

REVISION OF THE PALEOGENE GENUS
GLYPTOSAURUS
(REPTILIA, ANGUIDAE)

ROBERT M. SULLIVAN

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 163 : ARTICLE 1 NEW YORK : 1979

REVISION OF THE PALEOGENE GENUS
GLYPTOSAURUS
(REPTILIA, ANGUIDAE)

ROBERT M. SULLIVAN

*Research Associate, Vertebrate Paleontology
Natural History Museum of Los Angeles County
The Museum, Michigan State University,
East Lansing, Michigan*

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 163 : ARTICLE 1 NEW YORK : 1979

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

Volume 163, article 1, pages 1-72, figures 1-26, tables 1, 2

Issued April 20, 1979

Price. \$4.35 a copy

ISSN 0003-0090

Copyright © American Museum of Natural History 1979

CONTENTS

Abstract	5
Introduction	6
Acknowledgments	7
Abbreviations	8
Brief History and Taxonomic Problems of the Genus <i>Glyptosaurus</i>	8
Stratigraphic and Paleogeographic Occurrences of the Members of the Glyptosaurinae	10
Stratigraphic and Geographic Occurrences	10
Depositional Environments	12
Correlation of Glyptosaurine-Bearing Units	12
Systematics	13
Subfamily Glyptosaurinae McDowell and Bogert, 1954	14
Tribe Glyptosaurini, New Tribe	15
<i>Glyptosaurus</i> Marsh, 1871	15
<i>Glyptosaurus sylvestris</i> Marsh	15
Cf. <i>Glyptosaurus sylvestris</i>	19
<i>Glyptosaurus</i> sp.	19
<i>Paraglyptosaurus</i> , New Genus	19
<i>Paraglyptosaurus princeps</i> (Marsh)	21
Cf. <i>Paraglyptosaurus princeps</i>	24
<i>Paraglyptosaurus yatkolai</i> , New Species	25
<i>Eoglyptosaurus</i> , New Genus	25
<i>Eoglyptosaurus donohoei</i> (White)	26
Cf. <i>Eoglyptosaurus donohoei</i>	26
<i>Helodermoides</i> Douglass, 1903	27
<i>Helodermoides tuberculatus</i> Douglass	28
Cf. <i>Helodermoides tuberculatus</i>	39
<i>Helodermoides mongoliensis</i> , New Species	40
(?) <i>Helodermoides</i> sp.	41
Glyptosaurinae Indeterminate	42
<i>Nomina Dubia</i>	42
<i>Placosaurus rugosus</i> Gervais, 1852	42
<i>Placosaurus waltheri</i> (Weigelt, 1929)	43
<i>Placotherium waltheri</i> (Weigelt, 1929)	43
<i>Glyptosaurus sphenodon</i> Marsh, 1872	44
<i>Glyptosaurus obtusidens</i> Loomis, 1907	44
Tribe Glyptosaurini, Genus and Species Indeterminate	44
Tribe Melanosaurini, New Tribe	45
Cf. Glyptosaurinae, Tribe, Genus, and Species Indeterminate	45
Cf. Anguidae, Indeterminate	47
Phylogeny	47
Review of the Characters of the Genus <i>Glyptosaurus</i>	47
Frontals	49
Osteoderms	50
Teeth	51
Pterygoid Teeth	52
Postorbital-Postfrontal Region	52

Prefrontal-Postfrontal Bones	52
Mandible	52
Summary	53
Review and Re-evaluation of the Characters of the Anguid Subfamilies	54
Primitive and Derived Characters of the Glyptosaurinae	58
Dermal Armor: Primitive Versus the Advanced Condition	58
Paedomorphosis and Functional Morphology of the Glyptosaurini and the Phylogentic Implications	61
Summary	66
Paleoecology and Extinction	67
Eocene Glyptosaurines	67
Oligocene Glyptosaurines	67
Distribution and Paleobiogeography	68
Extinction	68
Summary	69
Literature Cited	70

ABSTRACT

The Paleogene North American lizard *Glyptosaurus* (Reptilia, Anguidae) Marsh, 1871 is revised. Two new genera, *Eoglyptosaurus* and *Paraglyptosaurus*, are named. *Helodermoides* Douglass, 1903 is resurrected as a valid genus.

Glyptosaurus (*sensu stricto*) is known by one species, *G. sylvestris*; *G. nodosus* is placed in the synonymy of *G. sylvestris* from Grizzly Buttes, Wyoming (middle Eocene). The new genus *Paraglyptosaurus* (early-middle Eocene) includes the species *P. princeps* (Marsh, 1872), including as synonyms *G. rugosus* and *G. hillsi*. *Paraglyptosaurus yatkolai*, new species is based on a single frontal from the Wasatchian of New Mexico.

Glyptosaurus donohoei White, 1952 is referred to a new genus, *Eoglyptosaurus* (early Eocene). Two species of *Glyptosaurus* (*sensu lato*) are considered *nomina dubia*: *Glyptosaurus sphenodon* Marsh, 1872 and *Glyptosaurus obtusidens* Loomis 1907. *Glyptosaurus montanus* and *Glyptosaurus giganteus* are synonyms of *Helodermoides tuberculatus* Douglass 1903 (early-middle Oligocene).

The late Eocene Mongolian *Glyptosaurus* near *nodosus* Gilmore, 1943 is transferred to *Helodermoides* as a new species, *H. mongoliensis*. The late Eocene European species *Placosaurus* Gervais, 1852, its type *P. rugosus*, *Placosaurus waltheri* (Weigelt, 1929), and *Placotherium waltheri* (Weigelt, 1929) are considered *nomina dubia*.

Two tribes are designated: the tribe Glyptosaurini to include *Eoglyptosaurus*, *Paraglyptosaurus*, *Glyptosaurus*, and *Helodermoides* and the tribe Melanosaurini to include the other glyptosaurines *Melanosaurus*, *Arpadosaurus*, *Peltosaurus*, and *Xestops*.

The subfamily Glyptosaurinae is the most primitive subfamily of the Anguidae, and the subfamily Anguinae is the most derived based on dermal armor morphology, mandibular length, palatal teeth, presence or absence of limbs, presence or absence of premaxillary fenestrae, the nature of the postorbital-postfrontal association, and the state of fusion of various skeletal elements.

The tribe Melanosaurini is the most primitive tribe of the subfamily Glyptosaurinae and the tribe Glyptosaurini is the most derived based on the morphology of the epidermal scale impressions upon the dermal armor.

Helodermoides is viewed as the most derived glyptosaurinid and glyptosaurine. The primitive nature of *Helodermoides* is regarded as paedomorphic

owing to its late occurrence. The tribe Glyptosaurini as a whole is regarded as a paedomorphic lineage primarily based upon the disintegration of dermal armor into discrete hexagonal osteoderms.

Because of the primitive nature of *Odaxosaurus* it is removed from the subfamily Anguinae and designated Anguidae: *incertae sedis*.

SOMMAIRE

La classification du lézard Paléogène de l'Amérique du Nord, *Glyptosaurus* (Reptilia: Anguidae) est ici révisée. On désigne deux nouveaux genres, *Eoglyptosaurus* et *Paraglyptosaurus*. *Helodermoides* Douglass, 1903 est rétabli comme genre légitime.

On connaît une espèce de *Glyptosaurus* (*sensu stricto*), *G. sylvestris*; *G. nodosus* se classe avec le *G. sylvestris* des Grizzly Buttes de l'État du Wyoming (Éocène intermédiaire). Le genre nouveau *Paraglyptosaurus* (Éocène inférieur et intermédiaire) comprend l'espèce *P. princeps* (Marsh, 1872) avec comme synonymes *G. rugosus* et *G. hillsi*. *Paraglyptosaurus yatkolai* n. sp. est basé sur un seul os frontal du Wasatchian de l'État du Nouveau Mexique. *Glyptosaurus donohoei* White, 1952 représente un nouveau genre, *Eoglyptosaurus* (Éocène inférieur). On considère comme *nomina dubia* deux espèces de *Glyptosaurus* (*sensu lato*): *Glyptosaurus sphenodon* Marsh, 1872 et *Glyptosaurus obtusidens* Loomis, 1907. *Glyptosaurus montanus* et *Glyptosaurus giganteus* sont synonymes du *Helodermoides tuberculatus* Douglass, 1903 (Oligocène inférieur et intermédiaire).

L'Éocène supérieur *Glyptosaurus* near *nodosus* Gilmore, 1943 du Mongolie s'affilie à *Helodermoides* en tant qu'espèce nouvelle *H. mongoliensis*. Les espèces Éocène supérieur d'Europe *Placosaurus* Gervais, 1852, le type *P. rugosus*, *Placosaurus waltheri* (Weigelt, 1929) et *Placotherium waltheri* (Weigelt, 1929) sont également considérées comme *nomina dubia*.

On désigne deux tribus: la tribu Glyptosaurini qui comprend *Eoglyptosaurus*, *Paraglyptosaurus*, *Glyptosaurus* et *Helodermoides* et la tribu Melanosaurini qui comprend les autres glyptosaurines *Melanosaurus*, *Arpadosaurus*, *Peltosaurus* et *Xestops*.

La sous-famille des Anguïdés la plus primitive est celle des Glyptosaurinae et la sous-famille Anguinae est la plus dérivée si l'on considère la morphologie du derme de l'armure, la longueur des mandibules,

les dents du palais, la présence ou l'absence de membres, la présence ou l'absence de fenêtres prémaxillaires, la nature de l'association postorbitale-postfrontale, et l'état de fusion des différents éléments du squelette.

La tribu Melanosaurini est la tribu la plus primitive de la sous-famille Glyptosaurinae et la tribu Glyptosaurini est la plus dérivée, compte-tenu de la morphologie des impressions des écailles de l'épiderme sur l'armure du derme.

On considère *Helodermoides* comme le genre le

plus dérivé des Glyptosaurinae et des Glyptosaurini. À cause de son apparence tardive, la nature primitive d'*Helodermoides* est considérée comme étant paédomorphique. En se basant principalement sur la désintégration de l'armure du derme en ostéodermes hexagonaux distincts, on considère la tribu Glyptosaurini comme formant dans l'ensemble, une lignée paédomorphique.

À cause de la nature primitive d'*Odaxosaurus* on le transfère de la sous-famille Anguinae et on a désigné Anguinae: *incertae sedis*.

INTRODUCTION

... Thus according to men's opinions, did these things come into being, and are now; and in time they will thus grow up and then pass away. To each of these men assigned the seal of a name.

Parmenides of Elea
(circa 500 B.C.)

The lizard infraorder Anguimorpha (Diploglossa) is one of the most interesting, diverse, and specialized lizard groups known. Two main lineages have been recognized by McDowell and Bogert (1954): the superfamily Anguioidea (Diploglossa) and the superfamily Varanoidea (Platynota). The latter superfamily includes 10 families, of which six are extinct. The diversity of the superfamily Anguioidea is not nearly so great, consisting only of three families (Xenosauridae, Anniellidae, and Anguinae), all of which have living representatives. The overall diversity of this infraorder has been considered by some students, notably Romer (1956), to be a reflection of an artificial grouping, not representative of the evolutionary relationships between these families of lizards.

Members of the Anguimorpha have been recognized in the fossil record as early as the Late Jurassic (Hoffstetter, 1965, 1966). Some of the modern families were established by the Late Cretaceous (Estes, 1964; Hoffstetter, 1966) and it is here that the Anguinae made its first appearance, although with initial low diversity.

It was not until the early Eocene, however, that the family Anguinae underwent what appears to have been an "explosive radiation" with the appearance of the Glyptosaurinae, a group characterized by having their entire body covered with thickened tubercular osteoderms

(osteoscutes). The subfamily Glyptosaurinae was originally based on the genus *Glyptosaurus*, including those fossil anguids with hexagonal osteoderms on the skull (McDowell and Bogert, 1954; including the European genus *Placosaurus*), but the subfamily definition has been recently expanded to include other fossil anguid genera (Meszoely, 1970; see below).

Glyptosaurines are among the most common Tertiary fossil lizards known, and have been found in early Cenozoic rocks in the United States, Europe, Asia, and more recently, Ellesmere Island, Canada. The first discovery was reported in his description of *Placosaurus rugosus* by Paul Gervais (1859).¹ In North America, during the year 1870, Othniel Charles Marsh of Yale College conducted a series of field expeditions that led to the discovery of

¹The original description of *Placosaurus* appeared in the first edition (1852) of *Zoologie et Paléontologie Française* by Paul Gervais. This edition was unavailable for this study. However, the second edition, published in 1859, was used by me and is supposed to be unaltered in regard to the description of *Placosaurus*. In this text, where I refer to the establishment of *Placosaurus*, I use the citation of the first edition (1852). The second edition (1859) is the citation used for discussing *Placosaurus* and is listed in Literature Cited.

glyptosaurine material at Grizzly Buttes, Wyoming; this material was the basis for his description of *Glyptosaurus sylvestris* (Marsh, 1871). Since that time numerous specimens of these fossil lizards have been collected, mostly from the United States.

There have been relatively few studies dealing with glyptosaurines. Camp (1923) was the first to review the taxonomic status of the glyptosaurs (*sensu* Marsh, 1872), and to give them familial rank. Gilmore (1928) has offered to date the most comprehensive study of *Glyptosaurus*. Broader reviews of the taxonomic status of glyptosaurines and other anguid subfamilies have been completed by Hoffstetter (1962b) and, more recently, by Meszoely (1970). Meszoely's study was the first to include revision of both living and fossil anguids and contributed much to our understanding of the group. He recognized four subfamilies within the family Anguidae: the Anguinae, Diploglossinae, Gerrhonotinae, and Glyptosaurinae; of these only the Glyptosaurinae is extinct. Meszoely documented the importance of making comparisons of the fossil anguids in the context of the living representatives of the family. Living anguids are known, however, by only a few genera, and most are not found as fossils. Of those that are, such as *Ophisaurus*, studies show that they have changed little since the middle Eocene (Meszoely and Haubold, 1975; Meszoely and Ford, 1976).

The interrelationships of the subfamilies of the Anguidae have been difficult to assess, a problem resulting as much from lack of fossil representatives of the living subfamilies as the unusual nature of the extinct Glyptosaurinae, the principal problem being the recognition of sufficient characters in common among both living and extinct groups necessary for the recognition of phylogenetic lineages. Groupings have been proposed by both Hoffstetter (1962b) and Meszoely (1970).

Problems in taxonomy within the Anguidae still exist for both fossil and living representatives. The subfamily Diploglossinae, for example, has been recently reviewed by Strahm and Schwartz (1977) in an attempt to determine means for generic separation of members in this subfamily, as there has been an historic

problem concerning the generic separation of *Celestus* and *Diploglossus*. On the other hand, the question of synonymy of the glyptosaurine genera *Placosaurus* and *Glyptosaurus* (e.g., McDowell and Bogert, 1954) has continued to this day.

Nevertheless, the unity of the genus *Glyptosaurus* has been unquestioned up to this time. However, while reviewing the genus *Glyptosaurus*, it became apparent, quite early in this study that it could be separated into a number of related anguid genera. Furthermore, many of the species of *Glyptosaurus* previously established, notably those erected by Marsh (1871, 1872), Loomis (1907), and Gilmore (1928), were based on relatively incomplete material, resulting in a plethora of invalid species.

A revision of the genus *Glyptosaurus* Marsh is presented here. Attention is given to problems below the familial level in terms of taxonomy and phylogeny. This study has been made possible by securing all known glyptosaurine material, described or undescribed. The specimens discussed herein represent well over 100 years of collecting in the Rocky Mountain and Great Plains regions of the United States and yet constitute a very small percentage of the fossil vertebrates recovered from these Eocene and Oligocene deposits. They represent a group of lizards, however, that was persistent and moderately diverse at its time, and which is the best represented in the fossil record.

ACKNOWLEDGMENTS

This study was made possible through the help and assistance of many individuals. For the loan of the specimens and information regarding them I thank Dr. Eugene Gaffney and Ms. Charlotte Holton (the American Museum of Natural History); Drs. Walter Coombs (Amherst College); David Berman and Mary Dawson (Carnegie Museum); Larry Martin and Robert Wilson (University of Kansas); Donald Baird (Princeton University); C. Bertrand Schultz, Michael Voorhies, Prof. Lloyd Tanner, Mr. R. George Corner, and the late Mr. Paul Edwards (University of Nebraska); Frederick Collier, Robert Purdy, Robert J. Emry, and Nicholas Hotton (National Museum of Natural

History, Smithsonian Institution) and John Ostrom and Ms. Mary Ann Turner (Yale Peabody Museum).

Stimulating conversations regarding fossil lizards and related matters were conducted numerous times throughout this study with Drs. Richard Estes and Richard Etheridge (San Diego State University); Mr. Floyd Richey (University of Chicago) and Mr. Jacques Gauthier (University of California-Berkeley). Discussions regarding the stratigraphic ranges and last occurrences of glyptosaurines were conducted with Dr. J. Alan Holman (Michigan State University) and Mr. Spencer Lucas (Yale University). Other discussions regarding mammalian biogeography and cladistics were conducted with Dr. Michael Novacek (San Diego State University) and Mr. John Chiment (University of California-Berkeley) and I am grateful for their help.

I thank Dr. Thomas Fritts (formerly from the San Diego Museum of Natural History) and Dr. Richard Etheridge for making recent lizard material available for my study.

Thanks to Dr. J. Howard Hutchison (University of California-Berkeley) and Mr. Jacques Gauthier for bringing to my attention the glyptosaurine material in the collections of the University of California Museum of Paleontology, including the recently discovered lizard fossils from Ellesmere Island, Canada.

Special thanks to Drs. Robert Hoffstetter (Museum National d'Histoire Naturelle, Paris) and Jean-Claude Rage (Université Paris VI) for photographs and correspondence regarding *Placosaurus*.

Drs. Richard Estes, Richard Etheridge, J. Alan Holman, and Charles A. M. Meszoely (Northeastern University) critically read the

manuscript and I am grateful for their comments and suggestions.

Finally, I am grateful to Drs. John D. Lynch and C. Bertrand Schultz (University of Nebraska) who encouraged me to continue my studies on *Glyptosaurus* and especially to the late Mr. Daniel A. Yatkola (University of Nebraska) who inspired interest in fossil lizards while I was in attendance at the University of Nebraska.

This study was completed in residence at San Diego State University and was partially funded by a grant from Sigma Xi, which is gratefully acknowledged.

This work is dedicated to the memory of Daniel Yatkola and Paul Edwards of the University of Nebraska.

ABBREVIATIONS.

- AC, Pratt Museum, Amherst College, Amherst, Massachusetts.
AMNH, the American Museum of Natural History, New York, New York.
CM, Carnegie Museum, Pittsburgh, Pennsylvania.
F:AM, Frick Collection, the American Museum of Natural History, New York, New York.
KU, University of Kansas, Museum of Natural History, Lawrence, Kansas.
PU, Geology Museum, Princeton University, Princeton, New Jersey.
UCMP, University of California Museum of Paleontology, Berkeley, California.
UNSM, University of Nebraska State Museum, Lincoln, Nebraska.
USNM, United States National Museum, Smithsonian Institution, Washington, D.C.
TT, Texas Tech Museum, Lubbock, Texas.
YPM, Peabody Museum of Natural History, Yale University, New Haven, Connecticut.

BRIEF HISTORY AND TAXONOMIC PROBLEMS OF THE GENUS *GLYPTOSAURUS*

The genus *Glyptosaurus* was the first fossil anguid lizard to be recognized in North America. Marsh (1871) gave the description of *Glyptosaurus sylvestris*, based on an assemblage of skeletal elements consisting of a ventral shield, fragment of a jaw bearing three teeth and a left frontal. The latter bone element, the type (USNM 16523), was cited by Gilmore (1928) as the only bone upon which the genus rests because its association with the other elements

is questionable. Marsh (1871, 1872) named seven other species in addition to *G. sylvestris*. Loomis (1907), Douglass (1908), Gilmore (1928), and White (1952) have also described additional species (table 1). Gilmore in his classic monograph (1928) was the first to review the genus *Glyptosaurus* since Marsh's original descriptions. Gilmore (1928) established two new species of *Glyptosaurus*: *G. giganteus* and *G. hillsi*, and syn-

TABLE I
Classifications of the genera *Glyptosaurus*, *Placosaurus*, and *Placotherium*

(WEIGELT) 1929										
GERVAIS 1852	MARSH 1871, 1872	DOUGLASS 1903	LOOMIS 1907	DOUGLASS 1908	GILMORE 1928	emend. Kuhn 1940	GILMORE 1943	WHITE 1952	MESZOLELY, et al., 1978	SULLIVAN This Paper
<i>Placosaurus rugosus</i>										<i>nomen dubium</i>
	<i>Glyptosaurus sylvestris</i>									<i>G. sylvestris</i>
	<i>G. nodosus</i>									<i>G. sylvestris</i>
	<i>G. ocellatus</i>				<i>G. sylvestris</i>					<i>G. sylvestris</i>
	<i>G. anceps</i>				<i>Ototriton anceps</i>					<i>O. anceps</i>
	<i>G. princeps</i>									<i>Paraglyptosaurus princeps</i>
	<i>G. rugosus</i>									<i>P. princeps</i>
	<i>G. sphenodon</i>									<i>nomen dubium</i>
	<i>G. brevidens</i>				<i>G. sylvestris</i>					<i>G. sylvestris</i>
		<i>Helodermoides tuberculatus</i>			<i>Glyptosaurus tuberculatus</i>					<i>Helodermoides tuberculatus</i>
			<i>Glyptosaurus obtusidens</i>							<i>nomen dubium</i>
				<i>Glyptosaurus montanus</i>						<i>Helodermoides tuberculatus</i>
					<i>Glyptosaurus hillsi</i>					<i>Paraglyptosaurus princeps</i>
					<i>G. giganteus</i>					<i>Helodermoides tuberculatus</i>
						<i>Placotherium waltheri</i>				<i>incertae sedis</i>
						<i>Placosaurus waltheri</i>				<i>nomen dubium</i>
							<i>Glyptosaurus near nodosus</i>			<i>Helodermoides mongoliensis</i>
								<i>Glyptosaurus donohoei</i>		<i>Eoglyptosaurus donohoei</i>
										<i>Paraglyptosaurus yatkolai</i>

onymized *Helodermoides* Douglass (1903) with *Glyptosaurus*. He also synonymized *Glyptosaurus ocellatus* (Marsh, 1871) and *Glyptosaurus brevidens* (Marsh, 1872) with the species *G. sylvestris*. *Glyptosaurus anceps* (Marsh, 1871) was recognized by Gilmore (1928) as *Ototriton*, a member of the family Amphisbaenidae. *Glyptosaurus sphenodon* (Marsh, 1872) and *Glyptosaurus obtusidens* (Loomis, 1907) were retained by Gilmore (1928) as valid species because he lacked conclusive evidence that would permit him to synonymize them with other species of the genus. More recently, the number of species of *Glyptosaurus* has increased to 11, with the description of *Glyptosaurus donohoei* (White, 1952).

There has been little agreement as to the taxonomic position of *Glyptosaurus* and supposedly related genera (*Peltosaurus*, *Xestops*, *Melanosaurus*) since their initial discovery. Marsh (1872) suggested that *Glyptosaurus* be placed in its own family Glyptosauridae. Camp (1923) agreed with Marsh's proposal, and established criteria for the separate familial classification, but was opposed by Gilmore (1928) and more recently by Meszoely (1970). The characters used by Camp (1923) to show that *Glyptosaurus* and other extinct anguid genera (the European Eocene form *Placosaurus* Gervais, 1852) constitute a family unto themselves have been shown by Meszoely (1970) to be invalid. Additional support based on caudal vertebrae has been given by myself (Sullivan, in press). Cope (1877), without characterizing the family, informally used Placosauridae for some Wasatchian Age osteoderms from New Mexico. Because he recognized the similarities of these osteoderms to those of *Glyptosaurus* and the European *Placosaurus rugosus*, he based the family name on the latter, which has

taxonomic priority. *Glyptosaurus* and the other North American genera *Odaxosaurus* (= *Pancelosaurus* Meszoely, 1970, see Meszoely, Estes and Haubold, 1978), *Melanosaurus*, *Peltosaurus*, *Xestops*, *Arpadosaurus*, *Helodermoides*, and the new genera herein described as *Eoglyptosaurus* and *Paraglyptosaurus* are all considered to belong to the family Anguidae.

