EXTRINSIC VERSUS INTRINSIC LINGUAL MUSCLES: A FALSE DICHOTOMY?

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ABSTRACT. The muscular tongue of amniote vertebrates is traditionally described as a composite of two muscle types: extrinsic muscles originate outside the tongue and insert within it; intrinsic muscles arise and insert completely within the tongue. Whole-tongue movements are attributed to the former, lingual shape change to the latter. This dichotomous view of tongue structure and function has endured since the mid-19th century, despite persistent indications of its inadequacy. A histologic analysis of the musculi genioglossus and verticalis in mammals and the musculus (m.) hyoglossus in lepidosaurian reptiles finds that the "extrinsic" m. genioglossus contributes extensively to the "intrinsic" m. verticalis; the verticalis "muscle" is composed of fibers from at least three nominally separate muscles, both extrinsic and intrinsic (genioglossus, longitudinalis inferior, intrinsic verticalis fibers); and the "extrinsic" m. hyoglossus in lepidosaurs comprises both extrinsic and intrinsic parts, which may be histochemically differentiated. Current models of the tongue as a muscular hydrostat suggest that it functions as an integrated functional unit and that the traditional atomistic, dichotomous view is inaccurate and misleading. The notion of individuated "muscles" is inapplicable within the tongue and should be replaced by reference to "fiber systems."

> Apart from simplifying matters to the student of anatomy, the division of the lingual muscles into extrinsic and intrinsic groups is of no proper scientific significance (Abd-El-Malek, 1938: 26)

INTRODUCTION

The evolution of tetrapod vertebrates from piscine ancestors was attended by the appearance of a mobile, muscular tongue. The tongue, in effect, assumed the ancestral role of water in the dynamics of feeding and is used by tetrapods today to capture, support, manipulate, transport, and swallow prey in the terrestrial environment. These functions depend on the capacity of the tongue, and the associated hyobranchial apparatus, to generate complex movements in three dimensions, within the mouth and without. The form and internal anatomy of the tongue vary widely among tetrapods, as does the nature and extent of its movements (e.g., Livingston, 1956; Schwenk, 2000a). Mammals, lepidosaurian reptiles and terrestrial turtles possess the most muscular and architecturally intricate tongues among tetrapods, and these evince the greatest complexity of motion. Contradictions about the muscular constituents of these amniote tongues and their role in generating tongue movement is the subject of this paper.

The tongue of most nonarchosaurian amniotes is a large, muscular mass, often with little or no internal skeletal support. The corpus of the tongue comprises orthogonal arrays of interweaving muscle fibers, the pattern of which is taxonomically variable. Despite extensive comingling of muscle fibers within the tongue, early anatomists treated the tongue like any other part of the musculoskeletal system and partitioned it into nominally discrete muscles. Initially, virtually all tongue muscles were thought to arise from elements of the skeleton outside the tongue (e.g., the mandible, hyobranchium, and styloid process of the skull in mammals) and the muscles were divided on the basis of their separate origins (Barnwell, 1976). However, by the early 19th century it was recognized that some muscle fibers arise and insert entire-

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ly within the tongue and several "intrinsic muscles" were thus recognized in addition to the better known "extrinsic muscles" (Barnwell, 1976). Intrinsic muscles were identified on the basis of their direction (transverse, longitudinal, or circular) and position (superior/dorsal or inferior/ventral) within the tongue.

The distinction between extrinsic and intrinsic muscles was formalized by Salter (1852; in Barnwell, 1976) who, in addition, attributed different kinds of tongue movement to the two muscle types: extrinsic muscles were said to move the whole tongue by virtue of their external skeletal attachments, whereas intrinsic muscles were thought to "move the tongue on itself." Thus, by the mid-19th century, two parallel dichotomies were established in the literature: an anatomical division of the tongue into extrinsic and intrinsic muscles, and a functional division relating the former to whole tongue movements and the latter to changes in tongue shape.

