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Research paper

Embryological evidence of a new type of seromucous labial gland in neotropical snail-eating snakes of the genus *Sibynomorphus*

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ABSTRACT

Snail-eating dipsadine snakes of the genera *Sibynomorphus* and *Dipsas* share infralabial glands divided into a distinct lateral portion along the lower lip (il1) and a ventrolateral portion along the mandible (il2). While il1 is constituted by several small and individual glands with their short ducts opening along the margin of the lower lip, il2 is constituted by a single hypertrophied gland with a single duct that opens laterally at the level of the intermandibular raphe. This unique condition seems to be restricted to the goo-eating dipsadine snakes. Here, we describe the embryonic development of the labial glands in the goo-eating dipsadine snakes *Sibynomorphus mikanii* and *S. neuwiedi*. Our results indicate that il2 developed independently from il1, being formed through a hypertrophied invagination instead of deriving from several small independent invaginations, as is the case for il1. Additionally, il2 showed a distinct timing of development, starting in younger embryological stages, prior to the development of il1 and other labial glands. The pattern of embryonic development observed for il2 supports the hypothesis that this gland evolved separately from the infralabial glands in both *Sibynomorphus* and *Dipsas*, as a novel, independent protein-secretion system associated with their specialized feeding behaviors.

1. Introduction

Although there is a significant amount of information available on the embryonic development of the venom or Duvernoy's glands of advanced caenophidian snakes (Kochva, 1965; Shayer-Wollberg and Kochva, 1967; Gygax, 1971; Ovadia, 1985), few authors offered detailed descriptions on the developmental aspects of the labial and oral glands in general. Buchtová et al. (2007) suggested that labial glands and teeth originate in a very similar way i.e., through the thickening of the epithelium followed by the invagination of the epithelial laminae into the mesenchyme. However, the development of the labial glands shows marked differences in respect to the venom or Duvernoy's glands. While the latter two develop from a single invagination on the caudal portion of the dental lamina of the maxillary bone (Vonk et al., 2008; Tucker, 2010), labial glands develop from a number of serial and non-compound epithelial thickenings followed by epithelial laminae invaginations into the mesenchyme along the upper and lower lips (Kochva, 1965; Gygax, 1971; Buchtová et al., 2007). This pattern of development agrees with the morphology present in adult snakes, in which labial glands are formed by a group of small, serial glands with short ducts arranged along the lip and separated from each other by septa of connective tissue (Smith and Bellairs, 1947; Kochva, 1978; Underwood, 2002).

In adult individuals of the dipsadine snakes genera *Sibynomorphus* Fitzinger, 1843 and *Dipsas* Laurenti, 1768; infralabial glands are divided into two distinct portions: a lateral strip-like portion along the lower lip (il1), and a ventrolateral portion along the mandible (il2). While il1 is mucous and is formed by short ducts, il2 is frequently constituted by seromucous cells and has a single "mandibular" duct that opens at the level of the intermandibular raphe (Zaher et al., 2014). However, il1 and il2 can be closely associated in the anterior region of the mouth, making it difficult to distinguish them in that region. Additionally, apart from the single duct of il2, some short ducts are also visible more posteriorly and appear to connect il2 with il1 or il2 directly with the oral epithelium, suggesting a single embryological origin and posterior differentiation (Zaher et al., 2014). These conflicting observations on adult individuals require an embryological study of the development of il1 and il2 portions in order to determine their identity.

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Table 1
General morphology descriptions and stages of development in the analyzed specimens. *Abbreviations*: HL, head length; SVL, snout-vent length.

