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A COMPARATIVE STUDY OF CROTAPHYTUS HOLBROOK (IGUANIDAE)

A Thesis

Presented to the

Department of Zoology and Entomology

Brigham Young University

In Partial Fulfillment

of the Requirements for the Degree

Master of Arts

---

by

Wilbur Gerald Robison, Jr.

August 1960

This thesis, by Wilbur Gerald Robison, Jr., is accepted in its present form by the Department of Zoology and Entomology of the Brigham Young University as satisfying the thesis requirement for the degree of Master of Arts.

Typed by Betty D. Harrison

August 1960

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Dr. Howard C. Nielson of the Statistics Department assisted in the statistical analyses.

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INTRODUCTION

It is becoming increasingly evident that the numerous comparative descriptions of certain saurian groups, which have been based mainly on external characters need to be supplemented by accounts of their internal anatomy, ecology, physiology, cytology, and genetics, as suggested by Huxley (1940:1), in order to fully understand the taxonomic and phylogenetic positions they hold. Perhaps this need is epitomized by the long confused case of the genus Crotaphytus Holbrook.

The purpose of this study is to describe and compare features of the anterior myology and osteology among members of the genus Crotaphytus for use, in addition to external characteristics, in determining if it is justifiable to separate Gambelia Baird as a monotypic genus, as proposed by Hobart M. Smith (1946:158-166).

It is hoped that the descriptions and plates herein will also aid in, and encourage gross anatomical studies of many different reptiles, add to our understanding of homologies, and indicate some of the structures which are important phylogenetically and taxonomically.

MATERIALS AND METHODS

The principal subspecies used for this study have been Crotaphytus wislizeni wislizeni Baird and Girard and Crotaphytus collaris baileyi Stejneger. However, four specimens of Crotaphytus collaris auriceps Fitch and Tanner from Grand County, Utah, and three of Crotaphytus collaris collaris Say from Anderson County, Kansas, and Stephens County, Texas, were dissected.

A male and female of Crotaphytus reticulatus from Webb and Dimmit Counties, Texas (snout to vent lengths 115 and 110 respectively) were the only representatives of this species examined.

The sixty-nine lizards of Crotaphytus w. wislizeni included in this study came from Navajo County, Arizona; Owyhee County, Idaho; Clark, Lander, Lincoln, Nye, Storey, and White Pine Counties, Nevada; and from Beaver, Emery, Garfield, Grand, Iron, Juab, Kane, Millard, Sanpete, San Juan, Tooele, Utah, Washington, and Wayne Counties, Utah.

The seventy-eight members of Crotaphytus c. baileyi used were collected in Coconino, Gila, and Navajo Counties, Arizona; Chihuahua, Mexico; Ada and Owyhee Counties, Idaho; Clark County, Nevada; and Emery, Garfield, Grand, Juab, Kane, Millard, Tooele, Utah, Washington, and Wayne Counties, Utah.

The majority of specimens was well preserved in formalin. However, a few were killed freshly by injecting water into the abdomen and the subcutaneous sinuses. This caused an expansion of the muscles as a result

of osmotic pressure, thus permitting the recognition of aspects which are not so evident in preserved material. Other specimens were injected or subcutaneously painted with 45% aceto-carmine to make the thin, superficial layers of muscle opaque enough to be seen clearly.

Skeletons were prepared by bacterial action or by an overnight soaking of a fresh, skinned lizard in 50% ammonium hydroxide, with a subsequent short period of boiling in water. The latter method gave better results. One disarticulated skeleton was prepared from a lizard preserved in formalin. The lizard was skinned and soaked in several changes of water for two weeks. It was then changed to 50% ammonium hydroxide and left for two months, after which time even the skull was disarticulated.

It should be mentioned that the skull measurements included in the statistical analysis section were made from preserved specimens, carefully dissected, and not from skulls distorted by the cleaning techniques. All the measurements are in millimeters and were made with the aid of a hand micrometer and a dissecting microscope.

REVIEW OF LITERATURE

The taxonomic history of this group is rather complicated. The genus Crotaphytus was first proposed by John E. Holbrook (1842:79-83), although the type species was collected and described earlier by Thomas Say (James, 1823:252) as Agama collaris. In April of 1852 Spencer F. Baird and Charles Girard (1852a:69)* added Crotaphytus wislizeni to the

*I follow Taylor (1935:411-412) in considering this manuscript to have been published before Stansbury's report (Baird and Girard, 1852b).

genus, and four months later they described the same species from a different locality as Crotaphytus gambelii (Baird and Girard, 1852c:126). In December that same year Edward Hallowell (1852:207-208) gave a more lengthy description of this species, naming it Crotaphytus fasciatus. A third species, Crotaphytus reticulatus, was named by Baird (1858:253).

The status of the species Crotaphytus insulanus Van Denburgh and Slevin (1921:96) and that of Crotaphytus dickersonae Schmidt (1922:638) have been questioned by Burt (1928b:6-10) and Allen (1933:7), but are retained as full species by Smith and Taylor (1950:93).

Hobart M. Smith (1946:158-166) separated the species wislizeni into the genus, Gambelia, having obtained this name from Baird (1959:7), who used it while describing Crotaphytus reticulatus, as follows: "More closely related to Crotaphytus collaris than to Crotaphytus (Gambelia) wislizenii." This, however, is not the original usage of the word, since an identical statement was published a year earlier by the same author in

his original description of Crotaphytus reticulatus (Baird, 1958:253). Robert C. Stebbins (1948:219) and Karl P. Schmidt (1953:3) did not accept the division of Crotaphytus, as proposed by Smith' (1946:158-166).

A complete list of the synonymy of this genus and its species is too long and involved to be included here, but can be obtained by reference to Boulenger (1885:203-204), Cope (1900:245-261), Van Denburgh (1922:104-131) and Smith and Taylor (1950:91-94).

Crotaphytus is mentioned in a minority of anatomical publications and, in them, is given only superficial treatment. The only one devoted solely to this genus or any of its members is that by Dwight D. Davis (1934). Unfortunately his descriptions are vague as well as inconsistent with fact.

It appears that Cope (1892:246-247) was the first to do extensive osteological studies on the North American genera of lizards. Later studies are those by Camp (1923), Williston (1925), Goodrich (1930), George (1955), Oelrich (1956), and Romer (1956). Two helpful statistical studies of the osteology of related genera are those by Phleger (1940) and Lundelius (1957).

One of the best early studies of lizard myology is that of Mivart (1867), while probably the most extensive comparative work on American lizards was done by Camp (1923). Other related studies are those by Adams (1919), Romer (1924), Edgeworth (1935), Olson (1936), Brock (1938), Evans (1939), George (1948), Kesteven (1944), Watson (1954), Oelrich (1956), and Sathe (1959). Other works available on related forms, which are pertinent, are mentioned in their respective sections.

MYOLOGY

The literature to date reveals no account of the myology of C. wislizeni and only Davis (1934) has published on C. collaris. The author has therefore prepared the following description of their anterior musculature, as a prerequisite to its use for comparative purposes.

The two forms are similar except in the few cases mentioned and explained separately for each. Notes are also made on certain aspects of the myology of C. reticulatus.

The axial musculature was compared in C. wislizeni and C. collaris and found to be the same. However, no description of these muscles has been included.

THROAT MUSCULATURE

Intermandibularis (posterior and anterior profundus; Plates 1, 7, and 8) is one continuous sheet of thin muscle with various points of origin, which lies superficial to the majority of the throat musculature and just deep to the skin. Posteriorly it is of a single muscle fiber in thickness, becoming increasingly thicker anteriorly.

Although not separable, it is convenient to consider this muscle as being of two parts: 1) intermandibularis posterior and 2) intermandibularis anterior profundus. The intermandibularis has been found to be separable into these two parts in Ctenosaura by Oelrich (1956) and by the author in Sceloporus and Dipsosaurus.

The intermandibularis anterior profundus portion of this muscle lies just anterior to the intermandibularis posterior part, and is separable from it, only by having a more dorsal origin. The two become continuous mesially. This anterior profundus part arises from the mesial surfaces of the splenial and coronoid bones and by a tendon along the crista dentalis. Its anterior fibers traverse the throat anteromesially to insert on the ventral mid-line raphe with its partner, deep to the intermandibularis anterior superficialis. Its posterior fibers emerge to the ventral surface by means of three or four interdigitations with the first mandibulohyoideus muscle and then pass transversely to insert on the mid-line raphe.

The intermandibularis posterior part of this muscle may be delimitated anteriorly by the most posterior interdigitation of the anterior profundus section with which it becomes continuous mesially. Posteriorly, this muscle is separated from the constrictor colli by a narrow area of aponeurosis lacking muscle fibers. It arises from the lateral surface of approximately the posterior one-half of the mandible. The margin of its origin begins at the retroarticular process of the articular and passes anteroventrally across the supra-angular and angular and then anteriorly on the ventral surface of the dentary. A few of its fibers pass dorsally just posterior to the pterygomandibularis and mesial to the depressor mandibularis, to take origin from the deep fascia of the latter. Its fibers pass transversely and slightly anteriorly to insert on the ventral mid-line raphe which widens into an aponeurotic sheet posteriorly, leaving a broad gap between the insertions of the partners from opposite sides.

A posterolateral part of this muscle is overlain by the insertion of the posterior bundle of the depressor mandibularis in C. wislizeni.

The posterior division of the intermandibularis posterior which was reported for Ctenosaura Pectinata by Oelrich (1956:48-49) was not observed in these species.

Intermandibularis Anterior Superficialis (Plate 1) is a short, band-like muscle connecting the mandibular rami in the area between the origins of the genioglossus and the first mandibulohyoideus. It lies superficial to the intermandibularis anterior profundus, the second mandibulohyoideus, and the genioglossus muscles. It is deep only to the skin.

Arising from the oral membrane, the anterior fibers of the intermandibularis anterior profundus, and the ligament along the crista dentalis, its fibers pass posteromesially to insert with those of its fellow on the mid-line raphe.

Posteriorly its fibers blend into those of the intermandibularis anterior profundus.

Mandibulohyoideus I (Plate 1) is a long, slightly triangular muscle, extending two-thirds of the length of the mandible. It lies lateral to the second mandibulohyoideus muscle, mesial to the mandibular rami, and anterior to the insertion of the sternohyoideus. It runs deep to the intermandibularis muscle and superficial to the genioglossus, hyoglossus, third mandibulohyoideus, and the pterygomandibularis muscles. Anteriorly its fibers interdigitate three or four times with those of the intermandibularis anterior profundus.

The first mandibulohyoideus originates along the ventromesial sur-

face of the dentary and a small part of the angular, from the posterior border of the intermandibularis anterior superficialis, posteriorly to the mass of the pterygomandibularis. It passes posteromesially to insert just posterolateral to the insertion of the second mandibulohyoideus, along the anterolateral border of the distal three-fourths of the first ceratobranchial.

Mandibulahyoideus II (Plate 1) is a narrow, elongate muscle which is pointed at both ends and lies mesial to first mandibulohyoideus and closely alongside its fellow on the ventral mid-line. It is deep to the intermandibularis muscle, superficial to the tongue, the genioglossus, and the hyoglossus.

This second mandibulohyoideus muscle originates by a narrow tendon which is possibly an anterior extension of the mid-line raphe, from the capsule of cartilage overlying the mandibular symphysis. It takes origin on this tendon at about the level of the inferior alveolar foramen and runs posteriorly to insert on the anterior border of the proximal end of the first ceratobranchial, anteromesial to the insertion of the first mandibulohyoideus.

Mandibulohyoideus III (Plate 2) is a thick band-like muscle running almost parallel to the mandibular ramus, across the mass of the pterygomandibularis and more or less attached to it by connective tissue. It lies dorsal to the first mandibulohyoideus, ventral and lateral to the genioglossus and the hyoglossus, and between the ceratohyal and the pterygomandibularis.

The third mandibulohyoideus arises from the ventromesial surface of

the dentary and the angular between the anterior and the posterior mylohyoid feramina, dorsal to the origin of the first mandibulohyoideus. It passes posteriorly to insert narrowly on the lateral surface of the ceratohyal, distal to its midpoint.

Genioglossus (Plates 1 and 2) is a thick, band-like muscle occupying, with its partner, all of the space between the mandibular rami, just ventral to the tongue and anterior to the basihyal. It is located dorsal to the first, second, and third mandibulahyoideus, and the intermandibularis muscles.

This muscle takes origin along the ventral and mesial surfaces of the anterior one-sixth of the mandibular ramus, bordering Meckel's canal dorsally. Its mesial fibers run directly posteriorly, while the lateral ones turn dorsally and somewhat laterally and then pass posteriorly. However, the genioglossus in these species is not clearly divisable into a medialis and a lateralis as in Ctenosaura pectinata (Oelrich, 1956:55). The fibers of this muscle insert on the lateral surface of the tongue and, by interdigitations, into the body of the hyoglossus.

Hyoglossus (Plate 2) is a thick, broad muscle lying lateral to the basihyal and the second ceratobranchial, and medial to the mandible, the third mandibulohyoideus, and the pterygomandibularis. It is dorsal to the first and second mandibulohyoideus muscles and the anterior portion of the third mandibulohyoideus. It lies ventral to the ceratohyal and the oral membrane.

The hyoglossus muscle originates along the anterolateral face of the distal two-thirds of the first ceratobranchial, just dorsal to the inser-

tion of the first mandibulohyoideus muscle. It passes anteriorly to interweave with the genioglossus near the proximal end of the hypohyal and to form the main body of the tongue.

Branchiohyoideus (Plate 2) is a thin, narrow muscle, lying dorsal to the hyoglossus between the ceratohyal and the first ceratobranchial of the hyoid bone. Dorsally it contacts the oral membrane which, in turn, lies ventral to the massive pterygomandibularis muscle.

The branchiohyoideus arises from the posteromesial surface of the posterior two-thirds of the ceratohyal, including its mesial process. It passes posteriorly, somewhat parallel to the two hyoid limbs, to insert near the distal end of the first ceratobranchial.

Sternohyoideus (Plates 1, 2, 7, and 8) is an extensive muscle sheet occupying the area posterior to the first ceratobranchial bone and anterior to the sternum and clavicle. It lies deep to the intermandibularis and the constrictor colli, anteriorly, and to the episternocleidomastoideus, the trapezius and a small part of the levator scapulae superficialis, posteriorly. It is superficial to the levator scapulae profundus, the pharyngeal membrane, the trachea, the clavicle, and the clavodeltoideus.

This muscle folds back upon itself to result in superficial and deep layers. The fold is along the midventral line, leaving the lateral margins and the main bodies of the two depths easily separable from one another. The lateral fibers of the superficial sheet run anteromesially and those of the deep group pass anterolaterally. However, mesially the fibers of both layers become increasingly anteriorly directed until all are running parallel and become continuous in the area of the fold.

Because of the divergent origins and directions of the fibers, and the increased thickness of the mesial portion, both sheets appear separable into several different muscles. Nevertheless, the two layers of muscle can be removed intact, laid on a flat surface, and separated to open the mesial fold; thus demonstrating a continuous muscle sheet. Lateral stretching and teasing do not reveal natural divisions. This technique and others were used on a series of ten specimens of both species measuring from 43 to 60 snout to vent (Fitch, 1956:238 reports hatchlings to measure 41), as well as older ones. The results were the same in all cases.

Davis (1934:19), in the same lizard, considers the superficial layer as divisable into three parts, one of which he calls omohyoideus. He fails to mention the deep layer. Oelrich (1956:51-52) finds the two layers to appear continuous, but because of their different origins and directions, treats them as being separable into omohyoideus and sternohyoideus in Ctenosaura pectinata. Kesteven (1944:245-246) in studying Physignathus finds enough suggested separation in young specimens to treat these layers as consisting of three parts; and he considers these to represent the similar, though more distinct, divisions observed in Varanus.

I have found several heads of origin and a diversity of fiber direction in both layers. It therefore seems unwise to make any division, even on the basis of apparent homology, without a careful embryological study.

The sternohyoideus arises by various heads from the suprascapula, clavicle, sternum, and interclavicle. One of its many heads originates

with the episternocleidomastoideus from the tough fascia which extends between the lateral process of the interclavicle and the sternum. Another head takes tendinous origin, mesially, from the mid-point of the interclavicle. Its fibers run anteriorly, obliquely crossing each other in many instances, and insert on almost the entire posterior surface of the first ceratobranchial and a proximal portion of the second ceratobranchial.