Remarkably, this dichotomous view of tongue form and function has endured in the literature to the present time (e.g., Sonntag, 1925; McGregor, 1938; Bennett and Hutchinson, 1946; Cooper, 1953; Livingston, 1956; Oelrich, 1956; Sondhi, 1958; Bowman, 1968; Perkell, 1969; Warwick and Williams, 1973; Miyawaki, 1974; Barnwell et al., 1978b; Langdon et al., 1978; Hellstrand, 1980, 1981; Tanner and Avery, 1982; Schwenk, 1986; Smith, 1988; Delheusy et al., 1994; Herrel et al., 1995). For example, in describing a lizard tongue, Oelrich (1956: 54) stated: "The extrinsic muscles, genioglossus and hyoglossus, control the motions of the tongue; the intrinsic muscles control its shape." Hellstrand (1980: 187) began his paper on the cat tongue by pointing out that it "is provided with muscles termed *extrinsic* or *intrinsic* according to whether they run partly or totally within the tongue. Functionally, the extrinsic muscles are usually classified as protruders or retractors and the intrinsic as shaping or modeling agents." In *Gray's Anatomy* (Warwick and Williams, 1973: 1239, 1240) it is noted that within the human tongue, "there are two sets of muscles, extrinsic and intrinsic; the former have attachments outside the tongue, the latter are contained within it." Each extrinsic muscle is said to move the tongue in some way, that is, retract, depress, or elevate it. In contrast, it is held that the intrinsic muscles, in toto, are "mainly concerned in altering the shape of the tongue."

Despite the persistence of the dichotomous descriptive convention, those who have investigated tongue anatomy in some detail have often questioned the accuracy or appropriateness of the dichotomy—anatomically, functionally, or in both ways (e.g., Bennett, 1935; Abd-El-Malek, 1938; Bennett and Hutchinson, 1946; Sondhi, 1958; Barnwell et al., 1978a; Langdon et al., 1978; Cave, 1980; Lowe, 1980; Kier and Smith, 1985; Schwenk, 1986; Smith, 1986, 1992; Smith and Kier, 1989; Sokoloff and Deacon, 1992; Napadow et al., 1999). Some authors have expressed doubt, even while beginning with the conventional view. Oelrich (1956: 55), for example, noted that extrinsic and intrinsic fibers interlace within the tongue and admitted that the intrinsic muscles "do not maintain their integrity throughout, but at some levels are intermingled to such an extent that their identity is obscured." Schwenk (1986: 137) pointed out that in tuatara (*Sphenodon*), the "distinction is not always demonstrable in every part of the tongue because both intrinsic and extrinsic fibers interlace complexly." Barnwell et al. (1978a: 8) concluded that the nominally intrinsic musculus (m.) longitudinalis superior of the human tongue "is comprised of both intrinsic and extrinsic fiber groups." It is telling that many writers seem compelled to state the conventional view, despite their evident dissatisfaction. This ambivalence is clear, for example, in a textbook account that virtually contradicts itself within the space of two sentences: "Generally, 'movements' other than those that basically alter the shape of the tongue are the result of contractions of the extrinsic muscles, though one group seldom functions alone. The overlapping, intermingling, and decussating nature of the intrinsic and extrinsic muscle groups permit the fine coordinated effort so necessary in speech" (Hiatt and Gartner, 1982: 239–240).

Others have rejected the traditional dichotomy altogether. For example, in his study of cat tongue anatomy and function, Abd-El-Malek (1938) concluded with the remark quoted at the outset of this paper, suggesting that the dichotomy is no more than a convenience, without scientific merit. He particularly rejected the functional dichotomy, suggesting that "most, if not all, of the intrinsic muscles are involved in every movement of the tongue. Indeed, in many movements both intrinsic and extrinsic muscles so called, are working together." Other authors take the radical view that all putative intrinsic muscle fibers are nothing more than extensions of extrinsic muscles (Lesbre [1922] in Cave [1980] for the horse, *Equus*; Cave [1980] for the rhinoceroses, *Rhinoceros*, *Ceratotherium*, and *Diceros*; and Sondhi [1958] for the monitor lizard, *Varanus*). According to Cave (1980: 128): "The so-called intrinsic tongue muscles are not therefore, morphological entities but merely continuations of the extrinsic muscles." Sondhi (1958: 175) concluded: "While there can be no doubt that the 'intrinsic muscles' can be distinguished from each other in certain regions of the tongue, the fact that they arise directly as a result of the change in course of certain bundles of the [extrinsic] hyoglossus fibres indicates that they do not deserve the status of independent muscles." It is worth noting that the studies of Lesbre and Cave were based on gross dissection without the benefit of histologic sections, and Sondhi's sections were of poor quality.

