The osteology and myology of the head and thorax regions of the obesus group of the genus Sauromalus Dumeril (Iguanidae)

David F. Avery
Wilmer W. Tanner

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THE OSTEONEGY AND MYOLOGY
OF THE HEAD AND THORAX REGIONS
OF THE OBESUS GROUP
OF THE GENUS
SAUROMALUS DUMERIL (IGUANIDAE)

by
David F. Avery
and
Wilmer W. Tanner

Biological Series — Vol. V, No. 3
DECEMBER 1964
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Sauromalus obesus obesus
Taken at the Nevada Test Site on rocky hill north of Mercury, June 7, 1960, by Dorald M. Allred. BYU 17435.
**INTRODUCTION**

The osteological and myological structures of the chuckwallas, genus *Sauromalus*, have long been neglected. Other studies dealing with the taxonomy, physiology, ecology, and general anatomy of *Sauromalus* and of related genera have been made by various workers. Those which are pertinent to this study are cited below. The present study is an attempt to understand the anatomy of the head and neck of *Sauromalus*, to compare it with related genera and to indicate as nearly as possible the phylogenetic position of this genus in the family Iguanidae.

The taxonomy of *Sauromalus* has been reviewed in some detail by Shaw (1945); however, a brief summary of the systematics of the genus, with special reference to the *obesus* group, is pertinent to this paper.

Dumeril (1856) established the genus *Sauromalus* for the species *ater* whose type locality is still unknown. However, Shaw (1945) limits the range of *ater* to those islands off the southeast coast of Baja, California. A series of specimens, collected at Fort Yuma, California, by the Mexican Boundary Survey and Lieut. Ives Expedition, was described as *Euphyrynge obesus* by Baird (1858). This genus and species was placed in synonymy under *Sauromalus ater* by Stejneger (1891) and was so considered until 1922 (Schmidt).

Stejneger's paper also distinguished material from Angel de la Guarda Islands, Gulf of California, Mexico, as being different from *Sauromalus ater* Dumeril and the latter being different from *S. ater* of California and Arizona. He reserved judgment on the *ater* problem for lack of specimens, but named the material from Angel de la Guarda Island, *Sauromalus hispidus*.

The Albatross Expedition of 1911 also collected material in Baja and the Islands of the Gulf of California. Dickerson (1919) studied these specimens and from them described three new species. The *interbrachialis* from La Paz proved to be the same as Stejneger's unnamed, doubtful specimen from Espiritu Santo Island. Dickerson also named the species *variatus* from San Esteban Island, Gulf of California, and *townsendi* from Tiburon Island, Gulf of California.

Schmidt (1922), who placed *interbrachialis* in synonymy under *ater*, distinguished northern populations of *ater* from southern ones by their greater number of ventral scale rows and resurrected Baird's name *obesus* for the northern population. In the same year Van Denburgh described *S. slevini* from Monserrate Island, Gulf of California, Mexico.

Shaw (1941) studied material from Santa Catalina Island, Gulf of California, Mexico, and described *S. klauberi*. In 1945 he gave full taxonomic treatment to the genus and named *S. australis* from Baja, California and *S. obesus tumidus* from southwestern Arizona. Shaw also concluded that the type locality of *S. ater* must be some island in the Gulf of California rather than the mainland of southwestern United States. This suggestion has helped considerably because the name *ater* had been a source of much confusion to present-day workers. Clifford (1958) described *S. shawi* from San Marcos Island, Gulf of California, Mexico. Recent acquisitions from North Central Arizona and South Central Utah permitted Tanner and Avery (1964) to describe *S. obesus multiforaminatus* from near Hiite, Utah.

In a systematic study of the genus *Uromastus* by Mittleman (1942), a phylogenetic tree for the family Iguanidae was proposed and the primitive position of the genus *Sauromalus* indicated.

Much of the available literature dealing with this genus is concerned with listing and describing of old and new collecting localities. Some such papers are Bocourt (1870-1909), Belding (1887), Moquard (1899), Van Denburgh and Slevin (1921), Tanner (1927), Bailey (1930), Bogert (1930), Dunn (1931), Cowles (1936), Taylor (1936), Gloyd (1937), Shaw (1946 and 1950), Murray (1955), Gates (1957), W. Tanner (1958), and Smith and Hensley (1959). Distribution patterns in the Great Basin have been discussed by Banta (1961).

Some behavior and physiological studies have also been published. Atsatt (1939) described color changes as controlled by temperature and light. Cowles and Bogert (1941) discussed the thermal requirements of *Sauromalus*, among other genera. Guibe (1954) investigated thermoregulation of reptiles, while Saint-Girons (1956) analyzed the cyclic activities of thermoregulation, and

The anatomy of the genus has not been completely neglected as studies concerning the lungs (Salt 1943), blood (Dill and Edwards 1935) and teeth (Hotton, 1955) have been made.

Other studies include food habits both in nature (Shaw 1939) and in captivity (Mayhew 1963), and a paper by Conti and Crowley (1939), describes a new bacterial species from the skin of Sauromalus varius Dickerson. Lewis and Wagner (1964) named a new hemogregarine from Sauromalus spp. which is vectored by a new mite parasite named by Newell and Ryckman (1964).

Sauromalus and closely related forms have not been overlooked as fossils, Para-sauromalus, possibly the stem stock for Sauromalus, was named by Gilmore (1928) from fragments of a jaw bone and teeth found in sediments of the Middle Eocene, Wind River Formation, of Alkali Creek, Fremont County, Wyoming. These specimens were provisionally referred to as Iguanidae because of resemblances of the dentition to that of Sauromalus. Brattstrom (1953-54) reported bits of skin, dentaries, foot bones, skulls, and vertebrae of Sauromalus in late Paleocene deposits in Gypsum Cave, Nevada, where they lay in conjunction with the Ground Sloth, Nototherium and the Camel, Camelops. Although this material is referred to as being in late Paleocene deposits, it is more likely of recent age. Gypsum Cave is well within the present range of Sauromalus o. obesus and Brattstrom indicates that the fossils closely resemble the modern species.

A basis for morphological study of the Iguanidae has been laid by Davis (1934) and Robison and Tanner (1962), who made a detailed analysis of the osteology and myology of the head and throat regions of Crotaphytus, and Oelrich (1956), who studied the head of Ctenosaurus pectinata.

Some other papers are of importance because they deal with related material. Parker (1880) studied the structure and development of the lizard skull. Cope (1892) was the first to do extensive osteological studies on genera of North American lizards. Studies by Camp (1923), Williston (1925), Goodrich (1930), George (1935), Oelrich (op. cit.), Romer (1956), and Robison and Tanner (op. cit.) have added considerable information to our knowledge of lizard osteology. Statistical studies of the osteology of related genera were made by Phleger (1940) and Lundelius (1957).

Lizard myology began with Mivart (1867) and was followed by the work of Adams (1919), Camp (1923), Romer (1924), Davis (1934), Edgeworth (1935), Olson (1936), Brock (1958), Evans (1939), Kesteven (1941), George (1948), Watson (1954), Oelrich (1956), Sathe (1959), and Robison and Tanner (1962).

The family Iguanidae is unique in its phylogenetic position among modern saurians. This was pointed out by Stokely (1950) in his report on the osteology of the wrist of Sceloporus. In his consideration of the wrist elements he discovered an intermediate bone. This wrist element had been considered to be a primitive character and at one time was thought to be restricted to amphibians and extinct reptiles. The possession of this structure by one genus in the family Iguanidae warranted a more detailed study of related forms such as Sauromalus. Romer (1956) indicates the presence of an intermediate in unspecialized lizards which he does not identify.

