



Hemipenial morphology of *Epictia vellardi* (Laurent, 1984) (Leptotyphlopidae, Serpentes) with the proposition and discussion of two general hemipenial patterns within the genus *Epictia*

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Abstract

Scolecophidia (Squamata, Serpentes), commonly known as blindsnakes, wormsnakes or threadsnakes comprises a group of small snakes, with relatively few systematic and morphological studies when compared to Alethinophidia. Since the external morphology is very conserved amongst scolecophidians, internal morphological studies—such as the hemipenial morphology—are useful to unravel several systematic issues within the group. We aimed to describe the hemipenial morphology of *Epictia vellardi* (Epictinae, Leptotyphlopidae) based on 16 organs belonging to eight specimens. The organ is unilobed, with the body conspicuously narrower than the base and with the apex slightly expanded, without any macroscopic ornamentation. The comparison of the hemipenial morphology of *E. vellardi* with other hemipenes of *Epictia* spp. allowed us to identify two general morphological patterns for the genus, which are proposed and discussed in detail in the present study. The results found herein may be extremely relevant for future hemipenial descriptions. In addition, independent characters found in Types I and II (such as ornamentation, shape of base, body and apex) should be regarded for future systematic and evolutionary morphology studies within Leptotyphlopidae, in addition to assisting in the taxonomy and identification of species of the genus.

Keywords Hemipenis · Ornamentation · Scolecophidia · Threadsnares

Introduction

Scolecophidia (sensu Miralles et al. 2018), commonly known as blindsnakes, wormsnakes or threadsnakes, consists of a group of snakes with relatively few studies (Francisco et al. 2018) regarding their evolution and natural history when compared to Alethinophidian snakes and, therefore, several issues related to its systematics still remain (Mez-zasalma et al. 2016). This taxon currently comprises about 440 species (Uetz et al. 2020) allocated in the family Leptotyphlopidae (approx. 150 species) and in the superfamily Typhlopoidea (approx. 290 species) (Uetz et al. 2020).

Morphological characters are so far the most common source of information applied as diagnostic features for taxa

within Leptotyphlopidae (Francisco et al. 2018). However, the reduced size of individuals hampers the conduction of internal morphological studies, since most of those techniques demand invasive procedures to assess anatomical data. In addition, due to their fossorial habit, the representativeness of these snakes in scientific collections is extremely low, with many species currently known exclusively from their holotype or type series (e.g., *Epictia rioignis*, Koch et al. 2019), adding even more limitations to the conduction of morphological studies that demand destructive approaches.

Considering that scolecophidians exhibit a very conserved external morphology (Martins et al. 2019a), the use of morphological data—such as hemipenial morphology—is particularly useful in the delimitation of species (Arnold 1986; Dowling and Savage 1960) and the distinction of cryptic species (Arnold 1986; Eberhard 1985, 2009; Myers and McDowell 2014; Passos et al. 2018). However, despite studies on hemipenial morphology being widely used in snakes in general, descriptive works on hemipenial morphology in Leptotyphlopidae are still scarce (Martins et al. 2019a).

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Representatives of Leptotyphlopidae are distributed in Africa and in the Neotropics (South America, Central America and the Antilles), with a smaller number of species occurring in the south of North America, in Arabia and southwest of Asia (Adalsteinsson et al. 2009; Martins et al. 2019a). Despite its wide distribution in the world, little is known about its systematics and ecology, even though they occur in a variety of habitats such as deserts, forests, swamps, savannas and modified habitats (Adalsteinsson et al. 2009; Martins et al. 2019a). This family is divided into two subfamilies: Leptotyphlopinae, with approximately 50 species (Uetz et al. 2020), and Epictinae, with approximately 90 species (Uetz et al. 2020). The subfamily Leptotyphlopinae is composed of four genera: *Epacrophis*, *Leptotyphlops*, *Myriopholis* and *Namibiana*; while Epictinae is composed of ten genera: *Epictia*, *Mitophis*, *Rena*, *Rhinoguinea*, *Rhinoleptus*, *Siagonodon*, *Tetracheilostoma*, *Tricheilostoma*, *Trilepida* and *Habrophallos*. The genus *Epictia* currently represents the most diverse among the Leptotyphlopidae family (Martins et al. 2019a), with 45 currently known species that occur in Mexico and throughout Central and South America (Martins et al. 2019a; Wallach 2016; Uetz et al. 2020).

