Gross Morphology and Distribution Patterns of Lingual Papillae in Some Geomyid and Heteromyid Rodents

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There have been few studies of lingual morphology and associated papillae of rodents since a 1924 study restricted mostly to Old World taxa (1). This is especially applicable to the North American superfamily Geomyoidea. We examined the distribution patterns and types of lingual papillae for three geomyids and 12 heteromyid rodent species. All member taxa have a single circunivallate papilla, widespread filiform papillae, and fungiform papillae, which are restricted anteriorly on the tongue surface. The two families can be distinguished on the basis of variation of these characters. No further resolution is afforded within the geomyids. However, subfamilial levels of variation can be distinguished within the Heteromyidae, and findings are suggestive of specific differences between member species of the genera *Perognathus, Chaetodipus,* and *Dipodomys*.

INTRODUCTION

The rodent superfamily Geomyoidea is an ancient assemblage comprised of two distinct families. The gophers (Geomyidae) are heavily built, fossorial animals which feed primarily on subterranean roots and leafy vegetation. The kangaroo rats, pocket mice, and their allies (Heteromyidae) are more delicate in structure, and range from bipedal to scansorial forms which forage mostly for seeds.

Many aspects of the anatomy of heteromyid rodents have been investigated, from the molecular and cytogenetic levels to gross morphology. Three rather distinct subfamilial lineages are recognized by Hafner and Hafner (2): the primitive Heteromyinae (*Heteromys* and *Liomys*), the Perognathinae (*Perognathus* and *Chaetodipus*), and the relatively derived Dipodomyinae (*Dipodomys* and *Microdipodops*). Perceptions of interrelationships among the more specious genera (*Perognathus, Chaetodipus*, and *Dipodomys*) are less obvious. There is no recent study of comparable breadth for the Geomyidae.

A superficial but taxonomically diverse survey of the external lingual morphology for 11 families of rodents led Sonntag (1) to conclude that distinctive lingual characters are observable at the familial and often generic level, and that little variation occurs at the specific level. Few subsequent studies have detailed external aspects of tongue structure for other mammals (3-8). Particularly neglected have been the distribution and types of lingual papillae among rodents. Additionally, the only pertinent reference in the literature for any member of the superfamily Geomyoidea is Sonntag's (1) citation of an 1888 observation that a single circumvallate papilla occurs in the gopher, *Geomys bursarius*.

The purpose of this study was twofold: first, to provide the first preliminary assessment of variation in the surface anatomy of representative geomyoid rodents, especially as pertains to lingual papillae; and second, to determine if such differences are as taxonomically distinct for the Geomyoidea as has been reported for other rodent taxa.

METHODS AND MATERIALS

Specimens were collected from wild populations or were borrowed from the collections of the Museum of Texas Tech University (TTU) and the Museum of Natural History of Los Angeles County, CA (LACM). Given the destructive nature of the technique employed (below), we were reluctant to borrow more than single representatives of each species. Emphasis was therefore placed on taxonomic diversity, although more than one specimen of some species were examined where possible. The lower jaw and hyoid musculature of each fluid-preserved whole specimen was exposed by first peeling back the skin from the lower jaw. The base of the tongue was then

carefully severed with a scalpel, far enough back to include the entire field of surface lingual papillae. The severed tissue was then gently pulled back from between the jaws with forceps. Following removal from the body, each tongue was stored in a glass vial of 60:40 2-propanol:water with a tag containing specific identification, and acronym and catalog number for the originating institution. Examinations took place with a light microscope under variable magnifications. Tongues were kept moist during examinations and illustration sessions, and Giemsa stain was applied to the surface of each tongue to provide the contrast necessary for illustration of the surface anatomy with a camera lucida attachment.

Tongues in vials were retained with those specimens on deposit at Midwestern State University, or were returned to the lending institutions.

