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ECOSYSTEMS

Morphological description of the digestive tract of the Amazonian Diving Lizard *Uranoscodon superciliosus* (Linnaeus, 1758) and its associations to the diet and foraging mode

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Abstract: The study aimed to characterize the digestive tract of *Uranoscodon superciliosus* and its associations to the diet and foraging behavior already described for the species. Five lizards were captured in forest areas near the city of Manaus, Amazonas, Brazil. Tongue, oesophagus, stomach, small and large intestines fragments were collected, fixed, and processed for light microscopy. Hyaline cartilage was present in the center of the tongue, and the papillae from the apex and glands from the radix showed positive reaction to Alcian blue. The oesophagus presented a folded mucosa, covered by an epithelium with mucous and goblet cells positive to PAS and Alcian blue. There was presence of gastric glands in the cardic and fundic stomach regions, plus all the regions reacted positively to PAS. Fold and villi variations in both small and large intestine were noted, as well as the number and arrangement of goblet cells. Mucous and goblet cells from the small intestine were positively stained in PAS, while only the goblet cells were Alcian blue positive. These findings indicate that the Amazonian Diving Lizard's digestive tract organs, mainly the tongue and stomach, present morphologies associated to ambush-type foraging and a specific diet largely based on small invertebrates.

Key words: Amazon, digestive organs, microscopy, morphology, reptiles.

INTRODUCTION

The reptile (Chordata, Reptilia) digestive tract varies according to feeding habits, but is generally short and simple compared to birds and mammals (Mader 2006, Devoe 2010). The digestive tract comprises the oral cavity and digestive organs, namely the oesophagus, stomach, and small and large intestines (Kardong 2010). It is believed that the digestive tract of the first mammals was very similar to that of reptiles, as both taxonomic groups use to share the same insectivorous diet in primordial times, adapting structurally and morphologically over time to different carnivorous, omnivorous or herbivorous diets (Guard 1980).

Today, carnivorous, omnivorous and insectivorous reptiles present a simpler digestive tract compared to herbivorous reptiles, which present other tract adaptations and details (Guard 1980, Rodrigues-Sartori et al. 2008, Magalhães et al. 2010). These adaptations are noted mainly in the oral cavity, with dentition changes according to prey capture capacity (Guard 1980, Mader 2006, Devoe 2010). With regard to lizards (Lepidosauria, Squamata), carnivorous and insectivorous species such as the gecko *Hemidactylus mabouia* (Moreau de Jonnès, 1818) present shorter stomach, followed by a long small intestine compared to the large intestine (Rodrigues-Sartori 2014), whereas herbivorous lizards, such as *Iguana iguana* (Linnaeus, 1758) exhibit varying small intestine lengths according to the amount of consumed plant matter, with potentially large colons and cecae, which are important for plant matter fermentation and digestion (Troyer 1984, O'Grady et al. 2005). In addition to dietary adaptations, digestive tract lizard characteristics may also vary according to foraging mode, size, habitat, and even seasonality (Iwasaki 2002, Mader 2006, Devoe 2010).

Tropidurid lizards (Iguania, Tropiduridae) comprise an ecologically diverse group of exclusively neotropical species (ca. 136 spp.), whose geographical distribution includes South America and the Galapagos Islands (Frost et al. 2001, Carvalho et al. 2020). Forty-two species are known in Brazil, most belonging to the genus *Tropidurus* with some, such as *Eurolophosaurus* spp. and *Strobilurus* spp., endemic (Costa & Bérnils 2018, O'Shea 2021), inhabiting from dense and humid forests to rocky and sandy habitats, to anthropic environments (Arruda et al. 1961, Da Rocha 1995, Rodrigues et al. 2018, Da Costa et al. 2020, Carvalho et al. 2020). Although variations may be noted between species, most tropidurid lizards' diets feed on similar food items, like insects, arachnids, larvae and, in some cases, plants (Arruda et al. 1961).

A very curious species belonging to this family, albeit little known regarding its bioecological aspects, is *Uranoscodon superciliosus* (Linnaeus, 1758). This species is known by many popular names, such as Tamaquaré in Brazil and "diving lizard" in other countries, the latter name associated to its peculiar escape behavior of diving and remaining submerged in water when threatened (Howland et al. 1990, Campos & Magnusson 2010). This arboreal lizard is an endemic species of the Amazon basin, usually inhabiting the banks of rivers and streams (Howland et al. 1990, Vitt et al. 1999, Faria et al. 2019). *U. superciliosus* has been described as a typical ambush predator, spending much of its time camouflaged on tree branches and feeding mainly on soil invertebrates, such as ants, earthworms, millipedes, cockroaches, crickets and, sometimes, small vertebrates, such as frogs and birds (Howland et al. 1990, Gasnier et al. 1994, Picelli et al. 2019).

Morphological studies are paramount in understanding digestive processes associated to animal nutrition, also serving as additional tools for physiological, pathological, and phylogenetic investigations (Rodrigues-Sartori et al. 2011, 2014). In this context, considering the scarcity of morphological and ecological *U. superciliosus* data, this study aimed to understand this species feeding strategy through a digestive tract morphology analysis.

MATERIALS AND METHODS

Study area and lizard capture

This study was conducted between 2018 and 2019 at the Federal University of Amazonas Experimental Farm (FEX-UFAM, 2°38'57.6"S, 60°3'11"W), located 80 km north of Manaus, in the state of Amazonas, Brazil. The research area is part of the Amazonian upland ('*terra firme*') rainforest, exhibiting high pluviometric density and flora and fauna variety (Rojas-Ahumada et al. 2012, Faria et al. 2019). Five lizards were captured manually during an active nocturnal search carried out along the banks of small streams and transported to the UFAM Human and Comparative Morphology Laboratory, at the Manaus *campus*, where they were euthanized via an associated 2% lidocaine and thiopental injection and dissected for digestive tract removal (Sebben 2007). All five *U. superciliosus* specimens were males, with a mean snout-vent length (SVL) of 119.4 ± 31.6 mm (84–160 mm) and mean body mass of 73 ± 26.7 g (45–110 g).

All procedures were approved by the UFAM ethics committee on animal use (protocol number 012/2016) and authorized by the Brazilian Ministry of the Environment (SISBIO number 53851 and SISGEN AA6199D).

Histological analyses

For gross morphology, the digestive tract was collected and analyzed under a Zeiss stereo microscope (Carl Zeiss, Jena, Germany) at 0.6 to 1.2 × magnification, to visualize the folds in the oesophagus, stomach, small and large intestines. Images were captured using a coupled Zeiss Axiocam digital camera and processed by the ZEN 2 v. 2.0 software (Carl Zeiss Microscopy GmbH 2011).

Tongue, oesophagus (proximal, medium and distal regions), stomach (cardic, fundic and pyloric regions), small intestine (proximal, medium and distal regions) and large intestine (proximal and distal regions) fragments were fixed in a 10% buffered formaldehyde solution and processed for light microscopy analyses as follows: (i) dehydration in a graded alcohol series (70%, 80%, 90% and 100% for 30 minutes each), (ii) one xylol diafanization bath, and (iii) a second xylol diafanization bath for 30 minutes, followed by paraffin inclusion for one hour. The tongue fragments were included in the sagittal position while tubular and hollow organs (oesophagus, stomach, small and large intestines) were included transversally. After the inclusion process, 4 µm-thick sample sections were obtained employing a microtome and submitted to hematoxylin and eosin staining (adapted from Magalhães et al. 2014) Alcian Blue (AB) staining was made with pH 1.0 for sulfated acid glycosaminoglycans evidence, while Periodic acid-Schiff (PAS) staining was used for neutral glycosaminoglycans evidence. The histological sections were then analyzed under a Leica DM4B microscope (Leica Microsystems, Heerbrugg, Switzerland) at 4 to 400 × total magnification. Images were captured using a coupled Leica DMC4500 digital camera and processed by the LAS v 4.8 software (Leica Microsystems Suiza Limited 2015).