The purpose of this paper is to present an account of the anterior osteology and myology of Sauromalus and to investigate its phylogenetic relationships with other Iguanids. All musculature was drawn from an adult specimen of Sauromalus obesus multiforaminatus, BYU 29994, and is enlarged approximately one and one half times natural size. Other specimens of obesus subsp. were dissected for comparative purposes.

We express our gratitude to those who have aided us in the preparation of this study. We are especially grateful to Dr. J. Keith Rigby for aiding us with the paleontology and to Mr. Ed Kassay and Mr. James Hopkins for their aid in providing us with live specimens to skeletonize and dissect. To those who have been so kind as to read and criticize this study we are grateful and express our thanks.

MATERIALS AND METHODS

Sauromalus obesus obesus Baird and Sauromalus obesus multiforaminatus Tanner and Avery are the principal subspecies used in this study. A specimen each of Dipso-saurus dorsalis Baird and Girard, Sceloporus magister uniformis Phelan and Brattstrom and Ctenosaurus hemilopha (Cope) were also dissected for comparative purposes.

Two specimens of Sauromalus o. multiforaminatus (BYU 29994 and 21732) from
Crossing of the Fathers, Kane Co., Utah, were examined. Four specimens of Sauromalus o. obesus (BYU 21729, 21723, 21728, 21731) came from Calimesa, California. With the exception of BYU 21728 all were males, with snout-vent lengths of 162 mm., 176 mm., 170 mm., and 170 mm., respectively.

A specimen of Dipsosaurus dorsalis (BYU 21726) from Calimesa, California, measuring 133 mm. in snout-vent length, was also dissected and compared with Sauromalus. An adult Sceloporus magister uniformis (BYU 21730) from Washington County, Utah, was also dissected.

All specimens were preserved in formalin. A skeleton of Sauromalus o. multiforaminatus and two skulls of S. o. obesus were prepared by different methods. The skeleton was prepared by soaking a skinned specimen in 50% ammonium hydroxide for two weeks, with poor results being obtained. A more successful method was to clean the skulls and soak them in Clorox bleach for one hour. Both articulated and disarticulated skulls were studied.

All specimens are accessioned in the natural history collections of Brigham Young University.

The photographs were taken with an X-ray machine using eleven milliamps at one and one half seconds with a medium KVP. By using the X-rays as negatives, the image was enlarged and printed on glossy paper. All work on the intermediate bone was done from these photographs, which proved ample when viewed with a dissecting microscope.

Specimens (all BYU) and species used for the X-ray photographs are as follows: Sauromalus o. multiforaminatus, 11734 and 11736; Sauromalus o. obesus, 21733; Dipsosaurus dorsalis, 21727; Crotaphytus c. baileyi, 18921; Crotaphytus w. wislizeni, 16748; Holbrookia m. maculata, 12821; Callisaurus d. gabbi, 21270; Sceloporus m. magister, 15236; Uta s. stansburiana, 14980; Uta (Urosaurus) o. ornata, 192; Phrynosoma c. frontale, 15236; and Ctenosaura hemilopha, 14618.

OSTEOLOGY

Since an exhaustive study of all skeletal elements is not the primary purpose of this paper, the following discussion will be limited with few exceptions to the skull and wrist bones.

Skull. — In general the skull of Sauromalus can be considered to be open with prominent dorsolateral orbital fenestrae dominating the central region of the skull. Posteriorly, in a dorsolateral position, is a large temporal fenestra on each side. Such a structure is a deviation from the typical diapsid condition seen in the fossil ancestors of modern lizards. Ventrally, the orbit floor is also open with an inferior orbital foramen and a pyriform process on each side.

An excellent account and discussion of the skull of Ctenosaura pectinata was published by Oelrich (1956:11-39), who described the skull as, "... streptostylic, possessing a freely movable quadrate bone which is attached dorsally to the paraoccipital process in two places by a syndesmosis and ventrally to the quadrate process of the pterygoid bone by a diarthrosis... kinetic in that the maxillary segment can be elevated and depressed, hingelike, on the occipital segment." Such characteristics can also be demonstrated in fresh specimens of Sauromalus, a genus now considered to be closely related to Ctenosaura.

Romer (1956:55-217) also gives a rather complete account of the reptilian skull with one section reserved for lizards. In his discussion he figures the dorsal and ventral portions of the skull of Iguana.

A fresh chuckwalla skull forms a compact structure which provides for both strength and lightness. The skull is highly complex and the following discussion will serve as a basic description of structures illustrated on Figures 1 and 2. Oelrich (1956) divides his discussion into the occipital and maxillary segments. For convenience such a grouping will here also be followed.

The Occipital Segment forms a median axis for the rest of the skull. It consists of two parts, (a) the Brain Case (basisphenoid, basioccipital, prootic, exoccipital, supraoccipital, and the associated semi-circular canals) and (b) the Foramen Magnum (enclosed by the basioccipital, exoccipitals, and supraoccipital). A tripartate occipital condyle is located on the posterior end of the basioccipital and the lateral exoccipitals. Basisphenoid (Fig. 1) is the main bone on the floor of the cranium. It is bordered posteriorly by the basioccipital. Dorsally the basisphenoid is attached to the prootic bone and ventrally it articulates with the pterygoids. This bone forms points of origin for the inferior part of the protractor pterygoideus muscle.

Basioccipital (Fig. 1) forms the posterior part of the floor of the brain case and provides areas of attachment for ventral axial musculature. Posteriorly it bears an occipital condyle, and anteriorly joins the basisphenoid and dorsolaterally the exoccipital and prootic bones. This bone provides at-
tachment for the third bundle of the longissimus dorsi muscle.

Prootic forms the anterolateral wall of the brain case and houses part of the membranous labyrinth. At its posterior end the prootic joins the supraoccipital, basisphenoid, basioccipital, and exoccipital. Its anterior borders consist of a series of membranes which form the tunnel for the optic nerve.

The prootic bone provides points of origin for the pseudotemporalsis and the protractor pterygoideus muscles.

Exoccipital is formed by the fusion of exoccipital and opisthotic bones. It forms the posterolateral wall of the brain case and the lateral parts of the occipital condyle. Part of the exoccipital houses the posterior portion of the membranous labyrinth. Medial-lateral articulations form with the parietal, supratemporal, and quadrates bones. At its most lateral projection the exoccipital forms an articulation with the prootic.

The paraoccipital process of this bone serves as an area of insertion for the longissimus dorsi of the axial musculature. The tip of the process receives the insertion of the episternocleidomastoidoideus muscle.

Supraoccipital forms the roof of the posterior part of the brain case and the dorsal rim of the foramen magnum. It also houses the dorsal part of the membranous labyrinth. Sutures join the supraoccipital to the prootic bone anterolaterally, the exoccipital posteriorly, and the parietal at its anterior extreme.

Orbitosphenoid is a vertical element surrounding the optic foramen. The anterior border forms the posterior margin of the optic foramen and the inferior process forms an area of origin for the superior rectus muscle. The orbitosphenoid also has connections with the prootic bone and the alar process of the basisphenoid.

A combination of bones in the anterior region of the skull is referred to as the Maxillary Segment. It consists of four parts, (a) the Palate (pterygoid, ectopterygoid, vomer, palatine, premaxilla, and maxilla), (b) Orbits (frontal, postfrontal, and jugal), (c) Nasal Capsule (nasal, prefrontal, lacrimal, and septomaxilla), and (d) Temporal Fenestra (parietal, supratemporal, postorbital, squamosal, quadrat, and epipterygoid). These bones are discussed as listed above.

Pterygoid (Figs. 1 and 2) forms the most posterior part of the palate. They are paired bones sutured at the mid-line and comprise the major area of motion between the occipital and maxillary regions. The anterior portion of the pterygoid is sutured to the palatine bone dorsally and the ectopterygoid

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Fig. 1. Skull of Sauropternus obesus multiforaminatus, BYU 21734.  
A. Lateral view of skull, x 5.  
B. Medial view of right mandible, x 2.
bone laterally. A caudolateral portion of the pterygoid articulates with the quadrate bone. At its anterior end there are facets with which the pterygoid articulates with the basipterygoid and columella.

At the ventral border, the pterygoid forms the posterior limit of the oral cavity and contributes an area for origin of the pterygomandibularis muscle. On a dorsal ridge, medial to the columellar fossa, is an area of insertion for the levator pterygoideus muscle. The insertion of most of the protractor pterygoideus muscle is located on the medial surface of the quadrate process of the pterygoid bone. The posterior fibers of the pterygomandibularis muscles arise along the ventrolateral border of the lateral side of the quadrate process.

**Ectopterygoid** (Figs. 1 and 2), forms a brace between the palate and the external roofing bones, e.g. parietals, etc. It is bordered laterally by the jugal and the posterior process of the maxilla. Medially the ectopterygoid connects with the pterygoid. Dorsally it forms the posterolateral part of the floor of the orbit.

**Vomer** (Fig. 2), a pair of bones, forms the most anterior part of the palate, the medial borders of the fenestra vomeronasalis externum and the medial borders of the fenestra exochoanaalis. At its posterior end the vomer is attached to the palatines dorsally and the medial surface of the maxilla. At the mid-line the vomers support the nasal septum and the cartilage of Jacobson's organ. At the extreme anterior end the vomer connects with the maxilla.

**Palatine** (Figs. 1 and 2) forms the main part of the palate, the floor of the orbit and nasal capsule. This bone has three processes: the anterior, or vomerine, forms the posterior floor of the olfactory capsule; the pterygoid process, which attaches dorsally to the pterygoid, forms the medial rim of the inferior orbital fossa and the floor of the orbit; and the maxillary process attaches dorsally to the prefrontal and ventrally to the jugal and maxillary bones.

**Premaxilla** (Figs. 1 and 2), the most anterior bone of the skull, joins the maxilla laterally and the nasal bones dorsally. It forms the rostrum of the skull.

**Maxilla** (Figs. 1 and 2) forms the major lateral surface of the snout. The ventral margin bears a single row of pleurodont teeth. There are three protrusions from the main region of the maxilla. The first protrusion is the premaxillary process which overlays, and is attached to, the maxillary process of the premaxilla. Its medial part attaches to the vomer whereas the dorsal extension forms the inferior rim of the fenestra exonarina.

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Fig. 2. Skull of *Sauromalus obesus multiformianatus*, BYU 21734.

A. Dorsal view, x 4.
B. Ventral view, x 4.
The posterior process of the maxilla is attached to the jugal and lacrimal bones dorsally, and to the ectopterygoid medially. This process forms the lateral part of the rim of the inferior orbital foramen.

The third process of the maxilla extends dorsally to form the lateral wall of the nasal capsule, the posterior rim of the fenestra exornarina anteriorly, and dorsally attaches to the nasal and prefrontal bones.

The maxilla attaches to the palatine bones along the medial border of the palatine shelf. Nasal (Figs. 1 and 2) forms the sloped top of the snout and partially covers the nasal capsule. The nasals attach posteriorly to the frontals, anteriorly to the premaxillae, and laterally to the prefrontals. Part of the anterior border of the nasal bone forms the dorsal border of the fenestra exornarina. Prefrontal (Figs. 1 and 2) forms the anterior angle of the orbit. Medially it attaches to the frontal and nasal bones, ventrally to the maxilla and posteriorly to the lacrimal.

Lacrimal (Fig. 1) is a small bone on the anteroventral rim of the orbit. Dorsally it is attached to the prefrontal, anteriorly to the maxilla, ventrally to the jugal, and ventromedially to the prefrontal. Septomaxilla is found within the nasal capsule where it covers Jacobson's Organ and houses the anterior part of the nasal capsule. Ventrally, it connects with the vomer and maxilla.

Frontal (Figs. 1 and 2) forms the dorsal border of the orbits and the anterior roof of the brain case. At its posterior extreme the frontal is attached to the parietal and postfrontal bones. Anteriorly, it is sutured to the nasal and the prefrontal. The pineal foramen penetrates the postero medial portions of this bone.

Postfrontal (Figs. 1 and 2) forms a small part of the postero dorsal margin of the orbit. Posteriorly this bone is sutured to the frontal, and laterally to the postorbital and the parietal.

Jugal (Figs. 1 and 2) forms the ventral border of the orbit and a small part of the supratemporal arch. Anteriorly it attaches to the maxilla, ventrally to the lacrimal and palatine bones, and medially to the ectopterygoid. The dorsal surface forms the anteroventral wall of the orbit.

Parietal (Figs. 1 and 2) forms the roof of the posterior part of the skull. It articulates with the frontal and postfrontal anterolaterally and with the postorbital posteriorty and ventrally. Posteriorly the parietal overlays the supratemporal and articulates with the exoccipital and supraoccipital.

The anterior two-thirds of the dorsal surface of the parietal gives origin to the pseudotemporalis superficialis muscle, and the posterior one-third gives origin to the adductor externus medius. The posterior tip of the supratemporal process supplies the origin for a part of the adductor externus profundus muscle. Laterally the parietal bone gives origin to the levator pterygoideus. The posterior border of the parietal provides attachment to the origin of the depressor mandibularis and the insertion of the spinus dorsi, longissimus dorsi, and episternocleidomastoides muscles.

Supratemporal provides support for the posterolateral angle of the parietal bone. Posteriorly, it articulates with the exoccipital, squamosal, and quadrate.

On the medial border of the anterior part is a partial origin for the adductor mandibularis externus profundus muscle and on the lateral border is the origin of the adductor mandibularis externus medius muscle. Postorbital (Figs. 1 and 2) forms part of the posterior rim of the orbit. The dorsal part is sutured anteriorly to the postfrontal and posteriorly to the parietal bone. The anteroventral border has connections with the jugal and the posteroventral border to the squamosal.

The ventral free border of the postorbital gives origin to the anterior half of the levator angularis oris muscle whereas the medial surface of the posterior half gives origin to the adductor mandibularis externus superficialis muscle. Squamosal (Figs. 1 and 2) is attached to the postorbital bone on the posterolateral border of the skull. The expanded posterior part of the squamosal is attached to the dorsal surface of the supratemporal and the quadrate.

The lateral surface of the squamosal provides an area of origin for the adductor mandibularis externus superficialis and part of the levator angularis oris muscle. The medial surface gives origin to the adductor mandibularis externus medius muscle. Quadrate (Figs. 1 and 2) is found at the posterolateral angle of the skull where it provides the articulating area between skull and lower jaw. It also forms the seat of the middle ear and attachment for the adductor musculature and tympanic membrane.

Mesially the quadrate is attached to the parietal, dorsally to the supratemporal, and laterally to the squamosal bone. Other parts of its dorsal surface provide for the origin of the adductor mandibularis superficialis and adductor mandibularis externus medius muscles. The medial half and its crest serve as origin for the adductor mandibularis posterior muscle. The posterior end of this area attaches to the prootic bone and the quadrate process of the pterygoid.
The tympanic crest serves as a place of attachment for the tympanic membrane and the origin of the adductor mandibularis externus superficialis muscle.