NECK MUSCULATURE

Constrictor Colli (Plates 1, 4, and 7) is the most superficial muscle of the cervical region and is overlain only by the connective tissue of the skin and a few scattered fat pads. Dorsally it lies on parts of the depressor mandibularis and episternocleidomastoideus and ventrally on the sternohyoideus. It is of only one muscle fiber in thickness.

This muscle arises from the superficial dorsolateral fascia of the neck extending almost as far as the posterior margin of the depressor mandibularis. It passes ventrally, just posterior to the retroarticular process of the articular bone, to insert on the extensive ventral aponeurosis which shortly anteriorly serves for the insertion of the intermandibularis. Its insertion is widely separated from that of its partner across the mid-line of the throat.

Episternocleidomastoideus (Plates 1, 2, 5, 7, 8, and 9) is a thick, ribbon-like muscle obliquely crossing the lateral surface of the cervical region. Anterodorsally it is deep to the depressor mandibularis. Otherwise it lies superficial to the sternohyoideus, the tympanic membrane, the distal ends of the ceratohyal and the ceratobranchial bones,

and to the two levator scapulae muscles. It arises just anterior to the pectoralis and borders the trapezius posteriorly.

In Crotaphytus wislizeni this muscle originates by a single head, along with a bundle of the sternohyoideus, from the lateral process of the interclavicle and a tough fascia, which extends from the main body of the sternum to that process. In Crotaphytus collaris the episterno-cleidomastoideus has two heads of about equal size. The lateral one arises as does the single head in Crotaphytus wislizeni, whereas the mesial one takes tendinous origin, with some fibers of the sternohyoideus, from the central column of the interclavicle. In some specimens of Crotaphytus wislizeni a small mesial sliver of muscle fibers was seen to take origin similarly to those of the mesial head in C. collaris, but never was this more than a faint sliver. In both species the muscle runs anterodorsally, deep to the depressor mandibularis and constrictor colli, to insert on the distal half of the parietal crest, lateral surface of the paraoccipital process of the exoccipital bone, and the fascia of the dorsolateral angle of the neck.

The origin of this muscle in C. reticulatus is similar to that described for C. collaris.

Depressor Mandibularis (Plates 4, 7, and 8) is a massive muscle lying on the lateral surface of the cervical region and bordering the auditory meatus anteriorly. The constrictor colli overlies most of its body. Anteriorly it is superficial to some of the posterior fibers of the adductor mandibularis externus medius and the posterior border of the tympanum. Posteriorly it passes superficial to the anterior fibers of the trapezius

and the episternocleidomastoideus; the distal ends of the ceratohyal and ceratobranchial bones, and the tympanic membrane.

Three bundles of the depressor mandibularis are recognizable in Crotaphytus wislizeni (anterior, lateral, and posterior) but only the posterior one is distinctly separable in its body from the others.

The anterior bundle takes origin from the anterolateral surface of the posterolateral parietal wing and the parietal crest. It passes posteroventrally to become continuous laterally with the body of the lateral bundle and insert with it, by a strong tendon on the retroarticular process of the articular bone.

The lateral bundle arises posteriorly from the fascia along the dorsolateral angle of the neck, approximately in the region of the first three cervical vertebrae, and deep to origin of the constrictor colli. Anteriorly the bundle originates from the entire posteromesial surface of the parietal wing and part of the parietal crest, which it traverses and passes ventrally to lie lateral to, and unite with, the anterior bundle. The anterior and posterior fibers of this entire bundle converge ventrally to insert with those of the anterior bundle, on the retroarticular process.

The posterior bundle (cervicomandibularis) is separable in its entirety from the others, except in extremely old (large) specimens in which it becomes somewhat attached, near its origin, to the lateral bundle. Its origin is from the superficial dorsal fascia of the mid-line of the neck just posterior to that of the lateral bundle, and deep to the origin of the constrictor colli. It passes anteroventrally along the posterior border of the lateral bundle and continuing past the insertion

of the anterior and lateral bundles to insert ventrolaterally on the superficial fascia of the intermandibularis and the skin.

Only two bundles of the depressor mandibularis can be distinguished in Crotaphytus collaris, and these are not separable from one another. The anterior group of fibers arises from the parietal and the anterior part of the superficial dorsal fascia, while the posterior group originates, just posterior to it, by the same fascia. The muscle fibers of both bundles converge ventrally, the posterior ones coming to lie lateral to the anterior group. All insert by a common tendon on the retroarticular process of the articular bone.

The character of this muscle in C. reticulatus is the same as that explained for C. wislizeni.

TEMPORAL MUSCULATURE

Pterygomandibularis (Plates 1 and 3) is an extremely large muscle which covers almost the entire posterior half of the mandible and has its main mass between the mandibular rami, just lateral to the trachea. It is overlain by the intermandibularis posterior, laterally, and the oral membrane, ventromesially. It lies dorsal to the third mandibulohyoideus and the hyoglossus muscles.

The pterygomandibularis originates, by a heavy tendon, from the ventral projection of the ectopterygoid, and part of the transverse process of the pterygoid. It also originates by a tendinous sheath from the remaining part of the tranverse process, and the ventrolateral border of the quadrate process of the pterygoid, as well as from the ventral border of the basipterygoid process of the basisphenoid in the region of

its articulation with the pterygoid.

Its fibers run posteriorly and then posterodorsally, to cover the ventral and lateral surfaces of the angular, articular, and supra-angular. Most of the fibers insert on the dorsal, mesial, and ventral surfaces of the articular, including its retroarticular and angular processes. A line of inserting fibers passes posterodorsally across the lateral surfaces of the angular and the supra-angular, continuing posteriorly along the condyle of the quadrate and the insertion of the depressor mandibularis, leaving only the posterior supra-angular foramen between it and the adductor mandibularis externus superficialis. A tendon, serving for the insertion of many of its fibers, runs lengthwise through the muscle mass in a posterior direction, and attaches to the angular process of the articular.

Levator Angularis Oris (Plate 7) is the most superficial muscle of the infratemporal fossa. It is overlain only by the extensive infratemporal fascia and the skin, and covers more than half of the lateral surface of the adductor mandibularis externus superficialis.

This thin muscle arises from the mesial surface of the superficial infratemporal fascia, the ventrolateral surfaces of the squamosal and the posterior part of the jugal, and from the anterodorsal angle of the tympanic crest. Its fibers run anteroventrally and insert on the dorsomesial surface of the mundplatt near the posterior border of the coronoid.

Adductor Mandibularis Externus Superficialis (Plates 1, 3, 4, 7, and 8) is an extensive muscle of the infratemporal fossa, which mesially is scarcely distinguishable from the adductor mandibularis externus medius. It is

deep to the levator angularis oris anterodorsally, and to the superficial infratemporal fascia posteroventrally.

It takes origin from the ventral surfaces of the postorbital, squamosal, and a portion of the jugal; and from the dorsal and anterior surfaces of the quadrate, as well as the lateral surface of the tympanic crest. Its fibers run anteroventrally, somewhat more ventrally than those of the levator angularis oris. They insert along the beveled, dorsolateral surface of the supra-angular, passing just dorsal to the posterior supra-angular foramen and covering the anterior supra-angular foramen. The more anterior fibers insert on the lateral and posterolateral surfaces of the coronoid and the lateral surface of the bodenaponeurosis.

Adductor Mandibularis Externus Medius (Plates 4, 7, 8, and 9) is a massive muscle which lies immediately mesial to the adductor mandibularis externus superficialis and dorsolateral to the adductor mandibularis externus profundus, from which muscles, it is only faintly separable. It also lies posterolateral to the pseudotemporalis superficialis, except for a few of its anteromesial fibers which are dorsal to the same.

The fibers of this muscle take origin from the mesial surface of the squamosal, the anterolateral surfaces of the supratemporal and the posterolateral parietal wing, the dorsolaterally beveled surface of the parietal, and from the anterior and dorsal surfaces of the quadrate bone. The fibers run anteroventrally, the dorsal ones being more anteriorly directed, and insert along the dorsomesial surface of the supra-angular, the posterior surface of the coronoid, and the lateral, posterior, and mesial sides of

the bodenaponeurosis.

Adductor Mandibularis Externus Profundus (Plate 10) is a massive muscle and is not clearly separable from the adductor mandibularis externus medius dorsolaterally. It is located ventrolateral to the pseudotemporalis superficialis, dorsal to the prootic, and lateral to the brain case and the supraoccipital.

This muscle originates from almost the entire posteromesial border of the posterolateral wing on the parietal, from the paraoccipital process of the exoccipital, and from the dorsolateral surface of the posterior process of the prootic bone. From its parietal origin this muscle turns ventrally and then anteroventrally to enter the infratemporal fossa, passing ventral to the supratemporal and the posterolateral parietal wing and dorsal to the exoccipital and the posterior process of the prootic. Here it joins with another head from the prootic and then continues anteroventrally to insert by the bodenaponeurosis to the posterior surface of the coronoid, and separately to the base of the coronoid.

The adductor mandibularis externus group is treated as three separate muscles only for convenience. Perhaps it should be considered a single mass (Adams, 1919) with slips as described above.

Pseudotemporalis Superficialis (Plate 10) is a divergent, massive muscle which lies ventromesial to the adductor mandibularis externus medius, posterior to the orbit, anterolateral to the cranial cavity, lateral to the epipterygoid, and lateral to the pseudotemporalis profundus. Some of its posterior fibers are sandwiched between the adductor mandibularis externus profundus and the adductor mandibularis externus medius.

The pseudotemporalis superficialis originates from the dorsolaterally beveled lateral margin of the parietal, part of the anterolateral surface of the parietal wing, the lateral surfaces of the anterior semicircular canal, and the alar process of the prootic, and all but the internal surface of the dorsal one-third of the epipterygoid. The anterior fibers of this muscle run ventrally while the posterior ones pass anteroventrally. They insert, with the pseudotemporalis profundus, on the mesial surface of the bodenaponeurosis, the posteromesial border of the coronoid to its base, and then posteriorly along the dorsal border of the articular to about its mid-point.

Pseudotemporalis Profundus (Plate 11) is an almost pyramid shaped muscle just posteromesial to the pseudotemporalis superficialis. It is lateral to the epipterygoid bone and to the levator pterygoideus muscle.

This muscle arises from the anterior, lateral, and posterior sides of the ventral two-thirds of the epipterygoid bone. It runs ventrally and inserts, in common with the pseudotemporalis superficialis muscle, on the posteromesial border of the coronoid and along the dorsal surface of the articular bone to its mid-point.

Adductor Mandibularis Posterior (Plate 11) is a broad, thin muscle, lying lateral to the tympanic cavity and the protractor pterygoideus muscle, and mesial to the mandible and to the adductor mandibularis externus muscles.

Some of its fibers arise from the lateral and mesial surfaces of an aponeurosis which runs between the mesial crest of the quadrate and Meckel's cartilage. Other fibers take origin from the posterior process of the prootic bone. They all pass anteroventrally and insert on the

dorsal surface of the articular bone with some of the fibers of the pseudotemporalis muscles, and on Meckel's cartilage.

Levator Pterygoideus (Plates 11 and 12) is a triangular shaped muscle which lies just posteromesial to the epipterygoid bone and the pseudotemporalis profundus muscle. It is anterolateral to the protractor pterygoideus and lateral to the prootic membrane of the cranial cavity.

This muscle takes origin by a flat tendon from the ventral surface of the parietal, just mesial to the epipterygoid, and posteriorly along the lateral margin of the parietal to its mid-point. Additional fibers arise from the dorsolateral surface of the prootic membrane. Its fibers fan out posteroventrally and insert, with a few anterior fibers of the protractor pterygoideus, on the proximal dorsal surface of the quadrate process of the pterygoid, beginning somewhat posterolateral to the fossa columella and extending anteromesially, to end just mesial to the epipterygoid.

Protractor Pterygoideus (Plates 11 and 12) is a broad, fairly short muscle which forms the anterolateral wall of the tympanic cavity. It lies posteromesial to the levator pterygoideus and lateral to the basisphenoid and the anterior parts of the prootic.

This muscle arises from the lateral surface of the anterior inferior process of the prootic, the posteroventral end of the pila antotica, and from the posterior and lateral surfaces of a tendon which runs from the anterior inferior process of the prootic to the region of the condyle on the anterior tip of the basipterygoid process of the basisphenoid. The fibers of the protractor pterygoideus fan out, running posteroventrally,

and insert on the dorsal and mesial surfaces of the quadrate process of the pterygoid. This insertion runs from just posteromesial to the fossa columella, posteriorly, almost to the mesial crest of the quadrate. Some of its anterior fibers insert with those of the levator pterygoideus, but the majority remain posteromesial to this muscle.

PECTORAL GIRDLE AND BRACHIAL MUSCULATURE

The descriptions of the brachial muscles were made with the arm stretched out laterally and the palm of the hand down for the dorsal view, and up for the ventral view.

Trapezius (Plates 4, 7, 8, and 9) is an extensive, superficial muscle located on the dorsolateral surfaces of the cervical and thoracic regions. It is the most superficial muscle of the area with the exception of the depressor mandibularis and the constrictor colli.

It arises from the dorsolateral fascia of the neck from the axis posteriorly to about the first thoracic vertebra* and then posteriorly

*I consider six cervical vertebrae after Camp (1923:359).

to the seventh, by the dorsal aponeurosis of the mid-line of the neck. The anterior fibers of this muscle pass posteroventrally along the border of the episternocleidomastoideus, and the posterior ones, anteroventrally, somewhat dorsal to the scapula. Thus, they converge to insert on the crest (probably a reminant of the cleithrum of lower forms) of the anterior margin of the suprascapula, and on the superficial fascia along the clavicle and the anterior margin of the pectoralis to the origin of episterno-

cleidomastoideus.

This muscle is of varying thicknesses. Posteriorly it is considerably developed, this being the major part to insert on the suprascapula. However, anteriorly it comes to be only one muscle fiber in thickness. In many specimens an anterior slip was observed to be separate from the main sheet in its body, and to become more or less associated with the episternocleidomastoideus.

Latissimus dorsi (Plates 4, 5, 7, 8, 9, and 10) is a sheet-like muscle which covers an extensive portion of the lateral body surface. Its anterodorsal fibers are overlain by the trapezius muscle while the remaining ones are deep only to the skin. It is superficial to part of the scapulodeltoideus and serratus muscles, and the suprascapula.

This muscle arises from the superficial fascia of the back and the deep fascia of the dorsal mid-line, between the first and the tenth thoracic vertebrae. Its anterior fibers run posteroventrally and its posterior ones, anteroventrally. They all converge and pass between the tendons of origin of the anconaeus coracoideus and anconaeus scapularis muscles, to insert tendinously on the processus latissimus dorsi of the shaft of the humerus.

Levator Scapulae Superficialis (Plates 4, 5, 8, 9, 10, and 11) is a broad, fan-shaped muscle which lies mostly anterior, but partly superficial, to the suprascapula. It is dorsal to the levator scapulae profundus, and superficial to the axial musculature and the posterodorsal fibers of origin of the sternohyoideus.

It lies deep to the constrictor colli, the trapezius, the epister-

nocleidomastoideus, the depressor mandibularis, the tympanic membrane, and the distal ends of the ceratohyal and the first ceratobranchial.

The levator scapulae superficialis originates, by means of a tendon, common to it and the levator scapulae profundus, from the diapophysis of the atlas. It runs posterodorsally and inserts on the anterior half of the lateral surface of the suprascapula.

Levator Scapulae Profundus (plates 3, 5, 8, 9, 10, and 11) is the ventral partner of the levator scapulae superficialis, and lies in approximately the same position with relation to the surrounding muscles, except that its posterior fibers of insertion run deep to those of the sternohyoideus muscle.

It takes origin, by a common tendon with the levator scapulae superficialis, from the diaphophysis of the atlas. Its fibers pass posterodorsally and insert along the anterior margin of the suprascapula just ventral to the insertion of the levator scapulae superficialis, and on the anterior surface of the acromial end of the clavicle.

