



Morphological variation within *Thamnodynastes pallidus* (Linnaeus, 1758) (Serpentes: Dipsadidae: Xenodontinae: Tachymenini)

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The genus *Thamnodynastes* is comprised of 19 valid species distributed throughout South America. *Thamnodynastes pallidus* is associated with the Amazon region and the Atlantic forest of northeastern Brazil, exhibiting a disjunct distribution. The characters employed in the definition of this species are controversial, and its morphological variation is poorly known. Some authors do not consider its distribution in the Atlantic Forest, attributing these specimens to *T. almae*. This study aims to compare the Amazonian and the Atlantic populations of *T. pallidus* by performing an analysis of morphological (colouration, morphometry, pholidosis and hemipenial morphology) and geographical variations. We examined 70 specimens of *T. pallidus* from the Atlantic Forest, and 61 from the Amazon Forest. A logistic regression selected the number of infralabials, number of subcaudals, and snout length as the only predictors that could discriminate the two populations. The distribution model shows regions with higher climatic suitability for *T. pallidus* spread across the Amazon basin and the Atlantic Forest. We provide sufficient evidence to characterise *T. pallidus*, and differentiate it from its congeners. Although we demonstrate the occurrence of variation with respect to some meristic and hemipenial characters between and within each population, we conclude that these variations are not sufficient to recognise them as distinct species.

Key words: Amazon Forest, Atlantic Forest, hemipenis, pholidosis, South America, Squamata

INTRODUCTION

Morphological variation has been studied in a wide range of organisms, and its study reveals a broad number of causes to account for it. For example, divergent selective (ecological) pressures can trigger and maintain phenotypic diversification (Glor et al., 2003; Langerhans et al., 2004; Stuessy et al., 2006). Morphological differences due to sexual dimorphism (Bruner et al., 2005), and seasonal climate oscillations (Poroshin et al., 2010) have also been reported. Among snakes, the scenario is similar, and many examples of morphological variation within and among populations (and among distinct species) exist (e.g., Shine, 1986; Forsman & Shine, 1997; Pizzatto & Marques, 2006; Martinez-Freiria et al., 2009; Pyron & Burbrink, 2009). Many studies relate morphology (colouration and morphometrics) and its variation to species evolution and/or ecology. However, most studies have considered morphological variation for taxonomic purposes.

The genus *Thamnodynastes* is comprised of 19 valid species distributed throughout South America from latitudes 10°N (Northern Colombia) to 37°S (Southern Argentina) (Cei et al., 1992; Franco & Ferreira, 2002; Bailey et al., 2005; Bailey & Thomas, 2007). The genus is composed of medium-sized species (maximum SVL length: 620 mm), with 17 or 19 rows of dorsal scales on the midbody, and posterior dorsal-scale reduction; keeled or smooth scales; usually one apical pit present in dorsal scales; a divided cloacal scale (except for *T. pallidus*); elliptical pupil; sexual dimorphism in ventral scales; and viviparity (Franco & Ferreira, 2002; Bailey et al., 2005).

As a brief taxonomic history, *T. pallidus* was described by Linnaeus in 1758 as *Coluber pallidus*. In 1824, Wagler, in Spix described *Natrix punctatissima* based on a specimen from Bahia (Brazil). Subsequently, in 1830, Wagler described the genus *Thamnodynastes*, designating the type-species as *N. punctatissima* Wagler, 1824, by monotypy. In 1899, Andersson synonymised

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Thamnodynastes punctatissimus under *Thamnodynastes pallidus*, after rediscovering the type of *Coluber pallidus* Linnaeus 1758 in the Royal Museum of Stockholm. Later, Bailey et al. (2005) stated that the holotype resurrected by Andersson (1899) was lost according to Lönnberg (1896), and designated a neotype for *T. pallidus* using the lectotype of its junior synonym, *Coluber strigilis* Thunberg, 1787, aiming at its nomenclatural stability. Bailey et al. (2005) defined the “*pallidus*” group including *T. pallidus*, *T. sertanejo*, *T. longicaudus*, and a fourth species not yet described. This group was diagnosed by the presence of a slender body and long tail; short head with large eyes; a blotched or striped ventral pattern; dorsal scales smooth and elongated, without pits; a short hemipenis, simple or shallowly bifurcated, with small slender spines and sulcus spermaticus bifurcating distally or simply opening into a nude area. *Thamnodynastes pallidus* and *T. sertanejo* differ from *T. longicaudus* by having 17 mid-dorsal scale rows (*versus* 19). Considering colouration, *T. pallidus* differs from *T. sertanejo* by the presence of four longitudinal ventral stripes in the former (*versus* blotched venter in the latter); from *T. longicaudus* by the number of dorsal scales as mentioned above, and by the absence of a dorsal series of dark blotches on the forebody (present in *T. longicaudus*) (Franco et al., 2003; Bailey et al., 2005).

