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Occurrence, Distribution and Functional Significance of Taste Buds in Lizards

KURT SCHWENK

The tongue and oral epithelium beneath and lateral to the tongue have been examined in 37 species of lizard representing all families except the Helodermatidae and Lanthonotidae. Taste buds occur in all species examined except *Varanus indicus* (Varanidae). They are found on the tongues of all remaining species except *Gonatodes antillensis* (Gekkonidae) and in the oral epithelia of all species except *Chamaeleo jacksoni* (Chamaeleonidae). Taste buds may be abundant, particularly in the Iguanidae, in which densities greater than 104/mm² occur. These observations are contrary to statements in the literature which have assumed taste buds to be rare or absent in lizards.

Lingual taste buds are more or less restricted to regions of thick, stratified squamous epithelium. They occur most frequently on the tongue tip and the ventrolateral margins of the foretongue, though they may be found anywhere.

Insufficient data exist to distinguish between taste and vomeronasal function as the basis for chemosensory-mediated behavior in lizards. It is, therefore, premature to assume the latter. Substrate licking might mediate gustation rather than vomeronasal function, particularly in iguanian lizards.

TASTE buds occur in the oral and pharyngeal epithelia of most vertebrates. They occur in cyclostomes (Johnston, 1905), sharks (Cook and Neal, 1921), lungfish (Parker, 1892), chondrosteans, holosteans, teleosts (Herrick, 1902), frogs (Jaeger and Hillman, 1976), salamanders (Farbman and Yonkers, 1971), caecilians (D. Wake, pers. comm.), crocodylians, birds (Bath, 1906), turtles (Korte, 1980), *Sphenodon* (Osawa, 1897), squamates (Nonoyama, 1936; De la Serna de Esteban, 1959; Burns, 1969; Kroll, 1973) and mammals (Graziadei, 1969).

Lizards have been little studied with regard to taste bud occurrence. Merkel (1880) and Holl (1887) described taste buds in the mouth and tongue of *Lacerta agilis* (Lacertidae). Willard (1915) noted taste buds in the oral epithelium and on the tongue of *Anolis carolinensis* (Iguanidae). Nonoyama (1936) found taste buds to be quite common on the tongues of *Eumeces latisc-*

cutatus (Scincidae), *Takydromus tachydromoides* (Lacertidae), *Gekko japonicus* (Gekkonidae) and *Japalura swinhonis* (Agamidae). Despite the ubiquity of taste buds in the mouths of other vertebrates and their presence in the mouth and on the tongue of those lizard species examined, recent reviews and textbooks have suggested that taste buds are uncommon in lizards and only rarely, if ever, found on the tongue (Porter, 1972; Romer and Parsons, 1977; Simon, 1983). This belief has led to the conclusion that taste, as one of several chemical senses, may be unimportant to lizards, or at least, is poorly understood (Simon, 1983). Consequently, the commonly observed squamate behaviors of tongue flicking and substrate licking usually have been interpreted solely in light of their possible role in vomeronasal function; taste, as a motivation for such behavior, has been neglected (c.f. Madison, 1977; Simon et al., 1981; Duvall,

1982). When taste has been considered, it has been dismissed as unimportant relative to vomeronasal function (Burghardt, 1970; Duvall, 1981), or dismissed due to lack of information (Burghardt, 1980; Simon, 1983).

In this paper I document the widespread occurrence and frequent abundance of taste buds in the oral epithelium and on the tongue of lizards. The significance of taste buds in lizard behavior is discussed.

MATERIALS AND METHODS

Lower jaws, including the tongue, were removed from 39 specimens (37 species) representing all lizard families except the Helodermatidae and the Lanthanotidae; all had been fixed in formalin and preserved in ethanol. Specimens were prepared for paraffin histology using standard techniques (Humason, 1979) and were serially sectioned at 6–10 microns. Sections were stained with either hematoxylin and eosin, hematoxylin and picro-ponceau, or Verhoeff elastin stain and picro-ponceau. These were examined for the presence of taste buds with a compound binocular microscope. Sufficient data for two additional species were provided by Nonoyama (1936).

Two living specimens (*Phrynosoma platyrhinos* and *Callisaurus draconoides* [Iguanidae]) were sacrificed for scanning electron microscope preparation. Lower jaws were removed, fixed in 4% glutaraldehyde (pH 7.2 in phosphate buffer), washed in phosphate buffer, dehydrated in an ethanol series, CO₂ critical point dried, sputter coated with gold-palladium and examined with an ISI-DS 130 SEM.

