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A new species of *Thamnodynastes* Wagler, 1830 from western Amazonia, with notes on morphology for members of the *Thamnodynastes pallidus* group (Serpentes, Dipsadidae, Tachymenini)

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Abstract

The genus *Thamnodynastes* is the most diverse within the tribe Tachymenini, with an extensive and complex taxonomic history. The brief descriptions and lack of robust diagnostic characters are the main sources for identification errors and for the difficulty to assess the diversity estimates of the genus. The *Thamnodynastes pallidus* group was briefly designated to encompass the most arboreal species of the genus, with thinner bodies and longer tails: *T. pallidus, T. longicaudus, T. sertanejo,* and a fourth undescribed species. After its designation, no other paper addressed this group and its morphological variation, especially for the hemipenis, is still undetermined. After the analysis of all species of *Thamnodynastes* we were able to corroborate the distinctiveness of the *T. pallidus* group and to accurately diagnose its fourth species from the western portion of the Amazonia lowlands. The new species is distinguishable from all congeners, except *T. sertanejo*, by the absence of ventral longitudinal stripes, 17/17/11 dorsal scale rows, and dorsal dark brown blotches on the anterior third of the body. The new species is distinguished from *T. sertanejo* by the higher number of subcaudals, lower number of ventrals, and smaller body and head sizes. We also provide additional diagnostic features for the *Thamnodynastes pallidus* group, including new data on hemipenial variation. Finally, we briefly discuss the defensive behavior and morphological characters associated with arboreality in members of the *T. pallidus* species group.

Keywords: Xenodontinae; color pattern; hemipenial morphology; natural history; defensive behavior

Introduction

The tribe Tachymenini comprises seven genera of widely distributed South American snakes. The genus *Thamnodynastes* Wagler, 1830 is the most diverse, with 20 species ranging from Argentina to the Guiana Shield lowlands and Tepuis, throughout the Amazon basin, with a trans-Andean distribution on the north coast of Colombia and Venezuela (Bailey & Thomas 2007, Franco *et al.* 2017). Even though a few studies have addressed the diversity of the

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genus (Cei *et al.* 1992; Franco & Ferreira 2003; Bailey *et al.* 2005; Coelho *et al.* 2013; Bellini *et al.* 2014; Nóbrega *et al.* 2016; Franco *et al.* 2017), the majority of information is restricted to a few species descriptions and anecdotal data on geographic distribution or natural history (Bergna & Alvarez 1993; Gorzula & Ayarzagüena 1996; Myers & Donnelly 1996; Bernarde *et al.* 2000; Franco *et al.* 2003; Manzanilla & Saìnchez 2005; Guedes *et al.* 2014).

The traditional morphological characters employed for recognition of *Thamnodynastes* species, mostly focused on the color pattern and scale counts, are highly conservative. Due to wide overlap of several quantitative characters, the meristic data alone is insufficient for the accurate diagnosis of many congeners. Consequently, a large gap of information is still present, including several issues on taxonomy, ecology, behavior and distribution of most species.

Bailey *et al.* (2005) erected the "*Thamnodynastes pallidus* group" to encompass the following most arboreal species of *Thamnodynastes*, with slender bodies and long tails, short head, large eyes, elliptical pupils and fewer dorsal counts: *T. pallidus* (Linnaeus, 1758)*, T. sertanejo* Bailey, Thomas & Silva-Jr., 2005, *T. longicaudus* Franco, Ferreira, Marques & Sazima, 2003 and a fourth undescribed species from the Upper Amazon. Bailey *et al.* (2005) also proposed additional characteristics for the group: "possession of a hood that is spread defensively; blotched dorsal and ventral pattern, or intricately striped; dorsal scales smooth, elongate and without apical pits; with dorsal scale rows reductions, involving the paravertebral rows once, and lateral rows one or more times; and short hemipenis, simple or shallowly bifurcate, with small slender spines not longer than the height of the sulcus spermaticus edges, terminal calyces poorly developed or absent, and the sulcus spermaticus bifurcates distally or simply opens onto a terminal clear space." Even though this arrangement was apparently consistent with the taxonomy, the authors provided no further information on the other species of the group, except for *T. pallidus* (Bailey *et al.* 2005). Furthermore, no other published work has provided additional information on the morphological variation of the *T. pallidus* group, especially dealing with hemipenial morphology.

The hemipenial morphology is an important character system, largely employed in the definition and diagnosis of several taxa (Dowling 1967; Keogh 1999; Zaher 1999; Harvey & Embert 2008; Jadin *et al.* 2010). Even though different degrees of intraspecific variation may occur (Zaher & Prudente 1999; Myers & McDowell 2014), hemipenes can provide valuable evidence for assigning species groups within a genus (Schargel & Castoe 2003). A very few detailed descriptions on *Thamnodynastes* hemipenes are already available (Cei *et al.* 1992; Bergna & Alvarez 1993; Nóbrega *et al.* 2016; Franco *et al.* 2017), and this deficit further creates more impediments to breakthrough the taxonomy of the genus.

After the analyses of species of the *Thamnodynastes pallidus* group, as well as of all currently recognized congeners, we were able to identify a fourth species of the *T. pallidus* group and provide new data on its morphological variation.

Material and methods

Eight hundred and sixteen specimens of all species of *Thamnodynastes* were examined, housed in 38 collections (Appendix 1). Institutional symbols followed Sabaj (2020). Additionally, type specimens of the species *T. hypoconia* (Cope, 1860) (ANSP 3747), *T. dixoni* Bailey & Thomas, 2007 (TCWC 44896) and *T. duida* Myers & Donnelly, 1996 (AMNH 36608) were examined exclusively by digital image.

Scale counts were taken considering the most informative characters for the genus according to Franco & Ferreira (2003). Terminologies for pholidosis and meristic characters followed Peters (1964), whereas ventral counting followed Dowling (1951). Dorsal scales were counted in three different portions of the body: anterior/mid-body/one head length before the cloaca; labials, temporals and ocular scales are shown on the "right/left" side of the head. Snout–vent length (SVL) and tail length (TL) were measured to the nearest 1 mm by stretching the specimen against a graduated ruler; when not possible, specimens were measured with a string, which was then stretched on a ruler. Head and scale measurements were taken to the nearest 0.1 mm with a digital caliper, exclusively on the right side of each specimen. Newborn individuals (SVL under 200 mm; Silva *et al.* 2019) were not considered for morphometric data. Measurements were converted to mean values to facilitate descriptions: "(mean value ± standard deviation, number of analyzed specimens)." Sex was confirmed by a small incision at the base of the tail, when the hemipenis was not everted. Color pattern was analyzed exclusively on preserved specimens, except for specimen AMNH 147707.

Sexual dimorphism was tested for ventrals and subcaudals data with a Welch Two Sample t-test in R v.3.6 (R Core Team 2013), which is a t-test adaptation that adjusts the number of degrees of freedom when the variances are

not necessarily equal to each other, and there are different sample sizes. Statistical analysis was performed with a significance level of 5% (a = 0.05).

Hemipenial preparation followed adapted protocols by Pesantes (1994), Zaher (1999) and Zaher & Prudente (2003). After preparation, hemipenes were stained with alizarin in a 70% alcohol solution to facilitate the visualization of structures (Harvey & Embert 2008), and sequentially photographed via a stereomicroscope (model Leica M205a), using the software Leica Application Suite (version 3.8). Hemipenial terminology followed Zaher (1999).

Geographic distribution records were obtained directly from collection catalogues. When not available, geographic coordinates were inferred from Google Earth Pro version 7.3.1.4507. When additional locality was not provided, the coordinate was considered as the geographical centroid from municipality headquarters. Even though this approach may represent a coarse approximation, since municipalities' extension can encompass very large areas in the Amazonia, we maintained the coordinate within the urban area in an attempt to designate an approximate point of reference. Maps were constructed with Quantum GIS software (QGIS Development Team 2019).

Results

Morphological definition of the **Thamnodynastes pallidus** *group*

After the compilation of extensive dataset for *Thamnodynastes*, based on examined specimens (Table 1), we were able to define the *Thamnodynastes pallidus* group to include *T. pallidus, T. longicaudus, T. sertanejo* and the new species as originally defined by Bailey *et al.* (2005), based on the unique combination of the following characteristics: smooth dorsal scales; highest dorsal scale reduction, from 17 or 19 rows at midbody to 11–13 near the cloaca (vs. 17 or 19 rows at midbody to 15 near the cloaca in other congeners); apical pits absent; loreal scale longer than wide; eye length larger than the distance between nostrils; nasal scale single (87%, *n*=174); long tail and highest subcaudal counts within the genus, ranging from 70–109; ventral color pattern composed of one slender dark brown stripe that transforms into two brown ventral stripes on the paraventral region, separated by a beige interspace (same color as the ventral background) only on the final two thirds of the body (*T. pallidus*), or two brown stripes separated by the beige interspace throughout the venter (*T. longicaudus*) (Fig. 1), or venter with sparse blotches, not forming stripes (*T. sertanejo* and the new species) (vs. one longitudinal stripe on the paraventral region, not separated by lighter interspace, on the first third or throughout the body venter, in all other congeners); iris light brown with a darker stripe crossing the pupil horizontally; unilobate or slightly bilobate hemipenes [vs. bilobate hemipenes in other congeners, unilobate condition present only in a few specimens of *T. strigatus* (Gunther, 1858) and *T. nattereri* (Mikan, 1828)], with a very short capitulum; hemipenial body completely covered with homogeneous small spines (vs. slightly or evidently enlarged spines on the first row of body spines in other congeners, except for *T. paraguanae* Bailey & Thomas, 2007, and some specimens of *T. dixoni* and *T. hypoconia*); base of the hemipenes covered with slightly smaller spines; and a subtle constriction separating the body and base of the hemipenes (Fig. 2).

We found a few specific differences in hemipenial morphology among species in the *T. pallidus* group. The capitulum can be completely covered with spines and show no calyces (*T. longicaudus, n*=2), completely covered with spinulate calyces (*T. pallidus, n*= 16), or covered with papillate (on the apex of each lobe) and spinulate calyces (on the base of capitulum and intrasulcar region) (*T. sertanejo, n*= 3); an apparent narrower region on the distal portion of the body may be present (*T. longicaudus*) or absent (*T. pallidus* and *T. sertanejo*); sulcus spermaticus branches are linearly oriented, extending up to the distal half of each lobe, and opening into a nude area separated by a thin wall (*T. longicaudus, T. pallidus* and *T. sertanejo*), or with a wider intrasulcar region ornamented by few spines (*T. longicaudus* and *T. sertanejo*), or the branches can simply merge into a single nude central area (*T. pallidus)*; hemipenial body in 7–11 transverse rows of spines (counted from the constriction that demarks the beginning of the body, until the intersection of body and capitulum, right before the presence of calyces), the first row with 12 (*T. longicaudus*), 13–18 (*T. pallidus*), or 25–27 (*T. sertanejo*) spines encircling the body (Fig. 2). Additionally, *T. pallidus* exhibits an exclusive variation of hemipenial bilobation, with a feeble bilobation in some specimens, and a unilobate condition in others. The hemipenis of *T. sertanejo* is also slightly bilobed, but not so conspicuously as some hemipenes of *T. pallidus* (Fig. 2).

After the analysis of all congeners, including all species from the *Thamnodynastes pallidus* species group (Table 1), we easily differentiated a new taxon based on external (i.e., color pattern and meristics) and internal (i.e., hemipenes) morphology, which we propose as the fourth member of the *T. pallidus* group, to be known as.

TABLE 1. Selected morphological variation of meristic and morphometric characters for the genus *Thamnodynastes* (updated from Franco *et al*. 2017); members of the *T. pallidus* species group are not considered here. Species with no available information are indicated with the symbol '–'. Abbreviations are as follow: **DO**=number of dorsal scale rows; **DO keeled**=presence or absence of keeled dorsals; **max.SVL**=maximum snout-vent length (in millimeters); **max.TL**=maximum tail length (millimeters);**VE**=number of ventral scales; **SC**=subcaudals; **ventral stripes**=number of longitudinal ventral stripes on the body; **M**=males; **F**=females. * Data from Franco & Ferreira (2003) (in parenthesis); ** Data from Bailey & Thomas (2007); *** Data from Myers & Donnelly (1996); and § Data from Myers & Donnelly (1996) (in parenthesis). Data for *T. corocoroensis* and *T. marahuaquensis* was based on our own analysis of each holotype, respectively, slightly differing from the original data given by Gorzula & Ayarzagüena (1996).