*Epterygoid* extends between the parietal and the pterygoid. Its dorsal tip appears to be held in place by the origin of the pseudotemporalis superficialis muscle. The upper one-third of this bone serves as the origin for the pseudotemporalis superficialis muscle. The ventral two-thirds serves the pseudotemporalis profundus muscle as origin.

The lower jaw consists of two paired rami which unite anteriorly in a mental symphysis and each articulates with the quadrate of the skull posteriorly. The dentary of each ramus bears a single row of pleurodont teeth (Fig. 1), whereas the remaining bones (articular, surangular, angular, splenial and coronoid) are edentate.

*Dentary* (Figs. 1 and 8) is the largest bone of the lower jaw and bears teeth on its dorsomedial border. At its posterior margins the dentary interdigitates with the coronoid, splenial, angular, articular, and surangular. The ventral border provides the origin for the anterior fibers of the mandibulohyoideus I and III and the genioglossus muscles.

*Articular* (Fig. 1) is that part of the mandible which articulates with the quadrate of the skull. This bone with its retroarticular process serves as the point for insertion for the depressor mandibularis, intermandibularis posterior, fibers of the pterygomandibularis, and adductor mandibularis externus muscles. The medial border is sutured to the splenial bone.

*Surangular* (Fig. 1) forms the lateral wall of the posterior third of the mandible. The dorsal border serves as the area of insertion for the adductor mandibularis externus muscle, and the intermandibularis posterior muscle inserts on its lateral surface.

*Angular* (Fig. 8) is a flat bone whose posterior part forms the ventral surface of the jaw between the articular and surangular. The anterior process of the angular attaches to the dentary. Part of this bone serves as the origin for the mandibulohyoideus I muscle.

*Splenial* is found on the mesial side of the jaw where it connects with the angular, articular, surangular, dentary, and coronoid bones. The intermandibularis anterior profundus muscle has its origin on this bone. *Coronoid* (Fig. 1) straddles the other bones of the jaw from a dorsal position. The two anterior extremities articulate with the dentary and surangular laterally, and the dentary, splenial, and articular bones ventrally.

The posterior, lateral, and apical surfaces give rise to the insertion of the adduc-

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Fig. 3. *Saurovallus obesus multiforaminatus*. BYU 21734. x 11.

A. Most anterior tooth on left side of upper jaw.
B. Eighth tooth from the posterior on left side of upper jaw.
C. Most posterior tooth on left side of upper jaw.
D. Most anterior tooth on left side of lower jaw.
E. Eighth tooth from the posterior on left side of lower jaw.
F. Most posterior tooth on left side of lower jaw.

*Saurovallus obesus*, BYU 21723. x 11.

G. Most anterior tooth on left side of upper jaw.
H. Eighth tooth from the posterior on left side of upper jaw.
I. Most posterior tooth on left side of upper jaw.
J. Most anterior tooth on left side of lower jaw.
K. Eighth tooth from the posterior on left side of lower jaw.
L. Most posterior tooth on left side of lower jaw.
tor mandibularis externus and adductor medius muscles, and provide an attachment surface for the bodenaponeurosis.

**Teth.** — The teeth (Fig. 3) are pleurodont and are borne by the dentary in the lower jaw and the premaxilla and maxilla of the upper jaw. The average number of teeth for each upper jaw is nineteen with the same number occurring in each dentary.

A tooth of Sauromalus obesus multiformatus may have a variable number of from three to six cusps. Those with six cusps appear to occur only in the anterolateral series with the most posterior teeth having the sixth cusp reduced or missing. In the most anterior teeth one to three cusps appear to be typical. The general pattern on all teeth appears to be a primary cusp with one to three accessory cusps on each side. The crowns are spatulate and about twice as wide as the root.

Gilmore (1928:27-28) described a fossil from the Middle Eocene, Wind River Formation of Fremont County, Wyoming. This specimen, *Parsauromalus olsoni*, consisted of two dentaries with fourteen teeth still intact. According to Gilmore, "The teeth present a style of crown structure not before observed among fossil sauria, its closest resemblances being with the living Sauromalus ater. . . . The teeth are pleurodont, . . . crowns laterally compressed, acutely spoon shaped, with tip directed inward as in Sauromalus." He also indicated that his type specimen represented an individual slightly larger than an adult Sauromalus ater.

Hotton (1953:96-97, 105, 107, 111-112) also gives a detailed description of Sauromalus dentition and compares it with several other Iguanid lizards. He concludes that "Dentition of Dipsosaurus d. dorsalis, Sauromalus obesus, and Ctenosaura similis are similar to each other and as a group are highly distinctive. Diets are also similar and highly distinctive."

**WRIST.** — An outstanding feature of the lizard wrist is the presence or absence of the intermediate bone. This bone has been regarded as highly characteristic of lower tetrapods, particularly the amphibians, extinct reptiles and turtles. As the above list suggests, possession of such a bone is an indication of primitiveness.

Until recently the possession of an intermediate bone by some lizards was not suspected. Its occurrence has been reported for families of the old world, primarily Agamidae and the cosmopolitan Scincidae. Camp (1923) indicates that the intermediate is always small and frequently absent in lizards, but does not specify the groups involved. Williston (1925) did not find the bone in the Sauria be examined. Barrows and Smith (1917) found the bone to be present in Xenosaurus grandis (Xenosauridae). Stokesley (1950:180-181) states, "I found no intermediate in the following species: Coelonyx variegatus (Gekkonidae); Agama caecicauda (Agamidae); Polychrus marromata, Uma notata, Cryptophytons wistizenii (Iguanidae). In a specimen of Sceloporus magister, an X-ray picture shows what I believe to be an intermediate, but I cannot identify it with certainty. . . . However, an intermediate was detected in specimens of each of the following species of the division Autarchoglossa: Ctenodaphthorops yulius, C. hypocrithus hedinyi, C. t. trossaltatus (Teiidae); Xantusia henshawi (Xantusiidae); Lacerta erhardtii riveti, L. pitugensis grossae, L. siulca campesiris (Lacertidae)." Romer (1956:382-383) has an excellent chapter on the carpals of reptiles and states, "The less specialized lizards have a carpal structure which is relatively primitive and readily derived from that seen in Sphenodon, but two modifications may be noted: (1) there remains but a single centrale, centrally placed; (2) the intermediate is greatly reduced in size (and readily overlooked) and may disappear completely." However, he does not specify to which groups the above descriptions apply.

The primitiveness of the intermediate bone is not in question. However, the extent of its occurrence in the family Iguanidae is not completely known. One may logically assume that members of the family Iguanidae (other than Sceloporus) should possess an intermediate. Phylogenetically the Iguanids are considered to be the stem group from which other lizard groups (Agamids for example) have evolved. Our investigations, including species belonging to ten genera of Iguanids, have confirmed the presence of the intermediate in other genera of this family.

The use of radiographs, in the search for such a delicate structure, has saved time by eliminating the making of serial sections or minute dissections. The resulting photographs show not only small bones, but also indicate a shadow where cartilaginous structures may occur.

The wrist in Sauromalus and most other Iguanids seen by us consists of from nine to eleven carpal bones which articulate between the metacarpals and the radius and ulna of the lower arm.

Carpals 1-5 (Figs. 4 and 5) are irregular-shaped bones which articulate at the proximal ends of the metacarpals thus forming the distal row of wrist elements. There are usually five, but one or more may be absent in some specimens. In an adult Sauromalus (Fig. 4) all five bones are present, where-
as in a juvenile (Fig. 4), only four are present.

Radiale (Figs. 4 and 5) is a large carpal found directly distal to the radius. It forms part of the proximal row of carpal elements and was constantly present in all genera examined.

Ulnare (Figs. 4 and 5) articulates at the distal end of the ulna and the proximal end of Carpal 5.

Pisiform (Figs. 4 and 5) is a large carpal shown in the X-ray photographs as being just lateral to the ulna. Several photographs did not show the pisiform to be present. In such cases it may have been obscured by the ulna.

Proximal Centrale (Figs. 4 and 5) appears to be a stable central element in the carpal pattern. It is usually found articulating between Carpals 2 and 3 distally, and the ulnare, radiale, and intermedium proximally. Distal Centrale (Figs. 4 and 5) can be told from the proximal centrale by its distal position. It appears to be a rather unstable bone and is not present in most specimens as is the case in the adult specimen of Sauromalus. It is interesting to note that in the juvenile (Fig. 4) this bone appears to be
Fig. 5. Ventral view of carpal bones from left manus.

G. Callisaurus draconoides gabbi. BYU 21270. x 5.
H. Urosaurus ornatus ornatus. BYU 192. x 5.
I. Uta stansburiana stansburiana. BYU 14980. x 5.
J. Phrynosoma coronatum frontale. BYU 15236. x 5.
K. Sauromalus obesus obesus. BYU 21738. x 5.
L. Holbrookia maculata maculata. BYU 12821. x 5.
M. Crotaphytus collaris baileyi. BYU 18921. x 6.

Present. Unfortunately, it may be confused with the distal centrale, which does not appear to be as constant. It is possible that both bones are unstable and that what may be the proximal centrale in one specimen may actually be the distal centrale in another. Romer (1956:380) indicates, "... loss of elements from the primitive reptilian carpal (or tarsal) pattern is commonly assumed to be due to fusion."

As observed in Fig. 4, the distal centrale is found mesial to the proximal centrale, distal to the radiale, and proximal to Carpals 1 and 2. **Intermedium** (Figs. 4 and 5) is definitely present in *Sauromalus* as indicated in Fig. 4. It is a shadowy structure appearing between the radius and ulna, and proximal to the proximal centrale. In the juvenile specimen (Fig. 4) the intermedium appears as a very faint dense area in the described position. Its shadowy appearance may indicate an incomplete ossification as would be expected.
MYOLOGY

A search of the literature reveals no previous account of the myology of the genus Sauromalus. The following account has been prepared by dissection and by using comparative studies of closely related genera.

Sauromalus, Ctenosaura and Crotaphytus appear to be closely related as indicated by the similarity in their musculature and those parts of the skeleton examined. Other studies now in progress which are concerned with other genera of Iguanidae such as Sceloporus, Uta and Phrynosoma should provide additional evidence of Iguanid phylogeny. Differences in habits and habitat are shown by minor variations of the basic myological pattern. The reader’s attention is drawn, in the text, to those differences considered to be comparatively significant. These are discussed in some detail below, but those myological patterns similar to Crotaphytus, as reported by Robison and Tanner (1962), and to Ctenosaura (Oelrich 1956), are not discussed further.

Specimens used for this study came from Glen Canyon, near Page, Arizona, and Crossing of the Fathers in Southern Utah. They are classified as Sauromalus obesus multiformatus Tanner and Avery. Specimens of Sauromalus obesus obesus (Baird), which were dissected and compared, came from Calimesa, California.

The throat integument is loosely attached to the underlying muscles and is not extendable into a dewlap as in many other Iguanids. However, there is a very distinct gular fold present.

The basic myology of Sauromalus has been dissected, illustrated, and compared with Crotaphytus (Robison and Tanner 1962) and Ctenosaura (Oelrich 1956). The following muscles were found to be similar to those in Crotaphytus and Ctenosaura and are listed below with their corresponding plate numbers. The plates of Robison and Tanner, and Oelrich, which figure the same muscle, are also listed for comparative purposes.

M. intermandibularis anterior superficialis (Fig. 6); Robison and Tanner — Plate 1; Oelrich — Figs. 36 and 37.

M. mandibulohyoideus I (Fig. 6); Robison and Tanner — Plate 1; Oelrich — Fig. 37.

M. mandibulohyoideus II (Fig. 6); Robison and Tanner — Plate 1; Oelrich — Fig. 38.

M. mandibulohyoideus III (Fig. 7); Robison and Tanner — Plate 2; Oelrich — Fig. 38.

M. genioglossus (Figs. 6 and 7); Robison and Tanner — Plate 2; Oelrich — Figs. 38 and 39.

M. hyoglossus (Fig. 7); Robison and Tanner — Plate 2; Oelrich — Figs. 38 and 39.

M. branchiohyoideus (Fig. 7); Robison and Tanner — Plate 2; Oelrich — Fig. 39.

M. sternohyoideus (Figs. 6, 7, and 13); Robison and Tanner — Plates 1, 2, 7, and 8; Oelrich — Fig. 38.

M. constrictor colli (Figs. 6, 9, and 12); Robison and Tanner — Plates 1, 4 and 7; Oelrich — Figs. 30 and 36.

M. pterygomandibularis (Figs. 6 and 8); Robison and Tanner — Plates 1 and 3; Oelrich — Figs. 32, 35, 37, and 39.

M. levator angularis oris (Fig. 12); Robison and Tanner — Plate 7; Oelrich — Fig. 30.

M. adductor mandibularis externus superficialis (Figs. 6, 8, 9, 12, and 13); Robison and Tanner — Plates 1, 3, 4, 7, and 8; Oelrich — Fig. 31.

M. adductor mandibularis externus medius (Figs. 9, 12, 13, and 14); Robison and Tanner — Plates 4, 7, 8, 9; Oelrich — Figs 32 and 40.

M. adductor mandibularis externus profundus (Fig. 15) Robison and Tanner — Plate 10; Oelrich — Figs. 33 and 41.

M. pseudotemporalis superficialis (Fig. 15) Robison and Tanner — Plate 10; Oelrich — Figs. 33 and 40.

M. adductor mandibularis posterior (Fig. 16) Robison and Tanner — Plate 11; Oelrich — Fig. 34.

M. levator pterygoideus (Figs. 16 and 17) Robison and Tanner — Plates 11 and 12; Oelrich — Figs. 34 and 35.

M. protractor pterygoideus (Figs. 16 and 17) Robison and Tanner — Plates 11 and 12; Oelrich — Figs. 35.

M. trapezius (Figs. 9 and 12) Robison and Tanner — Plates 4, 7, 8, and 9.

M. latissimus dorsi (Figs. 9 and 12) Robison and Tanner — Plates 4, 5, 7, 8, 9, and 10.

M. levator scapulac superficialis (Figs. 8, 10, 13, 14, 15, and 16) Robison and Tanner — Plates 4, 5, 8, 9, 10, and 11.

M. levator scapulac profundus (Figs. 8, 10, 11, 12, and 13) Robison and Tanner — Plates 4, 5, 8, 9, 10, and 11.

M. scapulodeltoideus (Figs. 7, 9, 10, and 13) Robison and Tanner — Plates 2, 4, 5, 7, and 8.

M. serratus (Figs. 10, 11, 14, 15, 16, and 17) Robison and Tanner — Plates 5, 6, 9, 10, 11 and 12.

M. pectoralis (Figs. 6, 7, 12, 13, 14, and 15) Robison and Tanner — Plates 1, 2, and 7.
Fig. 6. Ventral view of head and thorax musculature; superficial layer shown at left and first depth at right.
Fig. 7. Ventral view of head and thorax musculature; second depth at left and third depth at right.
Fig. 8. Ventral view of head and thorax musculature; fourth depth at left and fifth depth at right.
M. clavodeltoideus (Figs. 7, 12, 13 and 14) Robison and Tanner — Plates 2, 7, 8, and 9.
M. supracoracoideus (Figs. 8 and 12) Robison and Tanner — Plates 2, 3, and 7.
M. scapulohumeralis anterior (no illustration) Robison and Tanner — no illustration
M. coracobrachialis brevis (Fig. 8) Robison and Tanner — Plate 3.
M. coracobrachialis longus (Fig. 9) Robison and Tanner — Plates 2 and 4.
M. biceps (Figs. 7, 9, and 13) Robison and Tanner — Plates 2, 4, and 8.
M. brachialis inferior (Figs. 7 and 13) Robison and Tanner — Plates 2 and 8.
M. anconaeus humeralis lateralis (no illustration) Robison and Tanner — Plates 2 and 8.
M. anconaeus scapularis (Figs. 7, 9, and 13) Robison and Tanner — Plates 2, 4, and 8.
M. anconaeus coracoideus (Fig. 9) Robison and Tanner — Plate 4.
M. anconaeus humeralis medialis (Fig. 9) Robison and Tanner — Plate 4.
M. subscapularis I (no illustration) Robison and Tanner — no illustration.
M. subscapularis II (Figs. 11, 15, and 16) Robison and Tanner — Plates 6 10, and 11.
M. costocoracoideus (Fig. 16) Robison and Tanner — Plates 11 and 12.
M. internus sternocoracoideus (no illustration) Robison and Tanner — no illustration.
M. externus sternocoracoideus (no illustration) Robison and Tanner — no illustration.
M. sacrohamalis (Figs. 10, 14, 15, and 16) Robison and Tanner — Plates 5, 9, 10 and 11.
M. obliquus abdominis externus superficialis (Figs. 8, 10, 14, and 16) Robison and Tanner — Plates 3, 5, and 11.
M. obliquus abdominis externus profundus (no illustration) Robison and Tanner — no illustration.
M. intercostales externi (Figs. 11 and 17) Robison and Tanner — Plates 6 and 12.
M. intercostales interni (Fig. 17) Robison and Tanner — Plate 12.
M. obliquus abdominis internus (no illustration) Robison and Tanner — no illustration.
M. transversalis (no illustration) — Robison and Tanner — no illustration.

The following muscles have been found to differ significantly from those of Crotophytus and are discussed in some detail.
M. intermandibularis (Posterior and anterior profundus, Figs. 6, 12, and 13) is a continuous sheet of muscle originating at various points along the lower jaw bones and lies superficial to most of the throat musculature just deep to the skin. The posterior slip of this muscle is extremely thin from its belly to the insertion in the fascia of the midventral area.

The intermandibularis is separable into posterior and anterior parts in Sauromalus, with the posterior slip being one muscle fiber thick, with its belly about one-fourth as wide as the belly of the anterior slip. Oelrich (1956:48) also found the intermandibularis to be separable into these two parts in Ctenosaura pectinata. We found it to be similar in Ctenosaura hemilopha. Robison and Tanner (1962) describe a similar arrangement in Sceloporus and Diposaurus. In the specimens of these genera that we have examined, the posterior slip in Ctenosaura is very narrow and cordlike, being only one-tenth the width of the anterior part. In Diposaurus the division is similar to Sauromalus, with the posterior slip being from one-third to one-fourth the width of the anterior. Sceloporus shows both bellies widely separated, medially, but with the posterior belly being only about one-sixth the width of the anterior slip.

In Sauromalus the two slips are continuous at the origin with the main separation occurring along the mid-ventral line. The anterior slip arises from the mesial surfaces of the splenial and coronoid bones and from the crista dentalis, by a tendon. The anterior fibers extend anteromesially across the throat to insert on the ventral mid-line raphe. The posterior fibers also insert on the mid-line raphe after arising via several interdigitations with the first mandibulo-hyoides muscle along the ventral border of the jaw.

The intermandibularis posterior slip of this muscle arises as the last two or three interdigitations of the anterior profundus section with which it is continuous. Posteriorly, this muscle is continuous with the constrictor colli from which it can be delineated by the natural separations of the muscle fiber bundles. The posterior part of the muscle arises from the lateral surface of the mandible with its boundaries beginning at the retroarticular process of the articular and passes anteroventrally across the surangular, angular, and the ventral surface of the dentary. Its insertion on the midline raphe is characterized by a wide aponeurosis which leaves both sets of fibers from each side separated. The anteromedial portion of the posterior body in some specimens may be overlain by the insertion of the posterior bundle of the depressor mandibularis.
Fig. 9. Dorsal view of head and thorax musculature; superficial depth at left and first depth at right.
Fig. 10. Dorsal view of head and thorax musculature; second depth at the left and third depth at the right.
Fig. 11. Dorsal view of head and thorax musculature; fourth depth at left and fifth depth at right.
Fig. 12. Lateral view of head and thorax musculature; superficial depth.
Fig. 13. Lateral view of head and thorax musculature; first depth.
Fig. 14. Lateral view of head and thorax musculature; second depth.
Fig. 15. Lateral view of head and thorax musculature; third depth.
Fig. 16. Lateral view of head and thorax musculature; fourth depth.
Fig. 17. Lateral view of head and thorax musculature; fifth depth.
*M. episternocleidomastoideus* (Figs. 6, 10, 12, 13, and 14) is a neck muscle crossing at an oblique angle from the shoulder to the head. This muscle is overlain by the depressor mandibularis which covers its anterior end. Lying deep to the episternocleidomastoideus muscle are the sternohyoideus, the tympanic membrane, the distal ends of the ceratohyal and the ceratobranchial bones, and the two levator scapulae muscles.

The origin appears to be a single head arising from the lateral process of the interclavicle. Robison and Tanner (1962:6-7) have found this to be the case for *Crotaphytus wislizeni*, although there are two heads in *C. collaris* and *C. reticulatus*. Oelrich (1956:48) found a single head in *Ctenosaura pectinata*. We found this condition to also exist in *Sceloporus* and *Diposaurus*.

The insertion occurs on the distal half of the parietal crest, the lateral surface of the paroccipital process of the exoccipital bone and with some connection to the fascia of the dorsolateral angle of the neck. *M. depressor mandibularis* (Figs. 9, 12, and 13) is situated laterally with its anterior edge bordering the auditory meatus posteriorly. It is overlain by the constrictor colli. The anterior part of the depressor mandibularis is superficial to part of the posterior fibers of the adductor mandibularis externus medius and the posterior border of the tympanic membrane. Its posterior parts pass superficially to the anterior fibers of the trapezius and the episternocleidomastoideus, with some lying superficial to the distal ends of the ceratohyal and ceratobranchial bones, and the tympanum.

In *Saurophagus* this muscle is divisible into three bundles as Oelrich (1956:47) indicates for *Ctenosaura* and Robison and Tanner (1962:8) describe for *Crotaphytus wislizeni*.

The origin of the anterior bundle is from the anterolateral surface of the postero-lateral parietal wing and parietal crest. This bundle makes up the major part of the depressor mandibularis muscle and passes posteriorly with a tendinous insertion on the retroarticular process of the articular bone.

The intermediate bundle, in its posterior region, takes origin from the fascia along the dorsolateral angle of the neck, in the region of the first three cervical vertebrae, and ventral to the constrictor colli. This bundle has a common origin with the posterior bundle (cervicomandibularis) and a common insertion, ventrally, with fibers of the anterior bundle, on the retroarticular process.

The posterior bundle is separated by Robison and Tanner (1962:8) under the name cervicomandibularis, and is labeled by that name on Figures 6, 9, 12, and 13 to avoid confusion. Oelrich (1956:47) found it partially connected to the intermediate bundle in *Ctenosaura pectinata*, but described it as "... the cervicomandibularis, when separate ...". This muscle is completely separate from the other bundles except for a common origin in the superficial fascia of the dorsal mid-line of the neck, which it shares with the intermediate bundle. Its origin is just lateral to that of the intermediate bundle and ventral to the origin of the constrictor colli. It extends anterodorsally along the posterior border of the lateral bundle and continues past the insertion of the anterior and lateral bundles to insert on the superficial fascia of the intermandibularis and the skin.

Robison and Tanner (1962:8) have found the cervicomandibularis to be continuous with the other bundles in old or large specimens of *Crotaphytus*.

The following muscles have not been described previously for the genera involved in this paper, except for a general description of their disposition in *Crotaphytus* by Davis (1934:28).

*M. spinus dorsi* (Figs. 10, 11, 14, 15, 16, and 17) is a large muscle lying near the midline of the back and occupying the space between the neural spines and zygo-physe of the vertebrae.

This muscle has its origin on the main muscle mass of the caudal region with the main fibers extending anterodorsally to insert on the center of the posterior edge of the parietal bone of the skull.

*M. longissimus dorsi* is a thick muscle lying lateral to the spinus dorsi and ventral to the sacrolumbar. At its anterior extremes near the insertion it divides into three major bundles. The most medial of these emerges from the other two bundles to pass anteriorly and insert on the posterior border of the parietal bone. The second or medial bundle originates just posterior to the first and passes anteriorly at an oblique angle to insert on the exoccipital. The third or lateral bundle, the most posterior part of the longissimus dorsi, extends anteriorly directly to the basicoccipital, where it inserts.

**DISCUSSION**

**Osteology.** — The osteological characters of the Iguanid Lizards examined by us appear to be stable, as indicated by a comparison of the skull of *Saurophagus* (Figs. 1 and 2, pp. 3-8) with that of *Ctenosaura* as illustrated by Oelrich (1956), and the general
accounts of reptile osteology described by Williston (1925) and Romer (1956). The bones of the lizard wrist appear to be much less stable than those of the skull. Romer (1956:381) points out that fusion or complete loss of some wrist bones is common in lizards. To quote him, “Loss of elements from the primitive reptilian carpal (or tarsal) pattern is commonly assumed to be due to fusion. Sometimes this is the case, but often assumptions of fusion are unwarranted, and more frequently reductions appear to be due to actual loss of elements.”

The most unstable element of the wrist appears to be the distal centrale which is missing in adult Sauromalus (Figs. 4, A and 5, K) in Ctenosaura, Dipsosaurus, Crotophytus wislizeni, Holbrookia, Callisaurus, Secloporus, Uta and Urosaurus. This element is present in juvenile Sauromalus (Fig. 4, B). Crotophytus collaris and Phrynosoma. Romer (1956) indicates that this bone possibly fuses with the proximal centrale. This may explain why the distal centrale is present in juvenile Sauromalus and not in the adult. Fusion or deletion may occur later in life.

The intermedium has also been found to be variable in several genera. This wrist element (bone or cartilage) definitely occurs in the following genera: Sauromalus, Ctenosaura, Dipsosaurus, Crotophytus, Callisaurus, Secloporus, and Phrynosoma. It is a questionable structure in Uta, Urosaurus and Holbrookia. With the methods used in this study, an element as minute as the intermedium would be difficult to locate on small lizards such as the above genera. This may account for the absence of the intermedium in these groups. The possession of such a structure (intermedium) by the above iguanid genera implies that a considerable age or primitiveness may be associated with the family Iguanidae. This structure photographs well in some lizards such as Sauromalus, Ctenosaura, and Crotophytus indicating substantial ossification. In Dipsosaurus, Callisaurus, Secloporus, and Phrynosoma it appears as a faint shadow on the film, perhaps for lack of ossification. The genera Uta, Urosaurus, and Holbrookia appear not to have the structure; however, there is a space for it between the distal ends of the radius and ulna which suggest that if present the intermedium is cartilaginous.

The degree of ossification of this structure and other carpal is probably a function of the age of the individual. This is demonstrated in the genus Sauromalus in which the adult (Fig. 4, A) shows the intermedium distinctly, whereas a juvenile of the same subspecies (Fig. 4, B) shows no trace of the bone. There is, however, a space for it between the radius and ulna.

We recognize the need for using larger series in most genera than has been possible in this study particularly when considering elements so small and variable as carpals; however, the data presented seem significant, particularly that dealing with the intermedium and distal centrale.

**Teeth.** — The teeth (Fig. 3) of Sauromalus ocellatus multiforminatus and S. o. ocellatus show considerable similarity in their constant size, but differ slightly in shape and position of cusp. The cusps of the teeth of S. o. multiforminatus appear to be more angular than those of S. o. ocellatus. However, this may be due to the age of the specimens, illustrated. The angularity of the teeth on Fig. 3, A-F may indicate those of a young specimen while the more rounded cusps found in G-L represent a specimen more advanced in age. Position of the primary and accessory cusps is variable with no prominent trends recognized.

Age is also exhibited by tooth structure in another way. Old specimens have the accessory cusps completely worn away and the primary cusps reduced to a small swelling in both subspecies.

**Myology.** — Huntington (1903), Brock (1938), and Smith (1960) indicate that the musculature is an unstable morphological structure for major groupings such as orders and classes. For this reason it may be difficult to interpret homologies in the vertebrate categories above the family level. However, myology at the family level appears to be sufficiently stable to be used as a phylogenetic character. Piatt (1935), working with the North American genera of the family Plethodontidae, and Tanner (1952), working with Mexican and Central American groups of the same family, have indicated that the musculature is consistent enough to define genera. Robison and Tanner (1962) compared the myology of the two subgenera, Crotophytus and Gambelia, and found that the myology also remained constant. The lizards of the family Iguanidae, which we have examined, show little myological variation between generic groups. This is indicated by the fact that of the forty-eight muscles dissected in Sauromalus and compared (see pp. 11-25) with Crotophytus as described by Robison and Tanner (1962) and Ctenosaura by Oelrich (1956), only three show significant variation in configuration, origin, insertion, and size. Because the myology is relatively stable in the Iguanidae, it may be used as a tool for interpreting phylogenies between genera. Some muscles, such as the intermandibularis,
episternocleidomastoideus, and depressor mandibularis, differ between Sauromalus, Dipsosaurus, Ctenosaura, Sceloporus, and Crotaphytus, yet indicate close generic relationships between genera in the family Iguanidae.

*M. intermandibularis* is separable into anterior and posterior parts, with the posterior being over one-fourth as wide as the anterior. Such a separation is also discernible in Dipsosaurus and Sceloporus. In Dipsosaurus the posterior part is from one-third to one-fourth as wide as the anterior whereas in Sceloporus it is only about one-sixth the width of the anterior part. Oelrich (1956: 48) describes a separable condition in *Ctenosaura pectinata* with the posterior slip being figured as extremely small and widely separated from the anterior slip. Robison and Tanner (1962:2-3) described this muscle in *Crotaphytus* as complete, with the two slips being inseparable. In a single additional specimen of *C. collaris baileyi* examined, we found this to be the case. The morphology of this muscle indicates that Sauromalus, Dipsosaurus, Ctenosaura, and Sceloporus are more closely related to each other than any one is to Crotaphytus.