For this analysis, the tongue has been divided into three regions, tip, foretongue, and hindtongue (Fig. 1). The tongue tip is the bifurcated anterior end of the tongue, plus a small area immediately posterior to the bifurcation. The division between foretongue and hindtongue lies at the point halfway between the tongue tip and the posterior-most extent of the tongue's posterior limbs. As McDowell (1972) and Schwenk (in press) suggested, there may be a functional and evolutionary basis for this subdivision, as well as a topographic one.

Taste buds were identified on the basis of morphology and comparison with literature accounts. For each region, taste buds were scored as absent, present or abundant. "Abundant" signifies that two or more taste buds occurred in many or most sections of a region. "Present" indicates one to many observed. Thus, it was

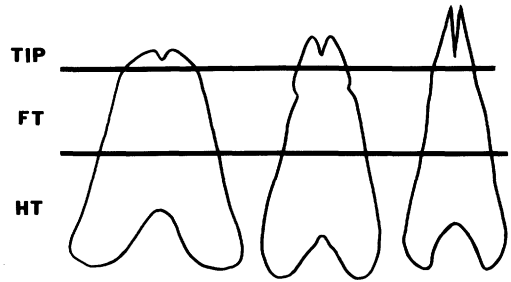


Fig. 1. Three morphological types of lizard tongue are shown to illustrate the tongue regions referred to in the text and Table 1. From left to right, an iguanid, an anguid and a lacertid. TIP = tongue tip; FT = foretongue; HT = hindtongue.

necessary to examine several or many sections in order to locate taste buds. "Absent" indicates that I found no taste buds in a given region. However, due to identification difficulties, small sample sizes, and sampling error, an absent score should not be regarded as absolute. At least, it indicates very low taste bud density.

Although taste buds may be common in the epithelium of the roof of the mouth, as in *Anolis carolinensis* (Willard, 1915) other than confirming the observation I did not search for them in this region.

RESULTS

Table 1 lists species examined and relative densities of taste buds in mouth and tongue. Quantification of taste buds is beyond the scope of this paper. Rather, I provide general data for a large number of species. However, some approximations are given to delimit the relative scale provided.

Nonoyama (1936) reported a total of ca 200 taste buds on the tongue of *Eumeces latiscutatus* (Scincidae) and ca 100 on the tongue of the lacertid *Takydromus tachydromoides*. These numbers correspond well with my observations of three other scincids and a lacertid (Table 1). The greatest total numbers of taste buds occurred on the tongues of iguanids. Although not counted over the entire tongue, I estimate between 500 and 600 taste buds in some species. The greatest density (ca 104/mm²) occurred on the tongue tip of *Phrynosoma platyrhinos* (Fig. 2A). Typical densities for an "abundant" score are about 25–75 taste buds per mm².

Taste buds occurred in all lizards except *Varanus*. They are most abundant in species of the

TABLE 1. DISTRIBUTION AND RELATIVE ABUNDANCE OF TASTE BUDS IN LIZARDS. ++ = abundant; + = present; - = absent; ? = unknown; juv = specimen used a juvenile; an asterisk indicates that data are from Nonoyama, 1936.

Family and species	Tongue tip	Foretongue	Hindtongue	Oral
Iguanidae				
<i>Anolis bonairensis</i>	++	+	++	++
<i>A. carolinensis</i>	+	+	+	+
<i>Basiliscus vittatus</i>	++	++	+	++
<i>Callisaurus draconoides</i>	++	+	+	++
<i>Crotaphytus insularis</i>	++	+	+	++
<i>Dipsosaurus dorsalis</i>	+	+	+	++
<i>Liolaemus monticola</i>	++	+	+	++
<i>Petrosaurus mearnsi</i>	++	+	+	++
<i>Phrynosoma cornutum</i>	++	+	+	++
<i>P. platyrhinos</i>	++	+	+	++
<i>Sceloporus occidentalis</i>	++	+	+	++
<i>Stenocercus</i> sp.	++	+	+	++
<i>Tropidurus</i> sp.	++	++	++	++
<i>Uma scoparia</i>	++	+	+	++
Agamidae				
<i>Agama</i> sp.	+	+	+	?
<i>Goniocephalus grandis</i>	+	+	+	+
<i>Stellio stellio</i>	-	+	+	++
<i>Uromastix hardwicki</i>	+	+	+	++
Chamaeleonidae				
<i>Chamaeleo jacksoni</i> (juv)	+	+	-	-
Gekkonidae				
<i>Gonatodes antillensis</i>	-	-	-	++
<i>Coleonyx variegatus</i>	-	-	+	++
Pygopodidae				
<i>Lialis burtonis</i>	+	+	-	++
Xantusiidae				
<i>Xantusia vigilis</i>	+	+	+	++
Scincidae				
<i>Dasia smaragdinum</i>	++	+	+	++
<i>Eumeces laticutatus</i> *	+	++	+	?
<i>E. skiltonianus</i>	++	+	+	++
<i>Scincella</i> sp.	++	+	+	++
Cordylidae				
<i>Cordylus polyzonus</i>	++	++	+	++
<i>Gerrhosaurus flavigularis</i>	+	+	+	++
Teiidae				
<i>Cnemidophorus tigris</i>	-	+	+	++
Gymnophthalmidae				
<i>Gymnophthalmus lineatus</i>	-	+	-	++
Lacertidae				
<i>Lacerta viridis</i>	+	+	+	++
<i>Takydromus tachydromoides</i> *	+	+	+	?
Dibamidae				
<i>Dibamus novaeguineae</i>	++	+	+	++

