An Examination of the Sensory Structures in the Oral Cavity of the American Alligator (*Alligator mississippiensis*)

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ABSTRACT The location and distribution of mucosal sensory structures of the crocodilian oral cavity are poorly understood. Although there are several descriptions of these structures in adults, nothing is known about their development. The purpose of this study was to document location, morphology, and relative abundance of these mucosal sensory structures in both hatchling and subadult alligators. Numerous mucosal sensory structures and pale staining dome-shaped papillae were observed only in the upper palate and tongue. In hatchlings, these papillae, which house either mechanoreceptive or chemosensory (taste buds) structures, were larger and more prevalent on the tongue than the upper palate. In the subadult, however, these papillae housed primarily mechanoreceptive structures and possibly degenerate taste buds. Although the presence of the mechanoreceptive structures in the palates of the suabadult alligator are to be expected, the loss of most taste buds is hitherto undocumented. Thus, there is morphological support for an ontogenetic shift in the role of the sensory palate, from a prey detection gustatory sensory system in hatchlings to a prey-manipulative mechanoreceptive system in subadults. J. Morphol. 275:1312-1320, 2014. © 2014 Wiley Periodicals, Inc.

KEY WORDS: aquatic vertebrate; taste bud; mechanoreceptor

INTRODUCTION

Avesuchians, a group encompassing both birds and crocodilians, share many common features. However, the structure of their oral cavities, at least superficially, appears to be quite different. The beak and associated oral cavities of birds contain numerous imbedded sensory organs. Both mechanoreceptive and chemoreceptive structures have been observed in several bird species. Grandy, Herbts, and Merkel corpuscles are mechanoreceptors (Iggo and Andres, 1982; Gentle and Breward, 1986). Herbst corpuscles are viewed as the avian Pacinian corpuscle, and are found in the skin of the bill and tongue of aquatic birds but not in nonaquatic birds (Iggo and Andres 1982). Gandry and Herbst corpuscles, however, are smaller encapsulated structures whose peripheral nerve endings are closely

associated with intracapsular tactile cells (Schwarztkopff, 1973). They differ in size and location, with the Gandry corpuscles being larger and unique to aquatic birds, and the Merkel corpuscles being smaller and thought to be distributed within many vertebrate species (Toyoshima 1993). Taste buds, a spherical unencapsulated group of cells residing within the epithelium whose bases are associated with sensory neurons, have been reported in many vertebrate taxa (Northcutt, 2004).

In crocodilians, however, the description of the sensory organs in the oral cavity appears to be less complete. In Crocodylus niloticus (Putterill and Soley, 2003, 2004, El-Sayyad et al., 2011), there is a general description of the sensory system in the palate of the adult crocodile, detailing the presence of three different types encapsulated mechanoreceptors, free nerve endings, and tastebuds, there is no information about either distribution or structural differences in sensory organs between hatchlings and adults. Even less is known about the mucosal sensory system in alligators. Ferguson (1981) examined the structure of the palate in Alligator mississippiensis, briefly describing the mucosal sensory system in the oral cavity of the hatchling without a description of the development of these sensory structures. There is little known about the mucosal

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Fig. 1. Anatomical view of pale staining tongue papillae of subadult Alligator. Black horizontal line indicates the part of the papillae that was measured. Stained with Pontamine sky blue. Scale bar: 0.5 mm (white line) [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

sensory system of the oral cavity of the hatchling alligator.

The aim of this study was to specifically examine the mucosal sensory system of the oral cavity in the hatchling and subadult A. mississippiensis. The ontogeny of these structures will be determined using both histological and anatomical techniques. Because no ontogenetic data exist on alligator oral sensory development, hypotheses can only be based on findings in other tetrapods. Because some cetaceans were observed to undergo a decrease in the number of taste buds postnatally (Komatsu and Yamasaki, 1980), with few reported taste buds in adults (e.g., Yamasaki et al., 1978; Komatsu and Yamasaki, 1980; Behrmann, 1988), it is hypothesized that the abundance and size of sensory structures (specifically taste buds which can be observed anatomically) may undergo an ontogenetic change (e.g., a decrease from birth onward). Alternatively, it may be hypothesized that bigger alligators have more or even bigger taste buds, as reported in cats (Robinson and Winkles, 1990) and mice (Zhang et at., 2008).

