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Iguanid Trigeminal Musculature and Its Role in the Phylogeny of the Iguanidae

by

Joseph Costelli

A dissertation submitted to the Graduate
Faculty in Biology in partial fulfillment
of the requirements for the degree of
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of New York

1973

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Introduction

The lizards (Lacertilia) are the most successful group of living reptiles, having, according to Porter (1972) eighteen living families with hundreds of highly diversified genera. The largest family of the Lacertilia, the Iguanidae, is a diverse group of lizards having about fifty living genera and 560 species. The family is confined almost exclusively to the new world, with representatives on Fiji, Tonga and the Galapagos Island, and two genera on Madagascar.

The three major classifications of the lizards were produced by Camp (1923) Hoffstetter (1955) and Romer (1956). All three classifications are presented below so that the position of the Iguanidae in each, may be compared.

Camp (1923)

- Suborder Sauria
  - Division Ascalabota
    - Section Gekkota
      - Family Gekkonidae
      - Family Uroplatidae
    - Section Iguania
      - Family Iguanidae
      - Family Agamidae
    - Section Rhiptoglossa
      - Family Chamaeleontidae
  - Division Autarchoglossa
    - Section Scincomorpha
    - Superfamily Xantusioidae
      - Family Xantusidae
    - Superfamily Scincoidae
      - Family Scincidae
      - Family Anelytropsidae
      - Family Feyliniidae
      - Family Dibamidae
    - Superfamily Lacertoidae
      - Family Gerrhosauridae
      - Family Lacertidae
      - Family Teiidae
    - Superfamily Amphisbaenoidae
      - Family Amphisbaenidae

Hoffstetter (1955)

- Order Sauria
  - Suborder Ascalabota
    - Infraorder Gekkota
      - Fam. Gekkonidae
      - Fam. Uroplatidae
      - Fam. Pygopodidae
    - Infraorder Iguania
      - Fam. Iguanidae
      - Fam. Agamidae
    - Infraorder Rhiptoglossa
      - Fam. Chamaeleontidae
  - Suborder Autarchoglossa
    - Infraorder Scincomorpha
      - Superfamily Xantusioidea
        - Fam. Xantusidae
      - Superfamily Scincoidea
        - Fam. Scincidae
        - Fam. Anelytropsidae
        - Fam. Feyliniidae
        - Fam. Dibamidae
      - Superfamily Lacerteidea
        - Fam. Gerrhosauridae
        - Fam. Cordylidae (Zonuridae)
        - Fam. Lacertidae

Romer (1956)

- Suborder Lacertilia
  - Infraorder Iguania
    - Fam. Iguanidae
    - Fam. Agamidae
    - Fam. Chamaeleontidae
  - Infraorder Nyctisauria (Gekkota)
    - Fam. Gekkonidae
    - Fam. Pygopodidae
  - Infraorder Leptoglossa (Scincomorpha)
    - Fam. Xantusidae
    - Fam. Teiidae
    - Fam. Scincidae
    - Fam. Lacertidae
    - Fam. Cordylidae (Zonuridae and Gerrhosauridae)
    - Fam. Dibamidae
  - Infraorder Diploglossa
    - Superfamily Anguoidae
      - Fam. Anguidae
      - Fam. Anniellidae
      - Fam. Xenosauridae
    - Superfamily Varanoidae (Platynota)

- Section Anguimorpha
  - Subsection Platynota
    - Superfamily Varanoidea
      - Fam. Varanidae
      - Fam. Dolichosauridae
      - Fam. Aigialosauridae
    - Superfamily Mosasauroidea
      - Fam. Mosasauridae
  - Subsection Diploglossa
    - Superfamily Pygopodoidea
      - Fam. Pygopodidae
    - Superfamily Anguioidea
      - Fam. Heledermatidae
      - Fam. Anguidae
      - Fam. Xenosauridae
      - Fam. Anniellidae
    - Superfamily Zonuroidea
      - Fam. Zonuridae

- Fam. Teiidae
- Infraorder Anguimorpha
  - Superfamily Anguioidea (Diploglossa)
    - Fam. Anguidae
    - Fam. Anniellidae
    - Fam. Xenosauridae
  - Superfamily Varanoidea (Platynota)
    - Fam. Varanidae
    - Fam. Helodermatidae
    - Fam. Lanthanotidae
    - Fam. Aigialosauridae
    - Fam. Mosasauridae
    - Fam. Dolichosauridae
- Order Amphisbaenea
  - Fam. Amphisbaenidae

- Fam. Helodermatidae
- Fam. Varanidae
- Fam. Lanthanotidae
- Fam. Aigialosauridae
- Fam. Mosasauridae
- Fam. Dolichosauridae
- Fam. Paleaophidae
- Infraorder Annulata (Amphisbaenia)
  - Fam. Amphisbaenidae

Most closely related to the Iguanidae, is its sister family the Agamidae, which is its ecological equivalent in the old world. The closeness of the two groups was recognized by Camp (1923) who placed them together in the Section Iguania. It was established, on the basis of characters such as hemipenes, musculature and squamation, that the family Gekkonidae is closely related to the Iguania. The gekkos were placed in the Section Gekkota. The Section Iguania, Gekkota and Rhiptoglossa, a highly specialized group derived from the Agamidae, make up the Division Ascalabota which is the more primitive of the two major divisions into which the lizards are grouped. All of the families fall in the Division Autarchoglossa.

The classification of Hoffstetter (1955) has elements of the Camp classification (1923) and of the Romer classification which appeared shortly after Hoffstetter's (1956). Hoffstetter raises the Sauria and Ophidia to the rank of orders. He removes the Amphisbaenidae from the Sauria and creates a separate order for that group. He maintains Camp's

Ascalabota-Autarchoglossa division giving each category the rank of suborder. He follows Camp in separating the Rhiptoglossa from the Iguania, and includes the Pygopodidae with the Gekkota as Romer was later to do.

Romer deemphasizes the Ascalabota-Autarchoglossa division by grouping the lizards in five infraorders, the Iguania, Nyctisauria, Leptoglossa, Diploglossa and Annulata. He includes the Family Chamaeleontidae with the Iguanidae and Agamidae in the infraorder Iguania instead of creating a separate section for it as Camp and Hoffstetter did. In addition Romer removes the family Pygopodidae from the Diploglossa and places it with the Gekkonidae forming the infraorder Nyctisauria. Porter (1972) follows Romers' treatment of the Iguanidae.

The major iguanid radiations have occurred on North, Central and South America and have produced several separate evolutionary lines. Forms have evolved with arboreal, terrestrial and scansorial specializations. Some are desert forms while others prefer more mesic habitats. One entire line is herbivorous while the remaining iguanids are insectivorous with some further specialized to eating ants.

The Iguanidae, because it is a closely, related yet highly diversified, group offers a fine opportunity for studying the variation of characters of great adaptive significance. The trigeminal musculature and entire jaw appartus form what must be a complex of such characters. The jaws are used for the crucial purpose of capturing, holding on to, killing and masticating the variety of food items taken by the different members of the family. The jaws are actually the only means the lizard has of manipulating its food and as such should reflect some of the dietary specializations of the various forms.

Being such a successful group the Iguanidae has several evolutionary lines each of which might be expected to show different jaw muscle adaptations. The present study is an attempt to:

1. discover the degree of variation present among the iguanid genera and subfamilies.
2. compare the iguanid jaw musculature to that of the families closest to the Iguanidae in the infraorder Iguania and to a few readily available, but more distantly related families.
3. compare the variation of the jaw musculature to that of another diet related character, dentition.
4. where possible, analyse the functional significance of the muscle and jaw variations.
5. set up, if possible, a classification and phylogency on the basis of jaw muscle characters alone.
6. determine if the variation in the jaw musculature supports the present classification or gives evidence for a different arrangement.

Literature

The earliest reference on lizard trigeminal musculature commonly found in the literature is to Meckels' System der vergleichenden Anatomie (1829). This is followed by Cuviers' Lecons d' Anatomie Comparee (1835) and Stannius' Handbuch der Zootomie (1856). Mivart (1867, 1870) described the jaw muscles of Iguana tuberculata and Chamaeleon parsonii. Sanders in a series of papers (1870, 1872, 1874) described the musculature of Platydactylus japonicus, Liolepis belli and Phrynosoma cornutum. Shufeldt (1890) worked on the musculature of Heloderma suspectum. In 1903 Bradley published a treatise entitled "The Muscles of Mastication and Movements of the Skull in the Lacertilia". This was followed by Versluys' paper on lizard jaw muscles (1904) and Edgeworths' paper of 1907 on the development of the head muscles of the chicken and the morphology of the head muscles of the sauropsida.

The great confusion in terminology created by the independent efforts of these early workers was rectified by the Lakjer in his classic paper entitled "Studien uber die Trigeminus-versorgte Kaumuskulatur der Sauropsiden", (1926). In this paper Lakjer compared the trigeminal musculature of 52 representatives of 31 families of lizard, snakes, turtles, crocodiles birds and rhynchocephalians. In doing so he consolidated all the work done before him and set up a muscle nomenclature which is still in use today.

After Lakjer came a series of papers by Lubosch (1933, 1938). In 1935 Edgeworth published a work on the cranial muscles of the vertebrates. Brock (1938) described the cranial muscles of the gecko and compared them to those of other gnathostomes. Save-Soderberg in 1945 published a work on the trigeminal muscles of the non-mammalian tetrapods. Poglayen-Neuwall (1953) described the trigeminal musculature of the snakes and crocodiles. In 1956 Oelrich published a very detailed anatomy of the head of Ctenosaura pectinata including a careful account of the jaw muscles. Haas (1960) compared the trigeminal muscles of Xenosaurus grandis and Shinisaurus crocodilurus in the hopes of discovering the relationships of the two genera. Avery and Tanner (1964) described the muscles of the head of Sauromalus and in 1971 published a study of the iguanine lizards in which the jaw musculature of the group was described.

As the reader can see most of the studies mentioned have dealt with surveys of large groups of animals usually taking one or two members of each family and assuming these are representative. Lakjer (1926) for example studied only four iguanids, Iguana tuberculata, Polychrus marmoratus, Tropidurus hispidus and Phrynosoma cornutum, out of some fifty iguanid genera. Other studies have dealt with the detailed anatomy of a single form such as Oelrich's paper on Ctenosaura (1956) and earlier papers by Shufeldt (1890), Mivart (1867, 1870) and Sanders (1870-73).

Up to this time no previous worker has done a detailed study of the jaw musculature of all of the major genera of a single family. Avery and Tanner (1971) have come closest with their study of the iguanines, but found very little variation for they were dealing with members of a single evolutionary line. As this study will show, there is considerable variation between the members of the Iguanidae, and four members of the group, no matter how well chosen, could not reveal all of the variation present.

Materials and Methods

In surveying the iguanid trigeminal musculature 56 species belonging to 38 genera, and representing all the iguanid subfamilies and problematical genera were dissected. Dissections were performed under an M5 Wild dissecting microscope equipped with a camera lucida. To standardize comparisons all dissections were carried out in a set series of steps, each removing a fixed layer of muscle. Each layer was described and drawn prior to removal. The same procedure was applied to the representatives of the non iguanid genera that were studied. A list of all the specimens dissected and their sources is presented below.

In addition, a large series of iguanid jaws and skulls were examined and measured to determine certain important skull ratios, characteristics and ontogenetic changes. The data from this work are summarized in the body of the paper and the exact specimens used and their sources and measurements are listed in the tables in the Appendix.

Specimens Dissected

Iguanids

Chalaradon madagascariensis	AMNH 12846
Oplurus quadrimaculatus	AMNH 47947
Iguana iguana	M. K. Hecht
Cyclura cornuta	AMNH 40835
Sauromalus obesus	AMNH 74437
Ctenosaura hemilopha	M. K. Hecht
Dipsosaurus dorsalis	R. Ruibal
Enyaliosaurus quinquecarinatus	AMNH 15997
Brachylophus fasciatus	Harvard 48955
Sceloporus cyanogenys	M. K. Hecht
Sceloporus undulatus	M. K. Hecht
Sceloporus orcutti	M. K. Hecht
Uta stansburiana	AMNH 14464
Urosaurus ornatus	AMNH 14659

Uma notata	M. K. Hecht
Callisaurus draconoides	AMNH 26169
Holbrookia texana	M. K. Hecht

Phrynosoma solare	M. K. Hecht
Crotaphytus collaris	M. K. Hecht

Morunasaurus annularis	USNM 6513
Leiosaurus catamarcensis	Harvard 96710
Ophryoessoides iridescens	Harvard 18791
Leiocephalus personatus	M. K. Hecht
Leiocephalus semilineatus	M. K. Hecht
Tropidurus torquatus	AMNH 93486
Platynotus semitaeniatus	Harvard 128435
Phrymaturus palluma	Harvard 2033
Leiolamus platei	AMNH 27581
Hoplocercus spinosus	AMNH series 93468
Stenocercus carrioni	AMNH 21848
Plica plica	AMNH 14117
Enyaliodes paraestabilis	AMNH 28870
Uranoscodon superciliosa	AMNH 36628

Basiliscus vittatus	M. K. Hecht
Corythophanes cristatus	AMNH 75202
Laemanctus serratus	AMNH 79030

Polychrus marmoratus	M. K. Hecht
Anolis cristatellus	M. K. Hecht
Anolis lineatopis	M. K. Hecht
Anolis agassizi	Harvard 130611
Anolis equestris	AMNH 78125
Xiphocercus valenciennesi	AMNH 72246
Derroptyx sp.	M. K. Hecht
Phenacosaurus heterodernus	Harvard 78529
Chamaelinorops wetmorei	Harvard 68691
Chamaeleolis chamaeleonides	AMNH 58901

Non-Iguanids

Agama sp.	M. K. Hecht
Gonatodes fuscus	M. K. Hecht
Hemidactylus turcicus	M. K. Hecht
Mabuya sp.	M. K. Hecht
Tupinambis tequixin	M. K. Hecht
Ameiva ameiva	M. K. Hecht
Zonurus sp.	M. K. Hecht
Varanus indicus	M. K. Hecht
Chamaeleon chamaeleon	M. K. Hecht
Xantusia vigilis	M. K. Hecht

Part 1

Description of Iguanid Trigeminal Musculature

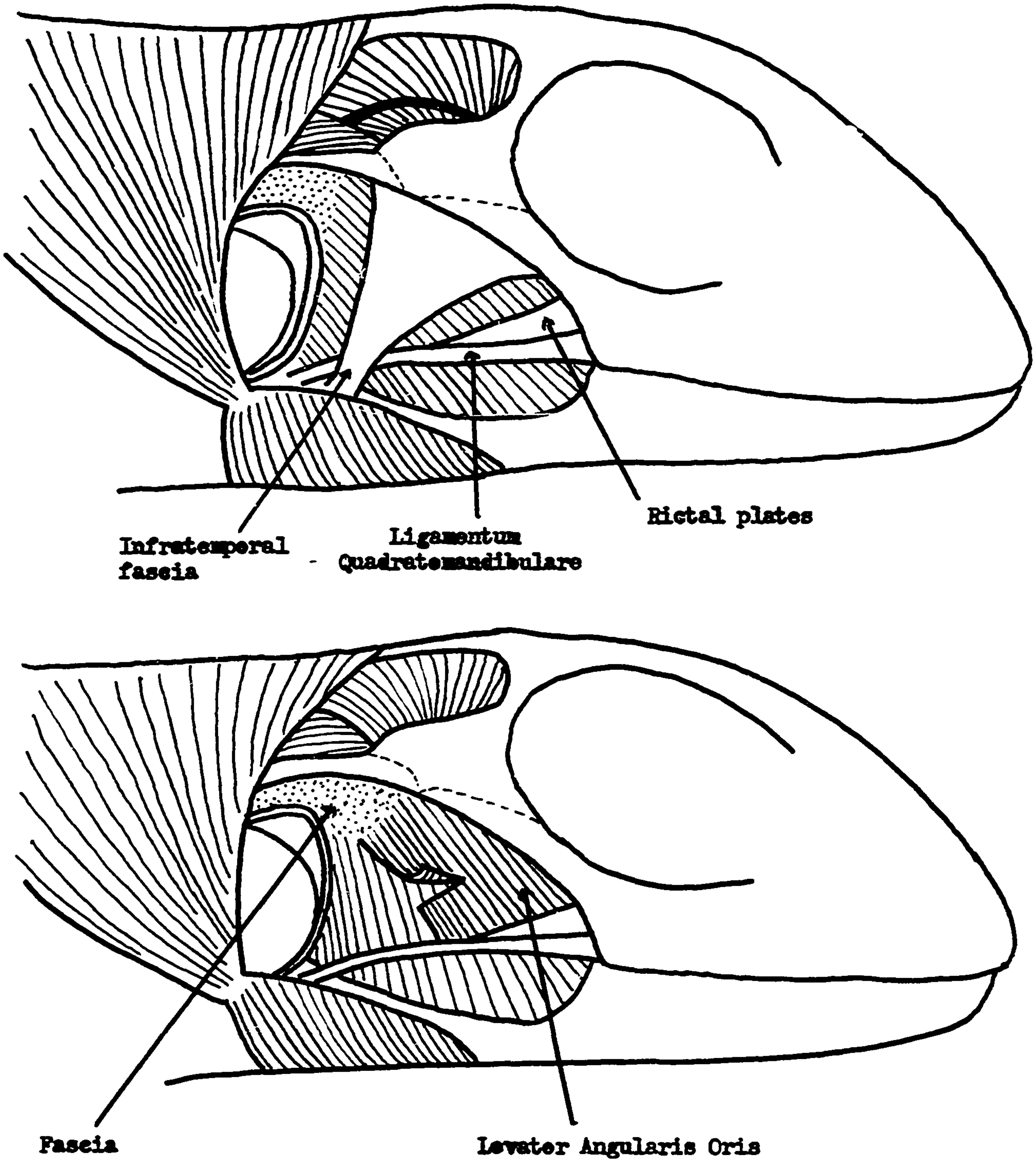
Iguanid Trigeminal Musculature

Ligamentum Quadratomandibulare

Upon skinning the temporal region, several connective tissue elements superficial to the actual trigeminal musculature are revealed. These are the ligamentum quadratomandibulare, the rictal plates or mundplatten and an extensive sheet of fascia, the infratemporal fascia, heretofore only poorly described (Fig. 1). The ligamentum is prominant in all iguanid genera, but absent in Dipsosaurus. The ligament is a tough band of connective tissue arising from the lateral surfaces of the surangular and articular, and the ventral lateral corner of the quadrate. As the ligament proceeds anteriorly it generally becomes broader and attaches to the ventral corner of the jugal. In most forms the ligament is continuous dorsally with the infratemporal fascia, and ventrally with the ventral edge of the outer rictal plate. In some forms the ligament may be fused to the outer rictal plate. This appears to vary at the species level. In Sceloperus cyanogenys it is fused while in S. orcutti and undulatus it is not. Among the other families of lizards the ligament is well developed in the Agamidae, Teidae, Varanidae and Cordylidae. It is highly reduced in the Scincidae and absent in the Gekkonidae, Xantusidae and Chamaeleontidae as a distinct structure.

Infratemporal Fascia

A large sheet of shiny fascia partially covers the infratemporal fossa in all iguanid genera. It shall be called here the infratemporal



Leiocephalus

Fig. 1 Superficial Features of the Trigeminal Musculature fascia. This fascia was mentioned by Oelrich in his study of the head of *Ctenosaura pectinata* (Oelrich, 1956), but not described in detail. Lakjer in his classic study of the jaw muscles of the sauropsida shows the fascia in three of his drawings each time labelling it differently.

The infratemporal fascia arises as a narrow band on the dorsal buccal surface of the surangular, anterior to the quadrate. It extends anterodorsally into a broad fascia which attaches along the posterior border of the jugal, the ventral border of the postorbital and usually continues onto the anterior half of the squamosal.

Immediately after originating on the mandible the fascia crosses exterior to the ligamentum quadratomandibulare. In most forms as it crosses the ligament it fuses with it in such a way that the fibres of the ventral border of the fascia become continuous with the fibres of the ligament. The remaining fibres fan out dorsally and posteriorly to cover the infratemporal fossa. The amount of coverage varies from genus to genus and is usually 2/3 to 7/8 of the fossa. The posterior border of the fascia is free of attachment in all forms except *Phrynosoma* where the posterior fibres attach to the overlying skin and *Crotaphytus* where the posterior fibres attach to the quadrate. Posterior to the fascia the underlying adductor superficialis can be seen filling the remainder of the fossa.

In *Crotaphytus*, *Ctenosaura*, *Leiocephalus*, *Dipsosaurus*, *Uta* and *Chalaradon* the fascia and ligament do not appear to be continuous. In these forms there is a space between the top of the ligament and the bottom of the fascia. Through this space the underlying rictal plates and muscle are visible. In *Crotaphytus*, *Ctenosaura*, *Leiocephalus* and *Uta* this gap can be attributed to anterior fibres of the fascia which insert on the skin and are removed in skinning. In the other forms however, no such cutaneous insertions were found.

Special pains were taken to describe the infratemporal fascia and ligamentum quadratomandibulare because their crossed condition appears to be an iguanid specialization. Amoung all the other families of lizards only the Varanidae were found to have a similar condition.

These structures show considerable variation among the other families. In the geckos *Hemidactylus* and Gonatodes there is no ligamentum quadratomandibulare. The jugal is absent and the squamosal is much reduced. The infratemporal fascia arises not on the surangular but on the surface of the superficialis muscle anterior to the quadrate. It fans out anterodorsally and inserts on the inferior border of the postorbital and parietal. In the gekkoes the parietal is extended laterally to meet the temporal bar. In the skink *Mabuya* the infratemporal fascia arises on the surangular and extends dorsally as a not very wide sheet of fascia and inserts at the junction of the jugal and squamosal. Ventrally the fascia is joined by a smaller triangular fascia arising as in the gekkoes from the surface of the superficialis. A thin slip of fascia extends from the ventral border of the infratemporal fascia and attaches to the rictal plates probably representing a much reduced ligamentum.

In the teiid *Ameiva* a very different condition exists. The ligamontum is continuous dorsally with a fascia which covers the entire infratemporal fossa. Exterior to this fascia is a separate narrow fascia resembling the infratemporal fascia as it is usually seen. It arises on the ventral half of the tympanie crest of the quadrate and extends anterodorsally to the usual insertion on the jugal and squamosal. In *Zonurus* the ligament is very strong and is solidly fused to the external rictal plate. Posteriorly the ligament is joined by a fascia originating on the surface of the superficialis muscle. The rictal plates are extremely large, extending all of the way back to the angle of the jaw where they make a firm attachment to the mandible. No infratemporal fascia is present. This may be correlated with the strong dermal armor covering the entire head.

In *Chamaeleon* there is no separate zygomatic ligament. The infratemporal fascia originates on the mandible, ventral to the quadrate and extends anteriorly to insert on the jugal. The dorsal half of the fossa is covered by a thin secondary fascia. In *Xantusia* the condition is essentially the same as *Chamaeleon* except that the thin second fascia is absent.

Rictal Plates

Medial to the infratemporal fascia and the ligamentum quadratemandibulare the rictal plates or mundplatten are found. These are two triangular plates of integument which extend posterior to the jugal. The inner one is continuous with the skin of the lower jaw and the outer one continuous with the skin of the upper jaw. The two rictal plates are continuous along their dorsal border. This border slopes downward as the plates are traced posteriorly. When the jaw is open the rictal plates partially open and flatten out providing extra skin at the angle of the jaw to accomodate the opening. When the jaw is adducted the rictal plates must be folded again along their dorsal crease so as to tuck away neatly. The folding is accomplished by the levator angularis oris muscle.

The rictal plates are of fairly constant size throughout the Iguanidae. They extend from 1/2 to 2/3 of the distance from the jugal to the quadrate. In Phrynosoma they extend almost the entire distance. Among the other families variation is found in the skinks and gekkoes which have very small rictal plates, half the size of the iguanid plates, and in the Chamaeleontidae and Cordylidae which have larger plates.

Adductor Mandibulae Group

The jaw musculature has been divided into three major portions according to the position of the parts with respect to the mandibular and maxillary branches of the trigeminal nerve (Luther, 1914; Lakjer, 1926). Both branches arise from the semilunar ganglion which sits in the trigeminal notch of the prootie. The maxillary branch V2, leaves the ganglion and courses through the infratemporal fossa in an anterolateral direction on its way to the orbit. The mandibular branch V3, travels ventrally and laterally to where it enters Meckels' fossa in the mandible (Fig. 6). The adductor mandibulae externus, the most exterior and therefore most easily accessable of the three parts of the adductor mandibulae lies lateral to both branches of the trigeminal nerve. Upon removing the adductor externus the two nerve branches are clearly seen. Most of the remaining muscle mass is the adductor mandibulae internus. It lies medial to both nerve branches. The small and often indistinct adductor posterior is found posterior to the mandibular ramus in the posteroventral corner of the infratemporal fossa (Fig. 6).

The adductor internus and externus are both large and clearly distinct separable muscle masses, filling the infra and supratemporal fossae and extending out to the posterior lateral corner of the mandible. The adductor posterior is quite small in comparison, and though always present in iguanids, it is never clearly separable from the externus.

Bodenaponeurosis

The great mass of adductor mandibulae muscle has widespread origins on the parietal, quadrate, prootic, exoccipital, pterygoid, epipterygoid, postorbital and squamosal. The mandible which must receive the force of contraction of all of this muscle has comparatively little surface area for muscle insertion. The surface area is oncreased by an extensive set of tendons and fascia known as the bodenaponeurosis. This consists of two strong extensions of the posterior and dorsal borders of the coronoid process (Fig. 2). The outer tendinous extension serves as the insertion of the adductor externus while the inner one receives the pseudotemporalis portion of the adductor internus. The maxillary ramus of the trigeminal passes anteriorly between the two branches of the bodenaponeorosis. The two tendens usually fuse ventral to the nerve, into one very thick tendon.

The external bodenaponeurosis is actually two sheets of fascia attached along their thickened anterior border. The outer of these sheets is long and narrow while the inner one is wide and extends posteriorly approximately half the width of the infratemporal fossa. Ventrally this inner sheet attaches along the medial ridge of the surangular forming an entensive trough just dorsal to Meckel's Fossa. In this arrangement the three outer surfaces of the external bodenaponeurosis provides insertion for the various subdivisions of the adductor externus. These will be described later.

The internal bodenaponeurosis is a simple unfolded sheet extending deeply into the pseudotemporalis muscle. At the muscle surface the sheet thickens to a tendon. The bipinnate insertion of muscle fibres on the various faces of all of the parts of the bodenaponeurosis considerably increases the force with which the jaw can be closed.

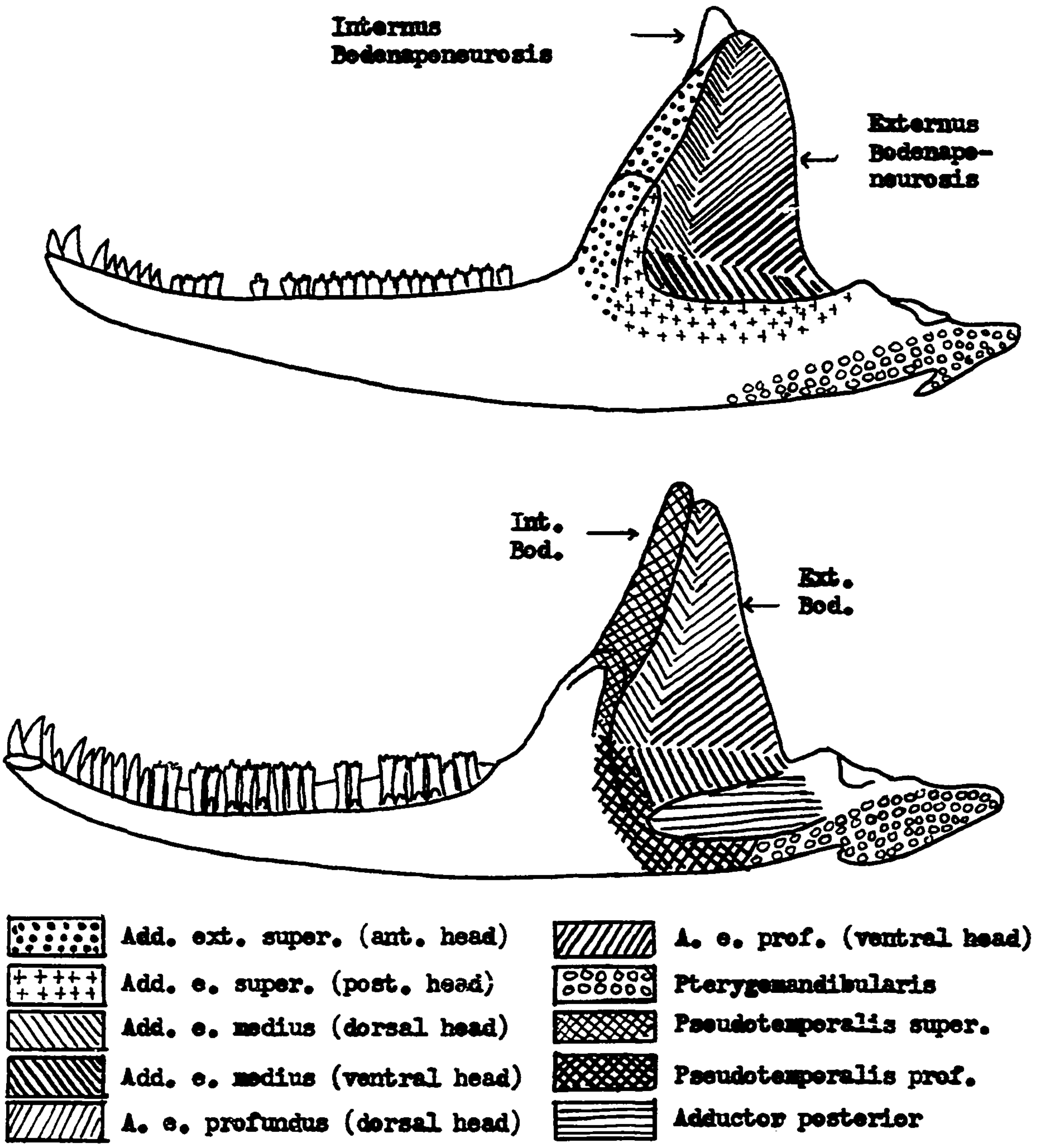


Fig. 2 Muscle Insertions on the Mandible and Bodenaponeurosis

Adductor Mandibulae Externus

The adductor externus is a very large muscle mass superficially occupying the entire infratemporal fossa in all iguanid species (Fig. 3). The extent of its presence in the supratemporal fossa varies at the genus level. It fills the entire fossa in Uma but is not seen at all in the supratemporal fossa of Urosaurus, Crotaphytus and Leiolaemus. All intermediates are also found and will be discussed further on. The muscle originates on the post orbital, squamosal, quadrate, parietal, exoccipital, prootic and supratemporal. These elements make up the temporal bar and posterior region of the temporal fossae. The externus inserts along the exterior bodenaponeurosis, the coronoid and surangular. It has a fairly complex internal structure and for purposes of analysis can be subdivided into superficialis, medius and profundus segments. These heads can be further subdivided into more or less consistently distinct regions. It must be remembered however that none of these represents a separate muscle mass isolated by connective tissue; with few exceptions this is all one muscle.

