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A comparative study of the head and thoracic osteology and myology of the skinks, Eumeces gilberti Van Denburgh and Eumeces skiltonianus (Baird and Girard)

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A COMPARATIVE STUDY OF THE HEAD AND THORACIC OSTEOLOGY AND MYOLOGY OF THE SKINKS, *EUMECES SKILTONIANUS* (BAIRD AND GIRARD) AND *EUMECES GILBERTI* VAN DENBURGH

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INTRODUCTION

The genus Eumeces was proposed by A. F. Weigmann in his Herpetologica Mexicana in 1834. Eumeces pavimentatus (Geoffroy-St. Hillaire) was designated the genotype.

The two species involved in this study belong to the skiltonianus group which are characterized by the presence of two dorsolateral and two lateral light lines on the body. Eumeces skiltonianus is found in the Pacific Coast States, British Columbia, Idaho, Montana, Utah, Nevada, northern Arizona, California, and Baja California. This species was described by Baird and Girard in 1852 with the type locality in Oregon. In 1896 Van Denburgh described a new species from southern California which he called Eumeces gilberti. In 1916 Camp wrote a paper disagreeing with the distinctness of this new species and considered all western skinks to belong to the same species (skiltonianus). Since that time the distinctness of these two forms has been verified by more thorough investigations on the basis of geographical distribution, size, color pattern, scale counts, and other external morphological characters. Taylor (1935) was the first to do a complete study of the genus Eumeces in which he fully recognized these two species; Smith (1946) further characterized them in his Handbook of Lizards; and Rodgers and Fitch (1947) set forth the distribution of gilberti and the distinguishing characters of that species. Tanner (1957) characterized skiltonianus, designated its type population, and described two new subspecies. The papers of

Rodgers and Fitch and Tanner set forth the external anatomical characteristics of these species. They also recognized that all subspecies of skiltonianus exhibit a striped pattern; whereas only the immature forms of gilberti have the striped pattern. Adults of gilberti are patternless and much larger than the adults of skiltonianus; the average snout-vent length for gilberti is about 88mm and for skiltonianus about 62mm. The external taxonomic characters of these two species seem to be complete; therefore, it is the purpose of this study to further clarify their taxonomic and phylogenetic relationships by comparing and examining the osteology and myology of their head and thorax regions.

Extensive literature reviews on general and specific osteology and myology have been done by other authors: Robison and Tanner (1962), Oelrich (1956), Avery and Tanner (1964), Jenkins and Tanner (1968), and Fisher and Tanner (1970). Only those references which are relevant to this report are given. An osteological comparison of the skulls of ten species within the genus Eumeces which included gilberti was done by Kingman in 1932. To date the only myological work within this genus available to the author is the publication by Edgeworth (1935), in which he describes E. schnideri.

MATERIALS AND METHODS

The subspecies used in this study are E. gilberti placerencis (5), g. rubricaudatus (3), E. skiltonianus skiltonianus (10), and s. utahensis (5).

The specimens of E. gilberti have the following numbers: Brigham Young University (31956-31958 inclusive, 32622, and 32623); Sacramento State College (303, 437, and 528). The specimens of E. skiltonianus have the following numbers: Brigham Young University (8721, 12467, 12468, 12472, 12474, 13750, 13756, 21939, and 31959-31965 inclusive).

Osteological material was prepared by skinning the specimens, removing the superficial muscles using forceps, placing the specimens in a 50% liquid bleach solution for 30 to 60 seconds and rinsing them afterwards in clear water. The last three procedures were alternated until the desired results were obtained. Care was taken not to destroy the osteological elements when removing the muscles with forceps nor to leave the specimens in the bleach solution for an extended length of time. Illustrations were produced by photographing the skulls through a binocular scope using 400 ASA, 35mm black and white film. The pictures were then enlarged to ten inches and traced onto mylar tracing sheets using a binocular scope for detail.

A full description of each element for E. gilberti is given under "G". If differences in skiltonianus are noted they are given under "S". A minimum of five skulls of each species is used for the description and comparative differences. All elements are discussed in alphabetical order.

Preserved specimens were carefully skinned for myological comparisons. Illustrations were obtained by taking measurements from the preserved specimens, enlarging them onto tracing paper, and then transferring them onto mylar tracing sheets.

A full description of each muscle for E. gilberti is given under "G". If differences in skiltonianus are noted they are given under "S". A minimum of four specimens of each species is used for the description and comparative differences. All elements are discussed in alphabetical order.

Inking for both types of illustrations was done with technical pens, numbers 0 and 00. Adhesive letters were used for lettering.

OSTEOLOGY

General Description of the Skull

This description represents the general osteological condition of both species. Differences are discussed later.

Generally the skull is delicate and for the most part completely ossified. The extremities are bounded by the rostrum, the occipital condyle, and the quadrates laterally. The rostrum is rounded and contains large narial openings which are bounded by the premaxillae, the nasals, and the prefrontals. The articulation between the nasals and the frontals marks a point of abrupt change in elevation with the frontals being higher. Anterodorsally the frontals contact the maxillae thus preventing the nasals from articulating with the prefrontals. The frontals form the medial margin of the orbits, whereas the prefrontals and postfrontals form the anterior and posterior margins of the orbits respectively. The parietal is slightly rugose and contains a centrally located parietal foramen. Its posterior margin is dorsoventrally slanted and has two lateral and two medial processes. The postorbitals articulate with the jugals either separately or in conjunction with the postfrontals. In some specimens the postorbitals are reduced to such an extent that only a small sliver of bone remains. The squamosals, however, do not come in contact with the jugals. A supratemporal fontanelle located posteriorly is bordered by the parietal, postfrontal, postorbital and squamosal elements. The occipital and otic regions are ventroposterior to the parietal and are generally highly fused. The fusion of elements does not always correspond directly with the size of the skull. The supraoccipital forms an ascendens process with the parietal. The basioccipital is generally fused with the other occipital elements, with the basisphenoid and also with the prootics. The parasphenoid is a slender pointed element attached to the ventral border of the interorbital septum and extends anteriorly. The anteromedial limb of the pterygoids contain a number of pleurodont teeth. The palatines contact only the maxillae, vomers, and pterygoids. Two pairs of Jacobsen's organs are housed in the vomers. The jugals have small spines extending posteriorly on their lateroventral margins. The maxillae and premaxillae contain cylindrical pleurodont teeth. The right premaxilla is larger and contains one more tooth than the left premaxilla. Two orbital fenestrae, two infraorbital fenestrae, two infratemporal fenestrae, and two posttemporal fenestrae are located in the skull.

Description of the Skull Elements

Basioccipital. (Figs. 2 and 3)

G. The basioccipital contributes to the cranium floor, is roughly hexagonal in shape, and forms the basal portion if not all of the occipital condyle. Kingman (1932) reported that the exoccipitals formed the lateral portions of the occipital condyle. In the present study, however, fusion obscures the possible presence of sutures with the exoccipitals. Articulation with the basisphenoid anteriorly and the prootics laterally are generally by fusion. If sutures are present, the basioccipital-basisphenoid suture is irregular and the basioccipital-prootic suture runs posteriorly and then dorsally, separating the prootic and opisthotic portions of the otic capsule and terminating on the ventral margin of the fenestrae ovali. The prominent basioccipital processes project ventrolaterally and in some cases have an epiphysis. These processes appear to be formed in part by the exoccipital and the paroccipital elements. Anterior to the above processes smaller protuberances are found which make up part of the otic capsules.

Basisphenoid. (Fig. 3)

G. The basisphenoid contributes to the anterior portion of the cranial floor. Anteriorly it contacts the rostroparasphenoid. Anterolaterally the basipterygoid processes emerge and enlarge distally into flangelike processes to articulate with the pterygoids by a cartilaginous pad. Lateral contact is generally made with the prootics by fusion of the two elements. The sella turcica is posterior to the basipterygoid processes. A small foramen located on the lateral surface of the basisphenoid forms a canal with the prootics.

Ectopterygoid. (Figs. 1 and 3)

G. The ectopterygoids have dorsal and ventral processes which enclose the lateral processes of the pterygoids. Contact is also made with the maxillae and jugals. These bones do not articulate with the palatines.

Epiotic. (Not figured)

G. The epiotics are part of the otic capsule and enclose the dorsal parts of the two vertical semicircular canals (Jollie, 1960).

They appear as large rounded protuberances when viewed from the foramen magnum and extend medially and dorsally. They fuse inside the braincase with the supraoccipital, the opisthotics, the paroccipital processes, and the exoccipitals.

Epipterygoid. (Fig. 2)

G. The epipterygoids are relatively straight ossified rods extending from a well developed socket on the dorsal margin of the pterygoids to the anterior descending processes of the parietal and posterior descending processes of the prootics. They have a slight lateral cant ventrodorsally.

Exoccipital. (Fig. 2)

G. The exoccipitals form the ventrolateral margins of the foramen magnum. They are fused with the supraoccipital dorsally and the basioccipital ventrally. Fusion in this area makes it difficult to determine if these bones contribute to the occipital condyle. Laterally they fuse with the paroccipital processes. Anteriorly they form the posterior margin of the fenestrae rotunda. One, two, or three hypoglossal nerve foramenae are located in the exoccipitals near the junction with the paroccipital processes. The jugular foramenae are bordered by these latter two bones.

Frontal. (Figs. 1, 2, and 3)

G. The frontal element forms the cranial roof between the orbits. The naterior lateral processes of the frontal always contact the maxillae. Posteriorly articulation is with the postfrontals and parietal. The suture with the parietal is slightly convex. The descending processes in the orbits are slender and contact the dorsal palatine limbs medial to the prefrontals.

S. Anteriorly this bone articulates with the nasals, prefrontals, and may contact the maxillae depending upon the extent of the anterior lateral processes of the frontal.

Interorbital Ossification. (Fig. 2)

This is an ossified element found in both species which is connected anteriorly to the internasal septum. It extends posterior and slightly ventral, and is found within the interorbital septum. In one specimen of E. gilberti it extended as far posterior as the braincase. It varies from short to long and from triangular to almost rectangular in shape.

Jugal. (Figs. 1, 2, and 3)

G. The jugals form the lateroventral margin of the orbits and the anterior margin of the infratemporal fenestrae. Their dorsoposterior margin generally articulates with the postfrontals and always with the postorbitals. They do not contact the squamosals. These bones articulate with the ectopterygoids ventrally. On their lateroposteroventral surface is a short posterior spine. Kingman (1932) stated that this projection suggests "the place of continuance of some element in the past". Anteroventrally the jugals are sandwiched between the lateral and medial processes of the maxillae.

Lacrimal. (Figs. 1 and 2)

G. The lacrimals are small rectangular splints of bone forming a portion of the ventroanterior margin of the orbits between the prefrontals and the maxillae. They are not always fused with the prefrontals. On their ventroposterior surface there is an arch of this element forming one to two foramenae which lead into the large lacrimal duct anteriorly.

Maxilla. (Figs. 1, 2, and 3)

G. The maxillae are the teeth-bearing bones of the skull ranging from 15 to 20 teeth per side, with an average of 19. Replacement teeth are present. The teeth are pleurodont. The medial surface is level with the palatine. The teeth are cylindrical, homodont, rounded at the tips, and extend slightly laterally. Dorsally the maxillae articulate with the nasals and with the frontals posteriorly. Anteriorly in the narial openings the maxillae send a slender process inward to meet the anterior process of the septomaxillae. The maxillae articulate with the premaxillae in the floor of the narial openings, and on the ventroanterior surface of the skull they overlap the lateral processes of the premaxillae. Posteriorly, articulation is with the prefrontals, the lacrimals, and the jugals. Ventrally, the maxillae articulate with the premaxillae and the vomers anteriorly, the palatines medially by the posterior palatine processes, the jugals posteriorly, the ectopterygoids medially, and with the prefrontals in the anterolateral portion of the orbits. The maxillae are not always fused with the lacrimals. The lateral surfaces of the maxillae contain six to eight supralabial foraminae of varying sizes and shapes.

S. The maxillae may or may not contact the frontal posteriorly. They have a range of 17 to 20 teeth per side, with an average of 18 and contain four to seven supralabial foraminae.

<u>Nasals</u>. (Figs 1 and 2)

<u>G</u>. The nasals cover most of the anterior dorsal surface of the skull. They contact the premaxillae and the narial openings anteriorly, the maxillae laterally, the frontal posteriorly, and do not articulate with the prefrontals. Three to five nasal foraminae are present, the posterior one being located near the junction of the prefrontals, nasals, and frontal elements. Sutures with the frontal are highly irregular and lobed.

<u>S</u>. The nasals may or may not contact the prefrontals. Two to four nasal foraminae are generally present. The suture with the frontal is not as irregular as that of <u>gilberti</u> unless articulation of the prefrontal and nasal elements is absent.

<u>Opisthotic</u>. (Fig. 1)

<u>G</u>. The opisthotics form the posterior portion of the otic capsule; the anterior portion being formed by the prootics (Smith, 1960). A suture separating these two bones terminates at the ventral margin of the fenestrae ovali. On the dorsal surface the opisthotics are fused with the epiotics and the prootics. The posterior portion of the opisthotics or the paroccipital processes connect the occipital region to the quadrate region. These processes are wide and generally fuse with the supratemporals and the quadrates and posteroventrally they contact the prootics.

<u>Os Palpabrae</u>. (Fig. 1)

<u>G</u>. The os palpabrae are irregular tearshaped bones which are attached to the dorsal posterior margin of the prefrontals by connective tissue.

Palatine. (Figs. 1, 2, and 3)

G. The palatines have a ventral and a dorsal limb. Posteriorly these two limbs join each other and articulate with the medial limb of the pterygoids. The ventral limbs articulate with the maxillae by the posterior palatine processes. The dorsal limbs are arched upward forming the wall of the internal naries and contact the descending processes of the frontal and the prefrontals. Anteriorly this limb articulates with the vomers. The dorsal limbs contact each other for about one-fourth their length before separating posteriorly to join the ventral limbs. The separated halves form a slight ventral ridge. The palatine canals are located in the ventral limbs just medial to the articulation with the maxillae.

Parasphenoid. (Figs. 1 and 2)

G. This element is a cartilaginous tapered rod extending in an anterior direction from the center of the basisphenoid and forming the ventral border of the interorbital septum.

Parietal. (Figs. 1, 2, and 3)

G. The parietal is a large posterior dorsal element which articulates with the frontal anteriorly and the postfrontals and the postorbitals laterally. The latter articulation is not present if the supratemporal fontanelle separates these two elements. The posterolateral processes contact the squamosals, the supratemporals, the paroccipital processes, the opisthotics, and the prootics. Medially two shorter processes extend posterior and lateral to the processes ascendens of the supraoccipital forming a metakinetic type of articulation (Romer, 1956). The posterior edge of the parietal including the medial and lateral processes slant ventrally with the result that the main body of the parietal is higher than the dorsal occipital region. The lateral borders of the parietal are slightly curved inward. Ventrally the descending wall laminae are drawn out and articulate with the anterodorsal border of the epipterygoids. A parietal foramen lies on the median line near the center of the bone. Articulation with the quadrate is absent.

Postfrontal. (Figs. 1 and 2)

G. The postfrontals contribute to the posterior margin of the orbits. Articulation is with the parietal medially and frontals anteriorly. Laterally contact is made with either the postorbitals or the postorbitals and the jugals. The suture with the postorbitals may be fused in some places.

Postorbital. (Figs. 1, 2, and 3)

G. The postorbitals vary in width and length, and frequently show a reduction of relative size when compared to other adjacent bones. They are found lateral to the postfrontals and medial to the squamosals. Anteriorly they articulate with the jugals and the postfrontals. The suture with the postfrontals may be fused in some places. Posteriorly these elements may articulate with the parietal depending upon the size of the supratemporal fontanelle. They do not articulate with the supratemporals.

S. The postorbitals vary in size, but are only occasionally reduced to the same degree as in gilberti.

Prefrontal. (Figs. 1 and 2)

G. The prefrontals articulate with the frontals medially and with the maxillae laterally. These elements have a large anterior orbital process which descends to contact the palatines, the frontals, and the lacrimals. In the anterior ventral portion of the orbit, articulation is made with the maxillae dorsally. A small foramen is either located in the descending process of the prefrontals or between the prefrontals and frontals.

S. The prefrontals articulate with the frontals medially, but may or may not articulate with the nasals.

Premaxilla. (Figs. 1, 2, and 3)

G. The right premaxillae is the larger and contains four pleurodont teeth as compared with three teeth on the left element. This unequalness is produced by the extension of the midline suture into the left element. These elements may be fused in places. The premaxillae border the narial openings medially and the maxillae and vomers ventrally.

