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ARTICLE

Hemipenial morphology and diversity in South American anoles (Squamata: Dactyloidae)

A.B. D'Angiolella, J. Klaczko, M.T. Rodrigues, and T.C.S. Avila-Pires

Abstract: Hemipenial morphology has provided useful characters to improve species identification and phylogenetic relationships in squamates. Here we provide hemipenial description and illustration of 13 South American anoles. At generic and specific levels, differences are mainly related to shape and ornamentation; intraspecific variation is low. An asulcate process, present in the hemipenis of most anole species studied, was highly variable among species and may be a useful taxonomic character in hemipenial morphology of this group.

Key words: Norops, *Dactyloa*, South America, hemipenis, male genitalia.

Résumé : La morphologie hémipéniale a fourni des caractères utiles pour améliorer l'identification des espèces et les relations phylogéniques chez les squamates. Nous présentons des descriptions et illustrations d'hémipénis de 13 anolis sud-américains. Aux niveaux du genre et de l'espèce, les différences sont principalement associées à la forme et à l'ornementation, et la variation intraspécifique est faible. Un processus sans sillon, présent dans l'hémipénis de la plupart des espèces d'anolis étudiées, varie considérablement d'une espèce à l'autre et pourrait constituer un caractère taxinomique utile de la morphologie hémipéniale de ce groupe. [Traduit par la Rédaction]

Mots-clés : Norops, *Dactyloa*, Amérique du Sud, hémipénis, organes génitaux mâles.

Introduction

Morphology of male genitalia provide helpful taxonomic characters in many groups of vertebrates and invertebrates (Keogh 1999; Lüpold et al. 2004; Yoshizawa and Johnson 2006; Köhler et al. 2007; Köhler 2010; Song and Bucheli 2010). Genitalia can be particularly useful in differentiating closely related species when overall body morphology is highly conserved (Keogh 1999). In squamates, male genitalia consist of a pair of blind-ended tubular structures known as hemipenes. Among different species, hemipenes may vary in size, shape, and aspects of ornamentation (Dowling and Savage 1960). In some groups hemipenial morphology is conservative (Klaver and Böhme 1986; Keogh 1999), whereas in others it displays significant intraspecific variation (Zaher and Prudente 1999; Köhler 2009; Nunes et al. 2012). The study of hemipenial morphology has provided important insights in the systematics of squamate reptiles, elucidating questions about species identification and phylogenetic relationships (Dowling and Savage 1960; Böhme 1991; Böhme and Ziegler 1997; Keogh 1999; G. Köhler et al. 2012; J. Köhler et al. 2012). In addition, because it is directly involved in the copulation process, modifications in its morphology may result in reproductive isolation (Arnold 1986; Köhler and Sunyer 2008; Köhler 2009; Nunes et al. 2012). Among lizards, hemipenial characters are most studied for members of the families Agamidae, Chamaleonidae, Dactyloidae, Gymnophtalmidae, Lacertidae, and Varanidae (Arnold 1973, 1986; Köhler and Veselý 2007; Rodrigues et al. 2008; Böhme and Ziegler 2009; Myers et al. 2009; Maduwage and Silva 2012; Nunes et al. 2012, 2014). In the last decade, anole hemipenes have gained more attention because of the work of G. Köhler and colleagues with mainland Central American species. These authors found several cases of geographically separated populations of putative closely related species with very distinct hemipenial morphology—usually a large and bilobate organ in one population contrasting with a smaller and unilobate one in the other population (Köhler et al. 2010, 2012; J. Köhler et al. 2012). Some of these studies revealed the importance of hemipenis in identifying cryptic diversity and helping to elucidate the taxonomy at the species level (e.g., Köhler and Sunyer 2008; Köhler and Veselý 2010). Klaczko et al. (2015) showed that anole hemipenial morphology evolved six times faster than other non-genital morphological traits and therefore can be directly related to reproductive isolation and the speciation process. On the other hand, in spite of such high variability between closely related species, Böhme and Ziegler (2009) showed that, at least for some groups of lizards, genital morphological characters are more informative than external characters for recovering phylogenetic relationships, once it is subject only to sexual selection.

