THE ANATOMY OF THE TONGUE OF RANA HEXADACTYLA.

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INTRODUCTION.

As is well known the frog's tongue is attached to the tip of the lower jaw by its anterior end, its hind end being free. The frog is capable of turning forward the hind end of the tongue to strike any insect prey and flick it back into the mouth. The movement is so quick and interesting to watch that it has attracted the attention of many workers. Dugès as early as 1827 expressed the opinion that the intrinsic muscles of the tongue were aided by the muscles of the jaw and of the hyoid. In 1857, Fixsen studied the structure of the frog's tongue and put forward the view that the genioglossus muscle acts as the protractor and that the hyoglossus muscle as the retractor of the tongue. This view was later supported by Weidersheim in 1882, by Ecker in 1889 and by Gaupp in 1901. In 1850 Kleine put forward the theory that the hyoglossus is the protractor and the genioglossus the rectractor muscle, while in 1894, Ferdinand, from his study of the tongues of several animals, was convinced that the hyoglossus acts both as the protractor and as the retractor. In 1901, Hartog made the suggestion that the tongue is projected by the pressure of lymph into the hollow spaces in the tongue and that the withdrawal of the fluid rectracts the tongue. In the same year Gaupp studied the anatomy of the tongue in great detail and supported Fixsen's conclusion that the genioglossus is the protractor and the hyoglossus the retractor muscle of the tongue. As neither a criticism of these views of Gaupp and Hartog nor a detailed study of the anatomy of the tongue has been published, the author has studied in detail the muscles of the tongue which aid it in projection and retraction. A detailed description of the structure and working of the tongue is further called for by the fact that even in the latest edition of the " Biology of the Frog " by Holmes—a handbook for students, the error of associating Gaupp's name with the lymph-pressure theory of tongue-projection has been repeated.

I am of the opinion, that the movements of the frog's tongue are brought about entirely by muscles, and that when the tongue is in a state of rest the long hyoglossi are contracted ; but that in functioning they are relaxed, and by their relaxation help the forward movement of the tongue from behind. The front part of the tongue being attached to the symphysis by the genioglossi, the posterior part is free to move forward ; the upper mucous secreting surface thus comes into contact with the prey, which adheres firmly to the tongue, and is thus drawn into the buccal cavity.

The hyoid and its muscles are also described so as to give a clearer understanding of the exact relations of the hyoid muscles with those of the tongue, and in order to determine the degree of participation of the hyoid muscles in the mechanism of the projection of the tongue. Further, as the hyoid apparatus participates in the movements of the

tongue in the Squamata, the relation of the hyoid and its muscles in the frog should be of interest for purposes of comparison. It may also be remarked that even the most detailed accounts of the hyoid muscles, hitherto given, are not clear in reference to the actions of the various muscles.

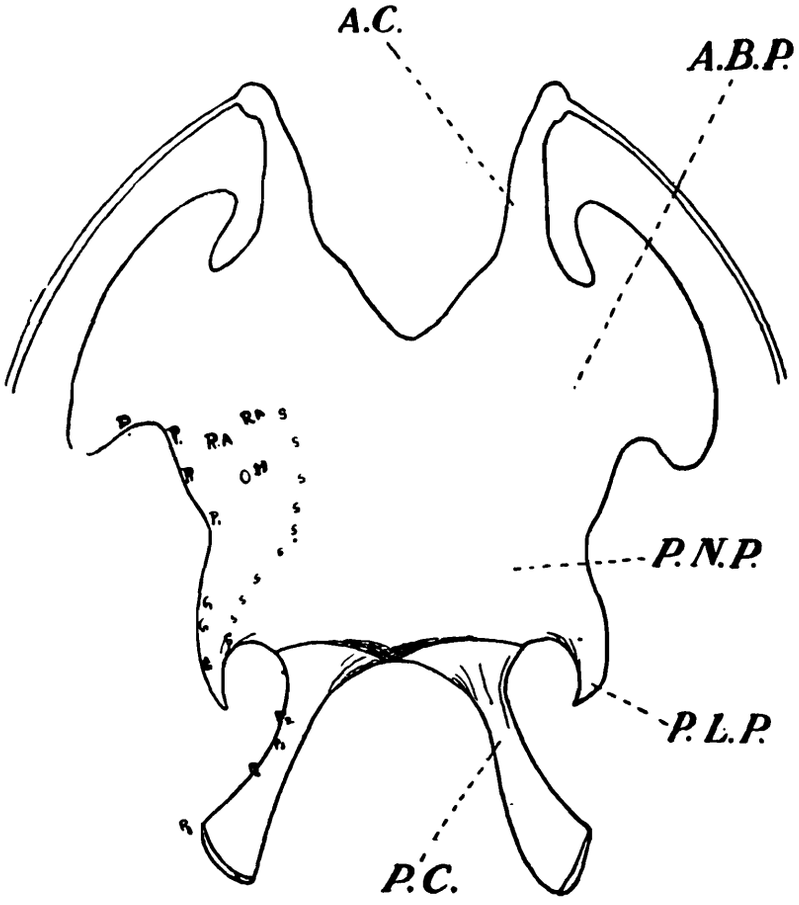
TECHNIQUE.

I dissected several freshly killed, as well as preserved specimens of *Rana hexadactyla*, and also studied the structure of the tongue of *Rana cyanophlyctis* from longitudinal and transverse sections of the entire tongue. The latter species was selected for its smaller size. The tongue was removed in every case with portions of the mandibular symphysis, the transverse muscles and the skin of the chin and the lower jaw, and was fixed in Bouin's picro-formol and embedded in paraffin. The sections were stained in alcoholic borax-carmine followed by Picro-indigo carmine, cleared in clove oil and mounted in Canada balsam.

THE HYOID APPARATUS.

(Fig. 1).

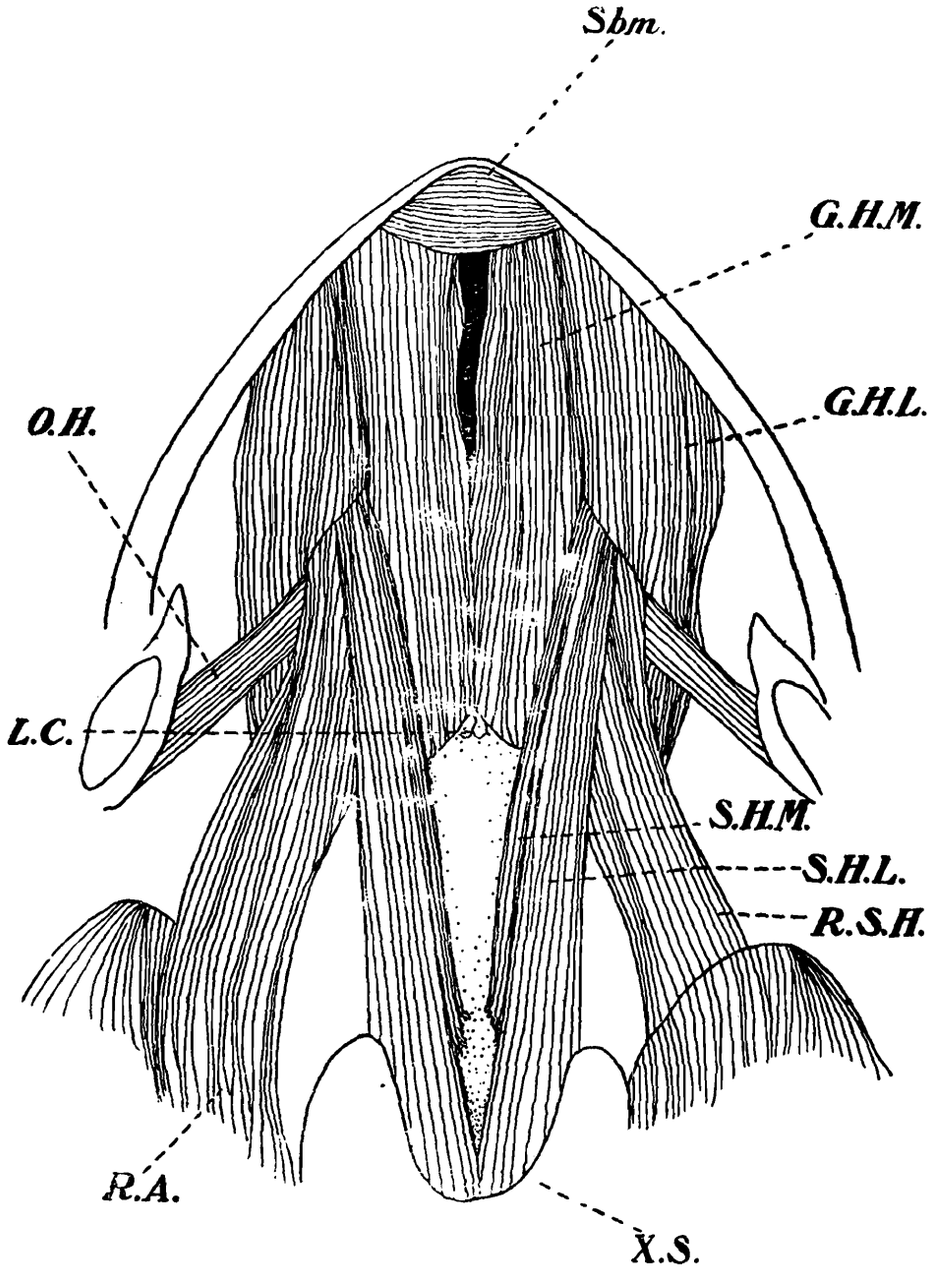
The hyoid (*os hyoideus*) consists of a thin cartilaginous plate broad in front and narrow behind. In the broad part, the antero-lateral



TEXT-FIG. 1.—The hyoid apparatus.