STAGES	DAYS AFTER OVIPOSITION	GENERAL MORPHOLOGY	STAGE Zehr (1962)	EXAMINED MATERIAL
Sibynomorphus mikanii				
1	10	SVL = 35 mm; HL = 2 mm; optic cup is pigmented and there is no signal of the choroid fissure; eyelids are not observed; cervical and mesocranial flexures are present; branchial clefts are closed; tip of the mandibular process reaches the same level of the anterior optic cup; maxillary process extends ahead the anterior border of the eye and it is not separate from the lateral nasal process; hindbrain is medially opened in the nuchal region; body is coiled and there is no scales or pigmentation.	26	MZUSP 18714; Appendix ASupplementary data – Fig. S1A, B
2	25	SVL = 55 mm; HL = 5 mm; eyelids are fused and cover the optic cup; maxillary process fuses to the nasal process and the mandibular tip reaches the nose; cervical flexure is not observed; external opening of the nostril is visible; endolymphatic sacs are visible in the occipital region; ventral body wall is fused at the first third of length; body shows no pigmentation or scales.	32	MZUSP 18715; Appendix ASupplementary data – Fig. S1C, D
3	32	SVL = 75 mm; HL = 7 mm; visible endolymphatic sacs; scales covering the whole body, except in the parietal region; hemipenes are everted, bilobated and sulcated; ventral scales are fused at the first third of the body length; pigmentation pattern is well developed.	36	MZUSP 18716; Appendix ASupplementary data – Fig. S1E, F
4	41	SVL = 115 mm; HL = 7.5 mm; egg tooth is present, vertically oriented, but not completely erupted; ventral body is totally fused except in the cloacal region; Ventral scale is paired; scales are not completely keratinized, especially in the axial region; scale morphology resembles adult condition; parietal region is scaled. Pigment pattern fully developed.	37	MZUSP 18717; Appendix ASupplementary data – Fig. S1G, H
Sibynomorphus neuwiedi				
1	Not recorded	SVL = 37 mm; HL = 3.5 mm; eyelids are not fused; maxillary process fuses to the nasal process and the mandibular tip reaches the nose; external opening of the nostril is visible; endolymphatic sacs are visible in the occipital region; ventral body wall is fused at the first third of length; body does not show pigmentation or scales.	32	MZUSP 22458; Appendix ASupplementary data – Fig. S1I, J

Here, we describe the staging of the embryonic development of the labial glands in the snail-eating dipsadine snakes *Sibynomorphus mikanii* (Schlegel, 1837) and *S. neuwiedi* (von Ihering, 1911) and demonstrate that both il1 and il2 portions of the infralabial gland are embryologically distinct labial glandular elements that attend distinct functions in adult snakes of the genus *Sibynomorphus*.

2. Materials and methods

2.1. Acquisition of embryos

Seven eggs from three clutches of *Sibynomorphus mikanii* and one embryo of *S. neuwiedi* were used. Embryos were provided by the herpetological collection of the Museu de Zoologia da Universidade de São Paulo (MZUSP) and the Museu Biológico do Instituto Butantan. Soon after laying, eggs were packaged into a plastic container filled with vermiculite. The incubation temperature and humidity were not controlled, varying according to the environment conditions. At intervals of 10, 23, 25, 29, 32, 36 and 41 days after oviposition (dao), embryos of *S. mikanii* were removed from the eggs. For the embryo of *S. neuwiedi*, the number of days since oviposition was not recorded. Each embryo was anesthetized according to animal ethics protocols prior to being fixed with a 5% formalin solution for two days after which they were transferred to a solution of 70% alcohol.

2.2. General morphology

The external morphology of the embryos was observed under a stereomicroscope (Nikon—model SMZ 1500) and each developmental stage was categorized according to the table of development previously established for *Thamnophis sirtalis sirtalis* (Zehr, 1962; Table 1). The embryos were then photographed and their total and head lengths were measured under a Leica M205A stereomicroscope equipped with a Leica DFC 425 digital camera and the LAS Core version 3.8 software to capture the images and to carry out the morphometry.

2.3. Histology

After external observations, the embryo's heads were decapitated at the level of the first cervical vertebrae, dehydrated and embedded in paraffin for histological and histochemical study. Before paraffin embedding, all heads, except the embryo of the first stage (10 dao) were divided sagitally into two halves. Serial transverse and sagittal sections (10 μm) were performed with a Microm HM 340-E microtome with disposable steel blades. In the first embryo these were only done in transverse sections. The sections were treated with hematoxylin-eosin (HandE) staining, for the general study of the tissues and submitted to the following histochemical staining procedures (Bancroft and Stevens, 1996): periodic acid-Schiff (PAS), alcian blue (pH 2.5), combined alcian

