body and up to 5th sub-caudal scale. Each branch of the *sulcus spermaticus* runs longitudinally to the tip of the lobes in which it inserts orbitally. The intra-sulcar region is covered with large calyces with strongly spinulated edges. The walls of the *sulcus spermaticus* are well defined with edges ornamented with numerous spinules which decrease gradually in length toward the apex of each lobe. Laterally, it possesses two oblique rows on each side of the hemipenis body with large hook-shaped spines that decrease gradually in length. The first basal spine of the first row is larger than any other spine that ornaments the hemipenis. The lobes are oblong, slightly differentiated from the hemipenis body, and bear large,

homogeneously distributed calyces with strongly spinulate edges. In asulcate view, basally the hemipenis has a small projection ornamented with two long hook-shaped spines. The basal projection is followed by a weakly ornamented or totally nude region. Medially, the hemipenis body possesses a globular projection ornamented with 4–5 hook-shaped rows of spines organized in an inverted “V” and decreasing in size toward the apex. The region between the capitation plane and the forked point of the lobes possesses numerous, dense spine rows organized in an inverted “V”.

***Ninia sebae* (Duméril, Bibron, and Duméril, 1854)**

Hemipenes extend from the caudal base to the 7th–8th sub-caudal scale, rarely 6th or 13th; shallowly forked; capitate on sulcate and asulcate sides; *sulcus spermaticus* centrifugal, bifurcate, the point of bifurcation always at the mid-point of the hemipenis body and up to 4th or 5th sub-caudal scale. Each branch of the *sulcus spermaticus* runs longitudinally to the tip of the lobes in which it inserts laterally (Fig. 2G). The intra-sulcar region is covered with numerous spinules and dense calyces with strongly spinulate edges. The walls of the *sulcus spermaticus* are robust and well defined with edges ornamented with numerous spinules, which decrease gradually in length toward the apex of each lobe. Basally, it possesses small hook-shaped spines, which are homogeneously dispersed. Laterally, it possesses only two lateral projections. The lateral projection of the right side is ornamented with a large basal hook-shaped spine that is larger than any other spine on the hemipenis body. Likewise, this projection is ornamented at the top with two oblique rows of spines that decrease in length toward the apex. The lateral projection of the left side is slightly smaller than the right projection and is ornamented with 2–3 rows of hook-shaped spines that are similar in size and decrease gradually in length toward the apex. The plane of capitation coincides with the bifurcation point of the *sulcus spermaticus*. The lobes are globular, clearly differentiated from the hemipenis body, and coated homogeneously with numerous calyces bearing large spinules. In asulcate view, basally the hemipenis possesses a small projection ornamented with a few small, hook-shaped spinules and two large hook-shaped spines in parallel. The basal region of spines is followed by a shallowly ornamented or totally nude region. Medially, the hemipenis body possesses a globular projection ornamented with 3–4 rows of hook-shaped spines of equal size organized in an inverted “V” (Fig. 2H). The plane of capitation is located just distal to the bifurcation point of the *sulcus spermaticus* (sulcate side). The region between the capitation plane and the forked point of the lobes possesses numerous, dense rows of spines organized in an inverted “V”.

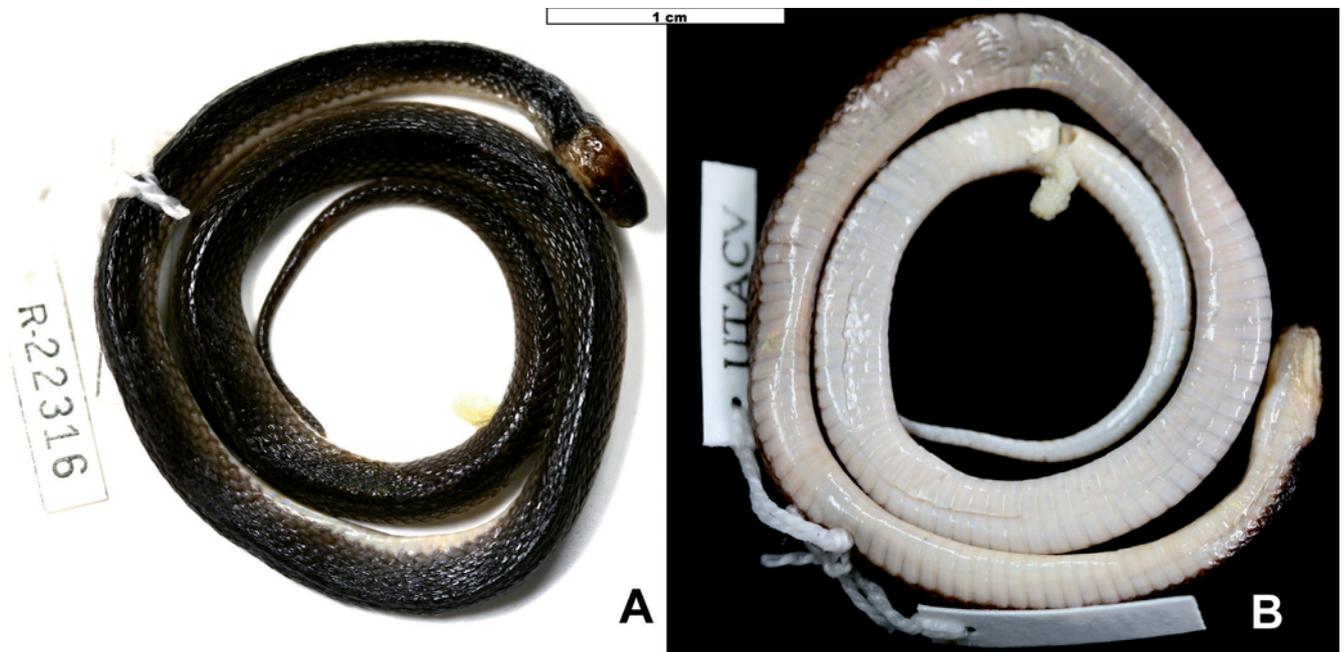


Figure 3. *Ninia franciscoi* sp. nov., holotype UTA-R 22316, male. (A) Dorsal view. (B) Ventral view.