RESULTS

The digestive tract was initially constituted by the tongue, which is located on the mouth floor, followed by the pharynx and oesophagus, the latter comprising a long and thin tubular organ connected to the stomach. The stomach is connected through the pyloric sphincter to the small intestine, which is, in turn, is connected to the large intestine, ending in the cloaca. The descriptions for each organ are detailed below.

Tongue

The tongue, non-bifurcated (Figure 1a) and positioned on the mouth floor, is mostly constituted by muscle. The tongue apex mucosa had its margin covered by a stratified squamous epithelium (Figure 1b), where transverse sections allowed cylindrical filiform papillae to appear clearly (Figure 2a, b). Near the area, it was possible to observe a single cartilage block located in the center of the organ, sharing space with skeletal muscle in different positions, but mostly longitudinally and transversally (Figure 1c). The lateral margin of the tongue's radix presented glands inserted partially between the epithelium and the dense irregular connective tissue, which after was followed by an extense area of skeletal muscle disposed in random directions (Figure 1d). After the tongue radix, it was observed the beginning of the pharynx, where the initial portion of a central canal composed mostly by cartilage blocks was seen.

The cylindrical filiform papillae and the glands, seen respectively in the apex and radix of the tongue, didn't react to PAS staining (Figure

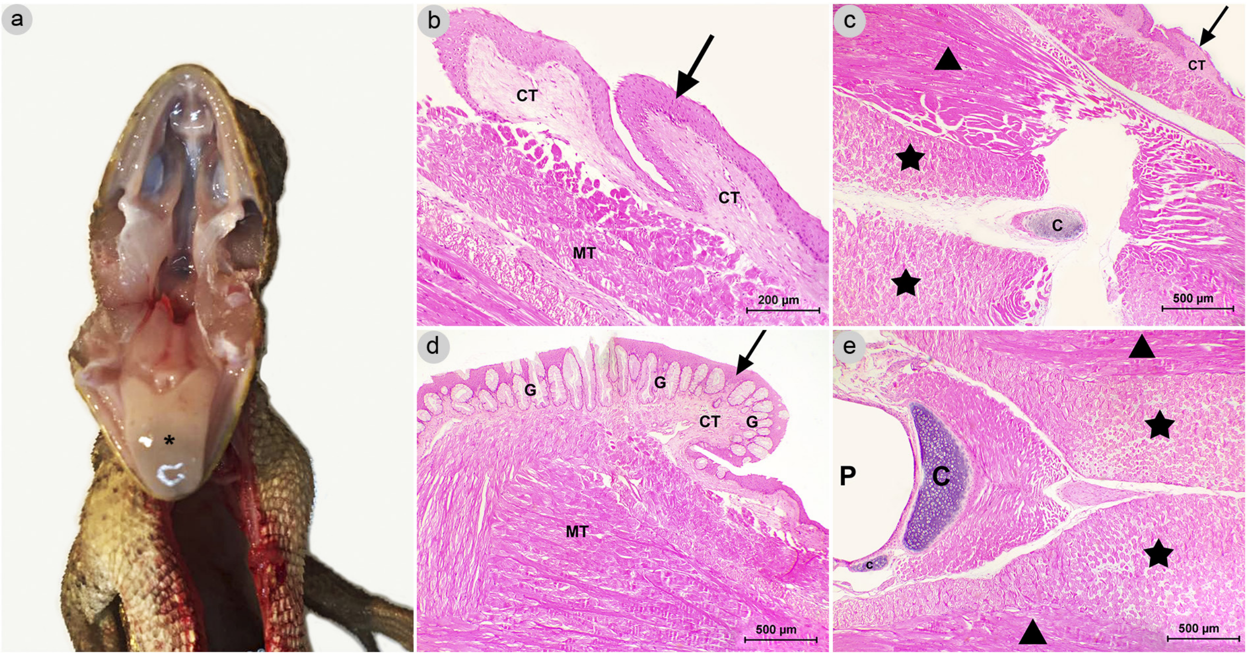

Figure 1. ***Uranoscodon superciliosus*** **tongue. (a) Macroscopic view of the tongue (black asterisk) on the mouth floor. (b) Photomicrography of the tongue apex. Lined by stratified squamous epithelium (black arrow), below dense irregular connective tissue (CT) and skeletal muscle tissue (MT) and (c) Hyaline cartilage block (C) located in the middle of skeletal muscle in transversal (star) and longitudinal (triangle) positions. (d) Photomicrography of the tongue radix. Glands (G) observed between the epithelium (black arrow) and the connective tissue (CT), followed by skeletal muscle tissue (MT) and (e) Beginning of the pharynx (P) marked by a central canal with hyaline cartilage blocks (C), with skeletal muscle bundles in the tongue radix, in both longitudinal (triangle) and transversal (star) dispositions. HE staining.**

2a, c). However, there was a strong reaction from the papillae and glands to Alcian blue staining (Figure 2b, d).

Oesophagus

The oesophagus is characterized as a long and thin hollow tube best observed alongside the pharynx, descending towards the caudal digestive tract region, and connected to the stomach. All oesophagus regions were macroscopically similar, with rectilinear and longitudinal folds, where was possible seeing an alternation between tall and short folds (Figure 3a). The transition from oesophagus to the stomach were signalized by the sudden change in the mucosa characteristics (Figure 3b).

The proximal oesophagus region presents a mucosa displaying long primary and secondary folds covered by a simple mucous cylindrical epithelium with goblet cells (Figure 4a). The epithelial tissue is supported by the *lamina propria*, constituted by loose connective tissue. A thin mucosal muscular, constituted by smooth muscle, separates the mucosa and submucosa (Figure 4a). The goblet cells of the three oesophagus' regions reacted strongly to PAS and AB, while the mucosa was weakly positive (Figure 5).

The submucosa, constituted by dense irregular connective tissue, fills the local folds (Figure 4b). The external muscular layer, located below the submucosa, presents two other smooth muscle layers, one inner circular layer and another outer longitudinal layer. The inner layer is thicker than the outer one, which presents dense irregular connective tissue forming septa, like muscular blocks. A serosa is noted following the external muscular layer and,