Many of the hemipenial morphological studies available for Leptotyphlopidae focus on the New World (NW) taxa (e.g., Bailey and Carvalho 1946; Cei 1993; Fabrezi et al. 1985; Orejas-Miranda 1962; Passos et al. 2005; 2006; Peters and Orejas-Miranda 1970; Pinto et al. 2010; Pinto and Curcio 2011; Pinto and Fernandes 2012; Savage 2002; Scrocchi 1990; Thomas 1975), with even more limited contributions for the leptotyphlopids of the Old World (OW) (e.g., Branch 1986). Almost all the works currently available are focused on the genera *Trilepida* (NW) and *Epictia* (NW), with few works available for the genera *Rena* (NW) and *Leptotyphlops* (OW); no descriptive works on the hemipenial morphology are available for the genera *Tetracheilostoma* (NW), *Tricheilostoma* (OW), *Rhinoleptus* (OW) and *Siagonodon* (NW)—in Epictinae—, and *Epacrophis* (OW), *Myriopholis* (OW) and *Namibiana* (OW)—in Leptotyphlopinae (Adalsteinsson et al. 2009; Martins et al. 2019a; Uetz et al. 2020). However, although there are a few available studies on the hemipenial morphology of representatives of *Epictia*, they are still punctual and scarce to allow an understanding of the dimension and morphological variety of this genus, with only 13 species having their hemipenial morphology described: *E. bakewelli* Oliver 1937, *E. striatula* (Smith and Laufe 1945), *E. diaplocia* (Orejas-Miranda 1969), *E. australis* (Freiberg and Orejas-Miranda 1968), *E. wynnii* Wallach (2016), *E. tenella* Klauber 1939, *E. resetari* Wallach (2016), *E. pauldwyeri* Wallach (2016), *E. martinezi* Wallach (2016), *E. magnamaculata* Taylor 1940, *E. albipuncta* (Burmeister 1861), *E. munoai* (Orejas-Miranda 1961) and *E. ater* Taylor 1940.

Given the insufficiency on the knowledge of threadsnakes morphology, herein we aim to describe in detail the hemipenis of *Epictia vellardi* (Laurent 1984). This species is currently distributed in Paraguay, Argentina (in Formosa), and Brazil (in Corumbá, in the State of Mato Grosso do Sul; and in the State of Mato Grosso) (Cabral et al. 2016; Costa and Bérnils 2018). We also provide a comprehensive discussion of the hemipenial morphology within the genus *Epictia*, with the definition of two patterns of hemipenial morphology within this taxon.

Materials and methods

The hemipenes of *Epictia vellardi* were described based on specimens from Reserva Particular do Patrimônio Natural Acurizal (Serra do Amolar, Corumbá, Mato Grosso, Brazil) housed at Coleção de Répteis of the Universidade Federal do Mato Grosso (UFMT). The morphology of the hemipenes was analyzed in situ from 16 organs belonging to eight specimens. The hemipenial terminology for description followed Dowling and Savage (1960), with modifications by Myers and Campbell (1981) and Branch (1986). Photographs were made with a Leica M205C stereomicroscope microscope, with an attached camera. The photos taken in various focal planes were combined in multifocal images with Leica Application Suite software version 3.6.0. Schematic drawings to illustrations of hemipenial general shape were conducted in Inkscape 1.0. The literature data on the hemipenial morphology of the genus *Epictia* are based on the citations given in the “Discussion”.

