THE MECHANISM OF THE THROAT-FAN IN A GROUND LIZARD, *SITANA PONTICERIANA* CUV.

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(Plate VII.)

INTRODUCTION.

Gular appendages have been described more often in arboreal lizards than in terrestrial ones. As early as 1826, Thomas Bell (2) has written about the structure of the dewlap in the Iguanid *Anolis* sp. In 1908, Gandolfi (6) worked out the muscles of the tongue of Agamids and Iguanids, but did not trace their function with reference to the hyoid. In 1919, von Geldern (7) explained the mechanism of the throat-fan in the " Florida Chameleon " (*Anolis carolinensis*), but concerned himself only with the hyoid muscles as he believed them to be the chief factors in it, though he suspected that " the muscles of the tongue probably play a part in the action " He does not mention or criticize Bell's naive explanation but refers to Chemin's account (4) of the gular appendage of *Calotes versicolor* which I have not been able to obtain. In view of the systematic significance of the throat musculature of lizards, a study of the muscles of the hyoid and of the tongue in their relation to the throat appendage of this animal should be of interest.

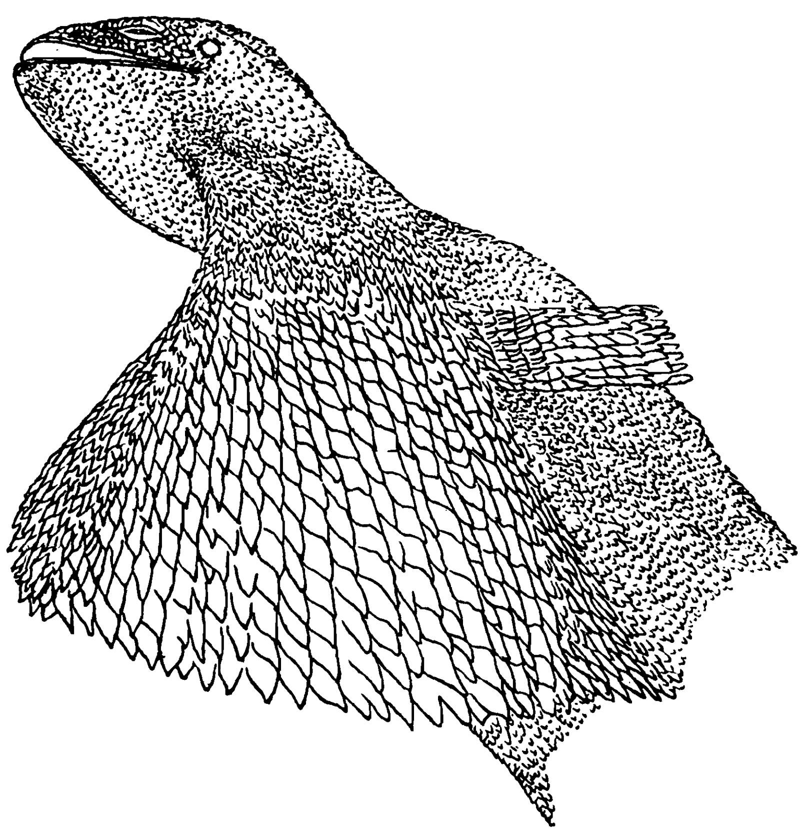
My thanks are due to Prof. S. G. Manavala Ramanujam of the Presidency College Madras, for his guidance and encouragement, for allowing me the use of his college library and for going through my manuscript and preparations ; to Dr. B. K. Das of the University College, Calcutta, for the formula of the picro-indigo-carmine stain ; to Rev. Gaebler and Prof. L. Narasu for translations of German references ; to the Principal of the American College, Madura, for permission to carry on this research in the college laboratory ; and, finally, to the Zoological Survey of India, Calcutta, for the loan of literature unavailable at Madras.

Sitana ponticeriana is purely a ground-lizard, having four toes, and is found all over India. It is more common in some districts than in others and frequents clumps of prickly herbs and cacti. As has been noted by Pycraft in his " Courtship of Animals " (1913), there is a strongly marked sexual dimorphism in this animal not only in size and build but also in the possession of a throat-fan in the male. Ordinarily the gular appendage in *Sitana* is folded fanwise under the breast but when the animal is excited, it is stretched out and again folded immediately—this process being repeated several times. In this process, the bright red and yellow colour-markings on the fan are alternately displayed and hidden. This action appears to depend not merely on the muscles of the hyoid but also involves the tongue muscles. These animals have been frequently observed in the field and no female was noticed by the author when the male was seen engaged in this display ; nor were several individuals seen at any time to be engaged in a collective display of their coloured gular folds. Even specimens caught and held in the hand displayed their fans.