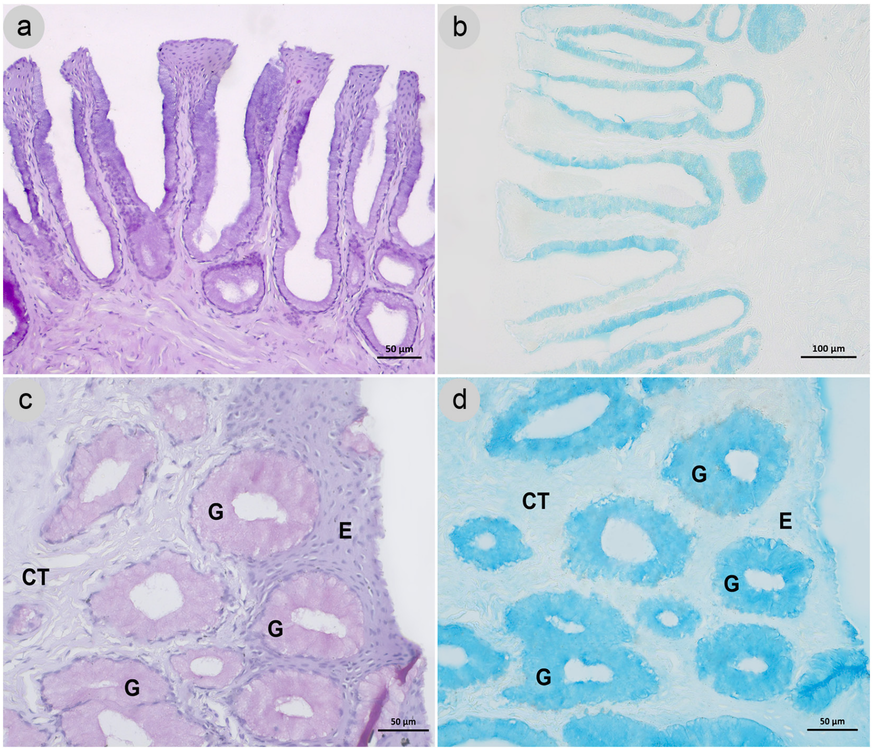

Figure 2. Histochemistry of the tongue of *Uranoscodon superciliosus.* (a) Papillae in the tongue's apex showing no reaction to PAS. (b) Papillae in the tongue's apex with positive reaction to AB. (c) Glands in tongue's radix papillae showing no reaction to PAS. (d) Glands in tongue's radix papillae with strong positive reaction to AB; epithelium (E), glands (G) and dense irregular conective tissue (CT).

when associated to other organs, is considered as an adventitious layer (Figure 4c).

The medium (Figures 4d, e) and distal (Figure 4f) oesophagus regions present similar characteristics to the proximal region, and the distal region presents thicker and shorter epithelium folds and a thicker mucosal muscular compared to the other oesophagus regions (Figure 4f).

Stomach

The stomach was a hollow 'J' shaped organ ending in a junction with the small intestine, termed the pyloric sphincter. The cardic region, after the oesophagus, and the fundic didn't present folds, probably because it presented a high quantity of food items inside the organ at the time of analysis (Figure 3b). The pyloric region, short and narrow, showed longitudinal thick folds, being more spaced from one another and going directly into the gastrointestinal sphincter (Figure 3c, d).

The cardic, fundic and pyloric regions exhibit a folded mucosa covered by a simple cylindrical epithelium containing mucous cells. The mucosa also exhibits depressions, named gastric pits, connected to the gastric glands. The lamina propria is located below the epithelium. The mucosal muscular is constituted by smooth muscle and the submucosa by a dense irregular connective tissue. The external muscular layer is divided into two other smooth muscle layers, an inner circular one and an outer longitudinal one (Figure 6).

Differences between the three stomach regions following the gastric pits and gastric glands are observed. Concerning the cardic region, the gastric pits in this area are shorter and the gastric glands more numerous within the mucosa (Figures 6a, b). The fundic region is similar to the cardic region, except for deeper gastric pits in some areas (Figure 6c). The pyloric region exhibits even deeper gastric pits, but less gastric glands, alongside a slightly thicker mucosal muscular, compared to the other

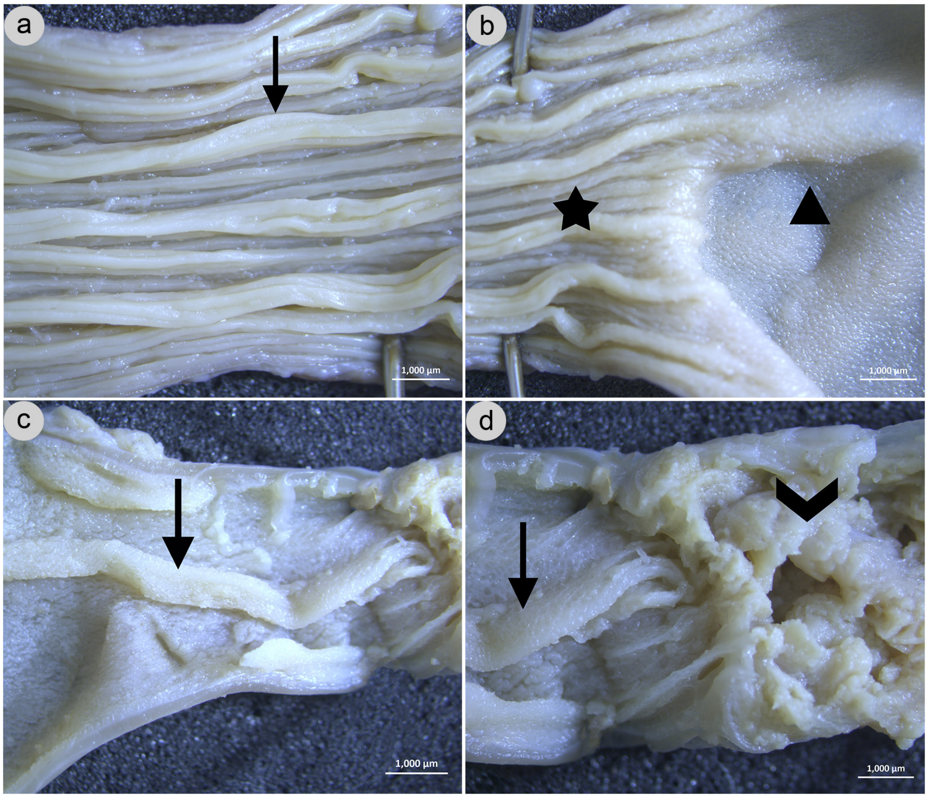

Figure 3. Gross morphology of oesophagus and stomach of *Uranoscodon superciliosus*. (a) Thick and rectilinear folds (black arrow) in all oesophagus' regions. (b) Gastroesophageal sphincter, with transition from oesophagus (star) and stomach's cardic and fundic regions (triangle). (c) Pyloric region, with longitudinal, thick and spaced folds (black arrow). (d) Gastrointestinal sphincter (arrowhead).

stomach regions (Figure 6d). The cardic, fundic and pyloric regions presented positive reaction to PAS coming from the epithelium and the gastric glands, whereas the pyloric region had a strong reaction than other regions (Figure 7a, c, e). None of the regions reacted positively to Alcian Blue (Figure 7b, d, f).

Small intestine

The small intestine (SI) had initially longitudinal zigzag folds, which were larger and more put together (Figure 8a). The medium and distal regions also presented zigzag folds, this time leaner and more anastomosed (Figure 8b, c).

The SI presents varied villi throughout its entirety, covered by a simple cylindrical epithelium with mucous and goblet cells (Figure 9). The goblet cells from the intestinal villi reacted strongly to PAS. However, this reaction was more intense in direction to the distal region of the organ, where mucous cells were strongly marked (Figure 10a, b, d). The goblet cells from all three regions were intensively marked in AB staining (Figure 10b, d, e). The lamina propria located just below the epithelial tissue is constituted by loose connective tissue, while the mucosal muscular is composed of smooth muscle and the submucosa, connected by dense irregular connective tissue (Figure 9a, b, c, d, e, f).