Thamnodynastes pallidus is the only species in the genus to exhibit an entire cloacal scale according to Franco & Ferreira (2002), and is recorded for localities in Venezuela, Suriname, French Guiana, east of Pará state, and for Pernambuco and Bahia states, in northeastern Brazil, exhibiting a disjunct distribution. Bailey et al. (2005) did not include in its distributional range specimens from northeastern Brazil, and considered *T. pallidus* to have both divided and entire cloacal scales. According to these authors, the species is distributed exclusively in the Amazon and the upper Orinoco watersheds, from central Bolivia to eastern Colombia, southern Venezuela and the Guianas, and to eastern Pará, Brazil. They also emphasise that the species occupies lowland areas, reaching maximum elevations of 400–450 m. Although Bailey et al. (2005) did not examine the specimens from northeastern Brazil mentioned by Franco & Ferreira (2002), they assigned them to *T. almae*. Recent studies corroborate Franco & Ferreira (2002) and confirm the occurrence of *T. pallidus* in northeastern Brazil (Hamdan & Lira-da-Silva, 2012). However the definition of this species and its geographic limits are still unresolved. Part of these taxonomic conflicts arise by the absence of a broad analysis of geographic variation comprising specimens from both Amazon and Atlantic Forest.

Considering the current scenario and the disjunct distribution of the species according to the above-mentioned records, the aim of this study was to compare the Amazonian and the Atlantic populations related to *T. pallidus* through an analysis of morphological and geographical variation, in order to understand definition and geographical limits of this species. We also performed a distribution modelling analysis to identify potential suitable areas for *T. pallidus*.

MATERIALS AND METHODS

Morphology

We examined specimens housed in the following museum collections: Coleção Herpetológica da Universidade Federal da Paraíba (CHUFPB), Museu de Zoologia da Universidade de São Paulo (MZUSP), Instituto Butantan (IBSP), Museu Nacional da Universidade Federal do Rio de Janeiro (MNRJ), Museu de Biologia Mello Leitão (MBML), Museu Paraense Emílio Goeldi (MPEG), Universidade Federal do Maranhão (UFMA), Museu de Zoologia da Universidade Estadual de Feira de Santana (MZFS), Museu de Zoologia da Universidade Federal da Bahia (MZUFBA), Laboratório Didático da Universidade Federal de Pernambuco (LDUFPE), Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul (MCP), Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul (MCN) and American Museum of Natural History (AMNH).

The selection of the most relevant characteristics for *Thamnodynastes* taxonomy was based on Franco & Ferreira (2002). We examined the following characters: loreal scale (present or absent), keels on dorsal scales (present or absent), condition of the cloacal scale (single or divided), number of preoculars (PreOc), postoculars (Posoc), supralabials (SL), infralabials (IL), temporals (T, first and second rows), dorsals (D), counted at three points of the body: on the neck (dorsals-N); on the midbody (dorsals-M); and near the cloaca (dorsals-T); Ventrals V, counted according to Dowling (1951); and the number of subcaudal scales (SC). We examined the dorsal and ventral colouration pattern following Franco & Ferreira (2002), and using the abbreviations proposed by Dowling (1951) and Peters (1964): “E – anterior ventral part lighter than posterior”; “H – anterior ventral part similar to posterior”.

The following measurements were taken using a ruler or digital calliper to the nearest 0.01 mm: snout length, measured from the tip of the rostral scale to the posterior margin of the preocular (SL), head length (HL), snout-vent length (SVL), tail length (TaL), and total length (TL). The method for hemipenial preparation and terminology followed Zaher (1999) and Zaher & Prudente (2003). Only one hemipenis per specimen was removed, everted and filled with coloured vaseline and stained with alizarin in a 70% alcohol solution to facilitate the visualisation of its structure (Uzzell, 1973).

Statistical analyses were performed using R software v.2.12.1 (R Development Core Team), and Systat v.13, with 0.05 as the significance level. Means and ± 1 standard deviation (SD) are presented throughout the text. We used Binary Logistic Regression (BLR; a special case of Generalised Linear Models [GLM] that uses binomial error structure and logit canonical function) to test the hypothesis that at least one of the predictors (our multivariate space) increased the probability of an individual being from the Amazon or Atlantic Forest (our two-level response variable). The logic for using BLR was due to the nature of the response variable and predictors, which is detailed (as are the procedures) in Crawley (2007) and Logan (2010). Separate null hypotheses were tested

for each estimated model parameter (i.e., if the log odds of an occurrence in one of the biomes are independent of each predictor variable and whether there is a significant relationship between the response and each predictor). The results of BLR should be interpreted as the probability p of a specimen or individual being from the Atlantic Forest (the mentioned reference level), given a specified predictor value. The multivariate space was composed of 19 predictors: 13 from (scale) counts: supralabials, infralabials, condition of the loreal scale, preoculars, postoculars (right and left), temporals (first and second rows), dorsals (dorsals–N: number of dorsal scales on a row of the neck; dorsals–M: on a row in the middle of the body; and dorsals–T: on a row near the cloaca), ventrals, subcaudals; and (iii) five continuous predictors (body-region measurements): head length, snout length, snout-vent length, tail length and total length. Before running the analysis, we examined the BLR requirements, especially regarding missing values, univariate and multivariate outliers, multicollinearity and overdispersion (lack of fit from binomial errors). Before we conducted the BLR analysis, we checked for the effects of gender on each predictor and for the influence of snout-vent length on numerical predictors (count and continuous predictors). We added this step into the analytical procedure, because the GLM results can be sensitive to model specification (i.e., the presence of interactions among predictors, covariates, etc.). In our opinion, due to the number of predictors and the sample size, this step was a better approach