The adductor mandibulae externus is innervated by the stout third branch of the mandibular ramus of the trigeminal. This branch leaves the mandibular ramus shortly after the ramus becomes distinguishable from the maxillary ramus. It enters the medial surface of the profundus head of the adductor externus. After passing through the profundus it branches to all parts of the medius and superficialis.

Adductor Externus Superficialis

This head of the externus is clearly separable into two distinct muscles, the levator angularis oris and the superficialis.

Levator Angularis Oris

The levator angularis oris is present in all iguanid genera. It is a thin sheet of muscle covering all but the posteroventral corner of the infratemporal fossa (Fig. 1). It lies medial to the infratemporal fascia and external to the superficialis muscle from which it probably arises. The levator appears to cover more of the infratemporal fossa in _Anolis_ and its close relatives due to the different shape of the fossa in this group. In the _Anolis_ group the infratemporal fossa tends to be squared off posteriorly because the squamosal passes very close to the quadrate leaving very little or no space dorsal to the quadrate. In these forms the levator originates on the inferior border of the postorbital and most of the inferior border of the squamosal. The origin then posses briefly onto the surface fascia of the superficialis muscle and then onto the dorsal half of the tympanic crest of the quadrate.

In most other iguanid genera the squamosal arches highly over the dorsal border of the quadrate creating a posterior extension of the infratemporal fossa in this region. Where such as extension exists the leavtor does not originate along the entire length of the squamosal. Instead it originates on the anterior part of the squamosal, passes onto the surface fascia of the superficialis and then onto the tympanic crest of the quadrate leaving the dorsal extension of the fossa covered only by the large sheet of fascia.

In all forms the fibres of the levator extend anteroventrally and insert on the dorsal border of the rictal plates. The insertion sometimes extends onto the medial surface of the inner plate. Upon contraction the dorsal edge of the plates are pulled causing them to fold.

The muscle is innervated by the tips of one or two twigs of the third branch of the mandibular ramus. These twigs come through the superficialis muscle to the inner surface of the levator, usually at about the center of the muscle. When the other parts of the trigeminal musculature contract to close to the jaw, the levator angularis oris also contracts, pulls on the dorsal edge of the plates and cause them to fold away.

In *Phrynosoma* the levator is very thick and covers all of the infratemporal fossa. Anteriorly its origin passes onto the jugal and posteriorly it covers the entire tympanic crest of the quadrate. In *Plica* the levator originates at the point of union of the jugal, postorbital and squamosal. The origin then immediately passes onto the surface fascia. As it does so it dips sharply ventrad and then sharply dorsal exposing a large area of surface fascia. Posteriorly it originates on the central quarter of the tympanic crest. In *Corythophanes* the levator originates on the point of union of the three temporal bones and then passes onto the fascia as in *Plica*, but in this case the origin continues ventrad on the fascia, anterior to the quadrate but never touching it. In *Leiocephalus*, *Dipsosaurus*, *Uta* and *Enyaliodes* the origin does not extend as far back as the quadrate, but ends on the fascia of the superficialis.

Among the other families of lizards the levator angularis oris is lacking as a separate entity in the Gekkonidae and Scincidae. In these families the reduced rictal plates attach directly to the surface of the anterior head of the superficialis muscle and are operated by this muscle rather than a separate sheet.

In *Varanus* the levator originates as several slips from the postorbital and squamosal, and one extensive sheet from the tympanic crest of the quadrate. These slips are quite thick and penetrate deeply into the surface of the superficialis muscle. All of the slips join to make a strong levator which occupies the ventral half of the infratemporal fossa. In *Chamaeleo* the levator originates on the surface fascia of the superficialis and the ventral 2/3 of the tympanic crest, filling as in *Varanus*, the ventral half of the fossa. In *Zonurus* the levator originates on the ventral face of the very much enlarged postorbital, and on the anterior half of the squamosal. There is no quadrate or fascia. The muscle fills the anterior half of the fossa and inserts on the dorsal medial border of the anterior half of the rictal plates. The posterior half of the plates are attached to the surface of the posterior head of the superficialis muscle by means of a sheet of fascia. Thus in *Zonurus* the very large rictal plates are operated by a strong levator angularis oris and the superficialis muscle. In the Teiidae and Xantusidae the levator resenbles that of the non anoline iguanid type.

Superficialis

The adductor ext. superficialis is found medial to the levator angularis oris and the rictal plates. It fills the entire infratemporal fossa and extends downward to varying degrees over the lateral side of the mandible (Fig. 3). It originates on the inner edge of the temporal bar, the tympanic crest of the quadrate and from two sheets of fascia which will be described below. It inserts on both surfaces of the outermost fold of the bodenaporeurosis and on the lateral surface of the surangular along the ventral border of the infratemporal fossa.

In all forms the superficialis can be divided into two heads. The anterior of these two originates on the medial surface of the postorbital. Its fibres pass ventrally and insert along the outer surface of the outer flap of the bodenaponeurosis. If the superficialis is highly developed the insertion may continue ventrally onto the coronoid and dentary. With the jugal removed this head can be seen as a long, narrow, almost vertically oriented segment occupying the most anterior part of the infratemporal fossa. In about half the genera (Table 1) the anterior head is immediately distinguishable from the posterior head because its fibres are oriented at a less acute angle than those of the posterior head. This is always the case in anolines and their allies. In a few genera, _Hoplurus_, _Basiliscus_ and _Polychrus_ the anterior head of the superficialis can be seen in the supratemporal fossa. This is because the fibres extend dorsally for a short distance before turning ventrad.

Among the other families the anterior head of the superficialis is usually conspicuous. It tends to be enlarged in those families where the postorbital expands to roof over the supratemporal fossa, ie. Cordylidae, Scincidae and Xantusidae.

The anterior superficialis is one of the more clearly separable heads. Its origin and insertion are shared by no other muscle. Medially it is completely separable from the pseudotemporalis which is part of the adductor internus. Laterally it is distinct from the levator angularis. Anterior to it there is no muscle and posteriorly it is distinct, though not separate, from the posterior head.

The posterior head originates on the inferior surface of the squamosal, the dorsal lateral surface of the quadrate as well as the tympanic crest. Fibres also arise from the most lateral portion of a fascia which originates on the anterodorsal border of the quadrate. This fascia extends anteroventrally and is fairly wide, entering deeply into the adductor externus and serving as part of the origin of the adductor externus medius as well as the superficialis. Fibres originate on the anterior and posterior face of the fascia. Finally there is a shiny fascia in the posterodorsal corner of the infratemporal fossa. This fascia covers the superficialis and gives rise to its most superficial fibres. This is the same fascia whose lateral surface is part of the origin of the levator angularis oris. In some forms, Hoplurus, Urosaurus, Dipsosaurus, Uranoscodon, Plica and Leiocephalus, the superficial fascia is joined by a second sheet of fascia originating at the junction of the postorbital and squamosal as a narrow band. This band fans out ventrally adding to the surface area available for muscle origination (Fig. 3).

The fibres arising from the superficial fascia are the outermost fibres of the muscle. They extend anteroventrad and form the ventral most edge of the posterior superficialis inserting along the lateral edge of the surangular. The insertion extends posteriorly, half of the distance from the coronoid to the quadrate. The fibres from the tympanic crest insert all along the surangular posterior to those from the superficial fascia and take over the ventral edge of the superficialis. Fibres from the posterior face of the quadrate fascia insert medial to those of the tympanic crest along the more dorsal reaches of the posterior half of the surangular. Fibres from the anterior surface of the quadrate fascia along with those from the squamosal slope anteroventrad to insert along the anterior lateral half of the surangular ventral and - or posterior to the ventral most extension of the anterior head.

The entire superficialis is innervated by two or three brances of the third trunk of the mandibular ramus. These pass into the medial surface of the muscle from the deeper muscle layers. One branch passes through the superficialis to innervate the levator angularis oris (Fig. 3). The insertion of the posterior superficialis covers the anterior surangular foramen causing the posterior inferior labial nerve to pass through the insertion as it courses anteriorly. This nerve does not however, inervate the superficialis.

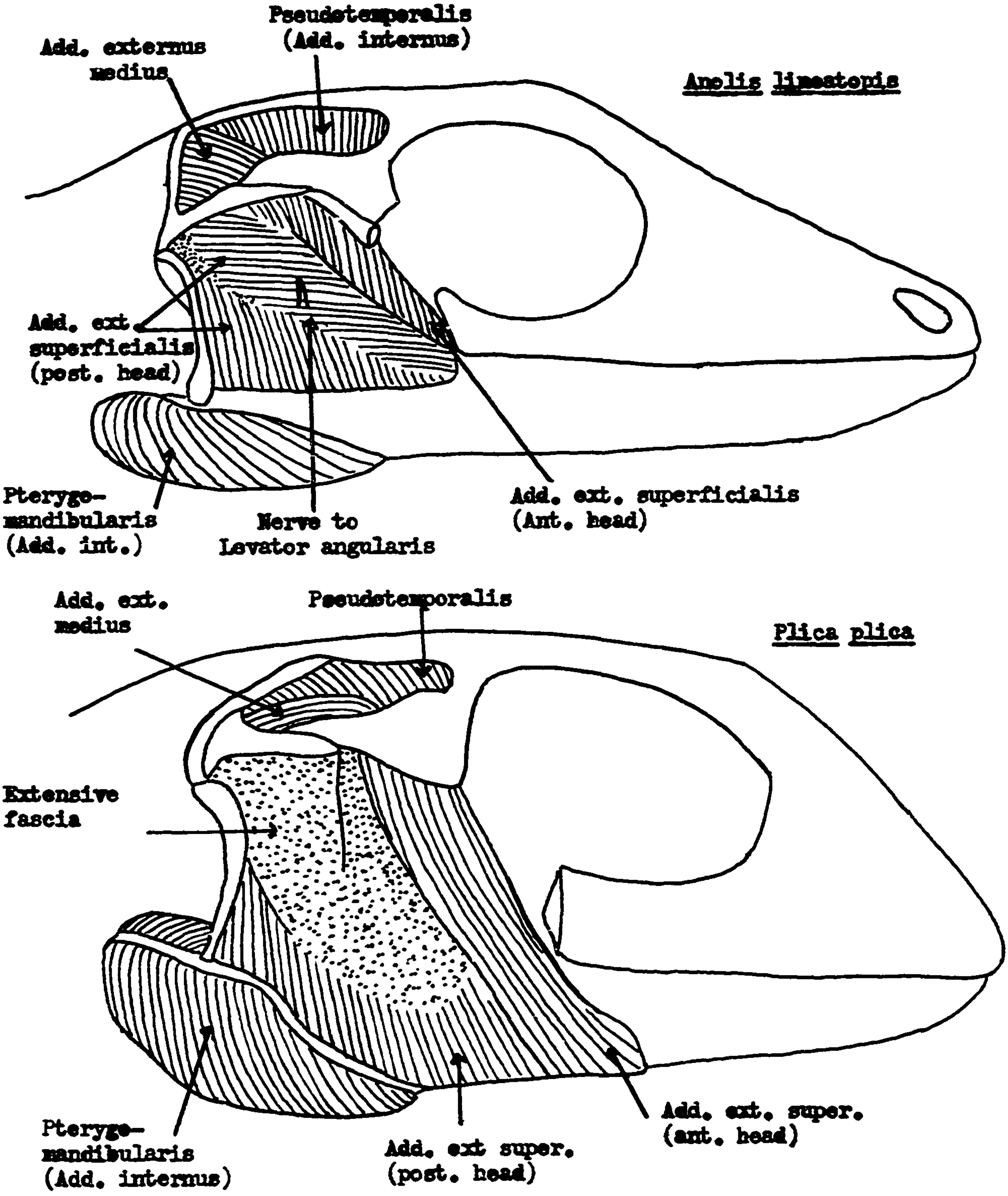


Fig. 3 Adductor Musculature, Superficial Depth

The superficial layers of the posterior superficialis are the most variable. In forms like *Anolis* and its close relatives *Chamaeleolis*,*Xiphocercus*, *Deiroptyx*, *Chamaelinorops*, the superficialis inserts along the dorsal lateral edge of the surangular and is very thin. Correlated with this the superficial fascia is small. In most other forms (Table 1) the superficialis extends further down the side of the mandible, and originates on a superficial fascia whose extent is proportionally increased. In *Plica* for example, the superficialis completely covers the side of the mandible and has a very extensive superficial fascia (Fig. 3).

Among the other families of lizards a very extensive superficialis extending most or all of the way down the side of the mandible seems to be the rule. The only exception is *Chamaeleo* where the muscle extends less than half the way down the mandible. In *Mabuya* and *Zonurus* extensive superficial fascia were not found at the origin of the superficialis but over the insertion of the muscle on the mandible. In these forms the supratemporal fossa is roofed over providing increased surface area for the origination of the superficialis. The enlarged superficialis requires increased insertional area which is furnished by the fascia over the origin. In *Ameiva* a tough fascia covers the entire muscle while in *Tupinambis* the fascia is just at the origin.

Adductor Externus Medius

The adductor medius is medial to and continuous with the posterior head of the superficialis. If the superficialis fibres inserting on the lateral side of the mandible are removed, an arbitrary separation can be made between the two heads and the medius can be seen filling the infratemporal fossa. The medius can usually be seen as two heads, one filling the infratemporal fossa and one extending into the supratemporal fossa (Fig. 4).

The fibres of the infratemporal or ventral head originate on the medial surface of the posterior half of the squamosal, the anterior medial and dorsal walls of the quadrate, and from both surfaces of the deeper portions of the fascia which originates on the anterior dorsal border of the quadrate and slopes anteroventrad. This is the same fascia whose lateral edges give rise to the posterior superficialis. The origins of the ventral head of the medius and the posterior superficialis are thus continuous and separation can be accomplished only at the insertion.

Fibres originating on the posterior face of the quadrate fascia and the anterior medial wall of the quadrate slope anteroventrad to insert along the medial and dorsal border of the posterior 2/3 of the surangular. Deeper fibres from this origin continue the insertion onto the trough of connective tissue created by the inner sheet of the externus bodenaponeurosis joining the surangular. Fibres from the anterior face of the quadrate fascia, the squamosal and the dorsal quadrate extend anteroventrad at a wider angle than the posterior fibres. They insert along the lateral and posterior surface of the coronoid and extend medially to fill the trough of the bodenaponeurosis. No variation was found in this head of the medius.

The supratemporal head of the medius represents the most dorsal extension of the adductor externus. It occupies the posterior part of the supratemporal fossa. The anterior part of the fossa is filled with the pseudotemporalis superficialis which is part of the adductor internus. The supratemporal or dorsal head originates on the lateral surface of the posterior half or so of the parietal, from the surface of the supratemporal and sometimes from the dorsal border of the posterior half of the squamosal. Its fibres pass anteroventrad into the infratemporal fossa where they insert on the anterior dorsal lateral surface of the inner sheet of the externus bodenaponeurosis. The entire insertion is dorsal to that of the infratemporal head.

Both heads of the muscle are innervated by the large third trunk of the mandibular ramus. The nerve passes through the inner surface of the medius at approximately its middle point. It breaks down into two or more branches which pass through the medius and extend to the superficialis.

The supratemporal head is a rather variable portion of the jaw musculature. As Table 1 shows, it usually fills less than half of the supratemporal fossa. However, in such genera as Urosaurus, Leiolamus and Crotaphytus the supratemporal head is not visible in the fossa, while in *Callisaurus*, *Uma* and *Phrynosoma* the supratemporal head fills all or most of the fossa. In *Callisaurus* and *Uma* the medius covers the pseudotemporalis by extending anteriorly over it as a sheet of muscle originating along the dorsal border of the parietal. In *Phrynosoma* the medius covers the entire fossa because the pseudotemporalis is greatly reduced. In *Leiolaemus* and *Crotaphytus* we have the opposite condition from *Callisaurus* and *Uma*. In these two the pseudotemporalis is extended posteriorly covering the origin of the medius. In *Urosaurus* the dorsal head of the medius is actually missing, not just covered. This obviously indicates a certain degree of evolutionary experimentation within the Iguanidae.

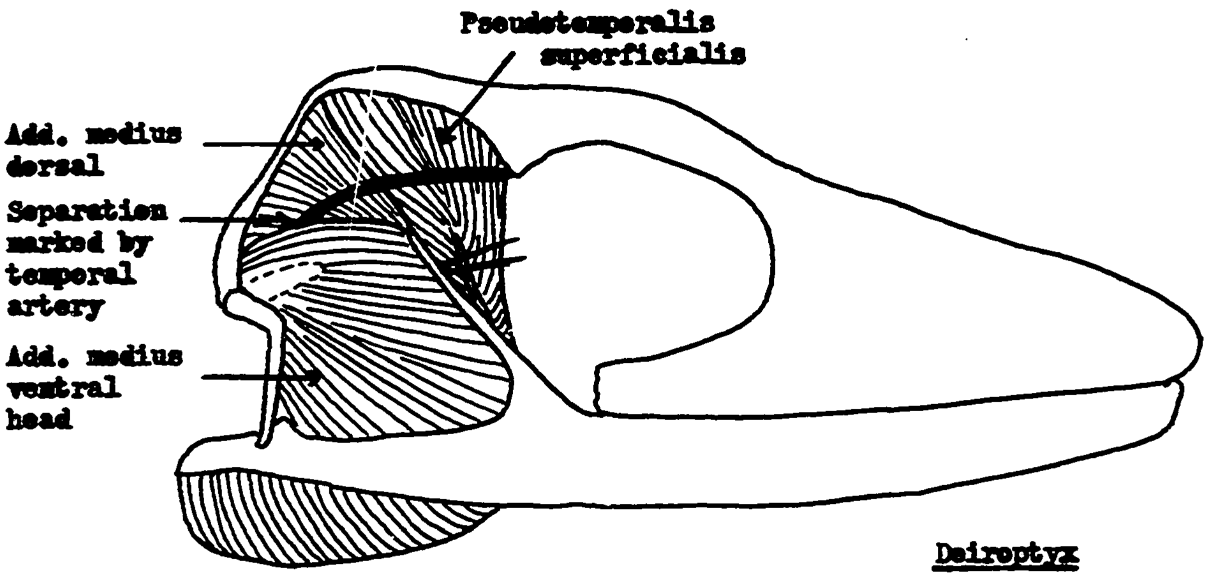
Comparison with other families is complicated by the fact that in some families the supratemporal fossa is reduced or lost. The fossa is present in the Teiidae, Agamidae, and Chamaeleontidae. The agamid and teiid fossa are similar to the iguanid fossa. The agamid fossa is filled more than half way with adductor medius while the teiid fossa is filled completely with pseudotemporalis superficialis. The dorsal adductor medius is lost in *Ameiva* and reduced to a tiny head under the superficialis in *Tupinambis*. The chamaeleontid fossa is greatly enlarged due to the large parietal crest, and is filled entirely with adductor medius, the pseudotemporalis being greatly reduced. In *Varanus* the fossa is reduced to a long narrow opening quite high on the side of the skull and is filled entirely with pseudotemporalis superficialis. The medius has a parietal origin but it is posterior to the fossa.

In the gekkoes the fossa is absent. The postorbital and squamosal are articulated along the length of the parietal creating a greatly enlarged infratemporal fossa. In the gekkoes the dorsal head of the medius is very extensive. It originates along the inferior surface of the parietal and fills all of the enlarged infratemporal fossa. In the Scincidae the supratemporal fossa is lost due to an enlarged postorbital which extends posteriorly between the squamosal and parietal covering the fossa. The dorsal head of the medius is again extensive filling all of the infratemporal fossa and covering the pseudotemporalis superficialis. In Xantusia the postorbital and squamosal articulate along the side of the parietal eliminating the supratemporal fossa. As in the skinks the dorsal head of the medius fills most of the enlarged temporal fossa. In Zonurus the fossa is filled over by the postorbital. The medius fills the entire infratemporal fossa and extends posteriorly through the posterior temporal fossa to originate on the lateral wall of the occipital crest which is well developed in Zonurus. This arrangement causes the posterior part of the medius to lie medial to the profundus. This is because the occipital crest is on the midline of the animal while the profundus originates on the lateral posterior edge of the parietal and on the exoccipital.

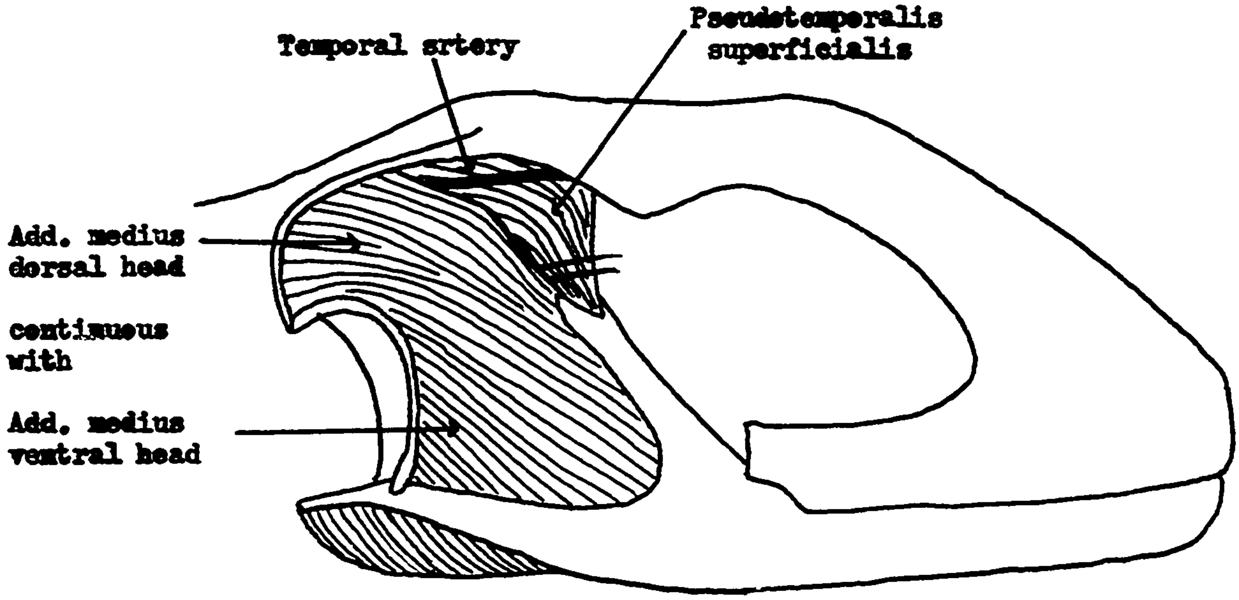
It seems that the supratemporal fossa may be lost either by a posterior enlargement of the postorbital as in the skinks, Zonurus and Xantusia, or by a lateral enlargement of the parietal to meet the temporal bar as in the geckos, or possibly by a combination of both factors. Whatever the method, the loss of the fossa appears to be always accompanied by the enlargement of the medius.

In most iguanid forms the two heads of the adductor externus medius are continuous, showing no external separation. However in the basiliscines and all the species of Anolis examined including Deiroptyx, Phenacosaurus, Xiphocercus, Chamaeleolis and Chamaelinorops there is a distinct separation of the two heads. The separation is always just dorsal or medial to the posterior end of the squamosal and is clearly marked by the temporal artery which passes between the two heads of the medius, continues over the supratemporal head of the medius and the pseudotemporalis superficialis and then leaves the fossa. In most other iguanid genera (Table 1) the temporal artery exists at the anterior border of the medius and passes over the pseudotemporalis superficialis (Fig. 4).

In Enyaliodes and Enyaliosaurus the temporal artery exits as in Anolis and its relatives but does not cause a conspicuous separation of the heads. Callisaurus and Uma show a separation of the medius, but in these forms the separation is not marked by the temporal artery. The artery passes between the medius and pseudotemporalis as in most forms, but is not visible superficially because the medius is greatly extended anteriorly covering the superficialis.



Deiroptyx



Sceloporus cyanogenys

Fig. 4 Comparison of Adductor Medius and Temporal Artery in Anoline and Sceloporine Lines

Adductor Externus Profundus

The adductor externus profundus is the deepest part of the adductor externus. It lies medial to the medius. Its fibres are continuous with those of the medius, but the two can be separated by means of their separate origins. Medial to the profundus lies the pseudotemporalis superficialis and profundus, the mendibular and maxillary ramus of the trigeminal and the braincase (Fig. 5).

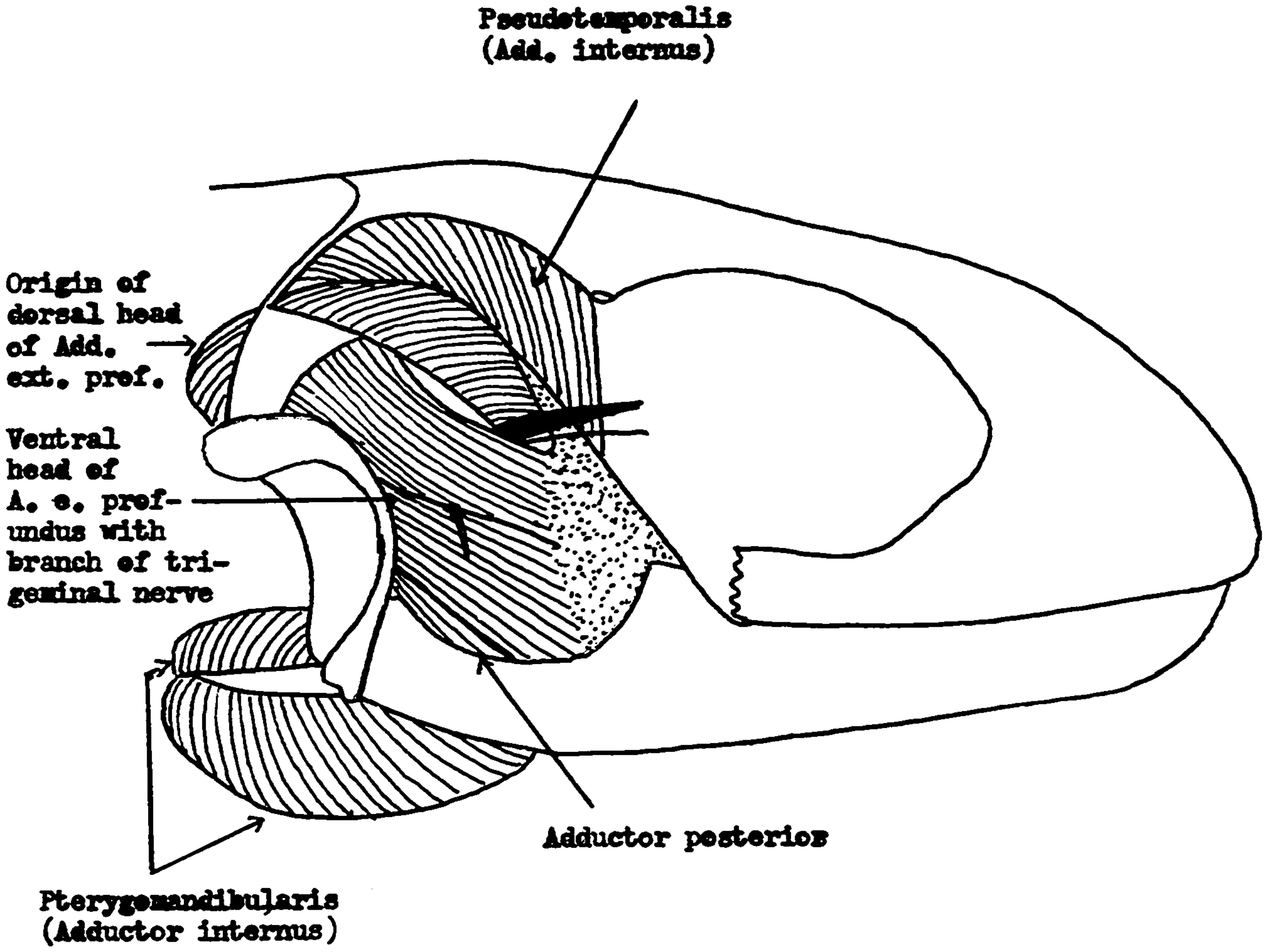
The profundus can be roughly divided into two heads. The dorsal head originates on the posterolateral tip of the parietal, and inferior surface of the supratemporal. The fibres from the posterior parietal form a conspicuous bulge which can be seen when looking at the head in lateral view after removing the epaxial musculature. Its fibres course medially for a short distance then pass anteriorly through the posterior temporal fossa dorsal to the exoccipital. They then pass anteroventrad to insert on the posterolateral side of the inner sheet of the externus bodenaponeurosis, posterior to the fibres of the medius. At the insertion the profundus fibres are indistinguishable from those of the medius. At the origin however, the profundus fibres are clearly identifiable because they pass out from the underside of the parietal while those of the medius come from the dorsal side of the parietal.