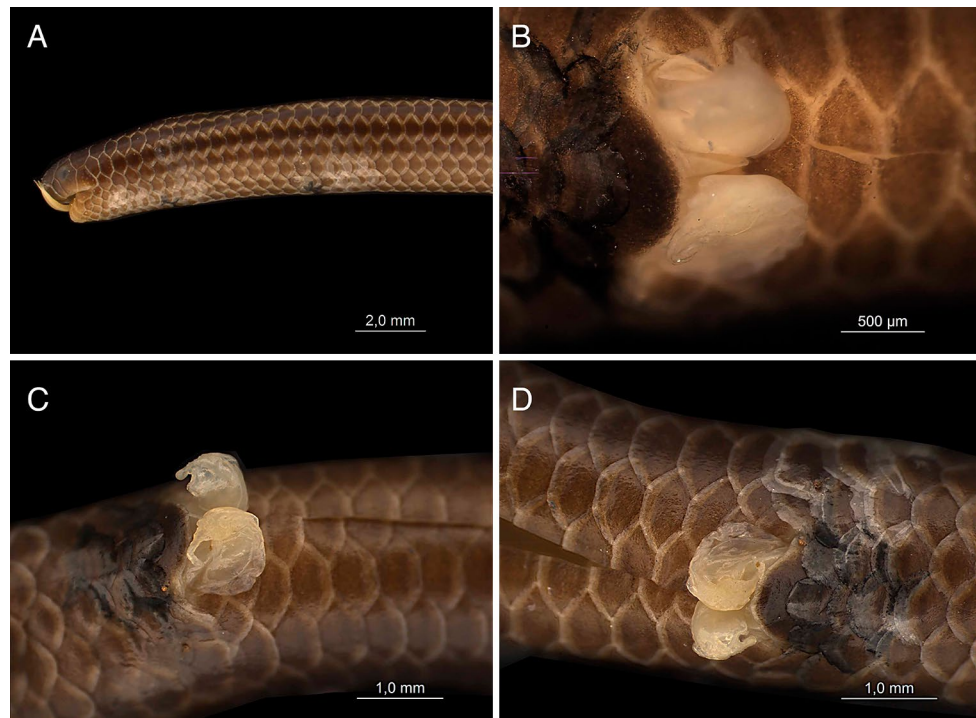
The identification of specimens was based on the species original description (Laurent 1984) and Francisco et al. (2012). We considered Wallach (2016) for species allocation in the following groups: *E. gr. albifrons*, *E. gr. goudotii* and *E. gr. phenops*.

Results

Our results are based on the examination of 2 organs fully everted and partially expanded (UFMT1343) and 14 organs partially everted and partially expanded (UFMT1297; UFMT1301; UFMT1348; UFMT1351; UFMT1355; UFMT1357; UFMT1502).

UFMT1343 (examined in situ, fully everted, partially expanded; Fig. 1): the organ is unilobed, approximately 2.6 mm in length from the base to the apex, with no macroscopic ornamentation. It has a wide base, narrowing along its body. The apex is spherical and wider than the body, being differentiated from the body by a conspicuous narrowing in the organ’s upper third. The spermatic groove has raised edges and exhibits a small lateralization in the region

Fig. 1 **a** Lateral view of the anterior region of *Epictia vellardi*; **b** hemipenes of *Epictia vellardi*, dorsal view; **c, d** hemipenes of *Epictia vellardi*, laterodorsal view; UFMT1343



adjacent to the cloaca in a counterclockwise direction, but at the base it follows a straight route to the apex.

We found no intraspecific variation in the organ base or body. We were not able to evaluate such variation in the apex given most organs were partially everted, and therefore had their apex inverted.

Discussion

Due to the relatively few studies regarding the scolecophidian systematics, several uncertainties of their representatives' relationship hypotheses still remain. Even though morphological characters are the most common source of information used to diagnose the Leptotyphlopidae taxa (Francisco et al. 2018), the majority of the systematic studies currently available for such group are based on molecular data (e.g., Adalsteinsson et al. 2009, Pyron and Wallach 2014, and Nagy et al. 2015), with most of the morphological data not yet phylogenetically tested. However, morphological data such as gland morphology (e.g., Martins et al. 2018), skull morphology (e.g., Salazar-Valenzuela et al. 2015; Koch et al. 2019; Martins et al. 2019a), head and neck myology (e.g., Martins et al. 2019b), visceral anatomy (e.g., Broadley and Wallach 2007a, b; Wallach 2016) and hemipenial morphology (e.g., Passos et al. 2006; Graboski et al. 2018; Martins et al. 2019a) have proven to be useful for the scolecophidian systematics.