TABLE 1. (CONTINUED.)

Family and species	Tongue tip	Foretongue	Hindtongue	Oral
Anguidae				
<i>Barisia viridiflava</i>	—	+	+	++
<i>Gerrhonotus coeruleus</i>	+	+	+	++
Anniellidae				
<i>Anniella nigra</i> (formerly <i>pulchra</i>)	—	+	+	++
Xenosauridae				
<i>Xenosaurus grandis</i>	+	+	+	+
Varanidae				
<i>Varanus indicus</i> (juv)	—	—	—	—

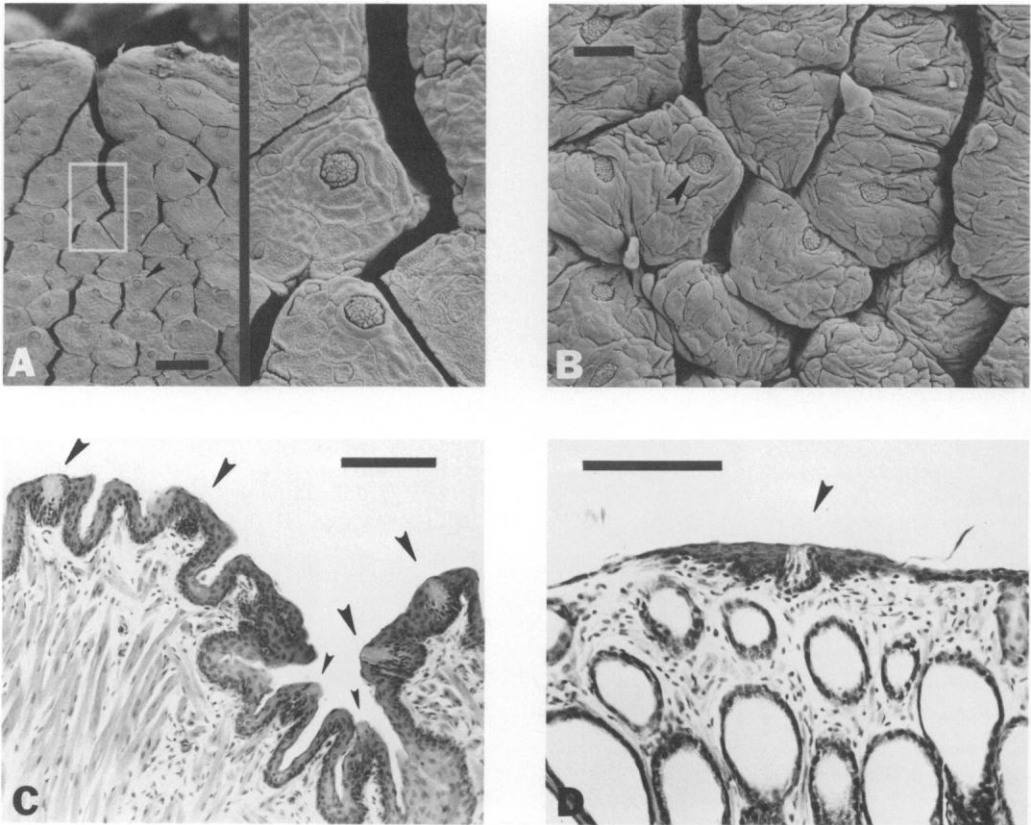


Fig. 2. Examples of lingual taste buds in iguanian lizards. A) Scanning electron micrographs (SEM) of the dorsal surface of the tongue tip in *Phrynosoma platyrhinos* (Iguanidae). On left, low magnification SEM shows distribution of at least one taste bud per papilla (arrows indicate example taste buds). Area enclosed in white box is shown on right at $5\times$ greater magnification. Taste bud pores with sensory cell apices are evident. Scale bar = $100\ \mu\text{m}$ on left, $20\ \mu\text{m}$ on right. B) SEM of papillae on the tongue tip of *Callisaurus draconoides* (Iguanidae), dorsal view. Note numerous taste buds (arrow). Scale bar = $25\ \mu\text{m}$. C) Transverse section ($8\ \mu\text{m}$) through the tongue tip of *Liolaemus monticola* (Iguanidae) showing taste buds in various planes of section (arrows). Hematoxylin and eosin. Scale bar = $100\ \mu\text{m}$. D) Transverse section ($8\ \mu\text{m}$) through the tongue tip of a juvenile *Chamaeleo jacksoni* (Chamaeleonidae). Note