than using a saturated model (where the main effects and all possible combinations of interactions among predictors are evaluated). We started the BLR analyses by specifying a full model (all predictors included) and then applied a reduced model for manual predictor selection, including predictors with both the lowest AIC (Akaike Information Criteria) value and significant p -value for each step. Differences between models (e.g., full vs. reduced models) were assessed via Chi-squared tests and we opted to use the results from the model with both the lower AIC (the simplest model) and with no departures from the assumed (binomial) error structure. For the sake of convenience, the odds of success (in our case, an individual occurring in the Atlantic Forest) were defined as the ratio of the probability of success over the probability of failure (of occurring in the Amazon).

Species distribution modelling

To identify potential suitable areas for *T. pallidus*, we used species distribution modelling (SDM) techniques. We gathered locality occurrence information from the literature, museum specimens and our own fieldwork and used Maxent, a method that has been demonstrated to perform well in a diverse set of modelling scenarios and is widely used in many studies in ecology, biogeography and conservation (Elith et al., 2006; Elith & Leathwick, 2009). A detailed explanation on how the maximum entropy principle applies to SDM can be seen in Elith et al. (2011). We performed 10 replications using a cross-validation procedure, where we divided our dataset

Table 1. Summary of the external variation found on the specimens of *Thamnodynastes pallidus* analysed on the present study for the Amazon and Atlantic Forest populations. Abbreviations: SL- supralabials, IL- infralabials, PreOc- number of preoculars, Posoc - postoculars, T - temporals, D- dorsals (counted in three points: on a row of the neck, in the middle of the body, and near the cloaca), V- ventrals, SC - subcaudal scales, and Cloacal - condition of cloacal scale (single or divided).

	Amazon (n=58)		Atlantic Forest (n=70)	
	Females	Males	Females	Males
SL	8/8 (n=35)	8/8 (n=23)	8/8 (n=40)	8/8 (n=30)
IL	8/8 (n=7)	8/8 (n=7)	8/8 (n=2)	9/9 (n=27)
	9/9 (n=28)	9/9 (n=15) 10/9 (n=1)	9/9 (n=37)	10/10 (n=1)
PreOc	1/1 (n=31)	1/1 (n=23)	1/1 (n=40)	1/1 (n=29)
	2/2 (n=3)			2/2 (n=1)
	2/1 (n=1)			
PosOc	2/2 (n=35)	2/2 (n=22) 3/2 (n=1)	2/2 (n=37) 3/3 (n=3)	2/2 (n=26) 2/3 (n=1) 3/3 (n=3)
T	2+3/2+3 (n=18)	2+3/2+3 (n=11)	2+3/2+3 (n=29)	2+3/2+3 (n=21)
	2+2/2+2 (n=1)	2+2/2+2 (n=7)	2+2/2+2 (n=8)	2+2/2+2 (n=3)
	2+1/2+3 (n=1)	2+1/2+3 (n=1)	2+2/2+3 (n=1)	2+2/2+3 (n=4)
	2+3/2+2 (n=2)	2+2/2+1 (n=1)	2+1/2+1 (n=1)	2+2/2+1 (n=1)
	2+3/2+1 (n=1)	2+3/3+3 (n=1) 3+3/2+3 (n=1)	2+2/2+3 (n=1) 3+3/2+3 (n=1)	3+3/3+3 (n=1)
D	17/17/13 (n=34)	17/17/13 (n=20)	17/17/13 (n=37)	17/17/13 (n=15)
	17/17/11 (n=1)	17/17/11 (n=3)	17/17/11 (n=3)	17/17/11 (n=14)
V	136–164 (n=34)	137–164 (n=23)	145–162 (n=39)	127–162 (n=30)
SC	73–98 (n=33)	70–99 (n=23)	81–101 (n=39)	82–104 (n=27)
Cloacal	single (n=32)	single (n=22)	single (n=40)	single (n=30)
	divided (n=1)	divided (n=1)		

Table 2. Descriptive statistics from meristic and morphometric variables for the two populations of *Thamnodynastes pallidus*. Range within parentheses. Dorsals-N: number of dorsal scales on a row of the neck; Dorsals-M: number of dorsal scales on a row in the middle of the body; Dorsals-T: number of dorsal scales on a row near the cloaca; SL: snout length distance from tip of snout to the tip of preocular; head length; SVL: snout-vent length; tail length; total length; “E”- anterior ventral portion lighter than posterior portion; “H”- anterior ventral portion is similar to posterior portion; A: absence of keels on dorsum; P: presence of keels on dorsum.

