Evolution of the iguanine lizards (Sauria, Iguanidae) as determined by osteological and myological characters

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EVOLUTION OF THE IGUANINE LIZARDS (SAURIA, IGUANIDAE) AS DETERMINED BY OSTEOLOGICAL AND MYOLOGICAL CHARACTERS

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David F. Avery and Wilmer W. Tanner

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TABLE OF CONTENTS

LIST OF TABLES .................................................................
LIST OF ILLUSTRATIONS ......................................................
INTRODUCTION .................................................................. 1
LITERATURE ...................................................................... 8
MATERIALS AND METHODS ..................................................
OSTEEOLOGY ................................................................ 9
   Skull and Jaws .............................................................. 9
   Teeth ........................................................................... 22
   Hyoid Elements ........................................................... 23
   Sterna and Ribs ............................................................ 23
MYOLOGY ..................................................................... 34
   Throat Musculature ....................................................... 34
   Neck Musculature ........................................................ 36
   Temporal Musculature ................................................... 38
OTHER CHARACTERS ............................................................
   Tongues ..................................................................... 40
   Hemipenes ................................................................. 67
DISCUSSION ................................................................ 67
   Osteology .................................................................. 67
   Myology ..................................................................... 69
   Tongues ..................................................................... 70
   Hemipenes .................................................................. 70
   Iguanine Distribution ..................................................... 70
ACKNOWLEDGMENTS ............................................................
CONCLUSIONS AND SUMMARY ........................................
LITERATURE CITED ..............................................................

LIST OF TABLES

Table Page
1. Skull Length and Width .................................................. 9
2. Skull Length and Height .................................................. 9
3. Basisphenoid Bones ...................................................... 10
4. Basioccipital Bones ....................................................... 10
5. Exoccipital Bones ........................................................ 11
6. Supraoccipital Bones ..................................................... 11
LIST OF ILLUSTRATIONS

<table>
<thead>
<tr>
<th>Figure</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Ventral view of skull</td>
<td>24</td>
</tr>
<tr>
<td>2. Ventral view of skull</td>
<td>25</td>
</tr>
<tr>
<td>3. Dorsal view of skull</td>
<td>26</td>
</tr>
<tr>
<td>4. Dorsal view of skull</td>
<td>27</td>
</tr>
<tr>
<td>5. Lateral view of skull</td>
<td>28</td>
</tr>
<tr>
<td>6. Lateral view of skull</td>
<td>29</td>
</tr>
<tr>
<td>7. Medial view of mandibles</td>
<td>30</td>
</tr>
<tr>
<td>8. Ventral view of hyoid bones</td>
<td>31</td>
</tr>
</tbody>
</table>
9. Ventral view of sternum .............................................. 32
10. Ventral view of sternum ............................................ 33
11. Ventral view of throat musculature; superficial layer shown at left and first depth at right ......................................................... 41
12. Ventral view of throat musculature; superficial layer shown at left and first depth at right ......................................................... 42
13. Ventral view of throat musculature; second depth at left and third depth at right ......................................................... 43
14. Ventral view of throat musculature; second depth at left and third depth at right ......................................................... 44
15. Ventral view of throat musculature; fourth depth at left and fifth depth at right ......................................................... 45
16. Ventral view of throat musculature; fourth depth at left and fifth depth at right ......................................................... 46
17. Dorsal view of throat and neck musculature; superficial depth at left and first depth at right ......................................................... 47
18. Dorsal view of throat and neck musculature; superficial depth at left and first depth at right ......................................................... 48
19. Dorsal view of head and neck musculature; second depth at left and third depth at right ......................................................... 49
20. Dorsal view of head and neck musculature; second depth at left and third depth at right ......................................................... 50
21. Dorsal view of head and neck musculature; fourth depth at left and fifth depth at right ......................................................... 51
22. Dorsal view of head and neck musculature; fourth depth at left and fifth depth at right ......................................................... 52
23. Lateral view of head and neck musculature; superficial depth ......................................................... 53
24. Lateral view of head and neck musculature; superficial depth ......................................................... 54
25. Lateral view of the head and neck musculature; first depth ......................................................... 55
26. Lateral view of the head and neck musculature; first depth ......................................................... 56
27. Lateral view of the head and neck musculature; second depth ......................................................... 57
28. Lateral view of head and neck musculature; second depth ......................................................... 58
29. Lateral view of head and neck musculature; third depth ......................................................... 59
30. Lateral view of head and neck musculature; third depth ......................................................... 60
31. Lateral view of head and neck musculature; fourth depth ......................................................... 61
32. Lateral view of head and neck musculature; fourth depth ......................................................... 62
33. Lateral view of head and neck musculature; fifth depth ......................................................... 63
34. Lateral view of head and neck musculature; fifth depth ......................................................... 64
35. Dorsal view of the tongue ..................................................... 65
36. Hemipenes .......................................................... 66
37. Phylogenetic relationships of the Madagascar Iguanidae and the genera of iguanine lizards ......................................................... 71
Ctenosaura pectinata (Wiegmann) taken 50 miles S.W. of Guadalajara (Hwy. 80) by Kenneth R. Larsen, 18 July 1970.
EVOLUTION OF THE IGUANINE LIZARDS (SAURIA, IGUANIDAE) AS DETERMINED BY OSTEOLOGICAL AND MYOLOGICAL CHARACTERS

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INTRODUCTION

The family Iguanidae is almost completely restricted to the Western Hemisphere with its main radiations occurring in North and South America. There are also representatives on Fiji, Tonga, and the Galapagos Islands in the Pacific Ocean. Two distinctly related iguanid genera are also found on Madagascar. These genera, Chalarodon and Oplurus, possess abdominal ribs and are therefore considered to be the most primitive members of the family. Although the iguanid lizards are familiar to most scientists interested in the tropics, their anatomy and evolution are still poorly understood.

Because the family Iguanidae is a large and diverse group of lizards, several distinct phylogenetic lines have been recognized. In this study we are concerned with that group of genera belonging to the iguanine line, which includes the following genera: Amblyrhynchos and Conolophus from the Galapagos Islands, Brachylophus from Fiji and Tonga Islands, Enyaliosaurus from Central America, Ctenosaura and Iguana from Central and South America, Cyclura from the West Indies, and Dipsoaurus and Sauromalus from North America.

Those iguanid lizards which have a discontinuous distribution all belong to the iguanine line, or are the most primitive members of the family. Explaining the discontinuous distribution pattern between the Western Hemisphere mainland iguanines, the Pacific Island forms, and their Madagascar relatives has proven to be an enigma for zoogeographers and herpetologists.

The purpose of this study is to establish the degree of relationship between the iguanines of the Galapagos, Fiji, and Tonga Islands with the mainland genera. We will also attempt to define more completely the relationships between the Madagascar genera and the iguanine line. In order to ascertain these relationships, the anterior osteology and myology of each genus has been investigated along with such specialized features as the tongue, hyoid bones, sterna and hemipenes. Hopefully the morphological relationships between the ten genera can be clarified by the use of these relationships, and the evolution and distribution of the iguanine iguanids can be explained. Of all the genera listed above, only Enyaliosaurus has not been studied in detail as only two skulls and one complete specimen were available for examination.

LITERATURE

Literature concerning the anatomy of lizards is varied, widely scattered and incomplete. Because of the large amount of material dealing with this subject, this discussion will be limited, with some exceptions, to that literature which pertains to the following anatomical features treated in this paper: namely the anterior osteology and myology, hyoid bones, sterna, the tongue, and the hemipenes.

One of the earliest discussions of the head-osteology or myology of lizards is that of Mivart (1867) who published a detailed account of the myology of Iguana tuberculata (Iguanidae). This work was followed by Mivart’s (1870) paper on the myology of Chamaeleon parsonii (Chamaeleonidae). The latter is detailed and when used with his paper on Iguana constitutes two of the most complete discussions of lizard myology in the literature.

Sanders (1870) published an account of the myology of Platydactylus japonicus (Gekkonidae) which is a comprehensive presentation but lacks adequate illustrations. Sanders (1872) again published a lizard myology, with an account on the musculature of Liolepis bellii (Agamidae). As with the earlier papers of Mivart, the paper is well illustrated. Gervais (1873) published a brief note on the skull and teeth of the Australian agamid Moloch. Notes and illustrations dealing with the myology of Phrynosoma coronatum (Iguanidae) were related by Sanders (1874).

Parker (1880) described the skull of Lacerta agilis, L. viridis and Zootoca vivipara (Lacertidae). That

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work was followed by De Vis's (1883) paper on the myology of Clammysodin saur us kingii (Agamidae). Unfortunately, his paper was poorly illustrated.

Boulenger (1885 to 1887) published his monumental catalogue of lizards in the British Museum in which are scattered his observations on the osteology of lizards, including a discussion of the distinctive cranial features of Amblyrhynchos, Brachylophus, Conolophus, Ctenosaura, Cyclura and Iguana (Iguanidae). Gill (1886) reviewed Boulenger's classification system for lizards and summarized the important osteological differences between the families. Boulenger (1890) further summarized his osteological observations on the distinctive cranial characters of the iguanid lizards related to Iguana. Even at this early stage of investigation, the iguanine line of evolution was recognized in the family Iguanidae as a natural group. All seven genera listed by Boulenger are today still considered to be iguanines. Boulenger (1891) published a series of remarks concerning the osteology of Heloderma and presented a conclusion for the systematic position of the family Helodermatidae.

E. D. Cope was also actively publishing on lizard anatomy during this period. Cope's (1892a) comments on the homologies of the posterior cranial arches in reptiles, and his conclusions in this matter have laid the foundation for understanding the components of the posterior skull of lizards by later workers. During the same year, Cope's (1892b) classic work on lizard osteology was published. Not only does Cope provide a comparison of the cranial osseous elements, but he describes in detail osteological features of the iguanines, Diposaurus and Sauromalus. This material was also incorporated into Cope's (1900) comprehensive taxonomic work.

The German worker Siebenrock, during the close of the 19th century, made several contributions to our knowledge of the anatomy of lizards. He published a brief paper on the skeleton of Uroplatus finbritius (Gekkonidae) (1892a) and a more lengthy discussion on the skulls of skinks, anurids and Gerrhosaurus (Cordylidae) (1892b). These papers were followed by Siebenrock's (1893) discussion of the skeleton of Brookesia superciliaris (Chamaeleonidae); an account of the skeleton of Lacerta simonyi (Lacertidae) (1894); and a comprehensive discussion on the skeleton of the agamid lizards (1895).

Bradley (1903) discussed the muscles of mastication and the movement of the skull in lizards. Broom (1903) named Paligiana whitei (Eschscholtz) from the Triassic beds of South Africa. This find is of considerable importance as it may represent an animal ancestral to lizards. The presence of this fossil also establishes the great geologic age of lizards in general. He also studied (1903b) the development of pterygoquadrate arch in lizards. Following these investigations, Beddard (1905) published notes on the skull of Uromastix (Agamidae), and in a separate paper discussed some aspects of Clammysodin saurus kingii and other agamids. Kingsley (1905) examined the reptile jaw bones and figured the medial surface of the Iguana (Iguanidae) mandible. Beddard (1907) examined the internal anatomy of several genera of lizards and described the uniqueness of various characters to particular families.

Bryant (1911) revised the iguanid genus Phrynosoma and its synonym Anota. In this paper he presented some osteological observations on the species and genera treated in the study.

A most useful paper on the phylogeny of jaw muscles in vertebrates was published by Adams (1919). Although the paper is concerned with reptiles in general it describes the jaw musculature of Iguana (Iguanidae) and Varanus (Varanidae) in particular. Kesteven (1917) analyzed the pterygoids and parasphenoids of reptiles and amphians.

Rice (1920) described the development of the skull in the skink Eumeces quingualineatus. Camp (1923) published his classic work on the classification of lizards, based on their anatomy. In this account, Camp described the anatomical structure of Sphenodon (Rhynchocephalia), Amphisbaenia (Amphisbaenidae), Coleonyx (Eublepharidae), Uroplatus (Gekkonidae), Typhlops (Typhlopidae), Tupinambis (Teiidae), Varanus (Varanidae), Gerrhosaurus, Zonuras, Chamaeleon (Cordylidae), Liias (Pygopodidae), Brachylophus, Phrynosoma (Iguanidae), Calotes (Agamidae), Chamaeleon (Chamaeleonidae), Xantusia (Xantusiidae), Trachysaurus (Scincidae), Lacerta (Lacertidae), Heloderma (Helodermatidae), Gerrhonotus (Anguidae), Xenosaurus (Xenosauridae), Ameiva (Anniellidae), and Gehco (Gekkonidae). Reese (1923) analyzed the osteology of Tupinambis nigropunctatus (Teiidae).

Broom (1924) discussed the origin of lizards by tracing the cranial elements of the fossil forms Youngina, Mesosuchus, and Pali guana (Eschscholtz). These genera were compared with modern skinks, chamaeleonids, varanids and agamids. Broom indicated the closeness of Pali guana to the modern lizards and suggested ways whereby Pali guana could have evolved into recent forms.

Dubeoq (1925) discussed the elevating muscles of the lower jaws in reptiles, and Williston published his treatise on the osteology of reptiles. This latter work is of interest as Williston figured skulls of Conolophus (Iguanidae), Varanus (Varanidae), Amphisbaena (Amphisbaenidae), and a chamaeleon. He also classified the Squamata in the Subclass Parapsida with the lizardlike fossil Araeoscelis.

Gilmore (1928) summarized the fossil lizards of North America and discussed the osteology of many forms as well as establishing the existence of some families of lizards in North America as early as the Upper Cretaceous. Nopfes (1928) presented a synopsis of the genera of reptiles. For each family he cited
osteological characteristics and summarized the fossil and recent genera found in each. Lastly, Simins (1928) analyzed skulls in the family Teiidae and separated the family into two divisions based on cranial osteology.

Goodrich (1930) published his major work on the structure and development of the vertebrates. In it he figured and described the skulls of Varanus (Varanidae) and Lacerta (Lacertidae). Edgeworth (1931a, 1931b) presented two papers on reptile anatomy in which he discussed the development of the eye, masti catory and hyoid muscles of Sphenodon (Rhynchocephalia) and an account of muscles used in opening and shutting the mouth of vertebrates. His remarks in the second paper were restricted to the lizard genera Lacerta (Lacertidae), Platy dactylus (Gekkonidae), and Calotes (Agamidae). Brock (1932) continued earlier investigations on lizard anatomy and the developmental stages in the skulls of the geckos Lygodactylus capensis and Pachydactylus maculos. Kingman (1932) studied the skull of the skink, Eumeces obsoletus.

Davis (1934) published a laboratory manual for Cro taphyatus (Iguanidae) which was one of the most complete studies on lizard anatomy. In the year 1935 important papers on lizard anatomy were published by Brock, Broom, and Edgeworth. Brock's discussion dealt with the problem of temporal bones in lizards, birds, and mammals. Most of Brock's comments were relegated to skinks and geckos. Broom's work also dealt with the temporal bones and correlated the information known for the fossil Paliguana and Youngina (Eosuchia) with the structure of the modern genera Iguana (Iguanidae), Agama (Agami dae), Chнемidophorus, Teis, Calliopistes (Teiidae), Varanus (Varanidae), Scapteira (Lacertidae), Gerrhonotus, and Anguis (Anguini dae) and Urop latus (Gekkonidae). The highlights of the year, for lizard anatomists, was the publication of Edgeworth's (1935) classic work on the cranial muscles of vertebrates. In this paper he describes the myology of Iguana (Iguanidae) and correlates it with members of the related families of lizards Chamaeleonidae and Lacertidae.

Davis (1936) reviewed problems of muscle terminology in reptiles. Howell (1936) presented a comprehensive study on the shoulder of reptiles. Much of the description contained in the paper pertains to the shoulder of Iguana (Iguanidae). Bahl (1937) published a comprehensive paper on the skull of Varanus (Varanidae). This is one of the most detailed accounts of lizard osteology in the literature.

Brock (1938) presented a discussion of the cranial muscles of geckos and El Toubi analyzed the osteology of Scincus scincus (Scincidae). The final paper of the decade was Evans' (1939) discussion of the evolution of the atlas-axis complex. This paper not only discussed fossil reptiles but also provided an account of the atlas-axis complex as it exists in Sphenodon (Rhynchocephalia) and Iguana (Iguanidae). In a later paper (1941a) he analyzed the skull of the chamaeleon Lophosaurus ventralis, and in a second paper (1941b) the skull of Acontias (Scincidae) and the affinities between snakes and lizards. During the same year Grimore (1941) published accounts of fossil lizards of the iguanid genus Acipre on from the Oligocene formations of Wyoming. In this paper he indicated the affinities of Acipre on to the more recent genus Cro taphyatus (Iguanidae). Malam (1941) provided a description of the cranial anatomy of Gerrhosaurus (Cordylidae).

Angel's (1942) synopsis of Madagascar lizards was published and the skeletal characteristics of Chalarodon and Ophiurus (Iguanidae) were reviewed. Hoffstetter (1942) reviewed the remains of fossil iguanids from the Eocene and Oligocene of Europe. Iyer, during the same year described the skeleton of Calotes versicolor (Agamidae). Mittleman (1942) presented a taxonomic summary of the genus Urosaurus (Iguanidae). He also discussed the general evolution of North American members of the family Iguanidae, and on the basis of osteology broke the family into lines of evolution, presenting a phylogenetic tree, in which he placed Ctenosaurus as a primitive ancestral type from which two main lines of evolution were formed. One line contained the sceloporous lizards and Parony soma while the other contained the crotaphytine lizards including Diplosaurus and Sauromalus. Mittleman also indicated that Diplosaurus, Sauromalus and Ctenosaurus are all very closely related.

The genus Uromastix (Agamidae) has been a popular subject of investigation among Old World workers. In 1942 the bony palate of this agamid was described and figured by Saksera. During the same year Young published on the cranial morphology of Xantusia (Xantusidae). DuBois (1943) analysed the skull of Cnemidophorus (Teiidae) and Iyer (1943) followed his earlier work with a detailed description of the skull of Calotes versicolor (Agamidae).

Kestevens' major paper on the evolution of the skull and cephalic muscles appeared in 1944. The musculature was described for Physignathus, Amphi bolurus (Agamidae), Anolis, Basiliscus (Iguanidae), Chameleo on (Chamaeleonidae), Tiliqua (Scincidae), Varanus (Varanidae), and Sphenodon (Rhynchocephalia). In the same year Zangerl examined the skull of the Amphibiaenidae. In this paper are figured skulls of Amphisbaena, Bipes, Geocalamus, Monapet sis, Leposternon, and Trogonophis, Prolacerta (Eosuchia) and the Protosaurian reptiles were discussed by Camp (1945) who indicated that the Lower Triassic Pro lacerta is intermediate between Youngina (Eosuchia) and modern lizards. In the same year Zangerl completed his analysis of the Amphibiaenidae with a discussion of the postcranial skeleton.

Pletzen (1946) examined the cranial morphology
of *Cordylyus* (Cordylidae) and discussed the cranial kinesis of that lizard. The genus *Xenosaurus* (*Xenosauridae*) was the topic of study for Barrows and Smith (1947). The authors described the osteology in detail and concluded that this lizard has affinities with the family Anguidae but should be retained in its own family. El Toubi (1947) published two papers; one describes the osteology of *Agama stellio* (Agamidae), and the other discusses the cranial osteology of *Uromastix aerugina* (Agamidae).

Broom (1948) described and figured the skull of *Phrynosoma cornutum* (Iguanidae). George (1948) examined the musculature of *Uromastix hardwickei* (Agamidae). The latter paper is accompanied by excellent figures dealing with limb musculature. El Toubi (1949) completed his investigation of *Uromastix aerugina* (Agamidae) and published an account of the postcranial osteology. Mahendra (1949) described in detail the skull of the gecko *Hemidactylus flaviviridis*.

Several papers were published in 1950 dealing with lizard anatomy. Bellairs presented the cranial anatomy of *Anniella* (Anniellidae); Detrie analyzed the skull of *Phrynosoma mcallii* (Iguanidae); Hames discussed the flexor muscles in the forearm and hand of lizards and mammals; Stokely surveyed the occurrence of the intermediate wrist bone in lizards; and Toerien also presented an account of the cranial morphology of *Anniella* (Anniellidae).

Only two papers dealing with lizard anatomy were published in 1951. Norris and Lowe discussed the osteology and myology of *Phrynosoma mcallii* (Iguanidae) and figured parts of the skull of several *Phrynosoma*. Webb presented the cranial anatomy of the geckos *Palmatogecko rangei* and *Oedura karrooica*.

El Toubi and Khalil (1952) summarized the structure of the cranium in Egyptian geckos. Barry (1953) added some observations to the cranial anatomy of *Agama* (Agamidae); and Brattstrom (1953) outlined the occurrence of Pleistocene lizards from California. Among the forms listed in Brattstrom's paper are skeletal remains of *Sceloporus*, *Crotaphythus* (*Iguanidae*), *Cuemidophorus* (Teiidae), and *Eumeces* (Scincidae).

George (1954) dealt with the cranial osteology of the agamid *Uromastix hardwickei* and figured the skull. McDowell and Bogert (1954) studied the skeletons of *Lanthanotus* (*Lanthanotidae*), and compared it with *Shinisaurus*, *Xenosaurus*, *Melanosaurus* (*Xenosauridae*), *Heloderma* (*Helodermatidae*), *Varanus* (Varanidae), *Aigialosaurus* (*Aigialosauridae*), *Tylosaurus* (*Mososauridae*), *Python* (*Boidae*), *Leptotyphlops* (*Leptotyphlopidae*), *Typlophos* (*Typlopidae*), *Pygopus*, *Delma*, *Liatis*, *Aprasia*, *Ophisops* (*Pygopodidae*), *Aristelliger* (*Gekkonidae*), *Colecouxy* (*Elephantaridae*), *Xantusia* (*Xantusiidae*), *Cordylus*, *Gerrhosaurus* (*Cordylidae*), *Peltoaurus*, *Diploglossus*, *Gerrhonotus*, *Anguis*, *Abronia*, *Celestus* (*Anguidae*), and *Anniella* (*Anniellidae*). The authors were able to present a phylogeny for the Anguimorphan lizards. This paper is well illustrated and is probably one of the best anatomical studies performed on lizards since Camp's paper in 1923. Poglayen-Newall discussed the jaw musculature of lizards in the same year.

Edinger (1955) discussed the parietal foramen in reptiles as to function and size and figured the skull roof of *Iguana* (*Iguanidae*). George (1955) completed an earlier work on *Uromastix hardwickei* (Agamidae). In his paper the postcranial osteology is discussed. Hoffstetter (1953) in the reptile volume of the French treatise on Paleontology reviewed general osteological features of the lizard skull and presented a summary of fossil lizard remains from Europe. Also Hotton (1955) surveyed the dentition and diets of North American Iguanidae. His analysis of teeth confirms the suspected close relationship between *Dipsosaurus*, *Saurophalus* and *Ctenosaurus*. Islam's description (1955) of the skull of *Vuomastix hardwickei* (Agamidae) is one of the most comprehensive yet presented for that genus.

The iguanid genus *Amblyrhynchus* was revised by Eibl-Eibesfeldt (1956). In this review the dorsal aspect of the skull of *A. c. cristatus* is figured. Islam completed his analysis of the skeleton of *Uromastix hardwickei* (Agamidae) in the same year. He described and figured aspects of the postcranial skeleton. Oelrich (1956) published his excellent, well illustrated account of the anatomy of the head of *Ctenosaura pectinata* (*Iguanidae*). In the same year Romer published his monumental work on the osteology of the reptiles. Besides giving a general account of the evolution of the reptile skeleton, Romer figured the skulls of *Varanus* (Varanidae), *Iguana* (*Iguanidae*), *Brookesia* (*Chamaeleonidae*), *Chaledos* (*Scincidae*), *Xantusia* (*Xantusiidae*), *Cordylus* (*Cordylidae*), *Amphisabaena* (*Amphisbaenidae*), and *Typhlops* (*Typhlopidae*).

Lundelius (1957) analyzed skeletal adaptations in *Sceloporus* (*Iguanidae*) and figured the skull. Brattstrom (1958) published two papers on fossil lizards. He recorded *Crotaphythus*, *Sceloporus*, *Saurophalus* (*Iguanidae*), and *Cuemidophorus* (Teiidae) from the Pleistocene sediments of California and in a second paper *Acrion* (*Iguanidae*) from the Oligocene formations of Wyoming. Savage (1958) investigated the genera *Urosaurus* and *Uta* (*Iguanidae*). After an anatomical analysis of iguanids Savage was able to separate the family into a sceloparine line and an iguanine line of evolution. The iguanine line is characterized by having an "S"-shaped nasal passage. Besides the eight iguanine genera outlined earlier, Savage included *Crotaphythus* in the iguanine line of evolution.

El Toubi and Kamal (1959) presented a well detailed and illustrated discussion of the skull of *Chalcides ocellatus* (*Scincidae*). The following year Haas (1960) presented a discussion of the trigeminus
muscles of Xenosaurus and Shinossauro (Xenosauridae). This paper is detailed and filled with exact illustrations. Hofer (1960) compared the skulls of Tupinambis (Teiidae) and Varanus (Varanidae). Jollie's discussion (1960) of the head skeleton of lizards is an excellent summary of evolution in that saurian. Besides detail, this paper contains illustrations of the skulls of Tupinambis (Teiidae), Anomphiboea (Amphibiaenidae), Anguis (Anguiniidae), and Uromastix (Agamidae). Lastly, Smith (1960) treated the theoretical development of chordate evolution of the lizard skeletons and musculature in detail.

Colbert (1961) published his book on the evolution of the vertebrates. In it he discussed the problem of lizard affinities with other reptiles and places them with the Diapsida. The paper by Sukhanov (1961) investigated the musculature of lizards and concluded it to be of two types: Scincio-Geckomorphous and Iguanomorphs. The author then presented a phylogeny of lizard families depending on their type of musculature.

Skeletal variations in Sator grandiceps (Iguanidae) were summarized by Etheridge (1962) while Kluge (1962) discussed the comparative osteology of Coleonyx (Eublepharidae). This latter paper is highly detailed and well illustrated. Another discussion of lizard anatomy was that of Robison and Tanner (1962) who outlined the anterior osteology and myology of Crotaphytus (Iguanidae). This paper is also well illustrated.

Estes (1963) reported on fossil lizards from the Miocene strata of Florida. Among those genera found were Leiocephalus (Iguanidae), Eumeces (Scinicipidae), Cnemidophorus (Teiidae) and unidentified Uromastix, Gekkonidae and Anguiniidae. Also during 1963, Harris' paper on the anatomy of Agama agama (Agamidae) was published. This is a well illustrated account in the form of a laboratory guide. Osteology and myology of the anterior body regions are well covered. Ostrum (1963) presented a short discussion on the lack of herbivorous lizards in the modern fauna. He indicated that this is probably because of the difficulties in eating caused by the streptostylar and kinetic nature of the skull.