A. B. P.—Anterior broad part; *A. C.*—Anterior cornua; *O. H.*—Insertion of omohyoidens; *P.C.*—Posterior cornua; P_1,P_5.—Petrohyoid insertions; *P. L. P.*—Postero-lateral process. *P. N. P.*—Posterior narrow part. *R. A.*—Insertion of Rectus abdominis continued as sternohyoideus; S_2.—Line of insertion of sternohyoideus. *G.*—Insertion of geniohyoideus.

margin is slightly constricted on either side to form a wing with an anterior and a posterior projection, and curves evenly from before backwards. The anterior margin bears a pair of elongated processes, the anterior cornua (A. C.). In the narrow part of the hyoid the postero-lateral margin is produced on either side into a pointed process (P. L. P.) which curves inwards. The posterior margin of the hyoid bears a pair of elongated processes, the posterior cornua (P. C.).



TEXT-FIG. 2.—View of deeper muscles. (The anterior parts of the sternum have been removed. *Same size.*)

G. H. L.—Geniohyiodeus lateral; *G. H. M.*—Geniohyoideus median; *L. C.*—Laryngeal cartilage; *O. H.*—Omohyoideus; *R. A.*—Rectus abdominis; *R. S. H.*—Rectus abdominus continued as sternohyoideus; *S. H. L.*—Strenohyoideus lateral; *S. H. M.*—Sternohyoideus median; *Sbm.*—submentalis; *X-S.*—Xiphisternum.

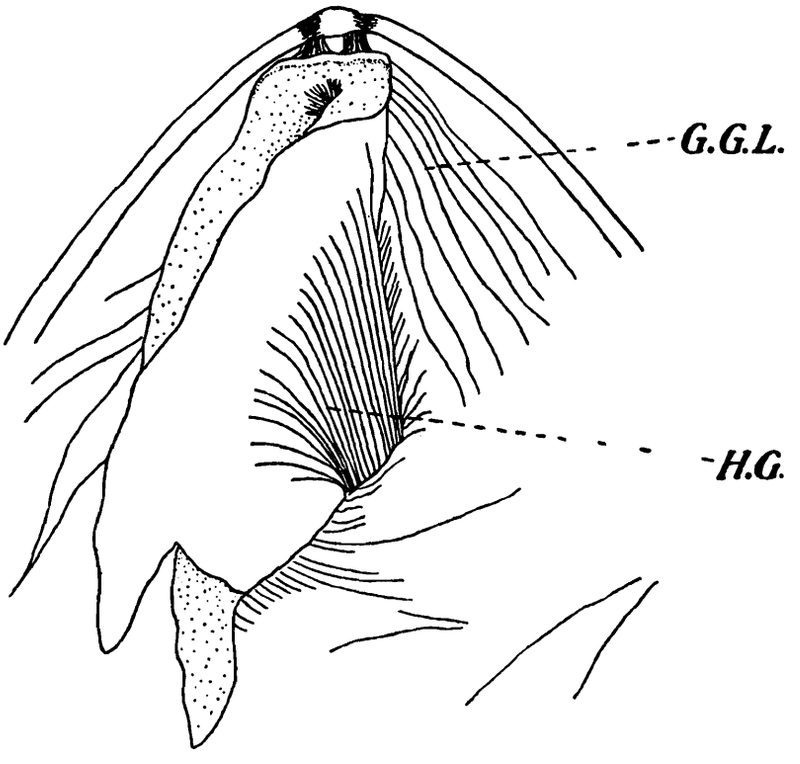
The anterior cornua consist of two parts, a stout proximal part terminating in a knob, and arising from the outer edge of this, a long slender distal part. The latter runs backwards almost parallel to the mandible near to the buccal floor and in close approximation to the fibrous tissues between the mylohyoid muscle and the buccal floor;

its distal ends are attached to the tympanic region. The posterior cornua are two flat bony rods, the anterior ends of which fit into corresponding notches in the posterior border of the hyoid plate: the posterior ends are flatter and have cartilaginous epiphyses.

The flat plate-like form of the hyoid apparatus is eminently adapted for affording attachment to various muscles, and for various movements connected with respiration. It is clear, however, that it does not play any direct part in the movements of the tongue.

TRANSVERSE MUSCLES.

M. Submaxillaris (Figs. 7-15. M. H.).—This forms the most ventral of the sheet of muscles of the lower jaw and corresponds to the mylohoideus of the higher animals. It covers the submaxillary area. Its fibres run transversely from one half of the lower jaw to the other. The most posterior fibres run close to the lower end of the septum maxillare. Some of the posterior most fibres have their origin in the fibrous tissue which lies between the skin and the septum maxillare as the latter bends anteriorly to the corner of the jaw. In *R. hexadactyla*, I have not been able to trace the origin of some of these fibres from the distal process of the anterior cornua, which curves round to the back part of the head, as Ecker seems to have found in the species that he examined. The rest of the submaxillaris has its origin on the superior border of the lower jaw, and extends across to unite with the muscle from the oppo-

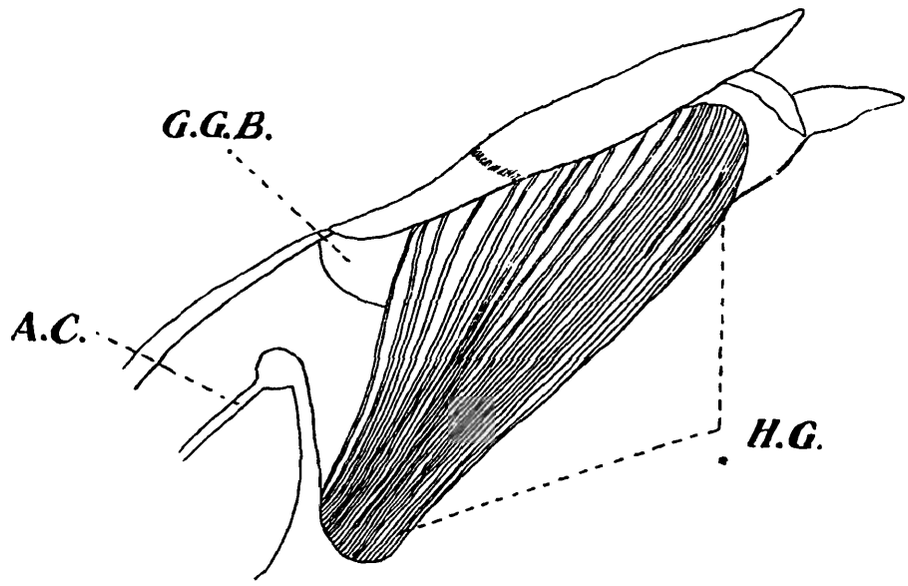


TEXT-FIG. 3.—View of tongue turned over to one side to show the "linguae peduncle". *G. G. L.*—Genioglossus lateralis; *H. G.*—Hyoglossi.

site side in the middle line by interdigitation. Anteriorly the fibres are directed obliquely forwards and the fibrous fascia in which they meet extends medially over the chin, *i.e.*, the angle of the symphysis, overlapping the submentalis muscle. Though the fibres of the submaxillaris muscle cannot be described as having a double origin, one

on the superior and the other on the inferior border of the jaw, as Kleine seems to have found, this muscle is unmistakably connected with the inferior edge of the lower jaw by a fibrous lateral extension of the fascia of the muscle. Through the space between the insertion on the superior border and the fibrous layer covering the lower edge run the nerves and blood vessels, as Ecker has described, but this alone does not account for the appearance of a twin insertion of the muscle fibres. The submaxillaris is also connected to the sides of the buccal floor by fibrous tissue developed on its fascia.

The Submentalis (Sbm. figs. 2, 7 and 8).—This is a very thick spindle-shaped muscle, the tendons of which are inserted on the dentaries on either side, while its short stout belly occupies the angle of the symphysis. The contraction of these fibres, which are arched ventrally, brings the sides of the lower jaw nearer and, according to Dugès and



TEXT-FIG. 4.—View of tongue partially drawn forwards.

A. C.—Anterior cornua; *G. G. B.*—Genioglossus basalis; *H. G.*—Hyoglossus.

Ecker, raises the premaxillae and closes the nostrils. It is not clear how the various functions assigned to the submentalis can be brought about, but it is probable that these fibres, which arch downwards and backwards, can by their contraction raise the floor of the mouth above it and push the genioglossi, which lie above it, upwards and forwards. In my opinion this muscle also serves to draw the two halves of the mandible together and lends to it the rigidity and firmness which the flexible cartilaginous union alone would not provide.

THE HYOID MUSCLES.

(Figs. 1 and 2).

