

TONGUE MUSCULATURE OF PASSERINE BIRDS

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INTRODUCTION

THIS paper has two aims: first, the presentation of a general picture of the tongue musculature of passerines; and, second, the correction of a number of bewildering errors in the only extensive description extant of the tongue musculature of the Raven (in Shufeldt, 1890), errors both of commission (descriptions and homologies) and of omission (undescribed muscles). A redescription seems to me desirable for two reasons: Shufeldt's 'Myology of the Raven' is the only commonly available English text which treats the entire musculature of a single passeriform species, and, as such, is frequently used as a guide by students who need to familiarize themselves with avian myology, although its numerous errors make for confusion in the mind of any student not already familiar with the subject; more important is the fact that, as the only complete description of the musculature of the Raven (*Corvus corax*), it is frequently referred to for purposes of comparison, by students working on the musculature of other groups of birds. Errors thus tend to accumulate and to be perpetuated.

The following description of tongue muscles is based on dissections of the Raven (*Corvus corax*), to which the details of origin, insertion and topographical relationships refer. I have dissected also a number of other North American passerines, in all of which the tongue musculature was found to be substantially as described below for the Raven. The forms examined include: CORVIDAE: *Aphelocoma californica*, *Corvus brachyrhynchos*, *Corvus corax*; TROGLODYTIDAE: *Heleodytes bruneicapillus*, *Thryomanes bewicki*, *Salpinctes obsoletus*; MIMIDAE: *Mimus polyglottos*, *Dumetella carolinensis*, *Toxostoma rufum*, *Oreoscoptes montanus*; TURDIDAE: *Hylocichla guttata*; LANIIDAE: *Lanius ludovicianus*; ICTERIDAE: *Sturnella neglecta*, *Quiscalus quiscula*, *Euphagus cyanocephalus*; FRINGILLIDAE: *Carpodacus mexicanus*, *Spinus psaltria*, *Amphispiza belli*, *Zonotrichia leucophrys*. Since these species represent several families of the suborder Passeres, and since they agree with the Raven in respect to the number and arrangement of the muscles, the description below may be taken as representative, in its general features, of passerine birds. Some differences in details have been noted; the finches, especially, exhibit well-defined variations and seem most likely to repay a comparative, functional or *biologisch-anatomische* study. The arrangement of the muscles in the following description is based on their development in ontogeny as presented by Edgeworth (1935). For terminology, I have depended chiefly on Gadow (1891), since his terms are

in most common usage among avian anatomists. There is included with each name, for the convenience of other students, a partial synonymy which indicates the terms employed by Shufeldt for the Raven, and by Gadow and by Edgeworth for birds in general.

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THE TONGUE MUSCULATURE

The term 'tongue musculature,' as here used, reflects a functional, rather than a morphological viewpoint. It is used to designate certain muscles which are functionally related in that their action effects movements of or in the hyoid apparatus, although they are of diverse origin. There are, of course, no intrinsic tongue muscles in birds.

Mandibular group

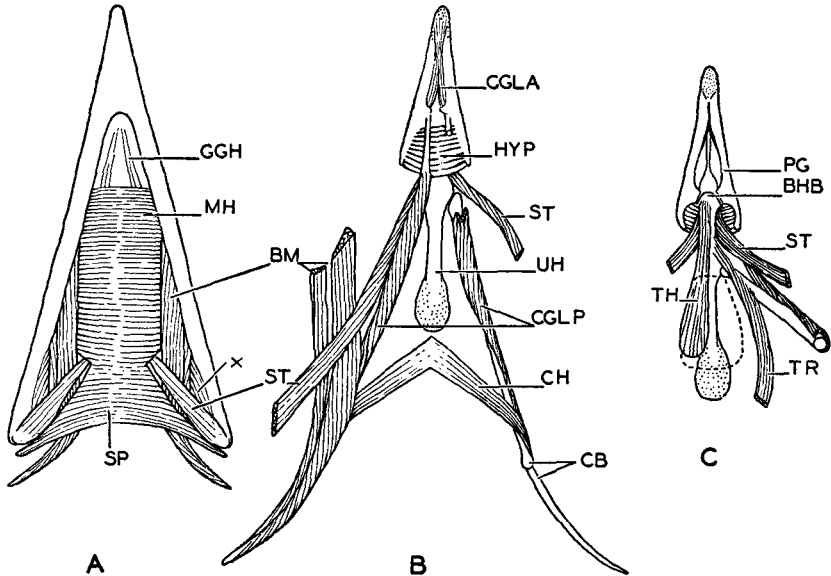
These are the muscles innervated by the mandibular branch of the fifth nerve. They are primarily masticatory muscles, but two of them belong, functionally, to the tongue musculature.

