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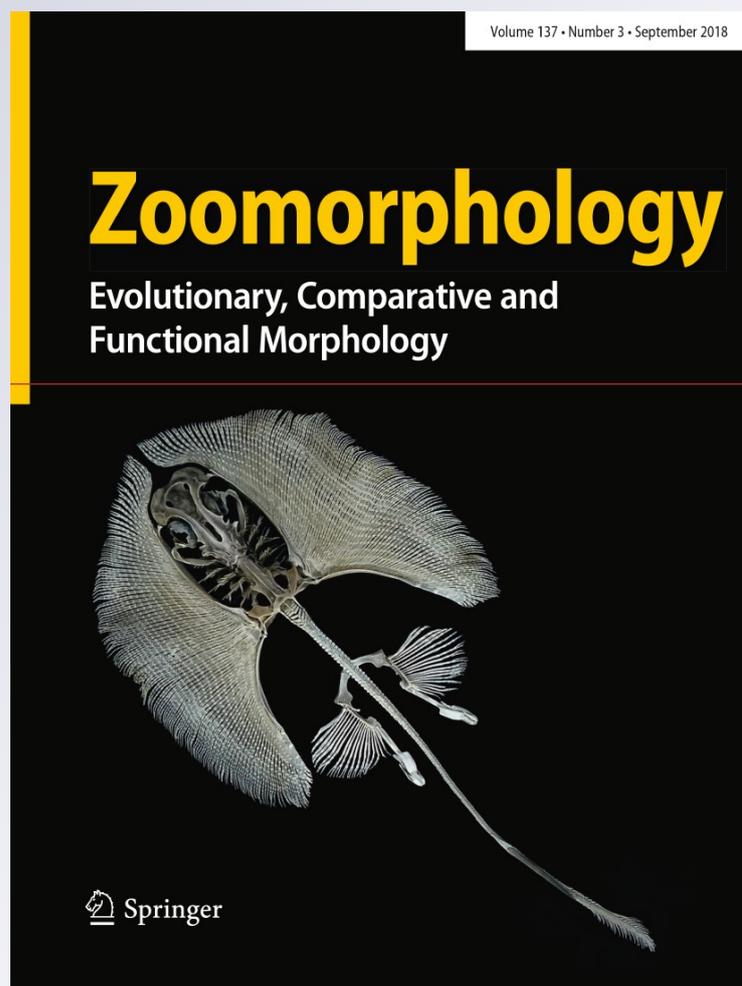
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Unveiling diversity under the skin: comparative morphology study of the cephalic glands in threadsnakes (Serpentes: Leptotyphlopidae: Epictinae)

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Abstract

The subfamily Epictinae contains about 75 currently recognized species of strictly fossorial snakes distributed along the Neotropics (subtribe Renina) and Equatorial Africa (subtribe Rhinoleptini). Although several studies have addressed some internal phenotypic characters complexes for the taxa included in this subfamily, most of the available data are limited to skull morphology and visceral topology. Additionally, many studies, when reporting glandular information, do not provide comparative data obtained through of a replicable methodology. In this study, we aimed to describe in detail the macrostructure of the cephalic glands for the members of the subfamily Epictinae. We provide herein the first report of a rictal gland for the infraorder Scolecophidia, as well as the first report of an infralabial accessory gland for the family Leptotyphlopidae. We highlight the utility of glandular qualitative characters for the systematics and even alpha taxonomy of this group of snakes that frequently exhibits a conserved external morphology. Furthermore, we also discuss possible functional aspects related to the Harderian gland in association to the *M. adductor externus superficialis* based on macrostructure observations of Epictinae specimens.

Keywords Fossorial snakes · Head glands macrostructure · Muscles · Functional anatomy · Phylogenetic inertia

Introduction

The family Leptotyphlopidae comprises about 140 species distributed almost exclusively in Africa (Leptotyphlopinae) and in the New World (Americas and Antilles; Epictinae except for subtribe Rhinoleptini also endemic from Africa) (Adalsteinsson et al. 2009; Uetz et al. 2018). The subfamily Epictinae contains about 75 species allocated in eight currently recognized genera. Despite the ancient cladogenesis and the complete isolation between these two main lineages of Leptotyphlopidae (Adalsteinsson et al. 2009), all living species present an entirely fossorial or semi-fossorial

lifestyle, actively eating on larvae or adults of social insects (Greene 1997; Cundall and Greene 2000; Webb et al. 2000). In leptotyphlopids, the preys are fully ingested through a very specialized mechanism named mandibular raking (Kley and Brainerd 1999), contrasting with a more widespread feeding mechanism of the Alethinophidian snakes by the pterygoidal walk (see Cundall and Greene 2000 for more details on snakes feeding). This feeding mechanism could provide food intake relatively fast—compared to widespread mechanism of the Alethinophidian snakes—which might be selected by the huge retaliatory response of social insects within their nests. The massive differences in the feeding mechanism, foraging pattern and diet play a fundamental role in many aspects of the leptotyphlopids natural history and, consequently, in their entire phenotype (Cundall and Greene 2000; Webb et al. 2000).