the presence of the taste bud (arrow) in a restricted zone of thick epithelium (see discussion). Large openings ventral to taste bud are glandular crypts. Hematoxylin and eosin. Scale bar = $100\ \mu\text{m}$.

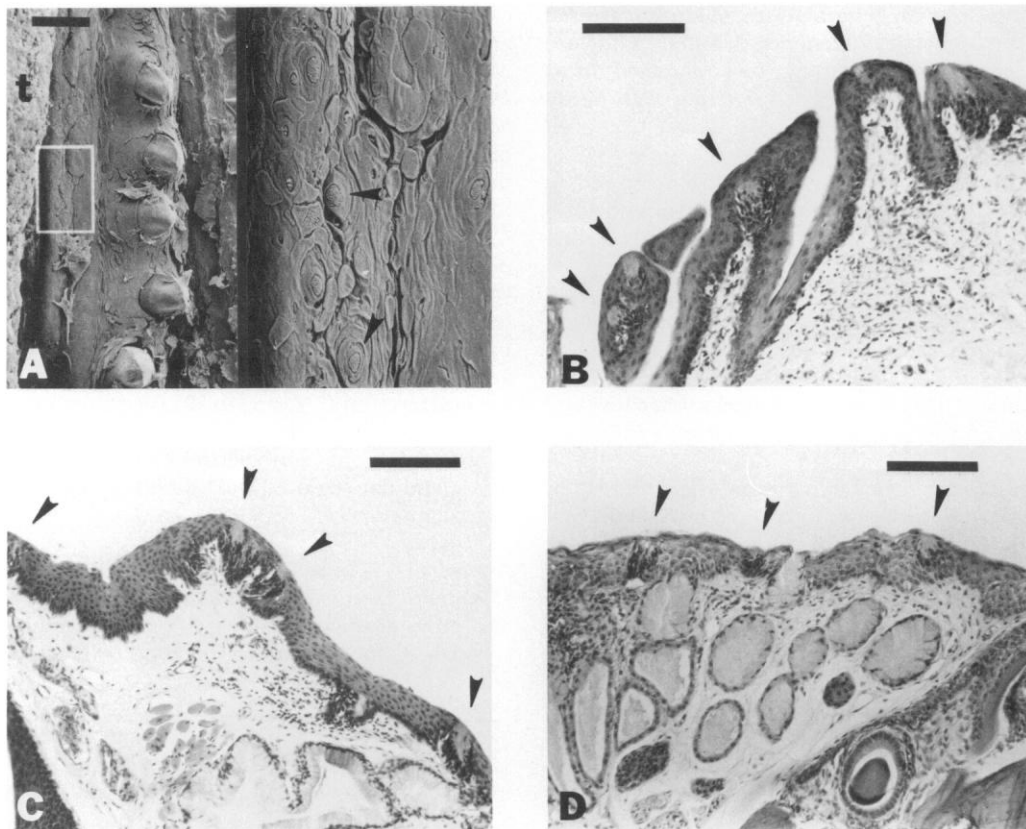


Fig. 3. Examples of oral taste buds in lizards. A) Low magnification SEM on left showing dorsal view of epithelial ridge ventrolateral to tongue (t) and medial to tooth row of *Callisaurus draconoides* (Iguanidae). Anterior is up. Portion of epithelial ridge enclosed in white box is shown on right at $5\times$ greater magnification. Example taste buds indicated by arrows. Scale bar = $200\ \mu\text{m}$ on left, $40\ \mu\text{m}$ on right. B) Transverse section ($8\ \mu\text{m}$) through the oral epithelium beneath the foretongue of *Liolaemus monticola* (Iguanidae). Arrows indicate taste buds in various planes of section. Hematoxylin and eosin. Scale bar = $100\ \mu\text{m}$. C) Transverse section ($8\ \mu\text{m}$) through ridge ventrolateral to foretongue of *Eumeces skiltonianus* (Scincidae). Taste buds indicated by arrows. Hematoxylin and eosin. Scale bar = $100\ \mu\text{m}$. D) Transverse section ($8\ \mu\text{m}$) through oral epithelium beneath tongue tip of *Gonatodes antillensis* (Gekkonidae) showing taste buds (arrows). Hematoxylin and eosin. Scale bar = $100\ \mu\text{m}$.