***Ninia franciscoi* sp. nov.**
(Figs. 3, 4A, 5C–D)

Holotype

UTA-R 22316, male (Fig. 3), from ca. 7.2 km Arima, Simla Research Station, Province of St. George, Trinidad (10°41'1"N, 61°17'W), collected 6 March 1988 by W.B. Montgomery and D. Resnick.

Diagnosis

Ninia franciscoi can be distinguished from all other congeners by the combination of the following characters: (1) an extremely long anterior temporal scale in contact with upper labials 5, 6, and 7; (2) temporal scale formula 1 + 2, with primary temporal scale 3x longer than lower posterior temporal (Fig. 4); (3) forked hemipenis (50–74%); (4) *sulcus spermaticus* centrolineal; (5) slender and acuminate-shaped lobes, strongly differentiated from the hemipenis body and homogeneously ornamented with large calyces; (6) Basally the hemipenis possesses a small pocket-shaped structure covered with small hook-shaped spines.

Description of holotype

An adult male, 319 mm total length; TL 69 mm; SVL 250 mm; tail/SVL ratio 27.6%; head clearly distinct from the body; head length = 10.49 mm; head width = 6.62 mm; rostral width > height; internasal width > length (1.39 × 0.90 mm); prefrontals longer than internasals, length slightly > width (2.42 × 2.22 mm; suture 2.22 mm);

frontal heart-shaped, width > length (2.96 × 2.74 mm); parietal length > width (4.32 × 2.62 mm; suture 3.30 mm); 1–1 supraoculars, length > width (1.50 × 0.98 mm), entering the orbit and contacting the postocular; single nasal; nasal contacting internasal, prefrontal, loreal, first and second upper labials; loreal single, length > height (1.62 × 0.98 mm), entering orbit and in contact with 2nd 3rd and 4th upper labial scales; 0/0 preoculars; 1/1 postoculars; temporal scales 1 + 2, where the anterior temporal scale is 3x longer than lower posterior temporal; anterior temporal scale extremely long and in contact with upper

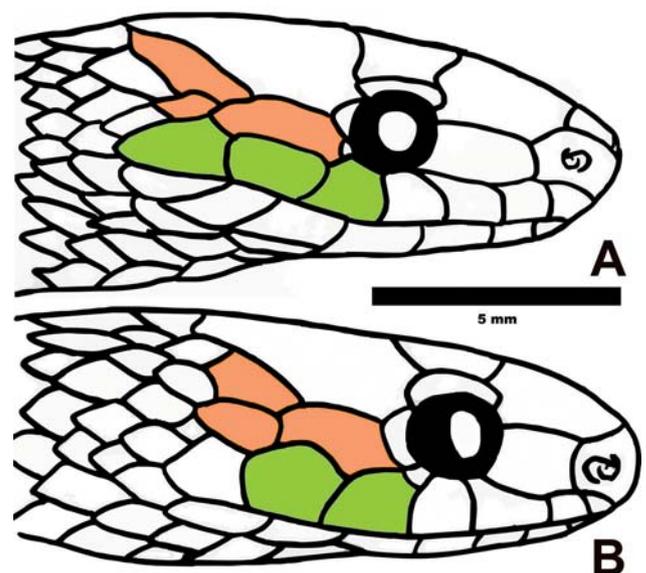


Figure 4. Comparisons between (A) *Ninia franciscoi* sp. nov. (holotype UTA-R 22316) and (B) *N. atrata* (syntype ANSP 3410). Orange = temporal scales. Green = supralabial scales in contact with anterior temporal scales.

labial scales 5, 6, and 7; 7/7 upper labials, width of all > length; 4th and 5th upper labials entering orbit and 5th in contact with the postocular scale; 8/7 lower labials, 1–5 in contact with two pairs of genials; small tubercles present on mental, all lower labials, and all chin-shields; dorsal scale rows 19/19/19, keeled, strongly striated, lacking apical pits; 143 ventrals; 55 paired sub-caudals; cloacal plate entire.

Color in preservative

Uniformly black-brown, except for the W-shaped, pale nuchal band; nuchal band cream colored with pale brownish tinge, with an anterior section of the band (dorsal to parietal scales) with darker brown pigmentation and posterior section of the band (dorsal to “neck” scales) with deep black pigmentation; ventral surfaces of head and body immaculate cream white; sub-caudal surface immaculate cream white.

Description of hemipenes

Hemipenes extend from the caudal base to the 8th–9th sub-caudal scale; forked; capitate, *sulcus spermaticus* centrolineal, bifurcate, point of bifurcation is at the mid-point of the hemipenis body and up to 4th–5th sub-caudal scale. Each branch of the *sulcus spermaticus* runs longitudinally to the tip of the lobes in which it inserts orbitally (Fig. 5B). The intra-sulcar region is covered with only large calyces. The plane of capitation is just proximal to the bifurcation point. The walls of the *sulcus spermaticus* are weak but well defined with edges ornamented with numerous spinules that decrease gradually in length toward the apex of each lobe. In sulcate view, basally the hemipenis possesses a small pocket-shaped structure

ornamented with small hook-shaped spines. Laterally, it possesses two oblique rows on each side of the hemipenis body with large hook-shaped spines, which decrease gradually in length. The first basal spine of the first row is larger than any other spine. The lobes are slender and acuminate-shaped, strongly differentiated from the hemipenis body and homogeneously ornamented with big calyces. In asulcate view, basally the hemipenis possesses a small, pocket-shaped structure ornamented with small, hook-shaped spines, two of which are prominent. The basal region of spines is followed by a shallowly ornamented or totally nude region (Fig. 5A). Medially, the hemipenis body possesses a globular projection ornamented with 4–5 rows of spines organized in an inverted “V” and increasing in size toward the apex. The plane of capitation coincides with the point in which the medial projection protrudes. The plane of capitation is located just distal to the bifurcation point of the *sulcus spermaticus* (sulcate side). The region between the capitation plane and the forked point of the lobes possesses numerous, dense rows of spines, organized in an inverted “V”.