The purpose of this paper is to explore the anatomical relationship between "extrinsic" and "intrinsic" lingual muscles in representative mammals and lepidosaurian reptiles. The mammalian genioglossus and verticalis muscles, and lepidosaurian hyoglossus muscle are investigated in detail and used as exemplars. Results of the morphologic investigation are considered in light of current models of tongue function in order to assess the structural and functional validity of the dichotomous view. Based on this analysis, a synthetic view of tongue form and function is proposed.

MATERIALS AND METHODS

Reference material included complete, serial paraffin sections of tongues from two mammalian species (domestic cat, *Felis catus*, three specimens; crab-eating macaque, *Macaca fascicularis*, three specimens) and more than 100 lepidosaurian reptile species (one to three specimens each), including tuatara (*Sphenodon punctatus*; Schwenk, 1986) and representatives of every major squamate clade (Schwenk, 1988, 2000b, unpublished data). The emphasis here is on the cat (Carnivora, Felidae) and generalized lizards (Squamata, Iguanidae) that putatively retain the plesiomorphic condition (Schwenk, 1986, 1988, 2000b). Histologic results were compared to literature accounts of tongue anatomy.

Sections were prepared using standard paraffin techniques (Presnell and Schreibman, 1997). Whole-tongue specimens were sectioned whenever possible to facilitate fiber tracing. Some previous studies have suffered from the myopic view offered by partial or fragmented specimens.

Both transverse and sagittal sections (6–10 μm) were prepared for most species, but only transverse sections were available for *Sphenodon* and some squamates (note that transverse tongue sections correspond to 'coronal' sections in the parlance of human anatomy). Sections were stained with hematoxylin and picro-ponceau or hematoxylin and eosin (Presnell and Schreibman, 1997).

In addition to paraffin sections, frozen tissue sections were available for several squamate species. These were stained for myosin adenosine triphosphatase and succinic dehydrogenase using standard techniques, as part of an ongoing histochemical study of tongue muscle fiber types (Schwenk and Anapol, in preparation). These data are preliminary and referred to here only in passing.

RESULTS

Genioglossus and Verticalis Muscles in the Cat

Preliminary observations indicate that the findings reported here for the cat are equally valid for the macaque. Based on consideration of the literature, the findings are likely to apply as well to many mammals with generalized tongues, including other carnivorans, opossums, and humans. However, with the exception of humans, detailed information is lacking for these and other species, including many with highly divergent tongue forms (e.g., monotremes: Doran and Baggett, 1970; Doran, 1973; and nectar-feeding bats: Greenbaum and Phillips, 1974; T. Griffiths, 1978). Therefore, the results of this study cannot necessarily be extrapolated to mammals as a whole.

When viewed in transverse section, most mammalian tongues are divisible into cortical and medullary regions. The cortex is distinguished by the presence of longitudinal fibers, whereas the core of the tongue is filled with transverse and vertical fibers. "Transverse" and "vertical" are convenient descriptors for these more-or-less perpendicular sets of fibers, but fibers of both groups are often quite oblique. Throughout most of the medullary zone, vertical and transverse fibers are organized into thin sheets of muscle that run across the width of the tongue, alternating one after the other along the tongue's length (Fig. 1). Tracing individual verticalis sheets through serial sections confirmed that in most of the tongue each sheet runs across the full width of the medullary core. However, in the anteriormost part of the tongue, a verticalis sheet may be interrupted across its width by invading bands of transversus. However, interpreting sections here is difficult because the sheets apparently do not run in a plane, becoming curved or cup-shaped, instead. Finally, some vertical fibers cross anteroposteriorly between adjacent sheets to form anastomoses (especially evident in the free, anterior part of the tongue; e.g., Fig. 3). Despite these complications, throughout most of the tongue the extreme regularity of the alternating vertical and transverse sheets is its most striking feature. The sheets of vertical and transverse fibers constitute the nominal intrinsic muscles, m. verticalis and m. transversus, respectively. In the cat they are separated into left and right moieties by a complete median septum.

