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Journal of Herpetology, Vol. 20, No. 2. (Jun., 1986), pp. 254-256.

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Journal of Herpetology, Vol. 20, No. 2, pp. 254-256, 1986
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A Preliminary Report on the Morphology and Distribution of Taste Buds in Gymnophiones, with Comparison to Other Amphibians

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As part of a study of the comparative and functional morphology of the head of members of the order Gymnophiona (caecilians, the limbless, elongate fossorial or aquatic amphibians) we have investigated the morphology and distribution of sensory receptors (see also Hetherington and Wake, 1979; Frittsch and Wake, 1986). We report for the first time the presence of taste buds in gymnophione amphibians. Tiepel (1932) reported that he was not able to find taste buds in *Hypogeophis*. We find them (so far) only in adults of the aquatic *Typhlonectes compressicaudus* and in aquatic larvae of an undetermined species of *Ichthyophis*. The taste buds lie not on the tongue, but in the oral mucosa between the teeth of the lower jaw in *Typhlonectes*, and in the mucosa of the palate and lower jaw near the teeth in *Ichthyophis*. A number of terrestrial forms examined do

not appear to have taste buds. The morphology of the taste buds is more similar to that of urodeles, particularly *Salamandra* (Jasinski and Miodonski, 1979), than to the taste discs and nonpapillate organs of frogs. This resemblance is probably plesiomorphic. Taste bud morphology of urodeles and gymnophiones is similar to that of fishes, and the anuran condition is presumed to be the derived state. We identify these structures as taste buds in gymnophiones for those of similar morphology have been demonstrated neurophysiologically to be functional taste buds in other taxa. In both anurans and urodeles (Jaeger and Hillman, 1976; Farbman and Yonkers, 1971; Fahrman, 1967; Fahrman and Schuchert, 1967; Düring and Andres, 1976; Graziadei and DeHan, 1971; Jasinski and Miodonski, 1979; West and Bernard, 1978; Whitear, 1976) the taste buds are distributed on both the tongue and the oral mucosa, rather than the mucosa alone. Jasinski and Miodonski (1979) comment on the variation among taxa in mucosal and glandular structure and taste bud morphology and distribution, citing unpublished data. Both terrestrial and aquatic frogs and salamanders have taste buds, whereas we have observed them only in aquatic adults and larvae of caecilians to date. As with the studies cited above, too few species have been sampled to draw conclusions about taxonomic or ecological implications of the presence or absence of taste buds among species.

Heads of 18 species representing 15 genera were fixed in 10% neutral buffered formalin or 4% phosphate-buffered glutaraldehyde; the former were stored in 70% ethanol. Most were serially sectioned and stained variously with hematoxylin-eosin, picro-ponceau, Mallory's azan, safranin red F, or toluidine blue. Glutaraldehyde-fixed lower jaws and tongues of *Dermophis mexicanus* and

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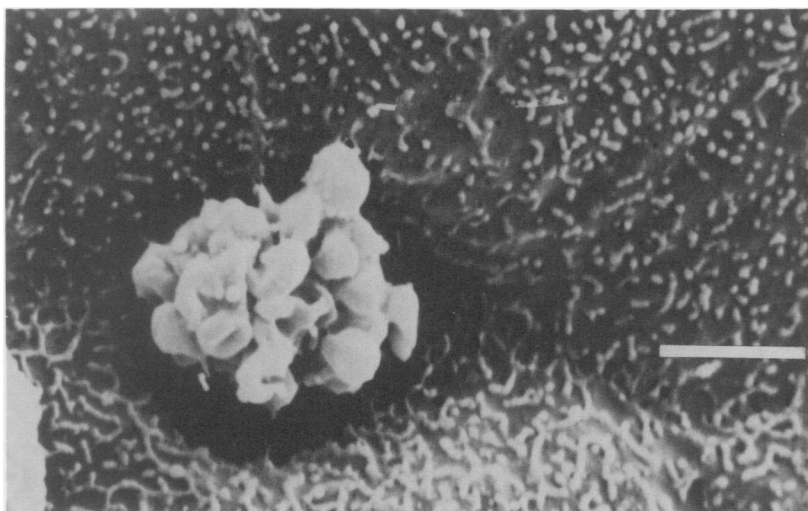


FIG. 1. Scanning electron micrograph of apical tuft of taste bud with approximately 21 filaments. Bar = 2.6 μ m.