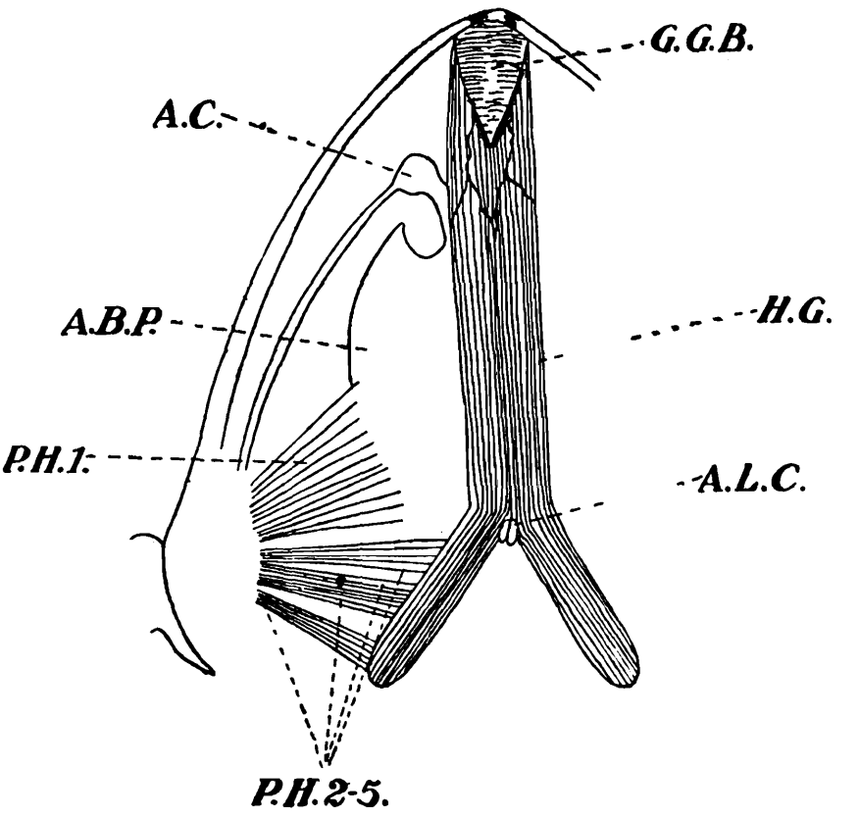
The Geniohyoideus.—The geniohyoideus of either side rises partly from the median tendon (*vide infra*) behind the symphysis and partly from the mandible where it lies external to the submentalis. The

median and lateral parts run backwards as one muscle but have separate insertions as follows :—

(*a*) The median division (G. H. M.) is inserted on a tendinous sheet which springs from the body of the hyoid between the proximal ends of the posterior cornua, and descending below is extended under the fasciae of the hyoglossi as they approach each other. This tendon sheet is in close union with the fibrous tissues which connect the anterior tips of the arytenoid cartilages with the hyoid ;

(*b*) the lateral bundle (G. H. L.), after running backwards with the median portion, separates from it to be inserted on the postero-lateral process of the hyoid.

The Sternohyoideus.—This is the anterior continuation of the *rectus abdominis*, which in the frog is considerably modified. It consists of three portions, a lateral and two median. The lateral part of the sternohyoideus (R. S. H.) of each side is really more ventral being the continuation of the rectus abdominis (R. A.) passing beyond the fifth "*inscriptio tendinae*" Running along close to but at a lower level than the median portions it ascends between the two divisions of the geniohyoideus, and its fibres, together with those of the median parts, become inserted on the lower surface of the hyoid plate. Of the two



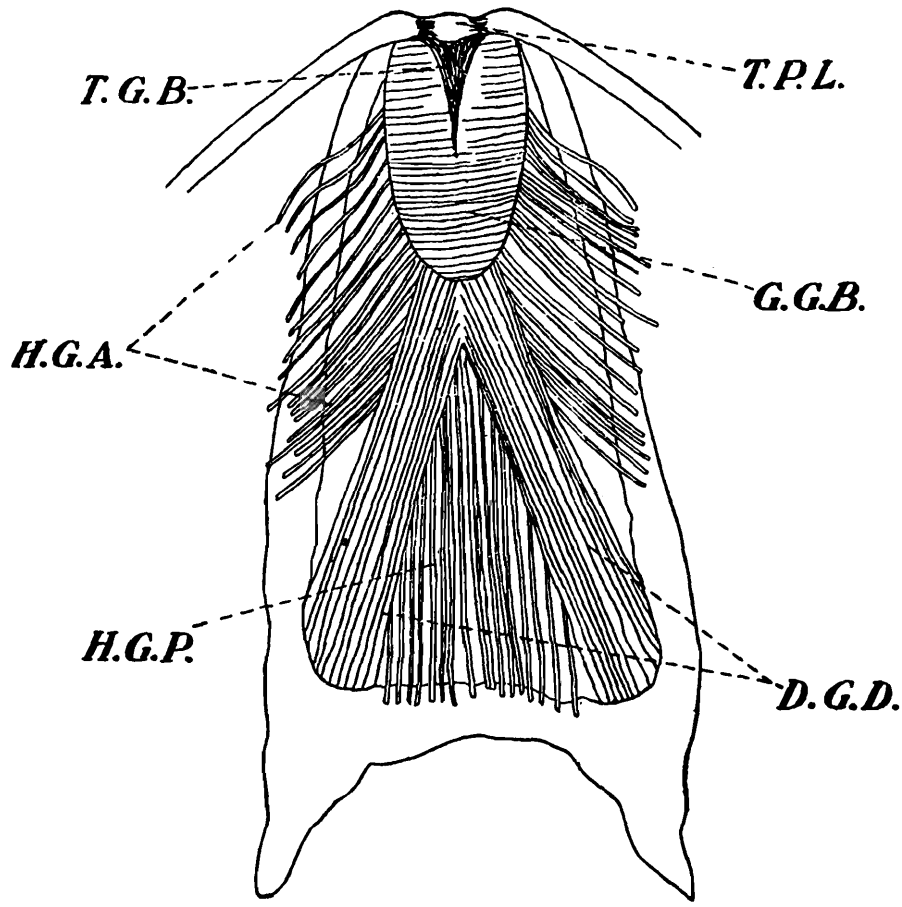
TEXT-FIG. 5.—View of deepest set of muscels.

A. B. P.—Anterior part of basilinguae plate ; *A. L. C.*—Anterior laryngeal cartilage ; *P. H.*$_{1\text{-}5}$.—Five bundles of petrohyoidei. (Other letters as in Fig. 4.)

median parts of the sternohyoideus, the outer (S. H. L.) is longer, and arises on the xiphisternum. Owing to its being close to its fellow of the opposite side both in origin and in the short length of its forward course, it appears as a single muscle but divides into two anteriorly. The second median part (S. H. M.) of the sternohyoideus is much shorter

and springs from the sides of the anterior end of the sternum proper. The median portions run with the lateral to their insertion on the hyoid plate.

The Omohyoideus (O. H.).—This is a comparatively slender muscle which arises on the anterior border of the bony scapula, descends anteriorly, and passing above the more superficial sternohyoideus reaches the hyoid bone between the divisions of the geniohyoideus, slightly external to the sternohyoideus.



TEXT-FIG. 6.—Ventral view of tongue with the Hyoglossus teased and spread out.

D. G. D.—Divergent bundles of genioglossus dorsalis; *G. G. B.*—Genioglossus basalis; *H. G. A.*—Hyoglossus anterior fibres. *H. G. P.*—Hyoglossus posterior fibres; *T. P. L.*—Tuberculum prelinguae—*T. G. B.*—Tendon connecting g. basalis with the geniohyoideus median.

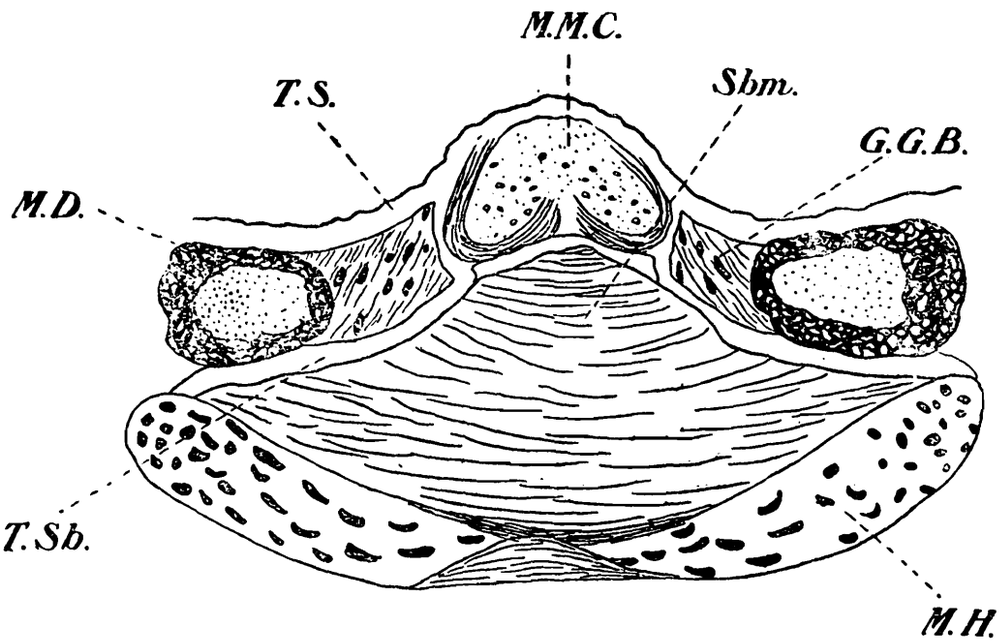
The Petrohyoidei. (Fig. 1 P_1—P_5).—The petrohyoidei arise from the prootic region of the skull, and curve round the pharynx to the ventral side in the region of the hyoid apparatus. From the nature of their insertion and from the difference in size of the muscles two groups can be recognized. The first, or *petrohyoideus anterioris*, is a thin flat muscle much wider than the rest. Though narrow at its origin it broadens as it descends. It is inserted on the sides of the posterior part of the hyoid, where the latter passes into the broader front part. *Petrohyoidei posteriores* are four in number, and curve round close to the pharynx spreading out to their insertion on the outer sides of the posterior cornua. Though they do not appear to have a direct and distinct insertion on the pharyngeal wall, it is not improbable that they function to some extent as constrictors of the pharynx.

The hyoid muscles appear to be adapted for moving the hyoid apparatus but not the tongue.

TONGUE MUSCLES.