Prootic. (Figs. 1, 2, and 3)

G. The prootics are very complex elements forming a major portion of the cranium and the otic capsules. Ventrally they articulate, sometimes by fusion, with the basisphenoid and the basioccipital. If these elements are not fused, the suture continues posterior to the ventral margin of the fenestrae ovali. The lateroventral portion of the prootics is thin and deeply concave. The lateral wall of the prootics contain a canal which comes from the basisphenoid and continues to the otic capsule. Posteroventrally fusion is made with the paroccipital processes. The anterior descending processes contact the posterodorsal margin of the epipterygoids.

Pterygoid. (Figs. 1, 2, and 3)

G. The pterygoids are "Y" shaped bones slightly less than one-half the length of the skull. The anterior limbs are large, heavy, and articulate with the palatines by an overlapping suture. These limbs have a depression in the center containing four to ten pleurodont teeth. The teeth are attached to the lateral side, face somewhat medially, may be in a single row, or in irregular groups; and they are more sharply pointed and smaller than those found elsewhere. The lateral limbs are sandwiched between the ventral and dorsal processes of the ectopterygoids. At the junction of these two bones the lateral surface of the pterygoids is flanged into the coronoid process. The posterior limbs curve inward anteriorly and then outward posteriorly to articulate with the quadrate, and then extend slightly beyond the quadrate articulation. In the middle of the pterygoids the basipterygoid processes articulate by a cartilaginous pad. Dorsal to the basipterygoid there is a socket into which the epipterygoids fit. Anterior to the basipterygoids, the pterygoids are highly concave medially and posterior to the above processes the pterygoids are highly convex medially.

Quadrate. (Figs. 1, 2, and 3)

G. The quadrates are large units articulating with the squamosal, supratemporal, and paroccipital elements posteriorly; and with the pterygoids anteriorly. The articulating surface with the pterygoids is saddle shaped.

Septomaxillae. (Fig. 1)

G. The septomaxillae are inverted cupshaped structures lying dorsal to Jacobsen's organ and extending anteriorly. They contact the premaxillae and the maxillae in the floor of the narial openings. There is a thin ridge of bone extending upward and outward from the anterior portion of the septomaxillae that is joined by an inward process from the maxillae.

Stapes. (Fig. 3)

G. The stapes are thin cylindrical bones with flared bases that fit into the fenestrae ovali. The lateral ends are somewhat expanded. These bones are directed posterolaterally and extend into the quadrate region.

Supraoccipital. (Fig. 1)

G. The supraoccipital forms the superior margin of the foramen magnum and generally fuses with the exoccipitals ventrally. Laterally they fuse with the opisthotics and with the epiotics inside the braincase. A slight midsagittal ridge is formed and the ascendens process extends posteriorly under the parietal and forms a metakinetic articulation with the medial posterior processes of the parietal.

Supratemporal. (Figs. 1, 2, and 3)

G. The supratemporals are small slivers of bones wedged between the squamosals and the parietal dorsally. Ventrally they contact the quadrates and the paroccipital processes.

Squamosal. (Figs. 1, 2, and 3)

G. The squamosals are larger than the postorbitals and have a medial expansion of variable width. They are separated from the jugals by the postorbitals and posteriorly they curve laterally and downward to articulate into a small depression of the quadrate. Posterior articulation is with the supratemporals and the parietal.

Vomer. (Fig. 3)

G. The vomers form the anteroventral surface of the skull. They are rolled laterally with the medial area being the more ventral. They are separated from each other by a deep medial longitudinal groove centrally. Anteriorly they become flat, constricted, and articulate with the premaxillae and the maxillae. They articulate posteriorly with the palatines. Anterior to the latter articulation two ventrally projected teethlike structures are present. The right and left halves are for the most part fused along their entire length. Each half contains one pair of Jacobsen's organs.

General Description of the Mandible

Since the mandibles of these two species are similar except for the differences described below, figures of both species are not given. E. skiltonianus, Figure 4, was chosen because of the more superior illustration and is typical for either species.

Each ramus is slightly bowed laterally. The rami are united anteriorly by the mental symphysis and articulate posteriorly with the quadrates. An open sulcus of Meckel's cartilage is located on their ventromedial surface. Each ramus consists of seven elements; the angular, the articular, the coronoid, the dentary, the prearticular, and the supra-angular. The surfaces are smooth. The dentary bears a single row of pleurodont teeth. The retroarticular processes are thin and spoonshaped. The prearticulars are generally fused with the articulars.

Description of the Mandible Elements

Angular. (Fig. 4)

G. The angular is located on the ventral surface of the mandibular ramus. It is projected dorsally in an anteroposterior direction. On the lateral surface of the ramus it contacts the supra-angular dorsally, the dentary anteriorly, and the prearticular posteriorly. On the medial surface of the ramus the angular articulates by a forward splint of bone between the dentary and the splenial elements. Dorsally, articulation is with the prearticular. This element contains a small foramen anteriorly.

Articular. (Fig. 4)

G. The articular forms the articulating surface of the mandible for the quadrate. This element is an ossification of Meckel's cartilage and is bordered by dermal elements. The articular process extends medially. The articular is generally fused with the supra-angular dorsally and with the prearticular ventrally. It does not contact the angular.

Coronoid. (Fig. 4)

G. The coronoid is an inverted "V" shaped element which is centrally located and projects dorsally. It has one lateral and two medial processes. The lateral process contacts the supra-angular ventrally and the dentary anteriorly. The anterior medial process lies along the posterior portion of the dentary. The posterior medial process contacts the supra-angular and the prearticular. Between the two medial processes a well developed coronoid fossa is found which contains anterior portions of the supra-angular and prearticular. These two latter elements are sometimes fused.

Dentary. (Fig. 4)

G. The dentary is the teethbearing bone of the mandible. This element extends posteriorly to a distance equal to the posterior medial process of the coronoid. Nineteen to 23 pleurodont teeth, with an average of 21, are located on the dorsal surface of the dentary. Meckel's cartilage is open ventrally and is equal in length to no more than one-half that of the dentary. The dentary contacts the splenial at the posterior end of Meckel's cartilage. Anterior articulation is with the anterior process of the coronoid, the supra-angular, and the angular. The lateral surface contains three to six mental foraminae of various sizes and shapes.

S. The dentary contains 18 to 22 teeth, with an average of 21, and contains three to seven mental foraminae.

Prearticular. (Fig. 4)

G. The prearticular is a major component of the medial surface of the ramus. It is generally fused with the articular posteriorly and sometimes fused with the supra-angular dorsally. Ventrally it comes in contact with the angular. This element forms the retroarticular process of the ramus. The mandibular fossa is located posteriorly and is formed by the supra-angular dorsally and the prearticular ventrally.

Splenial. (Fig. 4)

G. The splenial lies on the medial anterior portion of the ramus, ventral to the dentary. It sends forward two splinters of bone which enclose the posterior portion of the open sulcus of Meckel's cartilage prior to articulation with the dentary. This element extends posterior to the posterior margin of the posterior medial process of the coronoid. The splenial contains a foramen just posterior to the open portion of Meckel's cartilage.

Supra-angular. (Fig. 4)

G. Laterally the supra-angular covers the dorsal portion of the ramus between the dentary and the articular. It is generally fused with the articular posteriorly and forms the anterior portion of the articular process. It contacts the coronoid dorsally, the dentary anteroventrally, and the angular ventrally. On the medial surface it is sometimes fused with the prearticular. Posteriorly it contributes to the mandibular fossa with the prearticular. On the lateral surface two foraminae are located.

Description of the Hyoid Apparatus

The general morphology of the hyoid apparatus in both species is similar. Variations, however, were noted in the average ratios of the length of the entoglossal process to either the length of the proximal segment of the hyoid cornu or the length of the ceratobranchial 2. Gilberti being greater in both cases. A sufficient number of specimens was not available for statistical analyses. The hyoid apparatus is then represented by *E. gilberti* in Figure 5.

Hyoid Apparatus. (Fig. 5)

G. Unless stated differently, all elements are cartilaginous and highly calcified. The main body or the corpus is prolonged anteriorly into the entoglossal process. The latter is imbedded in the tongue musculature. The remainder of the corpus has two posterolateral projections which are connected to the other elements. The hyoid cornu consists of two segments. The posterior portion of the proximal segment is almost completely ossified and articulates between the corpus and the ceratobranchial 1. The remainder of this segment is tubular and connects to the distal segment of the hyoid cornu. The distal segment is initially flat and wide; it then becomes thicker and somewhat tubular, and distally it again becomes flatter. This segment has a calcified core throughout its length. The ceratobranchial 1 is completely ossified except near its articulation with its epibranchial. Medially it articulates with the proximal segment of the hyoid cornu. Initially it is tubular, toward the center it becomes wider, and distally it is tubular again and has a flared articulation with its epibranchial. The eipbranchial is a slender and pointed element. The ceratobranchial 2 is tubular and fused indistinguishably to the corpus.

Figure 1. Dorsal view of skulls.
A. *Eumeces gilberti* (9.2X) (SSC 303).
B. *Eumeces skiltonianus* (9.3X) (BYU 31960).

Key to Abbreviations

EC ---- Ectopterygoid
EN ---- External Nares
F ----- Frontal
IOF --- Infraorbital Fenestra
J ----- Jugal
L ----- Lacrimal
M ------ Maxilla
N ------ Nasal
NF ---- Nasal Foramen
OC ---- Occipital Condyle
OF ---- Orbital Fenestra
OP ---- Opisthotic
OSP --- Os Palpabra
P ------ Parietal
PAF --- Parietal Foramen

PAL ---- Palatine
PF ----- Postfrontal
PM ----- Premaxilla
PO ----- Postorbital
PR ----- Prootic
PRF ---- Prefrontal
PT ------ Pterygoid
PTF ---- Posttemporal Fenestra
Q ------- Quadrate
S ------- Squamosal
SM ------ Septomaxilla
SO ------ Supraoccipital
ST ------ Supratemporal
STF ---- Supratemporal Fontanelle

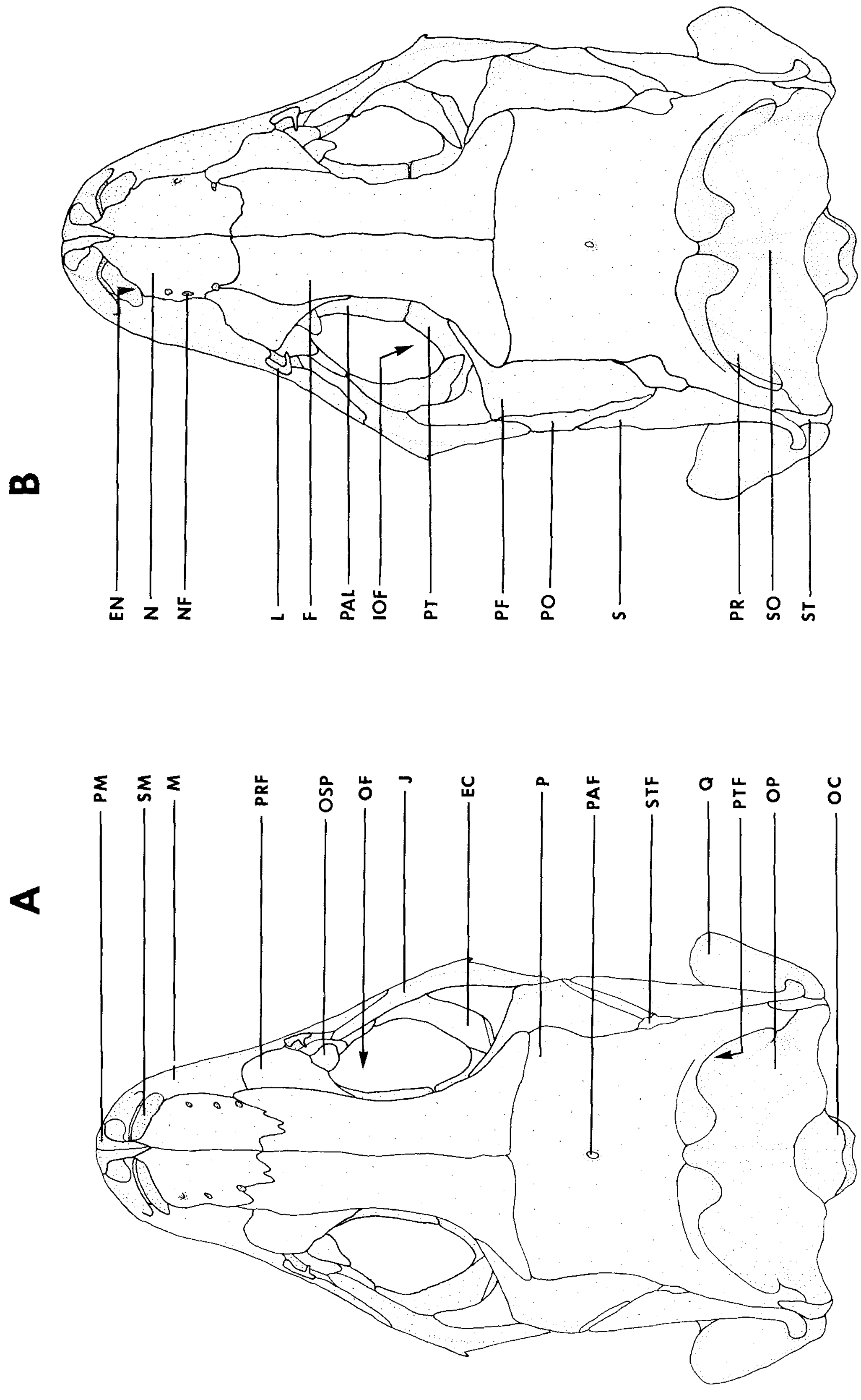
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Figure 2. Lateral view of skulls.
A. Eumeces gilberti (8.9X) (SSC 303)
B. Eumeces skiltonianus (9.3X) (BYU 31960)

Key to Abbreviations

BO ------ Basioccipital
EO ------ Exoccipital
EP ------ Epipterygoid
F ------- Frontal
IO ------ Interorbital Ossification
J ------- Jugal
L ------- Lacrimal
M ------- Maxilla
N ------- Nasal
OF ------ Orbital Fenestra
P ------- Parietal
PAL ---- Palatine
PF ------ Postfrontal
PM ------ Premaxilla
PO ------ Postorbital
PR ------ Prootic
PRF ----- Prefrontal
PS ------ Parasphenoid
PT ------ Pterygoid
Q ------- Quadrate
S ------- Squamosal
SLF ---- Supralabial Foramen
ST ------ Supratemporal