The subfamily status has varied somewhat in recent times. McDowell and Bogert (1954) erected the subfamily Glyptosaurinae under the family Anguidae to include *Glyptosaurus* and the European *Placosaurus* and *Placotherium*. Under the subfamily Diploglossinae, McDowell and Bogert (1954) included the genus *Xestops*. *Melanosaurus* Gilmore (1928) was included in its own subfamily, Melanosaurinae, and referred to the family Xenosauridae.

Genera included in the subfamily Glyptosaurinae by Meszoely (1970) are *Glyptosaurus*, *Peltosaurus*, *Melanosaurus*, *Xestops*, *Arpadosaurus*, and *Placosaurus*; the European *Placosauriops* and *Placosauroides* have recently been synonymized with *Xestops* of North America (Meszoely, Estes and Haubold, 1978).

Gilmore (1928) realized the shortcomings in working with the material of *Glyptosaurus* and wrote: "The fragmentary nature of the material upon which the species of *Glyptosaurus* have been founded makes the work with this genus very difficult. . . . It will be observed that many of the species are distinguished on very slender evidence."

Through the years additional specimens of glyptosaurus (*sensu* Marsh) have been collected, however, and it is of interest now to review the status of these early Tertiary lizards in the light of the new material gathered since the time of Gilmore's work.

STRATIGRAPHIC AND PALEOGEOGRAPHIC OCCURRENCES OF THE MEMBERS OF THE GLYPTOSAURINAE

STRATIGRAPHIC AND GEOGRAPHIC OCCURRENCES

The Glyptosaurinae as herein defined are known from one occurrence in the middle Pal-

eocene deposits of San Juan County, New Mexico, from Eocene deposits of North America, Europe, Mongolia, and from the early and middle Oligocene of North America. Geo-

logical deposits containing these lizards span the Rocky Mountain region from Northern New Mexico and they are also known from late Eocene deposits in Southern California (Schatzinger, MS), and Ellesmere Island, Canada (Estes and Hutchison, 1978) (fig. 1); the vast majority of specimens, however, occur in the intermontane basins of the Rocky Mountain region and the floodplain deposits of the Great Plains.

Marsh (1871, 1872) failed to provide any specific information regarding the locality of the original specimens uncovered. The type specimen of *Glyptosaurus sylvestris* was collected by C. T. Ballard at Grizzly Buttes, Wyoming, on the third trip of the Yale Expedition of 1870. All glyptosaurine material uncovered by Marsh's field parties of 1870-1873 was from either Grizzly Buttes, Millersville, or Henry's Fork, Wyoming, and all are of Bridgerian Age (Wood et al., 1941). Precise stratigraphic occurrence and locality are not known for many of these early, yet important, finds.

Cope's expedition of 1874 into northern New Mexico yielded remains of fossil anguids that he designated "Placosauridae" (Cope, 1877). These fragmentary remains are from the San Jose Formation [Wasatchian (Lucas, personal commun.)]. The assignment of Wasatchian Age was originally based on the presence of mammals, which include pantodonts, taeniodonts, the condylarth *Phenacodus*, and the bird *Di-tryma*.

To date the oldest known glyptosaurines come from the middle Paleocene (Torrejonian) deposits of San Juan County, New Mexico (see cf. Glyptosaurinae, tribe, gen. and sp., indet., below). This important specimen serves to extend the Glyptosaurinae down to the middle Paleocene and is represented by right and left dentary fragments, fragment of right maxilla as well as some unidentifiable bone fragments. This specimen was collected from the Nacimiento Formation by the American Museum of Natural History Expedition of 1913.

Hills (1888, 1889) gave a detailed account of the Huerfano River Basin in Colorado, which yielded the type *Glyptosaurus hillsi* (Gilmore, 1928). Loomis offered precise stratigraphic and geographic information regarding the occurrence of vertebrate fossils in the Wasatch beds of the Big Horn Basin, Wyoming, which in-

cluded the type *Glyptosaurus obtusidens* (Loomis, 1907).

Stratigraphic and geographic data on occurrences of glyptosaurines in the Oligocene are more complete than those from the Eocene. Douglass (1903) reported on the type of *Helodermoides tuberculatus* from the White River beds of Pipestone Springs, Montana, and reported a few years later on the type of *Glyptosaurus montanus* (Douglass, 1908), based on a specimen found in the "Titanotherium beds" north of the Big Hole River at the southeastern base of McCarty's Mountain, Beaverhead County, Montana; both reports give fair accounts on locality. Both of Douglass's specimens are from the lower Oligocene (Chadronian) deposits. Middle Oligocene (Orellan) deposits, which have been referred to by early stratigraphers as the "Oreodon beds"



FIG. 1. Important glyptosaurine localities in North America. 1. San Diego, California (Unitan); 2. San Juan Basin, New Mexico (Torrejonian and Wasatchian); 3. Huerfano Basin, Colorado (Wasatchian); 4. Nebraska Badlands (Chadronian-Orellan); 5. Big Badlands, South Dakota (Chadronian-Orellan); 6. Uinta Basin, Utah (Unitan); 7. Bridger Basin, Wyoming (Bridgerian); 8. Natrona County, Wyoming (Chadronian); 9. Pipestone Springs, Montana (Chadronian); 10. Ellesmere Island, Canada (Wasatchian).

of the White River Formation, have been the site of many glyptosaur finds, among which was Gilmore's type specimen of *Glyptosaurus giganteus* (Gilmore, 1928). The most nearly complete account of stratigraphic horizons of glyptosaurines and other fossil vertebrates was made by Emry (1973) in his study of Chadronian White River Formation deposits in Natrona County, Wyoming.

Outside the United States fossil anguids are known from the Wasatchian Age Eureka Sound Formation of Ellesmere Island, Canada, and are presumed to be Glyptosaurinae (Estes and Hutchison, 1978). Specimens of glyptosaurines are also known from the Shara Murun Formation (upper Eocene) near Baron Sog, Inner Mongolia (Gilmore, 1943; Radinsky, 1964), middle Eocene deposits from Geiseltal (Kuhn, 1940) and the upper Eocene deposits of Ste. Radegonde Près d'Apt of France (Gervais, 1859). To date no post-Eocene glyptosaurine remains are known outside the United States.

DEPOSITIONAL ENVIRONMENTS

Accounts of the depositional history of the Eocene and Oligocene sediments of the Rocky Mountain region and adjacent areas have been given by Love (1960), Love, McGrew and Thomas (1963), Clark, Beerbower and Kietzke (1967) and Robinson (1972). Briefly, the early Eocene of the Rocky Mountain region was characterized by the development of well-defined basins during a time of crustal deformation and volcanic activity. This volcanic activity increased with the onset of the middle Eocene and continued through late Eocene times coinciding with a decrease in crustal deformation (Love, 1960; Love, McGrew and Thomas, 1963; Robinson, 1972). The middle and late Eocene was a time of lake formation throughout what is now Wyoming (Robinson, 1972). Robinson (1972) also reported that there is a major hiatus in the Rocky Mountains between the middle and late Eocene sediments and the overlying Oligocene deposits that points to a major erosional or non-depositional episode during this time, despite the fact that these Eocene sediments are overlain by the

Oligocene sediments without significant discordance.

Lower Oligocene sedimentation of the Great Plains region has been studied by Schultz and Stout (1955) and more extensively by Clark, Beerbower and Kietzke (1967). The Chadron Formation in which many specimens of *Helodermoides tuberculatus* have been found, has been interpreted by Clark, Beerbower and Kietzke (1967) as being primarily channel fill-stream deposits, floodplain deposits, river bank deposits, and ponds. According to Robinson (1972), the early Oligocene deposits, while not extremely thick, are of a wide extent and those of the middle Oligocene (Orellan) of Schultz and Stout (1955) are less so, pointing to the possibility of another broad regional upwarping (Robinson, 1972).

CORRELATION OF GLYPTOSAURINE-BEARING UNITS

Of particular interest is the correlation of the lower and middle Eocene formations of the Rocky Mountain region that bear the remains of the glyptosaurine lizards described in this study. Precise stratigraphic data are lacking for the earlier collected material as noted previously, but their geographic location is generally known. Robinson (1972) published a correlation chart for these important Eocene deposits in the Rocky Mountain region that is adapted herein (fig. 2). These basal deposits are shown to be contemporaneous with each other, occupying the lower half of Eocene time. Thus the Willwood, Wasatch, Huerfano, and Wind River formations are considered to be of Wasatchian Provincial Age of Wood et al. (1941). The sediments of the Bridger Formation are not as extensive as the above-mentioned formations and represent a smaller amount of Eocene time (Savage, 1975). Two specimens of *Glyptosaurus* and one specimen of (?) *Helodermoides* are known from the Uinta Formation of Utah and represent the only known specimens of fossil anguid lizards from the Uintan. There are no known glyptosaurines from the Duchesnean Age (late Eocene) of Robinson (1972) in North America.

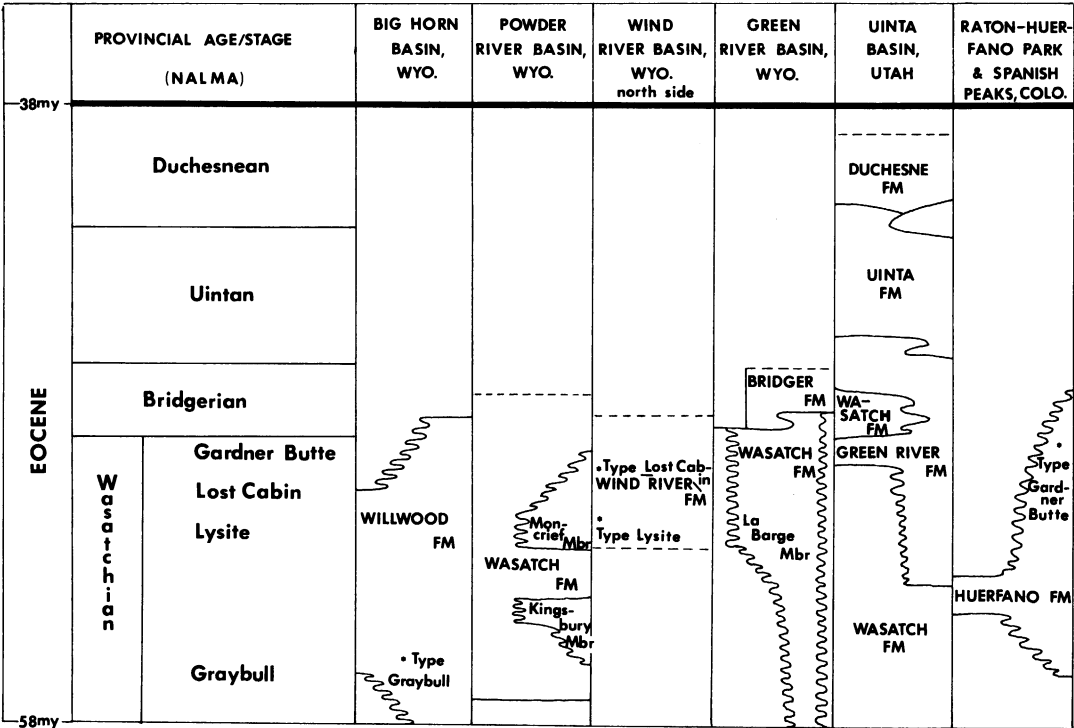


FIG. 2. Correlation of important Eocene glyptosaurine-bearing deposits of the Rocky Mountain region (modified after Robinson, 1972).

SYSTEMATICS

Past taxonomic work by Marsh (1871, 1872), Douglass (1903, 1908), Loomis (1907), Gilmore (1928, 1943), and White (1952) on the members of the genus *Glyptosaurus* (*sensu lato*) has been based, by and large, on fragmentary material. As a result these workers were influenced by differences in the size of specimens as well as observable differences in the osteoderms that covered the frontal bone(s). These characters are variable and are not in themselves particularly useful in assigning these fossil lizards to a particular taxon. Variations in size, particularly in the Oligocene forms, can be interpreted as ontogenetic variation within one

species. This is also evident among the Eocene forms, but to a lesser extent because less material is available. Differences in osteoderms and their distribution vary greatly within a species and they are not particularly useful in generic classification.

I have attempted to reclassify these fossil anguids primarily on skull morphology in association with dentition and osteoderm arrangement. I believe that this is the best approach given the fact that these fossil anguids are known from few remains. The following classification is adopted:

A CLASSIFICATION OF THE GLYPTOSAURINAE

CLASS REPTILIA

ORDER SQUAMATA

FAMILY ANGUIDAE COPE, 1864

SUBFAMILY GLYPTOSAURINAE McDowell and Bogert, 1954, Torrejonian-(?)Valentinian.

TRIBE GLYPTOSAURINI, new tribe

GENUS *GLYPTOSAURUS* MARSH, 1871, Wasatchian-Uintan; North America.*Glyptosaurus sylvestris* Marsh, 1871, Wasatchian-Bridgerian; North America.GENUS *PARAGLYPTOSAURUS*, new genus, Wasatchian-Bridgerian; North America.*Paraglyptosaurus princeps* (Marsh 1872), Wasatchian-Bridgerian; North America.*Paraglyptosaurus yatkolai*, new species, Wasatchian; North America.GENUS *EOGLYPTOSAURUS*, new genus*Eoglyptosaurus donohoei* (White 1952), Wasatchian; North America.GENUS *HELODERMOIDES* DOUGLASS, 1903, (?)Uintan-Orellan; North America, late Eocene; Mongolia.*Helodermoides tuberculatus* Douglass, 1903, Chadronian-Orellan; North America.*Helodermoides mongoliensis*, new species, late Eocene; Mongolia.

TRIBE MELANOSAURINI, new tribe

GENUS *ARPADOSAURUS* MESZOELY, 1970*Arpadosaurus gazinorum* Meszoely, 1970, Wasatchian; North America.GENUS *MELANOSAURUS* GILMORE, 1928*Melanosaurus maximus* Gilmore, 1928, Wasatchian; North America.GENUS *PELTOSAURUS* COPE, 1872*Peltosaurus granulosus* Cope, 1873, Chadronian-Whitneyan; North America.*Peltosaurus abbotti* Gilmore, 1928, Orellan; North America.GENUS *XESTOPS* COPE, 1873*Xestops vagans* (Marsh, 1872), Wasatchian-Bridgerian; North America.*Xestops abderhaldeni* (Kuhn, 1940), middle Eocene; Europe.*Xestops stehlini* (Hoffstetter, 1962), late Eocene; Europe.*Xestops weigelti* (Kuhn, 1940), middle Eocene; Europe.

SUBFAMILY GLYPTOSAURINAE

MCDOWELL AND BOGERT, 1954

TYPE: *Glyptosaurus* Marsh, 1871 (*sensu lato*).

KNOWN DISTRIBUTION: Middle Paleocene-late(?) Miocene (Torrejonian-Valentinian) of North America, middle and late Eocene of Europe, and late Eocene of Asia.

REVISED DIAGNOSIS: Anguids with robust tuberculated dermal armor; frontals usually wide, either fused or separate; palatine and pterygoid teeth in large ovoid patches, vomerine teeth absent.

The Glyptosaurinae differ from the subfamilies Gerrhonotinae, Diploglossinae, Anguinae, and the genus *Odaxosaurus* in the possession of robust (thick) tuberculate dermal armor (osteoderms) and well-defined ovoid patches of palatal teeth on the pterygoid and palatine bones and no teeth on vomerine bones. The subfamily differs from the Diploglossinae,Anguinae, and the genus *Odaxosaurus* by possessing a relatively elongated mandible and maxilla with a high tooth count (between 20 and 30), and differs from the Gerrhonotinae, Diploglossinae, and Anguinae in the possession of well-developed limbs; condition not known with certainty in *Odaxosaurus*. The Glyptosaurinae differ from the Anguinae and Diploglossinae in the absence of the premaxillary fenestrae¹; condition not known with certainty in *Odaxosaurus*.DISCUSSION: The subfamily Glyptosaurinae was first erected by McDowell and Bogert (1954). In this subfamily they placed only the genus *Glyptosaurus* and its European ally¹Meszoely (1970) used the term "premaxillary foramen" for the opening formed at the palatal junction of the maxilla and the premaxilla. Richard Estes, Jacques Gauthier, and myself prefer to call these openings "premaxillary fenestrae" so as not to confuse these with the foramina located on the labial side of the premaxilla.

Placosaurus Gervais, 1852. They erected the subfamily on the basis of three specializations that they believed were significant at the subfamilial level. These were: (1) "disintegration of the typical large and regular head osteoderms (and presumably the overlying epidermal scutes) of anguids"; (2) "the widening of the frontals (which may or may not be fused) between the orbits to form a moderately large orbital roof, the frontal being conspicuously wider between the orbits than anteriorly"; and (3) "the great increase in size." Meszoely's definition of the subfamily included only one character, that of the possession of tubercular dermal armor (Meszoely, 1970). For further discussion of the characters of the subfamily Glyptosaurinae see Review of the Characters of the Genus *Glyptosaurus* Marsh, 1871 below.

TRIBE GLYPTOSAURINI, NEW TRIBE

TYPE: *Glyptosaurus* Marsh, 1871 (*sensu stricto*).

KNOWN DISTRIBUTION: Early Eocene-middle Oligocene (Wasatchian-Orellan).

DIAGNOSIS: Glyptosaurines that differ from the only other glyptosaurine tribe, Melanosaurini, in the possession of hexagonal osteoderms that cover the entire skull.

DISCUSSION: This tribe is erected for the glyptosaurine genera that possess discrete hexagonal osteoderms that cover the entire skull. Four genera are included: *Glyptosaurus* Marsh, 1871, *Helodermoides* Douglass, 1903, *Eoglyptosaurus*, new genus and *Paraglyptosaurus*, new genus (see below). I believe that the possession of subequal hexagonal osteoderms on the skull implies a lineage distinct from the other glyptosaurines. The European species *Placosaurus rugosus*, *P. waltheri*, and *Placotherium waltheri* are placed within this tribe, although they are *nomina dubia* whose generic distinction cannot be verified (see below).

GLYPTOSAURUS MARSH, 1871

TYPE SPECIES: *Glyptosaurus sylvestris* Marsh, 1871, p. 456.

KNOWN DISTRIBUTION: Late early Eocene through early late Eocene (Late Wasatchian-Uintan) of North America.

DIAGNOSIS: A genus of glyptosaurinids exhibiting the following characters: frontals distinct, covered with hexagonal tubercular osteoderms arranged in five or six rows between the orbits; teeth obtuse, not inflated, striations confined to crown, maxilla straight, body and cephalic osteoderms with concentric or radiating pattern of tubercles.

Glyptosaurus differs from *Helodermoides* in having concentric ring pattern of tubercles on osteoderms, cephalic osteoderms generally non-inflated with five rows between orbits, obtuse tooth type, tendency for fusion of osteoderms to underlying bone, flattened frontals and presumed open supratemporal fenestrae. Differs from *Paraglyptosaurus* in having separate frontals, non-inflated obtuse tooth type, straight maxilla, curved jugal blade and less tendency for fusion of dermal armor to underlying bone. Differs from *Eoglyptosaurus* in having separate frontals, and broader cephalic osteoderms.

DISCUSSION: The type of the genus is based on the single left frontal (fig. 3a and b) designated *Glyptosaurus sylvestris* by Marsh (1871). See also specific discussion.

Glyptosaurus sylvestris Marsh

Figures 3; 4a and b; 5a and b

Glyptosaurus nodosus Marsh, 1871, p. 458.

Glyptosaurus ocellatus Marsh, 1871, p. 458.

Glyptosaurus brevidens Marsh, 1872, p. 305.

TYPE SPECIMEN: USNM 16523 (Marsh, 1871, p. 456), left frontal (fig. 3a and b).

LOCALITY: Grizzly Buttes, Wyoming.

HORIZON: Bridger Formation (Bridgerian).

DIAGNOSIS: Same as for genus.

HYPODIGM: AMNH 5113 (referred to *G. princeps* by Gilmore, 1928, pp. 103-104, p. 184, pl. 15, fig. 5) fig. 3e-h). Both frontals, left prefrontal, right maxilla, part of the left maxilla, pterygoid fragment and body osteoderms. Grizzly Buttes, Wyoming, Bridger Formation (Bridgerian). Collector: Albert Thompson, June 15, 1903.

AMNH 5902 (fig. 5i and j), both frontals, anterior fragment of parietal, left supratemporal process, right acetabulum, left squamosal, two dentary fragments, ramus fragment, proximal part of left humerus, proximal part of tibia, thoracic vertebral fragment, unidentified bone

fragments and osteoderms. Grizzly Buttes, Wyoming. Bridger (B_2) Formation (Bridgerian). Collector: William J. Sinclair, 1905.

AMNH 7590 (fig. 4a and b), complete right frontal, parietal, right jugal, posterior part of right ramus and part of left surangular, body

and cephalic osteoderms and unidentified bone fragments. Simpson's Quarry, near Gardner, Colorado. Huerfano Formation (Wasatchian). Collector: Peter Robinson, 1952.

AMNH 11045, left frontal. Fossil Creek, Gardner, Colorado. Huerfano Formation

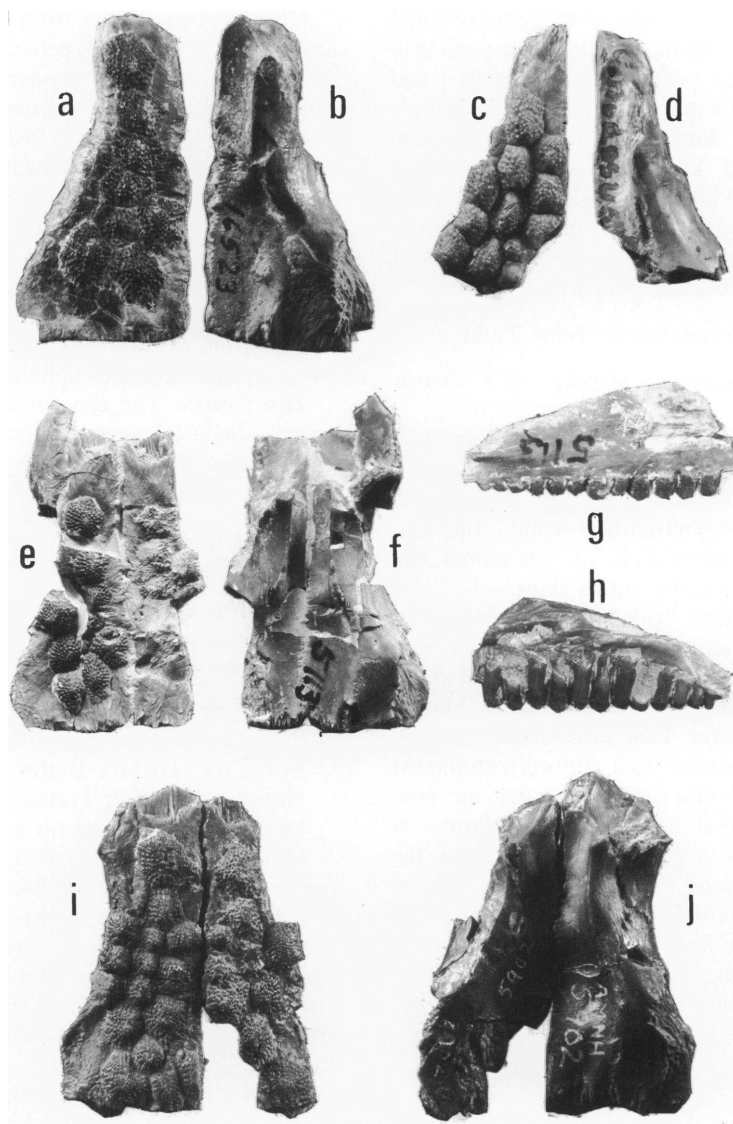


FIG. 3. *Glyptosaurus sylvestris*, USNM 16523 (type), left frontal. a. Dorsal view. b. Ventral view. X1.4.; USNM 16520 (type of *Glyptosaurus nodosus* Marsh, 1871), left frontal. c. Dorsal view, d. Ventral view. X1.4. AMNH 5113, left and right frontal. e. Dorsal view. f. Ventral view, right maxilla. g. Labial view. h. Lingual view. e and f X.9, g and h X1.4.; AMNH 5902, left and right frontal. i. Dorsal view. j. Ventral view. X1.1. All are from the Bridger Formation of Grizzly Buttes, Wyoming.