	Amazon (n=58)	Atlantic Forest (n=70)
Infralabials	8.77±0.46 (8–10)	8.99±0.21 (8–10)
Supralabials	8±0 (8–8)	8±0 (8–8)
Temporals (primary)	2.02±0.13 (2–3)	2.03±0.17 (2–3)
Temporals (secondary)	2.51±0.67 (1–3)	2.75±0.47 (1–3)
Preoculars	1.03±0.18 (1–2)	1.01±0.12 (1–2)
Postoculars (right)	2.02±0.13 (2–3)	2.09±0.28 (2–3)
Postoculars (left)	2±0 (2–2)	2.10±0.30 (2–3)
Loreal	1±0 (1–1)	1±0 (1–1)
Dorsals–N	17±0 (17–17)	17±0 (17–17)
Dorsals–M	17±0 (17–17)	17±0 (17–17)
Dorsals–T	12.82±0.56 (11–13)	12.517±0.87 (11–13)
Ventrals	151.02 ±6.83 (136–164)	152.78±5.70 (127–162)
Cloacal	96.7% (54) unique 3.28% (2) divided	100% unique
Subcaudals	84.85±9.85 (70–99)	91.77±5.43 (81–104)
Colouration	55.74% (33) E 44.26% (25) H	11.43% (8) E 88.57% (62) H
Keel	100% A	100% A
Snout Length (mm)	3.78±0.65 (2–5)	3.11±0.72 (1.00–4.60)
Head Length (mm)	15.43±2.59 (11–27)	15.53±2.53 (8.00–24.80)
SVL (mm)	386.41±73.16 (162–600)	336.250±77.027 (110.00–482.00)
Tail Length (mm)	154.46±26.36 (81–222)	140.91±35.28 (58–209)
Total Length (mm)	542.12±95.79 (292–764)	478.02±107.71 (205–679)

using 75% of the data for model calibration and retained 25% of the data to evaluate models. We report the mean and standard deviation of AUC test values for the 10 runs. We used Maxent with the R package dismo (Hijmans et al., 2013) and used the Maxent default parameters (Phillips & Dudik, 2008). The output model is projected in geographical space and the result can be interpreted as a map of environmental suitability for the species, where areas with higher values are climatically more favourable for the species.

We used the Bioclimatic environmental variables from the Worldclim project (Hijmans et al., 2005). These variables were downloaded from the WorldClim project at a 30" (1 km²) spatial resolution (available online at: <http://www.worldclim.org/>; Hijmans et al. 2005). The layers were cropped to span from latitude 13 to -25° and longitude -82 to -35°; this represents a larger spatial range than the distribution of the species, which also includes tropical and subtropical zones with bioclimatic conditions that are compatible with the occurrence of *T. pallidus*. To avoid over-fitting of the models and the use of redundant climatic variables, we identified highly correlated variables ($r > 0.9$) and excluded those that we considered biologically irrelevant. A similar procedure is described in Rissler & Apodaca (2007). We used a total of 10 abiotic environmental variables, which were: Bio 3

– Isothermality, Bio 4 – Temperature Seasonality, Bio 7 – Temperature Annual Range, Bio 10 – Mean Temperature of Warmest Quarter, Bio 11 – Mean Temperature of Coldest Quarter, Bio 14 – Precipitation of Driest Month, Bio 15 – Precipitation Seasonality, Bio 16 – Precipitation of Wettest Quarter, Bio 17 – Precipitation of Driest Quarter, and Altitude.

RESULTS

We examined 128 specimens of *T. pallidus*: 70 from the Atlantic Forest of northeastern Brazil (ATL) from the states of Bahia, Alagoas, Pernambuco, Paraíba and Sergipe; and 58 from the Amazon Forest (AMA) from the states of Acre, Amapá, Amazonas, Maranhão, Pará, Rondônia and Tocantins, Brazil, and also from Bolivia, Colombia, Guyana, French Guyana, Peru, and Suriname. Both populations were invariable for the following characteristics: rostral scale as wide as high, not visible dorsally; prefrontals and internasals paired, as long as wide; frontal, parietals and supraoculars longer than wide; nasals in contact with the first supralabials; one loreal in contact with the third supralabial; eight supralabials; dorsal scales smooth; four longitudinal stripes along the venter; and a postocular stripe. The remaining features exhibited a slight variation in both groups (Table 1), as follows: Temporals 2+3/2+3



Fig. 1. Dorsal and ventral view of *Thamnodynastes pallidus* from the Amazon population. Upper: MZUSP 18829 (Urbano Santos, Maranhão, Brazil), SVL: 351 mm; Tail Length: 141 mm; Lower: MZUSP 5771 (Berurí, Amazonas, Brazil), SVL: 310 mm; Tail Length: 130 mm.

(N AMA=29; N ATL=50), 2+2/2+2 (N AMA=15; N ATL=11), 2+1/2+3 (N AMA=5; N ATL=0), 2+1/2+1 (N AMA=0; N ATL=1), 2+3/2+2 (N AMA=2; N ATL=0), 3+3/2+3 (N AMA=1; N ATL=1), 3+3/3+3 (N AMA=0; N ATL=1). Dorsal scales 17/17/13 (N AMA=54; N ATL=52), 17/17/11 (N AMA=4; N ATL=17). Infralabials 9/9 (N AMA=43; N ATL=64), 8/8 (N AMA=14; N ATL=3), 10/9 (N AMA=1; N ATL=0), 10/10 (N AMA=0; N ATL=1). One preocular on both sides of the head (N AMA=54; N ATL=69), two preoculars on only one side of the head (N AMA=1; N ATL=0), and two preoculars on both sides of the head (N AMA=3; N ATL=1). Two postoculars on both sides of the head (N AMA=57; N ATL=63), three postoculars on only one side (N AMA=1; N ATL=0), and three on both sides (N AMA=0; N ATL=6). Ventral scales vary from 127–164 in the entire sample: in the Amazonian group, they range from 136 to 164 and in the Atlantic Forest group from 127 to 162 (Table 1). Subcaudal scales vary from 70–104 in the entire sample, ranging from 70 to 99 in the Amazonian group, and from 81 to 104 in the Atlantic Forest group. The cloacal scale is invariably single in the ATL group and shows very little variation in the Amazonian group, with only two specimens showing a divided cloaca (Tables 1 and 2).