Species	DO	DO keeled	max. SVL		max.TL		VE		SC		ventral stripes
			M	F	M	F	M	F	M	F	
T. almae	19/19/15	yes	624 (657*)	525 (595*)	185 (189*)	139 (166*)	146–157	144–154 (144–159*)	64–75	55–66	2–4
*T. ceibae***	19/19/13	yes	448	–	135	–	150	–	67	–	4
T. chaquensis	19/19/15	yes	577	501	233	197	136–152	135–155	55–72	48–65	2–4
T. chimanta	17/17/15	no	327	318	107	82	126–134	125–132	51–61	51–61	2
T. corocoroensis	19/19/15	no	–	260	–	75	–	132	–	56	2 (first third of the body)
T. dixoni	19/19/15	yes	523	525	155	163	147–162	141–154	53–73	58–69	2–4
*T. duida****	17/17/15	no	455	—	101	–	130	–	56	–	4
T. gambotensis	19/19/15	no	542	499	145	143	152–160	136–156	61–75	54–73	2–5
T. lanei	17/17/15	yes	438	431	158	176	137–158	135–154	73–87	75–88	4
T. hypoconia	19/19/15	yes	556	522	182	167	137–165	134–159	60–87	61–80	2–6

...Continued on the next page

TABLE 1. (Continued)

Species	DO	DO keeled	max. SVL		max.TL		VE		SC		ventral stripes
			M	F	M	F	M	F	M	F	
T. marahuaquensis	19/19/15	no	–	307	–	94	–	135	–	61	2
T. nattereri	19/19/15	yes	649	495	209	189	147–167	146–161	64–86	60–81	2–4
T. paraguanae	19/19/15	yes	485	550	125	160	137–157	132–152	55–72	53–65	2–4
T. phoenix	19/19/15	no	495	451	136	118	133–159	133–155	45–66	40–60	2–4
T. ramonriveroi	19/19/15	no	460	411	141	125	142–155	138–147	59–77	52–70	5
T. rutilus	19/19/15	no	477	414	190	142	127–135	115–132	68–79	65–69	2
T. strigatus	19/19/15	no	796	692	211 (212*)	159 (164*)	133–157	130–147	53-72 (52–68*)	47–71	2–4
T. yavi	19/19/15	no	296§	260 (262§)	94§	80	135§	130–131	66§	58–61 (57–61§)	2

FIGURE 1. Dorsal (left) and ventral (right) general color pattern for species of the *Thamnodynastes pallidus* group: *T. longicaudus* (IBSP 41045) from Rio de Janeiro, Brazil **(A)**; *T. pallidus* (MZUSP 19206) (SVL = 445 mm) from Maranhão, Brazil **(B);** *T. sertanejo* (MNRJ 8583) from Minas Gerais, Brazil (SVL = 493 mm) **(C)**. Scale bars = 2 cm.

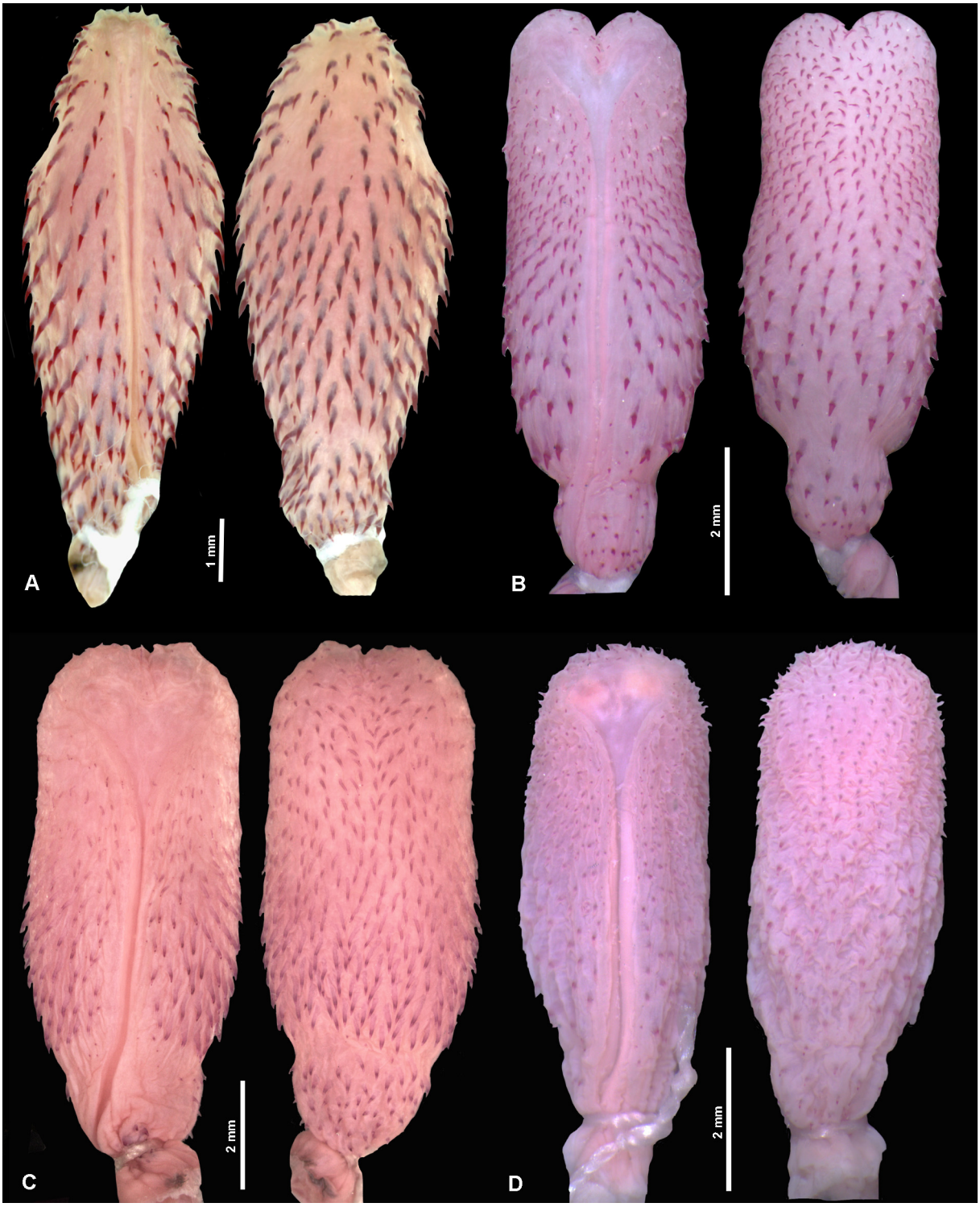

FIGURE 2. Sulcate (left) and asulcate (right) sides of the hemipenes for species of the *Thamnodynastes pallidus* group: *T. longicaudus* (IBSP 18676) from São Paulo, Brazil **(A)**; *T. pallidus* (MZUSP 18829) from Maranhão, Brazil **(B)**; *T. sertanejo* (MZUSP 21301) from Alagoas/Sergipe, Brazil **(C)**; and *T. pallidus* (MPEG 6842) from Pará, Brazil **(D)**.

***Thamnodynastes silvai* sp. nov.**
(Figs. 3–4)

Thamnodynastes cf. *pallidus* Dixon & Soini, 1977: 73; Dixon and Soini, 1986: 132.
Thamnodynastes pallidus Bartlett & Bartlett, 2003: 250, fig. 248.

Holotype. An adult male, SINCHI-R 2139 (Field Number JSH 948), collected by Juan Silva Haad on Isla Rondinã (no collection date), province of Mariscal Ramón Castilla, district of Ramón Castilla, department of Loreto, Peru (Fig. 3).

FIGURE 3. Dorsal (**A**), lateral (**B**) and ventral (**C**) views of head and dorsal (**E**) and ventral (**F**) views of body of the holotype of *Thamnodynastes silvai* (SINCHI-R 2139) from Ramón Castilla, Loreto Department, Peru. Scale bars = 3 cm.

***Paratypes* (*n*=30).** Seven adults and one juvenile from Loreto Department, Peru: female, AMNH 52125, collected by Harvey Bassler on March 1931 at Caballococha, Amazon River; male, AMNH 53581, collected by Harvey Bassler on December 16 1926 at Rean Rean, Suhuayo (near Contamana, Ucayali River); male, AMNH 52083 and female, AMNH 55472, without additional information; male AMNH 55643, collected by Harvey Bassler at Monte Carmelo, Requena Province (Uresti), no collection date; female, MHNC 3143 (Field Number 11) from Dos de Mayo (Sarayacu), Ucayali Province; male, USNM 197292 (Field Number AJ 933), collected on November 1970 at Iquitos; young male, CORBIDI 6072, from Requena Province (Jenaro Herrera) without additional information. Twelve adults collected by Dionisio Mafra at Yahuma island, Cayarú, Mariscal Ramón Castilla Province, Ramón Castilla district, Loreto Department, Peru: five females, SINCHI-R 2143 (Field Number JSH 1420), SIN-

CHI-R 2154 (Field Number JSH 1182), SINCHI-R 2148 (Field Number JSH 956), SINCHI-R 2147 (Field Number JSH 1034) and SINCHI-R 2151 (Field Number JSH 1585); and seven males, SINCHI-R 2140 (Field Number JSH 1051), SINCHI-R 2141 (Field Number JSH 1427), SINCHI-R 2163 (Field Number JSH 1062), SINCHI-R 2146 (Field Number JSH 963), SINCHI-R 2149 (Field Number JSH 704), SINCHI-R 2150 (Field Number JSH 1422), and SINCHI-R 2157 (Field Number JSH 1043). Five adults and one juvenile from Leticia, Amazonas department, Colombia: female, IAVH 2046 (Field Number OPM 518), collected by Oscar Pinto-Moreno at Amacayacu Natural National Park; young male, IAVH 854, collected by Juan Silva Haad on August 1978; two males, SINCHI-R 2144 (Field Number JSH 1127) and SINCHI-R 2169 (Field Number JSH 861); and two females, SINCHI-R 2142 (Field Number JSH 819) and SINCHI-R 2159 (Field Number JSH 150). One adult male, USNM 233065 (Field Number 807), collected on May 1952 at Maruma, Morona-Santiago Province, Ecuador (no collector information). Two adult females, SINCHI-R 2153 (Field Number JSH 373) and SINCHI-R 2162 (Field Number JSH 429), from Tabatinga, Amazonas State, Brazil. One adult female, MPEG 18835 (Field Number TCAP 2357), collected on July 29, 1994 by Marinus S. Hoogmoed and Teresa C. Ávila-Pires at the Mamirauá Ecological Station, Araçazinho lake (left bank of Paraná Apara), Uarini, Amazonas state, Brazil.

Diagnosis. Venter scattered with sparse dark brown blotches, not forming longitudinal ventral stripes; 12–21 dark brown blotches on the first third of the dorsum of the body, which progressively fade and turn into small brown spots on each side of the paravertebral region (Figs. 3–4); dorsal scale rows smooth, in 17/17/11 (70%, *n*=42) or 17/17/13 (22%, *n*=13) series; dorsals lacking apical pits; ventrals 124–137 in females and 127–148 in males; and subcaudals 80–97 in females, 83–101 in males (Table 2).

Comparisons. *Thamnodynastes silvai* differs from all congeners by having 17/17/13 or 17/17/11 dorsals [vs. 19/19/15 in *T. almae* Franco & Ferreira, 2003; *T. chaquensis* Bergna & Alvarez, 1993; *T. corocoroensis* Gorzula & Ayarzagüena, 1996; *T. dixoni*; *T. gambotensis* Perez-Santos & Moreno, 1989; *T. hypoconia; T. marahuaquensis* Gorzula & Ayarzagüena, 1996; *T. nattereri*; *T. paraguanae*; *T. phoenix* Franco, Trevine, Montingelli & Zaher, 2017; *T. ramonriveroi* Manzanilla & Sánchez, 2005; *T. rutilus* (Prado, 1942); *T. strigatus*; *T. yavi* Myers & Donnelly, 1996; and 19/19/13 in *T. ceibae* Bailey & Thomas, 2007], and ventral color pattern lacking longitudinal stripes (vs. at least some portion of venter with continuous or inconspicuous longitudinal stripes in all other *Thamnodynastes,* except for *T. sertanejo*). In addition, from the other species with 17 dorsals at midbody (*T. chimanta* Roze, 1958*, T. duida* and *T. lanei* Bailey, Thomas & Silva Jr., 2005), the new species differs by having 13 series of dorsals on the cloacal region (vs. 15 series in *T. chimanta, T. duida* and *T. lanei*); smooth dorsal scales (vs. dorsals markedly keeled in *T. lanei*); and 80–101 subcaudals (vs. 51–61 subcaudals in *T. chimanta,* 56 in *T. duida* and 73–88 in *T. lanei*) (Table 1). From the species of the *T. pallidus* group (*T. longicaudus*, *T. pallidus* and *T. sertanejo*), *T. silvai* differs by a set of characters (Table 2). Besides the absence of longitudinal ventral stripes, it differs from *T. longicaudus* by having 17/17/13 or 17/17/11 dorsals (vs. 19/19/13); from *T. pallidus* by divided cloacal (vs. single), the overall dorsal pattern, composed by several blotches on the first third of the body (vs. first third with several spots of lighter scales, yellow and whitish, bordered by dark brown or black markings in the scale interspaces, in a variegated pattern, sometimes forming smaller blotches), and wider and darker postocular stripe and supralabials spots (vs. postocular stripe and labial spots composed only by a thin dark line delineating the border, not colored internally) (Figs. 1, 3). *Thamnodynastes sertanejo* is the only other member of the genus with a blotched ventral pattern (not forming longitudinal stripes). Even so, *T. silvai* can be easily differentiated by head length 12.3–17.1 mm (vs. 16.1–25.8 mm in *T. sertanejo*), lower number of ventral counts, both for male and females (Table 2), and also by the overall dorsal body pattern: transverse dark brown or greyish bands separated by lighter bands (formed by three to five rows of beige scales) on the first third of the body, progressively vanishing into a homogeneous pattern with a few scattered small dark spots in mid-body that continue throughout the tail (vs. generally homogeneous first third of the body in *T. sertanejo*, with dark broad dorsal blotches separated by transverse bands of two or three rows of white scales, evident from the mid-body to tail) (Figs. 1, 3–4). Additionally, *T. sertanejo* also exhibits a few scattered black dots on the anterior portion of the venter, which may appear as larger black spots on the ventral posterior region (Fig. 1).