Comparisons with other species

The species was previously conflated with *Ninia atrata* (Dunn, 1935; McCranie and Wilson, 1995; Murphy, 1997) and is very similar to other species showing 19 dorsal scales without reductions such as *N. celata*, *N. espinali*. It differs from both by having (1) anterior temporal scale extremely long and in contact with upperlabial scales 5–7 and (2) temporal scales 1 + 2, where the anterior temporal scale is 3x longer than lower posterior temporal (Fig. 4). *Ninia franciscoi* sp. nov. can be distinguished from *N. atrata*, *N. celata*, *N. diademata*, *N. espinali*, *N. hudsoni*, *N. maculata*, *N. pavimentata*, *N. psephota* and *N. sebae* by having

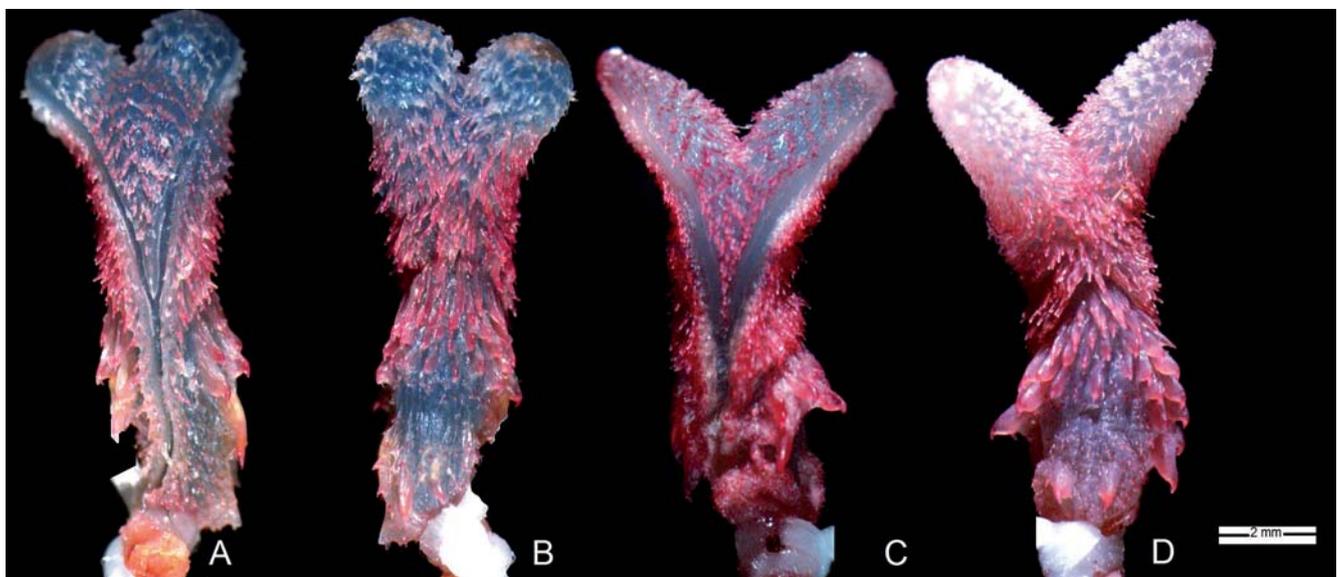


Figure 5. Comparisons among the hemipenial architecture of (A–B) *Ninia atrata* (AMNH 123767) and (C–D) *N. franciscoi* sp. nov. (holotype UTA-R 22316).

Table 2. Hemipenial characters comparisons among species of *Ninia*. The degree of apical differentiation follows Koegh (1999): simple (S), shallowly forked (SF), forked (F), and deeply forked (DF). Bifurcation point: at mid-point of the hemipenis (M); proximal to mid-point of the hemipenis (BM); distal to the mid-point of the hemipenis (AM).

Species	Sulcus spermaticus	Lateral projections	Basal hooks	Pattern of medial spines on asulcate side	Bifurcation point	Capitation	Degree of apical differentiation
<i>Ninia atrata</i>	Centrifugal	Absent	Present	Inverted “V”	M	Asulcate side	SF
<i>Ninia celata</i>	Centrifugal	–	–	Inverted “V”	M	–	SF
<i>Ninia diademata</i>	Centrolineal	Present	Absent	Inverted “V”	M	Asulcate side	SF
<i>Ninia espinali</i>	Centrifugal	Absent	Present	Lineal	BM	Asulcate side	SF
<i>Ninia franciscoi</i> sp. nov.	Centrolineal	Absent	Present	Inverted “V”	M	Sulcate and asulcate sides	F
<i>Ninia hudsoni</i>	Centrifugal	Absent	Present	Inverted “V”	BM	Non-capitate	SF
<i>Ninia labiosa</i>	Centrifugal	Present	Absent	Inverted “V”	M	Asulcate side	SF
<i>Ninia maculata</i>	Centrifugal	Absent	Absent	Inverted “V”	M	Non-capitate	SF
<i>Ninia pavimentata</i>	Centrifugal	Present	Absent	Inverted “V”	M	Sulcate and asulcate sides	SF
<i>Ninia psephota</i>	Centrolineal	–	Present	Inverted “V”	AM	Asulcate side	SF
<i>Ninia sebae</i>	Centrifugal	Present	Present	Inverted “V”	M	Sulcate and asulcate sides	SF

(1) a forked hemipenis (50–74%) with (2) slender and acuminate lobes, strongly differentiated from the hemipenis body and homogenously ornamented with larger calyces and (3) basally, hemipenis showing a small pocket-shaped structure covered with small hook-shaped spines (Fig. 5). Additional characters or character combinations that help distinguish *N. franciscoi* sp. nov. from all its congeners are summarized in Table 2.