Since there is much convergence in external features of anoline lizards, the description of hemipenial morphology is especially useful in efforts to provide additional phylogenetic characters for investigating their relationships. With that in mind, we present a detailed description of hemipenial morphology of 3 species of *Dactyloa* Wagler, 1830 and 10 species of *Norops* Wagler, 1830 occurring in South America.

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Table 1. Museum numbers and collection localities of South American anoles of the genera *Dactyloa* and *Norops* whose hemipenes were prepared for the present study.

Identification No.	Genus	Species	Locality	Country
MPEG28904	*Dactyloa*	*punctata*	Floresta Nacional de Caxiuanã, PA	Brazil
MPEG16011	*Dactyloa*	*punctata*	29 km North of Rio Branco, AC	Brazil
MPEG28866	*Dactyloa*	*punctata*	Floresta Nacional de Caxiuanã, PA	Brazil
MPEG21575	*Dactyloa*	*transversalis*	Floresta Nacional Serra da Cotia, RO	Brazil
MPEG21576	*Dactyloa*	*transversalis*	Floresta Nacional Serra da Cotia, RO	Brazil
MPEG4106	*Norops*	*auratus*	Boa Vista, RR	Brazil
MPEG4068	*Norops*	*auratus*	Boa Vista, RR	Brazil
MPEG18236	*Norops*	*brasiliensis*	Minaçu, GO	Brazil
MPEG12383	*Norops*	*brasiliensis*	Arari, Maranhão	Brazil
MPEG24491	*Norops*	*brasiliensis*	Tanguro, MT	Brazil
MPEG29707	*Norops*	*chrysolepis*	Laranjal do Jari, AP	Brazil
MPEG27374	*Norops*	*chrysolepis*	Serra do Acari, PA	Brazil
MPEG22197	*Norops*	*chrysolepis*	Porto Trombetas, Oriximiná, PA	Brazil
MPEG27367	*Norops*	*chrysolepis*	Urucará, PA	Brazil
MSH12316	*Norops*	*fuscoauratus*	Santa Isabel do Rio Negro, AM	Brazil
MPEGVXG14	*Norops*	*fuscoauratus*	Vitoria do Xingu, PA	Brazil
MPEGBP02	*Norops*	*fuscoauratus*	Bacia Rio Capim, Paragominas, PA	Brazil
MPEG29607	*Norops*	*fuscoauratus*	Afuá, Ilha do Marajó, PA	Brazil
MPEG20590	*Norops*	*fuscoauratus*	P. Walter, Juruá, AC	Brazil
MPEG28863	*Norops*	*fuscoauratus*	Floresta Nacional Caxiuanã, PA	Brazil
AMNHR-115871	*Norops*	*fuscoauratus*	Napo	Ecuador
AMNHR-133697	*Norops*	*fuscoauratus*	Amazonas	Venezuela
MZUSP27091	*Norops*	*fuscoauratus*	Napo, Limoncocha	Ecuador
MZUSP65666	*Norops*	*fuscoauratus*	Estação Ecológica de Saltinho, PE	Brazil
MZUSP81620	*Norops*	*fuscoauratus*	Apiacás, MT	Brazil
MZUSP16182	*Norops*	*fuscoauratus*	Canavieiras, BA	Brazil
AMNH151836	*Norops*	*fuscoauratus*	Guyana	Guyana
MBS024	*Norops*	*meridionalis*	Mina Guaporé, MT	Brazil
MBS010	*Norops*	*meridionalis*	Mina Guaporé, MT	Brazil
MPEG21781	*Norops*	*ortonii*	Floresta Nacional de Caxiuanã, PA	Brazil
MPEG26941	*Norops*	*ortonii*	Porto Urucu, AM	Brazil
MPEG31113	*Norops*	*ortonii*	Taracauá, AC	Brazil
MPEG22225	*Norops*	*planiceps*	São João Lucas, RR	Brazil
MPEG15814	*Norops*	*planiceps*	Inpa, Manaus, AM	Brazil
MPEG3922	*Norops*	*planiceps*	Coronel Mota, RR	Brazil
MSH12327	*Norops*	*planiceps*	Santa Isabel do Rio Negro, AM	Brazil
MPEG16765	*Norops*	*planiceps*	Reserva Duke, Manaus, AM	Brazil
MPEG15277	*Norops*	*scypheus*	Maraã, AM	Brazil
MCZ110284	*Norops*	*scypheus*	Sarayacu: Pastaza	Ecuador
MPEG27674	*Norops*	*tandai*	Maués, AM	Brazil
MPEG26931	*Norops*	*tandai*	Porto Urucu, AM	Brazil
MPEG27082	*Norops*	*tandai*	Mutum, Juruti, PA	Brazil
MPEG27673	*Norops*	*tandai*	Maués, AM	Brazil
MPEG29414	*Norops*	*tandai*	Itaituba, PA	Brazil
MPEG18924	*Norops*	*tandai*	Careiro da Varzea, AM	Brazil
MPEG30038	*Norops*	*trachyderma*	Itaituba, PA	Brazil
MPEG31114	*Norops*	*trachyderma*	Taracauá, AC	Brazil
MPEG30332	*Norops*	*trachyderma*	Rio Juruá, AC–AM	Brazil
MPEG20737	*Norops*	*trachyderma*	Porto Walter, Rio Juruá, AC	Brazil
MPEG17586	*Norops*	*trachyderma*	Santarém, PA	Brazil