Description of the holotype. Dorsals smooth in 17/17/11 rows; apical pit absent; ventrals 136 and divided subcaudals 98; cloacal semi-divided (division on half of the scale length); supralabials 8/8, 4–5th contacting eye; infralabials 10/9, 1–5th/1–4th contacting first pair of mentals, 5–6th/4–5th contacting the second pair; pair of mental shields, approximately the same size; temporals 2+3/2+3; nasal single; loreal elongate on the right side, slightly square on the left; preoculars 1/1 and postoculars 2/2; SVL 440 mm, TL 237.5 mm, head length 15.3 mm, head height 6.1 mm, head width 8.5 mm; distance between nostrils 2.5 mm, eye height 2.6 mm, eye length 3 mm, distance between eyes

5.4 mm, eye-mouth distance (approximately at the level of the fifth supralabial) 1.2 mm, eye-rostral distance 3.6 mm; internasal scale (length X width): 1.2 X 0.9 mm, prefrontal: 1.7 X 1.5 mm, frontal: 4.4 X 1.7 mm, parietal: 4.5 X 2.2 mm, loreal: 1.1 X 0.6 mm; prediastemal maxillary teeth 9 plus 2 slightly enlarged and grooved fangs.

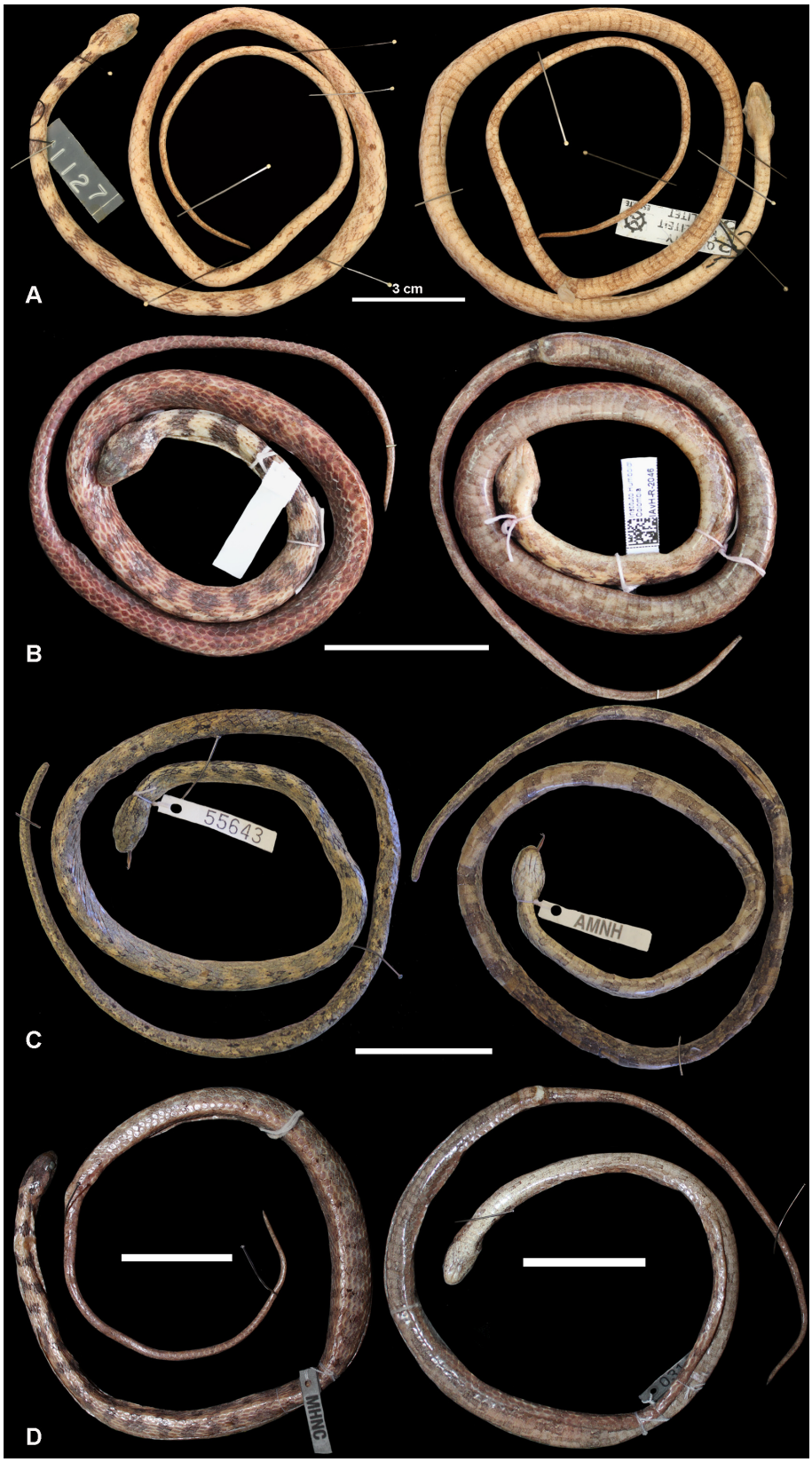

FIGURE 4. Color pattern variability in dorsal (left) and ventral (right) views of the paratypes of *Thamnodynastes silvai*: SINCHI-R 2144 **(A)** and specimen IAVH 2046 **(B)** from Leticia, Colombia; AMNH 55643 **(C)** and MHNC 3143 **(D)** from Loreto Department, Peru. Other scale bars = 4 cm.

TABLE 2. Morphological variation within species of the *Thamnodynastes pallidus* group. Measurements data are for adults, except for the single female specimen of *T. longicaudus*, represented by a newborn individual. **M**=Males; **F**=Females; **DO**=number of dorsal scale rows; **SVL**=snout-vent length; **TL**=tail length; **HL**=head length; **VE**=number of ventrals; **SC**=subcaudals; **ventral stripes=** number of longitudinal ventral stripes on the body. * Data complemented by Nóbrega *et al.* (2016); ** maximum SVL for *T. pallidus* in Nóbrega *et al.* (2016) = 600 mm.

		***Thamnodynastes silvai* sp.n.**	***Thamnodynastes pallidus***	***Thamnodyanstes longicaudus***	***Thamnodyanstes sertanejo***
DO		17/17/11 (*n*=42) or 13 (*n*=13)	17/17/13 (*n*=61) or 11 (*n*=10)	19/19/13 (*n*=9) or 19/19/15 (*n*=1)	17/17/11(*n*=24) or 13 (*n*=10)
SVL (mm)	**M**	292–440 (356.6±41, *n*=25)	283–520 (401.8±55.7, *n*=29)**	298–416 (343.1±40.9, *n*=7)	415–665 (568.3±67.1, *n*=19)
	F	251–388 (321.4±27.6, *n*=29)	253–451 (368.8±60.1, *n*=43)	163 (*n*=1)	390–655 (519.6±68, *n*=17)
TL (mm)	**M**	136–237.5 (170.4±24.1, *n*=20)	123–222 (165.8±23.6, *n*=27)	127–221 (179.1±31.8, *n*=7)	142–272 (215.3±30.7, *n*=18)
	F	120–173 (149.5±11.9, *n*=26)	97–190 (149.1±26.2, *n*=42)	76 (*n*=1)	132–231 (179±23.8, *n*=16)
HL (mm)	**M**	12.3–15.7 (14±0.8, *n*=24)	11.9–18.1 (15.2±1.8, *n*=29)	12.4–17.9 (14.4±1.8, *n*=8)	16.1–24 (21±1.8, *n*=19)
	F	12.3–17.1 (14.5±1.1, *n*=30)	11.2–18.8 (15.3±2, *n*=40)	–	17.2–25.8 (21.7±2.4, *n*=16)
VE	**M**	127–148 (137±4.8, *n*=27)	127–164 (*n*=53)*	133–147 (141±4.3, *n*=7)	152–167 (159±3.4, *n*=20)
	F	124–137 (128±2.9, *n*=30)	136–164 (*n*=73)*	142 (*n*=1)	140–151 (145±2.7, *n*=18)
SC	**M**	83–101 (94± 4.2, *n*=21)	70–104 (*n*=50)*	102–109 (106±2.4, *n*=7)	84–98 (91±3.7, *n*=20)
	F	80–97 (87±4.1, *n*=27)	73–101 (*n*=72)*	100 (*n*=1)	74–84 (79±2.7, *n*=17)
ventral stripes		absent	4	2– 6	absent

In preservative, dorsal surface of the head with intense brown pigmentation from the supratemporals to internasals, temporals light beige with several small brown dots; brown postocular stripe, extending from the postoculars to the rear corner of the mouth, where it continues as a blotch of seven scales in length; supralabial background light beige with a few small brown dots, brown blotches on the first three supralabials, and a small blotch right under the eye between supralabials four and five; infralabials background light beige with scattered small brown stains, reaching mentals, gulars and preventrals. Sixteen dorsal dark brown bands, two to four scale rows long, more prominent on the first third of the body, progressively losing pigmentation towards the tail, until fading into sparse dark brown spots on each side of the vertebral scale; beige stripe from the distal border of the parietals, extending eight scales onto the neck, bordered by two dark brown stripes (10 scales long) on each side; ventral background light beige with intense pigmentation of minute brown spots, darkening the overall ventral pattern towards the tail; diffuse dark brown blotches, concentrated on the paraventral portion, more evident from the second third of the body; ventral portion of the tail dark brown with more intense pigmentation than body (Fig. 3).

The hemipenis of the holotype is unilobed (although with divided retractor muscle), unicalyculate and non-capitated, with very short capitulum covered with small papillate calyces; few spinulate calyces on the proximal portion of capitulum on the asulcate side; hemipenial body covered with a few rows of small spines, 19 slightly larger spines

encircling first row; sulcus spermaticus divided at the base of the capitulum, with sulci ending in slightly enlarged area, on approximately half the capitulum length; subtle constriction between base and hemipenial body; base covered with several spines, approximately the same size as the body spines (Fig. 5).

Hemipenial morphology (*n*=15). *Thamnodynastes silvai* has a hemipenis pattern corresponding fairly well to the overall pattern of the *T. pallidus* group, more closely resembling the hemipenis of *T. longicaudus* (Figs. 2, 5). Additional prepared hemipenes exhibited little variation (Fig. 5), such as: capitular spinulate calyces can be more evident on the proximal portion of the capitulum, on the asulcate side (Fig. 5C); the sulci are short, after the sulcus spermaticus division, associated with a short capitulum in all analyzed specimens, and their termination can be slightly closer to the capitulum apex (Fig. 5B–D).