The throat muscles of several of these lizards were dissected and sections were made of the tongues from formaline-preserved specimens. The sections were cut about 8μ thick, stained in alcoholic borax carmine, followed by picro-indigo-carmine, cleared in xylol and mounted in balsam.

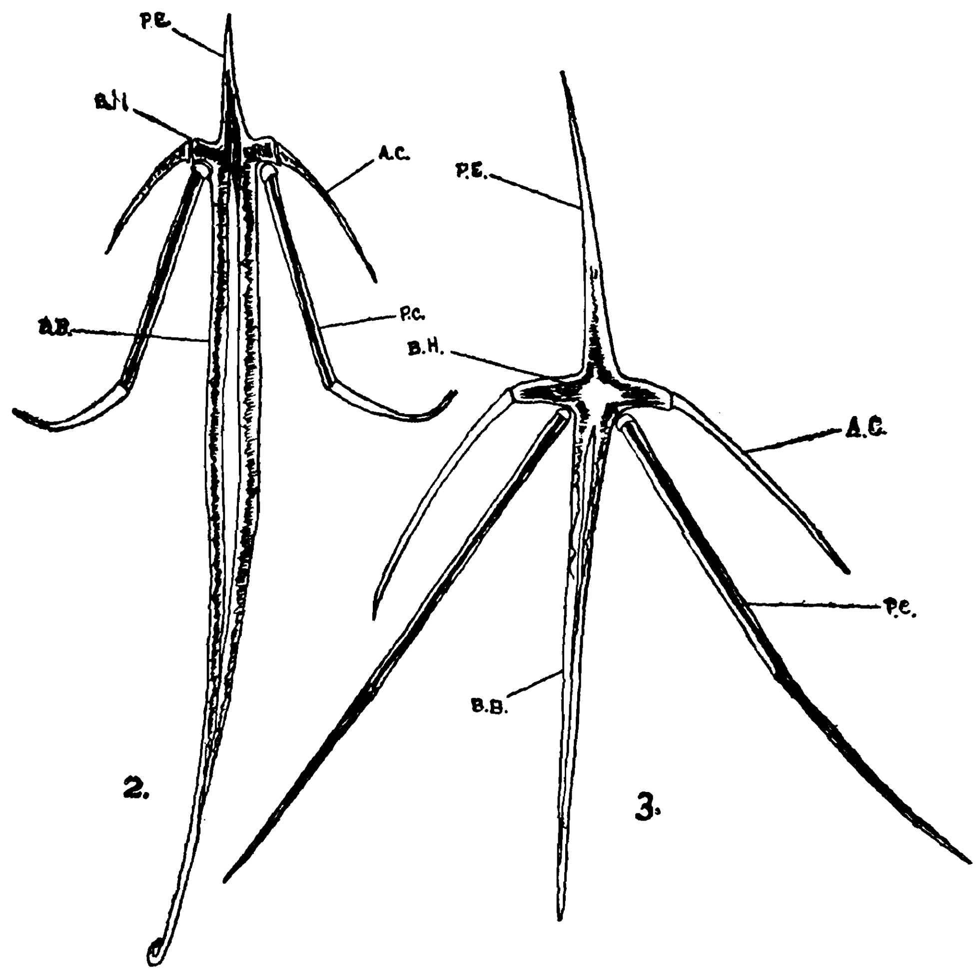
THE HYOID APPARATUS.

Text-figures 2 and 3 illustrate the hyoid apparatus of male and female *Sitana*. The difference between the hyoid apparatus of the two sexes will be obvious and are no doubt associated with the presence of the throat-fan in the male and its absence in the female. The hyoid of the male is nearly thrice as long and two-and-a-half times as large as that of the female. The wider basihyoid, the longer median process and the short weak basibranchials of the female are all unadapted to the function which they subserve in the male. It will, however, be noted that the hyoid apparatus of *Sitana* bears a general resemblance to that of *Anolis*. The basihyoid of *Sitana* is much more slender than that of *Anolis* and is cleft behind and continued into the basibranchial process which thus appears to be longer. The cleft of the basihyoid commences at



TEXT-FIG. 1.—Male *Sitana* with gular appendage stretched.