The first contributions on the Leptotyphlopidae anatomy have emerged in the nineteenth century with the works of Schlegel (1837) and Peters (1858, 1863). Later, in the course of almost 200 years, a dozen additional studies have been published on the topic, most of them focusing on the high-level classification of “Reptilia”, Squamata or

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Snakes (Lapage 1928; Bellairs and Boyd 1946; Haas 1962, 1973; McDowell 1986; Smith and Bellairs 1947; Rieppel and Zaher 2000), with reduced representativeness of taxa or morphological systems employed regarding the leptotyphlopids. In contrast, the studies with improved species representativeness (List 1966) or providing more detailed descriptions for a given character system (Brock 1932; Haas 1930a, b; Kley 2006; Pinto et al. 2015) regarding the leptotyphlopids are based usually on osteological and cartilaginous elements. Despite the apparently expressive amount of available studies, the knowledge on the cephalic glands of leptotyphlopids is restricted to the contributions of Taub (1966) and Gabe and Saint Girons (1967), which based their samples on the abundant species in scientific collections in broad comparative studies. As a result, the macro- and microstructure of the cephalic glands from several key species in the less sampled genera of leptotyphlopids still remain elusive. On the other hand, given the high species richness and the general conservative nature of the features from the external morphology (meristics, morphometrics and color patterns), it is primordial to study other character systems in addition to the available traditional external morphology in order to refine the taxonomic and systematic hypotheses for the group (Broadley and Wallach 1997a, b, 2007; Wallach and Hahn 1997).

Considering the relative scarcity of descriptive and comparative studies on the leptotyphlopids head glands, we aimed to describe in detail the cephalic gland morphology of members of the subfamily Epictinae.

Methods

We have examined 22 specimens from 18 species housed in 15 collections. We made a lateral subcutaneous incision longitudinally on the gular region until the left rictal region from each specimen with the aid of a scalper. The skin was posteriorly removed, and after total removal, the head was immersed in a 2% molecular iodine solution. The cephalic glands terminology follows Taub (1966) and Kochva (1978); for adductor muscles follows Haas (1973), Kardong (1980) and Cundall (1986) with modifications of Martins (2016); for skull elements follows Rieppel et al. (2009), and mandible elements follows Kley (2006). The photographs were taken with DFC 450 camera attached to a Leica stereomicroscope M205C and a Zeiss Axiocam using Axiovision Z-stack software attached to a Zeiss Discovery V12 stereomicroscope. Schematic drawings based on digital photos were prepared with Inkscape 0.92. We identified the specimens based on the original descriptions and recent taxonomic studies addressing Epictinae species, such as: Passos et al. (2006), Pinto (2010), Pinto et al. (2010), Pinto and Fernandes (2012), Pinto and Curcio (2011), Francisco et al.

(2012), McCranie and Hedges (2016) and Wallach (2016). In many instances, we examined the type material, topotypes and relevant comparative material in order to refine species' identifications. The supraspecific taxonomy adopted herein follows Wallach et al. (2014) and Uetz et al. (2018), except for *Rena unguistrostris* (sensu Adalsteinsson et al. 2009), which herein is considered as from the genus *Rena* and not *Siagonodon*, as proposed by Wallach et al. (2014), based on an unpublished manuscript.

Results

We report the presence of six cephalic glands in Epictinae: nasal glands, supralabial, infralabial, Harderian, rictal and infralabial accessory glands (Figs. 1, 2, 3). The rictal gland is present exclusively in *Epictia tenella* (Fig. 1b) and *Tetracheilostoma bilineatum*. A double infralabial accessory gland is present exclusively in *Mitophis leptepileptus* (Fig. 3) and a single infralabial accessory gland is reported for a few *Trilepida* species (Fig. 1d). A premaxillar gland is indistinct or absent in all species analyzed.

The nasal glands (Figs. 1, 3) are always paired, representing the second smallest gland in the head (larger than the infralabial accessory gland). Their shape is variable, being limited posteriorly by the eye or the anterior lamina of the premaxilla; anteriorly by the nostril and medially by the *nasal septum*, covering most of the ascending dorsal process of the septomaxilla and the anterior portion of the prefrontal descending lamina. We report the presence of variation concerning the (1) general shape of the gland and (2) its extension in relation to the nostril, being (a) exclusively posterior to the nostril, (b) posterior, dorsal and ventral to the nostril or (c) extend around the nostril; (3) in relation to its posterior limit, which may be (a) restricted to the anterior descending lamina of the prefrontal or (b) exceed the posterior limit to be posteriorly limited by the eye; (4) presence of a supralabial-nasal gland contact posteriorly. The interspecific variability is summarized in Table 1.

The supralabial glands (Figs. 1, 3) are paired and variable in shape, located ventrally to the eye, resting over the lateral lamina of the maxilla, and also in a small region of the anterior-ventral lamina of the premaxilla. The glands are delimited anterodorsally by the nasal glands, dorsally by the eye, anteroventrally by the anterior-lateral edge of the premaxilla, and posteriorly by the quadratomaxillary ligament. We detected variability concerning their (1) general shape, (2) anterior limit in relation to the nostril and (3) presence of an anterior extension to contact the opposite gland in the anterior lamina of the premaxilla. The interspecific variability is summarized in Table 2.

The infralabial glands (Figs. 1, 2, 3) are the most robust glands in the head, extending over the ventral and lateral