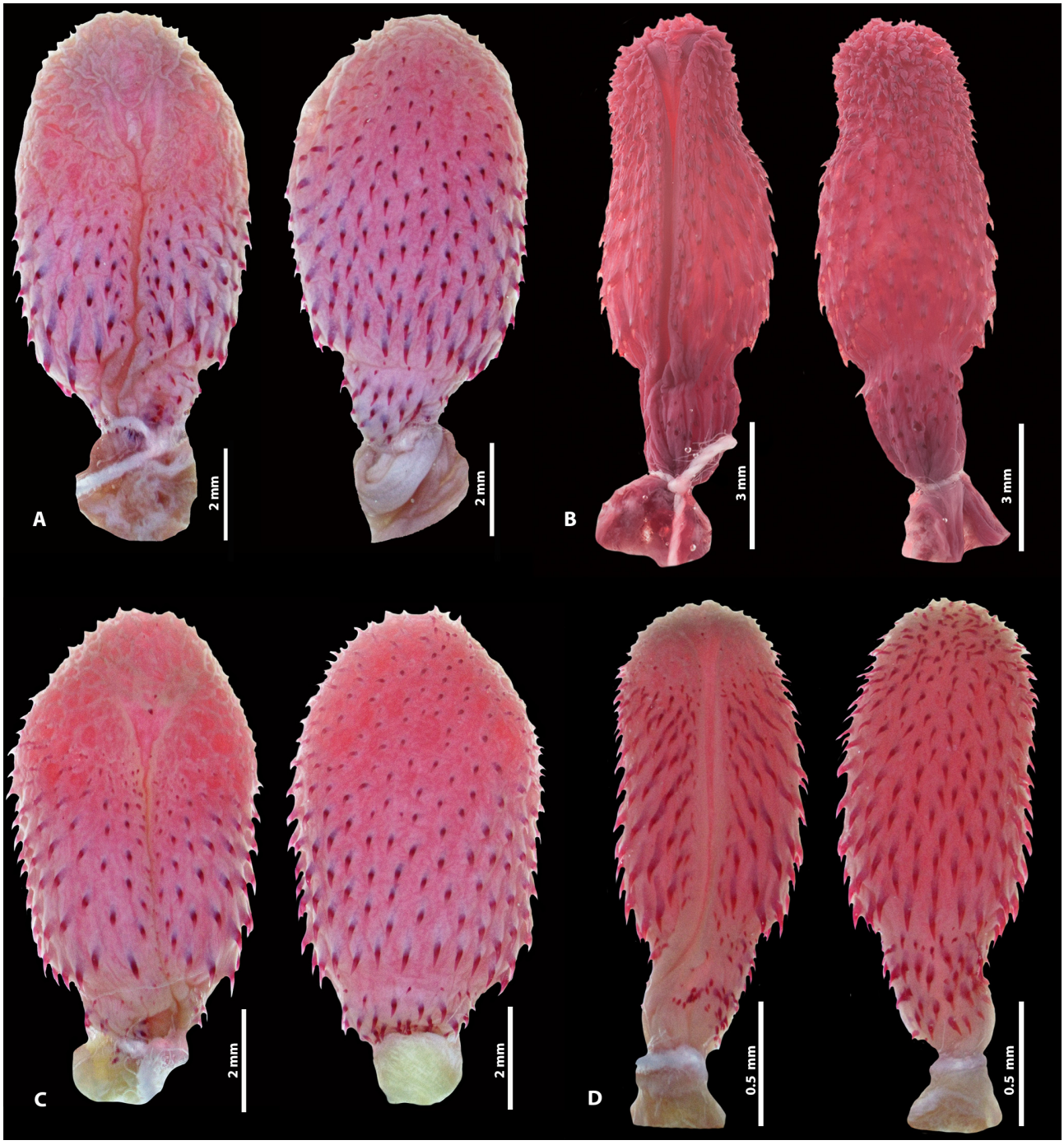

FIGURE 5. Hemipenial variation displaying the sulcate (left) and asulcate (right) sides of the organs of *Thamnodynastes silvai*: holotype (SINCHI-R 2139) **(A)**; AMNH 53058 (fully everted but not maximally expanded distally) from Iquitos, Loreto, Peru **(B)**; paratype SINCHI-R 2144 **(C)** and paratype SINCHI-R 2169 from Leticia, Colombia **(D)**.

Meristic and morphometric variation. Largest male (SINCHI-R 2139) SVL 440 mm and TL 237.5 mm; largest female (AMNH 55472) SVL 388 mm and TL 170 mm; smooth dorsal scales in 17/17/11 (70%, *n*=42), 17/17/13 (22%, *n*=13), 15/17/11 (3.3%, *n*=2), 17/17/12 (3.3%, *n*=2) or 17/17/10 (1.6%, *n*=1) series. Sexual dimorphism was reported for both ventrals (t =-8.4707, p<0.001) and subcaudals (t=-6.0197, p<0.001); ventrals 127–148 (137±4.8, *n*=27) and subcaudals 83–101 (94± 4.2, *n* =21) in males, ventrals 124–137 (128±2.9, *n* =31) and subcaudals 80–97 (87±4.1, *n* =28) in females; supralabials 8 (98%, *n*=52) or 8/7 (2%, *n*=1); 4–5th supralabials contacting eye (75%, *n*=38) or 3– 5th (28%, *n*=15); infralabials 9 (75%, *n*=43), 8/8 (8.7%, *n*=5), 9/8 (5.3%, *n*=3), 9/10 (3.5%, *n*=2), 10/9 (3.5%, *n*=2), 8/9 (1.7%, *n*=1) or 10/10 (1.7%, *n*=1); preoculars 1/1 (93%, *n*=52) or 1/2 (*n*=1); postoculars 2/2 (86%, *n*=49), 2/3 (*n*=1), 3/2 (*n*=2), or 3/3 (*n*=2); nasal scale single (98%, *n*=52) or semi-divided on the right side (*n*=1).

Color pattern variation. In preservative, examined specimens show head usually very pigmented with several small dots, from rostral to temporal scales, almost black in few specimens (USNM 233065, MHNC 3143). Head usually with two dark brown bands right after temporals, extending onto the neck, occasionally merged with first pair of dorsal blotches (USNM 203065, SINCHI-R 2142, 2139) (Fig. 4). These two bands may define a lighter central neck band (SINCHI-R 2153). Postocular stripe very distinguished, the same color as dorsal blotches, ending right after the corner of the mouth, and extending for 2 or 3 scales ventrally (IAVH 2046), or linearly extending on the side of the body (AMNH 52083) (Figs. 3, 4). Venter of the head light beige, with a few scattered brown dots concentrated more on neck region and laterally. Twelve to 21 dorsal bands on the first third of the body, defined into regular transverse bands (CORBIDI 6072, AMNH 52536) or irregularly shaped (e.g. IAVH 2046) (Fig. 4). Final dorsal two thirds of body and tail with more intensely pigmented variegate pattern (AMNH 52083, 53581), or with very subtle pigmentation, almost immaculate (AMNH 52858). All specimens (*n*=64) lack longitudinal ventral stripes, with ventral brown blotches dispersed throughout the belly and tail (Figs. 3–4). These blotches can be evenly spaced, occupying two ventral scales each (AMNH 53582, 55472), or more irregularly dispersed (IAVH 2046, USNM 233065) (Fig. 4). Most specimens with overall ventral darkening towards the tail, from beige or light cream on the head to an intensely pigmentated brown tail (IAVH 2046).

Color in life. The following pattern and coloration description of specimen AMNH 147707, from Pebas, Loreto Department, Peru, is from the field notes of Charles W. Myers (pers. comm. to Robert A. Thomas dated April 14, 1977): "Overall grayish brown above, with a few blackish brown spots and vague yellowish-brown areas that are paler than ground color and that occur at intervals to give an incipient banded pattern. The neck or hood region is banded with brown saddles and lighter brown interspaces (scales in the interspaces have pale yellow bases set in white skin). A pair of vague dark brown lines on rear of head and nape. Underside head and neck white, thence turning an increasingly dark grayish brown on venter, with squarish marks of still darker brown; these marks tend to be broken and/or bordered by streaks of whitish. Iris pale brown; pupil vertical. Tongue overall grayish black except for a broad brown band that encircles the base of fork."

Etymology. The specific epithet "*silvai*" is patronymic honoring the late Juan Silva Haad, physician at the hospital of Leticia for many years, who maintained a snake collection for over 50 years. He collected several species from Colombian, Peruvian and Brazilian Amazonia, including several of the *Thamnodynastes* specimens used in this description. He donated most part of his collection to the Sinchi Institute, with over 2,500 specimens of Amazonian snakes, which represented an immense contribution for the Institute's collection, and a valuable addition of important data for the study of Amazonian snakes. Unfortunately, he passed away on January 31, 2021, just a few weeks before the final reviewed version of the manuscript was accepted.

Distribution and natural history. Six females had three to six developed follicles with visible embryos (possibly in early stages of development due to their small size): SINCHI-R 2142 (3 follicles/embryos), SINCHI-R 2143 (6), SINCHI-R 2147 (4), SINCHI-R 2154 (5), SINCHI-R 2172 (5), and SINCHI-R 2173 (5); and one female (MPEG 18835) had three well-developed follicles with larger visible embryos, confirming a viviparous reproductive mode. The largest pregnant female (SINCHI-R 2147: SVL 323 mm, TL 173 mm) had four embryos. One specimen (AMNH 53582: SVL 321 mm, TL 152 mm) had a small frog (family Hylidae) in the stomach.

On July 29, 1994 at 14:15 h, during the flood season in the Amazon, Marinus S. Hoogmoed and Teresa C. Avila-Pires collected a female (MPEG 18835) in an isolated tree, emerging from a floating meadow (mixed vegetation) at the edge of a lake, completely surrounded by floating grassy mats along its banks. The specimen was slowly moving on the branches of a tree at a height of about 2m above the water surface. When collected (and later again when photographed), it flattened its head and anterior part of the body horizontally (forming a hood), which caused the thin skin between the scales to be stretched and exposed, suddenly showing a bold pattern of transverse, dark brown

spots on a lighter background (Figs. 6A–B). Within the spots, the edges of the scales were black, forming three to six horizontal short zig-zag lines (about three scales long) within the dark spots. Because of the abrupt change this behavior was interpreted as being defensive. No attempt to bite was made. We also report, for the first time, the same behavior for *T. pallidus*. Two specimens (SINCHI-R 2528 and 2529) displayed the hood-displaying performance while their photographs were being taken, during fieldwork in San José del Guaviare, Guaviare Department, Colombia, in June 15, 2017 (Figs. 6C–D).

Thamnodynastes silvai occurs in forested areas of Amazonia, along the triple frontier of Colombia, Brazil and Peru; extending southwest to the Loreto Department in Peru, northwest to the province of Morona-Santiago in Ecuador, and northeast to Uarini, state of Amazonas in Brazil (Fig. 7).

FIGURE 6. Defensive hood displaying behavior of *Thamnodynastes silvai* (MPEG 18835) **(A–B)**; and *T. pallidus* (SINCHI-R 2528–29) **(C–D)**. Photos A–B by T. Avila-Pires.

Discussion

It is well known that *Thamnodynastes* may not represent a monophyletic genus (Franco & Ferreira 2003; Zaher *et al*. 2009; Vidal *et al*. 2010; Grazziotin *et al*. 2012; Zaher *et al*. 2018), and a few authors have already mentioned the cryptic diversity associated with its members (Franco *et al.* 2017). The combination of taxonomic issues and deficiency of robust diagnostic characters have long perpetuated the difficulty to correctly assign individuals to species. Nevertheless, the *T. pallidus* species group represents an exception to this pattern.

Bailey *et al.* (2005) defined the *Thamnodynastes pallidus* group based on several characters of scale counts, body shape, color, behavior and hemipenial morphology; all of which we were able to corroborate. The hemipenes is very characteristic for the group, with no enlarged body spines and showing the most extreme reduction of bi-

lobation within the genus, with *T. longicaudus*, *T. silvai* and some specimens of *T. pallidus* exhibiting a unilobate condition. Some of the variation found within *T. silvai* and other species of the group, especially the variation related to shape, are associated with preparation biases, such as organ inflation. During the organ preparation, filling with stained petroleum jelly, some specimens are fully everted but not maximally expanded, while others are over expanded, causing the hemipenis to be larger. That could be due to the preservation status of the organ, or to muscle residues attached on the hemipenis' internal walls, which hinders its complete expansion.

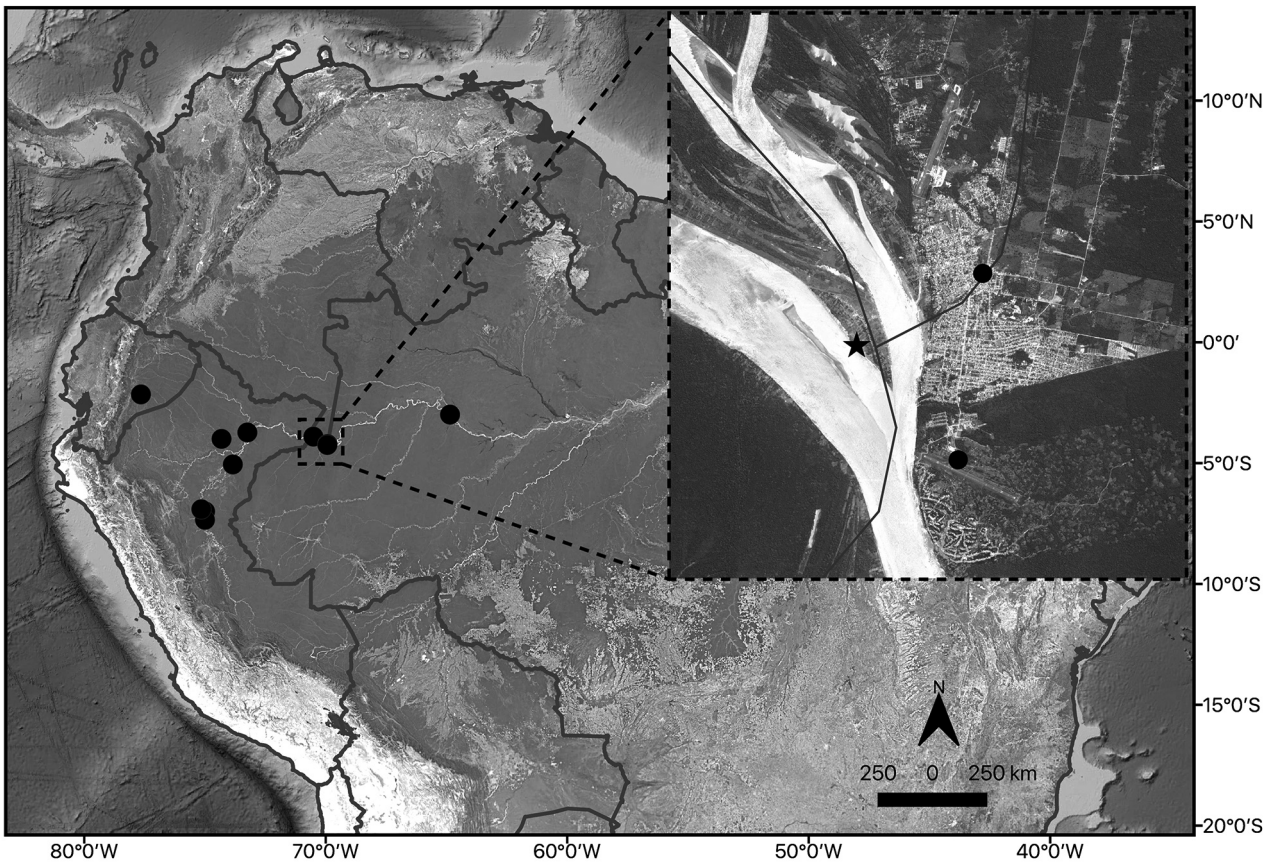

FIGURE 7. Know geographic distribution of *Thamnodynastes silvai*. On the right corner we detail the region of the type locality at the triple frontier between Colombia, Brazil and Peru. Black circles = examined specimens; black star = holotype.