M. mylohyoideus (*sic*, Shufeldt; mylohyoideus anterior, Gadow; intermandibularis, Edgeworth).—This is a thin transverse muscle sheet, extending between the rami of the mandibles (Text-fig. 1A, *mh*). Fibers from the two sides blend in the midline. Posteriorly, the sheet becomes continuous with a somewhat similar muscular layer, the serpihyoideus. The fibers of the mylohyoideus arise from the mandible dorsal to the inserting fibers of the branchiomandibularis (= geniohyoideus of Shufeldt) and not ventral to them as indicated by Shufeldt (1890, p. 21, fig. 5). This latter error was accepted by Burt (1930) and made the basis of a false comparison between ravens and woodpeckers.

M. ceratohyoideus (*sic*, Gadow; overlooked by Shufeldt [ceratohyoideus, Shufeldt = posterior ceratoglossus]; interkeratoideus, Edgeworth).—This is a very thin, short and strap-like muscle, extending obliquely forward from the ceratobranchiale to the midline, beneath and posterior to the urohyale (Text-fig. 1B, *ch*). Its origin is from the lateral side of the proximal piece of the ceratobranchiale at its distal end around which it makes a half turn to cross over the ventral side. At its origin it is covered by the branchiomandibularis and covers the posterior ceratoglossus. The entire muscle is hidden, in a superficial dissection, by the serpihyoideus, with the deep side of which the inserting fibers of both sides fuse in a median raphe.

This is a distinct muscle, though small, and readily seen also in passerines much smaller than the Raven, but it was overlooked by Shufeldt. Gadow does not describe its innervation, but thought it was "apparently" a

derivative of the ceratoglossus peculiar to birds. Edgeworth (1935) describes its derivation from the posterior part of the intermandibular muscle sheet.



TEXT-FIG. 1.—The tongue musculature of the Raven (*Corvus corax*). A: superficial dissection, ventral view. The skin and dermal musculature have been removed; a part of the pterygoideus (jaw muscle) is seen (x). B: deep dissection, ventral view. The mylohyoideus and serpihyoideus have been removed, and the entire hyoid apparatus has been separated from the mandible and floor of the mouth. The larynx, trachea and associated musculature are not shown. C: dorsal view; left side superficial, right side deep dissection. Shown in outline by the broken line is the thyroid cartilage, which lies on the dorsal side of the urohyale, and from the ventral surface of which the thyreohyoideus arises.

Abbreviations: *bhb*, basihyobranchiale; *bm*, branchiomandibularis; *cb*, ceratobranchiale; *cgla*, *cglp*, anterior and posterior ceratoglossus; *ch*, ceratohyoideus; *ggh*, genioglossus-geni-hyoideus; *hyp*, hypoglossus posterior; *mh*, mylohyoideus; *pg*, paraglossale; *sp*, serpihyoideus; *st*, stylohyoideus; *th*, thyreohyoideus; *tr*, tracheohyoideus; *x*, *M. pterygoideus*.

With respect to passeriforms other than those I have examined: Moller (1931) describes a muscle in *Zosterops annulosa* (Zosteropidae) without naming or homologizing it, which, on the basis of topographical relationships, seems to be this muscle. He gives no indication of it in other passeriforms studied by him.

Hyoid group

These are the muscles primarily derived from the hyoid muscle plate and innervated by the seventh nerve. Of them, two derivatives of the constrictor colli belong, functionally, to the tongue musculature.