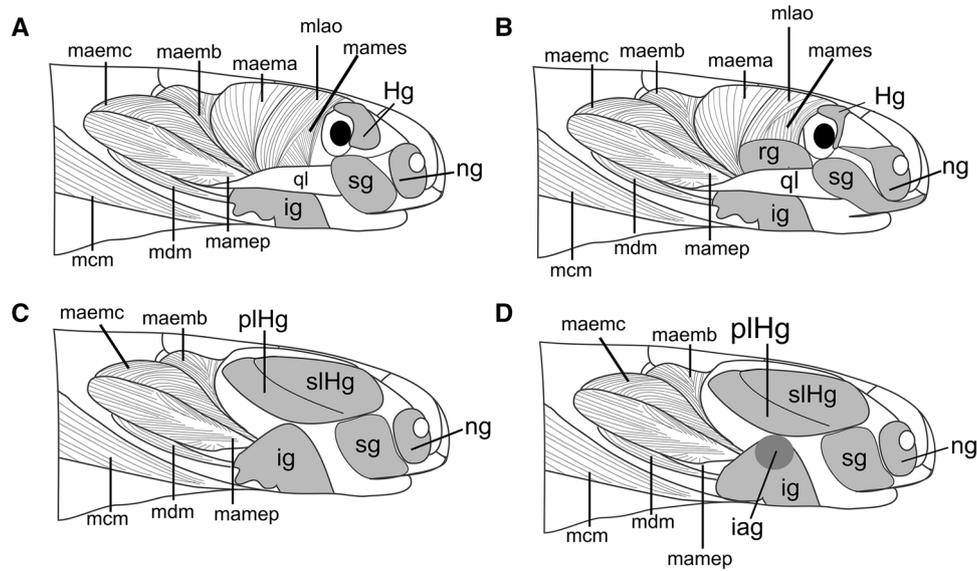
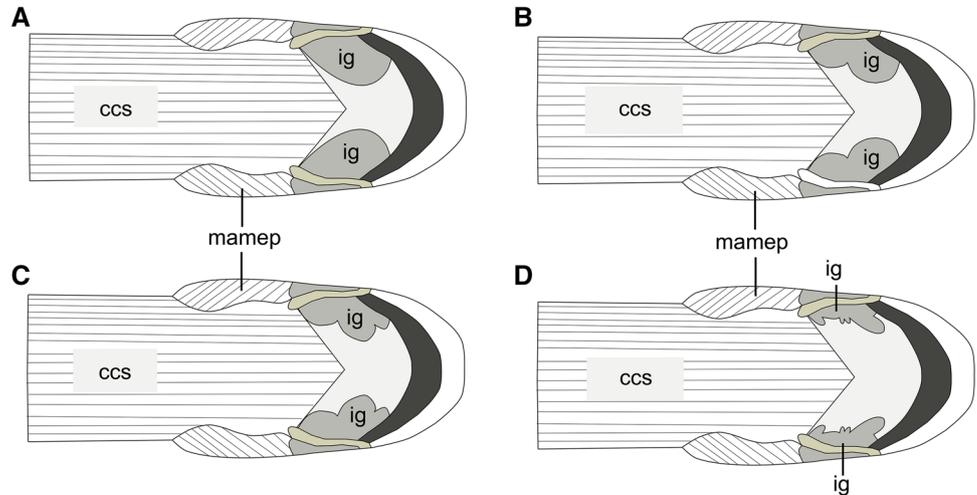


Fig. 1 Schematic illustrations of the cephalic glands in Epictinae (lateral view). **A:** Cephalic gland morphology and location in *Epictia* spp. (in exception of *Epictia tenella*), *Trilepida* spp., *Rena* spp., *Siagonodon cupinensis*, and *Tetracheilostoma bilineatum*, with no muscle removal. **B:** illustration of *Epictia tenella* with no muscle removal showing the rictal gland and the anterior extension of the supralabial gland. **C:** general gland pattern in *Epictia* spp. (in exception of *Epictia tenella*), *Trilepida* spp., *Rena* spp., *Siagonodon cupinensis*, and *Tetracheilostoma bilineatum* with removal of the eye, *M. adductor externus* medialis pars a, *M. externus superficialis*, *M. levator anguli oris*, and quadratomaxillary ligament, totally exposing the Harderian and infralabial gland in lateral view. **D:** general gland pattern in *Trilepida joshuai*, *Trilepida koppesi*, *Trilepida macrolepis*,

Trilepida brasiliensis, and *Trilepida salgueiroi* with removal of the eye, *M. adductor externus medialis* portion a, *M. externus superficialis*, *M. levator anguli oris*, and quadratomaxillary ligament, totally exposing the Harderian, infralabial, and infralabial accessory glands. Abbreviations: ig: infralabial gland; iag: infralabial accessory gland; maema: *M. adductor externus medialis* pars a; maemb: *M. adductor externus medialis* pars b; maemc: *M. adductor externus medialis* pars c; mamep: *M. adductor externus profundus*; mames: *M. adductor externus superficialis*; mcm: *M. cervicomandibularis*; mdm: *M. depressor mandibulae*; mlao: *M. levator anguli oris*; Hg: Harderian gland; ng: nasal gland; pIHg: postorbital lobe of the Harderian gland; ql: quadratomaxillary ligament; rg: rictal gland; sg: supralabial gland; sIHd: supraocular lobe of the Harderian gland

Fig. 2 Schematic illustrations of the variation in shape of the infralabial glands in Epictinae (ventral view after skin removal). **A:** illustration of the infralabial gland as a single lobe; **B:** bipartite lobe; **C:** tripartite lobe and **D:** irregular. Abbreviations: ccs: *M. costocutaneous superior*; ig: infralabial gland; mamep: *M. adductor externus profundus*



lamina of the mandible, from the anterior limit of the dentary until a short anteriormost region of the quadrate, and also a short lateral-ventral region of the head posterior to the supralabial gland. Two portions are distinct: a ventral and a dorsal–lateral portion. The ventral portion is slightly

variable in shape and size amongst Epictinae (Fig. 2). The dorsal–lateral portion of the gland ascends medially to the quadratomaxillary ligament, being partially covered by the inferior portion of the *Musculus levator anguli oris* and the *Musculus adductor externus superficialis* or by the rictal