All the members of the group share features that are associated with arboreality, such as a long tail, slender body and large eyes. It is well known that arboreality influences the morphology of snakes, as it imposes strong selective pressures towards narrower and more laterally compressed bodies, and relatively longer tails (Lillywhite & Henderson 1993; Pizzatto *et al.* 2007; Alencar *et al*. 2017; Harrington *et al.* 2018). These adaptations consequently reflect on other correlated characters present in the *Thamnodynastes pallidus* group such as number of subcaudals (longer tails show more subcaudals), and accentuated reduction of dorsal scale rows on the level of cloaca (i.e., less scale rows means slenderer bodies).

Bailey *et al.* (2005) also mentioned the shape of dorsals and "possession of a hood that is spread defensively" as characteristic of the *Thamnodynastes pallidus* group: *T. pallidus, T. longicaudus* and *T. silvai* in fact have apparently elongate dorsals. However, *T. sertanejo* has a more robust body, reflecting on dorsals format. The hood-displaying behavior is apparently exclusive for the *T. pallidus* group within the genus. This type of behavior is documented for *T. sertanejo* (Barbosa *et al.* 2006), *T. longicaudus* (Franco *et al.* 2003), and now for *T. pallidus* and *T. silvai*, the latter showing very conspicuous dark bands flaunted during the flattening of the neck (hood), similarly as in *T. longicaudus*. These dorsal bands seem to fit the usual dorsal color pattern found in arboreal snakes, which are predominantly dorsally brown or black, and/or patterned (Harrington *et al.* 2018).

Additional natural history notes and behavioral defensive display were documented for *Thamnodynastes silvai*. Dixon and Soini (1986) reported two specimens collected in the field, referred to as *Thamnodynastes* cf. *pallidus*, one from "beneath the bark of a standing dead log in the closed canopy forest" and the other "from a porch" in Iqui-

tos, Peru. The authors characterized the species as a rare semiarboreal snake, restricted to the primary forest. Bartlett & Bartlett (2003) described the defensive response of the new species (referred to as *T. pallidus* by the authors) as "to straighten out and become rigid, showing no signs of life", which can also occasionally strike and bite. William Lamar (pers. comm. to Robert A. Thomas) also reported a collected specimen from Puerto Miguel Village, Loreto, Peru (KU 220506) coiled on a tree branch about eye level during the day, in a seasonally flooded swamp forest. He also reported the presence of several *T. pallidus* in the same area, indicating the sympatry of these two species.

The characters associated with arboreality in the *Thamnodynastes pallidus* group could represent a unique condition within the genus, and further indicates the monophyletism of the group. However, it is not clear whether its species are in fact the most specialized or most arboreal species of the genus, as suggested by Bailey *et al.* (2005). Several species of *Thamnodynastes,* such as *T. lanei, T. nattereri, T. phoenix* and *T. strigatus,* can also show some degree of arboreality (Bernarde *et al.* 2000, Bailey *et al.* 2005, Lacerda *et al.* 2009). In fact, *T. lanei* and *T. nattereri*, which are frequently collected on vegetation, can also have longer tails, with 60–88 subcaudals; but not as long as the members of the *T. pallidus* group, with more than 90 subcaudals. Also, none of them show the extreme reduction of six dorsal scale rows, present in the *T. pallidus* group.

Several different evolutionary processes could lead towards arboreality and body shape adaptations in snakes, such as availability of new ecological opportunities and physiological pressures imposed by gravity (Sheehy *et al.* 2016; Alencar *et al.* 2017). Even though species of the *Thamnodynastes pallidus* group have longer tails and slender bodies, the frequency and types of habitat use have never been systematically tested to other congeners. Therefore, additional data on the natural history of other members of this genus is still needed to ascertain the specialized nature of the group.

Our results corroborate the recognition of the *Thamnodynates pallidus* group and provide important diagnostic characters for this cluster of species. Additionally, our data could indicate some degree of conservation threat for *T. silvai.* The majority of available specimens were collected prior to 1970, and the last registered specimen was found in 1994. In spite of a few sampling efforts by the Sinchi Institute around the type locality region, no other specimens of *T. silvai* were found. Similarly, there are very few records of the species in the literature (Dixon & Soini 1977, 1986; Bartlett & Bartlett 2003). Additional studies on ecology and fieldwork surveys are essential for further understanding conservation aspects of this new species.

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References

Alencar, L.R.V., Martins, M., Burin, G. & Quental, T.B. (2017) Arboreality constrains morphological evolution but not species diversification in vipers. *Proceedings of the Royal Society B: Biological Sciences*, 284, 1–9. https://doi.org/10.1098/rspb.2017.1775

Bailey, J.R., Thomas, R.A. & Silva Jr., N.J. (2005) A revision of the South American genus *Thamnodynastes* Wagler, 1830 (Serpentes, Colubridae, Tachymenini). I. Two new species of *Thamnodynastes* from Central Brazil and adjacent areas, with redefinition of and neotype designation for *Thamnodynastes pallidus* (Linnaeus, 1758). *Phyllomedusa*, 4 (2), 83–101. https://doi.org/10.11606/issn.2316-9079.v4i2p83-101

Bailey, J.R. & Thomas, R.A. (2007) A revision of the South American snake genus *Thamnodynastes* Wagler, 1830 (Serpentes: Colubridae, Tachymenini). II. Three new species from northern South America, with further descriptions of *Thamnodynastes gambotensis* Pérez- Santos and Moreno and *Thamnodynastes ramonriveroi* Manzanilla and Sánchez. *Memoria de la Fundación La Salle de Ciencias Naturales*, 166, 7–27.

Barbosa, A.R., Albuquerque, H.N. & Sousa, S.M. (2006) Descrição de desenvolvimento em cativeiro de uma nova espécie do gênero *Thamnodynastes* (Wagler, 1830) (Serpente: Colubridae) da Caatinga Paraibana. *Revista de Biologia e Ciencias da Terra*, 6 (1), 73–83.

Bartlett, R.D. & Bartlett, P. (2003) *Reptiles and Amphibians of the Amazon. An Ecotourist's Guide*. University Press of Florida, Gainesville, Florida, 291 pp.

Bellini, G.P., Giraudo, A.R. & Arzamendia, V. (2014) Comparative ecology of three species of *Thamnodynastes* (Serpentes, Dipsadidae) in subtropical-temperate South America. *The Herpetological Journal*, 24 (2), 87–96.

Bergna, S. & Alvárez, B. (1993) Descripción de una nueva especie de *Thamnodynastes* (Reptilia: Serpentes, Colubridae) del nordeste argentino. *Facena*, 10, 5–18.

Bernarde, P.S., Kokobum, M.N.C. & Marques, O. (2000) Utilização de hábitat e atividade em *Thamnodynastes strigatus* (Günther, 1858) no sul do Brasil (Serpentes, Colubridae). *Boletim do Museu Nacional*, Nova Série, Zoologia, 428, 1–8.

Cei, J., Bergna, S. & Alvárez, Y.B. (1992) Nueva combinación para el género *Thamnodynastes* (Serpentes, Colubridae) de Argentina. *Facena*, 9, 123–134.

Coelho, R.D.F., Souza, K., Weider, A.G., Pereira, L.C.M. & Ribeiro, L.B. (2013) Overview of the distribution of snakes of the genus *Thamnodynastes* (Dipsadidae) in northeastern Brazil, with new records and remarks on their morphometry and pholidosis. *Herpetological Notes*, 6, 355–360.

Dixon, J.R. & Soini, P. (1977) The reptiles of the upper Amazon basin Iquitos region, Peru. II. Crocodilians, turtles and snakes. *Contributions in Biology and Geology, Milwaukee Public Museum*, 12, 1–91.

Dixon, J.R. & Soini, P. (1986) *The reptiles of the upper Amazon basin, Iquitos region, Peru.* 2nd ed. Milwaukee Public Museum, Milwaukee, Wisconsin,154 pp.

Dowling, H.G. (1951) A proposed method of expressing scale reductions in snakes. *Copeia*, 131–134. https://doi.org/10.2307/1437542

Dowling, H.G. (1967) Hemipenes and other characters in colubrid classification. *Herpetologica*, 23 (2), 138–142.

Franco, F.L. & Ferreira, T.G. ["2002" (2003)] Descrição de uma nova espécie de *Thamnodynastes* Wagler, 1830 (Serpentes, Colubridae) do nordeste brasileiro, com comentários sobre o gênero. *Phyllomedusa*, 1, 57−74. https://doi.org/10.11606/issn.2316-9079.v1i2p57-74

Franco, F.L., Ferreira, T.G., Marques, O.A.V. & Sazima, I. (2003) A new species of hood-displaying *Thamnodynastes* (Serpentes: Colubridae) from the Atlantic forest in southeast Brazil. *Zootaxa*, 334 (1), 1–7. https://doi.org/10.11646/zootaxa.334.1.1

Franco, F.L., Trevine, V.C., Montingelli, G.G. & Zaher, H. (2017) A new species of *Thamnodynastes* from the open areas of central and northeastern Brazil (Serpentes: Dipsadidae: Tachymenini). *Salamandra*, 53 (3), 339−350.

Grazziotin, F.G., Zaher, H., Murphy, R.W., Scrocchi, G., Benavides, M.A., Zhang, Y. & Bonatto, S.L. (2012) Molecular phylogeny of the New World Dipsadidae (Serpentes: Colubroidea): a reappraisal. *Cladistics*, 1, 1−23. https://doi.org/10.1111/j.1096-0031.2012.00393.x

Gorzula, S. & Ayarzagüena, J. 1995 (1996) Dos nuevas especies del género *Thamnodynastes* (Serpentes: Colubridae) de lostepuyes de la Guayana Venezolana. *Publicación Asociación Amigos DonPana*, 6, 1–17.

Guedes, T.B., Nogueira, C. & Marques, O.A.V. (2014) Diversity, natural history, and geographic distribution of snakes in the Caatinga, Northeastern Brazil. *Zootaxa*, 3863 (1), 1–93. https://doi.org/10.11646/zootaxa.3863.1.1

Harrington, S.M., de Haan, J.M., Shapiro, L. & Ruane, S. (2018) Habits and characteristics of arboreal snakes worldwide: arboreality constrains body size but does not affect lineage diversification. *Biological Journal of the Linnean Society*, 125, 61–71. https://doi.org/10.1093/biolinnean/bly097

Harvey, M.B. & Embert, D. (2008) Review of Bolivian *Dipsas* (Serpentes: Colubridae) with comments on other South American species. *Herpetological Monographs*, 22, 54–105. https://doi.org/10.1655/07-023.1