(Figs. 3-16).

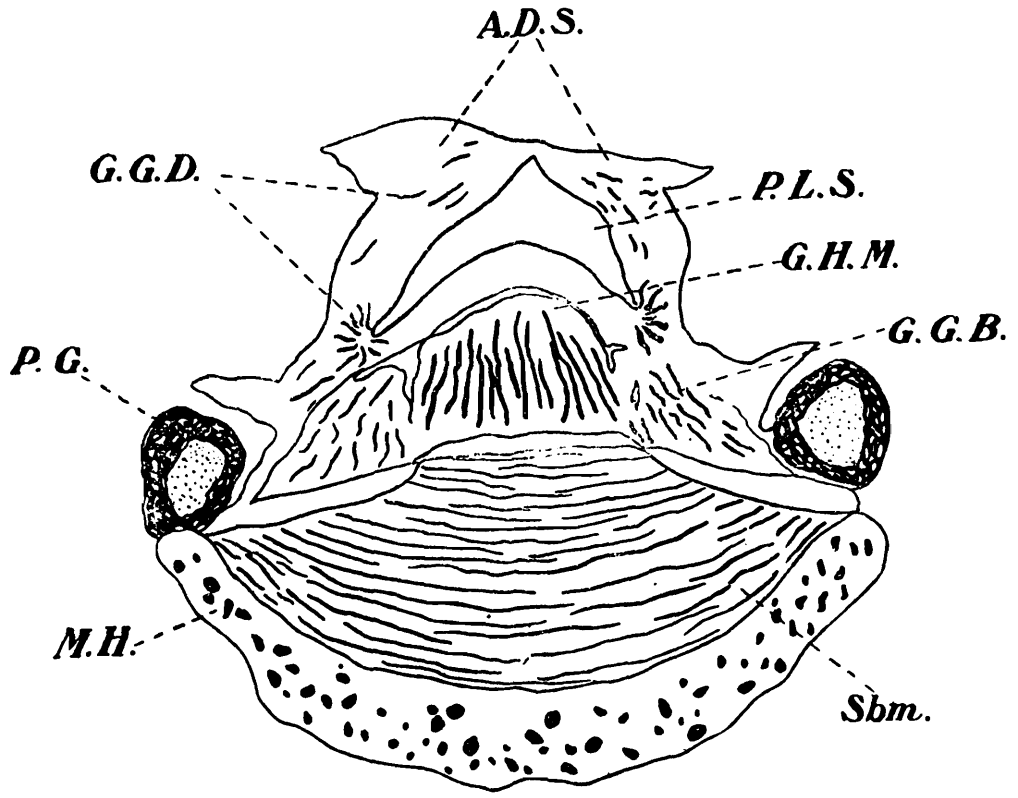
The two muscles of the tongue, the genioglossus and the hyoglossus, are both well developed, but, unlike the condition in the Reptilia, the genioglossus is chiefly a muscle of the tongue and is spread out on the buccal floor only as a very thin lateral extension. Further the genioglossal fibres are dorsal to those of the hyoglossus and not ventral to them as in the reptiles.



TEXT-FIG. 7.—Transverse section through mandibular symphysis.
G. G. B.—Genioglossus basalis; *M. D.*—Mandibular rami; *M. H.*—Submaxillaris; *M. M. C.*—Mentomeckelian cartilage (Tuberculum prelinguae); *Sbm.*—Submentalis; *T. S.*—Tendon sheet; *T. Sb.*—Tendon of submentalis.

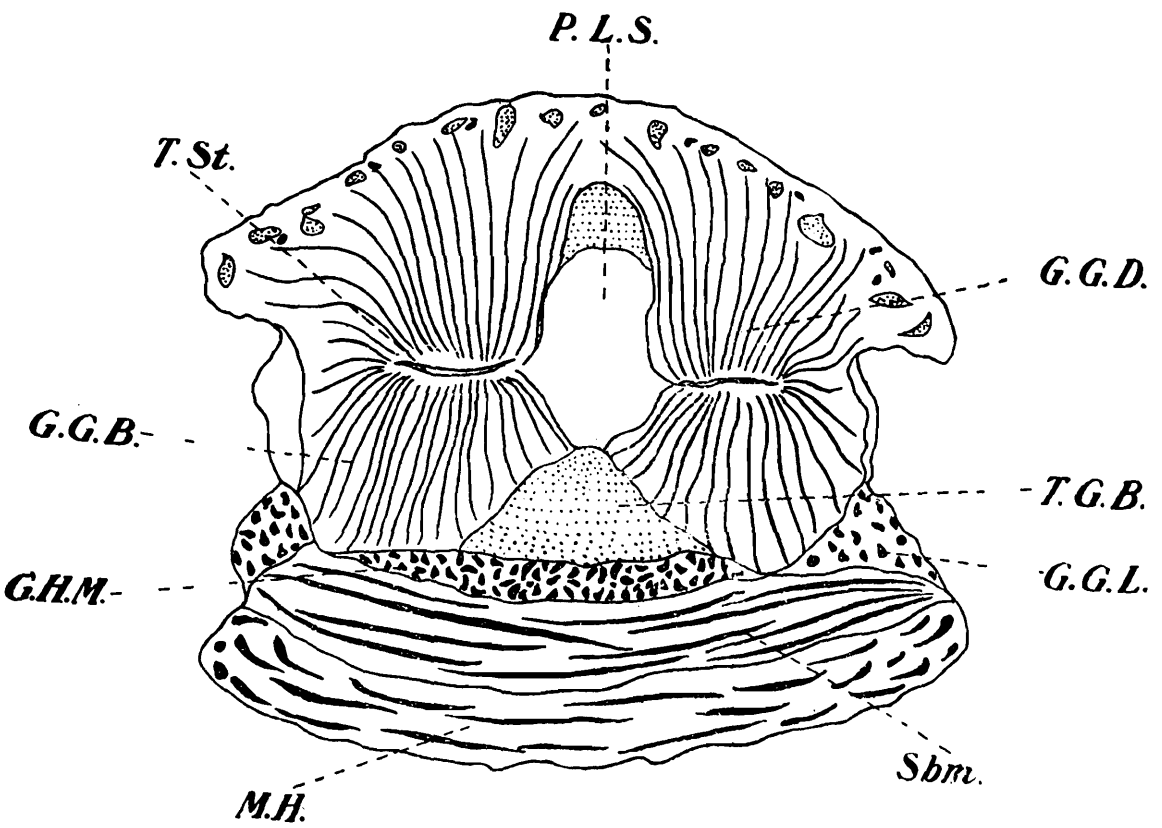
Genioglossus (figs. 3, 5).—Wherever present, in the frog and other animals, this muscle arises anteriorly at the symphysis of the lower jaw and extends backwards. Its origin in the frog, however, is not on the mandible itself but on a tendinous sheet springing from its superior aspect on either side of the *tuberculum prelinguae* (Fig. 6 T. P. L., Fig. 7 M. M. C.). The anterior fibres spring vertically from the lateral edges of the sheet, which stretches behind as two narrow strips, and the median fibres of the geniohyoideus arise below the central part of this tendinous sheet. The posterior fibres of the genioglossus spring both from above and below the two posterior extensions. As a consequence, the genioglossus appears to consist of a dorsal part arising from above the two tendinous strips, and a ventral and lateral part proceeding from their lower surface. The origin of the dorsal fibres from the posterior extensions of the tendinous sheet instead of from the upper surface of the sheet itself, indicates the apparently greater development of the ventral than of the dorsal part (which has a depression at its anterior end). Furthermore, as most of the fibres arise only from the posterolateral extensions of the tendinous sheet, the medial fibres incline towards one another, arching over the space between the two tendinous strips. A lymph sinus is formed at the anterior end of the tongue and is continued as a blind recess to some distance posteriorly. As the

course of the dorsal fibres varies from that of the ventral and the lateral fibres, the three parts of the genioglossus may be described separately.



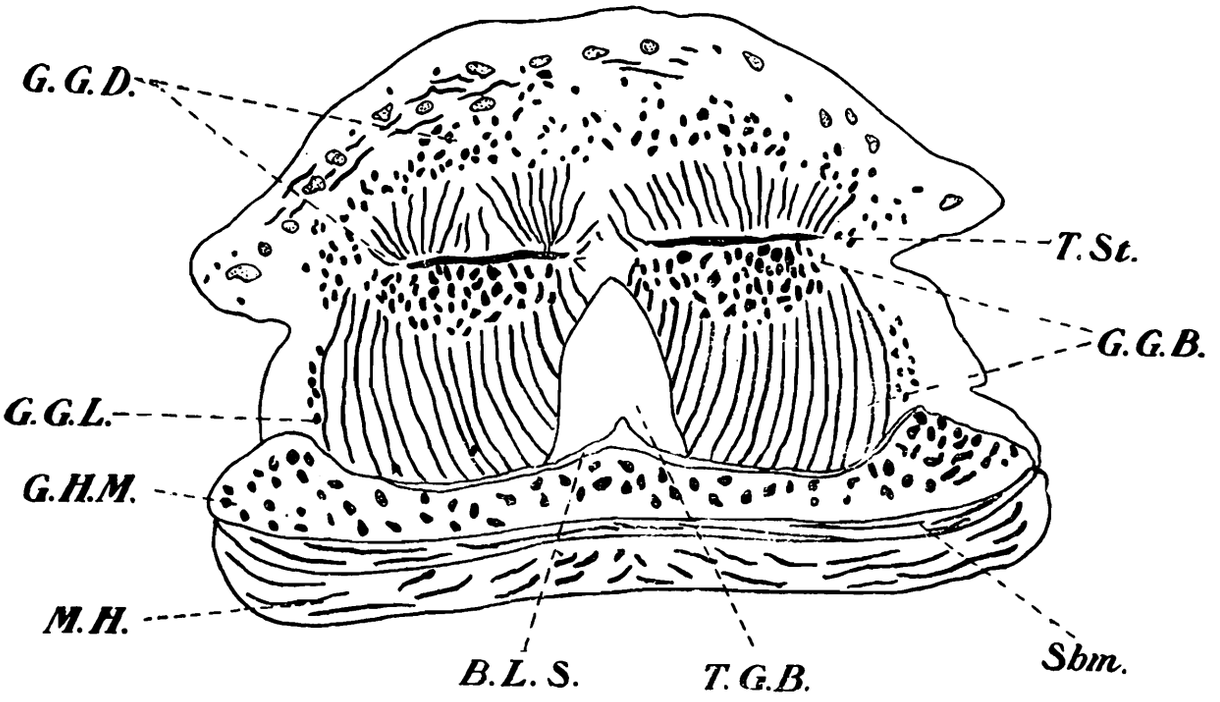
TEXT-FIG. 8.—Transverse section through the anterior end of tongue.
A. D. S.—Anterior edge of dorsal surface of tongue ; *G. G. B.*—Genioglossus basalis ; *G. G. D.*—Genioglossus dorsalis ; *G. H. M.*—Geniohyoidens median ; *P. G.*—Mandible ; *M. H.*—Submaxillaris ; *P. L. S.*—Prelingual sinus ; *Sbm.*—Submentalis.