Both populations have a brown dorsal surface of the head, with light-brown (slightly beige) body sides containing a posteroventral dark stripe that ranges from the postocular scales to three scales after the corner of the mouth. The venter of the head is predominantly

Table 3. Summary of the BLR analysis (reduced model). OR=odds-ratios. The intercept is not significant.

AIC=128.50; Schwarz's BIC=178.675				
Term	Estimate	Z	p	OR
Infralabials	-3.606	-3.333	0.001	0.027
Snout length	2.716	3.032	0.002	15.114
Subcaudals	-0.134	-2.947	0.003	0.875



Fig. 2. Dorsal and ventral view of *Thamnodynastes pallidus* from the Atlantic Forest population. Upper: MZUSP 5004 (Vicência, Pernambuco, Brazil), SVL: 369 mm; TaL: 154 mm; Lower: MZUSP 20355 (Cruz do Espírito Santo, Paraíba, Brazil), SVL: 405 mm; TaL: 162 mm.

immaculate. Small dark spots are present on the infralabials and supralabials. The dorsal region of the body is brown, with many black spots surrounding white spots. The anterior region of the body shows dorsal scales bordered by shades of yellow, more evident in juveniles. The venter of the body exhibits four dark longitudinal stripes from the beginning of the neck to the end of tail. The outermost stripes are separated by light spaces from the 60th ventral to the end of the body (Figs. 1 and 2).

Seventeen hemipenes were examined; 10 from the ATL group (CHUFPB 4534, CHUFPB 4535, CHUFPB 4536, CHUFPB 4548, CHUFPB 8840, CHUFPB 11147, CHUFPB 8845, MBML 2198, MZUSP 20356, MZUSP 5004) and seven from the AMA group (IBSP 13753, MZUSP 18829, MZUSP 19206, MPEG 6842, MPEG 10101, MPEG 11777, MPEG 20519). All hemipenes share a unilobed or slightly bilobed, unicalyculate and noncapitate hemipenes (Fig. 3). A slightly bilobed condition was found in hemipenes of specimens from Maranhão (AMA) and Pernambuco (ATL), whereas the remaining samples (AMA, from Pará state, and the remaining Atlantic Forest localities) showed the unilobed condition (Fig. 3). The capitulum is distributed on the distal portion of the organ and is formed by small spinulate calyces. The sulcus spermaticus divides at the base of the capitulum, but does not reach the apex. It expands distally denoting a heart-shaped termination, with spinulate calyces on the small intrasulcar region (Maranhão: MPEG 20519, MZUSP 18829 and Pará: MPEG 11777), or it is simple and expands into a small nude area and does not reach the apex (Paraíba: CHUFPB 4373, MZUSP 20356 and Pará: MPEG 6842). The hemipenial body is covered by spines that decrease subtly in size towards the distal end of the hemipenis on both sulcate and asulcate surfaces. All hemipenes exhibit many small spines at the base of the organ (Fig. 3).

Before running the BLR *per se*, we checked for correlations among predictors and for the influence of gender on predictors. As expected, snout-vent length is

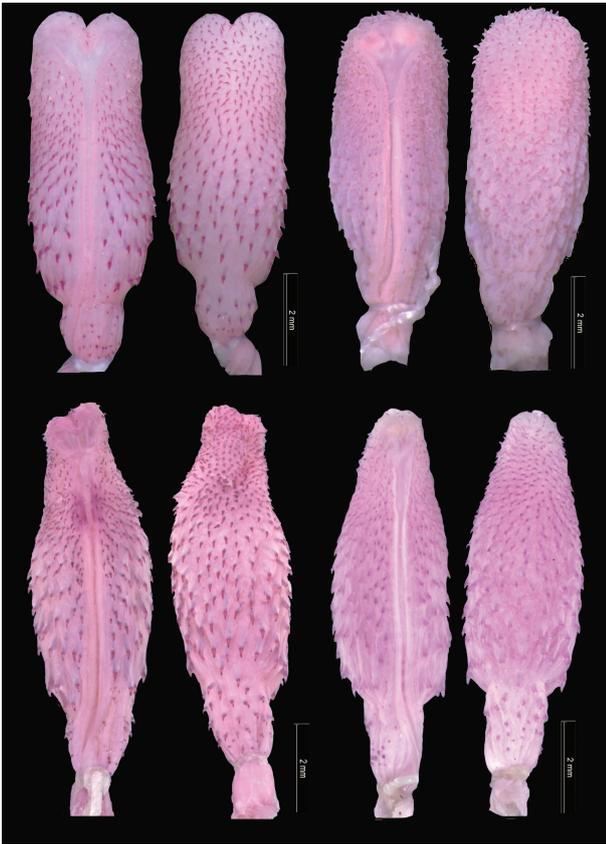


Fig. 3. Sulcate and asulcate side of the hemipenes of *Thamnodynastes pallidus* from the Amazon group (upper left: MZUSP 18829; upper right MPEG 6842), and from the Atlantic Forest group (lower left: MZUSP 5004; lower right MZUSP 20356).

