

CALIFORNIA STATE UNIVERSITY, NORTHRIDGE

CRANIAL AND CERVICAL MYOLOGY AND OSTEOLOGY  
OF THE ADULT CALIFORNIA NEWT (TARICHA TOROSA)  
IN RELATION TO ITS FEEDING

A thesis submitted in partial satisfaction of the re-  
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by

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ABSTRACT

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While anatomical studies of salamanders are not new, most have been done on a relatively few species and are mostly pure descriptive morphologies or superficial comparisons of many species. Somewhat surprisingly, the common California Newt (Taricha torosa) has not been fully nor accurately described. This study provides a detailed description of the head and neck anatomy of T. torosa. Osteological morphology is considered with particular reference to its relationship to the muscles. Muscle morphology is considered with particular reference to its probable functional importance in feeding. The study of cranial osteology indicates that the structure of the posterior portion of the skull is strongly influenced by the muscles. The muscle

anatomy indicates that the cervical muscles are strongly developed, while the tongue muscles and their skeletal supports suggest only limited mobility. An analysis of the jaw muscles indicates both the external and biceptate anterior levators are very strongly developed with the anterior levator slightly more important as an adductor. The mandibular depressor is found to be very inefficient. Contrary to the kinetic inertial model (Olson 1961), considerable reserve force when the jaws are closed is indicated. Large losses in efficiency are attributed to transverse displacement of the muscles.

## INTRODUCTION

The study of the morphology of bone or muscle is neither new nor a unique exercise, but most studies fail to consider bone and muscle as an integrated system. To be fully understood, bone must be considered in terms of the muscles, and the muscles in terms of their functions. Analysis of jaw muscle function by vector forces has been largely limited to mammals and their reptilian ancestors even though the amphibians offer a much simpler system and may be of great significance in understanding the primitive tetrapod condition. Aspects of the morphology of the rhipidistian and primitive amphibian jaws, as described by Olson (1961), suggest features of the modern salamander, Taricha torosa, which is being considered here.

Many features of the anatomy of several species of salamanders have been described, but few species have been considered in full detail. Hilton described the skeletons and cranial muscles of numerous salamanders, including Taricha torosa, in a series of papers (Hilton 1947, 1954, and 1959-1960). His descriptions are quite superficial and somewhat fragmentary, as are studies by Parker (1882) and Rhudy (1943) on the skulls of T. torosa. Detailed descriptions have been limited mainly to Salamandra, Amblystoma, Dicamptodon, and Necturus. Wake (1966) has done a comprehensive study of the skulls of plethodontids and with Ozeti (1969) described the tongue apparatus in salamandrids. Two specimens of Taricha torosa were included in the tongue study, but are only described in

generalized groupings. Smith's (1927) description of Triturus torosus (= Taricha torosa), is poorly detailed. Her description of the cranial muscles is rather confusing and inaccurate. In addition, based on the place of origin of her specimens and configuration of the vomerine teeth suggests that she studied Taricha granulosa rather than T. torosa.

Several classifications of salamander feeding methods have been described including Ozeti and Wake's (1969) "Gape and Suck", Regal's (1966) Classes One to Four, and Olson's (1961) Kinetic Inertial System.

"Gape and Suck", (or Saugschnappen), is of uncertain origin, but is defined by Ozeti and Wake as an adaptation to aquatic feeding. It is marked by a "water tongue" well developed and free on the sides, but lacking a posterior flap. Feeding is accomplished by a sudden opening of the mouth and expansion of the buccal cavity (with the possible aid of labial lobes in larvae and some aquatic adults). This type of feeding is applicable to Taricha torosa observed under aquarium conditions and it probably occurs during the breeding season in the wild, but most feeding is probably terrestrial. Even in the water the animals depend as much on a grasping lunge as on suction to capture prey.

Regal (1966) divided salamanders into four classes based on the degree of tongue development. Class I includes larvae and paedomorphic forms with little development of the tongue. Class

IV contains the advanced plethodontids with a very mobile tongue used, as in the anurans, to capture prey often of small size. The remaining plethodontids have slightly protrusible tongues and fall into Class III. Class II feeders have only partially free tongues used only to manipulate food in the mouth. This is characteristic of the ambystomids. The salamandrids, including Taricha torosa, are also Class II feeders, but probably evolved independently from the ambystomid/plethodontid line. Salamandrids have medial teeth paralleling the midline, unlike the transverse medial teeth of the ambystomids and plethodontids. Parallel medial teeth are a characteristic of Class I feeders and may indicate primitiveness in salamandrids.

Olson (1961) divided lower tetrapod feeding into kinetic inertial and static pressure systems. Salamanders are included with the kinetic inertial system feeders, which apply force only at the start of jaw closing, little force being applicable when the jaw is closed. The static pressure model includes strong pressure when the jaws are closed.

## MATERIALS AND METHODS

A total of nine animals were studied. Two specimens were from the collections of the biology department at the California State University, Northridge and were in breeding (i. e. aquatic) condition at the time of preservation, as indicated by the presence of a tail fin. The remaining specimens were purchased commercially and were in non-breeding (i. e. terrestrial) condition since tail fins were lacking. All specimens were from the Los Angeles area. They were kept in 70% denatured alcohol until used.

Five specimens were dissected for the muscle analysis. They were skinned and stained in 1:8 Borax-Carmine/Alcohol solution for two days and counterstained in 1% Picric Acid/Alcohol solution for one day. They were then dissected in water under a dissecting microscope with lighting applied from above.

The five specimens used for the cranial analysis (one specimen was used in both analyses) were skinned and then soaked in distilled water for one day, placed in a 4% potassium hydroxide (KOH) solution for a day, transferred for three days to a staining solution of 4% KOH with a few drops of Alizarin Red S solution added, and then returned to 4% KOH until almost clear (about a week). They were then passed through progressively concentrated solutions of glycerin/4% KOH (10%, 25%, 50%, and 75%), spending anywhere from one to several days at each station to achieve full clearing. Specimens were held in 75% glycerin until ready for analysis.

Examination of the specimens was done in 100% glycerin under a dissecting microscope with lighting applied from below.

Drawings were done with the aid of an ocular grid. Most drawings were done at 7X, although some were made at higher magnifications up to 25X. All drawings of osteological features, except one, are of the same specimen. Drawings of muscle morphology are from a single (different) specimen, with two exceptions. Measurements were made using an ocular scale at 10X.

## CRANIAL MORPHOLOGY WITH PARTICULAR REFERENCE TO THE MUSCLE ATTACHMENTS

The following description of the skull is based primarily on one specimen with major variations noted from the other specimens. Description of individual bones is divided into regional sections. The atlas and first thoracic vertebra are included because of their importance in muscle origins. Terminology is based primarily on Wake (1966) with variations in terms noted.

### BONES OF THE SKULL ROOF, INCLUDING THE ATLAS AND FIRST THORACIC VERTEBRA (Figure I)

The dorsal view of the cranium of Taricha torosa is considered by Rhudy (1943) to be smooth, except for some ridges and fossae, when compared to eastern and european newts (Notophthalmus and Triturus, respectively). The dominant features of the skull are the large temporo-orbital fenestrae that vacate most of the sides of the skull. They are occupied by the large eyes and jaw adductors. Medial to the temporo-orbital fenestrae are smaller supratemporal fenestrae, which are separated from the former by post-orbital arches (or supratemporal bars). The arches are absent in most other salamanders, but are reported to be heavier in eastern newts (Rhudy 1943). Their condition in Salamandra is uncertain; Francis (1934) denies their presence, but the illustration in Huene (1956) clearly shows them. The base of the skull seems wider in Taricha torosa than in most other salamanders. In the

front of the skull is a large dorsal fontanelle. It is usually smaller in other salamandrids and is absent in Necturus, Cryptobranchus, Amblystoma, and most plethodontids. There are nine bones that comprise the skull roof (plus the atlas and first thoracic vertebra). Unlike the condition in Amblystoma and some plethodontids, there are no septomaxillae present. Prenasals and quadratojugals are reported by DeBeer (1937) in Triton, but are not present in Taricha torosa.

Premaxilla: The anteriormost of the skull bones, the embryonically separate premaxillae, are fused at the midline to form a single bone which bears teeth along its ventral border. Dorsally, the premaxillae form the lower borders of the nasal fenestrae (external nares) and send projections along either side of the dorsal (internasal) fontanelle. The resultant premaxillae have a distinctive T-shape similar to those of some plethodontids (Wake 1966).

Maxilla: Lateral to the premaxillae, the maxillae are also tooth bearing bones. (They are absent in Necturus, but present in most other salamanders.) Teeth are borne on the front half of each bone only; the posterior suborbital process is toothless. The maxillae end well short of the jaw articulation area, but ligaments connect them to the articular end of each squamosal lateral to the external levator muscle. Other ligaments, from the medial side of the maxillae, connect to the processes of the pterygoids. The maxillae form the lower borders for the temporo-orbital fenestrae and the lateral borders of the nasal fenestrae. (The sub-

orbital processes on one side of two specimens were abnormally truncated with roughened ends.)

Nasal: Paired flat bones situated between the maxillae and the internasal projections of the premaxillae, the nasals form the upper borders of the nasal fenestrae and may reach the dorsal fontanelle behind the premaxillae. Posteriorly they border on the lacrimals, prefrontals, and frontals. The upper surface of the nasal is usually marked.

Nasal Cartilage (see Figure 4): An extension of the nasal capsules, the nasal cartilages fill most of the nasal fenestrae. In their centers are the much smaller nasal openings.

Lacrimal: Occurring at the anterior border of the temporo-orbital fenestrae, each lacrimal divides into two plates. The upper plates are part of the skull roof and bear markings similar to those on the surfaces of the nasals. The deeper plates are visible from above through a cleft between the upper plates and maxillae. Between the two plates runs the lacrimal duct (DeBeer 1934). The lacrimals lie between the frontals and maxillae, behind the nasals, and lateral to the prefrontals. Most authors (including Smith 1927) show the lacrimals and prefrontals as single paired bones, labeled the prefrontals.

Prefrontal: The small, somewhat rectangular, prefrontals lie between the nasals, frontals, and lacrimal bones.

Frontal: The frontals cover the forward part of the braincase

and form the anterior, upper margins of the temporo-orbital fenestrae. At their anterior ends the frontals contact the nasals, prefrontals, and lacrimals. They form the posterior border of the dorsal fontanelle. The main posterior contact is with the parietals. The suture between the frontals and parietals is somewhat sinuous. The junction is not always even so that one frontal may contact both parietals. The midline (sagittal) suture like the fronto-parietal (coronal) suture, is also sinuous particularly between the parietals. In one specimen a small, ovoid bony growth was seen in the right fronto-parietal suture and the frontals had several vacuities on their upper surfaces where the bone was much thinner. These abnormalities may have been pathological in origin.

The frontals send processes behind the orbits to contact corresponding processes of the squamosals, forming postorbital arches. The ventral surfaces of the arches are the origin for the external levator muscles (primarily from the squamosal). The arches form the lateral borders for the supratemporal fenestrae, through which the anterior levator muscles pass. Markings, evident on the frontals of all specimens, occur at the base of the arches and may indicate considerable stress in these areas. In one specimen, one arch was incomplete due to a short process of the squamosal (the frontal process ended bluntly at about its normal position). The effect of this abnormality on the external levator could not be determined, but must have caused some impairment of this normally

important muscle.

Parietals: Located between the frontals and occipito-otics, the parietals cover the middle part of the braincase and form the medial borders for the supratemporal fenestrae. The posterior portions of the bones are marked by pronounced trough-like fossae leading into the fenestrae. Along these fossae pass the superficial portions of the anterior levator muscles. The parietals seem to act as a pulley for the muscles as they pass into the fenestrae. The deep portions of the anterior levators take their origin from the parietals on the medial side of the supratemporal fenestrae near the frontal sutures. These deep muscles bulge into the fenestrae when contracted. The posterior border of the parietals is primarily with the occipito-otics along a ridge line, but may also contact the squamosals on the posterior edge of the fenestrae.

Occipito-otics (dorsal aspect): Forming the posterior part of the skull, the occipito-otics are paired on either side of the foramen magnum. On the upper surface, they are separated by a small, foramen-like suture covered by a small, oval piece of cartilage (the supraoccipital according to Smith 1927). Anteriorly, the occipito-otics contact the parietals and laterally the squamosals. They may or may not reach the supratemporal fenestrae. On the upper surface of the occipito-otics are large fossae, bordered dorsally along the parietal sutures by low crests or ridges. These fossae and ridges continue onto the squamosals and receive the in-

sertions of the dorsal trunk muscle. The posterior margins of the occipito-otics are broad and may brace the posterior processes of the squamosals, although, on one specimen the occipito-otics did not contact the squamosals fully. The occipito-otics are referred to as the exoccipitals, by most authors, after their principal component.

Squamosal (dorsal aspect): Situated lateral to the occipito-otics, the squamosals carry part of the insertion for the dorsal trunk muscles. Anteriorly, they contribute processes forming the posterior portions of the postorbital arches. Posteriorly, the squamosals send processes along the dorsal part of the lateral surface of the occipito-otics.

Atlas and First Thoracic Vertebra: While not part of the skull, these two vertebrae are the origins for two major muscles. The neural arch of the atlas gives rise to the superficial portion of the anterior levator muscles. The arch is a roughened knob and v-shaped marks are sometimes present indicating the direction of the muscles. The dorsal trunk muscles take their origins from the myosepta along the back (the first myoseptum is anterior to the atlas), but deeper elements arise from the upper body surface of the atlas and first thoracic vertebra. The atlas lacks a rib, the only precaudal vertebra to do so.

BONES OF THE ROOF OF THE MOUTH INCLUDING ATLAS AND FIRST THORACIC VERTEBRA (Figure 2):

As in most salamanders, the ventral view of the skull of Taricha torosa resembles an I with large orbital openings into the palate medial to the pterygoids. (The large openings allow the eyes to be drawn in, decreasing the mouth cavity space, thereby aiding in swallowing as in the anurans.) The vomerine teeth, as in other salamandrids, lie lateral to the parasphenoid paralleling the midline. In Taricha torosa the inward pointing vomerine teeth form a Y. Unlike the ambystomids and plethodontids, there is no palatine in Taricha torosa or other salamandrids. (It is probably present embryologically according to DeBeer 1937.) The internal nares are, consequently, incompletely bordered behind the vomers. The intervomerine fontanelle is fairly large in front of the vomerine teeth. Rhudy (1943) described the fontanelle as a figure 8 characteristic of the species. Although Smith (1927) illustrated such a figure for T. granulosa (?) none of the fontanelles I observed approached a figure 8. (The closest I found was a small foramen at the intervomerine contact in one specimen.) The ventral aspect of the skull includes seven bones, plus the atlas and first thoracic vertebra.

Premaxilla and Maxilla: Bearing the outermost row of teeth, the premaxillae and maxillae form the forward edge of the roof of the mouth.

Vomer: Situated posterior to the maxillae and premaxillae, the paired vomers are separated for most of their length by the

intervomerine fontanelle, but make a short contact behind it. Laterally, the vomers form the anterior border of the internal nares (there is no posterior border). Posteriorly, the vomers send tooth bearing processes lateral to the parasphenoid. The posterior portions of the toothed processes are ligamentous and lay ventral to the eye retractor muscles. The vomers are referred to as the prevomers and vomeropalatines by some authors.

Parasphenoid: Starting as a narrow, unpaired plate between the posterior processes of the vomers, the parasphenoid widens posteriorly and extends between the occipito-otics to form the lower border of the foramen magnum. The basioccipital, if present, is totally covered by, and may be fused to, the parasphenoid (DeBeer 1937). The posterior portion of the parasphenoid carries part of the insertion fossae for the subvertebral muscles on either side of the foramen magnum. Anterior to the latter is another pair of fossae, just dorsal to the ligamentous portion of the vomerine tooth processes, where the eye retractor muscles arise. Both sets of fossae extend onto the occipito-otics.

