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HEAD MUSCLES OF SALAMANDERS

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The adults of eight and the larvae of six families were studied and in these the majority of the world's genera were involved in the observations of the muscles.

It was found that there was a greater uniformity in the structures than the terminology employed in the past. As far as possible the classification of Francis '34, is followed with a more critical study of the nervous system and nerve distribution left for another time.

The muscles of the head and particularly of the throat have been the subjects of numerous, sometimes conflicting accounts. No other part of the body has been more difficult to understand and describe.

Many early observations before 1850 give information about the head muscles, such as Funk 1827, Carus 1828, Dugès 1834. Rusconi in 1854, was about the first to discuss the changes of muscles during metamorphosis. Later works are those of Wilder, 1892-6, Goppert, 1894-8 and Drüner, 1901-4. Other very valuable contributions were by Luther, 1914, Edgeworth, 1920, Smith, 1920, and more recently those of Eaton, '33-36, Francis '34 and Piatt '35-40, as well as a number of other writings dealing with special topics connected with amphibian muscles.

M. levator mandibulae anterior, Edgeworth '20, Francis '34, Eaton '36; temporalis, Funk 1827, Cuvier 1835, Fischer 1843, Lubosch 1914; pterygoidien, Rusconi 1854; pseudo-temporalis, Luther 1914. This is a triangular muscle from the frontal and perhaps parietal bones, inserted on the lower jaw. It is supplied by branches of the fifth cranial nerve. It helps to close the mouth.

M. levator posterior, Edgeworth '20, Francis '34, Eaton '36; cranio-mandibularis (part), Lubosch 1914; aductor mandibulae posterior, Luther 1914. It is from the frontal and the parietal bones to be inserted in the lower jaw back of the eye. It is supplied by a branch of the 5th cranial nerve. It aids in closing the mouth.

M. levator mandibulae profundus, Eaton '36; M; levator mandibulae (deep portion) Edgeworth '20; frontales, Funk 1827;

pterygoideus, Cuvier 1835, Fischer 1843, Owen 1866, Drüner 1901, Lubosch 1914, Luther 1914; pterygoidien, Rusconi 1854; ptergo-maxillaris, Hoffman 1873-4. This muscle under the superficial muscles mentioned above in many cases seems a part of them. It is variable in position and distribution among salamanders. It is supplied by branches of the fifth cranial nerve. It aids in closing the mouth.

Pterygoideus, Eaton '36, Lubosch '14 and others. This small muscle covered with the larger more superficial ones is from the pterygoid region of the skull to the lower jaw. It is supplied by the fifth cranial nerve. It helps close the mouth.

All these levator muscles just mentioned are really part of one system and distinctions between them are not always sharp. They vary in different forms.

M. levator mandibulae externus, Edgeworth, '20, Francis '34, Eaton '36; masseter, Funk 1827, v. Siebold 1828, Fischer 1843, Rusconi 1854, Schmidt, Goddard, van de Hoeven 1864, Owen 1899, Mivart 1869, v. Pessen and Rabinowicz 1891, Drüner 1901, Coghill 1901-6, Osawa 1902; temporal, Cuvier 1835; pre-tympano-maxillaris, Hoffman 1873-8; mandibularis externus, Lubosch 1914; aductor mandibulae externus, Luther 1914. This has its origin from the anterio-lateral edge of the squamosal and the anterior wall of the otic capsule. It is inserted on the posterior end of the dentary and lateral face of the coronoid process of the pre-articular region and in some cases to the skin of the corner of the mouth. It is served by the fifth cranial nerve. It aids in closing the mouth.

M. depressor mandibulae, Edgeworth '20, Francis '34; depressor maxillae inferioris, v. Seibold 1828; temporo-angulare, Duges 1834; digastricus, Fischer 1843; Stannius 1854-6, Osawa 1902; digastrique, Cuvier 1855, Rusconi 1854; occipito-mandibularis s. digastricus mandibulae, Owen 1866, digastris, Mivart 1869; digastric et depressor mandibulae, Humphrey 1872; cephalo-dorso-maxillaris s. digastricus maxillae, Hoffman 1873-8; c2md, Ruge 1897; cephalo-dorso-mandibularis, Drüner 1901.