Distribution and natural history

Ninia franciscoi sp. nov. occurs in the Northern Range of Trinidad at 240 m above sea level in rugged hills that parallel the north coast (Fig. 6). These hills support a semi-evergreen, seasonal forest and the fauna is considered South American, having been connected to the mainland as recently as 11,000 years ago (Murphy, 1997). Its natural history is unknown and the only information available was provided by the collectors, who reported that the holotype was collected during the day at the William Beebe Tropical Research Station, hidden under tin boxes. I found several parasitic worms (nematodes) in its stomach.

Etymology

Ninia franciscoi sp. nov. is named in honor of one of the most influential persons in my life, Francisco Sierra Corredor (1900–2005), my grandfather, who taught me how to find the secrets of the “nature goddess”.

DISCUSSION

The assessment of hemipenial morphology and caudal characters showed that they are a useful to diagnose *Ninia* spp. and, particularly, that hemipenial architecture

is an effective tool to clarify the identity of cryptic species. *Ninia sebae*, which is represented by four subspecies (*N. s. sebae*, *N. s. morleyi*, *N. s. punctulata*, *N. s. immaculata*; Schmidt and Rand, 1957) exhibits the greatest intraspecific variation in the genus. Smith (1996) analyzed the standard scale characteristics of *N. sebae*, finding significant differences among all subspecies and among the males and females of each complex. He distinguished and allocated the geographic variation of the subspecies as follows: (1) the banded group that corresponds to *N. s. sebae*, which is located in Mexico and the Guatemala highlands and (2) the unbanded group that corresponds to the populations from the upper Yucatán peninsula (*N. s. morleyi*), the Pacific coast and the Southwest of Guatemala (*N. s. punctulata*), and the northernmost Mexican locality at Cuautlaplan and southern Honduras, Nicaragua, and Costa Rica (*N. s. immaculata*). Additionally, one of his conclusions is that the populations of *N. s. punctulata* and *N. s. sebae* appear to be evolving in nearly complete

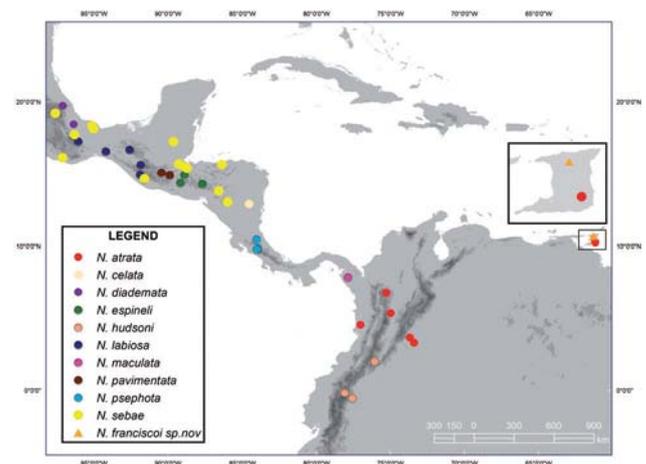


Figure 6. Geographic distribution of specimens of *Ninia* examined in this study.

genetic isolation, leading him to suggest that these taxa could be recognized as full species.

I contrast his hypothesis after analyzing nine localities that represent all the geographic variation of the species. The hemipenial morphology shows that all subspecies share the same hemipenial architecture and are morphologically homogeneous, which is consistent with the idea that the male genitalia are not correlated with ecological selection, food habits, or locomotion (Arnold, 1986; Branch, 1986; Jadin and Parkhill, 2011). Likewise, the molecular data examined by Ingrasci (2011) support the conservative hemipenial morphology unit exposed in *N. sabae*. Ingrasci (2011) found that across its large geographic range, all populations were recovered in a well-supported clade (PP1.0), which suggests that *N. sabae* does not have any substantial diversification. On the contrary, the intraspecific variation of the different populations, which derive from the ecological selection on such characters as color pattern and scale counts, obscure the morphological unity present in *N. sabae*. However, the sub-caudal meristic characters such as the insertion point of the muscle *retractor penis magnus* and the number of caudal scales agree with the geographic variation reported by Schmidt and Rand (1957) and Smith (1996). Therefore, the *N. sebae* complex must be considered as a single polymorphic species with four clear morphs that show intraspecific variation in hemipenial length, insertion point of the muscle *retractor penis magnus*, and geographic variation in the ventral and sub-caudal counts and color pattern.

I have treated the geographic variation of *Ninia diademata* and its subspecies with special attention because this complex shows variation in color pattern and caudal scales throughout a puzzling geographic distribution. Burger and Werler (1954) described all the subspecies of *N. diademata* and geographically located each morph as: (1) *N. d. labiosa*, distributed in moderate elevations of the Pacific slopes from Oaxaca, Mexico, to Guatemala; (2) *N. d. nietoi* and *N. d. plorator*, distributed on the Caribbean slopes from Puebla and Veracruz, Mexico, to Honduras; (3) *N. d. diademata* that occurs from the Caribbean versant of Veracruz south to Comitán, Chiapas. However, the descriptions of these subspecies were not clear and, consequently, none of these subspecies is particularly well distinguished from the others. Smith (1996) tried to resolve this ambiguity by analyzing standard scale characters and color patterns from 322 specimens that represented all the subspecies by discriminate analysis and multivariate statistical analyses. He concluded that there are no consistent differences that can be used to effectively diagnose subspecies or species using these characters.