(Wasatchian). Collector: AMNH Expedition, 1952.

USNM 16520 (type of *G. nodosus*, Marsh, 1871, p. 458; Gilmore, 1928, p. 105, p. 183,

pl. 14, figs. 4 and 4a) (fig. 3c and d), left frontal. Grizzly Buttes, Wyoming. Bridger Formation (Bridgerian). Collector: Othniel C. Marsh, 1870.

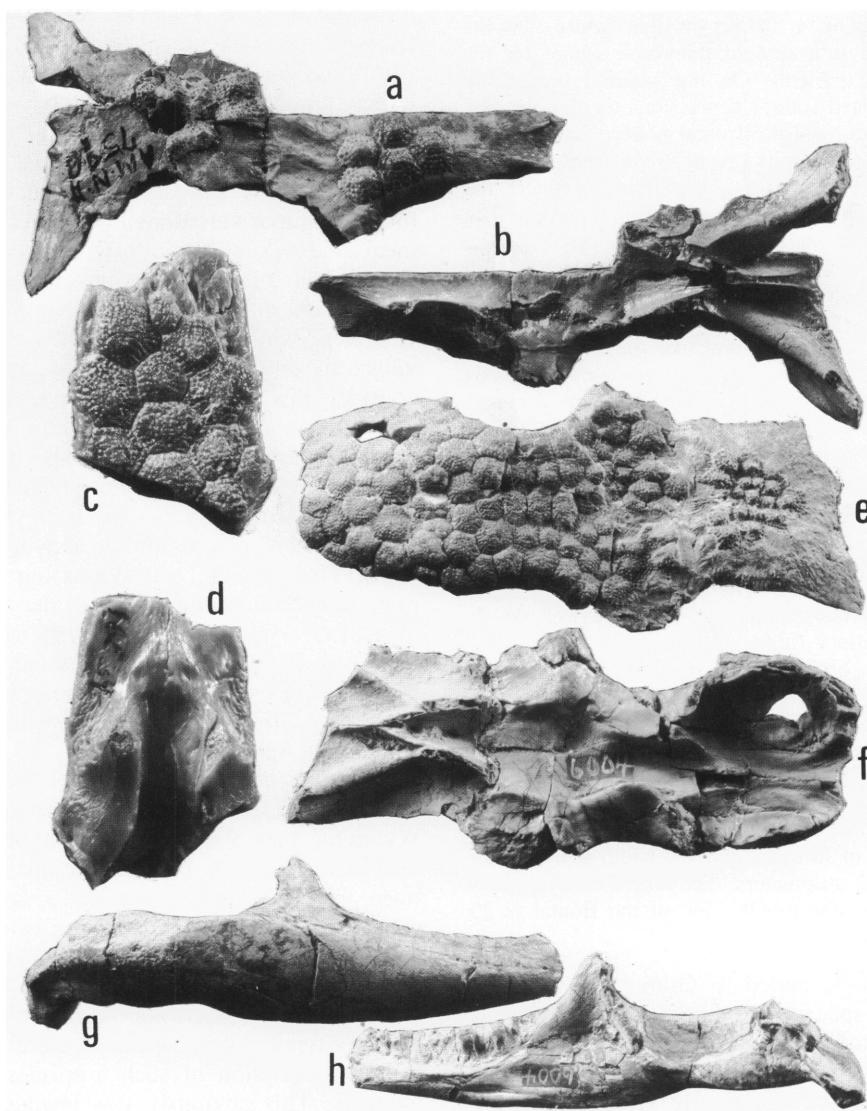


FIG. 4. *Glyptosaurus sylvestris*, AMNH 7590, right frontal and parietal. a. Dorsal view. b. Ventral view. Simpson's Quarry, near Gardner, Colorado. Huerfano Formation. X1. *Paraglyptosaurus princeps* (Marsh), new genus, USNM 16539 (type of *Glyptosaurus princeps* Marsh 1872), anterior part of frontal. c. Dorsal view. d. Ventral view. Grizzly Buttes, Wyoming. Bridger Formation. X1.4.; USNM 6004 (type of *Glyptosaurus hillsi* Gilmore 1928), frontal, parietal, nasals, parts of both pre- and postfrontals and maxillary. e. Dorsal view. f. Ventral view. X.8, right dentary. g. Labial view. h. Lingual view. Muddy fork of Huerfano River, above Gardner, Colorado. Huerfano Formation. X.6.

DISCUSSION: Marsh's description (Marsh, 1871) (see Review of the Characters of the Genus *Glyptosaurus* below) is still largely valid. Gilmore (1928) further described the type of *Glyptosaurus sylvestris* as follows:

The type frontal shows that it joined its fellow of the opposite side by a distinct median suture. On the posterior end is a straight transverse suture for the union of the parietal. On the external border are plainly indicated sutural depressions for the articulation of the pre- and postfrontal bones. These do not meet above the orbits as in *Heloderma*, but are separated by a space of 7.4 millimeters where the frontal contributes to the supraorbital border. The pointed anterior end of the frontal is missing. The dorsal surface, as Marsh observed, is covered with shields of "moderate thickness." The peripheral portion of most of the shields is flat or but slightly raised, with a decided nodelike elevation at their center. Their surfaces are covered with numerous small polished tubercles without definite arrangement, though there is a tendency, especially of the peripheral tubercles, to form in circular rows around the raised central portion. The shields are five and six sided and are so closely joined to one another as to entirely cover the underlying bone. Many of the lateral shields are detached and missing, thus showing the frontal surface to be smooth except for slight grooving. On the ventral side there are well developed longitudinal ridges that partially enclose the olfactory lobe of the brain. On its external side this ridge is strongly beveled, forming the supraorbital border. The olfactory ridges did not meet the median line to enclose the olfactory lobes as in *Heloderma*, but were widely separate as in *Peltosaurus* and other Anguidae. The frontal, as preserved, has a greatest length of 31 millimeters; a greatest width at the posterior end of 15.8 millimeters; width at the center of the orbit 12 millimeters. The length of five posterior shields on the middle row of the frontal is 20 millimeters.

Little can be added to Gilmore's redescription of this specimen, other than to say that it is, as he stated, adequate for generic diagnosis. *Glyptosaurus sylvestris* was extensively re-evaluated by Gilmore (1928). He synonymized the type species of *G. brevidens* and *G. ocellatus* with *G. sylvestris*. Type specimens of both these former species were unavailable for this study. His basis for synonymizing *G. brevidens* with *G. sylvestris* was the fact that he could not

see the differences in frontal thickness as described by Marsh (1872), and therefore concluded that they were specimens of the same species. As a result of the synonymy of this form, a number of post-cranial elements and other skull elements originally referred to *G. brevidens* became available for comparison of *G. sylvestris* with other forms.

My assignment of the hypodigm material is largely based on frontal morphology as this still remains the primary criterion for generic assignment. Assignment of individual specimens to *Glyptosaurus sylvestris* may be difficult as there are minor variations in tubercular arrangement and variations in osteoderm shape and size. Most of these variations concern the prominence of the concentric ring pattern of tubercles, which probably involves both individual and intraspecific variations, and I do not consider this variation taxonomically significant.

In size and shape the type specimen of *G. nodosus* (fig. 3c and d) is not unlike that of the type specimen of *G. sylvestris* (fig. 3a and b) and it is here placed into synonymy with the latter. The cephalic osteoderms are somewhat more inflated than those seen in the type specimen of *G. sylvestris* but this difference is unlikely to be more than individual variation. Both specimens are from the same locality and horizon, Grizzly Buttes, Wyoming, and Bridgerian Age.

The type of *G. sphenodon* (USNM 16524) from the Bridger Formation of Henry's Fork, Wyoming, may also be best considered a specimen of this species, but because this type specimen is so fragmentary *G. sphenodon* is considered a *nomen dubium* (see below).

Gilmore (1928) listed in the legend of one of his plates (Gilmore, 1928, p. 171, pl. 2) a species, *Glyptosaurus? microdus*. This was evidently a typographical error as there had never been a description of such a species of *Glyptosaurus*. This obviously was intended to read *?Xestops microdus* for the species that was re-described by Gilmore (1928, p. 148). The re-description of *?Xestops microdus* matches the illustration that appears in his plate 2. Meszely (1970, p. 125) designated this species of

Xestops along with three other species as being *nomina nuda*.

Cf. *Glyptosaurus sylvestris*

USNM 12709, posterior part of left maxilla. Two miles north of Lone Tree, Henry's Fork, Bridger Basin, Wyoming. Bridger Formation (Bridgerian). Collector: George F. Sternberg, 1930.

USNM 12845, part of right mandible, pterygoid and miscellaneous bone fragments. Little Dry Creek, Bridger Basin, Uinta County, Wyoming. Bridger Formation (Bridgerian). Collector: Charles W. Gilmore, 1930.

USNM 16654, posterior part of right frontal, part of parietal, ramus fragments, left jugal fragment, pterygoid, long bone fragments, vertebral fragments, cephalic and body osteoderms, and miscellaneous bone fragments. Northeast point of Twin Buttes, T14N, R109W, Sec. 10 or 15, Sweetwater County, Wyoming. Bridger (C) Formation (Bridgerian). Collector: Smithsonian Expedition, 1941.

YPM 1073, fragment of left frontal, vertebral fragments, body osteoderms and miscellaneous bone fragments. Grizzly Buttes, Wyoming. Bridger Formation (Bridgerian). Collector: George G. Lobdell, Jr., September 5, 1871.

YPM 1092 (fig. 5a and b), right dentary and part of ramus. Bridger Basin, Wyoming. Bridger Formation (Bridgerian). Collector: Yale College Scientific Expedition of 1873.

YPM 7590, fragment of jugal, vertebral fragments, and miscellaneous osteoderms. Associated with other bone fragments not referable to the Glyptosaurinae (probably *Saniwa*). Locality unknown. Gravel beds, formation unknown (?Bridgerian). Collectors: (?) Othniel C. Marsh and Joseph F. Page, August 28, 1871.

YPM 7592, posterior part of right frontal, osteoderms and vertebral fragments. Associated with crocodillian dentary and other dentary remains. Eocene (?Bridgerian), formation and locality unknown. Collector: George G. Lobdell, Jr., September 26, 1871.

YPM 7594, fragment of left maxilla. Eocene

(?Bridgerian), formation and locality unknown. Collector: R. E. Son, August 1873.

YPM 7596, posterior fragment of left maxilla. Millersville, Wyoming, (?Bridger Formation (?Bridgerian). Collector: R. E. Son, 1873.

Glyptosaurus sp.

Two specimens, CM 3405 and PU 11303, can be referred to the genus *Glyptosaurus*. Both of these specimens are too fragmentary to permit specific assignment and to my knowledge are the only two specimens of *Glyptosaurus* from the Uintan (late Eocene) of North America.

CM 3405, body osteoderms and crushed proximal part of right ramus. On the White River, near Ouray, Utah. Wagonhound Formation (Uinta B). Collector: Olof August Peterson.

PU 11303, fragment of frontals, right prefrontal, right jugal and posterior part of right maxilla, part of left maxilla, left jugal and unidentified bone fragments with osteoderms. Kennedy's Hole, White River, Utah. Uinta Formation, upper gray clays, *T. cornutum* beds. Collector: John Bell Hatcher, 1895.

DISCUSSION: PU 11303 is assigned to *Glyptosaurus* sp. on the basis of unfused frontal bones, tooth morphology (obtuse striated crowns), and osteoderms that display tubercles in a concentric ring pattern. CM 3405 is referred to this genus by the same concentricism of tubercles on body osteoderms.

These specimens extend the range of the genus *Glyptosaurus* to the Uintan (late Eocene) of North America.

PARAGLYPTOSAURUS, NEW GENUS

Glyptosaurus Marsh, 1871 (in part).

TYPE SPECIES: *Glyptosaurus princeps* Marsh 1872, p. 302.

KNOWN DISTRIBUTION: Early through middle Eocene (Wasatchian-Bridgerian) of North America.

ETYMOLOGY: From the Greek word *para* meaning near, beside, or parallel. In this case

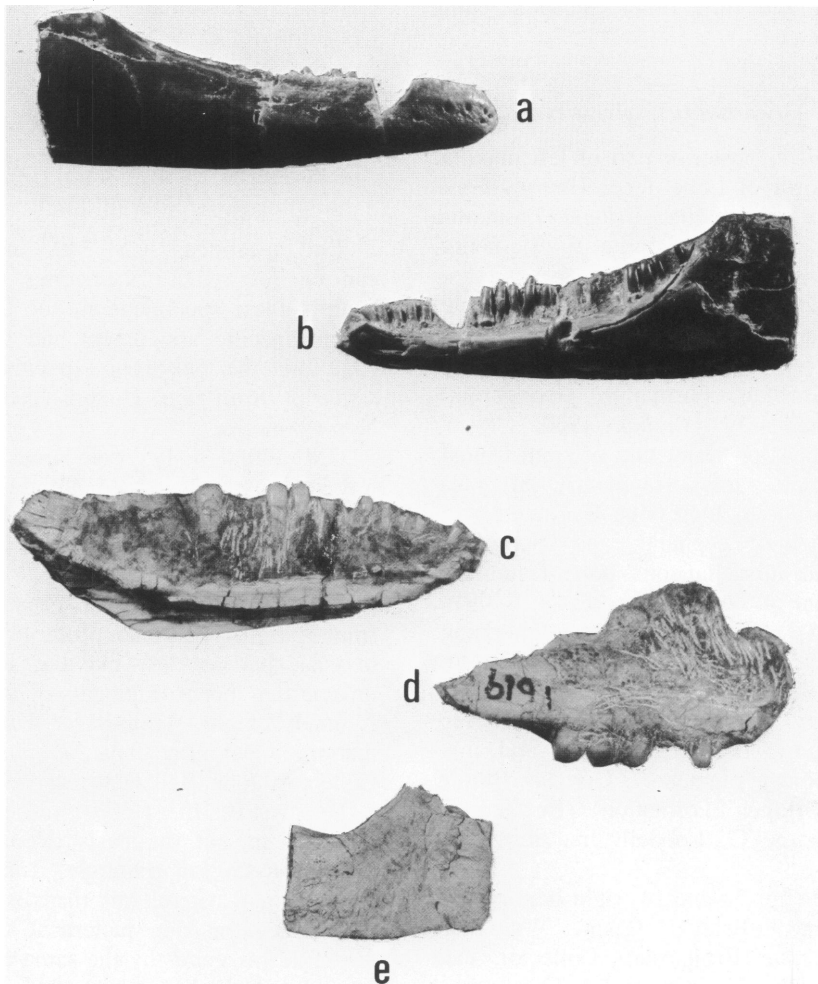


FIG. 5. cf. *Glyptosaurus sylvestris*, YPM 1092, right dentary and part of ramus. a. Labial view. b. Lingual view. Bridger Basin, Wyoming. Bridger Formation. X.7. *Paraglyptosaurus princeps*, AMNH 1619. c. Lingual view of left dentary. d. Labial view of right maxilla. Garcia Canyon, Colorado. Huerfano Formation. X1.4.; AMNH 6054. e. Labial view of left jugal blade. Grizzly Buttes, Wyoming. Bridger Formation. X1.4.

used to designate that this genus co-existed with the genus *Glyptosaurus*.

DIAGNOSIS: A glyptosaurinid exhibiting the following characters: frontals fused, cephalic osteoderms platelike, tubercles arranged in a concentric ring pattern that also takes the form of a radiating pattern from the center of the osteoderm on both the body and cephalic osteoderms; teeth obtuse with a tendency toward a rugose blunt crushing type, and some display

a heterodont condition in which the anterior teeth approach those seen in *Helodermoides* and the posterior teeth are massive crushing type; crowns of teeth heavily striated; maxilla curved; dentary massive; jugal blade forming an expanded right angled blade at its posterior margin; supratemporal fenestra open; skull flattened, elongate, and broad.

Differs from *Helodermoides* in having fused frontals, obtuse tooth type, concentric ring pat-

tern of tubercles on osteoderms, fusion of dermal armor to underlying bone, platelike cephalic osteoderms, curved maxilla and open supratemporal fenestrae. Differs from *Glyptosaurus* in having fused frontal, inflated obtuse tooth type with tendency toward a heterodont condition, curved maxilla and greater fusion of dermal armor to underlying bone. Differs from *Eoglyptosaurus* in having broad platelike osteoderms, inflated obtuse tooth type with tendency towards heterodont condition and a curved maxilla.

DISCUSSION: See specific discussion.

Paraglyptosaurus princeps (Marsh)

Figures 4c-h; 5 c-e; 6 and 7a-d

Glyptosaurus princeps Marsh, 1872, p. 302.

Glyptosaurus rugosus Marsh, 1872, p. 305.

Glyptosaurus hillsi Gilmore, 1928, pp. 107-113.

TYPE SPECIMEN: USNM 16539 (Marsh, 1872, p. 302) (fig. 4c and d), anterior fragment of frontal, anterior fragment of left dentary, pterygoid, mandibular fragments, cephalic and body osteoderms and unidentified bone fragments.

LOCALITY: Grizzly Buttes, Uinta County, Wyoming.

HORIZON: Bridger Formation (Bridgerian).

DIAGNOSIS: Differs from *P. yatkolai* in that it has flattened cephalic osteoderms and a well-developed midline row of osteoderms on frontal; lacks the characteristic lateral frontal osteoderms as seen in *P. yatkolai*.

HYPODIGM: AMNH 1614, central and posterior part of frontal, parietal fragments, maxilla, cephalic and body osteoderms, plus unidentified skeletal elements. Buck Spring, Alkali Creek, Wyoming. Formation unknown. Collector: Walter Granger, 1912.

AMNH 1618, incomplete parietal and body osteoderm. North of Gardner, Colorado. Huerfano Formation (upper beds) (Wasatchian). Collector: unknown, 1918.

AMNH 1619 (fig. 5c and d), left dentary and two right maxillae and tooth fragment (unassociated). Garcia Canyon, Colorado. Huerfano Formation (lower beds) (Wasatchian). Collector: unknown, 1918.

AMNH 6054 (figured in Gilmore, 1928, p.

173, pl. 4, fig. 4) (fig. 5e), parietal, left jugal fragment, right maxilla, body and cephalic osteoderms. Grizzly Buttes, Fort Bridger, Wyoming. Bridger Formation (Bridgerian). Collector: Walter Granger, 1903.

AMNH 6055 (figured in Gilmore, 1928, p. 185, pl. 16, figs. 1-6) (fig. 6a and b), frontal, parietal, left maxilla, proximal part of humerus (two humeri are present and are clearly from different genera), squamosal, jugal, disarticulated osteoderms. Grizzly Buttes, Wyoming. Bridger Formation (lower beds) (Bridgerian). Collector: Walter Granger, 1903.

AMNH 7455, frontal. Fossil Creek, Gardner, Colorado. Huerfano Formation (Wasatchian). Collector: Peter Robinson, 1952.

AMNH 7597, left maxilla. Fossil Creek, near Gardner, Colorado. Huerfano Formation (Wasatchian). Collector: unknown, (?)1952.

USNM 6004 (type of *Glyptosaurus hillsi* Gilmore 1928, pp. 107-113, figs. 62, 63, 65, 66, and 67; pl. 4, fig. 3; pl. 17) (fig. 4e-h), parietal, frontal, prefrontals, nasals, incomplete right postfrontal, left postfrontal, greater part of right mandible, left and right maxilla, anterior part of right dentary, both quadrates, pterygoid, ilium, thoracic vertebrae, and body osteoderms. Muddy Fork of Huerfano River, above Gardner, Colorado. Huerfano Formation (Wasatchian). Collector: R. C. Hills, 1889.

USNM 12590, nearly complete frontal and skull fragment. Levitt Creek, Uinta County, Wyoming. Bridger (B₃) Formation (Bridgerian). Collector: George F. Sternberg, 1930.

USNM 12844, anterior frontal fragment, right posterior part of frontal and body osteoderms. Between Levitt and Little Dry Creeks, Bridger Basin, Uinta County, Wyoming. Bridger Formation (Bridgerian). Collector: George F. Sternberg, July 10, 1930.

USNM 16526 (type of *Glyptosaurus rugosus* Marsh 1872, p. 305) (fig. 6c and d), posterior part of frontal. Grizzly Buttes, Uinta County, Wyoming. Bridger Formation (Bridgerian). Collector: T. G. Peck, 1871.

USNM 16599, anterior and right posterior part of frontal and unidentified bone fragment. West branch of Levitt Creek, Uinta County, Wyoming. Bridger (B₂) Formation (Bridgerian). Collector: Charles L. Gazin, 1940.

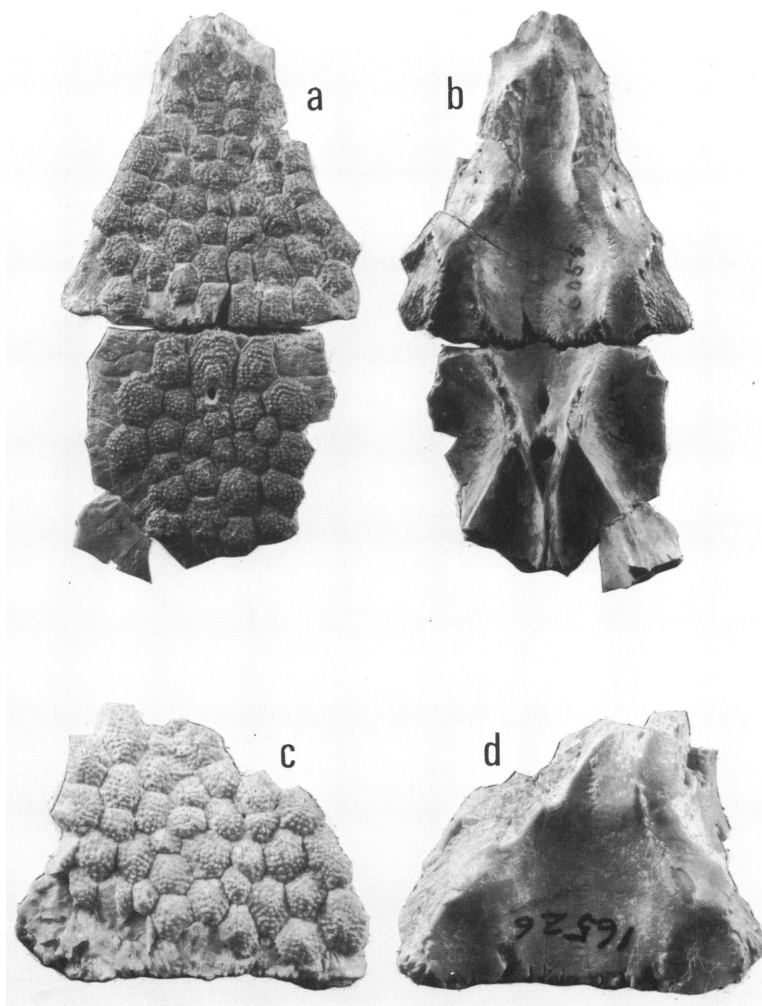


FIG. 6. *Paraglyptosaurus princeps*, AMNH 6055, frontal and parietal. a. Dorsal view. b. Ventral view. X1.4.; USNM 16526 (type of *Glyptosaurus rugosus* Marsh, 1872), posterior part of frontal. c. Dorsal view. d. Ventral view. X1.4. Both are from the Bridger Formation, Grizzly Buttes, Wyoming.