Avery and Tanner (1964) described the anterior osteology and myology of Saurornathus obesus (Iguanidae). This paper has several illustrations of that region. Brattstrom (1964) identified fossil lizards from cave deposits in New Mexico. Estes (1964) in a major publication described the fossil vertebrates from the Late Cretaceous Lance Formation of Wyoming. We note that no Iguanidae were recorded and that some of Gilmore's (1928) Cretaceous iguanids were transferred to other families. Estes and Tihen (1964) recorded Miocene-Pliocene vertebrates from Nebraska and listed among their finds Phrynosoma (Iguanidae), Cnemidophorus (Teiidae), Eumeces (Scinicipidae), and Gerrhonotus (Anguiniidae). Etheridge (1964) discussed the fossil record of Late Pleistocene lizards from the West Indies. Thecadactylus (Gekkonidae), Leiocephalus, Anolis (Iguanidae), Aneiva (Teiidae), and a braincase from an iguanine type lizard are listed among the remains. Etheridge (1964) also examined the skeletal morphology of the sceloparine lizards and presented a phylogenetic tree for the sceloparines. He removed Crotaphytus from the iguanine line of Savage (1958) and allied it to the sceloparines and Phrynosoma. He also indicated from osteological data, that the iguanine line of evolution is a natural grouping. Eyal-Giladi (1964) described the development of the chondrocranium of Agama stellio (Agamidae). Hollman (1964) described some Pleistocene amphibians and reptiles from Texas. The fauna does not differ appreciably from the modern fauna. Tilak (1964) reported on the osteology of Uromastix hardwickii (Agamidae).

Blanc (1965) described the skeleton of the Madagascar iguanid, Chalarodon. Etheridge (1965) examined some fossil lizards from the Dominican Republic and listed among the remains Aristelliger (Gekkonidae), Anolis, Leiocephalus (Iguanidae), Aneiva (Teiidae), and Diploglossus (Anguiniidae). Duellman (1965) utilizing external morphology suggests a close relationship between Enyathedaurus and Ctenosaura (Iguanidae). Gelback (1965) presented a most useful paper summarizing the Ploucine and Pleistocene amphibians and reptiles from North America. The paper also has an excellent bibliography. Ray (1965) analyzed the number of marginal teeth in Ctenosaura and Anolis. Weiner and Smith (1965) examined the osteology of the crotaphytiform lizards and illustrated the skulls of that group of iguanids.

Etheridge (1966) dealt with the systematics of Leiocephalus as based on the osteology of that iguanid genus. Lateral views of the mandibles are figured. Romer (1966) published his third edition of "Vertebrate Paleontology" which contains a summary of the evolution of lizards as well as illustrations of the skulls of Youngina, Prolacerta (Eosuchia), Sphenodon (Rhynchochelophila), and Polyglyphanodon (Iguanidae).

The morphological literature of 1967 includes a paper by Duda comparing the cranial osteology of Agama tuberculata (Agamidae) with the skulls of other agamids; and a discussion by Etheridge of the caudal vertebrae of lizards.

Criley (1968) described the cranial osteology of the Gerrhonotiform lizards and Gasc (1968) analyzed the osteology and morphology of Dibamus noraequinace (Dibamidae). Jordan (1968) discussed the muscles of the external ear in lizards in one paper, and cranial kinesis in the skulls of lizards in a second paper. The osteology and myology of Phrynosoma platyrhinos and P. hernandesii (Iguanidae) was treated by Jenkins and Tanner (1968) in a well illustrated paper. Montanucci (1968) compared the dentition of
the iguanid lizards *Iguana, Ctenosaura, Enyaliosaurius* and *Basiliscus* and Ssecy (1968) described the myology of *Sceloporus clarki* (Iguanidae). Romer (1968) presented a summary of lizard relationships to other reptiles and analyzed the fossil lizards of the Mesozoic.

Presch (1969) analyzed the evolution of species in the genus *Phrynosoma* (Iguanidae) by utilizing osteology.

Fisher and Tanner (1970) compared the head and thorax morphology of the Teiids (*Chelidophorius* and *Ameiva*), and Nash and Tanner (1970) compared the head and thorax anatomy of Skiltons and Gilberts skinks, genus *Eumecces* (Scincidae).

In summary the literature dealing with anterior osteology and myology of lizards is scattered and varied. Descriptions of skulls representing almost all families can be found. With the exception of such papers as Camp (1923), McDowell and Bogert (1954), Savage (1958), Etheridge (1964), and Presch (1969), little has been done, utilizing osteology, to analyze the evolutionary lines within families. The myology of lizards is even less well known with no attempt having been made to analyze the musculature of a particular family or evolutionary line within a family.

The fossil record of lizards is very incomplete, as indicated by the above summary, but the fossil record does indicate that lizards have been in existence since Triassic time and in North America since Cretaceous time. Little has been done to trace the degree of change between fossil osteology and recent genera.

Besides dealing with the osteology and myology of the head region, this paper utilizes the anatomy of the sternum. Some of the earliest discussions of the sternum are those of Howes (1891) and Parker (1891), who described the sternum of fossil reptiles. Sabatier (1897) examined reptile sterna and clavicles, and commented on their origin. One of the most complete, early attempts at discussing the osteology of the sternum, was that of Hanson (1919) who described the sterna of *Cucimodahorius* (Teiidae), *Anguis* (Anguiniidae), *Stellio* (Agamidae), *Varanus* (Varanidae), *Chirotes* (Amphisbaenidae), *Chamaeleo* (Chamaeleonidae), *Draco*, *Calotes* (Agamidae), and *Iguana* (Iguanidae).

Camp (1923) described the sterna of lizards in detail. He presented a summary of all elements as found in the recognized families and figured the sterna of *Gerrhosaurus* (Cordylidae), *Xenosaurus* (Xenosauridae), *Bachia* (Teiidae), and *Xantusia* (Xantusiidae). Gladstone and Wakeley (1932) presented a survey of the morphology of the sternum and its relationship to the ribs. Reese (1923) figured the sterna of *Tubinambis* (Teiidae). El Toubi (1947) included a description of the sterna in his account of the osteology of *Agama stellio* (Agamidae). The same author published a photograph of the sterna of *Uromastix aegyptia* (Agamidae) in 1949.

Islam (1956) figured the sterna of *Uromastix*, and Romer (1956) in his "Osteology of the Reptiles" discusses the evolution of the sterna and figures that of *Lacerta* (Lacertidae), and *Bachia* (Teiidae). Savage (1958) utilized the sterna in his discussion of *Uta* and *Urosaurus* (Iguanidae). He figured the sterna of both genera.

Potter (1961) described and figured the sterna of *Phrynosoma* (Iguanidae) as did Kluge (1962) for *Coleonyx* (Eublepharidae). Etheridge (1964) examined and figured the sterna of *Phrynosoma, Uma, Callosaurus, Holbrookia, Pseuderosaurus, Uta, Urosaurus and Sator* in his analysis of the evolution of the sceloprine line of iguanids and in 1965 discussed the abdominal skeletons of lizards and figured sterna and ribs of *Stenocercus, Amblyrhynchus, Anolis* and *Chalarodon* (Iguanidae). In the latter paper Etheridge notes four patterns of attachment of ribs to sterna, which is of value in separating the various groups of iguanid lizards. Weiner and Smith (1965), in their discussion of the crotophytiform lizards, figured the sterna of two species of *Crotophytus*. The sternal structure of *Leiocephalus* (Iguanidae) was also discussed by Etheridge (1966). The sterna and ribs of *Phrynosoma* (Iguanidae) are redescribed by Jenkins and Tanner (1968) and Presch (1969) presented and figured the sterna of *Petrosaurus, Uma* and *Phrynosoma* (Iguanidae).

The tongue and associated hyoid elements of lizards have received more attention than has the sternum. The earliest papers on the lizard hyoid or tongue are those of Lasama (1834) and Minot (1880). Each author presented a general discussion of hyoid elements in reptiles. Cope (1892), in his "Osteology of the Reptiles" discussed the hyoid bones and figured those of *Sphenodon* (Rhynchocephalia), *Chamaeleon* (Chamaeleonidae), *Gekko*, *Arbilestier*, *Phylodactylus*, *Thecadactylus* (Gekkonidae), *Eublepharis* (Eublepharidae), *Calotes*, *Phrynosoma*, *Uromastix* (Agamidae), *Holbrookia*, *Phrynosoma*, *Sceloporus*, *Uta*, *Saurornnax*, *Crotophytus*, *Anolis*, *Ctenosaura*, *Iguana* (Iguanidae), *Anguis*, *Dracaena*, *Gerrhonotus*, *Opisaurus* (Anguinidae), *Heloderna* (Helodermatidae), *Xenosaurus* (Xenosauridae), *Varanus* (Varanidae), *Scincus*, *Eumecces*, *Egerina*, *Litoplepisma*, *Gongyhus* (Scincidae), *Celestes* (Anguiniidae), *Gerrhosaurus*, *Zonurus* (Cordylidae), *Mancus* (Lacertidae), *Tubinambis*, *Cucimodahorius* (Teiidae), *Annella* (Anniellidae), *Chirotes*, *Amphisbaena* and *Rhineura* (Amphisbaenidae). Comig (1895) discussed the tongue musculature of reptiles and Chaine (1902) analyzed the musculature in the region of the hyoids. Although his paper is very general, he does describe some of the muscles of *Chamaeleon* (Chamaeleonidae). Beddard (1905) figured and described the hyoid bones of *Chlamydosaurus kingi* and *Physignathus* (Agamidae). Gandolfi (1908) described the tongue of agamids and iguanids. The musculature of the tongue
of Agama, Amphibolurus, Calotes, Liolaemus (Agamidae), Iguana and Cyclura (Iguanidae) are described. Camp (1923) also dealt with hyoids and tongues in his tome on lizard classification. The tongues were described in general and the hyoids of Coleonemys (Eublepharidae), Uropeltis (Gekkonidae), Brachylophus (Iguanidae), Calotes (Agamidae), Phrynosoma (Iguanidae), Gerrhonotus (Anguiniidae), Gerrhosaurus, Chamaegecko, Zonurus (Cordylidae), and Xenosaurus (Xenosauridae) were figured. Reese (1923) described and figured the tongue of Tupinambis (Teiidae) and Schwartzoff (1929) described the tongues of reptiles in general and proposed a phylogeny based on them. The tongue of Lacerta (Lacertidae), Ascalabotes (Gekkonidae), Ophidopsis, Anguis (Anguiniidae), Ablepharus (Scincidae), Varaunus (Varanidae), Ameiva (Teiidae), Calotes (Agamidae), and Chamaeleo (Chamaeleonidae) were discussed and illustrated by Grumman (1937), as was the hyoid of Agama stellio (Agamidae) by El Toubi (1947). The tongue of the anguimorphs Gerrhonotus (Anguiniidae), Shinisaurus (Xenosauridae), Varanus (Varanidae), Heloderma (Helodermatidae) and Lanthanotus (Lanthanotidae) were analyzed by McDowell and Bogert (1954). Oelrich (1956) described the hyoid of Ctenosaura (Iguanidae). Romer (1956) has also treated the hyoids of lizards and illustrated those of Heloderma (Helodermatidae) and Basiliscus (Iguanidae). The hyoids of Indian reptiles were described by Sondhi (1958) who figured the hyoid and tongue of Varaunus (Varanidae). Jollié (1960) described the hyoid of many genera of lizards and figured that of Amphibiae (Amphibiae). Goin and Goin (1962) figured the tongues of Mahaya (Scincidae), Varanus (Varanidae), Tachydromus (Lacertidae), Ophidopsis (Anguiniidae), Calotes (Agamidae), Gekko (Gekkonidae), Nesia (Scincidae) and Dibamus (Dibamidae). Kluge (1962) described the hyoid of Coleonemys (Eublepharidae) and Tilak (1964) presented the hyoid of Uromastix (Agamidae). Presch (1969) illustrated the hyoids of Phrynosoma coronatum and Sceloporus magister (Iguanidae).

The hemipenes have been considered by a few workers as being of evolutionary importance. One of the earliest comprehensive discussions is that of Cope (1896), who described the hemipenes of several genera of lizards and was able to create a key to separate some genera of Iguanidae by their hemipenes. Camp (1923) also utilized the hemipenes in his classification system. He also summarized Cope's work. Ortenburger (1923) suggested a method for preparing reptilian hemipenes for study. McCann (1946) also treated the subject of hemipenes in reptiles. The hemipenes of Uromastix hardwickii was examined by Charles (1953) and Majupuria (1957). Dowling and Savage (1960) discussed in detail the hemipenis of snakes. Their paper is a classic and is a primary source of information on structure and vocabulary concerning reptile hemipenes. The latest work on hemipenes is that of Rosenberg (1967) who described those structures in the Amphibiae.

Several other approaches have been used in studying the problem of saurian phylogeny. One structure that has been examined is the ear of lizards. Smith (1958) studied evolutionary changes in the middle ear of some agamids and iguanids. Baird (1960) surveyed the periotic labyrinth of reptiles. Hamilton (1964) examined the gross structure of the inner ear of lizards and was able to divide lizards into four groups on the basis of their ear structures. Schmidt (1964) examined the phylogenetic significance of the lizard cochlea and from his study was able to make some phylogenetic groupings between families.

Histological evidence is also useful in interpreting iguanid phylogeny. Hebard and Charipper (1955) studied the adrenal glands of several genera of lizards. The authors' work shows the natural grouping of lizards at family level and confirms the phylogenetic conclusions of Camp (1923) based on osteology and myology. The thyroid glands of iguanids and agamid were compared by Lynn, O'Brien and Herhenreader (1966). They concluded that both families are closely related.

In a study of pinworms in lizards, Gambino (1957) and Gambino and Heyneman (1960) found that the most primitive pinworms are specific to Dipsosaurus, Sauronatus, Ctenosaura, and Enyaliusaurous.

A further approach to saurian phylogeny has been through karyotype study. Several papers have described the karyotype of different genera of lizards but the paper by Gorman, Atkins and Holzinger (1967) is most useful in phylogenetic interpretations. Fifteen genera were examined, including Ctenosaura, Cyclura, Iguana and Sauronatus of the iguanine line. They found that the karyotype evolution in iguanids has been quite conservative and there appears to be very little difference in the chromosomes of the genera from Madagascar, Brazil, the Antilles and North America.

The results of such methods of study as histology, parasitology and cytology are suggestive but not sufficiently specific to be definitive. The complete solution to the problems of iguanid phylogeny must come therefore from studies of gross anatomy and particularly from osteology and myology.

The problems of iguanine distribution have been discussed by Beaufort (1951), Darlington (1957) and Carlquist (1965). All these considered the Pacific iguanids as waif populations resulting from rafting but were at a loss to explain the presence of iguanids.
MATERIAL AND METHODS

The descriptions of the osteology of the ten genera investigated are based on four or more skulls and jaws and two or more sterna and hyoids from each group. In all cases skeletons were cleaned by soaking in 50% ammonium hydroxide after defleshing, and then boiled for one to three hours in water and cleaned by hand. Final cleaning of sutures and bleaching was accomplished by immersion in Chlorox bleach for a few minutes. Many of the museum specimens were obtained as skeletons and required no cleaning.

One or two specimens of each genus were used for myological studies. All are preserved in 10% formalin or 70% alcohol. Tongues, hyoids, and hemipenes were removed from specimens destined to be skeletonized or from individuals on whom the myological studies had been completed. All three structures were preserved and stored in 70% alcohol.

All specimens are accessioned in one or another of the natural history collections of the following institutions: American Museum of Natural History (AMNH), Brigham Young University (BYU), University of Kansas (KU), Museum of Comparative Zoology, Harvard University (MCZ), Southern Connecticut State College (SCSC), and U. S. National Museum (USNM). Below is a summary list of materials utilized for this study.

Osteology

**Amblyrhynchus cristatus** Bell
- AMNH 24978, Galapagos Islands
- AMNH 75943, Galapagos Islands
- AMNH 76197, Galapagos Islands
- BYU 22810, Galapagos Islands
- MCZ 2006, Charles Island, Galapagos Islands

**Brachylophus fasciatus** Cuvier
- BYU 23743, Nukuafou, Tonga Island
- MCZ 5222, Fiji Islands
- MCZ 15008, Vunisea, Kadavu Island, Fiji Islands
- MCZ 15009, Vunisea, Kadavu Island, Fiji Islands

**Chalarodon madagascariensis** Peter
- MCZ 11508, Tulear, S. W. Madagascar
- MCZ 11522, Tulear, S. W. Madagascar
- MCZ 11531, Tulear, S. W. Madagascar
- MCZ 11532, Tulear, S. W. Madagascar

**Conolophus subcristatus** (Gray)
- AMNH 50797, Galapagos Islands
- AMNH 50798, Galapagos Islands
- AMNH 71304, Galapagos Islands
- MCZ 2027, Albrmarle Island, Galapagos Islands

**Conolophus pallidus** Heller
- MCZ 27772, Galapagos Islands

**Ctenosaura hemileopa** (Cope)
- BYU 30272, St. Eustatius, Saint Vincent and the Grenadines

**Ctenosaura pectinata** (Wiegman)
- BYU 22796, San Blas, Nayarit, Mexico
- MCZ 11350, Colima, Mexico
- MCZ 2176, Acapulco, Mexico
- MCZ 24904, Tepeh, Mexico

**Cyclura carinata** Harlan
- MCZ 59255, Sand Cay, Turks Island

**Cyclura cornuta** (Bonaparte)
- AMNH 57878, No data, probably Haiti
- AMNH 57968, No data, probably Haiti

**Cyclura macleayi** Gray
- MCZ 6915, Santiago, Cuba

**Enyalioides clarkei** (Baird and Girard)
- BYU 22806, Galapagos Islands

**Enyalioides palaeus** (Stejneger)
- BYU 23743, Nukuafou, Tonga Island
- BYU 21452, No data

**Dipsosaurus dorsalis** Baird and Girard
- BYU 21726, Palm Springs, California
- BYU 23761, Palm Springs, California

**Iguana iguana** Wiegman
- BYU 22795, El Zacatal, Campeche, Mexico
- BYU 22852, San Blas, Nayarit, Mexico
- MCZ 54989, Gorge of Tortugero, Costa Rica

**Iguana delicatissima** Laurenti
- BYU 38228, St. Eustatius

**Oplurus schei** (Dumeril and Bibron)
- BYU 3336, No data
- BYU 37188, Majunga, Madagascar
- BYU 37191, Majunga, Madagascar
- BYU 37192, Majunga, Madagascar

**Sauromalus obesus** (Baird)
- BYU 21734, Glen Canyon, Utah
- BYU 23762, St. George, Utah
- MCZ 23335, 35 miles West Sonora, Sonora, Mexico
- MCZ 8894, Buckskin Mountains, Arizona

**Sauromalus insignis** Stejneger
- MCZ 79777, Angel de La Guarda Island, Gulf of California

**Sauromalus shawi** Clift
- MCZ 85533, Isla San Marcos, Gulf of California

**Sauromalus varius** Dickerson
- MCZ 23331, No data
- BYU 30269, St. Eustatius Island, Gulf of California
- BYU 30270, St. Eustatius Island, Gulf of California
- BYU 30271, St. Eustatius Island, Gulf of California

Myology

**Amblyrhynchus cristatus** Bell
- BYU 22806, Galapagos Islands
- BYU 22810, Galapagos Islands

**Brachylophus fasciatus** Cuvier
- BYU 23743, Nukuafou, Tonga Island
- BYU 31955, Nukuafou, Tonga Island

(1970). These authors have reviewed the history of the drift theory and presented new evidence consisting of comparative radiometric ages, sea-floor spreading, and paleomagnetism. The fossil remains from Antarctica, Africa, and South America have also been cited.
An examination of the osseous elements of the iguanine lizards and the Madagascar iguanid reveals the following structures.

**Skull and Jaws**

The superficial elements of the skull of the iguanines and the Madagascar iguanids have been examined in detail. The analysis of the skull bones and jaws was made from two approaches. One approach was to examine the size of the bones by measuring length and width of each bone and then computing a percentage between length and width, which was then compared with similar data for identical bones in other genera. Tables presenting the means and the ranges of these values for each genus are presented throughout this chapter. All measurements are in millimeters.

A second approach to the study of the skull was made through observations and comparisons of the shape of the bones and their relationship to other bones. A summary of these observations and comparisons is presented in the text of this chapter. All observations and measurements are based on four to six individuals from each genus.

The skull of the iguanine lizard is streptostyly with a freely movable quadrate bone which articulates dorsally with the paroccipital process and ventrally with the quadrate process of the pterygoid. Such movement can be demonstrated in fresh and preserved specimens of all the genera examined. In general it may be said that the iguanine skull forms a compact and light, yet very strong cage for the brain and sense organs of the head.

The general shape of the skull is either elongated and flattened dorsoventrally or shortened and flattened laterally. Measurements of the length of the skull were taken from the tip of the premaxillary bone to the most posterior extension of the occipital condyle. Width of the skull was taken at the widest extension between the suborbital bars in the area of the orbit. Height measurements were taken at the posterior end of the maxillary bone and extending to the skull roof directly above that point. A summary of the ranges and means of these measurements is presented in Tables 1 and 2.

A survey of the means presented in those tables indicates that *Amblyrhynchus* (length-width, .789, length-height, .460) has the shortest and widest skull, whereas the longest and lowest skull is found among the continental genera *Sauromalus*, *Ctenosaura*, and *Cyclura*. Table 2 indicates that *Sauromalus* (.286) has the flattest skull of the iguanines, followed closely by *Ctenosaura* (.316) and *Cyclura* (.326) which also have a low skull roof.

### Table 1

**SKELETAL LENGTH AND WIDTH**

<table>
<thead>
<tr>
<th>Genus</th>
<th>Length</th>
<th>Width</th>
<th>Width-Length Ratio</th>
</tr>
</thead>
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<tr>
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<td>Min</td>
<td>Mean</td>
<td>Min. Mean.</td>
</tr>
<tr>
<td>Amblorhynchus</td>
<td>41.4</td>
<td>47.7</td>
<td>30.3</td>
</tr>
<tr>
<td>Brachylophus</td>
<td>27.3</td>
<td>30.7</td>
<td>18.6</td>
</tr>
<tr>
<td>Chalarodon</td>
<td>12.5</td>
<td>13.1</td>
<td>8.8</td>
</tr>
<tr>
<td>Cyclura</td>
<td>45.7</td>
<td>53.3</td>
<td>24.3</td>
</tr>
<tr>
<td>Dipsosaurus</td>
<td>22.2</td>
<td>22.3</td>
<td>12.8</td>
</tr>
<tr>
<td>Iguana</td>
<td>49.3</td>
<td>60.0</td>
<td>16.1</td>
</tr>
<tr>
<td>Ophiurus</td>
<td>18.2</td>
<td>21.1</td>
<td>11.2</td>
</tr>
<tr>
<td>Sauromalus</td>
<td>23.4</td>
<td>34.4</td>
<td>14.3</td>
</tr>
</tbody>
</table>

### Table 2

**SKELETAL LENGTH AND HEIGHT**

<table>
<thead>
<tr>
<th>Genus</th>
<th>Length</th>
<th>Height</th>
<th>Height-Length Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Min</td>
<td>Mean</td>
<td>Min. Mean.</td>
</tr>
<tr>
<td>Amblyrhynchus</td>
<td>41.4</td>
<td>47.7</td>
<td>30.3</td>
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<tr>
<td>Brachylophus</td>
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<td>Dipsosaurus</td>
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<tr>
<td>Ophiurus</td>
<td>18.2</td>
<td>21.1</td>
<td>11.2</td>
</tr>
<tr>
<td>Sauromalus</td>
<td>23.4</td>
<td>34.4</td>
<td>14.3</td>
</tr>
</tbody>
</table>

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*BYU 22801, Tulea, Madagascar*  
*BYU 22803, Tulea, Madagascar*  
*Conolophus subterratus (Gray)*  
*BYU 22811, Galapagos Islands*  
*Ctenosaura pectinata (Wiegmans)*  
*BYU 22796, San Blas, Nayarit, Mexico*  
*Cyclura mcalli Barbour and Noble*  
*BYU 22799, North Cay, Bahama Islands*  
*Dipsosaurus dorsalis Baird and Girard*  
*BYU 21726, Palm Springs, California*  
*BYU 22855, Palm Springs, California*  
*BYU 23760, Palm Springs, California*  
*BYU 23761, Palm Springs, California*  
*BYU 31954, Mesquite, Nevada*  
*Enyalioides clarkei (Bailey)*  
*KU 62447, Mexico*  
*Iguana iguana Wiegmans*  
*BYU 22795, El Zacatal, Campeche, Mexico*  
*BYU 22851, San Blas, Nayarit, Mexico*  
*BYU 22853, San Blas, Nayarit, Mexico*  
*Opisthoteuthis (Dumeril and Bibron)*  
*BYU 11504, Andrambolovato, Madagascar*  
*Saurorhynchus obscurus (Baird)*  
*BYU 21724, Glen Canyon, Utah*  
*BYU 23762, St. George, Utah*  
*BYU 31953, St. George, Utah*
For the sake of convenience the skull has been divided into a posterior occipital segment and an anterior maxillary segment.

The occipital segment forms a median axis for the attachment of the neck and articulation of the remainder of the skull. It consists of two parts, (a) the braincase (basisphenoid, basioccipital, prootic, exoccipital, supraoccipital, and the associated semicircular canals), and (b) the foramen magnum (enclosed by the basioccipital, exoccipital and supraoccipital). A tripartate occipital condyle is located on the posterior end of the basioccipital and the lateral exoccipital in all genera of iguanine lizards.

Basisphenoid

Basisphenoid (Figures 1 and 2) forms a portion of the floor of the braincase, is bordered posteriorly by the basioccipital, and is attached dorsally to the prootic bone. Anteriorly the bone is expanded into two anterolateral basipterygoid processes which articulate laterally, with the pterygoid bones. Anteromedially the basisphenoid is extended forward as the parasphenoid process. The basisphenoid forms points of origin for the inferior part of the protractor pterygoideus muscle.

Measurements of the length of the basisphenoid were made from the suture between basisphenoid and basioccipital, to the beginning of the parasphenoid process. A low ratio indicates that the bone is much longer than wide, whereas the higher ratios indicate bones that have lengths and widths almost equal.

Observations of the bone's position in the skull indicates some variability in the articulation between basipterygoid process and the pterygoid bone. This articulation occurs medial and posterior to an expansion of the pterygoid bone just posterior to the pterygoid's midpoint. This point of articulation is almost completely obscured ventrally by the pterygoid bone in *Amblyrhynchus*, *Chalarodon*, and *Ophius*. In *Dipsaurus* the articulation is visible ventrally but occurs dorsal to the ventral border of the pterygoid. In *Brachylophus*, *Conolophus*, *Ctenosaura*, *Cyclura*, *Iguana* and *Saurophalus* the anterior articulating portion of the basipterygoid process is partially obscured and two thirds of the articulation occurs on the ventromedial border of the pterygoid bones, rather than on the medial face.