Materials and methods

We examined the hemipenes of 13 anole species occurring in South America: *Dactyloa punctata* (Daudin, 1802), *Dactyloa phyllorhina* (Myers and Carvalho, 1945), *Dactyloa transversalis* (Duméril, 1851), *Norops auratus* (Daudin, 1802), *Norops brasiliensis* (Vanzolini and Williams, 1970), *Norops chrysolepis* (Duméril and Bibron, 1837), *Norops fuscoauratus* (D'Orbigny in Duméril and Bibron, 1837), *Norops meridionalis* (Boettger, 1885), *Norops ortonii* (Cope, 1868), *Norops planiceps* (Troschel, 1848), *Norops scypheus* (Cope, 1864), *Norops tandai* (Avila-Pires, 1995), and *Norops trachyderma* (Cope, 1875). We prepared from 2 to 14 hemipenes per species (Table 1), except for *D. phyllorhina*, of which description and comparisons were based on photos of a hemipenis of a specimen from Aripuanã, MT, Brazil, prepared by the late Gabriel Skuk. For hemipenis preparation, we followed a combination of techniques described in Pesantes (1994), Keogh (1999), Myers and Cadle (2003), and Zaher and Prudente (2003). To minimize possible variation caused by the eversion process, only partially or totally everted hemipenes were prepared, irrespective of being the right or left hemipenis. Once the preserved specimen was selected, one of the hemipenes was removed through a small incision at the base of the tail. In general, anole hemipenes have a very thin skin, and to avoid possible damages, 2% KOH was used only when the specimen was too old or when the lobes could not be totally everted with hot water. To allow a better visualization of ornamentation structures, the fully everted hemipenis was filled with colored Vaseline with the aid of a syringe with a sanded tip needle, to avoid damages to the hemipenis skin, and was subsequently conserved in 70% ethanol.

We obtained digital images of hemipenes in sulcate, asulcate, and lateral views. For the smallest hemipenes, we used a JVC camera KYF75U attached to a stereomicroscope, with the aid of Auto-Montage Pro version 5.02; all other hemipenes were photographed using a Nikon D90, with a macro lens of 105 mm.