This is a large muscle arising from the posterior edge of the squamosal and ear capsule and anterior portion of the fascia cephalo-dorsalis of Drüner and inserted on the end of the lower jaw below. It is supplied by a branch of the 7th nerve. It opens the mouth.

It is interesting to note that in many cases the closing muscles of the jaw are larger in total bulk than the opening ones.

In some larvae and adults, a division of the depressor mandibulae runs back to the ceratobranchial and is sometimes called ceratomandibularis. Such a division is found in Proteus, Necturus, Typhlomolge, Amphiuma. In Siren this is attached to the tip of

the ceratohyal. This connection to the ceratohyal I found in the larvae of Ambystoma, Dicamptodon and Rhyocotriton. It may occur in others, but I have not noticed it.

THROAT MUSCLES
SUPERFICIAL LAYER

M. INTERMANDIBULARIS, Edgeworth '20, Francis '34; mylohyoideus, v. Siebold, Carus 1828, Stannius 1854, Owen 1866, Coghill 1901-6; mylohyoideus et interhyoideus, Ealter 1887; mylohyoideus et interhyoideus posterior, Funk 1827.

This is a sheet of muscle across the floor of the mouth just under the skin. In the larva it consists of a small anterior, M. intermandibularis anterior as the M. i. posterior. Kesteven '41, prefers the name submentalis for the anterior portion, which seems better.

M. INTERMANDIBULARIS POSTERIOR, Drüner 1901, Luther 1914, Edgeworth 1920, Francis '34 and others. It arises from the inner or mesal edge of each side of the mandible in its middle portion. The fibers extend towards the middle line from each side to join a broad or narrower aponeurosis in the center. It is supplied by the N. mandibularis of the fifth cranial nerve.

It elevates the throat in breathing.

M.INTERHYOIDEUS, Edgeworth 1920, Francis '34, Piatt '35; M. constrictor pharyngis internus, v. Siebold 1828; mylohyoidien (middle part) Rusconi 1854; C2hv, Ruge '97; inter-os-quadrata, Drüner '01.

In adult Hynobiidae and Salamandridae this has been described as two muscles. Piatt '40, suggests that the more anterior should be known as the sub-hyoideus and the posterior the inter-os-quadrate, but in other families it may be called interhyoideus. So far as I have seen there are not two muscles in all Hynobiidae or Salamandridae and there may be two in other groups. Also the use of the name sub-hyoideus would merely add to the already great confusion as a well defined muscle in another place has been given this name.

This interhyoideus arises from the postero-mesal edge of the quadrate to spread out broadly over the caudal part of the mouth floor. Sometimes by means of fibers or a rather separate division it may reach quite cephalad under the fibers of the M. intermandibularis posterior. It is supplied by branches of the R. jugularis of the 7th cranial nerve.

It constricts the hyobranchial skeleton and the back part of the mouth, assisting in respiration and swallowing.

M. INTERHYOIDEUS POSTERIOR, Edgeworth '20, Francis '34; constrictor pharyngis externus, v. Siebold '28; myo-hyoideus (posterior part) Rusconi 1854; mylosternoideus, Walter 1887; C2vd, Ruge '97; quadrato-pectoralism Drüner 1901.

In the Plethodontidae in the adult two muscles may arise from this, or at least occupy this region; the quadrato-pectoralis whose origin may run over or near the angle of the jaw and a muscle said to be distinctive of this family, the gularis as recognized by Smith '20. The name interhyoideus inferior may be considered the right one in all groups but Plethodontidae and here it may be said to have a quadrato-pectoralis portion which is nearer the angle of the jaw and the gularis which takes origin farther back from fascia on the side of the neck. The insertion is into the connective tissue region of the gular fold. It is supplied by the gular branch of the 7th cranial nerve.

The function is to constrict the pharynx, aid in respiration or depress or tip the head to one side or the other.

M. genio-glossus, v. Siebold 1828, Fischer 1843, Mivart 1869, Drüner 1901, Francis '34 and others.

This muscle at the mandibular symphsis takes origin from this area and is inserted into the tongue. It may have median and lateral portions. It may show from the surface before the other muscles are removed or be represented by a few deep fibers or be entirely lacking. Free tongued forms do not have it as in some of the Plethodontidae, while others in this group may have it poorly developed. In some families it is found in some species but not in others. It is supplied by branches of the spinal nerve which is sometimes called the hypoglossus.