YPM 1072 (figured in Gilmore, 1928, as *G. sylvestris*, pl. 12, fig. 4) (fig. 7a and b), frontal, left postfrontal, distal end of left humerus, right ilium, fragment of left pterygoid, proximal end of left tibia, distal end of left femur, cephalic and body osteoderms and unidentified bone fragments. Grizzly Buttes, near Fort Bridger, Uinta County, Wyoming. Bridger (B₂) Formation (Bridgerian). Collector: Joseph F. Page, September 1, 1871.

YPM 7601 (fig. 7c and d), frontal. Locality and formation unknown (?)Millersville or Grizzly Buttes, Wyoming. (?)Bridger Formation (Bridgerian). Collector: unknown, 1874.

YPM 7602, posterior part of frontals, fragments of parietal, fragment of dentary, vertebral fragments and body osteoderms. Millersville, Wyoming. (?)Bridger Formation (Bridgerian). Collector and date unknown.

DISCUSSION: Gilmore (1928) established the

species *Glyptosaurus hillsi* with his description of a large Eocene anguid lizard from the Huerfano Formation (Wasatchian, Gardner Butte Member) near Gardner, Colorado. This species is strikingly different from species of *Glyptosaurus* and *Helodermoides* in a number of ways.

The frontals are fused, unlike the condition found in *Glyptosaurus* and *Helodermoides*. In addition five rows of platelike osteoderms lie between the orbits with a dominant middle row toward the anterior end of the frontal. This condition is evident in a number of specimens (fig. 4c and e; fig. 6a; 7a and c). The os-

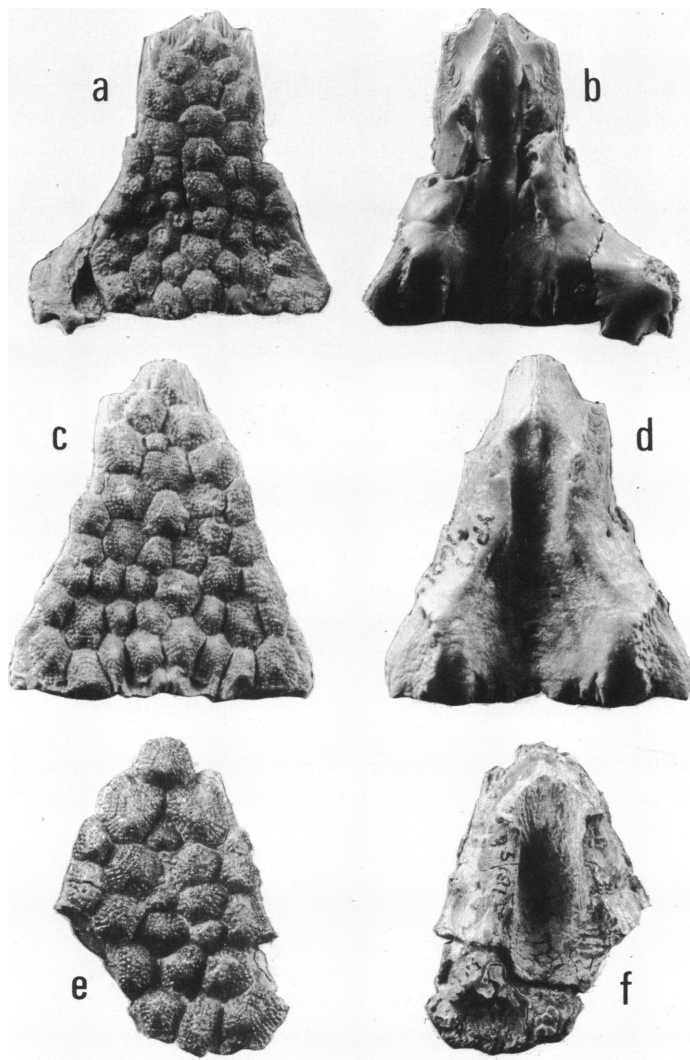


FIG. 7. *Paraglyptosaurus princeps*, YPM 1072, frontal and left postfrontal. a. Dorsal view. b. Ventral view. Grizzly Buttes, Wyoming. Bridger Formation. X1.; YPM 7601, frontal. c. Dorsal view. d. Ventral view. Locality and formation unknown, but probably Grizzly Buttes, Wyoming. Bridger Formation. X1.4. *Paraglyptosaurus yatkolai*, new species, AMNH 5181, nearly complete frontal. e. Dorsal view. f. Ventral view. Arroyo Blanco, New Mexico. San Jose Formation. X1.2.

teoderms are more prominent than those seen in the type of *Glyptosaurus* but this in itself does not seem to be a significant character. A concentric ring pattern of tubercles is very prominent as in some specimens of *G. sylvestris*. The maxilla is curved and robust as is the dentary, and the teeth are very large, of robust obtuse crushing type. The type of *Glyptosaurus princeps* Marsh (1872) has an anterior frontal fragment that corresponds exactly to the type of *Glyptosaurus hillsi* Gilmore (1928). In addition, the body osteoderms, mandible, and pterygoid fragments are indistinguishable, leaving little doubt as to their synonymy. A referred specimen (AMNH 6055, see fig. 6a and b), smaller than the two species of *Glyptosaurus* mentioned above, is indistinguishable from the type of *Glyptosaurus rugosus* (fig. 6c and d), and shows the same characters that distinguish these fossil agnathids from the others. This genus is distinct from its contemporary *Glyptosaurus* in having (1) fused frontals; (2) inflated crushing obtuse tooth type, and (3) curved maxilla and robust dentary. There are a few similarities that I believe reflect their genetic closeness. These similarities include subequal cephalic osteoderms with a concentric ring pattern of tubercles, and the presence of five rows of osteoderms between the orbits. Geologically they span about the same time, early Eocene to the end of the middle Eocene, with *Glyptosaurus* extending its range into the Uintan Age. The new genus *Paraglyptosaurus* is erected to include these contemporary robust forms previously referred to *Glyptosaurus* (*sensu lato*). The name *Paraglyptosaurus princeps* (based on USNM 16539) is chosen as the type species because of the number of specimens referable to this species.

Cf. *Paraglyptosaurus princeps*

AMNH 1617, six body osteoderms and vertebral fragments. Two miles north of Gardner, Colorado. Huerfano Formation (upper beds) (Wasatchian). Collector: AMNH Expedition, 1918.

AMNH 5109 (figured as *Glyptosaurus* sp. in Gilmore, 1928, p. 180, pl. 11, fig. 3), premaxilla, incomplete sections of left and right den-

taries, right mandibular fragments, six vertebral fragments, proximal end of humerus and unidentified bone fragments. Lower Alkali Creek, Wind River Basin, Wyoming. Wind River Formation (Wasatchian). Collector: AMNH Expedition, 1909.

AMNH 5196, dentary and maxilla fragment, osteoderms and miscellaneous bone fragments. South end of Promontory Bluff (?), near Gardner, Colorado. Huerfano Formation (Wasatchian). Collector: AMNH Expedition, 1918.

AMNH 7446, fragment of right dentary. Fossil Creek, near Gardner, Colorado. Huerfano Formation (Wasatchian). Collector: AMNH Expedition, 1952.

AMNH 7454, right maxilla fragment. Fossil Creek, Gardner, Colorado. Huerfano Formation (Wasatchian). Collector: AMNH Expedition, 1952.

AMNH 7592, cephalic and body osteoderms and miscellaneous bone fragments. Fossil Creek, near Gardner, Colorado. Huerfano Formation (Wasatchian). Collector: AMNH Expedition, 1952.

AMNH 7595, left dentary fragment. Fossil Creek, near Gardner, Colorado. Huerfano Formation (Wasatchian). Collector: AMNH Expedition, 1952.

AMNH 7596, right dentary fragment. Huerfano Basin, Colorado. Huerfano Formation (Wasatchian). Collector: Henry Fairfield Osborn, date unknown.

AMNH 7598, right dentary fragment. Garcier Canyon, Colorado. Huerfano Formation (Wasatchian). Collector: AMNH Expedition, 1952.

AMNH 7599, two parietal fragments. Fossil Creek, near Gardner, Colorado. Huerfano Formation (Wasatchian). Collector: AMNH Expedition, 1952.

AMNH 11044, fragment of maxilla. Lower Graybull Valley, Big Horn, Wyoming. Wasatch Formation (Wasatchian). Collector: AMNH Expedition, 1910.

PU 13271, posterior parts of left and right mandibles, anterior part of left dentary, maxilla fragment, cephalic and body osteoderms, parietal and miscellaneous bone fragments. One and one half miles east of Camp 1, Sand Coulee

Basin, Park County, Wyoming. Willwood Formation (Wasatchian). Collector: Glenn L. Jepsen, July 6, 1928.

USNM 215018, fragment of right maxilla. Divide between Sage Creek and Henry's Fork, Uinta County, Wyoming. Bridger (B₂) Formation (Bridgerian). Collector: Smithsonian Expedition, 1940.

YPM 7581, frontal fragment. Brizzly Buttes, Wyoming. Bridger Formation (Bridgerian). Collector: Othniel C. Marsh, September 5, 1870.

YPM 7583, anterior fragment of frontal. Locality and formation unknown (?Bridgerian). Collector: George B. Grinnell, September 3, 1870.

YPM 7584, proximal part of humerus, cephalic and body osteoderms, posterior part of left maxilla and miscellaneous bone fragments. Locality and formation unknown (?Bridgerian). Collector: Othniel C. Marsh, September 4, 1870.

YPM 7588, frontal fragment and three body osteoderms. Locality, formation, and collector unknown, September 4, 1871.

YPM 7595, fragment of left dentary. Millersville, Wyoming. (?)Bridger Formation (Bridgerian). Collector: R. E. Son, 1873.

YPM 7598, proximal end of humerus, mandibular fragments, cephalic and body osteoderms and miscellaneous bone fragments. Millersville, Wyoming. (?)Bridger Formation (Bridgerian). Collector: R. E. Son, 1873.

YPM 7599, right maxilla. Locality and formation unknown. Collectors: Lom and Chew, date unknown.

***Paraglyptosaurus yatkolai*, new species**

Figure 7e and f

TYPE SPECIMEN: AMNH 5181, nearly complete frontal (figured as *Glyptosaurus obtusidens* in Gilmore, 1928, pl. 15, fig. 6).

LOCALITY: Arroyo Blanco, New Mexico.

HORIZON: San Jose Formation (Wasatchian).

COLLECTOR: Expedition of the American Museum of Natural History, 1912.

DIAGNOSIS: Differs from *Paraglyptosaurus princeps* in having two prominent transversely-elongated anterior frontal osteoderms, with the

medial row of frontal osteoderms poorly developed. In addition the osteoderms are somewhat inflated unlike the platelike condition found in most specimens of *P. princeps*.

ETYMOLOGY: The species is named in honor of the late Daniel A. Yatkola (University of Nebraska).

DESCRIPTION: Gilmore (1928, p. 119) adequately described most of the diagnostic features of this specimen, however, a few additional features can be noted.

The frontal, unlike the frontal of *Paraglyptosaurus princeps*, lacks a prominent midline row of osteoderms. In addition, like *P. princeps*, it lacks any indication of a metopic suture on the ventral side of the frontal. Gilmore (1928, p. 119) stated that this specimen is represented by the "anterior half of coalesced frontals," however, the frontal is nearly complete dorsally, with only the posterior left corner, where it articulates with the left postfrontal, missing. Ventrally, the frontal is poorly preserved, especially around the periphery.

DISCUSSION: The type is the only specimen known of this species. It is so strikingly different in osteoderm form and arrangement, that I believe it to represent more than just a variation of *P. princeps*, to which it is related. This specimen was assigned to *Glyptosaurus obtusidens* Loomis by Gilmore (1928) on the grounds that both forms were from the earliest Wasatch deposits and thus represented the oldest known *Glyptosaurus* (*sensu lato*). For reasons given below *G. obtusidens* is considered a *nomen dubium* (see below).

***EOGLYPTOSAURUS*, NEW GENUS**

Glyptosaurus Marsh 1871 (in part).

TYPE SPECIES: *Glyptosaurus donohoei* White 1952, p. 186.

KNOWN DISTRIBUTION: Early Eocene (Wasatchian: Lost Cabin-Gardner Butte), of North America.

ETYMOLOGY: From the Greek word *eos* meaning dawn. In this case, used for the earliest recognized glyptosaurinid from the Lost Cabin Member of the Wasatch Formation of North America.

DIAGNOSIS: A glyptosaurinid exhibiting the following characters: frontals fused; cephalic osteoderm subconical; tubercles in a concentric ring pattern on cephalic and body osteoderms; five rows of osteoderms between orbits; teeth slender with obtuse crowns showing weak striations; homodont; maxilla straight; supratemporal fenestra open; skull elongated and flat.

Differs from *Helodermoides* in having fused frontals, obtuse tooth type, subconical osteoderms, tendency for fusion of dermal armor to underlying bone, open supratemporal fenestrae and elongated flattened skull. Differs from *Glyptosaurus* in having fused frontals, subconical osteoderms and greater fusion of dermal armor to underlying bone. Differs from *Paraglyptosaurus* in having uninflated homodont obtuse tooth type, straight maxilla, and subconical osteoderms.

DISCUSSION: See specific discussion.

Eoglyptosaurus donohoei (White)
Figures 8 and 9

Glyptosaurus donohoei White 1952, p. 186.

TYPE SPECIMEN: USNM 18316 (fig. 8a and b), crushed skull, incomplete left mandible, miscellaneous bone fragments and osteoderms.

LOCALITY: Boysen Reservoir, Fremont County, Wyoming, in SW1/4, Sec. 5, T4N, R6E.

FORMATION: Wasatch, Lost Cabin Member (Wasatchian).

COLLECTORS: Theodore E. White, Ernest L. Lundelius and John C. Donohoe, July 1948.

DIAGNOSIS: Same as for genus.

PARATYPE: USNM 18317 (fig. 8c and d), right dentary, maxilla, jugal cephalic, cheek and body osteoderms and miscellaneous bone fragments. Boysen Reservoir, Fremont County, Wyoming, SW1/4, Sec. 5, T4N, R6E (W.R.M.). Wasatch Formation, Lost Cabin Member (Wasatchian). Collectors: Theodore E. White, Ernest L. Lundelius, and John C. Donohoe, July 1948.

HYPODIGM: AMNH 7431 (fig. 8e-g; fig. 9), complete skull. Castillo Pocket, Quarry 1, Gardner, Colorado. Huerfano Formation (Wasatchian). Collector: J. Nocera, 1953.

DISCUSSION: This new genus is based on the

two specimens of *G. donohoei* reported by White (1952), as well as a third unpublished specimen (AMNH 7431), a beautifully preserved skull from the Huerfano Formation near Gardner, Colorado. These specimens resemble those referred to the contemporary *Paraglyptosaurus princeps* in that both species have fused frontals, similar arrangement of osteoderms between frontals as noted by White (1952), and elongated skull. *Eoglyptosaurus donohoei* (AMNH 7431) is so different from *Paraglyptosaurus princeps* (USNM 6004, = type of *Glyptosaurus hillsi*, Gilmore, 1928, see (fig. 4e-h) as to leave little doubt to their generic difference. *Eoglyptosaurus* differs from *Paraglyptosaurus* in that the maxilla is less curved, the teeth are more slender, homodont rather than showing the heterodont trend seen in *Paraglyptosaurus* and the possession of subconical osteoderms unlike the platelike osteoderm type seen on the frontal region of the latter genus.

The type of *Glyptosaurus donohoei* White (1952) (USNM 18316) agrees in every way with the species represented by AMNH 7431. The differences discussed above serve to separate it from its nearest relative *Paraglyptosaurus princeps*, and it is referred to a new genus, *Eoglyptosaurus*.

Cf. *Eoglyptosaurus donohoei*

AMNH 7454, maxilla fragment. Fossil Creek, Gardner, Colorado. Huerfano Formation (Wasatchian). Collector: AMNH Expedition, 1954.

UCMP 118364, parietal, right prefrontal, right posterior part of frontal, anterior part of right maxilla, coronoid region of right dentary, part of left dentary, right and left jugal fragments, fragment of medial part of right maxilla, fragment of left quadrate, right postfrontal, proximal end of right humerus, distal end of ?right humerus, cheek and body osteoderms, vertebrae and unidentified bone fragments. V77064, Big Piney North 3, Sublette Co., Wyoming. Wasatch Formation (Wasatchian). Barbara T. Waters, 1977.

YPM 8422, frontal, parietal, part of thoracic vertebra and unidentified bone fragment. 332b, 88-79, Big Horn Basin, Wyoming. Willwood

Formation (Wasatchian). Collector: YPM party, 1968.

Helodermoides Douglass, 1903

Glyptosaurus Marsh 1871, p. 456; Gilmore 1928, p. 113 (in part).

TYPE SPECIES: *Helodermoides tuberculatus* Douglass, 1903, p. 161, figs. 4 and 5.

KNOWN DISTRIBUTION: (?)Late Eocene-middle Oligocene (Chadronian-Orellan) of North America, late Eocene of Mongolia.

DIAGNOSIS: A glyptosaurinid exhibiting the following characters: frontals distinct, cephalic

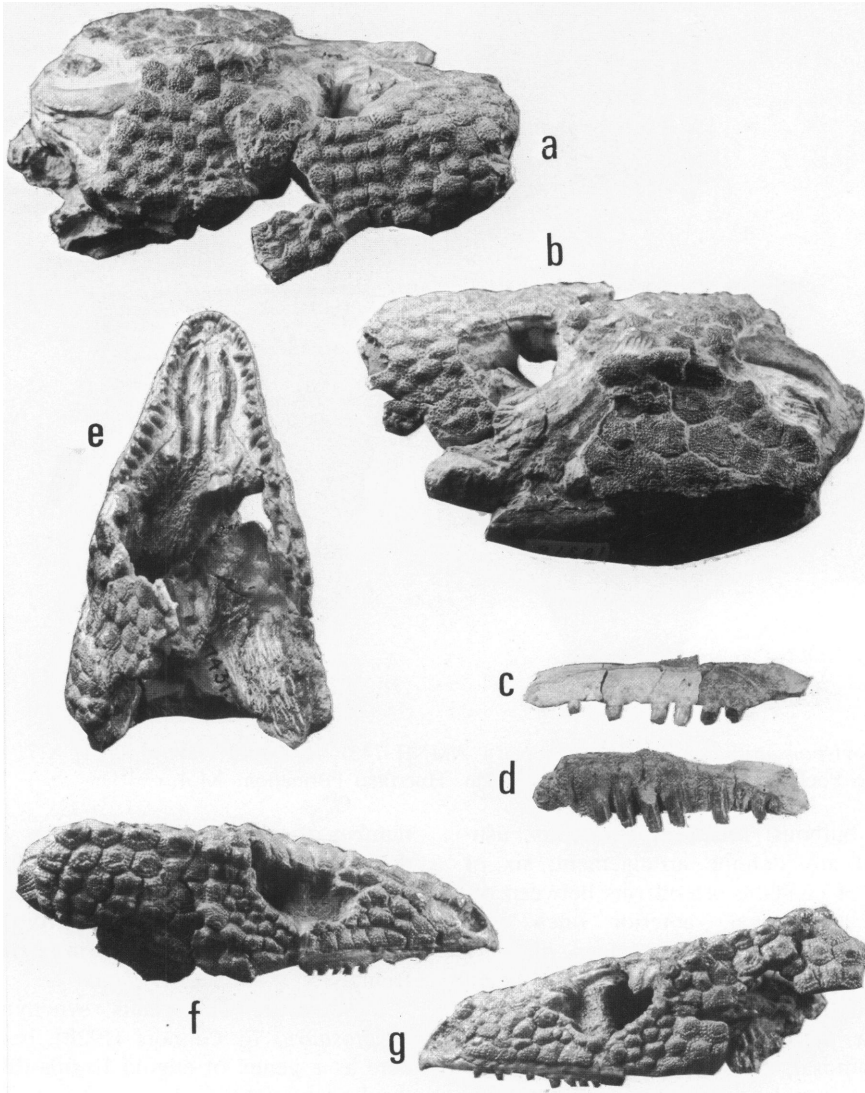


FIG. 8. *Eoglyptosaurus donohoei*, new genus, USNM 18316 (type of *Glyptosaurus donohoei* White, 1952), crushed skull. a. Dorsal view. b. Left lateral view. X.7.; USNM 18317 (paratype of *Glyptosaurus donohoei* White, 1952), right maxilla. c. Labial view. d. Lingual view. X1.4. Both from the Wasatch Formation (Lost Cabin Member) of Boysen Reservoir, Wyoming.; AMNH 7431, complete skull. e. Ventral view. f. Right lateral view. g. Left lateral view. Castillo Pocket, Quarry 1, Gardner, Colorado. X.7.

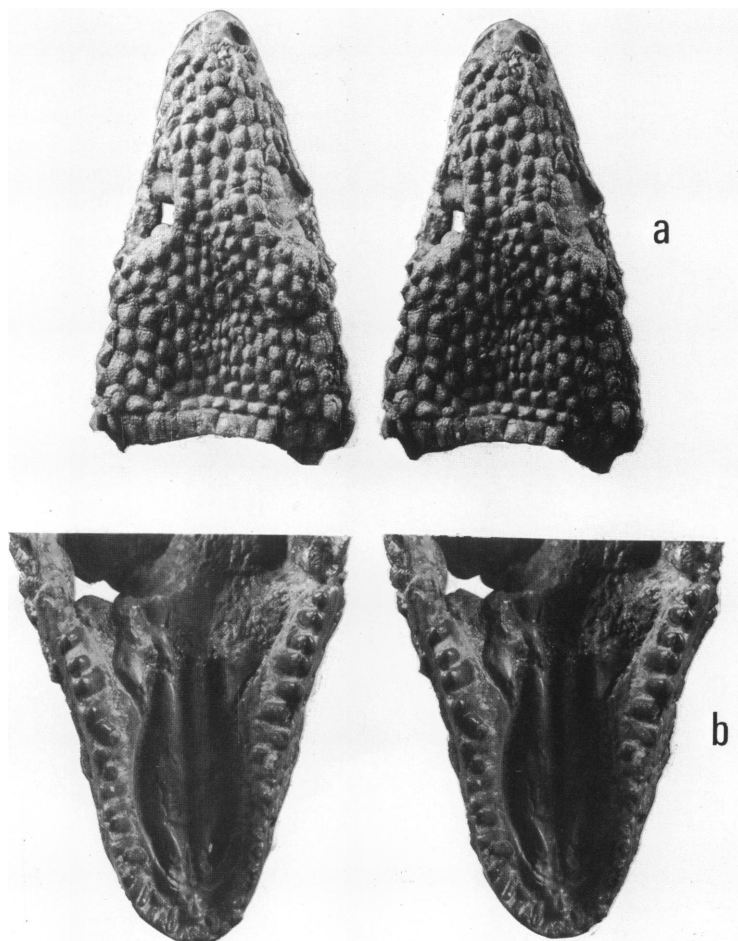


FIG. 9. *Eoglyptosaurus donohoei*, (stereo pair), AMNH 7431. a. Dorsal view of skull. X.7. b. Palate of skull. Castillo Pocket, Quarry 1, Gardner, Colorado. Huerfano Formation. X1.4.

osteoderms bulbous; tubercles numerous, usually without any definite arrangement; six or seven rows of cephalic osteoderms between orbits; teeth subconical, anterior ones with pointed crowns, posterior ones obtusely pointed, sharp and slightly recurved; jugal blade curved; maxilla straight; dentary moderately slender, not robust; supratemporal fenestra closed (squamosal, parietal, supratemporal, and postorbital in contact); skull highly vaulted.

Differs from *Glyptosaurus*, *Paraglyptosaurus*, and *Eoglyptosaurus* in having bulbous cephalic osteoderms, six or seven rows of osteoderms between orbits, slightly recurved homodont teeth, curved frontals, increase in the

number of tubercles per osteoderm without any definite arrangement, non-fusion of dermal armor to underlying bone and closure of the supratemporal fenestra. Differs from *Paraglyptosaurus* and *Eoglyptosaurus* in having separate frontals.

DISCUSSION: This genus, synonymized with *Glyptosaurus* by Gilmore (1928), is resurrected here as a genus of anguid lizards distinct from the Eocene genera.