RESULTS and DESCRIPTIVE ACCOUNTS

The geomyoid tongue is characterized by a tapered tip which is divided dorsally along the distal fourth of the tongue by a shallow, terminal groove. The intermolar eminence, an elevated region situated between the cheek teeth and described by Sonntag (1) as typical of most rodents, is not readily discernible when the

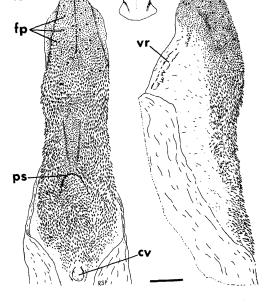


Figure 1. Illustration of dorsal (left), lateral (right), and cross-sectional (inset) views of tongue of representative geomyid rodent, *Geomys bursarius* (MWSU 18349). Labeled representative features are: ts, terminal sulcus; fp, fungiform papillae; ps, posterior sulcus bordering anterior margin of intermolar eminence; cv, circumvallate papilla; vr, ventrolateral ridge. Bar=2 mm.

tongue is extended. However, if the tongue is sufficiently contracted, this region protrudes prominently. It is then bordered anteriorly by a U- or V-shaped sulcus.

Lingual papillae cover the dorsum of the tongue and continue onto the sides. The most widespread structural type of these are the filiform papillae, which envelop the top, sides, and anterior tip of the tongue. These tiny structures are mostly monofid, and the sharp and tapered tips generally project posteriorly. Larger, circular-shaped fungiform papillae are prominently and somewhat uniformly distributed over at least the distal one-third of the tongue.

Largest and most conspicuous of lingual structures is the posteromedial circumvallate papilla. It is quite variable in shape, size, and surface topography, even between con-specific individuals. The shape is generally circular to ovoid. The dorsum is typically marked by minute bumps or projections which are difficult to resolve with light microscopy. This papilla resides in a craterlike depression bordered by marginal folds. Its prominence may be a transient feature. In some specimens, it is distinctly protruded, while in others it appears to be retracted into the depression. Given the extent of individual variation and the lack of resolving power with light microscopy, we are reluctant to attempt further detailed descriptions of this character. Distribution of the filiform papillae diverge around, and terminate, near the circumvallate papilla.

Family Geomyidae

Lingual morphology among gophers is conservative, for no consistent differences were found to distinguish the tongues of *Thomomys bottae* (n = 2), *Geomys bursarius* (n = 3), or *Cratogeomys castanops* (n = 2). The geomyid tongue is elongate and rather fusiform (Figure 1). From a dorsal perspective it is broadest at the base, becomes gradually constricted anteriorly, then broadens and tapers to the tip. In cross-section of the terminal third of the tongue, the sides are noticeably concave before flaring out to form a shelf usually visible from above.

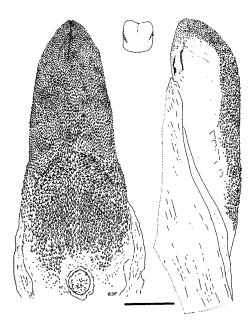


Figure 2. Illustration of dorsal (left), lateral (right), and cross-sectional (inset) views of tongue of representative heteromyid rodent, *Dipodomys ordii* (TTU 23506). Bar = 2 mm.

Fungiform papillae are small and most abundant near the tip of the tongue. Filiform papillae are monofid, with the minor exception of a few bi- and trifurcate papillae along the margins of the ventrolateral ridge. These are quite elongate and thorn-like along the lateral margins at the midbody of the tongue. Filiform papillae are smallest at the tongue tip and

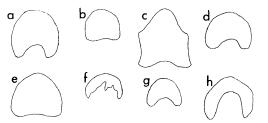


Figure 3. Distribution patterns of multifurcate filiform papillae on tongue dorsum, which comprise the intermolar eminence for eight species of *Dipodomys*: a) *D. agilis*; b) *D. compactus*; c) *D. deserti*; d) *D. elator*; e) *D. merriami*; f) *D. microps*; g) *D. ordii*; and h) *D. spectabilis*.

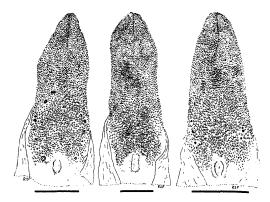


Figure 4. Illustration of dorsal views of tongue of three representative heteromyid rodents: (from left) *Chaetodipus nelsoni* (TTU 8023); *C. hispidus* (MWSU 18209); and *Perognathus flavus* (TTU 14552). Bars = 2 mm.

within a shallow trough in the vicinity of the midbody constriction, but also become smaller in size towards the posterior extent of their distribution. Most filiform papillae are oriented posteriorly, except for the vicinity of the apex of the intermolar eminence. This region, even if not elevated, is marked by a radiation of papillae outwards from a focal point just posterior to the midbody trough to form a whorl-like pattern.