MATERIALS AND METHODS Gross Anatomy

Five neonates (Snout Vent Length (SVL) ranging from 27 to 36.5 cm) and 11 subadults *A. mississippiensis* (Daudin, 1802; SVL ranging from 97.5 to 180 cm) were obtained from the Rockefeller Wildlife Refuge, Louisianna in accordance with the guidelines set by the Slippery Rock University Institutional Animal Care and Use Committee (protocol number 2007–2009). The oral cavity was divided into three regions: tongue, upper palate, and lower palate (the mucosal between the tongue and teeth in the lower jaw). Palates and tongues were excised. The exposed surface area was estimated by tracing the shapes of the tongues and upper palates onto paper, cutting them out, and weighing these paper cutouts against a known standard. The tongues and upper palates, then, had a solution of 1–2% pontamine sky blue, in 0.5% sodium acetate buffer (pH 8.3), spread on their surfaces (Berkhoudt, 1977). This was, then, allowed to dry for at least a day, when the pale staining dome-shaped papillae (PSDSP) were easily identifiable (see Fig. 1). These papillae (thought to correlate to taste buds: Berkhoudt, 1977) were counted and the diameters of 10 representative such regions were, then, estimated using calipers for each tongue and upper palate of 11 subadults. Data were then statistically analyzed.

Histology

Different specimens were used in this part of the study. The heads of five hatchling and three subadult American alligators (A. mississippiensis) were fixed in 10% formalin for at least a week. The tongue, lower palate, and upper palate from each were dissected out. For the hatchling, the entire structures (upper palate, lower palate and tongue) were, then, processed for paraffin histology. For the larger subadults, representative 1 cm² squares (from the central and peripheral regions) were excised for meach of the three areas (tongue, upper palate, and lower palate) and processed for paraffin histology. All tissues were processed and embedded in paraffin wax. The embedded tissue was sectioned at 10 μ m increments and stained using either Harris' Haematoxylin and Eosin or Masons' Trichrome.

Three-dimensional Reconstruction in Hatchling

One tongue specimen of a hatchling was selected for a threedimensional (3D) reconstruction. Scion Image software (release 4.02, National Institute of Health) was used for computer-based 3D reconstruction of the tongue, highlighting the taste buds. Serial sections were made, at 10 µm increments. For the reconstruction, every sixth section was digitally photographed using a Leica DMLB photomicroscope with a DKC-5000 Catseye Digital Still Camera System (Sony Electronics, Montvale NJ). The images were transferred to Adobe Photoshop 7.0 and saved as bitmap files. These files were aligned in sequence by superimposing them sequentially and manually rotating then to one another. Three-dimensional reconstruction was accomplished with Scion Image software (NIH) and were used to isolate and depict the distribution of the tastebuds on the dorsum of the tongue (see Rehorek and Smith, 2007 for further details).

Statistics

PSDSP were counted in all specimens in the oral cavity. No PSDSP were observed in the lower palate. A *t*-test was used to determine if there was a significant difference in total number of PSDSP between the tongue and upper palate. A 2-way ANOVA was used to determine the effects of alligator size and papillae position (Tongue or Upper Palate) on papillae diameter, using individual alligators as blocks. Finally, correlation coefficients were calculated to determine if there were significant relationships between PSDSP diameter and surface area of the upper palate and tongue surface area, respectively. Similarly correlations between PSDSP count and surface area were determined for both tongue and upper palate.

RESULTS Gross Anatomy

PSDSP were found on the tongue and upper palate, but not lower palate, of the larger subadult alligators (Fig. 1). In both, the neonates and the



Fig. 2. Pale staining dome-shaped papillae (PSDSP) density in the Alligator oral cavity (**A**: Tongue and **B**: Upper palate, respectively).

smaller subadults, these PSDSP were not easily identifiable and the entire surface was a dark blue color. In some of the larger subadults, posteromedial regions of the upper palate and tongue were devoid of any of these papillae.

There were significantly more (*t*-test 3.0, P < 0.016) PSDSP observed on the upper palate (1214.55 ± 158.28) than the tongue (453.55 ± 64.21). PSDSP density decreased with increasing size of oral cavity (Fig. 2). A 2-way ANOVA revealed that these papillae diameter was affected by oral cavity (upper palate or tongue) size, palate position, and their interaction (Table 1). Papilla diameter was positively correlated with the surface area of both the upper palate and the tongue (Table 2). The number of PSDSP was negatively correlated to the surface area of the upper palate, but not significantly correlated to the surface area of the tongue (Table 2).