I analyzed Smith's (1996) hypothesis using the hemipenial morphology of 16 specimens from the type localities of each morph, 13 from the Pacific slopes from Oaxaca, Mexico, to Guatemala (*N. d. labiosa*), one from

the Caribbean versant of Veracruz south to Comitán, Chiapas (*N. d. diademata*), and two from Puebla and Veracruz, Mexico, to Honduras (*N. d. nietoi* and *N. d. plorator*). Examination of these specimens indicates that they have obvious differences in their hemipenial architecture, including: (1) *sulcus spermaticus* centrolineal in *N. d. diademata*, *N. d. nietoi*, and *N. d. plorator* (centrifugal in *N. d. labiosa*); (2) calyces organized in longitudinal ridges present in *N. d. diademata*, *N. d. nietoi*, and *N. d. plorator* (lacking in *N. d. labiosa*). Moreover, the hemipenial characters group the subspecies as a morphological unit that allows clear diagnosis of two geographic sub-groups: (1) the *N. d. diademata* sub-group formed by *N. d. nietoi*, *N. d. plorator*, and *N. d. diademata*, distributed on the Caribbean slopes from Puebla and Veracruz, Mexico, to Honduras and (2) the *N. d. labiosa* sub-group that includes only *N. d. labiosa* populations, distributed at moderate elevations of the Pacific slopes from Oaxaca, Mexico, to Guatemala.

Likewise, the sub-caudal scales counts show significant differences between each complex ($\bar{X} = 95.5$, $n = 9$ in the *N. d. diademata* sub-group; $\bar{X} = 108.3$, $n = 13$ in the *N. d. labiosa* sub-group), which agrees with Burger and Werler (1954). Additionally, this result is supported by the molecular data offered by Ingrasci (2011), who, based on a Bayesian analysis of mitochondrial DNA, found deep divergence in the same two geographic sub-groups with high support for the node joining them (Fig. 7). Hence, I propose to elevate *N. d. labiosa* as a full species status and consider *N. diademata* as a single polymorphic species with three morphs (*N. d. diademata*, *N. d. nietoi*, *N. d. plorator*) with minor differences in ventral coloration, ventral and sub-caudal scale counts.

Ninia atrata has been thought to occur in disjoint populations distributed from Honduras, El Salvador, Colombia, Venezuela, Trinidad, and Tobago to southern Ecuador (Savage and Lahanas, 1991; Murphy, 1997,

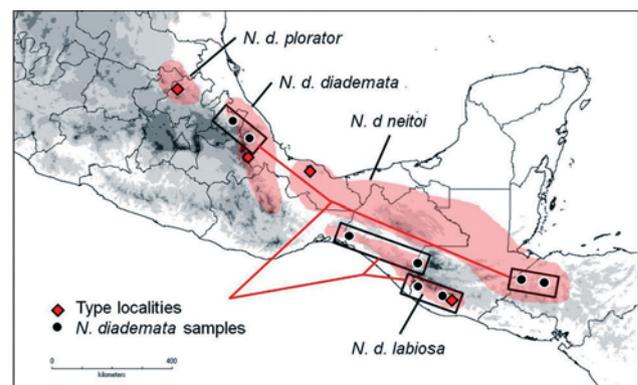


Figure 7. Map depicting relationships between two geographic sub-groups of *Ninia diademata* based on Bayesian analysis of mitochondrial DNA (Ingrasci, 2011). Boxes represent terminal clades or nodes. Lines represent branches; the length of the lines does not correspond to evolutionary distances. Red shading indicates approximate distributions of *N. diademata* sub-groups.

Savage, 2002). However, McCranie and Wilson (1995) demonstrated that within *N. atrata* sensu Dunn (1935) two undescribed species were concealed: one from Costa Rica (*N. celata*), the other from Honduras and El Salvador (*N. espinali*). As a consequence, the distribution of *N. atrata* is restricted to western Panama, Colombia, Ecuador, Venezuela, and Trinidad and Tobago (McCranie and Wilson, 1995; Savage, 2002). Following the original description by Hallowell (1845), the diagnostic characters of this taxon were redescribed by Burger and Werler (1954), McCranie and Wilson (1995), and Angarita-Sierra (2009) as follows: male SVL = 145–323 mm; female SVL = 170–426 mm; tail/body ratio = 28.2–30.2% (\bar{X} = 30%); head clearly distinct from body; rostral width > length; two internasals wider than long; two prefrontals longer than internasals, length slightly > width, in contact with ocular orbit; frontal heart-shaped, width > length; parietal length > width; 1/1 supraocular, each supraocular longer than wide, entering the orbit and contacting the postocular; single nasal; nasal contacting internasal, prefrontal, loreal, first and second supralabials; loreal single, length > height, entering orbit and in contact with supralabials scales 2, 3, and 4; 0/0 preoculars; 1/1 postoculars; usually 1 + 2 temporal scales formula, rarely 2 + 2, where the anterior temporal scale is 1.5–2x longer than lower posterior temporal, anterior temporal scale contact supralabial scales 5–6; usually 7/7 supralabials, occasionally 8/8 or 6/6, rarely 5/5, all supralabial scales wider than long, supralabials 3–4 entering orbit and 5 in contact with postocular scale; usually 7/7 supralabials, occasionally 8/8 or 6/6, rarely 5/5, supralabials 1–5 in contact with two pairs of genials; prominent tubercles present on mental, all infralabials, and all chin-shields in adult males; 1 dorsal scale rows 9/19/19 without reductions, keeled and strongly striated, lacking apical pits; 136–158 ventral scales in males, 133–169 ventral scales in females; paired sub-caudal scales, 36–70 sub-caudal scales in males, 41–65 sub-caudal scales females; anal plate entire; dorsal surfaces uniformly dark brown–black; nuchal collar present or absent, when present nuchal collar can be white, orange, red or pale yellow, W-shaped, or include parietal scales (see Angarita-Sierra 2009: figs. 3–4); venter immaculate.