The proximal portion of the SI exhibit elongated filiform villi containing goblet cells (Figures 9a, b). The medium portion is formed by leaf-like villi, mostly branched and containing more goblet cells (Figures 9d, e). The distal portions also exhibit leaf-like villi alongside digitiform and branched ones, smaller in height, with more numerous goblet cells in relation to the other SI portions (Figure 9f).

The external muscular layer of all portions is constituted by two other smooth muscle layers, one inner circular one and one outer

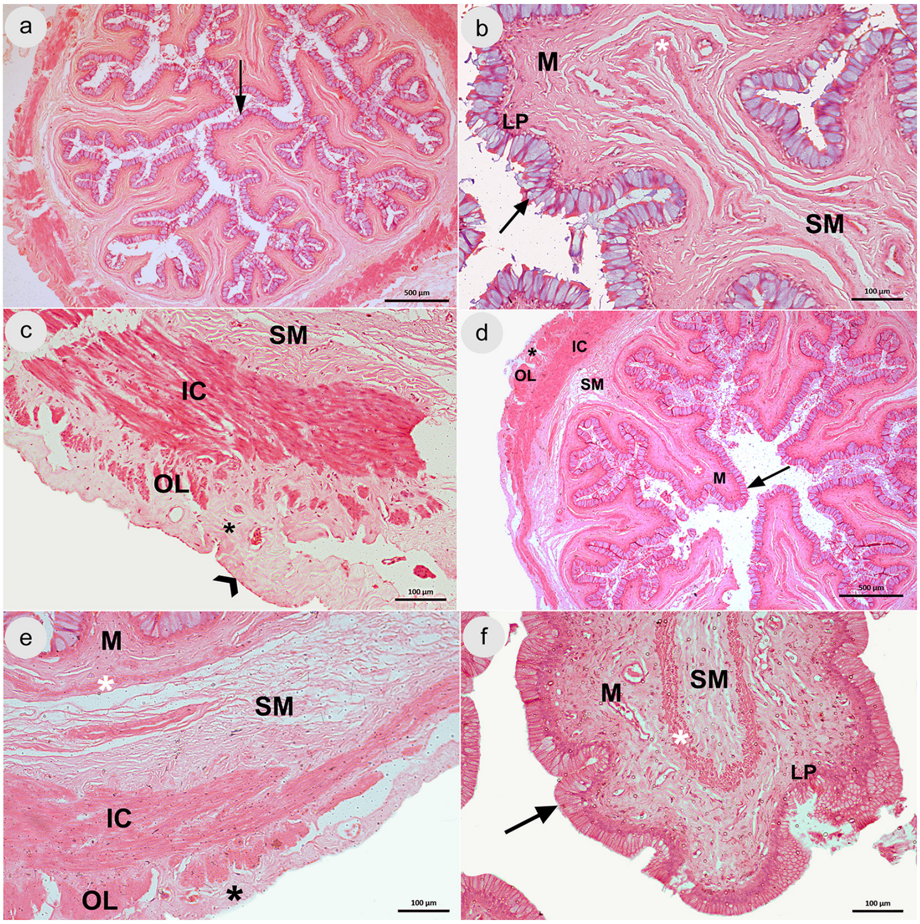

Figure 4. ***Uranoscodon superciliosus*** **oesophagus photomicrography. (a) Overview of the proximal region of the oesophagus. (b) Larger view of a proximal region fold. (c) Muscular layer in the proximal region. (d) Overview of the medium oesophagus region. (e) Larger view of medium oesophagus region layers. (f) Fold in the distal oesophagus region. Simple mucous cylindrical epithelium (black arrow); mucosa (M);** ***lamina propria*** **(LP); mucosal muscular layer (white asterisk); submucosa layer (SM); external muscular layer divided in two, a n inner circular (IC) and outer longitudinal (OL) layer; connective tissue septa associated with the outer longitudinal muscular layer (black asterisk); serosa (arrowhead). HE staining.**

longitudinal one, separated by a connective tissue septa with an externally identified serosa (Figures 9c). In addition, the external muscular layer decreases in size along the final portions (Figure 9f).

Large intestine

The proximal region of the large intestine started after the intestinal sphincter, formed by rectilinear longitudinal and thick folds (Figure 8d). This region presented wavy and anastomosed folds, organized in random direction, being spaced from one another (Figure 8e). A transition was seen between the proximal and distal regions, when the folds were closer together maintaining the same pattern. In the distal region was observed a zone were the folds had a transversal thickening, which can be related to a macroscopical demarcation of the rectum beginning (Figure 8f).

Both the proximal and distal large intestine regions present a folded mucosa covered by simple cylindric epithelium with many goblet cells, with longer distal region folds (Figures 11a, b, c). The lamina propria is constituted by loose connective tissue and the mucosal muscular, by smooth muscle, which becomes thinner and more noticeable towards the distal region. The submucosa is constituted by dense irregular connective tissue, with no differences between regions. The external muscular layer is formed by an inner circular layer and an outer longitudinal one, both constituted by smooth muscle (Figures 11a, b).

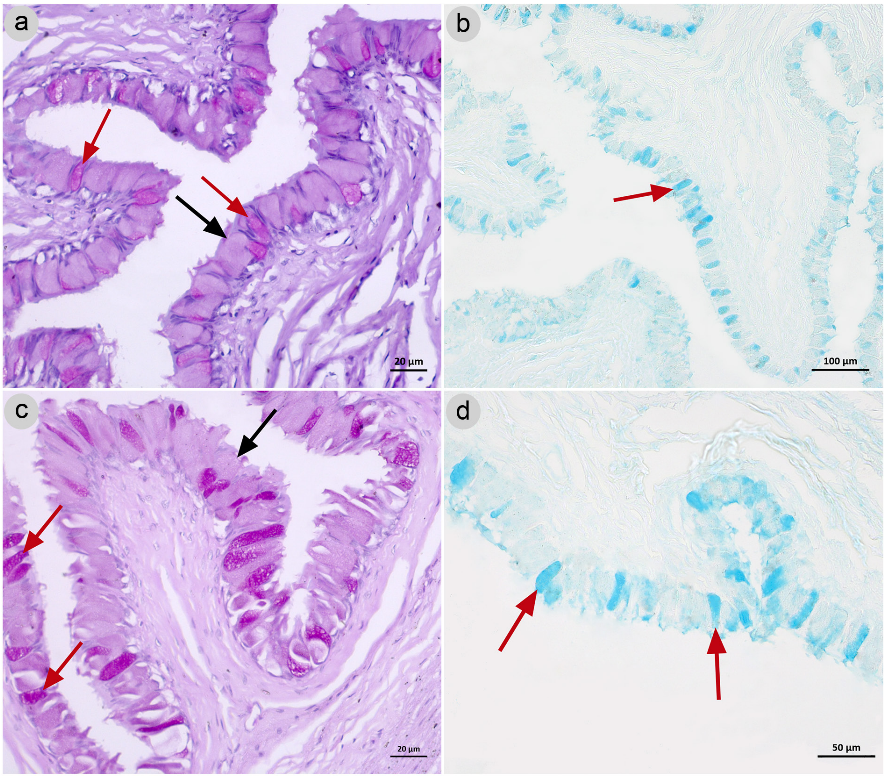

Figure 5. Histochemistry of the oesophagus of Uranoscodon superciliosus. (a) Proximal region with positive reaction to PAS. (b) Proximal region with positive reaction to AB. (c) Medium and distal regions with positive reaction to PAS. (d) Medium and distal regions with positive reaction to AB; simple mucous cylindrical epithelium (black arrow); goblet cells (red arrow) with strong and positive reaction in PAS and AB.