Iguanidae. They are rare or absent on the tongues of *Coleonyx variegatus* and *Gonatodes antillensis* (Gekkonidae), and virtually absent on the tongues of *Cnemidophorus tigris* (Teiidae) and *Gymnophthalmus lineatus* (Gymnophthalmidae). However, even when absent or scarce on the tongue, taste buds are always numerous in the oral epithelium beneath and lateral to the tongue (Fig. 3). Exceptions to this are *Varanus*, noted above, and *Chamaeleo*, in which taste buds were found in the tongue, but not in the oral epithelium.

In the following section I present more detailed information on the distribution of taste

buds on the tongue in individual lizard families. Relative numbers of taste buds are described in rank-order terms as follows: Abundant, numerous, scattered, rare, absent. In all cases except those noted above, taste buds were found to be abundant or numerous in the oral epithelium.

Iguanidae.—Taste buds are abundant or numerous in all regions, but most concentrated on tongue tip which may have one on every papilla (Fig. 2A–C). Posteriorly taste buds usually are located on ventrolateral papillae, rarely on filamentous papillae or glandular epithelia.

Agamidae.—In general, taste buds are scattered and more or less evenly distributed. They are numerous in places, e.g., foretongue of *Stellio stellio*, where they reach relatively high densities.

Chamaeleonidae.—Taste buds are scattered in the glandular portion of tongue tip and foretongue (Fig. 2D). A few occur within the "dimple" of the tongue bulb.

Gekkonidae.—I found only one taste bud on the dorsal surface of the hindtongue in *Coleonyx variegatus* and none in *Gonatodes antillensis*. Nonoyama (1936), however, found numerous taste buds on the tongue of *Gekko japonicus*.

Pygopodidae.—In *Lialis burtonis*, taste buds are numerous, almost abundant, on dorsal and ventrolateral papillae of foretongue. They become rare and finally absent in the glandular hindtongue.

Xantusiidae.—Taste buds are scattered and widely distributed in *Xantusia vigilis*. They are most frequent on dorsolateral margins of tip and foretongue.

Scincidae.—Taste buds are numerous or abundant on the tongue of all skinks examined. In most, they are particularly abundant on the tip. On the fore- and hindtongue they mostly occur on the ventrolateral surfaces, though they may occur on dorsal papillae, as well.

Lacertidae.—Taste buds are numerous on the ventrolateral surfaces of foretongue and become scattered in the glandular portion of the hindtongue. In *Lacerta viridis*, they are even present on the long tines of the forked tongue tip.

Teiidae.—Taste buds are rare in *Cnemidophorus tigris*. A few occurred on ventrolateral surfaces.

Gymnophthalmidae.—Only two taste buds were found on the ventrolateral surface of the foretongue in *Gymnophthalmus lineatus*.

Cordylidae.—Taste buds are abundant in *Cordylus polyzonus*, especially on tongue tip and foretongue. They occur on dorsal and ventrolateral surfaces. In contrast, the tongue of *Gerrhosaurus flavigularis* is relatively devoid of taste buds; they are scattered on the dorsal papillae

of the tongue tip, and become rare and restricted to ventrolateral margins posteriorly.

Dibamidae.—Taste buds are numerous in *Dibamus novaeguineae*, but are restricted to lateral margins of the dorsal surface. They are abundant on the tongue tip, becoming scattered and rare posteriorly.

Anguillidae.—Taste buds are rare or absent on the tongue tips of the two anguils studied; one taste bud was found on the dorsal surface of the tip in *Gerrhonotus coeruleus*. Elsewhere, taste buds are rare on the tongue of *Barisia viridiflava*, but are scattered in *G. coeruleus*. In the latter, they are most common on the sides of the foretongue at the transitional zone between glandular and non-glandular regions (McDowell's, 1972, zone of invagination).

Anniellidae.—*Anniella nigra* is similar to *Gerrhonotus coeruleus*. Taste buds are scattered, but are found most commonly on the ventrolateral surfaces of foretongue at the zone of invagination.