Scapulodeltoideus (Plates 2, 4, 5, 7, and 8) is a heavy, somewhat triangular muscle, lying superficial to the scapula and suprascapula, posterior to the insertions of the levator scapulae muscles, and to the origin of the sternohyoideus. It is overlain dorsally by parts of the trapezius and the latissimus dorsi, and ventrally by the skin and the clavodeltoideus.

This muscle arises from the posterior one-half of the lateral surface of the suprascapula and the acromial end of the clavicle. Its fibers converge ventrally, passing mesial to the clavodeltoideus and lateral to the ligament of the anconaeus scapularis, to insert on the proximal end

of the humerus.

Serratus (Plates 5, 6, 9, 10, 11, and 12) as here described may include the levator anguli scapulae and the rhomboideus (Mivart, 1867:776-777). I have chosen to treat this complex as divisable into dorsal and ventral portions.

The dorsal part consists of three ribbon-like slips of muscle which partially overlap one another, in such a way that they appear serratus-like from the dorsal view when the suprascapula is pried away from the lizard's body. This muscle is deep to the suprascapula, and, although it appears to be at least partially continuous with the ventral part, it lies mesial and somewhat dorsal to the ventral group.

The dorsal part arises by slips, from the lateral surfaces of the three cervical ribs. The slips pass slightly dorsolaterally, parallel to and slightly overlapping one another, and insert, separately, along the mesial surface of the suprascapula near its dorsal border.

The ventral part has two anterior slips which are continuous with those of the dorsal part near their origins, but have their main masses lateral and ventral to them. This part also has two posterior slips which are unaccompanied by partners of the dorsal group.

The ventral part originates, by separate fasciculae, from the distal regions of the last two cervical and the first two thoracic ribs, and from the intervening intercostales externi of the area. All the slips pass anterodorsally. The two anterior ones insert on the anterior half of the inner surface of the suprascapula, just ventral to the insertions of the dorsal group. The two wider, posterior slips, from the first and second

thoracic ribs, insert on the suprascapula, ventrolateral to the insertion of the slip from the last cervical rib, and along the posteroventral edge of the suprascapula, respectively.

Pectoralis (Plates 1, 2, and 7) is an extensive, superficial muscle of the breast. It overlies the sternum, sternal ribs, and the coracoid with their attached muscles. It is posterior to the clavicle and the clavodeltoideus, and anterior to the rectus abdominis externus. The origins of the paired pectoralis muscles separate along the ventral mid-line to allow for the tendinous origin of the sternohyoideus muscle from the interclavicle.

The pectoralis muscle arises from the inner angle of the clavicle, interclavicle, sternum, and the ventral mid-line fascia, continuing along the xiphoid rod to the sixth sternal rib. It follows this rib, arching posterolaterally and then anterolaterally along hyaline and finally myocomatal extensions bordering the rectus abdominis externus, and traverses ventral to the fourth and third and terminates near the second sternal rib. All the fibers of the pectoralis converge to insert on the deltopectoral crest of the humerus.

Clavodeltoideus (Plates 2, 7, 8, and 9) is a heavy muscle of the anteroventral shoulder region. It is located anterior to the supracoracoideus and the pectoralis, proximal to the brachialis inferior, ventral and lateral to the scapulodeltoideus, deep to the episternocleidomastoideus, and the sternohyoideus, and superficial to the scapulohumeralis anterior. The clavodeltoideus originates from the margins and the ventral surface of the proximal half of the clavicle. Its fibers run anterolaterally

across the ventral surface of the clavicle, and then turn dorsolaterally and posterolaterally, to pass mesial to the clavicle. This muscle inserts on the proximal end of the humerus.

Supracoracoideus (Plates 2, 3, and 7) is a deep chest muscle of triangular shape. It lies deep to the pectoralis muscle and the interclavicle, ventral to the coracoid and the large tendon of the biceps, posterior to the clavicle and the clavodeltoideus, and anterior to the coracobrachialis brevis.

The supracoracoideus muscle originates from the ventral surface of the anteromesial region of the coracoid. Its fibers pass posterolaterally, converging to insert on the delto-pectoral crest of the humerus.

Scapulohumeralis Anterior is a small, thin muscle located near the base of the scapula. It is anterior to the supracoracoideus, and deep to the clavodeltoideus and the inserting fibers of the scapulodeltoideus.

This muscle takes origin from the spinous process of the scapula, the anterolateral tip of the epicoracoid, the entervening membrane of the coraco-scapular fenestra, and the lateral surface of the scapula in the axillary region. The muscle runs posteriorly, lateral to the axillary region of the scapula. It then passes ventral to the tendon of origin of the anconaeus scapularis and over the margin of the glenoid fossa to insert on the distal surface of the humeral crest of the humerus, just dorsal to the insertion of the latissimus dorsi, and between the tendons of the anconaeus scapularis and the anconaeus coracoideus.

Coracobrachialis Brevis (Plate 3) is a short, stout muscle of the chest. It is located dorsal and posterior to the tendon of the biceps, and

anterior to the sternal attachment of the first thoracic rib.

This muscle takes origin from the ventral surface of the postero-lateral region of the coracoid. Its fibers run slightly posterolaterally and insert, shortly, on the head of the humerus in the concave region between the delto-pectoral and humeral crests, and on the proximal half of the posterior surface of the humerus.

Coracobrachialis Longus (Plates 2 and 4) forms the posterior surface of the upper arm. It is posterodorsal to the biceps and posteroventral to the anconaeus humeralis medialis.

This muscle originates from the ventral surface of the extreme posterolateral tip of the coracoid. It runs along the entire length of the humerus and inserts on the proximal surface of its ulnar process.

Biceps (Plates 2, 4, and 8) is a large ventral muscle of the upper arm. It is located posterior to the brachialis inferior, and anterior to the coracobrachialis brevis and the coracobrachialis longus muscles.

Its fibers arise near the proximal head of the humerus from a long, broad tendon which passes between the coracobrachialis brevis and supra-coracoideus, to originate just dorsal to the latter, from the ventral surface of the mesial border of the coracoid. The biceps muscle passes along the ventral surface of the humerus and shortly becomes united, to some degree, with the brachialis inferior. This united body of the two muscles passes between the radial and ulnar processes of the humerus and then bifurcates to insert on the ventral (flexor) surfaces of the proximal heads of the radius and the ulna.

This muscle is single in these species, as I do not consider the

brachialis inferior as its humeral head, after Mivart (1867:782-783).

Brachialis Inferior (Plates 2 and 8) is a large brachial muscle, located just anterior to the biceps and ventral to the anconaeus humeralis lateralis and the anconaeus scapularis.

This muscle arises just distal to the insertions of the clavodeltoideus and supracoracoideus muscles, from the delto-pectoral crest of the humerus, and also from the entire ventral surface of its shaft. The brachialis inferior runs along the anteroventral surface of the arm, becoming somewhat united with the biceps muscle distally. However, the majority, if not all, of its fibers insert on the radius, while most of those of the biceps insert on the ulna.

Anconaeus Humeralis Lateralis (Plates 2 and 8) lies dorsal to the brachialis inferior and anterior to the anconaeus scapularis, on the anterior surface of the upper arm.

The origin of this muscle is from the proximal head and the entire anterodorsal surface of the shaft of the humerus. Its body passes along the humerus and unites with the anconaeus scapularis. It inserts with all the other anconaeus muscles, on the olecranon process of the ulna and the above sesamoid.

Anconaeus Scapularis (Plates 2, 4, and 8) is a large member of the anconaeus group, which lies posterior to the anconaeus humeralis lateralis and anterodorsal to the anconaeus coracoideus.

Its origin is by a strong tendon which passes between the latissimus dorsi and the scapulodeltoideus, and attaches to the posterior surface of

the scapula. The muscle body passes dorsal to the glenoid fossa and the head and shaft of the humerus, to unite with the anconaeus humeralis lateralis and insert on the olecranon process of the ulna and the superficial sesamoid.

Anconaeus Coracoideus (Plate 4) is a small, dorsal muscle of the upper arm. It lies posteroventral to the anconaeus scapularis and anterodorsal to the anconaeus humeralis medialis.

It originates by means of a long, fine tendon which passes posterior to the inserting fibers of the lattissimus dorsi, to arise from the broad sterno-scapular ligament. The anconaeus coracoideus unites, shortly lateral to the latissimus dorsi, with the anconaeus scapularis and inserts with it on the olecranon process of the ulna and the adjacent sesamoid.

Anconaeus Humeralis Medialis (Plate 4) lies mostly deep to the anconaeus coracoideus, posteroventral to the anconaeus scapularis, and anterodorsal to the coracobrachialis longus.

This muscle arises from the humeral crest and the posterodorsal surface of the shaft of the humerus. It unites with the other anconaeus muscles to insert with them, on the olecranon process of the ulna, and on the patella-like sesamoid of the elbow.

Subscapularis I is a broad muscle which overlies the inner surface of the coracoid, ventrally, and borders the peritoneum dorsally. It is ventromesial to the second subscapularis and its dorsal surface is traversed near the middle by the ligament which serves for the insertion of the costocoracoid muscle.

The first subscapularis arises from the entire dorsal surfaces of the coracoid and the epicoracoid, including the membranes of all the fenestrae and of the spinous process of the scapula. Its fibers converge posteriorly and insert by a tendon, with the second subscapularis, on the humeral crest of the humerus.

Subscapularis II (Plates 6, 10, and 11) lies just dorsolateral to the first subscapularis, on the inner surfaces of the scapula and the suprascapula. It is lateral to some of the anterior fibers of the serratus, which come from the first sternal rib, and mesial to the scapulodeltoideus.

The second subscapularis originates from the scapula and suprascapula and passes posteroventrally to insert with the first subscapularis, by a tendon, on the humeral crest of the humerus.

Costocoracoid (Plates 11 and 12) is a broad, thin muscle, lying mesial to the first and second sternal ribs, some of the serratus muscles, the scapula, and the posterior portions of the first and second subscapularis muscles.

The costocoracoid arises from the anterior margin of the sternal region of the third thoracic rib. It runs anteriorly and inserts, just dorsal to the mid-region of the first subcapularis, on a ligament which extends between the inner surface of the sternum at the point of its articulation with the first sternal rib and the anterior border of the scapula, just dorsal to the spinous process.

Internal Sternocoracoid is a broad, thin muscle which lies on the inner surface of the sternum and is dorsal, in part, to the external sterno-

coracoid.

It arises along the dorsal surface of the posterolateral border of the sternum and from the sternal heads of the thoracic ribs. This muscle runs anterolaterally and inserts by a broad tendon on the inner surface of the mesial process of the coracoid and to part of the epicoracoid. This insertion is just anterolateral to that of the external sternocoracoid.

External Sternocoracoid is an extremely broad and short muscle which links the inner articulating borders of the sternum and the coracoid. It is superficial to the internal sternocoracoid, posteromesial to the first subscapularis, and anteromesial to the costocoracoid. Posteriorly its inner surface is traversed by the ligament of insertion of the costocoracoid.

This muscle arises from the entire anterolateral border of the sternum, just internal to its groove of articulation with the coracoid. It passes anteriorly and inserts by a flat tendon, on the epicoracoid, just posteromesial to the inserting tendon of the internal sternocoracoid.

LATERAL TRUNK MUSCULATURE

Sacrolumbalis (Plates 5, 9, 10, and 11) is an extensive muscle which parallels the longissimus dorsi over the full length of the dorsolateral surface of the body. It is dorsal to the serratus and superficial to the intercostal muscles.

The sacrolumbalis originates from the posterior end of the crest of the ilium. It passes anteriorly and inserts by tendinous bands, into the

ribs. The bands become more easily discernible anteriorly. Part of this muscle becomes continuous with the longissimus capitis, and inserts with it, by a tendon, on the spheno-occipital tubercle of the basioccipital.

Obliquus Abdominis Externus Superficialis (Plates 3, 5, and 11) is a thin, extensive sheet of muscle which covers most of the lateral surface of the body and is deep, only to the trapezius and the latissimus dorsi muscles. This muscle, with quite some difficulty, is separable into three parts. I will discuss these separately.

The first part is superficial to the second and anterior to the third part of this muscle. It is lateral and dorsal to the rectus abdominis externus, lateral and ventral to the sacrolumbalis, posterior to the scapula, and deep to the latissimus dorsi.

The majority of this muscle takes origin by separate heads, from aponeurotic tendons which interdigitate with the sacrolumbalis and attach to the lateral and posterior surfaces of the second through the eighth thoracic ribs near their dorsal articulations. Anteriorly, some of its fibers arise from the distal ends of the first and second thoracic ribs and from the entire posterior surface of the latter. All of its fibers run posteroventrally. The more anterior, thick, fibers from the first and second thoracic ribs insert on the xiphoid rod and the sternal part of the incomplete eighth thoracic rib, just deep to the origin of the pectoralis; and on part of the seventh thoracic rib. The remaining fibers insert along the lateral border of the rectus abdominis externus, posteriorly, to the thirteenth thoracic vertebra.

The second part lies deep to the first part, anterior to the third

part, and superficial to the intercostales and the obliquus abdominis internus.

This part arises just mesial, and somewhat ventral to the origin of the first part, and in this region is not clearly separable from it. The second part originates with separate heads, by flat tendons which are attached to the lateral and posterior surfaces of the second through the eighth thoracic ribs, at the level of the lateral border of the sacrolumbalis. Some of the tendons of origin interdigitate with the sacrolumbalis. The fibers of this part run posteroventrally and insert, by means of a thin fascia, on the dorsal border of the rectus abdominis, in a jagged line which lies closer to the ventral mid-line than the insertion of the first part. The region of this insertion extends from near the posterior extent of the eighth sternal rib, posteriorly, to approximately the area of the thirteenth thoracic rib.

The third part is posterior to the first. However, a few of its anterior fibers run mesial to those of the first part. The third part lies superficial to the obliquus abdominis internus and to the intercostales externi.

This part arises by flat tendons which interdigitate with the sacrolumbalis and attach to the lateral and posterior surfaces of the eighth through the thirteenth thoracic ribs. It takes further origin from the dorsolateral fascia of the back. Its fibers run posteroventrally and insert, by a short tendon, on the tubercle of the pubis, just superficial to the origin of the intercostales externi.

<u>Obliquus Abdominis Externus Profundus</u> lies immediately deep to the more

anterior fibers of the first part of the obliquus abdominis externus superficialis, and superficial to the intercostales interni and the sternal parts of the thoracic ribs.

This muscle takes origin from the distal ends of the first and second thoracic ribs and the intervening fascia. It runs posteroventrally and towards the ventral mid-line, to insert by separate slips, on the fourth through the sixth thoracic ribs. The posterior portion of each of these inserting fasciculae is overlain (serratus-like) by part of the next one posteriorly.

Intercostales Externi (Plates 6 and 12) lie between the three cervical ribs and ten of the thoracic ribs. They are deep to the second and third parts of the obliquus abdominis externus, the sacrolumbalis, the serratus complex, and the levator scapulae muscles; and are superficial to the intercostales interni and the obliquus abdominis internus.

Although discontinuous, due to the intervening ribs, this group may be considered as one muscle which originates by a tendon, from the tubercle of the pubis. Its fibers run anterodorsally and insert, separately, on the posterior surfaces of the tenth, ninth, and eighth thoracic ribs; and then continue anterodorsally, filling the spaces between all the remaining ribs. The fibers are attached to the entire length of the cervical ribs but extend, on the thoracic ribs, only from their dorsal heads to the articulations with their sternal components.

Intercostales Interni (Plate 12) lie immediately deep to the intercostales externi, in the spaces between the entire length of the thoracic ribs. Posteriorly they terminate, after attachment to the tenth thoracic rib,

by passing dorsally, and uniting with the fascia of the mid-line of the back. They are deep to the second part of the obliquus abdominis externus and superficial to the obliquus abdominis internus.

Obliquus Abdominis Internus is a very thin, sheet-like muscle which lies deep to the ribs, the intercostales interni, the rectus abdominis externus, the costocoracoid, the sternum, and the scapula; and is superficial to the transversalis.