The lack of studies related to the hemipenial morphology of Scolecophidia is mainly due to two factors: scarcity of specimens available in scientific collections and great difficulty in eversion of the hemipenis in situ, due to its small size and tissue fragility (Martins et al. 2019a; Pesantes 1994). Therefore, most available studies regarding the threadsnakes (Leptotyphlopidae) hemipenial morphology are based on organs previously everted (Martins et al. 2019a) or partially everted upon fixation.

The importance of such characters for diagnosing threadsnakes has already been previously highlighted in the literature. Passos et al. (2006) have suggested that hemipenial characters might be synapomorphic for threadsnakes of the genus *Trilepida*, and Martins et al. (2019a) have also suggested that the combination of a few hemipenial characters might be exclusive to the genus *Habrophallos*. Even though such characters have never been phylogenetically tested, the hemipenial morphology of scolecophidians allows us to unravel systematic issues within such group. Although such characters have been widely explored within snakes, those studies are still extremely underexplored within scolecophidians.

The results found herein are in accordance with the basic pattern of hemipenial morphology within scolecophidians, with organs being single and bearing an undivided *sulcus spermaticus* (Branch 1986; Wallach 1998 Unpubl. Thesis; Passos et al. 2006; Graboski et al. 2018; Martins et al. 2019a). Considering the hemipenis of *Epictia vellardi* and other *Epictia* spp., current available papers related to the

hemipenial morphology of representatives of *Epictia* seem to indicate the presence of two morphological patterns within this taxon (Fig. 2): (1) the first pattern (here called Type I) relates to an organ devoid of or has little ornamentation, with a conspicuously broad base and an evident constriction towards the body and apex (Fig. 2a, b); (2) the second pattern (here called Type II) includes organs without a clear distinction between the width of the body and the apex, with the base being the same width or slightly narrower than the body and apex, commonly presenting conspicuous and evident macro-ornamentations (such as flounces, calyces and papillae) in the base and/or body (Fig. 2c, d). Although the shape of the hemipenes may vary due to preparation artifacts (Passos et al. 2016; Zaher and Prudente 2003), we believe that the approximate shapes proposed herein reflect the actual morphology and the patterns for *Epictia* spp.

Available data on hemipenial morphology of *Epictia* spp. indicate that *E. australis* (Martins et al. 2019a; Scrocchi 1990), *E. magnamaculata* (Peters and Orejas-Miranda 1970; Wallach 2016), *E. munoai* (Branch 1986; Orejas-Miranda 1962), *E. pauldwyeri* (Wallach 2016), *E. resetari* (Peters and Orejas-Miranda 1970; Wallach 2016), *E. wynnii* (Wallach 2016), *E. tenella* (Bailey and Carvalho 1946; Martins et al. 2019a) and *E. vellardi* (present study) exhibit a Type I hemipenis, while *E. ater* (Martins et al. 2019a; Savage 2002; Wallach 2016), *E. diaplocia* (Martins et al. 2019a; Thomas 1975), *E. martinezi* (Wallach 2016) and *E. striatula* (Martins et al. 2019a; Peters and Orejas-Miranda 1970) have a Type II hemipenis (Table 1).

Four out of eight species that have a Type I hemipenis are currently allocated in the *Epictia* gr. *phenops* and four in the *Epictia* gr. *albifrons*; while two out of four Type II species are in the *Epictia* gr. *phenops* and two in the *Epictia* gr. *albifrons* (Wallach 2016) (Table 1), indicating that both patterns are found in both phenotypic groups known for the genus *Epictia*. Although hemipenial characters are

important to elucidate systematic questions, many of the species for which there is hemipenial description available are not included in recent phylogenetic hypotheses (e.g., Adalsteinsson et al. 2009; Pyron and Wallach 2014; Martins et al. 2019a; McCranie and Hedges 2016; Murphy et al. 2016; Nagy et al. 2015). A larger sample of these taxa in molecular and combined analyzes, as well as evolutionary studies, are essential to elucidate the issues related to hemipenial evolution in this group.