Helodermoides tuberculatus Douglass
Figures 10-18

Glyptosaurus montanus Douglass, 1908, pp. 278-281.

Glyptosaurus tuberculatus (Gilmore, 1928), pp. 113-115.

Glyptosaurus giganteus Gilmore, 1928, p. 119.

TYPE SPECIMEN: CM 707 (fig. 10a and b),

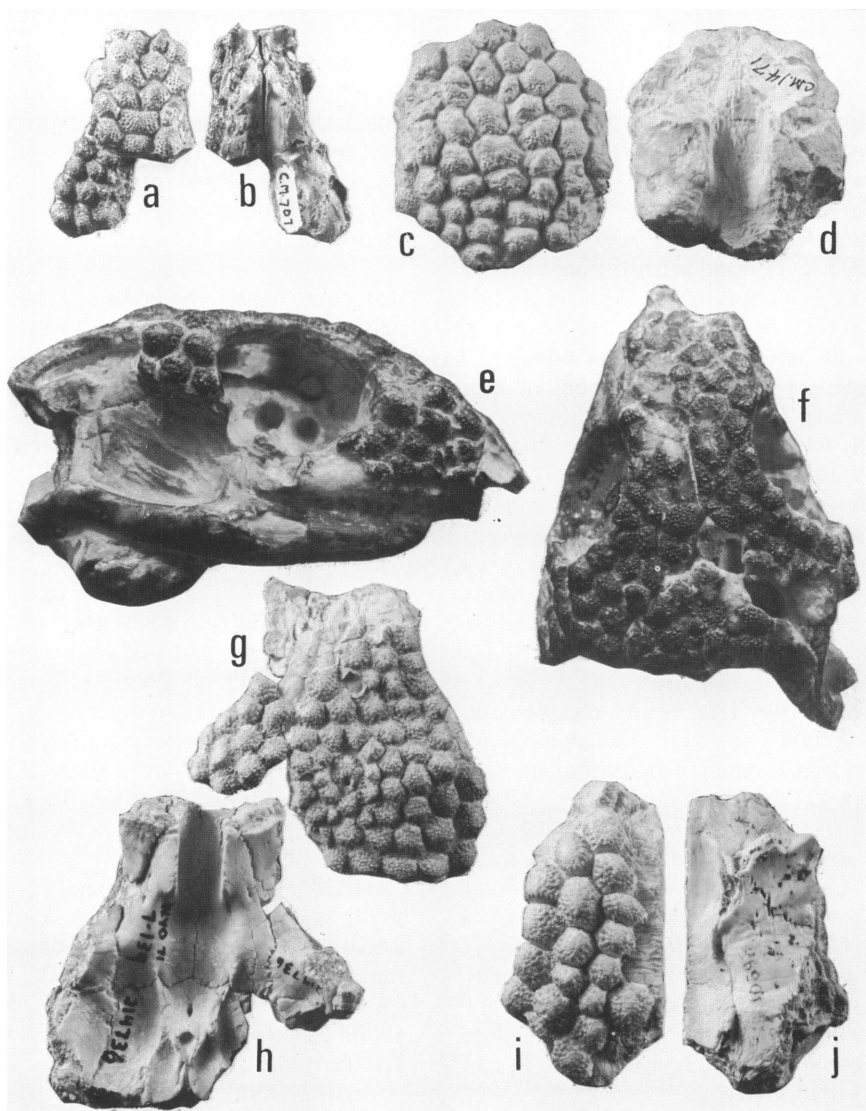


FIG. 10. *Helodermoides tuberculatus*, CM 707 (type) complete left frontal and anterior part of right frontal. a. Dorsal view. b. Ventral view. Pipestone Springs, Montana. Pipestone Springs beds, Titanotherium zone (Lower Oligocene). X.7.; CM 1417 (type of *Glyptosaurus giganteus* Gilmore, 1928), both frontals with posterior parts of prefrontals. c. Dorsal view. d. Ventral view. Jim Creek, Nebraska. White River Formation (Chadronian). X.7.; CM 1050 (type of *Glyptosaurus montanus* Douglass, 1908), complete skull and jaws. e. Right lateral view. f. Dorsal view. McCarty's Mountain, north of Dillon, Montana. White River Formation, Titanotherium beds (Chadronian). X1.4.; USNM 214736, left and right frontal, part of left and right pre- and postfrontals, parietal and part of right postorbital. g. Dorsal view. h. Ventral view. North fork of Lone Tree Gulch, Natrona County, Wyoming. White River Formation (Chadronian). X.9.; KU 10698, nearly complete left frontal and posterior part of left prefrontal. i. Dorsal view. j. Ventral view. Weld County, Colorado. White River Formation (Orellan). X1.

nearly complete left frontal and anterior part of right frontal, anterior part of left dentary and skull fragment with osteoderms. Associated with three fragments not referable to the *Glyptosaurinae*.

LOCALITY: Pipestone Springs, Jefferson County, Montana.

HORIZON: Pipestone Spring beds, Titanotherium zone (Chadronian).

Collector: Earl Douglass, 1899.

DIAGNOSIS: *Helodermoides tuberculatus* follows the generic description. It differs from the species *H. mongoliensis* (see below) in that the frontals are thicker and broader with six or seven rows of osteoderms between orbits.

HYPODIGM: AMNH 1611, fragment of right dentary, complete left frontal, posterior part of right frontal, four vertebrae and three body osteoderms. Pipestone Springs, Jefferson County, Montana. White River Formation (Chadronian). Collector: AMNH Expedition, 1902.

AMNH 3779, incomplete ramus, osteoderms, and unidentifiable bone fragments. Cameron Springs, Wyoming. Chadron Formation (Chadronian). Collector: Hessler, August 19, 1959.

AMNH 6800 (fig. 11c), nearly complete disarticulated skeleton and skull. Badlands, South Dakota. Chadron Formation (Chadronian). Collector: Glenn L. Jepsen, 1924.

AMNH 8313, fragments of parietal, left frontal and unidentified skull element. Veteran, Wyoming. Chadron Formation (Chadronian). Cook Collection. Collectors: Harold J. Cook and M. C. Cook, 1940-1945.

AMNH 8333, fragments of four frontals. Goshen Hole, Wyoming. "Manganese Pocket," Chadron Formation (Chadronian). Cook Collection. Collectors: Harold J. Cook and M. C. Cook, 1940-1945.

AMNH 8713, osteoderms and bone fragments. One-half mile southeast of Irvine, near Douglas, Converse County, Wyoming. Chadron Formation (Chadronian). Collectors: Morris Skinner, Ted Galusha, and party, 1958.

CM 1050 (type of *Glyptosaurus montanus* Douglass, 1903, pp. 278-281, figs. 1 and 2) (fig. 10e and f), nearly complete skull and jaws, incomplete humerus, distal ends of radius and ulna, osteoderms, and phalanges. Mc-

Carty's Mountain, north of Dillon, Montana. White River Formation, Titanotherium zone (Chadronian). Collector: Earl Douglass, July 13, 1903.

CM 1471 (type of *Glyptosaurus giganteus* Gilmore, 1928, p. 119, pl. 14, fig. 1) (fig. 10c and d), both frontals with posterior parts of prefrontals. Jim Creek, Sioux County, Nebraska. White River Formation, Oreodon beds (Orellan). Collectors: O. A. Peterson and J. A. Hermann, 1905.

CM 9975 (fig. 11a), nearly complete skull and gular region, body osteoderms, vertebrae, and ribs. South side of McCarty's Mountain, Madison County, Montana. White River Formation (?Chadronian). Collector: J. L. Kay, 1937.

F:AM 8690, central part of left frontal and anterior part of right frontal. Lusk area, Niobrara County, Wyoming. Chadron Formation (Chadronian). Collectors: Charles Falkenbach and party, 1943.

F:AM 8697, incomplete parietal. Middle of Lone Tree Gulch, Bates Hole area, Natrona County, Wyoming. Chadron Formation (Chadronian). Collectors: Morris Skinner and Ted Galusha, 1959.

F:AM 8698, incomplete parietal. Central fork of Lone Tree Gulch, Bates Hole, Natrona County, Wyoming. Chadron Formation (Chadronian). Collectors: Morris Skinner and Ted Galusha, 1959.

F:AM 8706 (fig. 12a and b), incomplete skull, jaws and anterior trunk region with osteoderms. Southwest fork of Lone Tree Gulch, Bates Hole, Natrona County, Wyoming. Chadron Formation (Chadronian), 30 ft. below 435 ft. Ash G. Collectors: Morris Skinner and Ted Galusha, 1957.

F:AM 8720, incomplete parietal, humerus and osteoderms. Two miles south of Ten Mile Bridge over Platte River, below Converse County, Wyoming. Chadron Formation (Chadronian). Collector: George F. Sternberg, 1945.

F:AM 8724, incomplete skull with body osteoderms. South side of pass, Seaman Hills, Natrona County, Wyoming. Chadron Formation (Chadronian), 20 ft. below purple white layer. Collectors: Charles Falkenbach and Morris Skinner, 1953.

F:AM 8725, articulated vertebrae and body osteoderms. South side of saddle, Seaman Hills, Natrona County, Wyoming. Chadron Formation (Chadronian). Collectors: Morris Skinner and Charles Falkenbach, 1953.

F:AM 8729, posterior part of right frontal (associated with limb bones not assignable to

H. tuberculatus with certainty). Pipestone Springs, Jefferson County, Montana. White River Formation (Chadronian). Collector: Charles Falkenbach, 1930.

F:AM 8757, fragments of frontals, left jugal, parietal, left dentary, right dentary, and unidentified fragments with osteoderms. Four

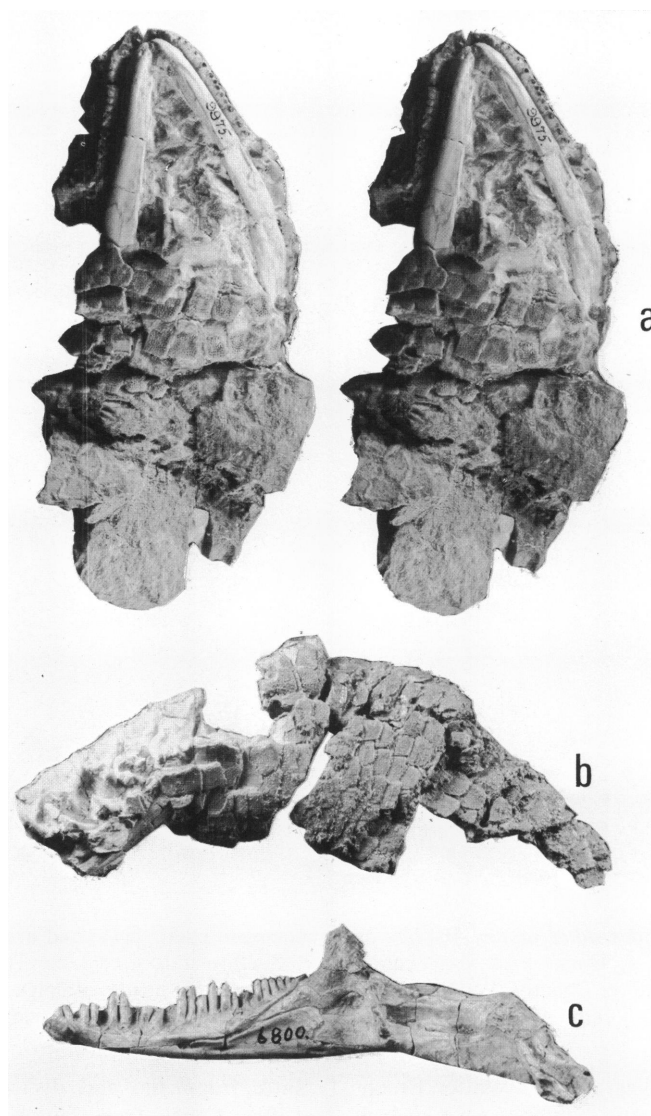


FIG. 11. *Helodermoides tuberculatus*, CM 9975, a. (stereo pair) gular region, ventral view. South side of McCarty's Mountain. White River Formation. X.7.; UNSM 4511. b. Thoracic section; articulated osteoderms and thoracic vertebrae. Two miles north of Crawford, Nebraska. Chadron Formation. X.5.; AMNH 6800. c. Lingual view of right mandible. Badlands, South Dakota. Chadron Formation. X.7.

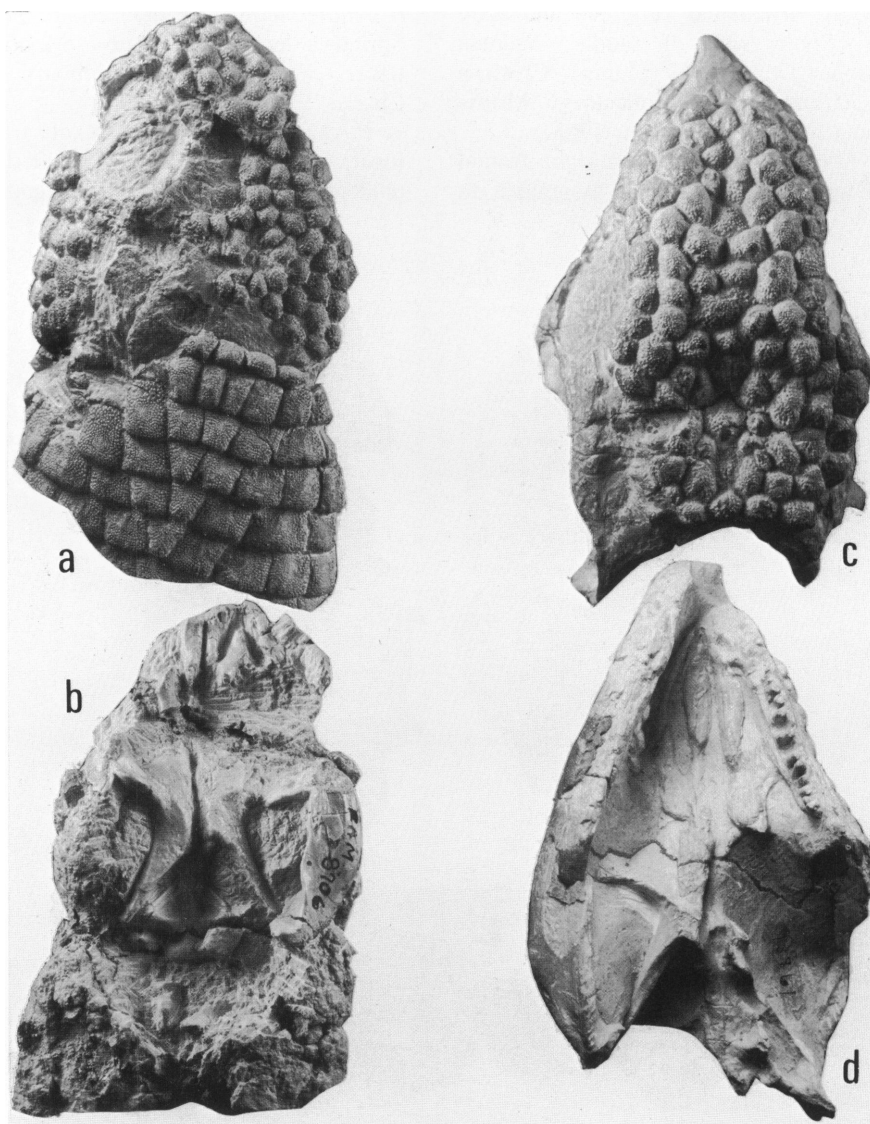


FIG. 12. *Helodermoides tuberculatus*, F:AM 8706, incomplete skull, jaws, and anterior trunk region with articulated osteoderms. a. Dorsal view. b. Ventral view. Southwest fork of Lone Tree Gulch, Bates Hole, Natrona County, Wyoming. Chadron Formation. X.7.; USNM 13861, nearly complete skull and right mandible. c. Dorsal view. d. Ventral view. Eight miles east of Douglas, Wyoming. Brule Formation. X.6.

miles south and 4 miles west of Walter Brecht Ranch, Dawes County, Nebraska. Chadron Formation (Chadronian). Collector: Morris Skinner, 1951.

F:AM 9166, disarticulated skull and skeleton, including right frontal, left nasal, right jugal and maxilla fragment, thoracic vertebra,

limb fragments and disarticulated osteoderms. Little Lone Tree Gulch, Bates Hole area, Natrona County, Wyoming. White River Formation (Chadronian), 45 ft. below Ash B. Collectors: Robert and Susan Emry, 1968.

F:AM 10160, right maxilla fragment. Two and one-half miles southeast of Jim Christian

Hills, Niobrara County, Wyoming. Chadron Formation (Chadronian), 30 ft. below purple white layer. Collectors: Morris Skinner and party, 1963.

F:AM 10161, right dentary fragment. South

of Kraft's, 2½ miles southeast of Jim Christian Hills, Niobrara County, Wyoming. Chadron Formation (Chadronian), 10 ft. above purple white layer. Collectors: Morris Skinner and party, 1963.

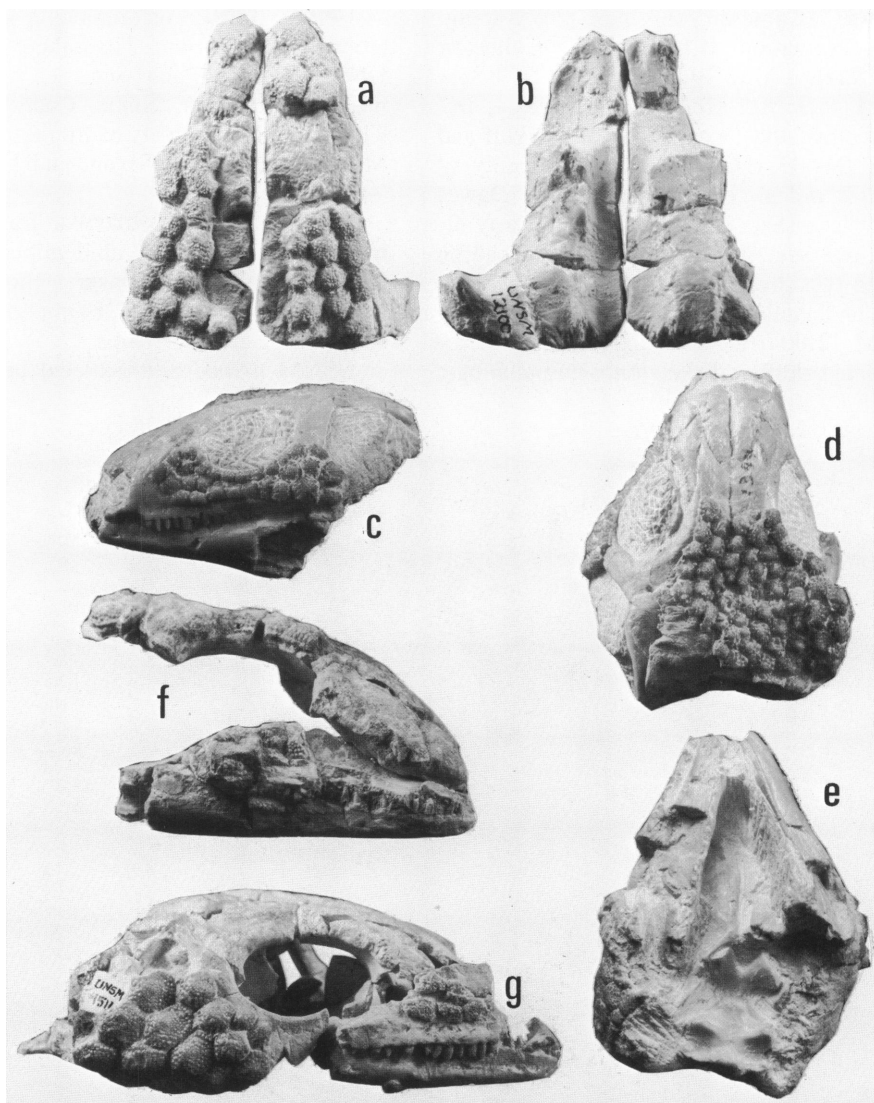


FIG. 13. *Helodermoides tuberculatus*, UNSM 12100, left and right frontals, nasals, right postfrontal and posterior parts of prefrontals. a. Dorsal view. b. Ventral view. North of Harrison, Nebraska. Chadron Formation. X.7.; TT 1344, nearly complete skull and jaws. c. Left lateral view. d. Dorsal view. e. Ventral view. Cameron Springs, Wyoming. Chadron Formation. X.7.; UNSM 214734, incomplete skull and jaws. f. Right lateral view. Middle fork of Blue Gulch, Natrona County, Wyoming. White River Formation (Chadronian). X.8.; UNSM 4511. g. Right lateral view of nearly complete skull. North of Crawford, Nebraska. Chadron Formation. X.7.

KU 10698 (fig. 10i and j), nearly complete left frontal and posterior part of left prefrontal. Weld County, Colorado. White River Formation (Orellan). Collector: Robert W. Wilson, July 11, 1956.

TT 1344 (fig. 13c-e), nearly complete skull and jaws. Cameron Springs, Wyoming. Chadron Formation (Chadronian). Collector: John F. Sutton, May 1972.

UNSM 4511 (fig. 11b; fig. 13g; fig. 14; fig. 17b and c; fig. 18d), nearly complete skull and skeleton. DW-13 (Harold J. Cook Locality of UNSM), 2 miles north of Crawford, Dawes County, Nebraska, east side of Highway 2, Sec. 26 and Sec. 35, T34N, R52W. Chadron Formation (Chadronian). Collectors: Robert M. Sullivan and Paul Edwards, July 1973.

UNSM 12100 (fig. 13a and b; fig. 18a-c), disarticulated skull and skeleton with pathologic

tail (see Sullivan, in press). SX-O (John Bell Hatcher Titanotheres Locality of UNSM), Sec. 4 and Sec. 9, T33N, R56W, north of Harrison, Sioux County, Nebraska. Chadron Formation (Chadronian). Collectors: Mylan Stout, David Nixon, and Larry Luebke, 1963.

UNSM 12101, incomplete parietal. SX-O (John Bell Hatcher Titanotheres Locality of UNSM), Sec. 4 and Sec. 9, T33N, R56W, north of Harrison, Sioux County, Nebraska. Chadron Formation (Chadronian). Collectors: Mylan Stout, David Nixon, and Larry Luebke, 1963.

USNM 10958, two maxillae fragments, fragment of parietal, and unidentified skull fragment. Hat Creek Basin, Sioux County, Nebraska. White River Formation. Collector: John Bell Hatcher, 1888.

USNM 10960, disarticulated head and body

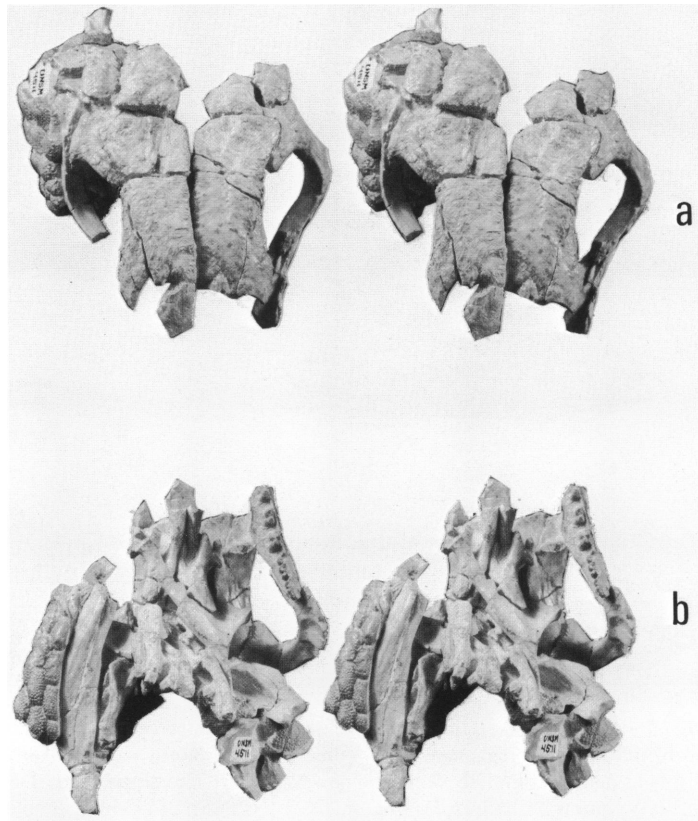


FIG. 14. *Helodermoides tuberculatus*, UNSM 4511, (stereo pair), incomplete skull. a. Dorsal view. b. Ventral view. North of Crawford Nebraska. Chadron Formation. X.5.

osteoderms. Hat Creek Basin, Sioux County, Nebraska. White River Formation. Collector: John Bell Hatcher, 1888.