Xenosauridae.—Although the tongue of *Xenosaurus grandis* is morphologically similar to that of anguils (Schwenk, unpublished data), it differs in having more taste buds. They are numerous over most of the tongue, becoming scattered in the glandular portion of the hindtongue.

Varanidae.—No taste buds were found in *Varanus indicus*.

DISCUSSION

This study and that of Nonoyama (1936) demonstrate that taste buds are not only present in lizards, but that they may be remarkably abundant. Furthermore, taste buds are not restricted to oral and pharyngeal epithelia, as has been suggested (Porter, 1972; Romer and Parsons, 1977; Simon, 1983). Indeed, they may reach their greatest densities on the tongues of some species. Of the 39 species considered, only two lacked lingual taste buds and in most they were numerous. Lingual taste buds were most abundant in the iguanid species I examined. They were also common in scincids, cordylids, agamids, *Xenosaurus* (*Xenosauridae*) and *Lialis* (*Pygopodidae*).

Three structural factors seem important in determining taste bud distribution. These are

degree of keratinization, presence of a glandular epithelium, and thickness of the epithelium. Taste buds occur principally in regions of stratified squamous epithelium of moderate to great thickness. They are rarely found within glandular epithelia and are not found on heavily keratinized surfaces, though they may be common in lightly keratinized epithelia (as in skinks and lacertids). Such structural parameters alone may largely explain observed distributions of taste buds in lizards. Thus higher densities of taste buds on the tongue tips of iguanids, for example, or the ventrolateral surfaces of the foretongue in most lizards, simply may reflect availability of suitable stratified squamous epithelium typical of these regions. The hind-tongue of most lizards is glandular (Schwenk, in press), which may result in the relatively fewer taste buds observed there. Consequently, one need not invoke adaptive explanations for the distribution of taste buds on the tongue.

The occurrence of taste buds in lizards (this study; Nonoyama, 1936), snakes (Burns, 1969; Kroll, 1973), amphisbaenians (De la Serna de Esteban, 1959) and *Sphenodon* (Osawa, 1897) suggests that their presence is primitive for Lepidosauria, hence few meaningful phylogenetic inferences may be made from these data. However, loss of taste buds in *Varanus* and reduction or loss of lingual taste buds in a teiid, a gymnophthalmid, gekkos (this study) and snakes (Nonoyama, 1936; Payne, 1945) could be interpreted as derived conditions.

The limited data presented here show that numbers of taste buds may be relatively variable among species or genera within a family (see Cordylidae and Gekkonidae, above). Such differences among related taxa suggest plasticity in the evolution of taste bud number. In contrast, there is consistency within some families (e.g., Iguanidae, Agamidae, Scincidae). Such contradictory patterns, as well as the small number of species sampled, suggest caution and limit phylogenetic speculation.

Simon (1983) stated that if taste buds are found on lizard tongues, we will need to examine the interaction of taste and vomeronasal function more carefully. This study demonstrates the ubiquity of both lingual and oral taste buds in lizards. Future studies utilizing tongue protrusion as a behavioral measure should consider its possible role in taste, as well as in vomeronasal function. I note in this context that the presence of oral taste buds, alone, is sufficient to implicate taste in lizard behavior. If tongue

flicks are capable of transporting chemicals to the vomeronasal organ (Kahmann, 1932; Oelofsen and Van Den Heever, 1979), then it is likely that oral taste buds could be similarly stimulated.

As taste receptors were heretofore thought to be rare or absent in lizards, virtually no studies exist which explicitly test for the presence of taste discrimination in lizards. An exception is Rensch and Eisentraut (1927), who tested the responses of heat-stressed lizards to treated drinking water. They observed avoidance behavior when the lizards were presented with water treated with "salty," "bitter," and "sour" substances. A positive response was noted when "sweet" solutions were used. However, in his thorough review of reptile chemical perception, Burghardt (1970) pointed out serious problems with the experimental protocol of this study. Nonetheless, the results are, at least, suggestive. Responses were elicited only after sampling of the water with the tongue. This observation may be significant in light of the discussion on chemosensory redundancy, below.