Family Heteromyidae

The heteromyid tongue (e.g., Figure 2) is a short, broad and tapered organ which also differs from the geomyid condition in the following ways: 1) body tapered, with less conspicuous midbody constriction; 2) ventral shelf less prominent, as visible in cross-section or from the dorsal perspective; 3) fungiform papillae with greater variation in size and distribution (over anterior half or more of dorsal surface); 4) ventrolateral ridge smooth, rather than with filiform papillae; and 5) intermolar eminence marked by broad polyfid (mostly bi- and trifurcate) filiform papillae, which are more uniformly oriented posteriorly. The circumvallate papilla appears to be especially variable, although this may be an artifact of preservation.

Subfamily Dipodomyinae. Characterization of the lingual morphology of this subfamily is based on six species of kangaroo rats: *Dipodomys agilis* (n = 1); *D. compactus* (n = 1); *D. deserti* (n = 1); *D. elator* (n = 3); *D. merriami* (n = 1); *D. microps* (n = 1); *D. ordii* (n = 4); and *D. spectabilis* (n = 1). Fungiform papillae occur over the anterior half of the tongue surface, and are especially concentrated at the tip. The considerable interspecific variation among representatives of this assemblage seems restricted to the intermolar eminence, as marked by the distribution of polyfid filiform papillae (Figure 3). For example, the distribution of these

papillae is quite broad in the single example of *D. deserti*, but is sparse and irregular among each of two specimens of *D. microps*.

Subfamily Perognathinae. In most respects, the lingual morphology of *Perognathus flavus* (n = 1), *Chaetodipus nelsoni* (n = 1), and *C. hispidus* (n = 2) are essentially similar to the Dipodomyinae (Figure 4). Nevertheless, some consistent differences were noted. The fungiform papillae are distributed over the surface of the tongue, except for the intermolar eminence, and many of these are proportionally quite large in *C. nelsoni*. Additionally, the broad polyfid filiform papilla comprising the intermolar eminence are less deeply forked than in the genus *Dipodomys*.

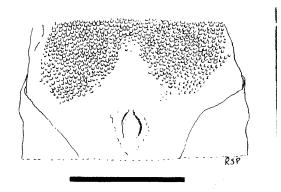


Figure 5. Illustration of posterodorsal view of tongue of *Liomys irroratus* (TTU 24418). Bar=2 mm

Subfamily Heteromyinae. Only a single specimen of ^{mm.} *Liomys irroratus* was available to represent this tropical-to-subtropical subfamily. In most respects, the lingual morphology resembles that of the *Perognathinae*, although the filiform papillae do not extend nearly so far posteriorly as in other geomyoid taxa. Furthermore, these are either small and blunted or are very weakly forked, rather than being simple conical structures (Figure 5). Although this subfamilial sample is restricted, the uniqueness of these distinguishing features lead us to believe that they likely characterize the species, and perhaps also the entire genus.

SUMMARY and CONCLUSIONS

Because the tongue is such a muscular and pliant organ, overall shape and certain morphological features are transient characters in life. Among preserved tongues of specimens, we found distortions due to dehydration, state of flexion at time of fixation, and molding against the palate or teeth— any of which are capable of confounding comparative analyses. The qualified definitions of such lingual features as overall shape, sulci, and prominences must therefore be accepted with caution. However, morphology and general patterns of distribution of filiform and fungiform papillae are not affected by such factors, and they are sufficiently variable to afford some systematic resolution among member taxa of the rodent superfamily Geomyoidea.

The family Geomyidae is distinguished by filiform papillae which are elongated and are almost entirely monofid. The ventrolateral ridge is marked by a few bi- and trifurcate filiform papillae. Fungiform papillae are small, and are restricted to the anterior one-third of the tongue. Representative species of *Thomomys, Geomys,* and *Cratogeomys* are indistinguishable for these familial characters.

Filiform papillae among the Heteromyidae are relatively short and stout. The intermolar eminence is adorned with broadened, polyfurcate filiform papillae, which contrast with the monofid condition elsewhere. The ventrolateral ridge is devoid of papillae. Each of the three subfamilies can be distinguished by the assessed characters. The potential of certain lingual features for specific or species group discrimination among pocket mice (size, distribution of fungiform papillae) and kangaroo rats (distribution patterns of polyfid papillae on the intermolar eminence) are deserving of further study.

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