Genioglossus dorsalis. (*G. G. D.*).—As mentioned above, this part of the genioglossus begins a little behind the ventral part. (Figs. 9



TEXT-FIG. 9.—Transverse section through " Conical bodied muscle ".
G. G. L.—Genioglossus lateralis ; *T. G. B.*—Tendon of genioglossus basalis ; *T. St.*—Tendon strips. (Other letters as in Fig. 8.)

and 10, T. St.). The first few fibres, springing from the two strips of tendon, radiate upwards into the surface of the tongue. The next few fibres run upwards and backwards, while the succeeding ones bend backwards to run parallel to the surface of the tongue. At about a sixth of the length of the whole tongue the lateral fibrous fascia of the whole genioglossus passes below the dorsal part of the muscle as an inward lateral extension, separating it from the thick cone-shaped genioglossus basalis. The lateral penetration of the fascia on either side is accompanied by fibrous extensions into the dorsal part of the genioglossus, dividing it into about three bundles. It is on this mass of fibrous tissue that the hyoglossal fibres are inserted (*vide infra*). The fibres of the dorsal part of the genioglossus serve to rotate its anterior end and to shorten the tongue, and as they diverge in the broad posterior region, they also serve to contract this part. As the cone-shaped genioglossus basalis extends backwards beyond the tendinous strips, the truncate

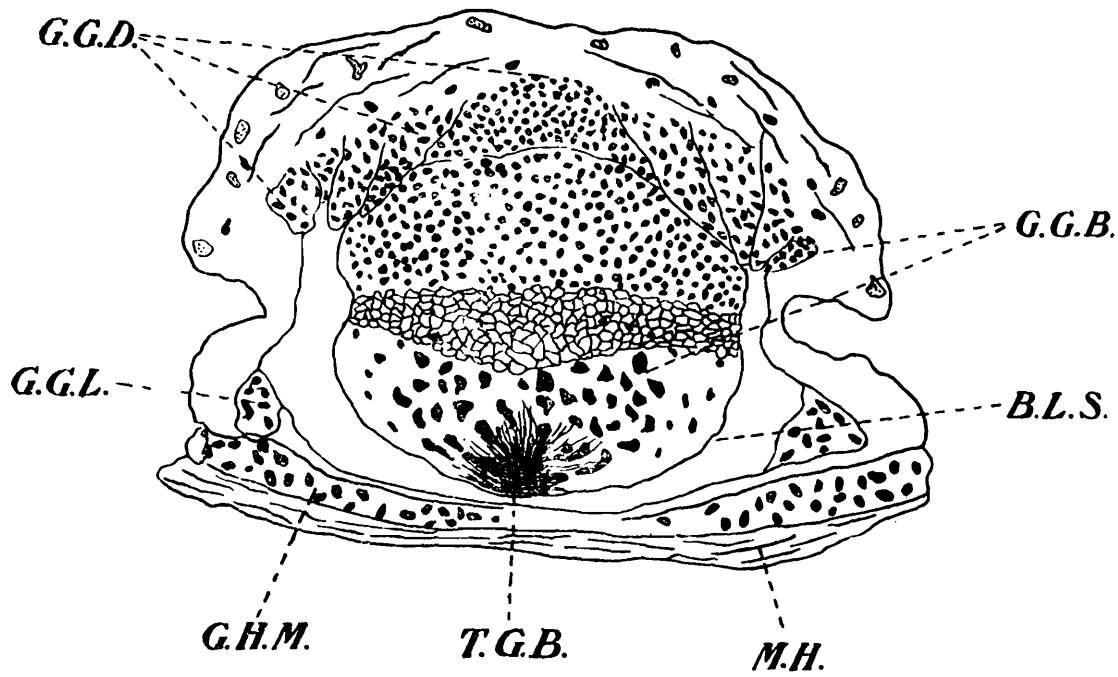


TEXT-FIG. 10.—Transverse section through middle part of "Conical bodied muscle". *B. L. S.*—Basilingual sinus. (Other letters as in Figs. 8 and 9.)

end of the median tendinous thickening of its ventral fascia curves upwards and separates the hindmost fibres of the genioglossus dorsalis into two divisions, which diverge (Fig. 6, D. G. D.) as they run into the tips of the tongue. Each division is formed of several bundles consisting of many fibres twisted as in a rope, and serves to draw up the tips of the tongue and to approximate them medially as well. Gaupp has not adequately explained the function of this muscle—especially its role in the play of the tongue.

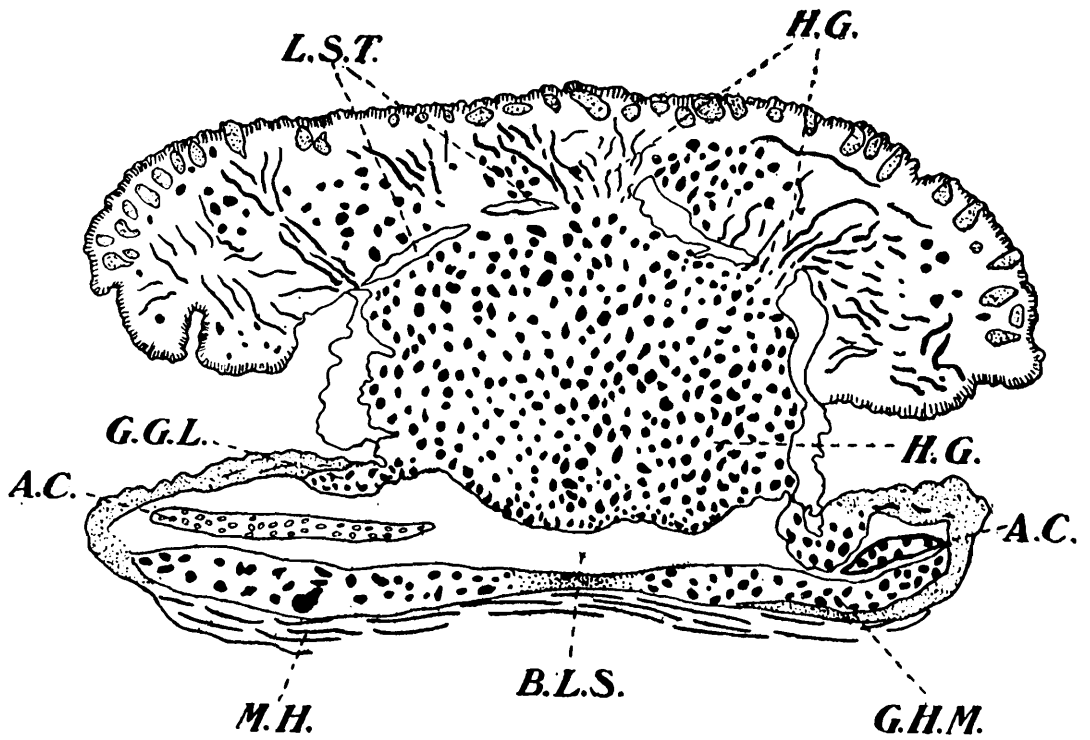
Genioglossus basalis. (*G. G. B.*).—This is a thick conical muscle, nearly one-third the length of the tongue, and lies at the front end of the tongue below the genioglossus dorsalis. The fibres of this muscle vary in their course. (*a*) The anteriormost fibres, which spring from the tendon sheet on either side of the *tuberculum prelinguae*, incline outwards and are inserted on the upper aspect of the tendinous sheath of the submentalis (*vide* fig. 8). A little behind where the tendinous

sheet of origin ends in two flat strips, the fibres are all oblique; those directed outwards end in fibrous tissues of the buccal surface of this part, while those which incline inwards are inserted on the upper fascia of the median geniohyoideus. (*b*) Still further behind, all the fibres incline towards a median insertion and a thick tendon (Figs. 9 and 10,



TEXT-FIG. 11.—Transverse section through hinder part of "Conical bodied muscle". (Letters as in Figs. 8, 9 and 10.)

T. G. B.) is formed on the middorsal region of the fascia of the median geniohyoideus. Near the posterior limit of the prelingual sinus (Fig. 9, P. L. S.) (*vide infra*) this tendon becomes separated from the geniohyoideus by the sinus basi lingualis (Fig. 10, B. L. S.) (*vide infra*) and



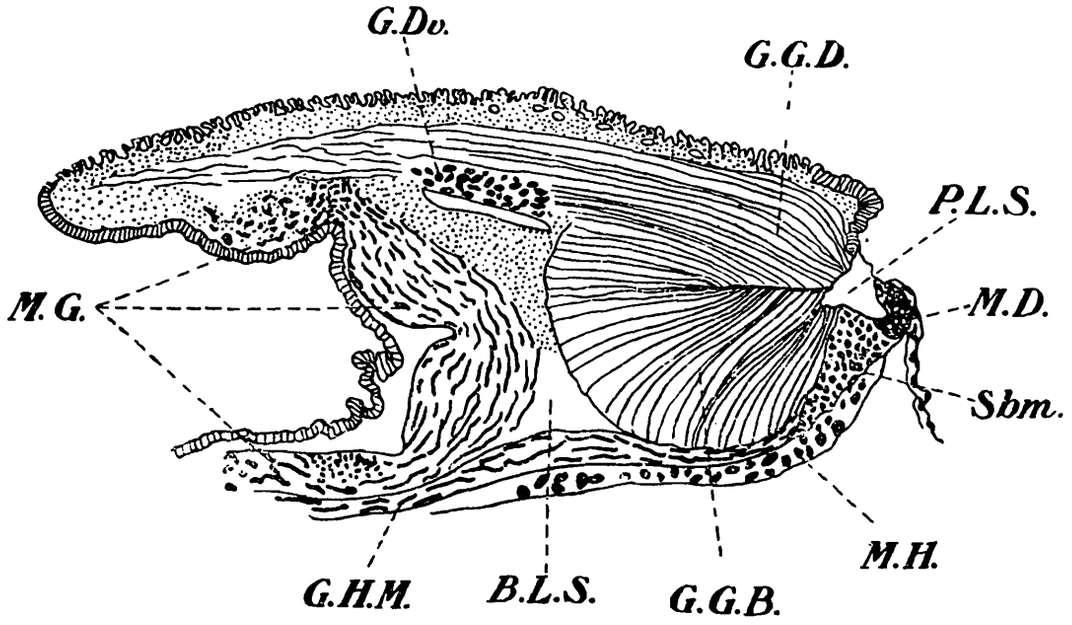
TEXT-FIG. 12.—Transverse section behind the conical muscle.

A. C.—Anterior cornua; *H. G.*—Hyoglossus; *L. S. T.*—Lymph sinuses of tongue. (Other letters as in Figs. 8, 9 and 10.)

runs within the ventral part of the genioglossus itself. Not only do these fibres of the ventral part of the genioglossus run inward from their lateral origins to the median tendon, but, owing to the great length of the more posterior fibres, run parallel to the long axis of the body for some distance and then turn downwards to their insertion (figs. 10 and 14). (*c*) The hindmost fibres are more or less horizontal and run nearly parallel to the tongue. As the fibres of the genioglossus basalis are much shorter than those of the genioglossus dorsalis, they form a thick cushion-shaped mass of muscle with a truncate hind end.

Genioglossus lateralis. (*G. G. L.*).—The fibres forming this division the genioglossus spring anteriorly from the fibrous tissues at the sides of the G. basalis, and spread backward fanwise, extending into the fibrous tissue below the buccal epithelium. They are few in number and lie far apart forming a sheet one fibre thick.

It is evident that the function of this peculiar and complicated muscle is to move the tongue forwards. The fibres of the dorsal part draw the posterior part of the tongue towards the tendinous sheet, which is thus made taut, resulting in the shortening of the tongue. The function of the several fibres of the basal part of the muscle differs according to their varied courses. The anterior-most fibres draw the tendon running along the lower side of the fascia, more forwards than upwards, while the fibres of the extreme posterior part draw the posterior end of the muscle distinctly forwards. The net result of the action of these fibres is to curve the hind end of the muscles upwards and forwards.



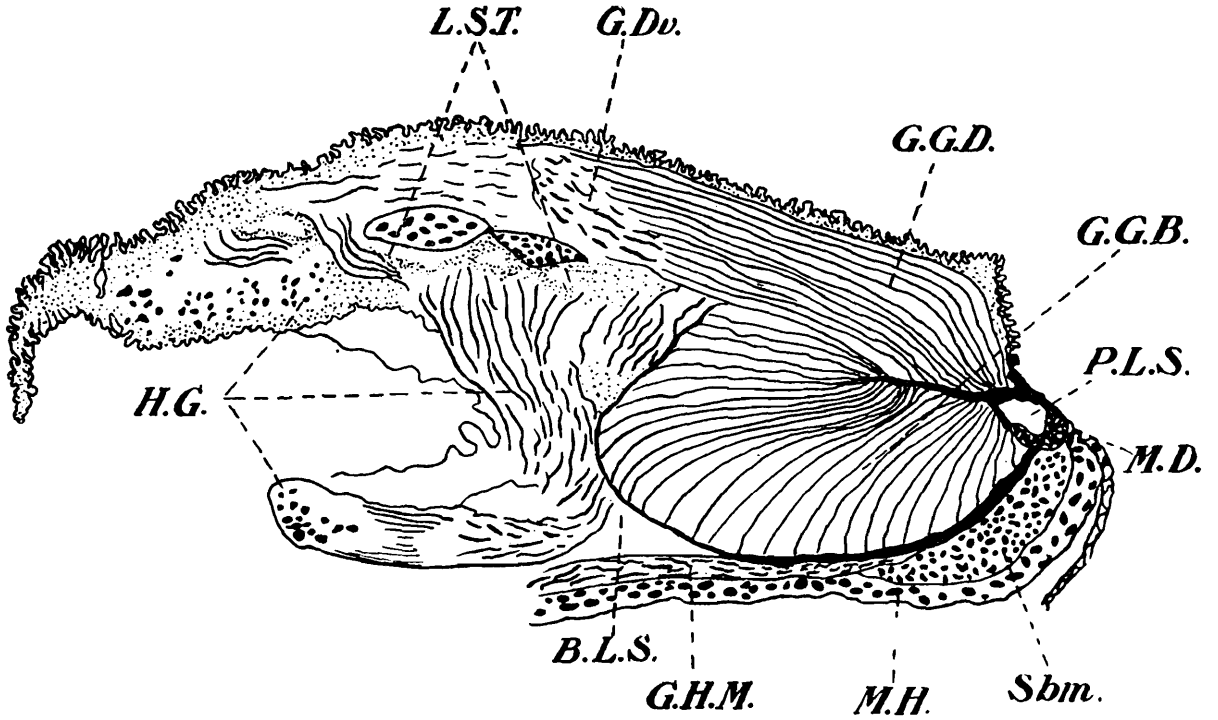
TEXT-FIG. 13.—Longitudinal section through median region.

G. Dv.—Genioglossus dorsalis divergent bundles. (Other letters as in Figs. 8 and 10.

This gives the pivotal movement necessary to enable the tongue to turn forward. As the ventral part of the genioglossus is attached at the front end to the submentalis and the geniohyoideus median, only the hinder end of the muscle is tilted forwards and upwards. The buccal floor is pulled forwards by the contraction of g. lateralis, thus facilitating the projection of the tongue. Here again owing to the

attachment of a part of the g. basalis to the buccal floor by the g. lateralis, as also by fibrous tissues, the front end of tongue cannot turn forwards.

Hyoglossus (*H. G.*) (figs. 4-17).—This is a paired muscle springing on either side from the distal end of the posterior cornua of the hyoid. It passes ventrally to the posterior cornu till the basihyoid is reached, then over the joint of the posterior cornua with the basihyoid, and, finally, joins its fellow of the opposite side, the two running forward close together and parallel to each other. Owing to the inconspicuousness of the fascia between them the two appear as one muscle in a transverse section. Running straight across the basihyoid, the hyoglossus turns upwards round its anterior curved edge, breaks out from its fibrous sheath and its fibres spread forward on either side of the ventral part of the genioglossus. The anterior-most fibres are inserted on the

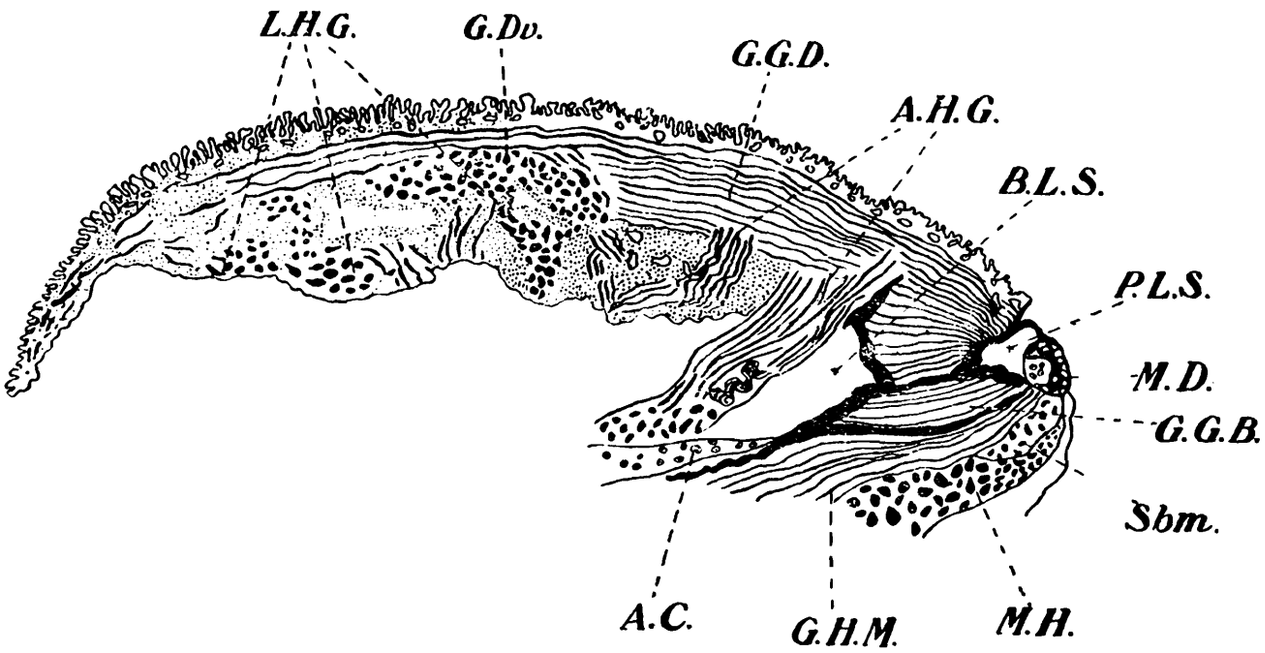


TEXT-FIG. 14.—Longitudinal section through slightly more median region. (Letters as in Figs. 8, 10, 12 and 13.)