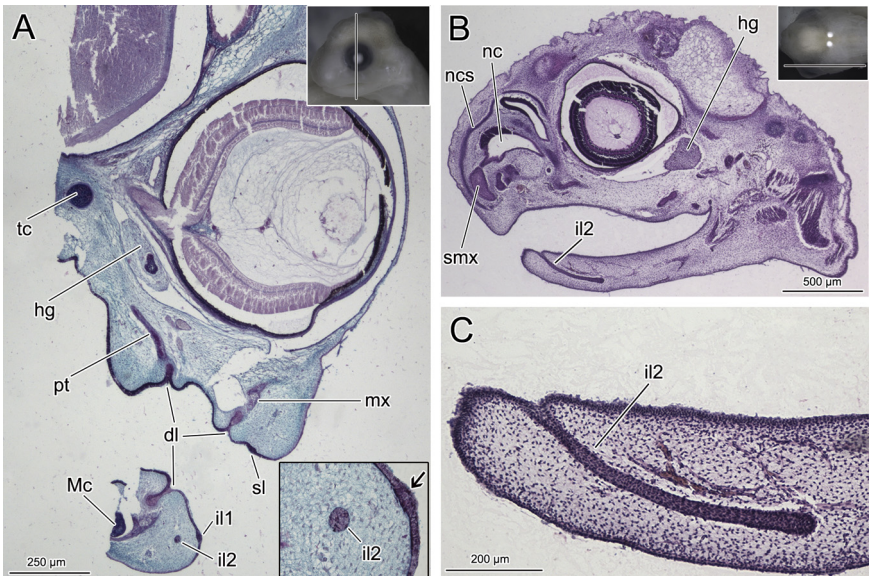

Fig. 1. *Sibynomorphus mikanii.* Stage 2 embryo. (A) Transversal section of the head showing the dental laminae (dl) of the dentigerous bones and the primordia of the labial glands in the upper and lower jaw. Insert shows a high magnification of the epithelial thickening of the dorsolateral part of the infralabial gland (arrow) and the invagination of the ventrolateral portion of the infralabial gland (il2); conjugated reaction of the alcian blue (pH 2.5) and PAS. (B) Sagittal section of the head showing the hypertrophied invagination of the ventrolateral portion of the infralabial gland (il2); section stained by HandE. (C) High magnification of the anterior figure showing the hypertrophied invagination of the ventrolateral portion of the infralabial gland (il2). Abbreviations: dl, dental laminae; hg, harderian gland; il1, lateral, mucous infralabial gland; il2, ventrolateral, seromucous infralabial gland; mx, maxilla; nc, nasal cavity; ncs, nasal capsule; pt, pterygoid; sl, supralabial glands; smx, septomaxilla; tc, trabecula. Panel at the upper right corner denote position of the sections. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

blue (pH 2.5) and PAS (Pearse, 1985; Kiernan, 2001). The PAS and alcian blue (pH 2.5) were applied for identification of neutral and acid mucosubstances, respectively.

Embryological development of the labial glands (supra and infralabial) was categorized into four stages previously established by morphogenesis. Only one embryo was used for each stage. Examined criteria were morphology and positive histochemical reation to alcian blue (pH 2.5) and PAS. We distinguished (see below) the more dorsolateral part of the infralabial gland from the more hypertrophied ventrolateral portion, as "lateral, mucous infralabial