Basioccipital

Basioccipital (Figures 1 & 2) forms part of the occipital condyle and the posterior floor of the braincase. It is the main point of attachment for ventral axial musculature. Anteriorly the basioccipital joins the basisphenoid and dorsolaterally it attaches to the exoccipitals and the prootic bones. The third bundle of the longissimus dorsi muscle attaches here.

Length and width measurements were made of the basioccipital with the length being taken from the suture between the basisphenoid and basioccipital to the posterior tip of the occipital condyle. The width of the bone was considered as the distance between the tips of the lateral extensions of the sphenoccipital tuberces. An examination of the ratio means in Table 4 indicates that the highest ratios for the basioccipital are possessed by *Brachylophus* (.709), *Ctenosaura* (.654), *Amblyrhynchus* (.653), and *Saurophalus* (.649) while *Dipsaurus* (.369) and *Conolophus* (.477) possess the lowest ratios. High ratios denote that lengths and widths are nearly equal for the bone.
on the prootic bone. Because of difficulties in measuring, the prootic was not studied in detail.

Exoccipital

Exoccipitals bones form the posterolateral wall of the braincase and the lateral parts of the occipital condyle. Mediolateral articulations form with the parietal, supratemporal and quadrate bones. The exoccipital also articulates at its most lateral projection with the prootic bone. The longissimus dorsi and episternocleidomastoideus muscles insert on the paraoccipital process of the bone.

The length of the exoccipital bone was measured from the lateral wall of the foramen magnum to the point of articulation by the paraoccipital process with the squamosal and quadrate bones. Width is represented as the distance between the exoccipital articulation with the supraoccipital bone and the union with the basisphenoid at the occipital condyle. As Table 5 indicates, the lowest ratio means for exoccipitals are possessed by *Dipsosaurus* (.594) and *Conolophus* (.626). The largest ratios are found in *Brachylophus* (.858), *Amblyrhynchus* (.830), and *Chalarodon* (.813). As with the other bones, near equal relationships between length and width are expressed as high ratios.

<table>
<thead>
<tr>
<th><strong>TABLE 5</strong> EXOCCIPITAL BONES</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Genus</strong></td>
</tr>
<tr>
<td><strong>Min.</strong></td>
</tr>
<tr>
<td><em>Amblyrhynchus</em></td>
</tr>
<tr>
<td><em>Brachylophus</em></td>
</tr>
<tr>
<td><em>Chalarodon</em></td>
</tr>
<tr>
<td><em>Conolophus</em></td>
</tr>
<tr>
<td><em>Corythosaurus</em></td>
</tr>
<tr>
<td><em>Cyclura</em></td>
</tr>
<tr>
<td><em>Dipsosaurus</em></td>
</tr>
<tr>
<td><em>Iguana</em></td>
</tr>
<tr>
<td><em>Ophius</em></td>
</tr>
<tr>
<td><em>Saurornthus</em></td>
</tr>
</tbody>
</table>

Orbitosphenoid

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 muscles at the eye. The orbitosphenoid also has connections with the prootic bone and the alar process of the basisphenoid. It was found to be absent in most of the cleaned skulls in the collections examined.

The 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, supra-temporal, postorbital, squamosal, quadrate and epipterygoid). These bones are discussed as listed above.

Pterygoid

Pterygoid (Figures 1, 2, 3, 4, 5 and 6) extends posteriorly as the posterior part of the palate. The pterygoids are paired bones sutured at the anterior end of the palatines, anterolaterally to the ectopterygoids and posteromedially to the basisphenoids. They comprise a major area of motion between the occipital and maxillary regions as the postero- lateral portions articulate with the quadrates which is movable. Articulating with the pterygoid on the dorsal border of the quadrat e projection is the columnella. At the ventral border, the pterygoid forms the posterior limit of the oral cavity and contributes an area for the origin of the pterygomandibularis muscle. On the dorsal ridge, medial to the columnella 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 quadrato process of the pterygoid bone. The posterior fibers of the pterygomandibularis muscles arise along the ventrolateral border of the lateral side of the quadrato process.

Measurements taken of the pterygoid bone include length; represented as the distance between the anterior portion of the pterygoid where it sutures with the
palatine and the most posterior tip of the quadrate process; and the width as the distance between the articulation with the basipterygoid process of the basisphenoid bone and the suture with the ectopterygoid bone. Table 7 summarizes these measurements and a survey of the ratio means indicates that the lowest pterygoid ratio (long, narrow bones) are possessed by Cyclura (.283), Sauromalus (.293), and Iguana (.309). The highest ratios (short, wide bones) are found in Brachylophus (.458) and Chalarodon (.435). The unique relationships of the pterygoid to the basipterygoid process of the basisphenoid bone have already been reviewed. The shape of the medial border of the pterygoid also controls the shape of the pyriform recess (Figs. 1 and 2) of the palate. This shape varies from a gradually widening slit as seen in Brachylophus, Chalarodon and Ophius to a more severe and rapid change in width of the recess as seen in Amblyrhynchus, Conolophus, and Cyclura. The remaining genera are intermediate between the above conditions.

Table 7

<table>
<thead>
<tr>
<th>Genus</th>
<th>Length</th>
<th>Width</th>
<th>Width-Length Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amblyrhynchus</td>
<td>23.9-28.8</td>
<td>8.4-10.3</td>
<td>0.39-0.46</td>
</tr>
<tr>
<td>Brachylophus</td>
<td>14-15.4</td>
<td>6.6-7.0</td>
<td>0.40-0.53</td>
</tr>
<tr>
<td>Chalarodon</td>
<td>5.6-5.7</td>
<td>2.4-2.6</td>
<td>0.41-0.46</td>
</tr>
<tr>
<td>Conolophus</td>
<td>32.5-34.6</td>
<td>8.18-8.2</td>
<td>0.34-0.37</td>
</tr>
<tr>
<td>Ctenosaura</td>
<td>18.7-24.5</td>
<td>5.8-7.5</td>
<td>0.28-0.35</td>
</tr>
<tr>
<td>Cyclura</td>
<td>29.1-39</td>
<td>7.3-13.5</td>
<td>0.25-0.33</td>
</tr>
<tr>
<td>Diplosaurus</td>
<td>10.1-12.1</td>
<td>4.1-4.2</td>
<td>0.33-0.35</td>
</tr>
<tr>
<td>Iguana</td>
<td>26.5-31.5</td>
<td>7.0-9.6</td>
<td>0.26-0.34</td>
</tr>
<tr>
<td>Ophius</td>
<td>8.4-11</td>
<td>2.9-3.9</td>
<td>0.31-0.37</td>
</tr>
<tr>
<td>Sauromalus</td>
<td>13.0-19.8</td>
<td>3.9-5.8</td>
<td>0.25-0.34</td>
</tr>
</tbody>
</table>

Ectopterygoid

Ectopterygoid (Figs. 1, 2, 3, 4, 5 and 6) forms a brace between the palate and the external roofing bones. Laterally the ectopterygoid sutures with the jugal and the posterior process of the maxilla, and mesially with the pterygoid. Dorally it forms the posterolateral part of the floor of the orbit.

Table 8

<table>
<thead>
<tr>
<th>Genus</th>
<th>Length</th>
<th>Width</th>
<th>Width-Length Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amblyrhynchus</td>
<td>7.2-9.8</td>
<td>1.8-2.4</td>
<td>0.25-0.27</td>
</tr>
<tr>
<td>Brachylophus</td>
<td>3.0-4.0</td>
<td>1.0-1.5</td>
<td>0.33-0.37</td>
</tr>
<tr>
<td>Chalarodon</td>
<td>1.4-1.4</td>
<td>0.6-0.6</td>
<td>0.40-0.43</td>
</tr>
<tr>
<td>Conolophus</td>
<td>10.9-15.5</td>
<td>5.0-6.5</td>
<td>0.40-0.46</td>
</tr>
<tr>
<td>Ctenosaura</td>
<td>3.5-5.6</td>
<td>1.4-2.3</td>
<td>0.40-0.43</td>
</tr>
<tr>
<td>Cyclura</td>
<td>6.1-10.8</td>
<td>2.2-4.3</td>
<td>0.55-0.47</td>
</tr>
<tr>
<td>Diplosaurus</td>
<td>2.3-2.6</td>
<td>1.4-1.5</td>
<td>0.55-0.60</td>
</tr>
<tr>
<td>Iguana</td>
<td>6.1-7.9</td>
<td>3.0-3.5</td>
<td>0.45-0.49</td>
</tr>
<tr>
<td>Ophius</td>
<td>2.2-2.6</td>
<td>0.9-1.1</td>
<td>0.49-0.49</td>
</tr>
<tr>
<td>Sauromalus</td>
<td>2.4-5.4</td>
<td>1.0-2.0</td>
<td>0.32-0.39</td>
</tr>
</tbody>
</table>

Vomers

Vomers (Figs. 1 and 2) are paired bones forming the most anterior part of the palate, the medial borders of the fenestra vomeronasalis externus and the medial borders of the fenestra exochoanalis. Posteriorly the vomer is attached to the palatines and dorsally to the medial surface of the maxilla. Medially the vomers support the nasal septum and the cartilage of Jacobson's organ. At the extreme anterior end the vomer sutures with the premaxilla.

The length of the vomer was measured from the anterior suture with the premaxilla to the most posterior point of the suture with the palatine bone. Width of the vomer was the distance between the medial border of the vomer at the ventral midline and the most lateral border where it attached to the maxilla. Table 9 summarizes the measurements of vomer bones and the ratio means show that the shortest, widest, vomers (highest ratios) are possessed by Chalarodon (.711) and the narrowest longest vomers (lowest ratios) are possessed by Amblyrhynchus (.253), Cyclura (.274), and Ctenosaura (.278).

The vomers possess a small blunt projection that protrudes from the lateral border of the bone into the opening of the fenestra exochoanalis and fenestra vomeronasalis externa and separates the opening. The possession of this anterolateral projection is seen in all ten genera. Some genera have a secondary projection which extends into the lumen of the fenestra vomeronasalis externa. This projection can be seen in Brachylophus, Ctenosaura, Cyclura, Iguana, and in Sauromalus.

Table 9

<table>
<thead>
<tr>
<th>Genus</th>
<th>Length</th>
<th>Width</th>
<th>Width-Length Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amblyrhynchus</td>
<td>11.2-13.0</td>
<td>2.8-3.2</td>
<td>0.20-0.25</td>
</tr>
<tr>
<td>Brachylophus</td>
<td>6.5-7.0</td>
<td>2.4-2.5</td>
<td>0.31-0.35</td>
</tr>
<tr>
<td>Chalarodon</td>
<td>1.3-1.9</td>
<td>1.3-1.4</td>
<td>0.70-0.71</td>
</tr>
<tr>
<td>Conolophus</td>
<td>12.2-13.6</td>
<td>4.1-5.5</td>
<td>0.33-0.37</td>
</tr>
<tr>
<td>Ctenosaura</td>
<td>7.2-9.7</td>
<td>2.9-4.2</td>
<td>0.27-0.33</td>
</tr>
<tr>
<td>Cyclura</td>
<td>11.6-18.2</td>
<td>3.1-5.7</td>
<td>0.23-0.35</td>
</tr>
<tr>
<td>Diplosaurus</td>
<td>3.9-4.2</td>
<td>2.0-2.1</td>
<td>0.47-0.49</td>
</tr>
<tr>
<td>Iguana</td>
<td>13.5-17</td>
<td>4.0-5.5</td>
<td>0.36-0.35</td>
</tr>
<tr>
<td>Ophius</td>
<td>3.1-4.2</td>
<td>1.4-1.6</td>
<td>0.36-0.39</td>
</tr>
<tr>
<td>Sauromalus</td>
<td>5.7-7.8</td>
<td>1.4-2.6</td>
<td>0.24-0.30</td>
</tr>
</tbody>
</table>

Measurements made on the ectopterygoid include the length, taken as the distance between the suture with the pterygoid and the suture with the jugal and maxilla. The width was measured as the greatest diameter of the bone at its point of union with the jugal and maxilla. These measurements are summarized in Table 8 and an examination of the ratio means shows that the lowest ratio (long, narrow bones) is found in Amblyrhynchus (.275) and the form with the highest ratio (short, wide bones) is Diplosaurus (.600).
Palatine

Palatine (Figs. 1, 2, 3, and 4) bones form 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 dor-sally to the pterygoid, forms the medial rim of the inferior orbital fossa and the floor of the orbit; and the maxillary process attaches dor-sally to the pre-frontal and ventrally to the jugal and maxillary bones.

The length of the palatine was taken as the distance from the anterior suture with the vomer bone at the midline to the most posterior extension of the suture with the pterygoid bone. The width of the palatine bone was considered to be the distance from the palatine medial border at the skull’s midline to the lateral suture between the palatine and the maxilla. Table 10 summarizes these measurements for the ten genera under discussion. The ratio mean column indicates that the shortest and widest bones (highest ratios) are possessed by Chalarodon (.846) while the longest and narrowest bones (lowest ratios) are found in Cyclura (466).

Table 10

<table>
<thead>
<tr>
<th>Palatine Bones</th>
<th>Length</th>
<th>Width</th>
<th>Width-Length Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Min. Mean Max.</td>
<td>Min. Mean Max.</td>
<td>Min. Mean Max.</td>
</tr>
<tr>
<td>Amblyrhynchus</td>
<td>12.0-13.2-14.4</td>
<td>7.7-8.6-9.2</td>
<td>604.653-721</td>
</tr>
<tr>
<td>Brachylophus</td>
<td>8.0-8.2-8.4</td>
<td>4.5-4.9-5.4</td>
<td>560.601-658</td>
</tr>
<tr>
<td>Chalarodon</td>
<td>2.8-2.8-2.9</td>
<td>2.3-2.4-2.5</td>
<td>821.846-862</td>
</tr>
<tr>
<td>Ctenosaurus</td>
<td>8.5-10.0-15.1</td>
<td>5.0-6.0-8.2</td>
<td>543.365-588</td>
</tr>
<tr>
<td>Diporosaurus</td>
<td>5.6-6.4-7.9</td>
<td>3.7-4.1-4.6</td>
<td>562.644-617</td>
</tr>
<tr>
<td>Iguana</td>
<td>11.2-15.9-20.1</td>
<td>7.4-9.1-10.6</td>
<td>432.596-674</td>
</tr>
<tr>
<td>Oplurus</td>
<td>5.9-7.5-12.0</td>
<td>3.5-3.6-5.3</td>
<td>441.532-576</td>
</tr>
<tr>
<td>Sauromalus</td>
<td>5.8-9.7-12.9</td>
<td>3.6-5.3-7.0</td>
<td>542.557-620</td>
</tr>
</tbody>
</table>

Premaxillae

Premaxillae (Figs. 1, 2, 3, 4, 5, and 6) is the most anterior bone of the skull, and joins the maxilla laterally and the nasal bones dorsally. It forms the rostrum of the skull.

The length of the maxilla was considered to be the distance from the anterodorsal tip of the bone to its dorsal union with the nasal capsule at the dorsal midline of the skull. The distances between the lateral sutures shared by the premaxilla with the maxilla on the ventral surface of the bones were considered to be the width of the premaxillae. The length and width values of the premaxilla are expressed in Table 11. The ratio mean column indicates the highest ratios (shortest, widest bones) is found in Conolophus (.914) while the lowest ratio (longest, narrowest bone) are found in Cyclura (.491), Ctenosaurus (.512) and Iguana (.521).

The suture between the posterodorsal portion of the premaxilla and the nasal bones differs from genus to genus, in the degree of penetration the premaxilla makes between the two nasal bones. In Amblyrhynchus, Conolophus, and Iguana, the penetration of the premaxilla is very shallow with that of Conolophus forming a shallow curve and penetrating the nasals very little. Deep penetrations of the premaxilla are found in Brachylophus, Chalarodon and Oplurus. Moderate penetrations are found in the remaining genera.

Table 11

<table>
<thead>
<tr>
<th>Premaxillary Bones</th>
<th>Length</th>
<th>Width</th>
<th>Width-Length Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amblyrhynchus</td>
<td>10.1-12.6-14.4</td>
<td>6.3-7.3-8.2</td>
<td>566-585-623</td>
</tr>
<tr>
<td>Brachylophus</td>
<td>7.5-8.5-9.8</td>
<td>4.2-4.7-5.6</td>
<td>442-558-629</td>
</tr>
<tr>
<td>Chalarodon</td>
<td>2.5-2.6-2.9</td>
<td>1.4-1.6-2.0</td>
<td>560-631-689</td>
</tr>
<tr>
<td>Conolophus</td>
<td>15.8-19.9-19.3</td>
<td>13.6-18.4-20.5</td>
<td>866-914-963</td>
</tr>
<tr>
<td>Ctenosaurus</td>
<td>8.0-11.0-15.0</td>
<td>4.1-5.7-8.4</td>
<td>464-512-560</td>
</tr>
<tr>
<td>Cyclura</td>
<td>11.7-21.6-29.1</td>
<td>5.1-10.7-15.0</td>
<td>435-491-568</td>
</tr>
<tr>
<td>Diporosaurus</td>
<td>4.0-4.9-6.5</td>
<td>2.5-3.1-4.3</td>
<td>607-629-661</td>
</tr>
<tr>
<td>Iguana</td>
<td>13.5-16.2-18.9</td>
<td>6.7-8.4-9.9</td>
<td>485-521-581</td>
</tr>
<tr>
<td>Oplurus</td>
<td>4.4-5.7-9.1</td>
<td>2.5-3.1-5.1</td>
<td>580-542-568</td>
</tr>
<tr>
<td>Sauromalus</td>
<td>4.7-7.3-12.3</td>
<td>2.6-4.3-6.3</td>
<td>509-603-676</td>
</tr>
</tbody>
</table>
widest bones (highest ratio) are found in *Amblyrhynchus* (619).

### TABLE 12

<table>
<thead>
<tr>
<th>Genus</th>
<th>Length</th>
<th>Width</th>
<th>Width-Length Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Amblyrhynchus</em></td>
<td>21.7-25.3-28.8</td>
<td>13.5-15.4-17.5</td>
<td>0.66-0.69-0.71</td>
</tr>
<tr>
<td><em>Brachylophus</em></td>
<td>15.0-17.4-18.9</td>
<td>6.0-6.6-7.5</td>
<td>0.50-0.56-0.59</td>
</tr>
<tr>
<td><em>Chalarodon</em></td>
<td>6.3-6.7-7.2</td>
<td>2.2-2.2-2.3</td>
<td>0.34-0.36-0.39</td>
</tr>
<tr>
<td><em>Conolophus</em></td>
<td>30.0-41.0-45.6</td>
<td>14.3-19.1-21.5</td>
<td>0.46-0.48-0.49</td>
</tr>
<tr>
<td><em>Conosaurus</em></td>
<td>16.1-21.3-29.3</td>
<td>5.5-8.0-11.7</td>
<td>0.34-0.37-0.39</td>
</tr>
<tr>
<td><em>Cyclura</em></td>
<td>23.4-40.6-54.3</td>
<td>8.4-15.5-23.4</td>
<td>0.35-0.38-0.40</td>
</tr>
<tr>
<td><em>Dipsosaurus</em></td>
<td>10.1-10.8-11.9</td>
<td>5.0-5.5-6.1</td>
<td>0.49-0.51-0.56</td>
</tr>
<tr>
<td><em>Iguana</em></td>
<td>77.6-35-0-40.6</td>
<td>11.4-13.5-16.5</td>
<td>0.38-0.39-0.43</td>
</tr>
<tr>
<td><em>Opimus</em></td>
<td>9.4-11.4-13.9</td>
<td>3.5-4.1-4.7</td>
<td>0.34-0.35-0.37</td>
</tr>
<tr>
<td><em>Sauromalus</em></td>
<td>15.1-18.9-27.1</td>
<td>4.3-7.2-10.8</td>
<td>0.35-0.37-0.39</td>
</tr>
</tbody>
</table>

### TABLE 13

<table>
<thead>
<tr>
<th>Genus</th>
<th>Length</th>
<th>Width</th>
<th>Width-Length Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Amblyrhynchus</em></td>
<td>17.2-20.3-24.1</td>
<td>6.3-7.5-8.4</td>
<td>0.38-0.39-0.41</td>
</tr>
<tr>
<td><em>Brachylophus</em></td>
<td>7.2-8.7-12.4</td>
<td>3.9-4.9-5.3</td>
<td>0.42-0.52-0.56</td>
</tr>
<tr>
<td><em>Chalarodon</em></td>
<td>2.3-2.5-2.7</td>
<td>1.3-1.4-1.3</td>
<td>0.42-0.45-0.48</td>
</tr>
<tr>
<td><em>Conolophus</em></td>
<td>15.6-22.2-26.1</td>
<td>8.6-10.6-11.9</td>
<td>0.40-0.49-0.51</td>
</tr>
<tr>
<td><em>Conosaurus</em></td>
<td>8.1-11.5-14.8</td>
<td>4.2-6.2-8.6</td>
<td>0.59-0.55-0.61</td>
</tr>
<tr>
<td><em>Cyclura</em></td>
<td>12.6-21.4-27.0</td>
<td>5.8-10.2-15.1</td>
<td>0.48-0.47-0.52</td>
</tr>
<tr>
<td><em>Dipsosaurus</em></td>
<td>6.8-7.2-7.5</td>
<td>2.9-3.6-3.9</td>
<td>0.42-0.50-0.54</td>
</tr>
<tr>
<td><em>Iguana</em></td>
<td>14.5-19.7-22.3</td>
<td>6.4-9.9-10.5</td>
<td>0.43-0.44-0.46</td>
</tr>
<tr>
<td><em>Opimus</em></td>
<td>4.5-5.3-7.7</td>
<td>1.9-2.4-3.7</td>
<td>0.42-0.48-0.50</td>
</tr>
<tr>
<td><em>Sauromalus</em></td>
<td>5.1-8.6-13.0</td>
<td>2.5-4.3-6.1</td>
<td>0.34-0.46-0.58</td>
</tr>
</tbody>
</table>

### Nasal

Nasal (Figs. 3, 4, 5 and 6) 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 exornata.

The measurement of length of the nasal bone was taken from the tip of the ventral border as it formed the fenestra exornata to the posterodorsal extension that sutured with the prefrontal. Width was defined as the widest portion of the bone from its medial suture with its opposite member to the most lateral extension of the bone where it sutured with the maxilla and prefrontals. These measurements are expressed in Table 13 where the ratio mean column shows the nasals with the greatest ratio of length to width (short, wide bones) are found in *Ctenosaura* (.555) and *Brachylophus* (.522), while those with the lowest ratio (long, narrow bones) are found in *Amblyrhynchus* (.375).

The basic shape of the nasal differs from genus to genus. The major differences include the amount of nasal bone that borders the premaxilla, the shape of the posterior border that sutures with the frontal bone, and the shape and position of the lateral border that sutures with the maxilla and prefrontals. The nasals border a large portion of premaxilla in *Brachylophus*, *Chalarodon* and *Opimus*.

### Prefrontal

Prefrontal (Figs. 3, 4, 5 and 6) forms the anterior angle of the orbit. Medially it attaches to the frontal and nasal bones, ventrally to the maxillae and posteriorly to the lacrimal.

Length measurements were taken from the suture between the prefrontal and lacrimal bones at the anterior lip of the orbit, to the suture between the prefrontal and frontal bones on the dorsal lip of the orbit. The width of the prefrontal bone was considered to be from the suture between the prefrontal and lacrimals to the medial point where the frontal, nasal, and prefrontal bones suture together as seen in Table 14. The prefrontals with the greatest ratio of length to width (shortest, widest bones) are possessed by *Amblyrhynchus* (.776). Those genera with prefrontals having the lowest ratio (long, narrow bones) include *Chalarodon* (.512) *Sauromalus* (.553), and *Brachylophus* (.571) (Table 14).

### Lateral

Lacrimal (Figs. 5 and 6) is a small bone on the...
anteroventral rim of the orbit. Dorsally it is attached to the prefrontal, anteriorly to the maxillae, ventrally to the jugal, and ventromedially to the prefrontal.

Measurements taken on the lacrimal include length as the greatest diagonal distance from the anterodorsal border as it sutures with the prefrontal and maxilla to the posterior border on the rim of the orbit as it sutures with the jugal. Width was considered as the vertical distance between the dorsal border of the lacrimal at the rim of the orbit to the ventral border of the lacrimal at its suture with the maxilla. Those measurements summarized in Table 15 show the lowest ratio (long, narrow bones) for the lacrimal bone is found in *Chalarodon* (.293). The highest ratio (short, wide bones) is that for *Conolophus* (.542), *Ctenosaura* (.532), *Cyclura* (.526), and *Brachylophus* (.523).

In shape the lacrimal differs from genus to genus. The most common form of the bone is that of a slightly curved rhomboid. This rhomboid shape is most perfectly reproduced in *Conolophus*, *Ctenosaura*, *Cyclura* and *Iguana*. In *Amblyrhynchus* the bone is reduced to a splintlike structure while in *Brachylophus*, *Chalarodon*, *Dipsosaurus* and *Oplurus* the rhomboid shape is distorted by the curvature of the bone to fit the rim of the orbit. In *Sauromalus* the bone has its dorsal part reduced so as to form a rough trapezoid shape.

**TABLE 15**

<table>
<thead>
<tr>
<th>Genus</th>
<th>Length</th>
<th>Width</th>
<th>Width-Length Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Amblyrhynchus</em></td>
<td>3.2-4.4</td>
<td>0.9-5.0</td>
<td>3.7-4.6</td>
</tr>
<tr>
<td><em>Brachylophus</em></td>
<td>2.4-3.3</td>
<td>0.6-3.9</td>
<td>2.8-4.5</td>
</tr>
<tr>
<td><em>Chalarodon</em></td>
<td>1.9-2.1</td>
<td>0.8-1.6</td>
<td>2.2-3.4</td>
</tr>
<tr>
<td><em>Ctenosaura</em></td>
<td>4.6-6.7</td>
<td>1.2-3.2</td>
<td>3.5-7.7</td>
</tr>
<tr>
<td><em>Cyclura</em></td>
<td>3.5-4.3</td>
<td>1.0-3.5</td>
<td>3.4-9.8</td>
</tr>
<tr>
<td><em>Dipsosaurus</em></td>
<td>2.2-2.6</td>
<td>0.4-1.6</td>
<td>1.7-1.8</td>
</tr>
<tr>
<td><em>Oplurus</em></td>
<td>1.3-1.8</td>
<td>0.4-0.9</td>
<td>1.0-1.5</td>
</tr>
<tr>
<td><em>Sauromalus</em></td>
<td>2.3-3.9</td>
<td>0.5-2.7</td>
<td>1.1-4.3</td>
</tr>
</tbody>
</table>

Septomaxilla

Septomaxilla is found within the nasal capsule where it covers Jacobson’s organ and houses the anterior part of the nasal capsule. Because of the difficulty in taking measurements of this bone, it has not been studied in detail.