Typhlonectes compressicaudus were dehydrated in an ethanol series, critical-point dried, sputter-coated with gold-palladium alloy, and examined and photographed with an ISI-DS 130 scanning electron microscope.

Scanning Electron Microscopy.—Taste buds of *Typhlonectes compressicaudus* are scattered through the oral mucosa of the labial margin of the lingual tooth row (Fig. 1A), but not on the tongue. The mucosal surface is of low, flat cells with irregular borders and numerous microvilli. The apical processes of the taste buds emerge in pores between mucosal cells. Taste buds have 8–25 processes with blunt tips; the processes end slightly above the mucosal surface (Figs. 1B, C).

Light Microscopy.—The taste buds of *Typhlonectes* are elongate, and the necks are long compared to taste buds of other amphibian taxa. That in Fig. 2A is 130 μm long and 70 μm wide at the widest part of the base. The tips of the apical processes are slightly higher than the mucosal surface. The pore is ill-defined in formalin-fixed material. We see some indication of the "light" cells, based on intensity of nuclear staining and association with apical filiform processes (and presumed by workers on frogs and salamanders to be the gustatory cells), and the "dark" or support/sustentacular cells, with secretory granules.

The taste buds of *Ichthyophis* sp. larvae are abundant on the palate, especially near the marginal teeth, and in the mucosa of the lower jaw, again near the teeth, but none have been observed on the tongue. The taste buds are proportionally shorter (50 μm \times 30 μm) than those of *Typhlonectes* adults, and have fewer cells (11 vs. 30 in a transverse section at the center of selected buds). Apical processes are apparent, the pore indistinct. Light and dark cells appear to be present (Fig. 2B).

In this paper we document the presence of taste buds in gymnophiones. Light and scanning electron microscopy indicate some aspects of structure of the buds. Our studies continue, incorporating other species and preparation of material for transmission electron microscopy. However, some comparisons with the taste buds of frogs and salamanders can be made at this time. Most attention has been paid to the taste buds of the tongue in the latter groups. We suggest that much of the observed variation may be related to the morphology of the tongue itself (presence or absence of papillae, presence or absence of glandular crypts, etc.), though the flattened taste discs that characterize the frog species examined are clearly derived relative to taste bud morphology in other taxa.

The large size reported for taste buds of *Necturus* (Farbman and Yonkers, 1971) may indeed be due to large cell size and greater cell number, but far too few taxa of amphibians have been examined to draw significant conclusions about cell size and systematic position. Unfortunately, there are no studies of the ontogeny of these organs in amphibians. The taste buds of larval and adult