USNM 12852, anterior part of right maxilla, anterior part of left dentary and posterior part of left frontal. One mile west of Pipestone Springs, Jefferson County, Montana. Pipestone Creek Formation (?Chadronian). Collector: George F. Sternberg, 1931.

USNM 13861 (figured as *Glyptosaurus giganteus* in Gilmore, 1938, pp. 16-21, fig. 5) (fig. 12c and d; fig. 15a) nearly complete skull and osteoderms. Eight miles east of Douglas, Converse County, Wyoming. Brule Formation (Orellan). Collector: George F. Sternberg, 1935.

USNM 13869 (figured as *Glyptosaurus giganteus* in Gilmore, 1938, p. 17, fig. 4 and pl.

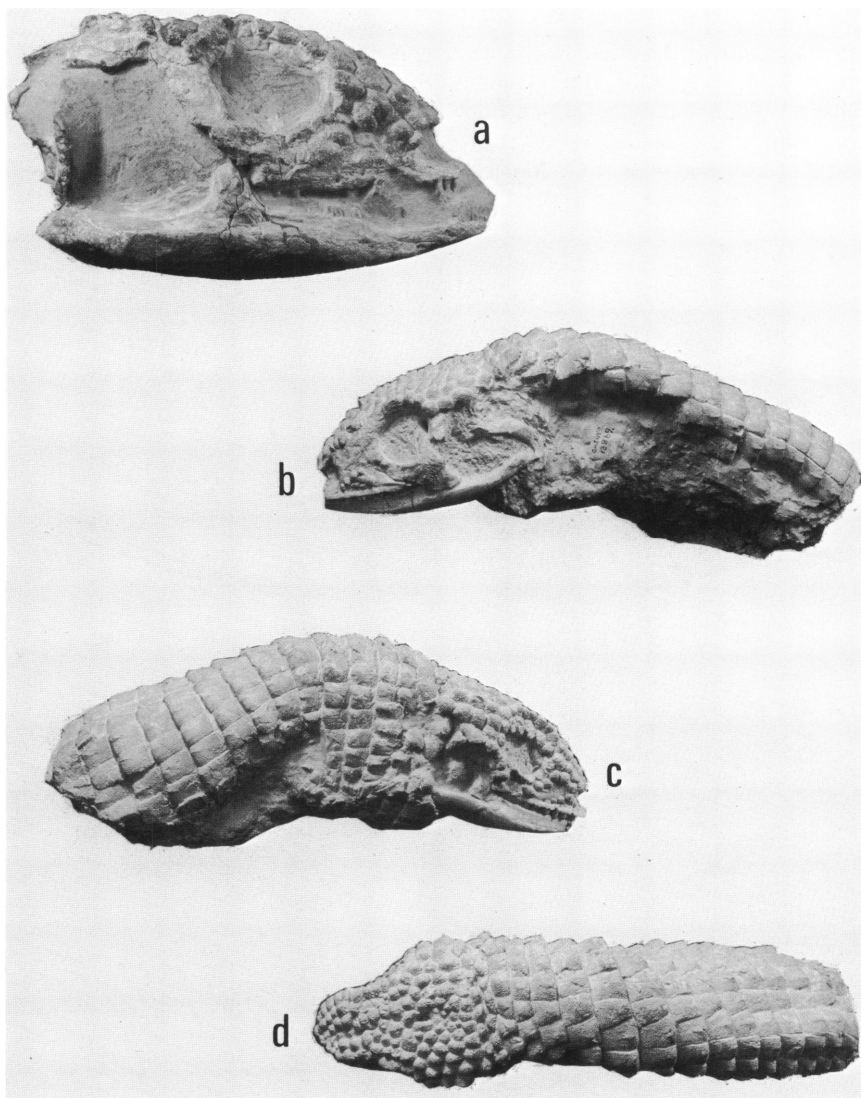


FIG. 15. *Helodermoides tuberculatus*, USNM 13861, nearly complete skull and right mandible. a. Right lateral view. X.6.; USNM 13869, nearly complete articulated skull and anterior thoracic region. b. Left lateral view. c. Right lateral view. d. Dorsal view. X.3. Both specimens are from east of Douglas, Wyoming. Brule Formation.

l) (fig. 15b, c, and d; fig. 16; fig. 17a), nearly complete skull and anterior thoracic region of lizard with articulated osteoderms. Eight miles east of Douglas, Converse County, Wyoming. Brule Formation (Orellan). Collector: George F. Sternberg, 1935.

USNM 15662, left frontal. Three miles south of Pipestone Springs, Jefferson County, Montana. Chadron Formation (Chadronian). Collector: Charles W. Gilmore, June 16, 1931.

USNM 214734 (fig. 13f), incomplete skull and jaws with fragments of disarticulated bones and osteoderms. Middle fork of Blue Gulch, Natrona County, Wyoming. White River Formation (Chadronian), 15 ft. below Ash G. Collectors: Robert J. Emry and Albert C. Myrick, 1971.

USNM 214735, crushed right maxilla and dentary, fragments of skull and osteoderms. Little Lone Tree Gulch, Natrona County, Wyoming. White River Formation (Chadronian), red silty claystone lens. Collectors: Robert J. Emry and Albert C. Myrick, 1971.

USNM 214736 (fig. 10g and h) frontals, fragments of prefrontals, postfrontals, parietal and right postorbital, miscellaneous skull fragments, with fragments of skeleton and osteoderms. North fork of Lone Tree Gulch, Natrona County, Wyoming. White River Formation (Chadronian), 7 ft. below Ash D. Collectors: Robert J. Emry and Albert C. Myrick, 1971.

DISCUSSION: *Helodermoides tuberculatus* was described by Douglass (1903), based upon

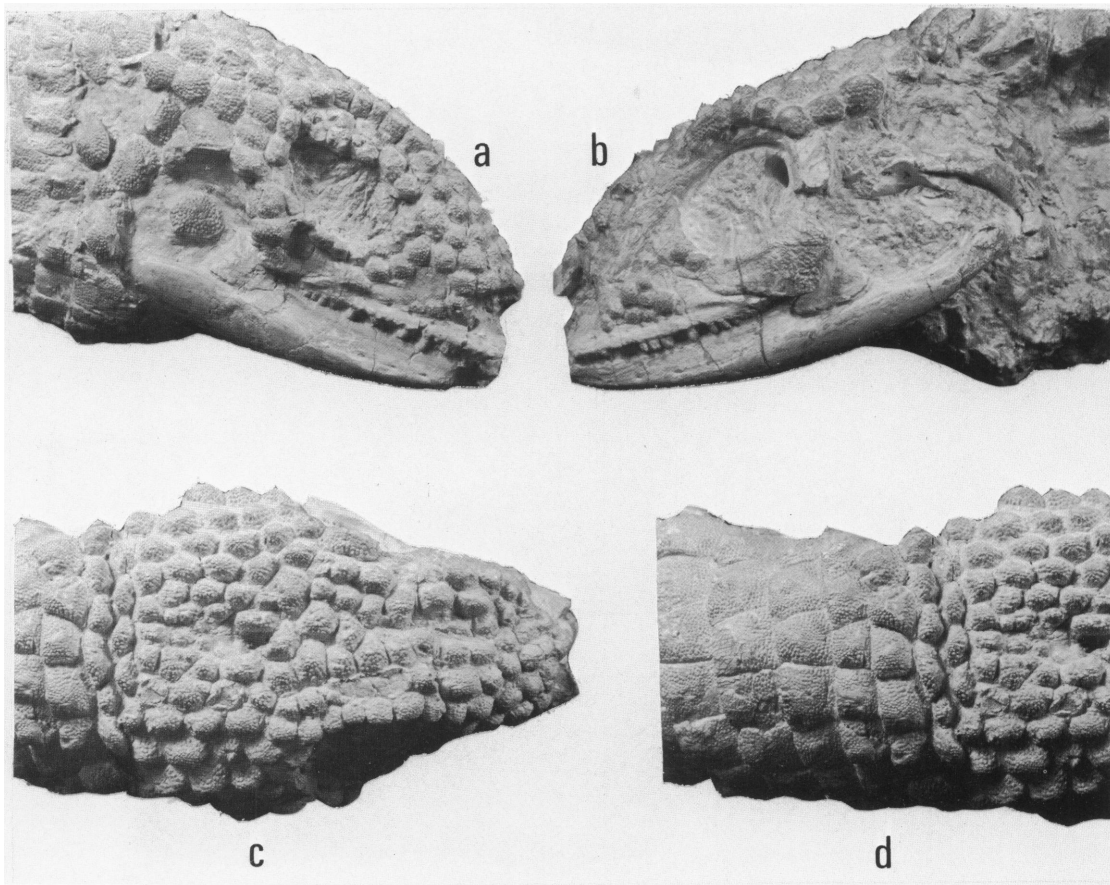


FIG. 16. *Helodermoides tuberculatus*, USNM 13869, nearly complete articulated skull and anterior thoracic region. a. Right lateral view of skull. b. Left lateral view of skull. c. Dorsal view of skull. d. Dorsal view of neck region. East of Douglas, Wyoming. Brule Formation. X.6.

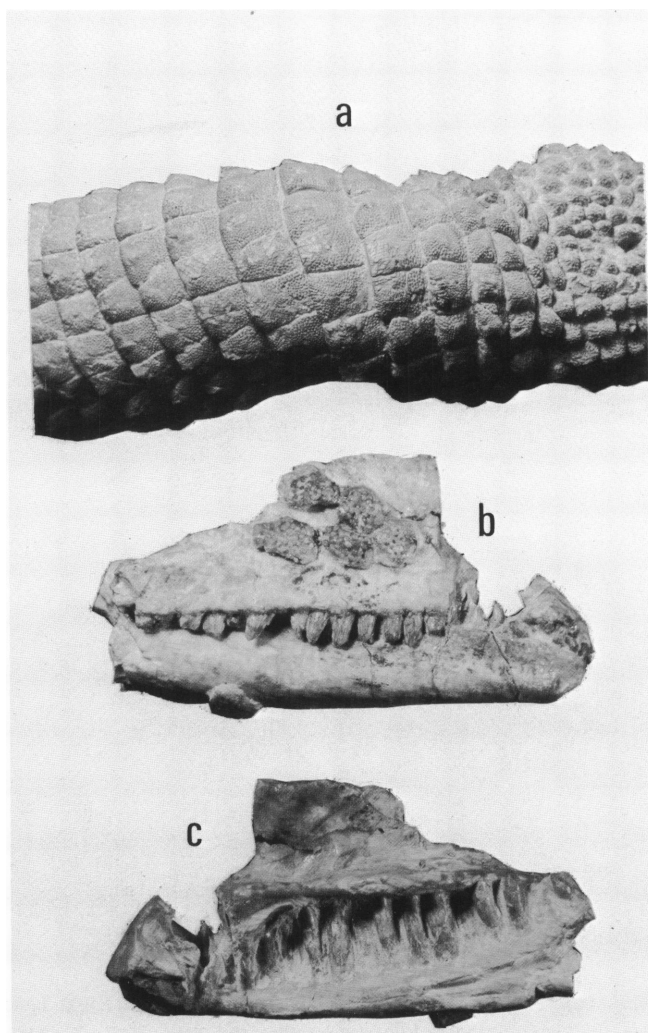


FIG. 17. *Helodermoides tuberculatus*, USNM 13869. a. Dorsal view of anterior thoracic region. East of Douglas, Wyoming. Brule Formation. X.5.; UNSM 4511, right maxilla, right dentary and premaxilla. b. Labial view. c. Lingual view. North of Crawford, Nebraska. Chadron Formation. X1.5.

two nearly complete articulated paired frontals covered with large bulbous hexagonal osteoderms. Associated with the frontals were a left dentary, skull fragment with six osteoderms, and three unidentified bone fragments, the latter not referable to the Glyptosaurinae. The dentary was unique among the previously known forms in that it bore very sharp teeth, which Douglass (1903) compared with *Heloderma* rather than with *Glyptosaurus*.

Gilmore (1928) synonymized *Helodermoides* with *Glyptosaurus* on the basis of osteoderm type. He was unable to detect any generic differences between the two forms, and thought that the difference in tooth type was not in itself sufficient for generic separation. Gilmore failed to make any direct comparison of *Helodermoides tuberculatus* with his type frontal of "*Glyptosaurus giganteus*" (CM 1471). Presumably Gilmore (1928) avoided this

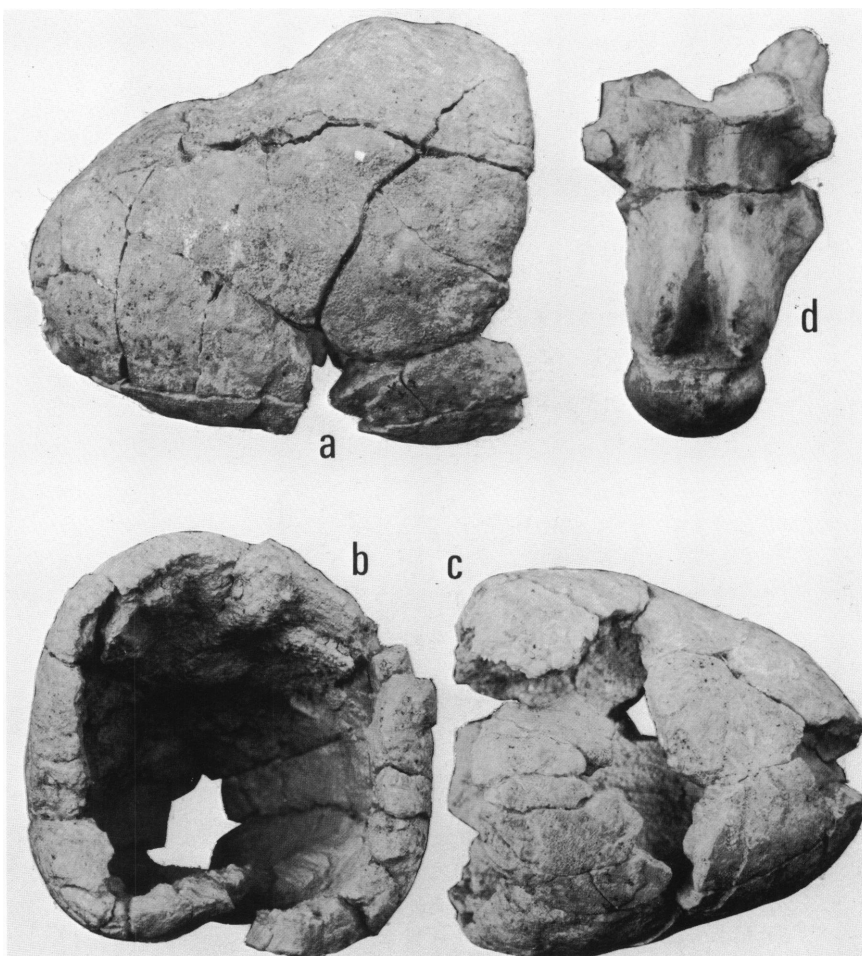


FIG. 18. *Helodermoides tuberculatus*, USNM 12100, pathologic tail. a. Right lateral view. b. Axial view looking toward the end of the tail. c. Ventral view (anterior to the left). North of Harrison, Nebraska. Chadron Formation. a and b X.9, c X.7.; USNM 4511. d. Ventral view of a caudal vertebra showing autotomic septum. North of Crawford, Nebraska. Chadron Formation. approx. X.7.

comparison because he failed to recognize the frontal condition as being separated in "*G. giganteus*." At the time of Gilmore's study these Oligocene lizards were known by only a few specimens. The type of "*Glyptosaurus montanus*" (Douglass, 1908) was the only other specimen known and it was sufficiently smaller, as to imply to Gilmore that there was a specific difference between them. However, since Gilmore's study, numerous specimens from the lower and middle Oligocene deposits of North America have been collected so that

these lizards represent the most complete series of fossil lizards presently known. A considerable size range is evident, from approximately 40 mm. skull length (CM 1050) to 95 mm. for USNM 13861. All these specimens display the following character states: (1) homodont sharp, subconical slightly recurved tooth type; (2) separate frontals; (3) straight maxilla; (4) closed supratemporal fenestra; (5) absence of the concentric ring pattern of tubercles on cephalic and body osteoderms; and (6) six to seven rows of cephalic osteoderms extending parallel to the

midline between orbits. In most cases the osteoderms are not fused to the underlying bone (see "Phylogeny" below). Close examination discloses that Gilmore's type frontal of "*G. giganteus*" has separate frontals, contrary to his description (Gilmore, 1928), and that it is nearly identical with the type of *Helodermoides tuberculatus* Douglass (1903), which has priority. Gilmore's subsequent description of *Glyptosaurus giganteus* (Gilmore, 1938) showed that there was a considerable variation among cephalic osteoderms within a single species, but he failed to recognize that *Helodermoides tuberculatus* was within that range of variation. His referred specimen of "*Glyptosaurus giganteus*" is very similar to Douglass's type of "*Glyptosaurus montanus*" (Douglass, 1908) except for size. A number of intermediate sizes of these Oligocene lizards are known whose similar morphology indicates that an ontogenetic series rather than taxonomic differences is involved. On the basis of the above character states, all the above specimens are considered to represent forms that are generically distinct from the Eocene genus *Glyptosaurus* and accordingly the genus *Helodermoides* is resurrected to include these forms. All of these North American Oligocene Anguid lizards are considered to represent one species, *Helodermoides tuberculatus* Douglass, 1903.

Cf. Helodermoides tuberculatus

AMNH 2189, two body osteoderms. Pipestone Springs, Jefferson County, Montana. White River Formation, Titanotherium beds (Chadronian). Collectors: Albert Thompson and F. B. Loomis, 1902.

F:AM 8694, thoracic vertebra. Central fork, Blue Ridge Gulch, Bates Hole, Natrona County, Wyoming. Chadron Formation (Chadronian). Collector: Expedition, 1959.

F:AM 8695, three thoracic vertebrae and unidentifiable bone fragment. Ledge Creek no. 4, Bates Hole, Natrona County, Wyoming. Chadron Formation (Chadronian). Collectors: Morris Skinner, Emry brothers and K. Wiechelman, 1963.

F:AM 8696, body osteoderms. South end of

Lone Tree Gulch, Bates Hole, Wyoming. Chadron Formation (Chadronian). Collectors: Morris Skinner and Ted Galusha, 1957.

F:AM 8713, osteoderms and unidentifiable bone fragments. One-half mile southeast of Irvine, near Douglas, Converse County, Wyoming. Collector: AMNH Expedition, 1958.

F:AM 9162, body osteoderms. Blue Gulch, Bates Hole area, Natrona County, Wyoming. Chadron Formation (Chadronian). Collectors: Morris Skinner, Emry brothers, and Kendrick, 1965.

F:AM 9201, body osteoderm. West end of Trunk Butte, Dawes County, Nebraska. Chadron Formation (Chadronian), 30' above base. Collectors: Morris Skinner and Lamb, 1953.

UNSM 63087, body osteoderm. SX-0 (John Bell Hatcher Titanotherium Locality of UNSM), Sioux County, Nebraska. Chadron Formation (Chadronian). Collector: UNSM field party, year unknown.

USNM 13805, basicranium. Pipestone Springs, Jefferson County, Montana. Pipestone Spring Formation (Chadronian). Collector: Charles W. Gilmore, 1935.

USNM 215096, body osteoderm. Head of Little Lone Tree Gulch, in NE1/4, Sec. 22 and N1/2 Sec. 23, T31N, R83W, Natrona County, Wyoming. White River Formation (Chadronian), 20-25 ft. below Ash D. Collectors: Robert J. Emry and Albert C. Myrick, 1971.

USNM 215137, cephalic and body osteoderms. Head of Little Lone Tree Gulch in NE1/4, Sec. 22 and N1/2 Sec. 23, T31N, R83W, Natrona County, Wyoming. White River Formation (Chadronian), 10-20 ft. above Ash E. Collectors: Robert J. Emry and Albert C. Myrick, 1971.

USNM 241322, four caudal vertebrae and proximal end of humerus. North fork of Lone Tree Gulch in SE1/4, Sec. 22, and north edge of NE1/4, Sec. 27, T31N, R83W, Natrona County, Wyoming. White River Formation (Chadronian), 0-5 ft. above Ash D. Collectors: Robert J. Emry and Albert C. Myrick, 1971.

USNM 243957, caudal and thoracic vertebrae, proximal and distal ends of both femurs, proximal ends of both humeri, acetabulum fragment of left ilium and ischium

and unidentified bone fragments. North fork of Lone Tree Gulch, Natrona County, Wyoming. White River Formation (Chadronian), 30 ft. below Ash D. Collectors: Robert J. Emry and Albert C. Myrick, 1971.

USNM 244220, partial skull. Little Lone Tree Gulch, Natrona County, Wyoming. White River Formation (Chadronian), pocket, 44 ft. below Ash B. Collectors: Robert J. Emry and Albert C. Myrick, 1971.

***Helodermoides mongoliensis*, new species**
Figure 19a and b

Glyptosaurus near *nodosus* Gilmore, 1943, p. 382.
Placosaurus cf. *nodosus* (Chow, 1957), p. 156.

TYPE SPECIMEN: AMNH 6669 (fig. 19a and b). Left frontal.

LOCALITY: Near Baron Sog, Inner Mongolia.

HORIZON: Shara Murun Formation (late Eocene).

COLLECTOR: Collected by the American Museum of Natural History Expedition of 1925.

ETYMOLOGY: Named for the general geographic locality from which this species was collected.

DIAGNOSIS: Differs from *Helodermoides tuberculatus* and *Glyptosaurus sylvestris* in that the frontals are constricted between the orbits and that there are only two complete rows of osteoderms over the orbit region of the frontal. It differs from *G. sylvestris* in that the individual tubercles are more crowded and approach those seen on *H. tuberculatus*.

DESCRIPTION: Gilmore (1943, p. 382) has adequately described this specimen, however, some additional characters not noted by Gilmore are worth mentioning.

The frontal is more constricted anteriorly than in all other glyptosaurines. Unlike the frontals in other North American Eocene glyptosaurines, this frontal is convexed (arched) rather than flat, a feature exhibited in *Helodermoides tuberculatus* of the North American Oligocene. The osteoderms on the frontal, which were noted by Gilmore (1943, p. 382) to resemble those of the type of *Glyptosaurus nodosus* (now synonymized with *Glyptosaurus sylvestris*, above), are also similar in morphol-

ogy to those seen in all known specimens of *Helodermoides tuberculatus*.

DISCUSSION: The type specimen described by Gilmore (1943) is the only specimen referable to this species at present. Although this specimen is without a doubt referable to the Glyptosaurini, I believe that it is distinct at the generic level from the type species of "*Glyptosaurus nodosus*" (Marsh, 1871, p. 458) which is now considered synonymous with *G. sylvestris* (see above) and can be properly referred to *Helodermoides*. The frontal is convex as in *Helodermoides tuberculatus* but is not as massive for similar sized lizards of that species. The frontal osteoderms are inflated as in *H. tuberculatus* but only form two distinct rows above the orbital region of the frontals. The tubercular arrangement shows no apparent concentric ring pattern as in the North American Eocene glyptosaurinids.

Chow (1957) described a specimen (V868) that consisted of "a right frontal, the proximal part of the left one, and part of the parietals, all covered with osteodermal scutes" which he assigned to the species *Placosaurus rugosus* Gervais. His assignment of the specimen to the genus *Placosaurus* was based on the belief that *Placosaurus* was synonymous with *Glyptosaurus* and that the former generic name had priority. He recognized the fact that this specimen was closer in morphology to the type of the North American *Glyptosaurus rugosus* (now *Paraglyptosaurus princeps*, see above) but believed that it was "hardly distinguishable from that of '*Placosaurus rugosus* Gervais' from the lower Ludian of Euzet described by Depéret (1917)." Chow then took the liberty to change the generic assignment of AMNH 6669 to *Placosaurus* cf. *nodosus*.

Chow's specimen (V868) was figured, but little can be said about its diagnostic characters. The figure (Chow 1957, fig. 1.) was labeled "right frontal," but it was apparently the right and left frontal bones. It is impossible to determine whether this specimen was joined by metopic suture dividing the frontals into left and right elements by his dorsal view of this specimen, but I assume they were paired, by his osteological description. The specimen appears to be the same size as *Helodermoides*

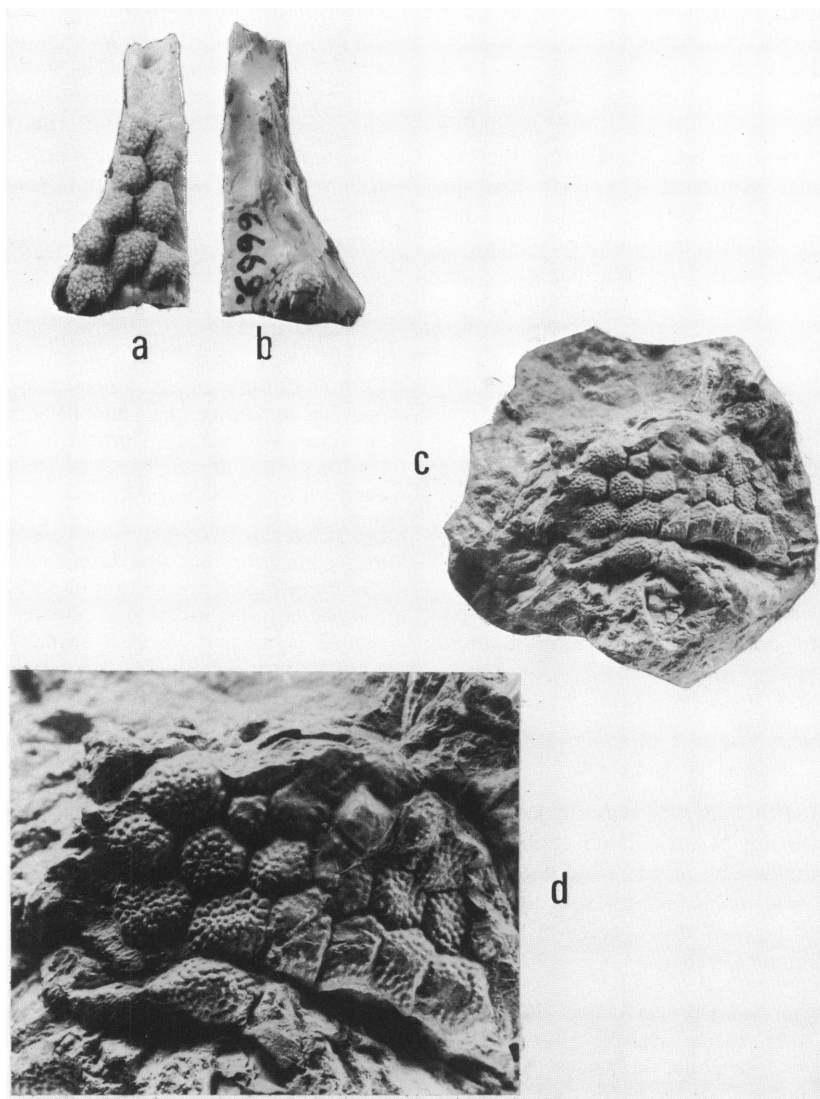


FIG. 19. *Helodermoides mongoliensis*, new species, AMNH 6669 (holotype), left frontal. a. Dorsal view. b. Ventral view. Near Baron Sog, Inner Mongolia. Shara Murun Formation (late Eocene). X1.6.; c and d. The type of *Placosaurus rugosus* Gervais, considered *nomen dubium* (see text), as it is diagnostic to tribe level only. Dorsal view of (?) frontal fragment. Ste. Radegonde pres d'Apt, France. a. X.8, b. X1.9.

mongoliensis and it would not be surprising that in the future, upon closer examination of this specimen, that it would be assignable to this species. *Placosaurus rugosus* is not considered a valid generic and specific identification for this specimen (see *nomina dubia* below).

(?)*Helodermoides* sp.

USNM 243961, posterior part of both frontals, parietal fragment, maxilla fragment, pterygoid fragment cephalic (cheek), and body osteoderms. White River Pocket, Ouray Quad-

range, Uinta County, Utah, SW1/4, Sec. 3, T9S, R20E. Uinta Formation (Uintan). Collector: Arthur Lewis, 1976.

DISCUSSION: This specimen, though quite fragmentary, serves as the basis for extending the range of *Helodermoides* down into the late Eocene of North America. The teeth that are preserved are typically of the subconical, homodont, sharp, slightly recurved type seen in the Oligocene species *H. tuberculatus*. The

concentric ring pattern of tubercles on the cephalic osteoderms is lacking as in *Helodermoides tuberculatus*, but is seen on the body osteoderms of this specimen. This intermediacy suggests that this form is transitional to the Oligocene species and may be best considered *Helodermoides* rather than *Glyptosaurus*. Specific assignment is not desirable owing to the fragmentary nature of the specimen.

GLYPTOSAURINAE INDETERMINATE

nomina dubia

Placosaurus rugosus Gervais, 1852.¹

Placosaurus waltheri (Weigelt, 1929).

Placotherium waltheri (Weigelt, 1929).

Glyptosaurus sphenodon Marsh, 1872.

Glyptosaurus obtusidens Loomis, 1907.

DISCUSSION: The following taxa discussed below are undiagnostic at the generic and specific level and are herein considered *nomina dubia*.

Placosaurus rugosus Gervais, 1852

Figure 19c and d

The genus *Placosaurus* was based on a specimen consisting of articulated cephalic osteoderms surrounded by matrix (fig. 19c and d). For historical purposes Gervais's original description of the type of this species is repeated here from Gilmore (1928).

C'est encore à un Saurien, mais dont il nous est impossible de fixer, même approximativement, les affinités, qu'il faut rapporter la plaque céphalique représentée par la fig. 2 de la pl. 64; c'est le dessus d'un crâne montrant les plaques osseuses des sourcils, et qui est recouvert lui-même de tubercles osseux irrégulièrement hexagonaux, mamelonnés à leur surface de tubercules émoussés que la fig. 2 a donne un peu plus grands que nature. Ni l'*Heloderme* du Mexique ni les *Scinocoidés* de la Nouvelle-Hollande, dont on a fait les genres *Cyclodus*, *Silubolëpis*, etc., n'ont les tubercles céphaliques aussi forts ni semblablement disposés.

¹Richard Estes (personal commun., 1979) reports that *Placosaurus rugosus* is probably a valid species based on recent reexamination by him of the type. The validity of *Placosaurus* will be dealt with in a forthcoming paper by me.

C'est ce qui m'a engagé à donner un nom générique nouveau au Saurien que cette plaque nous représenent; elle vient des marnes calcaires à Paléothériums et Chéropotames de la butte de Sainte-Radegonde, auprès d'Apt (assises proicènes).

Les tubercules à surface lisse, mais à peu près de même grandeur, qui sont représentés par la fig. 3, sont du même gisement. Doit-on les regarder comme étant de la même espèce que ceux de la fig. 2? C'est ce que je ne puis décider. Je me bornerai donc à constater la présence, dans ces terrains, de Sauriens constituant certainement un genre à part, et dont il serait intéressant de chercher d'autres débris.

La fig. 1 de la même planche donne l'image d'un fragment de mâchoire inférieure montrant l'empreinte ou la substance de huit dents postérieures d'un Saurien célodonte; elle ont une analogie éloignée avec celles des *Anguis*. Est-ce encore une autre espèce ou même un autre genre? L'examen de nouveaux ossements nous le fera connaître. Cette pièce vient aussi des calcaires marneux de la butte de Perréal ou Sainte-Radegonde.

Gervais's description of *Placosaurus rugosus* was first made in 1852 and reprinted in 1859. As noted earlier, I have only seen the second edition and without the plates and figures that Gervais referred to in the above quoted text. Dr. Robert Hoffstetter and Jean Claude Rage have, however, graciously furnished me with recent photographs (fig. 19c and d) of the type specimen of *Placosaurus rugosus* Gervais. This specimen appears to be assignable to any member of the Glyptosaurini save possibly *Eoglyptosaurus*. The inadequate description offers neither support to synonymy of *Glyptosaurus* with *Placosaurus* in which the latter has priority, nor does it support separation. Hoffstetter (in lett., 1976) has stated the following about the type specimen:

Pour *Placosaurus* l'espèce type *Pl. rugosus* a été fondée par P. Gervais (1852) sur un "fragment de crâne" portant des ostéodermes et provenant de Ste. Radegonde pres d'Apt (c'est-à-dire de l'Éocène supérieure, niveau de La Débruge dans la nouvelle définition de la limite Eocène-Oligocène). Le type est au Museum [the Museum National d'Histoire Naturelle in Paris, France], je ne crois pas qu'il y ait d'autre matériel provenant de Ste. Radegonde. . . .

De toute façon une identification précise sera difficile, car je pense que plusieurs genres sont représentés dans les fossiles européens rapportés à *Placosaurus*. La separation sans doute impossible à partir des ostéodermes céphaliques. . . .

Je viens de voir le specimen type (partie du plafond crânien, encore inclus dans la gangue). Cette gangue ("marne calcaire") est très différente des lignites du niveau repère, fossilifère, de la Débruge. Il faudra donc revoir le niveau stratigraphique et l'âge car la Débruge et Ste. Radegonde correspondent à la même localité géographique!

Gervais made the observation that this fossil lizard differed from the recent *Heloderma* and certain skinks in the arrangement and pattern of dermal armor. He was unable to assign "family affinities" to *Placosaurus rugosus*, presumably because of the inadequate material at hand as well as the fact that the Anguidae had not yet been defined. The previously collected European specimens were so fragmentary that, contrary to Gervais's observations, Boulenger (1918) believed many of the specimens described by Leenhardt (1906) were actually helodermatids.

Depéret (1917) was the first to suggest that the genus *Placosaurus* might be synonymous with the North American genus *Glyptosaurus*. This suggestion has been echoed by Gilmore (1928), Kuhn (1940), and McDowell and Bogert (1954). Meszoely (1970) suggested that they (*Placosaurus* and *Glyptosaurus*) may indeed be different genera but that a study of both the European and North American specimens was necessary. As suggested by the above personal communication with Dr. Robert Hoffstetter, the material referred to *Placosaurus* is characteristic of a number of glyptosaurine genera; the incomplete nature of the European material makes comparison with the North American material impossible at present. In North America more complete specimens are known and generic separation based on

cephalic osteoderms and other skeletal elements is possible. *Placosaurus*, the type *P. rugosus*, is considered a *nomen dubium*.

In the collections of Princeton University there is a right maxilla (PU 11494) that has been erroneously labeled *Placosaurus*. This specimen was originally referred to as *Lacerta lamandini* and is from the Eocene Phosphorites of Caylus, Tarn et-Garonne, France, and was collected by A. Rossinol. It is clearly anguid and very different from any of the North American genera. A large osteoderm seen on the side of this right maxilla indicates that we are dealing with a member of the tribe Melanosaurini (see below) rather than the Glyptosaurini in which *Placosaurus* belongs. It was suggested by Gilmore (1928) that this specimen was probably anguid and that it superficially approached the condition in dermal armor as seen in *Melanosaurus* in which I agree.

Placosaurus waltheri (Weigelt, 1929)

Kuhn, 1940, p. 467, pl. 1, fig. 6, pl. 2, figs. 5 and 6, pl. 5, figs. 1-3, pl. 7, figs. 3-6, pl. 8, figs. 3 and 4.

This species based on rectangular body osteoderms, and supposedly emended by Kuhn (1940), has been designated a *nomen dubium* by Meszoely, Estes and Haubold (1978) and is maintained here.

Placotherium waltheri (Weigelt, 1929)

Kuhn, 1940, p. 468, pl. 8, figs. 1, 2, 5, pl. 9, figs. 2 and 4.

The type specimen consists of (?)co-ossified posterior part of cephalic shield with various disarticulated (?)cephalic and body osteoderms and is from the middle Eocene deposits of Geiseltal, Germany.

DISCUSSION: I am at a disadvantage in discussing this form as it was unavailable for study, being housed in the Halle Museum in East Germany. However, from the figures of this specimen given by Kuhn (1940, pl. 8, figs. 1, 2, and 5, and pl. 9, figs. 2 and 4) indications are that this form may be a member of the tribe Glyptosaurini, unless the hexagonal osteoderms that are figured are from the cheek region of the lizard, thus making any tribe

assignment uncertain. The specimen was originally described as an edentate by Weigelt (1929a) who immediately reidentified it as a lizard (Weigelt, 1929b) and is represented by a series of fused osteoderms that form a large semicircular arch, that appears to represent the posterior part of the cephalic shield covering part of the dorsal neck region of the lizard, where the transition between hexagonal cephalic osteoderms and the rectangular body osteoderms occur. This same region is best preserved in a specimen of the North American species *Helodermoides tuberculatus* (USNM 13869, (fig. 16d). A certain amount of osteoderm variation is to be expected, making it impossible to assign this form to its own taxon or to other genera like *Helodermoides* or *Placosaurus*. This region is probably similar in all glyptosaurinids and somewhat variable thus making it not taxonomically useful below tribe level.

Mesozoely, Estes and Haubold (1978) considered this species to be *incertae sedis*, on the belief that it was generically distinct. Because of the absence of other skeletal elements and the inability to assign a generic name based on the external morphology of the osteoderms below the tribe level, I believe that this species should best be considered a *nomen dubium*.

Glyptosaurus sphenodon Marsh, 1872

Marsh, 1872, p. 306.

The species *G. sphenodon*, USNM 16524 (see Gilmore, 1928, pl. 18, figs. 12 and 13), represented by a small fragment of the right maxilla with remnants of two teeth, defies generic and specific assignment. The specimen was collected by T. G. Peck in 1871 from the Bridger Formation at Henry's Fork, Uinta County, Wyoming. On stratigraphic and morphologic grounds this specimen could either be *Glyptosaurus* or *Paraglyptosaurus*. Because of the fragmentary nature, *Glyptosaurus sphenodon* is considered a *nomen dubium*.

Glyptosaurus obtusidens Loomis, 1907

Loomis, 1907, p. 363.

The species *G. obtusidens*, AC 3612 (see Loomis, 1907, p. 364, fig. 3, or Gilmore, 1928, pl. 19, fig. 2), is represented by a frag-

ment of a right dentary bearing five teeth and associated body osteoderms, collected by the Amherst College Expedition of 1903 from the Wasatch Formation of Tatman Mountain, Big Horn County, Wyoming. Little can be added to the description of Loomis (1907) and the re-description of Gilmore (1928). Gilmore (1928) suggested that this fragment probably does not represent a separate species of *Glyptosaurus* (*sensu lato*), an opinion with which I concur. In addition this specimen cannot be assigned with any certainty to either the genus *Glyptosaurus* (*sensu stricto*) or any other glyptosaurine genus. An osteoderm was associated with the dentary (Loomis, 1907) but this is also undiagnostic below the subfamily level. Other specimens considered to be of this species (AMNH 5181, now *Paraglyptosaurus yatkolai*, new genus, new species [see above], and USNM 5380 considered herein as Glyptosaurini, genus and species indeterminate) were both referred to *G. obtusidens* on stratigraphic grounds only, because they were the only known glyptosaurines from the Wasatch Formation at the time of their description. Gilmore's retention on the basis of stratigraphic occurrence in the Wasatch is unsatisfactory since a number of fossil anguids from both tribes are of Wasatchian Age.

The teeth of the holotype (AC 3612) have slightly inflated shafts which differ from those of the early and middle Oligocene *Helodermoides tuberculatus*. The striations are confined to the crowns, as in all other fossil anguids. This specimen may be distinctive but a generic assignment is difficult or impossible at present. *Glyptosaurus obtusidens* is considered a *nomen dubium*.

TRIBE GLYPTOSAURINI, GENUS AND SPECIES,
INDETERMINATE

AMNH 1615, body and cephalic osteoderms. Wind River, Wyoming. Wind River Formation (Wasatchian). Collector: AMNH Expedition, 1909.

AMNH 11054, anterior part of frontal. Big Horn Basin, Wyoming. Wasatch Formation (Wasatchian). Collector: Walter Granger, 1911.

PU 22074, (?)frontal fragment, fragment of left jugal and three body osteoderms. Badlands north of Wind River Basin, Wyoming. Wind

River Formation, Lysite Member (Wasatchian). Collector: PU party, 1930.

USNM 5380, body and cephalic osteoderms. New Mexico. San Jose Formation (Wasatchian) (see Cope, 1877, pl. 32, figs. 26-36). Collector: Edward D. Cope, 1866 or 1867.

YPM 7580, osteoderms. Eocene. Locality, Formation and collector unknown, 1870.

YPM 7585, fragment of frontal, body osteoderms and two unidentified bone fragments. Locality unknown. (?)Bridger Formation (?Bridgerian). Collector: Yale College Expedition, 1871.

YPM 7586, body and cephalic osteoderms and miscellaneous bone fragments. Locality and formation unknown (?Bridgerian). Collector: Othniel C. Marsh, September 4, 1870.

YPM 7587, fragment of parietal. Locality unknown. (?)Bridger Formation (Bridgerian). Collector: Yale College Expedition, 1871.

TRIBE MELANOSAURINI, NEW TRIBE

TYPE: *Melanosaurus* Gilmore, 1928.

KNOWN DISTRIBUTION: Early Eocene-late Oligocene (Wasatchian-Whitneyan).

DIAGNOSIS: Glyptosaurines that differ from the only other Glyptosaurine tribe, Glyptosaurini, in the possession of shieldlike dermal armor that covers the frontal(s), parietal, and muzzle of the skull.

DISCUSSION: This tribe is erected for the glyptosaurine genera that have fused dermal armor covering the dorsal skull region, with variable impressions of enlarged epidermal scales over the frontal and parietal region. This tribe includes the genera *Arpadosaurus*, *Melanosaurus*, *Peltosaurus*, and *Xestops*. While not of primary concern for this study, these genera must be considered as they are closely related to the tribe Glyptosaurini and are considered here to form a monophyletic group with the other glyptosaurine genera (*sensu* Meszoely, 1970). Their relationship to the Glyptosaurinae is discussed below.

Cf. GLYPTOSAURINAE, TRIBE, GENUS AND SPECIES INDETERMINATE

The following material was seen during the course of this study, but could not be assigned below the subfamily level.

AC 2692, two dentary fragments. Wind

River Basin, Wyoming. Wind River Formation, Lysite Member (Wasatchian). Collector: Albert E. Wood, year unknown.

AC 3612 (type of *Glyptosaurus obtusidens* Loomis, 1907, p. 363, see above discussion of *nomina dubia*), dentary fragment. Tatman Mountain, Wyoming. Wasatch Formation (Wasatchian). Collector: Amherst College Expedition, 1903.

AMNH 1613, body osteoderms, vertebrae fragments and unidentified bone fragments. Alkali Creek, Wind River Basin, Wyoming. Wind River Formation (Wasatchian). Collector: AMNH Expedition, 1909.

AMNH 2089, right dentary. Graybull Valley, Big Horn, Wyoming. Wasatch Formation (Wasatchian). Collector: AMNH Expedition, 1910.

AMNH 2299, left dentary fragment. Wind River, Wyoming. Wind River Formation (Wasatchian). AMNH Expedition, 1905 or 1909.

AMNH 3783, dentary fragment and osteoderm. Reclusa Blowout, Powder River, Wyoming. Wasatch Formation (Wasatchian) (Posder River Local Fauna). Collector: Horace E. Wood II, 1951.

AMNH 3786, dentary fragment. Powder River, Wyoming, Sec. 26, T44N, R78W. Wasatch Formation (Wasatchian) (Powder River Local Fauna). Collector: Horace E. Wood II, 1951.

AMNH 3793, two dentary fragments. Drywell, Wyoming. Wasatch Formation (Wasatchian) (Powder River Local Fauna). Collector: Horace E. Wood II, 1951.

AMNH 5176, right mandible fragment. Big Horn Basin, Wyoming. Wasatch Formation (Wasatchian). Collector: Walter Granger, 1911.

AMNH 5187, left and right dentary fragments, fragment of right maxilla and unidentified bone fragments. Head of Kimbetoh Arroyo, San Juan County, New Mexico, New Mexico. Nacimiento Formation, lower level (Torrejonian). Collector: AMNH Expedition, 1913.

AMNH 7593, left dentary fragment and unidentified bone fragments. Fossil Creek, Gardner, Colorado. Huerfano Formation (Wasatchian). Collector: AMNH Expedition, 1952.

AMNH 7616, two articulated vertebrae. Garcia Canyon, Colorado. Huerfano Formation (Wasatchian). Collector: AMNH Expedition, 1952.

AMNH 11042, part of right dentary. Big Horn, Wyoming. Wasatch Formation, Graybull Member (Wasatchian). Collector: AMNH Expedition, 1916.

AMNH 11043, part of left dentary. Big Horn, Wyoming. Wasatch Formation, Graybull Member (Wasatchian). Collector: AMNH Expedition, 1916.

AMNH 11046, left dentary. Graybull Valley, Big Horn, Wyoming. Wasatch Formation (Wasatchian). Collector: AMNH Expedition, 1910.

AMNH 11047, left dentary. Big Horn Basin, Wyoming. Wasatch Formation (Wasatchian). Collector: Walter Granger, 1911.

AMNH 11048, left dentary. Big Horn Basin, Wyoming. Wasatch Formation (Wasatchian). Collector: Walter Granger, 1911.

AMNH 11049, fragment of left dentary. Big Horn Basin, Wyoming. Wasatch Formation (Wasatchian). Collector: Walter Granger, 1911.

F:AM 8701, vertebrae and unidentified bone fragments. South end of north fork, Lone Tree Gulch, Bates Hole, Natrona County, Wyoming. White River Formation (Chadronian). Collector: AMNH Expedition, 1959.

PU 13114, fragments of dentary, unidentified skeletal material and body osteoderms. Big Horn Basin, Wyoming. Willwood Formation, Graybull horizon (Wasatchian). Collector: William J. Sinclair.

PU 13455, incomplete right mandible. Alkali Creek, 5 miles northwest of Arminto, Wyoming. Wind River Formation, Lost Cabin Member (Wasatchian). Collector: P.U. Expedition, 1931.

PU 13456, incomplete left mandible. Alkali Creek, 5 miles northwest of Arminto, Wyoming. Wind River Formation, Lost Cabin Member (Wasatchian). Collector: P.U. Expedition, 1931.

PU 16748, two dentary fragments and maxilla fragment. Dry Creek, northeast of Emblem, northwest of Graybull, Wyoming. Willwood Formation, mid level (Wasatchian). Collector: Glenn L. Jepsen, 1954.

PU 17653, two dentary fragments. Red badlands west of Bridger Creek, 6 miles northwest of Lost Cabin, Wyoming. Wind River Formation (Wasatchian). Collector: P.U. Expedition, 1931.

PU 18100, fragment of right dentary, body osteoderms and bone fragments. Sec. 33, T56N, R100W, Park County, Wyoming. Willwood Formation, lower level (Wasatchian). Collector: P.U. Expedition, 1962.

PU 18132, right dentary and articulated (?) limb osteoderms. NW1/4 of Sec. 33, T55N, R100W, Park County, Wyoming. Willwood Formation, lower level (Wasatchian). Collector: P.U. Expedition, June 26, 1962.

PU 18198, body osteoderms. Sec. 31, T86N, R100W, Park County, Wyoming. Formation unknown. Collector: D. Burt, August 7, 1954.