front one-eighth of the length of the tongue. Other fibres are inserted in the fibrous tissues of the lower surface of the tongue on either side of the basal part of the genioglossus. The hyoglossal fibres are inserted between the two stout oblique bundles of the geniolossus dorsalis behind the genioglossus basalis. They are so numerous that they appear to form a peduncle by which the middle of the tongue is attached to the buccal floor. The distribution of the hyoglossal and genioglossal fibres in the tongue, will be clear from the diagram (fig. 16). The hyoglossal fibres which enter the middle of the tongue and radiate backwards to the hinder part of the tongue, appear to be short when the tongue is retracted, but when the tongue is swung out forwards, they appear to be long.

The surface of the tongue when projected is slightly reduced in area owing to the contraction of the genioglossus dorsalis, and when the tongue is resting the hyoglossal fibres running into the anteriormost

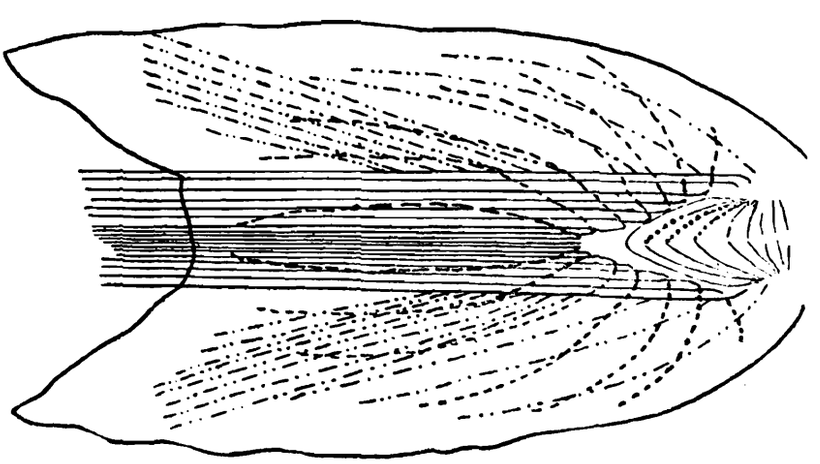
part of the projected tongue are really bent back. Even allowing for these facts, it is obvious that the hyoglossus running as it does from



TEXT-FIG. 15.—Longitudinal section through lateral part of tongue.
A. H. G.—Anterior hyoglossal fibres; *L. H. G.*—Lateral hyoglossal fibres. (Letters as in Figs. 8, 10, 12 and 13.)

its origin up to the middle of the retracted tongue, must be in a considerably contracted state, not unlike the very highly contracted hyoglossus of the Chameleon.

Some of the earlier investigators have maintained that there are three intrinsic muscles in the tongue of the frog, *viz.*—(*a*) the muscle, *transversum linguae*, present in the ventral region of the posterior part of the tongue, (*b*) a median longitudinal muscle present in the hinder part of the tongue, and (*c*) very fine muscle fibres spreading in a curve on the ventral surface of the whole tongue. Of these investigators

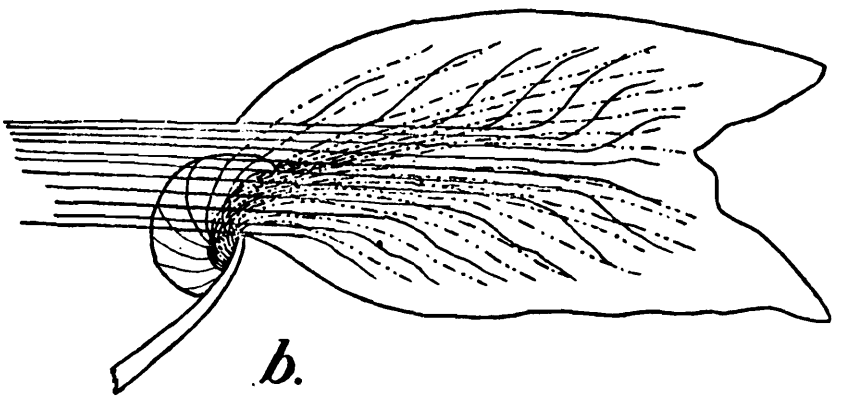


a.

TEXT-FIG. 16*a*.—Diagram to show the distribution of the hyoglossal and genioglossal fibres in a resting tongue, as seen from the Ventral Side.

———— = Genioglossus basalis fibres.
—· —· — — = Genioglossus dorsalis fibres.
- - - - - - - - = Hyoglossus fibres.

Gaupp alone appears to have made an accurate study of the microscopic structure of the intrinsic muscles, but beyond mentioning them he gives no description. A close study of serial transverse and longitudinal sections of the muscles shows that there are no intrinsic muscles in the tongue, and it is formed by the genioglossus and the hyoglossus alone. If the course of the genioglossus dorsalis be followed it is found that the fibres deviate in places to the borders of the tongue ; this is especially so in the part of the tongue behind the conical genioglossus basalis, where the posteriormost of the dorsal fibres run to the tip of the tongue as divergent bundles. These fibres serve to reduce the width of the tongue and may be mistaken for transversalis linguae. The greater number of the fibres of the genioglossus dorsalis runs backward through the entire length of the tongue to appear in the middle and posterior parts as several separate but similar bundles. All the fibres serve to shorten the tongue and so function as longitudinalis linguae ; they should not, however, be mistaken for a separate and distinct intrinsic muscle.



TEXT-FIG. 16*b*.—Diagram to show the distribution of the hyoglossal and genioglossal fibres in an extended condition of the tongue.

———————— = Genioglossus basalis fibres.
—·· —·· —·· — = Genioglossus dorsalis fibres.
– – – – – – – – = Hyoglossus fibres.

As already described, the fan-shaped hyoglossal fibres in the tip of the tongue appear to be independent fibres which curve and radiate in the ventral region of the tongue. It may be pointed out that the tongue is not capable of much movement within the mouth. The front portion of the tongue may be raised by the contraction of the submentalis while the whole tongue may be raised or lowered with the buccal floor by the movements of the hyoid. The length of the tongue may be reduced by the contraction of the longitudinal fibres of the genioglossus dorsalis and the breadth by the contraction of the divergent fibres of the same muscle. In this manner the tongue accomplishes the necessary adjustments after the retraction of the tongue into the mouth, and during swallowing.

THE MECHANISM OF THE TONGUE.

The sudden relaxation of the hyoglossus from a state of tonus enables the tongue to be pushed forwards, and as the tongue is attached to the tip of the lower jaw by the genioglossus which in contracting

gives an upward and forward jerk, the tongue turns over with the mandible as its fulcrum, till the posterior end is flung forward bringing the dorsal sticky surface of the tongue down on the prey. This mechanism of the tongue is comparable to that of a lever of the third order. The rôle, however, of the various parts of the genioglossus differs. The genioglossus lateralis aids in drawing the buccal floor forwards. The genioglossus dorsalis helps in the projection of the tongue in two ways: (1) by contracting and thus reducing the length of the tongue and (2) by the contraction of the longitudinal fibres, especially of the two twisted cord-like bundles which radiate from the point of origin of the hyoglossal fibres in the middle of the tongue to its tip, the tongue is made somewhat rigid along its long axis, enabling it to take the push of the hyoglossus. The genioglossus basalis, however, aids more directly in the projection of the tongue. The fibres of this conical muscle bring about by their contraction the tilting upwards and frowards of the posterior blunt end of the muscle, to such an extent as to give the anterior end of the tongue a pivotal motion. There are thus two protractor linguae working together and not a single protractor as previous investigators have maintained. In the retraction of the tongue the hyoglossi play a more prominent part than the genioglossus, though the latter, by the relaxation of its fibres, may facilitate it. The hyoglossi thus play an active part both in the projection and the retraction of the tongue, as in the Chameleons.

It will be obvious from the descriptions of the hyoid and its muscles, that they cannot have a share in the mechanism of projection of the tongue, as Dugès seems to have maintained.

DISCUSSION.

The explanations of the mechanism of projection of the tongue given by previous investigators fall into two main classes: (1) Hartog's theory of lymph-pressure, (2) theories of muscular action.