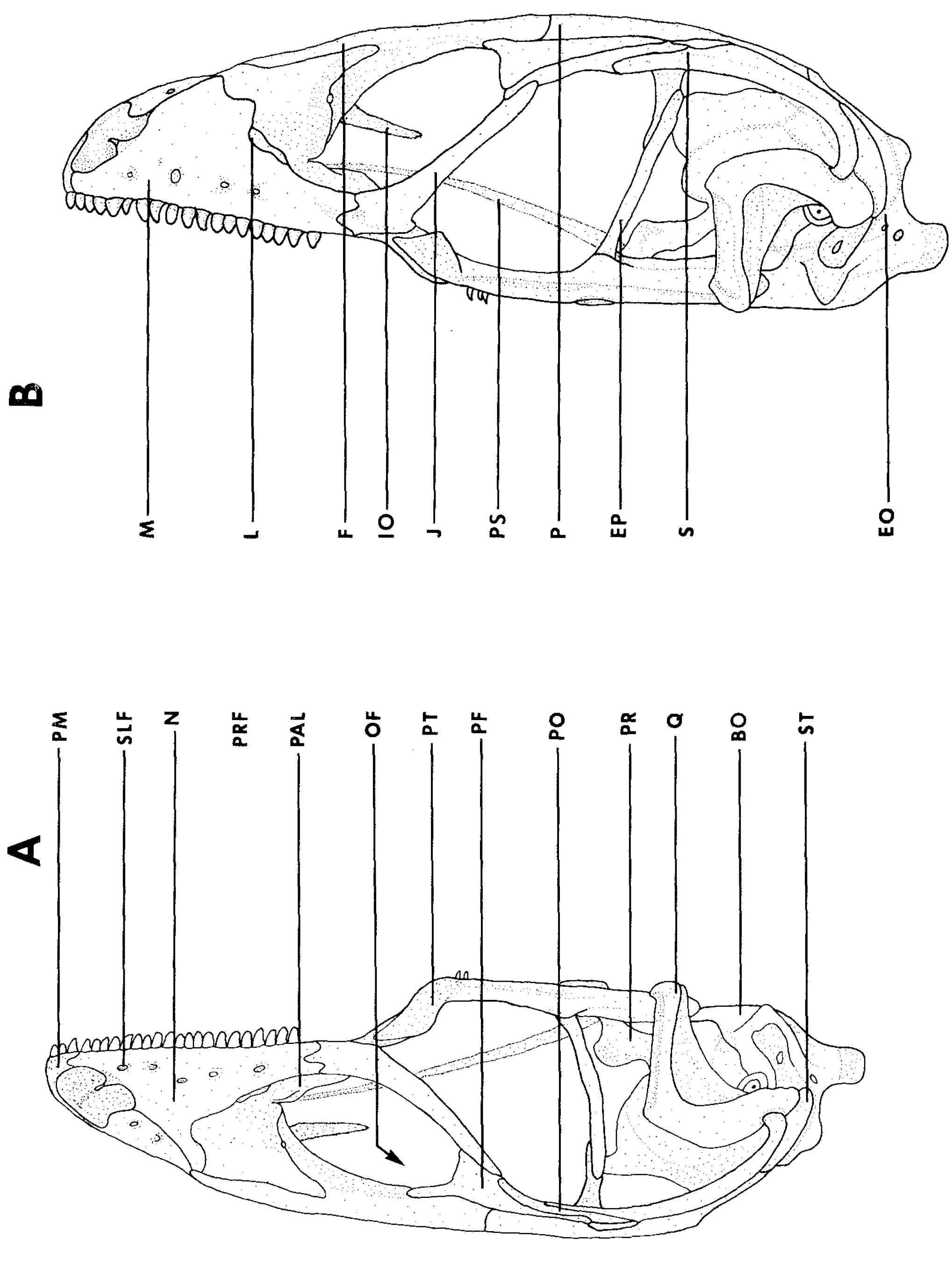
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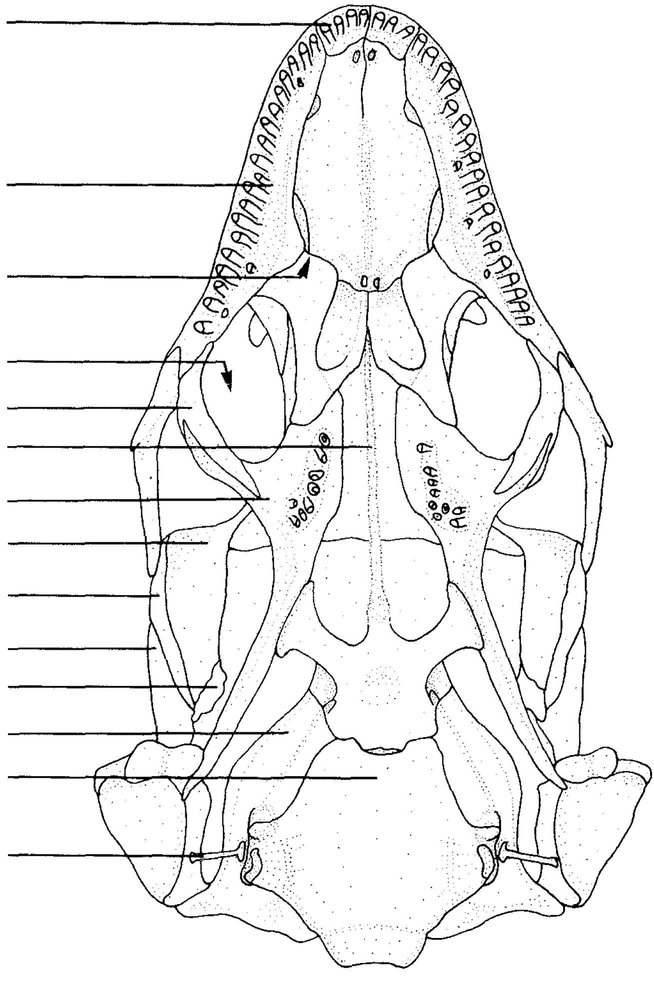
Figure 3. Ventral view of skulls.
A. Eumeces gilberti (9.2X) (SSC 303)
B. Eumeces skiltonianus (9.6X) (BYU 31961)

Key to Abbreviations

BC ------ Basioccipital
BS ------ Basisphenoid
EC ------ Ectopterygoid
IN ------ Internal Nares
IOF ---- Infraorbital Fenestra
ITF ---- Infratemporal Fenestra
F ------- Frontal
J ------- Jugal
M ------- Maxilla
OF ------ Orbital Fenestra
P ------- Parietal
PAL ---- Palatine
PF ------ Postfrontal
PM ------ Premaxilla
PO ------ Postorbital
POP ---- Paroccipital Process
PR ------ Prootic
PS ------ Parasphenoid
PT ------ Pterygoid
Q ------- Quadrate
S ------- Squamosal
ST ------ Supratemporal
STF ---- Supratemporal Fontanelle
V ------- Vomer
VOJ ---- Vomero-nasal Organs of Jacobsen

B



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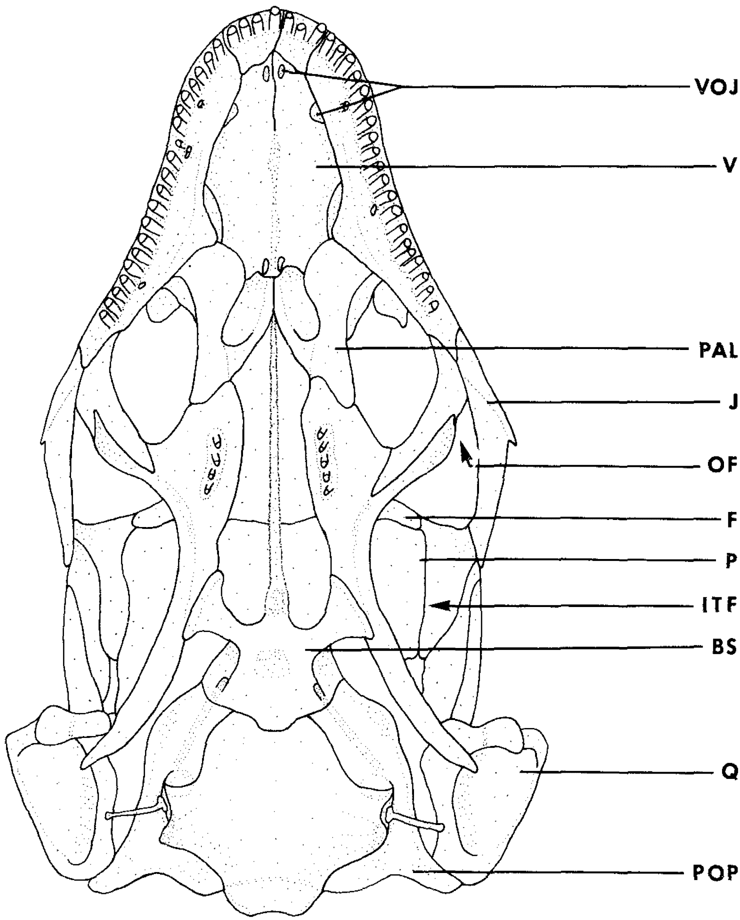

Figure 4. Mandible. Eumeces skiltonianus (9.3X) (BYU 12468)

A. Medial view

B. Lateral view

C. Dorsal view

Key to Abbreviations

A ------- Angular
AF ----- Angular Foramen
AR ----- Articular
C ------ Coronoid
D ------ Dentary
MC ----- Meckel's Cartilage
MEF ---- Mental Foramen
MF ----- Mandibular Foramen
PA ----- Prearticular
S ------ Splenial
SA ----- Supra-angular
SAF ---- Supra-angular Foramen
SF ----- Splenial Foramen

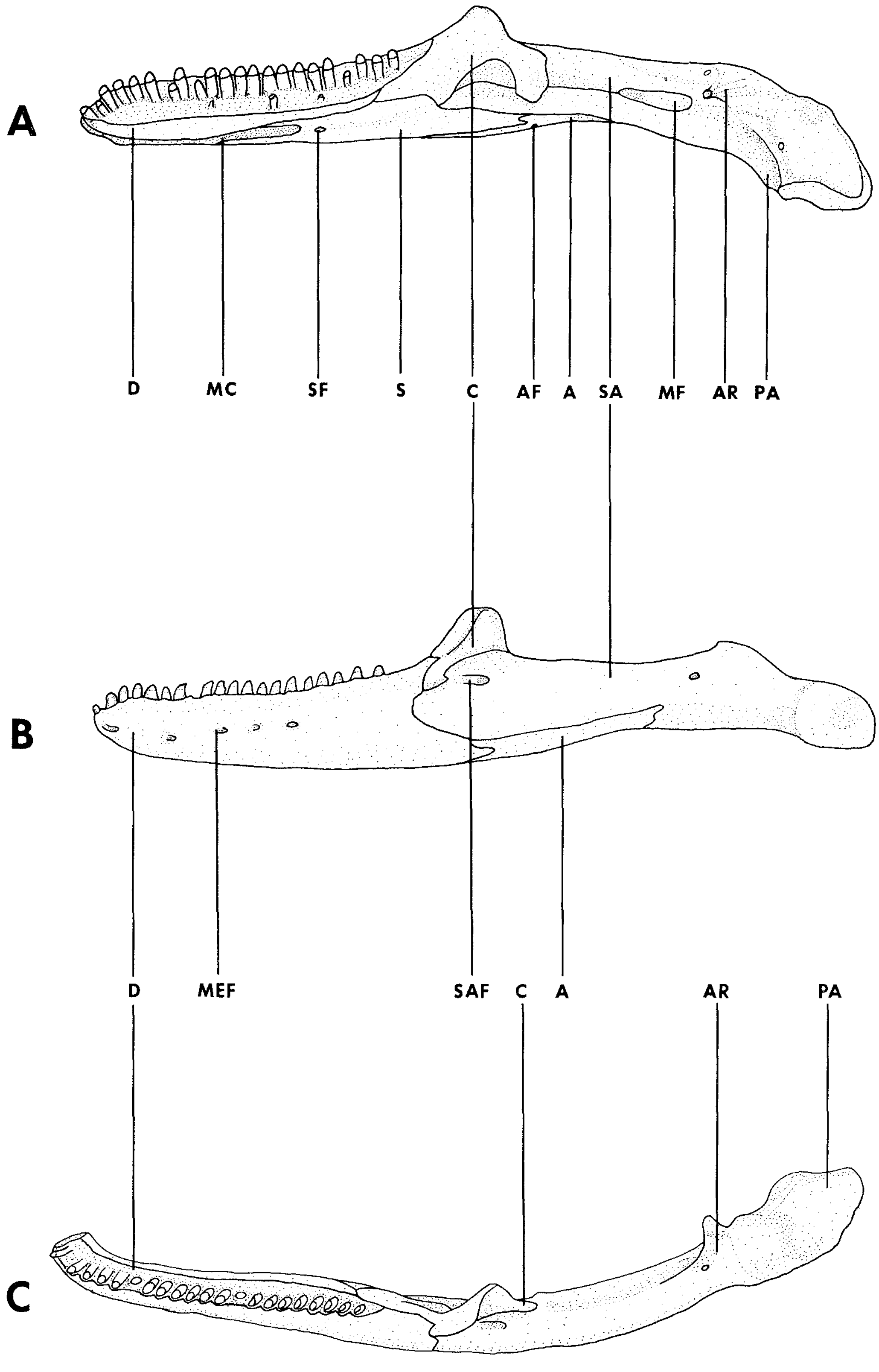
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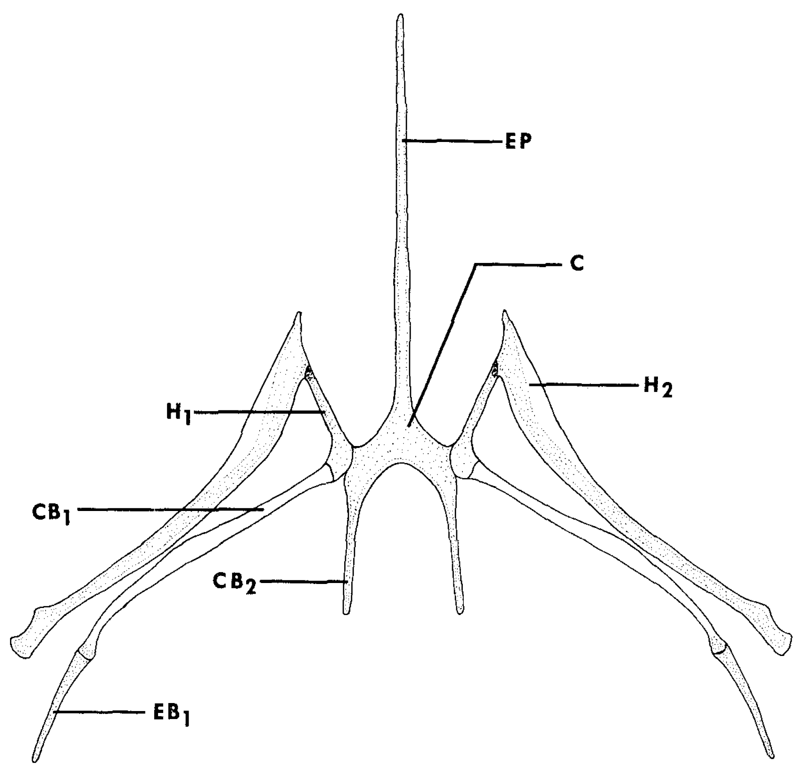
Figure 5. Dorsal view of hyoid apparatus. *Eumeces gilberti* (5.0X) (BYU 31956)

Key to Abbreviations

C ------- Corpus
CB_1 ----- Ceratobranchial 1
CB_2 ---- Ceratobranchial 2
EP ----- Entoglossal Process
H_1 ------ Proximal Segment of the Hyoid Cornu
H_2 ----- Distal Segment of the Hyoid Cornu


EP
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H_1
H_2
CB_1
CB_2
EB_1

MYOLOGY

General Description of the Myology

This description reflects the general myological condition of both species. Differences are discussed later.

Ventrally the intermandibularis anterior is subdivided, interdigitates with the geniohyoideus, and is continuous with the intermandibularis posterior. The sternohyoideus is separable into a superficial and a profundus layer; the medial border is partially separated from its partner by an elliptical space. This space is covered by fascia, but when uncovered, portions of the trachea, thyroid gland, clavodeltoidus, and the clavicle can be seen. The pectoralis is a large muscle covering the sternum and the scapula; posteriorly this muscle interdigitates with the rectus abdominus. Lateroventrally the pectoralis is covered by an anterior slip of the rectus abdominus which extends almost to the insertion of the pectoralis. A ligamentous fascia covers a large portion of the pectoralis and is connected to the anterior slip of the oblique abdominus rectus posteriorly, to the lateral process of the interclavicle and to the muscles immediately anterior to this process. There is only one mandibulohyoideus present. Both the clavodeltoideus and the coracobrachialis longus have a dorsal and a ventral origin on the clavicle and the scapula respectively. In the adductor muscle complex, the adductor mandibularis externus medius, the adductor mandibularis externus profundus, and the adductor mandibularis posterior are at equal depth. The second of these muscles extends through the posttemporal fenestrae to partially originate on the opisthotic and prootic elements. No levator anguli oris is present. The depressor mandibularis inserts on the retroarticular process and intermandibularis posterior, and in some specimens is separable into two bundles. The trapezius varies in thickness and in some specimens can also be separated into two bundles. The trapezius and the sternocleidomastoideus interdigitate ventrally to insert along with the sterohyoideus onto the interclavicle lateral process. There is both an anterior and a posterior scapulohumeralis. The obliquus abdominus externis muscle is divided into a superficial and a profundus layer. Dorsally the rectus capitis posterior is separated into an anterior and a posterior bundle; the former has a medial and a lateral slip. The obliquus capitis magnus and the longissimus cervicis are joined to the spinalis capitis by a myosepta. No longissimus capitis is present.

Description of the Myology

M. Adductor Mandibularis Externis Medius. (Figs. 6, 8, and 10)

G. This muscle is deep to the adductor mandibularis externus superficialis from which it is separated with difficulty. It lies dorsal to the adductor mandibularis externis profundus and is separated anteriorly from this muscle by a tendon from the bodenaponeurosis. These two muscles interdigitate posteriorly. The muscle originates from the prootic and opisthotic elements deep to the spinalis capitis and lies between the medial and lateral slips of the rectus capitis posterior. The muscle fibers extend in a lateral direction and as they enter the posttemporal fenestrae they turn anteroventrally, and have other origins on the beveled surface of the parietal, ventral surfaces of squamosals, postorbitals, jugals, and the dorsal surface of the quadrates. The fibers converge anteriorly to insert on the coronoid by way of the bodenaponeurosis.