Two natural "experiments" are suggested by the data presented here. First is the example of *Varanus*, in which no taste buds were found (although they may be present in the roof of the mouth, as they are in at least one lizard and in some, if not most, snakes [Willard, 1915; Burns, 1969; Kroll, 1973]). Despite this dearth of taste buds, the tongues of monitor lizards and snakes apparently are highly specialized for chemosensory function (McDowall, 1972; Schwenk, 1982) and are frequently protruded. The role of gustation is likely to be minimal in these animals. In contrast, chamaeleonids are often described as strictly visual lizards (Evans, 1961, 1967; Madison, 1977) due to their degenerate vomeronasal organs (Haas, 1937, 1947). Nonetheless, chameleons are known to lick the substrate (Parcher, 1974). This behavior might be explained by the presence of taste buds on the tongue tip (Fig. 2D); it is unlikely to be explained by vomeronasal function. These two examples, as well as limited neuroanatomical evidence (Willard, 1915) suggest separate, but complementary roles for taste and vomeronasal function in lizards. Given the large number of taste buds present, the presence of well-developed vomeronasal organs (Pratt, 1948; Parsons, 1970), and the frequency of tongue flicks and substrate licks observed (see introduction), it is likely that most lizards fall somewhere between the two extremes presented above.

If taste is important in some lizards, as suggested by the circumstantial evidence presented here, then the question arises as to why there is so much apparent chemosensory redundancy. Most lizards seem to have recourse to at least three chemosensory systems: Vomeronasal, olfactory and gustatory. Recently, a new chemosensory pathway was described in goldfish (Demski and Northcutt, 1983). If this system is a general phenomenon in vertebrates, as these authors suggested, then a fourth chemosensory modality may be added.

Burghardt (1980) discussed the apparent redundancy in olfactory and vomeronasal systems of reptiles. He concluded that the vomeronasal system, at least of snakes, is specialized for highly discriminatory perception of proximal chemical stimuli of low volatility. He noted that tongue contact is usually necessary to elicit courtship trailing and feeding responses in snakes. The implication is that olfaction is less discriminatory and operates over larger distances, putatively responding to chemicals of higher volatility. Burghardt's (1980) conclusions are an extension of the Cowles and Phelan (1958) hypothesis that olfaction in rattlesnakes is a highly sensitive, but relatively indiscriminate, sense that triggers tongue flicking and hence, vomeronasal function. Kubie et al., (1978) and Meredith and Burghardt (1978) used experimental and electrophysiological approaches to support the discrimination of olfactory and vomeronasal function in snakes. Duvall (1981) presented evidence supporting the Cowles and Phelan (1958) hypothesis for an iguanid lizard, *Sceloporus occidentalis*. Nearly the identical argument may be invoked to account for the apparent redundancy of olfaction and taste (Herrick, 1908). Herrick (1908) noted the anatomical distinctness of the olfactory and gustatory systems in vertebrates, but discerned no marked differences in the chemical stimuli to which each is sensitive. He proposed that the difference is one of response; olfaction is a distance sense to which the organism responds by moving toward or away from the source. Taste, on the other hand, acts only when a potential food item is in the mouth. Here the response is to swallow or reject. Taste, then, was seen by Herrick (1908) as a proximal, discriminatory sense.

I discuss Herrick's (1908) ideas to highlight the difficulty in distinguishing between vomeronasal and gustatory function. Both are implicated in proximal sampling of low or slightly volatile chemicals. Both seem to require the dis-

solution of these chemicals in an aqueous medium (Beidler, 1966; Parsons, 1970; Romer and Parsons, 1977). The tongue's role in stimulating each remains poorly understood in lizards. However, it seems likely that the tongue flick, without substrate contact, is capable of vomeronasal stimulation. This is particularly true of snakes and lizards that exhibit multiple tongue oscillations, which may serve to concentrate volatile chemicals for transfer to the vomeronasal organs (Gove, 1979; Burghardt, 1980). I submit that taste may be the principal chemosensory mode during substrate licking in lizards. Direct contact of the tongue with the substrate would make available chemicals of low volatility which would either stimulate lingual taste buds directly, or be transferred to oral taste buds lying in the epithelium beneath and lateral to the tongue. Vomeronasal function may be complementary, or even subsidiary, to taste during substrate licking.

Substrate licks, as opposed to air flicks, occur in all squamates, but are predominant in the Iguania (Iguanidae, Agamidae and Chamaeleonidae; Parcher, 1974; Gove, 1979; Duvall, 1981; Simon et al., 1981). In the Iguanidae and Agamidae, lingual and oral taste buds are often numerous (Table 1). In the Chamaeleonidae, they are not common, but may represent the only tongue-mediated chemosensory mode available (see above). Such reliance on substrate licking and the abundant presence of taste buds suggest that taste may be an important chemical sense in iguanian lizards.