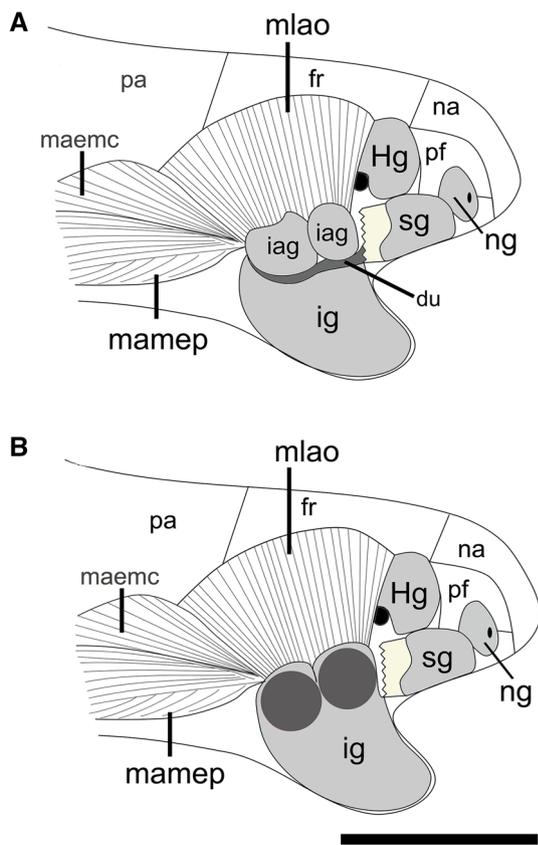


Fig. 3 Schematic illustrations of the cephalic gland shape and position in *Mitophis lepitepileptus* (lateral view after skin removal). **A**: lateral view, with no muscle removal and removal of the quadratamaxillary ligament (light yellow) illustrating the double infralabial accessory glands and its duct; **B**: lateral view with illustration of infralabial gland with removal of the infralabial accessory glands (area of insertion indicated by dark gray circles) and quadratamaxillary ligament (light yellow). Abbreviations: fr: frontal; Hg: Harderian gland; ig: infralabial gland; iag: infralabial accessory gland; mlao: *M. levator anguli oris*; Mamep: *M. adductor externus profundus*; na: nasal; ng: nasal gland; pa: parietal; pf: prefrontal; sg: supralabial gland. Scale: 0.5mm

gland (when present; Figs. 1, 2, 3). This portion is delimited posteriorly by the anterior fibers of the *Musculus adductor externus profundus* and anteriorly by the lateral edge of the dentary. A small and rounded portion of the lateral ascending infralabial gland might be exposed laterally between the *M. levator anguli oris* and the *Musculus adductor externus medialis* portion “a”. Additionally, these latter muscles penetrate the gland to insert in the dorsoposterior process of the dentary and in the coronoid, respectively. Inter- and intra-specific variations (when present) are described below.

Epictia ater ($n = 1$), *E. phenops* ($n = 1$), *E. tenella* ($n = 2$), *Rena dulcis* ($n = 2$), *R. segregata* ($n = 2$), *Trilepida brasiliensis* ($n = 1$), *T. dimidiata* ($n = 1$), *T. fuliginosa* ($n = 1$), *T. joshuai* ($n = 1$), *T. koppesi* ($n = 1$), *T. macrolepis* ($n = 1$) and *T. salgueiroi* ($n = 1$). Ventral portion of the

infralabial gland is composed by two circular distinct portions (Fig. 2b), with the anteriormost located posterior to the dental concha (mandibulae), presenting a marked concavity in the dorsoposterior process of the dental concha, followed by a posterior extension of the gland. In *E. tenella*, the anterior portion of the ventral part is twice the robustness compared to its posterior part. The dorsal–lateral ascending portion of the infralabial gland is triangular in shape, with its dorsalmost portion being overlaid by the ventralmost fibers of the *M. levator anguli oris* and in *Tril. brasiliensis*, also by the do *M. adductor externus medialis* “a”. In *R. dulcis* and *R. segregata*, a small circular portion projects prominently between the *M. levator anguli oris* and the anterior band of the *M. adductor externus superficialis*.

Mitophis lepitepileptus ($n = 1$). Ventral portion not delimited by two distinct circular regions (Fig. 2b), but presents a slight constriction at the level of the dentary dorsoposterior process. Its ascending dorsal–lateral portion is irregular, with its dorsalmost region marked by a concavity that accommodates the infralabial accessory gland.

Rena humilis ($n = 2$). Ventral portion composed by three distinct circular regions (Fig. 2c), the anteriormost located laterally to the dental concha, the medial resting laterally to the dorsoposterior process of the dentary, and the posteriormost lateral to the compound bone. The three regions are distinct by a marked constriction between the three portions. Its ascending dorsal–lateral portion is irregular but approximately trapezoidal, narrower dorsally. Its dorsalmost region is overlaid by the *M. levator anguli oris*.

Rena unguistrostris ($n = 1$). Its ventral portion is irregular (Fig. 2d), with an anteriormost circular portion, lateral to the dentary, between the posterior limit of the dental concha and the dorsoposterior process of dentary. This portion extends posteriorly, narrowing gradually, covering the lateral lamina of the compound bone. The ascending dorsolateral portion is irregular and not overlaid by the *M. levator anguli oris*.

Siagonodon cupinensis ($n = 1$). A single and broad ventral portion is present (Fig. 2a), without a medial constriction. It extends over the lateral lamina of the dental concha (in its posterior region) until the posterior limit of the compound bone. Its ascending dorsolateral portion is approximately trapezoidal in shape, being overlaid by the ventral fibers of the *M. levator anguli oris* and of the *M. adductor externus medialis* “a”.

Tetracheilostoma bilineatum ($n = 1$). Its ventral portion is single, ellipsoidal and wide (Fig. 2a), without constriction, extending from the posterior region of the dental concha until the posterior limit of the compound bone. Its ascending dorsal–lateral portion is trapezoidal, and is covered by the wide rictal gland.

Trilepida jani ($n = 1$). Its ventral portion was damaged during dissection and could not be described. Its ascending

Table 1 Qualitative variation of the nasal glands in Epictinae

	1	2	3	4
<i>Epictia ater</i>	Sc	b	a	b
<i>Epictia phenops</i>	Sc	b	a	b
<i>Epictia tenella</i>	St ($n=1$; 50%) or Dp ($n=1$; 50%)	c	b	a (50%; $n=1$) or b (50%; $n=1$)
<i>Mitophis lepitemileptus</i>	Ci	c	a	a
<i>Rena dulcis</i>	St (50%; $n=1$) or Sc (50%; $n=1$)	a ($n=1$;50%) or c (50%; $n=1$)	a	b
<i>Rena humilis</i>	St	a	a	a
<i>Rena segregata</i>	Sre	a	a	a
<i>Rena unguirostris</i>	St	a	a	a
<i>Siagonodon cupinensis</i>	Sre	a	a	a
<i>Tetracheilostoma bilineatum</i>	Dp	c	b	a
<i>Trilepida brasiliensis</i>	Sc	b	a	a
<i>Trilepida dimidiata</i>	Ci	c	a	a
<i>Trilepida fuliginosa</i>	Sc	b	b	a
<i>Trilepida jani</i>	Sc	b	a	a
<i>Trilepida joshuai</i>	Sc	c	a	a
<i>Trilepida koppesi</i>	Ci	c	a	a
<i>Trilepida macrolepis</i>	Dp	c	a	a
<i>Trilepida salgueiroi</i>	St	b	b	a

(1) Shape of gland: *ci* circular, *sc* semicircular, *st* subtriangular, *dp* drop-shaped, *ser* subrectangular; (2) extension in relation to nostril: (a) exclusively posterior to the nostril, (b) posterior, dorsal and ventral to the nostril or (c) extend around the nostril; (3) posterior limit: (a) restricted to the anterior descending lamina of the prefrontal or (b) exceed the posterior limit of the prefrontal to be posteriorly limited by the eye; (4) supralabial-nasal contact (a) present or (b) absent

dorsal–lateral portion is triangular and dorsally overlaid by the *M. levator anguli oris*.

The infralabial accessory gland (when present) may be single or paired, and rests dorsally and laterally to the ascending dorsal portion of the infralabial gland. A paired infralabial accessory gland is present exclusively in *M. lepitemileptus*, while a single gland is present, at least, in a few species of *Trilepida* (see “Discussion”). Detailed descriptions are provided below.

Mitophis lepitemileptus ($n=1$). A pair of circular glands rests laterally to the dorsal ascending portion of the infralabial gland (Fig. 3). In this species, a thin duct originates from the medial muscles inserts independently on these glands. Minor dissections revealed that such glands are not associated to the infralabial gland, being distinct in aspect and color.

Trilepida joshuai ($n=1$), *T. koppesi* ($n=1$), *T. macrolepis* ($n=1$), *T. brasiliensis* ($n=1$) and *T. salgueiroi* ($n=1$). In these species, a prominent circular portion rests in a concavity located on the dorsal–lateral portion of the infralabial glands (Fig. 1d). In all examined specimens, the infralabial accessory glands differ in color and aspect from the infralabial gland. Minor dissections revealed that in *T. brasiliensis*

and *T. salgueiroi* a duct exiting the gland, penetrating in the rictal plate and opening into the mouth.

The Harderian gland (Figs. 1, 3) is stout, covering the anterior, ventral, dorsal, medial and posterior regions of the eye, extending posteriorly to reach the descending lateral lamina of the parietal, medially to the *M. adductor externus superficialis* (Fig. 1c, d). In all species, a thick translucent fibrous capsule encloses the Harderian gland throughout all its extension. The gland splits into two distinct lobes: the supraocular lobe and the postocular lobe (Fig. 1c, d). Both supraocular and postocular lobes are covered by the *M. adductor externus superficialis*, being totally visible after total muscle removal. A small dorsal portion that lies anterior to the eye might be exposed in lateral view without the removal of the eye or the adductor muscles (Figs. 1a, b, 3). The supraocular lobe fits in the superior concavity of the orbit, covering the posterior lamina of the prefrontal bone, the descending lamina of the frontal and the small anterior region of the lateral lamina of the parietal. In dorsal and lateral view, the supraocular lobe is usually ellipsoidal. The postocular lobe is also ellipsoidal, extending posteriorly and exceeding the supraocular lobe to reach half the extension of the parietal bone.

Table 2 Qualitative variation of the supralabial glands in Epictinae

	1	2	3
<i>Epictia ater</i>	Sr	a	b
<i>Epictia phenops</i>	Sr	?	b
<i>Epictia tenella</i>	Sr (50%; =1) or Sc (50%; n = 1)	a or n/a	a (50%; n = 1) or b (50%; n = 1)
<i>Mitophis lepitepileptus</i>	Sbo	b	b
<i>Rena dulcis</i>	Lo	a	b
<i>Rena humilis</i>	Lo	a (50%; n = 1) or b (50%; n = 1)	b
<i>Rena segregata</i>	Lo	a (50%; n = 1) or b (50%; n = 1)	b
<i>Rena unguirostris</i>	Tra	a	b
<i>Siagonodon cupinensis</i>	Tra	a	b
<i>Tetracheilostoma bilineatum</i>	Tra	a	b
<i>Trilepida brasiliensis</i>	El	a	b
<i>Trilepida dimidiata</i>	Tra	a	b
<i>Trilepida fuliginosa</i>	Sr	a	b
<i>Trilepida jani</i>	Sr	b	b
<i>Trilepida joshuai</i>	Ci	b	b
<i>Trilepida koppesi</i>	Sr	a	b
<i>Trilepida macrolepis</i>	Sq	b	b
<i>Trilepida salgueiroi</i>	Sr	a	b

(1) Shape of gland: *ci* circular, *el* ellipsoidal, *sr* subrectangular, *sq* subquadrangular, *sc* semicircular, *sob* subovoid, *lo* losangular, *tra* trapezoidal, *n/a* not applicable (see number 3) (2) anterior limit in relation to the nostril: (a) reaches the posterior limit of the nostril, (b) does not reach the posterior limit of the nostril; (3) anterior extension to contact the opposite gland in the anterior lamina of the prearticular (a) present or (b) absent

A large and ovoid rictal gland (Fig. 1b) is reported for *E. tenella* and *T. bilineatum*. This gland is located posterior to the rictal plate and to the supralabial gland, overlaying a small anterior area of the ascending portion of the infralabial gland. The rictal gland fits into a concavity of the *M. adductor externus superficialis*, being dorsally limited by the *M. adductor externus superficialis* and posteriorly by the descending portion of the *M. levator anguli oris*.

Discussion

Internal anatomical characters have been applied to the systematics of snakes by several authors at least since the nineteenth century (e.g., Boulenger 1893; Cope 1894). These characters have proven to be useful in snakes systematics for both inferring phylogenetic relationships (e.g., Underwood 1967; Lee and Scanlon 2002; Lee et al. 2007), as well as in the recognition of cryptic species (Myers and McDowell 2014). The external morphology of Leptotyphlopidae is strongly conservative amongst Snakes, and therefore, internal anatomical data possibly provide informative characters that clarify the relationships of leptotyphlopoid genera (Passos et al. 2005, 2006; Pinto and Curcio 2011). The use of internal anatomical

characters does not represent an innovation for the taxonomy of the leptotyphlopids, since several studies included the visceral anatomy, skull and/or hemipenial morphology (Bailey and Carvalho 1946; Broadley and Wallach 1997a, b, 2007; Passos et al. 2006). Such studies have reinforced the need of additional internal anatomy in order to provide important characters for the systematics of this group. However, the large number of possible diagnostic features that the internal anatomical data of leptotyphlopids may provide are still poorly explored, and most studies have addressed skull and hemipenial morphology and, in this sense, as far as we know, the glandular macrostructure has not yet been employed as criteria in the alpha taxonomy of the group. The macrostructure variation found herein for the cephalic glands in Epictinae must be seen as useful characters in the systematics of leptotyphlopids. Our results reinforce the potential of this character system for the resolution of the unsolved taxonomy of the genus *Epictia* (Wallach 2016), especially those currently assigned to *E. tenella* (see discussion of supralabial glands). Considering the variation in gland morphology found in the present study, the presence/absence of infralabial accessory and rictal glands as well as an anterior elongation of the supralabial glands represent important features to be considered in future systematic studies of Leptotyphlopidae.

Concerning the currently recognized cephalic glands in snakes, so far, twelve oral and non-oral cephalic glands have been recognized (Taub 1966). The Harderian and the nasal glands are the only non-oral glands, while the remaining (infralabial, supralabial, Duvernoy, rictal, sublingual, temporomandibular, supralingual, anterior temporal, posterior temporal, and venom glands) represent the oral glands (Taub 1966). In snakes, most of the studies have focused on the venom and Duvernoy glands due to their toxicological properties and medical importance (see Fry et al. 2012 and references therein). Five cephalic glands have been described so far for Leptotyphlopidae: premaxillar, nasal, supralabial, Harderian and infralabial (Haas 1959; Taub 1966). To our knowledge, the present study is the first to identify a structure herein assigned as a rictal gland (observed exclusively in *E. tenella* and *T. bilineatum*) for Scolecophidia and an infralabial accessory gland for the family Leptotyphlopidae (*M. lepitempileptus* and *Trilepida* spp.).

According to Underwood (2002), rictal glands can be recognized by dissection with some confidence if they differ in color and texture and if their form is “discrete”. Although Smith and Bellairs (1947) argued that sections are required for certainty, we assign the wide structure herein named as rictal gland found in *E. tenella* and *T. bilineatum* based on Underwood’s criteria of identification of such glands. The wide rictal gland found in *E. tenella* and *T. bilineatum* lies posterior to the rictal area, and medial to the quadrato-maxillary ligament, as in other snakes (Underwood 2002). However, the pattern found in such species resembles the one found by McDowell (1986) for lizards and several Colubroids (sensu Grazziotin et al. 2012), where the “rictal gland” represents a skin invagination of the rictal region that extends posteriorly as a wide sac that rests on the *adductor* muscles (=rictal recess) and that can also represent (in some snakes) the insertion point to the *M. levator anguli oris*, *M. adductor externus superficialis* or *M. pterygoideus*. The relatively rigid aspect of the rictal glands found herein corroborates the idea that such structures are topographically the same as found in lizards (McDowell 1986) and in basal Henophidian snakes (Underwood 2002). In *E. tenella* and *T. bilineatum*, some fibers of the *M. adductor externus superficialis* insert in the dorsal and medial area of the rictal recess. The insertion of such muscles in the rictal recess also occurs in the true vipers of the family Viperidae, although its pattern of insertion is distinct from those found in leptotyphlopids. The level of development of the rictal gland (=rictal recess) in snakes is variable and might be reduced and almost indistinct or well developed, occupying a wide postmaxillary area, as in *E. tenella*, *T. bilineatum*, *Achalinus spinalis* (Xenodermidae), *Amplorhinus multimaculatus* (Lamprophiidae) and *Urotheca multilineata* (Dipsadidae) (McDowell 1986).