Frontal

Frontal (Figs. 3, 4, 5 and 6) forms the dorsal border of the orbits and the anterior roof of the braincase. At its posterior extreme the frontal is attached to the parietal and postorbital bones. Anteriorly, it is sutured to the nasal and the prefrontal. The pineal foramen penetrates the posteroomedial portions of this bone or the suture it shares with the parietal.

Table 16 represents length and width measurements of the frontal bone. Length was considered to be the distance from the most anteromedial suture shared with the nasals to the most postero-medial suture shared with the parietal bone. The width of the frontal was measured as the distance between the most lateral posterior projections as they sutured with the parietal and postfrontal bones. The greatest width to length ratio (short, wide bones) is to be found in *Ctenosaura* (.936) and *Brachylophus* (.907). The smallest ratio (long, narrow bones) is that of *Amblyrhynchus* (.629).

The shape of the frontal is basically the same for all genera but differs in some small features between genera. The greatest difference in shape occurs at the anterior end where the frontal sutures with the nasals and prefrontals. In *Conolophus* the anterior border interfingers with the nasals but is essentially straight. In *Brachylophus*, *Ctenosaura*, *Cyclura*, *Dipsosaurus*, *Iguana*, *Oplurus*, and *Sauromalus*, the anteromedial portion is triangle shaped and forms a wedge between the paired nasals. This triangle in *Dipsosaurus* is still more unique by being bifurcated at its tip by a secondary triangular projection of the nasal bones. In *Ctenosaura* and *Sauromalus* the lateral sides of the frontal’s triangular projection is further bifurcated by secondary triangles. The lateral sutures of this process in *Brachylophus* interfinger with the prefrontals and nasals but is essentially straight as it is in *Cyclura*. *Amblyrhynchus* and *Chalarodon* lack this anterior triangular projection and in its place possess a depression which fits around a triangular projection formed by the posterior borders of the nasals. Thus in the latter two genera the anterior portion of the frontal bone is bifurcated and sends a projection anteriorly which serves to separate the prefrontals and nasals for a portion of their length.

The frontals of *Amblyrhynchus*, *Brachylophus*, *Conolophus* and *Cyclura* are wider than long. In the other genera the frontals are longer than wide.

The placement of the pineal foramen in the frontal bone or the suture between the frontal and parietal bones is perplexing. The foramen was found to be in

**TABLE 16**

<table>
<thead>
<tr>
<th>Genus</th>
<th>Length</th>
<th>Width</th>
<th>Width-Length Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Amblyrhynchus</em></td>
<td>1.2-1.8</td>
<td>1.0-2.7</td>
<td>0.9-1.5</td>
</tr>
<tr>
<td><em>Brachylophus</em></td>
<td>1.0-1.4</td>
<td>0.8-1.5</td>
<td>0.9-1.4</td>
</tr>
<tr>
<td><em>Chalarodon</em></td>
<td>1.7-2.2</td>
<td>0.6-1.4</td>
<td>1.4-2.1</td>
</tr>
<tr>
<td><em>Ctenosaura</em></td>
<td>1.4-1.7</td>
<td>0.4-0.9</td>
<td>1.1-1.6</td>
</tr>
<tr>
<td><em>Cyclura</em></td>
<td>1.3-1.7</td>
<td>0.4-0.8</td>
<td>1.1-1.5</td>
</tr>
<tr>
<td><em>Dipsosaurus</em></td>
<td>1.5-2.0</td>
<td>0.9-1.0</td>
<td>1.4-2.3</td>
</tr>
<tr>
<td><em>Oplurus</em></td>
<td>0.8-1.3</td>
<td>0.3-0.7</td>
<td>0.6-1.1</td>
</tr>
<tr>
<td><em>Sauromalus</em></td>
<td>1.0-1.4</td>
<td>0.5-0.8</td>
<td>1.0-1.1</td>
</tr>
</tbody>
</table>
the suture between the two bones in all specimens examined of Brachylophus, Chalarodon, Ctenosaura, and Iguana. The foramen appears completely embedded in the frontal bones in one specimen each of Amblyrhynchus, Conolophus, and Oplurus, whereas other specimens of these genera possessed a foramen in the suture. In Cyclura the pineal foramen is found in the frontal bone in three of four specimens examined while it occurred in the frontal bone in all four specimens of Dipsosaurus and in five of six specimens of Sauromalus.

Postfrontal

Postfrontal (Figs. 3, 4, 5 and 6) 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.

The length of the postfrontal was measured as the distance between the extremities of its longest axis. The width was the distance between the parallel borders on the axis at right angles to the length. The values for these measurements are presented in Table 17 and it can be seen that the genus with the smallest ratio (longest, narrowest bone) is Chalarodon (.200), while Oplurus (.625) has the largest ratio (shortest, widest bones).

The postfrontal is usually splinterlike in shape as it is in all genera except Cyclura, Iguana and Oplurus. In Cyclura the anterolateral portion of the bone forms a short projection out over the postero dorsal part of the orbit in some individuals. This condition is especially well developed in Cyclura cornuta. In Iguana the lateral portions of the postfrontal is developed into a prominent knob on the anterodorsal face of the postorbital bone. In Oplurus the postfrontal is small, almost spherical in shape, and in at least one skull (MCZ 37191) this bone could not be located.

### TABLE 17
**POSTFRONTAL BONES**

<table>
<thead>
<tr>
<th>Genus</th>
<th>Length</th>
<th>Width</th>
<th>Width-Length Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Min.</td>
<td>Mean</td>
<td>Max.</td>
</tr>
<tr>
<td>Amblyrhynchus</td>
<td>6.9</td>
<td>8.0-10.3</td>
<td>3.9-4.2-4.6</td>
</tr>
<tr>
<td>Brachylophus</td>
<td>4.0</td>
<td>4.7-6.2</td>
<td>1.1-1.3-1.8</td>
</tr>
<tr>
<td>Chalarodon</td>
<td>0.5</td>
<td>0.5-0.5</td>
<td>0.1-0.1-0.1</td>
</tr>
<tr>
<td>Conolophus</td>
<td>10.4</td>
<td>14.0-16.7</td>
<td>2.3-3.5-4.4</td>
</tr>
<tr>
<td>Ctenosaura</td>
<td>3.8</td>
<td>4.8-5.8</td>
<td>0.8-1.1-1.7</td>
</tr>
<tr>
<td>Cyclura</td>
<td>6.5</td>
<td>9.4-12.4</td>
<td>1.9-2.7-3.9</td>
</tr>
<tr>
<td>Dipsosaurus</td>
<td>2.4</td>
<td>2.7-3.0</td>
<td>0.5-0.6-0.8</td>
</tr>
<tr>
<td>Iguana</td>
<td>4.6</td>
<td>7.0-9.4</td>
<td>2.0-2.7-3.2</td>
</tr>
<tr>
<td>Oplurus</td>
<td>0.2</td>
<td>0.2-0.3</td>
<td>0.1-0.1-0.3</td>
</tr>
<tr>
<td>Sauromalus</td>
<td>2.1</td>
<td>3.8-5.6</td>
<td>0.7-1.3-1.9</td>
</tr>
</tbody>
</table>

Parietal

Parietal (Figs. 3, 4, 5 and 6) forms the roof of the posterior part of the skull. It articulates with the frontal and postfrontal anteriorly and with the postorbital posteriorly and ventrally. Posteriorly the parietal overlaps the supratemporal and articulates with the exoccipitals and supraoccipital.

The anterior two thirds of the dorsal surface of the parietal gives origin to the pseudotemporalis supercilius 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 epiprostheleomastoideus muscles.

Measurements were taken on two areas of the parietal bone. The anterior two-thirds of the bone was to the eopterygoid. The dorsal surface forms the anteroventral wall of the orbit.

The length of the jugal is considered as the horizontal distance between the most anterior projections of the bone as it sutured to the lacrimal and maxillae, to the most posterior projection which sutured to the anteroventral border of the postorbital. The width was the widest distance between the two parallel borders at right angles to the length. Measurements of the jugal bones are presented in Table 18. The smallest ratio (longest, narrowest bone) of length to width is found in Ctenosaura (.136), Sauromalus (.141), and Oplurus (.148). The largest ratios (shortest, widest bones) are found in Amblyrhynchus (.207), Conolophus (.195), and Cyclura (.191).

The posterior extension of the jugal may extend so far posteriorly as to touch or overlap the squamosal, thereby completely covering the ventral border of the postorbital bone. Such a condition exists in Conolophus, Dipsosaurus, Iguana, and Oplurus. In the other genera the jugals and squamosals do not touch.

### TABLE 18
**JUGAL BONES**

<table>
<thead>
<tr>
<th>Genus</th>
<th>Length</th>
<th>Width</th>
<th>Width-Length Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Min.</td>
<td>Mean</td>
<td>Max.</td>
</tr>
<tr>
<td></td>
<td>Mean</td>
<td>Max.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Min.</td>
<td>Mean</td>
<td>Max.</td>
</tr>
<tr>
<td></td>
<td>Min.</td>
<td>Mean</td>
<td>Max.</td>
</tr>
<tr>
<td>Amblyrhynchus</td>
<td>18.1</td>
<td>19.0</td>
<td>24.7</td>
</tr>
<tr>
<td>Brachylophus</td>
<td>12.5</td>
<td>13.7</td>
<td>15.9</td>
</tr>
<tr>
<td>Chalarodon</td>
<td>6.1</td>
<td>6.4</td>
<td>6.8</td>
</tr>
<tr>
<td>Conolophus</td>
<td>26.2</td>
<td>32.4</td>
<td>38.2</td>
</tr>
<tr>
<td>Ctenosaura</td>
<td>14.0</td>
<td>19.2</td>
<td>27.3</td>
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<tr>
<td>Cyclura</td>
<td>24.0</td>
<td>38.5</td>
<td>50.8</td>
</tr>
<tr>
<td>Dipsosaurus</td>
<td>13.6</td>
<td>12.5</td>
<td>14.8</td>
</tr>
<tr>
<td>Iguana</td>
<td>20.0</td>
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<td>31.9</td>
</tr>
<tr>
<td>Oplurus</td>
<td>9.4</td>
<td>10.7</td>
<td>13.9</td>
</tr>
<tr>
<td>Sauromalus</td>
<td>11.9</td>
<td>15.9</td>
<td>24.1</td>
</tr>
</tbody>
</table>
subjected to length-width measurements, with the length being the distance along the midline, from the anterior suture with the frontal to the suture between the parietal and the supraoccipital. The width of the parietal was considered as the distance between the two most anterolateral projections of the bone where they sutured with the postorbital and postfrontals. The measurements are presented in Table 19. The greatest length width ratio (shortest, widest bone) is found in *Conolophus* (.751) while *Dipsosaurus* (.431), and *Brachylophus* (.448) possess the smallest ratio (longest, narrowest bones).

The second portion of the parietal to be measured was the wings or posterior dorsolateral projections of the bone that sutured with the supratemporal, squamosal, and articulated with the quadrate. The length of the parietal wings is the diagonal distance from the anterolateral portion of the parietal bone to the opposite posterior tip of the parietal wing. The width is the distance between the most postero-lateral surface of the two wings. The parietal wing ratios are summarized in Table 20 and show the greatest length width ratios (shortest, widest bones) to be possessed by *Dipsosaurus* (.945) and *Saurornatus* (.926). The lowest ratios (longest, narrowest bones) are those of *Brachylophus* (.765) and *Ctenosaura* (.781).

**Supratemporal**

Supratemporal provides support for the postero-

<table>
<thead>
<tr>
<th>TABLE 19</th>
<th>PARIETAL BONES</th>
</tr>
</thead>
<tbody>
<tr>
<td>Genus</td>
<td>Length</td>
</tr>
<tr>
<td>Ambyllophus</td>
<td>9.9-12.2-16.1</td>
</tr>
<tr>
<td>Brachylophus</td>
<td>5.6-6.5-7.4</td>
</tr>
<tr>
<td>Cheladoron</td>
<td>2.6-2.8-3.1</td>
</tr>
<tr>
<td>Conolophus</td>
<td>16.3-24.9-39.3</td>
</tr>
<tr>
<td>Ctenosaura</td>
<td>7.1-9.0-11.0</td>
</tr>
<tr>
<td>Cyclura</td>
<td>10.3-19.2-32.9</td>
</tr>
<tr>
<td>Dipsosaurus</td>
<td>3.4-3.9-4.3</td>
</tr>
<tr>
<td>Iguana</td>
<td>10.9-14.3-17.1</td>
</tr>
<tr>
<td>Opturus</td>
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<tr>
<td>Saurornatus</td>
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</tbody>
</table>

<table>
<thead>
<tr>
<th>TABLE 20</th>
<th>PARIETAL WINGS</th>
</tr>
</thead>
<tbody>
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<td>Genus</td>
<td>Length</td>
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</tr>
<tr>
<td>Cheladoron</td>
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</tr>
<tr>
<td>Conolophus</td>
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</tr>
<tr>
<td>Ctenosaura</td>
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</tr>
<tr>
<td>Cyclura</td>
<td>25.0-42.4-58.1</td>
</tr>
<tr>
<td>Dipsosaurus</td>
<td>12.6-13.6-14.4</td>
</tr>
<tr>
<td>Iguana</td>
<td>23.2-29.3-33.4</td>
</tr>
<tr>
<td>Opturus</td>
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</tr>
<tr>
<td>Saurornatus</td>
<td>12.9-19.7-29.0</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>TABLE 21</th>
<th>POSTORBITAL BONES</th>
</tr>
</thead>
<tbody>
<tr>
<td>Genus</td>
<td>Length</td>
</tr>
<tr>
<td>Ambyllophus</td>
<td>9.1-13.3-17.5</td>
</tr>
<tr>
<td>Brachylophus</td>
<td>5.5-6.4-7.8</td>
</tr>
<tr>
<td>Cheladoron</td>
<td>3.8-3.3-3.7</td>
</tr>
<tr>
<td>Conolophus</td>
<td>16.0-25.7-30.4</td>
</tr>
<tr>
<td>Ctenosaura</td>
<td>8.0-11.5-14.0</td>
</tr>
<tr>
<td>Dipsosaurus</td>
<td>5.4-6.4-7.1</td>
</tr>
<tr>
<td>Iguana</td>
<td>9.8-14.3-16.7</td>
</tr>
<tr>
<td>Opturus</td>
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<tr>
<td>Saurornatus</td>
<td>7.3-10.9-15.5</td>
</tr>
</tbody>
</table>

lateral angle of the parietal bone. Posteriorly, it articulates with the exoccipital, squamosal, and the 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. Because of the difficulties in measuring, this bone has not been studied in detail.

**Postorbital**

Postorbital (Figs. 1, 2, 3, 4, 5 and 6) 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 articulates with the jugal and the posteroventral border of 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.

The length of the postorbital was measured as the greatest distance between anteroventral and posteroventral projections. The width was considered as the distance from the ventral border to the tip of the dorsal projection where it sutured with the parietal and postfrontal bones. Table 21 shows that the greatest length width ratio (shortest, widest bones) is found in *Iguana* (.886), *Amblyrhynchus* (.882), and *Conolophus* (.876). The lowest ratio (longest, narrowest bones) is possessed by *Saurornatus* (.556) and *Cyclura* (.585).

The postorbital bone is roughly triangular in shape in all genera. Its ventral border has been discussed in the description of the jugal. This border is completely covered by the squamosal and jugal bones in *Conolophus*, *Dipsosaurus*, *Iguana*, and *Opurus*. In the other genera the central part of the ventral border is free. In *Amblyrhynchus* the anterior face of the dorsal process is enlarged and contributes to the knoblike structure of the postfrontal. The postorbital of *Cyclura* appears normal and does not contribute to the postfrontal knob over the orbit.
Squamosal

Squamosal (Figs. 1, 2, 3, 4, 5 and 6) is attached to the postorbital bone on the postero-lateral border of the skull. The expanded posterior part of the squamosal is attached to the dorsal surface of the supra-temporal and the quadrato.

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.

The length of the squamosal was measured as the distance between the most anterior and the posterior extremities of the bone. The width was the greatest distance between the parallel borders on an axis at right angles to the length. These measurements are presented in table 22 and show the greatest ratio (shortest, widest bones) to be found in *Amblyrhynchos* (0.736). The smallest ratio (longest, narrowest bones) occurs in *Chalarodon* (0.639).

The shape of the squamosal bone differs not only in size but in shape as well. The posterior projection of the bone has a dorsal and ventral hook-like projection in *Chalarodon* and *Ophius*. Those of *Ophius* are not as pronounced as those in *Chalarodon*. The posterior portion of the bone in other genera is swollen but the projections are in the forms of small triangular processes rather than curving hooks as in *Chalarodon* and *Ophius*. The greatest development of these triangular projections is found in *Amblyrhynchos, Conolophus, Ctenosaura, Cyclura, Iguana*, and *Saurornatus*. The squamosals take the form of a long split in *Dipsosaurus* and *Brachylophus*.

### TABLE 22

<table>
<thead>
<tr>
<th>Genus</th>
<th>Length</th>
<th>Width</th>
<th>Width-Length Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Squamosal bone</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Epiphythgoid

Epiphythgoid 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 as origin for the pseudotemporalis profundus muscle. This bone was not studied in detail.

Supratemporal fossa

Supratemporal fossa (Figs. 3 and 4) is the large cavity that dominates each half of the dorsal posterior third of the skull. It is bordered medially, postero-medially, and antero-medially by the parietal bone, antero-laterally by the postorbital, and postero-laterally by the squamosal.

Length and width measurements were taken of the supratemporal fossa, with length being the inside distance on the longest axis and width being the inside distance on the longest axis at right angles to the length. Table 24 shows the largest length-width ratios...
(shortest, widest opening) are possessed by Dipso-
saurus (.647), Sauromalus (.620), Amblyrynchus
(.616), and Conolophus (.609). The smallest ratio
(longest, narrowest opening) is found in Chalarodon
(.443).

### TABLE 24

<table>
<thead>
<tr>
<th>Genus</th>
<th>Length</th>
<th>Width</th>
<th>Width-Length Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amblyrynchus</td>
<td>12.5-15.2-18.3</td>
<td>6.3-9.4-11.9</td>
<td>504-616-781</td>
</tr>
<tr>
<td>Brachylophus</td>
<td>8.6-9.4-12.1</td>
<td>4.3-5.4-6.9</td>
<td>514-577-637</td>
</tr>
<tr>
<td>Chalarodon</td>
<td>3.4-3.6-4.3</td>
<td>1.5-1.6-1.9</td>
<td>428-443-462</td>
</tr>
<tr>
<td>Conolophus</td>
<td>18.0-20.8-34.0</td>
<td>12.0-17.8-21.2</td>
<td>.560-609.666</td>
</tr>
<tr>
<td>Deprasaurus</td>
<td>4.2-5.0-5.7</td>
<td>2.6-3.2-3.7</td>
<td>.619-647-687</td>
</tr>
<tr>
<td>Iguana</td>
<td>10.9-14.3-16.8</td>
<td>4.6-7.1-8.3</td>
<td>.422-499-567</td>
</tr>
<tr>
<td>Ophiurus</td>
<td>4.2-5.3-8.0</td>
<td>2.1-2.6-4.1</td>
<td>.500-524-586</td>
</tr>
<tr>
<td>Sauromalus</td>
<td>5.0-8.0-12.6</td>
<td>2.4-5.0-8.1</td>
<td>.480-620-672</td>
</tr>
</tbody>
</table>

**Orbit**

Orbit (Figs. 3 and 4) is the dominate lateral cavity
of the skull and in life is the area where the eye
is located. The orbit is basically circular and is bordered
dorsally by the frontal; anteriorly by the prefrontals,
lacrimal and jugals, ventrally by the jugal and poste-
riously by the postorbital and the postfrontal.

The length of the orbit was measured as the greatest
distance between lacrimal and postorbital. The width
was the greatest distance between jugal and frontal bones. These relationships are expressed in
Table 25 which shows the greatest length-width ratios
(most circular opening) to be found in Conolophus
(.969) and the smallest ratio (most elliptical opening)
in Chalarodon (.682).

### TABLE 25

<table>
<thead>
<tr>
<th>Genus</th>
<th>Length</th>
<th>Width</th>
<th>Width-Length Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amblyrynchus</td>
<td>12.4-14.3-16.3</td>
<td>10.9-15.4-19.5</td>
<td>.802-823-868</td>
</tr>
<tr>
<td>Brachylophus</td>
<td>11.3-13.9-14.2</td>
<td>9.0-9.3-10.9</td>
<td>.796-814-825</td>
</tr>
<tr>
<td>Chalarodon</td>
<td>5.2-6.2-7.3</td>
<td>3.9-4.2-4.5</td>
<td>.611-682-769</td>
</tr>
<tr>
<td>Conolophus</td>
<td>17.8-23.9-26.6</td>
<td>17.2-23.3-26.9</td>
<td>.958-969-985</td>
</tr>
<tr>
<td>Ctenosaura</td>
<td>12.1-15.3-18.3</td>
<td>7.6-12.0-14.1</td>
<td>.770-782-793</td>
</tr>
<tr>
<td>Cychura</td>
<td>16.8-25.6-33.1</td>
<td>12.8-20.7-27.5</td>
<td>.760-805-830</td>
</tr>
<tr>
<td>Deprasaurus</td>
<td>8.6-9.5-10.1</td>
<td>7.0-7.5-7.9</td>
<td>.770-790-813</td>
</tr>
<tr>
<td>Iguana</td>
<td>19.0-21.3-24.9</td>
<td>15.3-17.5-19.3</td>
<td>.715-825-867</td>
</tr>
<tr>
<td>Ophiurus</td>
<td>7.6-8.3-12.1</td>
<td>5.9-7.0-9.2</td>
<td>.760-795-839</td>
</tr>
</tbody>
</table>

**Exonarina**

Fenestra exonarina is the paired prominent opening on the dorsal rostrum of the skull. It is bordered medially and anterointervally by the premaxilla, laterally by the maxilla, and posterodorsally by the nasals. In life the fenestra

exonarina provides the opening for the external nares.

The length of the fenestra exonarina was considered to be the internal distance between the suture of the lateral projection of the premaxilla and the maxilla and the suture between the nasal and maxilla. The width was considered to be the greatest inside distance between the lateral border of the premaxilla and the anterior border of the maxilla. Table 26 represents a tabulation of these values and shows the greatest ratio (most circular opening) to exist in Brachylophus (.872) and the lowest ratio (most elliptical opening) to be found in Cychura (.443).

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, whereas the remaining bones (articular, surangular, angular, splenial and coronoid) are eden-
tate.

### TABLE 26

<table>
<thead>
<tr>
<th>Genus</th>
<th>Length</th>
<th>Width</th>
<th>Width-Length Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amblyrynchus</td>
<td>8.1-9.1-10.3</td>
<td>5.8-7.0-8.0</td>
<td>.716-764-817</td>
</tr>
<tr>
<td>Brachylophus</td>
<td>4.0-4.2-4.8</td>
<td>3.3-3.7-4.0</td>
<td>.804-872-951</td>
</tr>
<tr>
<td>Chalarodon</td>
<td>1.4-1.5-1.8</td>
<td>1.0-1.0-1.1</td>
<td>.611-664-714</td>
</tr>
<tr>
<td>Conolophus</td>
<td>11.7-15.4-17.5</td>
<td>8.5-11.9-13.6</td>
<td>.726-767-803</td>
</tr>
<tr>
<td>Ctenosaura</td>
<td>4.1-5.5-6.8</td>
<td>3.6-4.1-5.0</td>
<td>.700-743-806</td>
</tr>
<tr>
<td>Cychura</td>
<td>7.3-20.4-32.1</td>
<td>5.3-9.0-14.5</td>
<td>.428-443-452</td>
</tr>
<tr>
<td>Deprasaurus</td>
<td>3.2-3.8-4.2</td>
<td>2.0-2.3-2.5</td>
<td>.571-590-606</td>
</tr>
<tr>
<td>Iguana</td>
<td>8.2-11.7-14.3</td>
<td>5.5-7.8-8.7</td>
<td>.608-669-714</td>
</tr>
<tr>
<td>Ophiurus</td>
<td>1.9-2.5-4.2</td>
<td>1.4-1.8-2.1</td>
<td>.700-718-738</td>
</tr>
<tr>
<td>Sauromalus</td>
<td>3.0-4.6-6.8</td>
<td>2.1-4.1-5.0</td>
<td>.600-751-833</td>
</tr>
</tbody>
</table>

**Dentary**

Dentary (Figs. 5, 6 and 7) is the largest bone of the lower jaw and bears teeth on its dorsomedial border. At its posterior margins the dentary inter-
digitates with the coronoid, splenial, angular, artic-
ular, and surangular. The ventral border provides the
origin for the anterior fibers of the mandibulo-
hyoideus I and III and the genioglossus muscles.

Measurements taken on the dentary included the length as the distance from the anterior tip of the bone to the posterior most projection on the lateral surface of the mandible. The width of the dentary was that vertical distance between the top and the bottom of the mandible immediately in front of the coronoid. An examination of Table 27 reveals that the largest length-width ratio (smallest, widest bone) for the dentary is possessed by Amblyrynchus
(.297) and Conolophus (.282). The smallest ratio
(longest, narrowest bone) is that of Ophiurus (.147) and Chalarodon (.174).

The relationship between the postero lateral border of the dentary, the coronoid and the surangular differs from genus to genus. In Chalarodon and
Opiums the dentary is not overlapped by the coronoid on its posterodorsal surface. In Brachylophus, Ctenosaura, Dipsosaurus, Iguana and Sauromalus, the dentary is overlapped dorsally by the coronoid and the ventral border of the coronoid and its suture with the dentary is parallel to the ventral border of the mandible. The posterior suture of the dentary in Brachylophus, Ctenosaura, Iguana and Sauromalus is concave in nature. In Dipsosaurus this suture is convex. Amblyrhynchus, Conolophus and Cyclura have complex rounded or slanting suture between the ventral border of the overlapping coronoid and its suture with the dentary. The posterolateral suture in these genera is complex with two posteriorly pointing triangular projections being present in Amblyrhynchus and Conolophus. Cyclura possesses a smooth gently curving concave suture.

