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TONGUE MORPHOLOGY IN HORNED LIZARDS (PHRYNOSOMATIDAE: *Phrynosoma*) AND ITS RELATIONSHIP TO SPECIALIZED FEEDING AND DIET

Kurt Schwenk[1]

In lizards, the tongue is joined to the mandible by the median genioglossus medialis muscle and the larger, paired genioglossus lateralis muscles. These muscles run through a frenulum and along the sides of the tongue, forming its walls. In horned lizards, however, the genioglossus lateralis muscles fail to join the tongue for most of its length, forming separate ridges evident in the floor of the mouth lateral to the body of the tongue. This unique tongue morphology co-occurs with horned lizards' ability to consume large numbers of potentially lethal harvester ants, a diet enabled by a feeding mechanism in which ants are rapidly immobilized with strings of mucus before immediate swallowing. Circumstantial evidence implicates the unusual morphology of the genioglossus lateralis muscles in the mucus-binding system.

INTRODUCTION

The lizard family Phrynosomatidae comprises two clades: one with four genera of relatively generalized lizards, including the speciose genus, *Sceloporus*, and another, more phenotypically derived, arid-adapted clade, consisting of the 'sand lizards' and their sister group, the 'horned lizards' (*Phrynosoma* spp.) (Fig. 1) (Wiens et al., 2010, 2013). The genus *Phrynosoma* includes 17 nominal species that range across western North America from southern Mexico (possibly, northern Guatemala) to southern Canada (Canseco-Marquez et al., 2013; Nieto-Montes de Oca et al., 2014; Leaché and Linkem, 2015; Sherbrooke, 2003, 2020).

Horned lizards possess a bizarre morphology that has long been viewed as an iconic example of phenotypic specialization related to myrmecophagy (e.g., Pianka and Parker, 1975), a perception reinforced by the apparent phenotypic convergence between *Phrynosoma* and another unusual ant specialist, the agamid Moloch horridus (Pianka and Pianka, 1970). However, Greene (1982) and Schwenk (2000) pointed out that many other species of lizards regularly consume equal or greater quantities of ants, but lack any discernable phenotypic specializations associated with myrmecophagy. In fact, most of the convergent traits of *Phrynosoma* and Moloch are not a consequence of feeding on ants, per se, but of feeding on many small prey in open environments while exposed to visual predators (Pianka and Parker, 1975; Greene, 1982; Sherbrooke and Schwenk, 2008).

Although a specialized phenotype is not a necessary outcome of myrmecophagy, the horned lizard feeding apparatus does manifest several features correlated with diet. Meyers et al. (2006, 2018) described reductions in several traits related to prey crushing and processing in species that consume the largest numbers of ants, specifically in jaw adductor mass, bite force, dentition, and size/robustness of the skull and mandible. Reductions in these traits are consistent with the fact that highly myrmecophagous *Phrynosoma* species neither chew nor bite their prey before swallowing (Meyers and Herrel, 2005; Sherbrooke and Schwenk, 2008), in contrast to the vast majority of lizards (Schwenk, 2000). Nevertheless, the fact that horned lizards do not kill their ant prey before swallowing is notable given that the particular species horned lizards favor are harvester ants (*Pogonomyrmex* spp.), which are characterized by powerful, biting mandibles and a potentially lethal, venomous sting (Schmidt and Schmidt, 1989; Schmidt, 2019). Most lizards avoid dangerous prey (e.g., Hirth, 1963; Hasegawa and Tanigu-

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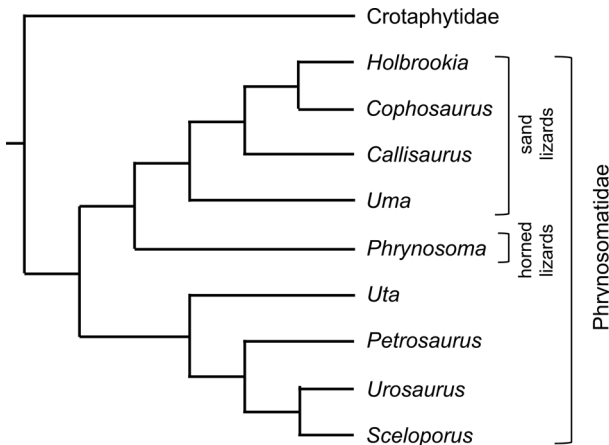e-mail: kurt.schwenk@uconn.edu

Fig. 1. Phylogeny of the Phrynosomatidae showing the relationships of the horned lizards (*Phrynosoma*) to other members of the family. Based on Wiens et al. (2010, 2013). Note that the sister group of Phrynosomatidae varies among different studies.

chi, 1996), but some take them occasionally, killing them immediately by means of biting or chewing, violent shaking, and/or crushing them against the substrate before further processing and swallowing (e.g., O'Connell and Formanowicz, 1998; Lappin and German, 2005).

Like all iguanians, horned lizards use the tongue rather than the jaws and teeth to capture prey (Schwenk and Throckmorton, 1989; Schwenk, 2000) and are, therefore, especially vulnerable to bites and stings on sensitive oral tissues. Furthermore, by failing to kill their prey upon capture, they remain susceptible to attack within the stomach because the ants are alive when swallowed. Sherbrooke and Schwenk (2008), however, showed that horned lizards possess several remarkable adaptations that protect them from injury during feeding. In contrast to other lizards in which feeding proceeds through a series multi-cycle stages, including ingestion (capture), processing (chewing), intra-oral transport, and swallowing, horned lizards collapse feeding into a single, combined ingestion-transport-swallow cycle. During this process, the tongue pushes the ant posteroventrally through a dense mat of large mucus-secreting papillae covering the sides of the tongue and the pharynx, unique to *Phrynosoma*. While this occurs, the ants are folded over and bound by strings of viscous mucus, incapacitating their weapons. Single-cycle feeding and the mucus-binding system significantly decreases handling time for each prey item while simultaneously protecting the lizards against injury or death. As for most features of the horned lizard phenotype, these specializations of the feeding apparatus are not a direct consequence of myrmecophagy, but rather an adaptive response specifically

to feeding on dangerous prey (Sherbrooke and Schwenk, 2008).