Basic hemipenial terminology follows Klaver and Böhme (1986). We refer to a "nude disk" when the lobes terminate in a flat and naked disk delimited by raised sulcal lips (Keogh 1999), whereas if a "naked area" is mentioned, no raised sulcal lips are present. We adopt the term "flounces" in reference to widely spaced, irregular, and nonoverlapping folds (Savage, 1997). Descriptions of hemipenes of some anole species mention the presence of an asulcate process (e.g., Köhler et al. 2007; Köhler and Smith 2008; Köhler and Sunyer 2008; Sunyer et al. 2008). In the present study, we differentiate two structures that may be present on the asulcate surface: (1) a fleshy projection that expands outward from the lobular crotch or bends toward the truncus and (2) a skin ridge (sensu Keogh 1999) formed by a series of raised fleshy tissue.

Results

All hemipenes of South American anoles are bilobed, with globular or tubular calyculated lobes showing a naked area or naked disk, and present a deep and bifurcated sulcus spermaticus. No mineralized structures are present (Fig. 1). Whereas several differences are observed at the generic and specific levels, intraspecific variation is relatively low.

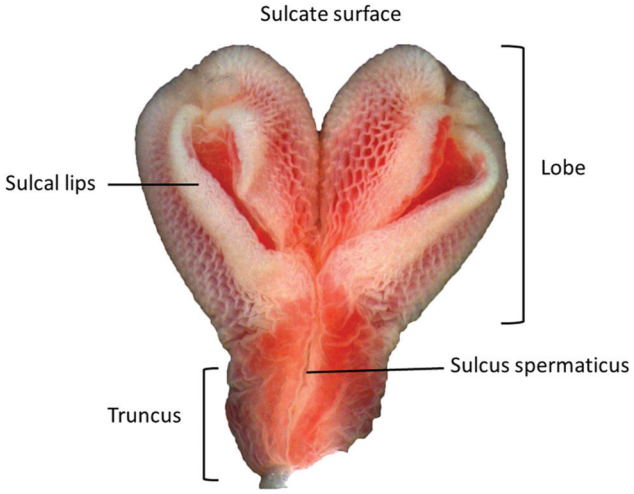
In *Dactyloa*, hemipenes of the three species examined show globular lobes, with a wide and elongate naked area in the sulcate surface. In contrast, lobes of most *Norops* tend to be proportionally smaller and the naked area form a round disk (except in *N. ortonii*, where an elongate naked area is present). Hemipenes of *D. transversalis* and *D. phyllorhina* are more similar to each other than to that of *D. punctata*. Both show a longer truncus, a skin ridge on the asulcate surface, and no triangular flap covered by folds between lobes, whereas in *D. punctata*, the hemipenial truncus is short, the lobes occupy almost the entire hemipenial extension, and a triangular flap is present between lobes on the asulcate surface.

Among the species of the *N. chrysolepis* group (sensu D'Angiolella et al. 2011), the hemipenes of *N. meridionalis*, *N. tandai*, and *N. chrysolepis* are very similar, presenting thick sulcal lips, a wide and subdivided fleshy projection between the globular lobes, and a thin skin pleat demarcating the asulcate and sulcate surfaces on truncus. *Norpos planiceps* and *N. brasiliensis* have both tubular-shaped lobes; naked disk in terminal position on lobes, delimited by a raised edge of skin; and a medial skin ridge on the asulcate surface of truncus. The hemipenis of *N. scypheus* is similar to those of *N. meridonalis*, *N. tandai*, and *N. chrysolepis* in having globular lobes and naked disks on lobes that extends from their base to almost the apex. However, it is also similar to those of *N. brasiliensis* and *N. planiceps* in lacking a fleshy projection between lobes, presenting instead a small skin lump medially on asulcate surface of truncus.