Even though the identities of some populations of the named forms of *N. atrata* have been resolved (see McCranie and Wilson, 1995; Savage and Lahanas, 1991; Savage, 2002), the cryptic characteristic of this taxon, such as color pattern, ventral and subcaudal counts, and size of cephalic scales, suggests that there might be > 1 undescribed species of *Ninia*. As part of an ongoing study of the *Ninia atrata* complex I have examined > 200 specimens that depict the entire distribution of the species. When I centered my attention on the population from Trinidad and Tobago ($n = 44$), I noticed the color pattern and morphometric relationship are closer to the Colombian trans-Andean populations than cis-Andean

populations described by Angarita-Sierra (2009). I compared the hemipenial morphology of different populations ($n = 10$), trying to represent the entire distribution of the *Ninia atrata* complex. Assessment of the hemipenial morphology of these specimens indicates that there are no consistent differences to effectively distinguish the populations. In general, the specimens of the populations from Trinidad and Tobago ($n = 2$) share the same hemipenial architecture of the Colombian populations (cis-Andean and trans-Andean populations evaluated). The only intraspecific variation exposed was the insertion point of the *muscle retractor penis magnus* and hemipenial length (Table 1).

Only one specimen from Trinidad (UTA-R 22316) showed hemipenial and cephalic scale morphology to distinguish it from all populations of *Ninia atrata* and from all other species of the genus, based on the following characters: (1) anterior temporal scale extremely long and in contact with upper labial scales 5–7 (anterior temporal scale contact with upper labials 5–6 in *N. atrata*); (2) temporal scales 1 + 2, where the anterior temporal scale is 3x longer than the lower posterior temporal (temporal scales 1 + 2, where the anterior temporal scale is 1.5–2x longer than the lower posterior temporal in *N. atrata*); (3) hemipenis forked (50–74%) (hemipenis shallowly forked in *N. atrata*); (4) lobes slender and acuminate, strongly differentiated from the hemipenis body (lobes shallowly differentiated from the hemipenis body in *N. atrata*); and (5) basally the hemipenis possesses a small pocket-shaped structure covered with small, hook-shaped spines (lacking pocket-shaped structure in *N. atrata*). Nevertheless, comparisons of standard scale counts and cephalic scale morphology of this specimen with the two syntypes of *Ninia atrata* from Caracas, Venezuela (females, ANSP 3410, 3412) show the same differences in temporal scales formula, contact of the anterior temporal scales, and size of the anterior temporal scales (Fig. 4). Therefore, the genus *Ninia* in Trinidad is represented by two sympatric species *Ninia atrata* (Dunn, 1935; Murphy, 1997; Boos, 2001) and *Ninia franciscoi* sp. nov. This new taxon may be part of the endemic herpetofauna distributed in the humid forest of the highlands of Trinidad, including *Leptophis stimsoni*, *Riama shrevei*, and *Erythrolamprus melanotus nesos* (Dixon and Michaud, 1992; Rivas *et al.*, 2005; Harding, 1995).

Finally, the survey of the hemipenial morphology and sub-caudal meristic characters reveals that hemipenial morphology is an excellent indicator of relationships at the specific level within *Ninia* while also showing strong morphological conservatism at the generic level. The hemipenial architecture suggests that the presence or absence of lateral projections divides *Ninia* in two units. The first unit lacks lateral projections and is composed of three South America species (*N. atrata*, *N. franciscoi* sp. nov., and *N. hudsoni*) and two Central American species

(*N. maculata* and *N. espinali*); the South American species differ in possessing basal hooks on the first oblique rows on each side of the hemipenis (sulcate side), absent in the Central American species. The second unit possesses lateral projections and is composed of five Central American species (*N. psephota*, *N. labiosa*, *N. diademata*, *N. pavimentata*, and *N. sebae*). Two groups can be distinguished within the latter unit as well; the first group consists of species with large tails and > 76 sub-caudal scales (*N. psephota*, *N. labiosa*, and *N. diademata*), whereas the second group includes species with robust walls of the *sulcus spermaticus* and poorly developed lateral projections

or only one developed lateral projection (*N. pavimentata* and *N. sebae*).

Although the main goal of this paper was not to provide a phylogenetic hypothesis of *Ninia*, hemipenial structures might give insights to understand the evolutionary trends of the genus and explore which features can be useful for future phylogenetic analyses. In seeking a cladistic approach of the relationships of *Ninia*, it is advisable to combine the hemipenial morphology with other features (e.g., scale counts, molecular data, osteological and myological characters) to clarify the phylogenetic relationships within the genus.