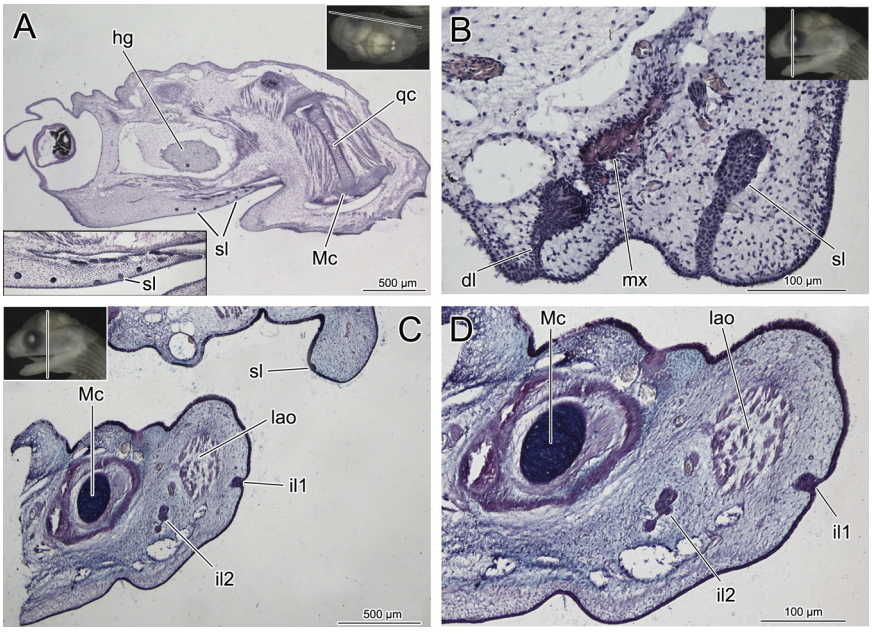

Fig. 2. *Sibynomorphus mikanii.* Stage 3 embryo. (A) Sagittal section of the head showing primordia of the supralabial glands; section stained by HandE. (B) Transversal section showing invagination of the supralabial glands; section stained by HandE. (C) Transversal section of the head in the post-ocular level showing epithelial thickenings of the supralabial glands and the mandible with the invagination of the dorsolateral part of the infralabial gland (il1) and branching of the ventrolateral portion of the infralabial gland (il2); conjugated reaction of the alcian blue (pH 2.5) and PAS. (D) High magnification of the anterior figure showing the mandible with the LAO between the two portions of the infralabial glands (il1 and il2) and beginning of the branching in the il2. Abbreviations: dl, dental laminae; hg, harderian gland; il1, lateral, mucous infralabial gland; il2, ventrolateral, seromucous infralabial gland; lao, muscle *levator anguli oris*; Mc, Meckel's cartilage; mx, maxilla; pt, pterygoid; qc, quadrate cartilage; sl, supralabial glands; tc, trabecula. Panel at the upper right and left corner denote position of the sections. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