Jadin, R.C., Gutberlet, R.L. & Smith, E.N. (2010) Phylogeny, evolutionary morphology, and hemipenis descriptions of the Middle American jumping pitvipers (Serpentes: Crotalinae: Atropoides). *Journal of Zoological Systematics and Evolution-*

ary Research, 48 (4), 360–365.
https://doi.org/10.1111/j.1439-0469.2009.00559.x
Keogh, J.S. (1999) Evolutionary implications of hemipenial morphology in the terrestrial Australian elapid snakes. *Zoological Journal of the Linnean Society*, 125, 239–278.
https://doi.org/10.1111/j.1096-3642.1999.tb00592.x
QGIS Development Team (2019) QGIS Geographic Information System. Open source geospatial foundation project. Available from: http://qgis.osgeo.org (accessed January 2019)
Lacerda, J.V.A., Assis, B., Santana, D.J. & Feio, R.N. (2009) Anurans in bromeliads, Parque Estadual da Serra do Brigadeiro, state of Minas Gerais, southeastern Brazil. *Check List*, 5 (4), 800–806.
https://doi.org/10.15560/5.4.800
Lillywhite, H.B. & Henderson, R.W. (1993) Behavioral and functional ecology of arboreal snakes. *In:* Seigel, R.A. & Collins, J.T. (Eds.), *Snakes: Ecology and Behavior*. McGraw-Hill, New York, New York, pp. 1–49.
Manzanilla, J. & Sánchez, D. 2004 (2005) Una nueva especie de *Thamnodynastes* (Serpentes: Colubridae) del macizo del Turimiquire, noreste de Venezuela. *Memoria de la Fundación La Salle de Ciencias Naturales*, 161–162, 61–75.
Myers, C.W. & Donnelly, M.A. (1996) A new herpetofauna from Cerro Yaviì, Venezuela: first results of the Robert G. Goelet American Museum-Terramar expedition to the northwestern Tepuis. *American Museum Novittates*, 3172, 1–56.
https://doi.org/10.1206/0003-0090(2001)261<0001:HOTYCM>2.0.CO;2
Myers, C.W. & McDowell, S.B. (2014) New taxa and cryptic species of Neotropical snakes (Xenodontinae), with commentary on hemipenes as generic and specific characters. *Bulletin of the American Museum of Natural History*, 385, 1–112.
https://doi.org/10.1206/862.1
Nóbrega, R.P., Montingelli, G.G., Trevine, V., Franco, F.L., Vieira, G.H., Costa, G.C. & Mesquita, D.O. (2016) Morphological variation within *Thamnodynastes pallidus* (Linnaeus, 1758) (Serpentes: Dipsadidae: Xenodontinae: Tachymenini). *The Herpetological Journal*, 26 (2), 165–174.
Pesantes, O.S. (1994) A method for preparing the hemipenis of preserved snakes. *Journal of Herpetology*, 28, 93−95.
https://doi.org/10.2307/1564686
Peters, J.A. (1964) *Dictionary of Herpetology*. Hafner, New York, 392 pp.
Pizzatto, L., Almeida-Santos, S.M. & Shine, R. (2007) Life-history adaptations to arboreality in snakes. *Ecology*, 88, 359–366.
https://doi.org/10.1890/0012-9658(2007)88[359:LATAIS]2.0.CO;2
R Core Team (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from: http://www.R-project.org/ (accessed 3 March 2021)
Sabaj, M.H. (2020) Codes for Natural History Collections in Ichthyology and Herpetology. *Copeia*, 108 (2), 593–669.
https://doi.org/10.1643/ASIHCODONS2020
Schargel, W.E. & Castoe, T.A. (2003) The hemipenes of some snakes of the Semifossorial Genus *Atractus*, with Comments on Variation in the Genus. *Journal of Herpetology*, 37 (4), 718−721.
https://doi.org/10.1670/7-02N
Sheehy, C.M., Albert, J.S. & Lillywhite, H.B. (2016) The evolution of tail length in snakes associated with different gravitational environments. *Functional Ecology*, 30, 1365–2435.
https://doi.org/10.1111/1365-2435.12472
Silva, W.S., Araújo. P.F., França, R.C., Pedrosa, I.M.M.C. & França, F.G.R. (2019) Offspring morphology and early growth of *Thamnodynastes pallidus* (Linnaeus, 1758) in the Brazilian Atlantic Forest (Serpentes; Thachymenini). *Herpetology Notes*, 12, 205–209.
Vidal, N., Dewynter, M. & Gower, D.J. (2010) Dissecting the major American snake radiation: a molecular phylogeny of the Dipsadidae Bonaparte (Serpentes, Caenophidia). *Comptes Rendus Biologies*, 333, 48–55.
https://doi.org/10.1016/j.crvi.2009.11.003
Zaher, H. (1999) Hemipenial morphology of the South American Xenodontine snakes, with a proposal for a monophyletic Xenodontinae and a reappraisal of colubroid hemipenes. *Bulletin of the American Museum of Natural History*, 240, 1−168.
Zaher, H. & Prudente, A.L.C. (1999) Intraspecific variation of the hemipenis in *Siphlophis* and *Tripanurgos*. *Journal of Herpetology*, 33 (4), 698−702.
https://doi.org/10.2307/1565589
Zaher, H. & Prudente, A.L.C. (2003) Hemipenes of *Siphlophis* (Serpentes: Xenodontinae) and techniques of hemipenial preparation in snakes: a response to Dowling. *Herpetological Review*, 34, 295−302.
Zaher, H., Grazziotin, F.G., Cadle, J.E., Murphy, R.W., Moura-Leite, J.C. & Bonatto, S.L. (2009) Molecular phylogeny of advanced snakes (Serpentes, Caenophidia) with an emphasis on South America xenodontines: a revised classification and descriptions of new taxa. *Papéis Avulsos de Zoologia*, 49, 115–153.
https://doi.org/10.1590/S0031-10492009001100001
Zaher, H., Yánez-Muñoz, M.H., Rodrigues, M.T., Graboski, R., Machado, F., Altamirano-Benavides, M., Bonatto, S.L. & Grazziotin, F.G. (2018) Origin and hidden diversity within the poorly known Galapagos snake radiation (Serpentes: Dipsadidae). *Systematic and Biodiversity*, 16 (7), 614–642.
https://doi.org/10.1080/14772000.2018.1478910

Appendix 1

Material examined

Localities are presented in the following format: "COUNTRY: **State:** *Municipality* or *Province* or *District* (specific locality). Specimens with analyzed hemipenes are indicated in parenthesis: (H).

***Thamnodynastes silvai* (*n*=33)**. BRAZIL: **Amazonas:** *Tabatinga*: SINCHI-R 2170. COLOMBIA: **Amazonas:** *Leticia*: SINCHI-R 2155, 2156, 2158, 2166; MPEG 18306, 18307, 18308. ECUADOR: **Morona-Santiago**: *Macuma*: USNM 233066. PERU: **Loreto**: AMNH 52858, 53494, 53582, 53585; *Cayarú, Mariscal Ramón Castilla Province*, *Mariscal Ramón Castilla:* SINCHI-R 2172; *Cayarú, Mariscal Ramón Castilla*, *Mariscal Ramón Castilla* (Yahuma Island): SINCHI-R 2138, 2145, 2152, 2160, 2164, 2165, 2167, 2168, 2171, 2173, 2174, (Rondiña Island): SINCHI-R 2161, 2175; *Iquitos*: AMNH 52536, 53058, 53059; *Orellana*: USNM 127123; *Rean Rean, Suhuayo* (near Contamana, Ucayali River): AMNH 53580. Without locality: AMNH 52859.

***Thamnodynastes almae* (*n*=29).** BRAZIL: **Alagoas-Sergipe**: (Xingó Hydroelectric Power Plant): MZUSP 20985, 20987–1003. **Bahia:** *Feira de Santana:* MZUEFS 801; *Rodelas*: IBSP 52135 (H) (holotype). **Paraíba:** *Areia* (Mata do Pau de Ferro): MZUSP 20375 (H), 20377; *Cabaceiras* (Bravo Farm): CHUFPB 4527; *Campina Grande*: IBSP 85059; *São José do Cariri* (11 km south from *Boa Vista*): CHUFPB 5918; **Pernambuco:** IBSP 83664; *Custódia*: MFCH 1863, 1848; *Floresta*: MFCH 1849–52, 1855, 1857, 1859, 1861, 1869; *Sertânia*: MFCH 1854 (H), 1866.

***Thamnodynastes chaquensis* (*n*=62).** ARGENTINA: **Buenos Aires:** *Ensenada*: MLP 1888 (H). **Chaco** (Antequera): FML 6608 (H); **Chaco: Comandante Fernández:** *Presidencia Roque Saenz Peña*: FML 26133; *La Mascota*: UNNEC 6716; **Chaco**: **General Güemes:** *Miraflores*: UNNEC 10467; *San Fernando* (Compania Las Mercedes): UNNEC 339 (H) (holotype); **Chaco:** (Tragadero River): UNNEC 7936; **Chaco: Veinticinco de Mayo:** *Machagai*: FML 1826; **Chaco: Doce de Octubre:** *Hermoso Campo*: UNNEC 41 (paratype); *Capital Solani*: MACN 36721 (paratype); *Colonia Benites*: MACN 36718 (paratype); *Las Garcitas*: MACN 36713 (paratype); *La Verde*: MACN 36719, 36720 (paratype); *Zaparinqui*: MACN 36717 (paratype). **Corrientes: Corrientes:** FML 2705, UNNEC 991, 6898; **Corrientes: Bella Vista:** MLP 320; **Corrientes: Ituzaingó:** *Isla Talavera*: UNNEC 12445. **Entre Ríos: Gualeguaychu:** *Ibicuy*: FML 13509; **Formosa:** UNNEC 223, 224 (paratypes); *Pozo del Tigre*: MACN 36728 (paratype); *Formosa* (El Bagual): MLP 652; *Formosa* (mouth of the Pilagá stream): UNNEC 8969; **Formosa: Matacos.** *Estancia La Florencia*: UNNEC 5636; **Formosa: Pilcomayo**: *Bouvier*: MNRJ 13419 (H), 13420; **Salta:** MLP 1616; **Salta, San Martín:** *Hickman*: FML 406, 428, 503 (H); **Salta, Rivadavia: (**Paraje Cañada de la Mujer): FML 25057. ARGENTINA without locality: MACN 1256, 1373, 3458 (paratypes). BOLIVIA: without locality: MNKR 3830, 3838, 3842, 4284, 4475, 4476, 4477, 5534; **Tarija:** *Nogalitos* (Baritú National Park, Bermejo River): MACN 33429; **Santa Cruz: Florida:** *Palmasola* (Tungas de Agua Dulce): MNKR 4331; *Pampagrande*: MNKR 2747; **German Busch:** MNKR 1137; *German Busch*: MNKR 1155 (H); *Puerto Busch* ("Portón"): MNKR 1360; **Vallegrande:** MNKR 5141. BRAZIL: **Mato Grosso:** *Barão de Melgaço*: MNRJ 7651; *Poconé*: UFMT 11220 (H). **Mato Grosso do Sul:** *Aquidauana* (Aguapé Farm): UFRGS 6164; *Corumbá*: MNRJ 21001–03; (Pantanal, Miranda and Abobral Rivers): ZUEC 2870. PARAGUAY: without locality: FML 11970; **Assunpción**: *Assunpción*: MNRJ 664, 666.

***Thamnodynastes chimanta* (*n*=13).** VENEZUELA: **Bolívar:** *Gran Sabana*: Chimanta Massif: FMNH 74044 (paratype); (Tepui Murey): MHNLS 10776; (Tepui Churi): MHNLS 10973, 11000, 11010; (Tepui Churi, Canaima National Park): MHNLS 20493–94, 20605; (Apacara Tepui): MHNLS 10970; (Valley between Torono and Chimanta Tepuis): MHNLS 10682 (H); (Tepui Acoplan): MHNLS 10984–85; (Tepui Amuri): MHNLS 11378.

***Thamnodynastes corocoroensis* (*n*=1).** VENEZUELA: **Bolívar: (**Tepui Corocoro): MHNLS 11376 (holotype).

***Thamnodynastes dixoni* (*n*=46).** COLOMBIA: **Arauca:** *Arauca*: (El Guafal Biological Station): IAVH 3144; *Puerto Rondón*: IAVH 1793–94, 2869, 7641; *Arauquita* (Vereda Normandia): IAVH 7631 (H); **Casanare:** *San Luis de Palenque* (Vereda El Tigre): ICN 12031; **Vichada:** *Cumaribo* (Corregimiento Santa Rita): IAVH 5143. VENEZUELA: **Amazonas:** *Atures* (about 6km south from Puerto Ayacuobro): EBRG 1950; (Fundo Copaiba, nearby Puerto Ayacucho): MHNLS 19864–65; *Puerto Ayacucho* (Puerto Ayacucho Airport): MBUCV 7088; (Experimental Station Amazonas): MHNLS 11580; *Puerto Ayacucho*: MHNLS 8436, USNM 80684; (Puente Cataniapo): EBRG 5863; (Orinoquia Camp, nearby Puerto Ayacucho): MHNLS 19047; **Anzoátegui:** (Unare Lake): EBRG 3336; **Apure: (**Hato La Guanota, 4 km west from San Fernando): *Mantecal*: EBRG 1977; (El Samán Road): EBRG 788, 789; (Hato El Frio): MHNLS 11602; **Bolívar:** (8 km north from El Manteco): EBRG 1211; (Guri Dam): MBUCV 837, 839–41, 844–45 (H), 846–47, 1832; **Cojedes:** *El Baul* (Hato Mataclara): EBRG 3670, 4295, 4410; *Rômulo Galegos* (Parcelamiento La Bianca, Sector Rincon Moreno): MHNLS 15130–31; (Road to El Baul): MHNLS 13304; **Guárico: (**Hato La Cruz Rubiera, Cazola Road): EBRG 2899; (H) *Calabozo*: MBUCV 8153 (H) (paratype); MBUCV 680; *San Rafael de Orituco:* MHNLS 9082; **Zulia:** *Catatumbo* (Los Cañaguatos): EBRG 1462 (H); *Jesus Maria Semprún* (San Martin Farm, Sector Águas Negras): MHNLS 18827–28**.**

***Thamnodynastes gambotensis* (*n*=60).** COLOMBIA: **Atlántico:** without locality: ICN 2084; (Soplaviento Lake): IAVH 80; *Barranquilla:* ICN 2002–04, MLS 727–28, 731, AMNH 126467; *Luruaco* (El Ceibal Farm): ICN 11225, ICN 9974 (H); (Magdalena River): ICN 117; **Bolívar.** *Cartagena.* MLS 732; IAVH 4167 (H); *Santa Catalina*: ICN 9973, 9975–76; *Zambrano* (Zambrano-Bolívar, Andaluz): IAVH 4199–201; **Boyacá:** *Macanal*: MLS 729. **Casanare:** ICN 213 (H); **Cesar:** *El Paso* (Potrerillo): ICN 11607; *Chimichagua* (La Ceja Swamp): ICN 11611, 11613, 11616; **Córdoba.** *Ciénega de Oro:* ICN 12130; *Montelíbano* (Tierradentro, Vereda Candelaria, Gundena Farm): ICN 11615; *Montería*: MLS 1944, 2187,

2403, 2496–97, 2502, 2950; *Montería* (Ciénaga Martínica): ICN 10569, (Estación Piscícola CVS): ICN 10371, 10372, (Martínica): ICN 10359, 10371, 10378, 10383–84, 10386; *Pueblo Nuevo* (Cintura, border of Carate channel): ICN 10374; La Vaqueta: ICN 11327; *Santa Cruz de Lorica:* ICN 10370, 10376 (H), 10389; **Magdalena:** *Ciénaga*: USNM 144175; *San Lorenzo*: IAVH 163; *Santa Marta* (Sector Los Cocos): IAVH 12, 83; (Vía Parque Isla Salamanca): IAVH 73; **Sucre:** *Coloso:* IAVH 3304 (H); *San Marcos* (Ciénaga de Gamboa, San Marcos Station): IAVH 4182, 4186, 4188; *Sincelejo* (La Palma): IAVH 1973; *Sincelejo*: ICN 0442.