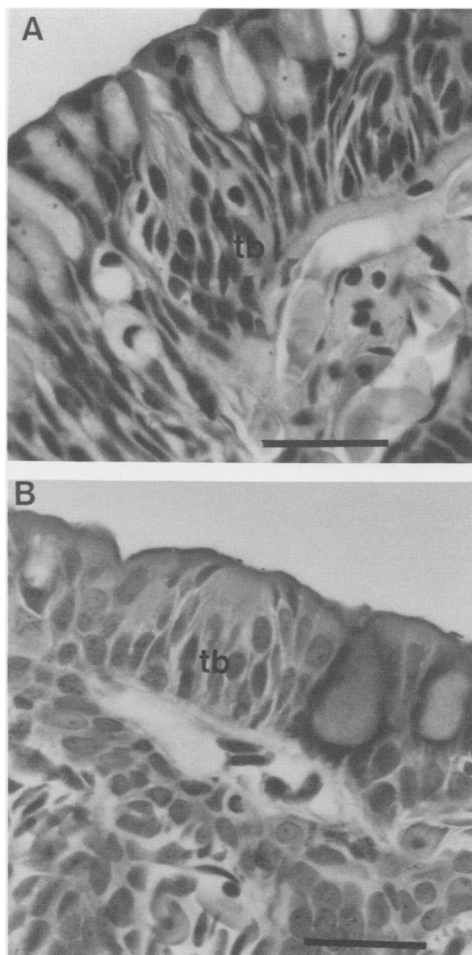


FIG. 2.A. Light micrograph of taste bud (tb) of *Typhlonectes compressicaudus*. Note elongate filaments of sensory cells. Bar = 56 μm . B. Light micrograph of taste bud (tb) of *Ichthyophis* sp. larva. Bar = 25 μm . The taste bud is relatively shorter and stouter than that of *T. compressicaudus*, but the apical filaments of each reach the surface of the mucosa. Both have the characteristic support and sensory cells and capillaries immediately below the basement membrane. Large goblet cells lie beside the taste buds.

caecilians, so far as is known, are noteworthy for three reasons: 1) the presence only in aquatic forms, larval or adult; 2) rather simple structure, similar to that of many fishes and some salamanders; and 3) distribution in the oral mucosa, but not on the surface of the tongue. Fishes are unusual for their extensive distribution of taste buds, not just in the mucosa but also over the external surface of the body.

Taste buds in the frogs and salamanders ex-

amed have been shown to be both chemo- and mechanoreceptors (Rapuzzi and Casella, 1965), but the two functions are separately innervated (Sato, 1976; West and Bernard, 1978). The simple structure but mucosal restriction of taste buds in gymnophiones may suggest chemoreception of ions as water passes into the mouths of aquatic larval and adult caecilians as they feed.

Acknowledgments.—We thank R. F. Inger, Field Museum of Natural History, for permission to section the head of an *Ichthyophis* larva, Tom Hetherington and Kath Thomas for sectioning many heads, and the Electron Microscope Laboratory at the University of California, Berkeley, for use of its facilities. We particularly acknowledge the support of this research by the National Science Foundation through grants BSR 83-05771 to MHW and PCM 82-12240 to the Electron Microscope Laboratory.

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Accepted: 21 June 1985.

Journal of Herpetology, Vol. 20, No. 2, pp. 256-259, 1986
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Evidence for Interactions Over Calling Sites Between Males of the Frogs *Ranidella signifera* and *R. riparia*

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Ranidella riparia and *R. signifera*, two small leptodactylid frogs, are usually allopatric, but their distributions meet in a narrow zone of sympatry in the southern Flinders Ranges of South Australia (Odendaal and Bull, 1982). Both species breed during winter and spring (June-October) in creeks flowing down from the ranges. Near the area of overlap, *R. riparia* normally occupies fast-flowing creeks with rocky beds and limited creekside vegetation, whereas *R. signifera* is found in slow-flowing creeks with muddy substrates and more extensive vegetation (Odendaal and Bull, 1982).

Previously we showed that *R. signifera* tadpoles were swept away more easily in flowing water (Odendaal and Bull, 1980), and had lower survival than *R. riparia* tadpoles in enclosures exposed to creek flow (Odendaal and Bull, 1983a). We suggested that *R. signifera* could not persist in the fast-flowing creeks where its tadpoles were poorly adapted. We found no equivalent explanation for the restriction of *R. riparia* whose tadpoles survived equally well whether or not exposed to creek flow (Odendaal and Bull, 1983a). We found no evidence that tadpoles of *R. signifera* competitively inhibit those of *R. riparia* (Odendaal et al., 1982; Odendaal and Bull, 1983a; Odendaal et al., 1984). We report, in this paper, investigations of the hypothesis that adult males of the two species compete because they overlap in the microhabitats which they use for calling sites.

Observations were made in the southern Flinders Ranges of South Australia during winter and spring when both species were breeding. Char-