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Histology of Hatchling

Both the upper palate and the dorsum of the tongue were lined by a relatively thick stratified squamous epithelium (5–6 cells thick). This epithelium was thrown into a series of papillae: either filiform (tapered protrusions) or low PSDSP. It was within the submucosa of these PSDSP that the superficial cutaneous sensory structures were found. Within these PSDSP reside one of two sensory structures: 1) in some PSDSP the taste bud was seen (Fig. 3A), an intraepithelial structure, consisting of numerous taste cells, the apices of which were directly exposed to the surface. Numerous taste buds were observed on the tongue, few in the upper palate and none in the lower palate. There appeared to be no pattern to the distribution of the taste buds on the hatchling tongue (Fig. 3B). 2) Subepithelial structures whose lamellae are perpendicular to the epithelium (Fig. 3C), which were identified as Merkel cell neurite complexes (as per von Düring and Miller, 1979), were more common than the taste buds in the PSDSP. Deeper in the submucosa of the tongue resided numerous neurovascular bundles and Pacinian corpuscles. The posterior portion of the tongue housed numerous large subepithelial salivary (von-Ebners) glands not seen on the anterior third of the tongue.

The lower palate was lined by a thinner epithelium (up to three cells thick). The entire structure was thrown into folds, and had no papillae of any sort. As a result, there were few, if any, taste buds or Merkel cell neurite complexes in this region. The folds themselves contained numerous neurovascular bundles, but not to the extent of the upper palate or tongue.

Histology of Subadult

Stratified squamous keratinized epithelium (4–5 live cells thick) with numerous dome-shaped projections was observed covering the upper palate and dorsum of the tongue. These dome-shaped projections corresponded to the PSDSP observed anatomically.

The PSDSP, like that of the hatchling, usually housed one of two structures. 1) Spherical intraepithelial structures (Fig. 3D,E), which were

 TABLE 1. Two-way ANOVA table for effects of papillae position

 on oral cavity size (surface area of tongue or upper palate)

 papilla diameter (T = tongue, UP = upper palate)

Source	Sum-of- squares	df	Mean- square	F-ratio	Р
Alligator size Papillae position (Tor UP)	$\begin{array}{c} 0.287\\ 0.4 \end{array}$	$10\\1$	$\begin{array}{c} 0.029\\ 0.4 \end{array}$	42.868 597.623	$<\!$
Interaction Error	$\begin{array}{c} 0.104 \\ 0.133 \end{array}$	10 198	$\begin{array}{c} 0.01 \\ 0.001 \end{array}$	15.523	< 0.001

ALLIGATOR ORAL CAVITY STRUCTURE

TABLE 2. Range of papillae diameter (PDR) and papillae count range (PCA) for the upper palate and tongue, respectively

	PDR (mm)	CDSA ($n = 11$)	PCR	CPSA $(n = 9)$
Upper palate Tongue	0.15 - 0.35 0.15 - 0.4	$\begin{array}{l} r=0.24,P<0.01\\ r=0.74,P<0.001 \end{array}$	$\begin{array}{c} 111-669 \\ 159-338 \end{array}$	r = -0.69, P < 0.05 r = 0.34, P > 0.05

The correlation coefficient for the correlation of PDR (with surface area: CDSA) and PCR (with surface area: CPSA) are given for the upper palate and tongue, respectively.

cellular in the smaller subadults but contained a spherical degenerative region in the larger subadults, were seen in some cases. Only the occasional, peripherally located taste bud was observed in the upper palate, mainly in the smaller subadult specimens. 2) Subepithelial Merkel cell neurite complexes were also observed (Fig. 4A,B). Closer examination of these clusters also revealed a few pale staining Merkel cells in the adjacent stratum basal. Additionally, the epithelium superior to this subepithelial Merkel cluster appeared a little thicker, producing a small dome. Sometimes the submucosal Merkel cell clusters were associated with the intraepithelial structures.

The sharp (filiform) projections, found mainly on the tongue, housed small whorls of cells that project into papillary ridges and relay deeply toward presumptive nerve fibers; they resembled Meissner's corpuscles: a series of encapsulated nerve terminals (Fig. 4C). The deeper submucosa consisted of dense irregular connective tissue with infiltrating neurovascular bundles and deep small Pacinian or Herbst corpuscles (Fig. 4D). Large blood vessels were observed deep in the submucosa. There were numerous neurovascular bundles traversing the submucosa. The posterior two thirds of the tongue housed numerous large subepithelial salivary (von-Ebners) glands, which were often infiltrated by lymphatic tissue.

A thinner stratified squamous keratinized epithelium (2–3 cells thick) was observed covering the lower palate (Fig. 4E). There was no clear evidence of any intraepithelial or encapsulated submucosal structures. The mucosa was thrown in longitudinal folds, which housed relatively superficial blood vessels and a few nerve tracts.

DISCUSSION

From these results two conclusions can be made: first that the alligator's oral cavity has numerous mucosal sensory structures. These mucosal sensory structures can be subdivided functionally based on which modality is being served: mechanoreceptive and chemosensory. Second, the precise nature of these mucosal sensory systems changes during post-natal ontogeny. This morphological ontogenetic shift appears to support a concurrent behavioral shift in feeding behavior.

Mucosal Sensory Structures: Mechanoreceptors

The observations of this study do, in part, support those of both Ferguson (1981) and Putterill and Soley (2003, 2004), although both studies described fewer mechanoreceptive structures. In this study, four types of mechanoreceptors were found in the oral cavity of the subadult alligator.

- 1. Filiform papillary tactile sense organs (Fig. 4C): These were found exclusively in the filiform papillae. These consist of specialized connective tissue cells in the papilla, which are in contact with nerve endings, superficially resembling Meissner's corpuscles. Meissner's corpuscles play an important role in light discriminatory touch (Iggo and Andres, 1982). In subadult alligators, this suggests that these filiform papillary tactile sense organs are an important mechanoreceptive structure purely because there are so many filiform papillae to be found on the dorsum of the tongue.
- 2. Pacinian and Herbst corpuscles (Fig. 4D): Pacinian corpuscles are found in the deeper submucosa and play an important role in deeper touch and vibration (Iggo and Andres 1982). Herbst corpuscles, a feature unique to birds, are found in the upper submucosal region. These are described as the avian homologue of the Pacinian corpuscle and are common on the bill and tongue of some birds (Iggo and Andres, 1982; Gentle and Breward, 1986; Crole and Soley, 2009). Although some studies suggest there are some ultrastructural and locational differences (Watanabe et al., 1985) between Herbst and Pacinian corpuscles they are functionally similar.
- 3. Merkel cell neurite complexes are present basally in the PSDSP (Figs, 3C, 4A,B). These were the sole mechanoreceptive structure observed in the oral cavity of the hatchling alligator. Putterill and Soley (2003) describe these as a subepithelial cellular mass, whereas Ferguson (1981) identifies them as a subepithelial Merkel cell neurite complex. Similar structures have been observed in beak skin of chickens, quail (Halata et al 2003), and two species of turtle (von Düring and Miller 1979).
- 4. Epidermal Merkel cells are present in the adjacent stratum basale (Fig. 4B). Such Merkel cells are not seen in birds (Halata et al., 2003), but are common in reptile skin (von Düring and





Fig. 3. Histological view of taste bud (black arrow) in the upper palate of the hatchling Alligator (**A**). Three-dimensional reconstruction of the neonate alligator tongue. Blue indicates outline of the tongue. Spots on tongue indicate the location of taste buds (**B**). Histological view of Merkel cell neurite complex structure (black arrows) in the upper palate of the hatchling alligator tongue (**C**). Histological view of epithelial structure (black arrows) in the upper palate of a subadult alligator (**D**) with a higher magnification of one of the intraepithelial clusters (black arrow) (**E**). Stained with Hematoxylin and Eosin (A, B, C) or Mason's Trichrome (D, E). A = Anterior, D = Dorsum. Scale bars: 58 μ m (A), 102 μ m (C), 102 μ m (D), and 34 μ m (E). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com]