This muscle takes origin by means of a tendinous aponeurosis, from the inner surfaces of all the ribs posterior to the first thoracic; and from the lumbar fascia. Its fibers run anteroventrally and insert, with separate slips, by aponeurotic tendons, on the inner surfaces of the sternum and the ventral heads of the thoracic ribs. The insertion continues posteriorly, along the dorsal surface of the rectus abdominis, just mesial to the insertion of the second obliquus abdominis externus. A few of its anterior fibers insert on the ligament of the costocoracoid, and continue as far anterior as the second thoracic vertebra. Posteriorly, this muscle terminates in the region of the femur by attachment to a fine ligament which passes dorsally, over the femoral muscles, and becomes lost in the lumbar fascia.

Transversalis contacts the peritoneal membrane, internally and the obliquus abdominis internus, externally.

The transversalis arises by means of a fascia which extends from the pelvis to the neck region. The muscle fibers originate along the portion of this fascia, which lies between the second thoracic vertebra and the femur. They run almost vertically, but somewhat posteroventrally, and

insert on the inner surfaces of the thoracic ribs, the lateral border of the sternum, and the dorsal surface of the rectus abdominis externus.

STATISTICAL ANALYSIS OF OSTEOLOGICAL AND OTHER MORPHOLOGICAL DIFFERENCES

Osseous elements, unlike muscles, lend themselves very well to accurate measurements. Therefore, an analysis of their size relationships has been included here, rather than a description of their structure and articulations, which would be very similar for both forms. The detailed description of the cranial osteology of the closely related genus Ctenosaura by Oelrich (1956) is a very useful reference. Important structural differences in the bones of the two species, here studied, are mentioned in the discussion.

Other morphological features which have been thought to be of taxonamic importance are included in this analysis.

I have followed Richmond (1956) and Walker (1953) on the formulas and symbols used for the t-test.* I recognize that a certain amount of

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* n = sample size

$\bar{X}$ = sample mean

s^2 = sample variance

$$t = \frac{\bar{x}_1 - \bar{x}_2}{\sqrt{\frac{s_1^2}{n_1} + \frac{s_2^2}{n_2}}}$$

$$\text{degrees of freedom} = \left[\frac{\left(\frac{s_1^2}{n_1} + \frac{s_2^2}{n_2}\right)^2}{\left(\frac{s_1^2}{n_1}\right)^2 \frac{1}{n_1+1} + \left(\frac{s_2^2}{n_2}\right)^2 \frac{1}{n_2+1}} \right] - 2$$

error can be expected, due to relative growth changes, when a t-test is used with a system of ratios (Lundelius, 1957:65). However, since the samples are reasonably large and include fair growth series, it is felt that this error is negligible. Phleger (1940) discusses the use of a relative growth formula for such studies.

The following is a detailed list of the measurements and counts which appear in various combinations, and somewhat abbreviated, in the subsequent data:

1. Total skull length taken from the tip of the snout (premaxilla) to the posterior end of the paraoccipital process of the exoccipital bone.
2. Maximum skull height taken from the ventral surface of the mandible, in the anterior region of the angular, to the most elevated point of the frontal bone, just anterior to the fronto-parietal suture.
3. Width of skull at the ectopterygoid, measured from the lateral projecting tip of its lateral process to the same tip of the other ectopterygoid.
4. Width of skull at the quadrate, measured from the anterodorsal corner of the tympanic crest to the same point on the opposite side.
5. Snout to quadrate, measured from the anterior tip of the premaxilla to the posterior surface of the tympanic crest.
6. Snout to parietal, measured from the anterior tip of the premaxilla to the posterodorsal margin of the parietal proper.

7. Snout to orbit, measured from the former to the posterolateral surface of the prefrontal.
8. Parietal width measured across its narrowest part, between the dorsolateral crests which border the supratemporal fossae.
9. Length of premaxilla, measured from its anterior to its posterior tips as seen from a dorsal view.
10. Length of fronto-parietal suture, measured between the lateral tips of the frontal and parietal bones at their junction.
11. Length of the nasal bone, measured from the fenestra exonarina to its posterior tip.
12. Width of the orbit, measured across its widest part, from the frontal to area of the transverse process of the ectopterygoid bone.
13. Length of the orbit, measured from its anterior extension between the prefrontal and the lacrimal to the notch just lateral to the dorsal process of the postorbital.
14. Greatest length of the fenestra exonarina.
15. Number of teeth or tooth sockets in the entire premaxilla.
16. Number of teeth or tooth sockets in the maxilla of both sides averaged.
17. Number of dentary teeth or indicated tooth spaces of both sides averaged.
18. Body width, measured at its widest point while pressing the specimen firmly against a flat surface.
19. Distance from snout to vent.

20. Distance between the mesial margins of the external nares.
21. External width of the temporal region, taken at its widest point.
22. Length of the rostral scale, measured from side to side.
23. Length of the labial adjacent to the rostral, measured from its anterior to posterior margins.
24. Length of the mental scale, measured from side to side.
25. Length of the labial adjacent to the mental, measured from its anteromesial to its posterolateral margins.
26. Number of scales bordering the mental posteriorly, between the infralabials.
27. Sternum width, measured across its widest point in the region of the articulation of the third thoracic rib (first one to articulate with the sternum anteriorly).
28. Sternum length, measured from the anterior point of the interclavicle to the region between the two xiphoid rods.
29. Width of the interclavicle, measured near its mid-point.
30. Width of the clavicle, measured at its widest point.
31. Length of the origin of the depressor mandibularis, measured from its beginning near the mid-point of the parietal wing, along the dorsal fascia of the neck, to its posterior extremity.
32. Total length of the hyoid, measured from the anterior tip of the hypohyal to the distal ends of the second ceratobranchials. The terminology of Camp (1923) has been used with respect to the hyoid.

33. Length of the second ceratobranchials of the hyoid, measured from the posterior extremity of the basihyal to their distal ends.

34. Length of the anterolateral projection of the basihyal (basal portion of ceratohyal), measured from the junction of the hypohyal with the basihyal to the proximal end of the ceratohyal.

35. Width of the ceratohyal in the region including the process which serves for part of the origin of the branchiohyoideus muscle.

36. The egg counts listed as observed by the author were made from eggs measuring over four milimeters in average diameter per group, which were found in preserved specimens.

In the subsequent statistical data a difference in sample means is considered significant if it is too great to have happened by chance alone; therefore indicating an actual difference in the parent populations. With the exception of egg complement and the length of the premaxilla, there were no borderline cases; thus the differences determined at the .05 level are also significant at the .01 level of significance. The actual value with which the computed t has been compared is 2.0 in most cases. Those cases in which the t value is greater than 4, the probability of obtaining such different sample means by chance alone, if the population means are actually equal, is less than .00006.

C. wislizeni	C. collaris

Depressor mand. length at origin/total skull length

$n = 16$	$n = 16$
$\bar{X} = 41.57$	$\bar{X} = 34.74$
$s^2 = 11.85$	$s^2 = 17.51$

$t = 5.07$

Significant

Body width/snout to vent length

$n = 20$	$n = 20$
$\bar{X} = 32.04$	$\bar{X} = 37.88$
$s^2 = 11.1$	$s^2 = 21.4$

$t = 4.58$

Significant

Total skull length/snout to vent length

$n = 16$	$n = 16$
$\bar{X} = 25.42$	$\bar{X} = 28.14$
$s^2 = .620$	$s^2 = 1.55$

$t = 5.816$

Significant

External temporal width/total skull length

$n = 16$	$n = 20$
$\bar{X} = 74.66$	$\bar{X} = 80.53$
$s^2 = 11.21$	$s^2 = 20.5$

$t = 4.46$

Significant

Distance between external nares/total skull length

$n = 12$	$n = 20$
$\bar{X} = 16.76$	$\bar{X} = 17.56$
$s^2 = 2.00$	$s^2 = 3.57$

$t = 1.35$

Not significant

Rostral length/length of adjacent labial

$n = 16$	$n = 20$
$\bar{X} = 3.11$	$\bar{X} = 2.816$
$s^2 = .14$	$s^2 = .25$

$t = 1.33$

Not significant

Mental length/length of adjacent labial

$n = 20$	$n = 20$
$\bar{X} = 2.27$	$\bar{X} = 2.18$
$s^2 = .0412$	$s^2 = .0678$

$t = .272$

Not significant

Number of scales posterior to mental

$n = 13$	$n = 16$
$\bar{X} = 4.31$	$\bar{X} = 2.5$
$s^2 = 1.559$	$s^2 = .35$

$t = 4.81$

Significant

Skull width at ectopterygoid/total skull length

$n = 20$	$n = 20$
$\bar{X} = 61.86$	$\bar{X} = 63.07$
$s^2 = 7.59$	$s^2 = 7.26$

$t = 1.41$

Not significant

Skull width at quadrate/total skull length

$n = 20$	$n = 20$
$\bar{X} = 67.32$	$\bar{X} = 68.98$
$s^2 = 9.5$	$s^2 = 7.7$

$t = 1.79$

Not significant

Maximum skull height/total skull length

$n = 20$	$n = 20$
$\bar{X} = 43.88$	$\bar{X} = 45.44$
$s^2 = 7.27$	$s^2 = 8.24$

$t = 1.772$

Not significant

Snout to quadrate/total skull length

$n = 20$	$n = 25$
$\bar{X} = 92.56$	$\bar{X} = 93.11$
$s^2 = 3.1$	$s^2 = 2.6$

$t = 1.09$

Not significant

Snout to parietal/total skull length

$n = 20$	$n = 25$
$\bar{X} = 85.51$	$\bar{X} = 82.45$
$s^2 = 3.5$	$s^2 = 4.8$

$t = 5.05$

Significant

Snout to orbit/total skull length

$n = 20$	$n = 25$
$\bar{X} = 40.54$	$\bar{X} = 35.94$
$s^2 = 2.00$	$s^2 = 1.2$

$t = 11.95$

Significant

Fronto-parietal suture length/total skull length

$n = 20$	$n = 20$
$\bar{X} = 73.99$	$\bar{X} = 72.59$
$s^2 = 13.5$	$s^2 = 17.5$

$t = 1.12$

Not Significant

Parietal width/total skull length

$n = 20$	$n = 25$
$\bar{X} = 20.17$	$\bar{X} = 17.45$
$s^2 = 5.5$	$s^2 = 14.8$

$t = 2.92$

Significant

Premaxilla length/total skull length

$n = 20$	$n = 25$
$\bar{X} = 22.43$	$\bar{X} = 20.82$
$s^2 = 4.25$	$s^2 = 3.97$

$t = 2.64$

Significant

Nasal length/total skull length

$n = 20$	$n = 25$
$\bar{X} = 17.77$	$\bar{X} = 17.78$
$s^2 = 3.4$	$s^2 = 2.5$

$t = .019$

Not Significant

Fenestra exonarina length/total skull length

$n = 20$	$n = 25$
$\bar{X} = 17.45$	$\bar{X} = 13.62$
$s^2 = 1.6$	$s^2 = 1.22$

$t = 10.66$

Significant

Width of orbit/length of orbit

$n = 20$	$n = 25$
$\bar{X} = 82.63$	$\bar{X} = 81.60$
$s^2 = 4.5$	$s^2 = 4.3$

$t = 1.633$

Not Significant

Number of premaxillary teeth

$n = 20$	$n = 25$
$\bar{X} = 6.15$	$\bar{X} = 6.32$
$s^2 = .134$	$s^2 = .2267$

$t = 1.35$

Not Significant

Number of maxillary teeth

$n = 20$	$n = 25$
$\bar{X} = 19.23$	$\bar{X} = 17.38$
$s^2 = 4.21$	$s^2 = 2.01$

$t = 3.43$

Significant

Number of dentary teeth

$n = 20$	$n = 25$
$\bar{X} = 23.20$	$\bar{X} = 22.56$
$s^2 = 3.0$	$s^2 = 6.4$

$t = 1.00$

Not Significant

Sternum width/sternum length

$n = 20$	$n = 30$
$\bar{X} = 62.24$	$\bar{X} = 69.51$
$s^2 = 12.4$	$s^2 = 20.7$

$t = 6.35$

Significant

Clavicle width/sternum length

$n = 20$	$n = 30$
$\bar{X} = 12.53$	$\bar{X} = 9.62$
$s^2 = 3.05$	$s^2 = 1.5$

$t = 6.45$

Significant

Interclavicle width/sternum width

$n = 20$	$n = 30$
$\bar{X} = 15.645$	$\bar{X} = 15.59$
$s^2 = 7.25$	$s^2 = 9.0$

$t = .07$

Not Significant

Second ceratobranchial length/total hyoid length

$n = 20$	$n = 25$
$\bar{X} = 31.4$	$\bar{X} = 44.05$
$s^2 = 11.7$	$s^2 = 11.9$

$t = 12.28$

Significant

Anterolateral projection of basihyal/total hyoid length

$n = 20$	$n = 25$
$\bar{X} = 20.29$	$\bar{X} = 14.5$
$s^2 = 2.94$	$s^2 = 2.96$

$t = 11.2$

Significant

Width of ceratohyal at process/total hyoid length

$n = 20$	$n = 25$
$\bar{X} = 6.042$	$\bar{X} = 7.1$
$s^2 = .962$	$s^2 = 1.32$

$t = 3.33$

Significant

Egg complement

$n = 21$	$n = 47$
$\bar{X} = 5.14$	$\bar{X} = 6.7$
$s^2 = 4.039$	$s^2 = 11.4$

$t = 2.37$

Significant

It appears advisable to list the data on egg counts in detail. I dissected 41 females of C. wislizeni ranging from 75 to 115 snout to vent measurement, and 42 of C. collaris from 75 to 105 snout to vent. The ovaries of 27 of the former and 24 of the latter contained an average of 18.3 and 17.7 eggs which were less than 3.6 in diameter, respectively. The remaining lizards contained eggs measuring 4 or more in diameter, and these cases have been listed individually, below. Small eggs were also found along with these large ones. Their number averaged approximately 15 in both species.

The reports of other observers have been included; in which cases, the egg counts are indicated by the authors' names and references. Otherwise, the locality of collection and the Brigham Young University museum number, where possessing one, identifies them.

Three subspecies of C. collaris are included, though C. collaris baileyi is represented by a majority of specimens. Egg sizes are given where available. One specimen (B.Y.U. 445) laid 3 eggs prior to their measurement.

Crotaphytus wislizeni

Eggs	Size	Author or Locality	Specimen
2	---	Richardson 1915:408	---
4	---	" " "	---
2	---	" " "	---
5	13.6x22.2	Shaw 1952:72	---
6	over 18	Johnson 1948:260	---
1	"large"	Camp 1916:522	---
6	16-20 long	Bently 1919:89	---
6	4-5	38 mi. E. Kanab; Kane, Utah	11381
5	9-9.8	5 mi. SW. Oak City; Millard, Utah	11354
7	3.8-4.2	Desert Exp. Sta.; Millard, Utah	4302
5	4.0	Battle Mt.; Lander, Nevada	2918
7	10-11x14-15	Boulder Dam; Clark, Nevada	460
9	9.5-10x11.5-12	St. George; Washington, Utah	515
4	12x17-19	Dugway; Tooele, Utah	14848
6	7	6 mi. N. Goshen; Utah, Utah	12196
8	5	Owyhee County, Idaho	2835
6	11-12	Star Spring; Garfield, Utah	12187
6	10-12x14-17.5	10 mi. S. Cisco; Grand, Utah	12857
4	5	Elberta; Utah, Utah	---
6	6-6.5x7.5-8	Temple Junction; Emery, Utah	---
3	6-8x9-11	" " " "	---
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Crotaphytus collaris

Eggs	Size	Author or Locality		Specimen
8	---	Anderson	1942:208	---
7	---	Burt	1928:10	---
9	---	"	" "	---
16	---	Burt and Hoyle	1934:198	---
10	18.3-21x12-13.1	Clark	1946:136	---
21	11.1x16	Ditmars	1907:115	---
8	---	Greenberg	1945:229	---
6	---	"	" "	---
6	---	"	" "	---
8	16.96x19.08	Hallowel	1856:239	---
2	---	Johnson, et al.	1948:259	---
7	11.4-11.7x18.4-20.3	Shaw	1952:73	---
12	---	Fitch	1956:236	---
7	---	"	" "	---
7	---	"	" "	---
6	---	"	" "	---
5	---	"	" "	---
5	---	"	" "	---
5	---	"	" "	---
5	---	"	" "	---
3	---	"	" "	---
6	---	"	" "	---
6	---	"	" "	---

Crotaphytus collaris (Continued)

Eggs	Size	Author or Locality	Specimen
10	---	Fitch 1956:236	---
8	---	" " "	---
8	---	" " "	---
10	---	" " "	---
4	---	" " "	---
5	---	" " "	---
7	4	Moab; Grand, Utah	1625
6	10-12x14-15	10 mi. S. Cisco; Grand, Utah	12855
5	9-10x10-12	Dewey Bridge; Grand, Utah	12856
4	8-9	Castair Canyon; Kane, Utah	11385
4	5-6	Adairville; Kane, Utah	14659
3	6.5	La Verkin; Washington, Utah	444
4	10-11x12-13	Topaz Mt.; Juab, Utah	9069
4	13-13.5x23-26	Lynndyl; Millard, Utah	445
6	4	Fillmore; Millard, Utah	8753
5	9-10	" " "	8755
8	4.5	15 mi. S. Hinckley; Millard, Utah	4310
4	4	Gold Hill; Tooele, Utah	4306
3	7	Melba; Ada, Idaho	507
11	10x14	5 mi. N. Brekenridge; Stephens, Tex.	13117
5	8-9	5 mi. E. Winslow; Navajo, Arizona	13573
6	7-9	" " " " " "	13574
5	3-4.5	Boulder Dam; Clark, Nevada	2935
5	5	Sheep Island; Clark, Nevada	4307
315			

DISCUSSION

MYOLOGICAL COMPARISONS

Muscles, being the most changeable of morphological structures, as pointed out by Brock (1938:736), present many problems when used for comparative purposes. Huntington (1903) comments on the difficulties involved in using muscles to determine phylogeny. The problems are augmented, on the generic level, by the limited number of myological studies available.