The m. transversus fibers originate from the median septum and run radially across the width of the tongue to insert into the lamina propria of the lingual tunic dorsally, laterally, and ventrolaterally. Some m. verticalis fibers originate from the lamina propria of the tongue's ventral surface and run dorsomedially to the lamina propria of the dorsal surface (but see below). In the lateral part of the tongue, dorsolaterally running transversus fibers cross dorsomedially running verticalis fibers in an X-like pattern (i.e., perpendicular, but approximately 45° to the vertical). Toward the midline verticalis fibers become more nearly vertical (see below).

The m. genioglossus is one of the major extrinsic muscles of the tongue and is assumed to be its principal protractor and protruder. In the cat, the m. genioglossus originates medially from two heads on the mandible near the symphysis. A ventral head gives rise to fibers that run posteriorly, inserting onto the anteroventral surface of the basihyal. Fibers from a larger dorsal head run posterodorsally in a fanlike array, penetrating the tongue midventrally along the posterior two thirds of its length. The most anterior of these fibers curve sharply dorsad as they enter the tongue's medullary core and run vertically to the

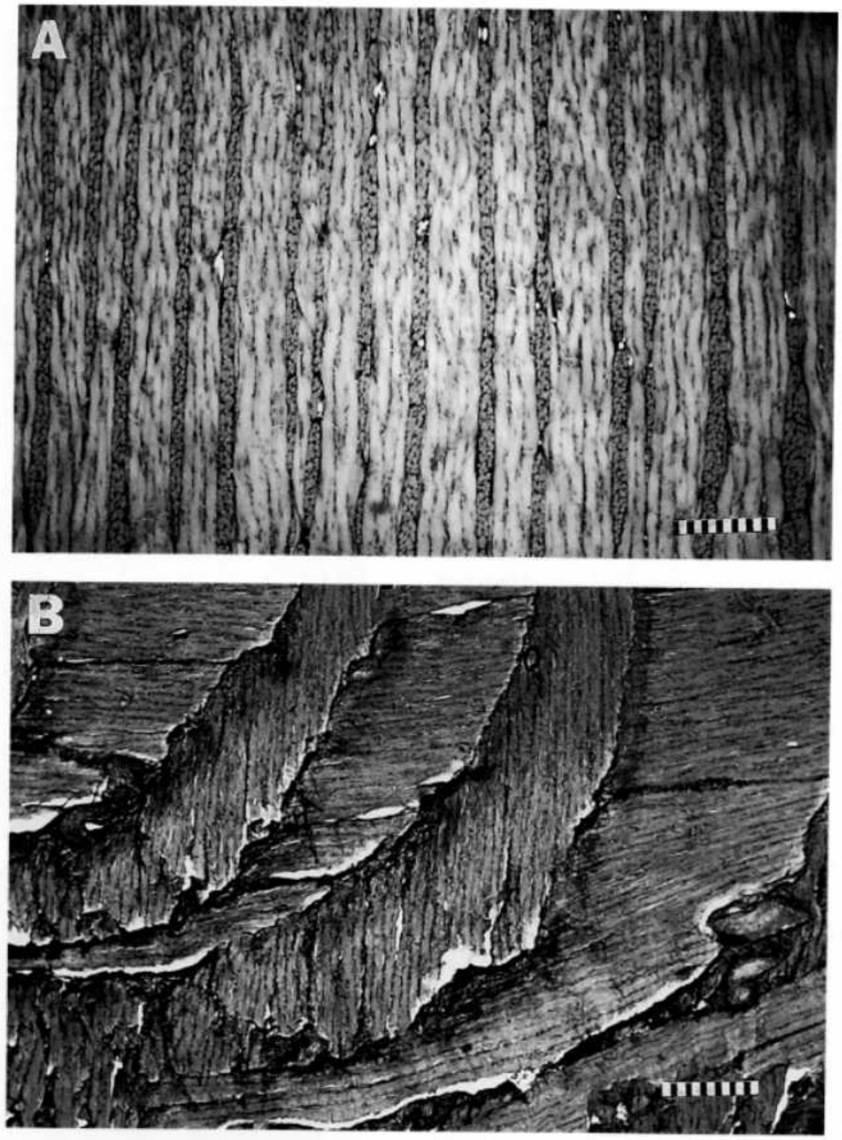

Figure 1. Alternating sheets of vertical (musculus [m.] verticalis) and transverse (m. transversus) muscle fibers in the medullary core of the cat midtongue. Note extreme regularity of alternating sheets. (A) Parasagittal section; verticalis sheets are thicker than transversus sheets in this region. Anterior is to the left. Scale bar = 0.2 mm. (B) Transverse section near the midline, in the ventromedial portion of the tongue's right half; medial septum to the right. Section is slightly oblique relative to plane of transversus and verticalis sheets so that it passes through several adjacent layers. As for (A), note extreme regularity of alternating pattern. Darker-staining tissue at the margins of each sheet is collagenous connective tissue of the thin fascial plane separating each sheet. Note that the ventralmost transverse fibers run ventrolaterally and the dorsalmost fibers run laterally. Dorsal to these, out of the photographic frame, the transverse fibers run dorsolaterally, that is, the transverse fibers radiate laterally from their midline origin on the median septum. Scale bar = 0.2 mm.