Fig. 4. Histological sections of the subadult alligator oral cavity. Histological view of sensory structures in the tongue of the subadult including subepthelial (Merkel cell neurite complex) structure (black arrow) in the tongue of a subadult alligator (**A**) with a higher magnification of the same structure (black arrow) and some epithelial Merkel cells (white arrow) (**B**), Meissner's corpuscle (black arrow) in the tongue papilla (**C**) and Pacinian corpuscle (black arrow) in deep dermis (**D**). The lower palate of subadult alligator shows none of the sensory structures described (**E**). Stained with either Hematoxylin and Eosin (C) or Mason's trichrome (A, B, D, E). Scale bars: $41 \mu m$ (A, C), $12 \mu m$ (B, D), and $83 \mu m$ (E). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com]

Miller, 1979). This combination of the Merkel cell neurite complex with the epithelial Merkel cells is a type of tactile sense organ or touch papilla. These particular sensor organs are found in the skin of all reptilian orders (von Düring and Miller, 1979). Ferguson (1981) also described free nerve fibers into the epithelium of the palatal epithelium of alligators.

Mucosal Sensory Structures: Taste Buds

The chemosensory structure in the alligator oral cavity is the taste bud. However, the distribution, structure, and thus function, of taste buds is different between hatchlings and subadults.

Hatchlings. Although the precise timing of taste bud inception in the alligator is unknown, these structures are fully developed in hatchlings. In both mammals and birds, the taste buds develop prenatally, although generally ontogenetically earlier in mammals than in birds (Ferrell, 1984; Hosley and Oakley, 1987; Ganchrow and Ganchrow, 1989). Prenatal studies of alligator need to be carried out to determine taste bud inception time.

Taste buds were restricted to the upper palate and tongue in the hatchling alligator. In most other vertebrates, with exception of Ratite birds (Crole and Soley, 2009), taste buds were found to be spread throughout the oral cavity (Schwenk, 1985, 1986; Ganchrow and Ganchrow, 1989). The mucosa of the lower palate in alligators consists of a thinner epithelium (not thick enough to support taste buds) and many mucosal folds. This suggests a greater level of flexibility (rather than chemosensitivity) of the lower palate mucosa.

The microvilli in hatchling alligator taste buds, like those of most nonmammalian vertebrates, are exposed at the surface of the oral cavity (Schwenk, 1985; Ganchrow and Ganchrow, 1989; Hansen et al., 2002; Crole and Soley, 2009; Barreiro-Iglesias et al., 2010; El-Sayyad et al., 2011). This is in contrast to mammals and some birds, wherein the microvilli are not open to the surface, and the chemicals are only accessible although a narrow taste pore (Moore and Elliott, 1946; Northcutt, 2004; Gartner and Hiatt, 2009).

Subadults. The structure and function of taste buds in subadult alligators is different to that of the hatchling. First, there is a distinction between true taste buds (wherein microvilli are in contact with the oral surface) and intraepithelial taste bud-like structures (which are enclosed structures, separated from the oral surface by a few layers of squamous cells). The true taste buds are few, and found only in peripheral locations in the smaller subadults, whereas the intraepithelial structures, housed within PSDSP, are more predominant.

These PSDSP, housing at least some of the large intraepithelial taste bud-like structures, are larger and fewer in the larger subadults, indicating both somatic growth of the papillae and loss of papillae. Additionally, these PSDSP are significantly larger in the tongue than in the upper palate. However,

there was also a significant effect of alligator size and a significant interaction. Thus, although these papillae were larger in the tongue at all ages, the magnitude of the difference between papilla diameter of the tongue and upper palate was greatest in larger alligators.

Taste buds were present throughout the upper palate and dorsum of the tongue in the hatchling alligator (Ferguson, 1981; this study) but were restricted to the peripheral areas of these same regions in the adult/subadult crocodilian (Putterill and Soley, 2003; this study). Thus, somewhere between hatchling and subadulthood taste buds are capped by squamous cells, thereby rendering them nonfunctional (and thus becoming anatomically identifiable as PSDSP).

Based on the anatomical observations, it appears that taste buds, taste bud-like structures, and their papillae (PSDSP), are sheared off with age (papilla-free zones of the upper palate), leaving behind a flat, keratinized surface.