Lymph-pressure theory. Hartog alone appears to have been responsible for this theory, though Holmes in his "Biology of the frog" has associated it with Gaupp also. That some body-fluid must be responsible for the extension of protrusible organs is an explanation which may appear plausible on the analogy of protrusible probosces and erectile organs in certain animals, but that such an explanation does not hold good in the case of the frog's tongue is apparent. The movements of the frog's tongue are quicker than those of the Chameleon because it is smaller and needs no preliminary adjustments, and the rapid whisking of the tongue cannot be due to the rushing in of a fluid and its running back almost at once. Hartog suggests that the lymph is squeezed into the tongue when it is to be projected. From the position of the tongue in the buccal cavity it is difficult to imagine how the tongue can be raised, rotated and thrown forwards by the mere rush of lymph into the tongue. The only possibility is that, the tongue will remain in a state of turgescence so long as the flow of lymph into the cavities of the tongue is maintained. Hartog proved his contention both by injecting air and some fluid into the mylohyoid to induce turgescence in the tongue and thus force it out of the mouth. "If

melted cocoa butter coloured with Carmine or alkanet is injected and the pressure kept up till the mass sets ", he says " it is found that the mass fills an enormous lymph sac (between the mylohyoid and the body of the hyoid) which extends through the median intermuscular fissure in the tongue, sending branches between the fan-shaped ramifications of the intrinsic muscles on the margin of the tongue and into its terminal dilatations " Hartog's evidence for the existence of the lymph spaces and the intermuscular fissure is based on his experiment only. The tongue is a fairly compact muscular organ with a few small lymph lacunae, actually within its substance, though there are two large sinus connected with it (*vide* figs. 8-12) while Hartog's theory presupposes the existence of large spaces and cavernous tissues in the tongue itself.

Theories of muscular action.—Fixsen, Kleine, Weidersheim, Ferdinand and Gaupp were convinced that the tongue is operated only by muscles. The theories of these authors may be grouped in two classes : (1) Theory of Fixsen, and (2) theories of other authors.

1. *Fixsen's theory.*—Fixsen made the suggestion that the genioglossus is concerned with the projection of the tongue and the hyoglossus in its retraction. This view was supported by Ecker and others who had no accurate knowledge of the anatomy of the genioglossus. It was confirmed by Gaupp who has described the important part " *Genioglossus pars basalis* " more accurately. As has been pointed out above the " genioglossus pars basalis " has a structure which is adapted to move its blunt hind end forwards and upwards. But it seems improbable that this muscle *alone* is responsible for the projection of the whole tongue, as Gaupp maintains. Accurate measurements of the length of this conical muscle show it to be a third of the total length of the tongue measured from its attachment to the base of the cleft tips. In specimens of *R. cyanophlyctis* the length of the genioglossus basalis was 2 mm. while that of the tongue was 6·4 mm. In *R. hexadactyla* the g. basalis was 7 mm. long and the tongue 22 mm. The ratio, in these cases, of the length of the conical muscle to the entire length of the tongue is even less than a third. Considering the relatively small size of the genioglossus basalis, it seems very improbable that it could vault over the tip of the lower jaw and take with it the whole tongue, nearly twice as long as itself, and the heavy and thick hyoglossi. A close examination of the course of the fibres of the genioglossus basalis shows that all the fibres of the muscle are not concerned in this forward and upward movement, which, therefore, cannot have the maximum force the entire muscle is capable of. As has been pointed out in the general account of the genioglossus basalis there are three classes of fibres, the vertical, the obliquely horizontal, and the horizontal. In longitudinal sections through the thickest part of this muscle these fibres occur in the ratio of 9 : 21 : 6. The second set of fibres most suited to give the muscle a forward and upward movement preponderate but do not form the entire muscle. Even if these fibres contract very forcibly the depth of the muscle is such that the posterior end may at the most be rotated through about 45°. In view of all this, it is difficult to resist the conclusion that Gaupp has by referring to it as the *protrusor linguae,* over-

emphasised the significance of the genioglossus basalis. Further Gaupp has not explained the function of g. dorsalis.

It is true, however, that the genioglossus as a whole has a share in the projection of the tongue. The genioglossus reduces the length of the tongue while increasing its rigidity. The genioglossus basalis gives a slight upward and forward jerk to the anterior end of the tongue. This facilitates the turning forward of the tongue when the relaxed hyoglossi also give it a push. Thus both the muscles are used in the forward movement of the tongue while the hyoglossus by its forcible contraction helps directly in retraction also. Inserted as the hyoglossal fibres are to the middle and the posterior parts of the tongue, farther from the front hinge than the genioglossus, they are very effective in working the tongue on the principle of the third order of levers.

2. *Theories of Kleine and Ferdinand.*—These are based on vague conceptions of the function of the hyoglossi which really have a double rôle. Kleine put forward the view that the powerful hyoglossi alone rotate the tongue forwards and that the genioglossi are responsible for its retraction. Ferdinand also appears to have ascribed a double rôle to the hyoglossus, namely, that of projection and retraction of the tongue. Although both these investigators connected the forward movement of the tongue with the action of the hyoglossi, they failed to note the degree of participation of the genioglossi in this movement. The hyoglossi by themselves would be inefficient as protrusor linguae; for, the tongue is a fleshy flabby structure, and if the front end of the tongue by which it is attached, sags down, all the force the hyoglossi can impart would be lost and the tongue would not have the precision of movement, directness of aim, and the rigid extension which make it so useful in capturing prey. The forward rotation of the tongue round the tip of the lower jaw along. thus bringing about the reversal, of surfaces necessary to bring the sticky dorsal surface downwards, the reduction of the length of the tongue necessary to enable it to pass out of and back into the mouth, and the degree of firmness necessary to take the force imparted by the hyoglossi, cannot be achieved without the genioglossi. It is significant, however, that both Kleine and Ferdinand considered the hyoglossi more responsible for the movements of the tongue than the genioglossus.

The mechanism of the projection of the frog's tongue is interesting from various points of view other than that of anatomy alone. It has been stated by Weidersheim and others that the intermaxillary glands at the front end of the buccal roof secrete mucous which is taken up by the tongue as it turns forward, so that its free end thus becomes extremely sticky. The assumption in such a statement is that the tongue is longer than the height of the gape of the mouth, and that consequently the free end of the tongue hits against the front part of the buccal roof. I have found the tongue to be actually longer than would be necessary to do this. In over thirty dead frogs the tongue was measured from the tip of the lower jaw to that of the upper jaw by a pair of callipers. Owing to postmortem rigidity, the jaws had to be forced open and the measurements were recorded when the jaws were at an angle of not less than 75° It is obvious that a muscular organ like the tongue would

be much shorter in the dead frog than in the living, and the jaws in the living frog would probably not be opened so wide as to make an angle of 75°, and, therefore, the measurements of the gape of the mouth were somewhat exaggerated. In spite of this, the ratio between the gape of the mouth and the length of the tongue was found to be 2·62 : 2·91. This shows that the tongue is so long that it cannot come out of the mouth without hitting the upper jaw. Though the free end of the tongue may come into contact with the secretion of the intermaxillary glands, it is very improbable that the tongue should rub against the sharp maxillary teeth or against the vomerine teeth, and in view of these facts, it may be concluded that though the tongue is long, it is actually reduced in length in order to come out through the mouth. In sections of the tongue the entire upper surface appears to be glandular, and the sticky secretion of mucous on the surface of the tongue is probably the product of these glands rather than that of the intermaxillary glands. It is noteworthy that in the two species of frog that I have studied, namely, *Rana hexadoctyla* and *R. cyanophlyctes* the animal uses its tongue only occasionally. From the few observations that I have been able to make these frogs make a dash for an insect which flies in the air close to its snout or swims in water and seize it between the jaws, rather than secure it with the tongue. When the prey is, however, settled on the ground the tongue is used as a predacious organ.

The exact picture of the whole process of tongue projection is difficult to portray because of its extreme rapidity. It is not surprising, therefore, to find that the popular sketches by different observers of the various stages of the process, differ so widely. A careful study of the anatomy of the tongue shows the impossibility of the anterior region of the tongue being swung forwards for the conical genioglossus basalis is attached anteriorly to the geniohyoideus and submentalis, and, however, much these muscles may aid in the movements of the tongue they will not permit the genioglossus to project forward as a whole.

If I am correct in my belief that the hyoglossus is kept contracted when the tongue is at rest, and is relaxed when projected, then this muscle belongs to the interesting group of muscles which are said to be always in a state of " Tonus " The " Tonus " muscles are known to occur in some invertebrates and the higher vertebrates but their occurrence in cold-blooded vertebrates has been observed by only a few investigators. The structure and working of the " Tonus " muscles are reserved for a separate treatment, and it is hoped that a thorough investigation of the innervation, histology and mechanism of action of these muscles will shed considerable light on the general physiological and physical problems connected with muscular tissues.

CONCLUSION.

1. The submaxillaris and the lymph spaces below the hyoid by their form and relation to other muscles and those of the tongue, are not adapted to participate in the projection of the tongue. Of the transverse muscles the submentalis may serve by its contraction to lift the

front part of the tongue; this facilitates the front part of the tongue turning forwards.

2. The hyoid muscles and the hyoid apparatus, unlike those of the Lacertilia, are adapted to enable the buccal cavity to perform various other movements rather than to participate in the tongue projection.

3. The tongue is pushed forward slightly by the relaxation of the contracted hyoglossi. Owing to the attachment of the tongue to the mandible by the genioglossi, and the upward and forward movement of the fibres of the genioglossus basalis this forward push is converted into a rotatory motion and the tongue turns forwards as if hinged at the front end.

4. The tongue consists of only two muscles—the hyoglossus and the genioglossus. The hyoglossus remains in a contracted or tonic state when the tongue is at rest, and relaxed when the tongue is pushed out of the mouth. The genioglossus is peculiarly modified; its dorsal part serves to reduce the length and breadth of the tongue while the ventral or basal part serves to give the anterior part of the tongue a forward pivotal movement.

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