If the tongue is at rest, the muscle may draw it to the front of the mouth and arch its surface, but if the tongue is fully extended the contraction of the muscle tends to retract it into the mouth. When the tongue is drawn towards the front of the mouth the muscle may press out a sticky mucous from the tongue for the purpose of capturing insects or other live food.

DEEP MUSCLES

M. genio-glossus sometimes seen near the surface is frequently either absent or deeply buried under other muscles.

M. genio-hyoideus, Carus 1828, Fischer 1843, Mivart 1869, Osawa 1902, Francis '34; rectus linguialis, Funk 1827; levator maxillae inferioris s. geniothyroideus, von Siebold 1828, Stannius 1854-6; levator maxillae inferioris longus, Schmidt, Goddard, van de Hoven 1864; genio-branchial, Humphrey 1872; maxillo-hyoideus, Hoffman 1873-4; genio-hyoideus s. rectus superficialis hypobranchialis anterior, Drüner 1901.

This is a pair of strong longitudinal muscles arising from the inner edge of the lower jaw either side of the middle line and inserted for the most part into the os triangulare and to some extent to the tissue near or in the central region when there is no os triangulare. The hypoglossal nerve supplies fine branches to these muscles.

The action of these muscles is to depress the jaw, or whole head or pull forward the os triangulare and the heart region.

M. genio-hyoideus tertitus, was described by Drüner in 1901 as an abnormality, where a few lateral fibers pass from the jaw to the posterior end of the ceratohyal. A similar condition has been described where fibers pass from the posterior cornu of the hyoid to the anterior part of the lower jaw, according to Francis '34. He suggests also that this may represent the M. genio-hyoideus lateralis described by Smith '20, in Eurecea.

The muscles under the name of M. genio-hyoideus tertius have the same nerve supply and same general function as M. genio-hyoideus.

In a number of cases fibers run from the mandible not far from the middle line, under the M. genio-hyoideus and end at or near the upper end of the ceratohyal. This may or may not be the muscle given the name M. genio-hyoideus tertius. To me it seems a slip from M. genio-hyoideus of Smith.

M. subhyoideus, Drüner, '04, Francis '34; ceratoglossi externi, Funk '27; os hyoides protrahens, Carus 1828; geiohyoideus lateralis, Drüner 1901; genio-hyoideus lateralis, of Smith.

Lateral to the genio-hyoideus on each side is this variable muscle about which there is some confusion with the subhyoideus or genio-hyoideus lateralis.

Although a muscle in this position, lateral to the M. genio-hyoideus is found in salamanders generally; its form and connections are variable and different perhaps also as to homology and origin and should perhaps have the name applied to it depend upon the group to which the animal possessing it belongs.

In general it arises from the posterior end of the cerato-hyal which it may partly enclose and run slightly diagonally forward to be inserted on the dorsal side of the aponeurosis of the M. intermandibularis. Drüner '01, describes a slip from this muscle to the lower jaw; in another of the Hynobiidae, Salamandrella, I found fibers running in that direction but not connecting with the jaw. In Hynobiidae and Salamandridae this muscle is supplied by the jugular branch of the 7th cranial nerve. It seems to be derived from the interhyoideus of the larva as its nerve supply might indicate. Smith '20, in a plethodont Eurecea describes the development of a muscle here called M. genio-hyoideus lateralis, derived not from the interhyoideus, but from the M. genio-hyoideus, whose nerve supply is not from the 7th cranial, but from the first spinal. Piatt '40, has investigated the nerves of this muscle in a number of the plethodontidae and finds the first spinal nerve is concerned in every case. According to Piatt then, the muscle in Salamandridae and Hynobiidae should be called subhyoideus and the term genio-hyoideus lateralis should be restricted to Plethodontidae.

The genio-glossus lateralis of Ambystomidae is said by Piatt to be homologous with the genio-hyoideus lateralis of Plethodontidae, but its relations are different, so the name genio-hyoideus lateralis need not be used.