The effects of age on taste bud density in other vertebrates indicate no consistent pattern. Fewer taste buds were observed in aging mice (Shin et al., 2012) but taste buds density did not change over time in postnatal rhesus monkeys (Bradley et al 1985), humans (Miller 1988), and chickens (Ganchrow and Ganchrow, 1989). Entirely new populations form in rabbits over several weeks (Miller 1988). This is in contrast to the condition in the striped dolphin (*Stenella coeruleoalba*) in which there is a postnatal reduction in taste buds, ending up with possibly no taste buds in the adult (Yamasaki et al. 1978; Komatsu and Yamasaki, 1980).

Although there is broad similarity between this study and previous crocodilian studies (Weldon and Ferguson, 1993; Putterill and Soley, 2003, 2004; El-Sayyad et al., 2011), there are refinements detected in this study. First, closer examination of the light micrographs provided by some of these authors (Weldon and Ferguson, 1993; Putterill and Soley, 2003, 2004) shows both a taste bud (located peripherally) and a taste bud-like structure. The peripherally located taste buds are consistent with the observations of this study. However, Putterill and Soley (2003, 2004) initially describe the taste bud-like structures and from then on refer to them all as taste buds (both taste buds and taste bud-like structures).

Second, a closer examination of the scanning electron micrograph (SEM) provided by Weldon and Ferguson (1993) and histological micrographs provided by El-Sayyad et al (2011) reveal that the surface of the papilla is covered by two concentric rings of squamous tissue. As a result, the receptor cells are no longer in contact with the chemical environment (separated from it by several squamous cells layers and a thin stratum corneum). Comparison to the SEMs of other vertebrates with similarly exposed taste buds (Wake and Schwenk, 1986; Northcutt et al., 2000; Abbate et al., 2010) reveals the presence of several processes with blunt tips. These would be the microvilli which make up the border of the taste bud that are exposed to the oral surface. Thus, the alligator taste bud is not in contact with the oral surface, is unlikely to function in gustation and they are not functional taste buds. Instead, they appear to be degenerative structures. In rats, degenerated taste buds are a rounded bud-like bulge in the epithelium. The degenerate taste buds appear as clusters of heterogeneous cells with numerous vacuoles (Farbman 1969; Cano and Rodriguez-Echandia, 1980), much like the intraepithelial structures of subadult alligators (this study).

Why do Alligators Have a Sensory Palate?

Alligators may use chemoreception to locate food. They submerge their heads and wave their heads from side to side prior to seizing their food (Weldon et al., 1990; Banta et al., 1992). Furthermore, they appear to use contact chemoreception, whereby they are in direct contact with the potential food source. Thus, it was proposed that the chemoreceptive system in use may be the gustatory system (Scott and Weldon, 1990).

For hatchlings (and smaller subadults), this would mean that they are detecting smaller organisms underwater (generally invertebrates: Delany and Abercrombie, 1986). Of the three potential cephalic chemical senses, taste is the most likely candidate. Olfaction is receptive mainly to airborne particles, thus is more limited in water. Avesuchians have no vomernonasal organ (see Hillenius and Rehorek, 2005 for review). Thus, tasting the water appears to be plausible alternative. As alligators get older (and thus larger) their prey are larger (including larger vertebrates: Delany and Abercrombie, 1986). Concurrently, older alligators have fewer taste buds. One possible explanation may be that alligators experience a reduction in reliance on taste for foraging (i.e., visual cues may be used, as the prey is now large enough to be seen). A similar conclusion was reached for the Striped dolphin (S. coeruleoalba: Komatsu and Yamasaki, 1980). Alternatively, or even additionally, the few remaining taste buds may be sufficient for some essential functions (e.g., adult alligators reject chemically protected food: Weldon and Ferguson, 1993).

Alternatively, alligators may not just use mechanoreception during foraging, but rather mechanoreception may be used for food manipulation within the oral cavity. As alligators are inertial feeders (in which the inertia of the food is used to move the prey to the back of the oral cavity), they may additionally use their tongues, in part, to manipulate the food into the appropriate orientation (Cleuren and De Vree 2000). To determine the position of the food, they need sensory information from their oral cavity. This could be the role of the array of epithelial and submucosal mechanoreceptive structures. Similar observations were made in the emu, where Crole and Soley (2009) concluded that taste may not be important for emu food selection.