M. Adductor mandibularis Externis Profundus. (Fig. 10)

G. This muscle lies ventral to the adductor mandibularis externis medius, and dorsal to the adductor mandibularis posterior. It is separated anteriorly from the latter two muscles by a tendon. They interweave posteriorly. The muscle originates on the anterior and anterodorsal surfaces of the quadrate, and on the lateral surface of the prootic. Insertion is on the bodenaponeurosis and also on the medial base of the coronoid.

M. Adductor Mandibularis Externis Superficialis. (Figs. 6, 9, and 15)

G. This thin superficial muscle is scarcely distinguishable from the deeper muscles. The muscle is separated by the bodenaponeurosis that extends from the coronoid and almost to the posterior margin of the muscle. It arises from the ventral surface of the squamosal, the dorsoanterior surface of the quadrate, and the anterior margin of the jugal. Insertion is on the bodenaponeurosis and the lateral surface of the supra-angular.

M. Adductor Mandibularis Posterior. (Fig. 10)

G. This muscle is deep to the adductor mandibularis externis superficialis and ventral to the adductor mandibularis externis profundus. It is separated anteriorly from the latter muscle by a tendon; posteriorly the fibers of these two muscles interweave. Origin is on the anterior surface of the quadrate with insertion on the medial dorsal surface of the supra-angular, the mandibular fossa, and on the most anterior surface of the articular.

M. Anconaeus Coracoideus. (Fig. 6)

G. The anconaeus coracoideus is a small dorsal muscle arising by a tendon, posterior to the insertion of the latissimus dorsi, from the sterno-scapular ligament and uniting with the anconaeus scapularis prior to insertion onto the olecranon process of the ulna. This muscle is found posterior to the anconaeus scapularis and antero-dorsal to the anconaeus medialis humeralis.

M. Anconaeus Humeralis Lateralis. (Fig. 15)

G. This muscle originates medial to the insertion of the scapulodeltoideus and clavodeltoideus from the proximal head and the anterior surface of the humerus. It then unites with the anconaeus scapularis to insert onto the olecranon process of the ulna. Some fibers will interdigitate distally with the brachialis inferior. This muscle is located anterior to the anconaeus scapularis and dorsal to the brachialis inferior.

M. Anconaeus Humeralis Medialis. (Fig. 6)

G. This muscle originates from the proximal end of the humerus, below the sterno-scapular ligament, and from the posterodorsal surface of the shaft of the humerus. It then unites with the other anconaeus muscles for a common insertion onto the olecranon process of the ulna. This muscle lies posterior to the anconaeus coracoideus and anterior to the coracobrachialis longus.

M. Anconaeus Scapularis. (Figs. 6 and 15)

G. This large upper arm muscle originates on the sterno-scapular ligament dorsal to the scapulodeltoideus and clavodeltoideus. It then follows the humerus to join tendonously with the other anconaeus muscles. The muscle is divided into two bundles. The anterior bundle fibers extend first lateroventrally, then parallel to the humerus, and then ventromedially. This muscle is posterodorsal to the anconaeus humeralis laterlis and anterior to the anconaeus coracoideus.

M. Biceps. (Figs. 15 and 17)

G. The beceps brachii is a large ventral muscle that inserts tendonously onto the proximal head of the ulna and radius. The muscle continues along the humerus and forms a broad tendon which is connected to the head of this muscle. The origin is on the medial ventral border of the scapula. On the humerus the muscle lies between the brachialis inferior and the coracobrachialis longus. Just lateral to the deltopectoral process an anterior slip is attached tendonously to this process. On the scapula a thin layer of the supracoracoideus covers the anterior portion of this muscle.

M. Brachialis Inferior. (Fig. 17)

G. This ventral muscle originates on the lateroanterior surface of the deltopectoral process and the anteroventral surface of the shaft of the humerus. Insertion is primarily on the radius; however, some fibers interdigitate distally with the biceps brachii to also insert on the ulna. This muscle is located anterior to the biceps and posterior to the anconaeus humeralis lateralis.

M. Branchiohyoideus. (Fig. 17)

G. This straplike muscle originates on the lateral three-fourths of the ceratobrahcial 1 and inserts on the posterior and ventral surfaces of the central portion of the hyoid cormu. This muscle is superficial to the sternocleidomastoideus and trapezius laterally, and is strongly attached to these two muscles by connective tissue.

M. Clavodeltoideus. (Figs. 6, 9, 12, 13, 15, 16, and 17)

G. This complex muscle inserts by a tendon onto the delto-pectoral process near the origin of the brachialis inferior and the insertion of the scapulodeltoideus. Some of the fibers interdigitate with the scapulodeltoideus prior to insertion. From the insertion the muscle fibers extend in two directions to originate on the clavicle. One bundle of fibers extends anteromedially under the clavicle bar, rotates ventrally and laterally to originate on the medioventral surface of the clavicle. The other bundle of fibers extends anteromedially under the clavicle-interclavicle bar to insert on the dorsomedial surface of the clavicle.

M. Constrictor Coli. (Figs. 6, 9, and 15)

G. This is a wide cervical muscle originating on the mid-dorsal fascia and the tympanic fascia. Insertion is with its partner in the median fuocia. This muscle is strongly attached laterally and ventrally by fascia to the trapezius, the sternocleidomastoideus, the pectoralis. In some specimens fat tissue is found in abundance on the ventral and lateral surfaces.

M. Coracobrachialis Brevis. (Fig. 17)

G. This posterior arm muscle originates on the medioventral surface of the scapula with the fibers converging laterally to insert onto the deltopectoral process and onto almost the entire length of the posteroventral surface of the humerus. This muscle is located anterior to the coracobrachialis longus and is deep to the biceps.

M. Coracobrachialis Longus. (Figs. 6 and 15)

G. This muscle has a dorsal and a ventral slip which have a common insertion onto the ulnar process of the humerus. The ventral slip is considerably larger and originates on the posterolateroventral tip of the scapula. The dorsal slip originates from the dorsal surface of the scapula just posterior to the origin of the subscapularis 2. It leaves the scapula dorsal to the origin of the ventral slip and shortly terminates into a long slender tendon to insert onto the ulnar process.

M. Costocoracoideus. (Not figured)

G. This broad thin muscle originates from the first sternal rib, extends anteriorly to insert onto the sternum and the sterno-scapular ligament.

M. Depressor Mandibularis. (Figs. 6, 9, and 15)

G. This muscle originates from the middorsal fascia, the dorsoposterior surface of the squamosal, and the most lateral surface of the parietal. The anterior muscle fibers converge centrally, attach to the dorsoposterior edge of the quadrate, the posterior margin of the tympanic fascia and then insert onto the retroarticular process by a wide tendon. The more posterior fibers converge anteroventrally to insert lateroventrally onto the superficial fascia of the intermandibu-laris posterior. This muscle is not easily distinguishable nor easily separable into anterior and posterior bundles. It is deep to the constrictor colli and superficial to the geniohyoideus, the sternocleidomastoideus, the trapezius, and the most posterior edge of the adductor mandibularis externus superficialis.

S. This muscle is easily separable into anterior and posterior bundles. The anterior bundle is extremely small and originates from the dorsoposterior surface of the squamosal, terminates as a wide tendon, and then joins with the posterior bundle to insert onto the retroarticular process. It is deep to the posterior bundle and superficial to the sternocleidomastoideus. The posterior fibers of the posterior bundle originate and insert similarly to *gilberti*.

M. *External Sternocoracoideus.* (Not figured)

G. The external sternocoracoideus originates from the anterolateral border of the sternum with fibers extending anteriorly to fuse with the internal sternocoracoideus for a tendonous insertion onto the scapula, medial to the origin of the subscapularis muscles.

N. *Genioglossus.* (Figs. 10 and 15)

G. The genioglossus originates from the anteromedial one-fifth of the mandible and inserts posteriorly by medial and lateral slips onto the hyoglossus and tongue fascia. It is strongly attached dorsally to the oral membrane. There is a small slip of this muscle which attaches anteromedially to the skin fascia. The muscle is lateral to the entoglossal process and the trachea, and medial to the mandibulohyoideus I.

M. Geniohyoideus. (Fig. 15)

G. The origin of the geniohyoideus is along the anterior margin of the ceratobranchial 1 and the posteroventral one-third of the entoglossal process of the hyoid apparatus. The muscle fibers continue anterolaterally, interdigitate with six or seven slips from the intermandibularis anterior, and insert along the medial surfaces of the dentary and angular. It is deep to the intermandibularis anterior, the constrictor coli, and the depressor mandibularis. The body of the muscle is superficial to the pterygomandibularis, the mandibulohyoideus 1, the hyoglossus, the genioglossus, and the trachea.

S. The only difference noted is that this muscle is interdigitated with five to seven slips from the intermandibularis anterior. (See M. Intermandibularis Anterior)

M. Hyoglossus. (Fig. 16)

G. The hyoglossus is a thin sheet muscle that originates from the anterior side of the ceratobranchial 1 and inserts anteriorly with the tongue fascia and with interdigitation by medial and lateral slips of the genioglossus. This muscle is deep to the geniohyoideus and superficial to the oral membrane, the mandibulohyoideus 1, and portions of the hyoid apparatus, the branchiohyoideus, and the pterygiomandibularis.

M. Intermandibularis Anterior. (Fig. 15)

G. This ventral muscle originates from the medial surface of the mandible and inserts with the oppostie muscle in the median fascia. Posteriorly the muscle becomes thinner and is continuous with the mandibularis posterior. This muscle is divided into six or seven medially fused slips which are irregular in size and which interdigitate with the geniohyoideus. In the specimens studied the number slips were approximately equally divided between six and seven.

S. This muscle is subdivided into five to seven medially fused slips which are irregular in size and which interdigitate with the geniohyoideus. A subspecific difference is observed. The number of slips in skiltonianus range from five to six, whereas in utahensis the number of slips range from six to seven.

M. Intermandibularis Posterior. (Figs. 9 and 15)

G. This thin sheet muscle originates ventral to the adductor mandibularis externis superficialis by fascia from the ventrolateral surface of the angular and the prearticular, and also from the fascia covering the quadrate. Insertion is ventrally with its partner in the median fascia. The muscle begins just posterior to the last slip of the intermandibularis anterior and terminates slightly posterior to the tympanic cavity. It is deep to the depressor mandibularis posteriorly. This muscle is superficial to the anterolateral portion of the pterygomandibularis.

M. Internal Sternocoracoideus. (Not figured)

G. This thin rectangular muscle arises from the posterolaterodorsal surface of the sternum and unites anteriorly with the external sternocoracoideus for a common tendonous insertion onto the scapula, medial to the origin of the subscapularis muscles.

M. Intercostalis Externis. (Fig. 14)

G. This muscle originates from the posterolateral edge of the ribs and inserts onto the anterolateral edge of the following posterior rib. This muscle is deep to the obliquus abdominus profundus and to the sacrolumbalis and superficial to the intercostalis internis. It does not cover the intercostalis ventrally and the muscle becomes thicker as it moves dorsally. Dorsally and anteriorly, fibers of this muscle join with those of the sacrolumbalis and obliquus abdominus profundus to insert onto the ventrolateral surface of the axis.

M. Intercostalis Internis. (Figs. 14 and 17)

G. The fibers of this muscle originate from the ribs and insert onto the following posterior rib. On the ventral surface the muscle is nearly parallel to the bilateral axis of the body, and as it extends dorsally the fibers change to a vertical and slightly posterior direction. It is deep to the intercostalis externis and superficial to the obliquus abdominus internis.

M. Latissimus Dorsi. (Figs. 6, 7, 9, and 15)

G. The fibers of the latissimus dorsi originate from the ligamentum nuchae, converge ventrally, and pass most medially between the anconaeus coracoideus and anconaeus scapularis to insert tendonously onto the shaft of the humerus. These muscle fibers are deep to the skin and are superficial to the posterior portion of the scapulo-deltoideus.

M. Levator Pterygoideus. (Fig. 12)

G. This muscle is deep to the pseudotemporalis profundus. It originates from the lateral surfaces of the prootic and parietal descending processes. Fibers extend ventrally to insert onto the lateral and medial surfaces of the pterygoid, just posterior to the fossa columella.

M. Levator Scapulae Profundus. (Figs. 12 and 16)

G. This narrow somewhat triangular muscle originates in common with the levator scapulae superficialis from the atlas and inserts posteriorly onto the clavicle bar, ventral to the levator scapulae superficialis. It is superficial to the esophageal membrane and deep to the trapezius.

M. Levator Scapulae Superficialis. (Figs. 7 and 12).

G. This muscle arises from the atlas with the levator scapulae profundus and inserts onto the anterolateral surface of the suprascapula. This muscle is thick anteriorly but becomes thinner and fanshaped posteriorly. It is deep to the lateral trunk muscles and is lateral to the rectus capitis anterior.

M. Longissimus Cervicis. (Figs. 8, 12, 13, and 17)

G. This muscle is located ventral to the obliquus capitis magnus. Its origin is by fusion with the myosepta between the obliquus capitis magnus and the lateral bundle of the spinalis capitis. The fibers extend in a ventroanterior direction to insert tendonously onto the basioccipital process.

M. Mandibulohyoideus 1. (Fig. 16)

G. The origin of this muscle is from the ventromedial surface of the dentary and the angular, and inserts onto the most anteroventral surface of the distal segment of the hyoid cornu. One to two slips of the intermandibularis anterior interdigitates with this muscle. It is superficial to the oral membrane and the medial portion of the pterygomandibularis, and lies lateral to the genioglossus. This muscle is deep to the hyoglossus and the geniohyoideus.

M. Obliquus Abdominus Externis. (Figs. 6, 9, and 15)

G. This sheet muscle originates anterolaterally from the ribs of the sixth and seventh vertebrae and laterally from the sacro-lumbalis. Insertion is with the pectoralis and rectus abdominus ventrolaterally.

M. Obliquus Abdominus Internis. (Fig. 14)

G. This thin, loosely arranged sheet muscle originates from the inner surface of the ribs and inserts anteriorly onto the esophageal membrane, the sternum, and the ventral heads of the thoracico-lumbar ribs. The fibers are superficial to the transversalis and deep to the intercostalis internis. They extend in a dorsal and slightly posterior direction.

M. Obliquus Abdominus Profundus. (Figs. 13 and 17)

G. This muscle has the same origin as the externis muscle except that some fibers will continue anterodorsally and become almost parallel with the sarcrolumbalis to interdigitate with that muscle and the intercostalis externis to insert onto the axis. Insertion is also by individual slips onto the sternal ribs with the most lateral fibers being attached to the most posterior rib. This muscle is generally heavier than the externis muscle.

M. Obliquus Capitis Magnus. (Figs. 8, 12, and 13)

G. This muscle originates from a myosepta with the lateral slip of the spinalis capitis. The myosepta extends lateroventrally from the fifth vertebrae to the atlas. Insertion is on the supratemporal, the paroccipital process, and the parietal.

M. Pectoralis. (Figs. 15 and 16)

G. The pectoralis is a thick muscle having its origin from the lateral process of the interclavicle, the sternum, the mesosternum and the ribs which are attached to the mesosternum, and the first two thoracico-lumbar ribs. Its origin along the ribs is in a steplike fashion laterally, with the most lateral slip fusing with the rectus abdominus. All fibers converge to insert tendonously onto the delto-pectoral process of the humerus. This muscle is deep to the skin and to a lateral slip of the rectus abdominus. It overlies a broad ligament from the interclavicle lateral process to the sternum and the posterior portion of the scapula with its attached muscles.

M. Protractor Pterygoideus. (Fig. 12)

G. The anterior portion of this muscle is deep to the pseudotemporalis profundus. Origin is from the anterolateral surface of the prootic. Fibers extend lateroventrally and posteriorly to insert onto the pterygoid and the quadrate process of the pterygoid.

M. Pseudotemporalis Profundus. (Fig. 11)

G. This muscle is deep to the adductor mandibularis externis profundus and the adductor mandibularis externis medius. It originates from the descending processes of the prootic and the parietal; and also from the lateral, posterior and anterior surfaces of the epipterygoid.

Some of the dorsal fibers originate from the ventral surface of the parietal. The muscle continues in a nearly anteroventral direction to insert onto the base of the coronoid and posteriorly onto the supra-angular and the mandibular fossa.

M. Pseudotemporalis Superficialis. (Fig. 11)

G. This muscle is located medial to the adductor mandibularis externis medius and dorsolateral to the adductor mandibularis externis profundus. Origin is from the ventral surface of the parietal medial to the supratemporal fontanelle. Fibers extend ventrally to insert tendonously onto the dorsal surface of the coronoid.