about its level of articulation with the posterior cornu. In front the basihyoid is continued into a short pointed median process called by Geldern " processus entoglossus ", or by Gandolfi " the tongue bone " The two pairs of appendicular processes—the two visceral arches of Beddard (1)—lie nearly parallel as in *Anolis*, but in the latter the anterior cornu nearly equals the posterior in size, as can be seen from Geldern's figures. There are also other minor features of difference as, for instance, the body of the basihyoid in *Sitana* is not so flat and broad as is figured for *Anolis,* but has its sides raised up so as to enclose a deep groove between them and consequently the anterior cornu of each side, which is attached to the raised-up side of the basihyoid, is more clearly dorsal to the basihyoid in *Sitana* than in *Anolis.* Beddard (1) describes a



TEXT-FIG. 2.—Hyoid apparatus of male *Sitana* (× 3). A.C. Anterior cornu; B.B. Basibranchial; B. H. Basihyoid; P.C. Posterior cornu; P.E. Processus entoglossus.

TEXT-FIG. 3.—Hyoid apparatus of female *Sitana* (× 7½). (Lettering as in fig. 2).

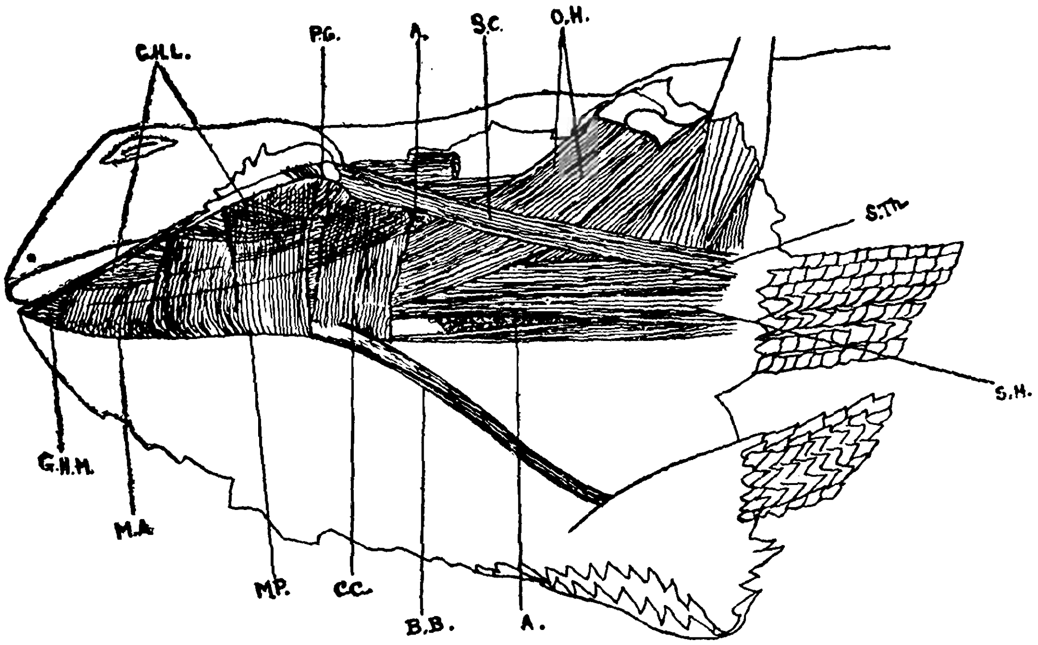
small piece in front of the anterior cornu in *Chlamydosaurus* and *Physignathus* and compares it to the thickened region of the hyoid of *Lacerta* figured by Parker, and suggests that if it were the remnant of an arch it could be homologised with the two hyoid arches of the Chelonia. In sections of the hyoid of *Sitana,* taken in front of the anterior cornu, a pair of very minute processes are seen. These are probably the reduced representatives of the thickenings figured by Parker for *Lacerta* rather than comparable to " the ossified segmented off bit " of Beddard in *Chlamydosaurus.*

MUSCLES OF THE HYOID.

1. *Sternohyoid* (S. H.) This, the anterior remnant of the rectus abdominis muscle of the lower vertebrate, has its origin on the sternum and

runs on either side of the basibranchial processes and ventral to the median portion of the sternothyroideus muscle. It is connected with the sternothyroideus by fascia, but it is inserted on to the most anterior part of the basibranchial processes, along with the omohyoid.

2. *Sternothyroideus* (S. Th.). This is a broad flat muscle springing from the sternum and being inserted all along the hind edge of the posterior cornu.