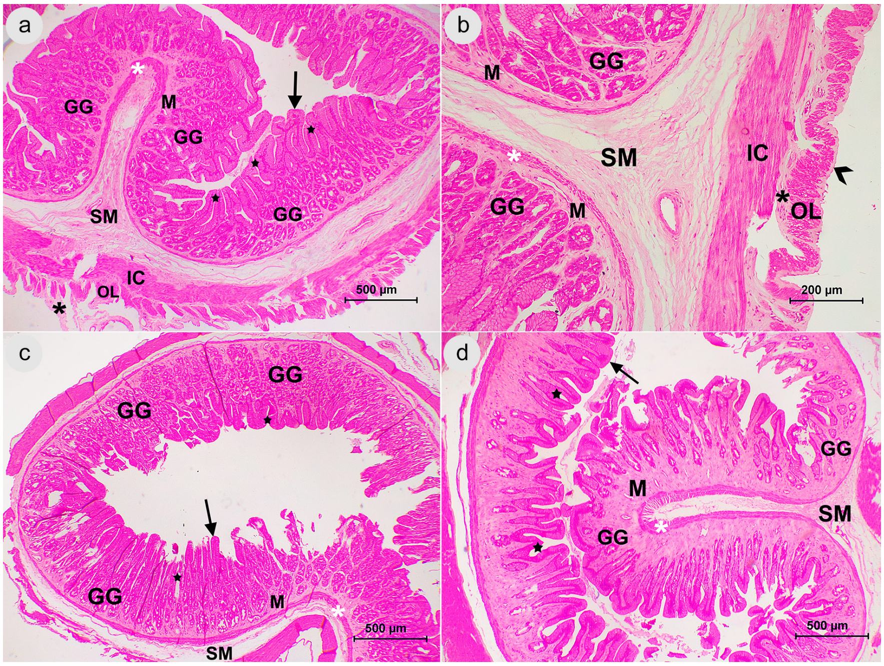

Figure 6. *Uranoscodon superciliosus* stomach photomicrography. (a) Overview of the cardic stomach region. (b) Larger view of the cardic region layers. (c) Overview of the fundic stomach region. (d) Overview of the pyloric region. Lining simple cylindrical epithelium (black arrow); mucosa (M); mucosal muscular layer (white asterisk); gastric pits (star); gastric glands (GG); submucosa (SM); external muscular layer divided in two, inner circular (IC) and outer longitudinal (OL) layer; connective tissue septa associated with the outer longitudinal muscular layer (black asterisk); serosa (arrowhead). HE staining.

DISCUSSION

Despite *Uranoscodon superciliosus* diet-related studies, which also include predation notes and foraging mode and stomach content descriptions (Howland et al. 1990, Gasnier et al. 1994, 1997, Vitt et al. 1999, Picelli et al. 2019), digestive tract characterizations are still lacking, making this the first study in this regard for this species. It is also important to note that studies

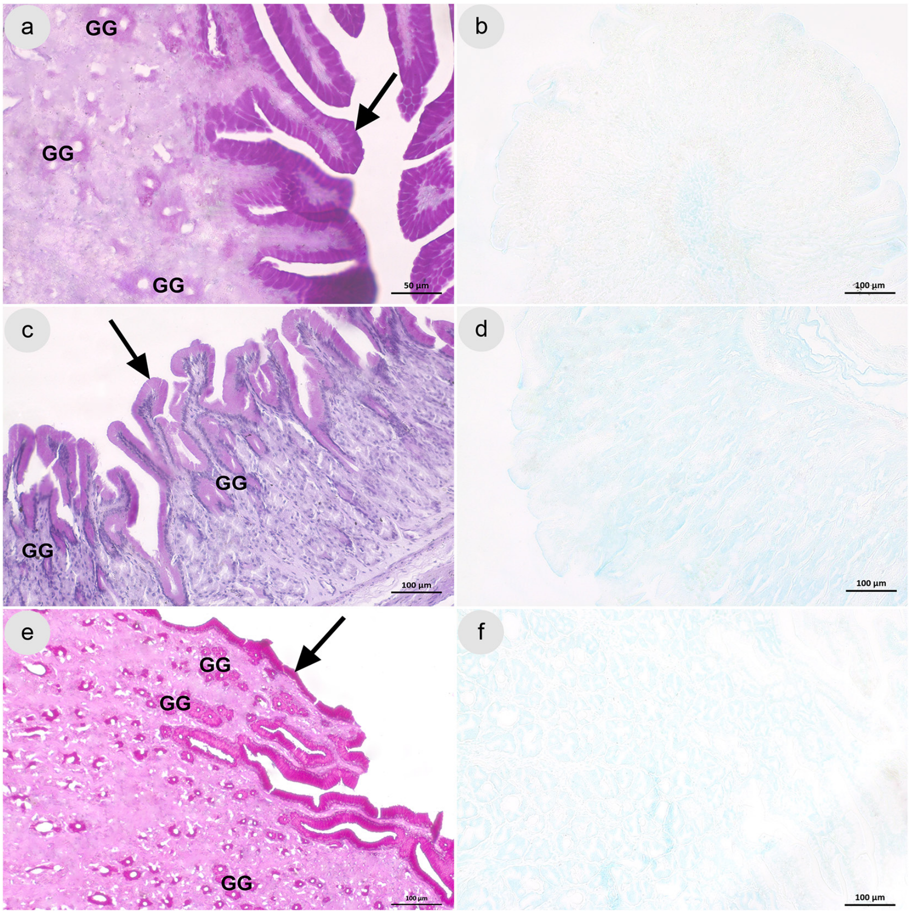

Figure 7. **Histochemistry of the stomach of *Uranoscodon superciliosus.* (a) Cardic region with positive reaction to PAS. (b) Cardic region without reaction to AB. (c) Fundic region with positive reaction to PAS. (d) Fundic region without reaction to AB. (e) Pyloric region with strong positive reaction to PAS. (f) Pyloric region without reaction to AB; lining simple cylindrical epithelium (black arrow); gastric glands (GG).**

concerning lizard and reptile histomorphological descriptions are still scarce, both in Brazil (Magalhães et al. 2010, 2014, Rodrigues-Sartori et al. 2014, Calais et al. 2016), and worldwide (Guard 1980, O'Grady et al. 2005, Koca & Gürcü 2011, Srichairat et al. 2018, Masyitha et al. 2020), especially compared to other vertebrates, such as mammals and birds. Furthermore, digestive tract studies are also mostly correlated with other goals, such as parasite identification (Grosset 2010, Rataj et al. 2011, Wolf et al. 2014), immunohistochemical analyses (Huang & Wu 2005, Liu et al. 2007, Mahfud et al. 2020) and specific cell assessments, *i.e.,* argyrophil cells (Shulan 2003, De-Chang 2006, Zhou et al. 2008). The lack of research on reptile digestive tract histomorphology implies in morphological data expansion challenges, creating barriers concerning the understanding of individual biology, evolutionary history, and the digestion process itself (Thongboon et al. 2019).

The digestive tract, comprising the tongue, oesophagus, stomach, and small and large intestines, is the most common organ assessed in lizard and reptile investigations (Luppa 1977, Mader 2006, Srichairat et al. 2018, Masyitha et al. 2020), with some assessments concerning accessory organs, such as the liver, gallbladder and pancreas (Srichairat et al. 2018).