lamina propria of the dorsal surface, but posteriorly the fibers become progressively more longitudinal, curving gently dorsad at their distal ends to meet the posterior surface of the tongue as it slopes downward to the root of the tongue. In (fetal) humans, the anteriormost fibers form a third bundle that turns sharply anterior as it enters the tongue, running to the tip (Langdon et al., 1978), but in the cat (Abd-El-Malek, 1938; this study) and several other mammals (Doran and Baggett, 1972), no comparable bundle is found and the most anterior genioglossus fibers run more or less vertically. The unattached, anterior part of the tongue is therefore devoid of genioglossus fibers.

In reconstructions of the genioglossus,

its fibers are often shown in sagittal view to end at the base of the tongue before penetrating the medullary core, or to run obliquely across the alternating sheets of vertical and transverse fibers toward the dorsal and posterior surfaces of the tongue (e.g., Kallius, 1910; Abd-El-Malek, 1938; Warwick and Williams, 1973; Crouch, 1978; Walker and Homberger, 1992). Independence of the genioglossus from the medullary, intrinsic fiber system is implied in these and other descriptions. In actuality, as genioglossus fibers turn dorsally into the tongue, they become confluent with the serially arranged sheets of verticalis fibers (Fig. 2A). As such, for most of the tongue's length, the medial portion of the verticalis muscle comprises genioglossus fibers. In other words, a large portion of the "intrinsic" verticalis muscle is composed of "extrinsic" fibers.

Although the previous observations seem to support the radical position of Cave (1980) and others suggesting that intrinsic fibers are merely extensions of extrinsic muscles, this view is vitiated by a full consideration of m. verticalis anatomy. Although the medial portion of each verticalis sheet comprises extrinsic genioglossus fibers, its lateral portion derives from purely intrinsic fibers that originate on the lamina propria of the ventral surface (Fig. 2B). Although medial genioglossus fibers are relatively vertical and lateral intrinsic fibers are oblique (running dorsomedially; see above), fibers of both sorts blend insensibly across the breadth of a single verticalis sheet to form a continuous structural unit. These units are repeated serially along the length of the tongue, alternating with sheets of m. transversus. Extrinsic and intrinsic components of the verticalis are also clearly evident in the opossum, *Monodelphis* (Smith, 1994, fig 2a).

Given the absence of genioglossus fibers in the anterior, free part of the tongue, one might expect the sheets of verticalis in this region to be uniformly intrinsic. Indeed, this is true laterally, as elsewhere in the tongue (Fig. 3A). However, in place of ge-