M. Pterygomandibularis. (Figs. 7, 10, 13, 15 and 17)

G. The pterygomandibularis originates tendonously from the pterygoid and the epipterygoid. The muscle continues posteriorly along the pterygoid, attaches to the pterygoid, the basipterygoid process, and then covers the ventrolateral surfaces of the angular, the articular, the medial surface of the supra-angular, and the medial dorsal surface of the retroarticular process. The muscle then extends dorsally around the posterior end of the retroarticular process to insert onto the condyle of the quadrate and the angular process of the articular. It is deep to all ventral and lateral muscles and is covered by an extensive fascia.

M. Rectus Capitis Anterior. (Figs. 14 and 17)

G. This is a thick straplike muscle originating by two slips from the ventral surface of the eighth and seventh vertebrae and their rib capitulae. Anteriorly the two slips fuse. The combined muscle interdigitates with its opposite partner and secondarily arises from the ventral spinous processes of the remaining anterior vertebrae. Insertion is, medial to the longissimus cervicis, onto the basioccipital and its process. The body of the muscle lies dorsal to the esophagus and ventral to the longissimus cervicis.

M. Rectus Capitis Posterior. (Figs. 8, 13, and 17)

G. Anteriorly this muscle is deep to the spinalis capitis and medial to the obliquus capitis magnus. In the vicinity of the seventh vertebrae the muscle is deep only to the dorsal fascia, is medial to the lateral portion of the spinalis capitis, and lateral to the ligamentum nuchae. This muscle is separated into anterior and posterior budnles by a myosepta with some interdigitation in the vicinity of the fourth vertebrae. The anterior bundle is divided into a lateral and a medial slip which are interdigitated but separable. The lateral slip makes the myosepta connection with the posterior bundle and originates from the second, third, and fourth vertebrae with insertion onto the paroccipital process, the parietal, and the supra-temporal. The medial slip originates from the atlas and inserts onto the prootic and the supraoccipital elements. The most anterior portion of the posterior bundle lies deep to the anterior bundle and inserts tendonously onto the axis.

M. Sacrolumbalis. (Figs. 6 and 9)

G. This superficial epaxial muscle originates from the crest of the ilium and inserts tendonously onto the ribs. Anteriorly, fibers of this muscle will join those of the intercostalis externis and the obliquus abdominus profundus to insert onto the ventrolateral process of the axis. This muscle interdigitates laterally with the obliquus abdominus muscles. This muscle is superficial to the intercostalis externis dorsally.

M. Scapulodeltoideus. (Figs. 6, 9, 12, and 13)

G. This triangular shaped muscle originates primarily from the lateral surface of the suprascapula with some fibers originating from the clavicle bar. Insertion is tendonously onto the deltopectoral process of the humerus. The muscle is ventral to the levator scapulae muscles and superficial to the scapulohumeralis muscles.

M. Scapulohumeralis Anterior. (Figs. 14 and 17)

G. This muscle has two slips. The dorsal slip inserts onto the anterior edge of the humerus next to the glenoid fossa beneath the sternoscapular ligament. The fibers continue dorsoanteriorly to originate from the most dorsoanterior surface of the scapular bar and the most ventroanterior surface of the suprascapula. The second slip, which is the longer, has the same origin but inserts onto the lateroventral border of the scapula. Centrally the two slips are joined by a myosepta.

M. Scapulohumeralis Posterior. (Figs. 8, 14, and 17)

G. This rectangular shaped muscle inserts onto the proximal end of the humerus next to the glenoid fossa, posterior to the insertion of the anterior muscle and medial to the insertion of the latissimus dorsi. The fibers continue anterodorsally covering some of the fibers of the serratus ventralis to originate from the posterolateral surface of the suprascapula and the scapular bar.

M. Serratus Dorsalis. (Fig. 8)

G. This muscle arises from the lateral surface of the first three cervical ribs by three slips and inserts onto the dorsal surface of the suprascapula. They slightly overlap one another by the posterior succeeding one.

M. Serratus Ventralis. (Figs. 8 and 13)

G. This is a wide straplike muscle which originates from the ribs of the sixth and seventh vertebrae, dorsal to the origin of the obliquus abdominus muscles. Insertion is onto the posteromedial border of the suprascapula and the dorsolateral portion of the scapula bar. This muscle is deep to the latissimus dorsi and the trapezius.

M. Spinalis Capitis. (Figs. 7, 8, 12, and 13)

G. This muscle originates along the cervical and thoracicolumbar vertebrae and inserts along the entire posterior portion of the parietal. Anteromedially, fibers insert tendonously onto the side of the supraoccipital ridge. The muscle has a medial and a lateral portion which are unseparable. The medial portion is superficial to the rectus capitis posterior and thins posteriorly to terminate near the seventh vertebrae. The lateral portion participates in a myosepta with some of the deeper muscles and continues posteriorly, lateral to the rectus capitis posterior.

M. Subscapularis 1. (Not figured)

G. This muscle has three slips which converge posteriorly to insert by a common tendon onto the humeral head. The most anterior slip originates from the anterodorsal border of the scapula. The most lateral slip of the two posterior slips originates from the scapula bar and the suprascapula; whereas the medial slip originates from the scapula bar. They both converge posteriorly to join the anterior slip.

M. Subscapularis 2. (Not figured)

G. The fibers of this muscle originate from the majority of the dorsal surface of the scapula and converge to insert onto the humeral head dorsal to the insertion of the subscapularis 1. This muscle is located between the anterior slip of the subscapularis 1 and the dorsal slip of the coracobrachialis longus, and lies lateral to the origin of the internal sternocoracoideus.

M. Supracoracoideus. (Fig. 17)

G. This ventral muscle has a wide origin from the anteromedial surface of the scapula with the fibers converging to insert tendonously onto the medial surface of the deltopectoral crest of the humerus. This muscle is located posterior to the clavodeltoideus and anterior to the biceps. On the scapula a thin layer of fibers will cover the anteroventral surface of the biceps. This muscle is thicker anteriorly.

M. Sternocleidomastoideus. (Figs. 6, 9, 11, and 15)

G. This wide, thick ribbonlike muscle originates from the posterior surfaces of the parietal, the squamosal, and the quadrate. It extends ventroposteriorly to insert onto the lateral process of the interclavicle. Near its insertion this muscle is fused with the trapezius. It is deep to the depressor mandibularis, the ceratobranchial

1, the branchiohyoideus, and the lateral portion of the trapezius. It is superficial to the neck muscles and to the insertion of the trapezius and the sternohyoideus.

M. Sternohyoideus. (Figs. 10, 12, 15, and 16)

G. The sternohyoideus is a thick sheet muscle having a superficial and a profundus layer. Some of the fibers slightly intermix medially and tend to become parallel to the bilateral axis; however, the muscle is easily separable into two layers. The ventral layer is slightly larger and originates from the posterior and ventral surfaces of the ceratobranchial 1 and medially from the corpus. Its fibers extend posterolaterally to insert onto the lateral process of the interclavicle and the clavicle-suprascapular bar, adjacent to the attachment of the trapezius. At its insertion this muscle joins with the sternocleidomastoideus and the trapezius. It is deep to portions of the sternocleidomastoideus, the trapezius, the depressor mandibularis, and the constrictor coli. The dorsal layer extends further laterally than the superficial layer and has its origin from the posterior surface of the ceratobranchial 1 and 2. Fibers continue posteromedially to insert onto the lateral process of the interclavicle. This layer is superficial to the pharyngeal membrane, the thyroid gland, and portions of the clavodeltoideus and the scapulodeltoideus. Medially, this muscle borders an elliptical space as previously mentioned in the General Description of the Myology.

M. Transversalis. (Fig. 14)

G. This loosely arranged muscle arises from a fascia which extends from the pelvis to the neck region and inserts ventrally onto the ribs, the lateral surface of the sternum, and the dorsal surface of the rectus abdominus. The fibers extend in a dorsoanterior direction, are superficial to the peritoneal membrane and are deep to the obliquus abdominus internis.

M. Trapezius. (Figs. 6, 7, 9, 11, 15, and 16)

G. The trapezius originates from the middorsal fascia and covers a majority of the lateral musculature. It narrows laterally to insert ventrally onto the clavicle bar and the lateral process of the interclavicle which in turn is attached to the sternum by a broad ligament. On the ventral surface the muscle fuses with the sternocleidomastoideus. In some specimens this muscle was attached to the pectoralis by a tendonous fascia. The trapezius is variable in thickness with the anterior fibers usually being thicker. Towards the center they become thinner and in some specimens can be separated into two bundles. In this case the anterior bundle inserts onto the lateral process of the interclavicle and the most ventral portion of the interclavicle-clavicle bar. The posterior bundle inserts onto the posterior border of the clavicle bar, dorsal to the sternocleidomastoideus.

Unnamed Muscle. (Not figured)

The following muscle was found in E. gilberti (BYU 31956). It is a thin horizontal straplike muscle originating by fascia from the ribs of the twelfth and thirteenth vertebrae and inserting onto the anterior edge of the insertion of the serratus ventralis, and also onto the suprascapula. This muscle is deep to the latissimus dorsi. It is not present in any other specimen of gilberti nor in skiltonianus.

Figure 6. Musculature dorsal view. *Eumeces gilberti* (3.7X) (BYU 31956).
A. Superficial depth
B. First depth

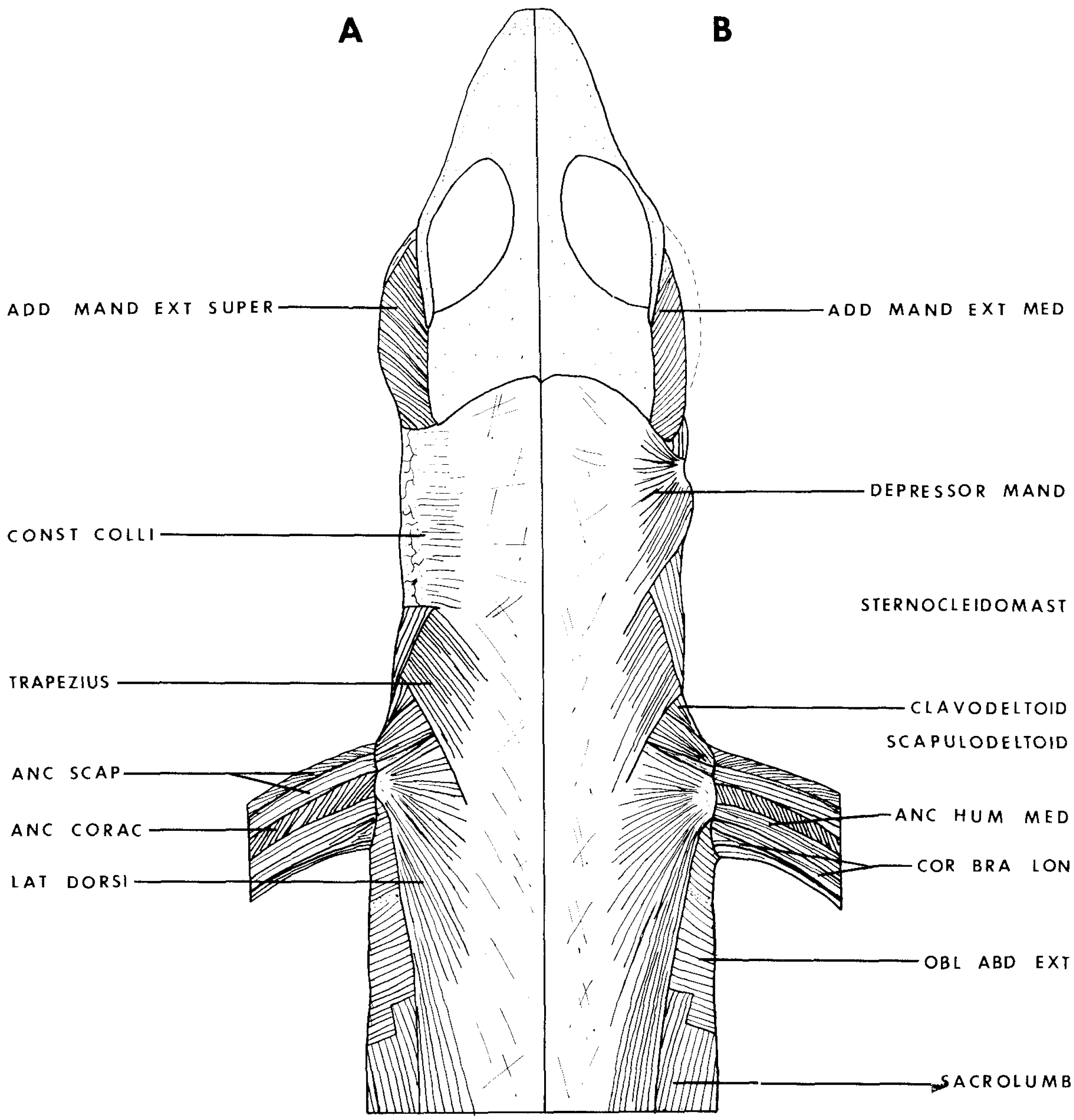

A
B
ADD MAND EXT SUPER
ADD MAND EXT MED
DEPRESSOR MAND
CONST COLLI
STERNOCLEIDOMAST
TRAPEZIUS
CLAVODELTOID
SCAPULODELTOID
ANC SCAP
ANC HUM MED
ANC CORAC
COR BRA LON
LAT DORSI
OBL ABD EXT
SACROLUMB

Figure 7. Musculature dorsal view. *Eumeces gilberti* (3.7X) (BYU 31956).
A. Second depth
B. Third depth

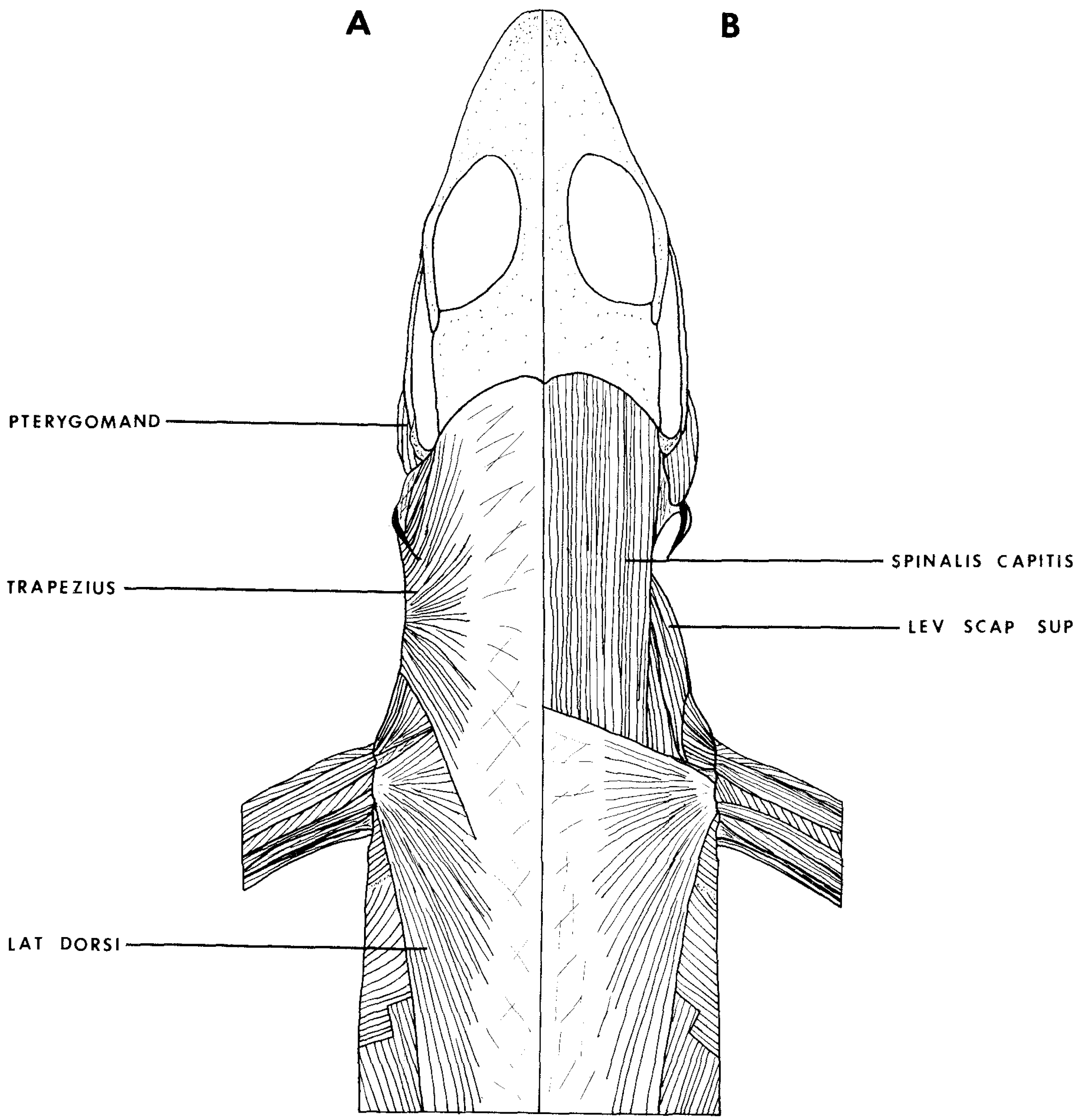

A
B
PTERYGOMAND
SPINALIS CAPITIS
TRAPEZIUS
LEV SCAP SUP
LAT DORSI

Figure 8. Musculature dorsal view. Eumeces gilberti (3.7X) (BYU 31956).
A. Fourth depth
B. Fifth depth