The hemipenis of *N. trachyderma* is similar to those of *N. brasiliensis* and *N. planiceps* in having tubular lobes, a terminal naked disk, and a medial skin ridge on the asulcate surface, extending from the midway on the truncus to the crotch. This later characteristic is also present in *N. fuscoauratus*. Hemipenes of *N. ortonii* and *N. auratus* are similar to each other in presenting globular lobes, a finger-shaped process projecting from the crotch on the asulcate surface, and truncus covered by well-delimited transverse folds. Besides, *N. ortonii* presents the naked area on lobes elongate, not forming a definite disk as in the other *Norops* examined, reminding to a certain extend those of *Dactyloa*.

Below we present the hemipenial description of all species studied (Figs. 2A–2N).

Fig. 1. Sulcate view of the hemipenis of *Norops trachyderma*, with indication of the main features used in hemipenial descriptions. Figure appears in color on the Web.



Dactyloa species

Dactyloa punctata (Fig. 2A)

Hemipenis bilobed, with globular lobes representing more than half of the hemipenis length. Sulcus spermaticus deep and bifurcated, with well-developed sulcal lips. It opens into a wide and elongate naked area extending laterally from the base of the lobes to the apex. Lobes densely calyculate outside this naked area. A triangular flap, covered by enlarged and irregular folds, present in the asulcate surface, initiating midway on the lobes and pointing toward the base of the hemipenis. Truncus short, wrinkled on both sulcate and asulcate surfaces, with a short and smooth base.

Dactyloa phyllorhina (Fig. 2B)

Hemipenis bilobed, with globular lobes representing about half of the hemipenis length. Sulcus spermaticus deep and bifurcated, with well-developed sulcal lips. It opens into a wide and elongate naked area extending laterally from the base of the lobes to the apex. Lobes densely calyculate outside this naked area. A skin ridge present in the asulcate surface, initiating midway on the lobes, where it is surrounded by enlarged calyces, and reaching the median region of truncus, where it is covered by enlarged and irregular transverse folds. Truncus wrinkled on both sulcate and asulcate surfaces.

Dactyloa transversalis (Fig. 2C)