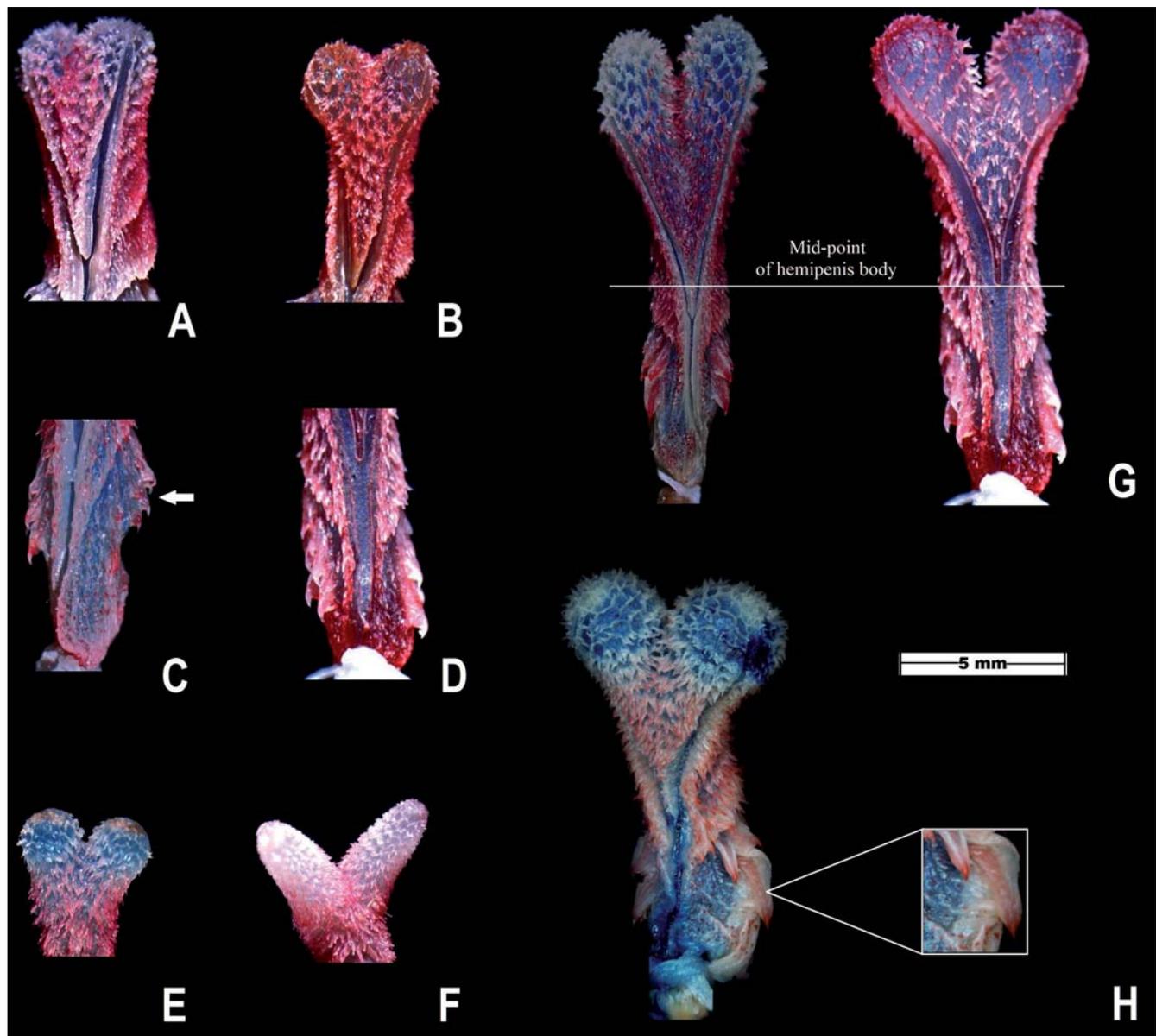


Figure 8. Hemipenial characters that assist in distinguishing among species of *Ninia*. **(A)** *sulcus spermaticus* centrolineal (AMNH 162268) versus **(B)** *sulcus spermaticus* centrifugal (UTA-R 1237). **(C)** Presence of lateral projection (UTA-R 7099) versus **(D)** absence of lateral projection (UTA-R 54000). **(E)** Shallowly forked (AMNH 123767) versus **(F)** forked (UTA-R 22316). **(G)** Left, bifurcation point of the *sulcus spermaticus* distal to mid-point of hemipenis body (USMN 232967) versus Right, bifurcation point of *sulcus spermaticus* at the mid-point of hemipenis body (UTA-R 54000). **(H)** Large hook-shaped spines (ICN 10787).

Key to the species of *Ninia*

The following key is based on hemipenial morphology and caudal characters and aims to assist in distinguishing among the species of *Ninia* throughout the entire geographic distribution.

- 1a. > 76 subcaudal scales; tail > 46% of SVL.....2
- 1b. < 76 subcaudal scales; tail < 46% of SVL.....3
- 2a. *Sulcus spermaticus* centrolineal; capitation only on asulcate side; lobes globular, weakly differentiated from hemipenial body that is as wide as lateral projections; asulcate side with calyces organized in longitudinal ridges (Fig. 8A).....
.....*Ninia diademata*
- 2b. *Sulcus spermaticus* centrifugal; capitation on sulcate and asulcate sides; lobes globular, clearly differentiated from slender hemipenial body; calyces not organized in longitudinal ridges on asulcate side (Fig. 8B)..... *Ninia labiosa*
- 3a. Hemipenial body with at least one lateral projection (Fig. 8C)4
- 3b. Hemipenial body without lateral projections (Fig. 8D).....5
- 4a. Hemipenial body with two well-developed lateral projections, projection of right side larger than projection on left side; lateral projection of right side (or left side in the specular view) ornamented with large, hook-shaped, basal spines that are larger than any other spine on hemipenis body; walls of *sulcus spermaticus* ornamented with numerous spinules that decrease gradually in length toward to apex of each lobe.....*Ninia sebae*
- 4b. Hemipenial body with two poorly developed lateral projections and ornamentation of 2–3 hook-shaped rows of spines of equal size; walls of *sulcus spermaticus* ornamented with numerous spinules that only extend over first part of hemipenial body to bifurcation point of *sulcus spermaticus* (rarely just distal to bifurcation point)
.....*Ninia pavimentata*
- 5a. Bifurcation point of *sulcus spermaticus* always at mid-point of hemipenis body6
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- 7a. Bifurcation point of *sulcus spermaticus* proximal to mid-point of hemipenis body; < 76 subcaudal scales; tail proportion ca. 31%10
- 7b. Bifurcation point of *sulcus spermaticus* just distal to mid-point of hemipenis body to sub-caudal scale 5; > 76 subcaudal scales; tail proportion ca. 38% *Ninia psephota*
- 8a. *Sulcus spermaticus* centrifugal; hemipenis shallowly forked (75–89%); lobes globular, clearly differentiated from body, which is slender or robust (Fig. 8E) *Ninia atrata*
- 8b. *Sulcus spermaticus* centrolineal; hemipenis forked (50–75%); lobes slender and acuminate, strongly differentiated from hemipenis body (Fig. 8F)*Ninia franciscoi* sp. nov.
- 9a. Walls of the *sulcus spermaticus* robust and well defined with edges ornamented with numerous spinules that decrease gradually in length toward apex of each lobe; tail proportion ca. 25%; < 132 ventral scales..... *Ninia celata*
- 9b. Walls of *sulcus spermaticus* weak and diffuse with edges poorly ornamented with few spinules that decrease gradually in length toward apex of each lobe; lacking lateral or medial projections; tail proportion ca. 40%; > 132 ventral scales*Ninia maculata*
- 10a. On asulcate side, region between capitation plane and forked point of lobes with 8–10 rows of spines forming parallel lines; bifurcation point of *sulcus spermaticus* always proximal to mid-point of hemipenis body and up to sub-caudal scale 3 *Ninia espinali*
- 10b. On asulcate side, region between capitation plane and forked point of lobes with numerous dense rows of spines forming inverted “V”; bifurcation point of *sulcus spermaticus* always slightly proximal to mid-point of hemipenis body and up to sub-caudal scale 5 or 6.....*Ninia hudsoni*