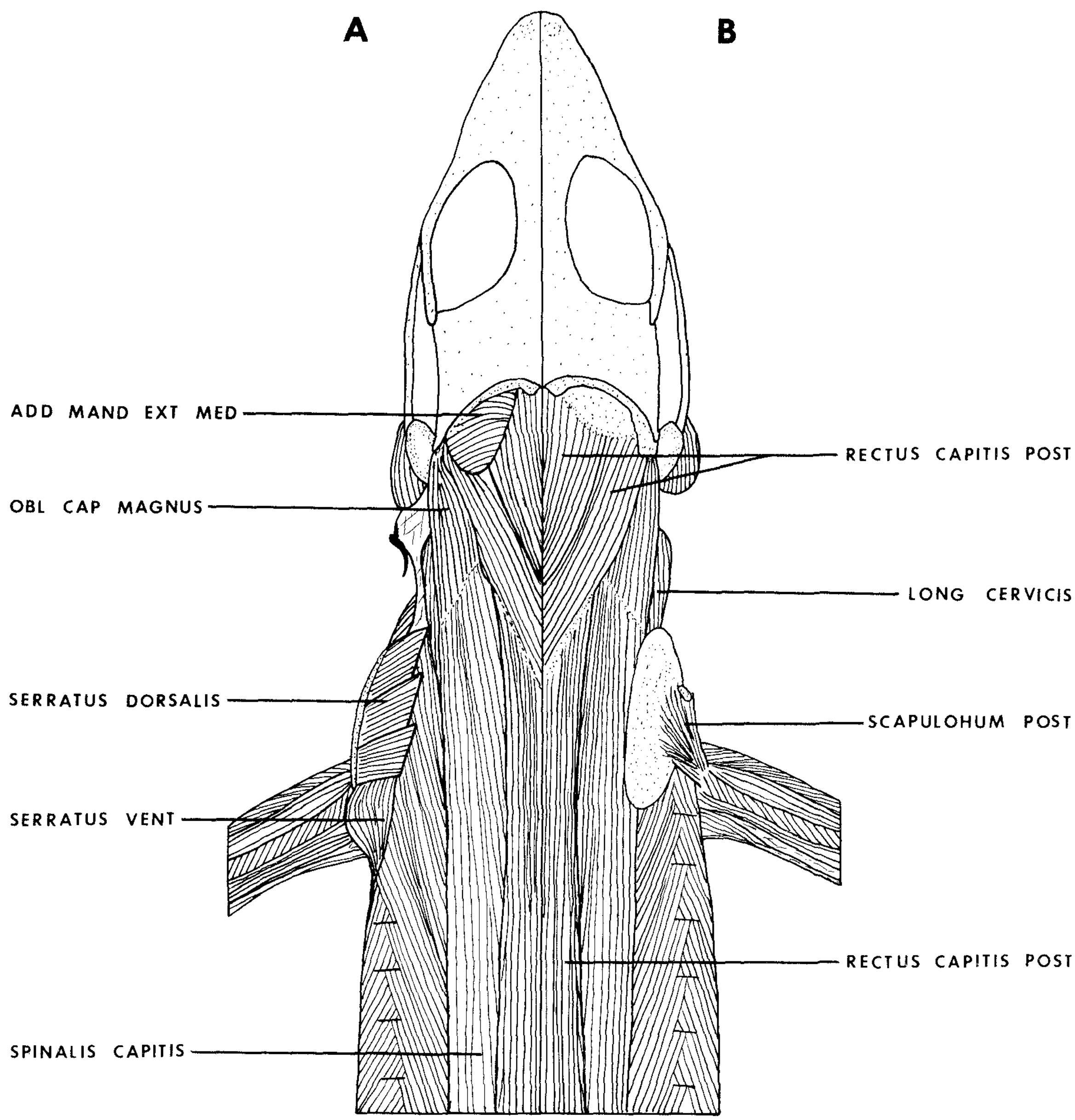
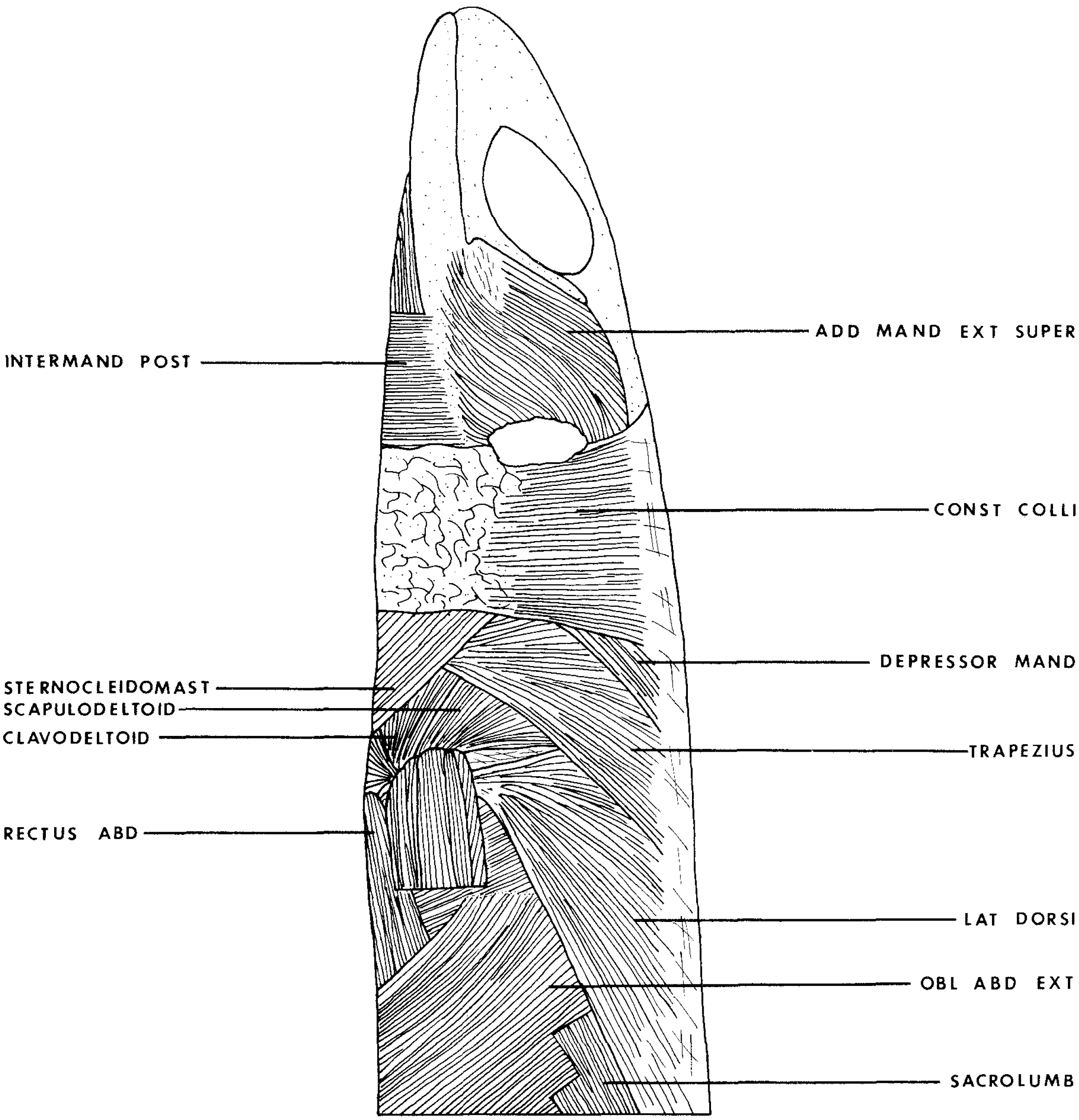

A
B
ADD MAND EXT MED
OBL CAP MAGNUS
SERRATUS DORSALIS
SERRATUS VENT
SPINALIS CAPITIS
RECTUS CAPITIS POST
LONG CERVICIS
SCAPULOHUM POST
RECTUS CAPITIS POST

Figure 9. Musculature lateral view. Superficial depth. *Eumeces gilberti* (3.7X) (BYU 31956).



ADD MAND EXT SUPER
INTERMAND POST
CONST COLLI
DEPRESSOR MAND
STERNOCLEIDOMAST
SCAPULODELTOID
CLAVODELTOID
TRAPEZIUS
RECTUS ABD
LAT DORSI
OBL ABD EXT
SACROLUMB

Figure 10. Musculature lateral view. First depth. A. Eumeces gilberti (3.7X) (BYU 31956). B. Eumeces skiltonianus (5.7X) (BYU 12474). Showing anterior and posterior bundles of the depressor mandibularis.

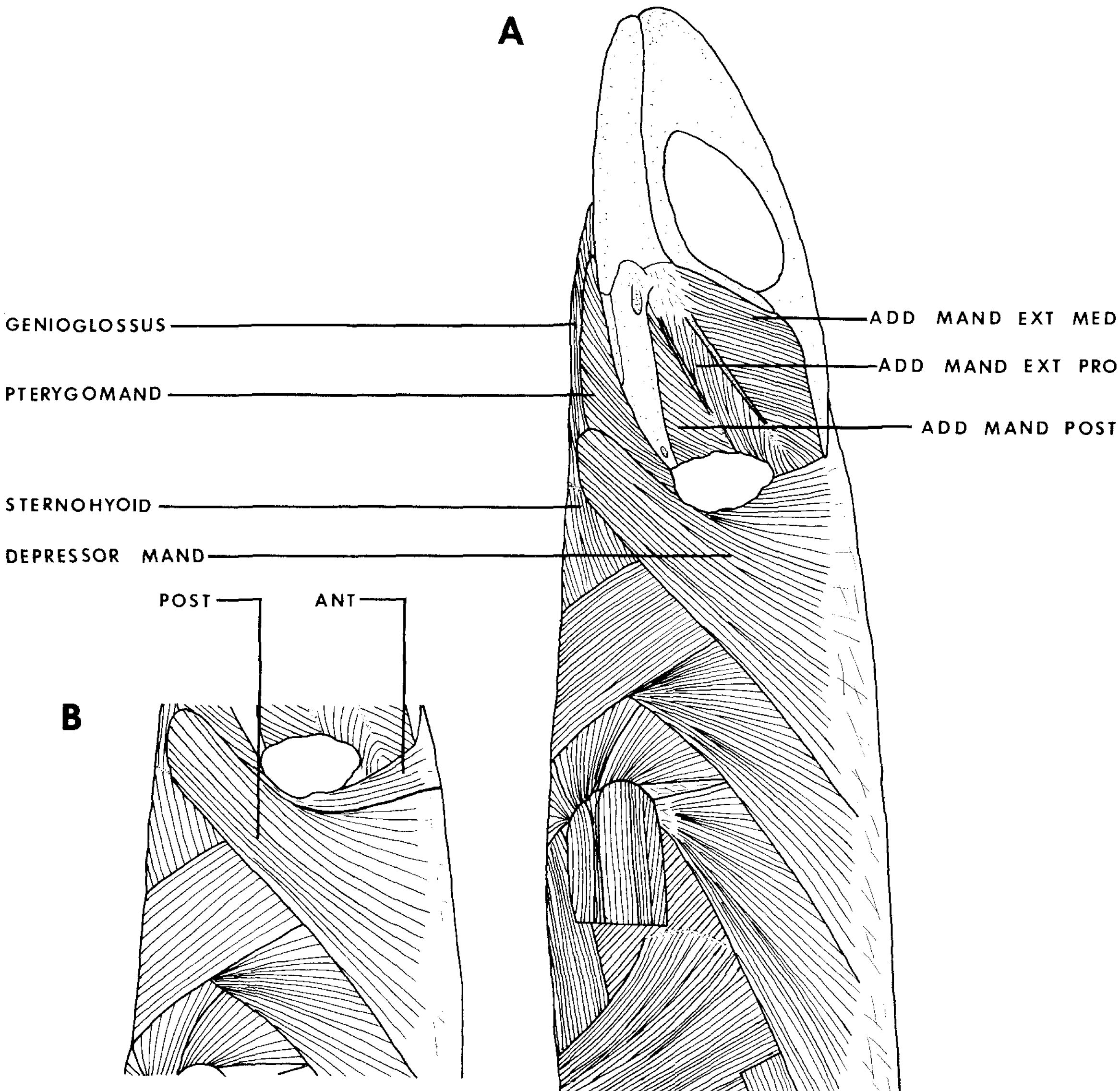

A
B
GENIOGLOSSUS
PTERYGOMAND
STERNOHYOID
DEPRESSOR MAND
POST
ANT
ADD MAND EXT MED
ADD MAND EXT PRO
ADD MAND POST

Figure 11. Musculature lateral view. Second depth. Eumeces gilberti (3.7X) (BYU 31956).

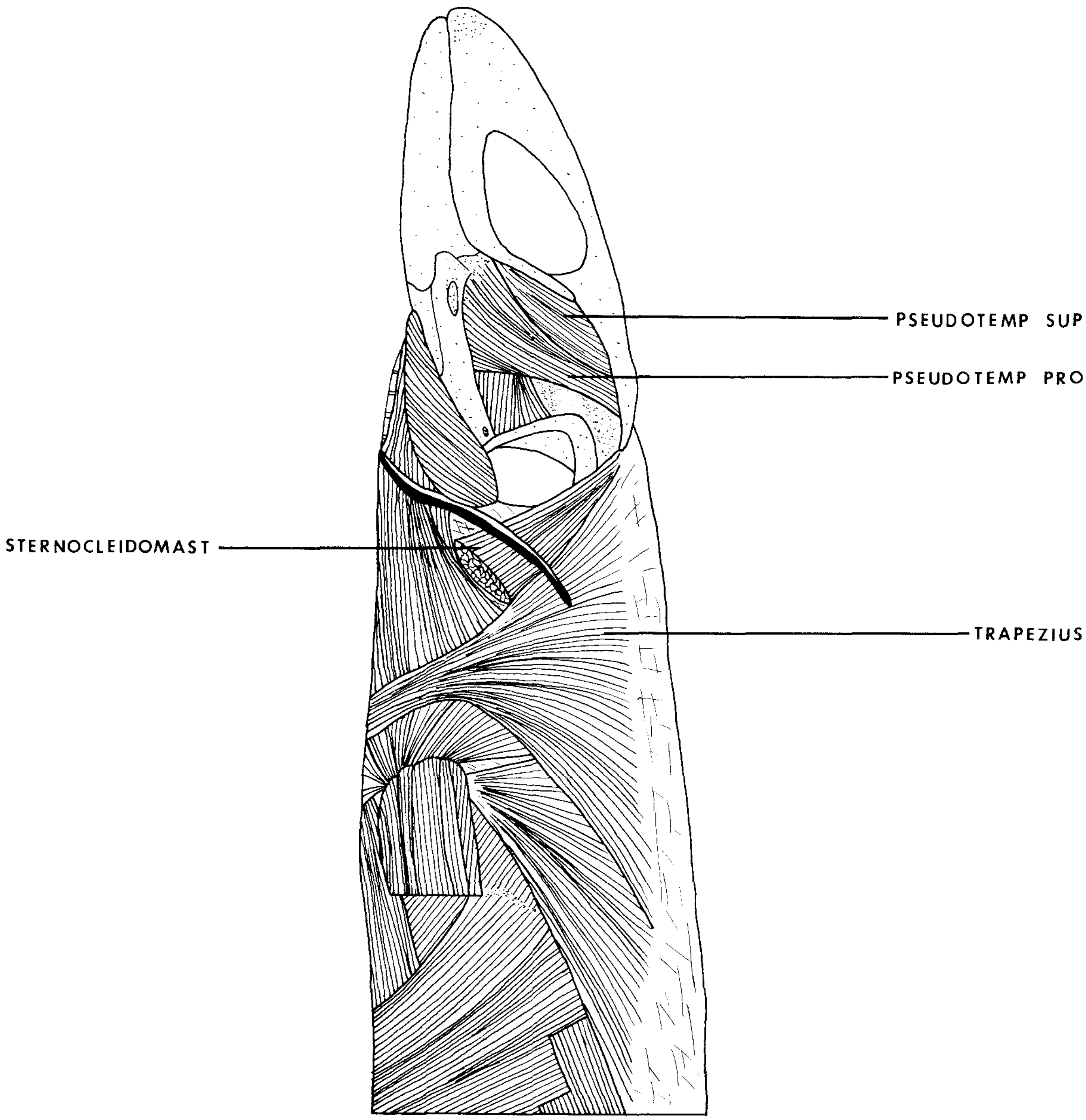

PSEUDOTEMP SUP
PSEUDOTEMP PRO
STERNOCLEIDOMAST
TRAPEZIUS

Figure 12. Musculature lateral depth. Third depth. Eumeces gilberti (3.7X) (BYU 31956).