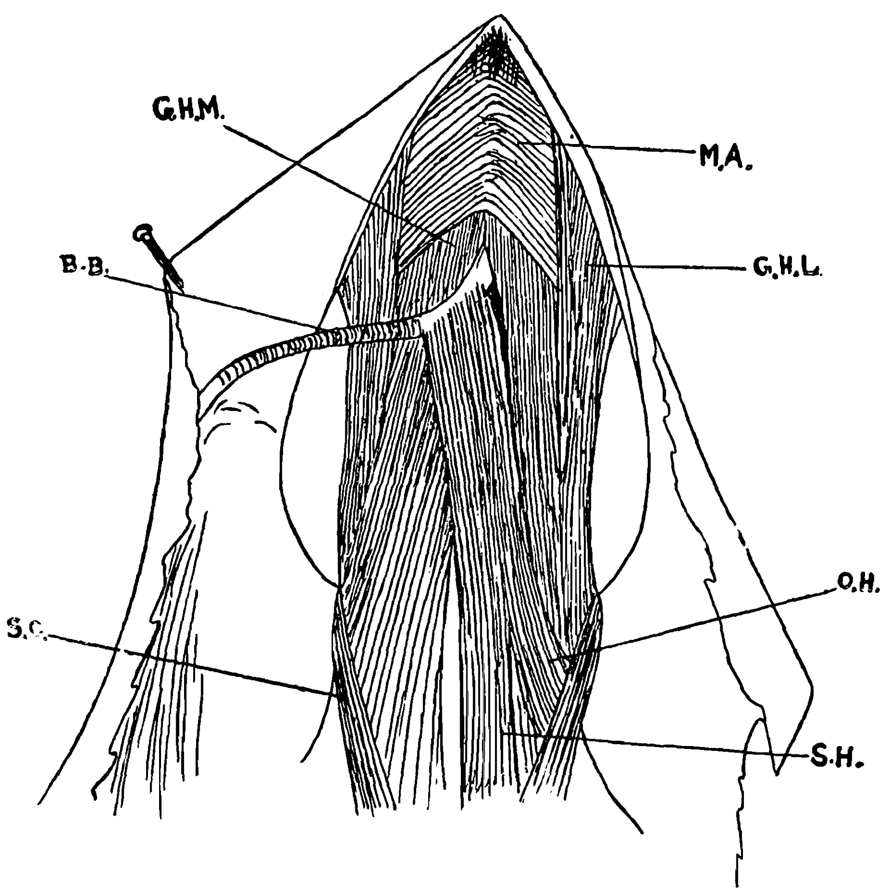


TEXT-FIG. 4.—Superficial muscles exposed (× 3). A. Adipose bodies; B.B. Basibranchial; C.C. Constrictor colli; G.H.L. Geniohyoideus, lateral bundle; G.H.M. Geniohyoideus, median bundle; M.A. Mylohyoideus anterior (M.A. profundus lies just below it); M.P. Mylohyoideus posterior; O.H. Omohyoideus; P.G. Pterygoideus; S.C. Sternocleidom; S.H. Sternohyoideus; S.Th. Sternothyroideus.

3. *The omohyoid* (O. H.) is a fairly thick flat double muscle. It starts from the anterior border of the scapula, runs obliquely in an anterior and ventral direction, parallel to the posterior cornu, to which it is attached along its outer border, and is finally attached along with the sternothyroideus to the basibranchial process.

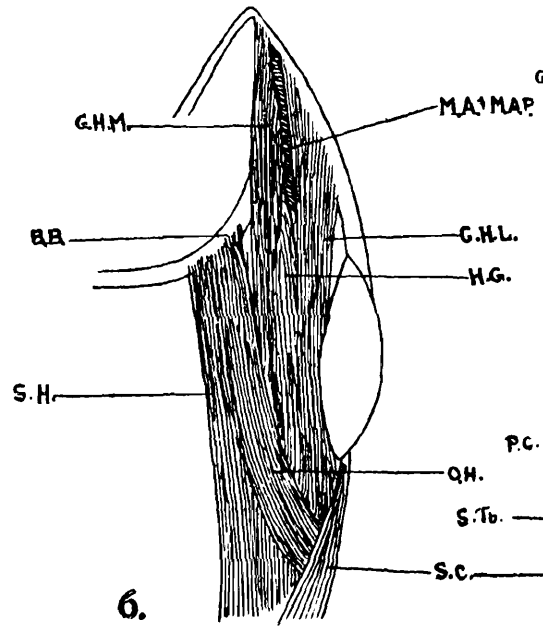
4. *The geniohyoideus* (G. H.) ties the hyoid anteriorly to the lower jaw. This in most lizards exists as many bundles which weave into the mylohyoid (*vide infra*) running transversely between the two rami of the mandible. There are four such divisions of the geniohyoideus in *Sitana*, which run between the corresponding portions of the mylohyoid. The most posterior is a short bundle, which, rising from the hind portion of the lower jaw and running dorsal to the last strip of the mylohyoideus, becomes attached to the curving end of the posterior cornu. This muscle has been regarded by Geldern and other earlier writers as a separate muscle and termed " Mandibulohyoid " and " Ceratomandibularis " It may, however, be pointed out that it is not unlike the two other muscles in front of it, which are similar to it in their course and function and which have been called geniohyoideus ; in this paper, therefore, the ' Mandibulohyoid ' of Geldern has been considered as a part of the geniohyoideus. The next bundle is very slender and lies under the first. The other two are fairly thick, the last and median being stoutest.