M. subarcualis rectus, Edgeworth '20; cerato-glossi-interni, Funk 1827; ceratoglossus, v. Siebold 1828; pre-stylo-peribranchial, Dugès 1834; cerato-hyoideus-internus, Fischer 1843, Mivart 1869, Hoffman 1873-8, Walter 1887, Drüner 1901; protacteur de la corne hyoidienne posterieure, Rusconi 1854; cerato-hyoideus, Stannius; cerato-hyoideus externus, Osawa 1902.

This arises from the posterior end of the first cerato-branchial cartilage, enclosing it in a muscular sheath. The fibers are inserted into the ventro-anterior border of the anterior end of the ceratohyal, in this way connecting extreme ends of the two cartilages. It is supplied by branches of the 9th and 10th cranial nerves.

Its contraction advances the branchial arches and associated parts connected with the copula in the extrusion of the tongue. It is a characteristic muscle in adults that have passed the larval period and is quite similar in appearance and position in Hynobiidae, Salamandridae, Ambystomidae and Plethodontidae.

M. sterno-hyoideus, Smith '20; rectus v. Siebold 1828; sterno-hyoideus superficialis, Furbinger 1873; rectus superficialis hypobranchialis s. sterno-hyoideus, Drüner 1901; with rectus abdominis superficialis or abdominus musculus rectus, Carus 1828; rectus cervicus superficialis, Edgeworth '20. A thin layer of muscle arises from the sternum and fascia near. This passes forward dorsally to the coracoids and ventral to the pericardium as a broad sheet with several insertions such as the following: at the junction of hypobranchial 1 and copula; on the tendon of the profondus portion of the muscle; more ventrally and mesially to the triangulare. Part of it is attached to the pericardium and sometimes fibers go on beyond the os triangulare to be inserted into the hypobranchial skeleton ventro-medially.

It is supplied by branches of the first three spinal nerves.

Its central fibers support the M. genio-hyoideus and its lateral fibers assist the abdomino-hyoideus in retracting the tongue.

M. abdomino-hyoideus, Smtih '20, Piatt '40; rectus cervicus profundus, Edgeworth '20, Francis '37; hebosteoglossus, v. Siebold 1828; sterno-hyoideus profundus, Furbinger 1873; rectus hypobranchus profundus s. abdomino-hyoideus, Drurer '01; with rectus abdominus profundus, M. epischio-hyoideus, Carus 1828; rectus cervicus profundus, Edgeworth '20, Francis '34.

This muscle forms the direct forward continuation of the M. rectus abdominus profundus. It passes forward about the lateral parts of the pericardium, mesial to the thyroid gland and between the hypobranchial cartilages 1 and 2, to be inserted on the dorsal side of the copula by a tendon. It may have an outer rather distinct slip which may be partly inserted into the first and second ceratobranchials as it passes between them. It is supplied by branches from the upper spinal nerves, or from the first, second and third.

It may retract the tongue or depress the head.

It is convenient to discuss some variations in the last two muscles at this time.

In *Salamandrella* of Hynobiidae, the sterno-hyoideus for the most part ends cephalad of the heart towards the middle line about the level of the os triangulare with a slip forward to the hyobranchial region. The abdomino-hyoid sends a mediam slip to the region of the os triangulare and another to the median portion of the hyobranchial apparatus while much of its substance passes between the first and second epibranchial to end on the dorsal side of the copula. In *Ambystoma maculata,* the broad sterno-abdominalis ends for the most part in the middle line on the os triangulare. The abdomino-hyoid sends a small slip to the os triangulare with little indication of terminations in the middle line until it terminates on the dorsal side of the copula. In *Rhyocotriton,* the abdomino-hyoid sends a small slip to the caudal surface of the os triangulare and several slender strands to the ventral side of the basibranchial and hyoid apparatus, but as in many others, most of its fibers end dorsally on the copula. In *Salamandra,* most of the abdomino-hyoid fibers end dorsally on the copula, but a few cross over to end ventrally and a few terminate on the os triangulare. The sterno-abdominalis broadens out to end largely in the region of the pericardium. In *Diemictylus viridescens,* sterno-hyoid fibers end in large numbers towards the middle line on the hyobranchial apparatus. The abdomino-hyoid with little indication of fibers on the os triangulare has a conspicuous small bundle which comes from underneath to end in the middle line of the copula. In *Cynops pyrogaster* the condition is much the same. In *Taricha torosa* there is a lateral slip to the os triangulare but none to the central ventral surface of the basibranchial. In *Plethodon glutinosus,* as the two muscles pass to the os triangulare, a lateral slip is sent to the latter and a small one to the median dorsal surface of the copula. The central part of the sterno-hyoid is broad. *Aneides* and *Pseudotriton* are similar with the median part of the sterno-hyoid broad from side to side.