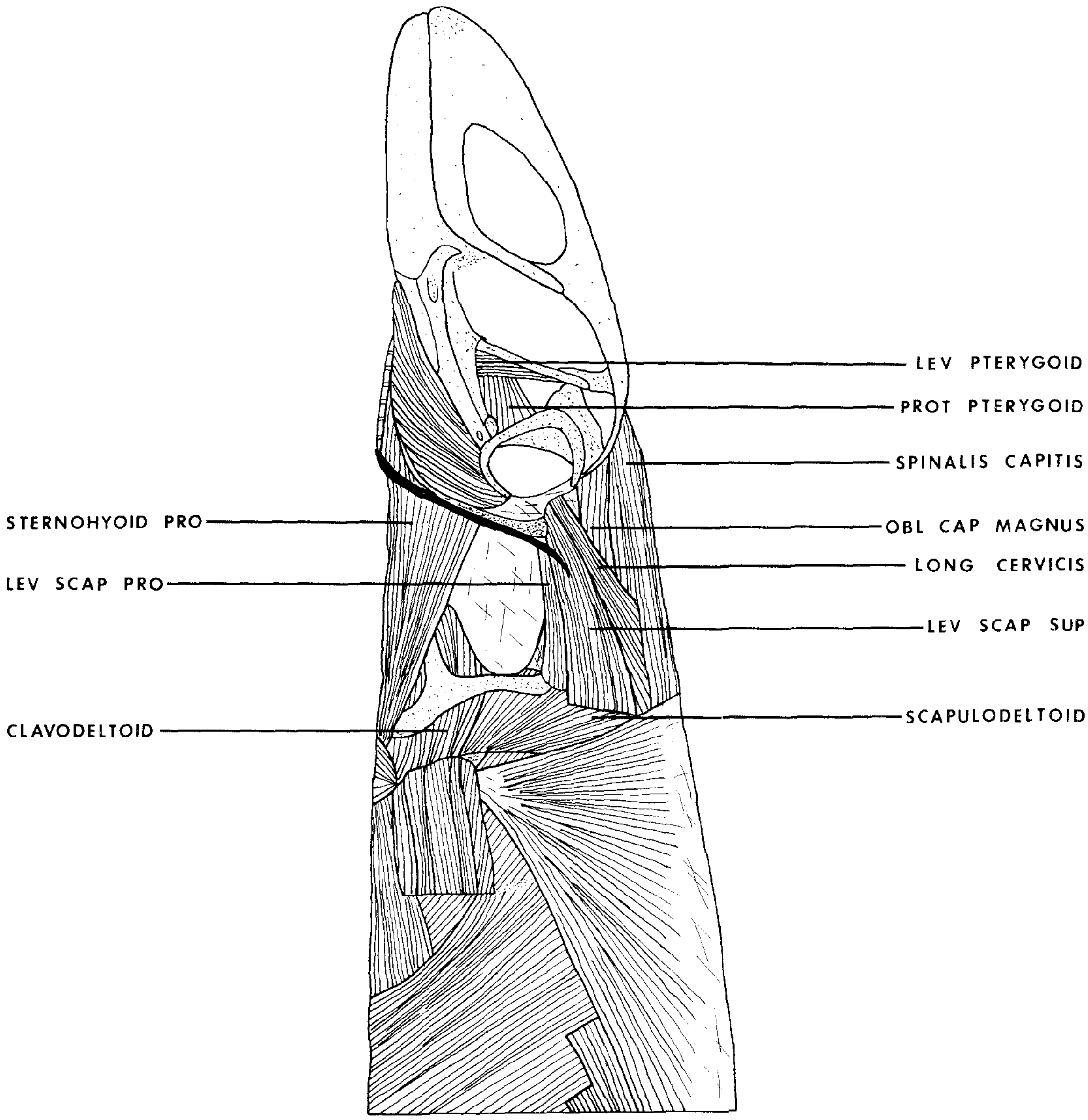

LEV PTERYGOID
PROT PTERYGOID
SPINALIS CAPITIS
STERNOHYOID PRO
OBL CAP MAGNUS
LONG CERVICIS
LEV SCAP PRO
LEV SCAP SUP
CLAVODELTOID
SCAPULODELTOID

Figure 13. Musculature lateral depth. Fourth depth. *Eumeces gilberti* (3.7X) (BYU 31956).

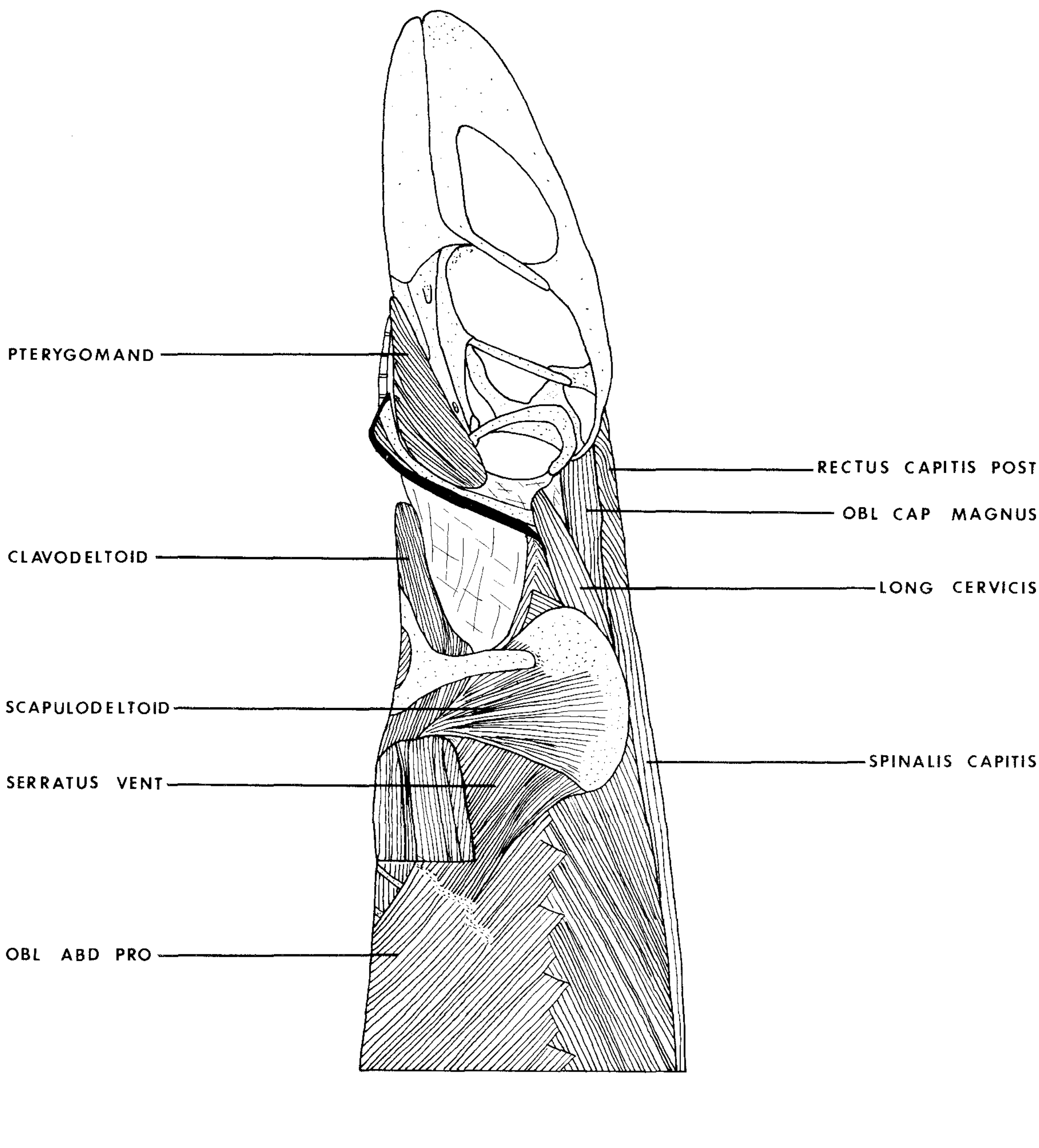

PTERYGOMAND
RECTUS CAPITIS POST
OBL CAP MAGNUS
CLAVODELTOID
LONG CERVICIS
SCAPULODELTOID
SPINALIS CAPITIS
SERRATUS VENT
OBL ABD PRO

Figure 14. Musculature lateral view. Fifth depth. *Eumeces gilberti* (3.7X) (BYU 31956).

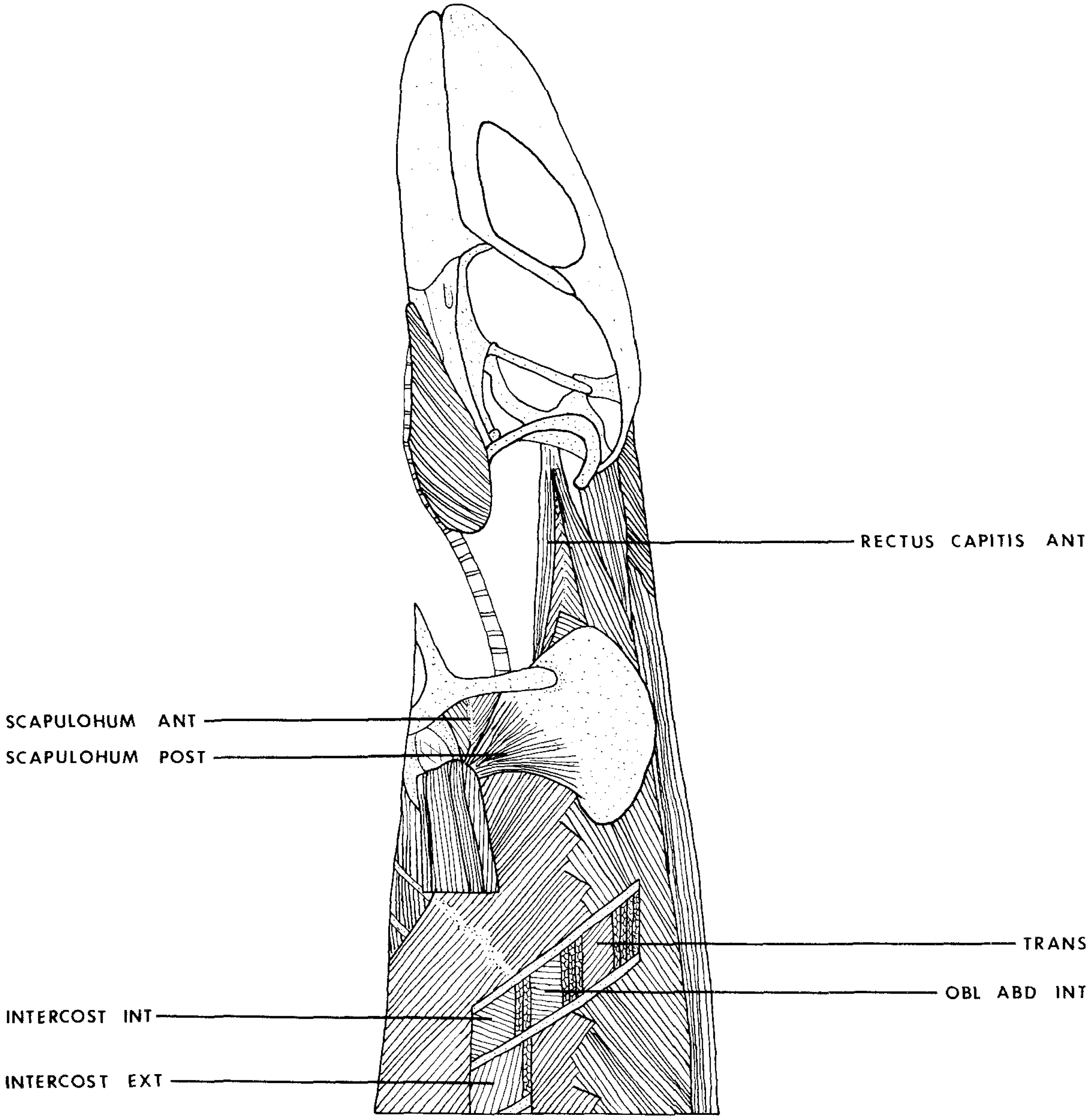

RECTUS CAPITIS ANT
SCAPULOHUM ANT
SCAPULOHUM POST
TRANS
OBL ABD INT
INTERCOST INT
INTERCOST EXT

Figure 15. Musculature ventral view. Eumeces gilberti (3.7X) (BYU 31956).
A. Superficial depth
B. First depth

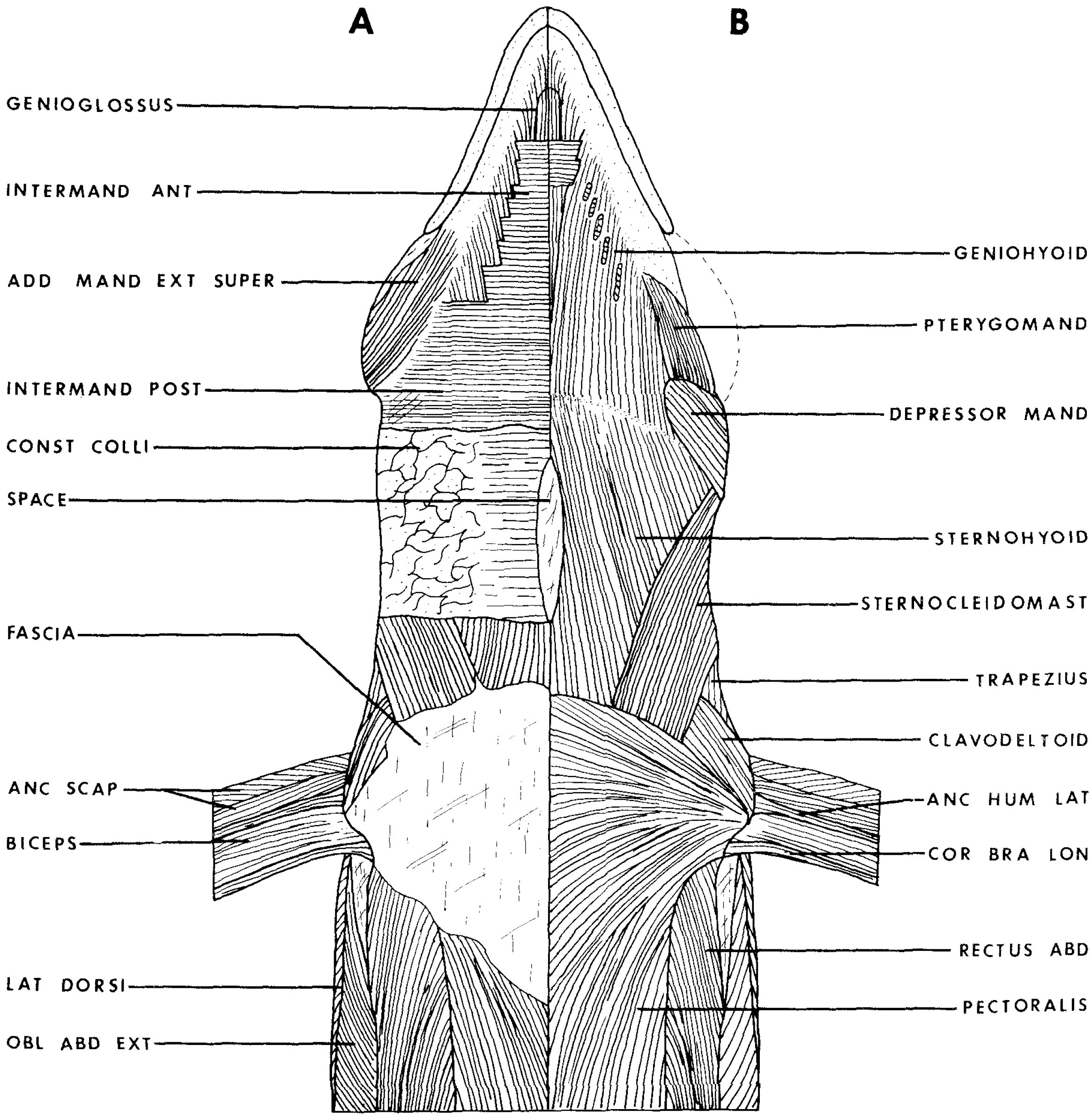

A
B
GENIOGLOSSUS
INTERMAND ANT
ADD MAND EXT SUPER
INTERMAND POST
CONST COLLI
SPACE
FASCIA
ANC SCAP
BICEPS
LAT DORSI
OBL ABD EXT
GENIOHYOID
PTERYGOMAND
DEPRESSOR MAND
STERNOHYOID
STERNOCLEIDOMAST
TRAPEZIUS
CLAVODELTOID
ANC HUM LAT
COR BRA LON
RECTUS ABD
PECTORALIS