*M. episternocleidomastoideus* arises as a single head in Sauromalus as reported by Robison and Tanner (1962:6-7) for Crotaphytus *wislizeni*. The above authors found two heads in *C. collaris* and *C. reticulatus*. Oelrich (1956:48) reports a single head in Ctenosaura *pectinata* with a small mesial slip. Those specimens of Dipsosaurus and Sceloporus examined also show a single head. The condition of a single head in the episternocleidomastoidius muscle suggests that Sauromalus and Dipsosaurus are intermediate forms between Ctenosaura and Crotaphytus.

The different configurations of this muscle between species in Crotaphytus may indicate that this muscle is variable and not suited for phylogenic comparisons in this genus, or these myological variations may indicate and support the distinction of at least subgeneric rank between the two groups (collaris and wislizeni) now recognized in Crotaphytus.

*M. depressor mandibularis* has three muscle bundles in Sauromalus as described by Oelrich (1956:47) for Ctenosaura. Robison and Tanner (1962:8) have found three bundles in Crotaphytus *wislizeni* and two bundles in *C. collaris*. The most posterior bundle, cervicomandibularis, appears to be variable in reptiles and has caused much confusion in the literature. As Robison and Tanner (1962:8) indicate this muscle fuses with the medial bundle in old specimens, creating a definite relationship between these two bundles. As a result the cervicomandibularis is considered to be a part of the depressor mandibularis complex in Sauromalus.

This study has shown that Ctenosaura and Sauromalus share in common with Dipsosaurus (1) an intermandibularis muscle distinguishable into anterior and posterior parts, (2) an episternocleidomastoidues muscle which arises by only one head, (3) a depressor mandibularis muscle which has three bundles instead of two as described for some species of Crotaphytus, (4) the possession of an intermedium bone in the wrist, and (5) an herbivorous diet.

The sharing of common characteristics by Sauromalus and Ctenosaura might be related to their similar habitats and diet (herbivorous), with each filling a comparable ecological niche. Dipsosaurus, a dune and sandy flats dweller, and Sauromalus, a rock dweller, both display these same myological characteristics, indicating that the groups involved are related through common ancestry.

Crotaphytus differs from Sauromalus in having (1) an intermandibularis muscle that is not divisible into anterior and posterior parts, (2) an episternocleidomastoidues muscle which arises by more than one head, (3) a depressor mandibularis muscle which has only two bundles in some taxa, and (4) a different diet (omnivorous).

The above differences in musculature indicate that Sauromalus is most closely allied to Ctenosaura and Dipsosaurus, with which it shares a herbivorous diet and similar osteological characters as previously discussed. Sceloporus exhibits all these characters except diet. Mittleman (1942:113) lists Sceloporus as a branch from Ctenosaura, with Urosaurus, Uta, and Sator being derivatives of the pre-Sceloporus line. Since Sceloporus appears to be related to Ctenosaura by the similarity in musculature, Phrynosoma should have characteristics intermediate between these two genera. Further study is needed to determine if such is the case. Both Sceloporus and Phrynosoma are known from Pleistocene fossils, as indicated by Gilmore (1928) and Brattstrom (1953).

Mittleman (1942:113) figures Ctenosaura as the base stock from which the genera of North American Iguanidae arose. Assuming he is correct, then the placing of Sauromalus and Dipsosaurus, as early derivatives of this line, is also seemingly plausible, for all three genera show close relationships. The range of Ctenosaura in Mexico may indicate that area to be the major region for Iguanid radiation in North America.
The fossil history of *Ctenosaura* is imperfectly known. An Eocene fossil, *Parasuromalus* (Gilmore 1928:27-28), may represent the ancestral stock for *Sauromalus*. Such evidence may indicate that this genus was well advanced toward its present form at this time and had branched away from the pre-Crotophytus line very early. Fossils of *Crotophytus* do not appear until Pliocene (Gilmore, 1928), with some occurrence in the Pleistocene of California (Brattstrom 1953). To date the fossil record is incomplete and the radiation of *Crotophytus* from the main Iguanid stock may have occurred at an earlier time. Present knowledge indicates, however, that this genus represents a later branch away from the main stock than that stock which gave rise to *Sauromalus* and presumably *Ctenosaura*.

CONCLUSIONS AND SUMMARY

Those anterior myological characters and the structures of the skull and wrist discussed previously and figured suggest that *Sauromalus, Ctenosaura, and Diplosaurus* form a separate and distinct natural grouping: *Iguana* should perhaps be included as well, but was not examined by us.

*Sauromalus, Ctenosaura, and Diplosaurus* share the following characteristics: (1) an intermandibularis muscle divisible into anterior and posterior parts, (2) an episternocleidomastoideus muscle which arises by only one head, (3) a depressor mandibularis muscle divisible into three bundles, (4) an herbivorous diet. The genus *Crotophytus* differs from the above genera by having (1) an intermandibularis muscle which is not divisible into anterior and posterior slips, (2) an episternocleidomastoideus muscle arising by more than one head, (3) a depressor mandibularis muscle with two bundles in some species, and (4) an omnivorous diet. *Sceloporus*, which has an omnivorous diet in some species and a carnivorous diet in others, shares basically the above indicated similarities with *Sauromalus, Ctenosaura, and Diplosaurus*.

An intermedium is present in *Sauromalus, Ctenosaura, Diplosaurus, Crotophytus, Callisaurus, Sceloporus, and Phrynosoma*. This structure is of a questionable nature in *Uta, Urosaurus, and Holbrookia*. The presence of the intermedium in the wrist of the above genera indicates a greater primitiveness in this feature for the family Iguanidae than for those families which lack the structure (Gekkonidae and Zonuridae). This verifies the position and early distinction of *Sauromalus, Ctenosaura, and Diplosaurus* as indicated by the many extinct groups of primitive reptiles as well as the family Agamidae (Stokely, 1950), which also possess the structure.

The ranges of the closely related genera *Sauromalus, Ctenosaura, and Diplosaurus* indicate that a radiation of Iguanid lizards took place in Mexico and Southwestern United States during middle Cenozoic time.

**Table 1. Summary of Utilized Characters**

<table>
<thead>
<tr>
<th>genus</th>
<th>Intermedium</th>
<th>Distal Centrale</th>
<th>Intermandibularis</th>
<th>Episternocleidomastoideus</th>
<th>Depressor mandibularis</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Sauromalus</em> — jv.</td>
<td>present</td>
<td>absent</td>
<td>1 slip</td>
<td>1 head</td>
<td>fused</td>
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<tr>
<td></td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
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<td></td>
<td>— adult</td>
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<td></td>
<td>X</td>
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<tr>
<td><em>Ctenosaura</em></td>
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<tr>
<td><em>Diplosaurus</em></td>
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<td><em>Sceloporus</em></td>
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<td><em>Crotophytus collaris</em></td>
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<td><em>C. wisliceni</em></td>
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<td><em>Holbrookia</em></td>
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<td><em>Callisaurus</em></td>
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<td><em>Uta</em></td>
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<td><em>Urosaurus</em></td>
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<td><em>Phrynosoma</em></td>
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</tbody>
</table>

*The musculature of these genera was not investigated.*

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