***Thamnodynastes hypoconia* (*n*=129).** ARGENTINA: without locality: MLP 724; **Buenos Aires:** *Federal District* (Ciudad Universitaria): MACN 32583; (Capitán River): MACN 24975; (Paraná River, Delta Island): FML 504 (H); **Buenos Aires: Atalaya:** MLP 5342; **Buenos Aires: Berisso**: *Los Talas*: MACN 28221; **Buenos Aires: Dolores:** *Dolores*: UNNEC 10121; **Buenos Aires: Ensenada:** MLP 109 (H), 118, 123, 125; **Buenos Aires: La Plata:** MLP 401, 419, 1396, 1401, 1421, 1431, 1448; **Buenos Aires: Magdalena:** MLP 1679; **Buenos Aires: Partido de La Costa:** *Punta Medanos:* MLP 684; **Buenos Aires: Punta Indio:** MLP 959, 1950; **Buenos Aires: Punta Piedras:** MLP 509: **Chaco:** MLP 5692, UNNEC 415, 6723; *Colonia Las Mercedes*: MNRJ 13423 (H); *Pampa Grande*: MLP 5028; *Roque Saenz Peña*: MLP 5027 (H); **Chaco: Bermejo:** *Laguna El Palmar*: UNNEC 5956, 6195; **Chaco: Comandante Fernández:** *La Mascota*: UNNEC 7154; **Chaco: San Fernando:** *Antequera*: FML 18160; *Compania Las Mercedes*: UNNEC 7480: **Corrientes:** without locality: MLP 1606; *Capital*: MNRJ 13424, UNNEC 11106; **Corrientes; Bella Vista:** MLP 319; **Corrientes: Ituzaingó:** *Estancia San Alonso*: UNNEC 7589; (Apipé Grande Island): UNNEC 10400; **Corrientes: Mburucuyá:** *Mburucuyá*: UNNEC 298, 4999; (Mburucuyá National Park): UNNEC 4641; **Corrientes: Mercedes**: UNNEC 10152; **Corrientes: San Miguel:** *San Miguel*: UNNEC 299, 10068, 10635; **Corrientes: Santa Lucia:** MLP 617. **Entre Ríos:** MLP 5034, 5365; **Formosa: Clorinda:** MLP 5032; **Formosa (**Guaycolec Reserve): FML 1982, UNNEC 7555; **Formosa: Laishi (**El Bagual Reserve): FML 11561, 14931, 14934, 23933, 23935–36; **Formosa: Patiño:** UNNEC 8958; **Formosa, Pilcomayo** (Rio Pilcomayo National Park): UNNEC 4840–41; **Formosa: Pirané:** FML 8290: **Missiones:** UNNEC 65; **Missiones: Apóstoles:** *Araza*: MLP 5652: **Santa Fé:** MLP 485, FML 1378; **Santa, Fé General Obligado,** *Villa Ocampo*: UNNEC 5194–95. BRAZIL: **Goiás:** *Niquelândia* (Serra da Mesa Hydroelectric Power Plant): MZUSP 21315, 21322–23, 21327–30, 21332, 21335 (H), 21337, 21339; **Minas Gerais:** without locality: UFMG 358; FUNED 2866; *Betim*: FUNED 247 (H); *Brumadinho*: UFMG 356, 525; *Cardeal Mota*: UFMG 249; *Contagem*: FUNED 250; *Corinto*: FUNED 243; *Florestal*: FUNED 1200; *Itaguara*: FUNED 681; *Nova Ponte*: FUNED 762, 780; *Ouro Preto*: FUNED 744; *Santana do Riacho* (Serra do Cipó): FUNED 1603; **Paraná:** *Paula Freitas*: MCP 16643;**Rio Grande do Sul:** *Caxias do Sul*: MCP 12194; *Bagé*: UFRGS 6170; *General Câm*ara: MCP 2096; *Guaíba*: MCP 3768; *Jaguarão* (Santa Ilza Farm): UFRGS 5210; *Jaguarão* (São Francisco Farm): UFRGS 5213; *Nova Santa Rita*: UFRGS 6249; *Pelotas:* MCP 12225; *Porto Alegre* (Salgado Filho Airport): UFRGS 1225; *Rio Grande* (Porto de Rio Grande): MCN 6467; *Rosário do Sul*: MCN 6440; *São Jerônimo*: MCP 2151; *São Sebastião do Caí*: MCP 8980; *Viamão*: UFRGS 3695; **Santa Catarina:** *Campo Belo do Sul*: UFRGS 4980; *Porto União*: MCP 16642; **São Paulo:** *Botucatu*: MNRJ 20856; *São Miguel Arcanjo*: FML 2802; **Tocantins:** *Goiatins*: UFMG 357; (Luis Eduardo Magalhães Hydroelectric Power Plant): MZUSP 14524, 14540, 15656–59; (Peixe Angelical Hydroelectric Power Plant): MZUSP 15425. PARAGUAY: without locality: MLP 299, FML 11969, USNM 11260, UMMZ 153077; **Itapúa**: *Isla Yacyretá:* MNRJ 13422, UNNEC 985–86. URUGUAY: **Colonia:** MLP 1758.

***Thamnodynastes lanei* (*n*=30).** ARGENTINA: **Corrientes: Ituzaingó:** *Isla Talavera*: UNNEC 568, 980. **Formosa: Formosa:** MACN (CENAI): 1918; **Pilcomayo:** *Riacho Negro*: UNNEC 4711. BOLIVIA: without locality: AMNH 22475, MNKR 3832; **Beni**: AMNH 2973; *Bella Vista:* MNKR 3624; **Santa Cruz:** *Santa Cruz de La Sierra*: MACN 3776; *Santiestevan* (Guabira): MNRK 970; *Isla Verde*, Cordillera (Bañadas): MNKR 2794 (H); **Trinidad** (60km from the city): MNKR 1745; **Pando:** *Manuripi* (Reserva Nacional de Vida Silvestre Amazônica): MNKR 2832. BRAZIL: **Amapá:** *Mazagão* (Vilanova): IBSP 80714; **Amazonas:** without locality: UMMZ 109082; *Urucará*: MPEG 23525; **Mato Grosso:** MLP 1856–57; (Gahyba Lake): MNRJ 370; *Cárceres* (São Luiz de Cárceres): MNRJ 66–61; **Mato Grosso do Sul:** *Corumbá* (Serra do Amolar, RPPN Acurizal): UFMT 0922; **Pará**. *Monte Alegre* (Serra da Partuma): MNRJ 662 (H); *Porto de Moz*: MZUSP 17760; **Rondônia:** *Porto Velho* (Santo Antônio Hydroelectric Power Plant): MZUSP 19031; (Jirau Hydroelectric Power Plant): MZUSP 19716–17, 19719, 19977 (H).

***Thamnodynastes longicaudus* (*n*=10).** BRAZIL: **Espírito Santo:** *Santa Teresa*: MNRJ 676; **Rio de Janeiro:** *Teresópolis*: IBSP 41045 (paratype); **São Paulo:** *Embu-Guaçu*: IBSP 20694 (paratype); *Guapiara*: IBSP 33706 (paratype); *Juquitiba*: IBSP 26561, 33702 (paratypes); *Salesópolis:* IBSP 18676 (paratype); *Salesópolis* (Boracéia Biological Station): AMNH 119774; *São Lourenço da Serra*: IBSP 59545 (holotype); between Bragança and Atibaia: IBSP 31890 (paratype).

***Thamnodynastes marahuaquensis* (*n*=1).** VENEZUELA: **Amazonas:** (north Tepui Marahuaca): MHNLS 12507 (holotype).

***Thamnodynastes nattereri* (*n*=68).** BRAZIL: **Bahia:** *Arataca:* MZUSP 20066; *Boa Nova* (Serra do Timorante): MNRJ 14935; *Camacan* (Serra Bonita)*:* MZUSP 20075; *Ilhéus:* MNRJ 2611; *Itambé:* MCNR 4398 (H); **Espírito Santo:** *Aracruz* (Barra do Sahy)*:* MBML 2904; *Dores do Rio Preto:* MBML 1812; *Guarapari* (Setiba): MBML 639, 1811; *Guarapari* (Paulo Cesar Vinha State Park): MPEG 22740; *Linhares:* MBML 883; *Santa Teresa:* MBML 181, 185, MNRJ 14075; *Serra*: MBML 1807; *Marechal Floriano:* MBML 780, 1814; *São Roque de Canaã*: MBML 539; **Minas Gerais:** *Araponga*: UFMG 352; *Araxá:* IBSP 84575; (Caparaó): MBML 1816, MZUSP 14406,14407; (Caparaó National Park): MBML 385; *Catas Altas:* MNRJ 18920; *Conceição do Mato* (Serra da Serpentina): MCNR 4020 (H), MZUSP 17891 (H); *Congonhas:* UFMG 359; *Cristália*: FUNED 2511; *Dores do Turvo*: FUNED 237; *Jaboticabas*: FUNED 1224; *Jaratinga*: FUNED 682; *Juiz de Fora*: FUNED 667; *Mariana*: FUNED 2456; *Miradouro*: FUNED 595; *Nova Lima:* UFMG 351; *Salto da Divisa*: MNRJ 12085; *Santa Bárbara* (Caraça Natural Park): FUNED 240; **Paraíba**: *Maturéia* (Pico do Jabre): MZUSP 20312, 20313;

Paraná: *Cruz Machado*: MCP 16919; *União da Vitória*: MCP 16936. **Rio de Janeiro:** *Maricá* (Ponta Negra): MNRJ 22226 (H); *Itaguaí:* IBSP 78373; *Resende* (Visconde de Mauá): MNRJ 21009; *Rio de Janeiro* (Bosque da Barra, Barra da Tijuca): MNRJ 20067, (Marapendi Natural Park): MNRJ 15195; (Botanical Garden): MNRJ 9348, (Prainha Municipal Park): MNRJ 10980; *Teodoro de Oliveira* (RJ 116, km 66,6): MNRJ 17723; **Rio Grande do Sul;** *Maquiné*: UFRGS 3614; *São Francisco de Paula*: MCP 11044; *São Francisco de Paula* (Colinas): MCN 7217. **Santa Catarina.** *Blumenau:* MCP 16920; *Humboldt*: MNRJ 678; *Porto União*: MCP 16871; *Praia Grande*: UFRGS 6291; *Rio Negrinho:* IBSP 86379, 86641. **São Paulo.** *Bananal* (Bananal Ecological Station): MZUSP 14260, 14329; *Cabreína*: UFMG 347; *Ilhabela:* IBSP 83429; *São Luiz do Paraitinga* (Serra do Mar State Park, Santa Virgínia): ZUEC 3613; *São Sebastião*: MZUSP 21219; *Salesópolis* (Boracéia): MZUSP 4105; *Ubatuba* (Serra do Mar State Park): ZUEC 3594, 3595.