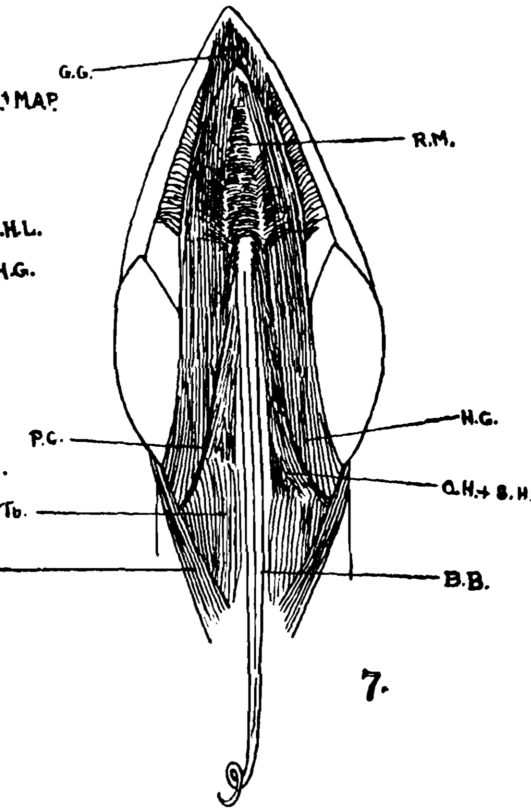
5. *The ceratohyoideus* (C. H.) is one of the factors of the hyoid mechanism and was held by Geldern to play the principal part in it. It is a short muscle which originates along the dorsal border of the posterior cornu and running forwards gets inserted on the anterior cornu. In its distal part the anterior cornu is almost surrounded by the fibres of this muscle. The latter becomes ligamentous anteriorly and is attached to the proximal part of the anterior cornu and the basihyoid.



TEXT-FIG. 5.—Dissection from ventral side. B.B. Basibranchial ; G.H.L. Geniohyoideus, lateral bundle ; G.H.M. Geniohyoideus, median bundle ; M.A. Mylohyoideus anterior ; O.H. Omohyoid ; S. C. Sternocleidom ; S.H. Sternohyoideus.

Function of the muscles. The sternothyroideus serves to draw the posterior cornu and with it the rest of the hyoid and the tongue backwards, *i.e.*, in a caudal direction. The sternohyoid and omohyoid muscles being inserted on the basibranchials serve to draw them backward and thus withdraw or fold the fan, after it has been stretched. The sternothyroideus and to a slight extent the omohyoids counteract the forward draw of the geniohyoideus and thus make the posterior cornu a fixed point about which the rest of the hyoid apparatus moves in the extension of the throat-fan and to which the muscles moving the tongue are attached. Further, the ceratohyoidei having their origin in the fixed posterior cornu and being inserted on the anterior cornu and basihyoid draw these latter structures towards its origin, *i.e.*, the fixed posterior cornu ; the basibranchial processes being continuous with the basihyoid are consequently swung forwards whenever the ceratohyoideus contracts. The whole hyoid apparatus illustrates the principle of the first order of levers; the basihyoid and its processus entoglossus forming the short power arm, the long basibranchial processes the weight arm, the fulcrum being provided about the articulation of the basihyoid with the posterior cornu.