The tongue is one of the lizard organs with the most morphological variations, due to different foraging modes, diets, and habitats (Iwasaki 2002). In active foraging species, the tongue is elongated and linked to a muscular arrangement associated to tongue-flicking, whereas ambush foraging species, such as *U.*

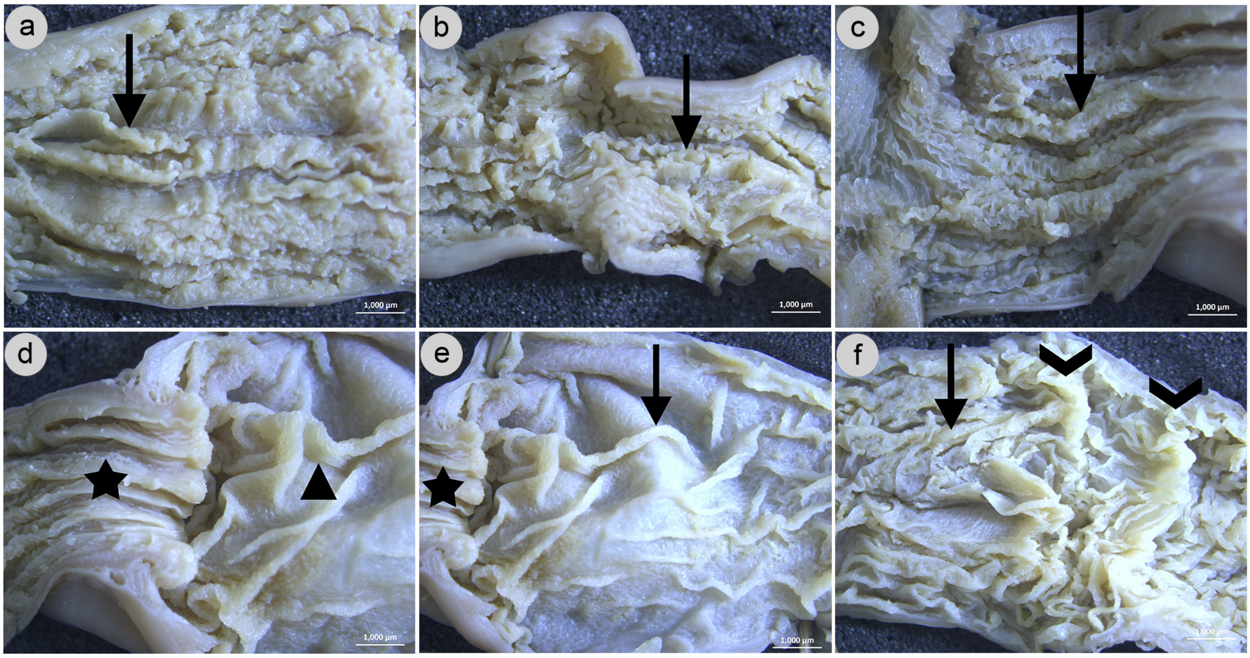

Figure 8. Gross morphology of the small and large intestines of *Uranoscodon superciliosus.* (a) Zigzag folds (black arrow) in the proximal portion of the small intestine. (b) Slender and anastomosed zigzag folds (black arrow) in the medium and (c) distal region of the small intestine. (d) Intestinal sphincter (star) and proximal region of the large intestine (triangle). (e) Curved and anastomosed folds (black arrow) in the proximal region of the large intestine. (f) Anastomosed and less spaced folds in the caudal region of the large intestine (black arrow) and transversal folds (arrowhead).

superciliosus, present less adapted patterns in this regard (Cooper 1995, Iwasaki 2002). The ambush foraging mode (also termed the sit and wait mode), does not involve large animal displacement, in contrast to active foraging, as predators remain still or display reduced movements, capturing less active prey (Huey & Pianka 1981, Zug et al. 2001, Silva & Araújo 2008). *U. superciliosus* does not have a bifurcated tongue, commonly observed in ambush foragers, whereas the bifurcation and tongue-flicking movement would be indicative of active foraging (Schwenk & Rubega 1985, Cooper 1995). The presence of cylindrical filiform papillae in the apex of the tongue, is often related to mechanical support during food manipulation and swallowing, as seen in the Sinai fan-fingered gecko *Ptyodactylus guttatus* Heyden, 1827 (Salem et al. 2017, Gewily et al. 2021). Despite the presence of lingual papillae, *U. superciliosus* did not have visible taste buds on the tongue, which has been observed in other lizard species. This absence may be explained by the fact that some lizards can display the taste buds in other parts of the oral cavity, instead of the tongue (Cizek et al. 2019).

The presence of a hyaline cartilage block in the center of the organ may be associated to tongue support inside the oral cavity and movement aiming at prey capture. A study investigating the chameleon *Chameleo chameleon* (Linnaeus, 1758), demonstrated that cartilage is responsible for tongue hardening for prey capture, without the need for fast locomotion (El Mansi & Fouda 2017). Although they present a relatively distant relationship, chameleons and tropidurids belong to the Iguania clade (Pyron et al. 2013) and share, among other characteristics, similar foraging modes, which may be associated to the presence

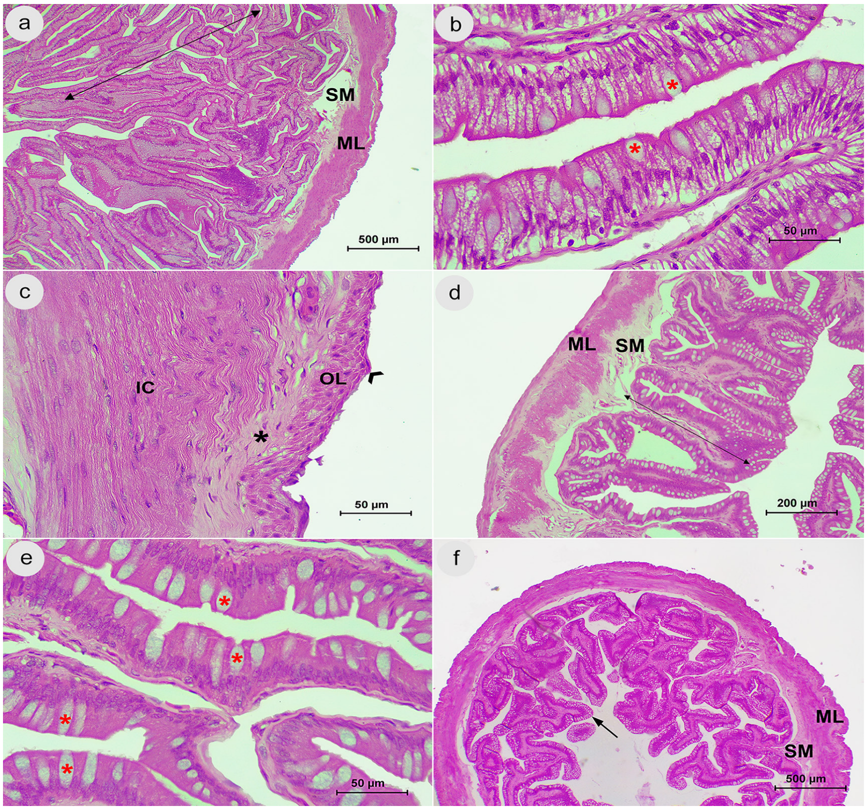

Figure 9. ***Uranoscodon superciliosus*** **small intestine photomicrography. (a) Overview of the proximal portion; presence of filiform elongated villi (two-head arrow). (b) Proximal portion villi. (c) Muscular layer of the proximal and medium portions. (d) Overview of the medium portion in the small intestine; digitiform villi (two-head arrow). (e) Larger view of medium portion villi. (f) Overview of the distal region in the small intestine. Simple cylindrical epithelium (black arrow); submucosa (SM); goblet cells (red asterisk); external muscular layer (ML); inner circular layer (IC); connective tissue septa between the two layers of the external muscular (black asterisk), outer longitudinal (OL) layer; serosa (arrowhead). HE staining.**