At the end of a horned lizard capture cycle, the hyobranchial apparatus pulls the tongue with the adherent ant downward very rapidly, evident externally as an extreme, ventral bulge of the pharynx (Meyers and Herrel, 2005; Sherbrooke and Schwenk, 2008), during which mucus-binding of prey occurs. Details of the mucus-binding mechanism remain unknown, but it is clear that the tongue plays a critical role in the process. Therefore, it is unlikely to be a coincidence that, as reported here, horned lizards possess a distinctive tongue morphology in comparison to other squamates. In this paper I describe the form of the tongue in horned lizards and show that the disposition of the musculus (m.) genioglossus lateralis, a major tongue protractor muscle, differs from all known sister and outgroup taxa. I explore possible functional consequences of the horned lizard morphology and consider preliminary evidence for its role in the unique mucus-binding system.

MATERIAL AND METHODS

Specimens. The species and specimens examined for this study are listed in Table 1. All specimens were formalin-fixed and preserved in 70% ethanol. Some are from my personal collection or were provided by colleagues, but most were obtained from museum collections. In most cases the lower jaw and tongue were removed, photographed and prepared for paraffin histology, although in some the tongue and surrounding tissues were excised, leaving the mandible intact. For a few specimens the entire head was removed and sectioned. Whole tongues were either photographed while immersed in 70% ethanol with a dissecting microscope (black and white images) or were photographed outside of fluid with a MacroscopicSolutions Macropod Pro® system (color images).

Histology. Complete, serial, paraffin sections were prepared of all specimens listed in Table 1 using standard methods (Presnell and Schreiber, 1997), with the exception that pure paraffin was used for embedding rather than a paraffin-polymer mixture. Specimens were sectioned at $7 - 10 \mu m$ (most at $8 \mu m$) and sections were stained with Ehrlich hematoxylin and eosin, Weigert iron hematoxylin and picro-ponceau (Presnell and Schreiber, 1997), or Periodic Acid Schiff-Alcian blue (Bancroft and Stevens, 1982). Histological sections were photographed with a Zeiss compound microscope. Multiple images were taken of each section and stitched together using software (Affinity Photo®).

Cinematography and Videography. Feeding in *Phrynosoma* platyrhinos was investigated using 16 mm

cine taken at 64 fps with a Bolex movie camera. Frame-by-frame analysis was used to examine tongue form during feeding with a Vanguard motion analyzer. Images of the tongue during prey capture were made from individual cine frames. Lingual prey capture in a variety of other iguanian and non-iguanian species was also captured using high-speed videography (Edgertronic SC1® high-speed video camera) and 35 mm photography during the course of other studies. Images from these studies were used only to verify that horned lizard tongue form deviates from what is observed during feeding in other lizards.

RESULTS

Tongue morphology. Figure 2 illustrates superficial tongue form in four species of *Phrynosoma* and four exemplars of other iguanian lizards, including a closely related sand lizard (*Uma scoparia*), two other phrynosomatids (*Sceloporus magister* and a second, unidentified *Sceloporus* species), and a more distantly related tropidurid (*Stenocercus* sp). There are three clear distinctions of horned lizard tongues compared to other lizards (Fig. 2): (1) The body of the tongue has a 'pinched waist', i.e., it narrows at a point slightly more than halfway along its length and then widens again at the 'posterior limbs'; (2) On each side of the tongue at its narrowed 'waist' there is a ridge of tissue, separated from it by a cleft, that fuses with the tongue at the distal end of each posterior limb. These ridges are distinct from the sublingual plicae (containing the sublingual glands), which lie lateral to the ridges and medial to the tooth rows; (3) The lateral ridges are covered by large papillae that extend onto the tongue's posterior limbs, over the larynx and into the pharynx.

The m. genioglossus lateralis in horned lizards. Serial transverse sections of the tongue in seven species of horned lizards reveal that the lateral ridges consist of the genioglossus lateralis muscles (GGL) (Fig. 3A – D). The paired GGL originate on the ventral edge of the mandible lateral to the symphysis, separate from the single, median origin of the m. genioglossus medialis (GGM) on the inner surface of the symphysis. Immediately posterior to their origins, the GGL and GGM join. The bulk of the latter remains as a single, undivided mass in the midline while the GGL run in the floor of the mouth on either side (Fig. 3B). The GGM forms a median elevation in the floor of the mouth that rises posteriorly to join the tongue ventral to the intrinsic verticalis musculature, forming a frenulum. As soon as it merges with the tongue the GGM sends a small, median group of fibers anteriorly toward the tip along the tongue's ventral surface (Fig. 3A) and two lateral extensions that climb up each side of the

tongue, forming its walls (Fig. 3B). Continuing posteriorly, the median part of the GGM disappears, leaving a large anatomical space within the frenulum. Simultaneously, some fibers of the GGL move medially into the frenulum to form its sides. The GGL fibers extend dorsally, entering the tongue ventral to the m. hyoglossus bundles and expand dorsolaterally on the sides of the tongue to its dorsal surface. As the GGL fibers extend dorsolaterally, they replace the GGM fibers that occupy this position anteriorly (compare Fig. 3B and C). Anteriorly, the major portion of the GGL remains in the floor of the mouth, but progressing posteriorly, these masses rise dorsally to form the lateral ridges observed grossly in Fig. 2 (Fig. 3B – D). Thus, for much of the tongue's length, the GGL forms both the walls of the tongue's corpus and the disjunct lateral ridges (Fig. 3C). These sepa-

TABLE 1. Species and Specimens Examined For This Study.