Episternocleidomastoideus.—The character of this muscle suggests that C. collaris and C. reticulatus are more similar than either is to C. wislizeni. There has been a natural selection in C. collaris and C. reticulatus for an enlargement of the mesial head which takes a more solid origin; while degeneration has left C. wislizeni with only a rudiment to represent it.

Accounts of this aspect of the episternocleidomastoideus in related lizards are difficult to find. However, Camp (1923:459) figures this muscle in Gekko verticillatus as having a single head, and Oelrich (1956, Plate 36), in his study of Ctenosaura pectinata, shows it with a small mesial slip of origin.

Depressor Mandibularis was found to have three recognizable bundles in C. wislizeni, the posterior of which is easily separable; whereas, only two, non-separable bundles are present in C. collaris. It was also found

that the origin of this muscle in C. wislizeni covers a greater area than does that of the same muscle in C. collaris, with respect to the skull length. The separable, posterior bundle in C. wislizeni is undoubtedly the homologue of the cervicomandibularis of other lizards. This muscle is found, throughout the various genera, to be present, absent, or fused in different degrees with the remainder of the depressor mandibularis (Camp, 1923 and Kesteven, 1944). Its state in the different cases does not follow any taxonomic system, but rather, appears to be connected with a greater or lesser degree of burrowing habits (Camp, 1923:448). The presence of the cervicomandibularis in C. wislizeni and its absence in C. collaris, then, suggests greater fossorial habits for the former, but does not give a clue as to their phylogenetic relation. C. reticulatus shows a closer relationship to C. wislizeni, with respect to this muscle, than to C. collaris.

OSTEOLOGICAL AND GENERAL COMPARISONS

External Number, Shape, and Size Relationships.—The statistical data indicate that C. wislizeni has a more slender and elongated body, a shorter skull, and a narrower head, proportionately, than does C. collaris. The different body shapes have resulted from selection for more streamlined forms, in the case of C. wislizeni, which have an advantage for life on the sandy desert flats where this lizard is usually found; whereas C. collaris has developed a stout body, as required by its more rugged habitat on the talus slopes at the desert's edge. The narrower head, as seen by the skull width/skull length comparisons, is only an external character and therefore must be interpreted as being the result of larger

temporal muscles in C. collaris.

No difference was found with respect to the distance between the external nares, nor in the rostral and mental sizes as related to the adjacent labials. However, it holds true that the number of postmentals is greater in C. wislizeni than in C. collaris (Smith, 1946:158). This character, then, is important taxonomically, but doubtfully of more than specific significance.

I was unable to find any important difference in the sizes of the body and caudal scales of the two species--first suggested as a distinguishing character by Baird and Girard (1852b:340). Seventy-two per cent of the C. wislizeni examined have an enlarged median row of internasals (Hallowell, 1852:207), irregular in all but one specimen. Thirty-eight per cent of the C. collaris also have an enlarged median row, which is regular in one specimen, from Castle Rock, Washington County, Utah. One individual of the latter species has two, regular median rows. I found just as much indication of a pregular fold in specimens of C. wislizeni as I could detect in those of C. collaris. The fringe of protruding scales bordering the ventral lamellae of the fourth hind toe, laterally, is constantly present, in varying degrees, in C. wislizeni; but is merely the result of an exaggerated extension of a similar border of scales in C. collaris.

Therefore, all these characters, as well as the difference in the dorsal scale pattern of the head and the number of suboculars, fit into the category of minor or unimportant taxonomic criteria in the case of these species.

Size Relationships of Skull Parts.—No difference was found in the relative skull width as measured in two places, the skull height, the nasal bone length, the extent of the fronto-parietal suture, or in the shape of the orbit. The fenestra exonorina and associated premaxilla lengths, the snout to orbit distance, and the snout to parietal distance are greater in C. wislizeni; whereas, the snout to quadrate distance is not, and the total skull length is actually less, proportionately, than in C. collaris. These data indicate that C. wislizeni has a more elongated snout, and that this length advantage is carried on through to the posterior border of the parietal. However, an immediate change takes place between that point and the quadrate, which results from a greater extension of the posterolateral wing of the parietal in C. collaris, accompanied by an elongation of the squamosal and other bones concerned.

The longer snout of C. wislizeni gives this species an advantage for burrowing in its typical habitat. It is interesting to note that only the snout is elongated, proportionately, and not the entire head as reported by Baird and Girard (1852a:69). The elongation of the posterior skull region in C. collaris producing a larger temporal fossa and a proportionately longer skull, is no doubt a result of correlation with the selection for larger temporal muscles in this species, as mentioned above. A similar condition was reported by Lundelius (1957) for Sceloporus olivaceus and S. undulatus.

The data show that the distance between the dorsolateral margins (crests) of the parietal proper is proportionally greater in C. wislizeni. It was also observed that this distance, in the species mentioned, increases slowly with age, whereas in C. collaris, after the sub-adult or

adult stage, it decreases. This results from a mesial movement of the crest, by demand of the developing temporal muscles as the parietal grows upward. The fact that this crest does not move mesially in C. wislizeni is another evidence of the lesser importance of the jaw muscles in this species.

Less obvious differences in the skulls are the more arched frontal, the less posteriorly inclined posterior margin of the fenestra exonarina as seen laterally, and the greater general bone thickness in the case of C. collaris. The two former characters have been modified in C. wislizeni for burrowing habits, while the latter is undoubtedly correlated with the greater jaw muscles of C. collaris. Cope (1892:202-203 and 1900:246-247) states that the pineal foramen is in the parietal in C. wislizeni, and in the frontal in C. collaris, bordering the coronal (fronto-parietal) suture in both cases. I have found this foramen present in the frontal and parietal of both species. However, it is usually found centered in the suture. Brattstrom (1953:177-178) notes some slight differences in the shape and size of the maxillae of C. wislizeni and C. collaris. George (1955) demonstrates some skull differences between Uromastix Hardwickii and U. aegyptia.

Number and Types of Teeth.—The number of premaxillary and dentary teeth is the same in both species, but C. wislizeni has more maxillary teeth, and they are narrower and slightly longer than those of C. collaris. The short, thick teeth of C. collaris are compatible with its heavier skull and more massive jaw muscles.

I find both species to possess pterygoid teeth, as reported for the

genus by Boulenger (1885:203). It is not clear why Camp (1923:365-366) lists one species of this genus as lacking such teeth.

Sternum and Related Parts.—The sternum is proportionately narrower in C. wislizeni, as correlated with its elongated body and fossorial habits. In this species the clavicle is wider, proportionately, to allow for its fairly large and regular perforation which lies deep to the origin of the clavodeltoideus muscle. Twenty per cent of the specimens of C. collaris observed had some type of a perforation in the clavicle; usually in the form of a slit, but never large or regular. The solid clavicle of C. collaris provides greater support for the pectoral apparatus. No difference was seen with respect to the interclavicle width.

Boulenger (1885:203) considers Crotaphytus as lacking a median sternal fontanelle, and Cope (1892:203 and 1900:247) states that C. collaris has one, whereas, C. wislizeni does not. I found at least a small median fontanelle to be present in all specimens of both species examined, except two of C. collaris from Elberta, Utah County, Utah; and Colonia Juarez, Chihuahua, Mexico (B.Y.U. 15185).

Hyoid Character.—The hyoid is very different in these species. The second ceratobranchials are proportionately shorter as well as weaker and less closely appressed in C. wislizeni. The length of the anterolateral projection of the basihyal is greater in C. wislizeni, while the mesial process, serving for the origin of the branchiohyoideus muscle is narrower.

It seems logical to attribute these hyoid differences to sexual selection, in C. collaris, for males with larger throat fans, and to assume that this was not a selective character in C. wislizeni. Supporting this

view is the fact that the latter species has not developed a bright coloration of the gular region in correlation with the throat fan, as has C. collaris (Burt, 1929:418). This may be an important factor in discouraging hybridization between these sympatric species.

Egg Complement.--Unfortunately, original observations on egg clutches for Crotaphytus are few; and these have been repeated, often without reference, by numerous authors. The report of Ditmars (1907:115) of 21 eggs laid by a female C. collaris has almost become legendary; in spite of the fact that all subsequent observers have reported strikingly fewer eggs.* Those which

*I do not consider the report of Strecker (1910:6), which has also been repeated many times, to have been based on an actual observation.

have observed egg clutches or large eggs within females are: Bently (1919:89), Camp (1916:522), Johnson (1948:260), Richardson (1915:408), and Shaw (1952:72), for C. wislizeni; and Anderson (1942:208), Burt (1928a:10), Burt and Hoyle (1934:198), Clark (1946:136), Ditmars (1907:115), Fitch (1956:236), Greenberg (1945:229), Halowell (1856:239), Johnson et al. (1948:299), and Shaw (1952:73) for C. collaris. The details of these reports are listed above.

The high counts of small eggs within the ovaries of both species, as compared to the number of eggs finally laid, suggests a pattern similar to that found in Eumeces skiltonianus (Tanner, 1957:82-89). However, the fact that small eggs are still present when others are ready to be laid raises the possibility that atrophy does not take place as in the skink, but that a few eggs are induced to enlarge to laying size, while the others remain for use at a later date. The data at hand are insufficient to allow

a decision.

The average number of eggs which I have determined for C. collaris is slightly lower than that of 7.55±.7 found for 29 clutches by Fitch (1956:235). However, this difference is not significant (t = .971). Although my analysis of data suggests a borderline difference between the egg complements of the two species, if the exceptional observations of Ditmars (1907:115) and Burt and Hoyle (1934:198) are not included, this difference is not significant even at the .05 level of significance (t = 1.86).

There is some reason to question the validity of these extreme egg counts. Uncontrolled conditions existed in both cases, since Ditmars (1907:115) apparently had several lizards within the same enclosure, and the observation of Burt and Hoyle (1934:198) was made in the field. If the true mean of the number of eggs per clutch is around 6.7, as suggested by the present analysis, the statistical probability that a clutch with 21 eggs would occur by chance alone is so small that it can be considered extremely unlikely.

The present study is limited by the fact that I have assumed that the number of large eggs (over 4mm. in diameter) in female lizards is a good indication of the actual number laid per clutch. A certain amount of bias can be expected because all of the subspecies of C. collaris were not represented by equal numbers. Further studies are necessary before the egg complement can be used as a taxonomic character for these species.

CONCLUSION

Smith (1946:158-159) used ten characters to distinguish Gambelia as a genus. Only half of these are true differences between C. wislizeni and C. collaris: 1) the external shape of the head, 2) the number of postmentals, 3) the number of suboculars, 4) the general character of the dorsal head scales, and 5) the character of the scales which border the ventral lamellae on the lateral surface of the fourth toe.

Additional differences between the two species are: 1) the character of the episternocleidomastoideus and the depressor mandibularis muscles, 2) the body proportions, 3) the relative size and shape of the skull and its component bones, 4) the number of maxillary teeth, 5) the shape of the sternum, 6) the width and character of the clavicle, and 7) the relative sizes of the hyoid parts. C. reticulatus is intermediate between the two species of this study with respect to the episternocleidomastoideus and the depressor mandibularis.

Many of the characters found to be different are a direct result of the adaptations of these sympatric species to their respective habitats. None are of generic significance.

The evidence at hand indicates that there is no justification for separating Gambelia from Crotaphytus.

SUMMARY

The anterior musculature of C. wislizeni and C. collaris is described in detail and compared. Size and number relationships of the skull and its component bones, the sternum, the clavicle, the parts of the hyoid, the general body form, certain scales and teeth, and the eggs per clutch were determined for large samples of both species and then statistically compared. The general character of many structures is also compared and notes are made on C. reticulatus.

The differences encountered by this study, as well as the valid ones of those listed by Smith (1946:158-159) are all considered unimportant generically and Gambelia is given no generic status.

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PLATES

EXPLICATION OF PLATES

The drawings were made from adult specimens of Crotaphytus wislizeni and are shown enlarged to approximately four times the actual lizard size.

Plate 1.---Ventral view of head and thorax; superficial layer shown at right and first depth at left.

Plate 2.---Ventral view of head and thorax; second depth on the right and third depth on the left.

Plate 3.---Ventral view of head and thorax; fourth depth on the right and fifth depth on the left.

Plate 4.---Dorsal view of head and thorax; superficial layer shown at right and first depth at left.

Plate 5.---Dorsal view of head and thorax; second depth on the right and a view of the left side with the suprascapula pried away from the body.

Plate 6.---Dorsal view of head and thorax; the dorsal serratus group cut on the right and the two anterior slips of the ventral group cut on the left.

Plate 7.---Lateral view of head and thorax; superficial layer.

Plate 8.---Lateral view of head and thorax; first depth.