The lower head of the profundus originates on the posterior process of the prootic and from a sheet of fascia extending ventrally from the exoccipital, medial to the quadrate and dorsal to the quadrate process of the pterygoid. Its fibres pass anteroventrad, ventral to those of the dorsal head and insert on the bodenaponeurosis ventral to the insertion of the dorsal head.

The separation between the two heads is roughly marked by the third branch of the mandibular ramus. This nerve passes between the two heads, innervates them and then divides into two or more branches which pierce the medius and superficialis.

The adductor externus profundus is fairly constant throughout the iguanidae. In Corythophanes which lacks a posterior temporal fossa t the dorsal head of the profundus which would normally pass through this fossa is also absent. In Phrynosoma the profundus appears to be missing. The posterior temporal fossa is present but no muscle passes through it. The lower head is either very greatly reduced or absent altogether.

Among the other families the profundus shows slight variation. In Xantusia the posterior temporal fossa is absent, eliminating the dorsal head of the medius in this family. In Chamaeleon the dorsal head is also absent possibly due to the fact that the parietal on which it normally originates, is extended into a very large mid dorsal spine, and does not extend laterally to meet the quadrate and squamosal as is the usual case. In Zonurus the dorsal origin of the profundus actually lies lateral to the medius. This is because the origin of the medius extends posteriorly onto the occipital crest which lies on the middle of the animals body.



Ctenosaura hemilopha

Fig. 5 Adductor Profundus

Adductor Mandibulae Internus

The adductor internus is divided into two completely separate muscle masses, the pseudotemporalis and the pterygomandibularis both of which lie medial to the maxillary and mandibular divisions of the trigeminal nerve (Fig. 6). In contrast to the adductor externus which is a single complex but unified structure, few generalizations can be made about the pseudotemporalis and the pterygomandibularis even though they are classified together. The two muscles lie at right angles to each other. The pseudotemporalis fills the anterior temporal region with fibres running roughly dorsoventrad while the pterygomandibularis fills the space between the mandible and the pterygoid with fibres running in an anterior posterior direction. The origin and insertions are completely different as are their innervations.

Pseudotemporalis

The pseudotemporalis is a very large muscle mass which when well developed occupies the anterior half of the temporal region (Fig. 6). In a skinned but undissected specimen it may be seen in the supratemporal fossa anterior to the medius. In the infratemporal fossa it may be seen only after the externus is removed. It lies medial and anterior to the externus, medial to the maxillary ramus and anterior to the mandibular ramus. It is anterior to the prootic and forms the posterior wall if the orbit.

In some forms it is divisable into two heads the superficialis

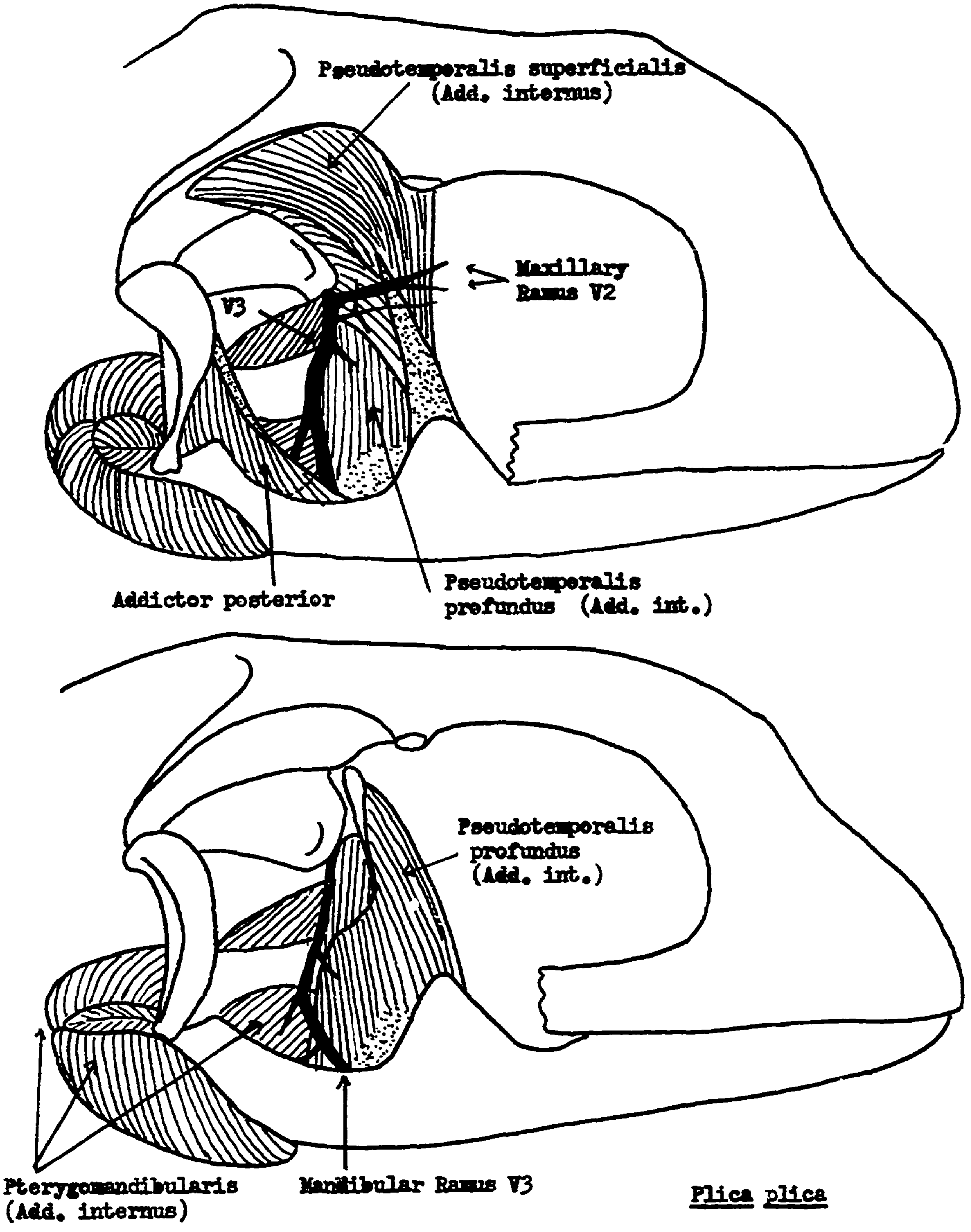


Fig. 6 Pseudotemporalis Superficialis and Profundus

and the profundus. The superficialis originates on the anterior lateral or dorsal surface of the parietal, the lateral surface of the alar process of the prootic and the lateral surface of the dorsal third of the epipterygoid. Its fibres pass ventrally to insert bipinnately on a sheet of fascia, the internus bodenaponeurosis. Some fibres insert directly on the dorsal edge of the coronoid bone. The muscle is innervated by the first branch of the mandibular ramus of the trigeminal nerve. The first branch along with the second, which is sensory (Oelrich, 1956) passes anteriorly over the superficialis next to the maxillary ramus often looking like part of it. Closer inspection however always reveals these branches as offshoots of the mandibular ramus.

Less conspicuous than the superficialis is the profundus. This is a triangular muscle anterior to the mandibular ramus. Its origin is covered by the superficialis dorsal to it. It originates on all but the medial surface of the ventral two thirds of the epipterygoid. Its fibres fan out to insert along the posterior edge of the coronoid and down onto the anterior half of the articular, ventral and medial to Meckels' Fossa. The fibres sometimes extend onto the medial surface of the sheet of the externus bodenaponeurosis which forms the trough above Meckels' Fossa. The profundus is innervated with the superficialis by the first branch of the mandibular ramus. It also receives a nerve entering its posterior surface at about the midpoint of the muscle. This nerve comes off the fourth branch of the mandibular ramus. The main trunk of the fourth branch passes ventrally to innervate the pterygomandibularis.

In some cases the two heads of the pseudotemporalis are not separable (Table 1). Oelrich (1956) reports partial fusion of the two in some specimens of Ctenosaura pectinata. Even where the heads are not separable, the fibres of the profundus can be seen passing out from under the superficialis at a different angle.

The profundus does not vary much throughout the Iguanidae, or even throughout the Lacertilia. Whether separable or not it is always present. In Plica it is quite large, its origin extending all of the way up the anterior border of the epipterygoid. In Varanus it is also large, its origin extending onto the parietal.

The pseudotemporalis superficialis however, is considerable more variable. In most forms it fills approximately the anterior two thirds of the supratemporal fossa. In Urosaurus it fills the entire fossa. In Holbrookia and Uma the muscle fills less than half of the fossa, the remaining space being occupied by the adductor medius. In Phrynosoma the pseudotemporalis superficialis is reduced to a very small slip which originates on the underside of the anterior tip of the parietal and inserts on the anterior dorsal border of a very extensive internus bodenaponeurosis. Because of its great reduction the superficialis and profundus heads are widely separated and do not touch. It appears as if the internus bodenaponeurosis remained large or increased in size as the superficialis retreated in an attempt to keep the two in contact.

The chart listing the extent of the superficialis is not, as one might expect, the exact reciprocal of the chart listing the extent of the supratemporal head of the medius. This is because the origin of one muscle can extend under or over the origin of its neighbor. In Callisaurus for instance, the medius extends more than half of the length of the supratemporal fossa while the pseudotemporalis superficialis does the same. This is possible because the superficialis origin extends posteriorly under the medius origin. The reverse is true in Crotaphytus where the superficialis covers the origin of the medius.

In comparing the data on extent of the superficialis and the condition of the temporal artery (Table 1), it is interesting to note that those forms such as Crotaphytus and Leiolamus in which the superficialis is extended posteriorly to cover the medius, have a temporal artery which is buried within the superficialis tissue. Since the anterior edge of the medius is covered by the superficialis the artery has no choice but to continue through the muscle. The same condition also exists in Tropidurus although the posterior extension of the superficialis is slight.

In Basiliscus, Corythophanes and Laemanctus large crests have evolved by posterodorsal elongation of the parietals. These crests provide greatly increased surface area for the origin of the equally enlarged pseudotemporalis superficialis. The tendency for crest formation exists also in the anolinae, and reaches greates fruition in such forms as Chamaeleolis. In terms of muscle the anoline crest differs from the basiliscine in that the former serves as origin for both the pseudotemporalis superficialis and the dorsal head of the adductor medius while the latter gives rise to the pseudotemporalis only. The basiliscene medius originates on the unexpanded parietal lateral to the crest and does not follow the pseudotemporalis all of the way up the crest as it does in the anoles.

The difference in musculature of the parietal crest clearly separates the anolinae and basiliscinae as two distantly related groups.

Among the other families of lizards the pseudotemporalis superficialis shows a great deal of variation (Table 1). It is absent in the gekkoes and chamaeleons and reduced in the Agamidae, Scincidae, Cordylidae, and Xantusidae. In _Agama_ it covers less than half of the parietal but is still visable in the supratemporal fossa. In the Scincidae, Cordylidae, and Xantusidae the muscle is further reduced and is not visable superficially. This is due to the fact that these forms lack a supratemporal fossa and tend to have large anteriorly extended adductor medius which together with the anterior head of the adductor superficialis cover the pseudotemporalis superficialis. Remembering the fact the gekkoes which also lack a supratemporal fossa, have lost the superficialis completely, it is tempting to speculate that loss of the fossa tends to lead to reduction or loss of the superficialis, and along with it an enlargement of the medius.

On the other hand, based on the specimens I dissected, the pseudotemporalis superficialis is well developed in the Varanidae and Teiidae, filling the entire supratemporal fossa in these groups. In _Varanus_ the fossa is slightly reduced with an extensive adductor medius posterior to it while in the Teiidae the fossa is fully developed.

Pterygomandibularis

The pterygomandibularis is one of the largest and most complex of the jaw muscles. It covers the posterolateral and ventral sides of the mandible. In ventral view it covers the posterior end of the mandible and extends foreward to its origins along the ectopterygoid, the posterior border of the pterygoid and the lateral sides of the quadrate process of the pterygoid extending as far medial as the basipterygoid processes. In lateral and ventral view the muscle is completely covered by the intermandibularis posterior which is a thin extensive sheet of throat muscle. The pterygomandibularis is bordered posteriorly and medially by the first ceratobranchial and ceratohyal. Its posterior most insertion on the retroarticular process is covered to varying degrees by the insertion of the depressor mandibulae and cervicomandibularis muscles. The medial ventral surface of the muscle forms the dorsal lateral walls of the pharynx and as such are covered with oral epitheliem. The pterygomandibularis shows a highly pinnate organization and is the only adductor muscle to be oriented in the anterior posterior plane (Fig. 7).

The pterygomandibularis originates from three sources. The first is a tough tendon arising from the posterior edge of the ectopterygoid. This tendon is continuous medially with a very extensive sheet of fascia which arises from the posterior edge of the transverse process of the pterygoid. This sheet of fascia which covers the belly of the muscle

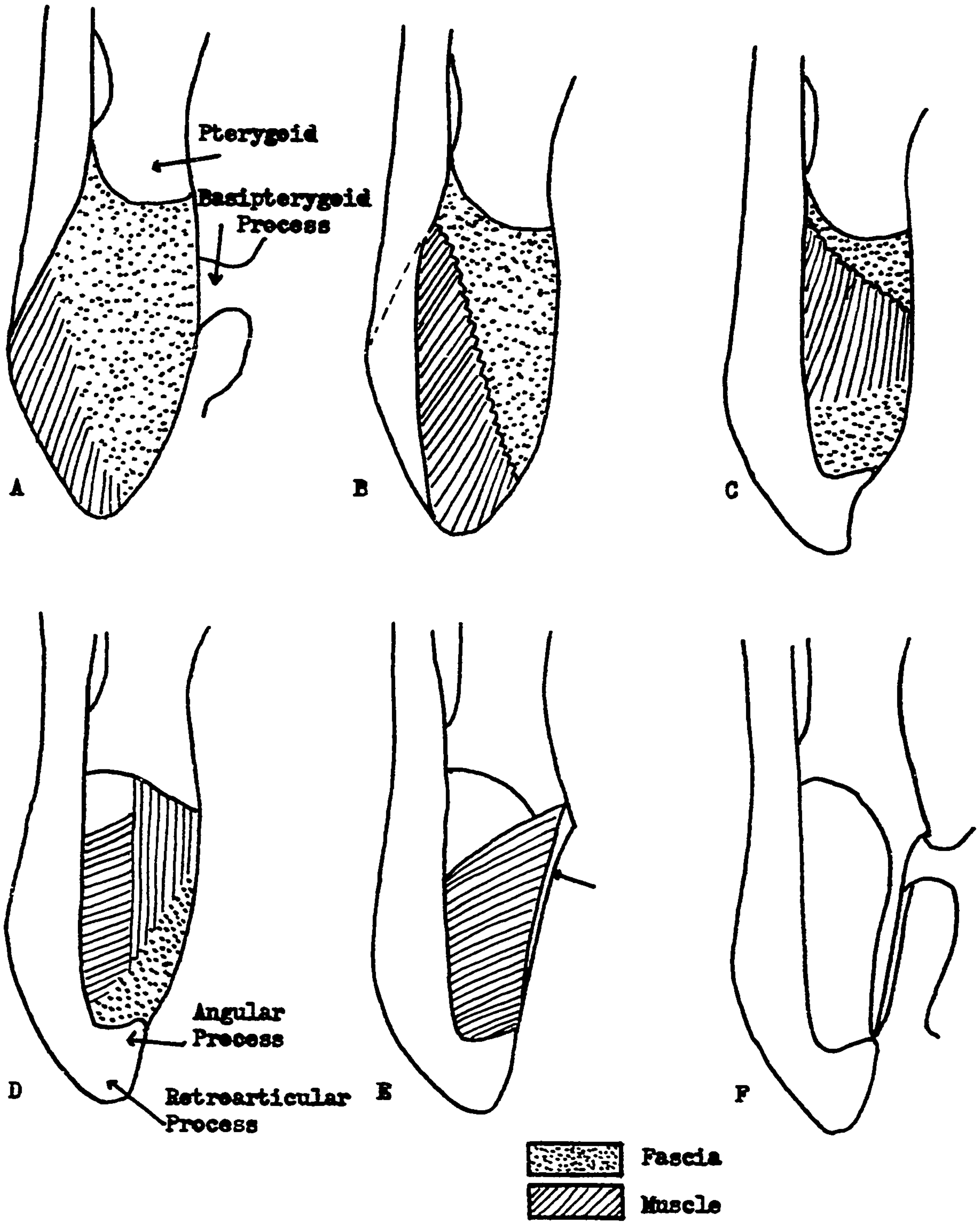


Fig. 7 Pterygomandibularis at Various Depths (Diagrammatic Representation)

plus the transverse process form the second part of the origin. The fascia extends medially to the ventral border of the quadrate process of the pterygoid. The lateral surface of this process is the third origin of the pterygomandibularis. Fibres also arise from the joint capsule of the basipterygoid process and quadrate process of the pterygoid.

The fibres from the first two origins fan out to insert all along the posterior end of the mandible to cover the articular along with its posteriorly directed retroarticular process and its anteromedially directed angular process. There is almost always a sheet of fascia extending anteriorly between the angular process and the main body of the articular. This fascia increases the insertional area for fibres coming from the shiny fascia of origin number two.

The fibres from the first two origins use the articular condyle as a fulcrum to adduct the jaw. Compared to the muscles so far discussed this is unique in that the muscle originates and inserts on opposite sides of the fulcrum it is operating. All of the other adductors originate and insert on the same side of their fulcrum.

The small amount of space allotted to this section of the muscle is very efficiently used. Rather than fill the space with a small number of long fibres extending from bony origin to bony insertion, the space is filled with a great number of short fibres many of which originate and insert on extensive sheets of fascia. This second arrangement greatly increases the force of contraction of the muscle. This type of set up is found in all of the muscles discussed so far, but it seems to be most highly developed in the pterygomandibularis, probably because of the angle at which the muscle is operating.

The fibres coming from the third insertion are seen only after the fibres from the first two origins have been removed. They pass ventrolaterally from the lateral wall of the quadrate process to insert along the dorsal and medial surface of the articular, ventral to Meckels' fossa. These operate directly on the mandible and work on one side of the fulcrum. Fibres coming from the anterior end of the quadrate process of the pterygoid and from the basipterygoid processes pass posteriorly to insert on a tendon which joins the angular process. Fibres originating on the posterior most tip of the quadrate process extend posteriorly over the angular process to the dorsal tip of the retroarticular process. Oelrich (1956) suggests that these fibres assist in abducting the jaw. Their position certainly supports this interpretation, but this means that while the rest of the pterygomandibularis is working to adduct the jaw, these fibres are working in opposition trying to abduct it. The selective advantage of this is unclear.

The pterygomandibularis is innervated by the fourth branch of the mandibular ramus. This long branch leaves the mandibular ramus a short distance after the third branch. It passes over the protractor pterygoideus to the floor of the infratemporal fossa where it enters the dorsal surface of the pterygomandibularis. This fourth branch also sends a small branch anteriorly to the posterior edge of the pseudotemporalis profundus.

The pterygomandibularis shows almost no variation among the genera of the iguanidae. The exception is Phrynosoma in which the muscle is greatly reduced and less pinnately organized. In Agama the muscle is strong and inserts upon an elongated retroarticular process. To the skink Mabuya the origin extends onto the dorsal surface of the pterygoid and the base of the epipterygoid. The angular process here is much reduced.

Adductor Posterior

The adductor posterior is the least conspicuous of the three divisions of the adductor mandibulae. It lies posterior to the mandibular ramus in the posteroventral corner of the infratemporal fossa (Fig. 6). It is a single muscle lying medial to the lower head of the adductor externus profundus. The muscle originates on the medial and lateral surface of a fascia which comes off of the dorsomedial corner of the quadrate. Its fibres fan out anteroventrally passing medial to the bodenaponeurosis to Meckel's fossa where they insert on Meckel's cartilage. Its fibres are continuous with those of the profundus making the determination of the exact limits of the muscle difficult. The insertion of the adductor posterior however is quite distinct. The fibres entering Meckel's fossa are clearly separable from the fibres of the pterygomandibularis which insert on the angular ventral to the fossa, and those of the adductor externus which insert on the bodenaponeurosis and surangular dorsal to the fossa. The muscle is innervated by the fifth branch of the mandibular ramus. The fifth branch leaves the ramus just before the ramus enters Meckel's fossa. The innervation is very difficult to find and was actually seen in the very largest specimens after considerable parts of the jaw were removed.

Constrictor Dorsalis Group

The constrictor dorsalis muscles include the levator pterygoideus, the protractor pterygoideus and the levator bulbi muscles. These muscles lie medial to the adductor internus. The two pterygoideus muscles lie posterior to the epipterygoid and ventral to the prootic and function in elevating and protracting (pushing foreward) the maxillary segment via the pterygoid. The bulbi muscles lie medial to the levator pterygoideus and extend anteriorly to operate the lower eyelid. None of these muscles are concerned with adducting the mandible. All of them are innervated by separate branches of the trigeminal nerve, independently of the three major rami.

Levator Pterygoideus

The levator pterygoideus is a laterally compressed strap of muscle lying posterior and slightly medial to the epipterygoid and the pseudotemporalis profundus (Fig. 8). It is anterior to the prootic and the mandibular ramus. It is lateral to the origins of the protractor pterygoideus, the levator bulbi muscles and the profundus ramus of the trigeminal. It originates on a band of fascia which comes off the ventrolateral surface of the parietal just anterior to the prootic and posterior to the dorsal tip of the epipterygoid. The muscles usually extends about two thirds of the way up from the pterygoid to the parietal, the remaining third of the distance being filled by the fascia. The fibres extend ventrally to insert on the dorsal surface of the pterygoid

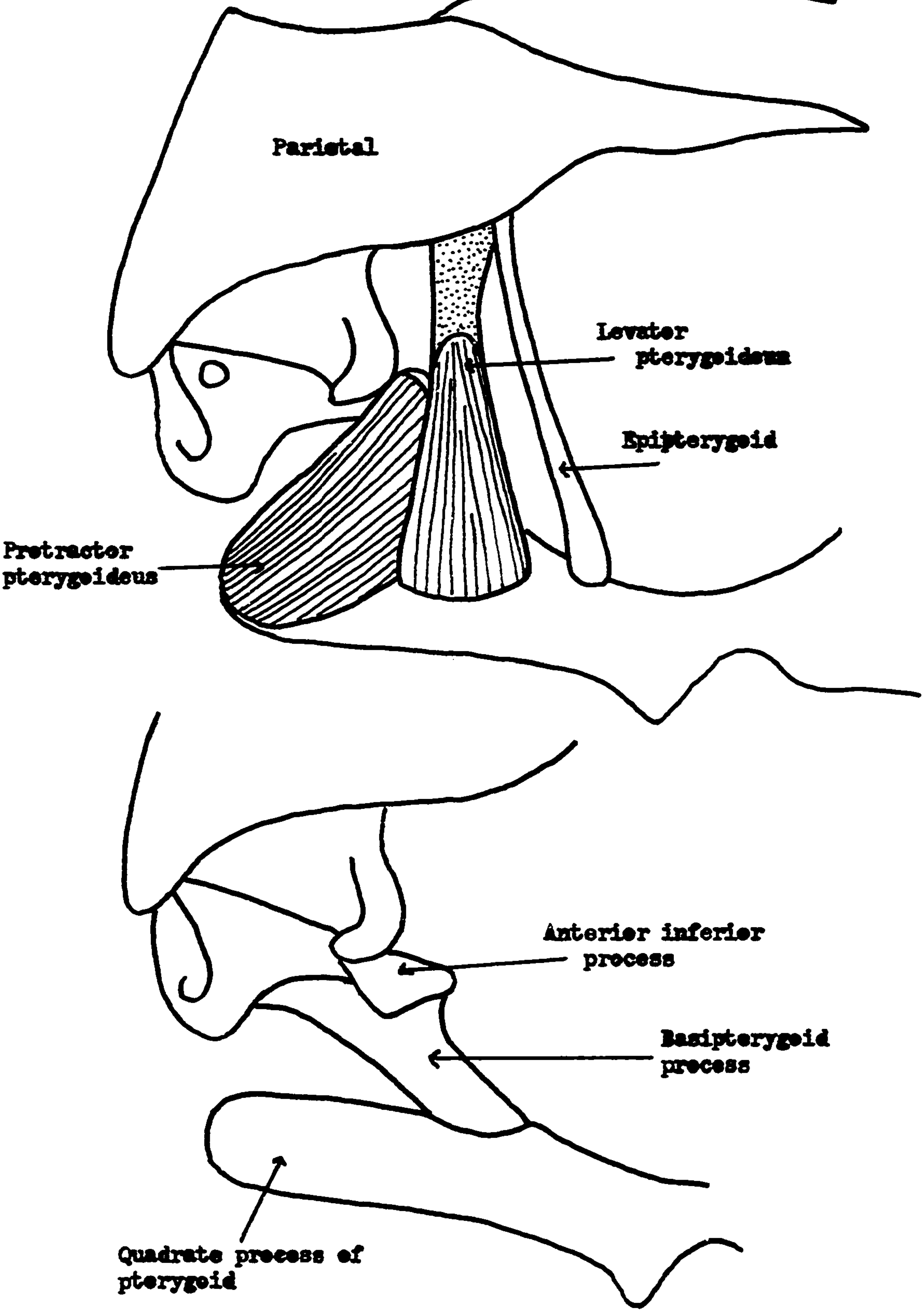


Fig. 8 Levator and Protractor Pterygoideus of *Anolis cristatellus*.

as far anterior as the medial border of the epipterygoid and as far posterior as the mandibular ramus. Innervation is by a separate branch of the trigeminal entering the medial side of the muscle.

Protractor Pterygoideus

The protractor pterygoideus lies medial and posterior to the levator pterygoideus (Fig. 8). It is ventral to the prootic, ventrolateral to the profundus division of the trigeminal and forms the lateral wall of the tympanic cavity. It originates anterior to the ganglion on the lateral surface of the anterior inferior process of the prootic and the adjoining alar process of the basisphenoid. The origin continues onto a tendon which extends from the pila antotica which is immediately anterior to the inferior process of the prootic, to the anterior dorsal surface of the basipterygoid process. All the fibres fan out posteriorly to insert all along the medial surface of the quadrate process of the pterygoid. In a few cases the insertion extends onto t the dorsal surface of the pterygoid. Innervation is by a separate branch of the trigeminal entering the lateral side of the muscle.

Variation in the protractor and levator pterygoideus among iguanids appears to be minimal, size being the only variation. Subtle size differences however, are difficult to detect and quantify due to the great variation in skull size in the group. Obvious differences were found in the large anolines _Anolis equestris_ and _Chamaeleolis_ which seem to have much reduced levators. In _Phrynosoma_ the levator appears to be short but this may be due to the increased height of the skull. Among the other families the greatest variation occurs in the Chamaeleontidae where due to the loss of cranial kinesis both levator and protractor muscles as well as the epipterygoid are gone. In Zonurus the protractor appears to be greatly reduced. In the gekkoes the fascia origin of the levator passes medial to the very much enlarged alar process of the prootic. It is interesting to note that reduction or enlargement seems to occur usually in only one of the two muscles. There was no case in which both were obviously enlarged or reduced except of course in Chamaeleon where both are lost.

Levator Bulbi

The levator bulbi muscles lie medial and anterior to the levator pterygoideus, medial to the epipterygoid and pseudotemporalis profundus and ventromedial to the eye. The muscle is composed of a ventralis and dorsalis segment. The ventralis originates from the ventral surface of a ligament which comes off the membranous braincase medial to the prootic and extends anteroventrad, medial and ventral to the eye. The fibres of the ventralis insert on the dorsal surface of the membrane of the pyriform recess. In a few forms such as Dipsosaurus they insert on the pterygoid lateral to the recess. The dorsalis arises from the dorsal surface of the distal end of the ligament. Its fibres fan out anterolaterally to form a thin sheet which passes ventral to the eye and inserts on the fascia of the lower eyelid. The ventralis anchors the dorsalis medially insuring that the force of contraction will be passed medially and not posteriorly, allowing for efficient lowering of the eyelid. In addition to this medial fibres of the dorsalis insert on the fascia of the palatine process of the pterygoid anchoring the anterior end of the muscle. Innervation is by a separate branch of the trigeminal extending anteriorly to the muscle, travelling with it a good distance before penetrating the surface.

The lavator bulbi muscles showed almost no variation in the Iguanidae and only a small amount of variation throughout the other families. Because of this and the fact that they do not function in adduction or cranial kinesis I tended to deemphasize them in my study. All families had dorsalis and ventralis segments in similar arrangement to that found in the Iguanidae.

Dentition

Up to now most studies of adaptation to diet have been focussed on variations in dentition. Indeed dentition seems to be a much more plastic character than the rather conservative trigeminal musculature. Before moving on to the analysis of the muscle data it might be interesting to digress for a moment to see how extensive the dental variation is.

Hotton (1955) studied the variation in 16 iguanid species belonging to 11 sceloporine and iguanine genera, including Crotaphytus and Phrynosoma. The diets of these were carefully studied and the food animals were grouped according to the degree of their activity and the heaviness of their intergument. Hotton lumped all of the herbivorous forms in one group, came up with the five types of diet listed below, and correlated these with five types of dentition.

	DIET	DENTITION	FORMS
A.	Vegetable matter	Teeth with high degree of lateral flattening, crowns with bladelike cutting edges, teeth highly cuspidate first cusped teeth far anterior on mandible, profile variable	Dipsosaurus, Sauromalus, Ctenosaura
B.	Animals of low activity and intermediate integument-Ants	Extremely blunt, stout peglike teeth, no cusps	Phrynosoma

	DIET	DENTITION	FORMS
C.	Animals of high activity and intermediate integument - Grasshoppers	Teeth moderately to highly cuspate, first cusped tooth midway along maxilla, front teeth higher, sharper, more conical than back teeth, slight lateral compression at apex of tooth.	Crotaphytus Gambelia Holbrookia Sceloperus
D.	Diet highly varied and with high proportion of animals of intermediate activity and integument. Leafhoppers	Teeth rather highly cuspidate, first cusped tooth anterior to middle of maxilla, front teeth slender sharp and conical, little or no compression at crown, much like type E	Uta *Urosaurus *Sator *Petrosaurus
E.	Diet rather varied with high proportion of food with high activity and heavy integument. Bees and wasps	Teeth poorly cuspidate, first cuspate tooth posterior to middle of maxilla, teeth slender, conical up to apex where they taper to sharp point, back teeth as high as front, little or no crown compression.	Callisaurus Urosaurus

* Added to Hottons classification by Etheridge (1964).