Occipito-otic (ventral aspect): Paired on either side of the foramen magnum, the occipito-otics are a fusion of the exoccipitals and otic capsules (the periotics or prootics). Posteriorly, the occipito-otics carry part of the insertion fossae for the subvertebral muscles medial to the otic fenestrae. The otic fenestrae, which are covered by opercular plates, are described later.

According to DeBeer (1937) and Monath (1964) the columellar plates and styles develop more anteriorly in the fenestrae ovalis in larval salamanders. While they are retained in ambystomids and some plethodontids, they are completely fused to the exoccipital in salamandrids and there is no trace of them in Taricha torosa. Anteriorly, the occipito-otics bear part of the origin fossae for the eye retractor muscles. Large foramina for the eye muscle nerves occur on the anterior surfaces inside the temporo-orbital fenestrae, but they usually lack the large surrounding bony collars seen in Figure 2.

Pterygoid (ventral aspect): Situated between the occipito-otics and quadrates, the pterygoids send flattened processes anteriorly. Ligamentous continuations of these processes contact the medial surface of the maxillae. Ventrally, the pterygoids support the dorsal epithelium of the mouth. The pterygoids are referred to as the palatoquadrates by DeBeer (1937) and the palatopterygoids by Wischnitzer (1967).

Quadrate: Situated lateral to the pterygoids, the block-like quadrates form the joint with the mandibles.

Atlas and First Thoracic Vertebra: The subvertebral muscles take their origin from the ventral surfaces of these two vertebrae and from the rib of the first thoracic. Besides the usual contacts with the paired occipital condyles, the atlas sends a flattened process from its ventral side into the foramen magnum. This

process makes minor contacts with the skull.

#### OCCIPITAL ASPECT OF THE SKULL (Figure 3):

Dominating the occipital view of the skull is the large diamond-shaped foramen magnum. Lateral to the broad occipito-otics are the jaw suspensions.

Occipito-otic: On either side of the foramen magnum, the occipito-otics comprise most of the occipital view. Lateral and somewhat below the foramen magnum are large, flat, circular occipital condyles which project out from the occipito-otics. Below and medial to the condyles, on the inside surfaces of the foramen magnum, are flat areas which contact the ventral plate of the atlas. Ventral to each condyle are fossae for insertion of the subvertebral muscles. The paired fossae extend onto the parasphenoid, which underlies the foramen magnum. Lateral to the condyles and opening somewhat ventro-laterally are the large, ovoid otic fenestrae, which are surrounded by heavy, bony collars projecting from the occipito-otics. Covering the fenestrae are cartilaginous opercular plates. The opercular muscles insert onto these plates. Dorsal to the condyles and otic fenestrae are large, triangular flat areas where the major cucullar muscles insert. Lateral projections of the occipito-otics (usually) make contact with the posterior processes of the squamosal. Near the points of contact insert the ribbon-like cephalo-dorso-subpharyngeal muscles. Dorsally the occipito-otics are dominated by the insertion fossae of the dorsal trunk muscles.

Jaw Suspension (Occipital Aspect): Consisting of the quadrates sandwiched between the pterygoids and squamosals, the jaw suspensions are firmly bound to the occipito-otics and are quite immobile. (It has been suggested by Hilton, 1960, that they are movable in Amblystoma to aid in swallowing large prey.) The suspensions are flared outward at an angle of about  $50^{\circ}$ .

LATERAL ASPECT OF THE SKULL (Figure 4):

The side view of the skull is dominated by the large temporo-orbital fenestra. Anterior to this is the more completely covered snout. Posterior to the fenestra is the jaw suspension.

Maxilla: Forming most of the side of the snout, the maxilla sends a toothless process below the orbit. The process ends as a flattened sheet well short of the jaw articulation. A ligament, lateral to the external levator, connects the maxilla to the articular end of the squamosal.

Marginal Teeth: Born on the dorsomedial margin of the maxilla, premaxilla, and dentary (lower jaw) the teeth of most specimens were as shown in Figure 4: large, uneven, pointing strongly inward, and with large gaps in the tooth row. The teeth of one specimen, however, were shorter, more even in size, more erect, and had fewer gaps. These differences may be related to its breeding (and therefore aquatic) condition. All teeth are pedicillate.

Orbitosphenoid: Occuring between the vomer and frontal bones, the orbitosphenoid forms most of the back wall of the orbit. At its

posterior suture with the occipito-otic is the large foramen for the optic nerve. This bone is also referred to as the sphenethmoid (Romer 1970).

Pterygoid: The body of the pterygoid lies deep to the quadrate. It sends a flattened process toward the suborbital process of the maxilla. It contacts the medial side of the maxilla by a ligament. The process is solid on the medial (ventral) surface, but laterally, the dorsal and ventral margins fold over to leave a thinner central portion. The posterior levator muscle takes its origin from the body of the pterygoid lateral to the process.

Squamosal: Appearing uniquely T-shaped in lateral view, the squamosal is the main muscle-bearing bone of the lateral skull aspect. The squamosal is divided by a sharp crest or spine into anterior and posterior portions (fossae). (The spine may be divided by a cleft in some cases, probably due to the passage of a nerve.) The anterior portion includes the postorbital arch process. The anterior fossa and underside of the arch are the origin for the external levator muscle. The posterior portion forms a large fossa by sending a process posteriorly. The posterior fossa is the origin for the mandibular depressor. The squamosal lies lateral to the quadrate, but usually tapers to an end at or just short of the jaw articulation. (One specimen extended slightly beyond.) The squamosal does not contribute to the jaw articulation. Inserting on the articular end of the squamosal are the tendon of the

quadratopectoral muscle and the ligament from the postorbital process of the maxilla. There is no quadratojugal between the squamosal and quadrate as reported in Triton by DeBeer (1937). In most other salamanders, the squamosal is much simpler with smaller fossae and no processes.

Quadrate: Situated deep to the squamosal, the quadrate forms the articulation for the lower jaw. The posterior margin of the quadrate is very scarred by the insertion of the interosssaquadrate muscle. The posterior, dorsal portion of the quadrate is cartilaginous.

#### THE MANDIBLE (Figures 4, 5, and 7)

Ventral Aspect: The mandibles form a parabolic arch which, when closed, lies just inside the upper lateral tooth margin. The mandibles are joined together anteriorly at the mental symphysis. The symphysis is cartilaginous and may be flexible in a live animal although posterior projections of the dentaries may inhibit this by increasing the area of contact at the symphysis. Each mandible is composed of four bones: the dentary, articular, prearticular, and angular. Francis (1934) does not include the angular for Salamandra. Smith (1927) lists the dentale (dentary), articular, splenial, and a fused coronary-surangular for Taricha granulosa (see p. 2).

Lateral Aspect: Most of the outside surface of the mandibles is dominated by the dentary. Only the anterior half of the dentary

bears teeth (on its dorsomedial surface). Behind the orbit, the dorsal edge of the dentary turns downward to taper to an end lateral to the articular. For convenience, I shall refer to this point of downturning as the dentary point. The external levator muscle inserts posterior to the dentary point.

Dorsal and Medial Aspect: Wedged between the dentary and the prearticular, the block-like articular carries the surface which articulates with the quadrate. The dentary lies on the lateral surface of the articular, but does not connect to it. From the dentary point, a projection folds over to form most of the anterior medial surface of the mandible. Lateral fibers of the genioglossal muscle take their origin along its length. Medial fibers of the genioglossal and the geniohyoid muscles arise from near the symphysis. The dentary bears the tooth row on its upper medial side and folds in on the lower surface to form the ventral surface of the anterior half of the mandible. This ventral surface is labeled the splenial by Smith (1927). The posterior intermandibular muscle arises from the ventromedial surface of the dentary. The angular and prearticular are strongly attached to the articular. The angular lies ventral to the articular and the mandibular depressor muscle inserts on its posterior end. The angular folds onto the medial surface behind the dentary. The prearticular forms most of the posterior medial surface of the mandible and extends anteriorly between the folds of the dentary. The prearticular sends a broad plate or flange

dorsomedially. Onto this dorsal process inserts the anterior (by a tendon) and posterior levators. This is termed the coronoid process by Francis (1934), but unlike the coronoid process of mammals, it serves only to decrease the transverse displacement of the deep levators. Smith (1927) considered the prearticular to be a fusion of the coronary (or coronoid) and surangular. The embryologically tooth bearing coronoid (DeBeer 1937) may be involved, but the surangular is phylogenetically lateral and cannot be involved (see Romer 1970). The core of the mandible, from the articular forward, is filled by Meckel's cartilage according to Smith (1927).

#### DETAILS OF THE JAW ARTICULATION (Figure 6)

The jaw joint is formed by the cartilages of the quadrate and articular. The quadrate cartilage has evident twin condyles not clearly reflected in the bone. The anterior condyle is directed laterally at about  $45^{\circ}$ . Riding at an angle to the quadrate is the cartilage of the articular. The articular has less well defined condyles. The articular condyles form a saddle which rotates through the trough in the quadrate cartilage.

#### THE BRANCHIAL ELEMENTS (Figure 7)

In most salamandrids the branchial skeleton consists of three parts; the ceratohyoid, first branchial arch, and the urohyal. The first branchial arch is composed of several elements. The amount of ossification in the branchial skeleton is greater than in most salamandrids. The elements also seem heavier and are probably

less mobile than in most other species. The nomenclature which I have followed complies with most authors.

Ceratohyoid: Situated as bony rods close to the base of the skull, the ceratohyoids extend into the floor of the mouth as cartilaginous plates. From the posterior tips of the ceratohyoids, the subhyoid muscles arise. Smith (1927) stated that the ceratohyoids in her specimens (T. granulosa?) connected to the squamosals, but my observations do not support this for T. torosa.

First Branchial Arch: The first branchial arch is composed of elements from several sources and the naming of the parts of this arch varies with the authors (see DeBeer 1937, Romer 1970). The outermost bony rods, the first epibranchials, lie ventroposterior to the ceratohyoids. (DeBeer and Romer refer to the epibranchials as the ceratobranchials.) They are separated from medial bony rods, the first ceratobranchials, by wide zones of cartilage. Extending from these zones of cartilage are arches of cartilage, the second ceratobranchials. (The ceratobranchials are termed hypobranchials by DeBeer and Romer.) Smith (1927) reported some ossification of the second ceratobranchials in T. granulosa (?), but I found none in T. torosa. The ceratobranchials join into a medial cartilaginous rod, the copula. The copula is also referred to as the basihyoid or first basibranchial, but probably is a fusion of both. I found the copula to be consistently cartilaginous, although Hilton (1947) reported some ossification in his specimens of T. torosa.

The copula underlies the tongue. From its tip, paired cartilaginous processes, or radii, project laterally and somewhat anteriorly. (Smith, 1927, termed these cornua, but they are not equivalent to the cornua of higher animals.) The number of radii seems variable; Smith (1927) and Hilton (1947) illustrate two pair, Ozeti and Wake (1969) illustrate one pair, and I found both conditions occurring (see Figure 16). The anterior pair are variably present (one specimen had only one). When present, they project horizontally or even slightly ventrally. The posterior pair of radii are always present. They are larger than the anterior pair, and point dorso-laterally into the tongue. The interradiial muscle, when present, spans this second pair dorsal to the copula. The cervical rectus muscles insert partially (superficial elements) on the posterior edge of the first ceratobranchial (tuberosities occur, but are not universal) and partially on the tip of the copula (deep elements). The deep elements pass through the space between the ceratobranchials. The first subarcual muscles arise from the tip of the epibranchials. Other muscles, which are doubtfully present, are the hypoglossal (copula to tongue), basiradials (ceratobranchials to the tip of the copula), and radioglossals (radii into tongue).

Urohyal: In most salamandrids the urohyal lies in the gular region. Also termed the second basibranchial, os triangulare, or os thyreoideum; the Y-shaped urohyal is the usual origin for the

geniohyoid muscles. This bone is not present in Taricha torosa and the geniohyoids connect by two inscriptions directly to the abdominal rectus muscle.

## MUSCLE MORPHOLOGY AND FUNCTION IN FEEDING

This description of the cranial and cervical musculature is based on one specimen with major variations noted from four others. Description of the individual muscles is divided into functional sections. Terminology is based on Ozeti and Wake (1969) and Edgeworth (1935). Important alternative names are noted. Embryonic origins are from Edgeworth (1935).

### THE JAW MUSCLES (Figures 8, 9, and 10)

The jaw muscles include the openers (depressors or abductors) and closers (levators or adductors) of the mandible. There is only one mandibular depressor muscle, although the geniohyoid muscle may assist in this function. The mandibular levators in Taricha torosa and most other salamanders are divided into three main muscles; anterior, posterior, and external levators (probably equivalent to the anterior, middle, and posterior levators of Olson, 1961). (There are twice as many adductors and abductors in anurans according to Starrett, 1968.) The levators have their embryonic origins, along with the intermandibular muscle, as mandibular arch muscles; the depressor is derived from hyoid arch muscles.

M. levator mandibulae externus (LME): The external levator is a broad, thick muscle that fills most of the temporo-orbital fenestra behind the eye. It is also referred to as the masseter (Smith 1927), but the homology is uncertain. Its embryonic point of origin is on the quadrate, but in the adult the external levator arises from the

anterior fossa of the squamosal and the ventral surface of the post-orbital arch. The LME inserts posterior to the dentary point, where the bone tapers to the level of the jaw articulation. From its insertion the fibers of the external levator are angled backward away from the large eye. The functional significance of this arrangement will be discussed later when I analyse the jaw muscles.

The absence of the postorbital arch in other salamanders must surely effect the size and importance of their external levators. This muscle is large in caecilians, but is reduced in anurans. It is very large in lizards (Starrett 1968).

M. levator mandibulae posterior (LMP): This muscle is also termed the pterygoid (Smith 1927, Eaton 1936). The posterior levator lies deep to the LME. Its embryonic origin is on the quadrate, but takes much of its adult origin from the body of the pterygoid. The LMP inserts on the prearticular posterior and lateral to the tendon of the anterior levators. I found this muscle to be poorly separated from the external levator so that they were often removed together during dissection. When separated from the LME, the posterior levator is a thin muscle which angles strongly posteriorly from its insertion. Its small size and angled insertion imply that the LMP is only a minor levator. It is, however, the major levator muscle in anurans, although minor in lizards (Starrett 1968). It was either weakly developed or absent in fossil amphibians (Olson 1961).

M. levator mandibulae anterior (LMA): This muscle is also termed the temporal (Smith 1927) or craniomandibular (Eaton 1936, Hilton 1960). The anterior levator arises in two heads which share a common insertion by a broad tendon onto the anterior portion of the dorsal process of the prearticular. The embryonic origin is from the wall of the chondrocranium, but in the adult the LMA is divided into a deep portion posterior to the orbit and superficial portion extending over the skull roof.

The anterior levator may be the earliest jaw adductor in tetrapods and is believed to have been large in ancestral forms. This is evidenced by the tendon scars on rhipidistian and fossil amphibian jaws. The muscle was probably divided into two heads even in these fossil forms (see Olson 1961). The anterior levator is reduced in frogs, but large in lizards (Starrett 1968).

The deep portion of the anterior levator (LMAd) is squeezed into the narrow area between the eye and superficial portion (LMAs). It has its origin on the side of the parietal, near the coronal suture in the anterior half of the supratemporal fossa. The LMAd is narrow in response to its crowded location, but is of considerable depth and expands into the fossa when contracted. The insertion is by a common tendon with the superficial portion. Its action is a simple dorsally directed pull on the mandible, for which action it is well placed. The deep portion is not described by Smith (1927) for her specimens (probably T. granulosa).

Unlike other tetrapods, the superficial portion of the M. levator mandibulae anterior (LMAs) has shifted its origin from the crowded temporal region completely off the skull and onto the arch of the atlas in T. torosa. This long, cylindrical muscle runs over the medial insertion of the dorsal trunk muscle and along a trough in the parietal, then turns ventrally and passes through the posterior half of the supratemporal fossa to insert on the mandible. The parietal serves as a pulley over which the LMAs pulls as it changes direction.

The posterior extension of the superficial anterior levator is very common in salamanders other than neotenic forms. Although some, such as Salamandra (Francis 1934) retain some contact with the occipital, others, such as Ensatus (Eaton 1936), extend this muscle even further onto the thoracic vertebrae. Limiting the origin to only one vertebra may allow greater movement of the head in Taricha torosa. The function of the superficial portion of the LMA despite its arrangement is a simple dorsal pull similar to the deep portion.

The superficial portion of the anterior levator is surely the posterior temporal of Smith (1927). She includes this muscle with an anterior temporal that must be, from the description of its origin, the dorsal trunk muscle of other authors. What she calls the ventral portion may be the major cucullar muscle, even though she describes that muscle separately. She associates these muscles

together as part of the dorsal latissimal in her animals (T. granulosa?) even though this would seem unlikely.

M. depressor mandibulae: This muscle is the main or sole jaw open (depressor). It has also been referred to as the digastric (Smith 1927). The embryonic derivation is from the hyoid levator muscle. Embryonically it originates on the otic capsule, but in the adult it fills the posterior squamosal fossa. While the depressor is often doubled or covered by other muscles in other salamanders, I found it to be a single large muscle clearly visible behind the LME in T. torosa. Other studies on Taricha disagree: Hilton (1960) shows the muscle doubled in T. torosa and Smith (1927) describes a thinner second origin from the dorsal fascia in T. granulosa (?). The depressor is very broad and thick, but makes a narrow insertion onto the posterior end of the angular. The insertion is similar to that of the mammalian triceps, but unlike the triceps the depressor does not enjoy a true posterior process to work upon. Consequently, although the muscle is well positioned relative to its insertion, its efficiency suffers from the short lever arm. (I will discuss this further when I analyse the jaw muscles.)

#### THE CERVICAL MUSCLES (Figures 8, 9, 11, and 17)

The cervical muscles connect the head to the trunk and function in moving the head. Observations on live T. torosa demonstrate the importance of these muscles in feeding on large food items. Head bobbing and shaking are important in tearing the food, manipu-

lating it into the mouth, and then aiding the tongue to work it over the vomerine teeth so that it can be swallowed. There are seven cervical muscles in adult T. torosa.

M. dorsalis trunci: The dorsalis muscle is a continuation of the epaxial body muscles which inserts on the dorsal surface of the skull on either side of the foramen magnum. This muscle is broad and thick and is characterized by transverse myosepta along its length. Of the fibers that insert onto the skull, superficial elements arise from the first myoseptum, which occurs anterior to the atlas. Deeper elements, however, arise directly from the upper body of the atlas and first thoracic vertebra. The superficial portion of the anterior levator covers and somewhat restricts the more medial fibers. The insertion of the dorsal trunk muscle is behind the crestlike suture between the occipito-otic and parietal and extends onto the dorsal surface of the squamosal. The function of the dorsalis is to raise the head and possibly to aid in opening the mouth. The dorsal trunk muscle is surely the anterior temporal of Smith (1927). She describes it as arising from the second, third, and fourth vertebrae in T. granulosa (?).

M. subvertebralis: This is the ventral counterpart of the dorsal trunk muscle. It forms a broad, thick sheet that inserts on the ventral surface of the occipito-otics and parasphenoid on either side of the foramen magnum medial to the otic fenestrae. The origin of the subvertebral is the centra of the atlas and other vertebrae

and their ribs. Its function in lowering the head is antagonistic to that of the dorsal trunk muscle.

M. cucullaris major: The major and minor cucullar muscles derive from the fourth branchial levator, but with the reduction of the branchial elements at metamorphosis the muscle is modified into two distinct elements and functions. The major cucullar in adult T. torosa, is a large muscle dorsal to the branchial elements. Its origin is from the leading edge and medial surface of the procoracoid and it inserts broadly on the posterior surface of the occipito-otic ventro-lateral to the dorsal trunk muscle. (It is overlain by a glandular mass dorsal to the branchial elements which absorbed much of the carmine stain. This caused me originally to believe that the muscle was largely tendinous. In one specimen fibers of the major cucullar were confluent with those of the minor, indicating the relationship of these muscles.) The function of the major cucullar muscle is apparently to turn the head in the sideways jerks that are used by T. torosa to tear large food items. (According to Monath, 1965, the major cucullar adds to the opercular muscle as part of the hearing mechanism in some plethodontids.)

M. cucullaris minor: The minor cucullar muscle, like the major, is derived from the branchial levators. In the adult this muscle becomes associated with the shoulder girdle and not with the head. Its origin is from the procoracoid and it inserts into the dorsal fascia or skin. Its function is in locomotion and not of concern here.

M. cephalo-dorso-subpharyngeus: This ribbon-like muscle is a remnant of the second, third, or fourth arcual levator. (The laryngeal dilator in Salamandra is a serial homologue not found in Taricha torosa; Francis 1934.) The origin of this muscle is from the ventral esophagus just dorsal to the aortic arches. It passes dorsal to the branchial elements, looping around the ceratohyoid in one specimen, to insert lateral to the major cucullar muscle on the occipito-otic near the squamosal. In the adult the cephalo-dorso-subpharyngeal muscle acts as a constrictor of the esophagus or to reject unacceptable food items by pulling the esophagus up and forward. There is also a constrictor or sphincter laryngis in the larynx.

M. opercularis: Also referred to as the scapular levator (Smith 1937; Monath 1965), the opercular muscle is a thick triangular sheet arising from the anterior edge of the scapula and suprascapula and inserting on the opercular plate of the otic fenestra. Francis (1934) believed, and I concur, that this muscle seems far too large to be concerned only with hearing. While its use in hearing is, without question, a major function of the muscle, I believe that it also functions in turning the head.

Smith (1927) described the scapular levator of T. granulosa (?) as "a long, thin muscle arising from the occipital bones, passing backward to be inserted on the anterior, upper margin of the cartilaginous scapula". This may be the opercular muscle, but the

"long, thin" description better fits the cephalo-dorso-subpharyngeal.

#### THE SUPERFICIAL VENTRAL MUSCLES (Figure 12)

The superficial ventral muscles are the outermost layer of the floor of the mouth. There are three such muscles in adult Taricha torosa.

M. intermandibularis posterior: As the name implies this muscle lies between the mandibles. It is also referred to as the mylohyoid (Smith 1927). The intermandibular muscle originates embryonically from the mandibular arch like the jaw adductors. An anterior portion may be present in larvae, but is not found in adult T. torosa. The adult muscle is a very thin sheet the origin of which extends from the medial border of the mandible near the symphysis (varying somewhat) to about four-fifths of the distance of the articulation. The insertion is into the midventral fascia. The length of the muscle fibers were quite short in some specimens causing a much wider sheet of fascia to occur. Contraction of this muscle would tense the fascia, thereby, raising the floor of the mouth and the tongue. This would aid in swallowing and respiration.

M. interossaquadrata: This muscle is also referred to as the interhyoid (Francis 1934) and the gularis (Eaton 1936; Hilton 1952 and 1960). In adult Taricha torosa it forms a single, fan-shaped muscle, although in other salamanders, such as Salamandra (Francis 1934), it is often double. In T. torosa it arises from the

posterior edge of the quadrate, which is deeply scarred from the attachment. (It takes its origin from the dorsal fascia in plethodontids, according to Hilton 1952.) The insertion is into the midventral fascial just dorsal to the posterior end of the intermandibular muscle which overlaps it just slightly. It extends to just in front of the shoulders where its fibers often contribute to the quadratopectoral muscle (see below) indicating a relationship between the two muscles. (In some specimens, however, the muscle did not reach the origin of the quadratopectoral muscle.) The function of the interossaquadrate appears to be the same as that of the intermandibular muscle: to lift the floor of the mouth and the tongue, thereby aiding in swallowing and respiration. This muscle is not described by Smith (1927) for T. granulosa (?).

M. quadratopectoralis: Extending from a triangular fascia between the shoulders, the quadratopectoral muscle inserts by a short tendon on the articular end of the squamosal spine. The muscle is rather thin in T. torosa. According to Hilton (1960) the quadratopectoral muscle is variously developed in other salamanders without any apparent taxonomic consistency. The muscle resembles the sternomastoid of mammals and may function similarly to turn or lower the head. The quadratopectoral muscle is the stylohyoid of Smith (1927), but she describes it as inserting on the mandible in T. granulosa (?).

DEEPER VENTRAL MUSCLES (Figures 13, 14, 15, and 16)

The deeper ventral muscles are primarily concerned with the movement of the tongue and its skeletal support. I found only six distinct muscles in Taricha torosa. Ozeti and Wake (1969) list four more muscles which I could not confirm.

M. subhyoideus: Also referred to as the ceratohyoid (Eaton 1936), the subhyoid muscle is a thin sheet from the tip of the ceratohyoid. The typical insertion is into the midventral fascia just deep to the intermandibular muscle, and anterior to the interosquadrata. In one specimen a smaller, deeper slip inserted on the mandible near the symphysis, just dorsal to the geniohyoid muscle. Although this condition is the one described by Hilton (1960) for the subhyoid muscle for T. torosa, it must be considered exceptional in my sample for this species. A similar configuration of the subhyoid muscle occurs normally in other salamanders, such as Salamandrina (Ozeti and Wake 1969). Contraction of the subhyoid muscle would pull the ceratohyoid medially, thereby squeezing and lifting the tongue. The subhyoid is not mentioned by Smith (1927) for T. granulosa (?), but may have been included in the subarcual rectus muscle (below).

M. subarcualis rectus I: Like the subhyoid muscle, the subarcual is derived from the branchial musculature. It is one of a series of embryonic muscles, but is the only one to remain in the adult. In Taricha torosa, the subarcual is a thick muscle extending from the posterior surface of the tip of the epibranchial (which

it totally surrounds) to insert onto the cartilaginous plate of the ceratohyoid. While the muscle might draw the hyoid plate posterior (opposing the subhyoid muscle), the subarcual could also draw the branchial elements forward bringing the tongue (which is attached to the copula) with them. Contraction on only one side would turn the branchial arch and tongue. Smith (1927) seems to combine the subarcual rectus with the subhyoid muscle as a single branchiohyoid muscle in T. granulosa (?).

M. geniohyoideus: This muscle is a paired, thin ribbon along the midline ventral to the branchial elements. Its embryonic origin, along with the cervical rectus muscle (see below), is from the anterior myotomes of the body. According to Edgeworth (1935) the other "glossal" muscles (presumably the genioglossal, etc.) derive from the geniohyoid. In the adult, the geniohyoid inserts on the mandible near the symphysis. In most salamanders, including Salamandra (Francis 1934; Ozeti and Wake 1969), the origin is from the urohyal. Taricha torosa lacks this branchial element and the geniohyoid muscle arises from the abdominal rectus by two myosepta, the anterior being where the urohyal should be and the posterior shared with the superficial cervical rectus muscle. The function of the geniohyoid muscle is unclear. It could support the branchial elements and by contracting raise the floor of the mouth. It might also lower the head. Another possible function, mentioned by Francis (1934) and Olson (1961), is to act as an extra jaw depres-

sor. Contraction of the geniohyoid muscle (with the aid of gravity), would tend to hold the mandible steady while the dorsal trunk muscles lift the head, effecting an opening of the mouth. Primitive extinct amphibians and rhipidistians show a weakly developed mandibular depressor muscle and may have used this method to open their mouths (Olson 1961).

M. rectus cervicis: A direct continuation of the abdominal rectus, the cervical rectus muscle is divided into two parts; the superficialis and profundus. The cervical rectus muscle is probably the sternohyoid of Smith (1927), although she describes it as inserting on the hyoid arch in T. granulosa (?).

The M. rectus cervicis superficialis lies ventral and medial to the profundus. The muscle takes most of its origin from the abdominal rectus by a myoseptum shared with the geniohyoid. About a third to a half of the muscle comes from the medial surface of the scapula, however. This is the omohyoid muscle of Ozeti and Wake (1969) and the pectoriscapular muscle of Francis (1934). The insertion of the superficial cervical rectus muscle is on the posterior edge of the first ceratobranchial. Contraction of this muscle would draw the branchial element and associated tongue posteriad.

The M. rectus cervicis profundus takes its origin directly from the abdominal rectus without an apparent myoseptum. It passes through the space between the first and second cerato-

branchials and inserts on the tip of the copula or into the tongue. (In one specimen, the profundus noticeably thinned into fascia over the second ceratobranchial, but did not insert on the bone.) The function of the deep portion of the cervical rectus muscle would seem to be the same as that of the superficial portion: to pull the branchial elements and tongue posteriad. It may also laterally rotate the copula and tongue. Francis (1934) suggested that the cervical rectus may also lower the head. Retraction of the tongue aids in producing the suction in aquatic feeding.

M. genioglossus: According to Hilton (1960), this muscle should be weakly developed, but I found the genioglossal clearly present. The muscle occurs as two unique lateral and medial elements.

The lateral elements of the genioglossal muscle occur as a very thin sheet of scattered fibers in the floor of the mouth. Most of the fibers arise and insert within the mouth floor, and only a few reach the mandibular symphysis. Contraction of the fibers would weakly tense the floor of the mouth.

The medial elements of the genioglossal muscle are more definitely formed into thin ribbons. The origin is from either side of the mandibular symphysis and the insertion is into the tongue. The medial genioglossal is divided into superficial and deep portions. The superficial portion inserts directly into the tongue and serves to pull it forward. The deep portion, however, crosses over to

insert on the opposite side of the tongue. Contraction of either antimeric slip of the deep medial genioglossal would tend to turn the tongue.

M. interradialis: I found this muscle only in the last dissection, but in this specimen it was well developed. The interradiial muscle inserts on the tips of the second pair of radii (presence of the first pair of radii is variable). It arches dorsally over the copula and anterior fibers of the deep portion of the cervical rectus. Contraction of this muscle would bend the radii causing a thickening of the tongue.

Muscles not found: In my dissections I could not find evidence for four muscles described by Ozeti and Wake (1969) for Taricha torosa. The first three muscles (the hyoglossal, basiradiial, and radioglossal) are reported for the tongue, but I found the tongue of T. torosa a round disk devoid of muscles. These may be fused with the deep cervical rectus muscle.

M. hyoglossus: This muscle is reported to extend from the copula into the tongue. Ozeti and Wake (1969) admitted it may be vestigial and Francis (1934) described it as small in Salamandra.

M. basiradialis: This muscle is described as originating from the dorsal apex of the copula and inserting on the ventral lateral margin of the second radii near its tip.

M. radioglossus: This muscle is supposed to run from the radii into the tongue. Ozeti and Wake (1969) admitted it is questionably present.

M. hebosteopsiloideus: In many salamanders this muscle divides off the deep cervical rectus to insert into the urohyal or myoseptal connection of the geniohyoid. Absence of the urohyal in Taricha torosa makes the loss of the muscle understandable.

#### THE EYE RETRACTOR MUSCLE (Figure 17)

There are eight eye muscles developed in salamanders (four recti, two obliques, a levator, and the retractor). These muscles are described by Hilton (1956) and I did not concern myself with them except for the special case of the M. retractor bulbi. The eye retractor deserves special consideration because of its importance in feeding. Contraction of this muscle pulls the eye into the socket, partially filling the mouth cavity. This aids in swallowing much as the same action does in the anurans. The origin of the retractor is from the anterior ventral surface of the occipito-otic and parasphenoid deep to the last few vomerine teeth. It inserts on the back side of the eye around the optic nerve.

The muscle that restores the eye to its normal position, the M. levator bulbi, was not dissected out, but may be of significance to feeding. This muscle, composed of four parts, underlies the

eye and acts to lift the eye and possibly lift the lower eyelid. Hilton (1956) suggests the eye levator may aid in breathing, but contraction would also increase the size of the mouth cavity increasing the suction during aquatic feeding.

FUNCTIONAL ANALYSIS OF THE JAW MUSCLES (See also Appendix I)

To gain a better insight into the workings of the jaw apparatus, I attempted to measure the muscles of Taricha torosa. Analysis of vectors and levers gives information on the relative efficiency and importance of these muscles. This is the first time, to my knowledge, that this form of analysis has been applied to an amphibian. Previous use of this technique has been limited to mammals (Herring and Herring 1974, Hiieme 1971, Martin 1967) and pelycosaur reptiles (DeMar and Barghusen 1972). The amphibian system is far simpler and may be closer to the primitive tetrapod condition.

Measurements of important parameters were taken with an ocular micrometer at 15X. After conversion into millimeters, the values for right and left paired elements were averaged and are given in Table I. To facilitate comparison, these values were standardized as percent of the snout-occiput length, which is equal to two elevenths ( $2/11$ ) the snout-vent length. These values are given in Table II. The average values will be used for analysis.

A considerable degree of uncertainty must be attributed to these values, particularly for displacement, as considerable interpretation of where to measure was involved.

Mandibular Length: This measurement was taken from the midpoint of the articulation to the anterior end of the mandible when

viewed from the side. (A diagonal measurement may be more valid.) It represents the action lever arm in efficiency calculations. (In mammals the distance to the first molar is used.)

Dentary Point Length and Height: These measurements define the force lever for the external levator muscle. Length was taken from the articulation to the anteriormost fibers of the external levator. Height was taken from the level of the articulation to the level of the anteriormost fiber.

Insertion Length: This defines the force lever length for a muscle. Since most muscles insert broadly, the muscle is measured along its midline (the central strand).

Displacement Values: The three dimensional arrangement (displacement) of a muscle can be resolved into three vectors (horizontal, vertical, and transverse) all at right angles to each other. These values were taken relative to the mandible for the central strand. Vertical measurements were taken perpendicular to the horizontal axis of the mandible. For all muscles except the external levator, this can be taken as representing the effective movement of the muscle. Horizontal measurements were taken parallel to the mandible. Transverse measurements were taken perpendicularly across the mandible (coronally). Horizontal and transverse values (except for the external levator) are wasted movement by the muscle, assuming the only function of the muscles is to open or close the jaw (i. e. there is no transverse or horizon-

tal jaw movement). The true length of the muscle has to be calculated from these values. The true length can be taken as representative of the total movement of the muscle.

Width and Thickness: According to Hiieme (1971) the strength of a muscle depends on the number of strands in it. Actually counting the number of strands is not very practical, but an estimate of the strength can be gained from the cross-sectional area. Since I was interested in only an approximation of relative strength, measuring the muscle width and thickness (depth) with an ocular micrometer was simple and adequate. The approximate area can be calculated by multiplying the two values.

Extreme difficulty was found with the posterior levator. This muscle did not cleanly separate from the overlying LME and part of the posterior levator may be included in the external levator measurements. In specimens four and five, so little of the posterior levator remained after excising the LME that meaningful measurements were impossible.

With these measurements we can estimate the relative efficiency and importance of the individual jaw muscles. The efficiency, calculated as the product of the leverage ratio and the movement ratio, is expressed as percent. The leverage ratio is the ratio of the force lever length (insertion length) to the action lever length (mandibular length). The movement ratio is between effective movement and total movement of the muscle. The relative

importance of the muscle is dependent on its effective force, calculated by multiplying the efficiency and cross-sectional area (i. e. total force) of the muscle. We can now consider the individual muscles. The formulae and results of calculations used in the following analyses, as well as vector diagrams, are given in Appendix I.

The M. depressor mandibulae is a simple case for analysis. There is only a slight horizontal displacement of the muscle so that most of the displacement inefficiency comes from transverse sources. The calculated true length is 40.2% of the snout-occiput length. This is very close to the vertical displacement length of 38%. The depressor suffers heavily, however, from its short working lever length (only seven as compared to 80 for the mandibular length). The resultant efficiency rating is only 8.3%, a very small value. The muscle is very large, the largest cross-sectional area of any jaw muscle (325). The large size of the muscle results in a respectable force despite its seemingly inefficient arrangement. (The geniohyoid muscle and gravity may also aid in opening the jaw, however.)

The M. levator mandibulae posterior is also a simple muscle for analysis, but difficulty in separating it from the overlying external levator muscle makes this analysis questionable. From the few observations made this muscle is not particularly important, at least for simple jaw closing. Both horizontal and trans-

verse displacement values are large. The effective (vertical) length of 21 compares poorly with the true length of 30.4. The working lever length is also shorter than for the other levator muscles and a very low efficiency of 9.5% results. This is the lowest efficiency of any levator. The size of the muscle also seems small, although few actual measurements could be taken. The cross-sectional area of 52 is probably too low, but does give an indication of the size. The calculated force of 4.9 is very small and the muscle seems relatively unimportant as an adductor. It may help position the mandible, however.

The deep portion of the M. levator mandibulae anterior is also simple. There is only a minor horizontal displacement of the muscle, which can be ignored. Inefficiency is caused by the transverse displacement, which is large despite the medially directed dorsal process of the prearticular on which the muscle inserts. The vertical measurement (27) compares well with the true length (32.5) despite the displacement. The working lever arm is longer than that of the posterior levator and an efficiency rating of 13.5% is indicated, significantly higher than for the posterior levator. The deep anterior levator, although narrow in width, is very thick and a cross-sectional area twice that of the posterior levator is indicated. The calculated force (14.6) is about three times the force of the posterior levator.

The superficial portion of the M. levator mandibulae anterior

would seem at first to present a difficult condition to analyze since the muscle extends so far from the insertion. The "parietal pulley" merely allows the levator to change direction. The muscle's efficiency is dependent on its arrangement between the parietal and insertion. This arrangement is similar to that of the deep portion and a similar efficiency rating seems reasonable. The cross-sectional area is slightly larger than that of the deep portion and the final force rating (20.8) is higher. The combined force of the anterior levator is 35.4, or seven times the force of the posterior levator.

The M. levator mandibulae externus presents the most complex situation since its working lever arm (posterior to the dentary point) does not parallel the action lever arm (the mandible). The external levator inserts on a slanted surface that compensates for the posterior orientation of its fibers. This relationship is similar to the way in which the temporal muscle works on the coronoid process in mammals (DeMar and Barghusen 1972). Presence of an angled insertion means the effective movement is not equivalent to the vertical displacement, but is at a right angle to the line of insertion (the dorsal edge of the dentary posterior to the dentary point). The angle at the articular can be calculated from the length and height of the process (the tangent relationship). This angle is about  $20^{\circ}$ . Using the vertical and horizontal displacement values, the angle by which the externus muscle is deflected from

the perpendicular (again a tangent relationship) is calculated to be  $28^{\circ}$ . The angle the externus makes with the lever arm becomes obvious if a line parallel to the mandible is made at the insertion. The angle of the fibers with the process equals the angle of the process ( $20^{\circ}$ ) plus  $90^{\circ}$  minus the angle of the fibers from the perpendicular ( $28^{\circ}$ ). The resultant angle is  $82^{\circ}$ , indicating that the muscle is not fully effective (which would be at  $90^{\circ}$ ). We can now calculate the efficiency of the muscle. The total length of the external levator is calculated to be 38, but the effective movement is not equal to the vertical displacement. The effective length must be considered at right angles to the lever. The right angle to the lever must be  $20^{\circ}$  off the true vertical. The length at right angle to the lever can be calculated by dividing the vertical displacement by the cosine of  $20^{\circ}$ . The effective length comes to 34.6. Comparing this to the actual length we have one component of the efficiency rating. Combined with the lever arm ratio, a total efficiency of 15.9% is calculated. This is the highest rating for any jaw muscle. The muscle is also the largest single levator and the net force (28.6) is higher than any other calculated for an individual muscle, although it is slightly less than the combined force of the anterior levators (35.4).

## CONCLUSIONS

Some broad conclusions can be drawn from the analysis of the jaw muscles:

1.) Muscle efficiency is never greater than 20%. Most of the loss in efficiency is due to differences in lever lengths. Gape capability must, therefore, outweigh efficiency in determining structure.

2.) Large losses in efficiency are due to transverse displacements. Transverse differences may have some function beyond simple jaw closing, possibly in respiration (Szarski 1962).

3.) The mandibular depressor is particularly hindered by a short working lever arm. It is at its most efficient position when the jaw is closed and will lose efficiency as the jaw opens. (This would be appropriate for a gape and suck feeder needing to open the mouth quickly to capture prey.)

4.) The posterior mandibular levator is very inefficient as a jaw adductor at all times. It will lose even more efficiency as the jaw opens.

5.) The anterior levator (both portions) is at its greatest efficiency when the jaw is closed. The mechanical efficiency will decline as the jaw opens. The greater overall length of the superficial portion would allow a greater amount of movement for the muscle while retaining physiological efficiency (Hildebrand 1974). This may mean the LMAs is the most efficient levator when the jaw

is fully opened, despite the mechanical arrangement, and may initiate the jaw closing.

6.) The external levator has not reached its full efficiency when the jaw is closed. As the jaw opens it will further decline in efficiency.

This analysis of the jaw muscles indicates that the levators are just starting to achieve their maximum efficiency when the jaw is closed. This would, of course, be useful in holding prey that is still alive or needs to be torn by head shaking. This implies that this is not a pure kinetic-inertial system as defined by Olson (1961), but has considerable force available when the jaws are occluded and approaches a static-pressure system.

## SUMMARY

The cranial and cervical anatomy of Taricha torosa can best be understood in relation to its feeding. Taricha and other salamandrids lack the food capturing tongues of anurans and advanced salamanders (plethodontids). Instead they must rely on grasping with the jaws to capture prey. In addition, T. torosa feeds for part of the year in the water and shows adaptations for gape and suck feeding.

The skull shows considerable reduction from the primitive solid roof. The opening of the sides of the skull and the consequent development of an arch are similar to the pattern seen in reptiles (similar to Sphenodon according to Smith 1927). Similarity, as well, in relative dominance of the external and anterior levators is indicated (Starrett 1968).

The shape of the skull is largely determined by the muscles that attach to it. There is little of the posterior skull that is not involved with and sculptured by muscle origins and insertions. The large temporo-orbital fenestra is filled by the large eye (which can be pulled into the opening to aid in swallowing) and the levator muscles. The presence of the postorbital arch is rare among salamanders and may be a primitive feature as suggested by Hilton (1947), but more likely it is an adaptation to allow an increase in the size of the external levator. This muscle may be more important in this species than in other salamanders. The ending of

the maxilla well anterior to the jaw articulation may also be an adaptation to remove hindrances to the action of the levator. Extending the origin of part of the anterior levator off the skull, while neither unique nor as extensive as in other salamanders, is complete. This removes it from the crowded temporal region and may increase its physiological efficiency (see p. 48). Limiting the origin to a single vertebra may allow more movement of the head. Use of the parietal as a pulley for part of the anterior levator may not be unique, but the clearly defined trough is not indicated for forms lacking a postorbital arch. The squamosal differs from the squamosal in other salamanders, not only in contributing to the postorbital arch, but in the posterior process that forms the fossa for the origin of the large depressor muscle. Limiting the depressor to the skull allows for greater head movement. The base of the skull is also broader than in other salamanders. This may be to brace the posterior process of the squamosal, but may also be related to the large cervical muscles attaching to the skull. (The crested insertion of the dorsalis muscle supports this contention.) The larger cervical muscles would indicate that the importance of head movement is greater in this species. This is evident in the feeding, particularly in the water.

The mandible shows two major adaptations to the insertion of the jaw adductors: the dentary point that increases the efficiency of the external levator and the dorsal process of the prearticular

that helps to reduce the transverse displacement of the anterior levator. Major mechanical inefficiencies of the arrangement of the skull are the considerable transverse displacement of the jaw muscles and the lack of a real posterior process for the depressor. These inefficiencies are common in salamanders, however.

The branchial elements of salamandrids are far less mobile than in plethodontids, and T. torosa they are larger and more ossified than in most other salamandrids. The tongue, associated with the copula of the first branchial, is only moderately developed and limited in its movement. Lack of tongue mobility would limit T. torosa to larger food items than plethodontids and even some salamandrids. This puts an emphasis on the jaw and cervical muscles to capture, hold, and tear food. The reserve force remaining when the jaws are closed is thus clearly important. The highly sculptured skull of Taricha torosa, so formed in relation to these muscles, is the result of this emphasis.

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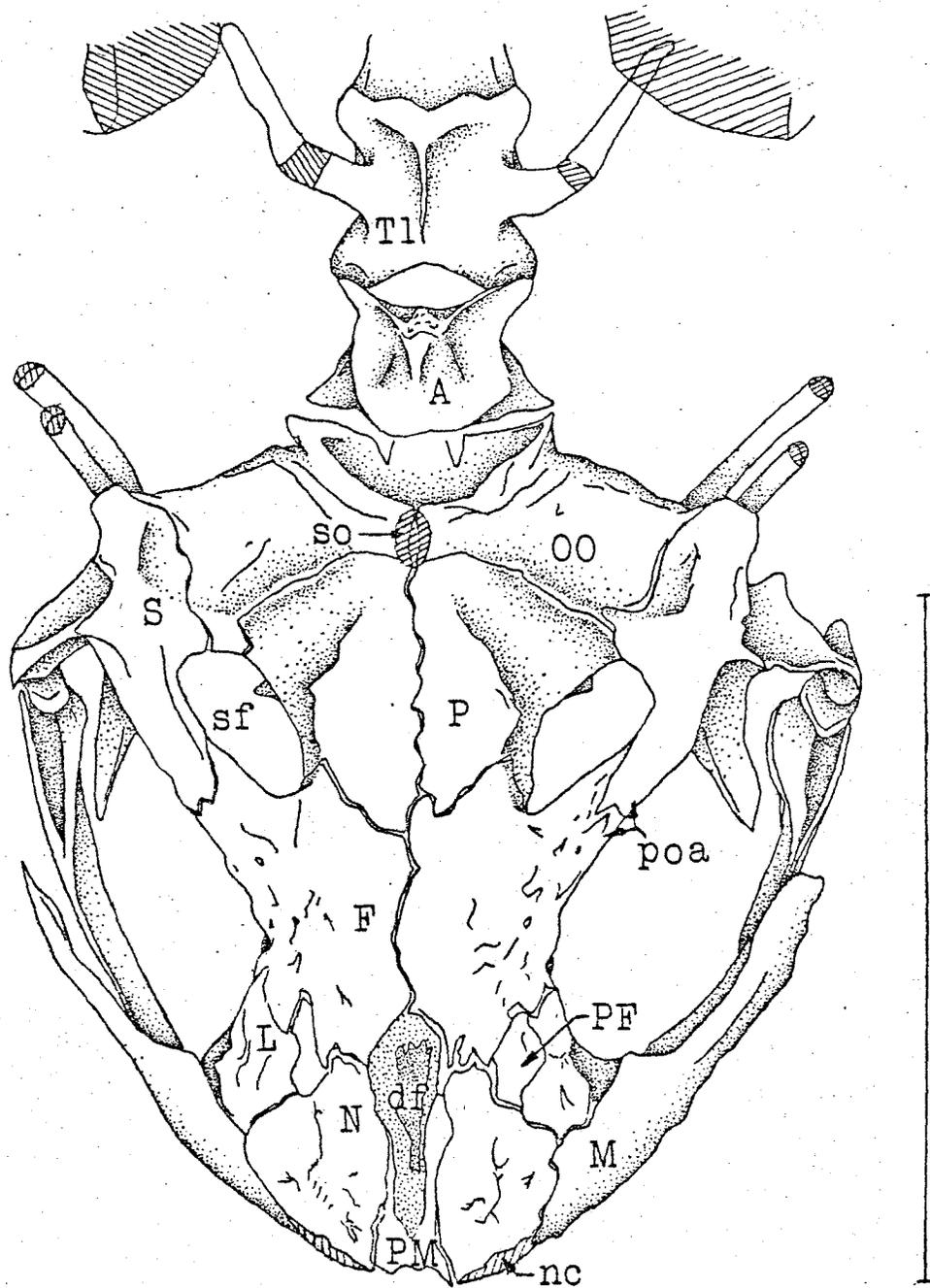
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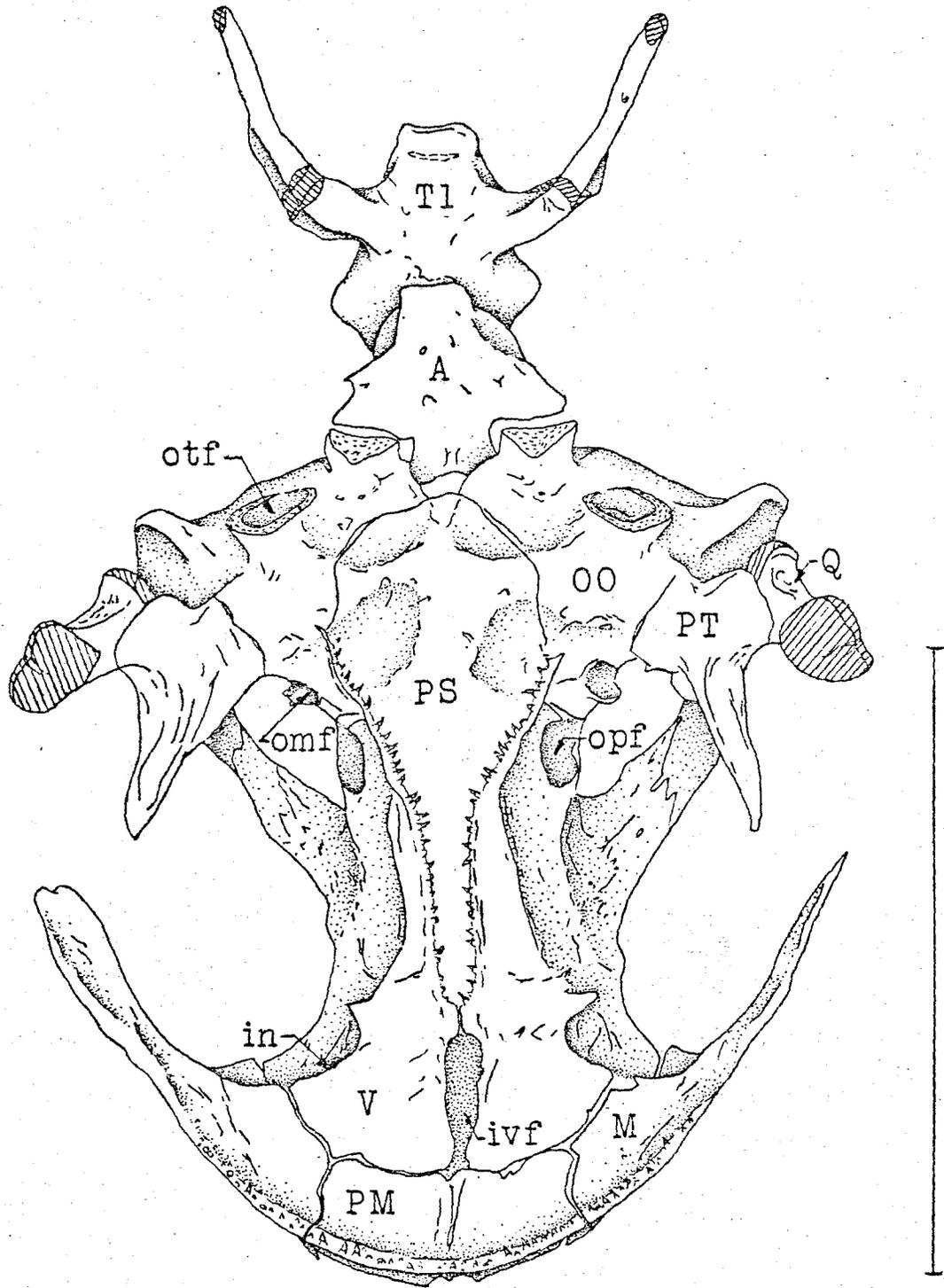
## FIGURE 1

Dorsal view of the skull and first two vertebrae. 7X. Abbreviations: A, atlas; df, dorsal fontanelle; F, frontal; L, lacrimal, M. maxilla; N, nasal; nc, nasal cartilage; OO, occipito-otic; P, parietal; PF, prefrontal; PM, premaxilla; poa, postorbital arch; S, squamosal; sf, supratemporal fenestra; so, supraoccipital cartilage; T1, first thoracic vertebra and rib. (Scale indicates one centimeter.)



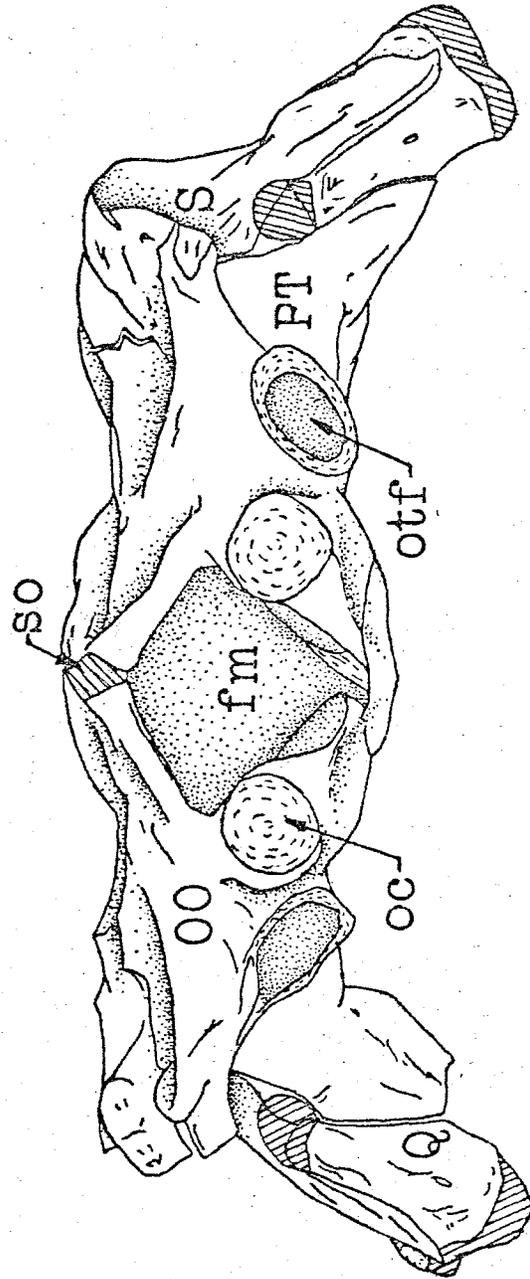
## FIGURE 2

Ventral view of the skull and first two vertebrae. 7X. Abbreviations: A, atlas; in, internal nares; ivf, intervomerine fontanelle; M, maxilla; omf, oculomotor foramen; OO, occipito-otic; opf, optic foramen; of, otic foramen; PM, premaxilla; PS, parasphenoid; PT, pterygoid; Q, quadrate; T1, first thoracic vertebra and rib; V, vomer. (Scale indicates one centimeter.)



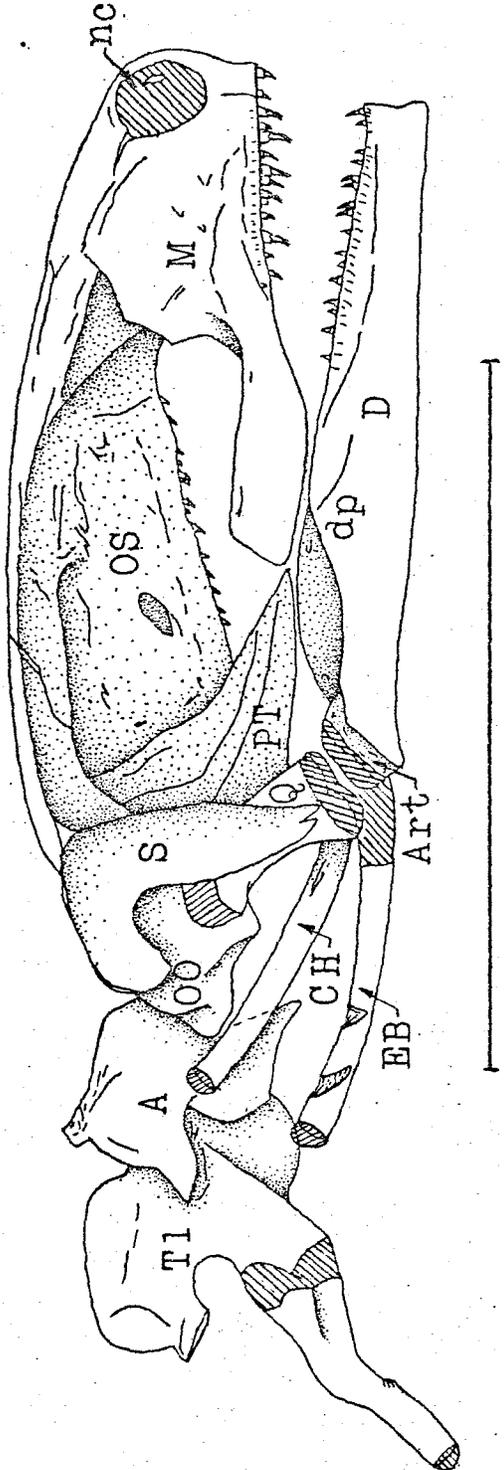
## FIGURE 3

Occipital view of the skull. 7X. Abbreviations: fm, foramen magnum; oc, occipital condyle; OO, occipito-otic; of, otic foramen; PT, pterygoid; Q, quadrate; S, squamosal; so, supraoccipital cartilage. (Scale indicates one centimeter,)



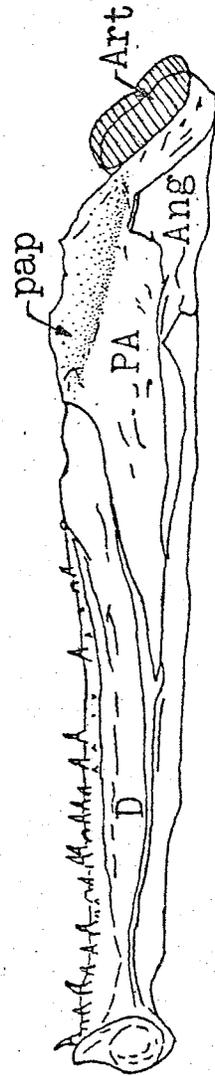
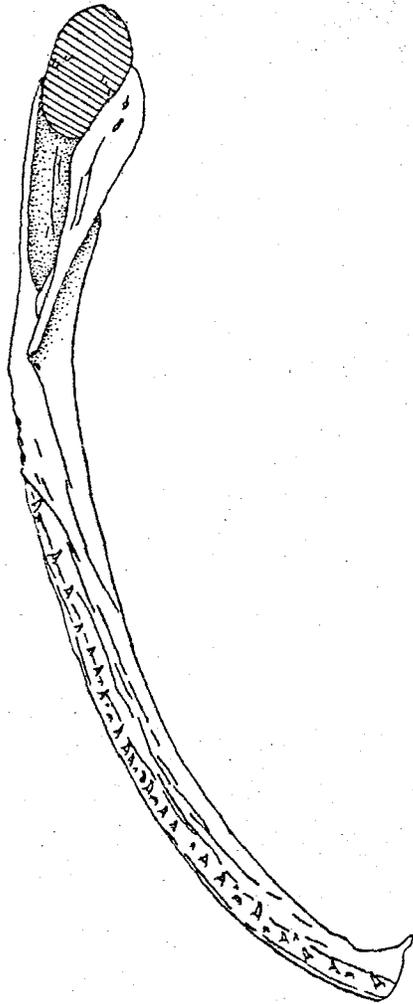
## FIGURE 4

Right lateral view of the skull and mandible. Branchial elements and first two vertebrae in situ. 7X. Abbreviations: A, atlas; Art, articular; CH, ceratohyoid; D, dentary; dp, dentary point; EB, first epibranchial; M, maxilla; nc, nasal capsule; OO, occipito-otic; OS, orbitosphenoid; PT, pterygoid; Q, quadrate; S, squamosal; T1, first thoracic vertebra and rib. (Scale indicates one centimeter.)



## FIGURE 5

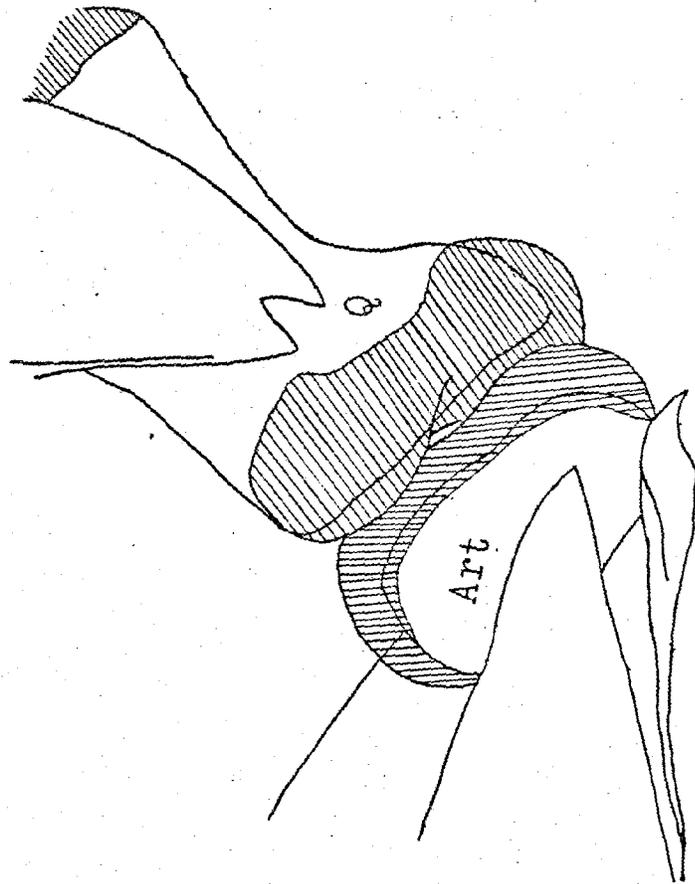
Dorsal and medial views of the right mandible. 10X. Abbreviations: Ang, angular; Art, articular; D, dentary; PA, prearticular; pap, dorsal process of the prearticular. (Scale indicates one centimeter.)



## FIGURE 6

Detail of the jaw articulation. Left lateral view. 25X.

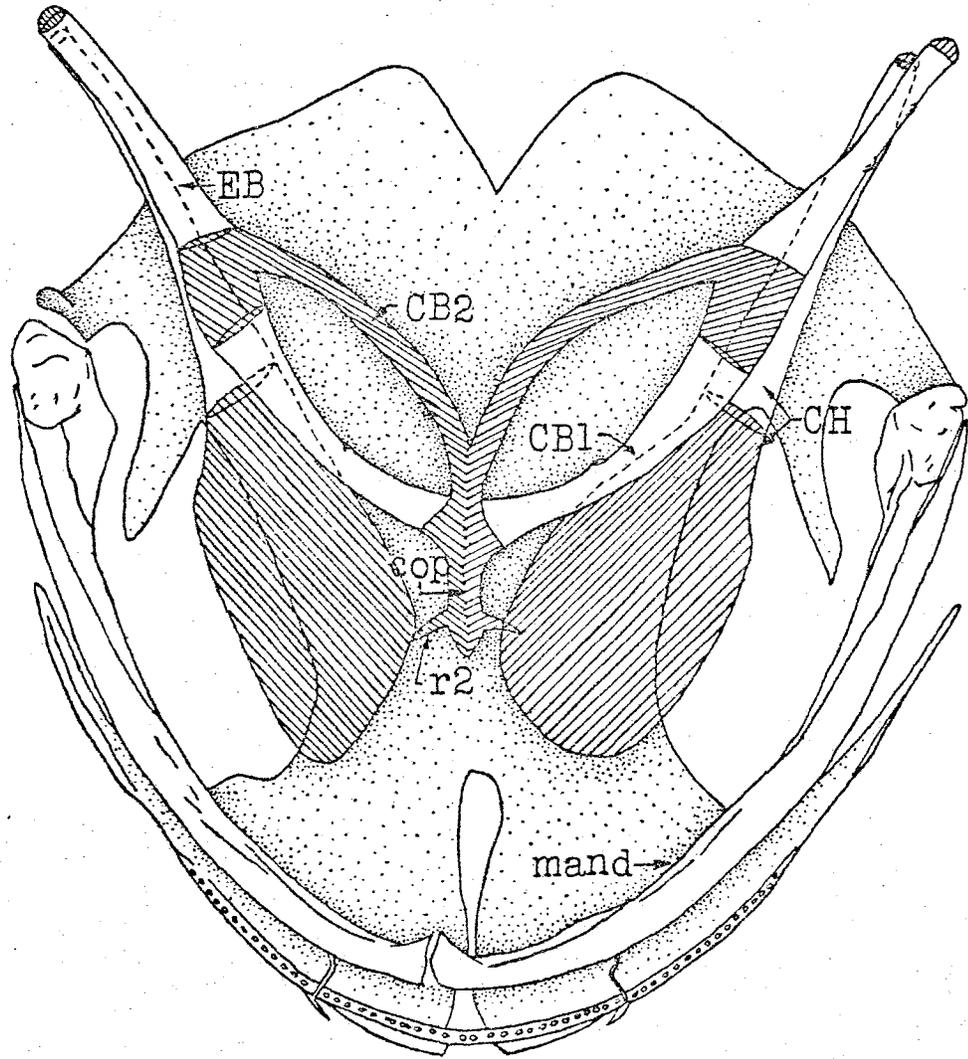
Abbreviations: Art, articular; Q. quadrate.



## FIGURE 7

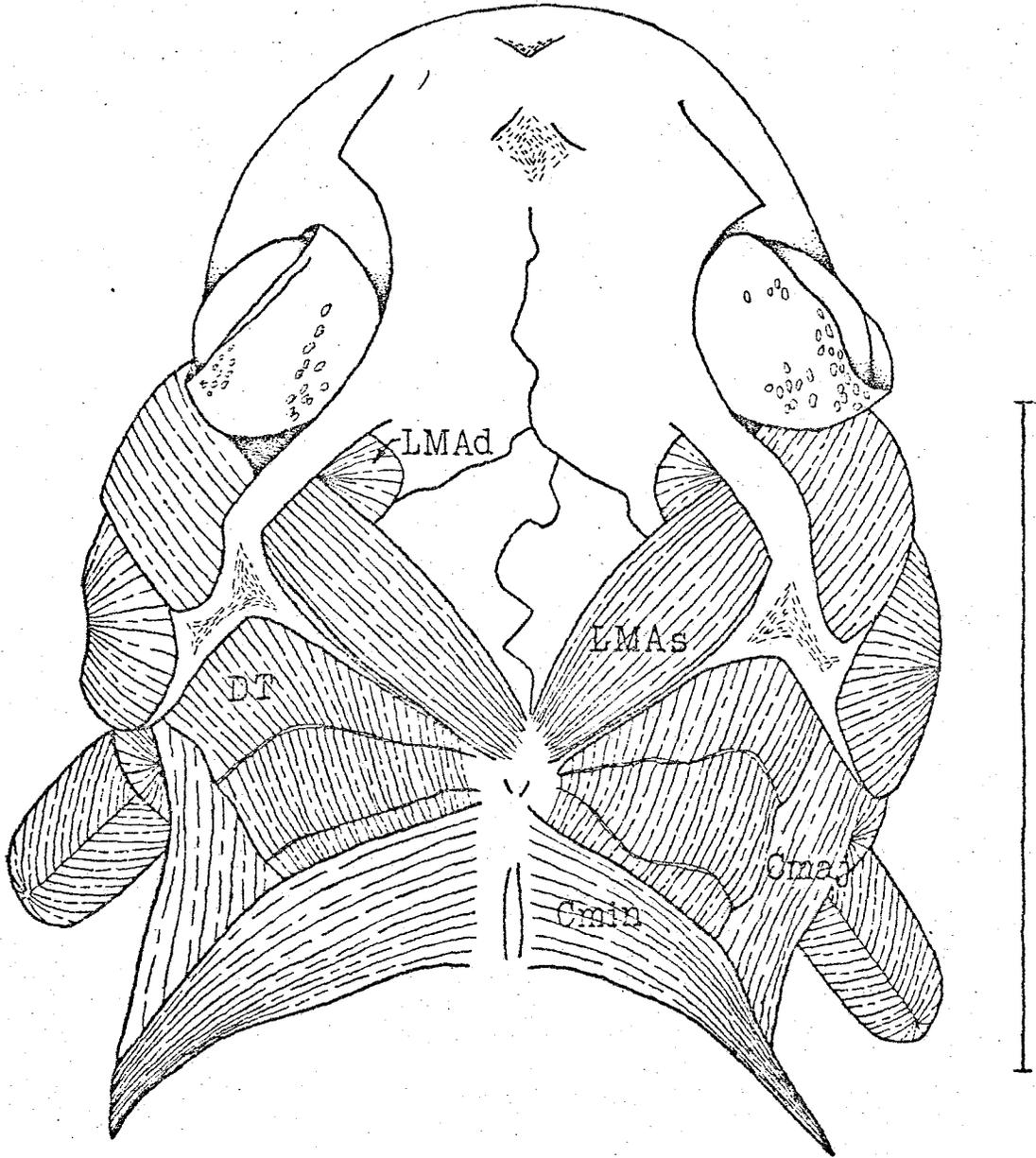
Ventral view of the mandibles and branchial elements in situ.

7X. Abbreviations: CB1, first ceratobranchial; CB2, second ceratobranchial; CH, ceratohyoid; cop, copula; EB, epibranchial; mand, mandible; r2, second radius. (Scale indicates one centimeter.)



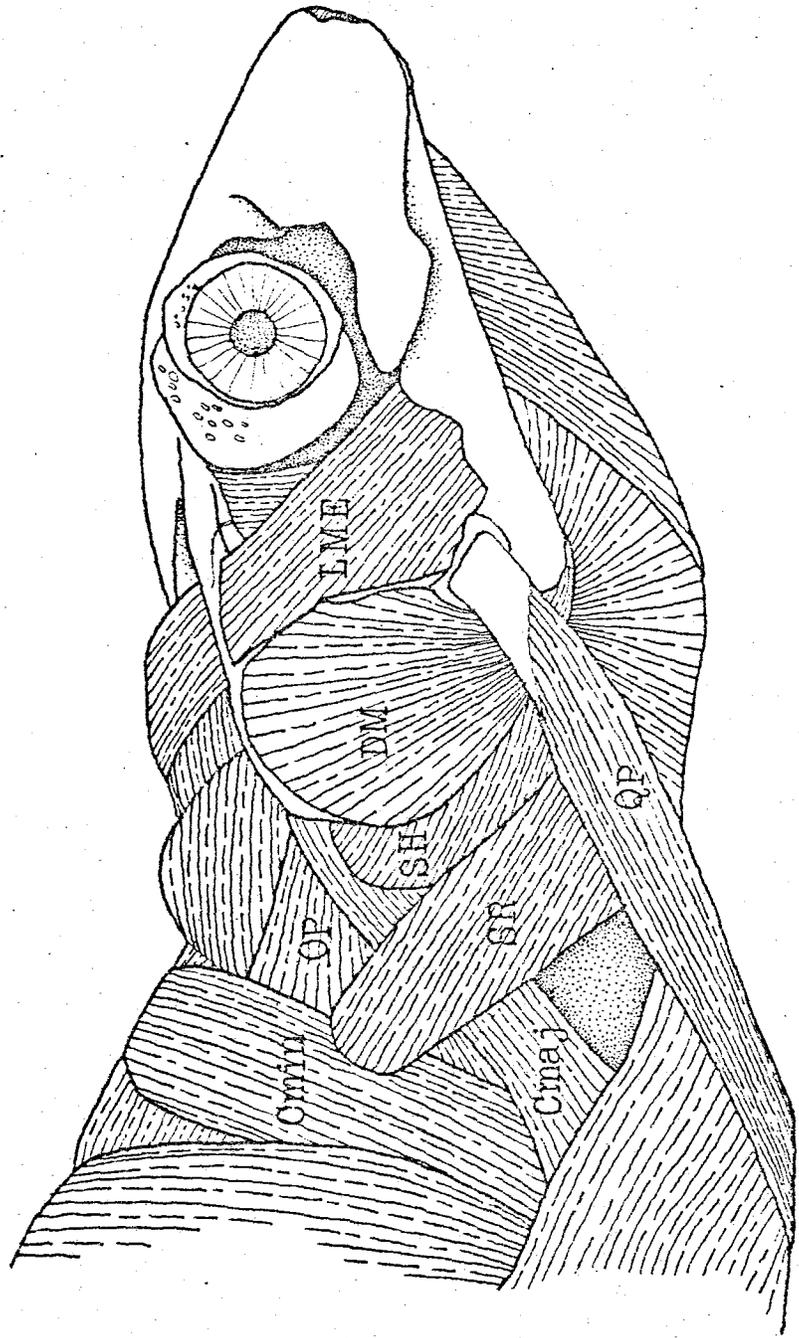
## FIGURE 8

Dorsal view of the superficial muscles. 7X. Abbreviations: Cmaj, M. cucullaris major; Cmin, M. cucullaris minor; DT, M. dorsalis trunci; LMA<sub>d</sub>, M. levator mandibulae anterior - deep portion; LMA<sub>s</sub>, M. levator mandibulae anterior - superficial portion. (Scale indicates one centimeter.)



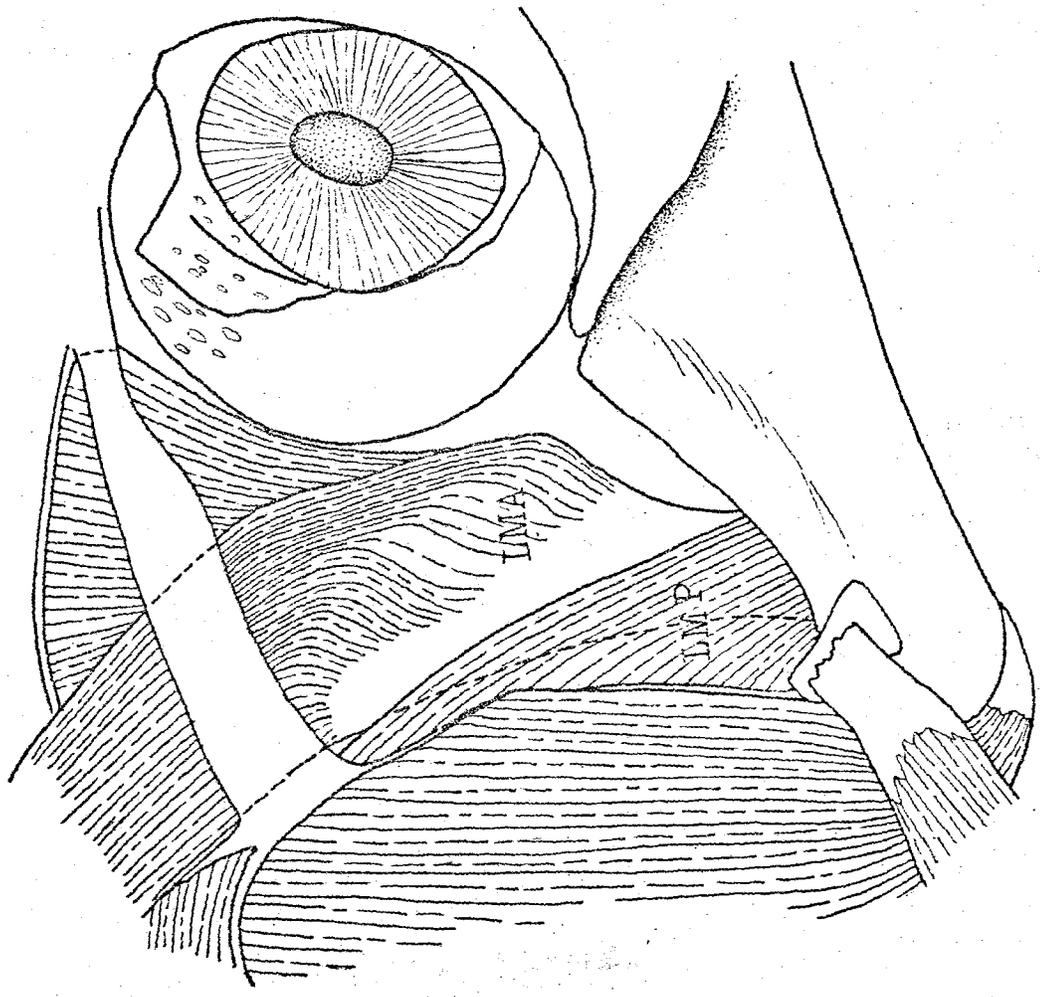
## FIGURE 9

Right lateral view of the superficial muscles. 7X. Abbreviations: Cmaj, M. cucullaris major; Cmin, M. cucullaris minor; DM, M. depressor mandibulae; LME, M. levator mandibulae externus; OP, M. opercularis; QP, M. quadratopectoralis; SH, M. subhyoideus; SR, M. subarcualis rectus I. (Scale indicates one centimeter.)



## FIGURE 10

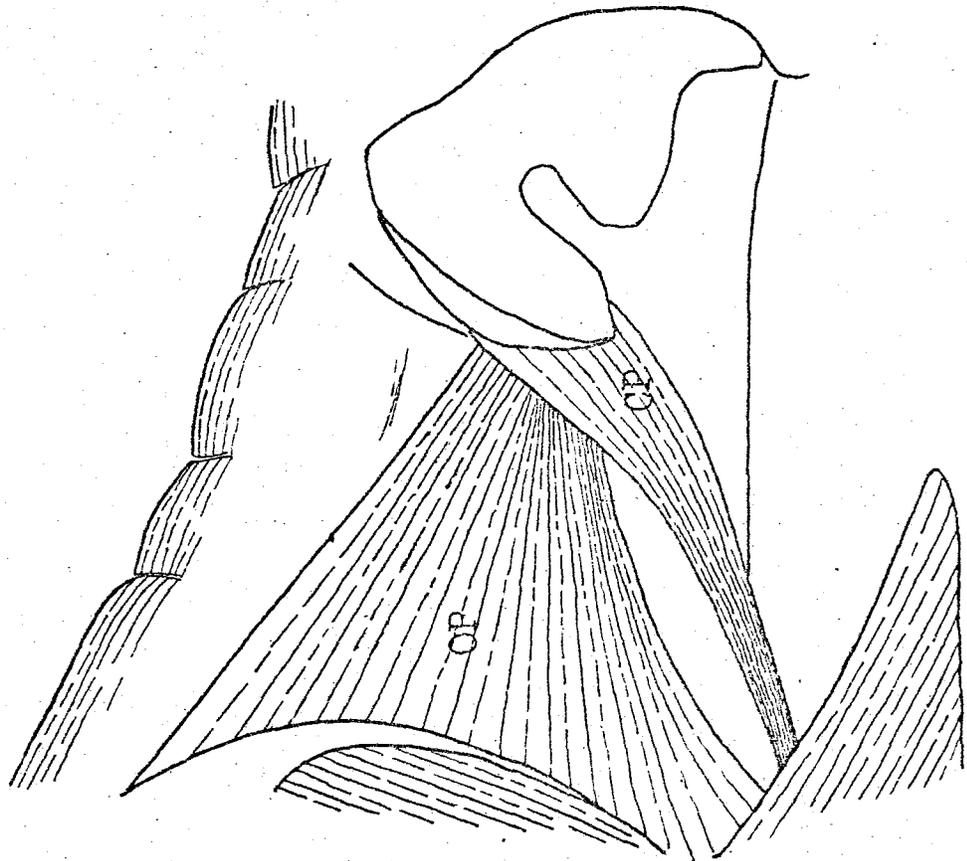
Detail of the insertion of the deep adductors. M. levator mandibulae externus removed. 15X. Abbreviations: LMA, M. levator mandibulae anterior; LMP, M. levator mandibulae posterior.



## FIGURE 11

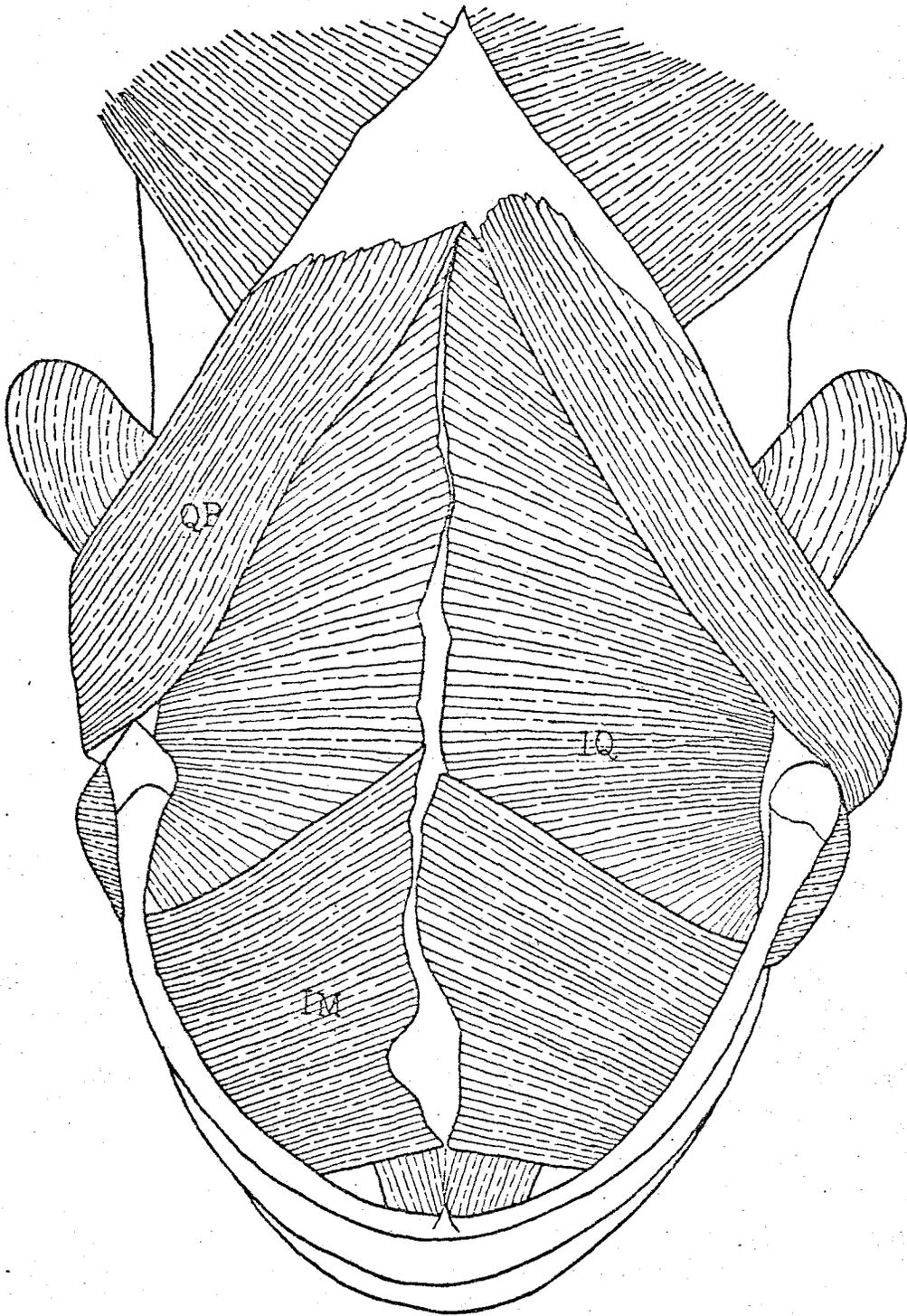
Detail of the right cervical muscles. Major and minor cucullar, mandibular depressor, all ventral, and branchial muscles removed.

10X. Abbreviations: CP, M. cephalo-dorso-subpharyngeus; OP, M. opercularis.



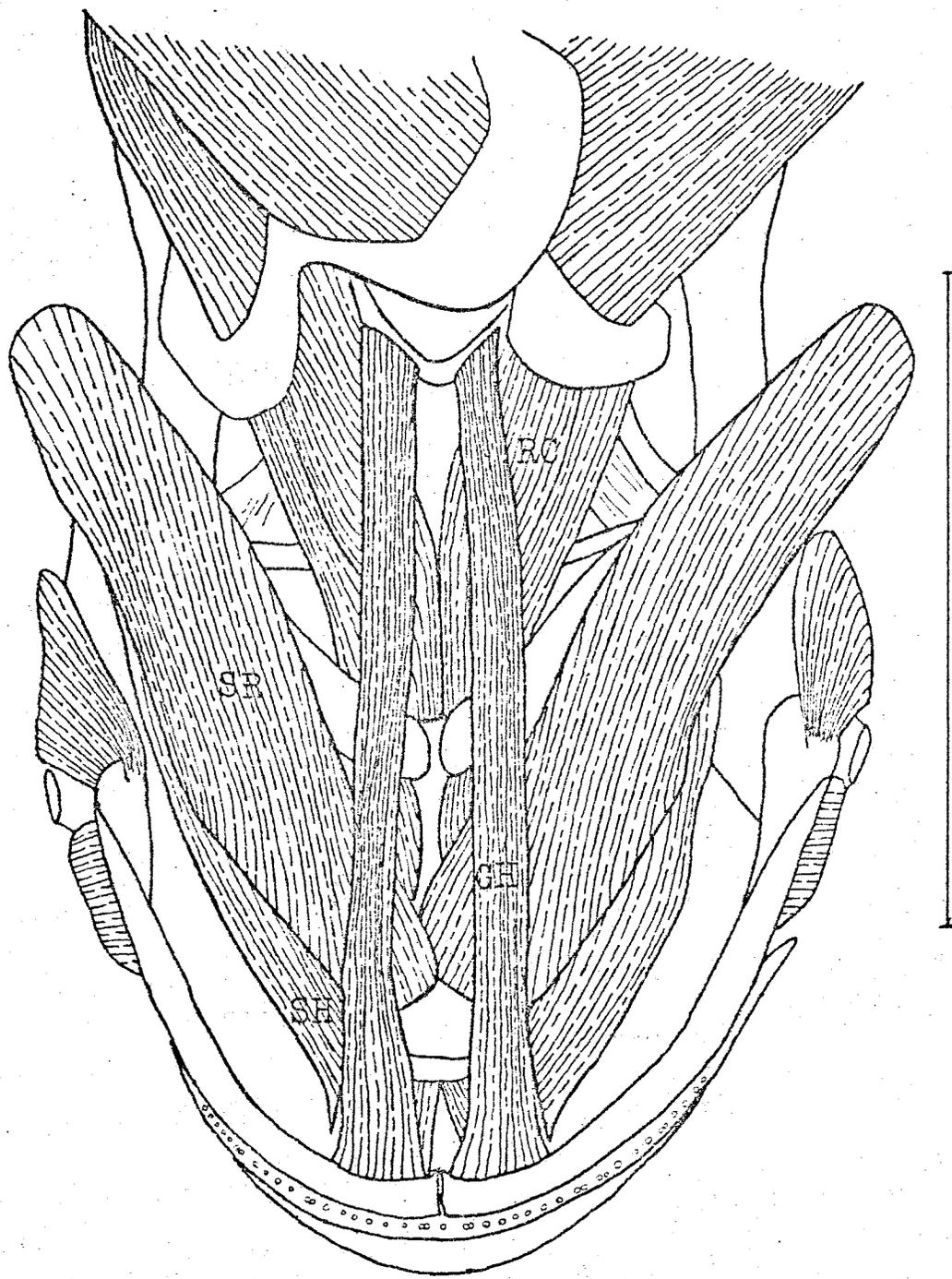
## FIGURE 12

Superficial ventral muscles. 7X. Abbreviations: IM, M. intermandibularis posterior; IQ, M. interossaquadrata; QP, M. quadratopectoralis. (Scale indicates one centimeter.)



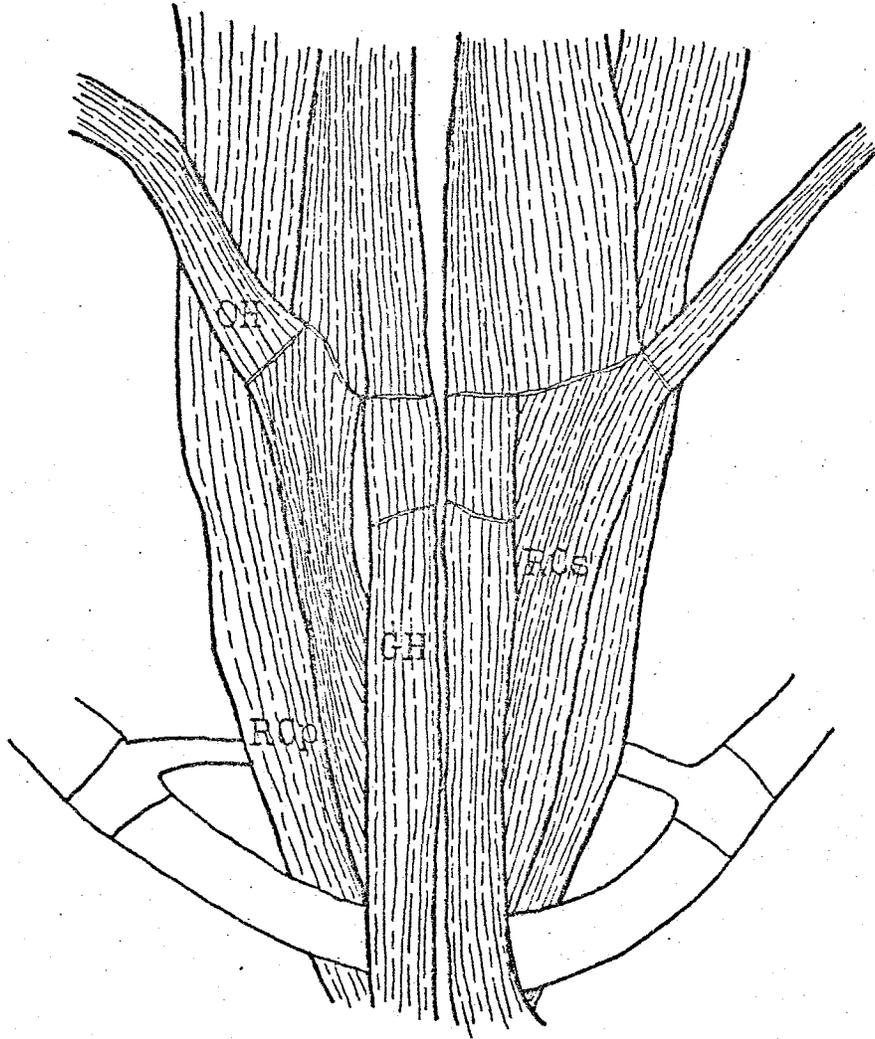
## FIGURE 13

Deeper ventral muscles (branchial muscles). 7X. Abbreviations: GH, M. geniohyoideus; RC, M. rectus cervicis; SH, M. subhyoideus; SR, M. subarcualis rectus I. (Scale indicates one centimeter.)



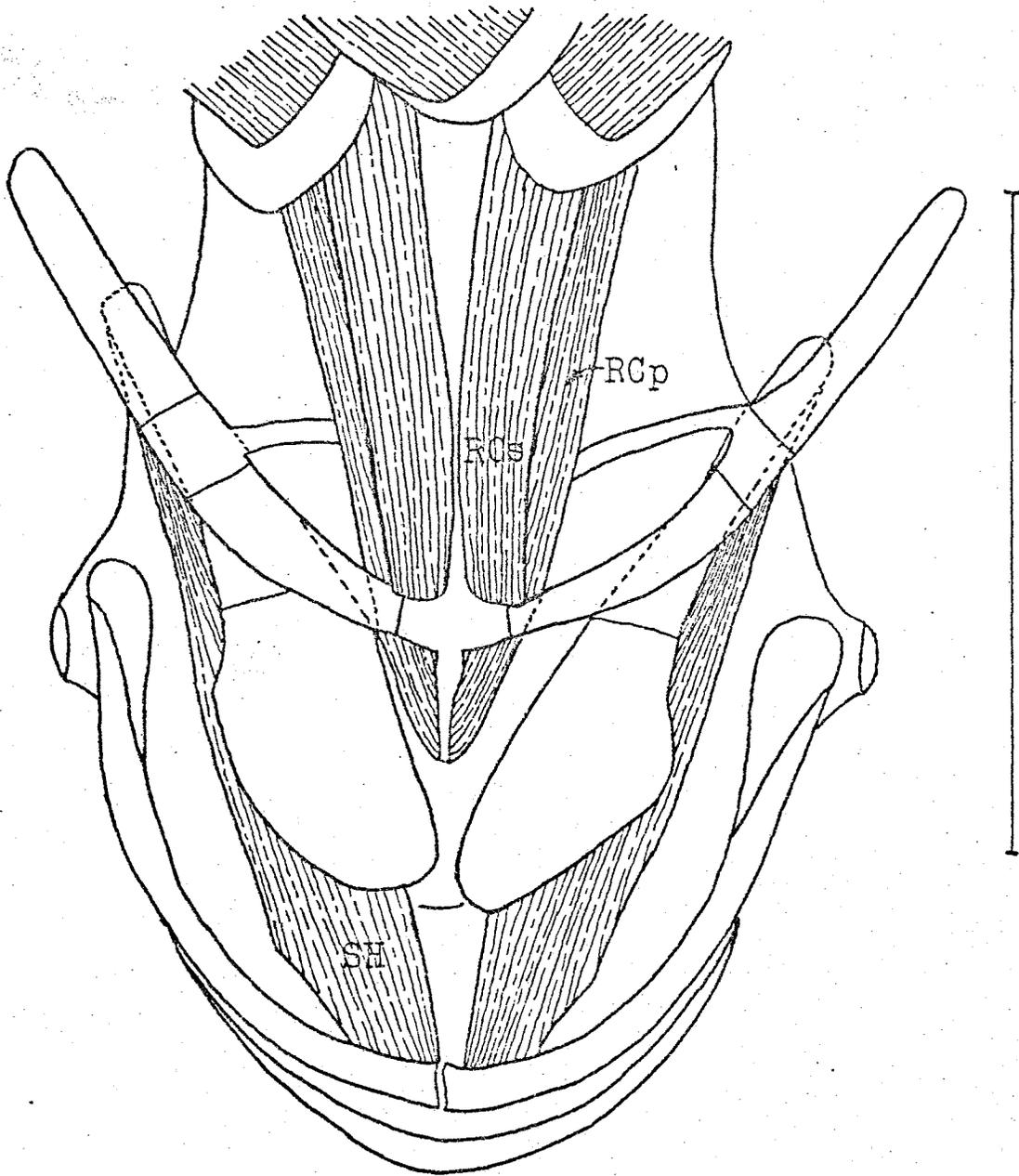
## FIGURE 14

Detail of the origin of the cervical rectus and geniohyoid muscles. 10X. Abbreviations: GH, M. geniohyoideus; OH, M. omohyoideus; RCp, M. rectus cervicis profundus; RCs, M. rectus cervicis superficialis.



## FIGURE 15

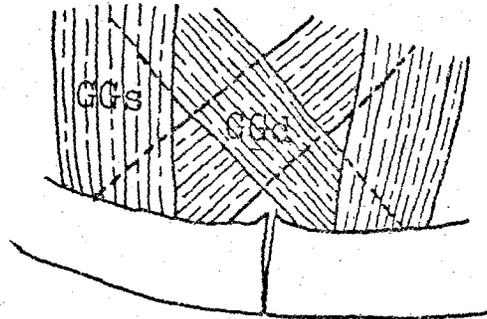
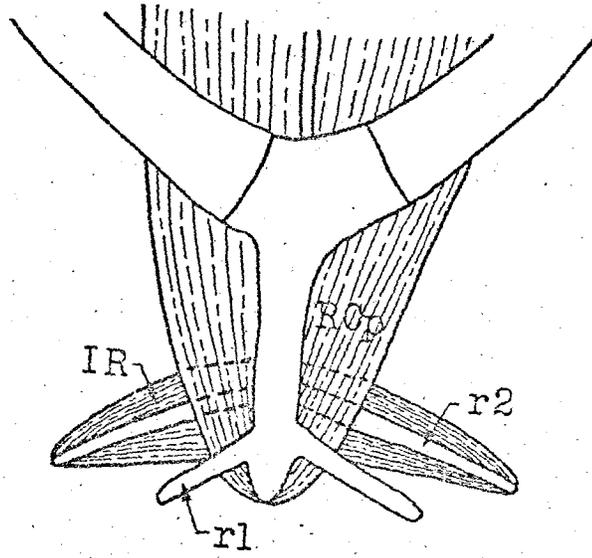
Cervical rectus muscle and the unusual deep slip of the subhyoid muscle. 7X. Abbreviations: RCp, M. rectus cervicis profundus; RCs, M. rectus cervicis superficialis; SH, M. subhyoideus. (Scale indicates one centimeter.)



## FIGURE 16

Muscles of the tongue region and an example of a double radii.

15X. Abbreviations: GGd, deep portions of the medial M. genioglossus; GGs, superficial portions of the medial M. genioglossus; IR, M. interradiialis; r1, first radius; r2, second radius; RCp, M. rectus cervicis profundus.



## FIGURE 17

Muscles of the ventral skull. 7X. Abbreviations: RB, M. retractor bulbi; SV, M. subvertebralis. (Scale indicates one centimeter.)

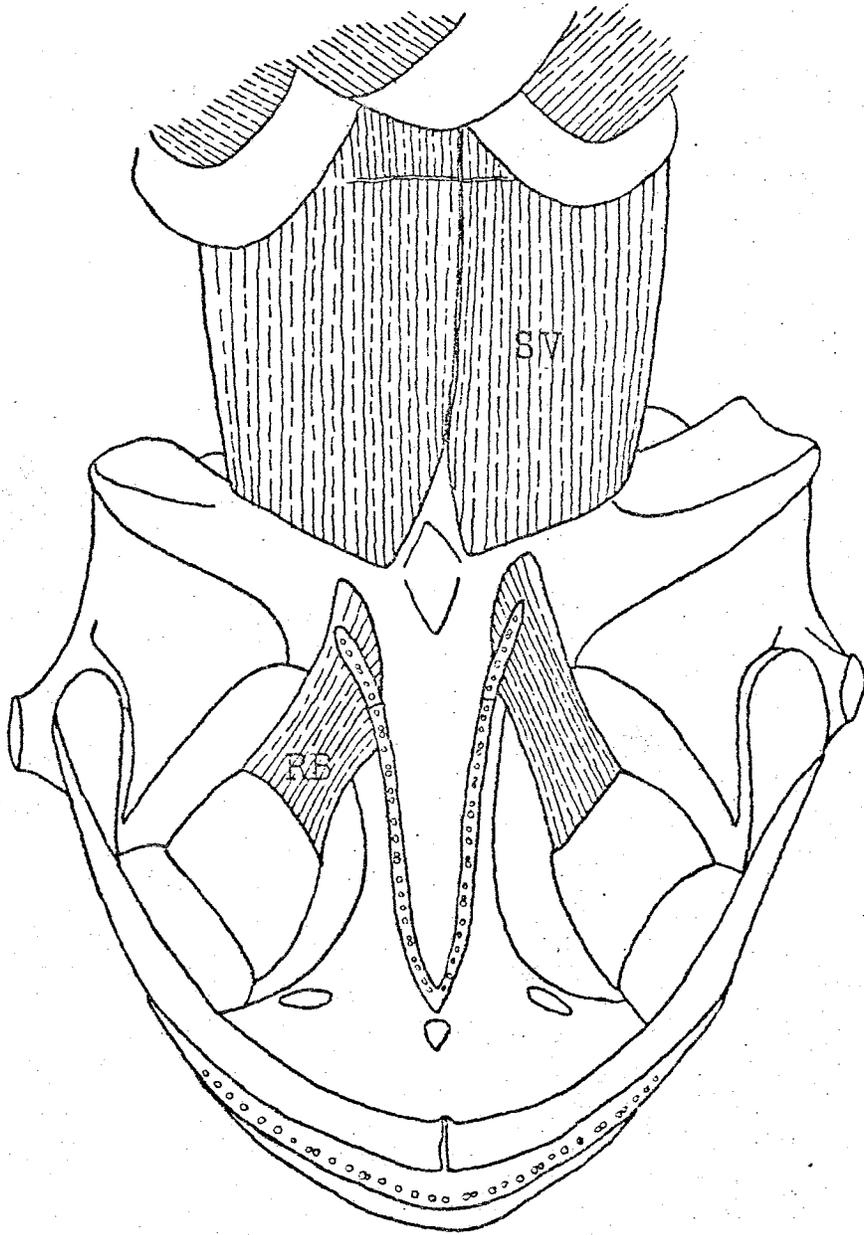


TABLE I

MEASUREMENTS OF PARAMETERS FOR THE FUNCTIONAL  
ANALYSIS OF THE JAW MECHANISM (mm)

MEASUREMENT	SPECIMEN				
	1	2	3	4	5
Snout-Vent Length	67.1	63.1	70.3	67.3	65.1
Mandibular Length	10.0	8.3	10.0	10.8	9.2
Dentary Point Length	2.9	3.5	2.9	2.9	2.5
Height	0.8	1.3	1.4	1.0	0.8
LME					
Insertion Length	1.3	1.7	1.7	1.9	1.7
Displacement					
Vertical	3.5	3.9	3.7	3.5	3.3
Horizontal	2.2	2.1	1.8	2.1	1.5
Transverse	1.7	2.5	2.5	1.9	1.7
Cross-sectional Width	2.9	2.3	2.0	2.1	1.9
Thickness	1.3	1.0	1.1	1.5	1.3
DM					
Insertion Length	-	0.8	0.8	0.8	0.8
Displacement					
Vertical	4.6	5.0	4.8	4.2	4.2
Horizontal	0	0.6	0.6	0	0
Transverse	2.1	1.7	1.5	1.3	1.7
Cross-sectional Width	3.4	3.0	3.2	2.9	2.8
Thickness	1.3	1.6	1.5	1.5	1.6

TABLE I (continued)

MEASUREMENT	SPECIMEN				
	1	2	3	4	5
LMP					
Insertion Length	-	1.3	1.2	-	-
Displacement					
Vertical	2.1	3.3	2.2	-	-
Horizontal	1.3	2.1	2.2	-	-
Transverse	-	1.9	2.3	1.5	1.9
Cross-sectional					
Width	1.0	1.5	2.2	-	-
Thickness	-	0.5	0.3	-	-
LMA					
Insertion Length	0.9	1.5	1.7	1.9	2.1
Displacement					
Horizontal	0	0	0	0	0
Transverse	-	2.3	2.1	2.1	2.6
LMA <sub>d</sub>					
Vertical	4.5	3.1	3.2	2.5	2.9
Width	1.9	1.0	0.6	0.8	0.6
Thickness	1.0	1.5	1.9	1.3	1.5
LMA <sub>s</sub>					
True Length	5.3	5.4	8.0	7.9	7.5
Width	1.9	1.5	1.8	1.8	1.7
Thickness	1.2	2.0	1.2	1.3	0.8

ABBREVIATIONS (Tables I and II): DM, M. depressor mandibulae; LMA, M. levator mandibulae anterior; LMA<sub>d</sub>, deep portion of the LMA; LMA<sub>s</sub>, superficial portion of the LMA; LME, M. levator mandibulae externus; LMP, M. levator mandibulae posterior.

TABLE II

MEASUREMENTS OF PARAMETERS AS PERCENT OF THE  
SNOUT-OCCIPUT LENGTH

MEASUREMENT	SPECIMEN					Mean
	1	2	3	4	5	
Mandibular Length	82	73	78	88	77	80
Dentary Point Length	23	31	23	24	21	25
Height	6	11	11	9	7	9
LME						
Insertion Length	10	15	13	15	14	14
Displacement						
Vertical	28	34	29	29	28	30
Horizontal	18	18	14	17	13	16
Transverse	14	22	20	16	14	17
Cross-sectional Width	24	20	15	17	16	18
Thickness	11	9	19	12	11	10
DM						
Insertion Length	-	7	7	7	7	7
Displacement						
Vertical	37	44	38	34	36	38
Horizontal	0	6	5	0	0	2
Transverse	17	15	12	10	10	13
Cross-sectional Width	18	26	25	24	24	25
Thickness	11	14	12	12	14	13

TABLE II (continued)

MEASUREMENT	SPECIMEN					Mean
	1	2	3	4	5	
LMP						
Insertion Length	-	11	10	-	-	11
Displacement						
Vertical	17	29	28	-	-	21
Horizontal	10	18	17	-	-	15
Transverse	-	17	18	15	18	17
Cross-sectional						
Width	8	13	17	-	-	13
Thickness	-	5	3	-	-	4
LMA						
Insertion Length	8	13	13	15	18	13
Displacement						
Horizontal	0	0	0	0	0	0
Transverse	-	20	16	17	17	18
LMAd						
Vertical	37	27	25	21	25	27
Width	15	9	5	6	5	9
Thickness	8	13	15	11	13	12
LMAs						
True Length	44	47	63	65	63	56
Width	15	13	15	11	13	12
Thickness	20	17	9	10	7	11

## APPENDIX I

ANALYSIS OF THE JAW MECHANISM IN T. TOROSA

## FORMULAE, DIAGRAMS, AND RESULTS

## ABBREVIATIONS:

Dh, height of the dentary point; Dl, length of the dentary point; E, efficiency; F, effective force; h, horizontal displacement; La, action lever (mandibular length); LE, effective length; Lf, force lever (insertion length); LT, true length; th, cross-sectional width; tr, transverse displacement; v, vertical displacement; w, cross-sectional width.

## GENERAL FORMULAE:

$$LT = \sqrt{(v)^2 + (h)^2 + (t)^2}$$

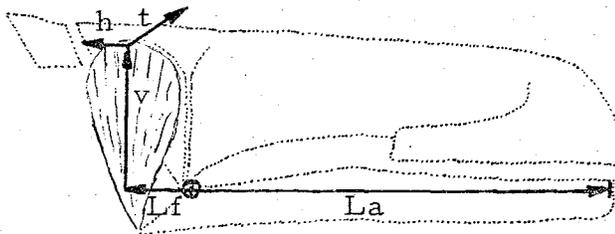
$$E = \frac{LE}{LT} \times \frac{Lf}{La} \times 100\%$$

$$F = (w) \times (th) \times (E)$$

(Values used in the calculations are given in Table II)

## DIAGRAMS AND RESULTS

## M. DEPRESSOR MANDIBULAE



$$LE = v$$

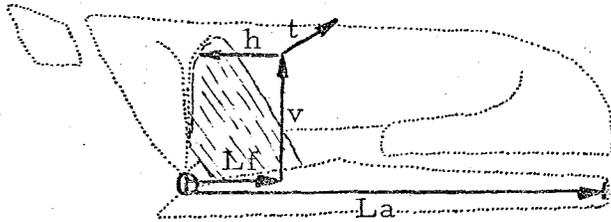
$$LT = 40.2$$

$$E = 8.3\%$$

$$F = 27.0$$

## APPENDIX I (continued)

## M. LEVATOR MANDIBULAE POSTERIOR



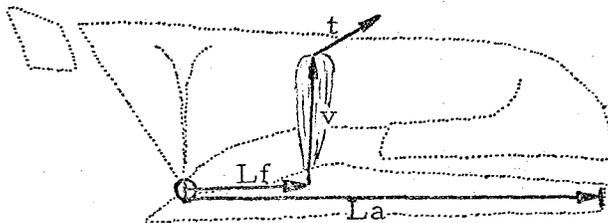
$$LE = v$$

$$LT = 30.4$$

$$E = 9.5\%$$

$$F = 4.9$$

## M. LEVATOR MANDIBULAE ANTERIOR (DEEP PORTION) (LMAd)



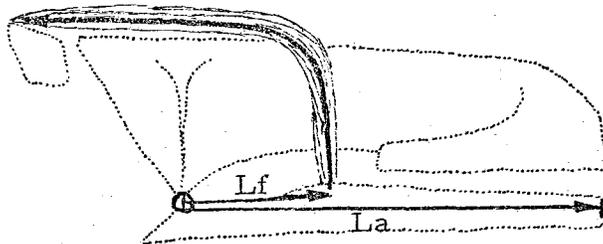
$$LE = v$$

$$LT = 32.5$$

$$E = 13.5\%$$

$$F = 14.6$$

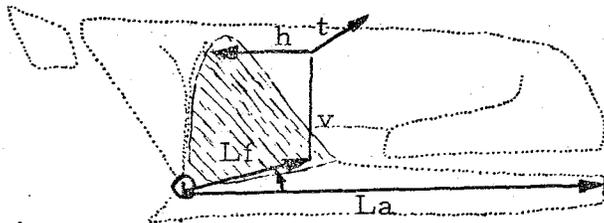
## M. LEVATOR MANDIBULAE ANTERIOR (SUPERFICIAL PORTION)



$$E = E \text{ of LMAd} = 9.5\%$$

$$F = 20.8$$

## M. LEVATOR MANDIBULAE EXTERNUS



$$LE = 34.6$$

$$LT = 38$$

$$E = 15.9\%$$

$$F = 28.6$$

(For the derivation of the effective length of the M. levator mandibulae externus see the next page.)

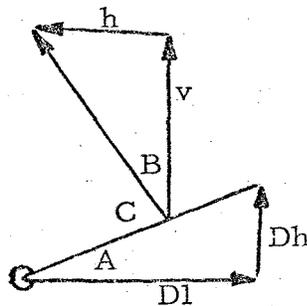
## APPENDIX I (continued)

DERIVATION OF THE EFFECTIVE LENGTH OF THE M. LEVATOR  
MANDIBULAE EXTERNUS: DIAGRAMS, FORMULAE, AND RESULTS

## ABBREVIATIONS FOR IMPORTANT ANGLES:

$\angle A$ , angle of the dentary process;  $\angle B$ , angle of the fibers from the vertical;  $\angle C$ , angle of the fibers from the dentary margin;  $\angle D$ , angle of the effective length from the vertical.

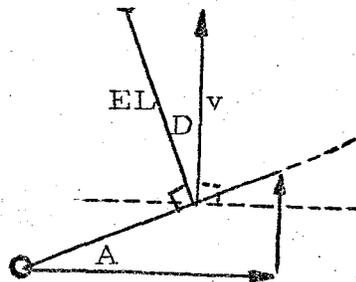
## DIAGRAMS AND FORMULAE



$$\text{Tangent } \angle A = \frac{Dh}{DI}$$

$$\text{Tangent } \angle B = \frac{h}{v}$$

$$\angle C = \angle A + (90^\circ) - \angle B$$



$$\angle D = \angle B + \angle C - (90^\circ)$$

or  $(90^\circ) - \angle A$

$$EL = \frac{v}{\text{cosine } \angle D}$$

## RESULTANT VALUES FOR THE MAJOR ANGLES

$$\angle A = 20^\circ$$

$$\angle C = 82^\circ$$

$$\angle B = 28^\circ$$

$$\angle D = 20^\circ$$