strongly correlated with tail and total length. Since the absence of multicollinearity is a prerequisite of logistic regression, we removed tail and total length from the analysis, because snout-vent length gave the greatest F value in preliminary ANOVAs (type of biome [‘Amazonian’ or ‘Atlantic’] as independent variable – results not shown). For BLR, we first defined a full model, into which all variables (except for tail and total length) described in the material and methods section were included as predictors. The full model gave an AIC of 128.50 and selected the number of infralabials (Estimate=-3.606; $Z=-3.333$, $p=0.001$), number of subcaudals (Estimate=-0.134; $Z=-2.947$, $p=0.003$), and snout length (Estimate=2.716; $Z=3.896$, $p=0.002$) as the only predictors that could discriminate the two populations (Table 3). The reduced model results are shown in Table 2 and there was a significant difference between the full and the reduced models ($\chi^2=73.722$, $df=17$, $p<0.001$).

According to distributional data from the literature, from museum specimens, and from our own fieldwork, we conclude that *T. pallidus* occurs in the Guianas, Suriname, Bolivia, Venezuela, Colombia, Ecuador, Peru, and in north and northeastern Brazil. The distribution model shows broad regions with higher climatic suitability for *T. pallidus* spread across the Amazon basin and the Atlantic Forest. Regions with particularly high suitability are seen on the northeast coast of Brazil, the central Brazilian Amazon, the coast of the Guianas, northern Bolivia, eastern Peru and Colombia (Fig. 4).

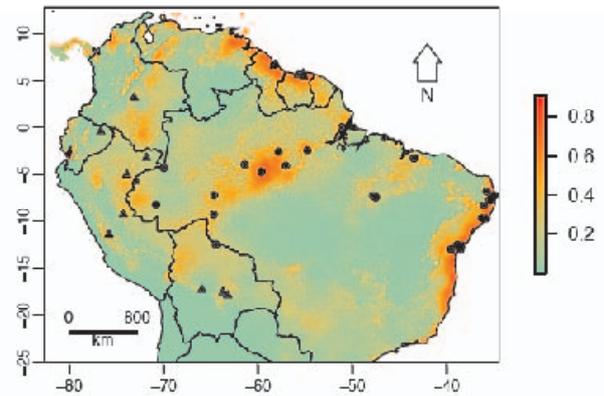


Fig. 4. Maxent distribution model of *Thamnodynastes pallidus*, warmer colours indicate areas with more suitable climatic conditions for the species to occur. Circles represents localities from museum and fieldwork records, triangles represent occurrence localities obtained from the literature.

DISCUSSION

As reported above, no significant quantitative and qualitative variability was found between individuals of the two populations for the following characteristics: shape of the frontal, parietal, rostral, snifisal and supraocular scales; unevenness of the internasal scales; the position of the nasal and loreal scales; the number and position of supralabials; the number of preoculars; colouration of the dorsal portion of the head, dorsum and venter, or the general aspect of the hemipenes. Four specimens exhibited two preoculars at least on one side of the head. This second preocular consists of a small scale placed below the larger preocular. Therefore the normal number of preoculars in *T. pallidus* is one scale, and individuals with two scales should be considered as an abnormality. Nonetheless, some characteristics showed intra- and interpopulational variation: the number of infralabials, the number of subcaudals, and snout length.

The presence of sexual dimorphism was expressed by the dorsal scale reduction (males: 17.17.11 for the ATL population and females 17.17.13), by the number of ventrals in both populations, and by the number of subcaudals for the Atlantic population, with higher scale counts for males in both cases. Male-biased sexual dimorphism in ventral scale number counts (males with more ventrals) is documented for several members of Tachymenini, and is considered to be a diagnostic trait for the tribe (Zaher et al., 2009).

Variation in colouration patterns, morphometric and hemipenial characteristics, and pholidosis, among or within snake populations, is commonly reported (Mitchell, 1977; Christman, 1984; Castellano et al., 1994; Heatwole et al., 2005). Some of these studies report morphological variation due to sexual dimorphism, ecology, environment, geographical gradients, and natural selection. Even with the relatively large sample used here, any attempt to associate the between-population morphological variation observed in this study would be

merely speculative (except for sexual dimorphism) for two main reasons: (i) the lack of field observational attempts in both biomes (e.g., microhabitat use) and (ii) the paucity of intense sampling in the region that separates the biomes (or even in putative natural corridors that could link them).