During the literature review carried out in this study, we identified some challenges that hindered the correct allocation of some hemipenes in Type I or Type II patterns. Considering *E. magnamaculata*, the first descriptive work on its hemipenial morphology was held by Peters and Orejas-Miranda (1970). In this study, two specimens (AMNH 103852 and AMNH 103864) from Providence Island (Colombia) were analyzed, with their hemipenis having a broader and more rounded basal part, followed by an elongated naked body. In the next quarter of the body, calyces are present, which proximally are larger and gradually reduce their size distally. The distal half is gradually larger in diameter, with the apex wider than the hemipenis body. However, this same species was analyzed by Wallach (2016), who described the organ of one specimen (FMNH 282651) from Roatán Island (Honduras). In this study, the hemipenis has a gradual narrowing towards the apex and with a spermatic groove without ornamentation, except for the presence of some papillae at the distal tip. A second specimen described by Wallach (2016), based on a partially everted organ (LACM 127623), presents an error of location, since in the appendix of material examined and in the caption of the hemipenis image (Fig. 15 of the mentioned article) the location mentioned is Cozumel Island (Mexico), but in the description of the hemipenis is actually from Guanaja Island (Honduras). In addition, Wallach (2016) accidentally switches the description of the hemipenes with

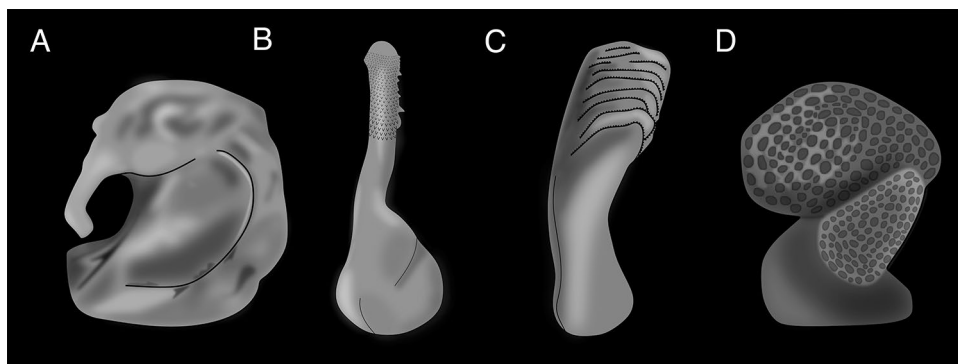


Fig. 2 Schematic drawing of everted hemipenes of *Epictia* spp., illustrating the morphological variation between the Type I and Type II patterns. **a** *E. vellardi*, Type I, based on original hemipenis description from the present study; **b** *E. resetari*, Type I, based on Fig. 3

from Peters and Orejas-Miranda (1970); **c** *E. ater*, Type II, based on Fig. 15G from Wallach (2016), with evident flounces at the apex; **d** *E. martinezi*, Type II, based on Fig. 15 M from Wallach (2016), with evident calyces at the apex

Table 1 Morphological patterns division of the representatives of the genus *Epictia* (Epictinae, Leptotyphlopidae) with described hemipenes