of cartilage blocks on *U. superciliosus* tongues. In addition, the glands found in the radix of the tongue are similar to the pattern of the glands found in other lizard species, like the ones seen in the lizard *Laudakia stellio* (Agamidae, Squamata), where acid and neutral mucin secretion was observed, and the ones seen in some chamaleon species, where tubular glands were disposed in the connective tissue (Wassif 2002, Koca et al. 2007, Fouda et al. 2015). The papillae in the apex and the glands in the radix of the tongue reacted strongly to Alcian Blue, indicating positive reaction to the presence of sulfated acid glycosaminoglycans. The presence of this type of GAG's was already observed in the tongue of different lizards, and is normally related to prey capturing functions, lubrication and protection of the epithelium against microorganism growth (Koca et al. 2007, Taha 2013, Salem et al. 2017, Srichairat et al. 2022a).

The esophageal mucosa containing folds has already been described in lizards, turtles and some species of fish (Rodrigues et al. 2008, Magalhães et al. 2014), being necessary for distension of the esophageal tube to allow the ingestion of larger prey (Magalhães et al. 2014). The number of folds varied according to the need for a larger extension area (Sricharait et al. 2018).

Unlike most reptiles, *U. superciliosus* does not present epithelium cilia in the oesophagus, suggesting that individuals depend on specific movements and gravity for food loading in the digestive tract (Zug et al. 2001). However, some *U. superciliosus* records indicate it also preys on giant earthworms, larger prey than usual for this species (Picelli et al. 2019). In fact, this species mostly feeds on small invertebrates with cylindrical and limp bodies (Howland et al. 1990, Gasnier et al. 1994), indicating that certain oesophagus morphology structures, such as

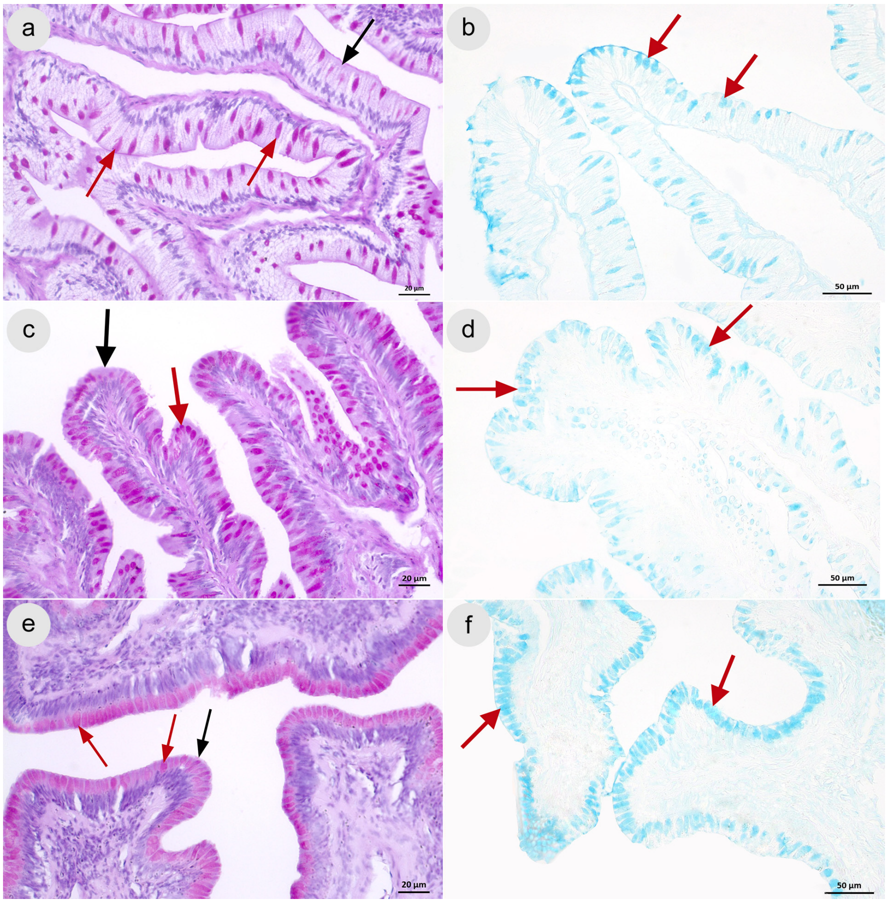

Figure 10. Histochemistry of the small intestine of *Uranoscodon supercilosus.* (a) Proximal region with positive reaction to PAS. (b) Proximal region with strong positive reaction to AB. (c) Medium region with strong positive reaction to PAS. (d) Medium region with strong positive reaction to AB. (e) Distal region with strong positive reaction to PAS. (f) Distal region with strong positive reaction to AB; simple cylindrical epithelium (black arrow); goblet cells with strong and positive reaction in PAS and AB (red arrow).

epithelium cilia are probably unnecessary. Furthermore, the presence of goblet cells may aid in food loading into the digestive tract, as described for other reptiles (Przystalski 1980). All the three regions from the oesophagus reacted positively to PAS and AB, indicating the presence of neutral and sulfated acid glycosaminoglycans coming especially from the goblet cells. The same was reported in other lizards, like Argentine giant tegu *Salvator merianae* Duméril & Bibron, 1839 and the African five-lined skink *Trachylepis quinquetaeniata* (Lichtenstein, 1823), the last one presenting a strong reaction to sulfated mucins presence (Awaad et al. 2022, Betancourt et al. 2022). Both neutral and sulfated acidic mucins play an important role in the lubrication of the esophageal epithelium, being also related to pH homeostasis and to the digestion process before the food gets to the stomach (Awaad et al. 2022, Betancourt et al. 2022, Srichairat et al. 2022b). Thus, the abundance and positive reaction to PAS and AB presented by goblet cells may be due to the fact that most of the prey consumed by *U. superciliosus* have integuments composed of sclerotized structures (e.g., insect exoskeletons) (Gasnier et al. 1994, Hickman et al. 2019).