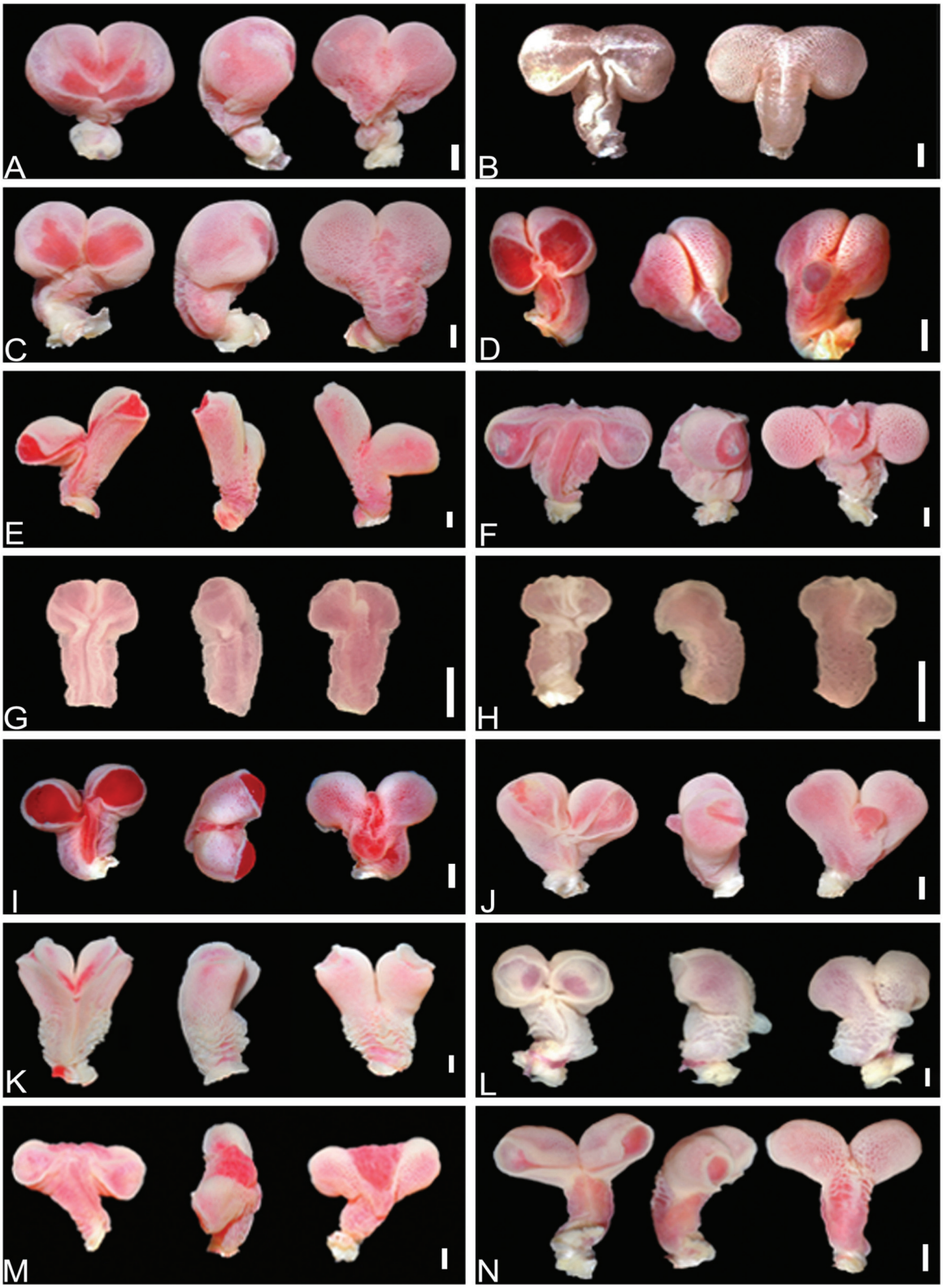
Hemipenis bilobed, with globular lobes representing at least half of the hemipenis length. Sulcus spermaticus deep and bifurcated, with well-developed sulcal lips. It opens into a wide and elongate naked area extending laterally from the base of the lobes to the apex. Lobes densely calyculate outside this naked area. Enlarged and irregular calyces cover the asulcate surface between lobes. Truncus with a shallow medial skin ridge surrounded by transverse folds.

Norops species

Norops auratus (Fig. 2D)

Hemipenis bilobed, with globular lobes representing about half of the hemipenis length. Sulcus spermaticus deep and bifurcated, with poorly developed sulcal lips. It opens into a round naked disk extending laterally from the base of the lobes to the apex. Lobes densely calyculate outside the naked disk. A fleshy finger-shaped process projects from the crotch on the asulcate surface, surrounded by enlarged calyces. Asulcate and lateral surfaces of

Fig. 2. Hemipenes of *Dactyloa* and *Norops* species studied in sulcate, lateral, and asulcate views: (A) *Dactyloa punctata*; (B) *Dactyloa phyllorhina*; (C) *Dactyloa transversalis*; (D) *Norops auratus*; (E) *Norops brasiliensis*; (F) *Norops chrysolepis*; (G) *Norops fuscoauratus*; (H) *N. fuscoauratus* with pigmentation; (I) *Norops meridionalis*; (J) *Norops ortonii*; (K) *Norops planiceps*; (L) *Norops scypheus*; (M) *Norops tandai*; (N) *Norops trachyderma*. Figure appears in color on the Web.



truncus covered with well-delimited transverse folds; oblique or longitudinal wrinkles on the sulcate surface.

***Norops brasiliensis* (Fig. 2E)**

Hemipenis bilobed, with tubular lobes representing about half of the hemipenis length. Sulcus spermaticus deep and bifurcated, with well-developed sulcal lips. It opens into a flat and naked disk on terminal region of each lobe. Lobes densely calyculate outside naked disk. A shallow medial skin ridge is present on the asulcate surface, from midway on the truncus to the crotch. Truncus covered with calyces distally and with flounces basally on both sulcate and asulcate surfaces.

***Norops chrysolepis* (Fig. 2F)**

Hemipenis bilobed, with globular lobes representing about half of the hemipenis length. Sulcus spermaticus deep and bifurcated, with well-developed sulcal lips becoming thicker at the lobes. It opens into a round naked disk that extends laterally from the base of the lobes to almost the apex. Lobes densely calyculate outside the naked disk; separated by a large, naked, triangular expansion that pushes them to the sides, giving the hemipenis a "T" shape. An extension of this expansion, with wrinkled surface, projects shortly towards the truncus and is followed by a medial and shallow skin ridge that extends towards the base of the hemipenis. A thin skin pleat extends from the basal region of the hemipenis to the base of the lobes laterally, demarcating the asulcate and sulcate surfaces. Truncus covered with flounces on both asulcate and sulcate surfaces.

***Norops fuscoauratus* (Figs. 2G and 2H)**

Hemipenis bilobed, with globular lobes representing less than half of the hemipenis length. Sulcus spermaticus deep and bifurcated, with poorly developed sulcal lips. It opens into a round naked disk that extends laterally from the base of the lobes to the apex. Lobes densely calyculate outside the naked disk. A medial skin ridge from the distal part of truncus to the crotch on asulcate surface. Truncus covered with flounces on both asulcate and sulcate surfaces. Some of the hemipenes show small pigmented spots on truncus; however, the amount of pigmentation varies among specimens and localities, and in a same locality, there are specimens with pigmented hemipenes and specimens with nonpigmented hemipenes (e.g., Guyana: Potaro-Siparuni; Brazil: Pacoti-CE and Porto Velho-RO).

***Norops meridionalis* (Fig. 2I)**

Hemipenis bilobed, with globular lobes representing about half of the hemipenis length. Sulcus spermaticus deep and bifurcated, with well-developed sulcal lips that become thicker at the lobes. It opens into a round naked disk that extends laterally from the base of the lobes to almost the apex. Lobes densely calyculate outside the naked disk. A fleshy projection between lobes on asulcate surface that becomes a triangular pleat toward the truncus. A thin skin pleat extends from the hemipenial base to the base of the lobes laterally, demarcating the asulcate and sulcate surfaces. Truncus shows a naked region below the triangular pleat projection on asulcate surface and longitudinal wrinkles on sulcate surface.

***Norops ortonii* (Fig. 2J)**

Hemipenis bilobed, with globular lobes representing more than half of the hemipenis length. Sulcus spermaticus deep and bifurcated with well-developed sulcal lips, which become shallow midway on the lobes. It opens into an elongate naked area, extending laterally from the base of the lobes to the apex. Lobes densely calyculate outside the naked area. A finger-shaped process projects from the crotch on the asulcate surface, surrounded by enlarged calyces. Asulcate and lateral surfaces of truncus covered with transverse folds.

***Norops planiceps* (Fig. 2K)**

Hemipenis bilobed, with tubular lobes representing about half of the hemipenis length. Sulcus spermaticus deep and bifurcated, with well-developed sulcal lips. It opens into a flat and naked disk on terminal region of each lobe. Lobes strongly calyculate outside naked disk. A fleshy skin ridge on asulcate surface, from midway on the truncus to the crotch. Truncus covered with calyces distally and with flounces basally on both sulcate and asulcate surfaces.

***Norops scypheus* (Fig. 2L)**

Hemipenis bilobed, with globular lobes representing about half of the hemipenis length. Sulcus spermaticus deep and bifurcated, with well-developed sulcal lips. It opens into a round naked disk that extends laterally from the base of the lobes to almost the apex. Lobes densely calyculate outside the naked disk. A delicate soft skin lump present medially on truncus asulcate surface. Truncus covered with flounces.