### TABLE 27

<table>
<thead>
<tr>
<th>Genus</th>
<th>Length</th>
<th>Width</th>
<th>Width-Length Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Min. Mean Max.</td>
<td>Min. Mean Max.</td>
<td>Min. Mean Max.</td>
</tr>
<tr>
<td>Amblyrhynchus</td>
<td>20.5-28.3 3-4 3</td>
<td>7.5 - 11 7 - 11 9</td>
<td>57.1-11 11.2 - 11 7</td>
</tr>
<tr>
<td>Brachylophus</td>
<td>19.8-21.4 23 1</td>
<td>4.0 - 7.5 - 8.5</td>
<td>11 11.2 - 11 11.2</td>
</tr>
<tr>
<td>Chalarodon</td>
<td>8.1 - 9.2 9.0</td>
<td>1.3 - 2.0 - 2.5</td>
<td>14 14.2 - 14 14.3</td>
</tr>
<tr>
<td>Conolophus</td>
<td>40.4-51.2 55 6</td>
<td>8.7-10.7 - 11 7</td>
<td>21 21.3 - 21 21.5</td>
</tr>
<tr>
<td>Ctenosaura</td>
<td>19.5-26.7 35 6</td>
<td>3.4 - 5.2 - 5.5</td>
<td>17 17.1 - 17 17.2</td>
</tr>
<tr>
<td>Cyclura</td>
<td>29.5-51.7 47 2</td>
<td>6.5-10.5 - 11 0</td>
<td>19 19.1 - 19 19.2</td>
</tr>
<tr>
<td>Dipsosaurus</td>
<td>12.9-14.7 13 5</td>
<td>3.3 - 3.6 - 3.9</td>
<td>24 24.3 - 24 24.6</td>
</tr>
<tr>
<td>Iguana</td>
<td>30.0-24.0 47 5</td>
<td>6.7 - 9.0 - 10.0</td>
<td>21 21.2 - 21 21.4</td>
</tr>
<tr>
<td>Oplturus</td>
<td>13.2-17.4 17 2</td>
<td>2.1 - 2.4 - 3.1</td>
<td>12 12.1 - 12 12.3</td>
</tr>
<tr>
<td>Sauromalus</td>
<td>13.6-20.0 29 4</td>
<td>2.5 - 3.6 - 5.5</td>
<td>14 14.1 - 14 14.3</td>
</tr>
</tbody>
</table>

### Articular

Articular (Figs. 5, 6 and 7) is that part of the mandibles 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 serrated to the splenial bone.

The length of the articular bone was measured from its most anterior projection on the medial surface where it sutured to the coronoid and splenial to the most posterior tip of the retroarticular process. The width was taken from the most ventromedial projection of the angular process to the opposite border of the articular bone where it sutured with the surangular on the mandible’s lateral surface. These measurements are summarized in Table 28 which shows the greatest length-width ratio (shortest, widest bones) to be found in Conolophus (.390) and the lowest ratio is possessed by Chalarodon (.200).

The angular process of the articular bone differs in shape and size from genus to genus. This projection was also subjected to length-width measurements. The length was taken as the greatest length of the mandible and was contrasted with the width of the articular which in part is a result of the size of the angular process. The ratio between those measurements is expressed in Table 29 which shows Conolophus (.219) to have the greatest ratio (shortest, widest bones), while the smallest ratios (longest, narrowest bones) are those of Chalarodon (.105) and Oplturus (.120).

As previously indicated, the shape of the angular process (Figure 7) differs from genus to genus. The projection which extends medially from the posterior ventromedial surface of the articular bone is either a small rounded bump as in Amblyrhynchus and Iguana, or a pointed spinelike anteriorly pointing projection as in the remaining genera. The smallest projection is that of Amblyrhynchus. Of the pointed projections, that of Cyclura is the most massive and pronounced, whereas the projection in Conolophus is nearly as large. The angular process of Ctenosaura and Sauromalus is less massive and projecting than that of Cyclura and Conolophus. It is similar in shape but less pointed in the last two genera. In Brachylophus, Chalarodon, Dipsosaurus and Oplturus, the angular projection is more triangular shaped than hooklike. In all four genera the anterior face terminates as a sharp spine. The process of Brachylophus and Oplturus is more sharply curved and hooklike than that of Chalarodon and Dipsosaurus.

### TABLE 28

<table>
<thead>
<tr>
<th>Genus</th>
<th>Length</th>
<th>Width</th>
<th>Width-Length Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Min. Mean Max.</td>
<td>Min. Mean Max.</td>
<td>Min. Mean Max.</td>
</tr>
<tr>
<td>Amblyrhynchus</td>
<td>18.4-25.0 30.0</td>
<td>5.9 - 9.1 - 10.8</td>
<td>.58 - .58 - .58</td>
</tr>
<tr>
<td>Brachylophus</td>
<td>16.0-17.4 18.4</td>
<td>4.3 - 5.3 - 6.4</td>
<td>.24 - .24 - .24</td>
</tr>
<tr>
<td>Chalarodon</td>
<td>6.3 - 6.3 6.7</td>
<td>1.2 - 1.2 - 1.4</td>
<td>.19 - .19 - .19</td>
</tr>
<tr>
<td>Conolophus</td>
<td>34.2-52.0 61.5</td>
<td>11.7-21.1 - 21.7</td>
<td>.32 - .32 - .32</td>
</tr>
<tr>
<td>Ctenosaura</td>
<td>14.1-21.4 21.2</td>
<td>4.6 - 6.4 - 10.6</td>
<td>.23 - .23 - .23</td>
</tr>
<tr>
<td>Cyclura</td>
<td>24.2-24.5 57.8</td>
<td>4.7 - 12.0 - 20.3</td>
<td>.18 - .18 - .18</td>
</tr>
<tr>
<td>Dipsosaurus</td>
<td>8.9-11.1 12.6</td>
<td>3.0 - 3.6 - 4.1</td>
<td>.29 - .29 - .29</td>
</tr>
<tr>
<td>Iguana</td>
<td>23.3-31.9 38.7</td>
<td>7.4 - 8.6 - 9.1</td>
<td>.22 - .22 - .22</td>
</tr>
<tr>
<td>Oplturus</td>
<td>8.3-11.3 15.8</td>
<td>1.9 - 3.0 - 4.9</td>
<td>.29 - .29 - .29</td>
</tr>
<tr>
<td>Sauromalus</td>
<td>14.8-20.7 23.5</td>
<td>7.8 - 5.5 - 9.3</td>
<td>.18 - .18 - .18</td>
</tr>
</tbody>
</table>

### TABLE 29

<table>
<thead>
<tr>
<th>Genus</th>
<th>Length</th>
<th>Width</th>
<th>Width-Length Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Min. Mean Max.</td>
<td>Min. Mean Max.</td>
<td>Min. Mean Max.</td>
</tr>
<tr>
<td>Amblyrhynchus</td>
<td>35.0-48.4 57.1</td>
<td>6.4 - 9.5 - 11.5</td>
<td>.18 - .18 - .18</td>
</tr>
<tr>
<td>Brachylophus</td>
<td>32.2-33.6 35.6</td>
<td>4.2 - 5.4 - 6.6</td>
<td>.10 - .10 - .10</td>
</tr>
<tr>
<td>Chalarodon</td>
<td>12.0-12.0 13.4</td>
<td>1.0 - 1.3 - 1.8</td>
<td>.08 - .08 - .08</td>
</tr>
<tr>
<td>Conolophus</td>
<td>66.6-85.1 107.6</td>
<td>11.6-21.3 - 21.7</td>
<td>.17 - .17 - .17</td>
</tr>
<tr>
<td>Ctenosaura</td>
<td>30.2-43.1 60.4</td>
<td>3.9 - 6.3 - 10.6</td>
<td>.12 - .12 - .12</td>
</tr>
<tr>
<td>Cyclura</td>
<td>48.6-84.1 117.3</td>
<td>7.9 - 14.5 - 21.1</td>
<td>.16 - .16 - .16</td>
</tr>
<tr>
<td>Dipsosaurus</td>
<td>19.9-33.2 25.4</td>
<td>3.5 - 4.4 - 4.4</td>
<td>.16 - .16 - .16</td>
</tr>
<tr>
<td>Iguana</td>
<td>50.0-65.4 77.2</td>
<td>7.5 - 8.6 - 9.2</td>
<td>.12 - .12 - .12</td>
</tr>
<tr>
<td>Oplturus</td>
<td>18.2-24.3 33.7</td>
<td>1.9 - 3.0 - 4.9</td>
<td>.10 - .10 - .10</td>
</tr>
<tr>
<td>Sauromalus</td>
<td>22.4-33.4 43.1</td>
<td>2.8 - 5.5 - 9.3</td>
<td>.11 - .11 - .11</td>
</tr>
</tbody>
</table>
Surangular

Surangular (Figs. 5, 6 and 7) forms the lateral wall of the posterior third of 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. The surangular's length is taken as the longest anterior-posterior axis on the lateral surface of the mandible. The width is considered to be the longest dorsal-ventral axis in the area of the anterior sutures with the dentary and coronoid on the mandible's lateral surface. Table 30 indicates the largest length-width ratio (shortest, widest bone) is found in Amblyrhynchos (.425) and the smallest ratio (longest, narrowest bone) in Sauromalus (.270) and Iguana (.278).

### Table 30: Surangular Bones

<table>
<thead>
<tr>
<th>Genus</th>
<th>Length</th>
<th>Width</th>
<th>Length-Width Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amblyrhynchos</td>
<td>11.9-16.31.6</td>
<td>5.8-6.9-8.9</td>
<td>365-425-487</td>
</tr>
<tr>
<td>Brachylophus</td>
<td>9.2-9.6-10.0</td>
<td>3.4-3.6-3.9</td>
<td>369-377-399</td>
</tr>
<tr>
<td>Chalarodon</td>
<td>5.9-9.3</td>
<td>1.0-1.1</td>
<td>344-352-366</td>
</tr>
<tr>
<td>Conolophus</td>
<td>23.5-34.3-62.1</td>
<td>9.0-15.2-18.0</td>
<td>289-343-365</td>
</tr>
<tr>
<td>Ctenosaura</td>
<td>11.4-16.8-25.4</td>
<td>3.1-4.7-6.6</td>
<td>271-296-309</td>
</tr>
<tr>
<td>Cycloeca</td>
<td>20.1-24.0-44.3</td>
<td>5.0-10.2-15.1</td>
<td>248-296-340</td>
</tr>
<tr>
<td>Diplosaurus</td>
<td>6.5-7.3-8.7</td>
<td>2.4-2.7-3.0</td>
<td>344-356-369</td>
</tr>
<tr>
<td>Iguana</td>
<td>20.0-25.2-30.4</td>
<td>5.4-7.0-8.5</td>
<td>270-278-299</td>
</tr>
<tr>
<td>Ophidius</td>
<td>5.0-6.1-8.2</td>
<td>1.4-1.8-2.6</td>
<td>280-293-316</td>
</tr>
<tr>
<td>Sauromalus</td>
<td>8.8-13.3-19.6</td>
<td>2.1-3.6-6.0</td>
<td>229-270-306</td>
</tr>
</tbody>
</table>

Splenial

Splenial (Fig. 7) 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.

The splenial’s length was considered to be the longest anterior-posterior axis and the longest dorsal-ventral axis as taken in the width. Table 31 indicates the largest ratio (shortest, widest bone) is found in Chalarodon (.405) and the smallest ratio (longest, narrowest bone) is that of Cycloeca (.149).

The splenial bone is a fusiform splinter shape in all ten genera but it is pierced by the anterior inferior alveolar foramen in different places in different genera. This foramen is completely enclosed within the bone in Amblyrhynchos and Ophidius. In Brachylophus the anterior tip of the bone forms the posterior border of the foramen. In Chalarodon, Conolophus, Ctenosaura, Cycloeca, Iguana and Sauromalus, the foramen is partially enclosed by the anterior dorsal border of the splenial. In Diplosaurus the foramen is found in the dentary and is separated from the splenial by a projection of the coronoid.

Angular

Angular (Figs. 5, 6 and 7) 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 mandibulohyoides I muscle.

The angular is roughly fusiform and its length was measured between the most anterior and most posterior projections. The width was the greatest distance between the opposite borders on an axis at right angles to the length. These measurements are summarized in Table 32 which indicates the greatest ratio (shortest, widest bone) to be that of Diplosaurus (.223) and the shortest ratio (longest, narrowest bone) to be Sauromalus (.107).

### Table 31: Splenial Bones

<table>
<thead>
<tr>
<th>Genus</th>
<th>Length</th>
<th>Width</th>
<th>Length-Width Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amblyrhynchos</td>
<td>12.4-16.1-19.5</td>
<td>2.8-3.8-4.1</td>
<td>202-214-225</td>
</tr>
<tr>
<td>Brachylophus</td>
<td>9.2-10.5-12.1</td>
<td>1.4-2.0-2.5</td>
<td>152-189-231</td>
</tr>
<tr>
<td>Chalarodon</td>
<td>3.0-3.5-4.4</td>
<td>0.5-0.5-0.7</td>
<td>156-160-166</td>
</tr>
<tr>
<td>Conolophus</td>
<td>24.1-37.4-46.7</td>
<td>4.9-7.1-8.8</td>
<td>155-193-226</td>
</tr>
<tr>
<td>Ctenosaura</td>
<td>10.2-16.2-23.1</td>
<td>2.1-2.7-3.3</td>
<td>134-178-204</td>
</tr>
<tr>
<td>Cycloeca</td>
<td>16.4-31.8-34.1</td>
<td>2.5-4.3-5.6</td>
<td>129-139-152</td>
</tr>
<tr>
<td>Diplosaurus</td>
<td>7.6-8.0-8.3</td>
<td>1.6-1.8-1.9</td>
<td>227-223-230</td>
</tr>
<tr>
<td>Iguana</td>
<td>19.2-24.5-30.4</td>
<td>3.2-4.1-4.8</td>
<td>157-170-193</td>
</tr>
<tr>
<td>Ophidius</td>
<td>4.7-6.1-9.4</td>
<td>0.9-1.1-1.5</td>
<td>159-189-204</td>
</tr>
<tr>
<td>Sauromalus</td>
<td>6.5-10.1-14.5</td>
<td>0.5-1.3-2.4</td>
<td>107-107-165</td>
</tr>
</tbody>
</table>

Coronoid

Coronoid (Figs. 5, 6 and 7) straddles the other bones of the jaw from a dorsal position. The two anterior extremities articulate in most genera with the dentary and surangular laterally and the dentary, splenial and articular bone vertebrae. The posterior, lateral, apical surfaces give rise to the insertion of the adductor mandibularis externus and adductor medius muscles, and provides an attachment surface for the adductor muscle.

The coronoid length was measured as the distance from the dorsal tip of the bone to the tip of the ventral most projection on the lateral surface of the
The width was the distance between anterior and posterior borders where they contact the dorsolateral surface of the mandible. Table 33 shows the greatest ratio (shortest, widest bones) is found in Chalarodon (.941) and Amblyrhynchus (.935). The lowest ratio (longest, narrowest bones) is that of Conolophus (.571).

The shape of the bone differs greatly from genus to genus. The anterolateral projection of the coronoid takes different shapes in different genera. In Chalarodon and Oplurus this projection is missing and the dentary and surangular are not overlapped on the lateral surface. In Conolophus and Cyclura the projection overlaps the dentary and surangular ventrally and projects very little anteriorly on the lateral surface of the dentary. Amblyrhynchus has a similar condition, however, there is a small anterior projection extending forward over part of the dentary. In Brachylophysus, Ctenosaura, Iguana and Sauromalus the anterolateral projection overlapping the dentary and surangular is extended forward as an elongated triangular or rectangular process. The smallest angles of triangulation occur in Ctenosaura and Brachylophysus in which the projection is elongated and splintlike. In Iguana and Sauromalus the anterior apex of the projection is rounded. The conditions of Dipsosaurus is similar to that of Amblyrhynchus and Conolophus where the lateral projection of the coronoid bone is mostly ventral in nature. There is, however, in Dipsosaurus, a small rounded anterior projection on the anterior border of the process.

### TABLE 33

<table>
<thead>
<tr>
<th>Genus</th>
<th>Length</th>
<th>Width</th>
<th>Width-Length Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Min.</td>
<td>Mean</td>
<td>Max.</td>
</tr>
<tr>
<td></td>
<td>Min.</td>
<td>Mean</td>
<td>Max.</td>
</tr>
<tr>
<td>Amblyrhynchus</td>
<td>5.1</td>
<td>5.3</td>
<td>5.5</td>
</tr>
<tr>
<td>Brachylophysus</td>
<td>4.3</td>
<td>4.5</td>
<td>4.7</td>
</tr>
<tr>
<td>Chalarodon</td>
<td>3.1</td>
<td>3.2</td>
<td>3.4</td>
</tr>
<tr>
<td>Conolophus</td>
<td>2.8</td>
<td>3.0</td>
<td>3.2</td>
</tr>
<tr>
<td>Cyclura</td>
<td>2.5</td>
<td>2.7</td>
<td>2.9</td>
</tr>
<tr>
<td>Dipsosaurus</td>
<td>3.0</td>
<td>3.2</td>
<td>3.4</td>
</tr>
<tr>
<td>Iguana</td>
<td>3.5</td>
<td>3.7</td>
<td>3.9</td>
</tr>
<tr>
<td>Oplurus</td>
<td>3.0</td>
<td>3.2</td>
<td>3.4</td>
</tr>
<tr>
<td>Sauromalus</td>
<td>2.5</td>
<td>2.7</td>
<td>2.9</td>
</tr>
</tbody>
</table>

**Teeth**

Teeth are pleurodont and are borne by the dentary in the lower jaw, the maxilla and premaxilla of the upper jaw, and the pterygoid of the palate. The possession of teeth and the numbers in each genus are summarized in table 34.

Pterygoid teeth are found in many genera on the pterygoid bones and their numbers are variable among individuals. Of five skulls of _Amblyrhynchus_ examined, only two had pterygoid teeth and these varied between 3-7 per side. These teeth were very tiny or represented only by a few sockets. In four skulls of _Brachylophysus_, pterygoid teeth ranged in number from 1-8 per side. _Chalarodon_ had well developed teeth in all four skulls examined, but with few in number, ranging from 2-4 per side. In five skulls of _Conolophus_ only one had remnants of teeth. These remnants consisted of a few sockets on each pterygoid bone. In _Ctenosaura_ all skulls had numerous well developed teeth numbering from 3-14 per side. A similar situation existed in _Cyclura_ with 1-10 teeth per side, _Iguana_ with 8-27 teeth per side, and _Oplurus_ with 4-9 teeth per side. In _Sauromalus_ six skulls were examined and four had between 1-7 teeth per side. Teeth were absent in the other two skulls. Only in _Dipsosaurus_ were there no pterygoid teeth or their vestiges in the four skulls examined. Camp (1923:367) omits _Dipsosaurus_ from his list of Iguanidae lacking pterygoid teeth. This may be a mistake on his part or perhaps an examination of a larger series of skulls may reveal that some pterygoid teeth are present in some individuals of this genus.

Montanucci (1968:307-314) comments on the pterygoid teeth of _Iguana_ and _Ctenosaura_ and indicates that in _Iguana_ the teeth have taken over the function of gripping as the lateral teeth are specialized for shearing. In _Ctenosaura_ the pterygoid teeth share the gripping function with less specialized lateral teeth. He also indicates that there is a relationship between size of the skull and number of pterygoid teeth.

**Premaxillary teeth** are found in all ten genera. These are less cuspid than the lateral teeth in _Sauromalus_ (Avery and Tanner, 1964:7-8). Observations on other genera indicates this is also the case for _Ctenosaura_, _Cyclura_, _Iguana_, _Dipsosaurus_ and _Oplurus_. In the other genera the premaxillary teeth bear secondary cusps.

**Maxillary teeth** are present in all genera and number from 15 to 26 per side in skulls examined. From our observations and those of Montanucci (1968:307-315) there appears to be a size-number relationship in iguanids, with smaller skulls always having less teeth than larger skulls in the same genus.

The cusps of the teeth differ considerably between genera. According to the system of Hotton (1955:91) the cuspidate character of the teeth of all genera would fit the category “high degree.” The cusp number and shape varies within this category. _Chalarodon_, _Iguana_ and _Oplurus_ have small cusps and are poorly defined. _Brachylophysus_, _Ctenosaura_, _Cyclura_, _Dipsosaurus_ and _Sauromalus_ have cusps well defined but not separated by deep indentions. In _Amblyrhynchus_ and _Conolophus_ the lateral cusps are well defined and widely separated from the central cusp of the tooth. The number of cusps per tooth also varies from genus to genus. _Amblyrhynchus_, _Brachylophysus_, _Chalarodon_,
and *Ophthalmus* are all tricuspatate. *Conolophus*, *Ctenosaura* and *Dipsosaurus* are tricuspatate with a few teeth bearing up to five cusps. In *Cyclura* and *Sauromalus* teeth with up to seven cusps are common and in *Sauromalus*, as many as nine occur. The most highly cuspatate teeth belong to *Iguana* which exhibits up to 13 cusps per tooth in some individuals. Hutton (1955) and Montanucci (1968) attribute the number of cusps per tooth to the kind of diet and specialized functions (gripping, shearing, masticating) of the teeth. It appears that lizards with similar diet and eating habits have similar dentition.

Dentary teeth are found in all ten genera. The number of teeth per bone is slightly larger than that for the maxilla of the same lizard. This is because the upper teeth are found on the premaxilla as well. The sum of one half of the teeth of the premaxillae and all the maxillary teeth of one side should roughly equal the number of dentary teeth.

In general, teeth of the dentary are similar to those of the maxilla and premaxilla and the size-number relationship exists for them as well.

### TABLE 34

<table>
<thead>
<tr>
<th>Genus</th>
<th>Premaxilla</th>
<th>Maxillary</th>
<th>Dentary</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Amblyrhynchus</em></td>
<td>7-7</td>
<td>17-21</td>
<td>17-24</td>
</tr>
<tr>
<td><em>Brachylophus</em></td>
<td>5-6</td>
<td>16-19</td>
<td>18-21</td>
</tr>
<tr>
<td><em>Chalarodon</em></td>
<td>2-4</td>
<td>16-18</td>
<td>19-21</td>
</tr>
<tr>
<td><em>Conolophus</em></td>
<td>None</td>
<td>15-20</td>
<td>17-21</td>
</tr>
<tr>
<td><em>Ctenosaura</em></td>
<td>3-14</td>
<td>20-26</td>
<td>20-33</td>
</tr>
<tr>
<td><em>Cyclura</em></td>
<td>6-10</td>
<td>19-23</td>
<td>22-28</td>
</tr>
<tr>
<td><em>Dipsosaurus</em></td>
<td>None</td>
<td>16-19</td>
<td>20-23</td>
</tr>
<tr>
<td><em>Iguana</em></td>
<td>8-52</td>
<td>20-26</td>
<td>19-30</td>
</tr>
<tr>
<td><em>Ophthalmus</em></td>
<td>4-9</td>
<td>15-19</td>
<td>16-23</td>
</tr>
<tr>
<td><em>Sauromalus</em></td>
<td>0-7</td>
<td>16-20</td>
<td>15-25</td>
</tr>
</tbody>
</table>

**Hyoid Elements**

The hyoids of the iguanines (fig. 8) are basically alike in structure. The hyoid is always cartilaginous in nature and consists of a central disc, the basihyal, to which is attached an anterior process, the glossohyal or processes entoglossus; an anterolateral projection on each side, the hypohyal; and two ceratobranchials, projecting posteriorly on each side. The medial ceratobranchials (II) are paired and extend posteriorly. In *Iguana* these are involved in operating the dewlap. The lateral ceratobranchials (I) project posterolaterally from the basihyal and articulate with the hypohyal by means of a lateral cerohyal which extends between the lateral terminations of each cartilage.

Unfortunately hyoids are seldom preserved in museum collections. As a result only one or two hyoids from each genus were examined, but some differences between genera can be noted. The shape of the hyoid corresponds to the shape of the animal. Iguanines that are dorsoventrally flattened normally have short hyoids with a large lateral spread of the ceratohyal and ceratobranchial I’s. Such is found in *Conolophus*, *Cyclura*, and *Sauromalus*. Most of the remaining genera are compressed laterally, and the spread of lateral elements of the hyoid in these is less than in the dorsoventrally flattened forms.

The basihyal is broader than long in some dorsoventrally flattened forms such as *Sauromalus* but is elongated in *Conolophus*, *Ctenosaura*, *Cyclura*, and the other genera. *Sauromalus* also differs from the other genera in that the ceratobranchial II’s are spread apart in life.

Individual elements of the hyoid show some differences which may be of phylogenetic importance. The dorsomedia1 portion of the ceratohyal is enlarged into a triangular to spoon shaped flange in *Amblyrhynchus*, *Brachylophus*, *Conolophus*, *Ctenosaura*, *Cyclura*, *Dipsosaurus*, *Iguana*, and *Sauromalus*. In *Ophthalmus* this flange is extremely small and is absent in *Chalarodon*. All other elements of the hyoid differ in length but not in shape.

**Sternum and Ribs**

The sterna and ribs of the iguanines have been discussed by Etheridge (1965) who examined the relationships of the abdominal skeleton of iguanids to the sternum and figured those of *Amblyrhynchus* and *Chalarodon*. Etheridge indicates that abdominal or inscriptive ribs are associated with the sternum in at least four different ways in the family Iguanidae. Three of Etheridge’s four patterns include iguanines. In one type “all of the inscriptive ribs posterior to the xiphisternum are attached to their corresponding dorsal ribs and end free without reaching the ventral midline” (Etheridge, 1965:163). Included in this group are *Sauromalus* and some individuals of *Conolophus*, *Amblyrhynchus*, *Cyclura*, and *Ctenosaura*. A second type according to Etheridge (1965:163) “is similar to the preceding except that one or two of the inscriptive rib pairs, either the first or second, or both may join one another at the ventral midline to form continuous chevrons.” *Iguana*, *Brachylophus* and some *Conolophus*, *Amblyrhynchus*, *Cyclura* and *Ctenosaura* have this type of attachment. A third pattern involves *Chalarodon* and *Ophthalmus* and according to Etheridge (1965:166) “consists entirely of paired elements that are free of attachment either to their corresponding dorsal ribs or to one another at the ventral midline. Members of the pair may approach one another very closely, touch, or even overlap midventrally, but never join one another to form a continuous chevron”. It is perplexing to note that although Etheridge mentions having examined *Dipsosaurus*, he fails to assign it an abdominal skeletal type.
A. *Amblyrhychnus cristatus*. BYU 22810. x 1.25
B. *Brachylophus fasciatus*. MCZ 15009. x 2.0
C. *Chalarodon madagascariensis*. MCZ 11531. x 4.0
D. *Conolophus pallidus*. MCZ 79772. x 1.0
E. *Ctenosaura pectinata*. MCZ 2176. x 1.5

Key to symbols used in Figure 1.