The precise nature of information received by lizards through taste is speculative. However, taste is now known to be a more subtle sense than was once thought. The human taste bud responds to tens of thousands of chemicals ranging in molecular weight from one to 44,000 daltons (Beidler, 1975). Furthermore, taste buds can respond to a variety of molecules including proteins and fatty acids (Beidler, 1977). Beidler (1977) also pointed out that many salts, sugars, and acids are present in nature in high concentrations. He noted that amino acids and fatty acids are abundant enough in some animal secretions to allow high specificity of response. Thus, chemical cues to which lizards might respond through taste are not only generally present in the environment, but could be present in species-specific combinations in fecal and glandular deposits and on the body. Taste, rather than vomeronasal function, might be used to discriminate among species and possibly, indi-

viduals, allowing for the evolution of species-specific messengers and responses mediated through lingual contact.

A likely candidate for taste-mediated behavior is cloacal licking in male *Phrynosoma* (Tollestrup, 1981) and *Uta* (Ferguson, 1966). Another is the release of a species-specific visual display in *Sceloporus occidentalis* after substrate licking (Duvall, 1979). Duvall (1979) found that displays were only elicited after lingual contact with the substrate, never after air flicks of the tongue. This observation is consistent with the hypothesis that substrate licks mediate gustation, rather than vomeronasal function, in iguanian and possibly other, lizards. Air flicks are presumed to gather chemical messengers for transfer to the vomeronasal organ (see numerous references above). However, such behavior was not sufficient to elicit a response in *Sceloporus*. Taste, as a contact sense, is thereby implicated.

As Herrick (1908) suggested, taste may be particularly important in discriminating among food types. Experimental studies of snake feeding have shown that unpalatable prey are rejected only after prey has been attacked or held in the jaws (Burghardt, 1969; Burghardt et al., 1973). These authors suggested that gustation might discriminate among prey species. In contrast, Curio and Möbius (1978) found no behavioral evidence for the use of chemosensory cues during prey attack in an iguanid lizard (*Anolis lineatopus*). Such equivocal results emphasize the need for more comparative data and further highlight the difficulty in distinguishing among chemosensory modes.

Other lizard behaviors, commonly attributed to vomeronasal function, may be determined, at least in part, by taste. Until suitable experiments are designed to explicitly discriminate between vomeronasal and gustatory function in lizards, it is premature to attribute all chemosensory-mediated behaviors to vomeronasal function.

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Embryonic Development of Duvernoy's Gland in the Snake *Spalerosophis cliffordi* (Colubridae)

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The development of Duvernoy's gland was studied in embryos of the colubrid snake *Spalerosophis cliffordi*. Using serial sections the following aspects were considered: 1) Morphogenesis of the gland, 2) the appearance of several enzymes at different stages of development and 3) the appearance of PAS-positive substances. The young snakes hatched on the 57th day of incubation at 30 C. The primordium of Duvernoy's gland and the maxillary dental lamina appeared as a joint bifurcated ingrowth of the oral epithelium on the 19th day. The lateral branch gives rise to the gland primordium as perpendicular branches radiated from its main axis. Branching continued at later stages until the gland attained the general form of a compound acinar gland. Alkaline phosphatase first appeared in the peripheral region of the branches on the 25th day of incubation and acid phosphatase was first demonstrable in all parts of the gland on the 33rd day. The staining intensity of the two enzymes became stronger at later stages of development, with a maximum reaction several days before hatching. On the day of hatching the reaction was weaker and was located mainly in the ducts. The PAS-positive, diastase-labile substances appeared in the gland on the 30th day of incubation. Several days before hatching PAS-positive secretion was observed in the main duct. On the day of hatching diastase-stable material replaced part of the other PAS-positive substances.

THE embryonic development of Duvernoy's gland in the colubrid snake *Natrix tessellata* has been described in a previous paper (Ovadia, 1984). Using histochemical methods, the appearances of PAS-positive substances and enzymatic activities have been studied in respect to the morphogenesis of the gland. The morphological investigations in *Natrix* and other embryological studies show that, in all snakes studied so far, Duvernoy's and venom glands originate from a primordium in common with the maxillary dental lamina (Kochva, 1965; Shayer-Wollberg and Kochva, 1967; Gygas, 1971).

Developmental aspects other than morphological descriptions are rarely dealt with. It was therefore of interest to find out whether the development of Duvernoy's gland among various species of snakes shows similar differentiation of enzymatic activities and PAS-positive substances.

The previous paper described histochemical aspects of the gland embryogenesis in a water snake. The present work deals with the same aspects in the arid snake *Spalerosophis cliffordi*. The use of the same methodology makes it possible to compare the embryogenesis of this gland in two different species of colubrid snake, in