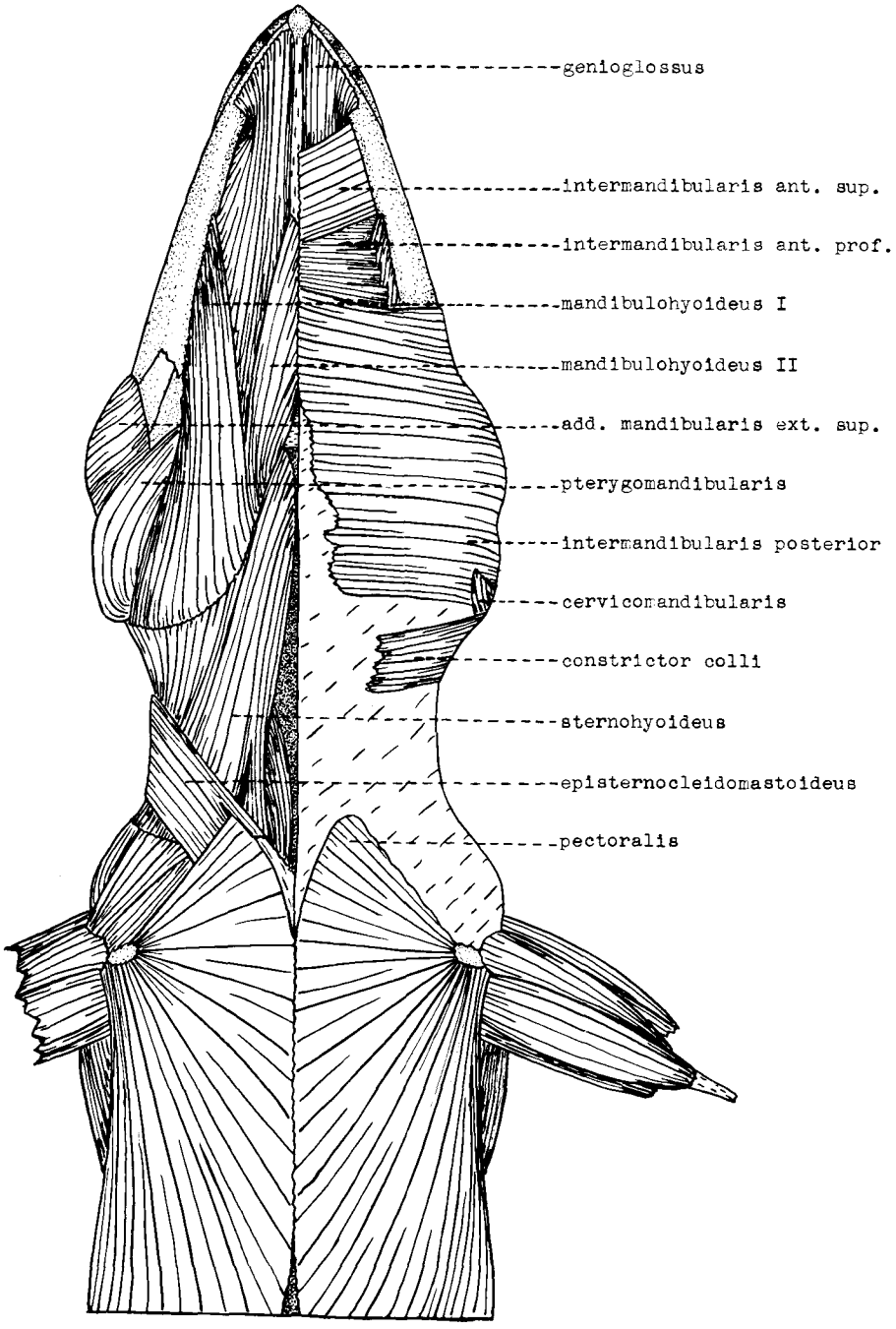
Plate 9.---Lateral view of head and thorax; second depth.

Plate 10.---Lateral view of head and thorax; third depth.

Plate 11.---Lateral view of head and thorax; fourth depth.

Plate 12.---Lateral view of head and thorax; fifth depth.

PLATE 1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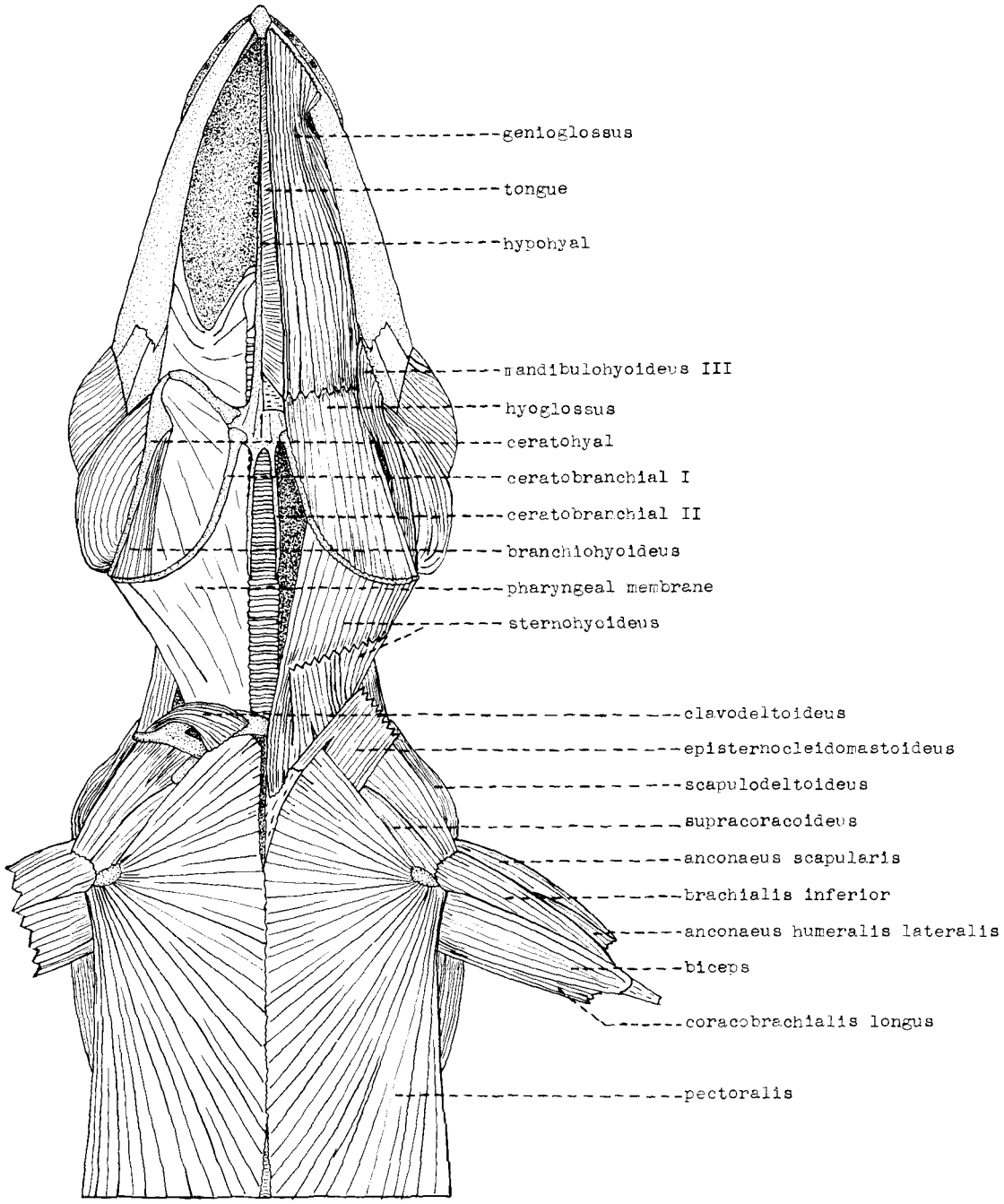
intermandibularis ant. sup.
intermandibularis ant. prof.
mandibulohyoideus I
mandibulohyoideus II
add. mandibularis ext. sup.
pterygomandibularis
intermandibularis posterior
cervicomandibularis
constrictor colli
sternohyoideus
episternocleidomastoideus
pectoralis

PLATE 2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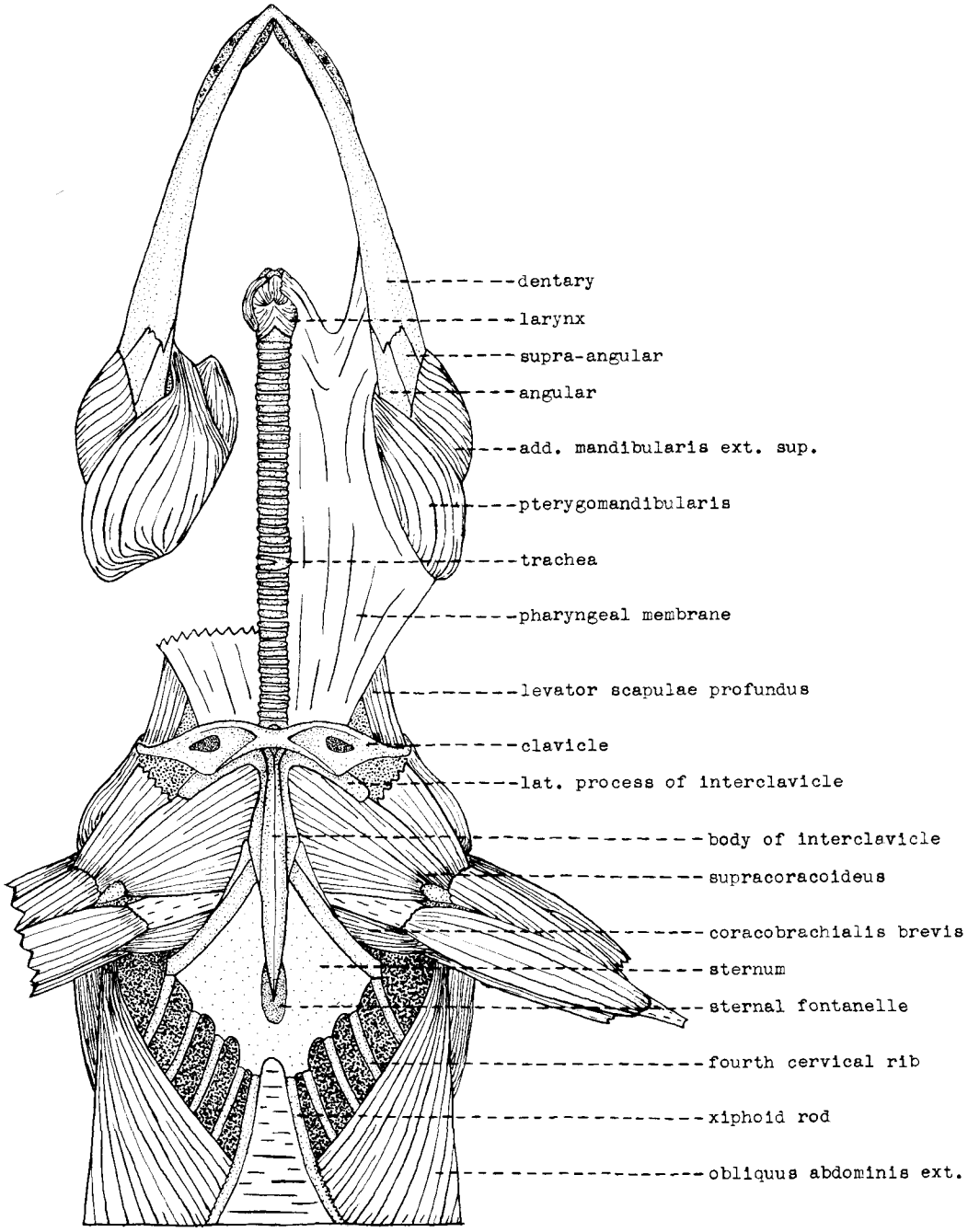
tongue
hypohyal
mandibulohyoideus III
hyoglossus
ceratohyal
ceratobranchial I
ceratobranchial II
branchiohyoideus
pharyngeal membrane
sternohyoideus
clavodeltoideus
episternocleidomastoideus
scapulodeltoideus
supracoracoideus
anconaeus scapularis
brachialis inferior
anconaeus humeralis lateralis
biceps
coracobrachialis longus
pectoralis

PLATE 3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larynx
supra-angular
angular
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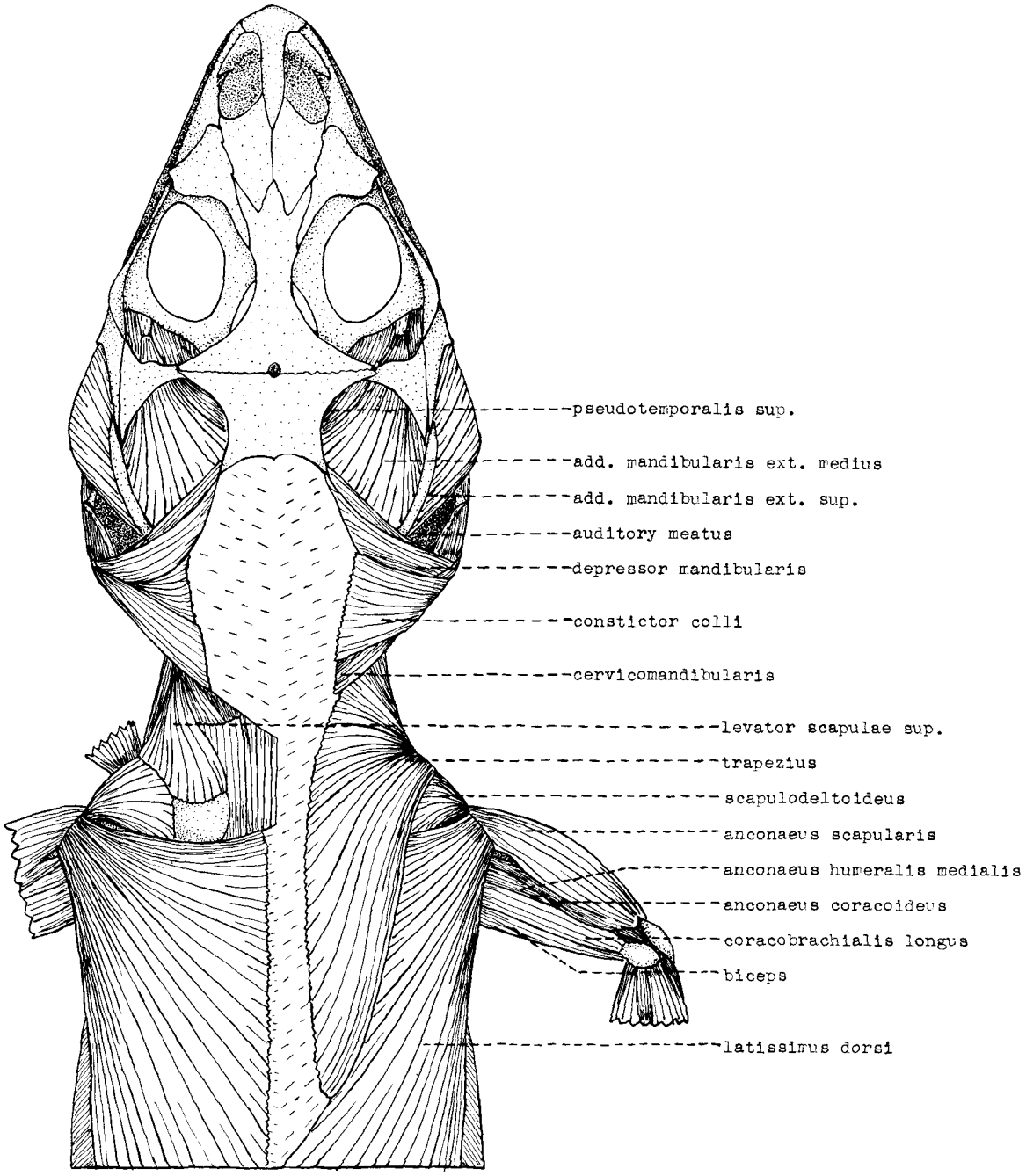
pterygomandibularis
trachea
pharyngeal membrane
levator scapulae profundus
clavicle
lat. process of interclavicle
body of interclavicle
supracoracoideus
coracobrachialis brevis
sternum
sternal fontanelle
fourth cervical rib
xiphoid rod
obliquus abdominis ext.