- ec-ectopterygoid
- fe-fenestra exonarina
- fr-frontal
- ju-jugal
- mx-maxilla
- na-nasal
- ob-orbit
- pal-palatine
- par-parietal
- pt-pineal foramen
- pm-premaxilla
- pot-postorbital
- prf-prefrontal
- ptf-ptyerygoid
- ptf-postfrontal
- qu-quadrato
de-
t-quadrate
- stf-supratemporal fossa
- so-supraoccipital
- sq-squamosal

Figure 1. Dorsal view of skull.
A. Cyclura macleayi. MCZ 6915, x 0.75
B. Dipsosaurus dorsalis. BYU 21726, x 2.0
C. Iguana iguana. BYU 22795, x 1.0
D. Oplurus sebae. MCZ 37191, x 3.0
E. Sauromalus obesus. BYU 21728, x 2.0

Key to symbols used in Figure 2.
ec-ectopterygoid
fe-fenestra exonarina
fr-frontal
ju-jugal
mx-maxilla
na-nasal
ob-orbit
pal-palatine
par-parietal
pl-pineal foramen
pm-premaxilla
pot-postorbital
prf-prefrontal
pt-pterzygoid
ptf-postfrontal
qu-quadratc
stf-supratemporal fossa
so-supraoccipital
sq-squamosal

Figure 2. Dorsal view of skull.
A. *Amblyrhynchus cristatus*. BYU 22810. x 1.25
B. *Brachylophus fasciatus*. MCZ 15009. x 2.0
C. *Chalarodon madagascariensis*. MCZ 11513. x 4.0
D. *Conolophus pallidus*. MCZ 79772. x 1.0
E. *Ctenosaura pectinata*. MCZ 2176. x 1.5

Key to symbols used in Figure 3:
- bo-basioccipital
- bp-basipterygoid process
- bs-basisphenoid
- ec-ectopterygoid
- ju-jugal
- mx-maxilla
- pal-palatine
- pm-premaxilla
- po-postorbital
- pp-parasphenoid process
- pr-pyriform recess
- pt-pterigoid
- pt-t-pterigoid teeth
- qu-quadrate
- sq-squamosal
- vo-vomer

Figure 3. Ventral view of skull.
A. *Cyrtora maceleyi*. MCZ 6915. x 0.75
B. *Dipsaurus dorsalis*. BYU 21726. x 2.0
C. *Iguana iguana*. BYU 22795. x 1.0
D. *Opimus schae*. MCZ 37191. x 3.0
E. *Sauromalus obesus*. BYU 21728. x 2.0

Key to symbols used in Figure 4.
bo-basioccipital
bp-basipterygoid process
bs-basisphenoid
ec-ectopterygoid
ju-jugal
mx-maxilla
pal-palatine
pm-premaxilla
po-postorbital
pp-preparasphenoid process
pt-pterigoid
ptt-pterigoid teeth
qu-quadratc
sq-squamosal
vo-vomer

Figure 4. Ventral view of skull.
A. *Amblyrhynchus cristatus*. BYU 22810. × 1.25
B. *Brachylophus fasciatus*. MCZ 15009. × 2.0
C. *Chalarodon madagascariensis*. MCZ 11531. × 4.0
D. *Conolophus pallidus*. MCZ 79772. × 1.0
E. *Ctenosaura pectinata*. MCZ 2176. × 1.5

Key to symbols used in Figure 5:
- an-angular
- ar-articular
- co-coronoid
- de-dentary
- ee-ectopterygoid
- ep-epitypogyd
- fe-fenestra exornina
- fr-frontal
- ju-jugal
- la-lacrimal
- mx-maxilla
- na-nasal
- ob-orbit
- pm-premaxilla
- po-postorbit
- pp-parasphenoid process
- prf-prefrontal
- pr-parietal
- pt-pterygoid
- ptf-postfrontal
- qu-quadrate
- sq-squamosal
- sr-surangular

Figure 5. Lateral view of skull.
A. Cycloche cleyi. MCZ 6915, x 0.75
B. Dipsosaurus dorsalis. BYU 21726, x 2.0
C. Iguana iguana. BYU 22795, x 1.0
D. Oplurus sebae. MCZ 27191, x 3.0
E. Sauromalus obesus. BYU 21728, x 2.0

Key to symbols used in Figure 6.

ar-articulare
cor-coronoid
de-dentary
ee-ectopterygoid
ep-epipterygoid
fe-fenestra exonatina
ju-jugal
la-lacrima
mx-maxilla
na-nasal
ob-orbit
pm-premaxilla
po-postorbital
pp-parasphenoid process
prf-prefrontal
pr-parietal
pt-pterigoid
ptf-postfrontal
qu-quadrat
sq-squamosal
sr-surangular

Figure 6. Lateral view of skull.
A. *Amblyrhynchus cristatus*. BYU 22810. × 1.75
B. *Brachylophus fasciatus*. MCZ 15009. × 2.0
C. *Chalarodon madagascariensis*. MCZ 11531. × 4.0
D. *Conolophus pallidus*. MCZ 79772. × 1.0
E. *Ctenosaura pectinata*. MCZ 2176. × 1.5
F. *Cyclus maccleyi*. MCZ 6915. × 10.75
G. *Dipsosaurus dorsalis*. BYU 21726. × 2.0
H. *Iguana iguana*. BYU 22795. × 1.0
I. *Ophurus sebae*. MCZ 37191. × 3.0
J. *Sauromalus obesus*. BYU 21728. × 2.0

Key to symbols used in Figure 7.
- alf-anterior inferior alveolar foramen
- an-angular
- anp-angular condyle
- co-coronoid
- de-dentary
- sp-splenial
- sr-surangular

Figure 7. Medial view of mandible.
A. *Amblyrynchus cristatus*. BYU 22810. x 10.75
B. *Brachylophus fasciatus*. BYU 23743. x 1.0
C. *Chalarodon madagascariensis*. MCZ 11522. x 4.0
D. *Conolophus ruber cristatus*. MCZ 2027. x 0.75
E. *Ctenosaura pectinata*. BYU 22796. x 10.75
F. *Cyclura carinata*. MCZ 59255. x 1.0
G. *Dipsoaurus dorsalis*. BYU 21726. x 1.5
H. *Iguana iguana*. BYU 22852. x 1.0
I. *Ophurus sebac*. MCZ 27188. x 3.0
J. *Sauromalus obesus*. MCZ 8894. x 1.5

Key to symbols used in Figure 8.

bh-basihyal
ch-ceratohyal
gh-glossohyal
hh-hypohyal

Figure 8. Ventral view of Hyoid Bones.
A. *Amblyrhynchus cristatus*. MCZ 2006. × 1.0
B. *Brachylophus fasciatus*. MCZ 15008. × 2.0
C. *Chalarodon madagascariensis*. MCZ 11531. × 4.0
D. *Conolophus pallidus*. MCZ 79772. × 1.0
E. *Ctenosaura pectinata*. MCZ 2176. × 1.5

Key to symbols used in Figure 9,
- cl-clavicle
- ic-interclavicle
- sc-ster nal cartilage
- sf-ster nal fontanelle
- sr-ster nal ribs
- xr-xiphisternal ribs

Figure 9. Ventral view of sternum.
A. *Cyclura macleyi*. MCZ 6915, x 1.0
B. *Dipsosaurus dorsalis*. BYU 21726, x 2.0
C. *Iguana iguana*. MCZ 54989, x 1.0
D. *Ophius gularis*. MCZ 37191, x 3.0
E. *Sauromalus obesus*. MCZ 8894, x 2.0

Key to symbols used in Figure 10.
- cl-clavicle
- ic-interclavicle
- sc-ster nal cartilage
- sf- sternal fontanelle
- sr- sternal ribs
- xr-xiphisternal ribs

Figure 10. Ventral view of sternum.
The several specimens of Dipsosaurus examined conformed to Etheridge's second type.

The sternum of all iguanines examined (Figs. 9 and 10) consists of a sternal cartilage which articulates laterally with four pairs of sternal ribs and posteriorly with two pairs of xiphoïd ribs. Anteriorly the sternal cartilage is attached to and partially surrounds a “T” shaped interclavicle. The arms of the “T” are of different lengths and leave the body of the interclavicle.

Sternal cartilage

Sternal cartilage corresponds in shape to general shape of the lizards. In dorsoventrally flattened forms the cartilage is wider than long. This situation exists in Sauronaltus and Amblyrhynchus and is about equally as wide as long in Ctenosaura and Cyclura. All other genera have elongated sterna.

The sterna in some forms is pierced by sternal fontanelles. Camp (1923: 409-410) reports fontanelles to be lacking in Chalarodon and Sauronaltus. He found a single median fontanelle in Iguana and Dipsosaurus. Two fontanelles were not recorded for any iguanines. We have found fontanelles to be lacking in Amblyrhynchus, Chalarodon, and Sauronaltus. A single central fontanelle exists in Brachylophus, Conolophus, Ctenosaura, Cyclura, Dipsosaurus, and Iguana. These openings usually surround the terminal end of the body of the interclavicle. The one sternum of Ophuris examined has two small fontanelles along the center line.

Interclavicle

Interclavicle differs in size of the body, the angles of the anterior arms to the body, and the length of the arms. The arms attach to the body at 90° angles in Amblyrhynchus, Brachylophus, Iguana, and Sauronaltus. The arms are attached at 45° angles in Chalarodon, Conolophus, Ctenosaura, Cyclura, and Ophuris. In Dipsosaurus the interclavicle arms are in an intermediate position between the two preceding groups. The arms are attached at approximately a 30° angle to the body.

The length of the interclavicle arms are short in Brachylophus and Dipsosaurus being about one quarter the length of the interclavicle body. The longest arms in relation to the body are those of Amblyrhynchus, Sauronaltus and Iguana, being about equal to the length of the body. In Ophuris, Ctenosaura, Chalarodon, Conolophus, and Cyclura the arms are two-thirds the length of the body.

MYOLOGY

In order to avoid confusion, the terminology used for the following description of the muscles is that of Robison and Tanner (1962), Avery and Tanner (1964), and Jenkins and Tanner (1968). Any deviations will be noted in the text.

Throat Musculature

M. Intermandibularis anterior superficialis

M. Intermandibularis anterior superficialis (Figs. 11 and 12) is a short straplike muscle connecting the rami of the mandibles in the area between the origin of the genioglossus and the first mandibulohyoideus muscle. The body lies superficial to the intermandibularis anterior profundus, mandibulohyoideus II and the genioglossus muscle. It is overlain superficially by the skin.

It arises from the oral membrane, the anterior fibers of the intermandibularis anterior profundus, and the crista dentalis ligament. The muscle insertion is with fibers of its opposite equivalent along the midline raphe.

This muscle is constant in all genera examined with the following exceptions. It was found to be absent in one juvenile Dipsosaurus examined and narrow and reduced in adults. The muscle was also found reduced and narrow in Iguana where it contributes to the anterior margin of the muscular contents of the dewlap. In the remaining genera the muscle is sheetlike with the width at least half the length.

M. Intermandibularis anterior profundus

M. Intermandibularis anterior profundus (Figs. 11 and 12) is a continuous sheet of muscle lying superficial to the majority of throat musculature and just deep to the skin. The muscle arises from the median surface of the splenial and cornoid bones and from the crista dentalis by a tendon. The anterior fibers extend anteromedially across the throat to insert on the ventral midline raphe. The posterior fibers also insert on the midline raphe after arising via several interdigitations with the first mandibulohyoideus muscle.

The muscle is relatively consistent in the iguanines examined. In Iguana the intermandibularis anterior profundus extends deep into the dewlap with the fibers ending about one-third the distance from the ventral border. It also forms the bulk of the muscular contents of the dewlap.

M. Intermandibularis posterior

M. Intermandibularis posterior (Figs. 11, 12, 24 and 25) is a thin sheet overlying the angle of the jaw and covering superficially, the posterior fibers of the intermandibularis anterior profundus. The muscle sheet is extremely thin in the posterior extremities
and thickens towards its anterior extremities. The posterior origin of this muscle is from the lateral surface of the mandible beginning at the midpoint of the retroarticular process. Anteriorly the muscle originates as the last two or three interdigitations of the anterior profundus muscle with which it is continuous. Its insertion on the midline raphe is characterized by a wide aponeurosis which leaves both sets of fibers from each side separated in some specimens.

Posteriorly the intermandibularis posterior is continuous with the constrictor colli from which it can be delineated by a natural separation of the muscle fiber bundles. The possession of this separation is variable in the genera examined. In Amblyrhynchus, Brachylophus, Charadriodon, Diposaurus, Iguana, and Ophurus the constrictor colli and intermandibularis posterior are closely associated along their entire common border. In Conolophus and Ctenosaura the two muscles are separated laterally at the angle of the jaw with part of the pterygomandibularis being visible between them. In Cyclura and Saurornatus the edges of the two muscles become more separated towards the midline raphe. In Iguana the intermandibularis posterior extends deep into the dewlap ending about a third of the way to the ventral border. It also forms the posterior portion of the dewlap’s muscular content.

M. Mandibulohyoideus I

M. Mandibulohyoideus I (Figs. 11 and 12) is a long triangular muscle which extends two-thirds of the length of the mandible, and lies lateral to the second mandibulohyoideus, mesial to the mandibular rami, and anterior to the insertion of the sternohyoideus. This muscle lies dorsal to the intermandibularis muscle and ventral to the genioglossus, hyoglossus, mandibulohyoideus III, and the pterygomandibularis muscles. At its anterior end, the mandibulohyoideus I interdigitates at right angles with the fibers of the intermandibularis anterior profundus.

The mandibulohyoideus I originates along the ventromesial surface 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 inserts just posterolateral to the insertion of the mandibulohyoideus II along the anterolateral border of the distal three-fourths of the first ceratobranchial.

There is no deviation from this pattern in the general examined.

M. Mandibulohyoideus II

M. Mandibulohyoideus II (Figs. 11 and 12) is a small elongated muscle tapering at both ends, lying mesial to the mandibulohyoideus I and inserting alongside its opposite equivalent on the midventral raphe. It lies deep to the intermandibularis muscle and superficial to the tongue, the genioglossus, and the hyoglossus.

The origin of the mandibulohyoideus muscle is a narrow tendon, an anterior extension of the midline raphe, from the capsule of cartilage overlying the mandibular symphysis. The muscle inserts on the anterior border of the proximal end of the first ceratobranchial, anteromesial to the insertion of the first mandibulohyoideus. A similar situation exists in all the genera examined.

M. Mandibulohyoideus III

M. Mandibulohyoideus III (Figs. 13 and 14) is a thick straplike muscle extending over the pterygomandibularis and with attachments to it by connective tissue. The course of this muscle is nearly parallel to the mandibular rami on each side. It lies between the ceratohyal and the pterygomandibularis.

In all genera this muscle arises from the ventromesial surface of the dentary and angular bones between the anterior and posterior myohyoid foramina. The narrow insertion of this muscle is on the lateral surface of the ceratohyal, distal to its midpoint.

M. Genioglossus

M. Genioglossus (Figs. 11, 12, 13 and 14) is a thick bandlike muscle in all genera which, with its partner on the opposite side, occupies a large area between the mandibular rami. Its position is ventral to the tongue and anterior to the basihyal. The first, second, and third mandibulohyoideus muscles and the intermandibularis muscle all lie ventral to it.

The genioglossus originates along the ventral and mesial surfaces of the anterior one-sixth of the mandibular ramus, and dorsal to Meckel’s canal. The mesial fibers extend posteriorly, while the lateral fibers turn dorsally and laterally before passing posteriorly.

M. Hyoglossus

M. Hyoglossus Figs. 13 and 14) is a thick broad muscle lying lateral to the basihyal and the second ceratobranchial and basial to the mandible, the mandibulohyoideus III and the pterygomandibularis. The mandibulohyoideus I and II muscles and the anterior portion of the mandibulohyoideus III lies superficial to it. The hyoglossus muscle lies ventral to the ceratohyal and the oral membranes.

The origin of this muscle is along the anterolateral face of the distal two-thirds of the first ceratobranchial and dorsal to the insertion of the mandibulohyoideus I muscle. The muscle traverses an anterior path to interdigitate with the genioglossus near the proximal end of the hypohyal and to form the main body of the tongue.

M. Branchiohyoideus

M. Branchiohyoideus (Figs. 13 and 14) lies dorsal to the hyoglossus, between the ceratohyal and the
first ceratobranchial of the hyoid bone. This muscle lies just ventral to the oral membrane which in turn lies ventral to the massive pterygomandibularis muscle.

The branchiomyoides has its origin from the post-ömerosal surface of the posterior two-thirds of the ceratothyal. Its path passes parallel to the two hyoid limbs, and inserts near the distal end of the first ceratobranchial.

In Sauromalus the insertion on the first cerato-branchial is narrow whereas the insertion in the other genera covers over half the distal portion of the first ceratobranchial.

M. Sternohyoides

M. Sternohyoides (Figs. 11, 12, 13, 14, 25 and 26) is an extensive muscle sheet, occupying a large area posterior to the first ceratobranchial cartilage and anterior to the sternum and clavicle. Its position is deep to the intermandibularis and the constrictor colli anteriorly, and to the episternocleidomastoidis, the trapezius, a small part of the levator scapulae profundus, pharyngeal membranes, trachea, clavicle, and the clavodeltoideus.

There has been considerable confusion in the literature concerning the limits of this muscle. Davis (1934:19) considers the superficial layer to be divisible into three parts in Crotaphytus. One of these muscles he calls the omohyoides. Robison and Tanner (1962:6) consider this muscle continuous in the same genus. Oelrich (1956:51-52) treats this muscle in Ctenosaura as being continuous but owing to the different origin and direction of the fibers, he separates the layers into omohyoides and sternohyoides. Kesteven's studies (1944:245-246) on the agamid, Physignathus, suggests a separation in young specimens and treats these layers as consisting of three parts which he considers to represent the similar, though distinct divisions present in Varanus. In the iguanines we have decided to treat the sternohyoides complex as three separate muscles: sternohyoides, sternothyroideus, and omohyoides.

The sternohyoides originates as several heads from the clavicle. Its oblique fibers extend anteriorly to insert on the posterior surface of the first ceratobranchial. In all the genera examined, the sternohyoides forms a broad elongated sheet of muscle with the exception of Ophurus where its appearance is narrow and cordlike.

M. Omohyoides

M. Omohyoides (Figs. 11, 12, 15, 16, 25, and 26) is sheetlike, and forms the lateral extension of the sternohyoides complex. In all genera examined it originates mesially from the lateral tip of the transverse process of the interclavicle with some fibers of the episternocleidomastoides. Laterally, the omohyoides takes its origin from the anterolateral surface of the clavicle and anterior border of the suprascapula.

The fibers of the omohyoides pass obliquely anterior to insert on the posterior margin of the first ceratobranchial and the proximal end of the second ceratobranchial cartilages.

In all of the iguanines examined except Chalarodon, the medial border is different to separate from the lateral border of the sternohyoides. The delinea- tion of both muscles must be made by comparing the origins and insertions. In Chalarodon the omohyoides is easily separated as the fibers of this muscle pass oblique to those of the sternohyoides.

M. Sternothyroideus

M. Sternothyroideus (Figs. 11 and 12) is the most medial extension of the sternohyoides complex and can be separated from the other members of this muscle group by its different origin and insertion. The name sternothyroideus is used as in Camp (1923:451) who figured this muscle as the deep member of the complex in Brachylophus.

The origin of this muscle is considered to be those fibers that arise from the interclavicle and sternum. These fibers pass anteriorly and parallel to the trachea to insert on the hyoid at the point of union between the basihyal and the hypohyal.

In the genera examined the lateral border of the sternothyroides and the medial border of the sternohyoides are difficult to determine except in Ophurus and Chalarodon where the borders of both muscles are separated in situ.

Neck Musculature

M. Constrictor colli

M. Constrictor colli (Figs. 11, 12, 17, 18, 23 and 24), the most superficial muscle of the cervical region, is overlain by the connective tissue of the skin and a few scattered fat pads. The constrictor colli lies superficial to parts of the depressor mandibularis and episternocleidomastoides, and is from one to two fibers thick.

The main origin of this muscle is on the superficial dorsolateral fascia of the neck which extends almost as far as the posterior margin of the depressor mandibularis. The muscle passes ventrolaterally posterior to the retroarticular process of the articular bone, and inserts on the extensive ventral aponeurosis at the midline, which also serves as the point of insertion for the intermandibularis posterior.

The relationships between the anterior border of the constrictor colli and the posterior border of the intermandibularis posterior have previously been described. The width of the constrictor colli is variable in the iguanines. The muscle is widest, covering most of the lateral surface of the neck, in Amblyrhythynchus, Chalarodon, Cychura, Iguana, and Sauro-
of the dorsal midline of the neck in common with the posterior fibers of the intermediate bundle, and ventral to the origin of the constrictor colli. It extends anteroven-trally along the posterior border of the intermediate bundle and continues past the insertion of the anterior and intermediate bundles to insert on the superficial fascia of the intermandibularis and the skin.

Some variations in the width of the anterior bundles occur in Iguana and Conolophus where the bundle is very narrow and in Amblyrhynchus where the bundle is thick and wide.

The cervicomandibularis also shows considerable variation in distinctness and relationship to the origin of the constrictor colli. Robison and Tanner (1962:8) indicate that this posterior bundle became indistinct in old forms of Crotaphytus. The problem of distinctness may be a function of age. Unfortunately the small sample sizes used in this study can lend no support to that theory.

In Brachylophus, Chalarodon and Dipsosaurus, the cervicomandibularis is extensive and its posterior border at the origin extends posteriorly beyond the posterior border of the origin of the constrictor colli, thereby making the cervicomandibularis the most superficial muscle, at its origin in that area of the neck. In all other genera examined, the cervicomandibularis is completely obscured by the more superficial constrictor colli.

M. Levator scapulae superficialis

M. Levator scapulae superficialis (Figs. 17, 18, 19, 20, 25, 26, 27, 28, 29 and 30) is normally considered to be a muscle of the pectoral girdle. Inasmuch as it originates on the neck, deep to the neck musculature it will be included with these muscles.

The levator scapulae superficialis is a broad fan-shaped muscle, lying mostly anterior, but partly superficial to the suprascapula bone. It is superficial to the levator scapulae profundus, the axial musculature and the posterodorsal fibers of the origin of the omohyoides.

The constrictor colli, trapezius, episternocleido-mastoideus, depressor mandibularis, tympanic membrane, distal ends of the ceratohyal, ceratobranchial bones, and the two levator scapulae muscles.

The depressor mandibularis can be subdivided into three bundles. 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 posteroven-trally with a tendinous insertion on the retroarticular process of the articular bone.

The intermediate bundle, in its posterior region, originates from the fascia along the dorsolateral angle of the neck, in the region of the first 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 intermediate bundle is sheetlike rather than forming a thick mass as does the anterior and posterior bundle.

When distinct the posterior bundle is considered a separate muscle, the cervicomandibularis (Figs. 17, 18, 23, 24, 25, and 26). It is separable from the other two bundles at its insertion and throughout most of its length. It takes its origin from the superficial fascia of the dorsal midline of the neck in common with the posterior fibers of the intermediate bundle, and ventral to the origin of the constrictor colli. It extends anteroven-trally along the posterior border of the intermediate bundle and continues past the insertion of the anterior and intermediate bundles to insert on the superficial fascia of the intermandibularis and the skin.

Some variations in the width of the anterior bundles occur in Iguana and Conolophus where the bundle is very narrow and in Amblyrhynchus where the bundle is thick and wide.

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The levator scapulae superficialis is a broad fan-shaped muscle, lying mostly anterior, but partly superficial to the suprascapula bone. It is superficial to the levator scapulae profundus, the axial musculature and the posterodorsal fibers of the origin of the omohyoides.

The constrictor colli, trapezius, episternocleido-mastoideus, depressor mandibularis, tympanic membrane, distal ends of the ceratohyal, and the first ceratobranchial all contribute to the superficial layer over this muscle.

The origin of the levator scapulae superficialis is in a tendon, common to it and the levator scapulae profundus. The tendon is attached to the diaphysis of the atlas. The muscle extends posterodorsally and inserts on the anterior half of the lateral surface of the scapula. There is little deviation in this pattern in the genera examined.

M. Levator scapulae profundus

M. Levator scapulae profundus (Figs. 19, 20, 27, 28, 29 and 30) is the deep partner of the levator...
scapulae superficialis, and has a similar position with relation to the surrounding muscles, with the exception that the posterior fibers of insertion pass deep to those of the omohyoideus muscle.

The origin is by a common tendon with the levator scapulae superficialis, from the diaphysis of the atlas. Muscle fibers pass posterodorsally to insert along the anterior margin of the suprascapula just ventral to the insertion of the levator scapulae superficialis, and to the anterior surface of the acromial end of the clavicle.

Temporal Musculature

M. Pterygomandibularis

M. Pterygomandibularis (Figs. 11, 12, 13, 14, 15 and 16) is a large muscle at the angle of the jaw covering a large part of the posterior half of the mandible. It reaches its largest size between the mandibular rami and lateral to the trachea. The intermandibularis posterior lies superficial to it laterally with the oral membrane bordering it ventromesially. The third mandibulo-hyoideus and the hyoglossus lie ventral to it.

The origin of the pterygomandibularis is in a heavy tendon arising from the ventral projection of the ectopterygoid, and the transverse process of the pterygoid. Some fibers also originate as a tendinous sheath from the remaining part of the transverse process, and the ventrolateral border of the quadrate process of the pterygoid with part from the ventral border of the basipterygoid process of the basisphenoid bone where this bone articulates with the pterygoid.

The main fibers of this muscle extend posteriorly and posterodorsally, to obscure the ventral and lateral surfaces of the angular, articular, and surangular bones of the mandible. The fibers insert on the dorsal, mesial, and ventral surfaces of the articular bone, including the retroarticular and angular processes. Some fibers form a line across the lateral surface of the angular and the surangular foramen. Between the foramen and the adductor mandibularis externus superficialis, a tendinous insertion extends lengthwise through the muscle mass in a posterior direction and attaches to the angular process of the articular.

M. Levator angularis oris

M. Levator angularis oris (Figs. 23 and 24), the most superficial muscle of the infratemporal fossa, is overlain by the infratemporal fascia and the skin. It covers part of the surface of the adductor mandibularis externus superficialis. It is this muscle which arises from the mesial surfaces of the superficial infratemporal fascia, the ventrolateral surfaces of the squamosal, the posterior part of the jugal, and the anterodorsal angle of the tympanic crest. The fibers pass anteroventrally to insert near the posterior border of the coronoid.

The size of the levator angularis oris differs in the genera examined. In all of the genera except Brachylophus and Dipsoaurus, the muscle covers over half the infratemporal fossa. In Brachylophus and Dipsoaurus the muscle is small and narrow, covering less than a third of the anterior part of the infratemporal fossa.

M. Adductor mandibularis externus superficialis

M. Adductor mandibularis externus superficialis (Figs. 23, 24, 25 and 26), of the infratemporal fossa, is an extensive muscle mass which mesially is scarcely distinguishable from the adductor mandibularis externus medius. It lies beneath the levator angularis oris at its anterior border and beneath the superficial infratemporal fossa at its posterior border.

The superficialis originates from the ventral surface of the postorbital, squamosal, jugal and quadrate bones, and from the lateral surfaces of the tympanic crest. The fibers, which extend anteroventrally, are more ventrally oriented than those of the levator angularis oris. They insert along the beveled, dorsolateral surface of the supra-angular, with fibers passing dorsal to the posterior supra-angular foramen and covering the anterior surangular foramen. The most anterior of these fibers insert on the lateral and posterolateral surface of the coronoid with parts inserting on the lateral surfaces of the bodenaponeurosis.