M. ceratohyoideus externus, Piatt '40, Easton '37.

This is often a large muscle from the ventral and basal end of the ceratobranchial. It is supplied by branches of the 9th and 10th cranial nerves. It moves the ceratobranchials and the ceratohyals. It is found in some gilled adults and in the larval forms of all groups. It is lost in adults without gills.

The other muscle often considered with it, is the subarcualis rectus 1, also found in gilled adults, larvae and adults without gills is often more prominent in the adult, where it replaces the M. ceratohyoideus externus. It is convenient to call this M. ceratohyoideus internus in comparison with the externus.

M. pectori-scapularis, Edgeworth 1920, Francis 1937; omohyoideus, Meckel 1869, Humphry 1872, Hoffman 1873-4, Ossava 1902; scapulo-post-hyoiden, Dugès 1834; pectori-scapularis internis, Furbinger 1873; pectori-scapularis s. omohyoideus, Walter 1877, Drürer 1901.

This is a small muscle which arises from the mesial surface of the ventral end of the scapula and is inserted at the lateral edge of the superficial part of the sterno-abdominalis. It serves to strengthen or brace the sterno-abdominalis.

M. hyoglossus, Fischer 1843, Drüner '01, Smith '20, Francis '37, Piatt '40. This small muscle has fibers from the dorsal side of the forward end of the copula into the tongue substance. It is supplied by branches of the first spinal nerve. It may compress the tongue, or change its shape slightly.

M. suprapendicularis, Smith '20, Piatt '40.

It arises from the medial border of the ceratohyal on each side. It is probably supplied by the first spinal nerve. It helps to force the tongue forward on contraction. It has been described especially in free-tongued forms among the Plethodontidae but is also found in some others.

MUSCLES ASSOCIATED WITH THE GILLS

M. ceratohyoideus externus and internus, already mentioned.

Subarcualis recti muscles, Edgeworth, 1920, Eaton '36, Piatt '40. These are usually two in number, the longest connects the first and last branchial arches and the second usually joins the last two arches. They are probably supplied by branches of the 9th and 10th cranial nerves. By their contraction the gill arches are brought together.

M. subarcualis obliqui, Edgeworth, 1920, Eaton '36, Piatt '40. These usually run from their origin on median muscles to be attached to the second or third arches or the last two arches. Probably supplied by the 9th and 10th cranial nerves. They help pull the arches forward.

M. protractor arcus ultimi, Hoffman 1878, Wilder 1891. In Siren and Proteus, from the base of the last ceratobranchial to the posterior side of the hypobranchial.

M. levatores arcuum, Fischer 1864; levatorarcus branchialis 1-4, Emerson '05, Eaton '36. These muscles vary in different larvae and adults in number and position. L.A.1 may arise from the posterior side of the squamosal and others up to 4 or 5 may form a fan-shaped group of muscles and fascia on the side of the body to be inserted at the base of the gill region. Probably supplied by branches of the 10th cranial nerve. They may pull the whole gill region closer to the head.

M. omo-arcualis, Piatt '36; prococoraco-branchialis, Wilder '91. This arises from the anterior angle between scapula and procoracoid and runs forward to be inserted on the last gill arch near the gill. It has been found in Proteidae, Sirenidae and the larvae of Hynobiidae. I have found it in Proteus, Necturus, Siren and Pseudobranchus adults.

Gill muscles (following Piatt '38)

There are two sets of delicate intrinsic gill muscles. The dorsal are the levatores branchiarum and the ventral the depressor branchiarum.