As previously pointed out by Underwood (2002), the homology hypothesis among the rictal glands in snakes is not clear and remains to be tested properly within a phylogenetic framework. Although we identified herein structures as rictal glands based on a putative topographic homology with other lizard and snakes (McDowell 1986; Underwood 2002), we are convinced that a complementary histological study including other semaphoronts should be a subject of future research interest in leptotyphlopoid systematics. There are at least two main hypotheses concerning the function of the rictal glands: (1) these glands are associated with mouth lubrication in fossorial snakes due to their diet based on low-palatable preys (Underwood 2002) or (2) they are related to production of seromucous secretion and may play a role of toxicity in some species (Phisalix and Caius 1918). However, there is no compelling histochemical evidence supporting the second hypothesis and, consequently, the first one is possibly more probable due to the specialized diet of these snakes.

Although we are likely the first in reporting a gland located at the postmandibular temporal region in Leptotyphlopidae, the glands in such region have also been previously reported in Typhlopidae as temporomandibular glands (Phisalix 1922), which are apparently very similar in position to the infralabial accessory glands reported herein. Phisalix (1922) described the temporomandibular gland based on a specimen of the family Typhlopidae, characterizing the gland by its mandibular enlargement, being located in a supra-aponeurotic region. Smith and Bellairs (1947) did not recognize a temporomandibular gland as a new structure and suggested they probably represent an enlargement of the infralabial glands in Typhlopidae. Taub (1966) follows the proposal of Phisalix (1922), considering the temporomandibular gland as distinct from the infralabial gland, also describing the gland as located posteroventrally to the eye, separated from the supralabial gland by a tendon. Posteriorly, after conducting a histochemical study of *Afrotiphlops punctatus*, Gabe and Saint Girons (1967) follow Smith and Bellairs (1947) in considering the temporomandibular gland in Typhlopidae as a widening of the infralabial gland, also describing the same condition for the leptotyphlopoid, *R. dulcis*. In fact, the infralabial gland in Epictinae projects dorsally accommodating medially between the descending fibers of the *M. levator anguli oris* and the *M. adductor externus medialis* portion “a” (Martins unpubl. data). In addition, in some specimens a rounded dorsal region of the infralabial gland emerges through the fibers of such muscle, and might erroneously suggest the inference of an indistinct and reduced gland that rests on the ascending portion of the infralabial gland. Despite the thorough dissections performed within this study, it was only possible to suggest the infralabial accessory glands as distinct from the regular infralabial glands only in a few

species (*M. lepitepileptus*, *Trilepida joshuai*, *T. koppesi*, *T. koppesi*, *T. brasiliensis* and *T. salgueiroi*). Such inference is based strictly on the presence of independent ducts—suggesting a differentiated secretor system from the infralabial glands—and also by differences in color and texture of glandular tissue, qualities which were used by Haas (1964) to identify a distinct infralabial accessory gland in *Liotyphlops albirostris*. Although Haas (1964) has identified such gland also based on histological sections of the head of *L. albirostris*, we tentatively assign such structures to an infralabial accessory gland based on topological and macrostructural qualities, until further histochemical studies provide precise evidence about its microstructure. Additionally, due to the reduced size of specimens and also by fragile nature of the ducts associated to these glands, we were not able to precisely identify the trajectory of the independent ducts and such data are still needed. Although an infralabial accessory gland is reported exclusively in Anomalepididae (Haas 1964, 1968), its shape and position are distinct from those found herein in the Epictinae. The infralabial accessory glands in Anomalepididae are elongate, thin and located in the anterior–ventral portion of the infralabial glands with independent ducts arising from them (Haas 1964, 1968). After Haas' studies, no additional work focused on the nature of such glands, and thus they still remain poorly understood regarding their morphology and function. The primary homology hypothesis (sensu De Pinna 1991) between the accessory infralabial glands from Anomalepididae to those found in Epictinae demands additional compelling evidence from the microstructure of such glands in both families, especially considering the relationships recovered by recent molecular phylogenies (Wiens et al. 2012; Reeder et al. 2015; Hsiang et al. 2015). Finally, even if future histochemical studies do not confirm such glands as independent from the infralabials, this “structure” could potentially represent a cluster of different types of cells that vary amongst Epictinae species, and its presence/absence might also contribute on the systematics of the group.

The supralabial glands, as well as the infralabial glands vary in shape both inter- and intraspecifically. This relative variation might be associated to the variability also found in the shape of the maxilla (A.R Martins in prep.), considering that such glands rest on the lateral laminae of maxilla. In one of the two specimens of *E. tenella* (MCZ 60801), the supralabial gland elongates anteriorly to contact the opposite supralabial gland in the premaxilla. This pattern is unique amongst all Epictinae species analyzed herein, as well as to other Scolecophidia (Phisalix 1922; Smith and Bellairs 1947; Haas 1964, 1968; Taub 1966; Gabe and Saint Girons 1967). The absence of such an elongation in the specimen from the Brazilian Amazonia (vs. its presence in the specimen from the Trinidad), as well as some “intraspecific variation” in the cephalic glands of the *E. tenella*, might suggest

this taxon represents a species complex. Although there is the need for corroboration of macrostructure differences with a more geographically representative sample, these data may be very relevant to solve the taxonomic problems in puzzling taxa.

In a similar pattern as the supralabial glands, the nasal glands also exhibited variation in size, shape and anterior/posterior limits. This variation might also be associated to the difference in the recess from the prefrontal bone that accommodates such glands, which also varies interspecifically in the Epictinae (Martins in prep.).