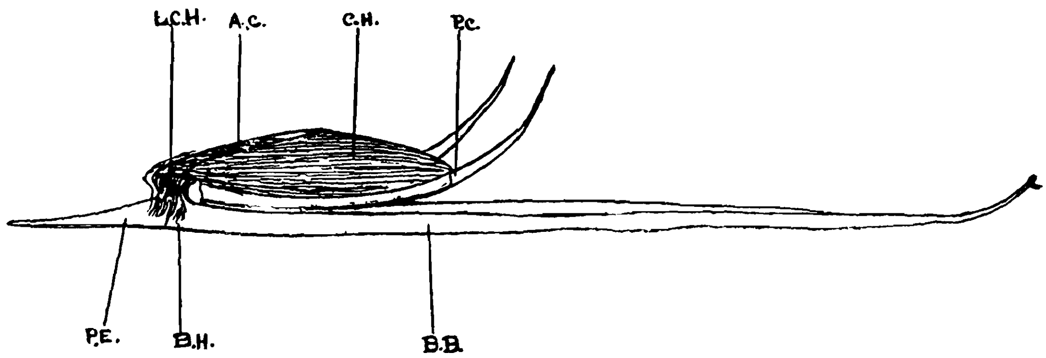


TEXT-FIG. 6.—View of deeper muscles. B.B. Basibranchial; G.H.L. Geniohyoideus, lateral bundle; G.H.M. Geniohyoideus, median bundle; H.G. Hyoglossus; M.A. Mylohyoideus anterior; O.H. Omohyoideus, ; S.C. Sternocleidom ; S.H. Sternohyoideus.

TEXT-FIG. 7.—View of still deeper muscles. B.B. Basibranchial; G.G. Genioglossus; H.G. Hyoglossus; O.H. and S.H. Omohyoid and sternohyoid cut; P.C. Posterior cornu; R.M. Ring muscle; S.C. Sternocleidom; S.Th. Sternothyroideus.

Constrictor colli (C. C.). Among the transverse muscles, the most superficial is the constrictor colli which Camp (3) figures in most lizards but it is only with difficulty made out in *Sitana.* Its fibres take their origin in the skin on the back of the neck, run down ventrally and extend as a sheet over the gorge, a little behind the mylohyoideus. This muscle aids in the process of swallowing.

The mylohyoideus (M. H.) is a transverse muscle running just beneath the skin on the ventral side of the head, between the rami of the mandible; two portions can be distinguished, namely, a mylohyoideus anterior and a mylohyoideus posterior. In *Sitana* the fibres of the mylohyoideus posterior run transversely across from one ramus of the mandible to the other. This sheet of muscle is laterally interrupted by the two lateral bundles of the geniohyoideus. The third lateral bundle of the geniohyoideus lies under the mylohyoideus posterior, and the median bundle runs below the mylohyoideus anterior (text-figure 4). The mylohyoideus anterior is contiguous with the posterior, as in some Agamids, and its fibres run obliquely forwards to meet in a median raphe. Just below the mylohyoideus anterior is another thin sheet of muscle which Camp has called mylohyoideus anterior profundus. Its fibres run obliquely backwards to meet in a median raphe. This muscle, though noticed



TEXT-FIG. 8.—Side view of hyoid apparatus. A.C. Anterior cornu ; B.B. Basibranchial ; B.H. Basihyoid ; C.H. Ceratohyoideus ; L.C.H. Ligamentous insertion of ceratohyoid ; P.C. Posterior cornu ; P.E. Processus entoglossus.

and described by Gandolfi, was left unnamed by him. Both Gandolfi and Camp found it to be present in Agamids and absent in the Iguanids. Camp has further found it in the Chameleons and is of opinion that it is additional evidence of the affinity between the two groups. The mylohyoideus, a breathing muscle in the lower vertebrates, not only aids breathing by pushing the tongue up and bringing the glottis into the nasopharyngeal groove but also assists swallowing.

THE MUSCLES OF THE TONGUE.

The hyoglossus (H. G.) is the most important of these. It is paired and fairly thick and takes its origin on the outer edge of the posterior cornu of each side, just dorsal to the attachments of the geniohyoideus and ventral to that of the ceratohyoideus. The hyoglossus of each side runs longitudinally, lying obliquely between the outer margin of the posterior cornu and the lateral margin of the tongue (*c.f.* pl. vii, figs. 1-4). The bony region of the posterior cornu first runs obliquely backwards and outwards and then takes a turn upward and outward in its distal part ; consequent on this, two regions can be distinguished, though feebly, in a cross section of the hyoglossus muscle—an inner and an outer. I shall first describe the course of the inner division.