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APPENDIX. SPECIMENS EXAMINED

Ninia atrata ($n = 11$). COLOMBIA: **Antioquia**: Guadalupe: Vereda Puentes de Acacias, Proyecto hidroeléctrico Porce, II 700 m, MHUA 14011, 14481; **Caldas**: La Victoria: Vereda El Llano, gravillera El Palmar, MHUA 14452; **Chocó**: Quebrada Docorodó, middle San Juan river (ca. 17 km airline SSW Noanomá), 04°33'N, 77°00'W, AMNH 123767; **Meta**: Lomalinda, UTA-R 3603, 3716; San Martín: Vereda La Castañeda, Palmeras del Meta, ICN 10760, 10787. TRINIDAD: UF 91620. TOBAGO: USMN 228099. VENEZUELA: within 200 mi of Caracas, ANSP 3410, 3412.

Ninia celata ($n = 1$). COSTA RICA: **Alajuela**: Cinchona, 1600 m, KU 35526.

Ninia diademata ($n = 13$). GUATEMALA: **Quezaltenango**: South slope Volcán Santa María, Finca El Faro, 4 km N El Palmar, UTA-R 22907, 22909, 22912, 22921, 22923; **Huehuetenango**: La Democracia, El Paraiso, Puente a Pera Roja, UTA-R 42291; **San Marcos**: Municipio Esquipulas Palo Gordo, Aldea Fraternidad, Finca La Esperanza, elevation 1550–1890 m, UTA-R 39507. MÉXICO: **Chiapas**: 10.94 km SE San Cristobal on Mexico Highway 190, 16°40.02'N, 92°34.26'W, UTA 8842; **Oaxaca**: Cerro Baúl, 19 km NW Rizo de Oro 16°33.60'N, 94°10.20'W, UTA-R 7698, 12367; Sierra Juárez, Vista Hermosa, 17°38.40'N, 96°21.00'W, UTA-R 8845; Sierra Mixes, 0.8 km South Totontepec 17°15.60'N, 96°02.40'W, elevation 1801 m, UTA-R 14151, 12370.

Ninia espinali ($n = 2$). EL SALVADOR: **Chalatenango**: Cerro Pital, KU 291246. HONDURAS: **La Paz**: 11 km NE Pequín, Canton Sabaneta, KU 183928.

Ninia franciscoi sp. nov. TRINIDAD: St. George, ca. 7.2 km Arima, Simla Research Station, UTA-R 22316.

Ninia hudsoni ($n = 3$). COLOMBIA: **Caquetá**: Florencia, 01°62'N, 75°62'W, ICN 7130. ECUADOR: **Pastaza**: Canton Pastaza, Barrilo Bella Vista, 01°50'487"S, 78°04'741"W, UTA-R 55950; River Siquino tributario River Villano, USNM 232967.

Ninia labiosa ($n = 2$). MEXICO: **Veracruz**: Carretera Xico-Xico Viejo, 19°44'32"N, 97°05'2155" W, UTA-R 53068; 3, 22 km north Monte Blanco, AMNH 42291.

Ninia pavimentata ($n = 7$). GUATEMALA: Baja Verapaz, Cerro Verde, UTA-R 7099; San Marcos, San Rafael Pie de la Cuesta, Aldea La fraternidad, elevation 1600 m, UTA-R 42402, 42405-08, 46560.

Ninia maculata ($n = 2$). HONDURAS: Olancho, Sierra de Botaderas Cauca, 15°38'382"N, 86°21'145"W, elevation 895 m, UTA-R 54000; PANAMA: Darién, USNM 50114.

Ninia psephota ($n = 3$). COSTA RICA: Cartago, Road empalme with Panamerican Highway, KU 35601; Heredia, UF 84192; San José, 20 km SE Cartago, KU 102523.

Ninia sebae ($n = 19$). GUATEMALA: Izabal, Sierra de Caral, Morales, Aldea Negro Norte, Cerro El Aguacate, elevation 1200 m, UTA-R 33033; Sierra de Santa Cruz, Finca Semuc, Chinamococh, UTA-R 26925; Sierra de Santa Cruz, Finca Semuc, 3 km NE Seyamch, UTA-R 29896; Municipio de Morales, Sierra de Caral, Aldea Negro Norte, UTA-R 37369; Quezaltenango, South slope Volcán Santa María, Finca El Faro, ca. 4 km N El Palmar, elevation 875 m, UTA-R 21418, 21625, 21645, 21649, 23425; Peten, Tikal, 1.4 km S Visitor Center Museum, UTA-R 41168. HONDURAS: El Paraiso, Las Manos, Finca Las Manos, 13°48.05'N, 86°34.42'W, UTA-R 41253; Olancho Sierra de Botaderas Cauca, 15°38'382"N, 86°21'145"W, elevation 895 m, UTA-R 53276. MEXICO: Oaxaca, Sierra Juárez, Metates, 17°42.00'N, 96°18.60'W, UTA-R 12374, 14154, 52616; Puebla, Catemaco, Falda ce volcán Santa Marta, El Bastonal, UTA-R 52616; Veracruz, 7.8 mi S Catemaco, Los Tuxtles, 18°20.40'N, 95°07.20'W, elevation 530 m, UTA-R 3079; Sierra de Tuxtla, ca. 3.5 km SSE Tebanca, UTA-R 12374. NICARAGUA: Jinoteca, Las Pilas, 13°2.80'N, 85°58.28'W, elevation 1535 m, UTA-R 44837.