MUSCLE CHANGES FROM GILLED LARVAE TO ADULTS THAT LACK GILLS

The intermandibularis anterior, or as Kesteven prefers it, the submentalis in some salamanders disappears in the adult, especially in the Hynobiidae, Salamandridae, Ambystomidae and Plethodontidae.

In the larva the large ceratohyoideus is lost when the adult stage is reached and in many cases the smaller internus becomes larger in many cases.

The thoracico-hyoideus of the larva transforms into the abdomino-hyoideus and the sterno-hyoideus of the adult. In the larva the muscle has a proliferation and an anterior growth of fibers which brings the origin on the dorsal surface of the first basibranchial to make the beginning of the abdomino-hyoideus. There is also a breaking down of the median portion of the thoracico-hyoideus and a differentiation of the ventral slip of the larval muscle into the sterno-hyoideus. (partly after Smith '20).

In some Plethodontidae there may be proliferation of the anterior end of the genio-hyoideus laterally, but this does not always last after transformation.

The subarcualis rectus muscles disappear in the adult when the gill arches are lost. Possibly some may be transformed into pharyngeal muscles.

The subarcualis obliqui of the larvae disappear in land stages. The levator archum muscles disappear as such in the adult to become dorsal pharyngeal muscles or contribute to them.

In several families, the so-called interhyoideus posterior or quadrato-pectoralis becomes two muscles, Piatt '40, considers those in Hynobiidae and Salamandridae to be sub-hyoides in front and the posterior portion the inter-os-quadrata. In Plethodontidae the two parts in the adult are a more ventral part of the quadrato-pectoralis and the gularis with fascia connections dorsally. These two differ in degree and form in various genera and species.

A cerato-mandibular division of the depressor mandibulae found in some larvae disappears in the adult.

Muscles found in the adult, gill lacking forms are as follow:

In some with attached tongues the genio-glossal may occur. In some Plethodontidae which have a small lingual cartilage such as the genera *Eurycea, Manculus, Pseudotriton* and *Gyrinophilus,* there is the small hypoglossus muscle.

In most free tongued Plethodontidae the surpapendicularis runs across the border of the tongue between the ceratohyals.

LARYNGEAL MUSCLES

M. dilator laryngeus, Edgeworth 1920, Francis 1937; dilator aditus laryngis, Henle 1839; dorso-laryngeus et dorso-trachealis, Fischer 1843, Wilder 1892-6; dorso-pharyngeus of dorso-laryngeus und dorso-trachealis, von Goppert 1894-8; dorso-laryngeus, Drüner 1901, Osawa 1902.

From the dorsal fascia, inserted on the lateral cartilage of the larynx. Supplied by branches of the 10th cranial nerve.

M. laryngeus dorsalis et ventralis, Edgeworth '20, Eaton '36 and others. Eaton recognizes a muscle each side of the larynx from the arytenoid cartilages with attachments to the ventral end of the last muscle. They dialate the larynx.

M. constrictor laryngis, Edgeworth '20, Eaton '36, Francis '37; constrictor aditus laryngis, Henle 1839, Fischer 1843, Drüner 1901; Ring of periartenoideus dorsalis, Wilder 92-6; spincter laryngis, Goppert 1894-8. This is a ring of muscle about the larynx ventral to the glottis. It receives branches from the 10th cranial nerve. It closes or restricts the cavity of the larynx.