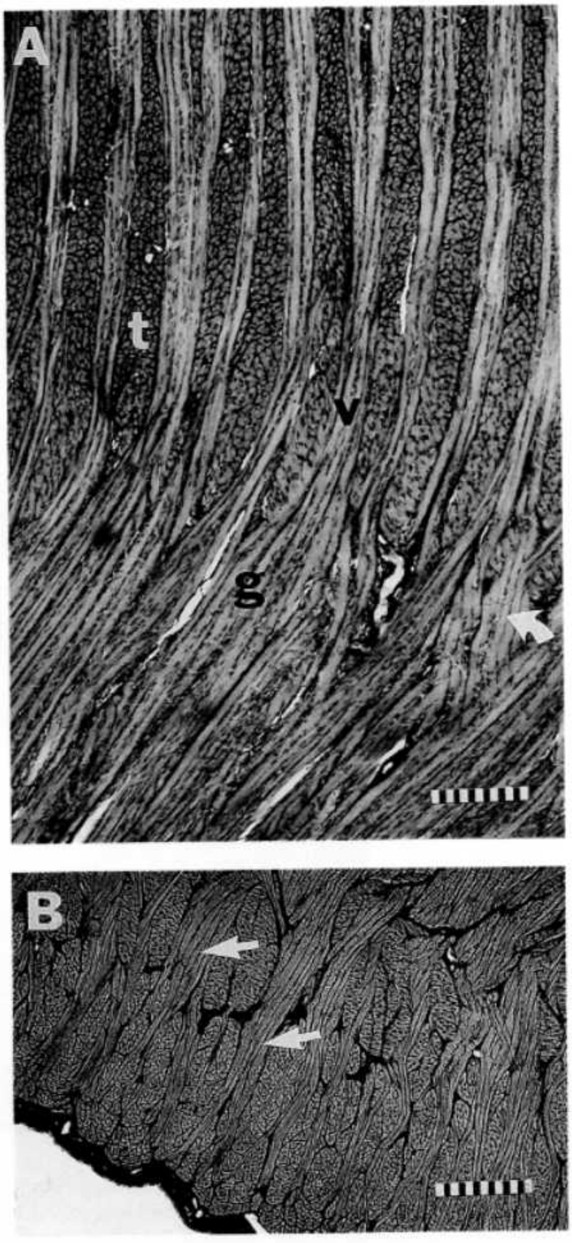

Figure 2. The relationship between musculus (m.) verticalis and m. genioglossus fibers in the cat tongue. (A) Parasagittal section near the midline, anterior to the left. Ventrally, the genioglossus muscle (g) penetrates the tongue's medullary core where it curves dorsad and is separated into separate layers by intervening sheets of transversus fibers (t). Thus, in this medial portion of the tongue the vertical fibers of the medulla, nominally m. verticalis (v), are actually contributed by the extrinsic genioglossus. However, note that some verticalis fibers continue a more vertical descent through the genioglossus to an intrinsic point of origin (curved arrow). Scale bar = 0.2 mm. (B) Transverse section through the ventrolateral part of the tongue's right side showing longitudinal fibers of lingual cortex and the origin of intrinsic verticalis fibers from the ventrolateral lamina propria (arrows). These lateral, purely intrinsic fibers, form an uninterrupted continuum within a single verticalis sheet with the medial genioglossus fibers. Scale bar = 0.2 mm.