Species	Hemipenis type	Group	Data source	Original identification in the literature
<i>E. albipuncta</i>	?	<i>E. gr. albifrons</i>	Fabrezi et al. (1985)	
<i>E. ater</i>	II	<i>E. gr. phenops</i>	Martins et al. (2019a), Savage (2002), Wallach (2016)	
<i>E. australis</i>	I	<i>E. gr. albifrons</i>	Martins et al. (2019a), Scrocchi (1990)	<i>Leptotyphlops australis</i> , in Scrocchi (1990)
<i>E. bakewelli</i>	?	<i>E. gr. phenops</i>	Wallach (2016)	
<i>E. diaplocia</i>	II	<i>E. gr. albifrons</i>	Martins et al. (2019a), Thomas (1975)	<i>Leptotyphlops tenella</i> , in Thomas (1975)
<i>E. magnamaculata</i>	I	<i>E. gr. phenops</i>	Peters and Orejas-Miranda (1970), Wallach (2016)	<i>Leptotyphlops goudotii magnamaculatus</i> , in Peters and Orejas-Miranda (1970)
<i>E. martinezi</i>	II	<i>E. gr. phenops</i>	Wallach (2016)	
<i>E. munoai</i>	I	<i>E. gr. albifrons</i>	Branch (1986), Orejas-Miranda (1962)	<i>Leptotyphlops munoai</i> , in Orejas-Miranda and Branch (1962)
<i>E. pauldwyeri</i>	I	<i>E. gr. phenops</i>	Wallach (2016)	
<i>E. resetari</i>	I	<i>E. gr. phenops</i>	Peters and Orejas-Miranda (1970), Wallach (2016)	<i>Leptotyphlops goudotii phenops</i> , in Peters and Orejas-Miranda (1970)
<i>E. striatula</i>	II	<i>E. gr. albifrons</i>	Martins et al. (2019a), Peters and Orejas-Miranda (1970)	<i>Leptotyphlops melanotermus</i> , in Peters and Orejas-Miranda (1970)
<i>E. tenella</i>	I	<i>E. gr. albifrons</i>	Bailey and Carvalho (1946), Martins et al. (2019a)	<i>Leptotyphlops tenella</i> , in Bailey and Carvalho (1946)
<i>E. vellardi</i>	I	<i>E. gr. albifrons</i>	Present study	
<i>E. wyzni</i>	I	<i>E. gr. phenops</i>	Wallach (2016)	

Based on the literature and novel data provided herein. The symbol “?” is used when we were not able to associate it with any Type categories. We considered Wallach (2016) for species allocation in the following groups: *E. gr. albifrons*, *E. gr. goudotii* and *E. gr. phenops*

their respective images (Fig. 15, I and J), considering that the image I presents the partially everted hemipenis and the image J presents the hemipenis completely everted. It is noticeable that both descriptions (Peters and Orejas-Miranda 1970; Wallach 2016) are extremely divergent, and this may indicate that one of these specimens was mistakenly identified, or may even point to the presence of a cryptic species within what it is currently classified as *E. magnamaculata*. To reach a conclusion, it would be necessary to analyze the specimen examined by Peters and Orejas-Miranda (1970), and, since we do not have access to these specimens, we take into consideration the description made by Wallach (2016) to classify the morphological pattern of the hemipenis of *E. magnamaculata*.

It was not possible to identify the type of hemipenis of *E. bakewelli* considering that its description available in Wallach (2016) was made exclusively from a specimen with partially everted hemipenis. Thus, as we do not have the description of the body and the apex of the organ, the species could not be associated with either morphological patterns. Similarly, the hemipenis of *E. albipuncta* could be associated with neither Types I nor II, since the organs used for description in Fabrezi (1985) were probably partially everted hemipenes. What the authors consider “terminal disk”—a flat structure at the apex of the hemipenis with a depressed central part—presumably represents the apical

region partially everted of the organ. Consequently, until there are new descriptions of the organ, we cannot allocate the species in any of the types proposed herein.