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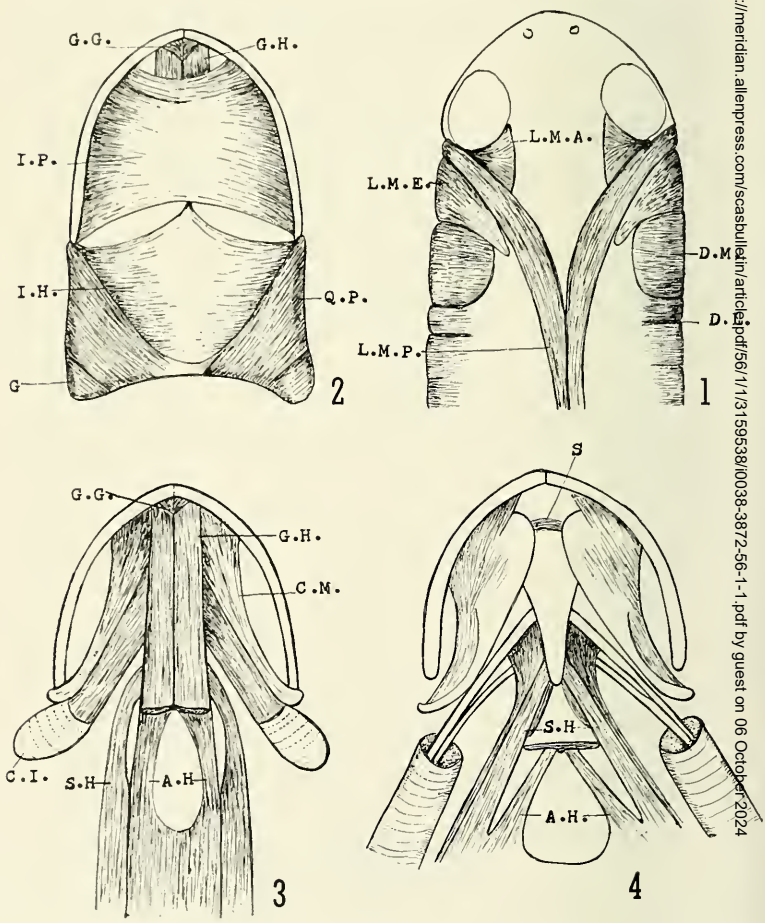

PLATE 1

Diagrams of the head muscles of adult salamanders. 1. From above. 2. From below. 3. Deeper layer from below. 4. Still deeper layer from below.

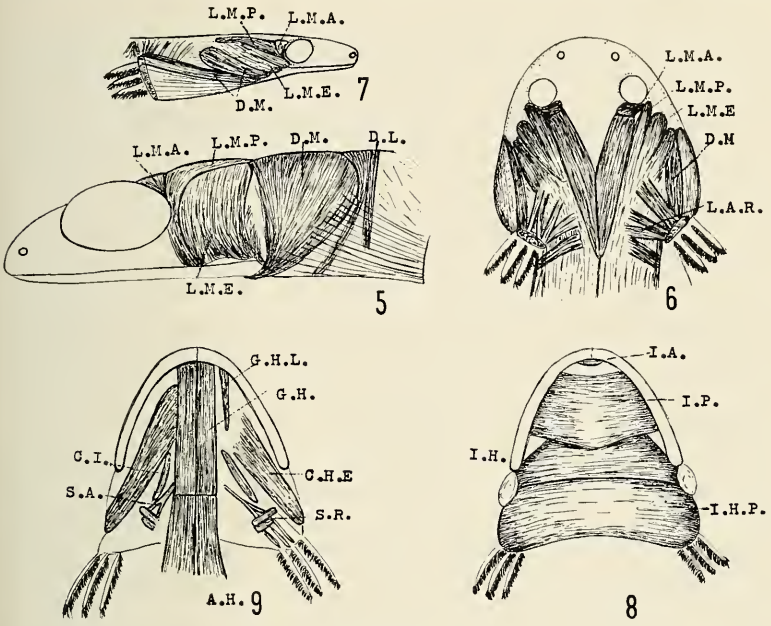

PLATE 2

5. Adult from the side. 6. Larva from above. 7. Larva from the side. 8. Larva from below, superficial muscles. 9. Larva from below, deeper muscles.

INDEX TO FIGURES

A.H., Abdomino-hyoides; C.H.E., Ceratohyoides externus; C.I., Ceratohyoides internus; C.M., Ceratomandibularis; D.L., Dialator laryngis; D.M., Depressor mandibulae; G., Gularis; G.G., Genioglossus; G.H., Geniohyoideus; G.H.L., Geniohyoideus lateralis; I.A., Intermandibularis anterior or submentalis; I.H., Interhyoideus; I.H.P., Interhyoideus posterior; L.A.R., Levatores arcum branchiarum; L.M.A., Levator mandibulae anterior; L.M.E., Levator mandibulae externa; L.M.P., Levator mandibulae posterior; Q.P., Quadrato-pectoralis; S., Suprapendicularis; S.A., Subarcualis obliqui; S.H., Sternohyoideus; S.R., Subarcuales recti.