The taxonomy of *Thamnodynastes* has been subject to divergence. Since the 1980s, several authors have published synonymisations, revalidations and descriptions of new species, which almost exclusively rely on morphological variation of few specimens (Perez-Santos & Moreno, 1989; Cei et al., 1992; Bergna & Alvarez, 1993; Gorzula & Ayarzagüena, 1996; Franco & Ferreira, 2002; Franco et al., 2003; Bailey et al., 2005; Bailey & Thomas, 2007).

Concerning *T. pallidus*, the cloacal scale condition is a disputed character: Franco & Ferreira (2002) and Pérez-Santos and Moreno (1989) reported that *T. pallidus* has a single cloacal scale. Roze (1966) and Dixon & Soini (1986) mentioned a divided cloaca, whereas Bailey et al. (2005) stated both conditions. From the 72 specimens examined by the latter authors, nine showed the divided condition. In our sample, we observed the two conditions only in the Amazonian population, with only two Amazonian specimens showing the divided condition. The geographical sample used by Bailey et al. (2005), Dixon & Soini (1986), and Roze (1966) was constituted by records from the Amazonian regions in Brazil, Peru, Venezuela, Colombia, French Guiana, Bolivia, Ecuador and Suriname. Even though the sample sizes in previous studies differ, the pattern might indicate that the divided condition, when it occurs, is restricted to Amazonian populations.

The cloacal scale is not the only source of taxonomic confusion. Bailey et al. (2005) suggested without further explanation, that specimens assigned to *T. pallidus* by Franco & Ferreira (2002) should be treated as *T. almae*, restricting *T. pallidus* to the Amazon. Alternatively, Franco & Ferreira (2002) affirmed that *T. almae* is a distinct species found only in the Caatinga biome. The differences between these two species, the number of dorsals-T (15 in *T. almae* and 13 in *T. pallidus*), the condition of the dorsal scales (slightly keeled in *T. almae* and smooth in *T. pallidus*), the number of subcaudal scales (59–66 in *T. almae* and 81–104 in *T. pallidus*), and the robustness of the body (*T. almae* being more robust than *T. pallidus*) are sufficient evidence to distinguish these taxa, and therefore eliminate further confusion.

The number of subcaudals within our samples (62–99 for the Amazonian population, and 81–104 for the Atlantic Forest), is higher than that previously mentioned by Franco et al. (2003) (a maximum of 99), based on Cunha & Nascimento (1993). A long tail is found within other members of the “*pallidus* group”, defined by Bailey et al. (2005), such as *T. longicaudus* (101–109, Franco et al. 2003), and *T. sertanejo* (74–98); and in *T. lanei* (74–90), the latter not included by Bailey et al. (2005) in the *pallidus* group. The other species of the genus exhibit a shorter tail, normally not reaching more than 80 subcaudals: *T. ceibae*, 67; *T. dixoni*, 57–62; *T. gambotensis*, 53–72; *T. paraguanae*, 57–72; *T. ramonriveroi*, 54–79 (Bailey & Thomas, 2007); *T. hypoconia*, 55–84 (Cei et al., 1992); *T. chimanta*, 48–59 (Roze, 1958; Myers & Donnelly, 1996); *T. duida*, 56; *T.*

yavi, 57–66 (Myers & Donnelly, 1996); *T. chaquensis*, 49–74 (Bergna & Alvarez, 1993); *T. corocoroensis*, 54; *T. marahuaquensis*, 61 (Gorzula & Ayarzagüena, 1996); *T. almae*, 59–66, *T. rutilus*, 57–79 and *T. strigatus*, 47–68 (Franco & Ferreira, 2002).

Considering the hemipenis, Bailey et al. (2005) characterise *T. pallidus* as “short, simple or very faintly bilobate, with sulcus simple, opening on a clear triangular space at tip”. Zaher (1999) diagnosed *Thamnodynastes* as having a poorly bilobate unicalyculate and noncapitate hemipenis, with a capitulum distributed on most of the distal half of the organ, and the sulcus spermaticus dividing distally at the base of the capitulum. We found a previously unreported variation in the pattern of the sulcus spermaticus in both populations. We characterise *T. pallidus* by the presence of a unilobed or slightly bilobed unicalyculate, and noncapitate hemipenis, with a simple sulcus expanding distally on a nude area or bifurcating distally on the base of the capitulum. In both cases, the sulcus does not reach the apex. Additionally, the base of the organ is formed by small spines, and is not nude.

Although we demonstrate the occurrence of variation with respect to some meristic and hemipenial characters between and within each population, we conclude that these variations are not sufficient to recognise them as distinct species. Thus, we recognise a single taxonomic lineage diagnosed by the presence of one preocular scale, 17/17/13 or 11 smooth dorsal scales, a single cloacal scale, slender body and long tail with four longitudinal ventral stripes, an unilobed or slightly bilobed hemipenis with small spines on the base of the organ, a hemipenial body covered by small spines, decreasing slightly towards the distal end of the hemipenis, and a sulcus spermaticus that is divided distally on the basis of the capitulum, which is formed by spinulate calyces.