M. Adductor mandibularis externus medius

M. Adductor mandibularis externus medius (Figs. 17, 18, 23, 24, 25, 26, 27 and 28) is a large muscle, faintly separated from and mesial to the adductor mandibularis externus superficialis and dorsolateral to the adductor mandibularis externus profundus. It is also posterolateral to the pseudotemporalis superficialis with the exception of its anteromesial fibers which are dorsal to that muscle. The origin of this muscle is from the mesial surface of the squamosal, the anterolateral surfaces of the supratemporal and the posterolateral wing of the parietal, the dorsolaterally beveled surface of the parietal, and from the anterior and dorsal surfaces of the quadrate bone. Fibers extend anteroventrally with the dorsal surfaces of the quadrate bone. Fibers extend anteroventrally with the dorsal ones being more anteriorly oriented than the ventral. These insert along the dorsomesial surface of the surangular, the posterior surface of the coronoid, and the lateral, posterior, and mesial sides of the bodenaponeurosis.

M. Adductor mandibularis externus profundus

M. Adductor mandibularis externus profundus (Figs. 29 and 30), a massive muscle, not clearly separable from the adductor mandibularis externus medius, is located ventrolaterally to the pseudotemporalis superficialis, dorsal to the prootic, and lateral.
to the braincase and the supraoccipital.

This muscle's origin arises from the entire posteromesial border of the posterolateral wing of the parietal, from the paroccipital 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 anterolaterally to enter the infratemporal fossa where it passes ventrally to the supratemporal and the posterolateral parietal wing and dorsal to the exoccipital and the posterior process of the prootic bone. At this point it joins with another head from the prootic and continues anterolaterally to insert by the bodenaponeurosis on the posterior surface and base of the coronoid.

The adductor mandibularis externus group has been considered as a single mass (Adams, 1919) with separate slips as described above. According to Oelrich (1956:41) this group is divided into three muscles on the basis of its relations to the three rami of the trigeminal nerve. This system has been followed here for the sake of convenience and clarity. No special differences were noted in the genera examined.

M. Pseudotemporalis superficialis

M. Pseudotemporalis superficialis (Figs. 17, 18, 29, and 30) is a divergent, massive muscle with a complex placement. It 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. The posterior fibers are trapped between the adductor mandibularis externus profundus and the adductor mandibularis externus medius.

The origin of the pseudotemporalis superficialis is 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 the internal surface of the dorsal one-third of the epipterygoid. Fibers of the anterior part pass ventrally while posterior fibers extend anterolaterally. The insertion is with the pseudotemporalis profundus, on the mesial surface of the bodenaponeurosis, the posteromesial border of the coronoid to its base and the dorsal border of the articular to its midpoint.

M. Pseudotemporalis profundus

M. Pseudotemporalis profundus (Figs. 31 and 32), a pyramid shaped muscle, lies just posteromesial to the pseudotemporalis superficialis, lateral to the epipterygoid bone and the levator pterygoideus muscle. This muscle arises from the anterior, lateral, and posterior sides of the ventral two-thirds of the epipterygoid bone. These fibers extend ventrally to insert with the pseudotemporalis superficialis muscle, on the posteromesial border of the coronoid bone and on the dorsal surface of the articular bone to its midpoint.

M. Adductor mandibularis posterior

M. Adductor mandibularis posterior (Figs. 31 and 32) is a wide straplike muscle, lying lateral to the tympanic cavity, the protractor pterygoideus muscle, and mesial to the mandible and to the adductor mandibularis externus muscles.

A few fibers arise from the lateral and mesial surfaces of an aponeurosis running between the mesial crest of the quadrate and Meckel’s cartilage. Other fibers take their origin from the posterior process of the prootic bone. All fibers pass anterolaterally to insert with some fibers of the pseudotemporalis muscles on the dorsal surface of the articular bone, and on Meckel’s cartilage.

### TABLE 35

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<thead>
<tr>
<th>Genus</th>
<th>Intermandibularis Posterior, position of posterior border</th>
<th>Sternothyroides lateral border</th>
<th>Constrictor Colli Width</th>
<th>Cervicomandibularis</th>
<th>Levator Angularis Oris</th>
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<td>X</td>
</tr>
<tr>
<td>Dipsosaurus</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Iguana</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Oplurus</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Sauromalus</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
</tbody>
</table>
M. Levator pterygoideus

M. Levator pterygoideus (Figs. 31, 32, 33, and 34), a triangular shaped muscle, lies posteromesial to the epipterygoid bone and the pseudotemporalis profundus muscle. It lies anterolateral to the protractor pterygoideus and lateral to the prootic membrane of the cranial cavity.

The origin is by a flat tendon from the ventral surface of the parietal bone, mesial to the epipterygoid, and posteriorly along the lateral margin of the parietal to its midpoint. Some fibers fan out posterolaterally to insert, with anterior fibers of the protractor pterygoideus, on the proximal dorsal surface of the quadrate process of the pterygoid bone, beginning posterolaterally to the fossa columella and extending anteromesially, to end mesial to the epipterygoid.

M. Protractor pterygoideus

M. Protractor pterygoideus (Fig. 31, 32, 33, and

OTHER CHARACTERS

Besides the osteology and myology, the structure of the tongue and hemipenes of iguanine lizards has been investigated.

Tongue

Only one tongue from each genus was examined with the exception of Diposaurus, where three tongues were utilized. Measurements were taken of total length, measured from the anterior tip to the most posterior extension of the tongue. Width was recorded as the greatest distance, at a right angle, to the length. Width in all cases was taken at the most posterior extremities of the tongue which is the widest region. The depth of both anterior and posterior indentation or clefts was also measured. Ratios were computed between length and width, length and depth of anterior cleft, and length and depth of posterior cleft.

The tongues (Figure 35) in all the iguanines are fleshy and protrusible with an arrowhead shape, a slight cleft anteriorly and a deeper cleft posteriorly, which surrounds the glottis laterally. The tongue is covered with "...velvety filamentous papillae..." (Oelrich, 1956:53) which are missing or very small at the most anterior tip and become increasingly larger posteriorly until, at the posterior extremity of the tongue, the papillae are fleshy and pointed rather than blunt.

As table 36 shows, the most elongated and narrow tongues are those of Ctenosaura (length times width ratio .491), Saurophalus (.530) and Cyclura (.539). The fattest tongues are found in Chalarodon (.705), Diposaurus (.698), and Ophurias (.691). The other genera show an intermediate situation for this character.

TABLE 36

<table>
<thead>
<tr>
<th>Genus</th>
<th>Length</th>
<th>Width</th>
<th>Anterior Cleft</th>
<th>Posterior Cleft</th>
<th>Length Width Ratio</th>
<th>Length Ant Cleft Ratio</th>
<th>Length Post Cleft Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amblyrynchus</td>
<td>.33</td>
<td>.19</td>
<td>.33</td>
<td>.55</td>
<td>.572</td>
<td>.034</td>
<td>.290</td>
</tr>
<tr>
<td>Brachylophus</td>
<td>.30</td>
<td>.15</td>
<td>.45</td>
<td>.58</td>
<td>.572</td>
<td>.039</td>
<td>.288</td>
</tr>
<tr>
<td>Chalarodon</td>
<td>.68</td>
<td>.48</td>
<td>.04</td>
<td>1.9</td>
<td>.705</td>
<td>.058</td>
<td>.279</td>
</tr>
<tr>
<td>Conolophus</td>
<td>.37</td>
<td>.22</td>
<td>.24</td>
<td>8.9</td>
<td>.694</td>
<td>.064</td>
<td>.239</td>
</tr>
<tr>
<td>Ctenosaura</td>
<td>.24</td>
<td>.12</td>
<td>.28</td>
<td>9.0</td>
<td>.491</td>
<td>.118</td>
<td>.368</td>
</tr>
<tr>
<td>Cyclura</td>
<td>16.5</td>
<td>8.9</td>
<td>0.6</td>
<td>6.1</td>
<td>.539</td>
<td>.036</td>
<td>.269</td>
</tr>
<tr>
<td>Diposaurus</td>
<td>11.5</td>
<td>8.0</td>
<td>1.7</td>
<td>3.6</td>
<td>.698</td>
<td>.147</td>
<td>.318</td>
</tr>
<tr>
<td>Ophurias</td>
<td>28.6</td>
<td>16.0</td>
<td>1.4</td>
<td>8.4</td>
<td>.559</td>
<td>.049</td>
<td>.293</td>
</tr>
<tr>
<td>Saurophalus</td>
<td>15.9</td>
<td>11.0</td>
<td>1.9</td>
<td>3.9</td>
<td>.691</td>
<td>1.19</td>
<td>.245</td>
</tr>
</tbody>
</table>

34), a broad, short muscle, which forms the anterolateral wall of the tympanic cavity. This muscle lies posteromesial to the levator pterygoideus and lateral to the basisphenoid bone, and the anterior parts of the prootic bone.

The origin of this muscle is from the lateral surface of the anterior inferior process of the prootic bone, the posteroverentral end of the pila antotica, and from a tendon which comes from the anterior inferior process of the prootic to the region of the condyle on the anterior tip of the basispterygoid process of the basisphenoid bone. Most fibers of the protractor pterygoideus fan out, posterolaterally, to insert on the dorsal and mesial crest of the quadrate. Some anterior fibers insert with those of the levator pterygoideus. The majority remain posteromesial to this muscle.

TABLE 36 TONGUE MEASUREMENTS
A. *Amblyrhynchus cristatus*. BYU 22806. x 0.35
B. *Brachylophus fasciatus*. BYU 31955. x 1.0
C. *Chalarodon madagascariensis*. BYU 22801, 22803. x 3.0
D. *Conolophus subcristatus*. BYU 22811. x 10.35
E. *Ctenosaura pectinata*. BYU 22850. x 0.5

Key to symbols used in Figure 11.
- cc-constrictor colli
- ep-episternocondylomastoideus
- g-genioglossus
- iap-intermandibularis anterior profundus
- ias-intermandibularis anterior superficialis
- ip-intermandibularis posterior
- mh1-mandibulohyoideus 1
- my1-mandibulohyoideus 1
- om-omhyoideus
- pe-pectoralis
- pt-pterygomandibularis
- sh-sternohyoideus
- st-sternothyroideus

Figure 11. Ventral view of throat musculature; superficial layer shown at left and first depth at right.
A. Cyclochila michalis. BYU 22799 \( \times 1.0 \)
B. Diplosaurus dorsalis. BYU 31954 \( \times 1.5 \)
C. Iguana iguana. BYU 22851 \( \times 0.75 \)
D. Oplurus sebae. BYU 11504. \( \times 1.25 \)
E. Sauromalus obesus. BYU 31953. \( \times 1.5 \)

Key to symbols used in Figure 12.
- cc-constrictor colli
- cp-episternocleidomastoideus
- ge-genioglossus
- iap-intermandibularis anterior profundus
- ias-intermandibularis anterior superficialis
- ip-intermandibularis posterior
- mhl-mandibulohyoideus I
- myl-mandibulohyoideus II
- om-omohyoideus
- pe-pectoralis
- pt-pterigomandibularis
- sh-sternohyoideus
- st-sternothyroideus

Figure 12. Ventral view of throat musculature; superficial layer shown at left and first depth at right.
A. Amblyrhynchos cristatus. BYU 22806. x 0.35
B. Brachylophus fasciatus. BYU 31955. x 1.0
C. Chalarodon madagascariensis. BYU 22801, 22803. x 3.0
D. Conolophus subcristatus. BYU 22811. x 0.35
E. Ctenosaura pectinata. BYU 22850. x 0.5

Key to symbols used in Figure 13.
- bh-brachiohyoideus
- ge-gemiglo^us
- hg-hyoglossus
- mHIII-mandibulohyoideus III
- pm-pharyngeal membrane
- pt-pterogomandibularis
- sh-sternohyoideus

Figure 13. Ventral view of throat musculature: second depth at left and third depth at right.
A. Cyclura nuchalis. BYU 22799, x 1.0
B. Diplosaurus dorsalis. BYU 31954, x 1.5
C. Iguana iguana. BYU 22851, x 10.75
D. Oplurus sebae. BYU 11504, x 1.25
E. Sauromalus obesus. BYU 31953, x 1.5

Key to symbols used in Figure 14.
- bh-branchiohyoideus
- ge-genioglossus
- hg-hyoglossus
- myIII-mandibulo-hyoideus III
- pm-pharyngeal membrane
- pt-pterigomandibularis
- sh-sternohyoideus

Figure 14. Ventral view of throat musculature; second depth at left and third depth at right.
A. *Amhlyrynchus cristatus*. BYU 22806. x 0.35
B. *Brachylophus fasciatus*. BYU 31955. x 1.0
C. *Chalarodon madagascariensis*. BYU 22801, 22803. x 3.0
D. *Conolophus subcristatus*. BYU 22811. x 10.35
E. *Ctenosaura pectinata*. BYU 22850. x 0.5

Key to symbols used in Figure 15.
- cl-clavicle
- ic-interclavicle
- lv-larynx
- om-omohyoideus
- pm-pharyngeal membrane
- pt-pterigomandibularis
- tr-trachea

Figure 15. Ventral view of throat musculature; fourth depth at left and fifth depth at right.
A. *Cyclura nuchalis*. BYU 22799. x 1.0
B. *Dipsosaurus dorsalis*. BYU 31954. x 1.5
C. *Iguana iguana*. BYU 22851. x 0.75
D. *Oplurus uriae*. BYU 11504. x 1.25
E. *Sauromalus aterius*. BYU 31953. x 1.5

Key to symbols used in Figure 15.
- cl-clavicle
- ic-interclavicle
- l-larynx
- pm-pharyngeal membrane
- om-omohyoides
- pt-pterigoideus
- tr-trachea

Figure 16. Ventral view of throat musculature; fourth depth at left and fifth depth at right.
A. Amblyrhynchus cristatus. BYU 22806. x 0.35
B. Brachylophus fasciatus. BYU 31955. x 1.0
C. Chalarodon madagascariensis. BYU 22801, 22803. x 3.0
D. Conolophus subcristatus. BYU 22811. x 0.35
E. Ctenosaura pectinata. BYU 22850. x 0.5

Key to symbols used in Figure 17.
am-adductor mandibularis externus medius
cce-constrictor colli
cm-cervicomandibularis
dm-depressor mandibularis
ld-latissimus dorsi
ls-levator scapulae superficialis
ps-pseudotemporalis superficialis
tr-trapezius

Figure 17. Dorsal view of head and neck musculature; superficial depth at left and first depth at right.
A. Cyclura nuchalis. BYU 22799. × 1.0
B. Diposaurus dorsalis. BYU 31954. × 1.5
C. Iguana iguana. BYU 22851. × 0.75
D. Ophius sebae. BYU 11504. × 1.25
E. Sauromalus obesus. BYU 31953. × 1.5

Key to symbols used in Figure 18.

- am-adductor mandibularis externus medius
- cc-constrictor colli
- cm-cervicomandibularis
- dm-depressor mandibularis
- ld-lattissimus dorsi
- ls-levator scapulae superficialis
- ps-pseudotemporalis superficialis
- tr-trapezius

Figure 18. Dorsal view of head and neck musculature; superficial depth at left and first depth at right.
A. Amblyrhynchus cristatus. BYU 22806. x 0.35
B. Brachylophus fasciatus. BYU 31955. x 1.0
C. Chalarodon madagascariensis. BYU 22801, 22803. x 3.0
D. Conolophus suberistatus. BYU 22811. x 0.35
E. Ctenosaura pectinata. BYU 22850. x 0.5

Key to symbols used in Figure 19.
ep-episternocleidomastoideus
lp-levator scapulae profundus
ls-levator scapulae superficialis
sd-serratus (dorsal part)
sl-sacrolumbalis

Figure 19. Dorsal view of head and neck musculature; second depth at the left and third depth at the right.
A. Cyclura michalis. BYU 22799, x 1.0
B. Diposaurus dorsalis. BYU 31954, x 1.5
C. Iguana iguana. BYU 22851, x 0.75
D. Ophorus sebae. BYU 11504, x 1.25
E. Sauromalus obesus. BYU 31953, x 1.5

Key to symbols used in Figure 20.
ep-episternocleidomastoideus
lp-levator scapulae profundus
ls-levator scapulae superficialis
sd-serratus (dorsal part)
sl-sacrolumbalis

Figure 20. Dorsal view of head and neck musculature; second depth at the left and third depth at the right.
A. *Amblyrhynchos cristatus*. BYU 22806, x 0.35
B. *Brachylophus fasciatus*. BYU 31955, x 1.0
C. *Chalarodon madagascariensis*. BYU 22801, 22803, x 3.0
D. *Conolophus subcristatus*. BYU 22811, x 0.35
E. *Ctenosaura pectinata*. BYU 22850, x 0.5

Key to symbols used in Figure 21.
- **ie**-intercostales externi
- **sd**-serratus (dorsal part)
- **sp**-spinus dorsi
- **ss**-subscapularis II

Figure 21. Dorsal view of head and neck musculature; fourth depth at left and fifth depth at right.
A. Cyclura nuchalis. BYU 22799. x 1.0
B. Diplosaurus dorsalis. BYU 31954. x 1.5
C. Iguana iguana. BYU 22851. x 0.75
D. Oplurus scutae. BYU 11504. x 1.25
E. Sauromalus obesus. BYU 31953. x 1.5

Key to symbols used in Figure 22.
ie-intercostales externi
sd-serratus (dorsal part)
sp-spinus dorsi
ss-subscapularis II

Figure 22. Dorsal view of head and neck musculature; fourth depth at left and fifth depth at right.
A. *Amblyrhynchus cristatus*. BYU 22806. × 0.35
B. *Brachylophus fasciatus*. BYU 31955. × 1.0
C. *Chalarodon madagascariensis*. BYU 22801, 22803. × 3.0
D. *Conolophus subcristatus*. BYU 22811. × 0.35
E. *Ctenosaura pectinata*. BYU 22850. × 0.5

Key to symbols used in Figure 23.
- am-adductor mandibularis externus medius
- as-adductor mandibularis externus superficialis
- au-auditory meatus
- cc-constrictor colli
- cm-cervicomandibularis
- dm-depressor mandibularis
- ep-episternocleidomastoideus
- ip-intermandibularis posterior
- la-levator angularis oris
- tr-trapezius

Figure 23. Lateral view of head and neck musculature; superficial depth.
A. *Cychra nuchalis*. BYU 22799. x 1.0
B. *Dipsosaurus dorsalis*. BYU 31954. x 1.5
C. *Iguana iguana*. BYU 33851. x 0.75
D. *Opisturus sebae*. BYU 11504. x 1.25
E. *Sauromalus obesus*. BYU 31953. x 1.5

Key to symbols used in Figure 24:
- am-adductor mandibularis externus medius
- as-adductor mandibularis externus superficialis
- au-antidorsal meatus
- cc-constrictor colli
- cm-cervicomandibularis
- dm-depressor mandibularis
- ep-episterno-clidomastoideus
- ip-intermandibularis posterior
- la-levator angularis oris
- tr-trapezius

Figure 24. Lateral view of head and neck musculature; superficial depth.
A. Amblyrhynchus cristatus. BYU 22806. x 0.35
B. Brachylophus fasciatus. BYU 31955. x 1.0
C. Chalarodon madagascariensis. BYU 22801, 22803. x 3.0
D. Conolophus subcristatus. BYU 22811. x 0.35
E. Ctenosaura pectinata. BYU 22850. x 0.5

Key to symbols used in Figure 25.

am-adductor mandibularis externus medius
as-adductor mandibularis externus superficialis
cm-cervicomandibularis
dm-depressor mandibularis
ep-episternocleidomastoideus
ip-intermandibularis posterior
ls-levator scapulae superficialis
om-omohyoideus
sh-sternohyoideus

Figure 25. Lateral view of head and neck musculature; first depth.
A. Cyclura nuchalis. BYU 22799.  x 1.0
B. Dipsosaurus dorsalis. BYU 31954.  x 1.5
C. Iguana iguana. BYU 22851.  x 0.75
D. Oplurus scut. BYU 11504.  x 1.25
E. Sauromalus obesus. BYU 31953.  x 1.5

Key to symbols used in Figure 26.
am-adductor mandibularis externus medius
as-adductor mandibularis externus superficialis
cm-cervicomandibularis
dm-depressor mandibularis
ep-episternocleidomastoideus
ip-intermandibularis posterior
ls-levator scapulae superficialis
om-omohyoideus
sh-sternohyoides

Figure 26. Lateral view of head and neck musculature; first depth.
A. Amblyrhynchus cristatus. BYU 22806. x 0.35
B. Brachylophus fasciatus. BYU 31955. x 1.0
C. Chalarodon madagascariensis. BYU 22801, 22803. x 3.0
D. Conolophus subcristatus. BYU 22811. x 0.35
E. Ctenosaura pectinata. BYU 22850. x 0.5

Key to symbols used in Figure 27.

am-adductor mandibularis externus medius
ep-episternocleidomastoideus
lp-levator scapulae profundus
ls-levator scapulae superficialis
pm-pharyngeal membrane

Figure 27. Lateral view of head and neck musculature; second depth.
A. Cyclura michalis. BYU 22799. x 1.0
B. Dipsosaurus dorsalis. BYU 31954. x 1.5
C. Iguana iguana. BYU 22851. x 0.75
D. Oplurus sebae. BYU 11504. x 1.25
E. Sauromalus obesus. BYU 31953. x 1.5

Key to symbols used in Figure 28.
- am-adductor mandibularis externus medius
- ep-episternocleidomastoideus
- lp-levator scapulare profundus
- ls-levator scapulare superficialis
- pm-pharyngeal membrane

Figure 28. Lateral view of head and neck musculature; second depth.
A. Amblyrhynchus cristatus. BYU 22806, x 0.35
B. Brachylophus fasciatus. BYU 31955, x 1.0
C. Chalarodon madagascariensis. BYU 22801, 22803, x 3.0
D. Conolophus subcristatus. BYU 22811, x 0.35
E. Ctenosaura pectinata. BYU 22850, x 0.5

Key to symbols used in Figure 29.
- ap-adductor mandibularis externus profundus
- lp-levator scapulae profundus
- ls-levator scapulae superficialis
- ps-pseudotemporalis superficialis

Figure 29. Lateral view of head and neck musculature; third depth.
A. *Cyclura nuchalis*. BYU 22799. x 1.0
B. *Dipsosaurus dorsalis*. BYU 31954. x 1.5
C. *Iguana iguana*. BYU 22851. x 0.75
D. *Oplurus scabre*. BYU 11504. x 1.25
E. *Saumalus obesus*. BYU 31953. x 1.5

Key to symbols used in Figure 30:
ap-adductor mandibularis externus profundus
lp-levator scapulae profundus
ls-levator scapulae superficialis
ps-pseudotentorialis superficialis

Figure 30. Lateral view of head and neck musculature; third depth.
A. *Amblyrhynchus cristatus*. BYU 22806. x 0.35
B. *Brachylophus fasciatus*. BYU 31955. x 1.0
C. *Chalarodon madagascariensis*. BYU 22801, 22803. x 3.0
D. *Conolophus subcristatus*. BYU 22811. x 0.35
E. *Ctenosaura pectinata*. BYU 22850. x 0.5

Key to symbols used in Figure 31.
- am-adductor mandibularis posterior
- lp-levator pterygoideus
- pp-protractor pterygoideus
- pt-pseudotemporalis profundus
- sc-scapula
- sd-spinus dorsi
- ss-suprascapula

Figure 31. Lateral view of head and neck musculature; fourth depth.
A. *Cyclura nuchalis*. BYU 22799. x 1.0
B. *Dipsosaurus dorsalis*. BYU 31954. x 1.5
C. *Iguana iguana*. BYU 22851. x 1.25
D. *Ophiurus sebae*. BYU 11504. x 1.25
E. *Sauromalus oebus*. BYU 31953. x 1.5

Key to symbols used in Figure 32.

am-adductor mandibularis posterior
lplevator pterygoideus
pp-protractor pterygoideus
pt-protractor pterygoideus
pt-pseudotemporalis profundus
sc-scapula
sd-spinus dorsi
ss-suprascapula

---

Figure 32. Lateral view of head and neck musculature; fourth depth.
A. *Amblyrhynchus cristatus*. BYU 22806, x 0.35
B. *Brachylophus fasciatus*. BYU 31955, x 1.0
C. *Chalarodon madagascariensis*. BYU 22801, 22803, x 3.0
D. *Conolophus suberiptatus*. BYU 22811, x 0.35
E. *Ctenosaura pectinata*. BYU 22850, x 0.5

Key to symbols used in Figure 33.
- cl-clavicle
- ic-interclavicle
- lp-levator pterygoideus
- pp-protractor pterygoideus
- sd-spinus dorsi
- se-serratus (dorsal part)
- sl-sacrolumbalis

Figure 33. Lateral view of head and neck musculature; fifth depth.
Key to symbols used in Figure 34.

*cl* - clavicle
*ic* - interclavicle
*lp* - levator pterygoideus
*pp* - protractor pterygoideus
*sd* - spinus dorsi
*se* - serratus (dorsal part)
*sl* - sacrolumbalis

Figure 34. Lateral view of head and neck musculature; fifth depth.
A. Amblyrhynchus cristatus. BYU 22810. x 1.25
B. Brachylophus fasciatus. BYU 23743. x 1.5
C. Chalarodon madagascariensis. BYU 22801. x 6.0
D. Conolophus subcristatus. BYU 22811. x 1.0
E. Ctenosaura pectinata. BYU 22796. x 1.5
F. Cyclophora nuchalis. BYU 22799. x 2.5
G. Diposaurus dorsalis. BYU 23761. x 3.0
H. Iguana iguana. BYU 22852. x 1.25
I. Ophurus sebae. BYU 11504. x 2.5
J. Saurornatus obesus. BYU 23762. x 1.5

Key to symbols used in Figure 35.
ac-anterior cleft
fp-filamentous papillae
gl-glottis
pc-posterior cleft
pp-pointed papillae

Figure 35. Dorsal view of the tongue.
A. *Amblyrhynchus cristatus*. BYU 22806. x 1.5. Left hemipenis.
B. *Brachylophus fasciatus*. BYU 23743. x 2.0. Left hemipenis.
C. *Ctenosaura pectinata*. BYU 22796. x 2.0. Left hemipenis.
D. *Diposaurus dorsalis*. BYU 23760. x 4.0. Left hemipenis.
E. *Iguana iguana*. BYU 22851. x 2.0. Left hemipenis.
F. *Sauromalus obesus*. BYU 23762. x 3.0. Right hemipenis.

Key to symbols used in Figure 36.
- *cr*-crease
- *cs*-calyculate surface
- *ss*-sulcus spermaticus

Figure 36. Hemipenes
Hemipenes

The vocabulary for descriptions of the hemipenes will follow that of Cope (1896) and Dowling and Savage (1960). Only the hemipenes (Figure 36) of Amblyrhynchus, Brachylophus, Ctenosaura, Dipsaurus, Iguana, and Sauromalus were available for study.