Thamnodynastes pallidus* (*n*=74).** BOLIVIA: **Beni:** *Bella Vista:* MNKR 3625; **Cochabamba:** without locality: AMNH 6779; *Carrasco* (Valle de Sajita): MNKR 365; **Santa Cruz:** *Guarayo* (Urubicha): MNKR 3429; *no other information*: UMMZ 60792, 63261; *Santa Cruz de La Sierra*: MACN 3860; *Yapaconí:* MNKR 31, 346. BRAZIL: **Alagoas:** *Maceió* (Mangabeiras Park): MZUSP 3499; **Amazonas:** *Berurí*: MZUSP 5771; *Mucuripe*: MZUSP 5760; *Tabatinga*: MCP 14090; **Bahia:** *Elísio Medrada* (APA Municipal Serra da Jibóia): MZUEFS 1173; *Mata de São João* (Camurujipe Reserve): MZUFBA 1744; *Salvador* (Pau da Lima Botanical Garden): MZUFBA 1534; *Santo Amaro*: MBML 2198 (H); **Maranhão:** *Carolina* **(**Estreito Hydroelectric Power Plant): MZUSP 18815, 19203, 19206 (H), 19211–13, 19215, 19218, 19220–21; *Urbano Santos* (Santo Amaro Farm): MPEG 20519 (H), 20520, (São Felipe Village): MZUSP 18829 (H); **Pará: Augusto Corrêa* (Cacoal): MPEG 3228, 6842 (H), 9177, 10101 (H); *Palestina do Pará* (Araguaia River, Jarbas Passarinho Port): MPEG 11777 (H); **Paraíba:** *Cruz do Espírito Santo* (Mata da Usina São João): MZUSP 20350, 20352–56 (H); **Pernambuco:** *Moreno* (Tapera Train Station; Mata do Toró): MCN 5377–79; *Vicência* (Água Azul): MZUSP 5004 (H); **Rondônia:** *Porto Velho* (Jirau Hydroelectric Power Plant): MZUSP 19460; **Tocantins:** *Filadélfia* (Estreito Hydroelectric Power Plant): MZUSP 19201; *Babaçulândia* (Estreito Hydroelectric Power Plant): MZUSP 19205. COLOMBIA: **Amazonas: (**Amacayacu Natural National Park): IAVH 3080 (H), 4192–93; *Leticia* (Santa Sofia Island): IAVH 3270–71 (H), 3272 (H), 3273; *Leticia*: IAVH 5597, 3408; *Yahuarcaca*: ICN 10572, (6 km north from Leticia): ICN 10533–34; (Leticia-Tarapacá Road): ICN 10530; **Meta:** *Villavicencio:* MLS 726; (Vereda Buenavista, Caño Carrillo): IAVH 5564; **Casanare:** (Guaicaramo Dam): MLS 730. VENEZUELA: (Tapirapecó Mountains, Tamaeuari Summit): MBUCV 7045; **Bolívar: (**Guaiquinima I): MHNLS 11020; *Mantopai* (Canaima National Park): EBRG 5111 (H). GUYANA: without locality: UMMZ 80500; **Berbice:** (Berbice west coast, east Demerara): AMNH 36134. PERU: without locality: AMNH 55870; **Loreto:** AMNH 54629. SURINAME: without locality: AMNH 8665, 130528 (H); **Paramaribo:** AMNH 104633.

***Thamnodynastes paraguanae* (*n*=32).** COLOMBIA: **Atlántico:** *Bocas de Ceniza*: ICN 2085; **Cesar: (**Curumaní-La Loma road): ICN 10888; *Chimichagua* (Caño Largo): ICN 11610 (H); (Pantano La Ceja): ICN 11609; **La Guajira.** AMNH 110023– 25; *Barrancas:* MLS 2411; *Dibulla:* IAVH 5654 (H). VENEZUELA; **Bolívar:** (Caño El Garzón, 18km south Parguaza River): MHNLS 9883; **Fálcon: (**Caño Santa Cruz): EBRG 3006; *Cerro Santa Ana* (Cerro Santa Ana): EBRG 5204, MHNLS 17096; *Peninsula de Paraguaná* (Chanaima): EBRG 4162; (Filo de Montecano, San José de Cocodite): EBRG 6058; (Parque Eolico Paraguana): EBRG 5906, 5974 (H); (Boca de Caño Reserve): EBRG 3000; *Paraguaná*: MBUCV 1468 (H) (holotype); UMMZ 217112 (paratype); **Zulia: (**Grano de Oro Farm, Palmar River): MHNLS 18611 (H), 16813; *Cabimas* (Sector la Pica Pica, eastern coast): MZUSP 22305; *El Carbón* (Guasare River): EBRG 3307; *Maracaibo*: USNM 56285; (Guajira): EBRG 5723; (campo Mara, Maracaibo vicinity): MBUCV 0025; *Páez* (Caño Santa Elena): EBRG 3269; (Las Mentiras): EBRG 3380; *Urdaneta* (La Mucura): MBUCV 8152; *Yaguasirú* (El Eneal): EBRG 3303–04 (H).

***Thamnodynastes phoenix* (*n*=114).** BRAZIL: **Alagoas**: *Piranhas* (Xingoì Hydroelectric Power Plant): MZUFBA 841, 844, 846, 1116, 1120; MZUSP 10864, 10868, 10875–79, 13342; FUNED 857, 860, 862, 866, 871; **Bahia:** *Alagoado*: MZUSP 10462; *Barreiras* (AcauaÞ Souza Farm): MNRJ 1955; *Barreiras*: IBSP 50432; *Brumado*: MZUSP 20621; *Capim Grosso* (Alegria Farm): MZUEFS 835; Campo Formoso (Gruta do Salitre): IBSP 31328; *Curaçaì* (Brotas): IBSP 43061, 43063, 43065, 43191; *Guanambi*: IBSP 50238, 54904 (H) (paratype), 70458; *Iramaia* (JacarandaÞ Farm): IBSP 42157; *Juazeiro* (Caraiìbas Metals): IBSP 37597; *Juazeiro*: IBSP 37461, 48692, 48941, 51719; *Morro do Chapeìu*: MZUSP 8957; *Mucujeî*: MZUSP 8956; *Palmeiras* (Campo SaÞo JoaÞo): MZUEFS 1263; *Paulo Afonso*: IBSP 44444, 44446; *Paulo Afonso* (Itaparica Hydroelectric Power Plant): MZUFBA S108, S115; *Paulo Afonso* (Sobradinho Hydroelectric Power Plant): MZUFBA 5366; *PoçoÞes*: MZUFBA 1556; *PoçoÞes* (SaÞo Feìlix do Amianto, Bom Jesus da Serra): IBSP 28194–95; *SaÞo Desideìrio* (PCH Siìtio Grande): MZUFBA 2315; *Queimadas*: MZUSP 10460, 10775; **Cearaì:** *Mauriti*: MFCH 1890, 1898; *Fortaleza* (Universidade Federal do Cearaì): FUNED 1018 (H); (Serra do Baturiteì): MZUSP 21180; **Goiaìs:** (Serra da Mesa Hydroelectric Power Plant): MZUSP 21009–20; **Minas Gerais:** without locality: UFMG 353; *Jaiìba*: FUNED 906; *Santana do Riacho*: UFMG 350; (Serra do Cipoì): IBSP 40521, UFMG 355; **Paraiìba:** *Cacimba de Areia*: IBSP 33401; *Patos* (Jardim Guanabara): IBSP 33399; *SaÞo Joseì dos Cordeiros* (Alma farm): CHUFPB 5894; **Pernambuco:** without locality: IBSP 41893; *Cabroboì*: MFCH 1872–73, 1875–77, 1882–83; *Custoìdia*: MFCH 1901; *Floresta*: MFCH 1880–81, 1884–85, 1888, 1896–97, 1899; *Petrolina*: MFCH 1902–03, IBSP 48317, 43820, 48322; *Petrolina* (Campus of the Universidade Federal do Vale do SaÞo Francisco): IBSP 87527 (H) (holotype); *Salgueiro*: MFCH 1887; *Sertâ̂nia*: MFCH 1889, 1895; (Itaparica Hydroelectric Power Plant): IBSP 52127; **Piauiì**. *Castelo do Piauiì*: MPEG 22766; (Uruçuiì-Uma Ecological Station): MZUSP 18146–47; *Pirarucara* (Sete Cidades National Park): MPEG 23344; *Valença do Piauiì*: MZUSP 5845; **Rio Grande do Norte:** *Natal*: IBSP 44508; **Sergipe:** *Canindeì de SaÞo Francisco*: IBSP 67952–53; **Tocantins:** *Mateiros* (Posto das Dunas, Pares do JalapaÞo): MNRJ 15196; *Mateiros*: CHUNB 28898, 41315; *Palmeiras do Tocantins* (Estreito Hydroelectric Power Plant): MZUSP 19105 (H).

***Thamnodynastes ramonriveroi* (*n*=30).** GUYANA: **East Berbice** (Rancho Dubulay): USNM 566282; (Rodway): AMNH 36117–18 (H). VENEZUELA: **Anzoátegui:** Turimiquire Massif: *Freites* (La Laguna Mountains): MNRJ 8128, MHNLS 15534 (paratype), EBRG 3962–63, 3958 (H), 3959–60, 3956, 3961 (paratypes), 3957 (holotype); (El Guanal Mountains): MHNLS 17688 (H); La Piedra Road, La Laguna Mountains): EBRG 3955 (paratype); **Bolívar:** AMNH 114776; **Delta Amacuro:** MBUCV 399; (Caño Guapoa): MHNLS 16215, EBRG 4533; (Caño Mariusa): EBRG 4510; (Caño Menelina): EBRG 1711; (Edelca Station, Caño Jarisi-Duina): MHNLS 10946; (Caño Pedernales, Volante Camp): MHNLS 13772, 13806; *Curiapo:* MHNLS 12977; *Delta Amacuro* **(**Bosque de Pantano, 2km from Pereira): MHNLS 13518; *Macareo* (Fundación La Salle): MHNLS 17727–29; **Sucre.** *Campona:* MHNLS 1217.

***Thamnodynastes rutilus* (*n*=10).** BRAZIL: **Goiás:** *Luiziânia* (Corumbá IV Hydroelectric Power Plant): MZUSP 17708; **Minas Gerais:** without locality: MNRJ 7508, UMMZ 109073; *Belo Horizonte*: FUNED 1102, 1452; *Esmeraldas*: FUNED 249; *Nova Ponte* (Nova Ponte Hydroelectric Power Plant): FUNED 809 (H), 1231; **Mato Grosso/Mato Grosso do Sul (**Ponte de Pedra Hydroelectric Power Plant): MZUSP 17609–10 (H), 17521.

***Thamnodynastes sertanejo* (*n*=38).** BRAZIL: **Alagoas/Sergipe:** (Xingó Hydroelectric Power Plant): MZUSP 21286, 21291–93, 21295–99, 21301 (H), 21303–07 (H), 21311; **Bahia:** *Paulo Afonso* (Itaparica Hydroelectric Power Plant): MZUFBA 39, 41, 43, 45–49, 102, 104, 141; *Poções*: MZUFBA 1568; **Minas Gerais.** *Manga* (Sossego Lake, Mocambinho): MNRJ 8583; **Paraíba:** *São José da Mata*: IBSP 85067–68; **Pernambuco.** *Cabroró*: MZUFBA 1907; *Custódia*: MFCH 1912; *Sertânia*: MFCH 1917, 1919, 1920, 1922 (H); **Rio Grande do Norte:** *Lagoa Nova* (Serra da Santana): IBSP 80223.

***Thamnodynastes strigatus* (*n*=33).** Without locality: BMNH 1946.1270 (holotype). ARGENTINA: **Buenos Aires:** *Berisso*: MLP 5318; *Ensenada*: MLP 668; *Zárate*: MLP 5026; **Chaco:** UNNEC 6726; **Corrientes:** *Corrientes*: UNNEC 327; *General Paz*: UNNEC 296; *Ituzaingó* (Isla Oculto): UNNEC 434; *Ituzaingó* (Isla Talavera): UNNEC 569; *Santo Tomé*: UNNEC 6173; FML 15752; **Entre Ríos:** *Concordia*: UNNEC 8931; **Misiones.** *San Pedro*: FML 7021; *Aristóbulo del Valle*: MLP 1619. BRAZIL: **Minas Gerais:** *Itamonte:* IBSP 22541 (H); **Paraná:** *São Mateus do Sul*: MCP 16540 (H); *União da Vitória*: MCP 16566; **Rio de Janeiro:** *Itatiaia* (Itatiaia National Park): MNRJ 14887; without locality: AMNH 23049; **Rio Grande do Sul:** *Barracão*: UFRGS 5786; *Cachoeira do Sul*: MCP 8827, 10570; *Eldorado do Sul*: MCP 18038; *Gravataí*: MCP 2158; *Guaíba*: MCN 7171; *Porto Alegre*: MCN 7299, MCP 4459; *Sananduva*: MCP 3947: **Santa Catarina:** *Abdon Batista*: MCN 16496; *Celso Ramos*: MCN 16348; *Itá*: MCP 2880; *Porto União*: MCP 16557; **São Paulo.** *Santana de Parnaíba*: MZUSP 14611 (H).

***Thamnodynastes yavi* (*n*=3).** VENEZUELA: **Amazonas**: Yavi Mountains: EBRG 3124 (holotype), 3125 (paratype), 3034.