In conclusion, the mucosal sensory system of the alligator palate is more complicated than previously thought. The hatchling taste buds exhibit a unique combination of structural and positional features, and thus, it is difficult to compare to other tetrapods. Alligators exhibit a more diverse array and density of mechanoreceptive structures than previously observed. Finally, morphological evidence supports the behavioral evidence for an ontogenetic shift in the role of the sensory palate in the alligator, much like that in cetaceans. In hatchlings, the sensory palate has a welldeveloped gustatory system, which may be used in prey detection. In subadults, the gradual loss of these taste buds (and thus the gustatory system) led to the dominance of a mechanoreceptive sensory palate, which now plays a role in prey manipulation. Further studies need to be conducted to determine both the mechanism of taste bud degradation and the role of these degraded structures in the increasingly mechanoreceptive oral cavity.

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LITERATURE CITED

- Abbate F, Guerrera MC, Montalbano G, Zichichi R, Germana A, Ciraico E. 2010. Morphology of the lingual dorsal surface and oral taste buds in Italian lizard (*Podarcis sicula*). Anat Histol Embryol 39:167–171.
- Banta MR, Joanen T, Weldon PJ. 1992. Foraging responses by the American alligator to meat extracts. In: Doty RL, Muller-Schwarze D, editors. Chemical Signals in Vertebrates VI. New York: Plenum press. pp 413–417.
- Barreiro-Iglesias A, Anadón R, Rodicio MC. 2010. The gustatory system of Lampreys. Brain Behav Evol 75:241-250.
- Behrmann G. 1988. The peripheral nerve ends in the tongue of the harbor porpoise *Phocoena phocoena* (Linne, 1758). Aquat Mammal 14:107–112.
- Berkhoudt H. 1977. Taste buds in the bill of the mallard (*Anas platyrhynchos* L.). Their morphology, distribution and functional significance. Neth J Zool 27(3):310–331.
- Bradley RM, Stedman HM, Mistretta CM. 1985. Age does not affect numbers of taste buds and papillae in adult rhesus monkeys. Anat Rec 212:246–249.
- Cano J, Rodriguez-Echandia EL. 1980. Degenerating taste buds in sialectomized rats. Acta Anat 106:487–492.
- Cleuren J, De Vree F. 2000. Feeding in Crocodilians. In: Schwenk K, editor. Feeding. Form, Function, and Evolution in tetrapod vertebrates. San Diego: Academic Press. pp 337– 358.

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- Crole MR, Soley JT. 2009. Morphology of the tongue of the emu (Dromaius novaehollandiae). II. Histological features. Onder J Vet Res 76:347–361.
- Delany MF, Abercrombie CL. 1986. American alligator food habits in northcentral Florida. J Wildl Manag 50(20):348–353.
- El-Sayyad HIH, Sabry DA, Khalifa SA, Abou-El-Naga AM, Foda YA. 2011. Studies on tongue or reptilian species *Psammophis sibilans*, *Tarentola annularis* and *Crocodylus niloticus*. Int J Morphol 29(4):1139–1147.
- Farbman AI. 1969. Fine structure of degenerating tastebuds after denervation. J Embryol Exp Morphol 22(1):55–68.
- Ferguson MJW. 1981. The structure and development of the palate in Alligator mississippiensis. Arch Oral Biol 26: 427–443.
- Ferrell F. 1984. Taste bud morphology in the fetal and neonatal dog. Neurosci Biobehav Rev 8(2):175–183.
- Ganchrow D, Ganchrow JR 1989. Gustatory ontogenesis in the chicken: An avian-mammalian comparison. Med Sci Res 17: 223–228.
- Gartner LP, Hiatt JL. 2009. Color Textbook of Histology. 3rd Ed. Philadelphia: Saunders Elsevier.
- Gentle MJ, Breward J. 1986. The bill tip organ of the chicken (Gallus gallus var. domesticus). J Anat 145:79-85.
- Halata Z, Grim M, Bauman KI. 2003. Freidrich Sigmund Merkel and his "Merkel cell", morphology, development, and physiology: Review and new results. Anat Rec 271A:225–239.
- Hansen A, Reutter K, Zeiske E. 2002. Taste bud development in the Zebrafish, *Danio rerio*. Dev Dyn 223:483–496.
- Hosley MA, Oakley B. 1987. Postnatal development of the vallate papillae and taste buds in rats. Anat Rec 218:216–222.
- Iggo A, Andres KH. 1982. Morphology of cutaneous receptors. Ann Rev Neurosci 5:1–31.
- Komatsu S, Yamasaki F. 1980. Formation of the pits with taste buds at the lingual root in the striped dolphin, *Stenella coeruleoalba*. J Morphol 164:107–119.
- Miller IJJR, 1988. Human taste bud density across adult age groups. J Gerontol Biol Sci 43(1):B26–B30.
- Moore CA, Elliott R. 1946. Numerical and regional distribution of taste buds on the tongue of the bird. J Comp Neurol 84(2): 119–131.
- Northcutt GR, Barlow LA, Braun CB, Catania KC. 2000. Distribution and innervation of tastes buds in the Axolotl. Brain Behav Evol 56:123–145.
- Northcutt RG. 2004. Taste buds development and evolution. Brain Behav Evol 64:198–206.
- Putterill JF, Soley JT. 2003. General morphology of the oral cavity of the Nile crocodile, *Crocodylus niloticus* (Laurenti, 1768). I. Palate and Gingivae. Onderstepoort J Vet Res 70: 281–297.
- Putterill JF, Soley JT. 2004. General morphology of the oral cavity of the Nile crocodile. *Crocodylus niloticus* (Laurenti,