Both propositions (Type I and Type II) reflect attempts to accommodate general hemipenial patterns within the genus *Epictia*. We must highlight that many *Epictia* spp. show modified patterns, as follows. Among the species classified as Type I, we could identify the following exceptions concerning the apex and ornamentation: *E. tenella* has its apex laterally expanded and dorsoventrally flattened (Bailey and Carvalho 1946); *E. munoai* does not have any macroscopic ornamentation, but has microscopic calyces and spinules in the medial portion of the hemipenis (Branch 1986; Orejas-Miranda 1962); *E. resetari* has spines and spinules in the distal half of the hemipenis terminal portion, which gradually decrease towards its most expanded apex (Peters and Orejas-Miranda 1970; Wallach 2016); *E. pauldwyeri* presents in its proximal portion a dozen scattered papillae (Wallach 2016); *E. wyzni* holds a series of rugae and papillae on the distal portion of its body, the proximal portion has seven circular folds with transverse rugae, and the distal portion is covered by six columns of papillae arranged in five transverse rows (Wallach 2016).

Considering the available biogeographic hypotheses (i.e., Adalsteinsson et al. 2009) and the available phylogenetic trees that include *Epictia* spp. (Adalsteinsson et al. 2009;

Martins et al. 2019a; McCranie and Hedges 2016; Murphy et al. 2016; Wallach 2016), Types I and II do not seem to be geographically or phylogenetically cohesive or exclusive. Thus, future broader phylogenetic and biogeographic analyses must consider the phenotypic variation seen in *Epictia* spp. In addition, the recognition of both patterns—and their variation—might be a first step into understanding the hemipenial evolution within this genus, as well as putative synapomorphies based on the organ. Recent molecular studies (Martins et al. 2019a) have recovered *Epictia* as the sister group of *Siagonodon* + *Habrophallos*. Even though the hemipenis of *Siagonodon* spp. have never been described, the suggested exclusive and diagnostic characters of the hemipenis of *Habrophallos* seem to be, in fact, synapomorphic. However, the absence of conspicuous macro-ornamentation (such as observed in Type I) seem to be a more typical pattern found in Epictini (sensu Martins et al. 2019a), as *Habrophallos*, *Mitophis*, *Trilepida* and *Rena* exhibit hemipenis with no evident macro-ornamentation as Type II *Epictia* spp. Therefore, such hemipenial types might be derived amongst Epictinae, and exclusive to a few taxa. However, this assumption still needs to be further elucidated with the description of additional organs/species.

Given the discussion above, one should also acknowledge that as such morphological types do not seem to be biogeographically or even phylogenetically cohesive, the wide diversity of hemipenial morphological characters may represent a mosaic of characters that evolved independently. The difference in shapes of the base, body and apex of hemipenis (e.g., widened base and narrow apex), the presence or absence of ornamentation (e.g., spines, papillae, calyces and flouces), the orientation of the hemipenis and of the sulcus, among others, should be analyzed independently.

This hypothesis should be tested in the future, considering available data for the taxa in relation to phylogenetic hypotheses available for the genus, also providing valuable data on the ancestral states of those putatively independent characters. Such efforts yet must reckon on additional hemipenial descriptions of *Epictia* spp. (and other Leptotyphlopidae) as well as the refinement of phylogenetic hypotheses for species of Leptotyphlopidae, and with the addition of more terminals for the genus. So far, we must conjecture that considering available data on the literature and the observation of previous phylogenetic hypotheses (e.g., Martins et al. 2019a), an ancestral for *Epictia* might have had a narrow and not ornamented base as exhibited in Type I.

In summary, the description of the *E. vellardi* hemipenis and the establishment of two hemipenial morphological patterns within the *Epictia* genus may aid in the taxonomy and identification of species pertaining to this genus. In fact, given the relatively conservative external morphology among the representatives of Scolecophidia, data on such organ are extremely relevant to clarify the systematics of

Leptotyphlopidae and their representatives, and should be regarded in future integrative phylogenetic studies, as well as comparative phylogenetic methods.

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Compliance with ethical standards

Conflict of interest The authors declare that there are no conflicts of interest or competing interests.

Ethics approval This study did not demand any ethics approval.

Consent to participate This study did not demand any consent to participate.

Consent for publication (include appropriate statements) All the authors agreed with the content and to submit this manuscript. We reinforced that we obtained consent from the responsible authorities at the institution where the work has been carried out.

Availability of data and material (data transparency) All specimens analyzed herein are housed at the Coleção de Répteis at the UFMT.

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