PLATE 4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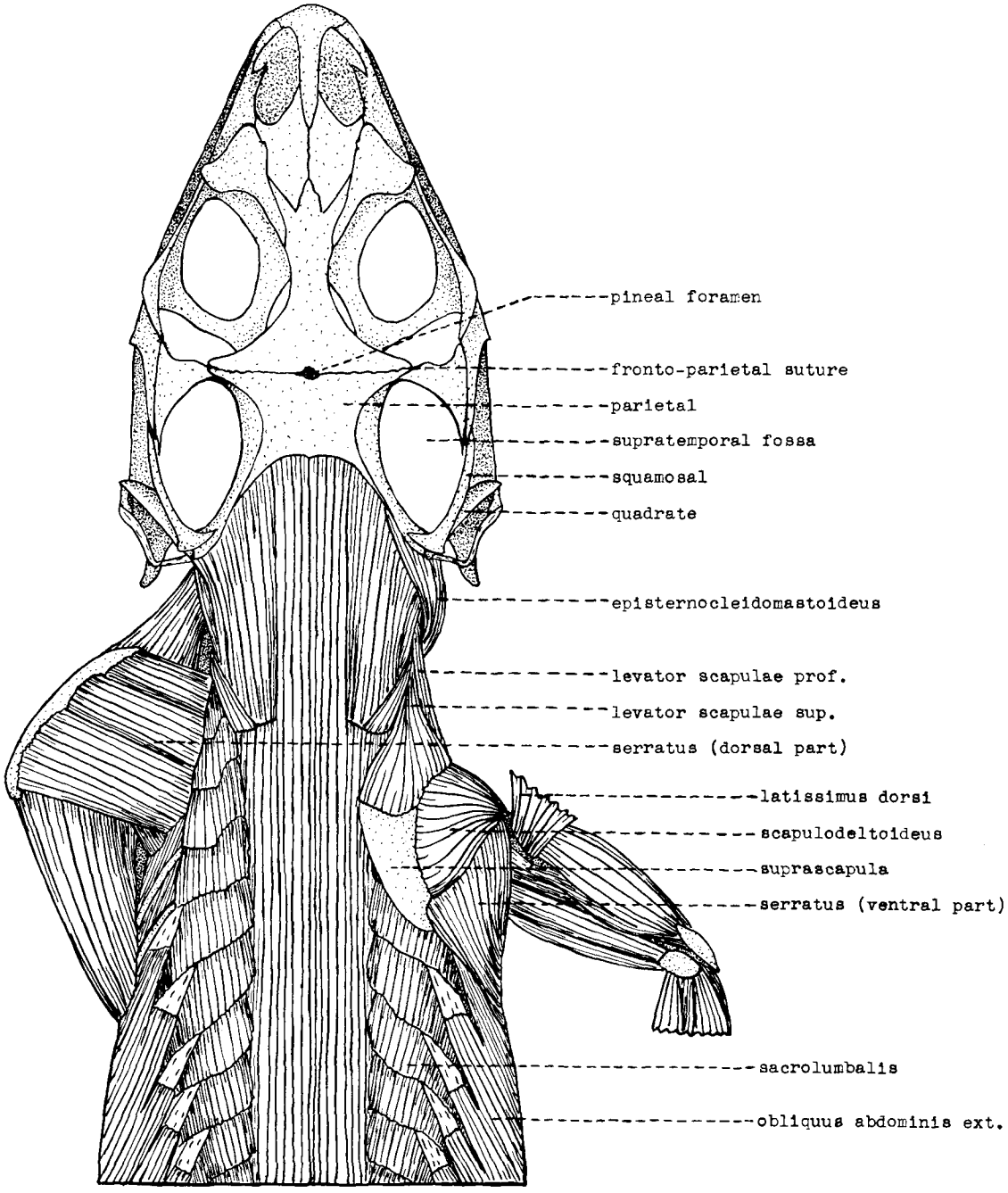
add. mandibularis ext. medius
add. mandibularis ext. sup.
auditory meatus
depressor mandibularis
constictor colli
cervicomandibularis
levator scapulae sup.
trapezius
scapulodeltoideus
anconaeus scapularis
anconaeus humeralis medialis
anconaeus coracoideus
coracobrachialis longus
biceps
latissimus dorsi

PLATE 5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fronto-parietal suture
parietal
supratemporal fossa
squamosal
quadrate
episternocleidomastoideus
levator scapulae prof.
levator scapulae sup.
serratus (dorsal part)
latissimus dorsi
scapulodeltoideus
suprascapula
serratus (ventral part)
sacrolumbalis
obliquus abdominis ext.

PLATE 6

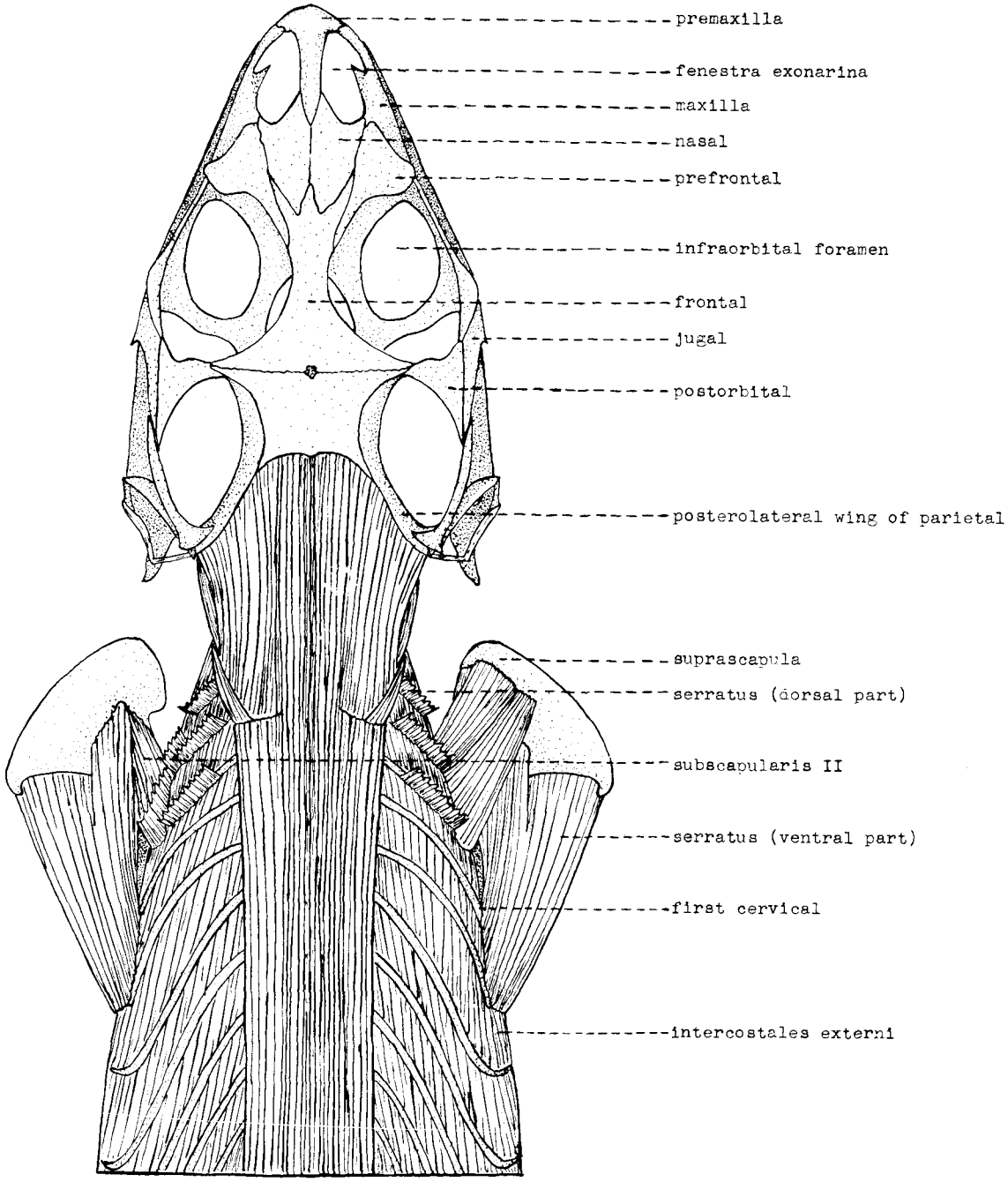
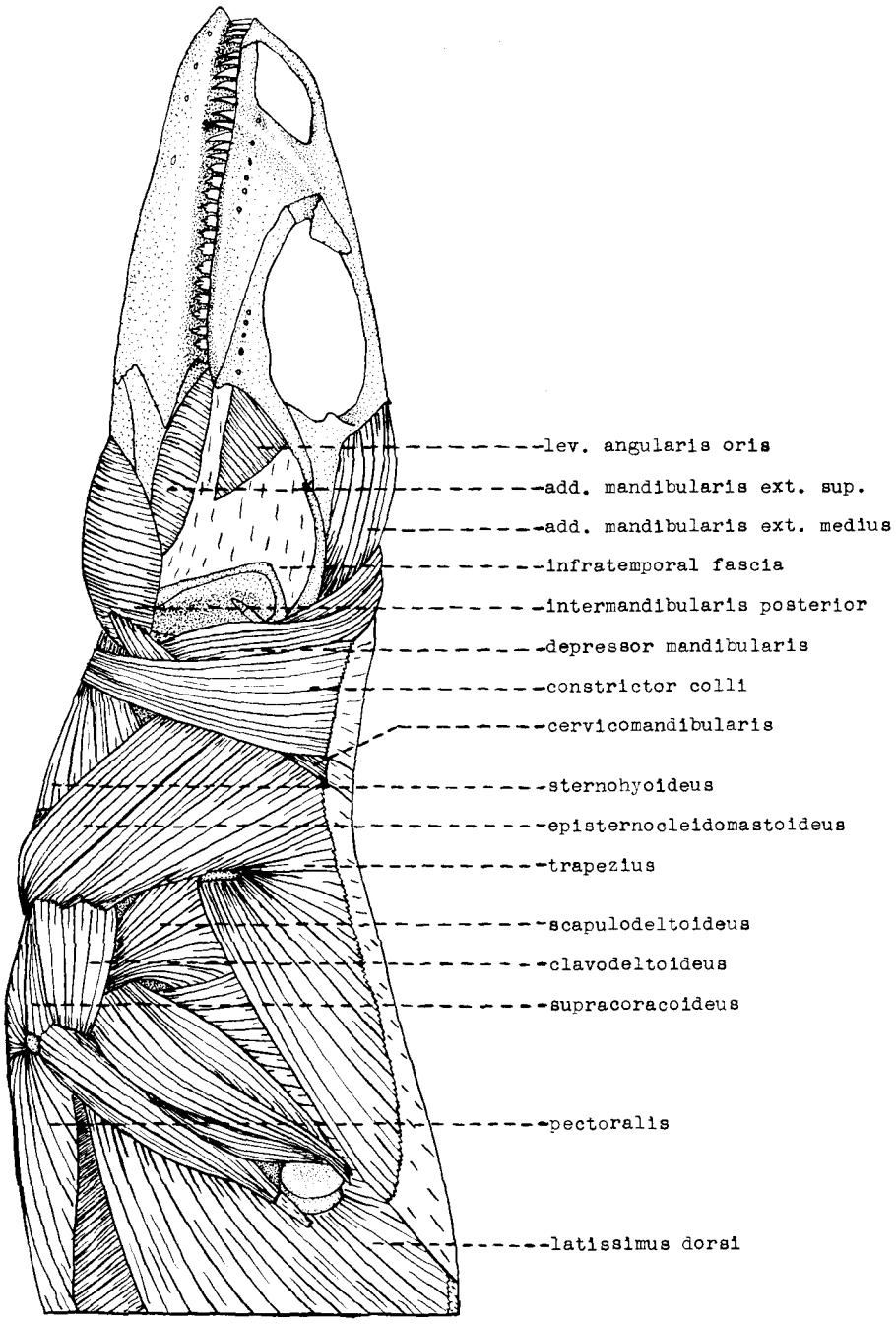

premaxilla
fenestra exonarina
maxilla
nasal
prefrontal
infraorbital foramen
frontal
jugal
postorbital
posterolateral wing of parietal
suprascapula
serratus (dorsal part)
subscapularis II
serratus (ventral part)
first cervical
intercostales externi

PLATE 7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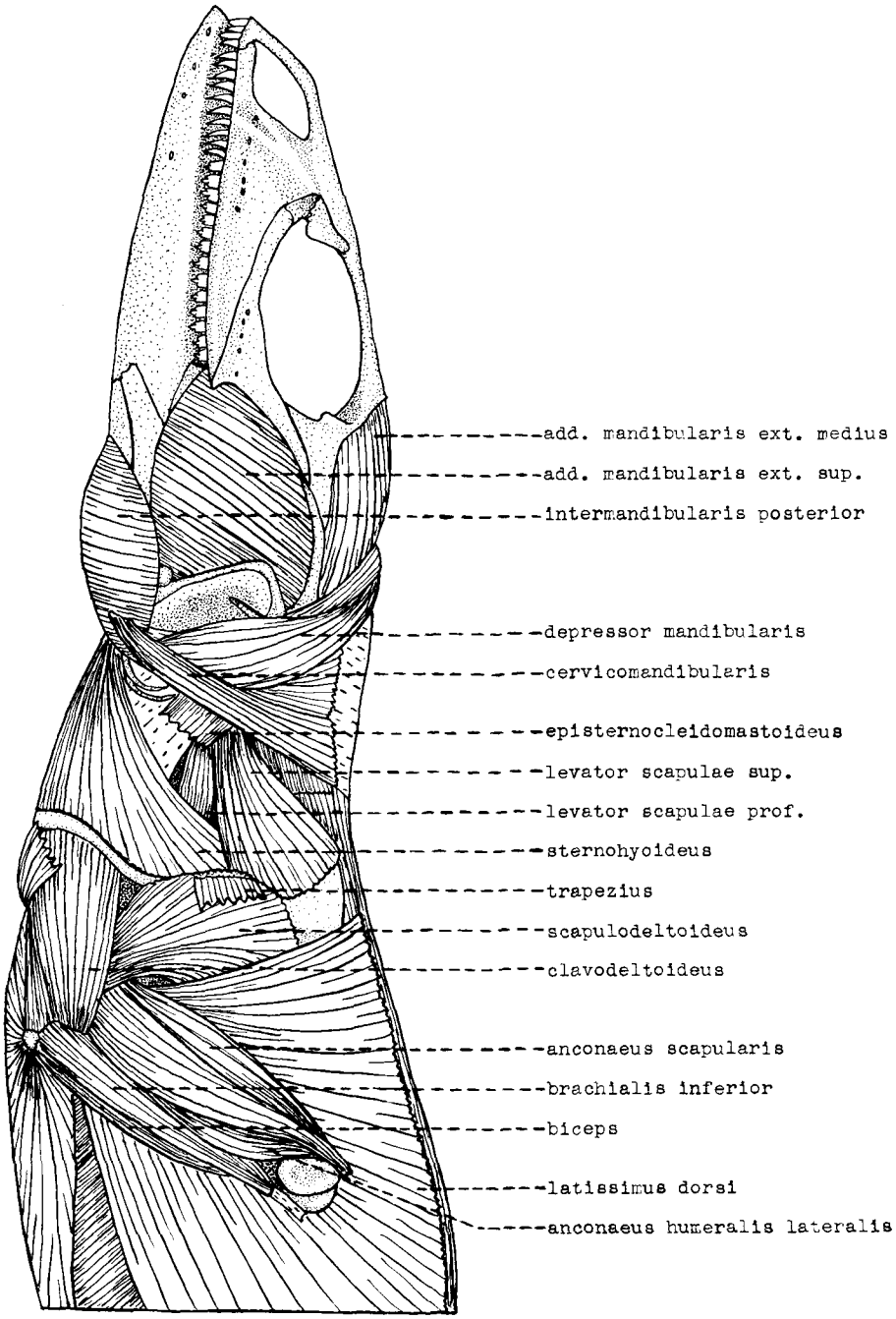
infratemporal fascia
intermandibularis posterior
depressor mandibularis
constrictor colli
cervicomandibularis
sternohyoideus
episternocleidomastoideus
trapezius
scapulodeltoideus
clavodeltoideus
supracoracoideus
pectoralis
latissimus dorsi