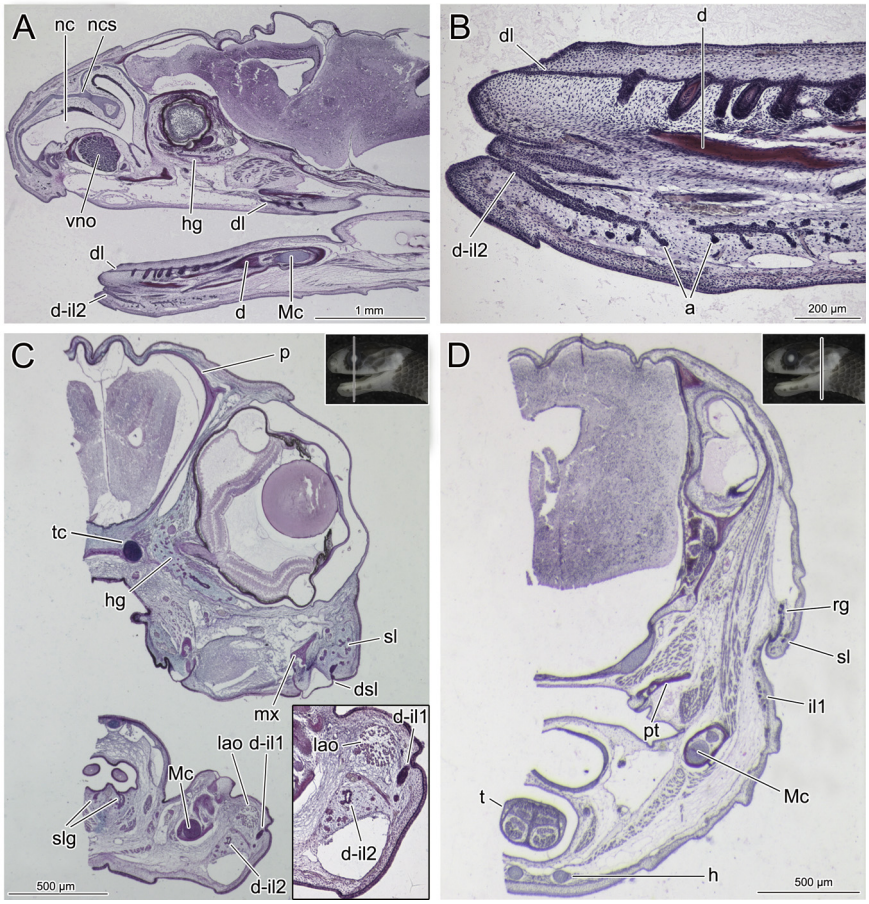

Fig. 3. *Sibynomorphus mikanii*. Stage 4 embryo. (A) Sagittal section of the head showing dental laminae of the dentigerous bone and position of the il2 gland; section stained by HandE. (B) High magnification of the anterior section showing initial third of the mandible with il2 branching and differentiation of the acini and duct (d-il2). The duct of il2 (d-il2) opens in the anterior region of the mouth. (C) Transversal section of the head at the level of the eyes showing the supra and infralabial glands branching and their respectives ducts. Insert shows details of the ducts in the il1 and il2 and LAO placed between both portions of the infralabial glands; conjugated reaction of the alcian blue (pH 2.5) and PAS. (D) Transversal section of the head at the level of the corner of the mouth showing supralabial, il1 and an invagination correspondent to the rictal gland (rg) located in a more medial region than supralabial glands; section stained by HandE. Abbreviations: a, acinus; d-il1, dl, dental laminae; duct of the lateral part of the infralabial gland; d-il2, duct of the ventrolateral portion of the infralabial gland; dsl, duct of the supralabial gland; h, hyoid; hg, harderian gland; il1, lateral, mucous infralabial gland; il2, ventrolateral, seromucous infralabial gland; lao, muscle *levator anguli oris*; Mc, Meckel's cartilage; mx, maxilla; nc, nasal cavity; ncs, nasal capsule; p, parietal; pt, pterygoid; rg, rictal gland; sl, supralabial glands; slg, sublingual gland; t, tongue; tc, trabecula;. Panel at the upper right corner denote position of the sections. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

gland" (il1) and "ventrolateral, seromucous infralabial gland" (il2), respectively (*sensu* Zaher et al., 2014).

All embryos and their histological sections of the head were deposited in the collection of the Museu de Zoologia da Universidade de São Paulo (MZUSP).

3. Results

3.1. *Sibynomorphus mikanii*

In the first stage of development (10 dao, Table 1, Appendix A, Supplementary Fig. S1) no structures related to muscles or cephalic glands, nor bone or connective tissues were observed. Mandibular and maxillary regions were constituted by a large number of mesenchymal cells.

At stage 2 (25 dao, Table 1, Appendix A, Supplementary Fig. S1) all dentigerous bones showed their respective dental laminae (Fig. 1A), and the primordia of the supra and infralabial glands, represented by the thickening of the ephitelium, appeared along the maxillary and mandibular region, respectively (Fig. 1A). The muscle *levator anguli oris* (LAO) was observed initially surrounding the corner of the mouth, along the rictal region. In the mandibular region, a hypertrophied ephitelial lamina was observed invaginating into the mesenchyme independently of the epithelial thickening in the maxillary and mandibular regions (Fig. 1A–C). This lamina measured approximately 0.7 mm long (Fig. 1B, C) and appeared to correspond to the il2, as shown throughout the following stages. The epithelial thickenings of both mandibular and maxillary regions as well as the hypertrophied ephitelial lamina in the mandibular region were PAS positive (Fig. 1A).

At stage 3 (32 dao, Table 1, Appendix A, Supplementary Fig. S1), the primordia of the labial glands were still present (Fig. 2A, C). The ingrowth of the epithelial laminae into the mesenchyme was particularly developed in the maxillary region (Fig. 2B). All thickenings of the epithelial laminae and their ingrowth into the mesenchyme of the labial glands were PAS positive (Fig. 2C, D). The epithelial lamina corresponding to the il2 started branching off along the mandibular region (Fig. 2C, D). The LAO was observed extending between the early il1 and il2 along the posterior region of the mandible (Fig. 2C, D).

At stage 4 (41 dao, Table 1, Appendix A Supplementary Fig. S1), both infra and supralabial glands, and more particularly il2, were observed branching off and starting differentiation of their acini and ducts (Fig. 3A–C). The duct of il2 extended longitudinally along the distal third of the mandible, opening in the anterior tip of the mouth (Fig. 3A, B). The ducts of the supralabial glands and il1 were

short and perpendicularly oriented relative to the gland, opening along of the upper and lower lips, respectively (Fig. 3C). The LAO extended anteriorly to the level of the eyes, being now positioned between two clearly differentiated il1 and il2 (Fig. 3C). More anteriorly, at the level of the nasal cavity, the LAO was not observed and the two portions of the infralabial glands (il1 and il2) were still undifferentiated. While both supralabial and il1 glands were closely associated with the upper and lower lip margins, respectively, il2 did not show any connection with the lower lip, extending along the lateral surface of the mandible (Fig. 3C). An epithelial invagination corresponding to the rictal gland was observed developing in the mesenchyme of the rictal region (Fig. 3D).

3.2. *Sibynomorphus neuwiedi*

Only one embryo of *S. neuwiedi* was available for this study, and it corresponded to stage 1 embryo of *S. mikanii* described above. Similarly to the latter, at stage 1 (dao not recorded, Table 1, Appendix A Supplementary Fig. S1) all dentigerous bones showed their respective dental laminae (Appendix A Supplementary Fig. S2), the primordia of the supra and infralabial glands, represented by the thickening of the epithelia, appeared along of the maxillary and mandibular region, respectively (Fig. 2B–D; Appendix A Supplementary Fig. S2). While the supralabial gland was represented by multiple, short independent invaginations measuring approximately 0.1 mm (Fig. 2B, C; Appendix A Supplementary Fig. S2), il2 was represented by a single hypertrophied invagination occupying practically the entire length of the mandible (Fig. 2A; Appendix A Supplementary Fig. S2). This last invagination measured approximately 1.0 mm in length, extending in a more ventrolateral position than the dental lamina of the dentary (Fig. 2C and D; Appendix A Supplementary Fig. S2). The LAO was observed surrounding the corner of the mouth, along the rictal region, and occupying a position between the two differentiated il1 and il2 (Fig. 2D; Appendix A Supplementary Fig. S2).

4. Discussion

Gygax (1971) stated that it is possible to describe the structure of the supralabial glands as single *glandlets*, a term used by this author to refer to the series of small, identically constructed glands that constitute the individual adult labial glands. Our results have shown a clear distinction in the development of these *glandlets* that originally compose the infralabial glands of *S. mikanii* and *S. neuwiedi* (Fig. 4). We verified that the mesenchyme invagination that extends over the first third of the mandibular region corresponds to il2, previously described by Zaher et al. (2014) in adult specimens of dipsadine snakes. Differently from other labial glands, this portion originates from a single and hypertrophied epithelial invagination instead of several short and individual ones (glandlet primordia). Additionally, the il2 of *S. mikanii* differs from other labial glands by invaginating earlier during embryogenesis (25 dao instead of 32 dao). Observations made on the only available embryo of *S. neuwiedi* seems to corroborate these results, with il2 already showing an epithelial invagination, while il1 remains in the earlier stage of cell proliferation (i.e, without any epithelial invagination).

Within the tribe Dipsadini, the genus *Geophis* also have infralabial glands divided in two distinct portions il1 and il2 (Gans, 1972; Zaher, 1999; Oliveira et al., 2014). However, only *Dipsas* and *Sibynomorphus* show a LAO separating il1 from il2 (Oliveira et al., 2014; Zaher et al., 2014). In embryos of *S. mikanii*, the LAO is already observed in the second stage of development, as a bundle surrounding the corner of the mouth. It is only in the fourth stage of development (41 dao) that the LAO acquires the adult morphology, extending anteriorly along the mandible and between the two