The highly cuspidate, compressed bladelike teeth of group A are used by iguanines for shearing vegetable matter. The blunt peglike teeth of Phrynosoma and certain ant eating forms of Sceloperus are an adaptation to food which does not have to be pierced or held onto. The slender, sharp and poorly cusped teeth of group E are necessary for piercing the heavy integument of bees and wasps while the highly cuspidate teeth of groups C and D are advantageous for grasping animals of intermediate activity and integument.

Hotton lumps group D with group E and comes up with four adaptive types of dentition for north americal iguanids, herbivorous, ant eating, predaceous type A (Animals of high activity and heavy integument) and B (Animals of intermediate integument).

Groups A and B fit nicely with Etheridge's scheme for relating the iguanid genera. All of the iguanines are herbivorous and *Phrynosoma* is highly specialized for ant eating. The predaceous types A and B however, do not assort according to the classification. *Uma*, *Holbrookia* and *Callisaurus* which Etheridge holds to be a closely related natural group contains predators of both types. Etheridge maintains that *Uma* fits in none of Hotton's categories and points out that a diversified genus like *Sceloporus* can and does have considerable variation in it. *Sceloporus* species range from groups B to C. The obvious conclusion is that dentition follows functional and not phylogenetic lines.

Montanucci (1968) carried the study further by comparing the dentition of three iguanines, *Iguana iguana*, *Ctenosaura similis* and *Enyaliosaurus clarki*, and *Basiliscus vittatus*. He found the teeth of *Iguana* to be highly compressed and serrate for use in shearing vegetable matter. The teeth of *Ctenosaura* and *Enyaliosaurus* are less compressed and not serrate but cuspate. This is an adaptation for nipping small leaves, blossoms and buds. The description of the dentition of *Basiliscus* seems to put it in group C or D of Hottons scheme. According to Borden (1943) *Basiliscus* has a very varied diet 78% of which are animals spread out over 29 orders and 22% of which is plant material some taken by accident and some by design.

PART II

DISCUSSION AND ANALYSIS

Taxanomic Characters

From the vast amount of description and comparison given up to this point we can now distill off those characters which seem to have taxonomic and, or functional significance within the Iguanidae and discuss them in detail. These are the characters chosen.

1. Extent of the adductor medius in the supratemporal fossa.
2. The presence of a superficial separation of the heads of the adductor superficialis.
3. The extent of the adductor superficialis.
4. The extent of the superficial fascia covering the superficialis.
5. The condition of the temporal artery.
6. The extent and size of the pseudotemporalis superficialis.
7. The separation of the heads of the pseudotemporalis.
8. The size of the gape of the jaw.
9. The size and shape of the parietal origin of the jaw musculature.
10. The presence of an enlarged parietal crest with accompanying enlarged jaw musculature.
11. The diet and habitat.

Most of these have been described at length in the preceeding text. Tables 1, 2 and 4 sumarize these data. In the following sections I will attempt to analyze the functional and taxonomic significance of these characters and their distribution among the iguanid genera.

It should be pointed out at the beginning that the number of characters furnished by the jaw apparatus is relatively small compared to the large large numbers of characters, derived from many systems, which are usually used in strictly taxonomic studies. The information obtained from the few available characters however, is sufficient to allow for the erection of a classification and phylogeny for the major groups which is, on the whole, quite consistent with the presently accepted arrangement of the family. In some cases, such as the sceloporines, lines within a subfamily can be substantiated.

Table 1 Summary of important iguanid jaw character differences.

	Genus	A Diet	B Habitat	C Extent of add. med. in supratemp. fossa	D Superficial s of add. superficialis
Madagascan	*Oplurus*	I	T	2	1
	Chalarodon	I	T	2	1
Iguanines	*Ctenosaura*	H	T	2	2
	Iguana	H	T	2	2
	Cyclura	H	T	2	
	Sauromalus	H	T	1	2
	Conolophus	H	T		
	Amblyrhynchus	H	T		
	Enyaliosaurus	H	T	2	1
	Dipsosaurus	H	T	2	1
	Brachylophus	H	T	2	2
Sceloporines	*Sceloporus*	I	T	2	1
	Uta	I	T	2	1
	Urosaurus	I	T	1	1
	Uma	I	T	5	2
	Holbrookia	I	T	4	2
	Callisaurus	I	T	4	2
	Phrynosoma	I	T	5	2
	Crotaphytus	I	T	2	2
Tropidurines	*Tropidurus*	I	T	2	1
	Leiocephalus	I	T	2	2
	Leiolaemus	I	T	2	1
	Hoplocercus	I	T	2	1
	Stenocercus	I	T	2	1
	Plica	I	A	2	1
	Enyaliodes	I	A	2	1
	Uranoscodon	I	A	2	2
	Morunasaurus	I	T	2	2
	Platynotus	I	T	2	1
	Phymaturus	I	T	2	1
	Leiosaurus	I	T	2	1
	Ophryoessiodes	I	T	2	2
Basiliscines	*Basiliscus*	I	A	22	2
	Corythophanes	I	A	2	2
	Laemanctus	I	A	2	1
Anolines	*Polychrus*	I	A	3	2
	Anolis	I	A	3	2
	Xiphocercus	I	A	2	2
	Deiroptyx	I	A	3	2
	Phenacosaurus	I	A	2	2
	Chamaelinorops	I	A	2	2
	Chamaeleolis	I	A	2	2

D Superficial sep. of add. superficialis	E Extent of superficialis	F Extent of superficial fascia	G Condition of temporal artery	H Size of pseudotemp. superficialis	I Separation of heads of pseudotemp.
1	4	3	4	2	
1	3	2	1	2	
2	4	3	1	2	*
2	2	3	1	2	-
	4	2	1	2	-
2	4	3	6	2	*
1	4	3	4	2	
1	2	3	1	2	-
2	3	3	1	2	-
1	3	2	1	2	*
1	2	3	1	2	*
1	3	3	1	1	*
2	2	2	1	4	*
2	3	2	1	4	*
2	2	2	1	2	-
2	2	1	2	5	*
2	2	2	1	1	*
1	4	2	1	2	*
2	3	3	1	2	*
1	3	2	1	1	*
1	3	2	1	2	
1	3	3	1	2	-
1	5	4	1	2	*
1	4	3	4	2	
2	3	4	1	2	*
2	4	3	4	2	-
1	4	3	1	2	-
1	4	3	1	2	-
1	3	3	1	2	-
2	3	3	4	2	-
2	2	2	4	2	*
2	1	2	4	2	-
1	2	1	4	2	-
2	2	2	1	2	-
2	1	1	4	2	*
2	1	1	4	2	*
2	1	1	4	2	*
2	1	1	4	2	*
2	1	1	4	2	*
2	1	1	4	2	*

Table 2 Jaw apparatus characters in non iguanids.

Group	A Diet	B Habitat	C Extent of add. med. in supratemporal fossa	D Superficial sep. of add. superficialis
Nyctisauria				
Gekkonidae *Hemidactylus turcicus*	I	A	- (4)	2
Gonatodes fuscus	I	A	- (4)	2
Iguania				
Agamidae *Agama* sp.	I	T	3	2
Chamaeleontidae *Chamaeleon chamaeleon*	I	A	4	1
Scincomorpha				
Xantusidae *Xantusia vigilis*	I	T	- (3)	1
Scincidae *Mabuya* sp.	I	T	- (4)	2
Teiidae *Ameiva ameiva*	C	T	0	1
Tupinambis teguixin	C	T	0	1
Cordylidae *Zonurus* sp.	I	T	- (4)	2
Diploglossa				
Varanidae *Varanus indicus*	C	T	0	2

D perficial sep. add. superfic- lis	E Extent of superficialis ialis	F Extent of superficial fascia	G Condition of temporal artery	H Size of pseudotemp. superficialis	I Separation of heads of pseudotemporalis
2	3	1		6	0
2	2	1		6	0
2	5	4	1	4	-
1	2	1	5	6	0
1	3	2		4	-
2	5	6		4	-
1	4	5	1	1	-
1	4	3	1	1	-
2	4	6	1	5	-
2	2	1	1	2	*

Legend Tables I and II

A. Diet
   - C. Carnivore
   - H. Herbivore
   - I. Insectivore

B. Habitat
   - T Terrestrial
   - A Arborial

C. Extent of the adductor externus medius in the supratemporal fossa. This is a measure of how far anteriorly and dorsally the adductor medius extends along the parietal in the supratemporal fossa.
   1. Adductor externus absent from the fossa at the surface
   2. Externus extends less than half the length of the parietal
   3. Covers half of parietal
   4. Externus extends more than half the length of the parietal
   5. Externus covers the entire supratemporal fossa
   - \- No supratemporal fossa present. This is followed by a measure of the extent of the muscle imagining a fossa to be present.

D. Is there a visable delineation between the two heads of the adductor superficialis at the surface of the muscle?

   - \- No separation can be made.
   - * A separation is present.

E. How far down the lateral side of the mandible does the adductor externus extend.
   1. Externus extends only to the top of the surangular.
   2. Externus extends less than halfway down the side of the mandible.
   3. Externus extends halfway down the side of the mandible.
   4. Externus extends more than half way down the side of the mandible.
   5. Externus extends to the ventral border of the mandible.

F. How extensive is the superficial fascia at the posterodorsal corner of the infratemporal fossa.
   1. Very little fascia present.
   2. Fascia covers just the posterodorsal corner of the fossa.
   3. Fascia extending halfway to the surangular.
   4. Fascia extending to the top of the surangular.
   5. Fascia covering the entire muscle.
   6. Fascia just at the insertion of the muscle.

G. How does the temporal artery pass through the supratemporal fossa.
   1. The artery exits at the anterior border of the medius and continues anteriorly over the pseudotemporalis superficialis.
   2. The artery passes through the fossa deep within the muscle and is not visable superficially.
   3. The artery passes through the pseudotemporalis superficialis and is not visable.
   4. The artery passes over the dorsal head of the medius and continues over the pseudotemporalis.

5. The artery passes through the medius and is not visable at the surface.
6. The artery exits through the pseudotemporalis and passes over it.

H. How far posteriorly does the pseudotemporalis extend.
1. It covers all of the parietal.
2. It covers more than half of the parietal.
3. It covers half of the parietal.
4. It covers less than half of the parietal.
5. Pseudotemporalis superficialis very small.
6. Pseudotemporalis superficialis absent.

I. Is the pseudotemporalis superficialis separable into two heads?
* Yes
\- No
0 The superficial head is lost

J. What is the shape of the parietal.
1. Crescentic
2. Triangular
3. Crescentic developing into triangular in mature specimens.

Adaptive Significance and the Distribution of Character States

Table 3 shows the number of genera in each subfamily or recognizable group, that have a particular character state. Such an analysis allows us to see at a glance which character states are present in the greatest number of genera and groups. It also gives a clear picture of the variation of the particular character in each group.

Knowing the distribution of each character state it is sometimes possible to deduce whether the character is of adaptive significance to the particular suite of characters being studied. If the various states of a character show more or less equal distribution among all of the subgroups of a family, it might be safely assumed that the character is not significant to the specific adaptations which distinguish the subgroups. For example, if half the genera in genus group I have character state A and the other half have character state B and the same situation is repeated in genus group 11, 111 and so on, it seems reasonable that this particular character is not associated with the suite of characters which have allowed each genus group to adapt to its particular niche. Niche is defined here as the particular role of the organism in relation to the ecosystem and will be used synonomously with adaptive zone. The character may however, be significant to the group of characters that separate one genus from the next. Thus when speaking of adaptive significance one must always specify the

Table 3 Distribution of Character States Among Iguanid Genera

	C. Extent of Medius in Supratemporal Fossa					D. Separation of Adductor Superficialis	
Subfamily	Character States*					States	
	1	2	3	4	5	1	2
Madagascan		2**					2
Iguanines		5				3	2
Sceloporus Group	1	3				1	3
Uma Group	1			2	2	4	
Tropidurines		8				2	6
Basiliscines		3				2	1
Anolines		6				6	
	2	24		2	2	18	14
	6	82		6	6 %	56	44

	G. Condition of Temporal Artery				H. Extent of Pseudotemporalis				
	Character States				Character States				
	1	2	4	6	1	2	3	4	5
Madagascan	1		1			2			
Iguanines	4		1	1		6			
Sceloporus Group	4				2	2			
Uma Group	3	1				1		2	1
Tropidurines	7		1		1	7			
Basiliscines			3			3			
Anolines			5			3			
	20	1	11	1	3	27		2	1
	60	3	33	3 %	9	81		6	3 %

* The condition of each state is explained in the legend to Table 1.
** The number of genera having the character in each state.

E. Extent of Superficialis

Character States

1	2	3	4	5
		1	1	
	2		4	
	2	2		
	3	1		
		5	2	1
1	2			
5	1			
6	10	9	7	1
18	30	27	21	3 %

F. Extent of Superficial Fascia

Character States

1	2	3	4	5
	1	1		
	1	5		
	2	2		
1	3			
	3	3	2	
1	2			
5	1			
7	13	11	2	
21	39	33	2 %	

I. Separation of Heads of the Pseudotemporalis

States

1	2
2	3
4	
3	1
5	1
1	2
5	1
20	8
72	28 %

J. Shape of Parietal

States

1	2	3
2		
4		5
4		
4		
8		
	3	
	6	
22	9	5
61	25	14 %

level one is referring to. To a strong selectionist every character is adaptively significant at one level or other.

In examining Table 3 and applying the criteria discussed above it can be seen that all the characters listed are significant to the radiation of the subgroups of the Iguanidae. In character C, the extent of the adductor ext. medius in the supratemporal fossa, there is obviously strong selection for character state 2 in every iguanid group except the Uma group where it would seem that selection has moved the genera to other adaptive zones. The same situation exists in character H, the extent of the pseudotemporalis. This character is roughly the reciprocal of character C.

Character G, the condition of the temporal artery, has a character state distribution which shows clustering at states 1 and 4. Character state 1 is associated with the adaptive zone or zones of the iguanines, sceloporines and tropidurines while character state 4 associated with the basiliscine, anoline zones. Characters E, the extent of the adductor e. superficialis and F, the extent of the superficial fascia show a good deal of variation at the genus level but both characters seem to be associated with the same two broad zones as character G.

Character D, the separation of the heads of the adductor e. superficialis, has only two states with almost equal distribution in each, in terms of number of genera. The distribution however, among the subgroups clearly shows the character to be tied up with the particular adaptations of the Uma group, the anolines and possibly the Madagascan iguanids. Over the remaining iguanids.

Character I, the separation of the heads of the pseudotemporalis, shows significance in all groups except the basiliscines and anolines. Character J very neatly separates the subfamilies on the crucial factor of parietal shape which is of obvious adaptive significance for it allows for an increase in the origin of the adductor musculature.

Jaw Adduction Strength

"Jaw adduction strength" or sinply "jaw strength" as used here and throughout the remainder of this paper, will mean simply, the force of adduction generated by the adductor musculature and transmitted to the mandible. The term "efficiency" will refer to the ability of the jaw apparatus to generate the maximum adductive force with the minimum effort or waste. Both terms will be used relatively for it is not the goal of this study to set up mathematical models to quantify them.

In examining a large series of iguanid skulls it becomes apparent that two cranial characters are functionally important with respect to the strength of the jaw apparatus. One is the shape and size of the parietal origin of the adductor musculature and the other is the length of the gape of the mandible. The parietal origin of the adductor musculature is found along the lateral edge of the parietal. The amount of muscle originating on the parietal can be readily determined by measuring the extent and shape of the very conspicuous muscle scar. Since the other major origins of the adductor musculature, the quadrate, prootic, epipterygoid and pterygoid vary little in size, the rather large variation of the size of the parietal scar can be correlated directly with the strength of the adductor mandibulae.

The mandible is of great importance for it is the structure which receives all of the force of the adductor musculature. The mandible acts as a lever whose fulcrum is the articular condyle. The depressor mandibulae which inserts posterior to the condyle causes the mandible to be abducted, while the adductor mandibulae inserting anterior to the condyle creates the opposite effect. The adductor mandibulae extends as far anterior as the coronoid process, anterior to which there is no adductor musculature. The gape, or length of the jaw anterior to the adductor musculature is therefore very important in estimating the force of contraction present at the tip of the jaws. If lizard A and B both have identical musculature, but A has a gape 20% longer than B, the laws of physics tell us that A will exert a lesser force at the tip of its mandible than B will. Even though lizards do most of their "chewing" with the more posterior parts of their jaw, such differences, if they do exist, could reasonably be expected to have some effect on the type of prey the lizard can capture and kill and would thus be under great selective pressure. Further, one might predict that goups of lizards eating different might have gapes of different lengths.

The gape length must be looked at in conjunction with the strength of the adductor musculature, as measured by the size of its parietal origin, for long jaws can be strengthened by increased adductor musculature. Thus gape length and parietal muscle scar can be used jointly to get a picture of the comparative jaw strength throughout the Iguanidae.

The force of adduction of the jaw can also be increased by increasing the extent of the adductor superficialis which can extend all or part way down the side of the mandible. The more extensive superficialis is usually accompanied by an enlarged superficial fascia. In

Cyclura the superficialis originates on a rather broad temporal bar and is probably proportionally strengthened.

Some lizards, especially the sceloporines tend to eliminate one or the other of the two muscles of the supratemporal fossa. It seems unlikely, from direct observation of the muscles involved, that there can be much difference in mass between the two smaller or one larger muscle arrangement. There may be however, greater efficiency in the simpler, one muscle set up and this may contribute to the strength of the jaw apparatus.

Parietal Origin of the Adductor Mandibulae

The shape of the parietal origin of the adductor mandibulae varies at the subfamily level in the Iguanidae. In the sceloperines, tropidurines, Crotaphytus and some iguanines (Dipsosaurus, Sauromalus and Enyaliosaurus), the parietal origin is in the shape of a crescent (Fig. 9 A). The anterior point of the crescent begins posterior to the orbit. The crescent thickens as it passes posterolaterally to join the quadrate and squamosal where the crescent again thins out. The dorsal border of the crescent is convex and the ventral border concave often having a slight point anteriorly where the epipterygoid articulates. When looking at the skull in dorsal view the two parietal origins are seen to be separated by varying amounts of parietal roofing the braincase. The more posteriorly one looks the further apart the parietal crescents are. This is due to their posterolateral orientation.

The large iguanines, Iguana, Cyclura, Amblyrhychus and Conolophus differ in that as they grow larger the parietal crescent which at first resembled that of Dipsosaurus and Sauromalus, becomes much wider at its middle and extends medially and dorsally until it meets its neighbor on the other side of the skull. In doing so it obliterates the roofing parietal between the two crescents and causes the two supratemporal fossae to meet on the dorsal midline. As growth proceeds a crest of bone begins to develope on the dorsal midline between the two fossae. This crest further increases the surface area of the muscle origin and at the same time keeps the two fossae separated. The larger the specimen the greater the crest will be, however it never reaches the dimen-

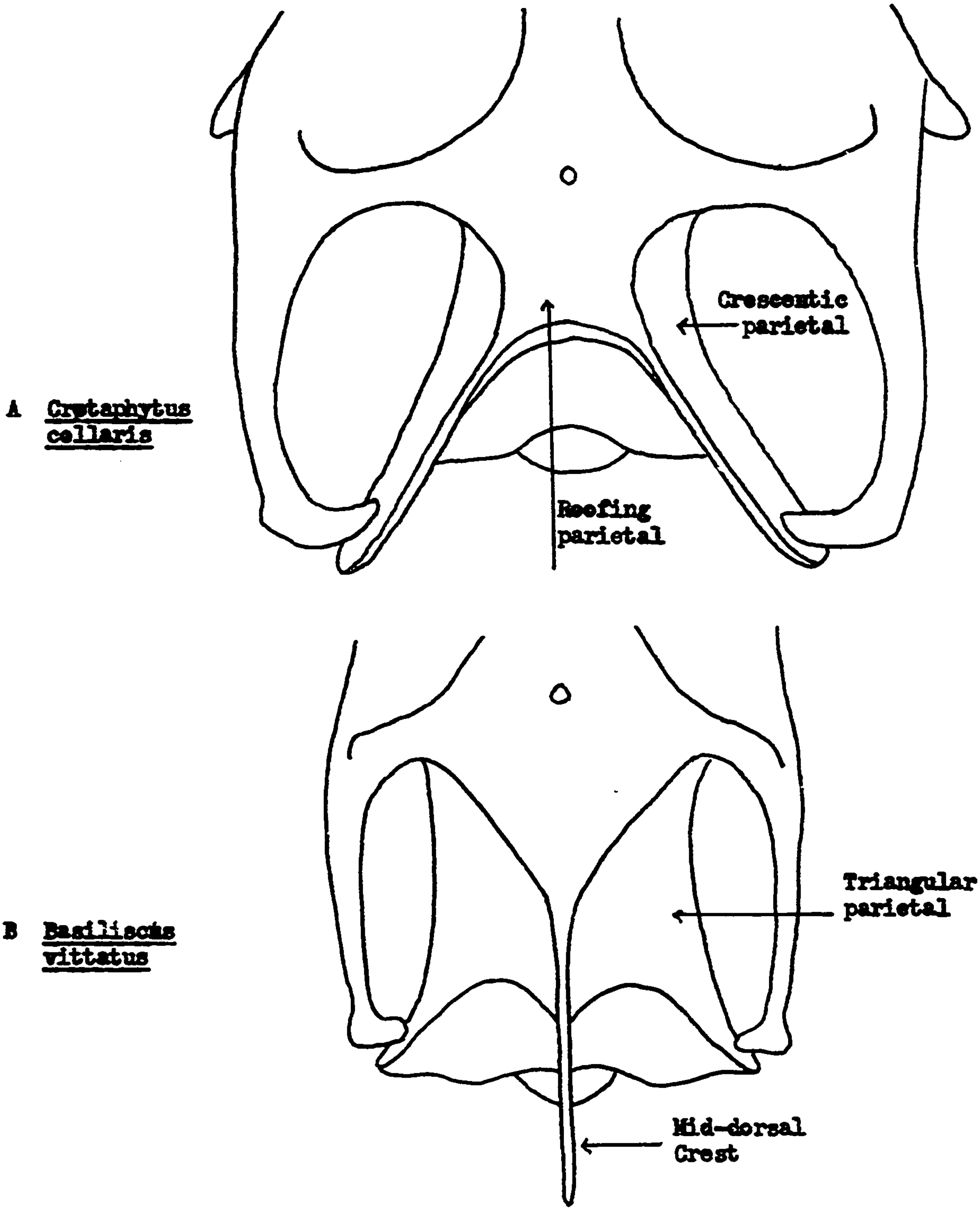


Fig. 9 Comparison of the Parietal Region of *Crotaphytus collaris* and *Basiliscus vittatus*.

sions of the crests found in the anolines and basiliscines.

In an initial experiment twenty skulls of Iguana iguana were measured for the following characters:

1. Total jaw length
2. Length from posterior border of coronoid process to tip of jaw
3. Greatest width of the parietal crescent
4. Smallest distance between parietal crescents.

In addition the presence or absence of a crest was noted. The ratio

$$\frac{\text{Maximum parietal crescent width}}{\text{Total jaw length}}$$

was calculated and the results plotted against jaw length which is taken as a measure of the total length, and thus age of the specimen (Fig. 10). The distance between parietal crescents was plotted directly against the jaw length (Fig. 11).

The results of these calculations were not linear. When the results are plotted however, it becomes quite clear that as the animal increases in size the parietal origin of the adductor mandibulae increases in area (Fig. 10), and it does so at the expense of the roofing parietal bone between the crescents (Fig. 11).

It will be seen later on the discussion of jaw length that the gape of Iguana decreases as the animal grows larger. The smaller gape accompanied by the enlarged surface area for the origin of the adductor musculature would seem to increase the force of adduction of the lower jaw in older, larger animals. This may allow the older Iguana to take

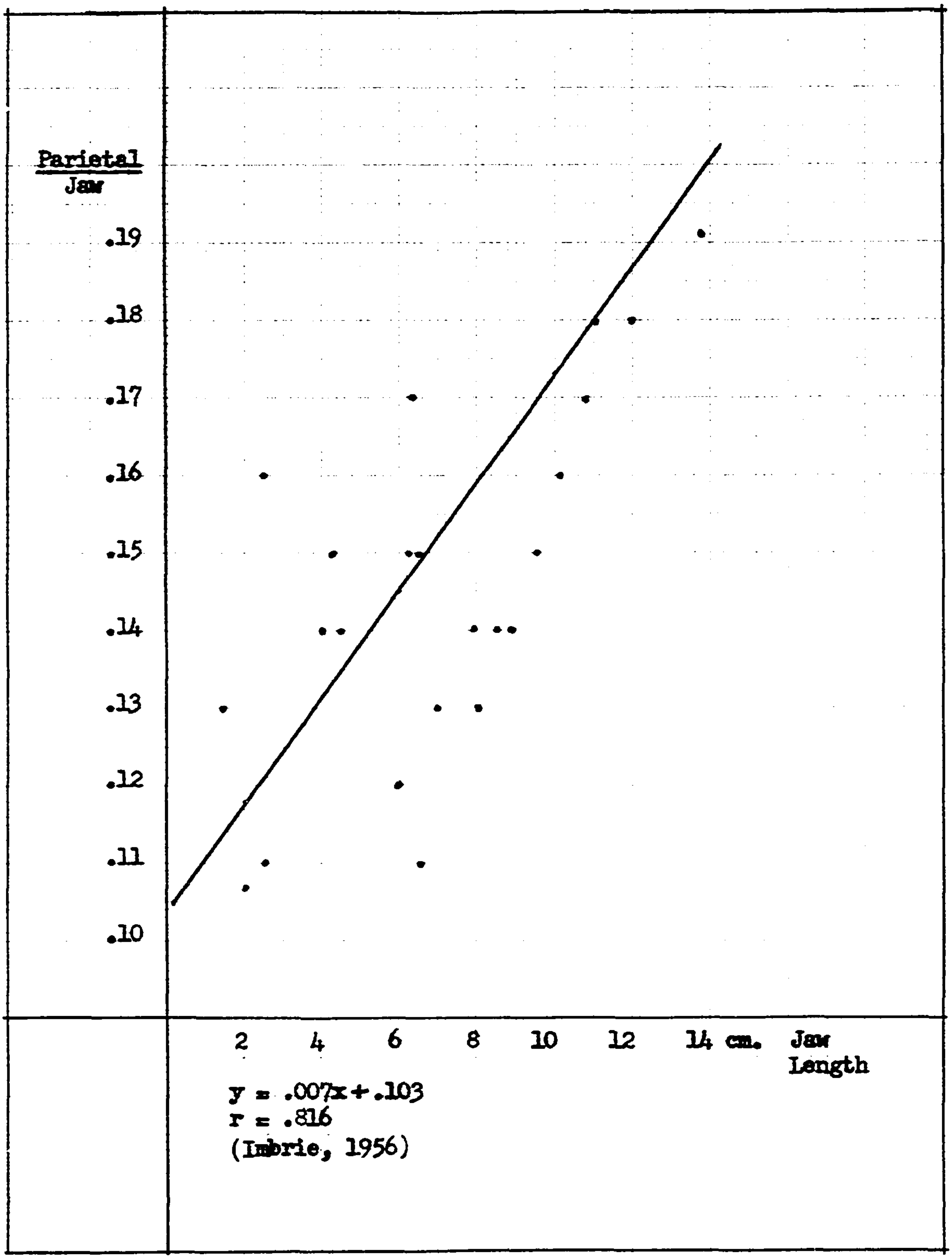


Fig. 10 Increase in the width of the parietal origin of the adductor mandibulae in *Iguana iguana*.

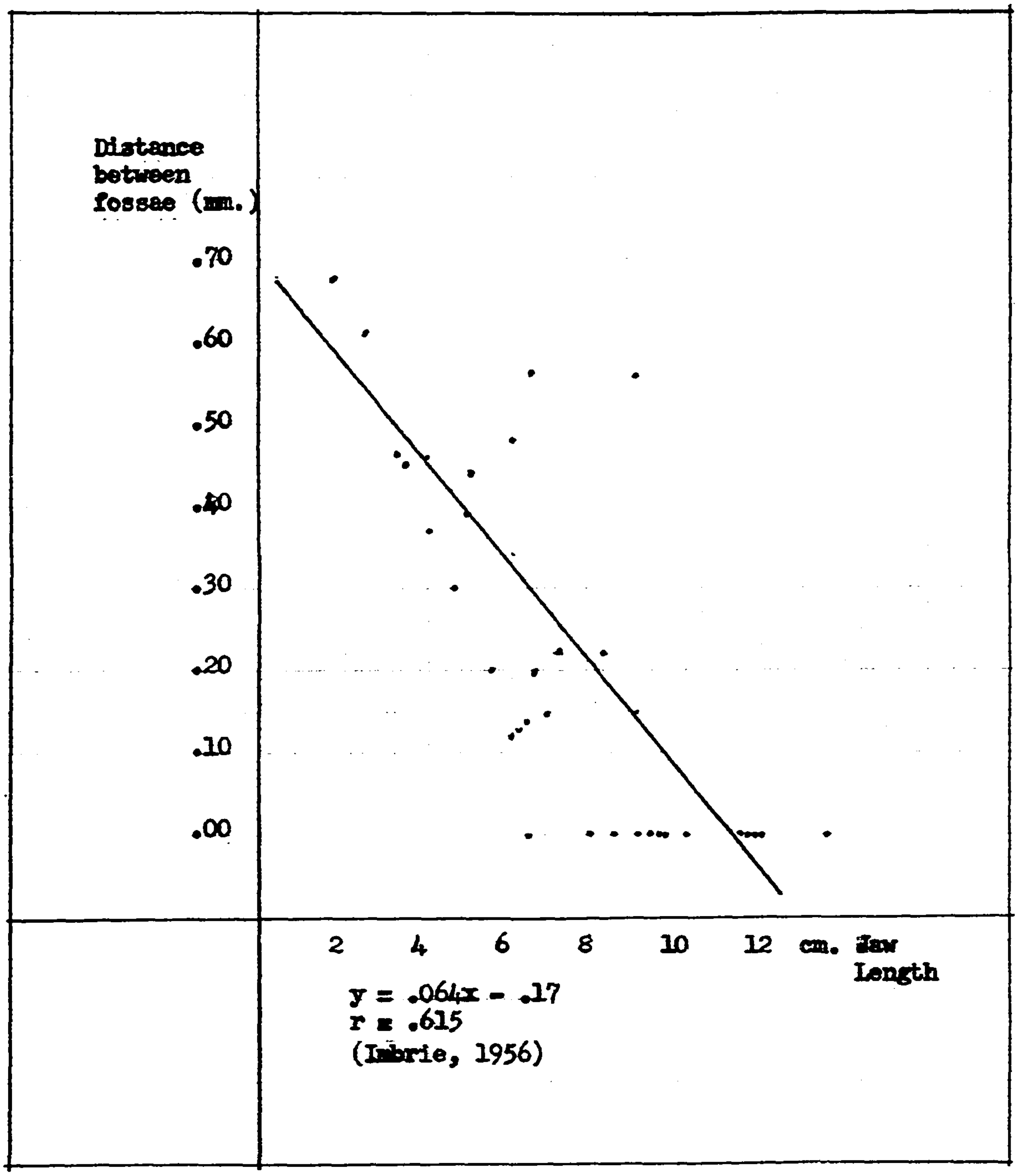


Fig. 11 Decrease in width of roofing parietal with age in *Iguana iguana*.

larger tougher vegetation.