Cope (1896) found the hemipenes to be undivided in Cyclura and Iguana, and bilobate in Ctenosaura, Dipsaurus, and Sauromalus. He also noted calyces covering the distal ends of all the above genera.

In our investigations, we have found the hemipenes of all the genera to be bulbous rather than bilobate in Sauromalus, Dipsaurus, Amblyrhynchus, and Iguana. Ctenosaura and Brachylophus are more bilobate than the above genera. However, Brachylophus has the most bilobate hemipenes of the group.

The sulcus spermaticus forms a broad, open curving groove on the posterior surface of the hemipenis in all genera except Brachylophus, where the sulcus is narrow and tightly closed forming a tube rather than a groove. In Ctenosaura, Sauromalus and Dipsaurus, a fold exists on the lateral border of the sulcus forming a small diverticulum in that area.

The distal half of the hemipenis is calyculate on the surface, whereas the base and proximal half is covered with irregular creases in all genera. All hemipenes lack spines or spinoose structures.

DISCUSSION

The phylogenetic relationships between the genera of iguanine lizards have not been analyzed. Boulegrer (1890) outlined some osteological characteristics for most of the genera but made no attempt at defining relationships. Cope, in 1892, discussed Dipsaurus and indicated it to be related to Crotaphytus by general appearance but different from it osteologically. Cope also analyzed Sauromalus and by virtue of the zygosphenal articulation, allied "... to Dipsaurus and the larger Iguanidae, but the separated ceratobranchials, and wide sternum are like that of the Phynosomas, with the exception of the fontanelles" (Cope, 1892:205). Camp (1923) in his basic work on the classification of lizards indicated Iguana, Cyclura, Sauromalus, Dipsaurus, and Amblyrhynchus to be related and intermediate in primitiveness. He also allied Brachylophus to Ctenosaura and Cyclura "... on the basis of details of the throat musculature, and number of abdominal parasterna" (Camp, 1923:416).

In 1942 Mittleman considered the relationships between Uta, Urosaurus and the iguanines Sauromalus, Dipsaurus, and Ctenosaura. He indicated that these latter three herbivores were a primitive ancestral stock closely related to Sceloporus and Crotaphytus. Savage (1958) outlined the iguanine characteristics and included Crotaphytus in that evolutionary line. Avery and Tanner (1964) were able to show several myological differences between Sauromalus and Crotaphytus and indicated these two genera were not in the same evolutionary line. Etheridge, in 1964, also examined the iguanines and separated the genus Crotaphytus from them, based on osteological differences.

As a result of previous studies, the existence of an iguanine evolutionary line has been well established. However, no conclusions have been made concerning the relationships between genera and the general phylogeny of the iguanine line.

Osteology

As previously indicated, length-width measurements of bones and bone shapes were utilized to analyze the osteological relationships between the iguanines. The ratio means of tables 1-34 were used to make these relationships clear. It has been assumed that a difference of forty or less points between means of the same bone indicates a close relationship. The possession of bones with similar shape is also an indicator of close relationship. Those genera sharing the most characters in common are considered to be the most closely related. A summary of the number of characters shared between genera is found in table 37.

<table>
<thead>
<tr>
<th>Genus</th>
<th>Amblyrhynchus</th>
<th>Brachylophus</th>
<th>Chalarodon</th>
<th>Cyclura</th>
<th>Dipsaurus</th>
<th>Enhydriscus</th>
<th>Eryciasauri</th>
<th>Iguana</th>
<th>Sauromalus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amblyrhynchus</td>
<td>12</td>
<td>8</td>
<td>22</td>
<td>8</td>
<td>10</td>
<td>13</td>
<td>11</td>
<td>17</td>
<td>13</td>
</tr>
<tr>
<td>Brachylophus</td>
<td>12</td>
<td>14</td>
<td>19</td>
<td>21</td>
<td>24</td>
<td>27</td>
<td>10</td>
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<td>17</td>
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<tr>
<td>Chalarodon</td>
<td>8</td>
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<td>11</td>
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<td>10</td>
<td>13</td>
<td>13</td>
<td>24</td>
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<tr>
<td>Cyclura</td>
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<td>19</td>
<td>11</td>
<td>22</td>
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<td>Dipsaurus</td>
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<tr>
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<td>22</td>
<td>31</td>
<td>16</td>
<td>17</td>
<td>28</td>
<td>18</td>
</tr>
<tr>
<td>Eryciasauri</td>
<td>13</td>
<td>27</td>
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<td>17</td>
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<td>9</td>
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<td>13</td>
<td>12</td>
<td>16</td>
</tr>
<tr>
<td>Sauromalus</td>
<td>17</td>
<td>22</td>
<td>11</td>
<td>22</td>
<td>32</td>
<td>28</td>
<td>17</td>
<td>13</td>
<td>15</td>
</tr>
</tbody>
</table>

Etheridge (1965:166) commented on the uniqueness of the abdominal skeleton of Chalarodon and Ophuras. These genera, by virtue of their abdominal skeleton, are either more primitive than, or as primi-
tive as, any member of the iguanine line. Because these two genera are isolated on Madagascar, one would assume that they are closely related. *Oplurus* and *Chalarodon* share 24 characters in common. This degree of relationship is higher than that of *Oplurus* or *Chalarodon* with any other genus. *Oplurus* also shares a number of close relationships with other genera. There are 19 characters shared in common between *Oplurus* and *Ctenosaura*, 18 between *Oplurus* and *Cyclura*, and 17 between *Oplurus* and *Brachylophus*. On the other hand, *Chalarodon* shows no close relationships with other genera except *Oplurus*. The only other high number of shared characters is that of *Chalarodon* with *Ctenosaura* (15).

It is obvious from the above that *Oplurus* is more closely related to the iguanines than *Chalarodon*. *Chalarodon* shows so few characters in common with the iguanines that we do not consider it to be closely related to the iguanine line of evolution. The high number of characters shared in common between *Chalarodon* and *Oplurus* is probably the result of a distant common ancestry between the two genera and common adaptations needed to meet the environmental demands of Madagascar.

Based on anatomy, we consider *Oplurus*, although primitive, to be more closely related to the iguanines than *Chalarodon*. Both are primitive, have been isolated for a long time, and have radiated. We consider the Madagascar iguanids to be the most primitive members of the family.

In regards to the iguanine line, the primitive iguanid *Oplurus* is more closely related to *Ctenosaura*, with 19 characters shared, and *Cyclura*, with 18 shared characters. This suggests that *Ctenosaura* is the most primitive of the Western Hemisphere iguanines. The primitiveness of *Ctenosaura* has been previously suggested by Mittleman (1942:113) who placed it as ancestral to all North American iguanid genera. This form may not be ancestral to all North American iguanid genera but is certainly ancestral to the Western Hemisphere iguanines. Besides possessing more characters in common with *Oplurus* than any other iguana, *Ctenosaura* also shares characters in common with *Conolophus* (22), *Cyclura* (31), *Iguana* (32) and *Sauromalus* (27). If *Ctenosaura* is not primitive, it is at least in the center of the evolution of the terrestrial Western Hemisphere iguanines.

*Cyclura* is very close to *Ctenosaura* in structure and in the number of osteological characters shared (31). *Cyclura* is also closely related to *Iguana* with which it shares 28 characters. *Cyclura* is an island form, probably evolved from the *Ctenosaura* line by isolation.

*Iguana* appears to have much in common with both *Cyclura* (28 characters shared) and *Ctenosaura* (32 characters shared). Together *Ctenosaura*, *Iguana*, and *Cyclura* form a closely related natural group and probably represent a primary radiation in the Central American area of the Western Hemisphere.

*Sauromalus* is a northern extension of the *Ctenosaura* type. *Sauromalus* shows 27 characters in common with *Ctenosaura* while 26 characters are shared with *Cyclura* and 24 with *Iguana*. It is logical to assume that *Sauromalus*, a desert form, has evolved from a *Ctenosaura* type organism, a more tropical form, rather than a *Cyclura* type. *Ctenosaura* and *Sauromalus* are both continental rather than island forms, such as *Cyclura*, and *Ctenosaura* and *Sauromalus* overlap ranges in Mexico and Baja, California.

*Conolophus* shares 22 characters each with *Amblyrhynchus*, *Ctenosaura*, *Cyclura*, and *Iguana*. This is an indication that this representative of the Galapagos Island fauna is derived from the Central American radiation rather than elsewhere.

After eliminating all characters shared in common between all five genera, one finds more are shared with *Ctenosaura* than *Cyclura*, *Iguana*, and *Amblyrhynchus*. The size of the interclavicle arms, the placement of the anterior inferior alveolar foramen in the splenial bone, the size and shape of the lacrimal bone, size and shape of the postfrontal, size and shape of the angular process in the lower jaw, size of the supraoccipital, size of the fenestra exornaria, size and shape of the angular bone, and size of the supratemporal fossa all link *Conolophus* with *Ctenosaura* rather than with either of the other three genera.

*Amblyrhynchus* is closely related to *Conolophus* with 22 characters shared, and to *Iguana* with 17 characters shared. An analysis of these shared characters shows that *Amblyrhynchus* is more closely related to *Conolophus* than to *Iguana*. After eliminating the characters shared in common by all three genera one finds that *Amblyrhynchus* shares 12 characters with *Conolophus* as opposed to 6 for *Iguana*. Among the characters shared in common with *Conolophus* are the size of the supraoccipital, palatine, jugal, quadrates, supratemporal fossa, fenestra exornaria, dentary and size of angular process. Also the posterior border of the dentary forms a complex interfinger suture with the surangular bone. The frontal bone in both is wider than long, and the pyriform recess widens posteriorly at a sharp angle in both genera. *Amblyrhynchus* shares with *Iguana* the size of the lacrimal bones, parietal wings, and the orbit. The angular process has a similar shape in both genera and the interclavicles are the same shape with arms equal in length to the body and attached to the body at a 90° angle. *Conolophus* and *Amblyrhynchus* are more closely related to each other than to other iguanines. *Amblyrhynchus* is probably derived from a *Conolophus-Ctenosaura* ancestor which invaded the Galapagos Islands from the mainland.

*Brachylophus*, from Fiji and Tonga Islands, is the most geographically isolated iguana. This genus shares a large number of characters with *Cyclura* (24), *Iguana* (22), *Ctenosaura* (21), and *Sauromalus* (21).
Obviously this close relationship to all these genera indicates a point of origin some place in the primary Central American radiation. Sauromalus being a Northern representative of this group is the least likely relative of Brachylophus. When all common characters between the five genera are eliminated we find the three characters, the size of the postfrontals, prefrontals and articular bones are shared between Brachylophus and Cyclura. Brachylophus and Ctenosau- ra share nasals, parietal wings, orbits, and articulars of similar size and shape. Iguana and Brachylophus have similar palatines, premaxillae, quadrates and vomers. Brachylophus, as with Conolophus, with which it shares 19 characters, is probably evolved from the pre-Ctenosaura-Iguana ancestral stock.

Dipsosaurus is the most problematical genus in the iguanine line. Osteologically, as pointed out by Cope (1892:201), Dipsosaurus is different from the other Iguanidae. This genus differs from all other iguanines in lacking pterygoid teeth, having a convex dentary suture with the surangular, interclavicle arms that attach to the inter-clavicle body at a 30° angle, and an anterior inferior alveolar foramen found in the dentary instead of the splenial bone. A summary of the characters shared with other genera shows that Dipsosaurus shares more characters in common with Brachylophus (27), than with any other genus. No other genus is even close in its relationship to Dipsosaurus. The size ratios of the frontals, parietals, jugals, nasals, squamosals, quadrates, postorbitalis, orbits, dentaries, surangulars, splenials, articulars, angulars, angular processes are similar. Also the interclavicle arms are one quarter the length of the interclavicle body, the sternal cartilage possess one fontanelle, the angular process is triangular, and the squamosals are splintlike in both genera. It seems obvious that Dipsosaurus and Brachylophus were derived from a common ancestry.

In summary, the osteological characters of the iguanine lizards indicate that Ophius has and Chalarodon are more closely related to each other than to the iguanines, and Ophius is the Madagascarian genus most closely related to the Western Hemisphere iguanines. Of the iguanines, Ctenosaura represents the ancestral stock from which Cyclura, Iguana, and Sau- romanus were evolved. Conolophus and Brachylophus are both early derivatives of this stock as well, with Amblyrhynchus having been derived from the Cono- lophus line, and Dipsosaurus and Brachylophus having a common ancestry.

Before leaving the osteology it is necessary to make mention of Enyaliosaurus. Measurements taken on the two skulls examined (USNM 48965 and USNM 21452) show a very close relationship between Enyaliosaurus and Ctenosaura. The ratio means of over half the skull characters checked confirm this relationship as indicated in table 37. Duellman (1965:599) examined the external morphology of Enyaliosaurus and states, “Enyaliosaurus doubtless is a derivative of Ctenosaura, all species of which are larger and have relatively longer tails with less well-developed spines than Enyaliosaurus. The evolutionary trend in Enyaliosaurus seems to have been towards smaller size with a relatively more robust tail having whorls of large spines. In this respect, E. palea- ris seemingly is primitive; E. quinquecarinatus is more advanced and probably is ancestral to the specialized species, E. clarki and E. defensor.”

From the above it is obvious that Enyaliosaurus is another example of the early pre-Ctenosaura radiation in Central America.

**MYOLOGY**

An examination of the muscles has revealed that the iguanines and the Madagascarian genera exhibit two basic patterns of muscle arrangement. In Amblyrhu- nyclus, Conolophus, Ctenosaura, Cyclura, Iguana, Ophiusus, and Sauromalus, the cervicomandibularis is hidden beneath the posterior origin of the constrictor colli. This same group of genera, plus Chalarodon, has a large levator angularis oris muscle. The remaining genera, Brachylophus and Dipsosaurus, appear to form a second natural group with the cervicomandibularis muscle extending beyond the posterior margin of the constrictor colli and with a small levator angularis oris muscle present. The fact that Ophiusus shares both characters with the larger group is an indication of its close relationship to the central iguanine stock. Chalarodon possesses only one of the characters and is probably the most distantly related of all the genera studied.

A few other myological characters are useful in determining relationships. The position of the adjoining borders of the intermandibularis posterior and the constrictor colli indicate a natural grouping between Conolophus, Ctenosaura, Cyclura, and Sauromalus. In these genera the borders are not connected along part of their length. In Amblyrhynchus, Brachylophus, Dipsosaurus, and Iguana, the borders of these muscles are connected for the entire length. These genera appear to have diverged away from the central stock. It is interesting to note that both Chalarodon and Ophiusus have the border of the intermandibularis posterior and the constrictor colli connected for the entire length. On the basis of myology, these two genera are not iguanine but may represent the most primitive condition in the family.

The branchiomyoideus has a wide insertion on the distal end of the first ceratobranchial in all of the
genera except Sauromalus. This deviation from the iguanine pattern is probably due to the unique shape of the hyoid in Sauromalus. Such a deviation probably represents a highly specialized condition rather than a primitive one.

The sternothyroideus is indistinguishable along its lateral border from the medial border of the sternohyoideus in all genera except Ophurus and Chalarodon where the two muscles are quite distinct. This character indicates a relationship between the two Malagasy genera that is lacking in the iguanines.

In summary the musculature shows the iguanines to be separated into an Amblyrhynchus, Conolophus, Ctenosaura, Cyclura, Iguana, and Sauromalus group, and a Brachylophus and Dipsosaurus group as determined by the position of the cervicomandibularis and levator angularis oris. The musculature further shows that Ophurus and Chalarodon form a natural grouping as indicated by the free lateral border of the sternothyroid.

Within the largest iguanine group of genera; Conolophus, Ctenosaura, Cyclura, and Sauromalus, there appears to be the most closely related members of the ancestral stock as indicated by each having incompletely connected borders between the constrictor colli and intermandibularis posterior muscle.

Before leaving the myology a brief discussion of Euryhaliosaurus is pertinent. An examination of one specimen of E. clarki (KU 62447) shows this individual to have a large levator angularis oris, a hidden cervicomandibularis, a narrow constrictor colli, and a sternothyroideus with its lateral border fused to the sternohyoideus. The possession of these characters allies Euryhaliosaurus closely with Ctenosaura and its close relatives.

Tongue

Camp (1923:374) states, “The broad, fleshy, partly smooth, partly papillate tongue of geckos and iguanids would seem histologically the least specialized and probably the more ancient type.” Unfortunately this primitive tongue does not show any clear evolutionary trends between the genera of iguanines. This may be because of the low sample size used in this study.

It may be noted, however, that the poorest development of pointed papillae at the posterior end of the tongue is found in Chalarodon and Ophurus. The depth of the posterior cleft is also more shallow in the above two genera. This is another indication of the uniqueness of the two Malagasy genera.

A single tongue from Dipsosaurus shows a small pointed tip at the anterior extremity of the tongue. This was not seen in larger individuals in any other genus and it may be that such a structure is a function of age and use. Older individuals may have worn this tip away leaving the rounded tip found in the other iguanines.

Hemipenis

The study of the hemipenis was hampered by a lack of material with four genera not being represented in the series.

The hemipenis of Brachylophus is unique among the six genera examined as the structure is bifid rather than bulbous. The sulcus spermaticus is tightly closed and tubelike rather than an open groove as found in Amblyrhynchus, Ctenosaura, Dipsosaurus, Iguana, and Sauromalus. These differences may suggest a more distant relationship between Brachylophus and the remaining continental iguanines.

A phylogenetic chart representing the relationships between the eleven genera, as determined by the above morphological characters, is seen in Figure 37.

Iguanine Distribution

Explaining the distribution of the iguanines has been especially perplexing for zoogeographers. One of the most recent statements on the subject is that of Carlquist (1965:395-396) who says, “Especially annoying to biogeographers is the presence of iguanas. Iguanas are inescapably a characteristically American family of lizards. To be sure, an iguana (Brachylophus) has mysteriously reached Fiji and Tonga, on which islands the genus is endemic. But how to explain that two iguana genera exist on Madagascar? Chalarodon, from the dry Southwest of the island, and Ophurus, with six species, are living evidence that iguanids did reach Madagascar. The best explanation seems to be that iguanas are a very ancient group of reptiles which have been extinguished on the African and Eurasian mainland, but managed, during their tenure there, to reach what were to become refuge islands for them and other creatures, Fiji and Madagascar, before they died out on the mainland.” Beaufort (1951:132) and Darlington (1957:212) also consider the Iguanidae to have evolved in the Old World.

The literature on fossil lizards such as Broom (1903), Broom (1924), and Camp (1945) indicates that lizards probably originated in Africa in Triassic times. By the beginning of the Cenozoic Era, the family Iguanidae was well established in North America (Gilmore 1928, Gilmore 1941, and Estes 1964).

The family Iguanidae may also have originated in the Old World tropics. The presence of Chalarodon and Ophurus on Madagascar is evidence of a long history in the African area. Current theory indicates that the ancestral iguanids spread to Europe and Asia and eventually to the Western Hemisphere. Fossils should mark the existence of iguanids on the Eurasian land mass. Some iguanids from Europe have been de-
Figure 37. Phylogenetic relationships of the Madagascar Iguanidae and the genera of iguanine lizards.
scribed by Hoffstetter (1942, 1955). However, according to Romer (1968:121), these are more likely agamids. There is no fossil record for iguanids from Asia.

Regardless of the fossil record, iguanids had to reach the Western Hemisphere from the Old World tropics. One of the more logical explanations of such a migration would be for the iguanids to spread northward through Europe, invade North America via the Bering Strait landbridge, and undergo a radiation in the Western Hemisphere. The development of better adapted families of lizards in the Old World tropics could have caused the extinction of the family Iguanidae in all areas where the families competed. Only in refugia, where the iguanids were isolated from these more successful families, would the iguanids survive. Members of the family Agamidae are ecological equivalents for many iguanids and are widespread in the Old World tropics. They may have caused the elimination of the Iguanidae where the two families overlapped. It is interesting to note that there are no agamids on Madagascar where iguanids still exist. Nowhere in the world except on Fiji do iguanids and agamids live side by side.

There is an alternative method by which the Iguanidae could have reached the New World tropics. The publication of several recent papers such as Hurley, Almeida, et. al., 1967, Heitzler 1968, Hurley 1968, Maxwell 1968, Hurley and Rand 1969, Kurten 1969, and McEllhenny and Lack 1970 lend new credence to the old theory of continental drift. All of the above papers indicate the existence of a large pre-Cretaceous land mass, Gondwanaland, which fractured in Cretaceous times to form Africa, South America, Australia, Antarctica, Southern India and Madagascar.

If the Iguanidae were widespread over Gondwanaland when this continental mass fractured in the Cretaceous, they would have been separated into separate populations on each of the above land masses. Of these continental areas only the Americas and Madagascar have not been invaded by Agamidae. These two areas are also the only areas that have iguanid lizards.

Continental drift would explain why the Madagascar genera are considered primitive to the rest of the family. They are closest to the family’s center of origin, and are relics of Cretaceous times. The drift theory would also explain why the iguane line is mostly southern and equatorial. They originated in that area in Gondwanaland and have spread little from their center of origin.

Regardless of the method of iguane migration to the New World, be it land bridge or continental drift, we are still faced with explaining the distribution of iguanines on the oceanic islands of the Western Hemisphere.

Cyclura is found in the Antilles and the Bahamas. This Ctenosaura derivative is widespread on the islands and is endemic to the area, having migrated and evolved there when these islands were connected to the mainland.

The origin of the Galapagos Islands has been debated for many years. Amblyrynchus and Conolophus, which are endemic to the Galapagos Islands, have been separated from the mainland genera for a long time, as indicated by their high degree of differences. If the islands are continental, these iguanids could have easily reached them. If the islands are oceanic Amblyrynchus and Conolophus must have migrated by rafting on logs or some other floating debris.

Baur (1891:310) considered the islands to have been connected to the mainland as late as Eocene times. Heller (1903:43-44) considered the islands to be volcanic and oceanic in nature. Chubb (1933:1-25) commented extensively on the volcanic nature of the Galapagos Islands and indicated a close affinity, geologically, to Cocos Island off Costa Rica. Svenson (1948:496-498) studied the plants of the Galapagos Islands and indicated a close affinity with South America. Finally, Vinton (1951:356-376) proposed a partial or complete land bridge from Costa Rica through Cocos Island to either a connection with the islands or terminating in a close proximity to the Galapagos land mass that later sank forming the present islands. This land bridge would have been developed in Mid-Tertiary time and would have provided means whereby turtles and iguanids could have gotten close enough to the islands to raft successfully.

As the land bridge never attached to the Galapagos Islands, these oceanic islands would have retained a considerable degree of uniqueness. Regardless of land connection or not, a pre-Ctenosaura-Iguana ancestor apparently did make the trip and later diverged into modern day Amblyrynchus and Conolophus.

The problem of Brachylophus on Fiji and Tonga Islands is to us the most perplexing problem in iguane distribution. If the iguanines were widespread in the world during late Mesozoic-early Cenozoic times and were widely scattered on the Gondwanaland continental nucleus, they should have occurred in Australia and Asia after the fracturing of that nucleus. From Australia or Southeast Asia it is a short trip by rafting to the Fiji and Tonga Island groups. If such a trip were accompanied by iguane elimination on the Asian and Australian land masses by agamids, Brachylophus would be left isolated on Fiji and Tonga.

Two factors disrupt the plausibility of this theory, however. If iguanines were widespread and gave rise to the Fiji and Tonga populations of Brachylophus via Asia and/or Australia, one would expect to find other relict populations on other Pacific Islands such as New Zealand, New Guinea, the Solomons, the Philippines, and Indonesia. These islands are all inhabited by agamids which could have eliminated
Brachylophus and other iguanines. Unfortunately the fossil record does not provide evidence of any Far Eastern Iguanidae, and we find today that agamids and Brachylophus do exist together on Fiji. This modern coexistence may be the result of Brachylophus or the agamids being recent invaders of the islands rather than long term residents.

A second fact disrupting the Far Eastern Theory for the origin of Brachylophus is the relationship of Brachylophus to Dipsosaurus, the North American iguaine. Did Dipsosaurus also raft from the Far East to North America? It seems highly unlikely. A more plausible explanation for the problem is that a Brachylophus-Dipsosaurus complex existed in the Western Hemisphere, closely related to the existing iguanine complex. Brachylophus in the South Pacific is probably the result of a few individuals that accidently rafted on floating debris to the Fiji and Tonga Island groups and a Northern survivor of this complex has evolved into the modern Dipsosaurus. Such a hazardous journey by log raft needs to occur only once with a gravid female to produce a viable island population.

Sauromalus represents the most northward extension of the iguaine line. Gilmore (1928:27-28) described the teeth of Parasauromalus olsoni from the Middle Eocene, Wind River Formation of Fremont County, Wyoming. This fossil form may represent the ancestral stock of Sauromalus and indicates the withdrawal of the modern Sauromalus from what once was a more extensive and northern range. According to Savage (1966:722-723), North and South America were connected in Paleocene and Pliocene times. The pre-Sauromalus stock may have invaded North America in Paleocene times before the land bridge was broken. This Sauromalus stock may have been separated from the Ctenosaura stock from Eocene to Pliocene times and evolved and diverged far enough from the parent stock to allow Ctenosaura to re-invade southern North America in late Pliocene times and overlap the Sauromalus range without competing ecologically.

CONCLUSIONS AND SUMMARY

The problem of phylogenic relationships within the iguaine phyletic line and the Madagascar iguanids have been investigated in order to explain the discontinuous distribution exhibited by the members of the family Iguanidae. Owing to inconclusive results from cytology and histological methods, the comparative morphology of the anterior osteology, myology, tongues, and hemipenes were used to determine relationships.

An examination of the above structures of the members of the iguaine phyletic lines and a comparison with the Madagascar iguanids indicates the following: (1) The Madagascar genera Chalarodon and Ophurus appear to be more closely related to each other than to other iguanid genera. (2) The Madagascar genus Ophurus is most closely related to the iguaine line of evolution. (3) Ctenosaura, Cychura and Iguana represent the main ancestral stock of iguanines in the Western Hemisphere. (4) Cychura is probably an early descendant of the Ctenosaura ancestral line. (5) Iguana and Ctenosaura evolved from a common ancestral stock. (6) Sauromalus is a northern derivative of the Ctenosaura ancestral line. (7) Conolophus is probably an early invader of the Galapagos Islands and is derived from the pre-Ctenosaura-Iguana iguaine ancestral stock. (8) Amblyrhynchus is a close relative of Conolophus and may be derived directly from a Conolophus ancestor. (9) Brachylophus is a derivative of the pre-Ctenosaura-Iguana ancestral stock and probably rafted to the Fiji and Tonga Islands from tropical America. (10) Dipsosaurus is more closely related to Brachylophus than any other iguaine and represents the northern extension of that generic complex. (11) The Madagascar iguanids and the Western Hemisphere iguanines were probably separated in post-Cretaceous times by continental drift which is thought to have resulted in a fracturing of Gondwanaland and the formation of Australia, southern India, Antarctica, Africa, Madagascar, and South America.

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