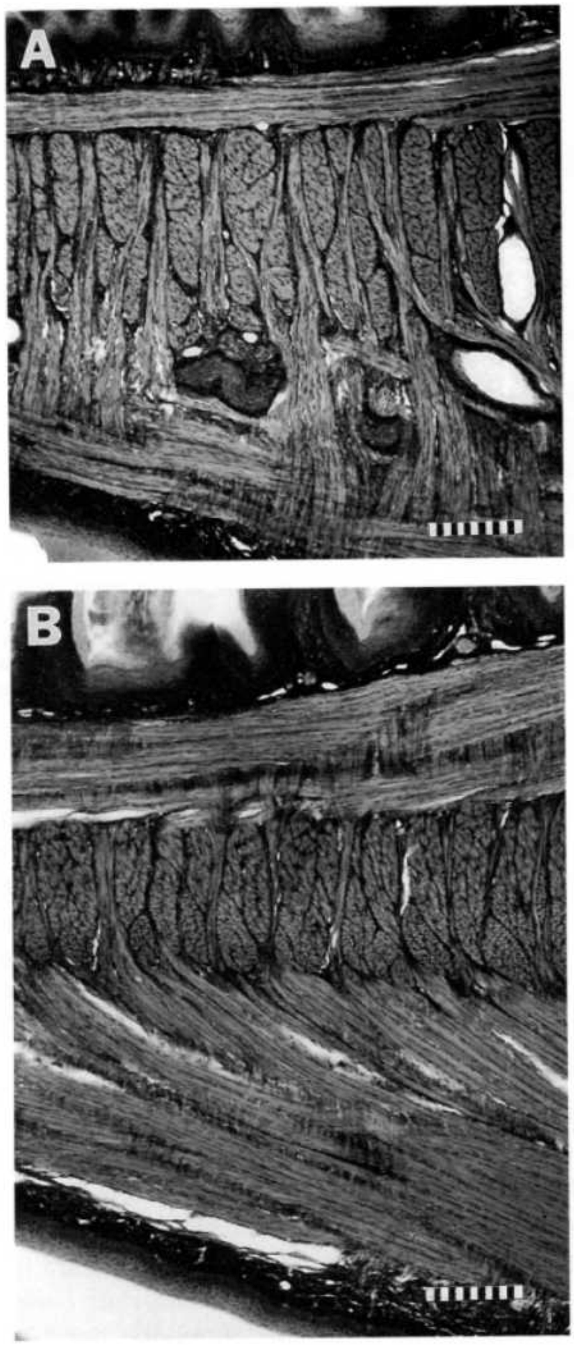

Figure 3. The free, anterior portion of the cat tongue in sagittal section. The tongue tip is toward the left. Note that longitudinal fibers run beneath the tongue's dorsal and ventral surfaces forming the cortex, whereas the medulla is filled by the alternating sheets of vertical and transverse fibers. These sheets are not so regularly disposed as they are posteriorly (Fig. 1) and anastomoses between verticalis sheets are frequent. (A) Section through lateral part of the tongue. Note that vertical fibers penetrate the cortex to arise and insert from dorsal and ventral laminae propria, that is, they are intrinsic fibers. The dark-staining structure just above the ventral longitudinal fibers is a nerve, kinked to permit extension during hydrostatic tongue elongation. The white areas are vascular spaces slightly distended by perfusion of the tongue. Scale bar = 0.2 mm. (B) Section more medial to (A), near to midline. In contrast to

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(A), vertical fibers are here contributed by the extensively developed ventral longitudinal system. These fibers represent musculus longitudinalis inferior, although it is possible that extrinsic styloglossus fibers also contribute. Compare to Figure 2A. Scale bar = 0.2 mm.

nioglossus fibers, the medial portion of each verticalis sheet is here occupied by ventral longitudinal fibers that turn dorsad into the verticalis (Fig. 3B). The ultimate origin of all ventral longitudinal fibers has not been traced with certainty, but most clearly belong to the intrinsic m. longitudinalis inferior. Among the ventral longitudinal fibers of the lingual cortex, longitudinalis inferior fibers are generally the most median (e.g., Barnwell et al., 1978b). Nonetheless, longitudinal fibers of the cortex are notoriously difficult to segregate according to source and it remains possible that some of the fibers contributing to the verticalis in the anterior part of the tongue derive from the extrinsic styloglossus muscle. Sections show that styloglossus fibers course anteroventrally along the sides of the tongue, joining the ventral longitudinal system anteriorly, but it is not certain that these fibers extend far enough anteriorly and medially to contribute to the verticalis in the free part of the tongue. Although (extrinsic) m. hyoglossus fibers are said to run within the ventral longitudinal system of some mammals (e.g., humans, Barnwell et al., 1978b), my sections (and those of Abd-El-Malek, 1938) indicate that in the cat, all hyoglossus fibers run anterodorsally into the dorsal longitudinal system.