The occurrence of *T. pallidus* extends to the Amazon region of Brazil, in the states of Acre, Amapá, Amazonas, Maranhão, Pará, Rondônia and Tocantins, and in the Atlantic Forest of northeastern Brazil in the states of Paraíba, Pernambuco, Alagoas, Sergipe, and Bahia. According to the distribution model, *T. pallidus* is more prone to occur in the rainforest of eastern South America, and western Brazil in Rondônia, Amazonas, and Acre states. The species also have a high probability of occurrence in the Central and Northern Amazonia, Pará state in Brazil, Northern Bolivia, Southeastern Peru, Northwestern Venezuela, French Guiana, and Suriname.

Widely distributed taxa are common (Borges-Nojosa et al., 2006; Sawaya et al., 2008; Pereira-Filho & Montingelli, 2011), but special attention is always conferred to species with disjunct distributions (Trauth, 1991; Scartozzoni & Marques, 2004; Passos & Fernandes, 2005). A possible explanation for the discontinuity in the distribution of *T. pallidus* is supported by recent studies that relate historical connections between the Amazon and Atlantic Forest (Thomas et al., 1998; Costa, 2003). In other words, the hypothesis that *T. pallidus* had a much broader distribution in the past and attained its recent distribution as a result of past climatic fluctuations that set forested environments (Amazon and Atlantic Forest) apart, is attractive.

The scenario might be more complex, involving past

climatic fluctuations and interactions with Brazilian central areas and other South American biomes (Costa, 2003; Colli, 2005; Carnaval & Moritz, 2008), which might also involve other Brazilian species of *Thamnodynastes*, such as *T. longicaudus* from the southern Atlantic Forest, *T. sertanejo* and *T. almae* from the Caatinga, *T. lanei* from the central region and Amazon region, and *T. chaquensis* from Chaco and Pantanal.

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APPENDIX

Specimens Examined

Thamnodynastes pallidus:

Atlantic Forest: Brazil: *Alagoas*: Rodovia AI-215: MNRJ 11400, MNRJ 11401; Mangabeiras: MZUSP 3499. *Bahia*: Elísio Medrado: Serra da Jibóia: MZFS 1173; Mata de São João: Reserva de Camurujipe: MZUFBA 1744; Salvador: Jardim Botânico: MZUFBA 1534; Santo Amaro: MBML 2198. *Paraíba*: João Pessoa: Mata do Buraquinho: CHUFPB 4534–4550, 8814, 8815, 8818, 8819, 8821, 8822, 8823, 8825, 8827, 8830, 8831, 8832, 8833, 8840, 8841, 8842, 8843, 8844, 8845, 8846, 8847, 8848, 8849, 8850, 8855, 9194, 9195, 9196, 11147, 12943, 12944, 12945, 12946, 12947, 13257; Cruz do Espírito Santo: Mata da Usina São João: MZUSP 20350, 20352–20356. *Pernambuco*: Moreno: Estação Ferroviária de Tapera: Mata do Toro: MCN 5377–5379; Vicência: Água Azul: MZUSP 5004. *Sergipe*: Indiaruba: Mata do Sabão: MNRJ 17238.

Amazon Forest: Brazil: *Acre*: Taracá: IBSP 18533. *Amapá*: Macapá: IBSP 18444. *Amazonas*: Berurí: MZUSP 5771; Borba: MNRJ 2625; Mucuripe: Rio Purus: MZUSP 5760; Rio Manjuru: AMNH 101960; São João, Solimões: AMNH 25159; Tabatinga: MCP 14090; *Maranhão*: Arari: MPEG 15237; Arari: Gancho do Arari BR-222: MPEG 18222, 15619; Pindaré-Mirim: Puraqueú: BR-222: MPEG 15704; Santa Luzia do Paruá: Paruá BR-316: MPEG 12840; Urbano Santos: Fazenda Santo Amaro: MPEG 20519, 20520; Urbano Santos: Povoado São Felipe: MZUSP 18829; UFMA 03, UFMA 06, UFMA 78, UFMA 89; UHE Estreito: MZUSP 18815, 19206, 19211, 19212, 19213, 19215, 19218, 19220, 19221; UHE Estreito: Carolina: MZUSP 19203. *Rondônia*: Forte Príncipe da Beira: Rio Guaporé: IBSP 22155; Porto Velho: UHE Jirau: Margem direita do Rio Madeira: MZUSP 19460. *Pará*: Augusto Corrêa: Cacoal: MPEG 3228, 6842, 9177, 10101; Chaves: Ilha do Marajó: Fazenda Santana: MPEG 18665, Palestina do Pará: Porto Jarbas Passarinho: Transamazônica: MPEG 11777; *Tocantins*: Guaraí: MZUSP 12681; UHE Estreito: Filadélfia: MZUSP 19201; UHE Estreito: Babaçulândia: MZUSP 19205. *Bolívia*: *Cochabamba*: AMNH 6779. *Santa Letícia*: MPEG 18303. *Colombia*: Boyaca: Guaicaramo: AMNH 46472. *GUIANA*: *Georgetown*: AMNH 2665, 36134. *Peru*: *Loreto*: Iquitos: AMNH 55870; *Orellana*: AMNH 54578, 54585, 54586, 54587, 54591, 54598, 54612, 54615, 54629; *Requena*: AMNH 52648. *Guiana Francesa*: IBSP 13753. *Suriname*: *Coppename River*: AMNH 73841; Paramaribo: AMNH 8665, AMNH 130528, AMNH 104633.