The development of the crest in larger specimens occurs also in Cyclura, Amblyrhynchus, and Conolophus. The other iguanines with the exception of Ctenosaura have crescentic parietal muscle scars throughout life.

In Ctenosaura the parietal origin is more extensive even in younger specimens. Only one small specimen was found where the temporal fossae were not confluent. The flattening of the skull prevents the formation of a crest in Ctenosaura.

In the anolines the parietal origin of the adductor mandibulae is greatly increased (Fig. 12 B). The crescent is developed into a triangle with its apex at the posteromedial corner of the parietal, squaring off this region of the supratemporal fossa. The two neighboring triangles on the skull meet at the dorsal midline and are usually separated by a small mid-dorsal crest. Very rarely are the origins separated by roofing parietal even in the smallest specimens.

The trend towards enlargement of the parietal origin and crest formation is further in the anolines by such forms as Xiphocercus, Anolis equestris, Chamaeleolis and Phenacosaurus. In Xiphocercus the enlargement is slight but enough to make the posterior end of the skull the highest. In forms without crests the skull reaches its maximum height at the frontoparietal articulation and maintains this height without much increase to the posterior edge of the parietals. In forms with crests the height increases posteriorly.

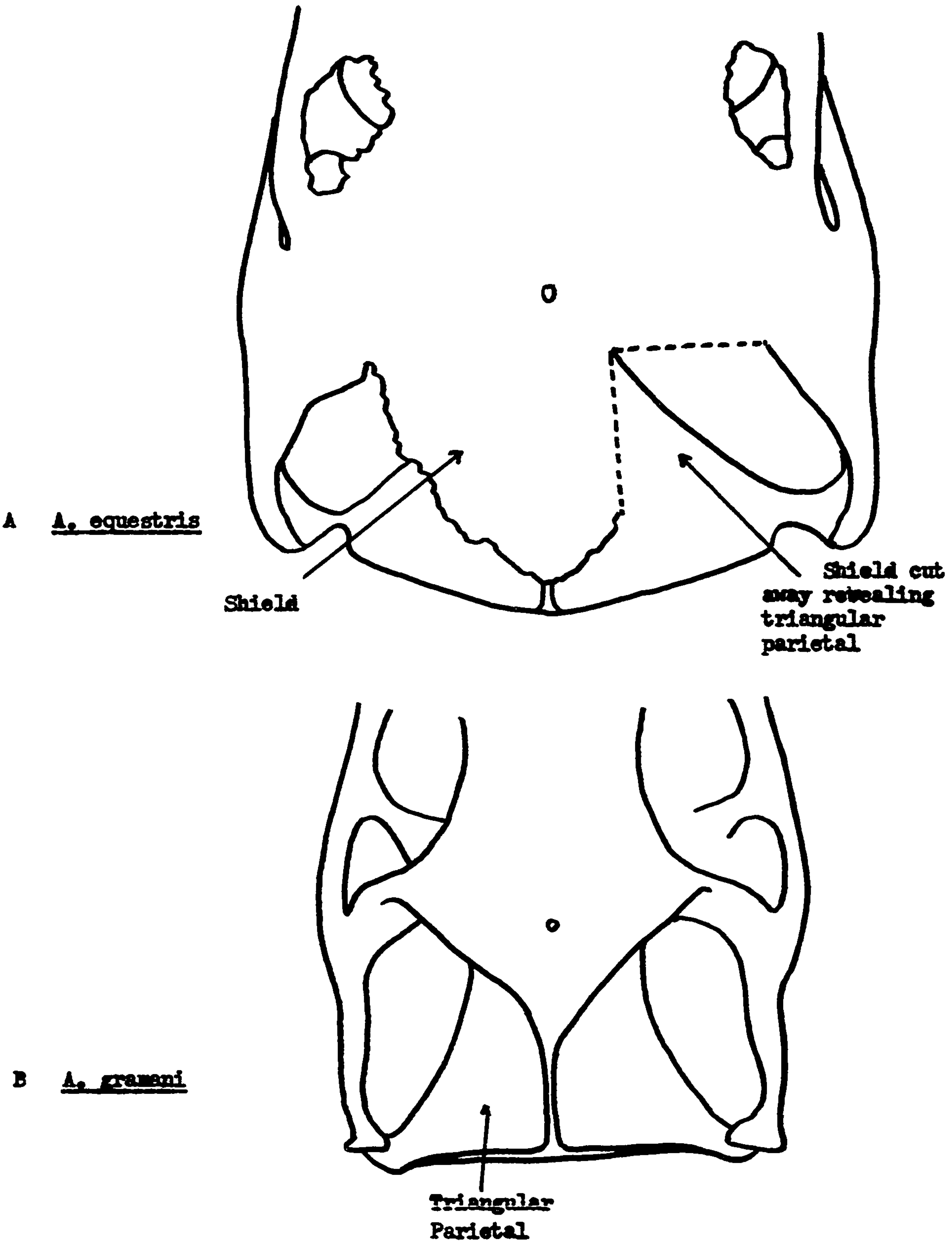


Fig. 12 Comparison of the Parietal Regions of *Anolis equestris* and *Anolis gramani*.

In the large *Anolis equestris* and the small *Phenacosaurus heterodermus* a mid dorsal crest is present along with an accessory plate of bone extending laterally from the dorsal border of the parietal triangle. This plate I shall call a shield. The shield narrows posteriorly and roofs the medial part of the supratemporal fossa (Fig. 12 A). The origin of the pseudotemporalis superficialis is extended onto the underside of the shield. In *Chamaeleolis* a crest is formed as in *Anolis equestris*, from parietal and accessory dorsal shield, but it is much higher adding more than 50% to the posterior height of the skull. The shield accompanies the crest to its very tip.

The enlargement of the parietal origin in the anolines is quite possibly correlated with an increase in the gape in this subfamily. The longer lever arm created by this increase certainly requires a stronger adductor muscle to maintain a good force of adduction. *Polychrus*, which Etheridge (1960) maintains is a primitive anole, has sceloporine parietals with a gape intermediate in size between the sceloporines and anolines.

The basiliscine parietal is greatly enlarged into a posterodorsally directed crest (Fig. 9 B). In *Basiliscus* the crest is not covered dorsally by a bony shield. In *Corythophanes* and *Laemanctus* however, a shield is present. In *Corythophanes* the shield is bony but differs from the anoline shield in that it extends only a little more than half of the length of the crest before tapering away completely. In *Laemanctus* the shield continues to the posterior most extension of the crest superficially resembling the shield of *Chamaeleolis*, but constructed of tough connective tissue, not bone. Muscle does not originate on the underside of this shield as it does on the bony shields of the anolines and *Corythophanes*.

Gape Ratio

To determine the size of the gape in any individual a gape ratio was calculated. For purposes of convenience and increased accuracy the gape was measured from the base of the posterior border of the coronoid process to the anterior tip of the jaw. The ratio Gape/Jaw Length was then calculated. The total jaw length, including the retroarticular process was used. The retroarticular process shows little variation in the Iguanidae and any attempt to exclude it from the jaw length would surely decrease measuring accuracy.

The first lizards to be examined for gape ratio happened to be a series of twenty Iguana iguana ranging in jaw length from 1.80 to 11.89 cm. Plotting the gape ratios against jaw length reveals that as the jaw length increases, ie., as the animal ages, the gape ratio decreases. The gape ranged from .63 in the smallest specimen to .56 in the largest. It would thus appear that as the individual Iguana ages its jaws become stronger by developing a shorter gape and, as seen earlier, an enlarged parietal origin (Fig. 13).

Further investigation found a similar growth curve to exist in Ctenosaura, Amblyrhynchus and probably Conolophus. Only very large specimens of Conolophus were available, but all of these had gape ratios appropriate to their size according to the Iguana, Amblyrhynchus, Ctenosaura curve. In addition, all of these genera increase the size

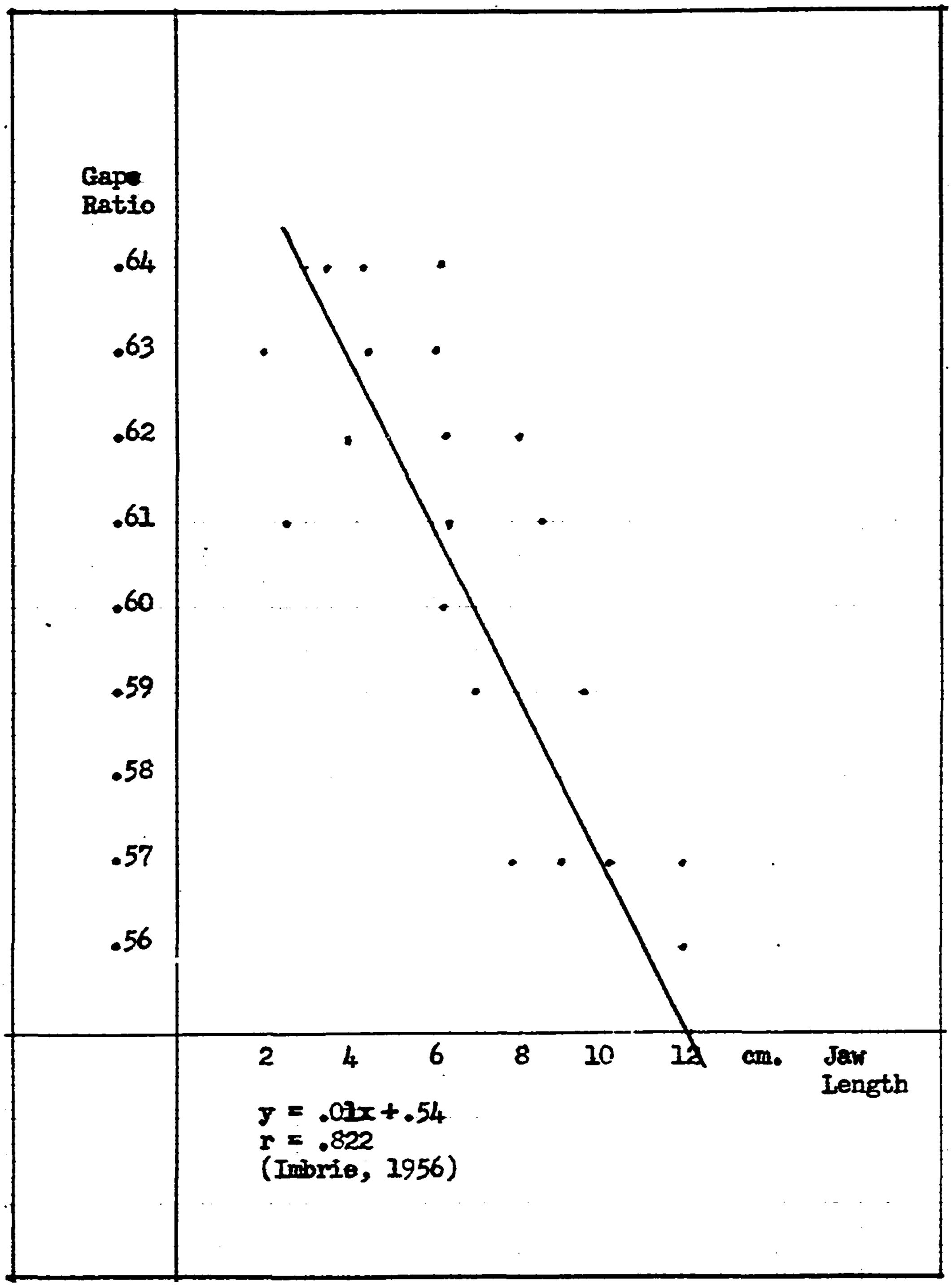


Fig. 13 Decrease in gape ratio with age in *Iguana iguana*.

of their parietal origin as they grow, thus they all develop stronger jaws. Only one specimen of Brachylophus was available but it too fit the curve.

Dipsosaurus, Sauromalus and Enyaliosaurus seem to have their own growth curve separate from that of the larger iguanines and below it on the graph (Fig. 14). Dipsosaurus which is a smaller animal than Sauromalus tends to have a larger gape, but the ratio is still small compared to the other iguanines of that size. These forms apparently start out with a shorter and therefore stronger jaw, and reach the minimum iguanine jaw ratio at a smaller size. It is interesting to note that none of these develop enlarged parietals or crests.

Cyclura stands alone with a series of gape ratios much higher than any other iguanines. It seems that they start out with higher ratios and keep them higher, but they to show some decrease with age. Older specimens of Cyclura develop parietal crests which help to strengthen the longer jaws. In addition the enlarged temporal bar gives rise to a strengthened adductor superficialis.

It is very interesting to note that the sceloporines also fit on the Iguana growth curve. Sceloporines tend to be small forms in comparison with the large iguanines. If the Iguana growth curve is extrapolated down to animals the size of sceloporines, the ratios predicted by the curve correspond to those actually found. The ratio went as high as .66 and .67 for some of the smaller specimens of Sceloporus and

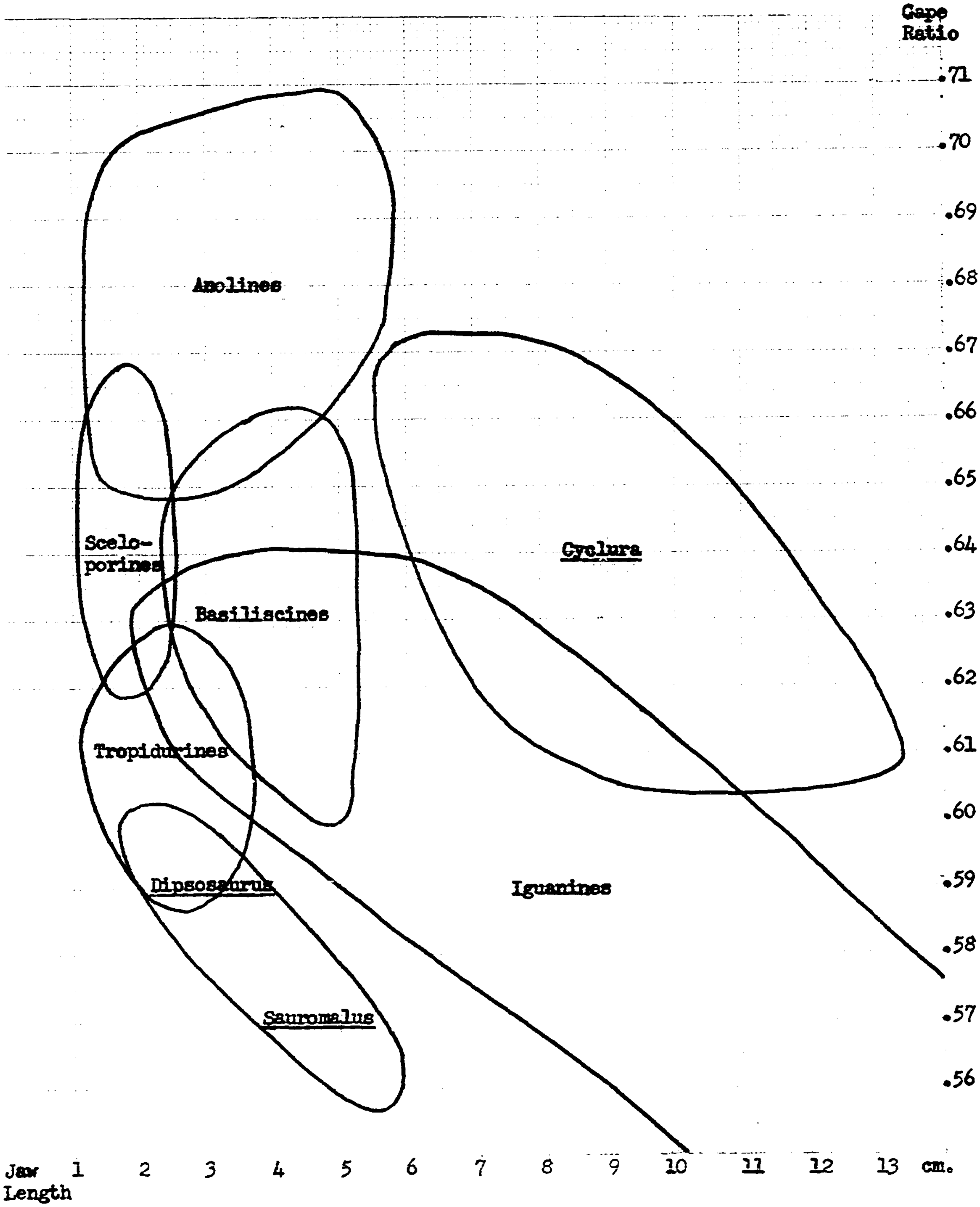


Fig. 14 Iguanid Gape Length

Table 4 Iguanid Gape and Parietal Characteristics

Genus	Gape Ratio	Space Between Parietals	Parietal Crest	Specimens
Chalarodon	.62	all specimens	none	2
Oplurus	.61-.63	all	none	3
Ctenosaura	.56-.62	none	none	13
Iguana	.56-.64	young specimens	older spec.	20
Conolophus	.57-.58		older spec.	7
Amblyrhynchus	.60-.62	young specimens	older spec.	6
Cyclura	.60-.64	young specimens	older spec.	12
Enyaliosaurus	.60-.63	all specimens	none	2
Sauromalus	.56-.61	all	none	8
Dipsosaurus	.59-.60	all	none	11
Sceloporus	.59-.66	all	none	21
Uta		all	none	
Urosaurus		all	none	
Holbrookia	.64-.66	all	none	4
Uma	.65	all	none	3
Callisaurus	.62	all	none	1
Phrynosoma	.63-.67	all	none	20
Crotaphytus	.60-.68	all	none	17
Tropidurus	.60-.63	all	none	3
Leiocephalus	.61-.62	all	none	2
Liolaemus	.59-.62	all	none	3
Hoplocercus	.59-.60	all	none	3
Stenocercus	.62	all	none	1
Morunasaurus	.60	all	none	1
Platynotus	.59	all	none	1
Leiosaurus	.63	all	none	1
Phymaturus	.58	all	none	1
Ophryoessoides	.63	all	none	1
Plica	.60	all	none	1
Enyalioides	.60	all	none	1
Uranoscodon	.60	all	none	1
Basiliscus	.60-.65	none	all spec.	7
Laemanctus	.66	none	all	1
Corythophanes	.62-.65	none	all	2
Polychrus	.66-.68	all	none	2
Anolis	.65-.71	rarely	some spec.	18
Deiroptyx	.69	none	none	1
Xiphocercus	.68	none	all (small)	1
Phenacosaurus	.70	none	all (small)	2
Chamaelinorops	.66-.67	none	all (small)	2
Chamaeleolis	.70	none	all	1

Phrynosoma. The rather long jaws combined with a small crescentic parietal origin throughout life would seem to indicate fairly weak jaws for the sceloporines.

Tropidurines, though similar in size to sceloporines tend to have a smaller gape and thus fall below the composite sceloporine, basiliscine, iguanine growth curve. Tropidurines have small crescentic parietal origins throughout life. Their slightly shorter jaws however, combined with an extensive adductor superficialis, probably give them an edge over the sceloporines in jaw strength.

The basiliscines also fit on the Iguana growth curve. They tend to be larger than the sceloporines and tropidurines, and to have smaller gapes. The very large parietal crests in this subfamily give the basiliscines probably the strongest jaws in the Iguanidae, despite the fairly long gape.

The anolines have the highest iguanid gape ratios, ranging from .65 to .71. There is no evidence of a change in ratio in larger specimens or species. The lower ratios overlap with these of the smallest sceloporines but from .68 to .71 only anolines are found. The enlarged parietal origin in the anolines can be interpreted as an adaptation probably for just maintaining the strength of the elongated jaws.

In summary their appears to be one major gape growth curve shared by the iguanines, sceloporines tropidurines and basiliscines with Dipsosaurus and Sauromalus falling below the curve and Cyclura above it. The anolines stand alone with ratios higher than any of the other iguanids.

Gape Length and Diet in the Iguanidae

There seems to be quite a close correlation between the length of the gape and the type of diet preferred by the iguanid lizard. Insectivorous iguanids have gapes of intermediate and long lengths while the herbivorous forms have definitely shorter gapes.

Insectivores, which are in the great majority in the Iguanidae, use their jaws for capturing, holding onto and killing organisms which are usually fairly active. The longer the gape, the better the chance the lizard has of capturing its prey and holding onto it. In killing prey the lizard will usually bite the organism several times, opening its jaws and freeing the organism for a short instant in time before it bites it again using both its upper and lower jaws. (Alexander, 1968). With each bite the prey is brought further back in the mouth until it is finally swallowed. The longer the jaws the less chance the lizard has of losing the prey during this process.

Herbivorous lizards, (Iguanines only, among the Iguanidae) of course consume non-motile food and would derive no advantage from a long gape. What is more important for the herbivore is that it be able to bite off a manageable piece of food from a food item which may be much larger than its mouth, a large fruit or piece of vegetation, for example. For this purpose the short, chopper like iguanine jaw is much more advantageous for it allows the entire force of the adductor musculature to be spread out over a shorter distance, thus actually strengthening the bite.

This combined with a shearing rather than a piercing dentition, makes for an efficient plant eating mechanism. In addition to this the larger iguanine herbivores also develop a stronger adductor musculature through the development of the triangular parietal. This probably allows them to take the larger, tougher vegetable matter that a larger animal would attempt to take.

It is very interesting to note that the herbivorous iguanids, almost without exception, are to some extent insectivorous as juveniles (Montanucci, 1968; Mayhew, 1963; Szarsky, 1962). It is interesting because it is a recapitulation of the ancestral insectivorous condition in the ontogeny of the herbivore. It also substantiates the relationship of gape length to diet because the young have gape ratios which are indistinguishable from insectivore ratios. As the lizard matures and gradually switches over to being almost exclusively herbivorous, the gape ratio becomes gradually shorter (Fig. 13).

It has been reported that <u>Iguana iguana</u> will take carrion (Loftin, 1965). This is not unreasonable, at least with respect to the jaw apparatus. The herbivore jaws and dentition should be almost as good at shearing off a soft piece of dead flesh from a stationary carcass as they are at shearing a piece of tomato from a large fruit (Fig. 13).

Primitive and Advanced Characters

Before discussing the trigeminal musculature from a taxonomic point of view it is necessary to discuss the criteria used in determining the primitive and advanced conditions of each character. A character state is considered primitive to the family if it is present in a large number of genera and a variety of subfamilies. The most parsimonius explanation of such a distribution is that the character state was present in the ancestral organism and has persisted in the various lines descendant from the ancester.

A character is advanced if it is found in just a few scattered genera within a family or in all or most of the genera of one or two subfamilies within a family. The simplest explanation of this distribution is that the character state developed independently in the scattered genera where it occurs. If it occurs in all of the genera of a subfamily, the character probably existed in the ancester of that subfamily. If the character is found in some of the genera of a subfamily it could mean that the group is split into two or more lines only some of which have evolved the trait. Table 3 lists the frequency of each character state among the iguanid genera and subfamilies and is thus useful in determining primitivness.

An organism is primitive with respect to the system studied if all or most of its characters have been assigned as primitive character states. It is advanced if most of its characters are advanced. Every degree of mixture of advanced and primitive characters is possible and was found in the present study.

A character which is primitive to the Iguanidae could be advanced or primitive to the lizards as a group. To determine the status of the character with respect to the Lacertilia, criteria similar to those described above must be applied at the family level. If the character is common throughout the other families it is primitive, if rare or absent it is advanced.

If the situation exists in which the primitive members of a group have for some reason become extinct without a trace, and leaving, the advanced forms in the majority, one might have trouble establishing what is primitive. Studing the other families however, would most likely clarify the situation. The condition most common in the other families, if it matched a minority condition in the family in question could be taken as primitive.

With these criteria established the condition of the characters used in this study can be analyzed:

1. Extent of the adductor medius in the supratemporal fossa. The most common condition is to have the medius cover less than half of the parietal. It is found in this character state in 82% of the genera and in every subfamily. It is clearly the primitive character state. Looking at the character in other families does not help for their seems to be a good deal of variation. The situation is complicated by the fact that many families lack a supratemporal fossa.

2. The Extent of the adductor superficialis

   No single character state has a clear majority of genera with respect to this character in the Iguanidae. However, throughout the other families of lizards the tendency is to have an adductor superficialis which extends more than halfway down the side of the mandible. Within the Iguanidae the more extensive superficialis is present in the most number of distinguishable groups thus having the widest distribution. For these two reasons a superficialis extending more than halfway down the side of the mandible will be taken as primitive and any variant as advanced.

3. Extent of the superficial fascia.

   The most common superficial fascia covers just the posterodorsal corner of the infratemporal fossa. It is present in the most number of genera and all of the subfamilies. It is therefore primitive to the Iguanidae. It is however, advanced for the Lacertilia for most of the other families have more extensive fascias.

4. Condition of the temporal artery.

   A temporal artery which exits at the anterior border of the adductor medius and passes anteriorly over the pseudotemporalis is the most common condition. It is found in the majority of the genera and all but one subfamily. It is also the most common condition in the other families which have a similar supratemporal region. It is therefore primitive among lizards.

5. Extent of the pseudotemporalis

   Eighty-one per cent of the iguanid genera have a pseudotemporalis which covers more than half of the parietal. The condition is found in everyone of the subfamilies and is obviously primitive to the Iguanidae. Most of the other lizard families have a smaller pseudotemporalis, possibly indicating that the larger muscle is advanced for the Lacertilia.

6. Size and shape of the parietal muscle origin.

   Sixty one per cent of the genera, in all but two of the subfamilies have crescentic parietals with expanses of roofing parietal between the crescentic muscle origins. This corresponds to the most common condition in the other families and is thus primitive. Triangular and crested parietals found in only a few groups are advanced.

7. Separation of the heads of the superficialis.

   The number and distribution of genera showing and not showing separation is about the same, both within the Iguanidae and within the Lacertilia making the determination of primitive or advanced state of the character impossible.

8. Separation of the heads of the pseudotemporalis.

   The separation of the pseudotemporalis seems to be primitive to the Iguanidae and advanced to the Lacertilia.

9. The gape

A range of gape values from .60 to .65 seems to be primitive to the Iguanidae for most of the genera and subfamilies fall within these values. Higher or lower values are advanced.

10. Habitat

The terrestrial, insectivorous habit is the most common in the Iguanidae and all the other lizard families. Even the few herbivorous forms are insectivorous as juveniles. These conditions are thus primitive.

Table 5 Distribution of advanced characters.

	Genus	Extent of Medius	Extent of Superficialis and Fascia	Temporal Artery	Condition of Parietal
Madagascan	*Oplurus*	P	P	P	P
	Chalarodon	P	P	P	P
Iguanines	*Ctenosaura*	P	P	P	A
	Iguana	P	A	P	P
	Cyclura	P	P	P	P
	Sauromalus	A	P	A	P
	Enyaliosaurus	P	P	A	P
	Dipsosaurus	P	A	P	P
	Brachylophus	P	P	P	P
Sceloporines	*Sceloporus*	P	P	P	P
	Uta	P	A	P	P
	Urosaurus	P	P	P	P
	Uma	A	A	P	P
	Holbrookia	A	P	P	P
	Callisaurus	A	A	P	P
	P *Phrynosoma*	A	A P	P	A
	Crotaphytus	P	P	P	P
Tropidurines	*Tropidurus*	P	P	P	P
	Leiocephalus	P	P	P	P
	Leiolaemus	P	P	P	P
	Hoplocercus	P	P	P	P
	Stenocercus	P	P	P	P
	Morunasaurus	P	P	A	P
	Platynotus	P	P	P	P
	Phymaturus	P	P	P	P
	Leiosaurus	P	P	P	P
	Ophryoessiodes	P	P	A	P
	Plica	P	P	P	P
	Enyaliodes	P	P	A	P
	Uranoscodon	P	P	P	P
Basiliscines	*Basiliscus*	P	A	A	A
	Corythophanes	P	A	A	A
	Laemanctus	P	A	A	A
Anolines	*Polychrus*	A	A	P	P
	Anolis	A	A	A	A
	Xiphocercus	P	A	A	A
	Deiroptyx	A	A	A	A
	Chamaelinorops	P	A	A	A
	Chamaeleolis	P	A	A	A
	Phenacosaurus	P	A	A	A

mporal tery	Condition of Parietal	Size of Pseudotemp.	Gape Ratio	Total of Advanced Characters	Average for Each Group
P	P	P	P	1	
P	P	P	P	0	.5
P	A	P	P	1	
P	P	P	P	1	
P	P	P	A	1	
A	P	P	A	3	
A	P	P	P	1	
P	P	P	A	2	
P	P	P	P	0	1.3
P	P	P	P	0	
P	P	P	P	1	
P	P	A	P	2	1.0
P	P	A	P	3	
P	P	A	P	2	
P	P	P	P	2	2.3
P	A	A	P	5	5.0
P	P	P	P	1	1.0
P	P	P	A	1	
P	P	P	A	1	
P	P	A	A	2	
P	P	P	A	1	
P	P	P	A	1	
A	P	P	A	2	
P	P	P	A	1	
P	P	P	A	1	
P	P	P	A	1	
A	P	P	A	2	
P	P	P	A	1	
A	P	P	A	2	
P	P	P	A	1	1.3
A	A	A	P	4	
A	A	A	P	4	
A	A	A	P	4	4.0
P	P	P	A	2	
A	A	P	A	5	
A	A	P	A	4	
A	A	P	A	5	
A	A	P	A	4	
A	A	P	A	4	
A	A	P	A	4	4.0

Iguanines, Sceloporines, Tropidurines and the Madagascan Iguanids

As far as the trigeminal musculature is concerned, these four groups form a closely related natural group, very similar to one another and quite distinct from the anolines and basiliscines. They all have wide skulls when compared with the advanced anolines and basiliscines. All except the larger individuals of the larger species of iguanines have narrow crescent shaped parietal muscle scars. These are considerably separated when seen in dorsal view, and give the supratemporal fossa a rounded appearance. The gape ratios of the four groups vary considerably. The adductor superficialis tends to extend down the side of the mandible and in some forms reaches its ventral border. The large superficialis is accompanied by an extensive superficial fascia. The anterior and posterior heads of the superficialis may or may not be separable. This character seems to vary even within the subfamilies. The two heads of the adductor medius are almost never separated. The temporal artery exits at the anterior border of the dorsal head of the medius and proceeds anteriorly over the pseudotemporalis. The dorsal head of the medius tends to be less prominent than in the anolines and basiliscines. Large shields or crests of bone or dense connective tissue are never found.

Madagascan Iguanids

According to Avery and Tanner (1971) the Madagascan genera Oplurus and Chalaradon are the most primitive in the Iguanidae. They are more closely related to each other than to any other genus. Of the two Oplurus is more closely related to the iguanine line, sharing a great many osteological and myological characters with Ctenosaura which Avery and Tanner take to be ancestral to the iguanines of the western hemisphere. Chalaradon shares few characters with the iguanines and is not considered closely related to that line. The similarities between Chalaradon and Oplurus are attributed by the authors to a "Distant common ancestry between the two genera and common adaptations needed to meet the environmental demands of Madagascar."

Table 4 which summarizes the distribution of primitive and advanced characters shows the Madagascan genera to be the most primitive in the family with regard to jaw musculature as well. In the supratemporal fossa both have a large pseudotemporalis and a smaller posterior, adductor e. medius. The adductor e. superficialis extends more than halfway down the side of the mandible.

The Madagascan forms have narrow crescent shaped parietals which give origin to the musculature of the supratemporal fossa. These crescents are separated by an expanse of roofing parietal.

The gape ratios of Oplurus and Chalaradon appear also to be primitive in that they sit at about the middle of the range of the iguanid values and overlap the ranges of all of the other subfamilies except the anolines.

The only advanced character found in the Madagascan forms is the position of the temporal artery in Oplurus. It is similar to the position of the artery in the anolines and basiliscines.

In considering jaw strength, Oplurus and Chalaradon are probably as strong as the smaller iguanines and tropidurines by virtue of their fairly extensive adductor superficialis.

Iguanines

Avery and Tanner (1971) and Mittleman (1942) select *Ctenosuara* as the most primitive North American iguanine by virtue of the great number of characters it shares with *Oplurus* and the other iguanine genera. They further suggest it is ancestral to all North American iguanines. *Cyclura*, *Ctenosaura* and *Iguana* are said to form a closely related natural group, probably representing a primary radiation in Central America. *Sauromalus* as well as *Conolophus* and *Amblyrhynchus* are all offshoots of the *Ctenosaura* line, with *Amblyrhynchus* coming off the *Conolophus* line. *Dipsosaurus* is most closely related to *Sauromalus*. *Enyaliosaurus* is another early offshoot of the *Ctenosaura* line.

Savage (1958) included *Crotaphytus* with the iguanines. Etheridge (1964) separated the two on the grounds that the characters they shared were also found in other groups, thus making it impossible to diagnose the group. Etheridge suggested that *Crotaphytus* is more closely related to the sceloporines. The jaw musculature tends to support this (Table 7).

With regard to the jaw apparatus *Ctenosaura* is a good choice for the most primitive. The only specialized character it has is a triangular rather than crescentic parietal adductor origin. All the other iguanines, plus the sceloporines and tropidurines have a crescentic parietal origin. The larger iguanines develop a triangular parietal origin as they grow older, but only *Ctenosaura* shows a triangular parietal origin throughout life. It seems very improbable that the triangular parietal is primitive. It may have evolved recently in this genus although the fossil record is inadequate to clarify the point.

The gape ratios of the subfamily seem to fit nicely with the information presented by Avery and Tanner. *Ctenosaura*, *Iguana*, *Conolophus* and *Amblyrhynchus*, it will be recalled, share the same growth curve with respect to gape. They all start out with large ratios which decreases as the animal grows. *Ctenosaura* and *Iguana* are the mainland forms inhabiting Central America. *Conolophus* and *Amblyrhynchus* invading the Galapagos Islands maintained the ancestral growth curve as did *Brachylophus* on Fiji. *Cyclura* another island form coming off of *Ctenosaura*, invaded the Antilles and Bahamas. *Cyclura* however, abandoned the ancestral growth curve and maintain the high juvenile gape ratio throughout life. *Sauromalus*, a northern desert form off the *Ctenosaura* line, and *Dipsosaurus*, another desert form closely related to *Brachylophus*, as well as *Enyaliosaurus*, a Central American form off the *Ctenosaura* line, have all independently developed a second growth curve of smaller gape ratios(Fig. 14). This may be correlated with their reduced size although the sceloporines which get to be much smaller, maintain the high ratio of the *Iguana* growth curve.

The large iguanines *Iguana*, *Conolophus* and *Amblyrhynchus* develop small parietal crests as they grow and lose the space between the parietal origins as they do so. The small iguanines maintain the space throughout life and develop no crests.

All of the iguanines except *Enyaliosaurus* have the temporal artery in the primitive condition, exiting at the anterior border of the adductor medius. *Enyaliosaurus* has developed an arterial configuration similar to that of the basiliscines, anolines, *Enyaliodes* and *Oplurus*.

Other examples of advanced characters are to be found in *Iguana* which has a small adductor superficialis, and *Dipsosaurus* which is the only iguanid studied to lack a ligamentum quadratomandibulare. *Sauromalus* has a very extensive pseudotemporalis which extends posteriorly to fill the entire supratemporal fossa. The dorsal head of the adductor medius is not seen until the squamosal is removed. The temporal artery exits through the pseudotemporalis due to its posterior extension.

The iguanines are all herbivorous, but it is well documented that the young of most forms will take insects. (Montanucci, 1968; Mayhew, 1963; Szarsky, 1962). It is most likely the herbivorous condition that allows the iguanines to attain their large size. Insectivorous lizards must be small and agile to get their prey. Herbivorous forms can grow large on their abundant and stationary food supply and then use their size for protection.

According to Throckmorton (1972), it is the primitive, fleshy nature of the iguanine tongue which allows the group to be herbivorous. Such a tongue is necessary for manipulating plant material. Where the tongue is modified as a slender organ of olfaction, Throckmorton maintains that herbivory is impossible.

Ostrom (1963) feels that the streptostylic quadrate of lizards precludes the possibility of a radiation of herbivorous lizards. To be properly digested, plant material must be well chewed. This requires a side to side grinding motion of the jaws. Ostrom feels that such motion is impossible because the adductor posterior which could provide it originates on a moveable quadrate. In order for the muscle to pull the jaw toward the midline its origin must be fixed. Ostrom maintains that streptostyly along with cranial kinesis are really adaptations for swallowing things whole and not for chewing. Snakes, where kinesis reaches its height, swall their food whole while all tetrapod herbivores except the lizards have fixed quadrates.

It seems possible that side to side movement could be achieved in lizards using the more dorsal fibres of the pterygomandibularis muscle. These fibres run from the lateral side of the quadrate process of the pterygoid to the ventromedial border of the mandible. Used independently and combined with proper grinding dentition, the pterygomandibularis could provide a combined adducting and grinding force.

The fact remains that the herbivorous iguanids do not chew their food any differently than the carnivorous iguanids. There seem to be no features in the musculature that one can point to as herbivorous specializations. The major adaptations seem to be in the serrate dentition which is necessary for shearing and grasping plant material.

Sceloporines

In his review of the sceloporines, Etheridge (1964) included eight genera and split them into three groups on the basis of the number of cervical vertebrae, a character which he believes to be conservative. The classification is as follows: *Uma*, *Holbrookia*, *Callisaurus* - 2 ribs; *Uta*, *Urosaurus*, *Sator*, *Sceloporus* - 3 ribs; *Petrosaurus* - 4 ribs. The *Uma* group is thought to be the most advanced. The tropidurines as a group are chosed by Etheridge as the closest relatives of the sceloporines. *Crotaphytus* and *Gambelia* are lumped in the genus *Crotaphytus* (Etheridge, 1964; Weiner and Smith, 1965). *Crotaphytus* is assigned as the closest North American relative to the sceloporines and is itself closest to *Petrosaurus*, both forms having the primitive 4 ribs.

Etheridge removes the genus *Phrynosoma* from the sceloporines stating that its position is analagous to that of *Chamaeleo* and the Agamidae. *Phrynosoma* obviously evolved from a primitive sceloporine but is so changed that very few characters are now shared between the two groups. Presh (1969) in his study of the genus *Phrynosoma* recommends that the group remain within the sceloporines as a fourth group of equal rank with *Petrosaurus*, the *Uta* group and the *Uma* group. Presh points out several characters which *Phrynosoma* has in common with the *Uma*. *Callisaurus*, *Holbrookia* group and suggests that the genus might have arisen from an ancestor of this line and not from a protosceloporine ancestor as Etheridge (1964) suggests. Presh's interpretation fits the jaw muscle data more closely than Etheridges'. The muscle modifications of *Phrynosoma* are similar to those of the *Uma* group but more striking.

In discussing the jaw musculature of the sceloporines, I will include *Crotaphytus* which, on the basis of jaw musculature, is more similar to the sceloporines than to the iguanines (Table 7) where some workers placed it (Savage, 1958). However, extensive studies by Avery and Tanner (1964) and Etheridge (1964) show *Crotaphytus* to be distinct from the iguanines and rather close to the more primitive sceloporines.

The sceloporines, along with *Phrynosoma* and *Crotaphytus* seem to have the weakest jaws in the Iguanidae. Table 4 and Figure 14 show them to have rather long gapes. The musculature is not strengthened either by increase of parietal origin or increase in the size of the adductor superficialis. The combination of rather long jaws and minimal muscular development seems to put the sceloporines at the botton of the list as far as jaw strength is concerned. However, being rather small lizards it is probable that their musculature is adequate for the size of the prey taken.

As a group the sceloporines can be recognized from the tropidurines by their longer gape, less developed adductor superficialis and variable supratemporal musculature. The pseudotemporalis superficialis and profundus tend to be separable in the sceloporines while separability is variable in the tropidurines. The small size of the adductor superficialis allows for separation of its two heads in most of the genera.

The sceloporine gape ratio ranges from .62 to .67, with .60 to .66 in *Crotaphytus* and .63 to .67 in *Phrynosoma.* Since the sceloporines tend to be smaller animals these ratios fit nicely along the *Iguana* - *Ctenosaura* gape ratio curve. Some of the highest ratios were found in the genus *Phrynosoma* (Table 4), indicating that there is no shortening of the jaw in this genus. The apparent shortening is due actually to a heightening of the skull.

The adductor superficialis extends halfway or less down the side of the mandible and is accompanied by a proportionally small superficial fascia. This gives a superficialis of only moderate strength to operate their rather long jaws.

A glance at Table 1 will reveal that the sceloporines seem to have done the most experimentation on the extent of the pseudotemporalis superficialis and adductor medius muscles in the supratemporal fossa. Only *Sceloporus* and *Uta* seem to have retained the primitive condition of this musculature. In this condition the pseudotemporalis takes up more than half of the parietal anteriorly, leaving the remainder of the parietal for the medius. In *Callisaurus*, *Uma*, *Phrynosoma* and to a lesser extent *Holbrookia*, the adductor medius is enlarged and extends anteriorly, covering the pseudotemporalis in *Callisaurus*, *Holbrookia* and *Uma* and replacing it almost entirely in *Phrynosoma*. In *Urosaurus* and *Crotaphytus* the opposite has happened. The pseudotemporalis has enlarged forcing the medius out of the supratemporal fossa. It is interesting to note that most of the experimentation is confined to the more advanced sceloporines *Callisaurus*, *Uma* and *Holbrookia*. This information supports Etheridges grouping of the genera.

There seems to be a trend in the sceloporines to reduce the number of muscles originiating on the parietal from two to one. Most genera have reduced the pseudotemporalis while one group has reduced the medius and only two genera, Phrynosoma and Urosaurus have succeeded in eliminating one or the other muscle. The advantage of this is unclear. It may be that a one muscle, one bone arrangement is more efficient. Fusion of centers of ossification and muscles have occured many times in other groups. The mammalian jaw musculature, not to mention the mammalian jaw are much simplified over their reptilian counterparts. With fewer parts come greater efficiency and possibly greater strength. It is possible that this is the method being explored by the sceloporines to increase their jaw strength. The only other iguanid genera trying this is the tropidurine genus Leiolamus and the iguanine Sauromalus. In these groups the pseudotemporalis grows over the medius posteriorly. However, both the tropidurines and iguanines as groups, are exploring other methods of strengthening their jaw apparatus.

Tropidurines

The tropidurines including, *Tropidurus*, *Leiocephalus*, *Leiolaemus*, *Hoplocercus*, *Stenocercus*, *Morunasaurus*, *Platynotus*, *Leiosaurus*, *Phymaturus*, *Ophryoessiodes*, *Plica*, *Enyaliodes* and *Uranoscodon* (Etheridge, 1959, 1964, 1966) separate fairly well from the sceloporines and iguanines on the basis of trigeminal musculature. All of them have very similar skull characteristics accompanied by similar musculature. The parietal as in the sceloporines and some iguanines is narrow and crescentic and therefore gives origin to a pseudotemporalis and adductor medius of average strength. The jaw mechanism is strengthened however by two factors. First, the tropidurine gape ratio is smaller than the ratio for sceloporines or small iguanines (excepting *Dipsosaurus* and *Sauromalus*). This strengthens the jaw by shortening the lever arm. Secondly the adductor superficialis appears to be consistenly enlarged, extending halfway or more down the side of the mandible (Table I). This is accompanied by proportionally enlarged superficial fascias, as well as additional accessory fascias serving as origin for the extra muscle. The combination of these two factors certainly make the tropidurine jaw stronger than the sceloporine jaw which has a longer gape and no enlarged musculature.

The two heads of the adductor superficialis tend to be less separable in the tropidurines due to the enlargement of the muscle by the addition of superficial fibres. The extent of the pseudotemporalis superficialis in the supratemporal fossa is fairly constant througout the group except for *Leiolaemus* where it extends posteriorly to cover the entire fossa. The extent of the dorsal head of the medius is also constant. The rather uniform picture of the musculature of the supratemporal fossa in the tropidurines and also the iguanines is in definite contrast to the condition found in the sceloporines where considerable variation occurs in this area.

The genera Plica, Uranoscodon, and Enyaliodes are arboreal and tend to be more similar to each other than to the terrestrial tropidurines (Tables 6,7,8). According to Etheridge (1959) their adaptations to being arboreal consist of having highly arched, broad and short skulls with a short preorbital region and a large orbit. These are quite different from the anoline arboreal adaptations, as Etheridge points out. As far as the jaw apparatus is concerned the arboreal tropidurines tend to have a more extensive adductor superficialis and superficial fascia than the terrestrial forms. Enyaliodes is special in that it has a temporal artery similar to that of the anolines and basiliscines. The arboreal tropidurines will be listed separately on all charts so that they can be studied as a group.

According to Etheridge (1966), larger individuals of certain larger species of the genus Leiocephalus in the West Indies develop enlarged, triangular parietal adductor origins just as the anolines do. Etheridge also reports that the West Indian species of Leiocephalus have a more extensive adductor superficialis than the South American members of that genus. These two pieces of information suggest that these island forms have developed increased jaw adduction strength. On the basis of this and many other characters Etheridge puts the West Indian forms in a separate genus from the South American forms. The name Leiocephalus is maintained for the island forms while the mainland forms are put in the genus Ophryoessoides. Leiocephalus is closest to the mainland genus

Leiolamus while Ophryoessiodes is closest to the genus Stenocercus.

Etheridge (unpubl.) has recently suggested that the genera Enyaliodes, Hoplocercus and Morunasaurus are the most primitive of the living iguanids, on the basis of skeletal characters. Table 5 shows these groups to be fairly primitive but not as primitive as the Madagascan forms on the basis of jaw musculature. Both Morunasaurus and Enyaliodes have advanced temporal arteries, and all have the shortened tropidurine jaw.

Basiliscines and Anolines

The basiliscines and anolines are two distinct natural groups, easily separable from each other and from the other iguanids, yet sharing some important characters. Both have laterally compressed skulls with much enlarged parietal origins. The origins are triangular in shape and meet on the dorsal midline giving the supratemporal fossa a squared off appearance. No space is present between the parietal origins on the dorsal surface of the skull. The adductor superficialis and superficial fossa are not extensive in either group. The anterior and posterior heads of the superficialis are usually separable. The dorsal and ventral heads of the medius are always separated by the temporal artery. Both groups have developed shields and crests, but with differing musculature.

Basiliscines

The genera Basiliscus, Laemanctus and Corythophanes form what appears to be a natural group within the Iguanidae. They share several important characters. All three genera have prominent crests formed by posterodorsal extension of the parietal. The crests all support the same distinctive type of musculature. The skulls tend to be laterally compressed with very large parietal origins. These are basically triangular in shape with large posterior crests. No space is present between the parietal origins when viewed dorsally. The gape ratio for the group varies from .60 to .66. The higher values belonging to Laemanctus and Corythophanes. The path of the temporal artery is constant in the group. It marks the separation of the two heads of the medius. The adductor superficialis does not extend far down the side of the jaw in any group. Two of the genera show a reduction in the posterior parietal origin of the adductor profundus, and two show separation of the anterior and posterior heads of the superficialis.

The crest of Basiliscus is the smallest and is just a simple projection of the parietal. In Laemanctus and Corythophanes the crests are larger and extend posteriorly over the neck. These two genera also show a tendency towards the formation of a shield. In Corythophanes the shield is bony and not well developed, extending only a little more than half the length of the crest before tapering away completely. In Laemanctus the shield continues to the end of the crest and is the same width all along its length. It is made of tough connective tissue.

The crest, regardless of its size in each genus, serves as the origin of the pseudotemporalis superficialis only, a sharp contract to the anoline condition. The larger the crest, the larger the origin of the muscle and the stronger it becomes. The prominent shield in *Laemanctus* does not serve as the origin of any muscle. It merely covers the pseudotemporalis, possibly for protection or display. The bony, posteriorly tapered shield of *Corythophanes* on the other hand, serves as added origin for the pseudotemporalis.

In all three genera the temporal artery comes through the adductor medius muscle separating it into dorsal and ventral heads, as in all the anolines. The differences however, is that the dorsal head of the basiliscine medius is less extensive than that of the anolines so that just a few fibres of the medius are seen dorsal to the artery. The position of the temporal artery aligns the basiliscines and anolines against the other subfamilies. However, since this condition of the temporal artery tends to pop up in distantly related groups such as *Oplurus* on Madagascar, *Enyaliosaurus* in the iguanines and *Enyaliodes* in the tropidurines it is difficult to use the character as evidence of a common ancestry for the baliliscines and anolines. It may simply be that the character is associated with the enlargement of the parietal musculature present in the anolines and basiliscines, but there is no enlargement in the scattered genera where the character is also found.

The adductor superficialis reaches just to the top of the jaw in *Corythophanes* and extends slightly further in *Basiliscus* and *Laemanctus*. The reduced superficialis is accompanied by a reduced superficial fascia.

The enlarged pseudotemporalis probably reduces the need for an extensive adductor superficialis. With respect to this character the basiliscines stand between the anolines and the rest of the Iguanidae.

The posterior parietal origin of the adductor profundus is fully developed in Basiliscus. It is greatly reduced in Laemanctus which has a strong post temporal fossa, and absent in Corythophanes which has no post temporal fossa. Fibres from the posterior parietal origin pass through the post temporal fossa. A reduction of the fossa would certainly lead to a reduction or less of the posterior parietal origin. The fact that the origin is reduced in Laemanctus which has a strong fossa indicates a definite tendency in the more specialized basiliscines to reduce this head regardless of the condition of the fossa. As demonstrated by Chamaeleolis, the reduction of the posterior head does not seem to be automatically associated with the development of a crest and shield. Chamaeleolis which has a similar crest arrangement has a strong posterior parietal origin.

Basiliscus is clearly the most primitive member of the subfamily as is seen by the condition of its crest and the presence of the posterior parietal origin of the adductor profundus. Laemanctus and Corythophanes show different specializations, the former bearing a prominent shield and the latter showing greatly enlarged eyes and an odd levator angularis oris.

Anolines

The genus *Anolis* including *Deiroptyx* and *Xiphocercus* (Etheridge, 1959), and the closely related but distinct genera *Chamaelinorops* and *Chamaeleolis* form a natural group quite distinct from the other iguanids. They all have the same suite of cranial and trigeminal muscle characters. To begin with the skull is laterally compressed as is the rest of the body. The portion of the parietal which gives rise to the adductor musculature is triangular and not crescentic. The apices of the left and right triangles converge on the dorsal midline eliminating any space between them. The gape is elongated with ratios ranging from .65 to .71. The ratio does not seem to alter as the lizard grows. The adductor ext. superficialis is not extensive, usually reaching just to the top of the surangular. The superficial fascia is likewise poorly developed. The two heads of the adductor ext. superficialis are always clearly separable. The adductor ext. medius is always clearly separated into dorsal and ventral heads by the temporal artery. The dorsal head of the adductor ext. medius is always prominent and where a crest is present it extends up onto the crest. The two heads of the pseudotemporalis are usually separable.

The lateral compression of the skull and body are adaptations to the arboreal habits of the anolines. The longer and narrower jaws are no doubt helpful in allowing the anolines to pick insects out of tight places. The increased jaw length most likely necessitated the increased parietal origin of the adductor musculature, in order to maintain sufficient force at the ends of the long jaws. The increase in size of the parietal origin along with the compression of the skull are probably responsible for the loss of the space between the left and right parietal origins. This space is also lost in the basiliscines which are also arboreal and fairly long gaped. The increased anoline gape ratio does not alter with age as it does in some iguanines. The anoline ratios are the highest in the family and they stay high in the larger forms.

The poorly developed adductor ext. superficialis must be a specialization in the anolines and also in the basiliscines, for almost every other lizard genus, regardless of family, has a larger superficialis. The reduction is probably made possible because of the increased parietal musculature, and is most likely correlated with the lateral compression of the skull.

The two heads of the adductor ext. superficialis are clearly separable because the superficialis is not extensive. When this muscle becomes extensive fibres are added to both heads by the superficial fascia. These additional fibres plus the superficial fascia itself make it difficult to separate the heads.

There is a clear separation between the heads of the adductor ext. medius. The dorsal and ventral heads look superficially like separate muscles and are separated by the temporal artery (Fig. 4). The dorsal head is larger and more conspicuous than in any other iguanid group. It covers half or almost half of the enlarged, triangular parietal origin. In forms like *Chamaeleolis* where a parietal crest is formed, the dorsal head of the a. e. medius extends along the entire length of the crest.

The temporal artery comes through the fibres of the a. e. medius in *Oplurus*, *Enyaliosaurus* and *Enyaliodes*, but in none of these does it clearly separate the medius into heads as it does in the anolines and to a much lesser extent in the basiliscines. The presence of this character in the three distantly related genera suggests a tendency for the trait to appear in iguanid groups, and is probably a case of parallelism. The trait must have been present however, in the ancestral anolines and basiliscines.

The position of the temporal artery does not seem to be related to the large size of the adductor ext. medius for Oplurus, Enyaliosaurus, Enyaliodes and the basiliscines all have the average small dorsal medius muscles. Uma and Callisaurus with very large dorsal medius heads, have no separation of the heads by the temporal artery.

Etheridge (1959) and other workers before him (Cope, 1900) have included the South American genus Polychrus with the anolines on the basis of a great many characters. The 20 out of a possible 22 characters which they share however, do not contain those characters unique to the anolines. As far as the jaw apparatus is concerned Polychrus is more similar to almost any other iguanid group than it is to the anolines. The only important character that shows similarity to the anolines is the enlarged gape. The Polychrus ratios range from .66 to .68, intermediate between the anoline and non-anoline values. Polychrus tends to have a slightly enlarged medius as some anolines have and shows separation of the heads of the adductor ext. superficialis as all anolines do. However, the adductor e. superficialis is too extensive to be anoline. It, as well as the temporal artery and the parietal are sceloporine in appearance. Polychrus is also the anoline not to have a separation of the two heads of the pseudotemporalis.

On the basis of this data alone Polychrus could not be closely allied to the anolines. The few jaw muscle characters they share are probably due to parallelism or convergence. Polychrus will be treated separately in all charts and graphs so that its characters and relationships will not be hidden.

Similarity Between Genera

Table 6 shows the similarity of each iguanid genus to every other iguanid genus with respect to jaw apparatus, diet and habitat. It does so by listing the number of these characters that each pair of genera share. Table 7 gives an idea of the similarity of each genus to each subfamily, genus group or important genus, by averaging the similarities of the particular genus to each member of the group in question. Table 8 compares the similarities of each major iguanid subgroup by averaging the similarities of the genera involved.

The data in Table 6 reveals that, with respect to jaw apparatus, 14 out of 31 genera are as or more similar to a genus in another subfamily than they are to the other genera in their own group. These 14 genera however, tend to be the least advanced of the family and include none of the *Uma* group, basiliscines or anolines (except *Polychrus*), and only one arboreal tropidurine. These groups because of their specializations are all more similar to their sister genera than to the genera in other subfamilies.

Table 7 shows 10 genera to be as or more similar to groups or subfamilies other than their own. These again tend to be the more primitive members of the Iguanidae and thus tend to resemble each other. *Oplurus* and *Chalaradon* for example, are as or more similar to the more primitive sceloporines and tropidurines than they are to each other. In agreement with Avery and Tanner (1971) *Oplurus* is slightly more similar to the iguanines than *Chalaradon* is. *Chalaradon* however, is consistently more similar to each remaining iguanid group than Oplurus is. Cyclura, Enyaliosaurus and Dipsosaurus are more similar to the primitive Madagascan forms than to the iguanines as a whole. Sceloporus and Uta are as or more similar to the Madagascan forms and primitive tropidurines than they are to the sceloporines as a whole. Tropidurus and Enyaliodes are more similar to the Madagascan forms than to the tropidurines.

Polychrus is more similar to the Uma group, Phrynosoma, Crotaphytus and the tropidurines than it is to the anolines to which it supposedly belongs. This is not surprising since the only character it shares with the anolines is the tendency to increase the jaw length. The remaining 21 genera behave as they should, showing greatest similarity to their own kind and little similarity to distantly related forms.

Phrynosoma shows the greatest similarity to the more advanced sceloporines of the Uma group and to Crotaphytus. Crotaphytus in turn shows a strong similarity to every iguanid genus, group or subfamily except the anolines. The anolines and basiliscines are closer to each other than to any other group. Both are equally similar to Polychrus. Most primitive groups are more similar to the more primitive Sceloporus group than to the advanced Uma group.

Table 8 shows a neater picture than the two preceeding tables. At the subfamily and genus group level only one group shares more characters with another group than it does with its own members. This occurs in the two Madagascan genera which are more similar to the terrestrial tropidurines and Sceloporus group than they are to each other. The iguanines are as similar to the Madagascan forms as to themselves and the primitive sceloporines are as similar to the tropidurines and Madagascan forms as to themselves. However, if the *Sceloporus* and *Uma* groups are combined in a single group, the sceloporines, and the arboreal and terrestrial tropidurines are combined in a single group, the tropidurines, the picture is cleared up considerably. The sceloporines then more similar to each other than to any other group, the Madagascan forms are more similar to themselves than to the sceloporines and also equally similar to the tropidurines as to themselves. However, the similarities of the subgroups should not be glossed over as they are real and probably represent a mixture of common ancestry and convergent evolution.

Table 6 Jaw Apparatus Similarities Between the Genera

	1.*	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.	16.	17.
1. *Oplurus*		8**	7	6	6	6	10	8	7	8	8	7	4	4	5	4	6
2. *Chalarodon*	8		6	6	7	5	7	8	7	11	9	8	6	7	8	5	8
3. *Ctenosaura*	7	6		9	7	8	8	8	8	6	7	5	4	5	6	2	6
4. *Iguana*	6	6	9		7	5	5	6	9	5	7	4	4	4	5	3	6
5. *Cyclura*	6	7	7	7		4	5	6	8	6	5	3	4	4	5	1	5
6. *Sauromalus*	6	5	8	5	4		8	6	7	4	5	4	4	4	5	4	4
7. *Enyaliosaurus*	10	7	8	5	5	8		9	8	6	7	5	3	3	5	3	5
8. *Dipsosaurus*	8	8	8	6	6	6	9		8	7	8	7	4	4	6	4	6
9. *Brachylophus*	7	7	8	9	8	7	8	8		8	8	7	6	7	6	5	7
10. *Sceloporus*	8	11	6	5	6	4	6	7	8		9	8	7	8	7	5	8
11. *Uta*	8	9	7	7	5	5	7	8	8	9		8	7	6	7	5	8
12. *Urosaurus*	7	8	5	4	3	4	5	7	7	8	8		6	7	6	5	7
13. *Uma*	4	6	4	4	4	4	3	4	6	7	7	6		9	9	8	9
14. *Holbrookia*	4	7	5	4	4	4	3	4	7	8	6	7	9		9	6	8
15. *Callisaurus*	5	8	6	5	5	5	4	7	6	7	7	6	9	9		6	9
16. *Phrynosoma*	4	5	2	3	1	4	3	4	5	5	5	5	8	6	6		7
17. *Crotaphytus*	6	8	6	6	4	4	5	6	7	8	8	7	9	8	9	7	
18. *Tropidurus*	9	10	7	5	7	5	8	8	6	9	9	6	6	6	8	4	7
19. *Leiocephalus*	8	9	7	7	5	6	7	8	9	9	9	8	6	7	8	5	8
20. *Leiolaemus*	7	10	5	4	5	4	6	7	7	9	7	8	7	7	7	5	8
21. *Hoplocercus*	7	10	6	4	5	5	6	8	6	10	8	7	6	7	7	4	8
22. *Stenocercus*	9	10	7	6	5	5	8	9	8	9	9	8	6	6	7	4	6
23. *Morunasaurus*	10	7	9	6	6	8	9	7	9	6	7	5	5	5	6	5	6
24. *Platynotus*	9	9	8	6	6	7	9	9	7	8	9	7	5	5	7	4	6
25. *Phymaturus*	9	9	7	6	7	7	8	10	7	7	9	7	5	5	7	4	7
26. *Leiosaurus*	9	9	6	7	6	6	8	10	10	9	9	7	5	5	6	4	6
27. *Ophryoessoides*	9	7	7	6	6	7	8	8	9	7	7	7	5	6	7	5	6
28. *Plica*	6	8	5	4	4	4	6	7	6	7	7	5	4	4	5	3	5
29. *Enyalioides*	9	7	6	4	4	6	9	7	6	6	7	5	3	3	4	3	4
30. *Uranoscodon*	6	8	6	5	4	5	5	6	8	7	7	5	5	6	7	4	6
31. *Basiliscus*	5	5	4	4	5	2	4	3	4	5	5	2	5	4	6	4	6
32. *Corytophanes*	5	4	4	3	5	2	3	2	4	5	4	2	4	4	4	3	5
33. *Laemanctus*	5	4	3	3	3	1	4	3	3	4	5	2	3	2	3	4	4
34. *Polychrus*	4	6	5	4	3	4	3	5	6	5	6	3	7	6	8	6	7
35. *Anolis*	4	3	4	2	1	3	2	1	3	2	2	1	2	2	3	3	2
36. *Chamaeleolis*	4	3	4	3	2	2	3	2	3	3	3	1	2	2	3	3	3
37. *Chamaelinorops*	4	3	4	3	2	2	3	2	3	3	3	1	2	2	3	2	3
38. *Phenacosaurus*	4	3	4	3	2	2	3	2	3	3	3	1	2	2	3	2	3

* The number refers to the number of the genus as listed on the left.
** The number of characters shared by the two genera.

16.	17.	18.	19.	20.	21.	22.	23.	24.	25.	26.	27.	28.	29.	30.	31.	32.	33.	34.	35.	36.	37.	38.
4	6	9	8	7	7	9	10	9	9	9	9	6	9	6	5	5	5	4	4	4	4	4
5	8	10	9	10	10	10	7	9	9	9	7	8	7	8	5	4	4	6	3	3	3	3
2	6	7	7	5	6	7	9	8	7	6	7	5	6	6	4	4	3	5	4	4	4	4
3	6	5	7	4	4	6	6	6	6	7	6	4	4	5	4	3	3	4	2	3	3	3
1	5	7	5	5	5	5	6	6	7	6	6	4	4	4	5	5	3	3	1	2	3	3
4	4	5	6	4	5	5	8	7	7	6	7	4	6	5	2	2	1	4	3	2	2	2
3	5	8	7	6	6	8	9	9	8	8	8	6	9	5	4	3	4	3	2	3	3	3
4	6	8	8	7	8	9	7	9	10	10	8	7	7	6	3	2	3	5	1	2	2	2
5	7	6	9	7	6	8	9	7	7	10	9	6	6	8	4	4	3	6	3	3	3	3
5	8	9	9	9	10	9	6	8	7	9	7	7	6	7	5	5	4	5	2	3	3	3
5	8	9	9	7	8	9	7	9	9	9	7	7	7	7	5	4	5	6	2	3	3	3
5	7	6	8	8	7	8	5	7	7	7	7	5	5	6	2	2	2	3	1	1	1	1
8	9	6	6	7	6	6	5	5	5	5	5	4	5	3	5	4	3	6	2	2	2	2
6	8	6	7	7	7	6	5	5	5	5	5	4	3	5	5	4	3	7	2	2	2	2
6	9	8	8	7	7	7	6	7	7	6	7	4	5	7	6	4	3	8	3	3	3	3
	7	4	5	5	4	4	5	4	4	4	5	3	3	4	4	3	4	6	3	3	2	2
7		7	7	8	8	6	6	6	7	6	6	5	4	6	6	5	4	7	2	3	3	3
4	7		8	9	10	9	8	10	10	9	7	8	8	7	4	6	3	5	2	3	3	3
5	8	8		8	9	10	9	9	9	10	10	77	7	9	4	4	3	6	3	4	4	4
5	8	9	8		10	9	6	8	8	10	7	7	6	7	3	3	3	3	6	2	2	2
4	8	10	9	10		10	7	9	9	10	8	8	7	8	4	4	4	6	2	3	3	3
4	6	9	10	9	10		8	11	11	12	10	8	8	8	3	3	3	4	2	3	3	3
5	6	8	9	6	7	8		10	9	9	10	6	9	8	5	6	5	5	4	4	4	4
4	6	10	9	8	9	11	10		12	11	9	8	9	7	3	4	5	6	2	2	2	2
4	7	10	9	8	9	11	9	12		11	9	8	9	7	3	4	5	6	2	2	2	2
4	6	9	10	10	10	12	9	11	11		10	8	9	7	3	4	5	6	2	2	2	2
5	6	7	10	7	8	10	10	9	9	10		6	8	8	5	5	5	5	4	5	5	6
3	5	8	7	7	8	8	6	8	8	8	6		8	9	4	4	4	6	3	4	4	4
3	4	8	7	6	7	8	9	9	9	9	8	8		7	5	5	4	5	4	5	5	5
4	6	7	9	7	8	8	8	7	7	7	8	9	7		5	5	4	7	4	5	5	5
4	6	4	4	3	4	3	5	3	3	3	5	4	5	5		10	9	6	8	8	8	8
3	5	6	4	3	4	3	6	4	4	4	5	4	5	5	10		8	5	8	8	9	9
4	4	3	3	3	4	3	5	5	5	5	5	4	4	4	9	8		5	8	8	8	8
6	7	5	6	6	6	4	5	6	6	6	5	6	5	7	6	5	5		6	5	5	5
3	2	2	3	2	2	2	4	2	2	2	4	3	4	4	8	8	8	6		8	10	10
3	3	3	4	2	3	3	4	2	2	2	5	4	5	5	8	8	8	5	8		11	11
2	3	3	4	2	3	3	4	2	2	2	5	4	5	5	8	9	8	5	10	11		12
2	3	3	4	2	3	3	4	2	2	2	5	4	5	5	8	9	8	5	10	11	12	

Table 7 Similarity of Each Genus to Each Subfamily or Group

	Madagascan Forms	Iguanines	*Sceloporus* Group	*Uma* Group	Sceloporines	*Phrynosoma*	*Cr ph*
Oplurus	8.0	7.2	7.7	4.3	6.0	4.0	6.
Chalarodon	8.0	6.5	9.3	7.0	8.2	5.0	8.
Ctenosaura	6.5	8.0	6.0	5.0	5.5	2.0	6.
Iguana	6.0	6.4	5.3	4.7	5.0	3.0	6.
Cyclura	6.5	5.8	4.7	4.3	4.5	1.0	5.
Sauromalus	5.5	6.2	4.3	4.3	4.3	4.0	4.
Enyaliosaurus	8.5	7.0	6.0	3.3	4.6	3.0	5.
Dipsosaurus	8.0	7.0	7.3	5.0	6.1	4.0	6.
Brachylophus	7.0	8.0	7.6	6.6	7.0	5.0	7.
Sceloporus	9.5	5.7	8.5	7.3	7.9	5.0	8.
Uta	8.5	6.5	8.5	6.7	7.6	5.0	8.
Urosaurus	7.5	4.6	8.0	6.3	7.7	5.0	7.
Uma	5.0	3.8	6.7	9.0	7.6	8.0	9.
Holbrookia	5.5	4.0	7.0	8.0	7.5	6.0	8.
Callisaurus	6.5	5.3	6.7	9.0	7.8	6.0	9.
Phrynosoma	4.5	2.8	5.0	6.7	5.8		7.
Crotaphytus	7.0	5.2	7.7	8.7	8.2	7.0	
Tropidurus	9.5	6.6	8.0	6.7	7.3	4.0	7.
Leiocephalus	8.5	6.6	8.7	7.0	7.7	5.0	7.
Liolaemus	8.5	5.[illegible]	8.0	7.0	7.5	5.0	8.
Hoplocercus	8.5	5.6	8.3	6.7	7.5	4.0	8.
Stenocercus	9.5	6.6	8.7	6.3	7.5	4.0	6.
Morunasaurus	9.5	7.5	6.0	5.3	5.6	5.0	6.
Platynotus	8.5	7.5	8.0	5.6	6.8	4.0	6.
Phymaturus	8.5	7.5	7.7	5.6	6.7	4.0	7.
Leiosaurus	8.5	7.2	8.3	5.3	6.8	4.0	6.
Ophryoessoides	9.5	7.2	7.0	6.0	6.5	5.0	6.
Plica	7.0	5.0	6.3	4.3	5.3	3.0	5.
Enyalioides	8.0	6.0	6.0	3.3	4.6	3.0	4.
Uranoscodon	7.0	5.2	6.7	6.0	6.3	4.0	6.
Basiliscus	5.0	3.6	4.0	5.0	4.5	4.0	6.
Corytophanes	4.5	3.2	3.7	4.0	3.9	3.0	5.
Laemanctus	4.5	2.8	3.7	2.7	3.2	4.0	4.
Polychrus	5.0	4.0	4.7	7.0	5.8	6.0	7.
Anolis	3.5	2.2	1.7	2.3	2.0	3.0	2.
Chamaeleolis	3.5	2.6	1.2	1.2	1.2	3.0	3.
Chamaelinorops	3.5	2.6	1.2	1.2	1.2	2.0	3.
Phenacosaurus	3.5	2.6	1.2	1.2	1.2	2.0	3.

Phrynosoma	*Crotaphytus*	Tropidurines (terr.)	Tropidurines (arb.)	Tropidurines	Basiliscines	*Polychrus*	Anolines
4.0	6.0	8.6	7.0	7.6	5.0	4.0	4.0
5.0	8.0	9.8	7.7	9.0	4.3	6.0	3.0
2.0	6.0	6.4	5.7	6.1	3.7	5.0	4.0
3.0	6.0	5.2	4.7	4.8	3.3	4.0	2.7
1.0	5.0	5.4	4.0	4.8	4.3	3.0	2.0
4.0	4.0	5.0	5.0	5.0	1.7	4.0	2.3
3.0	5.0	7.0	6.7	6.9	3.7	3.0	2.7
4.0	6.0	8.0	6.7	7.5	2.7	5.0	1.7
5.0	7.0	7.9	6.7	8.5	3.7	6.0	3.0
5.0	8.0	9.2	6.7	8.3	4.7	5.0	2.7
5.0	8.0	8.4	7.0	7.8	4.7	6.0	2.7
5.0	7.0	7.4	5.3	6.6	2.0	3.0	1.0
8.0	9.0	6.2	4.0	5.3	4.0	7.0	2.0
6.0	8.0	6.6	4.3	5.7	3.3	6.0	2.0
6.0	9.0	7.4	5.3	6.6	4.3	8.0	3.0
	7.0	4.4	3.3	4.0	3.7	6.0	2.7
7.0		7.2	5.0	6.4	5.0	7.0	2.7
4.0	7.0	9.0	7.7	8.1	4.3	5.0	2.7
5.0	7.0	8.7	7.7	8.2	3.7	6.0	3.7
5.0	8.0	9.0	6.7	8.0	3.0	6.0	2.0
4.0	8.0	9.7	7.7	8.8	4.0	6.0	2.7
4.0	6.0	9.5	8.0	8.8	3.0	4.0	2.7
5.0	6.0	8.4	7.7	8.3	5.3	5.0	4.0
4.0	6.0	9.8	8.0	9.4	4.0	6.0	2.0
4.0	7.0	9.8	8.0	9.4	4.0	6.0	2.0
4.0	6.0	10.2	8.0	9.6	4.0	6.0	2.0
5.0	6.0	8.9	7.3	8.5	5.0	5.0	4.7
3.0	5.0	7.6	8.5	7.8	4.0	6.0	3.7
3.0	4.0	7.2	7.5	7.3	4.7	5.0	4.7
4.0	6.0	7.8	8.0	7.8	4.7	7.0	4.7
4.0	6.0	3.6	4.7	4.0	9.5	6.0	8.0
3.0	5.0	4.0	4.7	4.3	9.0	5.0	8.3
4.0	4.0	3.2	4.0	3.4	8.5	5.0	8.0
6.0	7.0	5.4	6.0	5.6	5.3		5.3
3.0	2.0	2.2	3.7	2.7	8.0	6.0	9.0
2.0	3.0	3.0	4.7	3.5	8.0	5.0	9.5
2.0	3.0	3.0	4.7	3.5	8.3	5.0	10.5
2.0	3.0	3.0	4.7	3.5	8.3	5.0	11.3

Table 8 Similarity of Genus Group to Genus Group

	Madagascan Forms	Iguanines	*Sceloporus* Group	*Uma* Group	Sceloper
Madagascan Forms	8.0	6.8	8.3	5.7	7.0
Iguanines	6.8	6.8	5.6	4.7	5.1
Sceloporus Group	8.3	5.6	8.6	6.7	7.5
Uma Group	5.7	4.7	6.8	8.7	7.7
Sceloporines	7.0	5.1	7.5	7.7	7.7
Tropidurines (Terrestrial)	8.9	6.1	8.3	6.7	7.5
Tropidurines (Arboreal)	7.3	5.4	6.3	4.5	5.4
Tropidurines	8.3	5.8	7.8	5.8	6.8
Basiliscines	4.7	3.2	3.8	3.8	3.8
Anolines	3.5	2.5	1.4	1.6	2.4

up	Sceloporines	Trepidurines (Terrestrial)	Trepidurines (Arboreal)	Trepidurines	Basiliscines	Anolines
.7	7.0	8.9	7.3	8.3	4.7	3.5
.7	5.1	6.1	5.4	5.8	3.2	2.5
.7	7.5	8.3	6.3	7.8	3.8	1.4
.7	7.7	6.7	4.5	5.8	3.8	1.6
.7	7.7	7.5	5.4	6.8	3.8	2.4
.7	7.5	9.2	7.5	8.4	3.6	2.7
.5	5.4	7.5	8.0	7.7	4.5	4.3
,8	6.8	8.4	7.7	8.5	3.9	3.2
.8	3.8	3.6	4.5	3.9	9.0	8.1
.6	2.4	2.7	4.3	3.2	8.1	9.7

Character Combinations

Table 9 lists all of the major characters found in the iguanid jaw apparatus and shows which character combinations are found in the iguanids and which are not. An "X" indicated the combination is found and a blank indicates the opposite.

Long jaws are found associated with none of the traits characteristic of non anoline genera. They seem to be the exclusive property of the anolines. Short jaws are found in combination with almost every other character except a small adductor superficialis, a character found only in the anolines. The sceloporine type of temporal artery "1" is found with all characters except those found only in the anolines and basiliscines. The anoline type of temporal artery, because of its presence in _Oplurus_ and _Enyaliosaurus_ is found combined with almost every character except a modified pseudotemporalis which is characteristic of the _Uma_ group.

The standard pseudotemporalis "2" is found with every other character while the modified pseudotemporalis is found only with characters peculiar to the sceloporines. A greatly enlarged pseudotemporalis is found in combination with characters shared by the anolines and basiliscines only. The standard adductor medius "2" is found with every character except the modified pseudotemporalis of the _Uma_ group and _Phrynosoma_. The modified medius is found in the anolines as well as these last two groups and so is found with all characters except those characteristic of tropidurines, where it never occurs.

A small superficialis is found with anoline and basiliscine traits while the medium and large superficialis are found only with non anoline traits. Separability of the heads of the adductor superficialis is found with all characters except an enlarged superficialis which is characteristic of the tropidurines and which tends to obscure the separation.

Herbivory is found with all traits except strictly anoline characters such as long jaws and small superficialis and advanced sceloporine characters such as those of the Uma group. Insectovory, because it is so widespread is found with every character. A small parietal is found with non anoline traits while a large parietal is found with anoline and basiliscine characters. A parietal crest as one would expect, is found with characters shared by the anolines and basiliscines.

In some cases it is possible to say that the presence of one character functionally precludes the presence of another. Such is the case with the enlarged superficialis and separability of the heads of the superficialis, long jaws and small parietal, standard medius and modified pseudotemporalis. In other cases it is probably safe to say that the characters are fairly independent of one another and therefore are free to combine or not. This is probably the case with the anoline temporal artery which can be found with all but one character. In some cases it is obvious that characters must be united, such as the enlarged superficialis and the enlarged superficial fascia and the enlarged pseudotemporalis and parietal. These have been eliminated from the chart. There are few if any other characters which I can say must be associated. Probably elongated jaws and increased parietal size must go together for reasons discussed under the section on jaw strength. There are no long jawed forms without enlarged musculature. However, enlarged parietal and parietal musculature need not be accompanied by long jaws as can be seen in the basiliscines. Further, there are some characters which one would assume to be associated but are not. Such is the case of long jaws and an enlarged superficialis. The enlarged muscle would further strengthen the longer jaws in the anolines and basiliscines but it does not occur. There must be selection against this combination for a large superficialis is primitive and would probably be present in the anolines unless specifically eliminated.

	Character	1	2	3	4	5	6	7	8	9	10	11	12
1.	Long jaw				X	X		X	X	X			X
2.	Short jaw			X	X	X	X	X	X		X	X	X
3.	Temp. Artery 1*		X			X	X	X	X		X	X	X
4.	Temp. artery 4	X	X			X		X	X	X	X	X	X
5.	Pseudotemp. 2	X	X	X	X			X	X	X	X	X	X
6.	Pseudotemporalis modified		X	X							X		X
7.	Medius 2	X	X	X	X	X				X	X	X	X
8.	Medius modified	X	X	X	X	X	X			X	X		X
9.	Superficialis sm.	X	X		X	X		X	X				X
10.	Superficialis med.		X	X		X	X	X	X				X
11.	Superficialis lg.		X	X	X	X		X					
12.	Separation of superficialis heads	X	X	X	X	X	X	X	X	X	X		
13.	Herbivorous		X	X	X	X		X			X	X	X
14.	Insectivorous	X	X	X	X	X	X	X	X	X	X	X	X
15.	Parietal small		X	X	X	X	X	X	X		X	X	X
16.	Parietal triangular	X	X	X	X	X		X	X	X			X
17.	Crest	X	X	X	X	X		X		X			X
18.	Pseudotemporalis lg.	X	X		X	X		X		X			X

Table 9 Character combinations
* See legend to Table 1
for meaning of numbers.

3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
	X	X		X	X	X			X	X	X		X	X	X
X	X	X	X	X	X		X	X	X	X	X	X	X	X	X
		X	X	X	X		X	X	X	X	X	X	X		
		X		X	X	X	X	X	X	X	X	X	X	X	X
X	X			X	X	X	X	X	X	X	X	X	X	X	X
X							X		X		X	X			
X	X	X				X	X	X	X	X	X	X	X	X	X
X	X	X	X			X	X		X	X	X	X	X		
	X	X		X	X				X		X		X	X	X
X		X	X	X	X				X	X	X	X			
X	X	X		X						X	X	X	X		
X	X	X	X	X	X	X	X			X	X	X	X	X	X
X	X	X		X			X	X	X			X	X	X	
X	X	X	X	X	X	X	X	X	X			X	X	X	X
X	X	X	X	X	X		X	X	X	X	X				
X	X	X		X	X	X			X	X	X			X	X
X	X	X		X		X			X	X	X		X		X
	X	X		X		X			X		X		X	X	

Character combinations
* See legend to Table 1
for meaning of numbers.

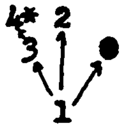
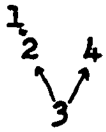
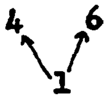
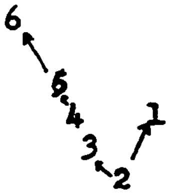
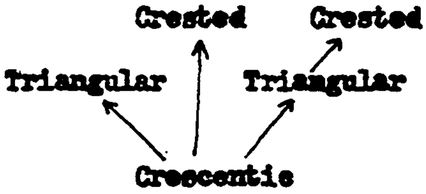
Direction of Evolution of Character States

As can be seen from an examination of the preceeding charts, the variation of each of the trigeminal muscle characters can be roughly set into character states. This does not infer however, that all of the characters show discontinuous variation. Such characters as; the extent of the medius in the supratemporal fossa; the extent of the adductor superficialis; the extent of the superficial fascia; the extent of the pseudotemporalis on the parietal and the gape ratio are most probably continuous. However, for ease of analysis, these characters can be treated as discontinuous by setting up character states representing convenient points along the continuum of the characters variation. Thus we can describe the adductor medius as covering none of the parietal, less than half of the parietal, half of the parietal and so on.

The existance of a continuum suggests a possible directionality in the evolution of the characters in question. If the primitive and derived states of each character can be deduced, as I believe they can for the trigeminal musculature, evolutionary trees can be made suggesting the probably phylogeny of the individual character. This proceedure was used by Marx & Rabb (1972) and is quite applicable to the trigeminal musculature.

Table 10 reveals that most of the characters show bidirectional evolution with the trait evolving towards both extreme ends of the continuum from a primitive condition somewhere between the two ends. The

Table 10 Direction of Evolution of Character States

Character	Number of States	Character Tree	Direction
1. Extent of adductor medius in supratemporal fossa	5		Tridirectional
2. Extent of adductor superficialis	5		Bidirectional
3. Separation of heads of the adductor superficialis	2		Unidirectional
4. Extent of the superficial fascia	4		Bidirectional
5. Temporal artery	3		Bidirectional
6. Extent of the pseudotemporalis on the parietal	6		Bidirectional
7. Shape of the parietal	4		Tridirectional
8. Gape Ratio	3		Bidirectional

*See legend to Table 1 for key to numbers.

characters showing this kind of evolution are the extent of the superficialis and the superficial fascia, the extent of the pseudotemporalis on the parietal, and the gape ratio.

Two characters show a tridirectional evolution with three conditions or trends evolving from the primitive state. The condition of the parietal and the extent of the medius in the supratemporal fossa show this evolutionary pattern. In the first character the parietal evolved from the primitive crescent to a triangle with some forms going on to develop a crest and shield. This occurs in the anolines and is one of the three lines. In a second line, the basiliscines, the primitive crescent evolves directly to a triangle with fully developed crest with no intermediate stages. In the third line, represented by the large iguanines a triangular parietal developes in the ontogeny of the individual.

The extent of the medius on the parietal is a tridirectional character. From the primitive condition, in which the medius covers less than half of the parietal, three separte lines evolve. In one the medius is lost (<u>Sauromalus</u> and <u>Urosaurus</u>). In the second, the anolines, the medius increased to half the parietal and in a separate third line, the advanced sceloporines, the medius covers almost the entire parietal.

The condition of the temporal artery and the separability of the heads of the superficialis show unidirectional evolution going from the primitive to the advanced condition. The temporal artery has three character states within the Iguanidae. One is the advanced condition found in the anolines and basiliscines. The other two are the primitive condition found in most other genera and a variation of the primitive condition due not to a change in the course of the vessel but to a change in the surrounding muscle.

This analysis clearly shows the evolution of individual characters to have proceeded in different directions in the different iguanid lines.

The Evolution of the Trigeminal Musculature

The iguanid trigeminal musculature furnishes insufficient data on which to erect an elaborate phylogeny. The most that can be done is to describe the probable ancestral condition and where possible, to indicate the broad lines of evolution.

Chalaradon on *Madagascar* has no advanced characters with respect to the jaw apparatus and thus probably represents the ancestral jaw condition. Avery and Tanner (1971) on the basis of many characters chose Oplurus as the more primitive genus. In terms of jaw apparatus however, Oplurus has an advanced temporal artery which eliminates it f from consideration, for this particular set of characters. The ancestral condition whether in *Chalaradon* or some other form close to it had the following set of characters:

1. an adductor medius covering less than half of the parietal
2. an extensive adductor superficialis and superficial fascia
3. a temporal artery exiting at the anterior border of the medius
4. a crescentic parietal
5. a pseudotemporalis covering more than half of the parietal
6. a gape ratio of .60 to .65
7. a clear separation of the heads of the pseudotemporalis
8. no parietal crest or shield
9. terrestrial
10. insectivorous

From this *Chalaradon*-like ancester evolved the iguanines which developed the habit of plant eating, and the sceloporines and tropidurines which remained insectivorous. Avery and Tanner (1971) take *Ctenosaura* as the most primitive Iguanine from which all other Western Hemisphere iguanines are derived. As far as the jaw apparatus is concerned *Cteno-*

saura is probably the most primitive iguanine genus, but it is still too advanced, by virtue of its specialized parietal, to be considered directly ancestral to the iguanines. Actually, there is no one specialization that the iguanine trigeminal musculature has consistently over the primitive Chalaradon condition except of course that the animals are herbivorous. Thus the primitive iguanine ancester probably had a jaw apparatus that would fit the description given for Chalaradon with the exception that the jaws were used on plants and not insects. Ctenosaura, if it lacked the advanced parietal would be a good possible ancester.

From this herbivorous, Chalaradon like ancester the iguanines radiated in Central America with each iguanine group developing its own specializations. One trend in the subfamily was towards increased size, a character which is often correlated with plant eating. The genera which grew larger developed enlarged parietal muscle origins and shorter stronger jaws during the ontogeny of the individual. The forms that remained small maintained the crescentic parietals and longer jaws. Data on gape ratio suggest that Ctenosaura, Iguana, are on the main iguanine line from which all of the other genera are offshoots.

The sceloporines and tropidurines are about as similar to each other as they are to the Madagasoan genera from which they appear to be derived. Etheridge (1964) suggests that the two groups split from a common line, off of the ancestral stock. The jaws musculature indicates that they came off of the Chalaradon like ancester separately, for the two groups share no characters which are unique to them, and both have developed quite different trigeminal muscle patterns.

The primitive sceloporine is again almost indistinguishable from a Chalaradon type organism. Within the subfamily the genus Sceloporus ranks as the most primitive, and with respect to jaw apparatus is indistinguishable from Chalaradon. The sceloporines as a group tended to reduce the extent of the adductor superficialis muscle and with it the extent of the superficial fascia. The more advanced sceloporines, those in Etheridges two ribbed group (1964), greatly increased the size of their adductor medius in the supratemporal fossa while Urosaurus in the more primitive three ribbed group went the other way and lost the adductor medius in the fossa. This indicates some sort of strong selection in these groups, against the ancestral condition. The selection might possibly be correlated with the fact that these groups invaded a desert habitat and were thus subjected to greatly changed selective forces.

Phrynosoma carried to an extreme, the trends started in the advanced sceloporines and also changed over to ant eating. Etheridge (1964) removed Phrynosoma from the sceloporines on the basis of a large suite of characters. With respect to jaw musculature alone I would not separate the two for all of the advanced characters seen in Phrynosoma are to be found also in Uma, Holbrookia and Callisaurus, indicating that Phrynosoma came from this group and is just continuing the trend. The possibility also exists that the similarities between Phrynosoma and the other advanced sceloporines are due to convergence and that Phrynosoma may have come off of the sceloporine line before the split into the two and three ribbed groups. On the basis of jaw muscle information alone I would discount convergence for reasons of parsimony. Presh (1969) reinstates Phrynosoma among the sceloporines and my findings support this action.

The genus *Crotaphytus* appears to be very primitive with respect to jaw musculature. Its only advanced character being an enlarged pseudotemporalis. The musculature alone gives no clue as to its origins. It could just as easily have evolved from the iguanines, sceloporines or the *Chalaradon* type ancestor. Its diet and distribution link it more closely to the sceloporines however.

The tropidurine ancestor retained the extensive adductor superficialis and developed a slightly shorter and thus more powerful jaw. While the sceloporines invaded and radiated in North America, the tropidurines went into South America. A typical primitive tropidurines is probably *Tropidurus* which has all the *Chalaradon* traits except for the shortened jaw. The tropidurines remained insectivorous and some became arboreal. Some genera increased the size of their adductor superficialis thus evolving in the opposite direction from the rest of the family with respect to this character.

We now come to the basiliscines and anolines which cannot be placed on our phylogenetic bush with any degree of accuracty or assurance. The ancestral basiliscine probably had triangular parietal muscle origins which met on the dorsal midline of the skull and some kind of dorsomedial, bony projection all of which allowed for the origin of an enlarged pseudotemporalis and a considerable strengthening of the jaw. It also had a temporal artery which exited through the adductor medius separating it into two heads. The primitive basiliscine adductor superficialis and superficial fascia are much reduced and the animal was probably arboreal. The primitive basiliscine condition, which corresponds to the condition in the genus *Basiliscus* is already quite advanced over what we have seen so far.

Being a Central American group it is improbable that they evolved from the sceloporines or tropidurines which are North and South American. Also these groups were already starting to specialize in directions which are different from what we see in the basiliscines. The iguanines and as shall be seen later, the anolines are also too specialized to have given rise to the basiliscines. The only valid source to consider is the ancestral Chalaradon typy organism. This ancester is sufficiently primitive to give rise to the basiliscines and was in the right place to do so.

However, if the basiliscines go back to the most primitive ancester and are thus probably as old as the iguanines or sceloporines, why are they represented by only three genera. It may be that the anolines filled many of the niches that the basiliscines might have if they had had no competition.

Basiliscus, Corythophanes and Laemanctus all evolved separately from the Basiliscus like ancester. This is obvious from the marked differences in crest arrangement in each group.

The ancestral anoline also had a triangular parietal muscle origin or was able to develop it in early ontogeny as some, more primitive modern anoles can. The organism had no parietal crest. It used its enlarged parietal for the origin of an enlarged pseudotemporalis and medius. This is a basic difference separating the anolines and basiliscines. Were it not for this difference the two groups could probably be linked with respect to jaw characters. The ancestral anoline also had a greatly reduced adductor superficialis and superficial fascia, and an elogated jaw. The organism was insectivorous and probably atboreal.

Again as in the basiliscines, almost all of the group specializations are already present in the most primitive members making it difficult to trace the groups origin. The genus Polychrus is thought by many workers (Etheridge, 1959; Cope, 1900) to closely related to the anolines. The data on jaw apparatus reveals Polychrus to be much more primitive than the anoles and actually more similar to many of the other groups. The only true anoline character it has is an elongated gape. For the origin of the anolines we must again go back to the ancestral *Chalaradon* like organism, for the most parsimonius arrangement. *Polychrus* probably represents a very early and not too successful experiment of character arrangements in the anoline line.

Within the anoline line some forms developed large shields such as *A. equestris* and others very large crests with covering shields such as *Chamaeleolis*. The genus *Anolis* underwent a great radiation in the Antilles and Central America. It is quire possibly this factor which limited the radiation of the basiliscines. As experiments in arboreal insectivores, the anolines are probably more successful.

A recent attempt to determine the intragroup relationships of the Iguanidae was carried out by Renous-Lecuru and Jullien (1972). On the basis of the innervation of the fore and hind limbs they were able to separate the Iguanidae into three groups. One of the groups contains only the Madagascan forms. The iguanines, anolines and basiliscimes all fall neatly into one or the other of the two remaining groups. The sceloporines and tropidurines however are split, with some members falling into each of the two groups

In the case of the sceloporines one group contains *Phrynosoma*, *Uma*, *Holbrookia* and *Uta*, and the other contains *Sceloporus* and *Urosaurus*. Except for the presence of *Uta* in the first group the split would be consistent with previous arrangements of the group. Their arrangement places *Crotaphytus* with the more primitive sceloporines which is also acceptable.

In the case of the tropidurines the two groups are also somewhat discordant. One of the groups contains advanced tropidurines while the other is a mixture of advanced and primitive tropidurines as well as very primitive iguanids (*Morunasaurus* and *Enyaliodes*). (Etheridge, unpubl.)

When the presence or absence of femoral and or preanal pores are added to the type of limb innervation, five groups are formed. The iguanines, basiliscines, anolines and sceloporines still assort as they did previously, however, the tropidurines are now split into four groups which seem to follow Etheridge's new arrangement. The primitive iguanids *Morunasaurus* and *Enyaliodes* fall in one group, two other groups contain only advanced tropidurines and a fourth group contains all of Etheridge's primitive tropidurines. The only discordance is the presence of *Uranoscodon* (advanced according to Etheridge) in this last group.

The information furnished by Lecuru and Jullien is thus, for the most part concordant with what is already known about the iguanid subfamilies and does not contradict any of my findings. Their work is especially welcome in the tropidurines where probably, the least amount of work has been done. The jaw musculature of the tropidurines gives no information as to intragroup relationships, therefore they will be treated as a single unit in my phylogeny.

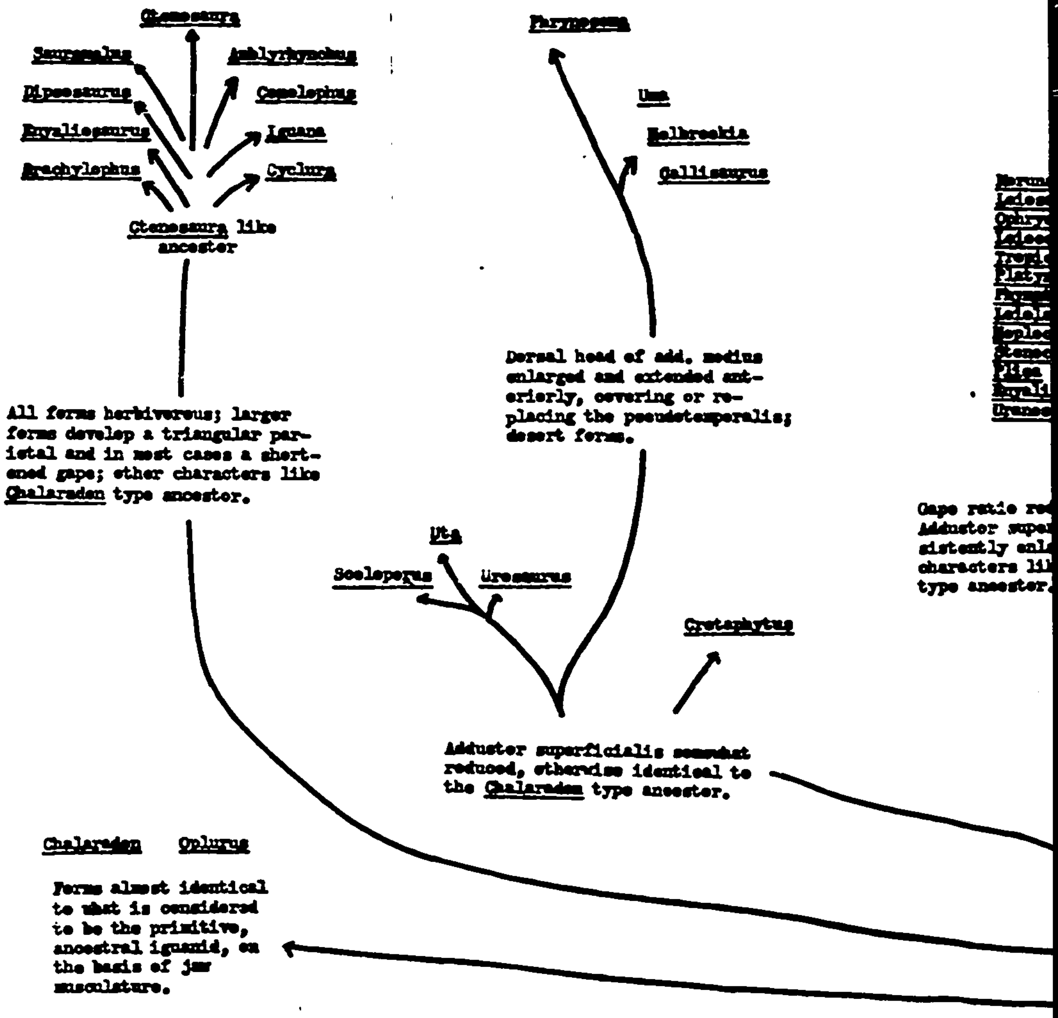
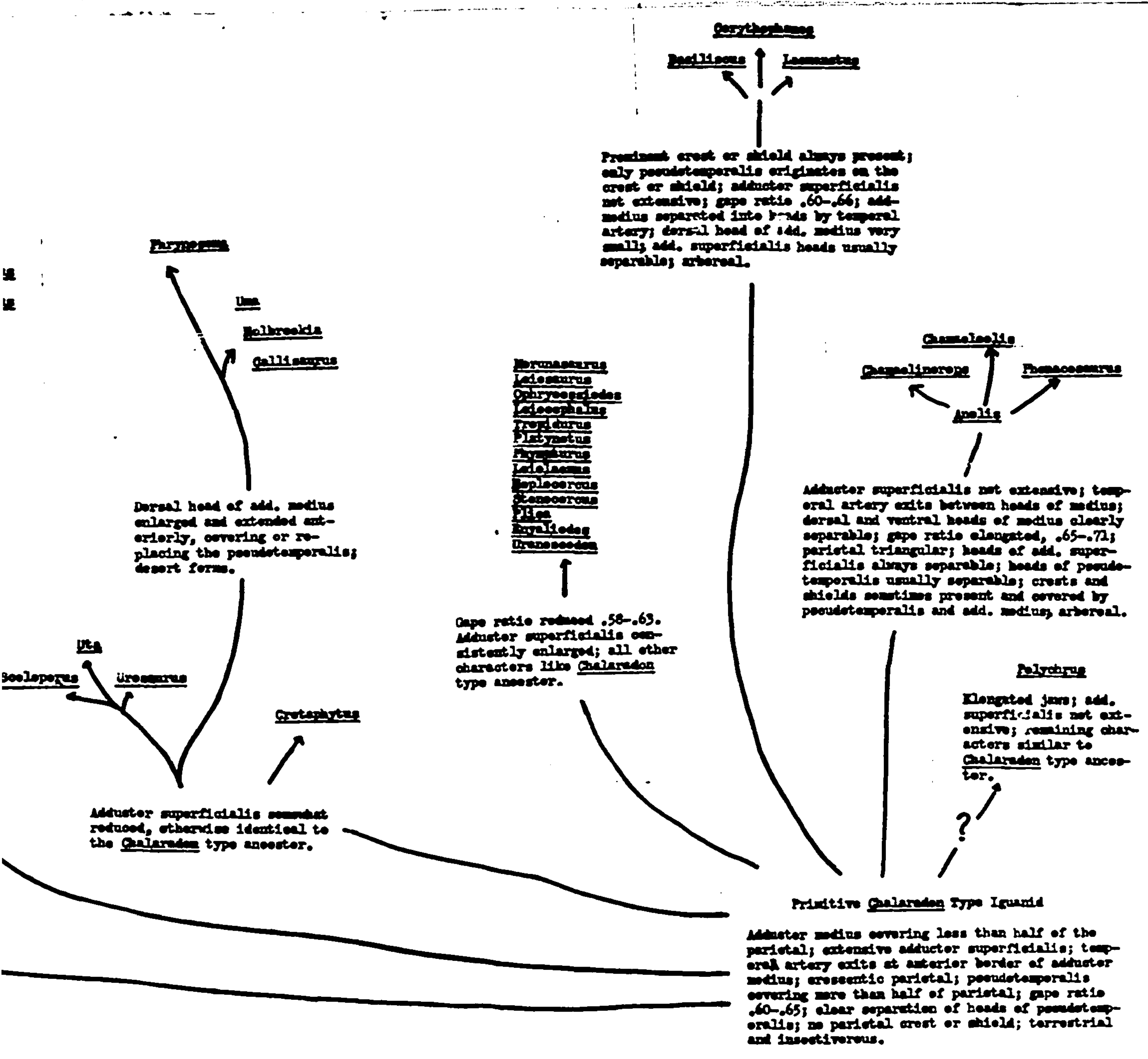


Fig. 15 Evolution of the Iguanid Trigeminal Musculature



of the Iguanid Trigeminal Musculature

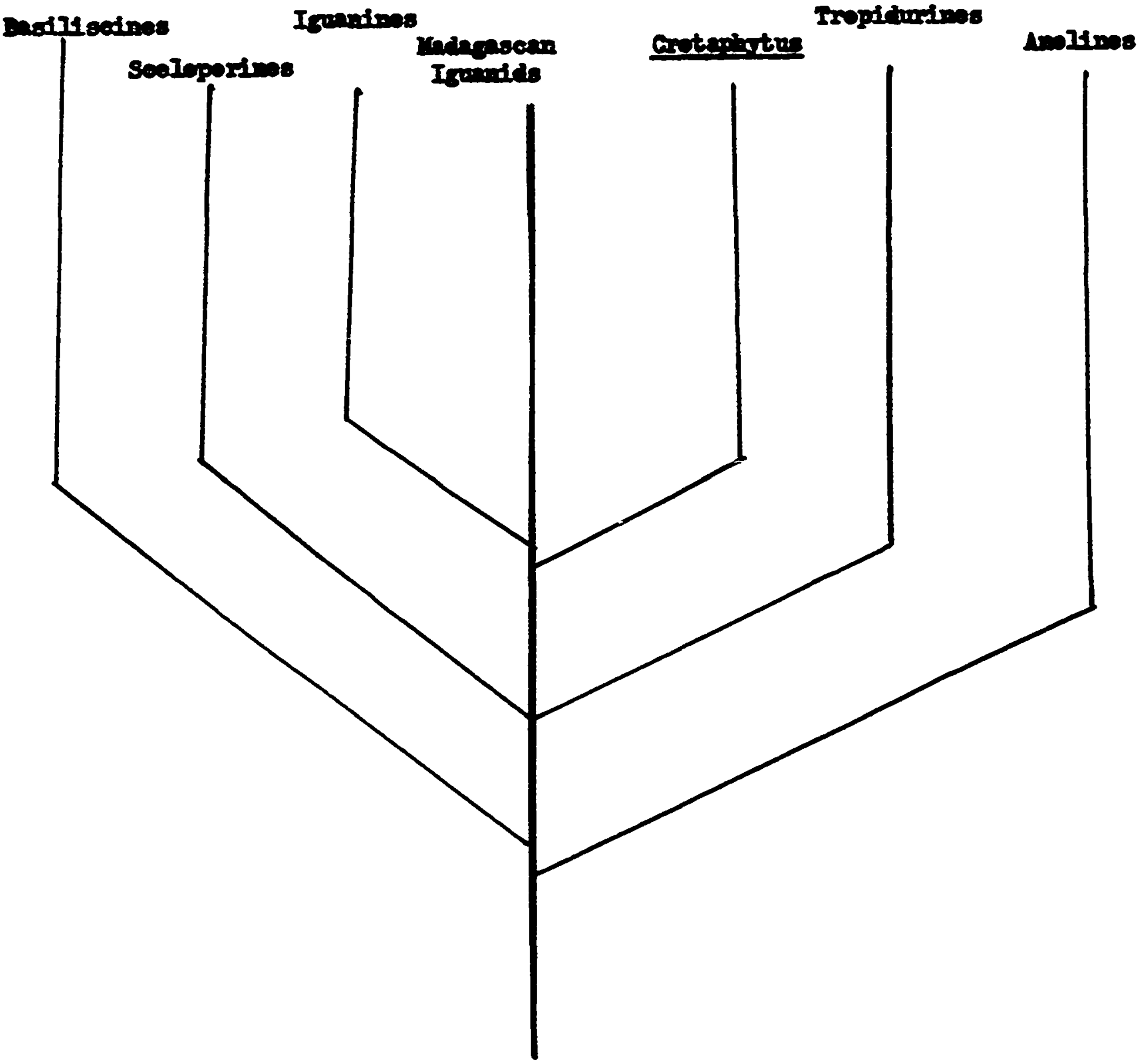


Fig. 16 Alternate Representation of Iguanid Evolution.

Summary & Conclusions

The trigeminal musculature and jaw apparatus of the iguanid lizards have been examined. The musculature has been described and the degree of infrafamilial variation recorded. Variation in jaw length and the extent of certain muscles have been used to estimate jaw strength. Ontogenetic changes, character combinations and problematical genera have also been investigated. The information gathered supports the following conclusions:

1. With very few exceptions, all of the elements of the trigeminal musculature as described by Lakjer (1926) are present in all of the iguanids examined.
2. Considerable muscular variation exists, but is confined mainly to the more superficial muscle layers.
3. Similar variation in other families would necessitate the extensive study of large and varied samples before valid interfamilial comparisons could be made.
4. Variation in trigeminal musculature and jaw length generally follow subfamilial lines.
5. The variation in jaw length and especially in the extent of the adductor superficialis and pseudotemporalis superficialis seem to indicate variation in jaw strength in the different subfamilies.
6. Marked ontogenetic changes involving decreased jaw length and expanding superficial musculature, both tending toward increased jaw strength occur in most of the larger iguanines.

7. Other than increased jaw strength in the larger forms, there seem to be no muscular specializations associated with the herbivorous condition of the iguanines.
8. The estimated jaw strength of the iguanid groups in decreasing order is: 1. Basiliscinae, 2. Anolinae, 3. Large Iguanines and Tropidurinae, 4. Small Iguanines, Madagascan genera, Sceloporinae and Phrynosoma.
9. The sceloporines show the most intragroup variation; the anolines and basiliscines show the least.
10. The existance of a more primitive Sceloporus, Uta, Urosaurus group and a more advanced Uma, Holbrookia, Callisaurus group within the sceloporines (Etheridge, 1964) is supported by the jaw musculature.
11. The most advanced jaw apparatus is found in the anolines, basiliscines and Phrynosoma, the most primitive in the Madagascan forms.
12. Crotaphytus has a primitive jaw apparatus and shows greatest similarity to the Sceloporines.
13. Phrynosoma is closest to the more advanced sceloporines whose muscle adaptations it has carried to an extreme.
14. Polychrus is not particularly close to the anolines, having only one of the four major characters that make up the anoline jaw character complex.
15. Superficially the anolines and basiliscines are more similar to each other than to any other group but these similarities appear to be due to convergence.

16. Dentition seems to correlate more closely with dietary variation than does jaw musculature.

17. Almost every character studied is found in combination with every other character somewhere within the Iguanidae indicating that almost all combinations have been tried and have proved successful.

18. Individual characters have shown unidirectional, bidirectional and tridirectional pattern of evolution.

19. The evidence obtained from the jaw apparatus suggests that each of the iguanid subfamilies is derived independently from an ancester similar in structure to the Madagascan Chalaradon.

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Appendix

Madagascan Forms and Iguanines

Species	AMNH Number	Jaw	Gape	Gape Ratio	Parietal Width	Dist.	Crest
Oplurus cyclurus	71462	2.50	1.50	.62	.23	.22	-
quadrimaculatus	71452	2.44	1.50	.61	.25	.26	-
	47947	1.88	1.19	.63			-
Chalarodon madagascar-	12846	1.23	.76	.62			-
iensis	71461	1.02	.63	.62			-
Dipsosaurus dorsalis	79962	2.38	1.40	.59	.27	.50	-
	77436	2.14	1.28	.60	.24	.50	-
	73238	2.32	1.38	.60	.20	.63	-
	75792	2.59	1.52	.59	.30	.55	-
	75551	1.90	1.18	.62	.15	.53	-
	68891	2.12	1.25	.59	.19	.53	-
	68708	2.15	1.28	.59	.20	.48	-
	75552	1.88	1.13	.60	.15	.52	-
	75603	1.99	1.19	.60	.22	.48	-
	75553	1.87	1.10	.59	.15	.46	-
	75554	1.88	1.10	.59	.19	.48	-
Sauromalus varius	73616	6.06	3.42	.56	.70	.60	-
hispidus	73516	3.94	2.28	.58	.43	.58	-
obesus	75606	3.02	1.82	.60			
	75098	3.73	2.19	.58	.33	.75	-
	75096	3.93	2.25	.57	.32	.60	-
	75097	4.00	2.30	.58	.39	.50	-
	73359	3.87	2.23	.58	.37	.41	-
	74814	3.92	2.31	.59	.38	.50	-
Amblyrhynchus cristatus	76197	4.60	2.76	.60	.84	.33	-
	24978	5.80	3.60	.62		.00	-
	75943	3.52	2.15	.61	.83	.00	-
	72806	10.61	6.01	.58	1.89	.00	*
	75942	3.85	2.28	.60	.76	.00	-
	75560	5.23	3.12	.60	1.09	.00	*
Brachylophus fasciatus	17701	3.26	2.00	.61	.50	.17	-
Enyaliosaurus quinquecarin-	77640	2.68	1.59	.60	.36	.33	-
atus	15897	2.20	1.40	.63			-

Species	AMNH Number	Jaw	Gape	Gape Ratio	Parietal Width	Par. Jaw	Dist.	Crest
Iguana iguana	72635	1.80	1.15	.63	.23	.13	.68	-
	75484	2.47	1.51	.61	.27	.11	.61	-
	82125	3.42	2.22	.64	.55	.16	.45	-
	62553	3.99	2.50	.62	.57	.14	.37	-
	81871	4.40	2.86	.64	.68	.15	.39	-
	71835	4.62	2.92	.63	.67	.14	.31	-
	62574	6.03	3.85	.63	.80	.13	.48	-
	87389	6.20	4.00	.64	1.05	.17	.13	-
	43302	6.30	3.78	.60	.94	.15	.20	-
	74629	6.43	3.91	.61	1.00	.15	.00	-
	97341	6.43	3.99	.62	.78	.12	.57	-
	74630	7.06	4.21	.59	1.00	.14	.22	-
	62552	7.86	4.55	.57	1.22	.15	.00	*
	74631	8.05	5.02	.62	1.12	.14	.22	-
	74627	8.50	5.20	.61	1.31	.15	.00	-
	97342	8.88	5.08	.57	1.38	.15	.56	-
	74736	9.43	5.58	.59	1.54	.16	.00	*
	3193474621	10.16	5.75	.57	1.73	.17	.00	*
	74628	11.75	6.64	.57	2.13	.18	.00	*
	32377	11.89	6.70	.56	2.25	.19	.00	*
Conolophus subcristatus	72806	10.53	5.97	.57				
	71304	10.00	5.84	.58	1.64		.00	*
	74620	9.22	5.40	.57	1.60		.00	*
	74576	9.00	5.20	.58	1.60		.00	*
	77970	9.86	5.64	.57	1.50		.00	*
	72305	[illegible]	6.18	.58	1.78		.00	*
	50797	10.65	6.08	.57	1.80		.00	*
Cyclura cornuta	57878	9.45	5.97	.63	1.75		.00	*
	57968	11.75	7.36	.63	2.55		.00	*
	50799	9.69	6.10	.63	2.00		.00	*
figginsi	74440	5.33	3.44	.64	.69		.44	-
	76875	6.35	3.96	.63	.79		.14	-
	76878	6.87	4.24	.62	.85		.15	-
	76876	5.74	3.86	.67	.75		.20	-
	76877	6.00	3.85	.64	.77		.12	-
	75624	11.53	7.34	.64	1.83		.00	*
	66631	10.95	7.09	.64				
	66630	9.39	5.99	.64	1.50		.00	*
	66632	13.30	8.10	.61	2.23		.00	*

Species	AMNH Number	Jaw	Gape	Gape Ratio	Parietal Width	Dist.	Crest
Ctenosaura							
acanthura	46483	10.55	6.13	.58		.00	-
pectinata	75526	6.05	3.83	.63		.00	-
	75523	8.27	4.75	.57		.00	-
	75528	5.58	3.32	.60		.00	-
	75529	4.62	2.88	.62		.00	-
	75474	4.66	2.92	.62		.28	-
hemilopha	57408	6.30	3.81	.60		.00	-
similis	69625	11.00	6.35	.58		.00	-
	69626	9.31	5.24	.56		.00	-
	38949	7.30	4.30	.58		.00	-
	69627	10.90	6.25	.57		.00	-
	71837	8.75	5.00	.57		.00	-
	66636	13.30	7.64	.57		.00	-
			Sceloporines				
Sceloporus							
orcutti	75085	2.88	1.70	.59		.60	-
	69089	2.14	1.32	.61		.53	-
magister	68986	2.45	1.53	.62		.60	-
cyanogenys	92179	2.37	1.50	.63	.13	.58	-
poinsettii	71302	2.22	1.40	.63	.11	.60	-
jarrovi	72630	1.70	1.10	.64	.10	.50	-
	75604	1.62	1.00	.62		.50	-
olivaceous	93186	2.18	1.43	.65	.12	.50	-
	93188	2.05	1.33	.65	.16	.49	-
	93190	2.00	1.28	.64	.10	.48	-
	93183	[illegible]	1.60	.65	.15	.62	-
	93184	2.20	1.42	.65	.14	.51	-
	93185	2.17	1.43	.65	.14	.53	-
undulatus	69964	1.64	1.10	.66			-
	69044	1.20	.75	.63			-
	99691	1.37	.84	.63			-
occidentalis	68714	1.69	1.05	.62			-
	68985	1.69	1.10	.65			-
	68984	1.67	1.05	.64			-
	68983	1.58	1.05	.66			-
	68942	1.73	1.07	.62			-
Holbrookia							
texana	Hecht	1.33	.86	.64			-
	"	1.46	[illegible]	.66			-
	"	1.34	.84	.64			-
	"	1.34	.84	.64			-

Species	AMNH Number	Jaw	Gape	Gape Ratio	Parietal Width	Dist.	Crest
Uma							
notata	Heckt	2.20	1.43	.65			-
	"	1.83	1.19	.65			-
inornata	68847	1.76	1.16	.65	.10	.50	-
Callisaurus draconoides	26169	1.69	1.04	.62			-
Phrynosoma							
asio	72636	2.06	1.37	.66			-
	74838	2.19	1.53	.69			-
	74839	2.24	1.42	.63			-
	19378	2.07	1.34	.64			-
cornutum	76206	1.59	1.00	.63			-
	99686	1.78	1.17	.65			-
	77117	1.63	1.10	.67			-
	90804	1.32	.84	.63			-
solare	70095	1.57	.99	.63			-
	1285	1.52	1.05	.67			-
modestum	1327	1.08	.69	.64			-
	74499	1.23	.79	.64			-
	74597	1.32	.90	.67			-
platyrhinos	77054	1.20	.80	.66			-
	77040	1.20	.80	.66			-
	68612	1.23	.81	.65			-
	77039	1.46	.99	.67			-
m'callii	77042	1.19	.79	.66			-
douglasi	70639	1.85	[illegible]	.64			-
	8237	2.00	1.28	.64			-

Crotaphytus

Species	AMNH Number	Jaw	Gape	Gape Ratio	Parietal Width	Dist.	Crest
Crotaphytus							
collaris	75090	2.84	1.80	.63	.26	.43	*
	82297	2.25	1.40	.62	.20	.40	-
	92890	2.55	1.60	.62	.18	.43	-
	103187	2.57	1.63	.64	.23	.36	-
	85625	3.25	1.95	.60	.28	.43	-
	84489	2.59	1.53	.60	.23	.43	-
	99690	2.40	1.49	.62	.20	.34	-
	73715	2.65	1.57	.60	.25	.31	-
	2363	2.81	1.74	.62	.29	.38	-
	74572	2.43	1.54	.63	.24	.43	-
	99687	2.06	1.30	.63	.20	.35	-
	99688	2.06	1.33	.64	.18	.37	-
	99689	2.86	1.80	.63	.28	.32	-
	73518	3.06	1.90	.62	.24	.40	-
wislizeni	75657	2.67	1.69	.63	.23	.41	-
	75083	2.32	1.54	.66	.20	.47	-
	73068	2.78	1.76	.63	.20	.47	-

Tropidurinae

Species	AMNH Number	Jaw	Gape	Gape Ratio	Crest	Dist.
Tropidurus albemarlensis delanonis	77624	1.55	.95	.61	-	.43
	90691	2.12	1.28	.60	-	.49
	92979	2.37	1.50	.63	-	
Leiolaemus multiformis	81801	2.19	1.29	.59	-	.30
	80140	1.40	.84	.60	-	.35
	80139	1.66	1.03	.62	-	.35
Leiocephalus carinatus	70575	1.66	1.02	.62	-	.40
	57461	2.19	1.37	.62	-	.19
	59988	2.06	1.28	.61	-	.21
	Hecht	1.99	1.28	.65	-	
	Hecht	2.32	1.45	.62	-	
Enyalioides praestabilis	28870	2.40	1.48	.60	-	
Stenocercus carrioni	21848	1.90	1.19	.62	-	
Hoplocercus spinosus	89398	2.39	1.41	.59	-	.30
	90658	2.12	1.28	.60	-	.25
		1.73	1.04	.60		
Plica plica	85313	3.64	2.18	.60	-	
	36628	2.77	1.66	.60	-	

Anolines

Species	AMNH Number	Jaw	Gape	Gape Ratio	Dist.	Crest
Polychrus marmoratus	71170	2.73	1.80	.66	.46	*
	71171	2.47	1.68	.68	.40	-
Anolis bonairensis	72641	1.80	1.23	.68	.34	-
equestris	73848	4.60	3.24	.70	.00	*
	75278	5.70	3.96	.70	.00	*
	72634	4.68	3.35	.71	.00	*
	75279	5.07	3.49	.69	.00	*
	74618	5.25	3.53	.67	.00	*
cristatellus	10413	1.84	1.19	.65	.00	-
	71592	1.84	1.20	.65	.00	-
carolinensis	70102	1.86	1.23	.65	.00	*
	70089	1.48	1.03	.69	.22	-
	70105	2.00	1.37	.69	.00	-
	70104	1.99	1.33	.66	.00	-
	70108	1.93	1.30	.67	.00	-
	75749	1.84	1.26	.68	.00	-
distichus	41271	1.39	..90	.65	.00	-
sagrei	68853	1.43	.93	.65	.00	-
	68854	1.53	1.00	.67	.00	-
lineatopis	74619	1.96	1.29	.65	.00	-
Phenacosaurus heterodermis	70631	1.83	1.28	.70	.00	*
Deiroptyx	Hecht	3.70	2.55	.69	.00	-
Xiphocercus valenciennesi	72246	2.50	1.69	.68	.00	*
Chamaelinorops wetmorei	12156	1.26	..85	.67	.00	*
	12105	1.20	.80	.66	.00	*
Chamaeleolis chamaeleonides	58901	5.16	3.60	.70	.00	*

Basiliscines

Species	AMNH Number	Jaw	Gape	Gape Ratio	Dist.	Crest
Basiliscus vittatus	74615	5.02	3.00	.60	.00	*
	17883	3.24	2.04	.63	.00	*
	17892	2.44	1.53	.63	.00	*

Species	AMNH Number	Jaw	Gape	Gape Ratio	Dist.	Crest
Basiliscus basiliscus	57769	3.29	2.05	.62	.00	*
	84490	3.98	2.29	.58	.00	*
	73847	4.09	2.59	.63	.00	*
Corythophanes cristatus	16390	2.99	1.95	.65	.00	*
	45202	2.81	1.75	.62	.00	*
Laemanctus serratus	79030	3.20	2.13	.66	.00	*

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