The presence of a folded stomach mucosa is related to the expansion of stomach walls during food ingestion (Rodrigues-Sartori et al. 2008, Pardiñas et al. 2020). In the macroscopic view, the similarity between cardic and fundic regions, both being different from the pyloric region, can also be seen in studies with lizards (Sricharait et al. 2018, Engelke et al. 2020). Although the folds in the first two regions are well observed in other reptiles, such as *V. salvator* and *H. mabouia* (Rodrigues-Sartori et

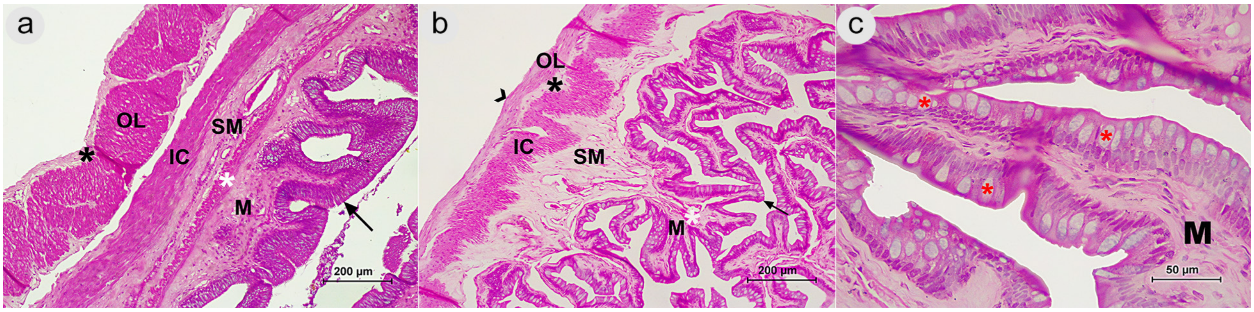

Figure 11. ***Uranoscodon superciliosus*** **large intestine photomicrography. (a) Overview of the proximal region in the large intestine. (b) Overview of the distal region of the large intestine. (c) Larger view of the folds present in the distal region. Simple cylindrical epithelium (black arrow); mucosa (M); mucosal muscular layer (white asterisk); submucosa (SM); inner circular layer (IC); outer longitudinal layer (OL) layer; connective tissue septa (black asterisk); serosa (arrowhead); goblet cells (red asterisk). HE staining.**

al. 2011, Sricharait et al. 2018), in the stomach of *U. superciliosus* were not visible, which can be explained by the fact that the organ was stuffed with food items in studied animal. Additionally, it was noted that the stomach became narrower after the pyloric area started with less longitudinal folds in this region, as in the cases of *Uromastyx aegyptia* (Forskål, 1775) and *Pelomedusa subrufa* (Bonnaterre, 1789) (Zaher et al. 2012, Abouelela & Reem 2020).

The mucous cells present in the epithelium of the three regions of the stomach showed neutral glycosaminoglycans, indicated by the positive staining reaction, and the secreted mucus has the function of gastric protection against chemical substances, mechanical injuries and external pathogens. A strong PAS reaction was also seen in the stomach of *I. iguana* (Serra-Campos et al. 2021). The gastric pits observed in the stomach of *U. superciliosus* are connected to the secretory portion of the gastric glands, through epithelium invaginations, and have also been reported in other lizard species (El-Bakry et al. 2012, Çakici & Akat 2013, Skrypka & Panikar 2020). Variations in pit depth are common in other reptiles and vertebrates in general (Khamas & Reeves 2011, Vieira-Lopes et al. 2014, Gogone et al. 2017).

The stomach of *U. superciliosus* had gastric glands that responded positively to PAS staining, indicating the presence of neutral glycosaminoglycan secretions. However, the lack of reaction to Alcian blue shows that no sulfated acid mucins were present, this absence also reported in *I. iguana* and *Ophisops elegans* Ménétries, 1832 lizards (Çakici & Akat 2013, Serra-Campos et al. 2021). Studies suggest that these gastric glands are responsible for secretions composed mostly by pepsinogens and HCl in lizard stomachs, as well as in other vertebrate species (Liquori et al. 2000, Rodrigues-Sartori et al. 2011, Thongboon et al. 2019).

The presence of larger and more abundant gastric glands in the cardic and fundic stomach regions indicate that chemical digestion begins when food enters this organ, as this process depends on pepsinogen and HCl secretion (Darias et al. 2007). The pyloric stomach region exhibits a thicker mucosal muscular than the other stomach regions, associated to the contraction movement associated to gastric gland secretion release stimulation (Chaves & Vazzoler 1984, Magalhães et al. 2010). Two layers of muscle are observed in two different dispositions, one inner and circular and the other outer longitudinal, according to Luppa (1977) and Zug et al. (2001), which play a role in the peristalsis movement of the pyloric stomach region.

The zigzag pattern observed macroscopically in the folds of the small intestine was also seen in the water monitor lizard *V. salvator,* where the size of the folds also varied between regions (Srichairat et al. 2018). Histologically the villi play an important role in increasing the absorption area of nutrients and varied along the different small intestine portions in *U. superciliosus* (Magalhães et al. 2010, Masyitha et al. 2020). A decrease in the size and number of villi along the small intestine was observed, which may be associated to a decreased absorption capacity and a transition to the large intestine, also observed in *Pogonna vitticeps* (Ahl, 1926) (Engelke et al. 2020) and the gecko *Hemidactylus mabouia* (Rodrigues-Sartori et al. 2014). The small intestine portions present villi type variations, ranging from filiform in the proximal portions to leaf-like in medium and digitiform and leaf-like in the distal. These variations have also been observed in other vertebrates, such as *Chelonia mydas* (Magalhães et al. 2010) and Podocnemididae chelonians (Magalhães et al. 2014).

The presence of two cellular types in the epithelium, *i.e.,* mucous cells and goblet cells, have been reported previously in other reptile species (Al-Thani & El-Sharif 1996, Ahmed et al. 2009). The histochemical analysis showed positive reaction to the presence of neutral glycosaminoglycans coming from mucous and goblet cells in the epithelium, plus positive reaction to sulfated acidic mucins coming from the goblet cells in all three regions of the SI. Neutral and acidic mucins displayed in the small intestine, especially by the goblet cells, play an important role in aminoacid absorption, epithelium hydration, protection against pathogens and chemical defense against enzymatic degradation of the mucus barrier, this last function being properly performed by the acidic glycosaminoglycans (Ferri et al. 1976, Al-Thani & El-Sharif 1996, Awaad et al. 2022).

The presence of a transverse fold area and the division of the large intestine in proximal and distal regions were also seen in the Nile crocodile *Crocodylus niloticus* Laurenti, 1768, where the organ was also mentioned as colorectum (Shaker & Ibrahium 2021). The large intestine exhibits functions related to hydroelectrolytic equilibrium, feces formation and mucus production by abundant goblet cells, contributing to feces sliding (Allen et al. 1986, Magalhães et al. 2010). Less folds with smaller lengths are associated to decreased absorption capability, as observed in other reptiles (Al-Thani & El-Sharif 1996, Engelke et al. 2020, Shaker & Ibrahium 2021).

In conclusion, the digestive tract morphology of *Uranoscodon superciliosus* corresponds to most other reptile descriptions, although some uncommon features for lizards are noted, such as villi type variations in the small intestine and the absence of epithelium cilia in the oesophagus. In contrast, the tongue presents the most morphological variations as a function of foraging mode and dietary habits. The stomach is differentiated into cardic and fundic regions and the pyloric region, mainly according to the depth of the gastric pits and number of glands. The small and large intestines follow previously described patterns for other vertebrates. The histochemistry analysis showed that neutral and sulfated acid glycosaminoglycans play different and important roles related to the organ's function. Thus, the digestive tract morphology of *U. superciliosus* and the foraging mode and diet of this species was described and correlated to these descriptions, comprising a potential study model for other reptile morphology assessments.

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GAB, AMP and MSM conceived and designed the study. AMP and ACR performed the fieldwork. GAB and ACR processed the data and performed the microscopic analyses. GAB interpreted the results and helped prepare the manuscript. AMP and MSM contributed to the critical reading of the manuscript and supervised the findings reported herein. All authors took part in the preparation, revision, and final approval of the final manuscript version.