In conclusion, the extrinsic genioglossus muscle makes a substantial contribution to the putatively intrinsic verticalis muscle. Anteriorly, the verticalis also includes fibers of a second intrinsic muscle, the longitudinalis inferior, and possibly extrinsic fibers of the styloglossus. The verticalis "muscle" thus includes fibers from three, or possibly, four different sources: intrinsic vertical fibers; intrinsic longitudinal fibers; extrinsic genioglossus fibers; and possibly,

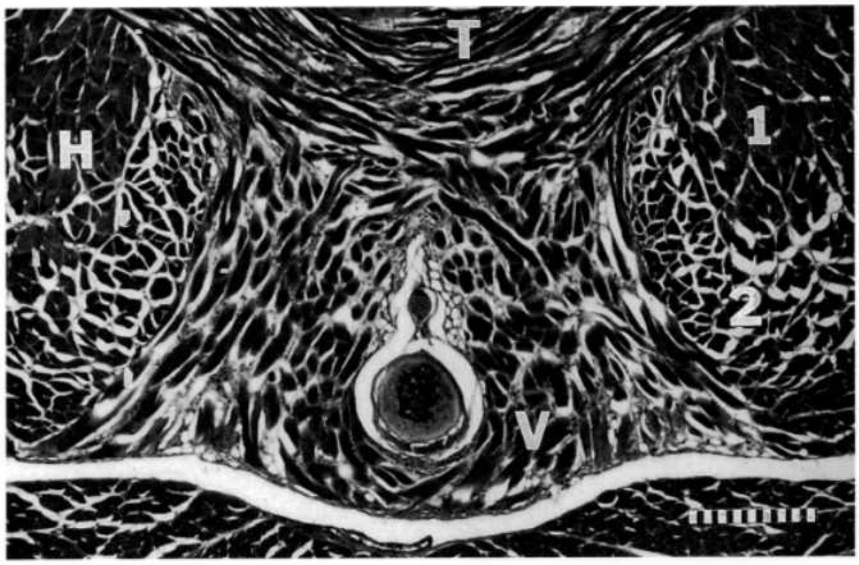

Figure 4. Transverse section through the midtongue of a lizard (*Holbrookia texana*, Iguanidae). The circular structure in the center is the lingual (entoglossal) process of the hyobranchium, which is surrounded by fibers of the midline intrinsic muscle, musculus (m.) verticalis (V). Dorsal to the verticalis is the m. transversalis (T) and on either side are the paired hyoglossus bundles (H); the lateral part of each bundle is cut off in the figure. Note that within each hyoglossus bundle the fibers are separated into two parts: a dense, more vertically oriented dorsolateral portion (1) and a more loosely organized, more longitudinally oriented ventromedial portion (2). Scale bar = 0.2 mm.

extrinsic styloglossus fibers. An individual sheet of verticalis occupies a transverse plane across the width of the tongue comprising a continuum of vertically oriented muscle fibers, yet within a given sheet, a large proportion of the fibers are contributed by a nominally separate muscle, usually from outside the tongue. Furthermore, the muscles making this contribution vary along the length of the tongue. Thus, the nominal m. verticalis satisfies neither the definition of "intrinsic," nor even the usual notion of a "muscle." Nonetheless, the serial coherence of the verticalis is maintained throughout the medullary core, despite the disparate sources of its constituent fibers.

The Hyoglossus Muscle in Lepidosaurian Reptiles

Lepidosaurs include the tuatara of New Zealand (*Sphenodon*) and the squamates, comprising lizards, snakes, and amphisbaenians. The lepidosaurian tongue, with few exceptions, is a highly mobile organ that rivals that of mammals in its internal complexity. However, unlike mammals, the principal longitudinal muscles of the tongue lie within its core and not its periphery. These are the hyoglossus muscles, evident in transverse section as two large, cylindrical or subcylindrical bundles (Fig. 4). In a few taxa (notably gekkotans) they subdivide anteriorly into multiple bundles, but in the vast majority of species they remain paired for the length of the tongue (Schwenk, 1988, 2000b).

As in mammals, the hyoglossus is one of the major extrinsic muscles of the lepidosaurian tongue. It is traditionally described as originating on the first ceratobranchial of the hyobranchial apparatus and inserting within the tongue near its tip (e.g., Gnanamuthu, 1937; Oelrich, 1956; Delheusy et al., 1994; Herrel et al., 1997, 1999) and is regarded as the principal retractor of the tongue.

Some studies have indicated that hyoglossus anatomy is more complex than suggested by conventional descriptions. In his figures of transversely sectioned *Sphenodon* embryos, Edgeworth (1935) identified a separate ventromedial bundle within the hyoglossal mass, which he called the