The Harderian gland has been traditionally associated to the physiological adjustments of the eye in Squamates (Smith and Bellairs 1947; Taub 1966), but a few alternative functions for this gland have been proposed: (1) corneal lubrication (Greer 1983); (2) an accessory salivary gland (as a source of digestive enzymes or as a lubricant; Young and Lennep 1978) and (3) vomerolfaction (Rehorek 1997). Although many of the functions assigned to the Harderian gland in Squamates still remain elusive, its main role for vomerolfaction in Snakes is most likely and is reinforced based on morphological studies (Rehorek 1997). In fact, the level of the development of the Harderian gland in Epictinae species with well developed eyes or those with a reduced eye-spot reinforces the supposition that this gland is not associated to eye lubrication in leptotyphlopids and is most likely associated to vomerolfaction and/or lubrication and/or digestion. Such inferences are possibly supported by evidences from Bellairs and Boyd (1946), based on the histological sections of the *Argyrophis diardii* (Typhlopidae). These authors report a unique structure in this species—well developed subbrillar cavity with a very few acins being discharged in this cavity—possibly related to its fossorial habits. A wide part of the acins discharge occur in a wide lacrimal duct (which possibly represents the Harderian duct itself), which therefore direct ventral-medially to open in the vomeronasal organ. A wide subbrillar cavity with acins discharging from the Harderian glands and lachrymal duct are also present in *Xenopeltis unicolor*, *Cylindrophus rufus* and amphisbenids (all of them with strictly fossorial lifestyle).

Notwithstanding, the Harderian gland represents the only cephalic gland in Epictinae that is associated with a lateral array of muscles. The *M. adductor externus superficialis* covers the postorbital portion of the gland, inserting posteriorly in the rictal plate. The position and trajectory of the *M. adductor externus superficialis* suggest its action as a “compressor glandulae” that squeezes the gland from an anterior–posterior course, generating a pressure on the lachrymal duct during mouth opening. Even if anatomical characteristics of the lachrymal apparatus are similar amongst fossorial Squamata (Bellairs and Boyd 1946), the putative association with the superficial adductor muscle would represent an evolutionary

novelty in Leptotyphlopidae to potentialize secretion in the vomeronasal organ and/or the oral cavity. The function of the Harderian gland as well as its association to the *M. adductor externus superficialis* needs further histochemical investigation in order to confirm whether its function is associated to vomerolfaction, lubrication or digestion, and also if muscle fibers are associated to connective tissues of the gland. If such assumptions are correct, then the nasal glands would represent the only non-oral gland in Leptotyphlopidae as a possible result of their biology (feeding mechanisms and ingested prey).

Finally, internal anatomical characters are extremely important considering that an understanding of variation and evolution of scolecophidian anatomy can play a major role in understanding the glandular diversification in snakes, as well as issues concerning the origin and evolution of venom in Squamata. Exploring such data in both systematics and functional perspectives from Scolecophidia is a challenge especially due to its small size, hampering minor dissections for macrostructural studies. For that reason, a histological approach is fundamental in the corroboration of homology hypotheses formulated on the basis of macrostructural investigation. This study provides insights in the topic although we are aware that additional data are still needed for the resolution of several functional and evolutionary issues introduced herein.

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Author contributions AM, PP and RP conceived the study. AM performed dissections, evaluated the characters state and produced the illustrations. All authors analyzed and discussed the findings and wrote the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Research involving human participants and/or animals This article does not contain any studies with human participants performed by any of the authors. All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

Ethical approval International, national, and/or institutional guidelines for the care and use of animals were followed.

Additional information

Material examined

Epictia ater (n = 1): **EL SALVADOR**: SAN MIGUEL: KU18384.

Epictia phenops (n = 1): **MEXICO**: OAXACA: FMNH 111477.

Epictia tenella (n = 2): **BRAZIL**: PARÁ: *Oriximiná*: Porto Trombetas: MNRJ 16827. **TRINIDAD AND TOBAGO**: TRINIDAD: *Guayaguayare*: MCZ 60801.

Mitophis leptepileptus (n = 1): **HAITI**: SUD-EST: *Soliette*: USNM275548.

Rena dulcis (n = 2): **UNITED STATES OF AMERICA**: OKLAHOMA: *Comanche*: OMNH35564, 35580.

Rena humilis (n = 2): **UNITED STATES OF AMERICA**: CALIFORNIA: *San Diego*: FMNH 33950, 34302.

Rena segregata (n = 2): **UNITED STATES OF AMERICA**: NEW MEXICO: *Doña Ana*: LACM, 134007, 134009.

Rena unguirostris (n = 1): **ARGENTINA**: TINOGASTA: *Palo Blanco*: FML 1773.

Siagonodon cupinensis (n = 1): **BRAZIL**: MATO GROSSO: Barra do Tapirapés: Guarantã do Norte: UFMT 5627.

Tetracheilostoma bilineatum (n = 1): **MARTINIQUE**: LE LAMENTIN: *without locality*: USNM 564808.

Trilepida brasiliensis (n = 1): **BRAZIL**: MATO GROSSO DO SUL: *Corumbá*: UFMT 1159.

Trilepida dimidiata (n = 1): **BRAZIL**: RORAIMA: *Boa Vista*: MZUSP 10090.

Trilepida fuliginosa (n = 1): **BRAZIL**: GOIÁS: *Luziânia*: CHUNB 40847.

Trilepida jani (n = 1): **BRAZIL**: MINAS GERAIS: *Ouro Preto*: LZV 813S.

Trilepida joshuai (n = 1): **COLOMBIA**: ANTIOQUIA: *Jericó*: IBSP 8919.

Trilepida koppesi (n = 1): **BRAZIL**: GOIÁS: *Aporé*: MNRJ 24715.

Trilepida macrolepis ($n = 1$): **BRAZIL**: PARÁ: *Paraupebas*: Floresta Nacional de Carajás: MPEG 23017.

Trilepida salgueiroi ($n = 1$). **BRAZIL**: ESPÍRITO SANTO: *Governador Lindemberg*: MNRJ 12132.

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