M. stylohyoideus (*sic*, Shufeldt and Gadow; gularis anterior, Edgeworth).—A long, thin, flat and tapering muscle, extending from the posterior end

of the mandible to the basihyobranchiale (Text-fig. 1, *st*). The origin is from the lateral face of the angulare, immediately anterior to the depressor mandibulae. The postero-medial edge of the muscle is closely bound to the antero-lateral edge of the serpihyoideus in this region. It then crosses the branchiomandibularis superficially, passes deep to the mylohyoideus and runs forward beside the posterior ceratoglossus, gradually crossing to its dorsal side, and acquiring a fleshy insertion along the lateral surface of the basihyobranchiale. The anteriormost portion of insertion lies between the hypoglossus posterior and the thyreochoideus (Text-fig. 1C). Shufeldt (1890, pp. 27-28, fig. 7) was in error in describing and figuring the insertion of this muscle in the Raven as on the head of the ceratobranchiale, although such an insertion is said to occur in some passeriform birds (cf. Moller, 1930, 1931: Nectariniidae, Meliphagidae, Coerebidae, Zosteropidae).

M. serpihyoideus (*sic*, Gadow; digastric, Shufeldt; gularis posterior, Edgeworth).—A double fan-shaped muscle lying posterior to the mylohyoideus, with which it apparently is continuous (Text-fig. 1A, *sp*). It arises, on either side, by a narrow band of fibers from the basitemporal plate, medial to the depressor mandibulae. These extend ventrad between the angle of the jaw and the muscle-wound ceratobranchiale and, turning mediad, spread out in a thin sheet of superficial muscle, the fibers from either side meeting in a median raphe and blending anteriorly with those of the mylohyoideus. On its deeper surface the inserting fibers of the ceratohyoideus join the raphe.

Apparently in some passeriforms the primary origin of the serpihyoideus from the mandible, just back of the stylohyoideus, rather than from the base of the skull, is retained (cf. Moller, 1930, 1931: Nectariniidae, Meliphagidae, Coerebidae, Zosteropidae).

Note: The two muscles of this group, which in some other birds are not separate, together constitute the mylohyoideus posterior of Gadow (= the gularis of Edgeworth).

Ventral muscle group

This group of muscles is derived from the branchial muscle plates, innervated by branchial nerves of the corresponding segments. Only the subarcuales recti of the first segment (ninth nerve) are represented in birds, and these have but one derivative.

M. branchiomandibularis (*sic*, Edgeworth; geniohyoideus, Shufeldt and Gadow).—A flat, stout muscle-bundle extending from the ceratobranchiale to the mandible (Text-fig. 1 A, B, *bm*), more or less clearly separable into lateral and medial portions. It is attached to the distal unit of the ceratobranchiale which it enwinds in a spiral half-turn. Leaving the ceratobranchiale in the region of the joint between proximal and distal portions,

it passes deep to the stylohyoideus and superficial to the mylohyoideus to the medial surface of the mandible, where it attaches over an extensive area. Shufeldt's description is substantially correct, but his text-figure, previously mentioned, shows the area of attachment to the mandible as dorsal rather than ventral to that of the mylohyoideus.

Hypobranchial spinal group

These are muscles derived from the ventral ends of occipito-spinal myotomes, innervated by the cervical plexus, the major contribution to which is made by the twelfth nerve. The group becomes separated in development into prehyoid derivatives, innervated by the lingual nerve, and posthyoid derivatives, innervated by the superior descending cervical nerve. The former include the geniohyoid-genioglossus, the ceratoglossals and the hypoglossals; the latter include derivatives of the rectus cervicis.

Prehyoidean hypobranchial spinal muscles

Mm. geniohyoideus-genioglossus (*sic*, Edgeworth; genioglossus, Gadow; overlooked by Shufeldt [geniohyoideus of Shufeldt and Gadow = branchiomandibularis]).—These vestigial muscles are represented by a few longitudinal fibers in the anterior part of the floor of the mouth, between the oral mucosa and the mylohyoideus (Text-fig. 1A, *ggh*). In gross dissection they appear to be stringy cords diverging posteriorly from the region of the symphysis toward the medial sides of the sublingual glands, and disappearing posterior to the base of the tongue. Teased fragments, placed under the microscope, quickly reveal their skeletal muscle nature. In serial sections of the head of a nestling Brown Thrasher (*Toxostoma rufum*), I was able to follow some of the more medial fibers to the ventral side of the posterior end of the paraglossale; the remainder faded out beneath the mucosa to the side of the base of the tongue.

Moller (1930, 1931) notes the occurrence of these muscles in the following passeriforms: *Cinnyris chalybaeus* (Nectariniidae); *Anthornis melanura* (Meliphagidae); and *Dacnis cayana* (Coerebidae). In each of these, insertion is on the ceratobranchiale and on the paraglossalia. In *Zosterops annulosa* (Zosteropidae) he describes muscle fibers arising from the mandible and inserting on the pharyngeal mucosa, that probably represent this muscle, which thus appears to have an arrangement in *Zosterops* similar to that in the passerines examined by me. To my knowledge there are no other reports of the occurrence of these muscles in passeriform birds.

M. ceratoglossus posterior (*sic*, Gadow; ceratohyoideus, Shufeldt [ceratoglossal of Shufeldt = ? tracheohyoideus]; hyoglossus posterior [not *hypo*-], Edgeworth).—A slim, nearly cylindrical muscle-bundle extending from the ceratobranchiale to the paraglossale (Text-fig. 1B, *cglp*), it arises from the

dorsal surface of the proximal unit of the ceratobranchiale, along most of its length; proximally, it crosses over ventrally toward the midline, becomes tendinous as it passes over the under side of the hypoglossus posterior, and is inserted on a tubercle on the ventro-medial border of the paraglossale, just in front of its articulation with the basihyobranchiale.

Shufeldt erroneously considered himself to be in agreement with Gadow in his use of the names ceratohyoideus and ceratoglossal; the error in synonymy has been carried along by Edgeworth (1935, p. 288).

M. ceratoglossus anterior (*sic*, Gadow; ?depressor-glossus, Shufeldt; hyoglossus anterior [not *hypo*-] Edgeworth).—A tiny bundle of muscle fibers within the tongue, on the under side (Text-fig. 1B, *cgl*a). This vestigial muscle arises by a delicate tendon just in front of the tubercle on the paraglossale on which the posterior ceratoglossus inserts; the muscle fibers spread out anteriorly over the under side of the cartilage of the tip of the tongue.

In serial sections of the head of a nestling Brown Thrasher (*Toxostoma rufum*) it may be seen that the point of origin of this muscle is 0.5 mm. anterior to the insertion of the (posterior) ceratoglossus; between the two is a marked localized thickening of the perichondrium of the paraglossal cartilage. It is precisely as though the inserting tendon of the ceratoglossus fused to the perichondrium for a short distance, then separated, became carneous, and continued on to the tip of the tongue. The evidence thus indicates that this tiny muscle on the under side of the tongue is a separated anterior portion of the ceratoglossus, such as has previously been reported to occur in *Gallus*, *Procellaria*, and *Palamedes* (Gadow, Edgeworth).

In two of the four passeriforms whose tongue musculature was studied by Moller (1931: *Dacnis cayana*, *Zosterops annulosa*) he mentions the occurrence of "Skelettmuskeln" around the paraglossalia, which he saw in sections of the tongue. These, possibly, represented the ceratoglossus anterior; otherwise, there has been no report of the occurrence of this muscle in passeriform birds.

The depressor-glossus of Shufeldt, according to him (1890, p. 30), "arises fleshy [in the Raven] from the entire under surface of the [basihyobranchiale], the fibers contract as they pass forwards, and become tendinous between the [paraglossalia], and as a delicate tendon so continue on to finally find an insertion at their tips, where they meet anteriorly (Fig. 17)." The fact is that there is no muscle in the Raven which answers this description, or which occupies the position of the muscle shown in his fig. 17 (p. 46). No muscle extends from the ventral surface of the basihyobranchiale to the paraglossalia. The ventral surface of the former is a thin keel, bare of muscle; the lateral faces are covered by the stylohyoideus. Except for the posterior ceratoglossus, which Shufeldt, under the name "ceratohyoideus," correctly described and figured, the only other muscle in this general region

is the hypoglossus posterior. But this is a *transverse*, rather than a longitudinal muscle such as shown by Shufeldt, and of such a nature that he could not have failed to recognize it, had he seen it.

M. hypoglossus posterior (*sic*, Edgeworth; hypoglossus obliquus, Gadow; overlooked by Shufeldt).—An apparently unpaired, transverse muscle, passing beneath the basihyobranchiale between the posterior ends of the paraglossalia (Text-fig. 1B, *hyp*). The anterior ends of the stylohyoideus are covered by the muscle, while the tendons of the posterior ceratoglossus pass over its ventral surface. Undoubtedly originating from paired primordia, the fibers coming from either side do not form a raphe, but overlap one another to form a continuous muscle extending from one paraglossale to the other. The muscle lies back of the joint formed by the basihyobranchiale with the two paraglossalia; contraction, therefore, would pull the posterior ends of the paraglossalia downward, and, consequently, elevate the tip of the tongue. If synergistic muscles (the two sets of ceratoglossals) opposed this action, then, conceivably, contraction of the hypoglossus could arch the dorsal surface of the tongue by depressing its edges.

Apparently, this conspicuous muscle has not previously been reported to occur in passeriform birds. In *Dacnis cayana* (Coerebidae), Moller (1931) describes and figures a muscle which probably is this; he does not give it a name. Apparently it is absent in the nectariniid, meliphagid and zosteropid species studied by him, since, although he examined sections of the tongue, he makes no mention of a muscle which could be interpreted as the hypoglossus posterior (Moller, 1930, 1931).

Posthyoidean hypobranchial spinal muscles

These are the derivatives of the rectus cervicis (system of the sterno-hyoideus, Gadow) which forms two bands, an external and an internal fasciculus. The former is attached posteriorly to the tip of the keel of the sternum (= cleiodotrachealis of Shufeldt). About the middle of the neck it is tightly bound to the skin, becomes free again and passes forward at the side of the trachea, to the anterior end of which it is more or less firmly attached. A pair of muscle bundles which appear to be the direct continuation of this fasciculus reach the hyoid apparatus. They are, therefore, the equivalent of the cricohyoideus of Edgeworth; for convenience in description the separate names employed by Gadow will be used here.

M. tracheohyoideus (Shufeldt: ? ceratoglossal, in part).—A flat muscular band extending from the latero-ventral side of the trachea to the dorso-medial face of the head of the ceratobranchiale; a few fibers continue on to the lateral face of the basihyobranchiale beneath the stylohyoideus (Text-fig. 1C, *tr*). This muscle is a continuation of the outermost part of the external fasciculus of the rectus cervicis.

M. thyroehyoideus (Shufeldt: sterno-hyoideus; ? ceratoglossal, in part).— This muscle extends from the thyroid cartilage of the larynx, over the head of the ceratobranchiale, to the dorsal surface of the basihyobranchiale, reaching to its very tip (Text-fig. 1C, *th*). Wide posteriorly, where it covers the ventro-lateral half of the thyroid cartilage, it narrows abruptly as it passes forward. Shufeldt's figures of these two muscles (his ceratoglossal and sternohyoideus) are puzzling. I am unable to reconcile them with the facts. No part of the rectus cervicis extends anteriorly *beneath* the ceratobranchiale, as shown in his ventral view (Fig. 17, p. 46, sternohyoideus); while the basihyobranchial attachment of his muscle extending forward from the ceratobranchial (Fig. 18, p. 35, ceratoglossal) occupies the actual area of attachment of the muscle extending forward from the ventral face of the thyroid cartilage.

SUMMARY

The musculature effecting movement of or in the hyoid apparatus, here termed "tongue musculature," was dissected in nineteen species of the following passerine families: Corvidae, Troglodytidae, Mimidae, Turdidae, Laniidae, Icteridae and Fringillidae. Some differences in detail were noted, but the number and general arrangement of the muscles were uniform in all species examined. The detailed description of these muscles is given for the Raven (*Corvus corax*); eight major errors in Shufeldt's 'Myology of the Raven' are corrected.

Three of the eleven muscles herein described have not been reported previously to occur in passerines (ceratohyoideus, ceratoglossus anterior, hypoglossus posterior); a fourth muscle (geniohyoideus-genioglossus) has heretofore been reported for but three forms.

The geniohyoideus-genioglossus is vestigial in passerines. The ceratoglossus anterior, differentiated off from the rostral end of the main body of the ceratoglossus, is minute (probably vestigial). The hypoglossus posterior is a transverse muscle in these passerines; its topographical relations are such that it could act either to elevate the tip of the tongue, or, with synergists, to arch the upper surface of the tongue both transversely and longitudinally.

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