The inner division of the hyoglossus runs horizontally parallel to the outer division. Towards the middle of the length of the tongue, the upper fibres of this inner division turn outwards and run obliquely over the outer division of the hyoglossus. Anteriorly more of these fibres assume this oblique course—some seven descend round the outer side of the outer division of the hyoglossus and become attached to its fascia, while some fibres get inserted into the side borders of the tongue, running across fibres of the genioglossus. In giving an account of the tongue muscles of Agamids other than *Sitana*, Gandolfi describes a " Ring Muskel um das Hyoglossus." I do not find such a muscle in *Sitana*. The muscle fibres which can be described as going round the outer hyoglossus are those of the inner division of the hyoglossus and as these rise from the posterior cornu, there is no muscle which has the same origin and course as Gandolfi describes for his " Ring Muskel um das Hyoglossus."

While the upper fibres of the inner division take this oblique course, the lower run close to the processus and become inserted on it. The set of upper fibres are separated from the lower by the " Ring muscle round the hyoid bone " (*vide infra*) passing outwards between them. This ring muscle encloses within it the lower part of the inner division of the hyoglossus, as well as the processus. The inner division of the hyoglossus thus has two insertions, one over and round the fascia of the outer division and another on the processus.

The outer division of the hyoglossus (*cf.* pl. vii, figs. 4 and 5) also has a part of its ventral fibres inserted on the processus along with the ventral portion of the inner division. Apart from this, the outer division runs forward to the extreme tip of the tongue and its fibres ascend into the dorsum of the tongue and in doing so cross the other muscles (*vide infra*) in a radiating manner. The function of the various divisions of the hyoglossi is obviously to draw in the tongue towards the posterior cornu. In such a retraction the fibres inserted on the processus will pull it back and thus swing open the throat-fan. The rest of the hyoglossus also will aid this, as in the front part of the tongue this muscle is bound to the processus by the other muscles which are attached to the fibrous extension from the " Ring muscle round the hyoid bone."

The Ring muscle (R. M.) (Gandolfi). The fibres of this muscle rise in the basihyoidal groove and run anteriorly for a very short distance. Where the basihyoid gives rise to the processus entoglossus, they take a lateral and downward course enveloping the processus on each side. The two lateral portions are separated in the middle line by a feebly developed " septum " formed by the fascial covering of the muscle. As the fibres of the ring muscle pass outwards and downwards round the processus, the lower part of the inner division of the hyoglossus becomes cut off on either side, as already described, and is thus enclosed between the ring muscle and the processus (*cf.* pl. vii, figs. 5 and 6). Immediately in front of the glottis this septum or fibrous plate takes a more dorsal position in the tongue (*cf.* pl. vii, figs. 6 and 7), the processus being still enclosed or surrounded by the ring muscle. This muscle has been distinguished by Gandolfi as the " Ring muskel um das Zungenbein ", but as no other " Ring muscle " is seen in *Sitana* I prefer to refer to this merely as the ring muscle. Towards the tip of the tongue this muscle passes into the connective tissue at the base of the front end of the tongue. As regards the function of this muscle in the tongue of Agamidae, Gandolfi conjectures that the contraction causes its fibres to thicken, which thus makes them exert a pressure all round ; that as the muscle is surrounded by almost inelastic connective tissue, it cannot expand ; and that as the motion towards the back is also impossible, the thickening of the muscle-fibres occurring during contraction manifests itself in a forward extension of the tongue.

This is improbable, for the muscles genioglossus and hyoglossus are responsible for the slight protrusion and retraction of the tongue that we can observe in Agamids. The course of the majority of the fibres is clearly circular and the muscle therefore must serve only to hold firmly on to the processus entoglossus and, because of its partial attachment to the basihyoid, it is able to fix the fibrous plate, so necessary for the play of the muscles which start from it.

The longitudinalis linguae (L. L.) is a muscle which takes its origin from the fibrous plate in front of the glottis and runs obliquely towards the surface of the tongue proceeding forwards to the tip below the papillae. By its contraction the tongue tip is curved or rolled up.

The transversalis linguae (T. L.) is a muscle whose fibres take their origin from the fibrous plate anterior to the glottis and pass laterally to the side borders of the tongue. This muscle serves to bring together the sides and makes the tongue narrower and thicker.

The genioglossus (G. G.) starts from the mandibular symphysis and its fibres get distributed to the tip and sides of the tongue as far back as the laryngeal region. The genioglossi of the two sides serve to draw the tongue forwards.