PLATE 8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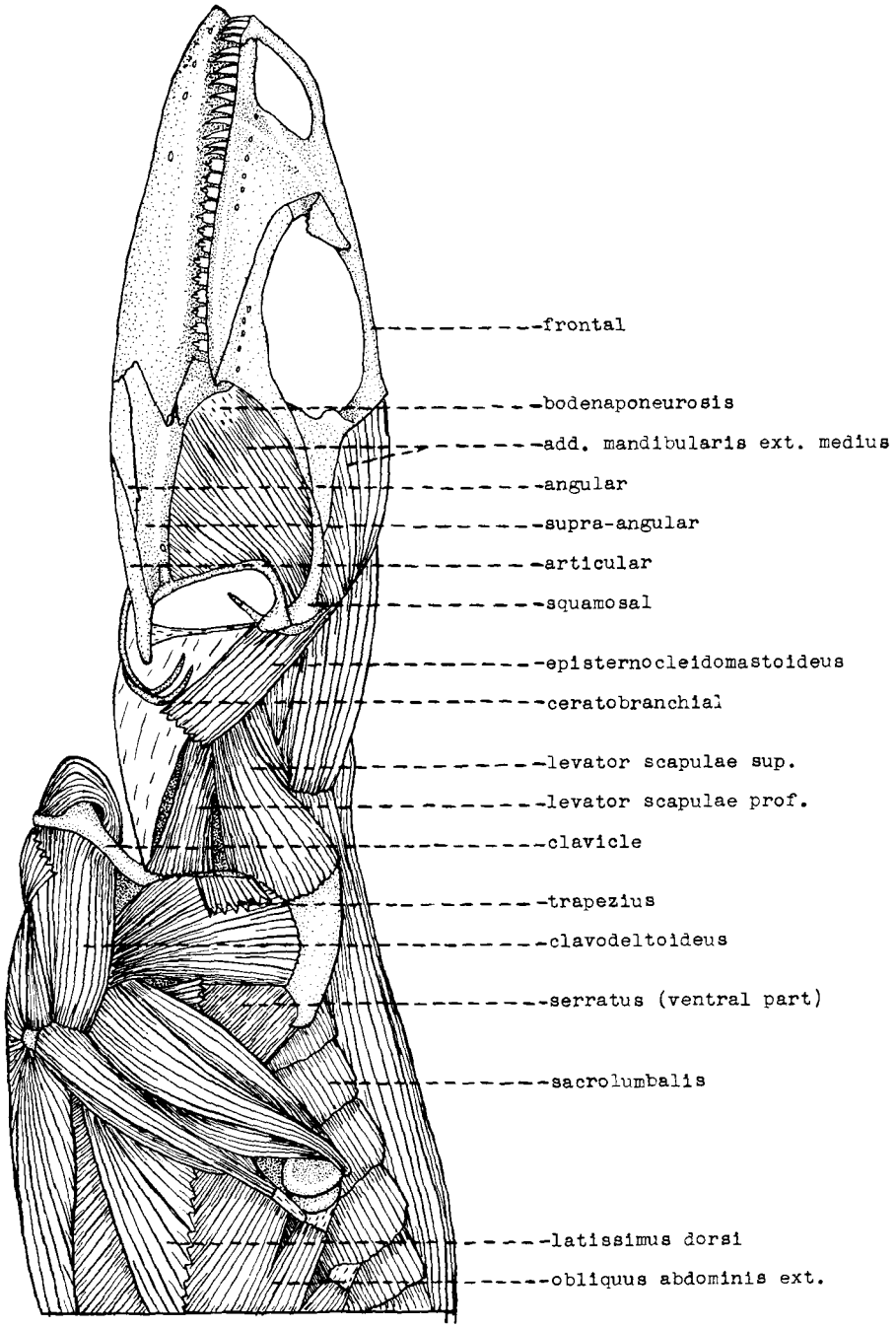
add. mandibularis ext. sup.
intermandibularis posterior
depressor mandibularis
cervicomandibularis
episternocleidomastoideus
levator scapulae sup.
levator scapulae prof.
sternohyoideus
trapezius
scapulodeltoideus
clavodeltoideus
anconaeus scapularis
brachialis inferior
biceps
latissimus dorsi
anconaeus humeralis lateralis

PLATE 9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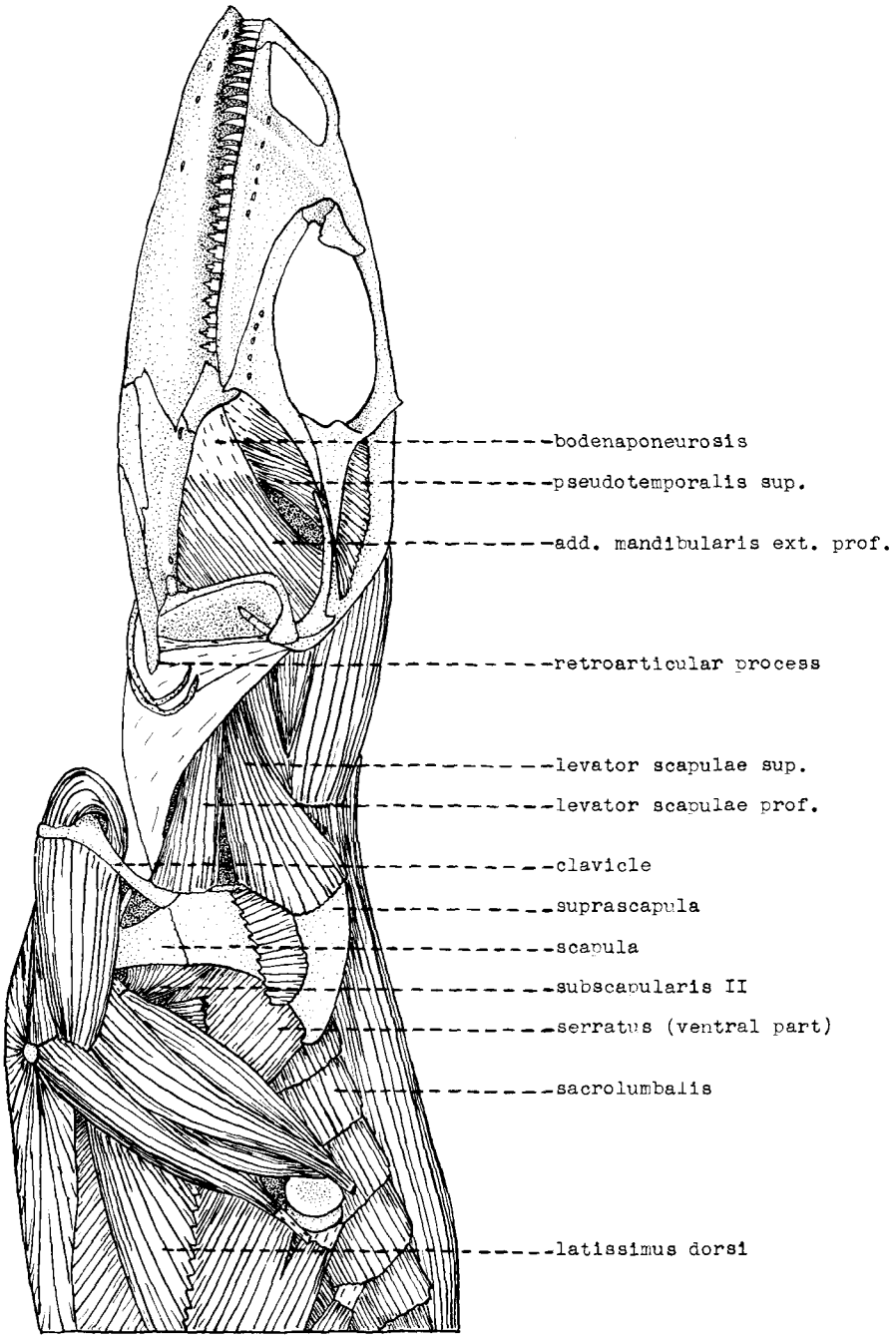
bodenaponeurosis
add. mandibularis ext. medius
angular
supra-angular
articular
squamosal
episternocleidomastoideus
ceratobranchial
levator scapulae sup.
levator scapulae prof.
clavicle
trapezius
clavodeltoideus
serratus (ventral part)
sacrolumbalis
latissimus dorsi
obliquus abdominis ext.

PLATE 10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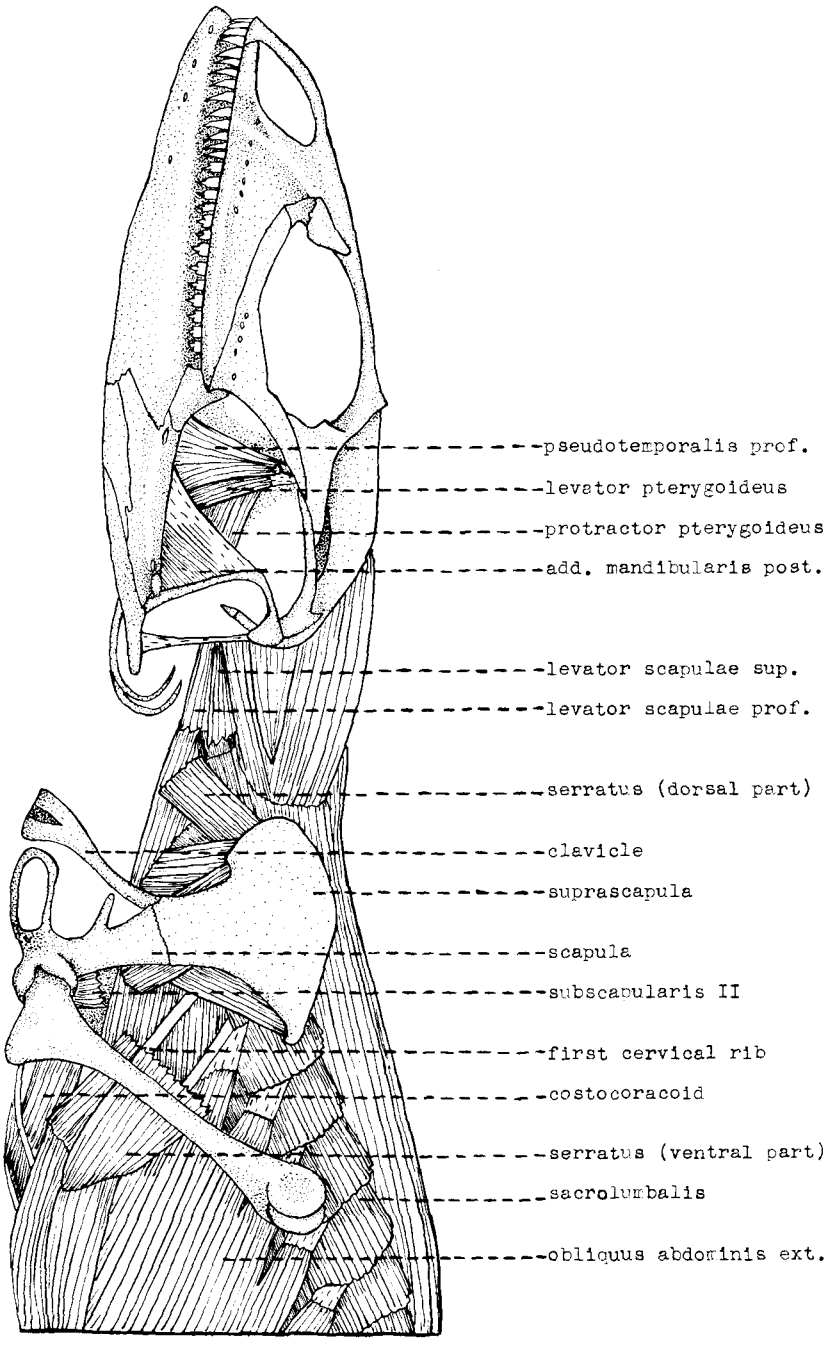
retroarticular process
levator scapulae sup.
levator scapulae prof.
clavicle
suprascapula
scapula
subscapularis II
serratus (ventral part)
sacrolumbalis
latissimus dorsi

PLATE 11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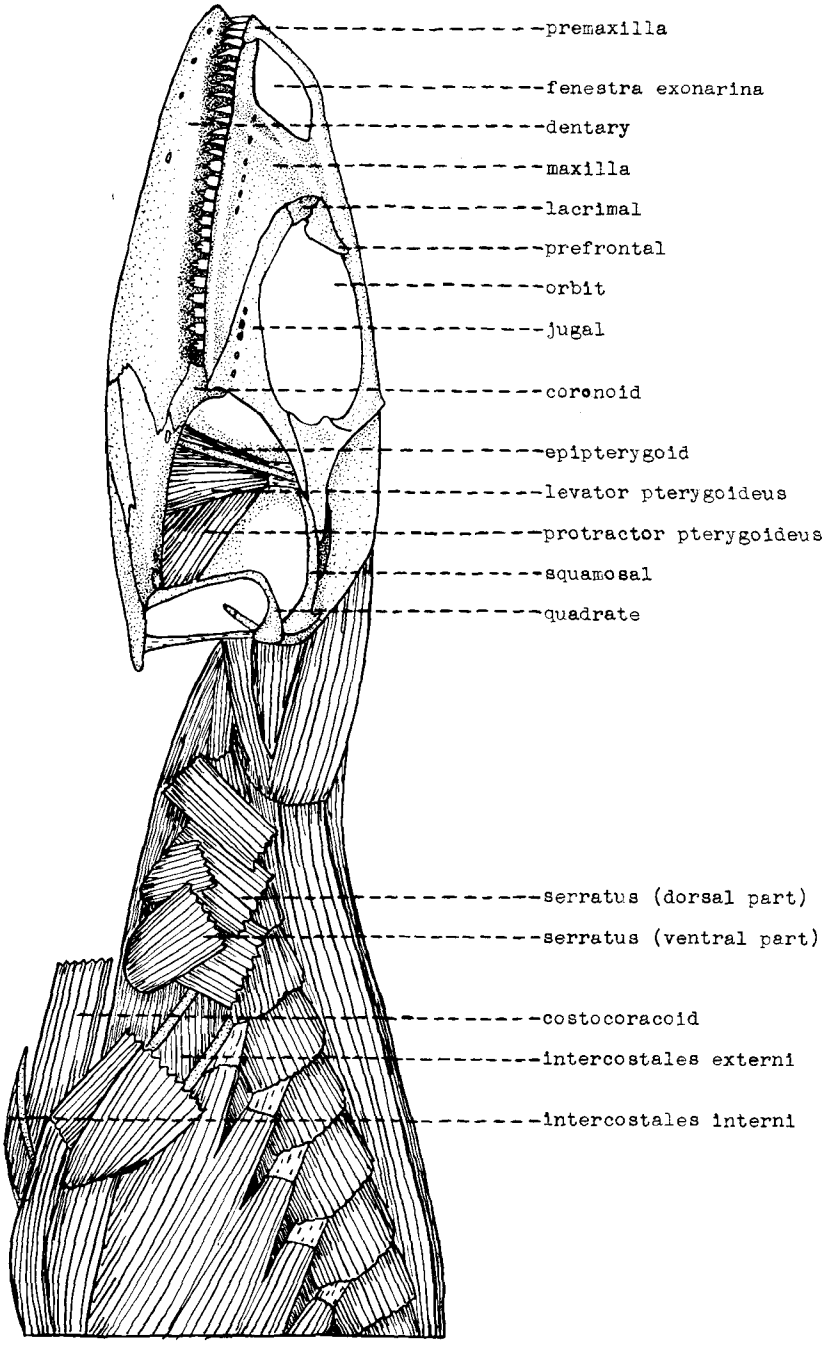
protractor pterygoideus
add. mandibularis post.
levator scapulae sup.
levator scapulae prof.
serratus (dorsal part)
clavicle
suprascapula
scapula
subscapularis II
first cervical rib
costocoracoid
serratus (ventral part)
sacrolumbalis
obliquus abdominis ext.

PLATE 12


premaxilla
fenestra exonarina
dentary
maxilla
lacrimal
prefrontal
orbit
jugal
coronoid
epipterygoid
levator pterygoideus
protractor pterygoideus
squamosal
quadrate
serratus (dorsal part)
serratus (ventral part)
costocoracoid
intercostales externi
intercostales interni

A COMPARATIVE STUDY OF *CROTAPYUTUS* HOLBROOK (IGUANIDAE)

An Abstract of a Thesis

Presented to the

Department of Zoology and Entomology

Brigham Young University

In Partial Fulfillment

of the Requirements for the Degree

Master of Arts

---

by

Wilbur Gerald Robison, Jr.

August 1960

This abstract of a thesis, by Wilbur Gerald Robison, Jr., is accepted in its present form by the Department of Zoology and Entomology of Brigham Young University as satisfying the thesis abstract requirement for the degree of Master of Arts.

Typed by Betty D. Harrison

August 1960

ABSTRACT

The anterior myology of Crotaphytus wislizeni and C. collaris is described in detail and a statistical analysis is made of the differences in the relative bone sizes, and the number of eggs per clutch, as well as other taxonomic characters previously applied to these species. The significant differences found with respect to the shape of the skull, that of the body, and the character of the hyoid are correlated with muscular development and habits of the two species. The descriptive material is accompanied by detailed myological and osteological illustrations of C. wislizeni. Comparative notes are made on C. reticulatus which is found to be intermediate between these species with respect to its myology. The results of this study indicate that Gambelia and Crotaphytus are synonymous.