Figure 16. Musculature ventral view. *Eumeces gilberti* (3.7X) (BYU 31956).
A. Second depth
B. Third depth

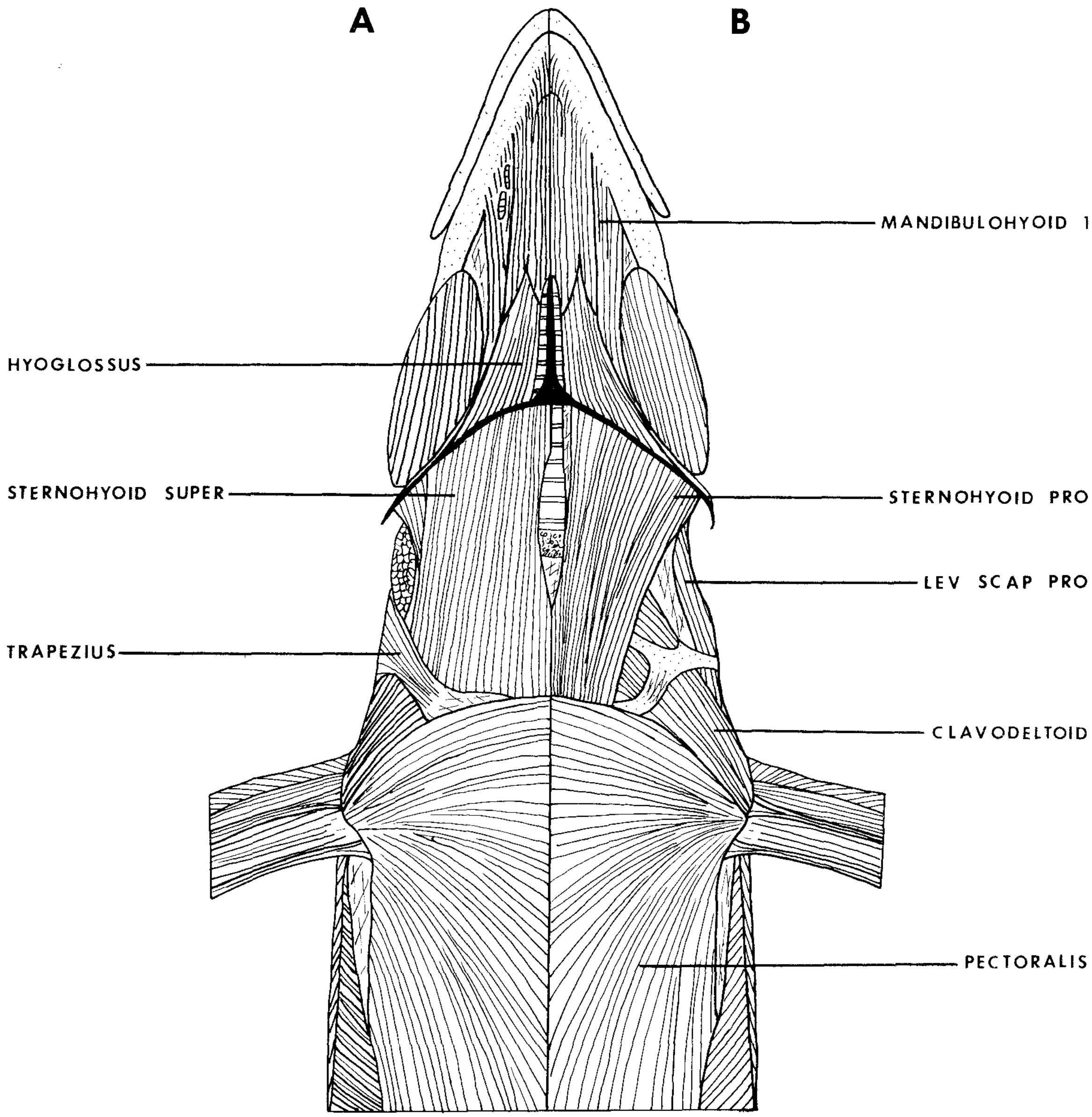
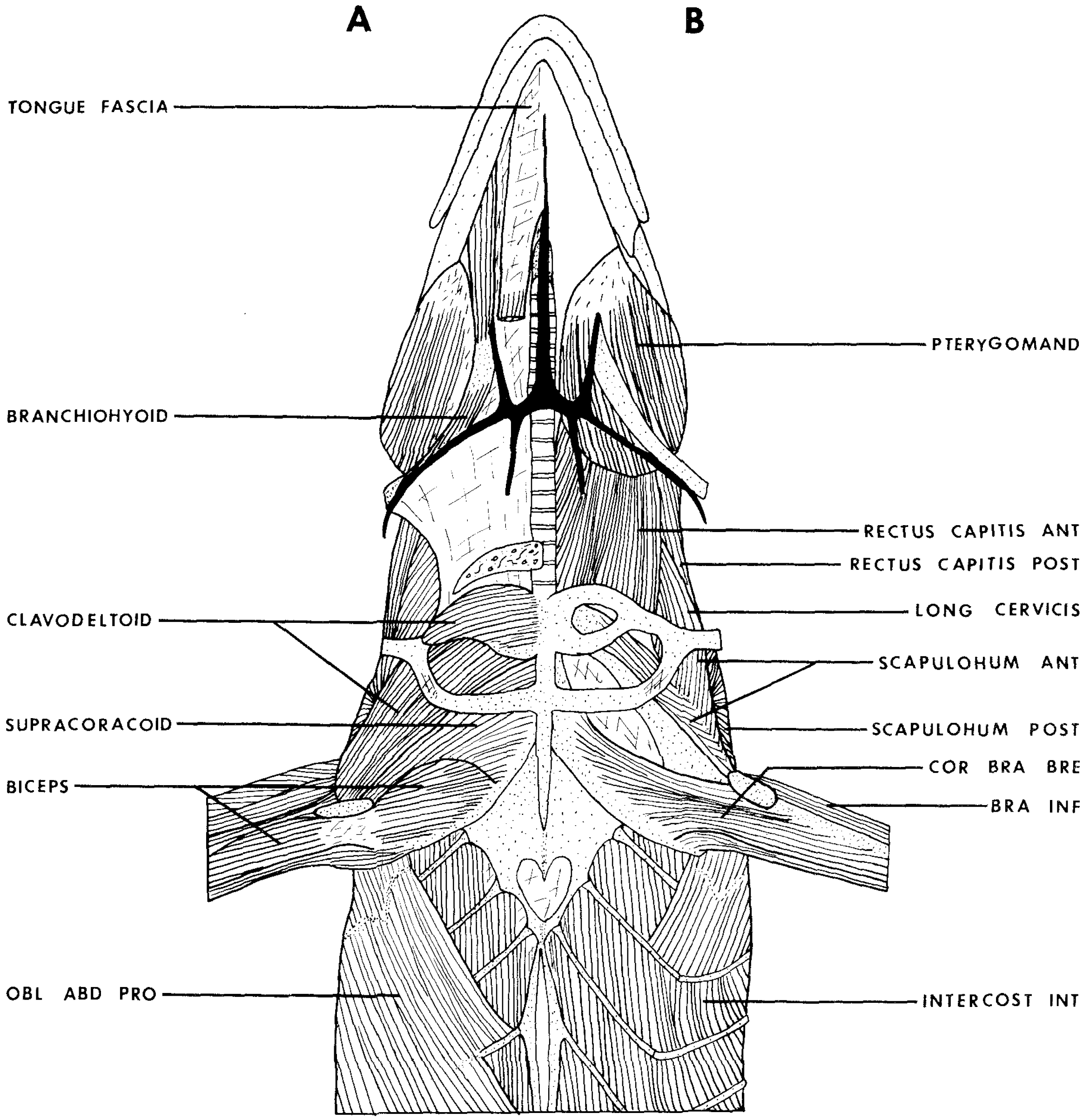

A
B
MANDIBULOHYOID 1
HYOGLOSSUS
STERNOHYOID SUPER
STERNOHYOID PRO
LEV SCAP PRO
TRAPEZIUS
CLAVODELTOID
PECTORALIS

Figure 17. Musculature ventral view. Eumeces gilberti (3.7X) (BYU 31956).
A. Fourth depth
B. Fifth depth


A
B
TONGUE FASCIA
BRANCHIOHYOID
CLAVODELTOID
SUPRACORACOID
BICEPS
OBL ABD PRO
PTERYGOMAND
RECTUS CAPITIS ANT
RECTUS CAPITIS POST
LONG CERVICIS
SCAPULOHUM ANT
SCAPULOHUM POST
COR BRA BRE
BRA INF
INTERCOST INT

DISCUSSION

Osteology

Upon comparing the lizard skull with other groups of the class Reptilia one finds according to Jollie (1960) "that all are specialized to some extent and none is strickingly more primitive in the totality of its structure than the others.". He further states that the variation of structures can be explained largely by adaptive modification and that the reptilia show "radiation rather than an anatomical heirarchy of groups.".

To determine what the ancestral lizard or the first lizard may have looked like one must rely on the fossil record and the anatomy of living lizards. Broom (1935) is of the opinion that lizards arose from Eosuchian stock in the Upper Triassic and then later developed osteoderms over the skull and the body regions. In the Middle Mesozoic some primitive groups retained the osteoderms while others lost them; thus giving rise to the living forms which have a variety of skull variations. All of the families within the infraorder Leptoglossa (scincomorpha) have osteoderms except the family Teiidae. The genus Ameiva within this family has os palpabre elements (Fisher and Tanner, 1970) which may be suggestive of cranial osteoderms sometime in the past. In families that still retain the osteoderms, Laurtidae and Scincidae, the supratemporal fenestrae are extremely reduced or lost in contrast with the teiids which have large fenestrae. The postfrontals being expanded in the former while in the latter the post-frontals are reduced, lost, or fused with the postorbitals.

Following is a discussion of the osteological comparisons between *E. gilberti* and *E. skiltonianus*. The variations noted are: 1. in *gilberti* the anterior lateral processes of the frontals prevent articulation of the prefrontals with the nasals; whereas, in *skiltonianus* articulation with the nasals and prefrontals can either be present or absent; 2. in *gilberti* the maxillae contain six to eight supralabial foraminae and 15 to 20 teeth, average 19, while in *skiltonianus* the maxillae contain four to seven supralabial foraminae and 17 to 20 teeth, average 18; 3. in *gilberti* there are three to five nasal foraminae compared with two to four in *skiltonianus*; 4. in *gilberti* the dentary have three to six mental foraminae and 19 to 23 teeth, average 21, compared with *skiltonianus* which has four to seven mental foraminae and 18 to 22 teeth, average 21; and 5. in *gilberti* the postorbitals frequently show a reduction of the relative size when compared to other adjacent bones while in *skiltonianus* the same degree of reduction is only occasionally observed. Condensing these variations it is found that: 1. the number of foraminae in the maxillae, nasals and dentary overlap and are variable within species with neither species showing a definite trend; 2. the same applies to the number of teeth in the maxillae and mandible; 3. in *gilberti* the nasal-prefrontal articulation is constant; whereas, in *skiltonianus* it is variable; and 4. in *gilberti* the postorbitals frequently show a reduction of the relative size when compared to other adjacent bones, while in *skiltonianus* this same degree of reduction is only occasionally observed.

Myology

In contrast with osteology, the homologies of muscles, and thus phylogenies, are difficult to trace when comparing different taxonomic categories. If significant changes are to be found, they are in the cranial myology. This area seems to be the most easily traceable among groups and in turn is phylogenetically the most important. Tanner (1952) working with the Plethodontidae found the throat musculature to be stable enough to define genera. This conclusion has been supported by other papers by Robison and Tanner (1962), Avery and Tanner (1964), Jenkins and Tanner (1968), and Fisher and Tanner (1970).

Smith (1960) lists a number of trends which have taken place in the musculature of the more primitive to the more advanced vertebrates. These are: 1. the loss of myosepta and the fusion of myotomes; 2. the separation of muscles into layers; 3. the expansion of muscles from a limited size; 4. the shifting of location of muscles; 5. the multiplication or fusion of muscle attachments; and 6. the subdivision of muscles.

In general these two species show both primitive and advanced characters. The presence of myosepta in the axial musculature would certainly indicate a primitive condition. The subdivision of the intermandibularis anterior, the rectus capitis posterior, the possible trend toward a complete separation of the trapezius and the depressor mandibularis and the distinct layers of the obliquus abdominus externis and sternohyoideus muscles would indicate an advanced condition.

When comparing the myology of these two species little difference is observed. The intermandibularis shows a subspecific difference in _E. skiltonianus_. In the specimens observed of the two _skiltonianus_ subspecies there was found to be a range of five to seven subdivisions of the intermandibularis anterior. In _skiltonianus_ the number of subdivisions tended toward the lower limit, whereas in _utahensis_ the number of subdivisions tended toward the higher limit. On the other hand both subspecies of _gilberti_ tended to orient themselves equally with six to seven subdivisions of this muscle. The only myological character found in this study which differentiates these two species consistently is the depressor mandibularis. In _skiltonianus_ this muscle is easily separated into an anterior and a posterior bundle, whereas in _gilberti_ this same muscle is somewhat interdigitated and not easily separable. All other muscules mentioned are similar in both species.

SUMMARY AND CONCLUSIONS

The differences observed from the osteology and myology are few and subtle, thus complicating the ideal situation of having a more definitive separation of these two species.

Neither species is consistent in having all of the anatomical characters equal. E. skiltonianus, however, does have more variation than gilberti. This species: 1. exhibits a wider range of variation in the number of slips of the intermandibularis anterior; 2. has two distinct bundles of the depressor mandibularis; and 3. has variation in the anterior suture pattern of the frontal, nasal, prefrontal and maxillae elements. E. gilberti on the other hand has: 1. only one distinct bundle of the depressor mandibularis; 2. a frequent reduction of the relative size of the postorbitals when compared to other adjacent bones; and 3. a more limited suture pattern in the anterior portion of the skull. The major anatomical difference between these two species seems to be size. From the specimens used in this study the average snout-vent length of gilberti is approximately 30mm greater than that of skiltonianus.

I believe that skiltonianus shows more anatomical plasticity than gilberti. Plasticity in this case would indicate a more recent gene flow between peripheral and central individuals, and genetic inconstancy which would provide more variation and more flexibility for adaptation and selection. When the geographical distribution of these two species is considered it also appears that skiltonianus has more flexibility.

Taylor (1935) has suggested that these two species may have arisen simultaneously from a common ancestral stock. On the basis of this anatomical study there is little reason to doubt their close relationship. However, it seems logical to propose an alternate suggestion; namely, that the anatomical variations of *skiltonianus*, when compared with similar characters in *gilberti*, indicate that *gilberti* may have arisen from *skiltonianus*.

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VITA

David F. Nash

A COMPARATIVE STUDY OF THE HEAD AND THORACIC OSTEOLOGY

AND MYOLOGY OF THE SKINKS, EUMECES SKILTONIANUS

(BAIRD AND GIRARD) AND EUMECES GILBERTI VAN DENBURGH

David F. Nash

Department of Zoology

Master of Science Degree, August 1970

ABSTRACT

Further clarification of the taxonomic and phylogenetic relationships of *Eumeces gilberti* and *Eumeces skiltonianus* is achieved by the comparisons of the skull, mandible elements, and the anterior myology of these two species. Figures are provided to compliment the descriptions.

The study confirms their close relationship and few differences are observed. *E. skiltonianus*, however, appears to have more anatomical plasticity which suggests that *E. gilberti* may have arisen from the former.

APPROVED: