

PROSAUPOD AND IGUANID JAW MUSCULATURE:
A STUDY ON THE EVOLUTION OF FORM AND FUNCTION

by

JENNIFER ELIZABETH FAIRMAN

Submitted to the Johns Hopkins University
in conformity with the requirements for
the degree of Master of Arts

Baltimore, Maryland
1999

*© Jennifer Elizabeth Fairman 1999
All rights reserved*

ABSTRACT



This project investigates modern lizards in order to assess the muscle origins, insertions and respective jaw musculature of two prosauropods, *Anchisaurus polyzelus* and *Plateosaurus engelhardti*. Through dissection and observation, iguanid jaw musculoskeletal anatomy is used as a paradigm for the evolution of herbivory in prosauropod dinosaurs.

It has been argued that prosauropods had an exclusively herbivorous diet based on such morphological conditions as dentition, offset jaw articulation, neck length and skull size. *Anchisaurus* is closely related to *Plateosaurus*, and thus, may have been a significant phylogenetic link in the evolution of herbivory in prosauropod dinosaurs. Here it is argued that *Anchisaurus* had a facultative omnivorous feeding style. Examination of the temporal fenestrae and jaw musculature in both herbivorous and omnivorous iguanid models is used to predict jaw musculature for both prosauropods with respect to diet.

Dissections and skeletonization of the omnivorous *Sceloporus magister*, the insectivorous *Ctenosaura hemilopha* and *Ctenosaura pectinata*, and the herbivorous *Iguana iguana* provided the basis for the modern comparative sample. Prosauropod skull materials included a skull cast of *Plateosaurus engelhardti* and an incomplete but articulated specimen of *Anchisaurus polyzelus*.

This work identifies a suite of skull structures and muscle locations that appear to relate to differences in feeding styles in the extant iguanids under study. These similarities include:

- (1) the oblique shift of the temporal fenestrae in relation to each other and the long axis of the skull,
 - (2) the dorsal shift of the supratemporal fenestra, and
 - (3) the overall lengthening of the jaw muscles, found in the *omnivorous* forms,
- and*
- (1) the relationship of the temporal fenestrae at right angles to each other and the long axis of the skull,
 - (2) the larger surface area of the parietal bone in the supratemporal fenestra, and
 - (3) the lateral location of the jaw muscles, in the *herbivorous* forms.

These features are also found in the prosauropod dinosaurs under study: the skull of *Plateosaurus engelhardti* exhibits temporal fenestrae that are located at a right angle with respect to each other and the long axis of the skull, whereas *Anchisaurus polyzelus* exhibits temporal fenestrae that are of an oblique relationship.

On the basis of the structural differences, within their phylogenetic context for both Iguanidae and Prosauropoda, it appears very likely that *Anchisaurus* was not an herbivore as previously thought, but rather an omnivore, similar to the extant iguanid *Sceloporus*. In this way, anchisaurids form an important link from the primitive carnivorous feeding habits of basal dinosaurs, through their own facultative omnivory, to the more strictly herbivorous plateosaurids.

ACKNOWLEDGEMENTS



This graduate thesis would not have been possible without the tutelage and support of many individuals. **David B. Weishampel** , Professor of the Department of Cell Biology and Anatomy at the Johns Hopkins University School of Medicine, who acted as preceptor and who initiated this project, gave me invaluable insight, provided *Plateosaurus engelhardti* skull materials, permitted access to his private collection and library, and granted the extraordinary opportunity to conduct research in his area of study; **Timothy H. Phelps** , Associate Professor of the Department of Art As Applied to Medicine at the Johns Hopkins University School of Medicine, who acted as departmental faculty advisor, provided the most valuable logistical critique and recommendations regarding content, layout and illustrations, and was a constant source of encouragement, *insisting I have fun*; **Kevin De Queiroz** , research scientist of the Department of Herpetology at the Smithsonian National Museum of Natural History, who identified iguanid specimens, loaned preserved iguanid specimens and skulls and provided access to the Smithsonian Herpetology Library; **Jacques A. Gauthier** , curator, **Mary Ann Turner** , collections manager, **Chris Chandler** , collections manager, and **Marilyn Fox** , curator at the Yale University Peabody Museum of Natural History, who provided the *Anchisaurus polyzelus* cranial specimen, access to the Yale Peabody Archives, bench space and a microscope with which to work; **Paul M. Barrett** of Cambridge University, for providing a copy of his dissertation; **Mason B. Meers** of the Florida Gulf Coast University, for providing fresh iguanid specimens; **Michael S. Linkinhok** er, Instructor of the Department of Art as Applied to Medicine at the Johns Hopkins University School of Medicine, who gave advice and guidance, and who contributed to my knowledge in the skeletonization of the iguanid specimens. I would like to thank the **Vesalius Trust** for generously granting financial support for this project. I extend my gratitude to **the faculty of the Department of Art as Applied to Medicine** as well as **my classmates** for their individual critique and support throughout this project. From each of them, I have learned so much. I sincerely want to thank both **William W. Scavone** and **Rudolf T. Fairman** for many months filled with encouragement and emotional support. Finally, I would like to thank my **family** , especially my **parents** and **grandparents** , as well as my **friends** for believing in me, and encouraging me to pursue my life's true passion. *Thank you all!* Without you, this reality would still be a big dream!

TABLE OF CONTENTS



<i>Abstract</i>	<i>ii</i>
<i>Acknowledgements</i>	<i>iv</i>
<i>Index of Tables</i>	<i>vi</i>
<i>Index of Figures</i>	<i>vii</i>

INTRODUCTION

<i>Phylogeny</i>	1
<i>Morphology</i>	5
<i>Cranial Kinesis</i>	5
<i>Dentition and Diet</i>	7
<i>Significance of Study</i>	10

METHODS

<i>Iguanids</i>	11
<i>Prosauropods</i>	13
<i>Illustrating data</i>	15

RESULTS

<i>Iguanids</i>	17
OSTEOLOGY	17
MYOLOGY	27
CIRCULATION AND INNERVATION	41
<i>Prosauropods</i>	45
OSTEOLOGY	45
MYOLOGY	61

DISCUSSION

<i>Commentary</i>	81
<i>Osteology</i>	82
<i>Myology</i>	83
<i>Conclusion</i>	87

<i>Appendix A - Abbreviations and Terminology</i>	88
<i>Appendix B - Specimen Inventory</i>	90
<i>References</i>	91
<i>Vita</i>	95

INDEX OF TABLES

page

42	TABLE 1: Adductor Jaw Muscles in Iguanidae	78	TABLE 5: Proposed Adductor Jaw Muscles in Prosauropoda
43	TABLE 2: Constrictor Jaw Muscles in Iguanidae	79	TABLE 6: Proposed Constrictor Jaw Muscles in Prosauropoda
43	TABLE 3: M. Depressor Mandibularis in Iguanidae	79	TABLE 7: M. Depressor Mandibularis in Prosauropoda
44	TABLE 4: Summary of Myological Differences in Iguanidae	80	TABLE 8: Summary of Myological Differences in Prosauropoda

INDEX OF FIGURES

<i>page</i>			
2	FIG. 1: Phylogenetic relationships of extant and extinct Sauria	31	FIG. 13: Iguanid myology, lateral view of Superficial and First depths, <i>Iguana iguana</i> , <i>Ctenosaura hemilopha</i> , <i>Sceloporus magister</i>
3	FIG. 2: Phylogenetic relationships within Dinosauria		
3	FIG. 3: Phylogenetic relationships within Iguanidae	33	FIG. 14: Iguanid myology, lateral view of Second and Third depths, <i>Iguana iguana</i> , <i>Ctenosaura hemilopha</i> , <i>Sceloporus magister</i>
6	FIG. 4: Osteological location of kinetic points in Iguanid cranium, <i>Ctenosaura hemilopha</i>	38	FIG. 15: Iguanid myology, lateral view of Fourth and Fifth depths, <i>Iguana iguana</i> , <i>Ctenosaura hemilopha</i> , <i>Sceloporus magister</i>
6	FIG. 5: Osteological location of kinetic points in Prosauropod cranium, <i>Plateosaurus engelhardti</i>	45	FIG. 16: Osteological location of fenestrae in Prosauropod cranium, <i>Plateosaurus engelhardti</i>
8	FIG. 6: Dentition of herbivorous and omnivorous Iguanids, <i>Iguana iguana</i> , <i>Sceloporus magister</i>	48	FIG. 17: Prosauropod cranial osteology, lateral view of <i>Plateosaurus engelhardti</i>
12	FIG. 7: Location of incisions, <i>Iguana iguana</i>	50	FIG. 18: Prosauropod cranial osteology, photographic views of <i>Anchisaurus polyzelus</i>
14	FIG. 8: Cranial reconstruction, skull cast, <i>Plateosaurus engelhardti</i>	51	FIG. 19: Prosauropod cranial osteology, lateral views of <i>Anchisaurus polyzelus</i>
17	FIG. 9: Osteological location of fenestrae in Iguanid cranium, <i>Sceloporus magister</i>	52	FIG. 20: Prosauropod cranial osteology reconstructed, lateral views of <i>Anchisaurus polyzelus</i>
19	FIG. 10: Iguanid cranial osteology, lateral views, <i>Iguana iguana</i> , <i>Ctenosaura hemilopha</i> , <i>Sceloporus magister</i>	56	FIG. 21: Osteology of posterior palate and braincase, lateral view, <i>Plateosaurus engelhardti</i>
25	FIG. 11: Iguanid mandibular osteology, medial views, <i>Iguana iguana</i> , <i>Ctenosaura hemilopha</i> , <i>Sceloporus magister</i>	62	FIG. 22: Prosauropod myology, sites of origin and insertion, <i>Plateosaurus engelhardti</i>
28	FIG. 12: Iguanid myology, sites of origin and insertion, <i>Iguana iguana</i> , <i>Ctenosaura hemilopha</i> , <i>Sceloporus magister</i>	63	FIG. 23: Prosauropod myology, sites of origin and insertion, <i>Anchisaurus polyzelus</i>

page

- 65 **FIG. 24:** Prosauropod myology,
 lateral view of Superficial depth,
 Plateosaurus engelhardti,
 Anchisaurus polyzelus
- 66 **FIG. 25:** Skull of *Sphenodon*
- 68 **FIG. 26:** Prosauropod myology,
 lateral view of First depth,
 Plateosaurus engelhardti,
 Anchisaurus polyzelus
- 70 **FIG. 27:** Prosauropod myology,
 lateral view of Second depth,
 Plateosaurus engelhardti,
 Anchisaurus polyzelus
- 72 **FIG. 28:** Prosauropod myology,
 lateral view of Third depth,
 Plateosaurus engelhardti,
 Anchisaurus polyzelus
- 75 **FIG. 29:** Prosauropod myology,
 lateral view of Fourth and Fifth
 depths, *Plateosaurus engelhardti*,
 Anchisaurus polyzelus

INTRODUCTION



*THE STUDY OF DINOSAURS HAS MUCH TO DO WITH THE HISTORY OF LIFE
AND OF THE EARTH, WITH THE NATURE OF NATURE, AND WITH WHO WE ARE...*

– Fastovsky and Weishampel, *The Evolution and Extinction of Dinosaurs*

The discovery of dinosaurs has given scientists direct insight to major trends of evolution, especially because they are connected to their modern forms through phylogenetic relationships. Consequently, knowledge of extinct vertebrates enriches our understanding of present-day vertebrates. This project presents a unique opportunity to research such a comparative study of extant and extinct forms in which an investigation of omnivorous and herbivorous jaw musculoskeletal anatomy in iguanid lizards is used as a paradigm for the evolution of herbivory in prosauropod dinosaurs.

This project investigates modern lizards in order to assess the muscle origins, insertions and respective jaw musculature of two prosauropods, *Anchisaurus polyzelus* and *Plateosaurus engelhardti*, through careful dissection and observation of iguanid jaw musculoskeletal anatomy. The musculoskeletal anatomy of the omnivorous *Sceloporus magister* (desert spiny lizard), the insectivorous *Ctenosaura hemilopha* (northern false iguana) and *Ctenosaura pectinata* (spiny tailed iguana), and the herbivorous *Iguana iguana* (common green iguana) serve as extant models for omnivorous and herbivorous prosauropod jaw musculature.

Phylogeny

THE PROSAUROPODS

Prosauropoda are among the earliest saurischian, or “lizard-hipped” dinosaurs, which existed world-wide between the Late Triassic and the Early Jurassic periods (210 to 190 million years ago) (see FIG. 1). They have been considered to represent the first phylogenetic radiation among the dinosaurs, especially among the archosaurs (which include dinosaurs, crocodiles, pterosaurs and birds) to have herbivorous members (NORMAN 1985). Prosauropoda were

relatively large-bodied bipedal or quadrupedal “sauropodomorphs” with lightly built skulls, long necks, and an especially long tail (GALTON 1990). They are taxonomically diverse, including genera such as *Massospondylus*, *Plateosaurus* and *Anchisaurus*. According to GALTON (1990:320), they can be distinguished from other dinosaurian taxa by several characteristics, including, “[a] skull about half the length of the femur, jaw articulation situated slightly below the level of the maxillary tooth row, dentition [consisting] of small, homodont or weakly heterodont, spatulate-shaped teeth with course, obliquely angled marginal serrations...” This taxon is currently considered to be monophyletic (GALTON 1990, UPCHURCH 1995, 1998). Iguanids are also monophyletic, but only distantly related to prosauropods.

Two genera of prosauropods, *Anchisaurus* (meaning *close-reptile*) and *Plateosaurus* (meaning *flat-reptile*), have been selected for study of jaw musculature pertaining to omnivorous and herbivorous diets, respectively (see FIG. 2). These two taxa, named by O. C. MARSH (1893), were later studied by FREIDRICH VON HUENE (1906, 1926), who recognized that they belong to a single major group that he called Prosauropoda and combined them with Sauropoda, thus comprising Sauropodomorpha (GALTON 1990).

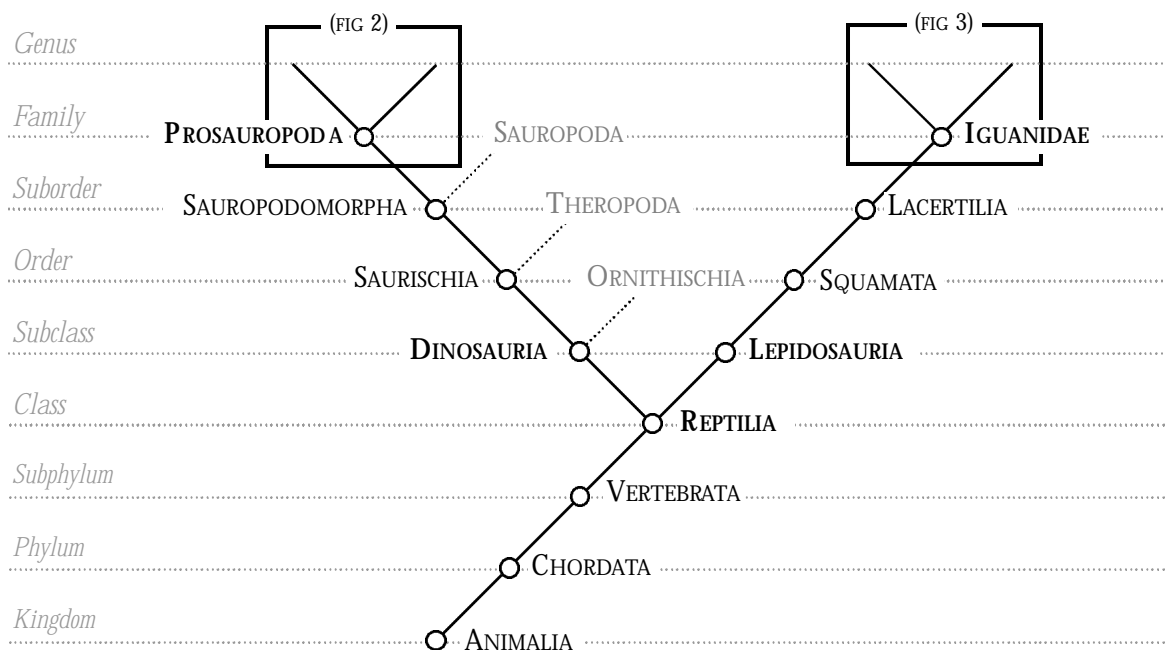


FIG. 1 - Phylogenetic relationships of extant and extinct Sauria

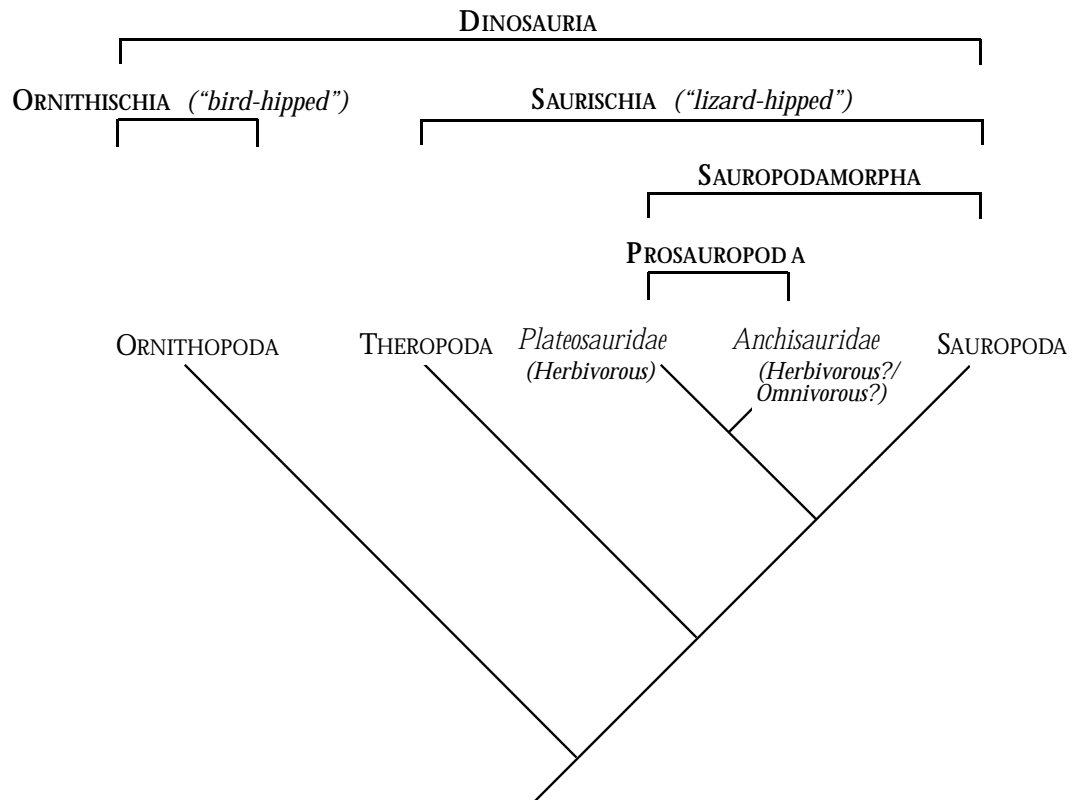


FIG. 2 - Phylogenetic Relationships within Dinosauria

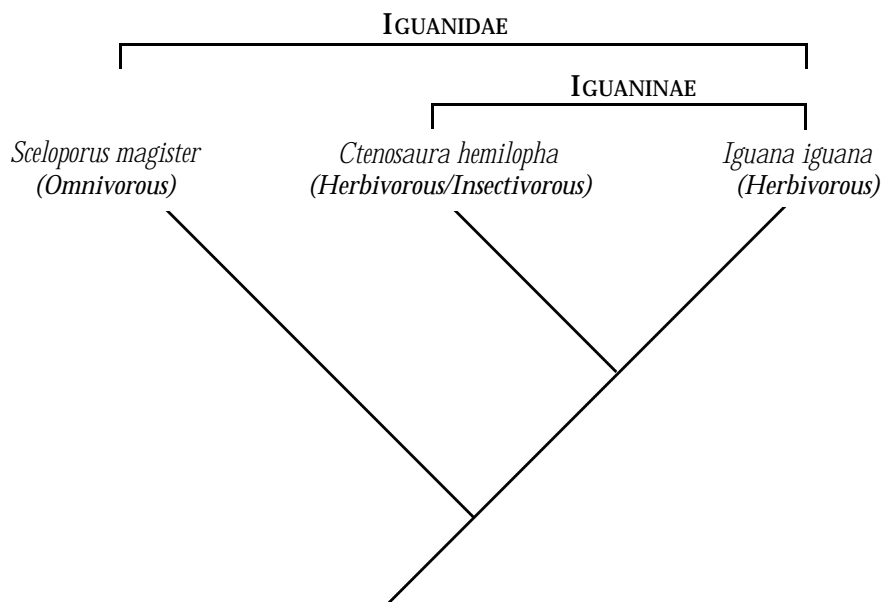


FIG. 3 - Phylogenetic relationships within Iguanidae

A cast of *Plateosaurus engelhardti* (AMNH 6810) was obtained from Dr. David B. Weishampel's private collection. This material is a complete disarticulated epoxy skull cast from the originally fully articulated and well preserved specimen from the Knöllenberg of Trössingen, Germany. Study of the skull *Anchisaurus polyzelus* (YPM 1883) was conducted at the Yale University Peabody Museum of Natural History. This specimen, the best-preserved skull of *Anchisaurus polyzelus*, is from the early Jurassic formation of Manchester, Connecticut, and is a holotype of *Anchisaurus colurus* (MARSH, 1891:267) which is a type of species of the genus *Yaleosaurus* (HUENE, 1932:122) (GALTON 1976).

THE IGUANIDS

According to SMITH (1946), there are four extant groups of reptiles: turtles, crocodiles, *Sphenodon* and Squamata, including snakes and lizards. The later group is further divided into families, including gekkonidae, chamaeleonidae, and iguanidae, among many others. Within the iguanids are those lizards whose feeding style appears to be most similar to that of the prosauropods (see FIG. 3). Members from three iguanid genera, *Iguana*, *Ctenosaura* (both iguanines), and *Sceloporus*, were used in this study. These phylogenetic relationships have been studied and described by DE QUERIOZ (1987).

The following abbreviations precede the identification numbers of the specimens used in this study and represent the institutional and personal names from which the specimens were borrowed:

AMNH	American Museum of Natural History, New York, NY
MEERS	Mason B. Meers, Private Collection, Florida Gulf Coast University
NMNH	National Museum of Natural History, Washington, DC
WEISHAMPEL	David B. Weishampel, Private Collection, Johns Hopkins University School of Medicine, Baltimore, MD
YPM	Peabody Museum of Natural History, Yale University, New Haven, CT

Morphology

According to KARDONG (1998), some of the earliest reptiles had skulls that resembled those of modern lizards. The skull roof consisted of several parts formed by the dermatocranium, providing opening for the orbits, the pineal organ (a dorsally located sensory organ) and the external nares. The dermatocranium was supported against the chondrocranium by a *columella* (the epipterygoid). The temporal region of the outer dermatocranium had openings for the attachment of jaw muscles. *Anapsids* had no temporal openings. *Synapsids* had only one opening. *Diapsids* had two temporal openings, the supra- and infratemporal fenestrae, which carried over into modern reptiles such as *Sphenodon* and crocodiles. In contrast, the infratemporal arcade, creating the lower border of the infratemporal fenestra, has been lost in modern lizards such as the iguanids. The loss of the infratemporal arcade opens the infratemporal fenestra directly with the pterygoid fossa (see FIGS. 9 and 16), and liberates the anterior portion of the skull from the quadrate bone, giving it freedom to move as it articulates dorsally with the braincase. This type of movement is called *streptostyly*. The variety of modification in the diapsid condition has also carried over to birds and snakes. The question of the evolution of temporal fenestrae has been argued to accommodate the strong adductor muscles ability to bulge during contraction. This particular feature is one which both the prosauropods and the iguanids developed in order to accommodate space and ample surface area for the attachment of the jaw muscles to the skull. The loss of the infratemporal arcade (present in prosauropods) produces a modified diapsid skull with an increased amount of movement in the iguanid skull with respect to that of the prosauropod skull.

Cranial Kinesis

Kinetism is the ability of the skull to move between two segments of the braincase (GALTON 1985). The reptilian skull exhibits various degrees of mobility. According to KARDONG (1998), cranial kinesis can be described as being one of three types, depending on hinge position: *prokinesis* (movement between the nasal and frontal bones, found in snakes and birds), *mesokinesis* (movement between the frontal and parietal bones, found in lizards), or *metakinesis* (movement between the parietal and supraoccipital bones, also found lizards) (see

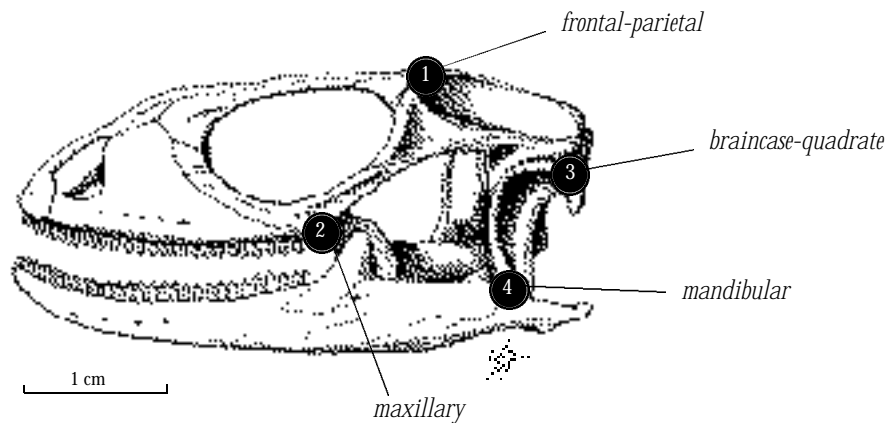


FIG. 4 - Osteological location of kinetic points in Iguanid cranium (*Ctenosaura hemilopha*)

FIG. 4). A skull can also be considered *monokinetic* (having one hinge) or *dikinetic/amphikinetic* (having two hinges), depending on the number of hinges the skull exhibits (KARDONG 1998). In contrast to the condition found in the skulls of lizards, GALTON (1985) noted that, because the frontals and parietals of prosauropods were firmly bound, prosauropod dinosaurs exhibited skulls that were not mesokinetic. This is especially apparent in the *Plateosaurus engelhardti* specimen under study (see FIG 5). GALTON concluded that the skull of *Plateosaurus engelhardti* was akinetic with certain features present in kinetic skulls (i.e. jaw constrictor muscles found in iguanids and inferred in prosauropods; see also below).

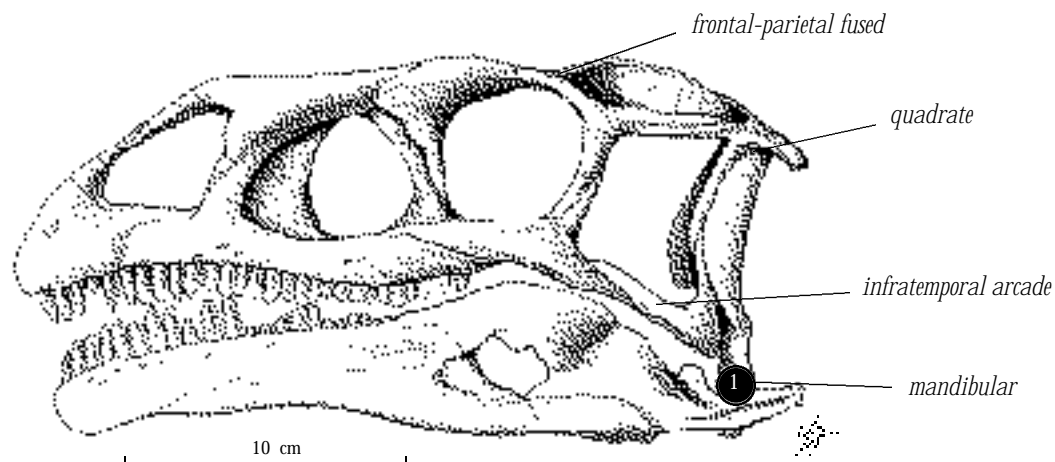


FIG. 5 - Osteological location of kinetic points in Prosauropod cranium (*Plateosaurus engelhardti*)

Dentition and Diet

According to IVERSON (1982), many scientists have previously referred to lizards as herbivores or carnivores, without regard for the individuality among species as lying along a carnivory-omnivory-herbivory continuum. In other words, some omnivores like the insectivorous *Ctenosaura hemilopha* or *C. pectinata*, lie very close to the herbivory end of the continuum, whereas the omnivorous *Sceloporus magister* lies further away. In addition, many “herbivores” are actually facultative omnivores. For example, *Iguana iguana*, whose diet generally consists of vegetation such as leaves, shoots, fruits, vegetables or dandelion flowers, has been found to occasionally feed on material such as mealworms, insects, baby mice or even dog food (BARRETT 1998).

Previous studies have suggested possible diets of these prosauropods through examination and analysis of the dentition and general skull form (GALTON 1984). Comparisons between prosauropods and modern vertebrates have included those of mammals, birds and modern reptiles. As mentioned previously jaw articulation in prosauropods, especially in anchisaurids, is ventrally offset with respect to the maxillary tooth row, a characteristic generally considered to apply to herbivorous vertebrates (GALTON 1985). This orientation of the jaw joint would have provided more force and even distribution of force for the breakdown of robust plant material. GALTON further argued that inappropriate comparisons between prosauropods and mammals have resulted in findings of reptilian-like feeding systems in prosauropods.

Comparisons have also been studied between both modern carnivorous and herbivorous reptilian models. Typically the dentition of the carnivorous reptilian models is subconical in shape with maximal crown width at the root-crown junction, and serrations are fine and perpendicular to the cutting edge. Teeth are spaced broadly apart. In contrast, dentition of the herbivorous models, such as that in *Iguana iguana*, is spatulate-shaped with anteroposteriorly expanded crowns (see FIG. 6). Serrations are coarse and are not perpendicular to the cutting edge, but rather are at a 45° angle. Teeth are spaced close together (see FIG. 11) (GALTON 1985). Because the dentition of prosauropods resembles that

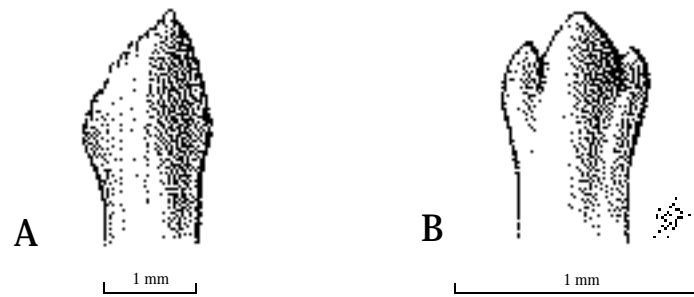


FIG. 6 - Dentition of herbivorous and omnivorous Iguanids. **A** *Iguana iguana*, **B** *Sceloporus magister*

of the undoubtedly herbivorous *Iguana iguana*, GALTON argued that the mechanical breakdown of food in the former most likely only included plant material.

It has also been argued that prosauropods may have been mixed family of herbivores and opportunistic omnivores (COOPER 1981, CROMPTON and ATTRIDGE 1986, GALTON 1979, 1984, 1985, 1986, 1990). COOPER (1981) studied another prosauropod genus, *Massospondylus*, whose masticatory apparatus resembled that of a carnivore. He stated that, given the distribution of the available plant material, which was quite resistant for chewing, prosauropods were inefficient herbivores. In fact, prosauropods may have been carnivorous or carrion feeders, facultatively feeding on insects, small reptiles, amphibians or mammals. However, in this argument, COOPER included *Plateosaurus*, which was argued by GALTON as clearly being herbivorous. GALTON (1985) categorized COOPER's arguments as to why or why not prosauropods were carnivorous as the following summary:

A. Supposed reasons why prosauropods were carnivorous:

1. Teeth relatively long
2. Presence of serrated edges to the teeth indicate a cutting function.
3. The shearing planes of the teeth were aligned along the jaws as is typical of all carnivores.
4. The closure of the maxillary teeth outside those of the dentary would have formed a very efficient shearing plane for cutting.
5. Relatively small, grasping hands armed with enormous trenchant claw which was as rapacious as that found in the most carnivorous of dinosaurs.
6. The carnivorous ancestry of prosauropods, descended from proterosuchian thecodonts.

B. Reasons why prosauropods were not predators on large prey:

1. Small size of the skull relative to the body length.
2. The lateral inflexibility of the axial skeleton.
3. The relatively weak dentition

C. Supposed reasons why carrion formed a major part of diet:

1. Large trenchant claw of manus used for ripping apart carcasses.
2. Cannibalism as major part of diet so it would not have been strictly dependent on food-chain cycles.
3. Explanation of herding.

D. Supposed reasons why prosauropods were not herbivores:

1. Absence of flattened, opposing crowns to the teeth meant that food could not be pulped prior to swallowing.
2. Virtually no lateral movement of the jaw was possible, and hence mastication of plant material was not possible.
3. Shearing planes of teeth were aligned along and not across the jaw.

GALTON (1985) concluded that prosauropods, including anchisaurids, were herbivorous and gives prosauropod herbivorous adaptations as the following:

E. Herbivorous adaptations in prosauropods:

1. Shape of teeth.
2. Form of serrations.
3. Orientation of crowns.
4. Offset jaw articulation.
5. Supplementary action of gastric mill.
6. Long neck and proportionately small skull.

In a recent study on the diet of extinct reptiles, BARRETT (1998) suggested that iguanids may serve as a model for potential prosauropod cranial anatomy and diet. BARRETT drew special attention to comparisons made between the dentitions of both of these taxons. He suggested that, perhaps, if the evidence supporting undoubtedly herbivorous iguanines are also opportunistic omnivores (feeding occasionally on insects), then we should conclude that prosauropods exhibiting the same kind of dentition should be accepted as being similar opportunistic feeders. The striking similarities he found in his studies suggests this to be true. In addition, he suggested that if this evidence is accepted, the dentition alone should not be the sole factor for determining prosauropod diet. In his phylogenetic analysis of

extinct reptiles, he suggests that prosauropods were a mixture of omnivorous dinosaurs, while sauropods were strictly herbivorous. In contrast, the diet of their common ancestor is unknown. He concludes that prosauropods probably had a diet dependent highly on plant material, but was supplemented by small prey and carrion. Because he suggested that the dentition alone is not as reliable a comparison for the analysis of diet in prosauropods, the present research on the morphology of extant iguanid lizard jaw musculature is being used in this study as a paradigm for deducing the diet of extinct reptiles.

Significance of Study

It can be argued that an exclusively herbivorous diet would support such characteristics as an elongated neck and strong tail, enabling prosauropods like *Anchisaurus* and *Plateosaurus* to reach plant material in high places. In this study, *Anchisaurus* is being considered to be very closely related to *Plateosaurus*, and thus, may have been a significant phylogenetic link in the evolution of herbivory in prosauropod dinosaurs. Here it is argued that *Anchisaurus* was not a predator on large prey, but may have been herbivorous with an opportunistic omnivorous diet (feeding occasionally on small prey). Examination of temporal fenestrae and jaw musculature in both undoubtedly herbivorous and omnivorous iguanid models is used to predict jaw musculature for both prosauropods with respect to diet. A similar approach to that of OSTROM (1961) was used in determining the muscle origins and insertions of the prosauropod crania.

Observation of phylogenetic relationships among prehistoric and modern vertebrates through basic scientific research makes this study significant. By observing the development of a modern vertebrate in relation to its extinct predecessors, one can better understand present-day anatomy and behavior. Not only does this project implement a comparison that will serve as a model for others, but also it will add to the existing body of evolutionary knowledge. Research methods such as those incorporated here may be applied to studies in forensic anthropology and functional morphology, anatomy, paleontology, and herpetology.

METHODS



The Iguanids

SPECIMENS:

The iguanid specimens obtained for this research were the omnivorous *Sceloporus magister* (desert spiny lizard), the insectivorous *Ctenosaura hemilopha* (northern false iguana) and *Ctenosaura pectinata* (spiny tailed iguana), and the herbivorous *Iguana iguana* (common green iguana) (see APPENDIX B). Four *Iguana iguana* specimens were: two preserved from Kevin De Queiroz at the National Museum of Natural History (USNM 68056, USNM 12265), one fresh from Mason B. Meers at the Florida Gulf Coast University (MEERS PRIVATE COLLECTION IV), and one preserved from David B. Weishampel from the Department of Cell Biology and Anatomy at the Johns Hopkins University School of Medicine (WEISHAMPEL PRIVATE COLLECTION III). Meers also provided two fresh *Ctenosaura pectinata* specimens (MEERS PRIVATE COLLECTION I, MEERS PRIVATE COLLECTION II). One preserved *Ctenosaura hemilopha* specimen (USNM 521637) and one preserved *Sceloporus magister* specimen (USNM EXCHANGE) were also obtained from De Queiroz. Finally, one *Iguana iguana* skull (USNM 220236) and one *Sceloporus magister* skull (USNM 220250) were provided by De Queiroz.

PRESERVATION:

All preserved specimens were stored in 70% EtOH solution in glass jars at room temperature, and were only removed from solution during dissection. All fresh specimens were kept in Ziploc bags in a freezer, and were thawed at room temperature when dissection was to be performed.

DISSECTION:

Dissections of iguanid jaw musculature were performed under a Nikon Dissection Microscope equipped with a camera lucida. To ensure standard comparisons, each layer was carefully dissected, described, sketched and photographed prior to its subsequent removal. Measurements were taken in millimeters.

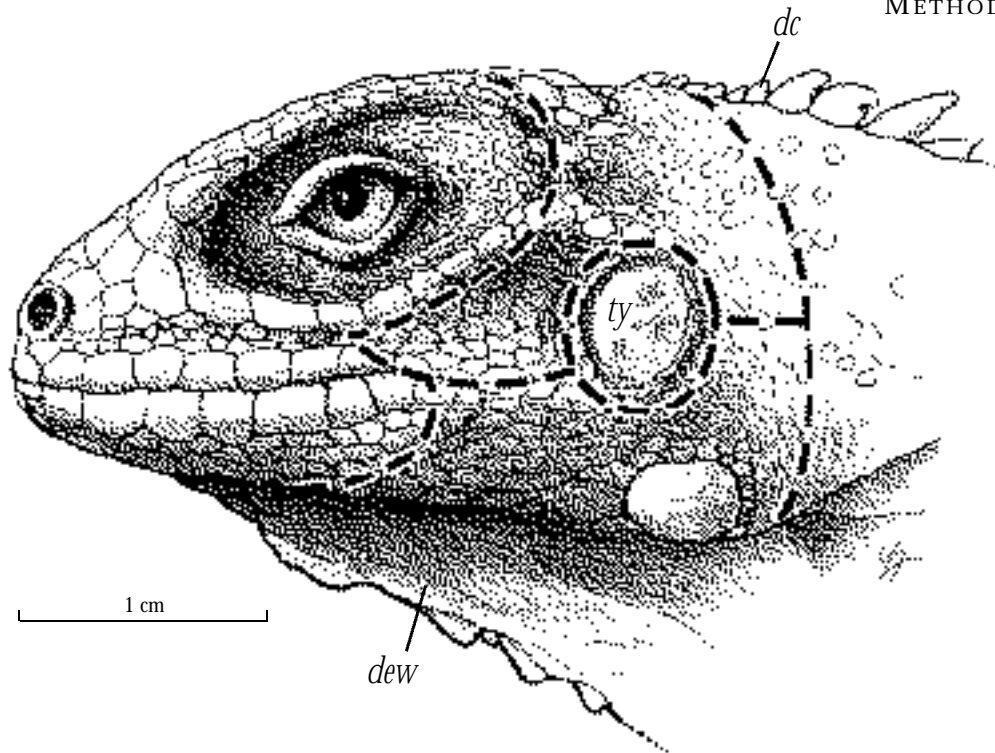


FIG. 7 - Location of incisions (*Iguana iguana*); *dc* dorsal crest, *dew* dewlap, *ty* tympanum.

Dissection begins with palpating posterior to the orbit and dorsal to the tympanic membrane, indicating the postorbital, a triangular-shaped bone which separates the supratemporal and infratemporal fenestrae. This should be noted before dissection occurs so as not to sacrifice any of the superficial structures to be studied. Using small dissection scissors and forceps, the initial incision begins dorso-ventrally on the lateral side of the neck, a few millimeters posterior to the tympanum (see FIG. 7). A second lateral incision was created cutting anteriorly toward the tympanum from the mid-way point of the initial incision. The cut was continued with a circumferential incision around the tympanic membrane. Continuing anteriorly from the tympanic membrane, a skin incision was made along the posterior angle of the mouth toward the ventral edge of the orbit. This cut was continued along the edge of the jugal bone (surrounding the posterior and ventral borders of the orbit) dorsally until terminating at the dorsal midline of the skull. Another cut was made from the posterior corner of the mouth, anteroventrally to the dewlap. Skin was carefully peeled away with small mosquito clamps from the anterior mandible. The dorsal and ventral flaps of skin were retracted with two pairs of mosquito clamps. Muscles were dissected with a pin probe and small forceps. After superficial and first depth structures were

examined, the postorbital and the anterior squamosal bones were removed with small forceps. Eventually, the tympanic membrane was removed as well.

To help prevent dehydration during dissection, 70% EtOH solution was added to the field using an eyedropper. Sketches were created with aid of a camera lucida attachment to the dissection microscope. Detailed notes were taken. Pictures were systematically shot with a Nikon 35mm SLR equipped with a 25-90macro lens on a well lit copy stand using Kodak Ektachrome 320T 35mm slide film.

SKELETONIZATION:

The crania of *Ctenosaura pectinata* (MEERS PRIVATE COLLECTION I) and *Iguana iguana* (MEERS PRIVATE COLLECTION IV) were skeletonized using a water and 20% bleach solution. Skin and muscles had been removed previous to skeletonization. The cranium of each specimen was placed in a separate beaker and warmed below boiling on a hot plate for approximately twelve hours each. Each cranium was checked periodically and tissue layers were subsequently removed.

The Prosauropods

The prosauropod specimens obtained were a complete and disarticulated cast of *Plateosaurus engelhardti* skull (AMNH 6810) and the original *Anchisaurus polyzelus* skull remains (YPM 1883). The skulls of *Plateosaurus engelhardti* and *Anchisaurus polyzelus* were reconstructed based on some of the characteristics found in the dissection and examination of the iguanids.

PLATEOSAURUS ENGELHARDTI:

Sketches of the osteology and muscle origin and insertion sites of *Plateosaurus engelhardti* were created with the unaided eye. The disarticulated bone casts were rearticulated using a water and Carbowax mixture. Because of its brittle quality, the Carbowax was replaced with low-temperature hot glue using a Surebonder mini glue gun. The fully articulated *Plateosaurus* skull was sketched. The hard palate was sketched separately in order to provide a more didactic understanding of the constrictor muscle region. Adductor and constrictor muscle

groups were sculpted onto the cast using Sculpey modeling compound and then labeled (see FIG. 8). Layers were sculpted from the deepest to the most superficial levels, following the organization of the iguanid condition. Some nerve branches and the temporal artery were placed in position using hand-colored rubber bands. These muscles were sketched systematically as each layer was applied for final transfer. Muscle layers were recorded on print film using a Canon EOS Elan IIE SLR camera with a 25-80 35mm lens and Kodak Gold 200 speed film.

ANCHISAURUS POLYZELUS:

The skull of *Anchisaurus polyzelus* was examined using both the naked eye and dissection microscope. The specimen was sketched dorso-laterally and ventro-laterally. Measurements were taken in millimeters. Muscle origin and insertion sites were located, examined and sketched. Photographs were taken of dorso-lateral, ventro-lateral, superior, ventral, anterior and posterior views of the specimen. Photographs were recorded using a Canon EOS Elan IIE SLR camera with a 25-80 35mm lens and Kodak Gold 200 speed film. The medial mandible of *Anchisaurus polyzelus* was reconstructed artistically based on the mandible of *Plateosaurus engelhardti*.

Illustrating the Data

The goal of this project is to provide visual and written clarification of omnivorous and herbivorous iguanid jaw musculoskeletal anatomy, omnivorous and herbivorous prosauropod cranial muscle origin and insertion sites, and respective prosauropod jaw musculature. Tone illustrations of six layers (named superficial to the fifth depth) of jaw musculature of the three iguanid species and the two prosauropods were created from careful annotations, measurements, sketches and slide photographs of the iguanid dissections and from the prosauropod cranial bones and bone casts. These illustrations were rendered using airbrushed lamp black watercolor and Staedtler Dynagraph film pencils on Laserline smooth surface illustration board. These illustrations were scanned on an Epson flat-bed scanner at a resolution of 300ppi, modified in Adobe Photoshop 5.0, and saved as EPS (Encapsulated

PostScript). These digital illustrations became placed files with word-story layout in QuarkXPress 4.0 Passport. Iguanid and prosauropod osteology and muscle origin and insertion maps were rendered using pen and ink Micron pens, Color-aid and Prismacolor black pencils on coquille board. Color maps and layouts were created using the scanned artwork and spot color layers in Adobe Photoshop 5.0 on a PowerMac 9600/233.

The final renderings of the *Anchisaurus polyzelus* specimen in its disarticulated and incomplete state (both right and left lateral) were scanned into the computer and the separate bones were color mapped with flat color in Adobe Photoshop 5.0 using a separate layer from the black and white rendering. The original renderings were compiled, then dropped out of the illustration leaving only the disarticulated bone maps. These bone fragments were reconstructed as left lateral view of the skull in Photoshop and a composite sketch was created with missing fragments indicated in dotted lines. This composite was then reconstructed and rendered in black and white. A new color map was applied to the final rendering.

Depiction of the inferred prosauropod jaw musculature was based on inferences made from the anatomical findings of the iguanid dissections and prosauropod cranial bone elements. Clay models of jaw muscles for herbivorous prosauropods were added to the *Plateosaurus engelhardti* (AMNH 6810) cranial bone casts in order to recreate herbivorous prosauropod jaw muscles.

RESULTS

The Iguanids

OSTEOLOGY

Vertebrates with two temporal fenestrae are considered members of Diapsida. These fenestrae are divided by a temporal bar called the supratemporal arcade (consisting of the posterior ramus of the postorbital and anterior ramus of the squamosal bones). All of the extant specimens examined in this project are members of Lepidosauria, a clade which includes all modern lizards and snakes, *Sphenodon*, and their ancestors (KARDONG 1998). These members have a dorsal opening, called the supratemporal fenestra, containing most of the origins of the adductor groups, and a lateral opening, called the infratemporal fenestra. The latter opens ventrally by an incomplete infratemporal arcade and connects with the pterygoid fenestra (see FIG. 9).

All iguanid skull materials described here are from *Iguana iguana* (USNM220236 AND MEERS PRIVATE COLLECTION I), *Ctenosaura hemilopha* (USNM521637) and *Sceloporus magister* (USNM EXCHANGE). The skull of the iguanids are typically small and lightly built. The relationship of the supratemporal fenestra to the infratemporal fenestra in these iguanids shifts obliquely with respect to diet. In the herbivorous *Iguana iguana*, the supratemporal fenestra is located

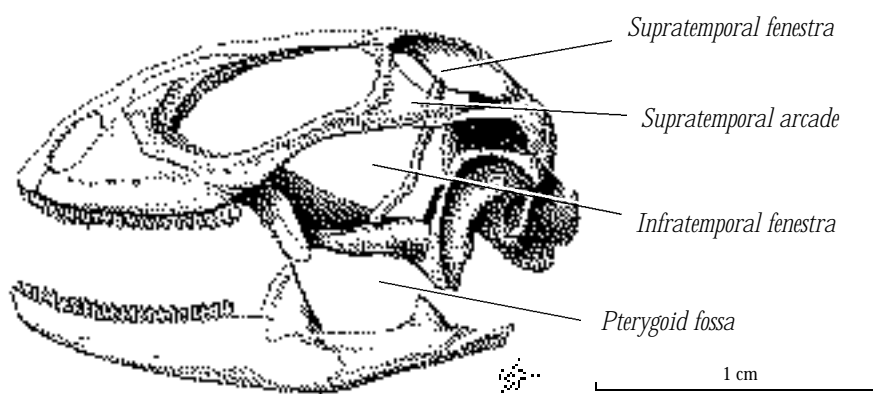


FIG. 9 - Osteological location of fenestrae in Iguanid cranium (*Sceloporus magister*)

at a right angle to the infratemporal fenestra and the long axis of the skull. In the insectivorous *Ctenosaura pectinata* and *C. hemilopha*, the supratemporal fenestra is located more posteriorly. In the omnivorous *Sceloporus magister*, this trend is shifted even farther. This relationship between the two fenestrae has a direct effect on the shapes and insertions of the jaw musculature under study.

The skull consists of 31 different bones and can be divided into three parts: the chondrocranium, the splanchnocranium, and the dermatocranium. Bones are paired with a few exceptions. Nomenclature used for osteology and myology has been implemented based on that of ROMER (1956) and EDGEWORTH (1935), respectively.

THE DERMATOCRANIUM (see FIG. 10)

Facial Series

Premaxilla (pm): This single element, produced by fusion of paired premaxillae, is located anterior-most in the skull and forms the anterior border of the external nares. The posterior extension of the premaxilla between the nares is the nasal process. The palatine process forms the anterior portion of the palate. The palatine process has two mandibular foramina for passage of the mandibular artery (OLDHAM 1975). There are also a small pair of foramina at the tip of the premaxilla for passage of nerves. This bone ventrally bears between four to six teeth. *Iguana iguana*, *Ctenosaura hemilopha*, *C. pectinata*, and *Sceloporus magister* present similar structures.

Maxilla (mx): This paired bone forms the majority of the lateral surface of the facial region of the skull. It constitutes the posterior border of the external nares. This bone also bears the remainder of the teeth of the upper jaw. The teeth are considered *homodont*, lacking much morphological differentiation among teeth within the upper and lower jaws. However, it should be noted that the herbivorous *Iguana iguana* bears serrated blade shaped teeth, while the omnivorous *Ctenosaura hemilopha*, *C. pectinata*, and *Sceloporus magister* all bear teeth with three prominent denticles (refer to FIG. 6). All teeth are *pleurodont*, located on the medial surface of the upper jaw as they are on the lower jaw (see FIG. 11). A row of labial foramina can be seen on the lateral surface of the maxilla for passage of several small nerve branches.

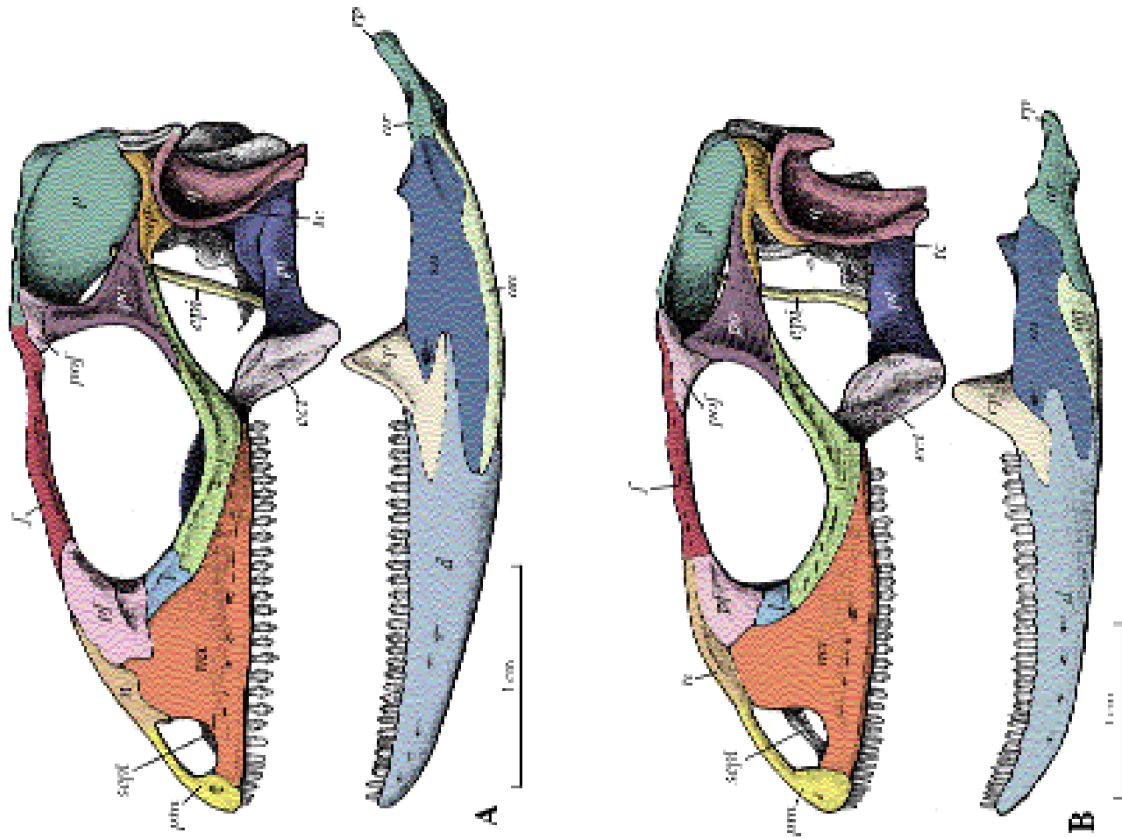


FIG. 10 IGUANID CRANIAL OSTEOLOGY, lateral views
A *Iguana iguana*, B *Ctenosaura hemilophos*, C *Sphaeromus magister*,
an angular, ar angular, cr quadrate, ep epipterygoid, f frontal, f jugal, f lacrimal,
of exopterygoid, of epipterygoid, f frontal, f jugal, f lacrimal,
na maxilla, n nasal, p parietal, pof postorbital foramen, pf prefrontal,
pm postmaxilla, pof postorbital foramen, pof postorbital foramen, pof postorbital,
q quadrate, q retroarticular process, sq squamosal, ty tympanic crest.

Septomaxilla (sept): This small bone can be seen within the external nares lying lateral to the nasal septum. During dissection, it is easy to sacrifice and was hardly noticeable in the *Ctenosaura pectinata*, *Ctenosaura hemilopha* and *Sceloporus magister* specimens. It supports the cartilaginous nasal capsule within the external nares (OLDHAM 1975).

Nasal (n): This single bone is located dorsal and posterior to the premaxilla along the midline of the skull. It articulates with the posterior tip of the premaxilla and the dorsal border of the maxilla, completing the edges of the external nares. Posteriorly, the nasal bone articulates with the frontal bone while posterolaterally, it articulates with the prefrontal bones.

Orbital Series

Prefrontal (pf): This paired bone forms the anterodorsal border of the orbits. It articulates with the frontal, lacrimal and nasal bones dorsomedially, ventrally, and anteriorly, respectively.

Lacrimal (l): This small paired bone forms the anterior border of the orbits. It articulates with the prefrontal and jugal bones dorsally and ventrally, respectively. According to KARDONG (1975), the lacrimal foramen is located medially.

Jugal (j): This paired arch-shaped bone forms the ventral border of the orbits articulating with the maxilla anteroventrally. Its anterior border also articulates with the lacrimal bone. Posteriorly, it forms the anterodorsal border of the infratemporal fenestra, the region, containing a majority of the jaw muscles under study. The posteroventral border of the arcade also serves as a site of origin for the *M. adductor mandibulae externus superficialis*.

Postorbital (po): This paired, triangular shaped bone is a landmark one should note before beginning dissection of the jaw muscles. Its anterior ramus articulates with the jugal while its posterior ramus articulates with the squamosal, forming the supratemporal arcade (refer to FIG. 6). This arcade divides the supratemporal fenestra from the infratemporal fenestra and also serves as a site of origin for the *M. adductor mandibulae externus superficialis*. Its dorsal

ramus articulates with the postfrontal bone. The postorbital forms the majority of the posterior border of the orbit.

Postfrontal (pof): This small paired bone rests on the dorsal border of the postorbital and the ventrolateral border of the frontal and parietal bones.

Skull Roof

Frontal (f): This single element, comprising the fusion of the paired frontals, forms the roof of the skull and the dorsal borders of the orbits. The parietal foramen lies at the medial point of the posterior border of the frontal and the anterior border of the parietal bones.

Parietal (p): This single bone, embryologically formed from fusion of the parietal pairs, is located posterior to the frontal bone and forms most of the roof of the brain cavity. It constitutes the posteromedial border of the supratemporal fenestra, and serves as the site of origin for many of the adductor and constrictor jaw muscles.

Temporal Series

Supratemporal (sut): This paired bone is located inferior to the parietal bone and can only be seen from a posterior view of the skull. This component is not found in prosauropods.

Squamosal (sq): This paired bone forms the posterior portion of the supratemporal arcade and the posterodorsal and posteroventral borders of the infratemporal and supratemporal fenestrae, respectively. The medial surface of the arcade also serves as a site of origin for M. levator anguli oris. Its dorsal edge is the site of origin for the ventral portion of the dorsal head of M. adductor mandibulae externus medius. Ventrally it articulates with the quadrate bone.

Quadrate (q): This concave “auricle-shaped” paired bone forms the lateral floor of the middle ear (OELRICH 1956). It is located at the posterolateral angle of the skull. Its anterolateral border is called the tympanic crest, which provides a surface for the attachment of the anterior border of the tympanum. The tympanic membrane was peeled away from the crest

during dissection. The ventral condyle of the quadrate forms the articulation with the mandible as a synovial joint. It also serves as a point of origin for Mm. adductor mandibulae externus superficialis et medius.

Palatal Series

Vomer (v): This single bone is located on the ventral aspect of the skull. It articulates with the posterior process of the premaxilla and constitutes the anterior-most aspect of the palate. Laterally this bone articulates with the medial surfaces of the maxilla.

Palatine (pal): This single bone is located on the ventral aspect of the skull articulating with the posterior aspect of the vomer. It forms the floor of the orbits and nasal capsule. It articulates dorsally with the pterygoids.

Pterygoid (pt): This paired bone forms the posterior-most section of the hard palate. Medially it bears small pterygoid teeth. The pterygoid articulates posteriorly with the quadrate along its elongated quadrate process and forms the dorsal border of the pterygoid fenestra. It also articulates posteromedially with the basisphenoids, anteriorly with the palatines and anterolaterally with the ectopterygoids. The pterygoid serves as a point of insertion for M. levator pterygoideus.

Ectopterygoid (ect): This paired bone is located anterior to the pterygoid and lies vertically on the lateral lower region of the skull, forming the anterodorsal border of the pterygoid fenestra. It articulates anterodorsally with the jugal and the maxilla and medially with the pterygoids. The pterygoid serves as a point of insertion for the first portion of M. pterygomandibularis.

Epipterygoid/Columella (epi/col): This element is a vertical, rod-shaped bone that articulates dorsally with the parietal and ventrally with the pterygoid bone. This bone helps to reinforce the structure of the cranium from the verticle forces of contraction and serves as a site of origin for M. pseudotemporalis profundus.

THE BRAINCASE

Basisphenoid (bs): This single bone forms a large portion of the floor of the braincase. It articulates with the pterygoid bones via a pair of basipterygoid processes. It is bordered by the basioccipital posteriorly, and articulates with the prootic bone dorsally. The basisphenoid forms the site of origin for *M. protractor pterygoideus*.

Basioccipital (bo): This single bone forms the remainder of the braincase floor. It forms a majority of the occipital condyle ventral to the foramen magnum. The basioccipital articulates anteriorly with the basisphenoid and dorsolaterally with the exoccipitals and prootics.

Exoccipital (exo): This single bone forms the posterolateral wall of the basicranium, the lateral aspects of the occipital condyle, the lateral borders of the foramen magnum and is located dorsal to the basioccipital. Ventrolaterally is the dorsally-located vagus foramen and the ventral hypoglossal foramina (OLDHAM 1975).

Supraoccipital (suo): This single bone forms the posterior component of the braincase and the dorsal border of the foramen magnum. It articulates with the parietal anteriorly, the prootic anteriolaterally and the exoccipital posteriorly.

Orbitosphenoids (os): These two c-shaped bones articulate with each other to enclose the optic foramen. This bone articulates with the alar process of the basisphenoid.

Prootic (pro): This bone is located anterior to the supraoccipital. It forms the lateral portion of the braincase and anteriorly, it rests against the epipterygoid. In addition to the basisphenoid, the prootic forms the site of origin for *M. protractor pterygoideus*.

THE MANDIBLE (see FIG. 11)

The lower jaw, referred to as the mandible, is comprised of six paired bones. It serves as a major insertion site for all of the jaw muscles except the constrictor group.

Dentary (d): This paired bone is located most anteriorly, and articulates with its counterpart at the mandibular symphysis. As its name implies, the dentary is the portion of the mandible where the dentition is found at its dorsal edge. As mentioned previously, the teeth are homodont in form and pleurodont in placement. Anteriorly, the dentary is pierced by several mental foramina for the exit of several small nerves. On its medial side, the dentary articulates posteriorly with the splenial the angular, the surangular and the coronoid process.

Coronoid (co): This bone is a fin-shaped small projection bearing the coronoid process. It is the dorsal-most bone of the mandible and serves as a major site of insertion for the adductor muscle group. The *bodenaponeurosis* (basal aponeurosis described below in the *Myology* section), a very thick tendinous sheet formed by the bottom edges of the adductor muscles, attaches at several different locations on the dorsal and posterior borders of the coronoid process.

Surangular [*Supra-angular*] (sa): This long bone lies posteroventrally to the coronoid and posterior to the dentary. Its medial surface bears a large mandibular foramen. The lateral portion of this foramen, along with the articular and angular bones, forms the posterior portion of the *Meckelian canal*. Its dorsal edge forms the site of insertion for M. adductor mandibulae externus superficialis laterally, and Mm. adductor mandibulae externus medius, profundus et posterior, medially.

Angular (an): This horizontally shaped bone is located ventral to the surangular and posterior to the dentary.

Articular (ar): This dagger-shaped bone is located at the posterior-most portion of the mandible. The mandibular joint (articular glenoid) articulates with the quadrate bone, forming a synovial joint for which to allow movement of the mandible. The retroarticular

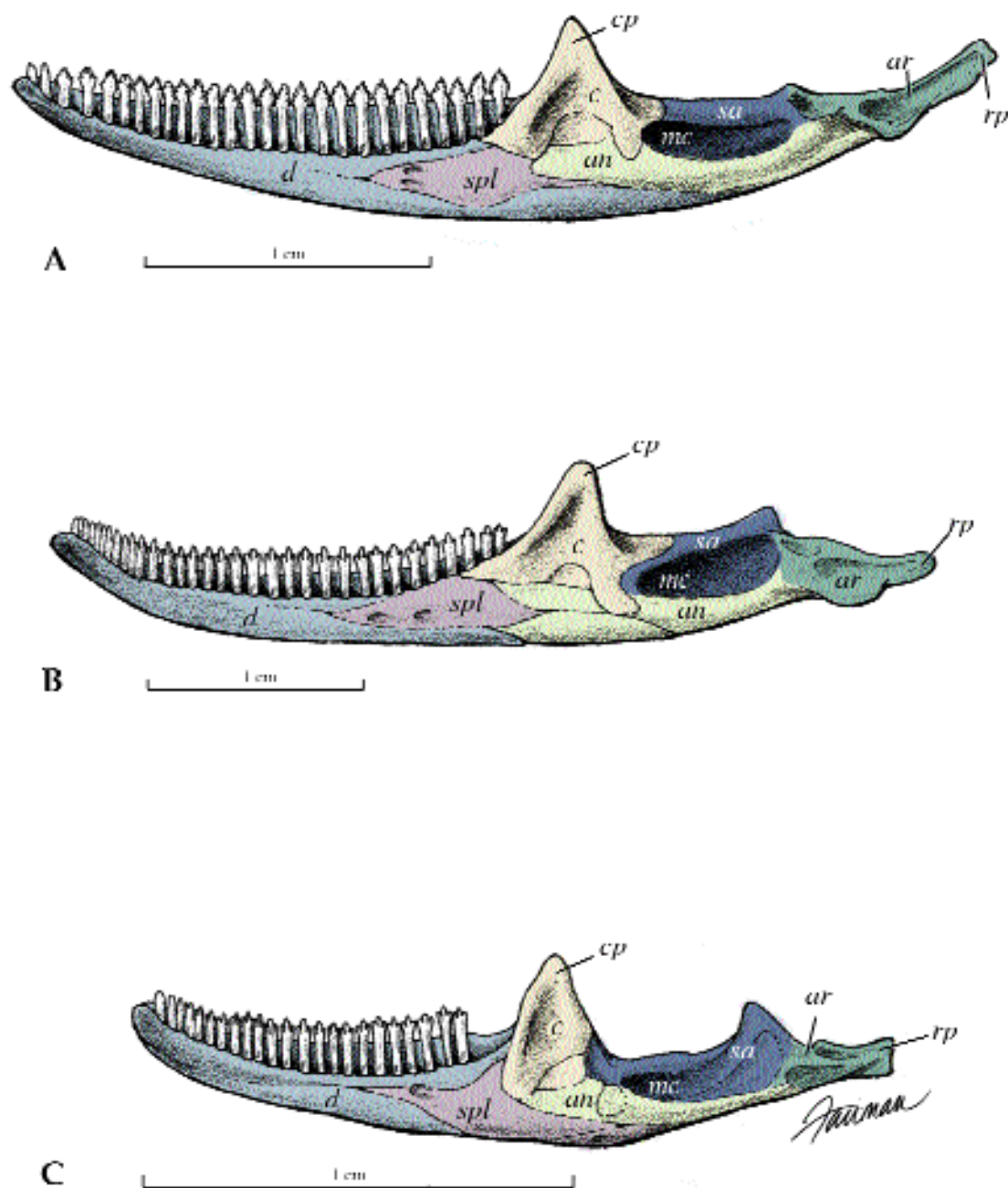


FIG. 11 - IGUANID MANDIBULAR OSTEOLOGY - medial views, A *Iguana iguana*, B *Ctenosaura hemilopha*, C *Sceloporus magister*; *an* angular; *ar* articular; *c* coronoid; *cp* coronoid process; *d* dentary; *mc* Meckelian canal; *rp* retroarticular process; *sa* surangular; *spl* splenial.

process projects posteriorly and receives fibers from M. pterygomandibularis. Anteriorly, the retroarticular depression serves as a site of insertion for the dorsal portion of M. pterygomandibularis. Its remaining fibers insert on the ventral, dorsal and angular surfaces of the articular. The apex of the triangular facet of the retroarticular process receives insertion fibers from M. depressor mandibulae. Along its lateral border, the tympanic crest is a site for the attachment of the ventral border of the tympanum.

Splénial (spl): This bone is visible only from the medial side of the mandible. It articulates with all of the bones of the mandible and completes the medial portion of the *Meckelian canal*. Two foramina pierce the splénial for the exit of several small nerves.

MYOLOGY

SUPERFICIAL STRUCTURES

Upon removal of the skin, several superficial structures are encountered lateral to the musculature. These will be addressed in this section. However, not all superficial structures are illustrated.

Mundplatt /*Rictal Plate* (mund): The *Mundplatt* [German for *mouth-plate*] is a triangular-shaped extension of the posterior corner of the mouth. It is formed by a double-layer, or invagination, of the skin from the upper and lower jaw (see FIG. 13). Its dorsal border serves as an insertion site for *M. levator anguli oris*. The *Mundplatt* serves to accommodate the opening of the mouth, and therefore is a protective cover for the posterior corner. *M. levator anguli oris* serves to tuck this accommodating integument when the jaw is adducted. The ventral length of the *Mundplatt* varies from species to species. The *Mundplatt* of *Iguana iguana* is short dorsoventrally while that of *Ctenosaura hemilopha* and *Sceloporus magister* present wider surfaces. Of the three species, *Ctenosaura hemilopha* appears to have a proportionately larger *Mundplatt*.

Ligamentum quadratomandibulare (lq): This ligament is a band of connective tissue that extends from the posteroventral corner of the jugal to the ventrolateral corner of the quadrate (see FIG. 13). It is dorsally continuous with infratemporal fascia while ventrally it connects with the *Mundplatt*, and is therefore hard to separate during dissection. This ligament is said to occur in all iguanids (COSTELLI 1973). It was found in *Ctenosaura hemilopha*, *C. pectinata* and *Sceloporus magister*, but was not found in any of the *Iguana iguana* specimens that were dissected for this project.

Infratemporal fascia (if): This thin, tendinous fan-shaped sheet of fascia covers the jaw musculature of the infratemporal fenestra. It is the most superficial structure, adherent to the skin and *Mundplatt* of the lower cheek. Its apex arises from the anteroventral corner of the quadrate and fans anterodorsally to insert on the ventral border of the squamosal and postorbital bones as well as the posterior border of the jugal. COSTELLI (1973) mentioned

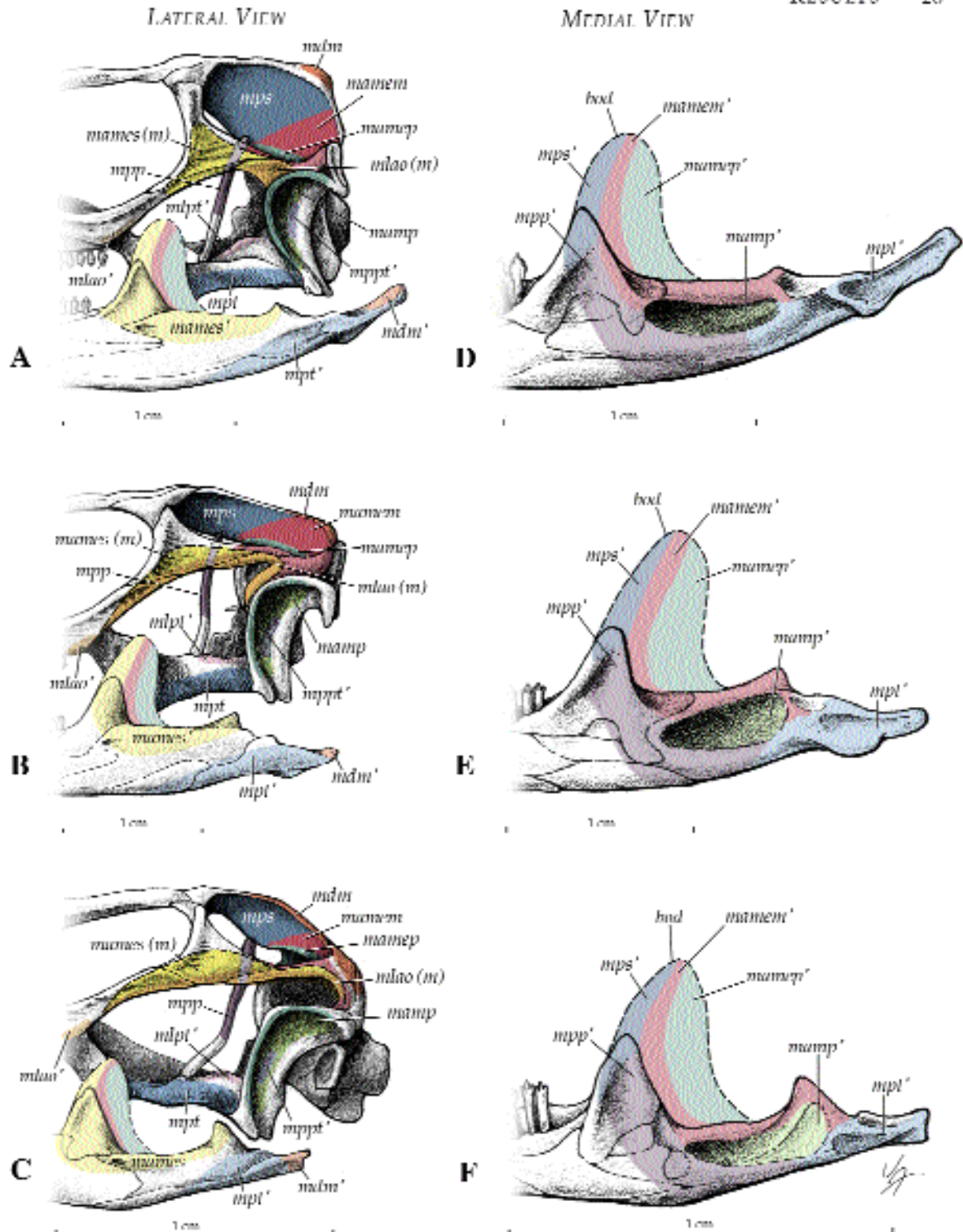


FIG. 12 - IGUANID MYOLOGY, SITES OF ORIGIN AND INSERTION; A,D *Iguana iguana*, B,E *Ctenosaura hemilophota*, C,F *Sceloporos magister*; *bd* bodenapuncusis; *ms* medial surface; *manms*, *manms*¹ M. adductor mandibulae externus medius origin, insertion; *manop*, *manop*¹ M. adductor mandibulae externus profundus origin, insertion; *manps*, *manps*¹ M. adductor mandibulae externus superficialis origin, insertion; *manp*, *manp*¹ M. adductor mandibulae posterior origin, insertion; *mls*, *mls*¹ M. depressor mandibulae origin, insertion; *mlp*, *mlp*¹ M. levator pterygoideus origin, insertion; *ppp*, *ppp*¹ M. pseudotemporalis profundus origin, insertion; *ppsp*, *ppsp*¹ M. protractor pterygoideus origin, insertion; *whs*, *whs*¹ M. urogenitalis superficialis origin, insertion; *whs*, *whs*¹ M. urogenitalis lateral origin, insertion.

that this fascia is found in all iguanid genera, but it was not found in any of the *Iguana iguana* specimens. This may be due to the difficulty in separating this extremely delicate and thin sheet of fascia from the skin, which was the case in *Ctenosaura hemilopha*, *C. pectinata* and *Sceloporus magister*. The amount of infratemporal space covered by the fascia varies according to species.

ADDUCTOR MANDIBULAE GROUP

Based on their relationship to the three rami of the trigeminal nerve, the adductor mandibulae group have been divided into three groups of muscles: the M. adductor mandibulae externus, M. adductor mandibulae internus and M. adductor mandibulae posterior (LAKJER 1926, OSTROM 1961, COSTELLI 1973, GALTON 1985). The M. adductor mandibulae externus group occurs lateral to the maxillary ramus of the trigeminal nerve. This nerve separates the externus muscles from the internus muscles as it travels anteriorly from the trigeminal foramen of the prootic to toward the orbit, medial to the jugal bone. Thus, M. adductor mandibulae internus is found medial to the maxillary ramus and anterior to the mandibular ramus of the trigeminal nerve. This nerve also exits the trigeminal foramen of the prootic, posterior to the maxillary ramus and travels ventrally and eventually turns anteriorly into the *Meckelian canal*, on the medial side of the mandible (see FIG. 11). M. adductor posterior is found posterior to the remaining constrictor muscles, medial to the mandibular ramus.

Bodenaponeurosis (bod): The *bodenaponeurosis* [*Boden* German for *basal* or *bottom*] consists of the tendon and fascia of the adductor mandibulae externus and internus muscle groups (pseudotemporalis portion). The adductor mandibulae muscle group, whose tripartite origins range from the parietal, quadrate, prootic, exoccipital, pterygoid, epipterygoid, postorbital and squamosal bones, requires an insertion that accommodates the widespread forces of contraction to the mandible. This insertion occurs on the small surface area of the medial surface, dorsal and posterior borders of the coronoid process (see FIG. 12) (COSTELLI 1973). This tendinous bundle of fascia is a strong structure that was difficult to separate and remove during dissection. The bodenaponeurosis is separated by the maxillary ramus (V_2) of the trigeminal nerve.

M. Adductor Mandibulae Externus (mame): This quadratopartite muscle spans from the supratemporal fenestra, to the dorsal border of the mandibular ramus. It will be described here in its separate parts:

M. Levator Anguli Oris (mlao): This most laterally-located jaw muscle occurs in the infratemporal fenestra medial to the infratemporal fascia and lateral to *M. adductor mandibulae externus superficialis* (see FIG. 13). It originates on the surfaces of the medial squamosal, the posterior jugal and anterior quadrate at the tympanic crest and it travels anteriorly and ventrally to insert on the dorsal and posterior edge of the *Mundplatt* laterally and medially. AVERY and TANNER (1971) state that the insertion site is on the posterior border of the coronoid, but this is a minor part of its insertion. Instead, its fibers mostly travel in a straight course as a flat sheet in order to insert onto the *Mundplatt* and pull the integument of the posterior corner of the mouth dorsally and posteriorly when the mouth is closed. It also serves to slightly levate the mandible. Its thickness is substantially decreased at its posteroventral edge and is easily separated from the underlying *M. adductor mandibulae externus superficialis*. Fibers from the mandibular ramus of the trigeminal nerve pierce its medial surface. *M. levator anguli oris* of *Iguana iguana* and *Ctenosaura hemilopha* are shorter and thicker than that of *Sceloporus magister*. This may result from the proportional differences between the infratemporal fenestrae of the three iguanids. According to COSTELLI (1973), this muscle is innervated by the third branch of the mandibular ramus (V_3) of the trigeminal nerve.

M. Adductor Mandibulae Externus Superficialis (mames): This muscle occurs in the infratemporal fenestra medial to *M. levator anguli oris* and lateral to *M. adductor mandibulae externus medius* (see FIG. 13). It originates on the surfaces of the medial squamosal, postorbital and jugal bones as well as on the anterior quadrate at the tympanic crest. The origin of this muscle in *Iguana iguana* and *Sceloporus magister* is fleshy, while, in *Ctenosaura hemilopha*, the origin gradually makes a transition from tendon to fleshy muscle as the tendon extends over almost half of the length of the belly of the muscle. It travels anteriorly and ventrally to insert on the dorsolateral portion of the lower jaw, covering the lateral and medial surfaces of the coronoid process, surangular

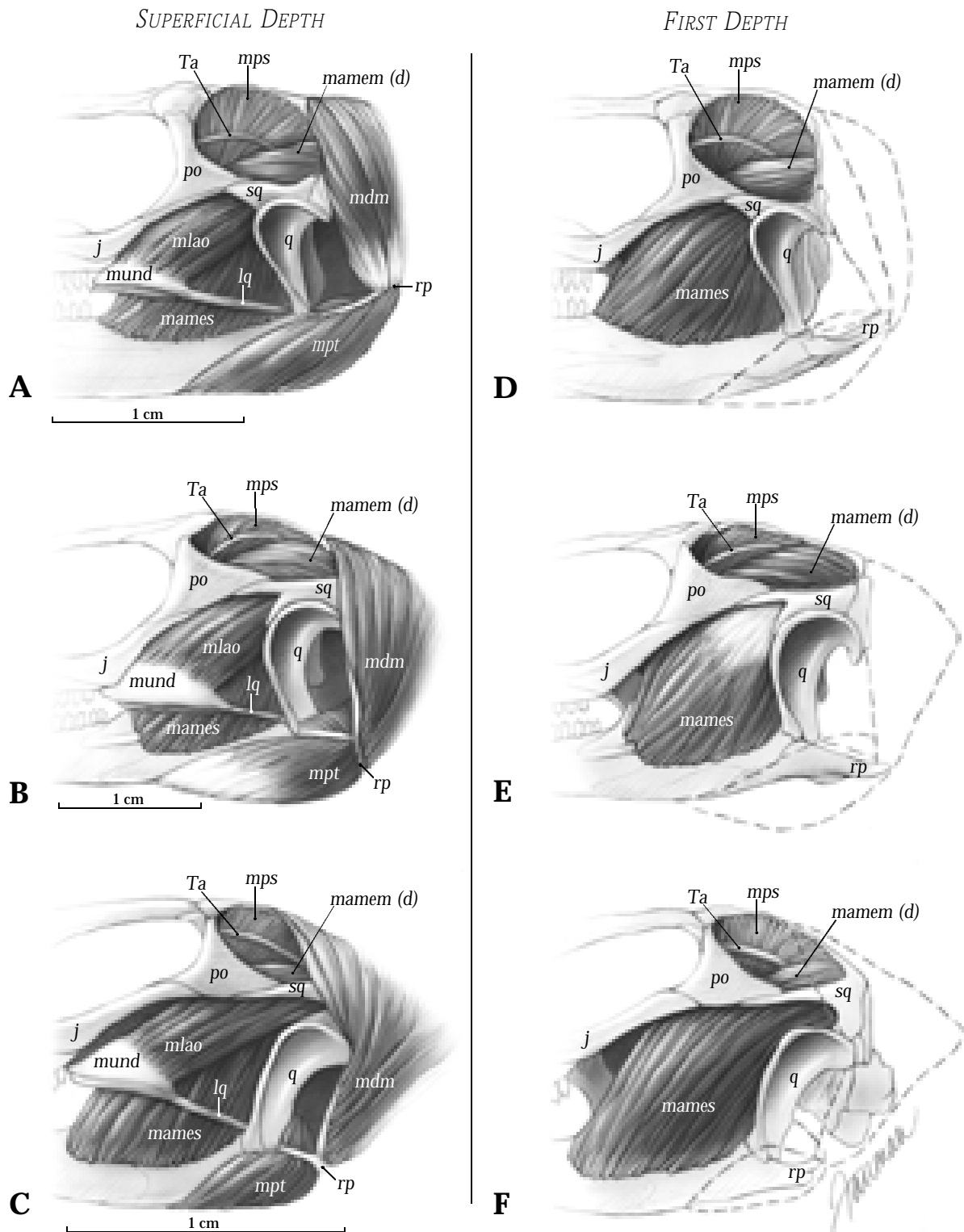


FIG. 13 - IGUANID MYOLOGY, LATERAL VIEWS, SUPERFICIAL AND FIRST DEPTHS; A, D *Iguana iguana*; B, E *Ctenosaura hemilopha*; C, F *Sceloporus magister*. j jugal; mamem (d) M. adductor mandibulae externus medius, dorsal head; mames, M. adductor mandibulae externus superficialis; mdm M. depressor mandibulae; mlao M. levator anguli oris; mps M. psuedotemporalis superficialis; mpt M. pterygomandibularis; mund Mundplatt; po postorbital; q quadratus; rp retroarticular process; sq squamosal; Ta temporal artery.

and the articular bones. This muscle can be divided into an anterior and posterior head. Its fibers for the most part travel in a straight course anteroventrally. However, its anterior fibers also tend to travel more ventrally and insert into the lateral-most portion of the bodenaponeurosis. This relatively thick muscle can be separated medially from the underlying M. adductor mandibulae externus medius. Nerve fibers from the mandibular ramus of the trigeminal are found piercing both its lateral and medial surfaces. M. adductor mandibulae externus superficialis of *Iguana iguana* is proportionately smaller than that of *Ctenosaura hemilopha*, which in turn is proportionately smaller than that of *Sceloporus magister*. This is due to the posterior shift of the location and shape of the squamosal bone in each of these iguanids respectively, thus creating a wider infratemporal fenestra in the more omnivorous species studied. The action of this muscle is to elevate the mandible. According to COSTELLI (1973), innervation is by the third branch of the mandibular ramus (V₃) of the trigeminal nerve.

M. Adductor Mandibulae Externus Medius (mamem): This muscle can be best visualized after removal of the postorbital and anterior squamosal bones (see FIG. 14). The M. adductor mandibulae externus medius can be divided into a dorsal and ventral head. Its dorsal head originates in the supratemporal fenestra, posterior to M. pseudotemporalis superficialis. The temporal artery separates these two muscles as it travels from the posterior orbit to the anterodorsal border of M. adductor mandibulae externus medius. This is an important landmark to look for in dissection, as M. pseudotemporalis superficialis and M. adductor mandibulae externus medius can be misidentified as being a single fan-shaped muscle filling the supratemporal fenestra. M. adductor mandibulae externus medius originates on the surfaces of the medial squamosal, supratemporal, lateral parietal and anterior quadrate. From the supratemporal fenestra, M. adductor mandibulae externus medius travels medial to the supratemporal arcade, twisting more ventrally, and enters the infratemporal fenestra, thus becoming the ventral head. This portion of M. adductor mandibulae externus medius is located medial to M. adductor mandibulae externus superficialis and lateral to M. adductor mandibulae externus profundus. It travels anteriorly and ventrally to insert on the dorsolateral portion of the lower jaw, to the coronoid process and the surangular and articular bones. Its

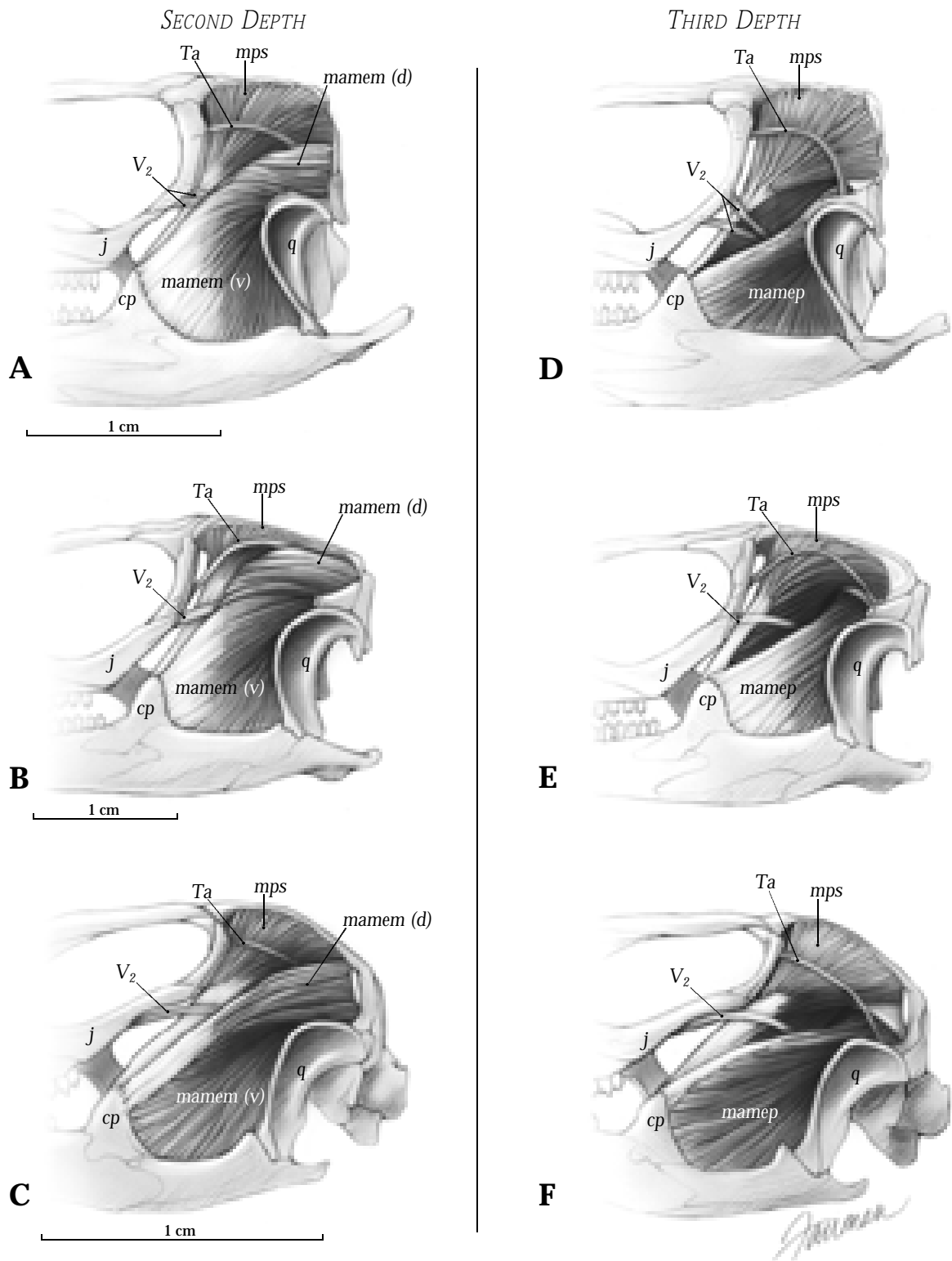


FIG. 14 - IGUANID MYOLOGY, LATERAL VIEWS, SECOND AND THIRD DEPTHS; A, D *Iguana iguana*; B, E *Ctenosaura hemilopha*; C, F *Sceloporus magister*; cp coronoid process; j jugal; mamem (d) M. adductor mandibulae externus medius, dorsal head; mamem (v) M. adductor mandibulae externus medius, ventral head; mamep M. adductor mandibulae externus profundus; mdm M. depressor mandibulae; mps M. pseudotemporalis superficialis; mpt M. pterygomandibularis; mund Mundplatt; q quadrate; Ta temporal artery; V₂ Trigeminal nerve, maxillary ramus.

aponeurotic insertion occurs mostly on the medial surfaces thereof. The ventral head of this muscle in *Iguana iguana* has the largest area of tendon. It covers most of the anterior and ventral portions of its insertion into the bodenaponeurosis. In *Ctenosaura hemilopha* the extent of the insertion is lessened. In *Sceloporus magister* the insertion becomes a strong fibrous band of tendon. The ventral head of M. adductor mandibulae externus medius is separated medially from the tendon of M. pseudotemporalis superficialis by the maxillary ramus of the trigeminal nerve. This can be visualized at the anterior border of the ventral head. This relatively thick muscle is extremely difficult to separate medially from the underlying M. adductor mandibulae externus profundus in *Iguana iguana* and *Ctenosaura hemilopha*. Nerve fibers from the mandibular ramus of the trigeminal are found piercing both its lateral and medial surfaces. Overall, the M. adductor mandibulae externus medius of *Sceloporus magister* is elongated most antero-posteriorly than that of *Iguana iguana* or *Ctenosaura hemilopha*. This is due to the oblique shift of the location of the infratemporal fenestra in this more omnivorous species. The action of this muscle elevates the mandible. According to COSTELLI (1973), innervation is by the third branch of the mandibular ramus (V_3) of the trigeminal nerve.

M. Adductor Mandibulae Externus Profundus (mamep): According to SECOY (1971), M. adductor mandibulae externus profundus is usually not found as its fibers are indistinguishable as being separate from the lateral M. adductor mandibulae externus medius. However, in *Sceloporus magister*, as well as *Iguana iguana* and *Ctenosaura hemilopha*, it was clearly found. This muscle is best visualized upon removal of the M. adductor mandibulae externus medius. The M. adductor mandibulae externus profundus muscle is the most medially located jaw muscle of the adductor mandibulae externus muscle group (see FIG. 14). Its dorsal head originates in the supratemporal fenestra on the ventral border of the parietal, the exoccipital and prootic bones. It leaves the supratemporal fenestra medial to the squamosal bone and travels anteriorly and ventrally into the infratemporal fenestra. It inserts into the bodenaponeurosis on the medial portion of the lower jaw, to the coronoid process and the surangular and articular bone. The ventral head of this muscle in *Ctenosaura hemilopha* has the largest tendon. It covers most of the posterior and ventral portions of its insertion into the bodenaponeurosis. In *Iguana*

iguana, it is lessened. In *Sceloporus magister*, this insertion becomes a strong fibrous band of tendon. The fibers of this muscle in *Sceloporus magister* run more anteroposterior as compared to that of the other two genera. The ventral head of M. adductor mandibulae externus profundus is separated medially from the tendon of M. pseudotemporalis superficialis by the maxillary ramus (V_2) of the trigeminal nerve. This can be visualized at the anterior border of the ventral head. Its action elevates the mandible. According to COSTELLI (1973), this muscle is innervated by the third branch of the mandibular ramus (V_3) of the trigeminal nerve.

M. Adductor Mandibulae Internus (mami):

M. Pseudotemporalis Superficialis (mps): This muscle is the largest jaw muscle occupying the supratemporal fenestra (see FIGS. 12 and 14), originating on the lateral surface of the parietal, the prootic and the epipterygoid bones. The dorsal portion of this muscle in *Iguana iguana* and *Sceloporus magister* is fleshy and fan-shaped (with fibers running more dorso-ventrally), whereas that of *Ctenosaura hemilopha* is fleshy and crescentic (with fibers running more anteroposteriorly). Once M. adductor mandibulae externus medius, is removed, the thickness of M. pseudotemporalis superficialis can be visualized quite clearly. Its posterior fibers form a thick wall of muscle filling much of the infratemporal fenestra. As it travels anteriorly and ventrally, its fibers become a convergent, strong, narrow slip of tendon which inserts into the medial portion of the bodenaponeurosis. The maxillary ramus (V_2) of the trigeminal nerve crosses lateral to this insertion. In *Iguana iguana*, two branches of this ramus were found traveling anteriorly toward the orbit. Muscle action is to elevate the mandible. According to COSTELLI (1973), this muscle is innervated by the first branch of the mandibular ramus (V_3) of the trigeminal nerve.

M. Pseudotemporalis Profundus (mpp): This muscle, most of which lies in the infratemporal fenestra, is located medial to M. pseudotemporalis superficialis (see FIG. 15). Its fleshy origin begins on the lateral surface of the parietal, the prootic and the epipterygoid bones. The fibers of this muscle run slightly anteriorly and dive ventrally toward the coronoid process where they insert the medial-most portion of the

bodenaponeurosis. The maxillary ramus (V_2) of the trigeminal nerve can clearly be seen running from the trigeminal foramen of the prootic crossing anteriorly and slightly dorsally over the belly of this muscle. The root of the mandibular ramus (V_3) of the trigeminal nerve is posterior to the epipterygoid bone and the posterior edge of the muscle. It passes ventrally toward the mandible and disappears medial to the surangular, suggesting its continued path through the mandibular fenestra of the *Meckelian canal*. In *Iguana iguana*, this muscle is completely fleshy except for its insertion into the bodenaponeurosis. It appears to consist of two separate muscle bellies; the second is posterior and medial to the first. These two muscles seem to diverge from their origin, yet converge again toward the mandible. In *Ctenosaura hemilopha*, this muscle is short and wide. Its origin is slightly tendinous, and appears to be continuous with the prootic membrane and rests lower on the epipterygoid bone. *M. pseudotemporalis profundus* of *Sceloporus magister* is the largest of the three species. Like the condition in *Iguana iguana*, two muscle bellies make up *M. pseudotemporalis profundus* in *Sceloporus magister*. However, in *Sceloporus magister*, these muscle bellies are more easily distinguishable and do not converge at their insertion. The anterior edge of *M. adductor mandibulae posterior* covers the insertion site of the second belly of *M. pseudotemporalis profundus*. *M. pseudotemporalis profundus* serves to slightly elevate the mandible and according to COSTELLI (1973), it is innervated by the first and fourth branches of the mandibular ramus (V_3) of the trigeminal nerve.

M. Pterygomandibularis (mpt): This pterygomandibularis muscle is the largest and most complex jaw muscle studied. It is best viewed from its ventral aspect, dorsal to the throat constrictor muscles. It originates with a very large tendon from the ectopterygoid and basipterygoid bones, and from the quadrate processes of the pterygoid bone. When viewed laterally, it eventually appears dorsolateral to the mandible (see FIG. 13). It runs posteriorly and covers most of the posterior aspect of the mandible. It inserts at the posterior-most aspect of the mandible with fibers attaching to the articular bone at the articular and retroarticular processes. The intermandibularis muscle (a throat constrictor muscle that will not be described) covers the lateral and ventral aspects of *M. pterygomandibularis*, and consequently was sacrificed during dissection. *M.*

pterygomandibularis can be divided into three portions on the basis of its three sites of origin. Its first portion originates on the posterior ectopterygoid with a very strong, thick tendon that continues medially. Eventually this tendon is joined by a thick fascial sheath at the transverse process of the pterygoid bone, its second origin. This sheath reaches the belly of the muscle and continues to the ventral aspect of the quadrate process of the pterygoid, becoming its third origin. This third portion can only be visualized after the first and second portions have been sacrificed. Fibers can also be visualized medial to the articular bone of the mandible, arising ventral to the tympanic cavity and diving ventrally to the quadrate process of the pterygoid. Thus, the retroarticular region of the mandible is surrounded by muscle fibers on both its lateral and medial surfaces. COSTELLI (1973) mentioned a very interesting functional and morphological characteristic of this muscle: when compared with the other jaw muscles studied in this investigation, M. pterygomandibularis is the only muscle which originates and inserts on both sides of the fulcrum lever of the mandible. This is not true of the other jaw muscles as they each insert onto the same side of their fulcrum lever. Of the three iguanids studied, *Ctenosaura hemilopha* seems to have the most robust M. pterygomandibularis. Its fascial covering is visualized both on its ventral and lateral aspects. *Sceloporus magister* has the smallest muscle belly. The action of this muscle is to elevate the mandible. According to COSTELLI (1973), this muscle is innervated by the fourth branch of the mandibular ramus (V_3) of the trigeminal nerve.

M. Adductor Mandibulae Posterior (mamp): The last muscle of the adductor mandibulae muscle group is M. adductor mandibulae posterior (see FIG. 15). It rests in the infratemporal fenestra anterior to the quadrate bone, originating on the quadrate and prootic bones and forming a triangular shaped muscle belly as it travels anteriorly and ventrally toward the mandible. Its tendinous insertion occurs at the medial surface of the surangular and articular bones. In *Iguana iguana*, this muscle is fleshy with its small anteroventral corner being tendinous. It consists of two separate muscle bellies, the second is visualized posterior and medial to the first. In *Ctenosaura hemilopha*, its insertion is much wider, occupying the entire ventral border of the muscle. M. adductor mandibulae posterior of *Sceloporus magister* is the widest of the three genera. The mandibular ramus (V_3) of the trigeminal passes medial to

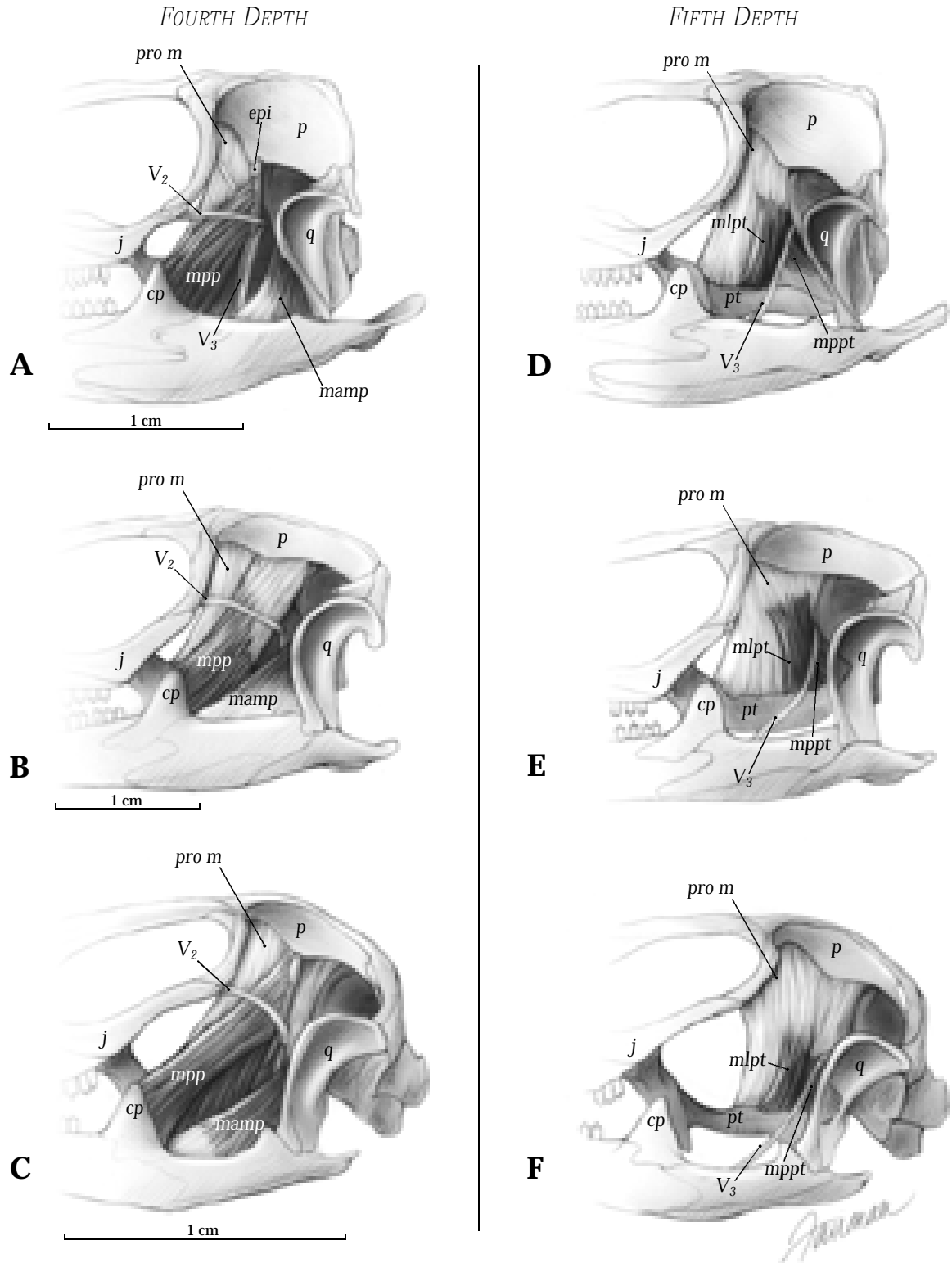


FIG. 15 - IGUANID MYOLOGY, LATERAL VIEWS, FOURTH AND FIFTH DEPTHS; A, D *Iguana iguana*; B, E *Ctenosaura hemilopha*; C, F *Sceloporus magister*. cp coronoid process; j jugal; mamp M. adductor mandibulae posterior; mlpt M. levator pterygoideus; mpp M. pseudotemporalis profundus; mppt M. protractor pterygoideus; p parietal; pro m prootic membrane; pt pterygoid; q quadrate; V_2 Trigeminal nerve, maxillary ramus; V_3 Trigeminal nerve, mandibular ramus.

this muscle. Its action is to elevate the mandible. According to COSTELLI (1973), this muscle is innervated by the fifth branch of the mandibular ramus (V_3) of the trigeminal nerve.

M. Depressor Mandibulae (mdm): This muscle originates on the posterior surface of the parietal bone (see FIG. 13). Its anterior fibers slightly cover the muscles of the supratemporal fenestra. The fibers of this muscle converge ventrally and insert on the retroarticular process of the mandible. The insertion slightly overlaps that of *M. pterygomandibularis*. Its anterior border forms the posterior edge of the tympanic cavity. The size of this muscle varies among the iguanids studied. In *Iguana iguana*, this muscle is very narrow and has a tendinous insertion. In both *Ctenosaura hemilopha* and *Sceloporus magister*, this muscle fans posteriorly over the lateral surface of the constrictor region of the throat and has a fleshy insertion. The action of this muscle is to depress the mandible. This is the only muscle that opens the jaw. This muscle is innervated by the maxillary ramus (V_2) of the trigeminal nerve.

CONSTRUCTOR DORSALIS GROUP

These muscles consist the remaining jaw muscles studied. They are located deep within the infratemporal fenestra.

M. Levator Pterygoideus (mlpt): This muscle is a small ribbon-shaped slip which originates on the ventral border of the parietal bone (see FIG. 15) and the prootic membrane. It continues ventrally and inserts onto the medial aspect of the pterygoid bone. The mandibular ramus (V_3) of the trigeminal nerve can best be visualized at this level leaving the trigeminal foramen of the prootic. It is seen traveling along the posterior edge of this muscle, continuing ventrally toward the mandibular fenestra of the *Meckelian canal*. The action of this muscle is to elevate the maxillary segment of the cranium. This muscle is innervated by the mandibular ramus (V_3) of the trigeminal nerve.

M. Protractor Pterygoideus (mppt): This muscle is a small slip located medial to *M. levator pterygoideus* (see FIG. 15). It originates on the prootic and basisphenoid bones and continues posteroventrally and inserts onto the deep anteromedial aspect of the quadrate and posterior

palate. This insertion is difficult to visualize without removing the tympanic crest of the quadrate bone. Therefore, this muscle has been illustrated transparently in FIGURE 15. The action of this muscle is to elevate and protract the maxillary segment of the cranium. This muscle is innervated by the mandibular ramus (V_3) of the trigeminal nerve.

M. Levator Bulbi (mlb): This muscle is not illustrated and therefore will not be discussed in great detail. *M. levator bulbi* is a small triangular-shaped muscle which originates on the supratrigeminal ligament, continuing anteroventrally near the piriform recess to insert onto the palatal membrane. The action of this muscle is to depress the palpebrae inferioris. Innervation by the mandibular ramus (V_3) of the trigeminal nerve.

CIRCULATION AND INNERVATION

The structures discussed here are major soft-tissue landmarks that divide the jaw muscles into their various relationships. Therefore, they will be described here as they are important structures to look for while dissecting the temporal fenestrae in iguanids.

Temporal artery (Ta): The temporal artery enters the anterior edge of the supratemporal fenestra (see FIGS. 13 and 14). It runs lateral to M. pseudotemporalis superficialis and disappears as it dives medially to the anterior border of M. adductor mandibulae externus medius. This is a landmark one should note when distinguishing the muscles of the supratemporal fenestra as this artery separates their origins.

Trigeminal branches (V₂ and V₃): The maxillary ramus (V₂) of the trigeminal nerve crosses the anterior edge of the infratemporal fenestra (see FIGS. 14 and 15). It continues over the tendon of M. pseudotemporalis superficialis and dives medial to the anterior border of Mm. adductor mandibulae externus medius et profundus. This nerve divides the adductor mandibulae externus muscle group from the internus muscle group. The mandibular ramus (V₃) of the trigeminal can be found deep to the adductor muscles as it exits the trigeminal foramen posterior to the maxillary ramus. It travels ventral and medial to all adductor structures and continues anteroventrally to the medial surface of the mandible where it exits the infratemporal fenestra through the mandibular foramen.

TABLE 1 - Adductor jaw muscles in Iguanidae

MUSCLE	ORIGIN	INSERTION	N*	ACTION
<i>M. adductor mandibulae externus (mame)</i>				
<i>levator anguli oris</i>	squamosal, postorbital & tympanic crest	posterior coronoid, dorsal <i>Mundplatt</i>	V ₃ 3 rd branch	elevates skin of mouth
<i>superficialis</i> (anterior/posterior)	jugal, quadrate, postorbital & squamosal	coronoid, surangular and articular	V ₃ 3 rd branch	elevates mandible
<i>medius</i> (dorsal/ventral)	squamosal, supratemporal, parietal & quadrate	coronoid, surangular and articular	V ₃ 3 rd branch	elevates mandible
<i>profundus</i> (dorsal/ventral)	parietal, exo-occipital & prootic	coronoid, surangular and articular	V ₃ 3 rd branch	elevates mandible
<i>M. adductor mandibulae internus (mami)</i>				
<i>M. pseudotemporalis superficialis</i>	parietal, prootic & epipterygoid	coronoid & articular	V ₃ 1 st branch	elevates mandible
<i>M. pseudotemporalis profundus</i>	parietal, prootic & epipterygoid	coronoid & articular	V ₃ 1 st & 4 th branch	elevates mandible
<i>M. pterygomandibularis</i>	basipterygoid process, ectopterygoid & pterygoid	articular	V ₃ 4 th branch	elevates mandible
<i>M. adductor mandibulae posterior</i>	quadrate & prootic	coronoid	V ₃ 5 th branch	elevates mandible

* branch of Trigeminal Nerve V, or Facial Nerve VII (COSTELLI 1973)

TABLE 2 - Constrictor jaw muscles in Iguanidae

MUSCLE	ORIGIN	INSERTION	N*	ACTION
<i>M. levator pterygoideus</i>	parietal and prootic membrane	medial pterygoid	V ₃	elevates maxillary segment of cranium
<i>M. protractor pterygoideus</i>	prootic & basisphenoid	quadrate	V ₃	elevates & protracts maxillary segment of cranium
<i>M. levator bulbi</i>	supratrigeminal ligament	palatal membrane (antero-ventrally near piriform recess)	V ₃	depresses palpebrae inferioris

* branch of Trigeminal Nerve V, or Facial Nerve VII (COSTELLI 1973)

TABLE 3 - M. depressor mandibulae in Iguanidae

MUSCLE	ORIGIN	INSERTION	N*	ACTION
<i>M. depressor mandibulae</i> (anterior/lateralis)	parietal bone	retroarticular process	VII	depresses mandible

* branch of Trigeminal Nerve V, or Facial Nerve VII (COSTELLI 1973)

TABLE 4 - Summary of myological differences, *Iguanidae*

MUSCLE	<i>IGUANA</i>	<i>CTENOSAURA</i>	<i>SCELOPORUS</i>
<i>M. adductor mandibularis externus (mame) - levator anguli oris</i>	large wing shape, fleshy insertion into <i>Mundplatt</i>	large muscle, small insertion to <i>Mundplatt</i>	small muscle, narrow insertion to <i>Mundplatt</i>
<i>superficialis</i>	fleshy origin	origin more tendinous	origin fleshy, proportionately widest
<i>medius</i>	aponeurotic, dorsal and ventral heads semi-continuous	aponeurotic, dorsal and ventral heads semi-continuous	aponeurotic, dorsal and ventral heads continuous
<i>profundus</i>	small tendinous anterior band, semi-tortuous fibers	large, wide tendinous anteroventral band, flat	small tendinous anterior band, semi-tortuous fibers
<i>M. pseudotemporalis (mami) superficialis</i>	fan-shaped, aponeurotic insertion	crescent-shaped	fan-shaped
<i>profundus</i>	small ribbon-shaped slip, fleshy origin	fan-shaped, more tendinous origin on epipterygoid and parietal	long slip to superior epipterygoid, thick tendinous insertion to coronoid process
<i>M. pterygomandibularis</i>	very large, narrow	large, wide and tendinous	small flat straight sheet
<i>M. adductor mandibularis posterior</i>	large, wide tendon ventally attached to articular	large, wide tendinous insertion on quadrate and articular	small wide insertion to articular
<i>M. levator pterygoideus</i>	small ribbon, small tendinous origin on prootic membrane	large ribbon	narrow ribbon with tendinous origin on prootic membrane
<i>M. protractor pterygoideus</i>	small insertion	wide insertion	wide insertion
<i>M. depressor mandibulae</i>	narrow, delicate, tendinous insertion	narrow slip but wider than <i>I. iguana</i> , narrow tendonous slip	very large, wide sheet, broad muscular insertion, tripartite
<i>M. levator bulbi</i>	large triangle	small flat triangle	small flat triangle

The Prosauropods

OSTEOLOGY

All prosauropod skull materials described here are from *Plateosaurus engelhardti* (AMNH 6810) and the *Anchisaurus polyzelus* (YPM 1883). The skull of these relatively large-bodied forms are typically small and lightly built.

Taphonomically, *Anchisaurus polyzelus* was obliquely deformed and slightly flattened to its present right dorsolateral and left ventrolateral configuration. Individual bones are variably disarticulated and some are missing. The right postorbital bone was left very well intact, though it is cracked in several locations. The mandible has been preserved almost to its natural configuration. The quadrates are close in their natural position and articulate with the mandible on the right side.

The skull of *Plateosaurus engelhardti* is an almost complete, well-preserved specimen. An epoxy cast of this specimen was received completely disarticulated and was used in this reconstruction.

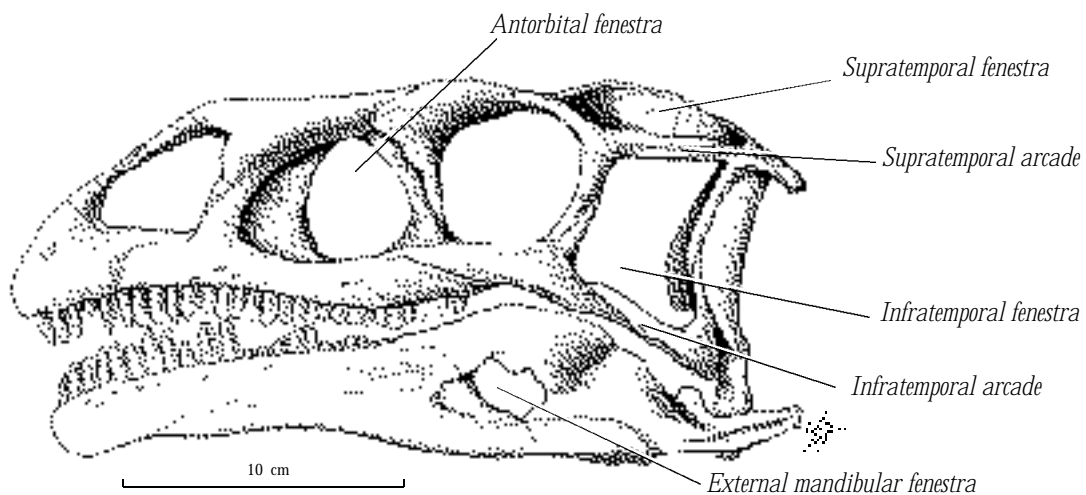


FIG. 16 - Osteological location of fenestrae in prosauropod cranium (*Plateosaurus engelhardti*).
 Note: the hard palate has been omitted from this illustration for clarity of the skull.

The oblique shift of the supratemporal fenestra to the infratemporal fenestra in iguanids with respect to diet may be applied to prosauropods. *Plateosaurus engelhardti* displays the same square relationship of its temporal fenestrae as the herbivorous *Iguana iguana* is oriented almost at a right angle with the infratemporal fenestra (see FIG. 16). There might be more support in speculating the diet of *Plateosaurus engelhardti* as being herbivorous with the additional display of herbivorous dentition. This relationship also applies to *Anchisaurus polyzelus* in that its temporal fenestrae shift to the oblique relationship like that of the insectivorous *Ctenosaura hemilopha* and *C. pectinata* or the omnivorous *Sceloporous magister*. This relationship between the two fenestrae has a direct effect on the shapes and insertions of the jaw musculature under study here. The jaw articulation in prosauropods is ventrally offset with respect to the tooth row, as in most herbivores.

The skull consists of 33 different bones and, like the iguanid skull, is divided into three parts: the chondrocranium, the splanchnocranium, and the dermatocranium. Bones are paired with a few exceptions:

THE DERMATOCRANIUM (see FIGS. 17-20)

Facial Series

Premaxilla (pm): This is a fairly flat, pair of bones located most anteriorly that form the anterior border of the external nares. In *Plateosaurus engelhardti*, the medial surfaces articulate with one another quite well. This bone also bears five teeth ventrally in *Plateosaurus engelhardti*, although, *Anchisaurus polyzelus* has only one tooth preserved on the right side. According to GALTON (1976), there were probably about five or six teeth per premaxilla. In *Anchisaurus polyzelus*, the premaxilla consist of the anterior-most four bone fragments anteriorly, an horizontal bar on the left lateral side, and three articulated fragments on the right. They are closely associated posteriorly with the maxilla on both sides.

Maxilla (mx): This paired bone, in addition to the nasal bone, forms the majority of the lateral surface of the facial region of the skull. The maxilla articulates posteriorly with the jugal, dorsally with the nasal and anteriorly with the premaxilla. It forms the posterior

border of the external nares and the anterior and ventral borders of the *antorbital fenestra*¹. In *Anchisaurus polyzelus*, the right maxilla is more complete than the left. This bone also bears the remainder of the teeth of the upper jaw. The teeth are considered homodont in form and thecodont (in sockets) in placement. In *Plateosaurus engelhardti*, there are 24 tooth positions on the left side and 20 on the right. Tooth height decreases anteroposteriorly from the middle of the tooth row. The same seems to be true of *Anchisaurus polyzelus* from the five teeth preserved on the left side. All teeth are thecodont.

Nasal (n): This pair of bones are located dorsal and posterior to the premaxilla along the midline of the skull. In *Plateosaurus engelhardti*, this element comprises most of the roof of the skull. However, most of the lateral surface, especially its posterolateral border is missing. Its dorsal surface has been well preserved except for its medial edges. These edges do not articulate very well with one another as they are incomplete. The nasal articulates with the posterior tip of the premaxilla and the dorsal border of the maxilla, completing the edges of the external nares. Ventrally, it contributes to the roof of the antorbital fenestra. Posteriorly, the nasal articulates with the frontal, while posterolaterally, it articulates with the prefrontals. In *Anchisaurus polyzelus*, only three small fragments of this bone have been preserved on the anterior border of the right lateral side.

Orbital Series

Prefrontal (pf): This paired bone forms the anterodorsal border of the orbits. It articulates with the frontal, lacrimal and nasal bones medially, anteroventrally, and anteriorly respectively. In *Plateosaurus engelhardti*, this bone is slightly incomplete anteriorly while *Anchisaurus polyzelus*, it is much narrower and represented by two twisted fragments on the right side.

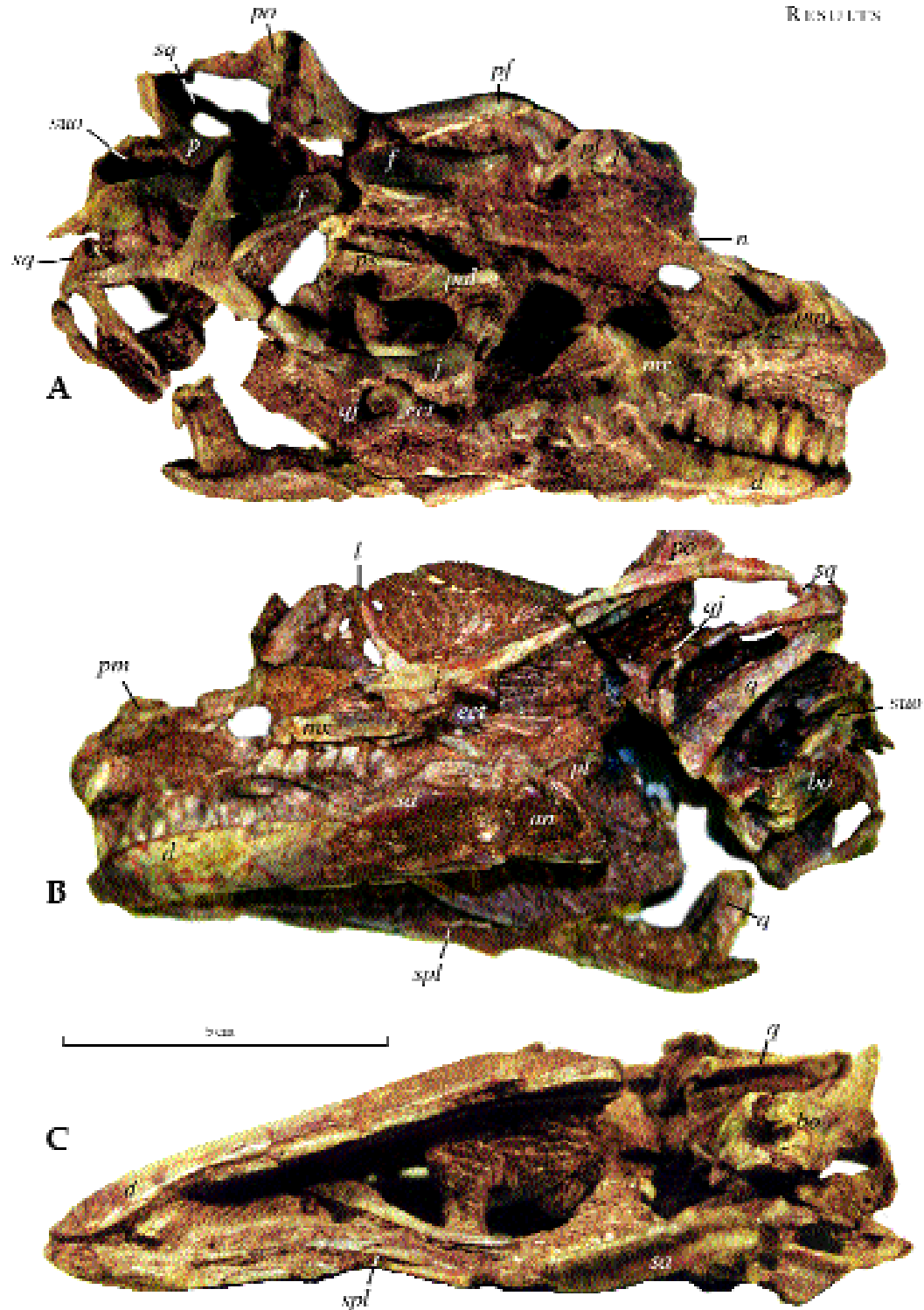
1 The antorbital fenestra is an opening in the skull usually bounded by the maxilla and lacrimal bones (in later forms this may also include the nasal or jugal bones). This opening is occupied by a pneumatic chamber (air sac) (WITMER 1997). The posterior nasal passage functions as the site of the middle respiratory turbinate in modern birds (WITMER 1989). The antorbital fenestra is a characteristic typically found in archosaurs whose modern descendants include crocodiles and birds (WITMER 1995). The antorbital fenestra distinguishes archosaurs from their diapsid relatives such as the iguanids.

Lacrima (l): This vertical paired bone forms the anterior border of the orbits and the posterior border of the antorbital fenestra. It articulates with the prefrontal and jugal bones posteriorly and ventrally, respectively. In *Plateosaurus engelhardti*, the ventral process of this bone has a very well preserved lateral facet for articulation with both the jugal and the posterior process of the maxilla. In *Anchisaurus polyzelus*, this bone is represented by a small ventrally-located bone fragment, comprising its ventral-most process. Another well-preserved vertical bar can be found on the left side of the specimen. Its articulation with the jugal has been preserved. According to GALTON (1984), its medial surface also articulates with the maxilla.

Jugal (j): This paired, Y-shaped bone forms the ventral border of the orbits. In *Plateosaurus engelhardti*, the jugal articulates with the maxilla anteroventrally and the lacrimal medially. Posteriorly, with its dorsal process articulating with the postorbital, it forms the anterior border of the infratemporal fenestra, the region which contains a majority of the jaw muscles reconstructed here. The posterior process articulates with the quadratojugal to form the infratemporal arcade. In *Anchisaurus polyzelus*, this bone is incomplete, but well represented on both sides of the skull. The left jugal articulates in its natural position with the surrounding lacrimal, maxilla and postorbital. The maxilla probably articulates slightly with the jugals anteroventrally (GALTON 1976).

Quadratojugal (qj): Not found in iguanids, this bone in prosauropods is flat, V-shaped, and articulates with the posterior process of the jugal. It constitutes the posteroventral corner of the infratemporal fenestra. In *Plateosaurus engelhardti*, the quadratojugal probably articulated with the ventral tip of the squamosal, although this could not be reconstructed in that particular configuration. Its articulation with the quadrate along its posterior edge was reconstructed without its dorsal process. In *Anchisaurus polyzelus*, this bone is a small fragment ventral to the right posterior jugal. According to GALTON (1976), its ventral surface rests more anteriorly than it does in *Plateosaurus engelhardti*.

Postorbital (po): This paired, triangular shaped bone is well preserved in both *Plateosaurus engelhardti* and *Anchisaurus polyzelus*. Its three processes separate the supratemporal fenestra,



Courtesy of the Yale University Peabody Museum of Natural History

FIG. 18 . PROSAUROPOID CRANIAL OSTEOLOGY, *Anchosaurus polyzelus*; A Right dorso-lateral view, B Left ventro-lateral view, C Ventral view; *ang* angular, *ar* articular, *bo* basoccipital, *bs* basisphenoid, *c* coronoid, *cp* coronoid process, *d* dentary, *et* ectopterygoid, *f* frontal, *j* jugal, *l* lacrimal, *mx* maxilla, *n* nasal, *p* parietal, *pal* palatine, *pf* prefrontal, *pm* premaxilla, *po* postorbital, *pt* pterygoid, *q* quadrate, *qa* quadratoangular, *ra* retroarticular process, *sa* surangular, *spl* splenial, *sq* squamosal, *ss* supraoccipital.

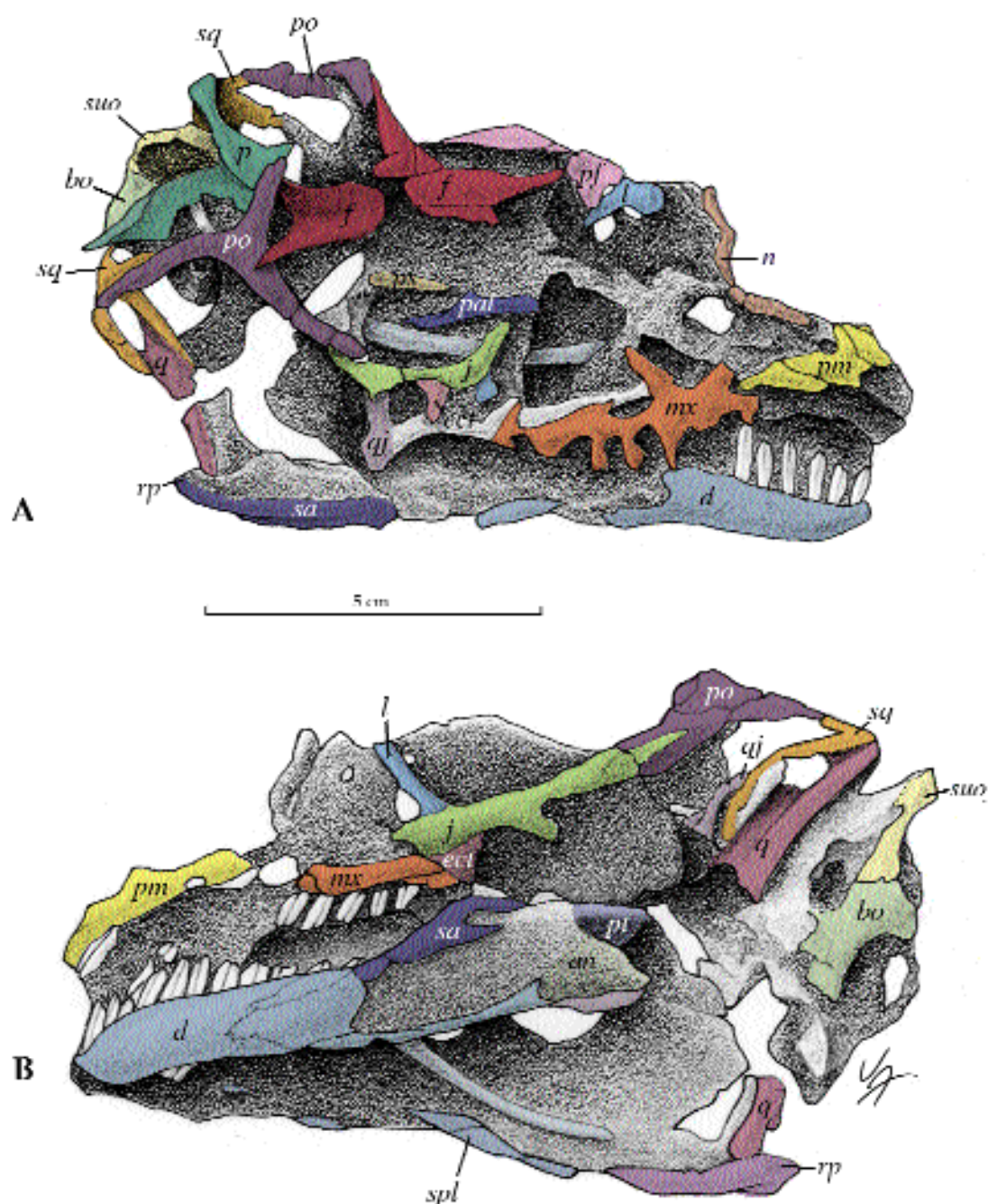


FIG. 19 - PROSAUROPOD CRANIAL OSTEOLOGY, *Anchisaurus polyzelus*, A Right dorso-lateral view, B Left ventro-lateral view; *an* angular, *ar* articular, *bo* basioccipital, *bs* basisphenoid, *c* coronoid, *cp* coronoid process, *d* dentary, *ect* ectopterygoid, *f* frontal, *j* jugal, *l* lacrimal, *mx* maxilla, *n* nasal, *p* parietal, *pal* palatine, *pl* prefrontal, *pm* premaxilla, *po* postorbital, *pt* pterygoid, *q* quadrate, *qj* quadratojugal, *rp* retromarginal process, *sa* surangular, *spl* splenial, *sq* squamosal, *suo* supraoccipital.

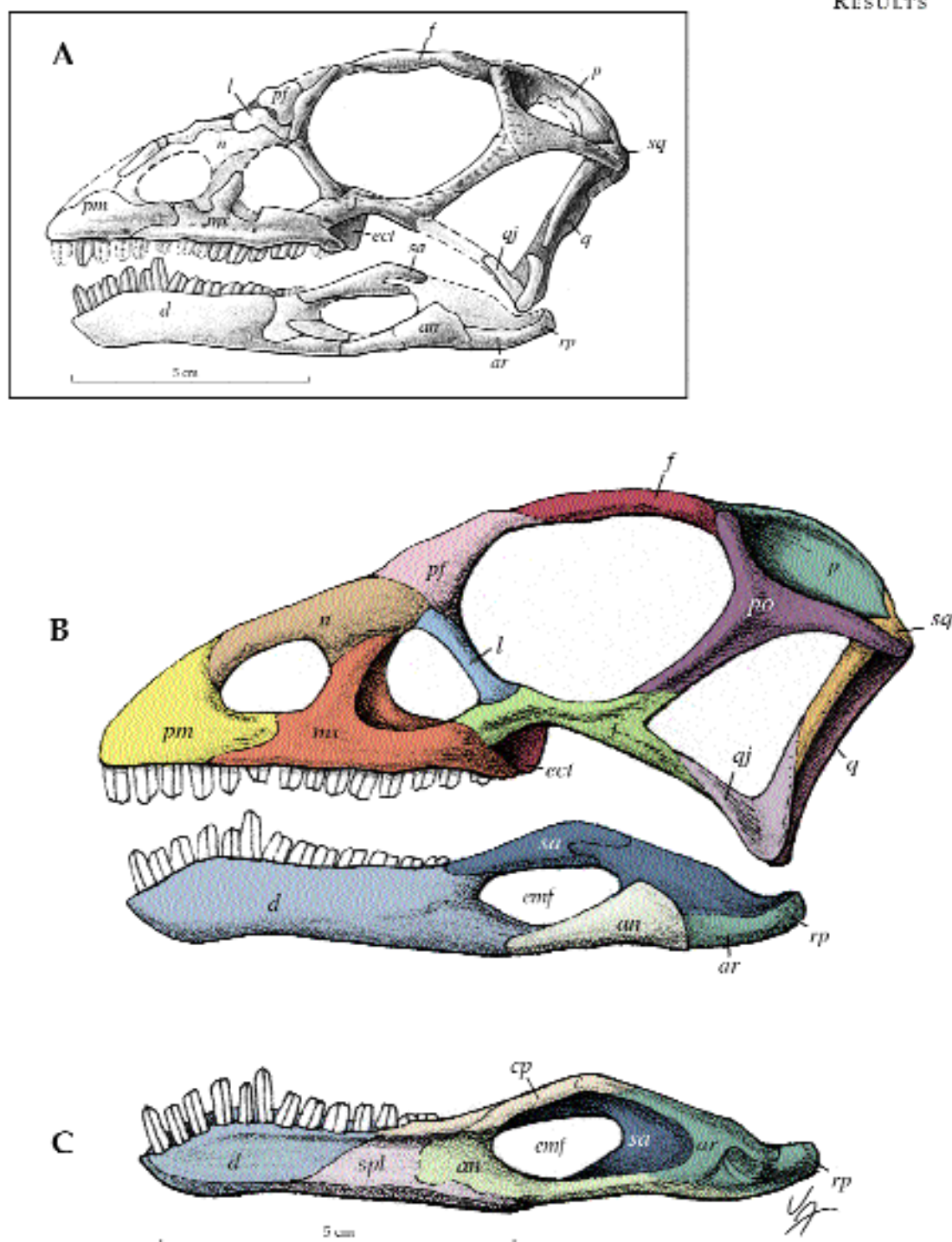


FIG. 20 - PROSAUROPOD CRANIAL OSTEOLOGY RECONSTRUCTED, *Anchisaurus polyzelus*. A Reconstruction model, B Left lateral cranium and mandible, C Right medial mandible; an angular, ar articular, bo basioccipital, c coronoid, cp coronoid process, d dentary, ect ectopterygoid, emf external mandibular fenestra, f frontal, j jugal, l lacrimal, mx maxilla, n nasal, p parietal, pf prefrontal, pm premaxilla, po postorbital, q quadrate, qj quadratojugal, rp retroarticular process, sa surangular, spl splenial, sq squamosal.

the infratemporal fenestra and the posterior border of the orbit. Its ventral ramus articulates with the jugal. Its posterior ramus articulates with the squamosal, forming the supratemporal arcade. This arcade divides the supratemporal fenestra from the infratemporal fenestra, as seen in iguanids. The medial postorbital portion of the arcade also serves as a site of origin for *M. adductor mandibulae externus superficialis*, as there is a slight horizontal facet for muscle attachment. In *Plateosaurus engelhardti*, the dorsal ramus of the postorbital articulates with the postfrontal. However, in *Anchisaurus polyzelus*, the dorsal ramus articulates with the frontal. According to GALTON (1984), the dorsal portion of the postorbital bone has been considered by others to be the postfrontal bone, limiting the ventral ramus to be the postorbital. However, GALTON notes that what was thought to have been a suture separating these two supposed bones was, in fact, a crack. Therefore, no postorbital bone will be discussed as it has not been found in either specimen examined.

Skull Roof

Frontal (f): This single bone, fused from right and left halves, forms the roof of the skull and the dorsal borders of the orbits. In *Plateosaurus engelhardti*, this bone is incomplete on its anterior border and is fused with the parietal on its posterior border. A prominent scar on its lateral surface very well may have served as a site of origin for *M. pseudotemporalis superficialis*; this was reconstructed in the *Plateosaurus engelhardti* and can be seen in FIGURE 22. In *Anchisaurus polyzelus*, this bone was preserved on the right side of the skull, but was broken into two major fragments. In contrast to *Plateosaurus engelhardti*, the frontal bone of *Anchisaurus polyzelus* constituted more of the dorsal border of the orbit, while the enlarged prefrontal in *Plateosaurus engelhardti* comprises the dorsal roof of the orbit.

Parietal (p): This single bone, located posterior to the frontal bone, forms most of the roof of the brain cavity as well as the dorsomedial border of the supratemporal fenestra. It is fused with the frontal bone anteriorly in *Plateosaurus engelhardti*, but in *Anchisaurus polyzelus*, it is separate from the frontal anteriorly, and well preserved on the right side of the skull. However, the two fragments are slightly shifted from one another. The posterior ramus of each parietal is twisted anterolaterally. In *Plateosaurus engelhardti*, the parietal may have served as the site of origin for many of the adductor and constrictor jaw muscles. A scar on

its posterolateral process is likely the site of origin for *M. adductor mandibulae externus medius*. Posteriorly, the posterior process of the parietal bones of both specimens articulates with the squamosal. Like *Plateosaurus engelhardti*, it presents well defined scars for muscle attachment.

Temporal Series

Squamosal (sq): In *Plateosaurus engelhardti* and *Anchisaurus polyzelus*, the squamosal is well preserved and is represented by a complete bone with four processes. This paired bone forms the posterior portion of the supratemporal arcade and the posterodorsal and posteroventral borders of the infratemporal and supratemporal fenestrae, respectively. The medial surface of the arcade as it articulates with the medial process was probably the site of origin for some of the adductor muscles. The ventral process of this element articulates with the quadrate bone.

Quadrate (q): This paired bone is located at the posterolateral angle of the skull. The ventral condyle of the quadrate forms the articulation with the mandible by a synovial joint. The also serves as a point of origin for *Mm. adductor mandibulae externus superficialis et medius*. In *Plateosaurus engelhardti*, its left lateral wing is missing. Thus, reconstructing an articulation with the ventral process of the squamosal was not possible. In *Anchisaurus polyzelus*, this bone was rotated 90° along its longitudinal axis (GALTON 1976).

Palatal Series

Vomer (v): In *Plateosaurus engelhardti*, this bone is represented by two longitudinal bone fragments. In *Anchisaurus polyzelus*, this bone is not seen as it rests medial to the maxillae. These two bones are located on the most anterior portion of the ventral aspect of the skull creating the first section of the palate. It articulates anteriorly with the posterior process of the premaxilla. The posterior edge of the vomer articulates laterally with the anterior border of the palatine bone.

Palatine (pal): This paired bone is located on the ventral aspect of the skull, articulating with the posterolateral aspect of the vomer, and forming the mid-region of the secondary palate.

In *Plateosaurus engelhardti*, the left bone is less complete than the right. In *Anchisaurus polyzelus*, it is represented only by a small fragment on the right side, dorsal to the arch of the jugal.

Pterygoid (pt): This paired bone forms the posterior-most section of the palate and forms the dorsal border of the pterygoid fenestra. In *Plateosaurus engelhardti*, a lateral view of the posterior palate can be seen in FIGURE 21. The posterior of the bone gives off a dorsal quadrate ramus and a ventral triangular-shaped basipterygoid flange. The pterygoid articulates laterally with the pterygoid process of the quadrate. The anterodorsal aspect of the bone gives off a wing-shaped process called the pterygoid flange. Between the medial surfaces of the quadrate rami of the pterygoid, the basipterygoid processes of the basisphenoid articulates with the posterior aspect of the pterygoid. In *Anchisaurus polyzelus*, this bone was represented as a small triangular-shaped process posterior to the left surangular, dorsal to the angular. This bone has several muscle scars for the insertions of M. pterygoideus (M. pterygomandibularis) and Mm. levator et protractor pterygoideus.

Epipterygoid (epi): This vertical process of the pterygoid bone is a separate ossification. It articulates dorsally with the parietal and ventrally with the pterygoid bone (the epipterygoid process). In *Plateosaurus engelhardti*, this articulation has been preserved. It may have served as a site of origin for M. pseudotemporalis profundus. In *Anchisaurus polyzelus*, the epipterygoid was not found because the sediment surrounding it had been removed. However, according to GALTON (1976), it was preserved posterior to the parasphenoid on the left side of the skull.

Ectopterygoid (ect): This is a crescent-shaped paired bone that, in *Plateosaurus engelhardti*, is located anterior to the pterygoid and lies vertically on the lateral lower region of the skull and forms the anterodorsal border of the pterygoid fenestra. It articulates anterodorsally with the jugal and the maxilla with its expanded lateral end. Its medial end is a flattened blade-like process that is overlapped by the pterygoid. In *Anchisaurus polyzelus*, this bone is represented on the left side of the skull by a small triangular element, posterior to the maxillary. On the right side, its articulation with the jugal is slightly twisted, but preserved, and can be visualized as a small extension ventral to the ventral edge of the jugal.

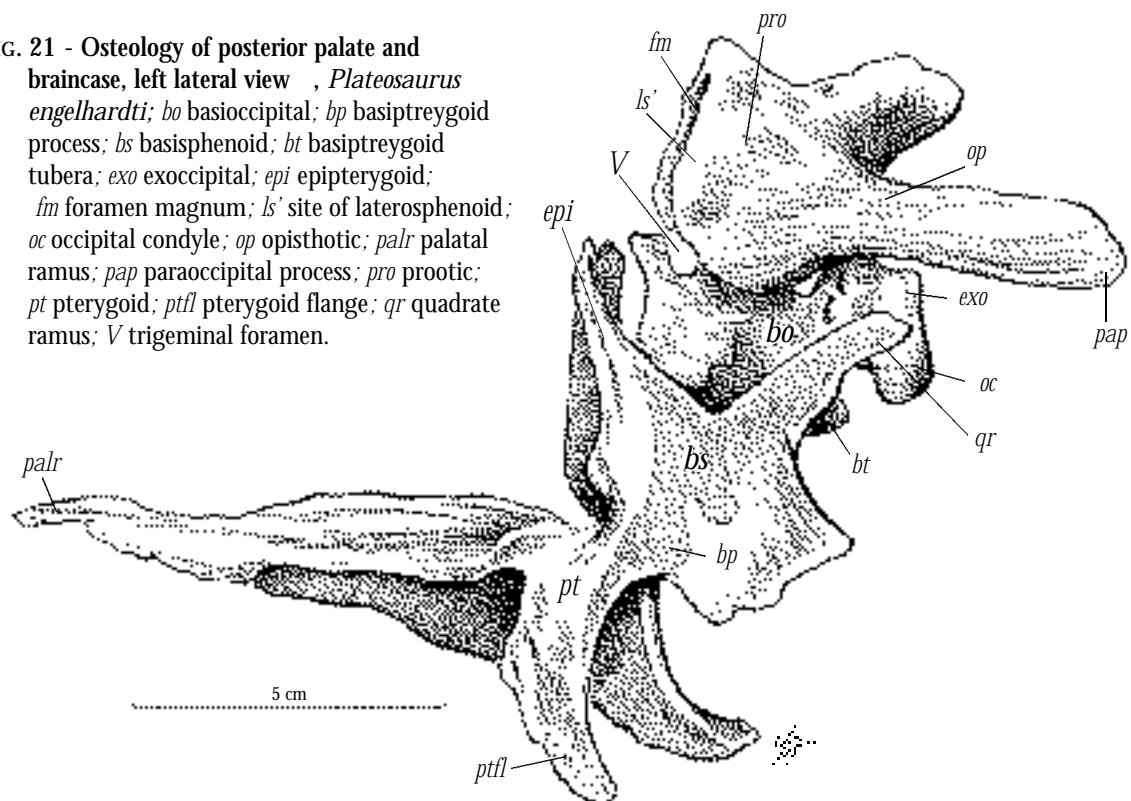
THE CHONDROCRANIUM (BRAINCASE) (see FIG. 21)

Basisphenoid (bs): This single bone forms a large portion of the floor of the brain cavity. It articulates with the pterygoid bones via a pair of basipterygoid processes. In *Plateosaurus engelhardti*, the basipterygoid processes fit tightly between the two quadrate rami of the pterygoid. In *Anchisaurus polyzelus*, the basisphenoid can be seen only posteriorly and laterally on the right side of the skull, ventral to the foramen magnum and the basioccipital.

Parasphenoid (ps): This single bone forms the anterior-most portion of the basicranium, projecting from the medial surface of the basipterygoid process (bp) of the basisphenoid (GALTON 1984). This bone is missing from *Plateosaurus engelhardti*.

Basioccipital (bo): This bone forms the remainder of the brain cavity floor as well as the majority of the occipital condyle ventral to the foramen magnum. In *Plateosaurus engelhardti*, the articulation of this bone with the basisphenoid has been preserved. In *Anchisaurus polyzelus*, this bone can best be seen on the posterior left side of the skull dorsal to the

FIG. 21 - Osteology of posterior palate and braincase, left lateral view, *Plateosaurus engelhardti*; bo basioccipital; bp basipterygoid process; bs basisphenoid; bt basipterygoid tubera; exo exoccipital; epi epipterygoid; fm foramen magnum; ls' site of laterosphenoid; oc occipital condyle; op opisthotic; palr palatal ramus; pap paraoccipital process; pro prootic; pt pterygoid; ptfl pterygoid flange; qr quadrate ramus; V trigeminal foramen.



basisphenoid. A dorsally-located paroccipital process has also been preserved in *Anchisaurus polyzelus*. According to GALTON (1976), its position has been twisted at the basioccipital-basisphenoid suture such that the braincase is directed dorsally at a 45° angle.

Exoccipital (exo): This bone forms the lateral borders of the foramen magnum and is located dorsal to the basioccipital. Ventrolaterally are the dorsal vagus and the ventral hypoglossal foramina. Ventral to these two foramina are another two hypoglossal foramina between the basioccipital et occipital.

Supraoccipital (suo): This is a single bone forming the posterodorsal component of the braincase and the dorsal border of the foramen magnum. It articulates ventrolaterally with the prootic bones. Its anterior-most portion articulates dorsally with the parietal.

Laterosphenoid (ls): This pair of bones forms the anterior-most portion of the basicranium. The anterior portion expands forming a facet for which to articulate with the frontal and parietal bones, dorsally, and the postorbital anterolaterally. It articulates with the prootic posteriorly and provides a surface for the insertion of M. protractor pterygoideus. Its anterior edge contributes to the posterior portion of the trigeminal foramen.

Orbitosphenoid (os): These two c-shaped bones articulate with each other to enclose the optic foramen.

Prootic (pro): This pair of bones is located anterior to the supraoccipital forming the lateral portion of the braincase. Anteriorly, it rests against the epipterygoid process. Posteriorly it articulates with the opisthotic. The laterosphenoid articulates the anterior surface of the prootic.

Opisthotic (op): This bone is a flat posterior projection of the lateral wall of the braincase, whose anterior suture with the prootic is indistinguishable. Its dorsal-most edge serves as a partial site of origin for M. depressor mandibulae as this muscle curves dorsomedially over the posterior ramus of the squamosal.

THE MANDIBLE (see FIGS. 17 and 20)

The lower jaw, referred to as the mandible, is comprised of six paired bones. It serves as a major insertion site for all of the jaw muscles except the constrictor group.

Dentary (d): This paired bone is located most anteriorly, articulates with its counterpart at the mandibular symphysis and forms the majority of the mandible in both prosauropod specimens. In *Plateosaurus engelhardti*, it is very well preserved and has 22 tooth positions on the left dentary; 18 tooth positions are found on the right dentary. As mentioned previously, the teeth are homodont and thecodont. Tooth height decreases as their location moves posteriorly. Though denticles are difficult to visualize in the cast model, some teeth bear rounded spatulate-shaped crowns. Anteriorly, the dentary is pierced by foramina on its lateral surface for the exit of several small nerves. The dentary articulates posteriorly with the splenial (on its medial side), the angular, the surangular, and the coronoid process. In *Anchisaurus polyzelus*, this bone is also well preserved, indicating 12 tooth positions on the left dentary and 6 tooth positions are found on the right dentary. The number of teeth suggest this specimen may have been adolescent. The surangular on the left side articulates with the posterior aspect of the left dentary, giving a very well preserved form for which the mandible could be reconstructed.

Coronoid (co): This bone is a ridge located on the medial side of the dorsal portion of the mandibular foramen. It probably served as a major site of insertion for the adductor muscle group. In *Plateosaurus engelhardti*, the coronoid extends above the surangular and marks the mid-portion of the mandibular foramen. In *Anchisaurus polyzelus*, this ridge cannot be seen. However, an elevation of the surangular suggests a similar structure to that found in *Plateosaurus engelhardti* probably existed and was an attachment site for adductor musculature by the insertion of a wide bodenaponeurosis.

Intercoronoid (ic): Not found in iguanids, this bone forms a ridge located on the medial side of the dorsal portion of the mandible. It probably served as an additional site of insertion for the adductor muscle group. In *Plateosaurus engelhardti*, it extends from approximately the mid-portion of the dentary at the tenth tooth position to the anterior surangular. On the

right mandible, it dorsally overlaps the splenial and articular bones. This bone was not found in *Anchisaurus polyzelus*.

Surangular [*Supra-angular*] (sa): This long bone lies posterior to the dentary and forms the dorsal-most portion of the mandible. Its medial surface bears a large mandibular foramen. In *Plateosaurus engelhardti*, its thicker dorsal edge probably provided the site of insertion for M. adductor mandibulae externus superficialis laterally, and the Mm. adductor mandibulae externus medius et profundus and M. pseudotemporalis muscles medially. In *Anchisaurus polyzelus*, the right surangular is located ventrally at the posterior-most portion of the mandible. Its dorsal prominence also suggests a similar insertion site for the adductor and pseudotemporalis muscles. In both prosauropods, a bodenaponeurosis similar to that of modern lizards probably existed as a common tendon for the reception of the collective forces of these jaw muscles.

Angular (an): This horizontal bone is located ventral to the surangular and posterior to the dentary. In *Plateosaurus engelhardti*, it forms the ventral portion of the mandibular foramen. On the medial surface of the mandible, it overlaps the posterior portion of the prearticular. In *Anchisaurus polyzelus*, the angular is not very well distinguishable. However, it is represented by a posteriorly-located triangular element on the left mandible and a horizontally-placed remnant on the right side. The mandible was represented in the reconstruction as having a foramen dorsal to the dorsal border of the angular, and the ventral border of the surangular.

Prearticular (pa): This medially-located bone forms the anterior border of the mandibular foramen. In *Plateosaurus engelhardti*, it is very well preserved, located posterior to the splenial. Its posterior portion becomes narrow as it overlaps the articular. In *Anchisaurus polyzelus*, this bone could not be seen. However, it was artistically reconstructed in a medial view of the mandible based on the anatomy of the mandible of *Plateosaurus engelhardti*. M. adductor mandibulae posterior probably inserted into the anterior portion of the external mandibular fenestra.

Articular (ar): This is a dagger-shaped bone located at the posterior-most aspect of the mandible. Its dorsally-located articulation, called the *articular condyle*, accommodates the ventral condyle of the quadrate in a synovial joint that allowed movement of the mandible. In *Plateosaurus engelhardti*, the articular is very well preserved and several muscle insertion scars can be visualized. The retroarticular process projects posteriorly and probably received fibers from M. pterygomandibularis. Anteriorly, the retroarticular depression serves as a site of insertion for the dorsal portion of M. pterygomandibularis and its remaining fibers insert on the ventral, dorsal and angular surfaces. The apex of the triangular scar on the retroarticular process probably served as a site for the insertion of M. depressor mandibulae. Along its lateral border is the tympanic crest, a site for the attachment of the ventral border of the tympanum. In *Anchisaurus polyzelus*, this bone may be the remnant on the right side where the quadrate articulates with the mandible, but further information on its morphology and sites of muscle attachment is unavailable.

Splenial (spl): This bone is only visible from the medial side of the mandible. In *Plateosaurus engelhardti*, it articulates with most of the bones of the mandible, overlapping the posterior portion of the dentary. Posteriorly, it articulates with the prearticular. It is overlapped dorsally by the intercoronoid process and completes the medial portion of the mandibular foramen. In *Anchisaurus polyzelus*, this bone is only represented by small ventrally-located fragments on both the right and left lateral sides.

MYOLOGY

The following description of jaw muscular reconstruction is based on the muscle groups found and described in the previously reported Iguanid Myology section.

SUPERFICIAL STRUCTURES

Although direct osteological evidence is lacking, it is assumed that superficial structures similar to those found in iguanids might be found in the prosauropod temporal fenestrae.

Mundplatt /Rictal Plate (mund): The *Mundplatt*, the extension of the posterior corner of the mouth found in iguanids, may have also existed in the prosauropods (see FIG. 24). Its dorsal border most likely served as an insertion site for *M. levator anguli oris* and *M. retractor anguli oris* in order to accommodate the opening of the mouth. The ventral length of the *Mundplatt* of *Plateosaurus engelhardti* may have resembled that of the herbivorous *Iguana iguana*, being shorter in height and longer in length (running along the ventral border of the infratemporal arcade) than that of *Anchisaurus polyzelus*.

Ligamentum quadratomandibulare (lq): This ligament is band of connective tissue extending from the posteroventral corner of the jugal to the ventrolateral corner of the quadrate. In prosauropods, an infratemporal arcade, consisting of the posteroventral ramus of the jugal and the anteroventral ramus of the quadratojugal, resided dorsal and lateral to its place. It is dorsally continuous with infratemporal fascia. Ventrally, it connects with the *Mundplatt*.

Infratemporal fascia (if): This thin tendinous sheet of fascia may have extended over the lateral-most adductor muscles and covered the majority of the infratemporal fenestra. Its apex originated from the anteroventral corner of the quadrate and fanned anterodorsally to insert on the ventral squamosal, ventral and posterior postorbital and posterior jugal.

ADDUCTOR MANDIBULAE GROUP

Similar to that of the iguanids, the adductor mandibulae group of muscles has been divided into the same three groups of muscles, according to their relationship to the three rami of the

trigeminal nerve: Mm. adductor mandibulae externus, internus et posterior (LAKJER 1926, OSTROM 1961, COSTELLI 1973, GALTON 1985). The M. adductor mandibulae externus muscle group presumably occurred lateral to the maxillary ramus (V_2) of the trigeminal nerve. This nerve would have separated the externus muscles from the internus muscles as it traveled anteriorly from the trigeminal foramen of the prootic to toward the orbit medial to the jugal bone. M. adductor mandibulae internus, hence, would have been found medial to the maxillary ramus (V_2) and anterior to the mandibular ramus of the trigeminal nerve. This nerve also exited the trigeminal foramen of the prootic, posterior to the maxillary ramus (V_2) and traveled ventrally and eventually turned anteriorly into the mandibular fenestra on the medial side of the mandible. M. adductor posterior was found posterior to the mandibular ramus (V_3). The remaining constrictor dorsalis muscles were medial to the mandibular ramus (V_3).

Bodenaponeurosis (bod): Just as in the iguanids, a thick aponeurotic tendon in prosauropods must have existed in order to accommodate the widespread forces of contraction to the mandible from the various muscles of both adductor mandibulae externus and internus muscle groups (pseudotemporalis portion). However, this tendon was wider than that of the iguanids (see FIGS. 22 and 23). The tripartite origins of the adductor mandibulae muscle group range from the frontal, parietal, quadrate, pterygoid, epipterygoid, postorbital and squamosal bones. The insertion of the bodenaponeurosis in prosauropods occurred on the elevated surface of the medial surface, dorsal and posterior borders of the ridge-shaped coronoid process of the medial mandible. The bodenaponeurosis was separated by the maxillary ramus (V_2) of the trigeminal nerve at the division between the externus and internus muscle groups.

M. Adductor Mandibulae Externus (mame): a tripartite muscle

M. Levator Anguli Oris (mlao): This muscle differs slightly in prosauropods than in iguanids (see FIG. 24) and here it is appropriate to make more general comparisons among reptiles. *Sphenodon*, a Lepidosaur with a similar skull structure to both iguanids and prosauropods, has an iguanid-like skull, with no antorbital fenestra, but with a complete infratemporal arcade (see FIG. 25). According to HAAS (1973:288-310), M.

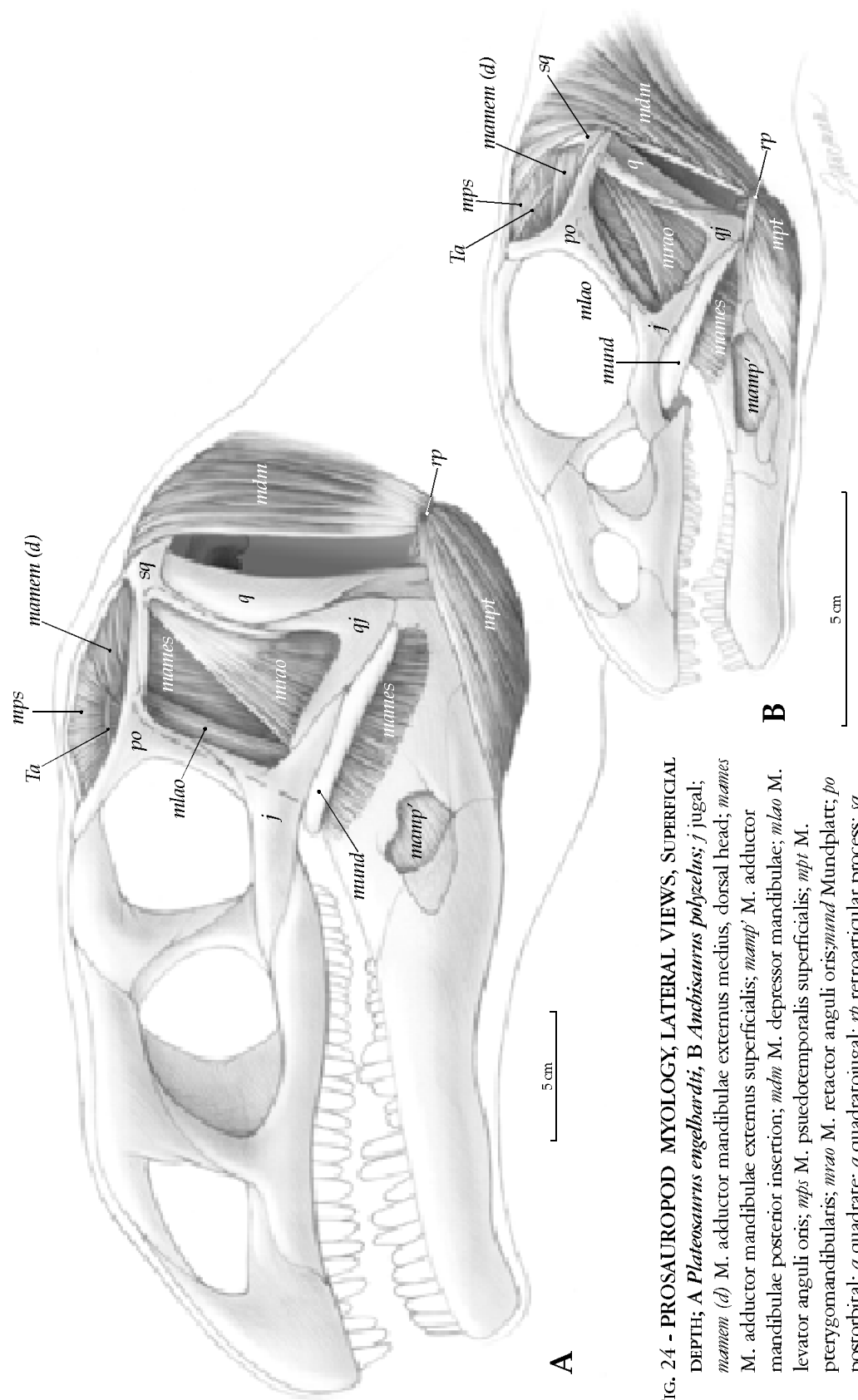


FIG. 24 - PROSAUROPOD MYOLOGY, LATERAL VIEWS, SUPERFICIAL DEPTH; A *Plateosaurus engelhardti*, B *Anchisaurus polyzelus*; *j* jugal; *mamem* (d) M. adductor mandibulae externus medius, dorsal head; *mames* M. adductor mandibulae externus superficialis; *mamp'* M. adductor mandibulae posterior insertion; *mmdm* M. depressor mandibulae; *mlao* M. levator anguli oris; *mips* M. psuedotemporalis superficialis; *mpt* M. pterygomandibularis; *mrao* M. retractor anguli oris; *mund* Mundplatt; *po* postorbital; *q* quadrate; *q* quadratojugal; *rp* retroarticular process; *sq* squamosal; *Ta* temporal artery.

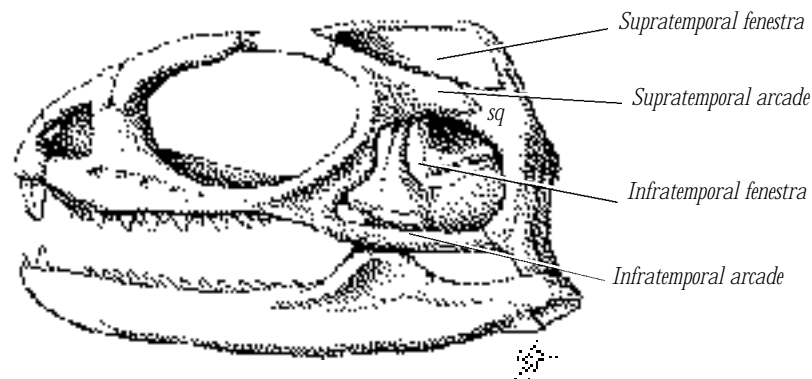


FIG. 25 - Osteological location of fenestrae in *Sphenodon* cranium; *sq* squamosal (after OSTROM 1961).

levator anguli oris, generally found in lizards, presents, “a more primitive arrangement in *Sphenodon*.” This muscle may have been one of two facial muscles (in addition to *M. retractor anguli oris*, to be described) that slightly elevate the mandible and pull the integument of the posterior corner of the mouth posterodorsally during adduction of the jaw. It probably resided in the infratemporal fenestra medial to the infratemporal fascia and lateral to *M. adductor mandibulae externus superficialis*. The extent of this muscle may have covered the anterior quarter of the fenestra. Originating on the surfaces of the ventral border the posterior ramus of the postorbital, the posterior border of the jugal and the infratemporal fascia medially. It traveled anteriorly and ventrally, medial to the infratemporal arcade, to insert into the medial surface of the anterior portion of the *Mundplatt*. As in herbivorous iguanids, *M. levator anguli oris* in *Plateosaurus engelhardti* may have been a shorter thicker muscle in proportion to that *Anchisaurus polyzelus*. In the latter prosauropod, this muscle may have followed the oblique edges of the ventral and dorsal rami of the postorbital and jugal, respectively. Fibers from its medial aspect may have inserted onto the ventral ridge of the coronoid process, lateral to a basal aponeurosis of the adductor muscles. This muscle was probably innervated by the third branch of the mandibular ramus (V_3) of the trigeminal nerve, like that of the iguanids.

M. Retractor Anguli Oris (*mrao*): This muscle is the only jaw muscle not previously described in the iguanid section as it is not found in these forms (see FIG. 24). However, it is found in *Sphenodon* (HAAS 1973). Because the cranial anatomy of *Sphenodon* is

considered primitive yet similar to prosauropods and to iguanids, this muscle may have existed in prosauropods. In addition to *M. levator anguli oris*, this muscle also aided in slightly elevating the mandible and pulling the integument of the posterior corner of the mouth posterodorsally during adduction of the jaw. It too most likely resided in the infratemporal fenestra medial to the infratemporal fascia and lateral to *M. adductor mandibulae externus superficialis*. The extent of this muscle may have covered almost half of the posterior section of the fenestra originating on the surfaces of the ventral border of the anterior ramus of the squamosal and the ventral edge of the postorbital. It traveled anteriorly and ventrally to insert into the posterior aspect of the medial surface of the *Mundplatt*. *M. retractor anguli oris* in *Plateosaurus engelhardti* may have been a wider muscle in proportion to that of *Anchisaurus polyzelus*. Fibers from its medial aspect may have inserted onto the ventral ridge of the coronoid process, lateral to the bodenaponeurosis of the adductor muscles. In keeping with iguanids, this muscle was probably innervated by the third branch of the mandibular ramus (V_3) of the trigeminal nerve.

M. Adductor Mandibulae Externus Superficialis (mames): This muscle occupied the superficial region of the infratemporal fenestra medial to *M. levator anguli oris* and lateral to *M. adductor mandibulae externus medius* (see FIG. 26). It originated on the surfaces of the medial squamosal, postorbital (and possibly the dorsal ramus of the jugal). The origin of this muscle in *Plateosaurus engelhardti* was most likely a fleshy origin. In contrast, the origin in *Anchisaurus polyzelus* was probably more tendonous, like that of *Ctenosaura hemilopha*, as indicated by the more oblique shape of the posterior region of the infratemporal fenestra. *M. adductor mandibulae externus superficialis* gradually would have made a transition from tendon to fleshy muscle as the tendon probably extended over almost half of the belly of the muscle. *M. adductor mandibulae externus superficialis* traveled anteriorly and ventrally, medial to the infratemporal arcade, to insert on the dorsolateral portion of the lower jaw, covering the coronoid process, surangular and articular. In *Plateosaurus engelhardti*, this muscle probably traveled more ventrally than anteriorly as compared to *Anchisaurus polyzelus*. Just as this muscle can be divided into an anterior and posterior head in iguanids, the prosauropod muscle might have had

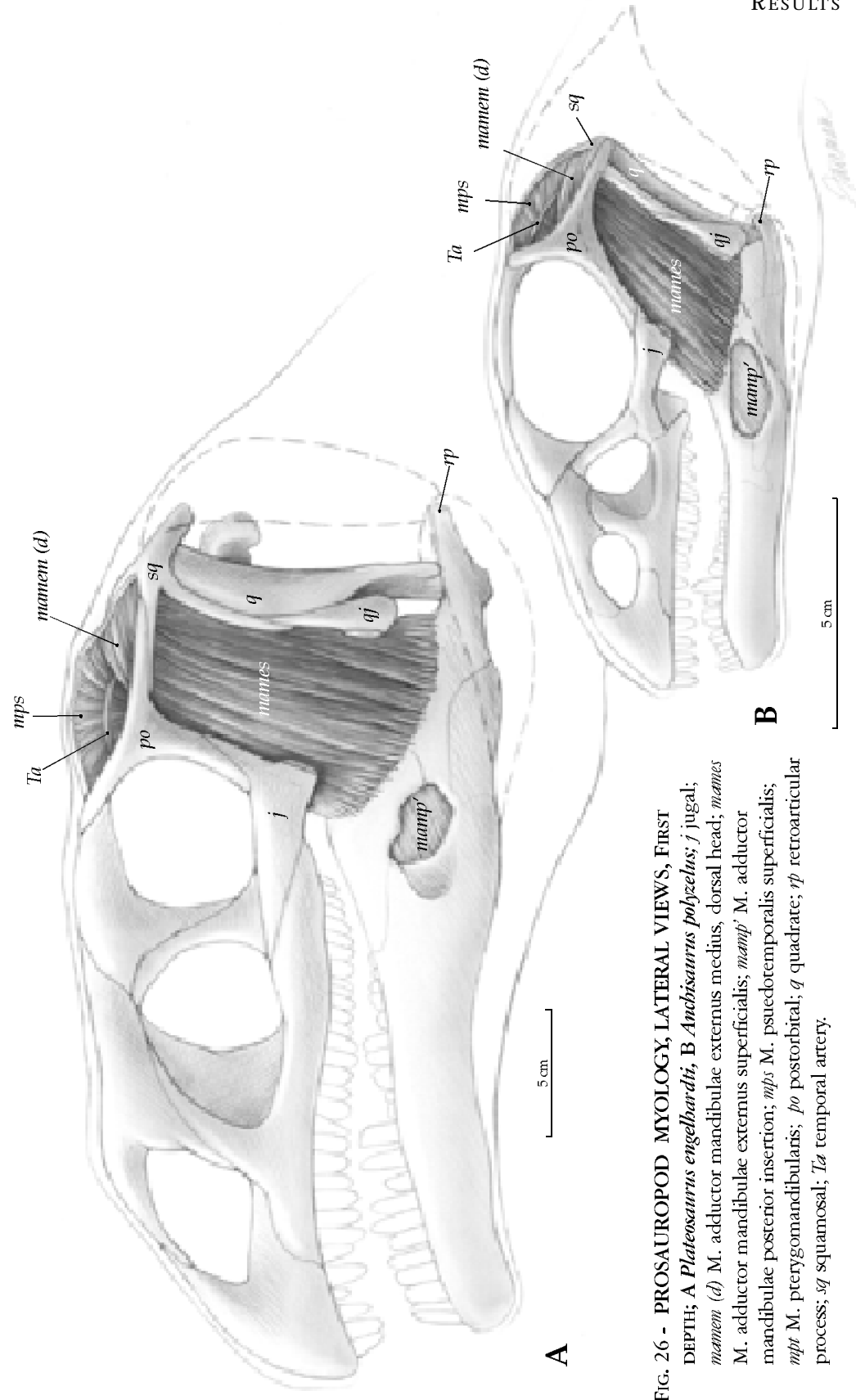


FIG. 26 - PROSAUROPOD MYOLOGY, LATERAL VIEWS, FIRST DEPTH; A *Platesosaurus engelhardti*, B *Anchisaurus polyzelus*; j jugal; *mamem (d)* M. adductor mandibulae externus medius, dorsal head; *mamem* M. adductor mandibulae externus superficialis; *mampt* M. adductor mandibulae posterior insertion; *mps* M. pseudotemporalis superficialis; *mpt* M. pterygomandibularis; *po* postorbital; *q* quadrate; *rp* retroarticular process; *sq* squamosal; *Ta* temporal artery.

fibers traveling in two orientations. Its anterior fibers may have traveled more ventrally and inserted into the anterior-most portion of the bodenaponeurosis. Its action was to elevate the mandible. As in the iguanids, this muscle was also likely to have been innervated by the third branch of the mandibular ramus (V_3) of the trigeminal nerve.

M. Adductor Mandibulae Externus Medius (mamem): This muscle would have originated on the surfaces of the medial squamosal, parietal, postorbital and anterior quadrate (see FIG. 27). Like in iguanids, this muscle could be divided into a dorsal and ventral head. Its dorsal head originated in the supratemporal fenestra, posterior to *M. pseudotemporalis superficialis*. In *Plateosaurus engelhardti*, the parietal bone has a distinct muscle origin scar that can be seen on the posterior-most portion of the supratemporal fenestra. Judging from this location, the fibers may have been more fan-shaped in orientation than that of *Anchisaurus polyzelus*. The shape of *M. adductor mandibulae externus medius* of the latter prosauropod would probably have resembled that of *Ctenosaura hemilopha* or *Sceloporus magister*, where the fibers are directed more antero-posteriorly. The temporal artery is likely to have traveled between *M. adductor mandibulae externus medius* and *M. pseudotemporalis superficialis*, from the posterior orbit to the anterodorsal border of *M. adductor mandibulae externus medius*. From the supratemporal fenestra, *M. adductor mandibulae externus medius* traveled medial to the supratemporal arcade, twisting more ventrally, and entered the infratemporal fenestra, thus becoming the ventral head. This portion of *M. adductor mandibulae externus medius* was located medial to *M. adductor mandibulae externus superficialis* and lateral to *M. adductor mandibulae externus profundus*. It traveled anteriorly and ventrally, passed medial to the infratemporal arcade and inserted on the dorsolateral portion of the anterior coronoid process, the surangular and the articular. Its aponeurotic insertion occurred mostly on the medial surfaces thereof. The ventral head of this muscle in *Plateosaurus engelhardti* may have had a larger area of tendon than in *Anchisaurus polyzelus*. It covers most of the anterior and dorsal portions of its insertion into the bodenaponeurosis. The ventral head of *M. adductor mandibulae externus medius* was separated medially from the tendon of *M. pseudotemporalis superficialis* by the maxillary ramus (V_2) of the trigeminal nerve. This occurred at the anterior border of the ventral

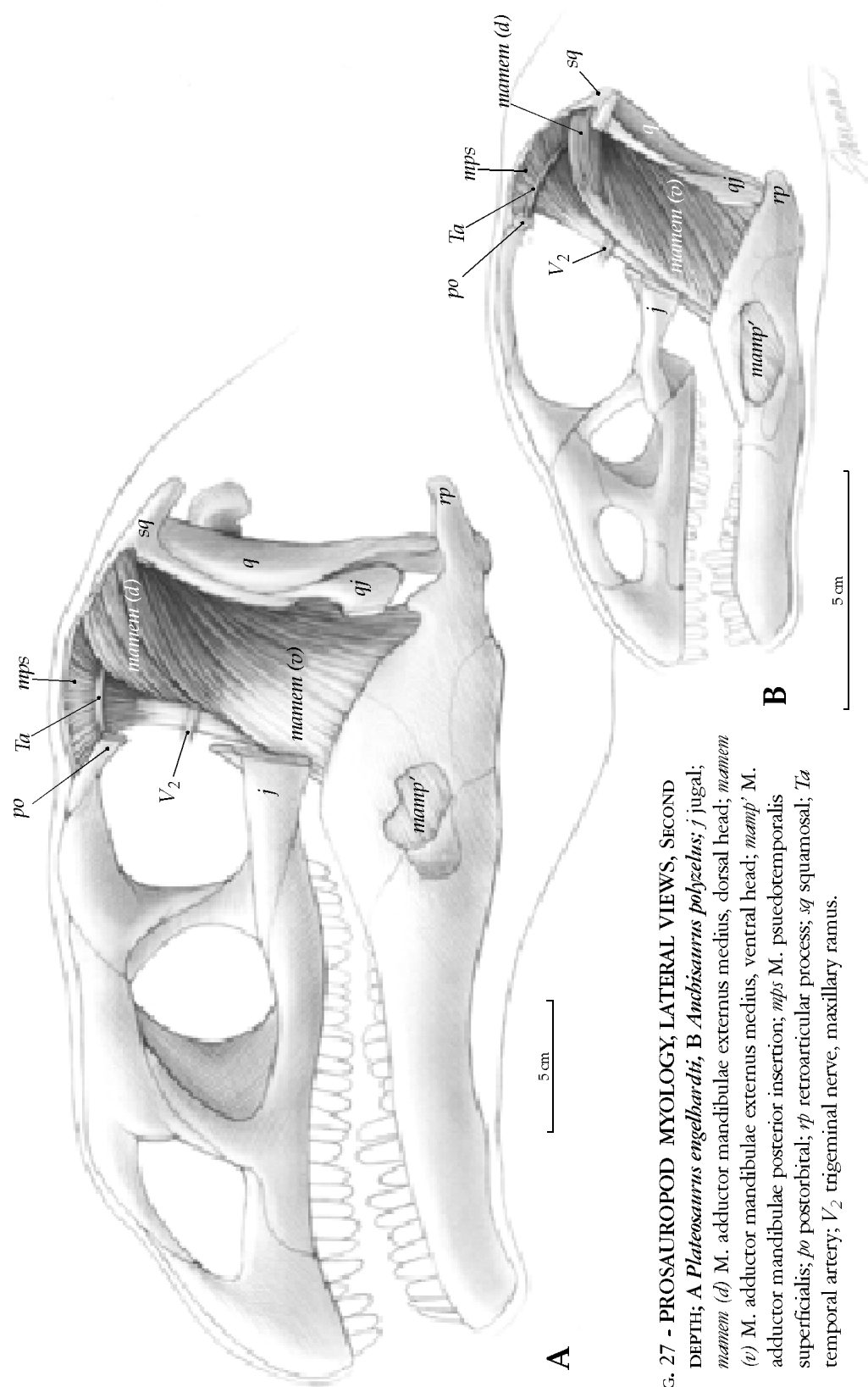


FIG. 27 - PROSAUROPOD MYOLOGY, LATERAL VIEWS, SECOND DEPTH; A *Plateosaurus engelhardti*, B *Anchisaurus polyzelus*; j jugal; *mamem (d)* M. adductor mandibulae externus medius, dorsal head; *mamem (v)* M. adductor mandibulae externus medius, ventral head; *mamp'* M. adductor mandibulae posterior insertion; *mps* M. pseudotemporalis superficialis; *po* postorbital; *rp* retroarticular process; *sq* squamosal; *Ta* temporal artery; *V₂* trigeminal nerve, maxillary ramus.

head. Overall, *M. adductor mandibulae externus medius* of *Anchisaurus polyzelus* was elongated most antero-posteriorly than that of *Plateosaurus engelhardti*, which ran more dorsoventrally, due to the oblique shift of the location of the infratemporal fenestra in *Anchisaurus polyzelus*. In both species, the action of this muscle elevated the mandible. This muscle was probably innervated by the third branch of the mandibular ramus (V_3) of the trigeminal nerve.

M. Adductor Mandibulae Externus Profundus (mamep): Medial to *M. adductor mandibulae externus medius*, *M. adductor mandibulae externus profundus* was the most medially located jaw muscle of the adductor mandibulae externus muscle group (see FIG. 28). Its dorsal head originated in the supratemporal fenestra on the medial surfaces of the parietal and squamosal. Exiting the supratemporal fenestra medial to the squamosal and traveling anteriorly and ventrally into the infratemporal fenestra. Passing medially to the infratemporal arcade, it inserted into the bodenaponeurosis on the medial portion of the lower jaw, to the coronoid process, and the surangular and articular bones. The ventral head of this muscle in *Plateosaurus engelhardti* probably possessed a small anterior band of tendon. In contrast, *M. adductor mandibulae externus profundus* of *Anchisaurus polyzelus* probably had a larger tendonous area covering most of the posterior and ventral portions of its insertion into the bodenaponeurosis. The anterior border of the ventral head of the profundus was most likely separated medially from the tendon of *M. pseudotemporalis superficialis* by the maxillary ramus (V_2) of the trigeminal nerve. Elevates the mandible, this muscle was probably innervated by the third branch of the mandibular ramus (V_3) of the trigeminal nerve.

M. Adductor Mandibulae Internus (mami):

M. Pseudotemporalis Superficialis (mps): This muscle was the largest jaw muscle occupying the supratemporal fenestra (see FIGS. 27 and 28). Anterior to *M. adductor mandibulae externus*, it originated on the lateral surface of the frontal, parietal bones, and may have been more anteriorly-located in prosauropods than in the iguanids because of the extension of the frontal portion of the fenestra. In *Plateosaurus engelhardti*, the posterolateral portion of the frontal and lateral parietal bones have a distinct origin scar

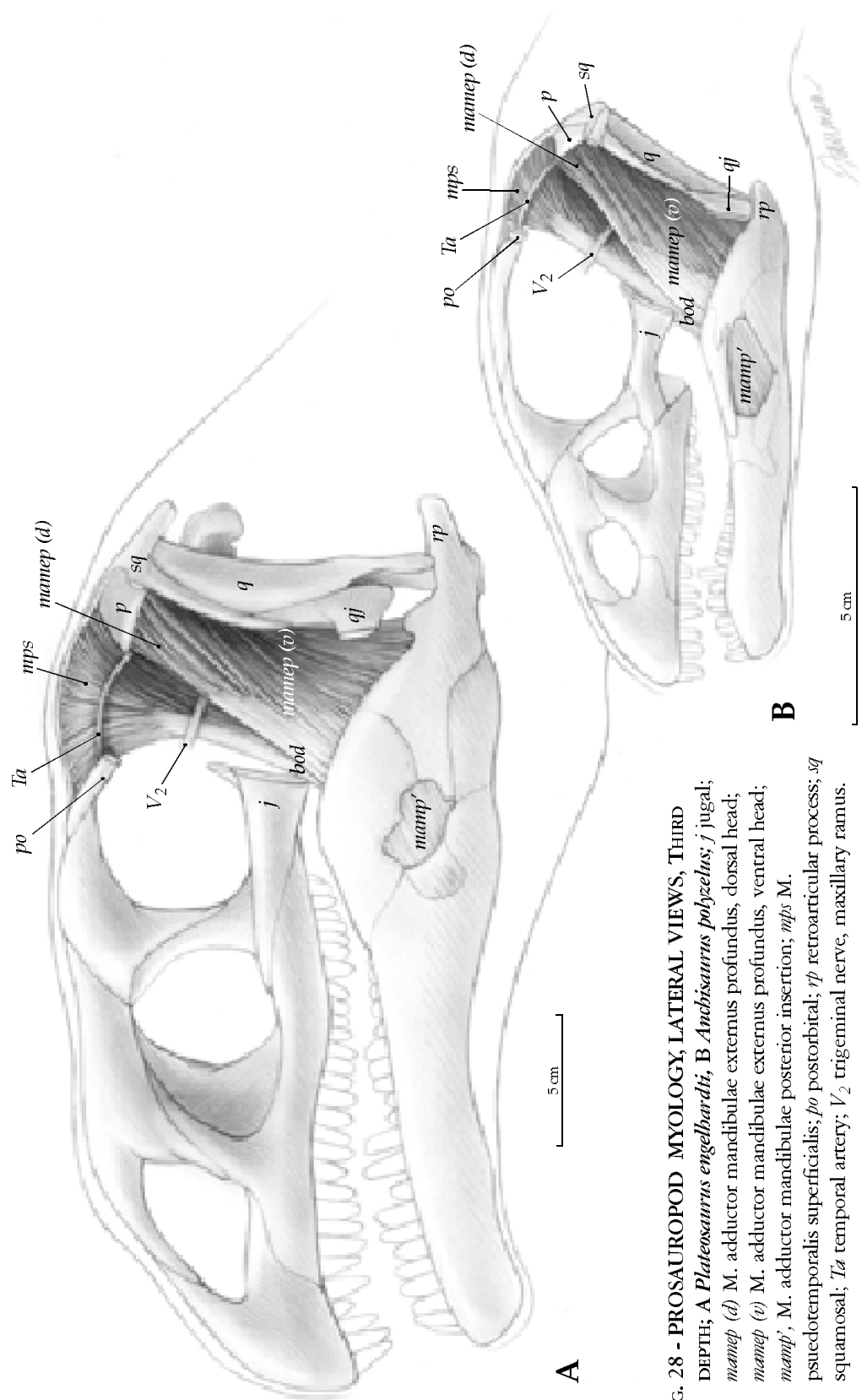


FIG. 28 - PROSAUROPOD MYOLOGY, LATERAL VIEWS, THIRD DEPTH; A *Plateosaurus engelhardti*, B *Anchisaurus polyzelus*; j jugal; *mam'ep (d)* M. adductor mandibulae externus profundus, dorsal head; *mam'ep (v)* M. adductor mandibulae externus profundus, ventral head; *mam'p*, M. adductor mandibulae posterior insertion; *mps* M. pseudotemporalis superficialis; *po* postorbital; *V2* retroarticular process; *sq* squamosal; *Ta* temporal artery; *V2* trigeminal nerve, maxillary ramus.

for this muscle that can be seen on the anterior-most portion of the supratemporal fenestra. The dorsal portion of this muscle in *Plateosaurus engelhardti* was probably fleshy and fan-shaped (with fibers running more dorso-ventrally). In contrast, *M. pseudotemporalis superficialis* in *Anchisaurus polyzelus* was probably fleshy and crescentic (with fibers running more anteroposteriorly). The thickness of this muscle might have been similar to that of iguanids. Its posterior fibers formed a thick wall of muscle filling much of the infratemporal fenestra. It traveled anteriorly and ventrally and its fibers became a convergent, strong slip of tendon that passed medial to the infratemporal arcade and inserted into the antero-medial portion of the bodenaponeurosis. The maxillary ramus (V_2) of the trigeminal nerve crossed over this insertion. The action of *M. pseudotemporalis superficialis* was to elevate the mandible. This muscle was likely innervated by the first branch of the mandibular ramus (V_3) of the trigeminal nerve.

M. Pseudotemporalis Profundus (mpp): This muscle was located directly medial to *M. pseudotemporalis superficialis* (see FIG. 29). Its fleshy origin begins on the ventrolateral surface of the parietal and the anterior ridge of the vertical ramus of the epipterygoid. Most of this muscle resided in the infratemporal fenestra. The fibers of this muscle ran slightly anteriorly and dove medially to the infratemporal fenestra and ventrally toward the coronoid process where they inserted into the medial-most portion of the bodenaponeurosis. Posterior to the epipterygoid bone and the posterior edge of the muscle, the root of the mandibular ramus (V_3) of the trigeminal nerve, passed ventrally toward the mandible and continued through the mandibular fenestra. *M. pseudotemporalis profundus* of iguanids consists of two separate muscle bellies, the second is visualized posterior and medial to the first. These two muscles may have existed in the prosauropods, given the larger surface area of the dorsal ramus of the epipterygoid bone. Its origin was probably slightly tendinous in *Anchisaurus polyzelus*, fleshy in *Plateosaurus engelhardti*. *M. pseudotemporalis profundus* in *Anchisaurus polyzelus* may have been proportionately larger than that in *Plateosaurus engelhardti* because of the oblique position of the elevation of the mandible to the supratemporal fenestra. The action of *M. pseudotemporalis profundus* elevated the mandible. This muscle was probably innervated by the first and fourth branches of the mandibular ramus of the trigeminal nerve.

M. Pterygomandibularis [*M. Pterygoideus* (GALTON 1984)] (mpt): In studying the complex structure of the iguanid *M. pterygomandibularis*, it is assumed the prosauropod structure might have been just as complex (see FIG. 24). The mandible and the palate of *Plateosaurus engelhardti* have sites for which this muscle could have inserted. GALTON (1984) divided this muscle into two parts that he called *pars dorsalis* and *pars ventralis*. It is possible, however, that this muscle was divided into three parts, as it is in iguanids, based on their sites of origin. *M. pterygomandibularis* *pars dorsalis* can thus be divided again into two separate parts, the first originating on the posteroventral aspect of the ectopterygoid. The fibers continued posteromedially to the pterygoid bone and the medial surface of the quadrate becoming its second origin. These two portions inserted ventromedially on the retroarticular process of the posterior mandible. The third part of the muscle most likely wrapped around the lateral side of the posterior mandible from the lateral pterygoid flange of the quadrate, thus surrounding the retroarticular process on both sides. This muscle elevated the mandible on both sides of its fulcrum lever. This muscle was probably innervated by the fourth branch of the mandibular ramus (V_3) of the trigeminal nerve.

M. Adductor Mandibulae Posterior (mamp): The last muscle of the adductor mandibulae muscle group is *M. adductor mandibulae posterior* (see FIG. 29). Similar to iguanids, it rested in the posteroventral corner of the infratemporal fenestra, anterior to the quadrate bone and medial to the quadratojugal portion of the infratemporal arcade. It originated on the quadrate bone at the pterygoid flange and extended anteriorly and slightly ventrally toward the medial surface of the mandible. Its tendinous insertion occurs at the anteromedial border of the inframandibular fenestra. Its action was to elevate the mandible. This muscle may have been innervated by the fifth branch of the mandibular ramus (V_3) of the trigeminal nerve.

M. Depressor Mandibulae (mdm): This muscle originated on the posterior surface of the squamosal bone (see FIG. 24). In *Plateosaurus engelhardti*, this muscle may have also originated at the tip of the paroccipital process adjacent to the squamosal and the parietal (GALTON 1985). Its anterior fibers may have covered part of the anterior process of the

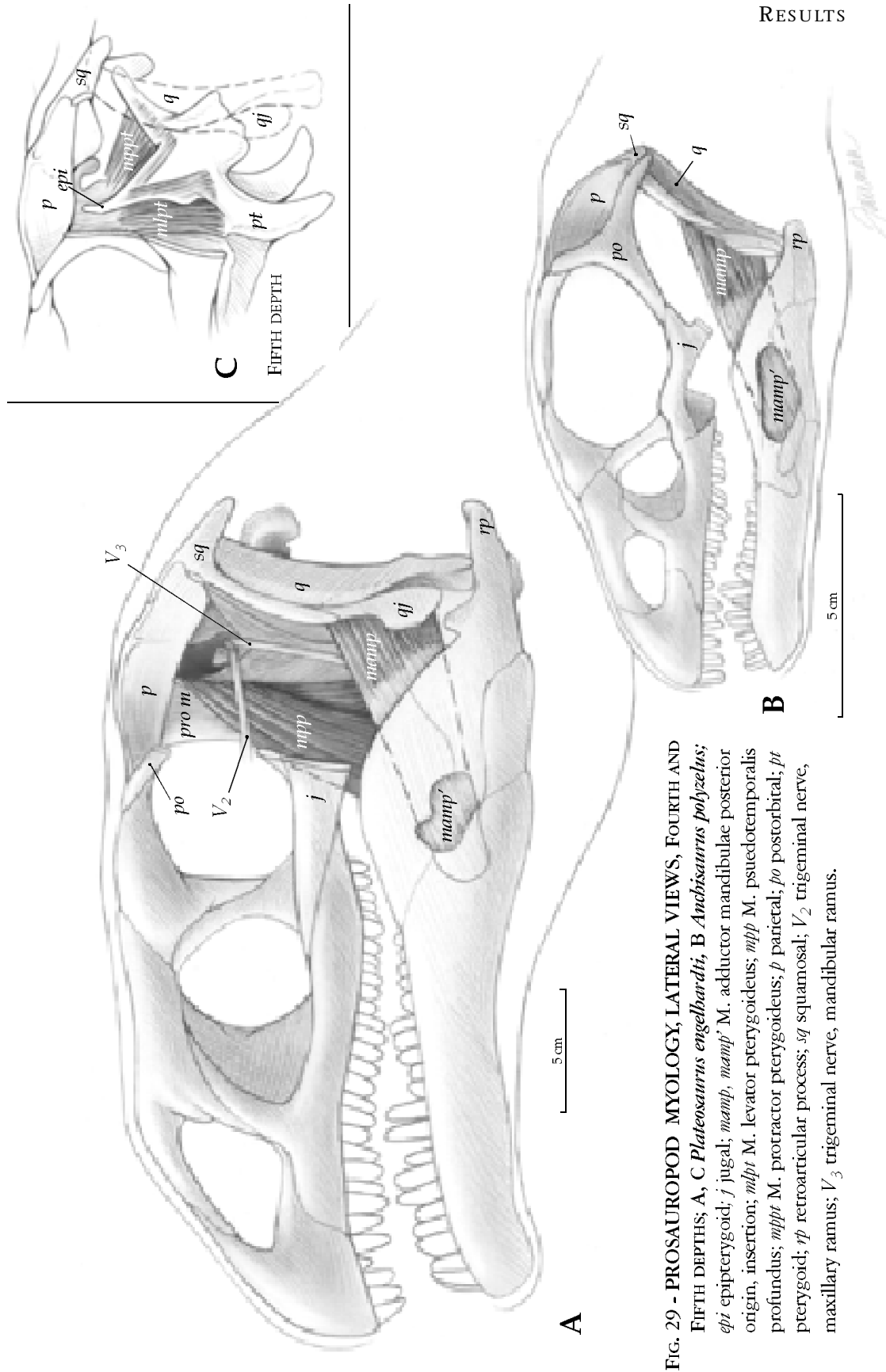


FIG. 29 - PROSAUROPOD MYOLOGY, LATERAL VIEWS, FOURTH AND FIFTH DEPTHS; A, C *Plateosaurus engelhardti*, B *Anchisaurus polyzelus*; *epi* epipterygoid; *j* jugal; *mamp*, *mamp'* M. adductor mandibulae posterior origin, insertion; *mlpt* M. levator pterygoideus; *mppt* M. pseudotemporalis profundus; *mlpt* M. protractor pterygoideus; *p* parietal; *po* postorbital; *pt* pterygoid; *rp* retroarticular process; *sq* squamosal; *V₂* trigeminal nerve, maxillary ramus; *V₃* trigeminal nerve, mandibular ramus.

squamosal, extending dorsally and overlapped the posterior aspect of the dorsal head of *M. adductor mandibulae externus medius*. The fibers of this muscle travelled ventrally and inserted on the retroarticular process of the posterior mandible. This insertion slightly overlapped the ventral aspect of *M. pterygomandibularis*. Its anterior border formed the posterior edge of the tympanic cavity. The size of this muscle varies among the iguanids studied and may have done the same in the prosauropods. This was the only muscle whose action was to depress the mandible. *M. depressor mandibulae* was innervated by the maxillary ramus (V_2) of the trigeminal nerve.

CONSTRUCTOR DORSALIS GROUP

These muscles are the last to be reconstructed in prosauropods. They are located deep in the infratemporal fenestra.

M. Levator Pterygoideus (mlpt): This muscle was probably very similar to that of the iguanids (see FIG. 29C). A small ribbon-shaped slip originated on the ventral border of the parietal bone and possibly on the ventrolateral surface of the laterosphenoid according to GALTON (1985). It continued ventrally and inserted onto the medial aspect of the pterygoid bone at the medial epipterygoid process and ventral epipterygoid bone. The mandibular ramus (V_3) of the trigeminal nerve would be seen at this level as it left the trigeminal foramen of the prootic. The action of this muscle was to elevate the maxillary segment of the cranium. However, because the prosauropod cranium is considered akinetic, this kinetic movement is limited. This muscle was innervated by the mandibular ramus (V_3) of the trigeminal nerve.

M. Protractor Pterygoideus (mppt): Like *M. levator pterygoideus*, this muscle probably resembled that of the iguanids (see FIG. 29C). It too was a small slip located medial to *M. levator pterygoideus*. It originated on the prootic and basisphenoid bones and continued posteroventrally to insert onto the deep anteromedial aspect of the quadrate. Its dorsal border would have run ventral to the trigeminal foramen. The action of this muscle was to elevate and protract the maxillary segment of the cranium. This muscle was innervated by the mandibular ramus (V_3) of the trigeminal nerve.

M. Levator Bulbi (mlb): This muscle is not illustrated and, therefore, will not be discussed in great detail. *M. levator bulbi* was a small triangular-shaped muscle that originated on the ligament dorsal to the trigeminal foramen and continued anteroventrally to insert onto the eyelid (GALTON 1985). The action of this muscle was to depress the palpebrae inferioris. Its innervation was likely the mandibular ramus (V_3) of the trigeminal nerve.

TABLE 5 - Proposed Adductor Muscles in Prosauropoda

MUSCLE	ORIGIN	INSERTION	N*	ACTION
<i>M. adductor mandibulae externus (mame)-</i>				
<i>levator anguli oris</i>	postorbital, jugal	<i>Mundplatt</i> , mandible	V ₃	elevates mandible
<i>retractor anguli oris</i>	squamosal, postorbital	<i>Mundplatt</i> , mandible	V ₃	elevates mandible
<i>superficialis</i>	medial postorbital & squamosal, jugal	lateral coronoid	V ₃	elevates mandible
<i>medius</i>	parietal, squamosal & postorbital, quadrate	anterodorsal coronoid	V ₃	elevates mandible
<i>profundus</i>	parietal, medial squamosal (laterosphenoid)	posterodorsal coronoid	V ₃	elevates mandible
<i>M. adductor mandibulae internus (mami) -</i>				
<i>M. pseudotemporalis superficialis</i>	frontal, parietal, epipterygoid	both portions insert to aponeurosis of anteromedial coronoid, posteromedial dentary	V ₃	elevates mandible
<i>M. pseudotemporalis profundus</i>	parietal, epipterygoid		V ₃	elevates mandible
<i>M. pterygoideus (pterygomandibularis)</i>				
<i>dorsalis</i>	ectopterygoid, pterygoid/quadrate	ventromedial surangular	V ₃	elevates mandible
<i>ventralis</i>	lateral pterygoid flange	lateral surangular	V ₃	elevates mandible
<i>M. adductor mandibulae posterior</i>	quadrate (pterygoid flange)	inframandibular fenestra	V ₃	elevates mandible

* branch of Trigeminal Nerve V, or Facial Nerve VII

TABLE 6 - Proposed constrictor jaw muscles in Prosauropoda

MUSCLE	ORIGIN	INSERTION	N*	ACTION
<i>M. levator pterygoideus</i>	parietal, epipterygoid laterosphenoid	pterygoid epipterygoid	V ₃	elevates maxillary segment of cranium
<i>M. protractor pterygoideus</i>	prootic, basisphenoid	quadrate- pterygoid flange/ pterygoid- quadrate flange	V ₃	elevates & protracts maxillary segment
<i>M. levator bulbi</i>	ligament dorsal to the trigeminal foramen	eyelid	V ₃	depresses eyelid

* branch of Trigeminal Nerve V, or Facial Nerve VII

TABLE 7 - Proposed M. depressor mandibulae in Prosauropoda

MUSCLE	ORIGIN	INSERTION	N*	ACTION
<i>M. depressor mandibulae</i> (<i>anterior/lateralis</i>)	posterior projection of squamosal and paraoccipital process	retroarticular process	VII	depresses mandible

* branch of Trigeminal Nerve V, or Facial Nerve VII

TABLE 8 - Summary of myological differences, *Prosauropoda*

MUSCLE	<i>PLATEOSAURUS</i>	<i>ANCHISAURUS</i>
<i>M. adductor mandibulae externus</i> (mame)- <i>levator anguli oris</i>	long slip	small slip
<i>retractor anguli oris</i>	tendinous origin	fleshy origin
<i>superficialis</i>	fleshy origin	origin tendinous, proportionately the widest
<i>medius</i>	aponeurotic, dorsal and ventral heads semi-continuous	aponeurotic, dorsal and ventral heads continuous, narrow tendinous band
<i>profundus</i>	small tendinous anterior band, semi-tortuous fibers	wide tendinous anterior band, continuous fibers
<i>M. pseudo-temporalis</i> (mami) - <i>superficialis</i>	fan-shaped, aponeurotic insertion	fan-shaped
<i>profundus</i>	small ribbon-shaped slip, fleshy origin	long slip to superior epipterygoid, thick tendinous insertion to coronoid process
<i>M. pterygoideus</i> (pterygomandibularis) <i>dorsalis/ventralis</i>	narrow, large fleshy insertion	smaller, wide tendonous insertion
<i>M. adductor mandibularis posterior</i>	large, wide tendon ventrally attached to external mandibular fenestra	small wide insertion to external mandibular fenestra
<i>M. levator pterygoideus</i>	small ribbon, small tendinous origin on prootic membrane	narrow ribbon with tendinous origin on prootic membrane
<i>M. protractor pterygoideus</i>	small insertion	wide insertion
<i>M. depressor mandibulae</i>	narrow, delicate, tendinous insertion	wide sheet, broad muscular insertion, tripartite

DISCUSSION



Commentary

Prosauropods have traditionally been considered strictly herbivorous forms (GALTON 1985). Through present research, I have been able to identify a suite of interrelated features that suggests that this interpretation is not accurate. These features build on BARRETT'S (1998) study, which demonstrates the diet of prosauropods was not completely herbivorous. In fact, BARRETT claimed that most authors tend to categorize primitive dinosaur feeding styles as being either exclusively herbivorous or carnivorous, disregarding the possibility of a full spectrum in omnivorous feeding styles. He also suggested that certain morphological features, like dentition, are not reliable determining factors in distinguishing diet. This results from the lack of paradigms for omnivorous tooth form and a weak iguanine paradigm for herbivorous tooth form. Because iguanids have often been regarded as exclusively herbivorous, many extinct taxa *de facto* have been considered herbivorous. However, there is now substantial evidence suggesting that iguanids show a trend from omnivory to herbivory and that prosauropods may have undergone similar transformation in diet. For example, in this study, it was found that the position temporal fenestrae in iguanids shifted from an oblique relationship (found in the omnivorous *Sceloporus magister*) to a position where the fenestrae were located at a right angle in relation to each other and the long axis of the skull (found in the herbivorous *Iguana iguana*). This temporal shift changed both the location of the jaw joint and the shape and angle of the muscles that are contained within the fenestrae. Various kinetic implications can be derived from these morphological changes.

BARRETT discussed the combination of omnivorous and herbivorous tooth form found in various taxa, which suggests the possibility of a continuum of omnivorous feeding style in prosauropods. Accepting this evidence, consideration of a ventrally-deflected jaw joint, a strictly herbivorous morphological feature, is a vague assumption if treated alone. Other anatomical structures must be examined, especially since iguanids have been found to have a full spectrum of feeding habits.

Osteology

In general form, the skull of prosauropods and iguanids (and all other diapsids) has both supratemporal and infratemporal fenestrae, although the latter have lost the infratemporal arcade. These fenestrae have been considered to be associated with the presence of strong jaw adductor muscles by providing a physical area for attachment and room for muscle bulging during contraction (KARDONG 1998). This condition may have played a significant role in the evolutionary relationships between herbivorous and omnivorous forms, principally because such cranial structures allow the skull to withstand stresses of muscular contraction, especially as it relates to diet.

One such morphological change in the skulls of the iguanids with respect to herbivorous feeding habit was identified in this study. In the omnivorous *Sceloporus magister*, the supratemporal fenestra is located at an oblique angle in relation to the infratemporal fenestra and the long axis of the skull. The supratemporal arcade is located slightly dorsally, causing the muscles of the supratemporal fenestra to also be dorsally located. In addition, the parietal surface of the supratemporal fenestra exhibits a smaller area for the attachment of the adductor jaw muscles. In the insectivorous and herbivorous *Ctenosaura hemilopha*, the angle of the supratemporal fenestra with respect to the infratemporal fenestra is decreased. The supratemporal arcade is moved slightly more dorsally than that of *Sceloporus magister*, making the supratemporal fenestra, and the muscles contained there, more dorsally placed. The surface area of the parietal portion of the supratemporal fenestra has also increased. Finally, in the herbivorous *Iguana iguana*, the supratemporal fenestra is located at a right angle to the infratemporal fenestrae and the long axis of the skull. The parietal surface is the largest of all three species. The supratemporal arcade has significantly shifted ventrally, causing the jaw muscles of the supratemporal fenestra to be more laterally located on the skull.

The ventrally-offset position of the mandibular joint with respect to the maxillary tooth row was once thought to relate directly to herbivory (GALTON 1985). However, based on the further observations of skull design in iguanids, this relationship should now be reconsidered. Among iguanids, the ventrally offset position of the jaw joint is found in *Sceloporus magister* as

well as in *Ctenosaura hemilopha* and *C. pectinata*, all of which are undoubtedly omnivorous and insectivorous, respectively. From the perspective of the prosauropods under consideration here, the use of a ventrally-offset jaw joint in both *Anchisaurus polyzelus* and *Plateosaurus engelhardti* cannot be used as a simple signature of a strictly herbivorous habit.

Other features and the trends they imply do, however, provide more ambiguous value in assessing diet in prosauropods. For example, in *Sceloporus magister*, an iguanid that has omnivorous feeding habits, the oblique arrangement of the temporal fenestrae the same as it is seen in the reconstruction of *Anchisaurus polyzelus* (YPM 1883). Even GALTON'S reconstruction (1979 FIG 14a), though slightly different in structure, displays an oblique relationship between the supratemporal and infratemporal fenestrae. In contrast, *Plateosaurus engelhardti*, as reconstructed in this study and as seen in GALTON'S studies (1979, 1984, 1985, 1986), exhibits temporal fenestrae that are at right angles with respect to each other as well as the long axis of the skull. This shift directly effects the shape and size of the jaw muscles in prosauropods just as they do in the iguanids studied.

In consideration of the mobility of the quadrate bone as it articulates dorsally with the skull roof, it is interesting to note that in iguanids the ventral aspect of this bone rotates posteriorly with respect to increasing herbivorous diet. The same is true of prosauropods: *Anchisaurus polyzelus* has a more anteriorly offset jaw joint in comparison to that of *Plateosaurus engelhardti*. This character may also attribute to the oblique shift of the temporal fenestrae in the omnivorous iguanid and prosauropod forms.

Myology

On the basis of these differences in skull structure that ultimately affected the shape and structure of the prosauropod jaw musculature, it is likely that *Anchisaurus* was a facultative omnivore rather than a strict herbivore and that *Plateosaurus* was a much more specialized herbivore. Changes in the shape and structure of this jaw musculature may have allowed modified movement of the skull with respect to different feeding habits (refer to TABLES 4 and 8). Because such similarities were found in the iguanids, it is concluded that not all

prosauropods were strictly herbivores, but that the omnivorous anchisaurids may represent a functional intermediate between the more primitive carnivory of archosaurs and thus a significant phylogenetic link in the evolution of herbivory in prosauropod dinosaurs.

SUPERFICIAL STRUCTURES

With respect to the superficial structures of iguanids, the question of the existence of a ligamentum quadratomandibulare and *Mundplatt* in prosauropods was considered. Because the *Mundplatt* was an extension of the skin at the posterior corner of the mouth, it was hypothesized that prosauropods had a similar structure that accompanied the opening and closing of the mouth. If this were true, then these dinosaurs likely also had a *Mundplatt* that served as a site of insertion for a muscle (or group of muscles) which pulled the integument away from the corner of the mouth when the jaw was adducted.

The question of how this might have been accommodated was investigated by examining the primitive cranial osteology of *Sphenodon*, a primitive relative of lizards and snakes, and thereafter to archosaurs, as presented by HAAS (1974). Like the skulls of prosauropods, that of *Sphenodon* has an infratemporal fenestra fully closed ventrally by an infratemporal arcade. *Sphenodon* has two superficial muscles that originate on the supratemporal arcade and insert onto the medial and lateral surfaces of the *Mundplatt*. Each aids in the retraction and elevation of the *Mundplatt* at the posterior corner of the mouth. He referred to these muscles as M. levator anguli oris (similar to that of the iguanids) and M. retractor anguli oris (not found in iguanids). The infratemporal arcade of the *Plateosaurus engelhardti* skull was examined for possible origin sites for M. levator anguli oris, at the posterior margins of the dorsal ramus of the jugal and ventral ramus of the postorbital bones, and for M. retractor anguli oris, at the anterior borders of the ventral ramus of the squamosal and quadrate bones. What had been previously determined as one large muscle scar on the medial surfaces of the postorbital for M. adductor mandibulae externus superficialis in GALTON'S study may in fact be the site for both M. adductor mandibulae externus superficialis and M. levator anguli oris. Small scars for these muscles were found in *Plateosaurus engelhardti* and are indicated in FIGURES. 22 and 23.

The infratemporal fascia may also have served not only as a covering of the infratemporal muscles, but also may have been partially an additional soft tissue insertion site for these two proposed muscles as the surface area of the supratemporal arcade is relatively narrow.

ADDUCTOR MANDIBULAE GROUP

M. adductor mandibulae externus: The adductor mandibulae externus muscle group in the iguanids is quadrupartite, including *M. levator anguli oris* and *M. adductor mandibulae externus superficialis*, *medius et profundus*. In prosauropods, the fifth muscle, *M. retractor anguli oris*, is added to this group (see above).

Due to the perpendicular shift of the temporal fenestrae with respect to one another, the jaw musculature in iguanids varies in size, shape and muscle fiber direction. The most noticeable difference between *M. adductor mandibulae externus superficialis* in the three iguanid genera studied is the prominent tendinous origin in *Ctenosaura hemilopha*.

In addition, the change in size and shape of *M. adductor mandibulae externus medius* was striking in this investigation. In *Sceloporus magister*, the dorsal head of this muscle is most continuous with its ventral counterpart. In contrast, *Ctenosaura hemilopha* and *Iguana iguana* have a tortuous and semi-continuous *M. adductor mandibulae externus medius*. These differences in muscle organization have been reconstructed in *Plateosaurus engelhardti* and *Anchisaurus polyzelus*.

M. adductor mandibulae internus: This muscle group showed significant differences with respect to diet in the iguanids studied. *M. pseudotemporalis superficialis* in *Ctenosaura hemilopha* was significantly more crescent-shaped than that of *Iguana iguana* due to the shape and location of the supratemporal fenestra. Because this same characteristic is found in *Anchisaurus polyzelus*, *M. pseudotemporalis superficialis* is considered to have been slightly more crescent-shaped in this species than that of *Plateosaurus engelhardti* with its fibers running more anteroposteriorly before diving ventrally and blending with the basal aponeurosis of the coronoid process.

M. pseudotemporalis profundus was reconstructed in *Plateosaurus engelhardti* in a similar fashion to that of *Iguana iguana* due to the location of the supratemporal fossa and the angle of the dorsal process of the epipterygoid bone. However, because of the lack of palatal material, *M. pseudotemporalis profundus* was not reconstructed in *Anchisaurus polyzelus*. However, inferences can be made from observing the differences between *M. pseudotemporalis profundus* in iguanids. In *Sceloporus magister*, *M. pseudotemporalis profundus* is an elongate tendinous ribbon, a condition that comes from the oblique shift of the supratemporal fenestra. Therefore, that *M. pseudotemporalis profundus* in *Anchisaurus polyzelus* can be inferred to have been similar. This difference between prosauropods suggests that these muscular details may have had indirect correlation with differences in feeding style.

Finally, the meckelian canal in iguanids served as a similar site as the external mandibular fenestra in prosauropods for the insertion of *M. adductor mandibulae posterior*. This muscle has a large tendinous insertion in both prosauropod and iguanid forms.

CONSTRUCTOR DORSALIS GROUP

Because cranial kinesis in prosauropods is significantly less than that of the iguanids, it is not obvious what sort of constructor apparatus prosauropods had? Unfortunately, the palate of *Anchisaurus polyzelus* is incompletely known and was therefore difficult to reconstruct. As a result, the constructor group of muscles was not reconstructed for this prosauropod. However, *Plateosaurus engelhardti* exhibits a well-preserved palate and basicranium, including a fused epipterygoid-pterygoid apparatus onto which *M. pseudotemporalis profundus* inserted. Though the prosauropod skull has extremely limited cranial kinesis, the presence of muscle scars for the insertion of *Mm. levator et protractor pterygoideus* suggests that the maxillary segment prosauropod skull may have had some kinetic ability.

M. DEPRESSOR MANDIBULAE

M. depressor mandibulae in iguanids showed significant change in structure with respect to herbivory. This is especially significant considering that this muscle is the only one that opens the jaw. Its insertion on the retroarticular process of the posterior mandible varies considerably between the herbivorous *Iguana iguana* and the omnivorous *Ctenosaura hemilopha*

and *Sceloporus magister*. M. depressor mandibulae in *Plateosaurus engelhardti* was likely not to fan out as it did in *Anchisaurus polyzelus*. This is especially true since the posterior ramus of the squamosal protrudes more posteriorly than that of *Anchisaurus polyzelus*. This muscle must have originated near the midline of the dorsal aspect of the parietal, covering a larger surface area on the lateral aspect of the anterior neck.

Conclusion

Noting the variations described above among iguanids as they relate to differences in diet, the assumption that all prosauropods were herbivorous is too general an argument to explain the phylogenetic relationships between herbivorous and omnivorous dinosaurs.

Given the similarities of skull structure and muscle locations in both the extant and extinct forms, it is reasonable to compare iguanid feeding style to that of prosauropods. These similarities include the oblique shift of the temporal fenestrae in relation to each other and the long axis of the skull, the dorsal shift of the supratemporal fenestra, and the overall lengthening of the jaw muscles, found in the omnivorous forms, and the relationship of the temporal fenestrae at right angles to each other and the long axis of the skull, the larger surface area of the parietal bone in the supratemporal fenestra, and the lateral location of the jaw muscles, in the herbivorous species. These features are also found in the prosauropod dinosaurs under study: the skull of *Plateosaurus engelhardti* exhibits temporal fenestrae that are located at a right angle with relation to each other and the long axis of the skull, whereas *Anchisaurus polyzelus* exhibits temporal fenestrae that are of an oblique relationship.

On the basis of the structural differences, within their phylogenetic context for both Iguanidae and Prosauropoda, it appears very likely that *Anchisaurus* was not an herbivore as previously thought, but rather an omnivore, similar to the extant iguanid *Sceloporus*. In this way, anchisaurids form an important link from the primitive carnivorous feeding habits of basal dinosaurs, through their own facultative omnivory, to the more strictly herbivorous plateosaurids.

APPENDIX A



Abbreviations and Terminology

an	<i>Angular</i>	if	<i>Infratemporal fascia</i>
an p	<i>Angular process</i>	j	<i>Jugal</i>
aof	<i>Antorbital fenestra</i>	l	<i>Lacrima</i>
ar	<i>Articular</i>	ls	<i>Laterosphenoid</i>
bo	<i>Basioccipital</i>	lq	<i>Ligamentum quadratomandibulare</i>
bod	<i>Bodenaponeurosis</i>	mame	<i>M. adductor mandibulae externus superficialis, medius, et profundus</i>
bp	<i>Basipterygoid process</i>	mames	
bs	<i>Basisphenoid</i>	mamem	
bt	<i>Basipterygoid tubera</i>	mamep	
c	<i>Coronoid</i>	mame'	<i>M. adductor mandibulae externus superficialis, medius, et profundus (insertions)</i>
col	<i>Columella (also Epipterygoid)</i>	mames'	
cp	<i>Coronoid process</i>	mamem'	
d	<i>Dentary</i>	mamep'	
dc	<i>Dorsal crest</i>	mami	<i>M. adductor mandibulae internus</i>
dew	<i>Dewlap</i>	mamp	<i>M. adductor mandibulae posterior</i>
dh	<i>Dorsal head</i>	mc	<i>Meckelian canal</i>
ect	<i>Ectopterygoid</i>	mdm	<i>M. depressor mandibulae</i>
emf	<i>External mandibular fenestra</i>	mlao	<i>M. levator anguli oris</i>
epi	<i>Epipterygoid (also Columella)</i>	mlb	<i>M. levator bulbi</i>
exo	<i>Exoccipital</i>	mlpt	<i>M. levator pterygoideus</i>
f	<i>Frontal</i>	mppt	<i>M. protractor pterygoideus</i>
fm	<i>Foramen magnum</i>	mpp	<i>M. pseudotemporalis profundus</i>
ic	<i>Inter coronoid</i>	mps	<i>M. pseudotemporalis superficialis</i>
		mpt	<i>M. pterygomandibularis</i>
		mrao	<i>M. retractor anguli oris</i>
		mund	<i>Mundplatt/Rictal Plate</i>

mx	<i>Maxilla</i>	ptp	<i>Pterygoid process</i>
n	<i>Nasal</i>	q	<i>Quadrate</i>
oc	<i>Occipital condyle</i>	qj	<i>Quadratojugal</i>
op	<i>Opisthotic</i>	qp	<i>Quadrate process</i>
os	<i>Orbitosphenoids</i>	qr	<i>Quadrate ramus</i>
p	<i>Parietal</i>	rt	<i>Retroarticular process</i>
pa	<i>Prearticular</i>	sa	<i>Surangular</i>
pal	<i>Palatine</i>	sept	<i>Septomaxilla</i>
palr	<i>Palatal ramus</i>	spl	<i>Splenic</i>
pap	<i>Paraoccipital process</i>	sq	<i>Squamosal</i>
pf	<i>Prefrontal</i>	suo	<i>Supraoccipital</i>
pm	<i>Premaxilla</i>	sut	<i>Supratemporal</i>
pof	<i>Postfrontal</i>	Ta	<i>Temporal artery</i>
pro	<i>Prootic</i>	V	<i>Trigeminal nerve</i>
ps	<i>Parasphenoid</i>	V _{1,2,3}	<i>Trigeminal rami: ophthalmicus, maxillaris, mandibularis</i>
po	<i>Postorbital</i>	tc	<i>Tympanic crest</i>
pt	<i>Pterygoid</i>	ty	<i>Tympanum</i>
ptf	<i>Pterygoid fossa</i>	v	<i>Vomer</i>
ptfl	<i>Pterygoid flange</i>	vh	<i>Ventral head</i>

APPENDIX B



Specimen Inventory

- | | |
|---|--|
| <p><i>Anchisaurus polyzelus</i>: YPM 1883, Manchester, Connecticut USA, partial skull (FIGS. 18-20), holotype of <i>A. colurus</i> Marsh, 1891:267 type specimen of species of the genus <i>Yaleosaurus</i> Huene, 1932:122 (GALTON, 1976).</p> | <p><i>Iguana iguana</i>: USNM 12265, (FIGS. 13-15) complete specimen prepared in 70% ethanol, cranium dissected.</p> |
| <p><i>Ctenosaura hemilopha</i>: USNM 521637, (FIGS. 13-15) complete specimen prepared in 70% ethanol, cranium dissected.</p> | <p><i>Iguana iguana</i>: USNM 68056, (FIGS. 13-15) eviscerated specimen prepared in 70% ethanol, cranium dissected.</p> |
| <p><i>Ctenosaura pectinata</i>: MEERS (PRIVATE COLLECTION) I, Fort Myers, Florida USA, complete specimen prepared fresh stored in a freezer, cranium dissected and skeletonized.</p> | <p><i>Iguana iguana</i>: WEISHAMPEL (PRIVATE COLLECTION) I, Baltimore, Maryland, USA complete specimen prepared in 70% ethanol, cranium dissected.</p> |
| <p><i>Ctenosaura pectinata</i>: MEERS (PRIVATE COLLECTION) II, Fort Myers, Florida USA, complete specimen prepared fresh stored in a freezer, cranium dissected.</p> | <p><i>Plateosaurus engelhardti</i>: AMNH 6810, Knollenmergel, Trossingen Germany, (FIGS. 8 and 17) complete epoxy skull cast.</p> |
| <p><i>Iguana iguana</i>: MEERS (PRIVATE COLLECTION) IV, Fort Myers, Florida USA, complete specimen prepared fresh and stored in a freezer, cranium dissected and skeletonized.</p> | <p><i>Sceloporus magister</i>: USNM EXCHANGE, (FIGS. 13-15), complete specimen prepared in 70% ethanol, cranium dissected.</p> |
| | <p><i>Sceloporus magister</i>: USNM 220250, (FIGS. 10 and 11) complete skull.</p> |

REFERENCES

- AVERY, David F.; TANNER, Wilmer W. 1971. Evolution of the Iguanine Lizards (Sauria, Iguanidae) as Determined by Osteological and Myological Characters. Brigham Young Universit. Science Bulletin, Biological Survey v. 12, no. 3:1-79.
- BARRETT, P. M. In press. Prosauropods and iguanas: speculation on the diets of extinct reptiles. In: The Evolution of Herbivory in Terrestrial Vertebrates, Sues, H. D., ed. Cambridge: Cambridge University Press.
- BAUMEL, Julian J.; KING, Anthony S.; LUCAS, Alfred M.; BREAZILE, James E.; EVANS, Howard E. 1979. Nomina Anatomica Avium. London: Academic Press.
- BELLAIRS, Angus d'A. 1970. The Life of Reptiles. v. 1. New York: Universe Books.
- BELLAIRS, Angus d'A; KAMAL, A. M. 1974. The Chondrocranium and the Development of the Skull in Recent Reptiles. In: Biology of Reptilia, v. 11; Gans, C. and Parsons, T. S., eds. London: Academic Press, Inc., Ltd:1-263.
- COOPER, Michael R. 1981. The prosauropod dinosaur *Massospondylus carinatus* Owen from Zimbabwe: its biology, mode of life and phylogenetic significance. Occasional Papers of the National Museums and Monuments, series b, v. 6, part 10:689-840.
- COSTELLI, Joseph. 1973. Iguanid Trigeminal Musculature and Its Role in the Phylogeny of the Iguanidae. Dissertation, City University of New York.
- CROMPTON, A. W.; ATTRIDGE, J. 1986. Masticatory apparatus of the larger herbivores during Late Triassic and Early Jurassic times. In: The Beginning of the Age of Dinosaurs, Padian, Kevin, ed. Cambridge: Cambridge University Press: 223-236.
- DE QUEIROZ, Kevin. 1987. Phylogenetic systematics of iguanine lizards: a comparative osteological study. University of California Publications in Zoology: v. 118:1-203.
- EDGEWORTH, Francis Henry. 1935. The Cranial Muscles of Vertebrates. Cambridge: Cambridge University Press.
- FROST, Darrel R.; ETHERIDGE, Richard. 1989. A Phylogenetic Analysis and Taxonomy of Iguanian Lizards (Reptilia: Squamata). Lawrence: University of Kansas.
- GALTON, Peter M.; CLUVER, M. A. 1976. *Anchisaurus capensis* (Broom) and a revision of the Anchisauridae (Reptilia, Saurischia). Annals of the South African Museum, v. 69, part 6:121-159.

- GALTON, Peter M. 1979. Prosauropod Dinosaurs (Reptilia: Saurischia) of North America. *Postilla*, v. 169:1-98.
- GALTON, Peter M. 1984. Cranial anatomy of the prosauropod dinosaur *Plateosaurus* from Knollenmergel (Middle Keuper, Upper Triassic) of Germany, Two complete skulls from Trössingen/Württ with comments on diet. *Geologica et Palaeontologica*, v. 18:139-171.
- GALTON, Peter M. 1985. Cranial anatomy of the prosauropod dinosaur *Plateosaurus* from Knollenmergel (Middle Keuper, Upper Triassic) of Germany, All the cranial material and details of soft-part anatomy. *Geologica et Palaeontologica*, v. 19:119-159.
- GALTON, Peter M. 1985. Diet of prosauropod dinosaurs from the late Triassic and early Jurassic. *Lethaia*, v. 18:105-123.
- GALTON, Peter M. 1986. Herbivorous adaptations of Late Triassic and Early Jurassic dinosaurs. In: *The Beginning of the Age of Dinosaurs*, Padian, Kevin, ed. Cambridge University Press: pp. 205-221.
- GALTON, Peter M. 1990. Basal Sauropodomorpha – Prosauropoda. In: *The Dinosauria*, Weishampel, David B.; Dodson, Peter; Osmólska, Halszka, eds. Berkeley: University of California Press:320-401.
- GEORGE, J. C.; Berger, A. J. 1966. *Avian Myology*. London: Academic Press.
- GUTHE, Karl F. 1974. Reptilian Muscle: Fine Structure and Physiological Parameters. In: *Biology of Reptilia*, v. 11; Gans, C. and Parsons, T. S., eds. London: Academic Press, Inc., Ltd: 265-354.
- HAAS, Georg. 1974. Muscles of the jaws and associated structures in Rynchocephalia and Squamata. In: *Biology of Reptilia*, v. 4; Gans, C. and Parsons, T. S., eds. London: Academic Press, Inc., Ltd: 285-490.
- HUENE, Freidrich von. 1906. Ueber die Dinosaurier der Aussereuropaeischen Trias. *Geologische und Palaeontologische Abhandlungen*. (N.F.) v. 8: 99-156.
- HUENE, Freidrich von. 1926. Vollständige Osteologie eines Plateosauriden aus dem Schwäbischen Keuper. *Geologische und Palaeontologische Abhandlungen*. (N.F.) v. 5:139-180.
- HYMAN, Libbie Henrietta. 1922. *Comparative Vertebrate Anatomy*. Chicago: The University of Chicago Press.
- IORDANSKY, N. N. 1974. The Skull of Crocodilia. In: *Biology of Reptilia*, v. 4; Gans, C. and Parsons, T. S., eds. London: Academic Press, Inc., Ltd: 201-262.

- IVERSON, John B. 1982. Adaptations to Herbivory in Iguanine Lizards. In: *Iguanas of the World: Their Behavior, Ecology and Conservation*. Burghardt, Gordon M.; Rand, Stanley A. , eds. Park Ridge: Noyes Publications: 60-75.
- KARDONG, Kenneth V. 1998. *Vertebrates, Comparative Anatomy, Function, Evolution*. Boston: WCB/McGraw Hill.
- KING, A. S.; McLelland J. 1979. *Form and Function in Birds*. London: Academic Press, v. 1.
- LAKJER, Tage. 1926. Studien über die Trigemini-Versorgte Kaumuskulatur der Sauropsiden. Copenhagen, C.A. Reitzel.
- LULL, Richard Swann. 1953. Triassic Life of the Connecticut Valley. Hartford, Connecticut Geological and Natural History Survey Bulletin, v. 81: 97-121.
- MARSH, O. C. 1893. Restoration of *Anchisaurus*. *American Journal of Science*. (3) v. 45:169-170.
- NORMAN, David. 1985. *The Illustrated Encyclopedia of Dinosaurs*. New York: Crown Publishers, Inc.
- OELRICH, Thomas M. 1956. The Anatomy of the Head of *Ctenosaura pectinata* (Iguanidae). *Ann Arbor: Museum of Zoology, University of Michigan*, no. 94:1-122.
- OLDHAM, Jonathan C.; SMITH, Hobart M. 1975. *Laboratory Anatomy of the Iguana*. Dubuque: Wm. C. Brown Company Publishers.
- OSTROM, John H.; 1961. Cranial morphology of the hadrosaurian dinosaurs of North America. *Bulletin of the American Museum of Natural History*, v. 122: art. 2:33-186.
- OSTROM, John H.; MCINTOSH, John S. 1966. *Marsh's Dinosaurs*. New Haven: Yale University Press.
- ROMER, Alfred Sherwood. 1956. *Osteology of the Reptiles*. Chicago: The University of Chicago Press.
- SCHUFELDT, R. W. 1890. *The Myology of the Raven (Corvus corax sinuatus)*. London: MacMillan and Co.
- SCHUMACHER, Gert-Horst. 1974. The Head Muscles and Hyolaryngeal Skeleton of Turtles and Crocodilians. In: *Biology of Reptilia*, v. 4; Gans , C. and Parsons, T. S., eds. London: Academic Press, Inc., Ltd:101-200.
- SECOY, D. M. 1971. The Myology of *Sceloporus C. Clarki* Baird and Girard (Reptilia: Iguanidae). *Brigham Young Univ. Sci. Bull.* v. 14, no. 1:1-22.

- SMITH, Hobart M. 1946. *Handbook of Lizards*. Ithaca, Comstock Publishing Company, Inc.
- SWINTON, W. E. 1954. *Fossil Amphibians and Reptiles*. Norwich: Jarrold and Sons, Ltd.
- THOMASON, Jeff J., editor. 1995. *Functional Morphology in Vertebrate Paleontology*. Cambridge: Cambridge University Press.
- UPCHURCH, Paul 1995. The Evolutionary History of Sauropod Dinosaurs. *Philosophical Transactions of the Royal Society of London*, v. 124:43-103.
- UPCHURCH, Paul 1998. The Phylogenetic Relationships of Sauropod Dinosaurs. *Zoological Journal of the Linnean Society*, series B, v. 349:365-390.
- VAN DERVENDER, Robert Wayne. 1982. Growth and Ecology of Spiny Tailed and Green Iguanas in Costa Rica, with Comments on the Evolution of Herbivory and Large Body Size. In: *Iguanas of the World: Their Behavior, Ecology and Conservation*. Burghardt, Gordon M.; Rand, Stanley A. , eds. Park Ridge: Noyes Publications: 162-183.
- WEISHAMPEL, David B. 1984. Evolution of Jaw Mechanisms in Ornithomimid Dinosaurs. In: *Advances in Anatomy Embryology and Cell Biology*, v. 87:1-110.
- WEISHAMPEL, David B.; FASTOVSKY, David E. 1996. *The Evolution and Extinction of the Dinosaurs*. Cambridge: Cambridge University Press.
- WEISHAMPEL, David B.; YOUNG, Luther 1996. *Dinosaurs of the East Coast*. Baltimore: The Johns Hopkins University Press.
- WITMER, Lawrence M. 1989. The craniofacial air sac system of Mesozoic birds (Aves). *Zoological Journal of the Linnean Society*. v. 100:327-378.
- WITMER, Lawrence M. 1995. Homology of facial structures in extant archosaurs (Birds and Crocodilians), with special reference to paranasal pneumaticity and nasal conchae. *Journal of Morphology*. v. 225:269-327.
- WITMER, Lawrence M. 1997. The evolution of the antorbital cavity of archosaurs: a study in soft-tissue reconstruction in the fossil record with an analysis of the function of pneumaticity. *Journal of Vertebrate Paleontology*. v. 17, supplement to no. 1:1-65.

VITA



The author was born on the 1st day of July, 1972 in Houston, Texas where she attended the High School for Health Professions. In August of 1987, she and her parents moved to Newport News, Virginia, where she graduated from Denbigh High School. She pursued her undergraduate studies at the University of Maryland, College Park and worked as an illustrator and graphic designer for the university's Department of Communication Services. In May of 1995 she received a Bachelor of Arts in studio art with a supporting area in the German language and a Bachelor of Science in biological sciences. Upon graduation she worked as a full-time contract illustrator for the USDA Systematic Entomology Laboratory at the National Museum of Natural History, Smithsonian Institution.

In August of 1997, she matriculated to the Department of Art As Applied to Medicine at the Johns Hopkins University School of Medicine in Baltimore, Maryland. She worked as an intern at Hurd Studios in Brooklyn, New York the summer of 1998. There she story-boarded and illustrated for patient education medical videos for public television. The author is the 1999 recipient of the Vesalius Trust Inez Demonet Award. She will receive her Master of Arts in Medical and Biological Illustration on the 27th of May, 1999.