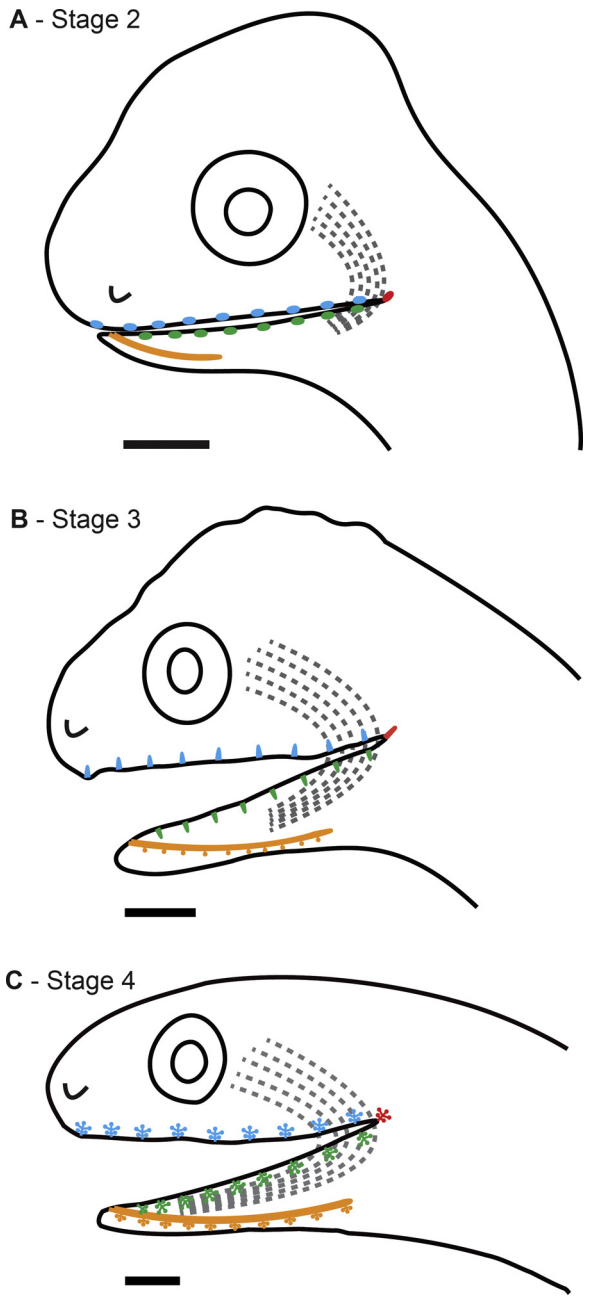

Fig. 4. Schematic representation of the stages of development in the labial and rictal glands of *Sibynomorphus mikanii*. (A) Second stage. (B) Third stage. (C) Fourth stage. Blue, supralabial glands; Red, rictal gland; Green, lateral and striped portion localized along of the lower lip (il1); Orange, ventromedial portion localized along of the mandible (il2); Grey, muscle *levator anguli oris*. Scale bars = 1 mm. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

portions of the infralabial glands (il1 and il2), to insert in the anterior tip of the dentary. The close contact observed between LAO and il2 suggests that the gland may well be indirectly stimulated to evacuate its content during muscular contraction of the LAO. Such indirect muscle action was also described by Jansen and Foehring (1983) for the Duvernoy's gland of *Thamnophis sirtalis*.

The developmental pattern verified in the labial glands of *S. mikanii* and *S. neuwiedi* are consistent with the morphology observed in adult individuals (see Zaher et al., 2014), where the il1 and supralabial glands show a typical morphological pattern of labial glands. That is, consisting of a series of small and individual glands (glandlets) with short ducts opening independently along

of the margin of the lips (Smith and Bellairs, 1947; Gygax, 1971; Kochva, 1978; Underwood, 2002). On the other hand, il2 shows a distinct morphological pattern, being arranged along the entire mandible and detached from the infralabial lip. This gland shows a single duct extending longitudinally along its whole length and opening into the anterior region of the mouth, instead of having a series of short ducts along its labial margin. The short ducts, which appear to connect il2 with il1 or il2 directly with the oral epithelium in adult individuals of *Dipsas* and *Sibynomorphus* (Zaher et al., 2014) are formed later during its embryonic development and may help in the release of secretion from il2 more posteriorly into the mouth. However, the main volume of secretion from il2 is more likely discharged through the main anterior duct of the gland.

The pattern of embryonic development verified in il2 suggests that oral glands in snakes may retain much more potential for morphological plasticity than previously expected, supporting the hypothesis that il2 may have evolved as a novel protein-secretion delivery system in goo-eating snakes, and more specifically in species of the genera *Sibynomorphus* and *Dipsas*. This system might also perform additional functions associated with the specialized feeding behavior found in dipsadine goo-eating snakes (Oliveira et al., 2014; Zaher et al., 2014). The independent origin and possible distinct functions of il2, as demonstrated here, corroborates the need to formally distinguish il2 from il1.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.jcz.2016.09.004.

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