Species	*N* (gross)	*N* (histology)		
		transverse	sagittal	total
Phrynosoma[1]				
P. asio	3	2	0	2
P. cornutum	2	1	0	1
P. coronatum[2]	1	1	1	2
P. douglassii	2	1	1	2
P. mcallii	1	1	0	1
P. orbiculare	1	0	1	1
P. platyrhinos	3	1	1	2
'Sand Lizards'				
Callisaurus draconoides	2	1	1	2
Cophosaurus texanus	1	1	0	1
Holbrookia maculata	1	1	0	1
Uma scoparia	1	1	1	2
Other Phrynosomatids				
Petrosaurus mearnsi	1	1	0	1
Sceloporus occidentalis	2	4	3	7
S. magister	2	0	0	0
Sceloporus sp. (Mexico)	1	0	1	1
Urosaurus graciosus	1	2	1	2
Uta stansburiana	1	1	0	2
Non-Phrynosomatid Ant-Specialists				
Moloch horridus	3	3	0	3
Anolis bonairensis	1	1	0	1
Liolaemus monticola	3	2	0	2
Other Outgroup Species				
Representatives of most lizard families				100

[1] Note that the sampled species include three of the four recognized clades within the genus *Phrynosoma* (Leaché and Linkem, 2015)

[2] *P. coronatum* has been subdivided into three species (*P. coronatum*, *P. blainvilli*, *P. cerroense*) (Montanucci, 2004; Leaché et al., 2009); it is not known to which of these putative species the specimen belongs.
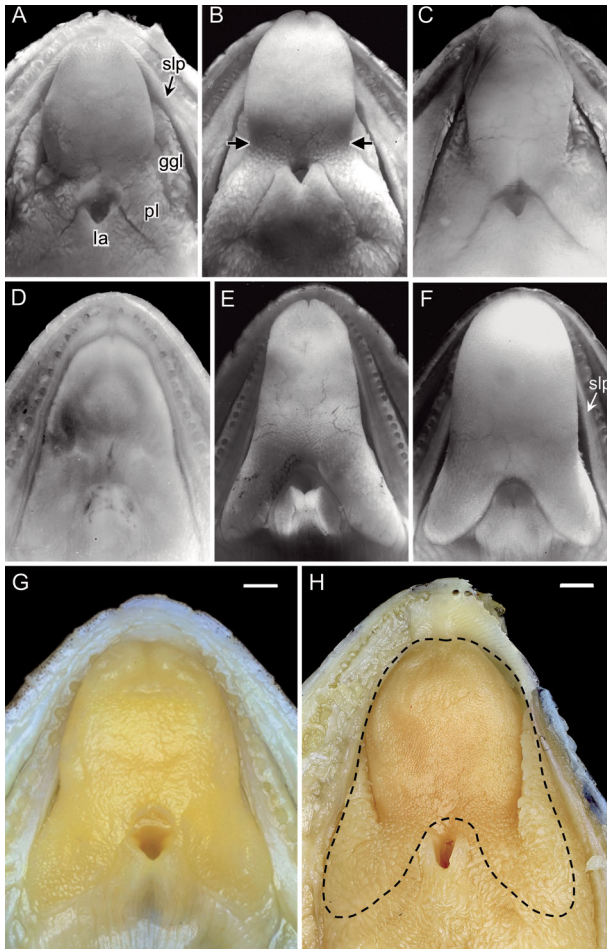
Fig. 2. Superficial tongue form in horned lizards (A – C, H) compared to other phrynosomatids (D, E, G) and a tropidurid (F). A, *Phrynosoma douglasii*; B, *P. orbiculare*; C, *P. cornutum*; D, *Uma scoparia*; E, *Sceloporus* sp.; F, *Stenocercus* sp.; G, *Sceloporus magister*; H, *P. platyrhinos*; ggl, lateral ridge containing the m. genioglossus lateralis; la, larynx; pl, posterior limb of the tongue; slp, sublingual plica. Arrows in B indicate the 'pinched waist' characterisitic of horned lizard tongues. Dotted line in H indicates the outline of the *S. magister* tongue in G (see text for explanation). Scale bar in G and H is 1 mm (scale was unavailable for A – F, but is similar).

Fig. 3. Transverse sections of the tongue in a horned lizard, *P. mcallii* (A – D) and a generalized phrynosomatid, *Uta stansburiana* (E – H), from anterior to posterior. Note the presence of the lateral ridges (lr) containing fibers of the m. genioglossus lateralis (ggl) in the horned lizard and their absence in *Uta*, in which all m. genioglossus lateralis fibers enter the frenulum and run along the sides of the tongue body. In section B, the arrows indicate the dorsolateral extent of the GGM. By section C, GGL fibers have replaced the GGM fibers in this position. In section G, note the vestiges of the m. genioglossus medialis (ggm) as it is replaced by the GGL posteriorly. Sections A-F stained with hematoxylin and eosin; sections G and F stained with iron hematoxylin and picro-ponceau; dl, dorsal longitudinal fibers; gh, m. geniohyoideus (mandibulohyoideus); ggl, m. genioglossus lateralis; ggm, m. genioglossus medialis; im, m. intermandibularis; lp, lingual process (hypohyal, entoglossal process) of hyobranchium; lr, lateral ridge; slg, sublingual glands; slp, sublingual plica; tr, transverse fibers (m. transversalis); v, m. verticalis. Scale bars are 400 μm.

rate parts of the GGL are reunited in the posteriormost part of the tongue as the lateral ridges merge with the tongue's posterior limbs dorsally (Fig. 3D). Fibers from both parts of the GGL turn medially and intermingle with each other and with dorsal transverse fibers (m. transversalis) on each side.

The m. genioglossus lateralis in other lizards. As described above, each GGL in *Phrynosoma* consists of two moieties — a medial part that extends dorsally within the frenulum, lateral to the GGM, to replace fibers of the GGM posteriorly in forming the sidewalls of the tongue; and a lateral part that thickens to form a raised,
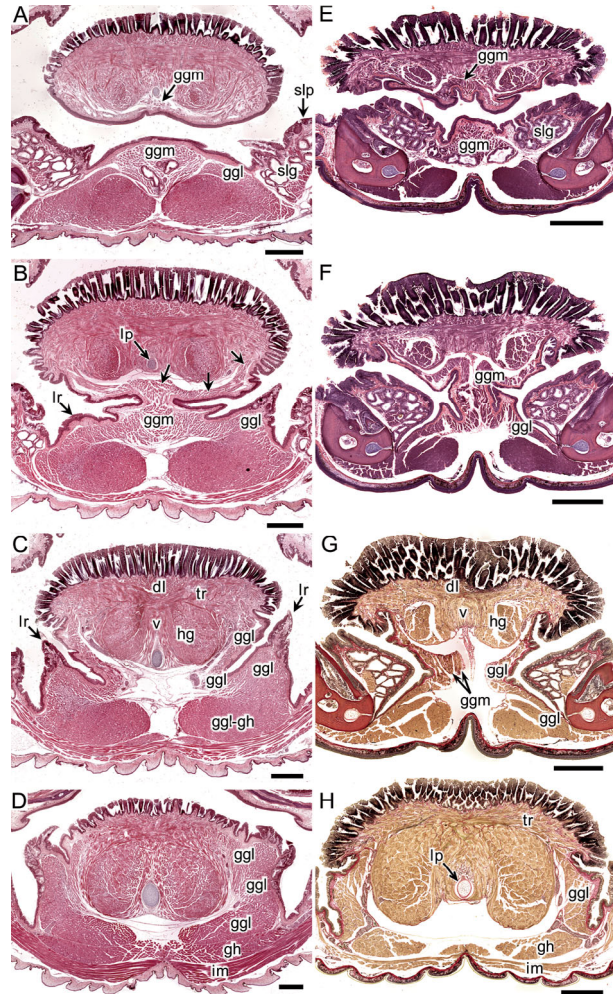
elevation or ridge in the floor of the mouth lateral to the tongue corpus, only joining it (and its own medial fibers within the tongue) posteriorly at the distal end of the tongue's posterior limb. In all other lizards, including *Phrynosoma*'s sister clade, the sand lizards, and other phryno-
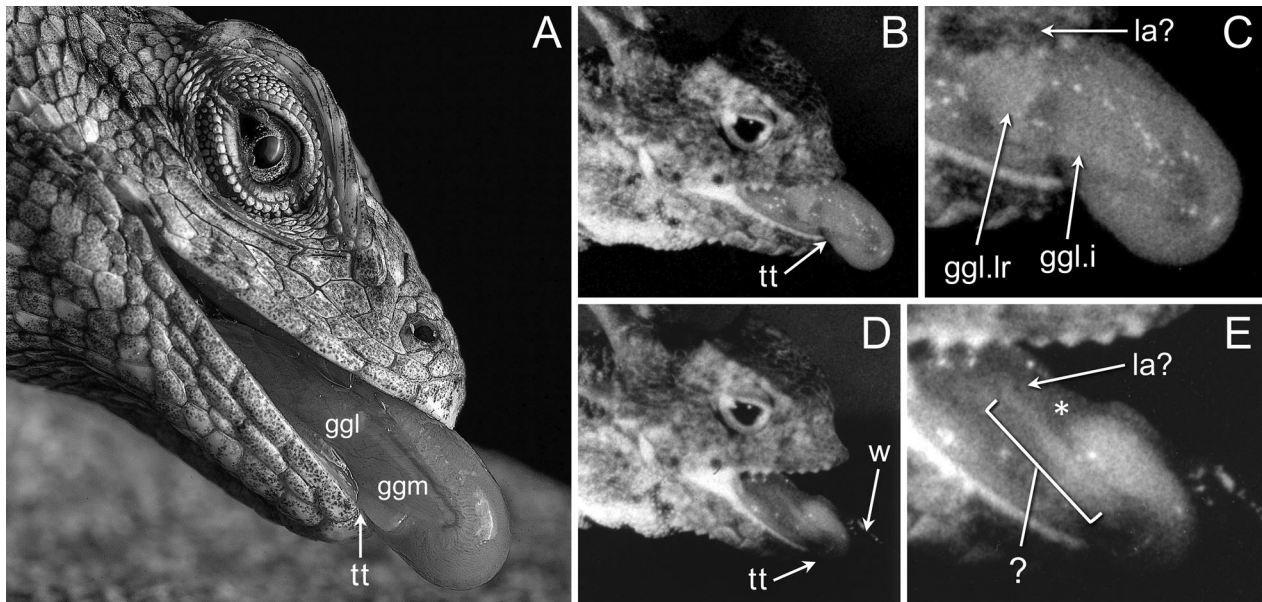
Fig. 4. Tongue form during feeding in a horned lizard (*P. platyrhinos*) compared to a generalized phrynosomatid (*Sceloporus occidentalis*): A, Lingual prey capture in a typical iguanian lizard (*S. occidentalis*) in which the mm. genioglossus lateralis and medialis are indistinct, forming the smooth sides of the tongue. Photo by Jackson Phillips; B, lingual prey capture in *P. platyrhinos* feeding on earthworms, which fail to adhere to the tongue, shows a novel conformation of the GGL during protrusion; C, enlarged view of B; D, during tongue retraction with an earthworm imperfectly held by the tongue, the hindtongue is momentarily compressed or retracted ventrally, creating an apparent pocket at the back of the tongue; E, enlarged view of D. The question mark indicates an unidentified band of tissue that remains during hindtongue deformation, perhaps the remaining mucosa: ggl, m. genioglossus lateralis; ggl.i, intrinsic component of the ggl that runs along the side of the tongue posterior to the ggm; during tongue protrusion it is extended anteriorly beyond the mandible; ggl.lr, the extrinsic component of the ggl that forms the 'lateral ridge' in the floor of the mouth when the tongue is at rest within the mouth; la, larynx; tt, tongue tip; w, earthworm; asterisk, putative location of a pit or pocket in which mucus-binding of prey might occur (see text).

somatids, only the medial component of the GGL is present, i.e., the part that contributes to the frenulum and forms the sides of the tongue. Although fibers running in the floor of the mouth lateral to the frenulum presumably belong to the GGL, in other species they never expand dorsally into lateral ridges.

Papillary morphology. A second unique feature of the tongue in horned lizards is the presence of large papillae that blanket the lateral ridges, the posterior limbs, the larynx and the pharynx (Fig. 2). The papillae are covered with a dense epithelium of mucous cells. These were described by Sherbrooke and Schwenk (2008) as a central part of the horned lizard mucus-binding system and will not be dealt with further here.

Tongue kinematics. The kinematic data are very preliminary for several reasons. They are based on low resolution 16 mm film taken at only 64 fps (i.e., 4× slower than real time). The film is of a single individual feeding on earthworm pieces, a highly unnatural prey type for horned lizards. The earthworm's wet surface prevented effective tongue adhesion (which was the point at the time the films were made), resulting mostly in failed capture attempts and aberrant kinematics. In particular,

capture attempts sometimes resulted in prolonged tongue protrusion and a large, persistent gape compared to the extremely rapid cycling typical of horned lizards feeding on insects. However, the persistent gape permitted observation of tongue form during the end of retraction when the jaws would typically be closed. Whether or not the observed tongue form accurately reflects normal behavior remains an open question. It is possible that the patterning of tongue deformation is stereotyped and therefore unchanged, as rapid motor patterns are often insensitive to sensory feedback once initiated. Indeed, observations are functionally suggestive and at least consistent with the novel tongue morphology described here. Nevertheless, the results described here are tentative and require confirmation with higher resolution, high-speed videography and ideally, high-speed radiographic studies.

Figure 4 shows two unusual aspects of tongue form observed in *P. platyrhinos* as compared to typical iguanians. When the tongue is extended during prey capture in a generalized phrynosomatid such as *Sceoporus occidentalis*, the GGL is evident as the featureless lateral wall of the tongue ventral to the papillary surface (Fig. 4A). In
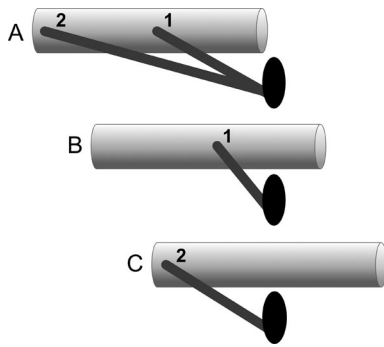
Fig. 5. A simple mechanical model illustrating one possible function of the specialized GGL in horned lizards. The mandible is represented by a vertical black oval and the tongue by a shaded gray cylinder. Alternative insertion sites of the GGL are shown by the dark gray bands: A, the tongue at rest. In most lizards the GGL inserts onto the body of the tongue anteriorly through the frenulum (conformation 1). In horned lizards, most if the GGL remains free of the tongue and inserts posteriorly on the tongue's posterior limb (conformation 2); B, shortening the typical GGL to 50% of its resting length results in modest protrusion of the tongue beyond the mandible; C, Shortening the horned lizard GGL to 50% of its resting length results in significantly greater protrusion.

contrast, the protruded tongue in a horned lizard (*P. platyrhinos*) shows what are probably the two parts of the GGL in a very different conformation (Fig. 4B, C). Both muscles originate from the inner surface of the mandible at the symphysis. A narrow band extends anteriorly toward the curled part of the tongue's dorsal surface. At the posterior end of the tongue, a broad band of muscle extends dorsally, appearing to loop over the posterior limbs of the tongue. I interpret the former muscle as the intrinsic component of the GGL that runs along the side of the tongue body and the latter as the disjunct, lateral part that forms the lateral ridges. With the tongue protruded beyond the mandible during protraction of the hyobranchial apparatus (Schwenk and Throckmorton, 1989; Schwenk, 2000), the intrinsic portion of the GGL is protruded along with it, changing its apparent function from a putative 'protractor' muscle to a de facto retractor. In contrast, the lateral, extrinsic part of the GGL does not extend beyond the mandible because the posterior limbs of the tongue to which it attaches remain within the jaw's margin. The muscle's origin from the mandible and insertion on the posterodorsal part of the tongue evident in the figure is consistent with the description of the resting muscle, above.

In conjunction with its counterpart on the opposite side, the extrinsic GGL fibers would 'girdle' the posterior end of the tongue. This conformation might account for the peculiar form of the tongue evident during tongue retraction in Fig. 4D, E, in which most of the hindtongue appears to have disappeared (compare Fig. 4C and E).

Conceivably, this momentary disappearance might have been caused by compression through contraction the GGLs' girdling fibers. If so, the remaining longitudinal band of tissue evident in Fig. 4E is difficult to interpret. Alternatively, or concurrently, the posterior end of the tongue was pulled ventrally by a component of the complex m. hyoglossus (Schwenk, 2001) while the hyobranchium was depressed.

DISCUSSION

Function. A simple explanation for the form of the GGL in horned lizards is that its more posterior insertion point affords greater tongue protrusion distance (Fig. 5). Smith (1984) suggested this as the reason for the more posterior insertion point of the GGL in most non-iguanian lizards compared to iguanians. Limited data suggest that horned lizards do, indeed, protrude their tongues relatively farther than other, comparably sized iguanians (Schwenk and Throckmorton, 1989; Meyers and Herrel, 2005), which may be aided by their unusually blunt, foreshortened snouts (Table 2).

The hypothesis of enhanced tongue protrusion distance may be correct, but observations of the tongue during feeding in *P. platyrhinos* suggest an alternative, or additional functional possibility. As Fig. 4C suggests, the putative role of the GGL (and GGM) as a tongue protractor in iguanian lizards might be incorrect, or at least, exaggerated. With the tongue fully protruded, the more anterior, intrinsic part of the GGL is extended completely beyond the mandible, which would be impossible by means of its own contraction. Therefore, the tongue must be protruded by another mechanism. In general, tongue movements are tightly correlated with hyobranchial movement in iguanians (Smith, 1984), and during tongue protrusion beyond the mandible, the hyobranchium is observed to protract anteriorly at the same rate as the tongue (unpublished data). This suggests that tongue protrusion in iguanians, at least, is driven primarily by hyobranchial protraction rather than m. genioglossus contraction (Schwenk and Throckmorton, 1989; Schwenk, 2000).

An alternative hypothesis for the derived morphology of the GGL in horned lizards is suggested by images captured fortuitously during feeding attempts in *P. platyrhinos* (Fig. 4). These suggest that the m. genioglossus lateralis might be involved in generating the novel tongue shapes observed in Fig. 4C and E. Given the caveats stated earlier about the preliminary and possibly aberrant nature of these results, I can only speculate here. However, it is suggestive that the peculiar, transient form of the tongue evident in Fig. 4E occurred at a point in tongue retraction that would correspond to the moment of mucus-binding in a normal bout of feeding on a harvester ant (with the jaws closed). If one makes this assumption

and assumes also that an ant, being smaller and more adhesive than an earthworm, would normally be moved to the posterior end of the tongue for swallowing, then it is possible that the rapid, ventral abduction of the posterior tongue surface would draw the ant downward and into a narrow, papilla-lined pocket (indicated by an asterisk in Fig. 4E) where it is compressed, folded and bound with mucus before it can bite or sting. The pocket could then be everted when it is aligned with the esophagus, ensuring that the ant is immediately swallowed.

Finally, it is worth noting that movements and shape changes of muscular tongues, particularly in mammals and lepidosaurs, are exceptionally difficult to interpret mechanistically owing to the complexity of their muscle fiber architecture and their capacity to function as muscular hydrostats (e.g., Kier and Smith, 1985). Traditional notions of insertions, origins and lever arm mechanics are not applicable within the tongue, which behaves more holistically and therefore, less predictably (Schwenk, 2001), making causal inferences of the sort I have attempted even less reliable.

Evolution. Given that the condition of the m. genioglossus lateralis described herein is unique to the genus *Phrynosoma*, and that sister and outgroup taxa share a different morphology, it is safe to conclude that the horned lizard condition is derived within squamates. Ancestrally, the GGL presumably were similar to the condition in other lizards in which it is closely associated with the m. genioglossus medialis within the frenulum and restricted to running within the walls of the tongue body.

There are three possible scenarios for the origin of the horned lizard condition: (1) the lateral ridges formed from de novo amplification and elevation of GGL fibers in the floor of the mouth lateral to the frenulum; (2) the ridges formed by cleavage of GGL fibers from the sides of the tongue, separating them from the tongue corpus; or (3) the ridges formed by failure of GGL dorsal extensions to enter or fuse with the frenulum established by the GGM. Several lines of evidence suggest a process involving a combination of scenarios 2 and 3. In Fig. 2H an outline of the *Sceloporus magister* tongue shown in

TABLE 2. Phenotypic Specializations in the Feeding Apparatus of Myrmecophagous Horned Lizards (*Phrynosoma*) And Their Inferred Functional Correlations (Relative to Sister and Outgroups)

No.	Specializations	Functional correlation[4]	Source(s)[5]
	Kinematic		
1	Extreme relative tongue protrusion distance (relative to head size)	a	3, 8
2	Ability to modulate tongue trajectory in response to prey movement within a few milliseconds[1]	a	2, 6
3	Ability to target ant at mid-body	b	2
4	Typical multi-cycle ingestion, processing, intraoral transport and swallow feeding stages collapsed into a rapid, single-cycle, combined ingestion-transport-swallow stage	b, c	9
5	Reduction in total prey handling time (feeding duration)	b, c	3, 8
6	Hyolingual manipulation of prey within pharynx during which living prey is balled and bound with mucus strands[2]	b	1, 9
	Morphological		
7	Smaller, less robust skull	d	4
8	Blunt, foreshortened snout	a	10
9	Shorter, more slender mandible	d	4
10	Shorter tooth row, fewer teeth	d	4
11	Smaller jaw adductor muscles	d	5
12	Weaker bite	d	5
13	Mucus-secreting pharyngeal papillae	b	1, 9
14	Stout, steeply tapered lingual process of hyobranchial apparatus[3]	?	10
15	Extremely reduced second ceratobranchials of hyobranchial apparatus	?	10
16	M. genioglossus lateralis remains separate from body of tongue for most of its length; extreme posterior insertion	e	1

[1] There are no comparative data to confirm that this trait is unique to *Phrynosoma*, but given the exceptionally short duration of the tongue protrusion phase of ingestion, it is likely to be.

[2] See text; the mechanics of this process remain unknown.

[3] Typical, but not universal within the genus; also present in some agamids and a few other species.

[4] (a) precise prey targeting; (b) protection against ant weapons; (c) maximize number of prey consumed, decrease chance of ant-mobbing; (d) lack of chewing, processing; (e) increase tongue protrusion distance; possible function during mucus-incapacitation mechanism

[5] (1) this study; (2) Fertschai et al. (2021); (3) Meyers and Herrel (2005); (4) Meyers et al. (2006); (5) Meyers et al. (2018); (6) Ott et al. (2004); (7) Schwenk (2000); (8) Schwenk and Throckmorton (1989); (9) Sherbrooke and Schwenk (2008); (10) personal observation.

Fig. 2G is superimposed on a *P. platyrhinos* tongue. The outline almost perfectly encompasses the lateral ridges of the latter, suggesting that if the ridges were joined to the sides of the tongue corpus, the *Phrynosoma* tongue would look nearly identical to the *Sceloporus* tongue, i.e., the ancestral condition. This supports the 'cleavage' scenario of lateral ridge evolution and would account for the peculiar 'pinched waist' appearance of the *Phrynosoma* tongue. Second, among phrynosomatids there are small variations in the way that GGL fibers contribute to the frenulum and enter the tongue. In some, the GGL participates with the GGM in forming a single, median, muscular frenulum, with the GGM attaching first to the ventral midline of the tongue and the GGL on either side next joining the tongue more laterally (*Sceloporus* spp., *Uma scoparia*). In other species, however (e.g., *Holbrookia maculata*, *Cophosaurus texanus*, *Uta stansburiana*, *Urosaurus graciosus*), the GGM initially forms a narrower median septum alone followed by independent dorsal extensions of GGL fibers from the floor of the mouth immediately lateral to the frenulum. As the GGL extensions approach the ventral side of the tongue, they simultaneously fuse with the existing frenulum, making it wider and forming its muscular sides. If the dorsal extensions of the GGL, or parts of them, failed to fuse with the frenulum, they would create independent, lateral ridges. This latter morphological pattern is consistent with scenario 3. The variations I have described are not phylogenetically consistent, i.e., similar patterns occur within both the sand lizard clade and the more generalized clade including *Sceloporus*. Furthermore, my histological samples do not include a sufficient number of individuals of any one species to assess adequately the extent of intraspecific variation in these traits, thus no firm conclusions can be drawn at this time.

The degree of morphological divergence documented here between horned lizard tongues and those of other species might seem unremarkable, but in the context of squamate tongue form, it is extraordinary. With very few exceptions, tongue morphology in squamates is unusually uniform at high taxonomic levels (Schwenk, 1988, 2000). All pleurodont iguanians, for example, share a strikingly consistent anatomy, including similar tongue shape, papillary form and distribution, and muscle fiber architecture. This morphological homogeneity is correlated with a shared set of similar tongue functions. Conversely, significant divergences in tongue form are associated with major changes in these functions and such fundamental changes typically occur only along the stems of major radiations, e.g., with the origin of families or higher groups (Schwenk, 1988, 2000). In other words, ecological differences among species within a family, in foraging behavior or diet, for example, are virtually never manifested in tongue morphology. When divergence does occur within an otherwise uniform group (e.g., the family Dactyloidae within the pleurodont iguanians; K. Schwenk, unpublished data), the different morphology similarly characterizes a large, monophyletic radiation independent of any associated ecological change. In contrast, the evolution of a distinct tongue form in horned lizards has occurred on a much finer evolutionary scale than expected. The 17 species of *Phrynosoma* share a morphology that differs from even their closest relatives, the sand lizards, and other members of their family, all of which retain the ancestral condition. The exceptional nature of such fine-scaled divergence suggests the action of unusually strong selection on horned lizards associated with a novel demand outside the broad functional scope of the ancestral phenotype. The obvious correlation is with horned lizards' unique capacity to feed on large numbers of lethal prey, suggesting that the modified tongue form in *Phrynosoma* is an adaptation associated with handling such dangerous prey during feeding, possibly related to the mechanism of mucus-binding.

CONCLUSIONS

Horned lizards possess a unique, derived form of the tongue in which a major part of the genioglossus lateralis muscle fails to join the body of the tongue for most of its length, appearing as an elevated ridge in the floor of the mouth lateral to the tongue. The paired GGL form a 'girdle' around the posterior end of the tongue that might aid in enveloping dangerous harvester ant prey within a papilla-lined pit that folds and immobilizes the ant with strings of viscous mucus before being ejected directly into the esophagus. The evidence for such a mechanism remains extremely circumstantial, but regardless, there is strong phylogenetic support for a functional correlation between the form of the genioglossus lateralis muscles and horned lizards' ability to incapacitate the weapons of their potentially lethal prey.

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REFERENCES

Bancroft J. D. and Stevens A. (1982), *Theory and Practice of Histological Technique*, Churchill Livingstone, New York.

Canseco-Marquez L., Muñoz A., García A., and Ponce P. (2013), "*Phrynosoma asio*," *The IUCN Red List of Threatened Species*, 2013, e.T198393A2524363; DOI: 10.2305/IUCN.UK.2013-2.RLTS.T198393A2524363.en.

Montes de Oca, A., Arenas-Moreno D., Beltrán-Sánchez E., and Leaché A. D. (2014), "A new species of horned lizard (genus *Phrynosoma*) from Guerrero, México, with an updated multilocus phylogeny," *Herpetologica*, **70**, 241 – 257.

Fertschai I., Sherbrooke W. C., Ott M., and Chagnaud B. P. (2021), "Avoiding being stung or bitten-prey capture behaviors of the ant-eating Texas horned lizard (*Phrynosoma cornutum*)," *Biol. Open*, **10**(3), bio058453; DOI: 10.1242/bio.058453

Greene H. W. (1982), "Dietary and phenotypic diversity in lizards: why are some organisms specialized?" in: D. Mossakowski and G. Roth (eds.), *Environmental Adaptation and Evolution*, Gustav Fischer, Stuttgart, pp. 107 – 128.

Hasegawa M. and Taniguchi Y. (1993), "Visual prey discrimination of queen and worker ants by a generalist lizard," *J. Ethol.*, **11**, 55 – 62.

Hirth H. F. (1963), "The ecology of two lizards on a tropical beach," *Ecol. Monogr.*, **33**, 83 – 112.

Kier W. M. and Smith K. K. (1985), "Tongues, tentacles and trunks: the biomechanics of movement in muscular-hydrostats," *Zool. J. Linn. Soc.*, **83**, 307 – 324.

Lappin A. K. and German M. (2005), "Feeding behavior modulation in the leopard lizard (*Gambelia wislizenii*): effects of noxious versus innocuous prey," *Zoology*, **108**, 287 – 295.

Leaché A. D. and Linkem C. W. (2015), "Phylogenomics of horned lizards (Genus: *Phrynosoma*) using targeted sequence capture data," *Copeia*, **103**, 586 – 594.

Leaché A. D., Koo M. S., Spencer C. L., Papenfuss T. J., Fisher R. N., and McGuire J. A. (2009), "Quantifying ecological, morphological, and genetic variation to delimit species in the coast horned lizard species complex (*Phrynosoma*)," *Proc. Natl. Acad. Sci. USA*, **106**, 12418 – 12423.

Meyers J. J. and Herrel A. (2005), "Prey capture kinematics of ant-eating lizards," *J. Exp. Biol.*, **208**, 113 – 127.

Meyers J. J., Herrel A., and Nishikawa K. C. (2006), "Morphological correlates of ant eating in horned lizards (*Phrynosoma*)," *Biol. J. Linn. Soc.*, **89**, 13 – 24.

Meyers J. J., Nishikawa K. C., and Herrel A. (2018), "The evolution of bite force in horned lizards: the influence of dietary specialization," *J. Anat.*, **232**, 214 – 226.

Montanucci R. R. (2004), "Geographic variation in *Phrynosoma coronatum* (Lacertilia, Phrynosomatidae): further evidence for a peninsular archipelago," *Herpetologica*, **60**, 117 – 139.

O'Connell D. J. and Formanowicz D. R., Jr. (1998), "Differential handling of dangerous and non-dangerous prey by naïve and experienced Texas spotted whiptail lizards," *Cnemidophorus gularis*," *J. Herpetol.*, **32**, 75 – 79.

Ott M., Ostheim J., and Sherbrooke W. C. (2004), "Prey snapping and visual distance estimation in Texas horned lizards, *Phrynosoma cornutum*," *J. Exp. Biol.*, **207**, 3067 – 3072.

Pianka E. R. and Parker W. W. (1975), "Ecology of horned lizards: a review with special reference to *Phrynosoma platyrhinos*," *Copeia*, **1975**, 137 – 154.

Pianka E. R. and Pianka H. D. (1970), "The ecology of *Moloch horridus* (Lacertilia: Agamidae) in western Australia," *Copeia*, 1970, 90 – 103.

Presnell J. K. and Schreibman M. P. (1997), *Humason's Animal Tissue Techniques. 5th edition*, Johns Hopkins Press, London.

Schmidt J. O. (2019), "Predator-prey battle of ecological icons: horned lizards (*Phrynosoma* spp.) and harvester ants (*Pogonomyrmex* spp.)," *Copeia*, **107**, 404 – 410.

Schmidt P. J. and Schmidt J. O. (1989), "Harvester ants and horned lizards predator-prey interactions," in: J. O. Schmidt (ed.), *Special Biotic Relationships in the Arid Southwest*, University of New Mexico Press, Albuquerque, pp. 25 – 50.

Schwenk K. (1988), "Comparative morphology of the lepidosaur tongue and its relevance to squamate phylogeny," in: R. Estes and G. Pregill (eds.), *Phylogenetic Relationships of the Lizard Families*, Stanford Univ. Press, Stanford, pp. 569 – 598.

Schwenk K. (2000), "Feeding in lepidosaurs," in: K. Schwenk (ed.), *Feeding: Form, Function and Evolution in Tetrapod Vertebrates*, Acad. Press, San Diego, pp. 175 – 291.

Schwenk K. (2001), "Extrinsic vs. intrinsic lingual muscles: a false dichotomy?" *Bull. Mus. Comp. Zool.*, **156**, 219 – 235.

Schwenk K. and Throckmorton G. (1989), "Functional and evolutionary morphology of lingual feeding in squamate reptiles: phylogenetics and kinematics," *J. Zool. Lond.*, **219**, 153 – 175.

Sherbrooke W. C. (2003), *Horned Lizards of North America*, Univ. of California Press, Berkeley.

Sherbrooke W. C. (2020), "Current names: a guide to recent name changes of horned lizard species," *Sonoran Herpetologist*, **33**, 4 – 10.

Sherbrooke W. C. and Schwenk K. (2008), "Horned lizards (*Phrynosoma*) incapacitate dangerous ant prey with mucus," *J. Exp. Zool. A*, **309**, 447 – 459.

Smith K. K. (1984), "The use of the tongue and hyoid apparatus during feeding in lizards (*Ctenosaura similis* and *Tupinambis nigropunctatus*)," *J. Zool. Lond.*, **202**, 115 – 143.

Wiens J. J., Kozak K. H., and Silva N. (2013), "Diversity and niche evolution along aridity gradients in North American lizards (Phrynosomatidae)," *Evolution*, **67**, 1715 – 1728.

Wiens J. J., Kuczyngski C. A., Arif S., and Reeder T. W. (2010), "Phylogenetic relationships of phrynosomatid lizards based on nuclear and mitochondrial data, and a revised phylogeny for *Sceloporus*," *Mol. Phylog. Evol.*, **54**, 150 – 161.