***Norops tandai* (Fig. 2M)**

Hemipenis bilobed, with globular lobes representing about half of the hemipenis length. Sulcus spermaticus deep and bifurcated, with well-developed sulcal lips that become thicker at the lobes. It opens into a round naked disk that extends laterally from the base of the lobes to almost the apex. Lobes densely calyculate outside the naked disk; separated by a large, naked, triangular expansion that pushes them to the sides, giving the hemipenes a "T" shape. An extension of this expansion, with wrinkled surface, projects shortly towards the truncus and is followed by a medial and shallow skin ridge that extends towards the hemipenial base. A thin skin pleat extends from the basal region of the hemipenes to the base of the lobes laterally, demarcating the asulcate and sulcate surfaces. Truncus covered with flounces.

***Norops trachyderma* (Fig. 2N)**

Hemipenis bilobed, with tubular lobes representing about half of the hemipenis length. Sulcus spermaticus deep and bifurcated, with poorly developed sulcal lips. It opens into a naked disk on the terminal region of each lobe. Lobes densely calyculate outside the naked disk. A fleshy medial skin ridge on asulcate surface, from about midway on the truncus to the crotch. Truncus distally ornamented with flounces on asulcate surface, surrounding the skin ridge, and shallow wrinkles on sulcate surface; base naked.

Discussion

The use of hemipenial characters in systematic studies of anoles has increased substantially in the past years (G. Köhler et al. 2012 and J. Köhler et al. 2012 and references therein). This sudden interest is due mostly to the discovery of a large number of potential informative characters, helping to diagnose morphologically similar species (Köhler et al. 2007; Köhler and Veselý 2010). In a variety of studies, divergent hemipenial morphology was the starting point for systematic revisions and (or) species description (Köhler 2009, 2010, 2011). In the present work, we show that intergeneric and interspecific hemipenial variations in South American anoles are high, with considerable differences in hemipenial shape and ornamentation.

South American anoles do not form a monophyletic group and the same applies to the South American radiation of *Norops*, which has their closest relatives in Central America and in the West Indies (Nicholson et al. 2012). An exception is the *N. chrysolepis* species group, which evolved in South America. D'Angiolella et al. (2011) revisited the taxonomy of the group, using both morphology and molecular characters. The hemipenial morphology variation is concordant with their recovered molecular phylogeny for this group, with closely related species presenting similar hemipenes. In addition, *N. meridionalis* shares with *N. tandai* and *N. chrysolepis* the presence of a thin skin pleat demarcating the asulcate and sulcate surfaces on truncus. Vanzolini and Williams (1970), based

on morphology and habitat use (grassland and forest, respectively), considered *N. meridionalis* as only superficially similar to the *chrysolepis* group. Molecular studies, however, recovered *N. meridionalis* within this group, sister to *N. tandai* and *N. chrysolepis* (Nicholson et al. 2006; D'Angiolella et al. 2011). Even though this relationship received weak support in both studies, our results corroborate it. Böhme and Ziegler (2009) found high levels of coincidence between molecular–genetic phylogenies and phylogenetic hypotheses proposed based on hemipenial morphology, and attributed this to the fact that genital morphology seems to be only subject to sexual selection, not being affected by environmental selective pressures. In the case of *N. meridionalis*, its divergent morphology might be related to its ecological adaptation as a grassland dweller, whereas hemipenial characters were not affected by such environmental selection, retaining the phylogenetic signal.

With the present study, we were able to observe that the most conspicuous feature of the anole hemipenes studied is the presence of asulcate processes, either as fleshy projections or as a skin ridge. This structure varied among the species in relation to form, extension, development, and ornamentation, suggesting it may be an important character for systematic and taxonomic future analyses.

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