1768). II. The tongue. Onderstepoort J Vet Res 71:263-277.

- Rehorek SJ, Smith TD. 2007. Concurrent 3-D Visualization of Multiple Microscopic Structures. In: Mendez-Vilas A, Diaz J, editors. Modern Research and Educational Topics in Microscopy, Vol. 3. Spain: Formatex. pp 917–923.
- Robinson PP, Winkles PA. 1990. Quantitative study of fungiform papillae and taste buds on the cat's tongue. Anat Rec 225:108–111.
- Schwartzkopff J. 1973. Mechanoreception. In: Farner DS, King JR, editors. Avian Biology Volume III. New York: Academic press. pp 417–477.
- Schwenk K. 1985. Occurrence, distribution, and functional significance of taste buds in lizards. Copeia 1985:91–101.
- Schwenk K. 1986. Morphology of the tongue in the tuatara, Sphenodon punctatus (Reptilia: Lepidosauria), with comments on function and phylogeny. J.Morphol 188:129–156. Scott TP, Weldon PJ. 1990. Chemoreception in the feeding
- Scott TP, Weldon PJ. 1990. Chemoreception in the feeding behavior of adult American alligators, *Alligator mississippien*sis. Anim Behav 39:398–405.
- Shin Y-K, Cong W-N, Huan S, Kim W, Maudsley S, Egan J, Martin B. 2012. Age-related changes in mouse taste bud morphology, hormone expression, and taste responsivity. J Gerontol A Biol Sci 67A(4):336–344.
- Toyoshima K. 1993. Are Merkel and Gandry cells two varieties of the same cell in birds? Arch Histol Cytol 56(2):167–175.
- von Düring M, Miller MR. 1979. Sensory nerve endings of the skin and deeper structures of reptiles. In: Gans C, editor. Biology of the Reptilia. New York: Academic press. Vol 9. pp 407-441.
- Wake MH, Schwenk K. 1986. A preliminary report on the morphology and distribution of taste buds in gymnophiones, with comparison to other amphibians. J Herpetol 20(2):254–256.
- Watanabe I-S, Usukura J, Yamada E. 1985. Electron microscope study of the Grandry and Herbst corpuscles in the palatine mucosa, gingival mucosa and beak skin of the duck. Arch Histol Jpn 48(1):89–108.
- Weldon PJ, Ferguson MWJ. 1993. Chemoreception in crocodilians: anatomy, natural history, and empirical results. Brain Behav Evol 41:239-245.
- Weldon PJ, Swenson DJ, Olson JK, Brinkmeier WG. 1990. The American alligator detects food chemicals in aquatic and terrestrial environments. Ethology 85:191–198.
- Yamasaki F, Komatsu S, Kamiya T. 1978. Papillary projections at the lingual margin in the striped dolphin, *Stenella coeruleoalba*, with special reference to their development and regression. J Morphol 157(1):33-47.
- Zhang G-H, Zhang H-Y, Deng S-P, Quin Y-M, Wang T-H. 2008. Quantitative study of taste bud distribution within the oral cavity of the postnatal mouse. Arch Oral Biol 53:583–589.