DISCUSSION.

Thomas Bell (1826) has described the extension of the throat-fan in *Anolis*, as the simple process of the hyoid being drawn back by the sternohyoid. According to him as the posterior tip of the basibranchial is fixed in the skin, it results in the basibranchials becoming arched on their lower side thrusting the skin fold downwards " like the ribs of an umbrella well opened " Unfortunately he did not study the musculature in detail and his theory though simple and attractive is untenable. Geldern, however, described the mechanism more correctly for the same animal. In *Sitana*, as in *Anolis*, the extension of the throat-fan is undoubtedly due to the levering action of the posterior part of the hyoid apparatus about a fixed fulcrum formed by the middle portion, the weight arm—the basibranchial processes—pushing the folded fan open. Geldern points out how in *Anolis* the ceratohyoideus by rising from the posterior cornu and being attached to the anterior cornu will pull these latter back and therefore the basihyoid also ; and though he did not work out the muscles of the tongue, believed that " they may play a small part in the action " The ceratohyoideus in *Sitana*, however, is slightly different. Its fibres run parallel to the anterior cornu from their origin of the posterior cornu and are inserted on the basihyoid and on the anterior cornu near its articulation with the former. This, it would be seen, gives a more effective pull upwards and backwards to the basihyoid.

Further, when the muscles of the tongue are worked out and studied in relation to those of the hyoid it is difficult to resist the conclusion that they, and especially the hyoglossus, take at least an equal share in the drawing back of the processus entoglossus and the basihyoid, and, therefore, in the extension of the fan. The hyoglossus besides being intimately connected with the basihyoid through other muscles—the Ring muscle for instance—has a ventral division of it inserted on the processus entoglossus and can retract the basihyoid to a considerable extent.

The folding of the fan is accomplished by the omohyoids and the sternothyroideus which pull the basibranchials upwards and backwards, aided by the relaxation of the other muscles, concerned in its protrusion. I find no trace of the muscle which Geldern found in *Anolis* and named myloceratoideus and which he describes as drawing the anterior cornu forwards during the retraction of the gular appendage.

I have been unable to obtain Chemin's article on the hyoid apparatus of *Calotes versicolor*, which Geldern criticises. In giving a resumé of Chemin's account of the hyoid mechanism, Geldern says, " the basihyoid is pulled ventrad by means of the sternohyoid (sternothyroideus ?) and the processus entoglossus is prevented from moving ventrad with the basihyoid by a band of tissue extending from one hyoglossus to the other and the basihyal would rotate as the fulcrum and swing the processus retrobasalis (basibranchials) forward " This view, however, cannot be supported by facts for the sternothyroidei, even in *Calotes*, are inserted on the posterior cornu as in most lizards and therefore the basihyoid cannot be pulled down except indirectly through its attachment with the posterior cornu and after all the sternothyroidei are more horizontal than oblique. Criticising Chemin's description Geldern says that " he cannot agree with the general statement that the mechanism in *Calotes* is essentially the same for all the Iguanidae. . . . Certainly it differs markedly in *Anolis*, where the processus entoglossus is not the arm of the lever and only acts as a hindrance to the production of the throat-fan " The processus entoglossus, though smaller in the male, must yet be regarded as playing a part in the mechanism of the throat-fan of *Sitana*, since it affords attachment for a part of the hyoglossus and forms with the basihyoid the power arm of the lever.

CONCLUSION.

1. The play of the gular appendage depends on the hyoid apparatus working as a lever through the muscles attached to it. Both the muscles of the hyoid and those of the tongue play a part. The basihyoid is pulled backwards not only by the ceratohyoideus but also by the hyoglossus through its attachment to the basihyoid process.

2. In its main features the mechanism of the dewlap in *Sitana* no doubt resembles that of the Iguanid *Anolis carolinensis*, described by Geldern. But this author paid no attention to the tongue muscles though he realised that they may play a part. In *Sitana*, undoubtedly, they do play an important part.

3. The similarity of the hyoid apparatus and the part it plays in the extention of the throat-fans in Lacertila need not necessarily be of systematic importance. Similarity of structure may have been possibly attained by similarity of functions. For one thing, the hyoid apparatus differs widely even among the Agamidae as, for instance, between *Calotes*, *Draco*, *Physignathus*, *Chlamydosaurus*, etc. Therefore, the similarity of this organ that exists in *Sitana*, an Agamid, and *Anolis*, an Iguanid, is not surprising.

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