PU 18324, right maxilla and various dentary fragments. Sec. 21, T54N, R97W, Big Horn County, Wyoming. Willwood Formation, lower level (Wasatchian). Collector: P.U. Expedition, 1954.

PU 20346, dentary and maxilla fragments and body osteoderms. East side of Little Sand Coulee, center north half of Sec. 19, T55N, R102W, Park County, Wyoming (Leo Hickey's Locality 6856E). Willwood Formation, lower level (Wasatchian). Collector: Alexander Gancarz, September 5, 1968.

PU 22071, two dentary fragments. Badlands north of Wind River Basin, Wyoming. Wind River Formation, Lysite Member (Wasatchian). Collector: P.U. Expedition, 1930.

PU 22072, right dentary. Three miles southwest of Basin, Big Horn County, Wyoming. Willwood Formation, Graybull Member (Wasatchian). Collector: A. Silberling, 1938.

PU 22073, right and left dentary fragment. Three miles southwest of Basin, Big Horn County, Wyoming. Willwood Formation, Graybull Member (Wasatchian). Collector: A. Silberling, 1938.

PU 22074, body osteoderms and jugal fragment. Locality, formation, collector and date unknown.

USNM 16524 (type of *Glyptosaurus sphenodon* Marsh, 1872, p. 306, see above discussion of *nomina dubia*), anterior part of right maxilla. Henry's Fork, Uinta County, Wyo-

ming. Bridger Formation (Bridgerian). Collector: T. G. Peck, 1871.

YPM 3946, left dentary and right jugal fragment. SW1/4, SW1/4 of Sec. 20, T49N, R96W, 3/4 miles NNE of Mueller Cabin, Wyoming. Willwood Formation, Lysite Member (Wasatchian). Collector: Tor Kreiger, July 18, 1961.

YPM 7582, body osteoderms and vertebra. (?) Fort Bridger, Bridger Basin, Wyoming. Bridger Formation (Bridgerian). Collector: Othniel C. Marsh, 1870.

YPM 7591, two osteoderms and maxilla fragment. (?) Bridger Basin, Wyoming. Bridger Formation (Bridgerian). Collector: Frederick Mead, September 5, 1871.

YPM 7593, proximal end of humerus, acetabulum, vertebrae fragments, body and cheek osteoderms and unidentified bone fragments. Grizzly Buttes, Wyoming. Bridger Formation (Bridgerian). Collector: George G. Lobdell, Jr., September 6, 1871.

YPM 7597, vertebrae fragments, proximal end of humerus, osteoderms, and unidentified bone fragments. Grizzly Buttes, Wyoming. Bridger Formation (Bridgerian). Collector: Yale College Expedition, 1873.

Cf. ANGUIDAE, INDETERMINATE

AMNH 7444, left dentary fragment. CCC Draw, Gardner, Colorado. Huerfano Formation (Wasatchian). Collector: AMNH Expedition, 1952.

F:AM 8693, articulated vertebrae and ribs. Bates Hole, Natrona County, Wyoming. White River Formation (Chadronian). Collector and year unknown.

F:AM 9163, five vertebrae fragments. North fork of Lone Tree Gulch, Natrona County, Wy-

oming. White River Formation (Chadronian). Collector and year unknown.

F:AM 9164, maxilla fragment. Middle fork of Lone Tree Gulch, Natrona County, Wyoming. White River Formation (Chadronian). Collector and year unknown.

F:AM 9165, dentary fragment. Middle fork of Lone Tree Gulch, Natrona County, Wyoming. White River Formation (Chadronian). Collector and year unknown.

F:AM 9167, fragment of vertebra. North fork of Lone Tree Gulch, Natrona County, Wyoming. White River Formation (Chadronian). Collector and year unknown.

F:AM 9168, caudal vertebra. Little Lone Tree, Bates Hole area, Natrona County, Wyoming. White River Formation (Chadronian). Collector and year unknown.

USNM 215049, vertebra fragment. South fork of Lone Tree Gulch, primarily in SE1/4, Sec. 27, T31N, R83W, but also in bordering parts of the NE and SW1/4s of the same section, Natrona County, Wyoming. White River Formation (Chadronian). Collectors: Robert J. Emry and Albert C. Myrick, 1971.

USNM 241320, vertebra. Head of Little Lone Tree Gulch, Natrona County, Wyoming, in NE1/4, Sec. 22, and in north 1/2 of Sec. 23, T31N, R83W. White River Formation (Chadronian) 20-30 ft. below Ash D. Collectors: Robert J. Emry and Albert C. Myrick, 1971.

USNM 241330, two vertebrae. South fork of Lone Tree Gulch, Natrona County, Wyoming, primarily in the SE1/4, Sec. 27, T31N, R83W but also in bordering parts of the northeast and southwest 1/4s of the same section. White River Formation (Chadronian), 40-50 ft. below Ash F. Collectors: Robert J. Emry and Albert C. Myrick, 1971.

PHYLOGENY

REVIEW OF THE CHARACTERS OF THE GENUS *GLYPTOSAURUS*

Because results of the present study differ from the former concept of what constituted the

genus *Glyptosaurus* a review of the characters utilized is necessary.

Three individuals have discussed what they believe to have been the character states dis-

played in the genus: Marsh (1871, 1872), Gilmore (1928), and Meszoely (1970).

Marsh (1871) characterized the genus *Glyptosaurus* as follows:

The head in this genus, for which the name *Glyptosaurus* is proposed, was covered with large osseous shields, symmetrically arranged and highly ornamented, resembling in this respect the modern *Heloderma*. Other parts of the body, especially the ventral region, were protected by rectangular, ornamented shields, united to each other by suture, and, in some of the species, these were carinate. The teeth are pleurodont, and, in the species in which they are preserved are round, with obtuse summits, not unlike those of *Trachydosaurus rugosus* Gray of Australia. The frontals show, especially in front, a distinct median suture, which forms a slightly obtuse angle with their posterior margin. The articular bone projects behind the cotylus far backward and downward, resembling in this respect the corresponding part in *Varanus niloticus*.

The dorsal and caudal vertebrae have the same general form as those of *Varanus*, but show traces of zygosphenic articulation especially in their rudimentary zygantral cavities. The tail was long and apparently rounded. Some of the species were larger than any existing American lizards.

In 1872 Marsh added to his list of *Glyptosaurus* characters:

In addition to the characters given when the genus *Glyptosaurus* was proposed, the following derived from a study of more complete specimens, may be mentioned. The entire body and tail were covered with ornamented osseous plates, most of them united by suture. The rami of the lower jaw were loosely attached at the symphysis. There were numerous small teeth, "dent en cardes," on the pterygoids. The malar arch was complete. The parietals were thick, and there was a parietal foramen. The pelvic arch and the limb bones resemble those in the Iguanas, but the posterior limbs were proportionally smaller. The caudal vertebrae, in some species at least, were divided transversely by a thin unossified septum, so that the centra break there readily as in many recent lizards. This genus and its allies evidently represent a distinct family which may be called the Glyptosauridae.

Later Gilmore (1928) reviewed Marsh's characters and summarized the osteological characters of *Glyptosaurus* as follows:

Skull.—Parietal undivided, expanded laterally, roofing over supratemporal fossa, with pineal foramen;

frontals usually separate; inferior plates of frontal straight or infolded, never fully inclosing olfactory lobes, nasals distinct; prefrontals elongate, extending above orbit but never meeting the postfrontal; postfrontal subtriangular; postorbital apparently present but excluded from orbital border; jugal large, massive, rectangular; articulating principally with postfrontal; occipital distinctly tripartite; supratemporal fossa roofed over by dermal scuta; tabulare present; columelli cranii present; supratemporal arch present; pterygoid wide with large patch or one or two narrow bands of teeth.

Jaws.—Meckel's groove closed except at anterior end; surangular extending forward, even with or beyond anterior suture of coronoid; splenial wide posteriorly, narrowly contracted anteriorly, strongly visible from a lateral view; surangular, articular, and prearticular coossified to form one bone; angular short, showing broadly in lateral view; angle strong, directed downward and inward; coronoid high.

Teeth.—Pleurodont; transversely compressed crowns, with beveled outer faces, sharp; posterior teeth blunt with low longitudinal ridge; crown surfaces smooth or striated.

Vertebrae.—Cervicals shortened, keeled; anterior dorsals with low but sharp median keel, rapidly subsiding into dorsals with convex ventral surfaces; precondylar constriction slight; condylar end set off by angular groove; diapophyses vertical, narrow; sacral vertebrae not coossified; caudal vertebrae with short transverse processes; chevrons pediculate, and placed posteriorly to the middle; neural spines of caudals moderate. No zygosphenic articulation.

Arch and limb bones.—Ilium with short, forward projecting process. Humerus with ectepicondylar foramen.

Dermal scuta.—Highly embossed tuberculate osteoderms on head and body. Those on the head more or less of equal size usually without definite arrangement, those of body rectangular and united laterally by suture, some with low carina.

Meszoely (1970) summarized the characters of the genus *Glyptosaurus* as follows:

The frontals, parietals, and cheek region are covered with numerous polygonal osteoscutal plates. These cranial osteoscutae, as well as those of the body, are covered with raised tubercular mounds, which are often arranged in concentric patterns. The frontals are distinct or fused; in the latter case the point of fusion is generally marked by a raised ventral ridge. The palatines and the pterygoids bear teeth. The postfrontals and prefrontals are narrowly separated

above the orbit. The parietal foramen is present, and the postorbital is excluded from orbit formation. The body scutes are rectangular, have a uniform width and are much longer than wide. They are covered with tubercular mounds that are arranged in a concentric pattern. A deep groove is present between the smooth anterior gliding surface and the sculptured area. The gliding surface is an anterior transverse band and comprises about one-quarter of the total length of osteoscutes. In every species some of the osteoscutes have feeble keels. Strongly jagged lateral edges indicate suturing between adjacent osteoscutes.

On the mandible the anterior extremities of the coronoid and the surangular are in line on a vertical plane on the labial surface. The dentary reaches posteriad between the above two bones to the supra-angular foramen.

An evaluation of these criteria is necessary and is given below.

FRONTALS: Marsh (1871) defined the genus *Glyptosaurus* based on the frontal specimen USNM 16523 (fig. 3a and b), which showed a "distinct median suture." In his original publication of the genus (Marsh, 1871), Marsh described three additional species (*G. nodosus*, *G. ocellatus* and *G. anceps*). The frontals in Marsh's type of *G. nodosus* were separate, those of *G. ocellatus* were apparently unfused also, but the type of this latter species was unavailable for this study. Its synonymy with *G. sylvestris* by Gilmore (1928) may be correct and is maintained here, but since this species is based on a patch of cranial scutes, assignment to the new genus *Paraglyptosaurus* is equally possible since both genera are known from the Bridgerian of Grizzly Buttes, Wyoming (see Gilmore, 1928, p. 182, pl. 13).

In many of his type descriptions of 1871 and 1872, Marsh failed to state the condition of fusion of frontals where known; it is therefore necessary to refer to Gilmore's redescrptions, although in two cases Gilmore also did not recognize the true state of the frontals of the species now synonymized with *Helodermoides tuberculatus* (*Glyptosaurus giganteus* Gilmore, 1928) and *Paraglyptosaurus princeps* (*Glyptosaurus hillsi* Gilmore, 1928), believing them fused in the former and partially fused in the latter.

The frontal bone has been used by both Gilmore (1928) and Meszoely (1970) as one of

the most diagnostic skeletal elements used in classifying fossil anguid lizards at both the generic and specific levels. Fusion and non-fusion of the frontal bone can be used along with other criteria for distinguishing different genera, as the condition appears to be consistent in the glyptosaurinids.

The unfused frontal state is best represented in the large sample of *Helodermoides tuberculatus* from the North American Oligocene. These Chadronian and Orellan lizards are represented by specimens ranging in frontal length from 16 mm. to 49 mm.; each displays the separate (paired) frontal condition. Fusion of frontals is uniform among specimens of the lower Eocene-middle Eocene genus *Paraglyptosaurus*, in which there is also a variation in frontal length from 33 mm. to 45 mm. Although the variation in the latter genus does not seem to be as great as in the former, this is due to the sample size rather than indicating any inconsistency. I therefore conclude that fusion develops very early in the ontogeny of these lizards, and thus it appears to be a character that can be used in conjunction with other characters when describing genera.

Meszoely (1970) stated that the "frontals are distinct in *Glyptosaurus sylvestris*, *G. nodosus*, *G. montanus* and *G. tuberculatus*. These bones are fused but with a prominent suture line or raised ridge marking the point of fusion in *G. rugosus*, *G. hillsi*, *G. princeps* and *G. giganteus*."

I agree with Meszoely's statement regarding species in which the frontals are distinct, except for his omission of the type "*G. giganteus*" which also displays unfused frontals, but the prominence of the suture lines exhibited in the latter forms varies. This condition is also seen in the type of *Arpadosaurus gazinorum* (fig. 20b) and is not diagnostic, probably occurring in all fossil anguids in which frontal bones are fused.

The sample of *Glyptosaurus* and *Eoglyptosaurus*, though not being represented by a number of specimens equivalent to the sample of *Helodermoides* and *Paraglyptosaurus*, also display consistently separate frontals in the case of *Glyptosaurus* and fused frontals in the case of *Eoglyptosaurus*. The frontal bone in both

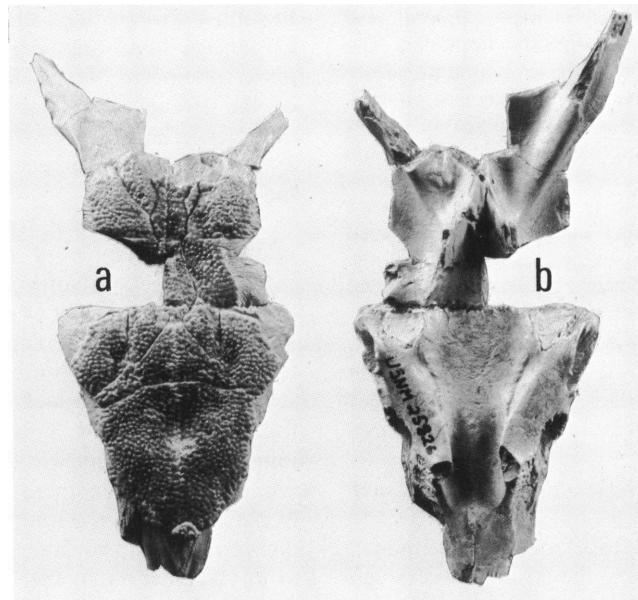


FIG. 20. *Arpadosaurus gazinorum*, USNM 25826 (type), complete frontal and nearly complete parietal with supratemporal processes. a. Dorsal view. b. Ventral view. North of Big Piney, Wyoming (Wasatchian). X1.

tribes occurs in both the fused and unfused state.

OSTEODERMS: A variety of interpretations have been offered regarding the encrusting dermal armor that covers the skull and body of these ancient lizards (McDowell and Bogert, 1954; Hoffstetter, 1962a; Meszoely, 1970). Past and present classification has been preoccupied with the description of the epidermal scale impressions (see Meszoely, Estes and Haubold, 1978) which have been usually presumed to be linked with the apparent break-up of the dermal armor as seen in the Glyptosaurini. Morphotypes range from the very faint epidermal shield markings on the frontal bone in *Melanosaurus* Gilmore, 1928, the intermediate condition seen in *Arpadosaurus* Meszoely, 1970 (fig. 20a), the well-developed enlarged cephalic shields of *Peltosaurus* and *Xestops*, and finally to the extreme conditions seen in *Eoglyptosaurus*, *Glyptosaurus*, *Paraglyptosaurus*, and *Helodermoides* where there is a presumed one to one correspondence of the epidermal scale to the underlying osteoderm. Past workers, in particular Gilmore (1928), have not emphasized dif-

ferences in the osteodermal armor among the forms included here in the Glyptosaurini. All the genera of the Glyptosaurini superficially resemble each other in the possession of hexagonal cephalic osteoderms, but I have shown above that size, arrangement, and tubercular pattern is as distinctly different among the Glyptosaurini as are the differences seen among the genera that comprise the Melanosaurini. Marsh originally described the dermal scutes on *Glyptosaurus* as being large, symmetrically arranged, highly ornamented, whereas body osteoderms were rectangular and laterally sutured, some of them keeled. Gilmore (1928) noted that *Glyptosaurus* displayed dermal scutes on the head of subequal size and that they were tuberculate (which is probably what Marsh meant when he said "highly ornamented"), but did not include it as a defining character of any particular species.

All known glyptosaurines and the fossil aniguid, *Odaxosaurus*, display rectangular body osteoderms. However, as shown on the more complete specimens, position on the body dictates shape, size, keeling, the amount of over-

lap, lateral suturing and the size and shape of the individual osteoderm. Specimens of *Helodermoides tuberculatus* exhibit osteoderms that are keeled with a prominent lateral suture whereas others may have a lateral gliding surface; variations of shape within an individual may include osteoderms that are rectangular to square, triangular to almost circular as well as the hexagonal type depending on their position on the body (e.g., see figs. 12a; 15c and d; 16a, c, d, and 17a).

Osteoderms on the dorsal side are much thicker than those on the ventral side, which tend to be more square as seen in UNSM 4511 (fig. 11b). Ovoid osteoderms are known from another specimen of *Helodermoides tuberculatus* (UNSM 12100) and may be from the limbs. Cheek osteoderms in both the Glyptosaurini and the Melanosaurini are hexagonal.

A concentric pattern of tubercles is seen in a few genera of the Glyptosaurinae, particularly in the Eocene genera *Eoglyptosaurus*, *Glyptosaurus* and *Paraglyptosaurus*, and is especially prominent in the latter genus. This concentric ring pattern of tubercles is absent in the Oligocene *Helodermoides* and in all other fossil anguids, except that some peripheral tubercles may show some concentricism as the result of osteoderm shape.

The low carina or keel occurs in all fossil anguids in which the body osteoderms are known. Keeling is confined to the dorsal side of the lizard and varies in prominence. Keeling has been reported in the osteoderms of *Xestops*, *Glyptosaurus* (*sensu lato*), *Arpadosaurus*, and *Melanosaurus* (Meszoely, 1970). Contrary to Meszoely (1970) keels are present in some *Peltosaurus* specimens, in particular UNSM 12102.

The prominent groove reported by Meszoely (1970) between the gliding surface and the sculptured area of the body osteoderm in *Glyptosaurus* (*sensu lato*) is present in all members of the subfamily Glyptosaurinae and in some other subfamilies of the Anguidae and is not diagnostic of *Glyptosaurus* (*sensu lato*) as implied by him. In all glyptosaurines the gliding surface varies in size according to its topographic position on the body and does not always comprise one-quarter of the entire

osteoderm for *Glyptosaurus* (*sensu lato*) as stated by Meszoely (1970).

Taxonomically, the external morphology of individual osteoderms is unreliable below the tribe level and particularly at the generic level. Hoffstetter (1962a) concluded on the basis of external morphology that the anguids could be divided into two groups: (1) the gerrhonotines (*sensu lato*) which include the fossil glyptosaurines and Recent gerrhonotines (*sensu stricto*), and (2) the anguines (*sensu lato*), which include diploglossines and anguines (*sensu stricto*). A recent study of the internal structure of the osteoderms of the genera in the Diploglossinae (Strahm and Schwartz, 1977) has resulted in the recognition of the genera *Celestus* and *Sauresia* which were previously included in the single genus *Diploglossus*. Possibly a study of histology of the different glyptosaurine osteoderms may reveal similar results.

TEETH: The teeth originally described by Marsh (1871) and Gilmore (1928) and were presumed associated with the type specimen of *Glyptosaurus sylvestris* have been subsequently lost. However, descriptions given by Marsh (1871) and Gilmore (1928) that they were "pleurodont, and, in the species in which they are preserved, are round, with obtuse summits. . . ." Other specimens of *Glyptosaurus sylvestris* from the Bridger Formation (fig. 3g and h; fig. 5a and b) show that the tooth type was as described by Marsh.

The teeth of *Paraglyptosaurus princeps* exhibited in USNM 6004 (type of *Glyptosaurus hillsi* Gilmore, 1928) and AMNH 1619 (fig. 4g and h; fig. 5c and d) are inflated and represent the extreme of the crushing tooth type found in the Glyptosaurini. A similar extreme crushing type is found in the type specimen of *Arpadosaurus gazinorum* (Meszoely, 1970).

Helodermoides deviates from other glyptosaurines in that the tooth type is a simple, subconical, slightly recurved tooth with an unstriated or faintly striated crown. Faint striations appear only in the largest specimens.

Teeth in other glyptosaurines have prominently striated crowns and are more or less homodont. One specimen of *Paraglyptosaurus princeps* (AMNH 1619, fig. 5c and d) shows a

heterodont condition in which the anterior teeth approach the sharp toothed condition seen in *Helodermoides* and the posterior teeth are of the obtuse blunt crushing type.

The striations that occur on the obtuse tooth type are external, forming crenulations in the enameloid covering. This morphology, evident in glyptosaurines and many other anguids, when coupled with regional variation makes it impossible to assign toothed elements to any taxon with certainty, a conclusion also reached by Meszoely (1970).

PTERYGOID TEETH: Another character of *Glyptosaurus* (*sensu lato*) used by Marsh and Gilmore was the presence of pterygoid teeth. All known fossil anguid lizards in which the pterygoid and palatine bones are known display teeth in large ovoid patches. Gilmore (1928) reported the condition of "pterygoid teeth in a narrow band, sometimes two parallel bands" in *Glyptosaurus sylvestris*. This was based on the type of *Glyptosaurus brevidens* which Gilmore (1928) synonymized with *G. sylvestris*. As the type of *G. brevidens* is lost I cannot confirm this description. No other specimens show such a band, and presence of pterygoid teeth among glyptosaurines is a primitive character perhaps characteristic only for the subfamily as expressed by Meszoely (1970), at least if large, oval patches are specified.

POSTORBITAL-POSTFRONTAL REGION: This region is preserved in only a few skulls of glyptosaurines (*Melanosaurus*, *Helodermoides*, *Paraglyptosaurus*, and *Peltosaurus*) and clearly shows that the postorbital is excluded from the orbit, save *Peltosaurus* where these two bones are fused. This condition has been reported in the Recent genera *Anguis*, *Ophisaurus*, and *Wetmorena*. The postfrontal and postorbital bones are fused in *Ophiodes* and *Diploglossus pleei* and separate in *Gerrhonotus* and *Abronia* with the postorbital gaining narrow exit into the orbit (Meszoely, 1970). I believe that the participation of the postfrontal and the exclusion of the postorbital in orbit formation is at best a subfamily state if not that of the family Anguidae in general with the exceptions where noted.

PREFRONTAL-POSTFRONTAL BONES: Meszoely (1970) stated that a character of *Glyptosaurus* (*sensu lato*) is the "narrow

separation" of the prefrontal and postfrontal bones above the orbit. Meszoely was probably referring to the Oligocene species *Helodermoides tuberculatus*, for some specimens the separation is small in comparison with the Eocene glyptosaurines including *Glyptosaurus* (*sensu stricto*), yet this apparent encroachment of the prefrontal and postfrontal on one another is probably the result of size, although wide separation of these bones is probably a derived condition for the Glyptosaurinae, resulting from increase in eye size and narrowing of frontal.

MANDIBLE: A few supposedly consistent characters of the bones in the mandible have been given by both Gilmore (1928) and by Meszoely (1970).

Meszoely (1970) stated in reference to *Glyptosaurus* (*sensu lato*) that: "All species in which the mandible is known display the characteristic labial suturing between dentary and postdentary bones, in which the anterior extremities of the coronoid and the surangular are on a vertical line, and the anterior inferior alveolar foramen is between the dentary and the splenial."

This labial suturing condition is recognized in the type of *Melanosaurus maximus* (AMNH 5168) as well as the type of *Paraglyptosaurus princeps* (USNM 16539) and in *Helodermoides tuberculatus* (CM 1050, type of *Glyptosaurus montanus*, see above). A specimen here referred to *Melanosaurus* (PU 21803) has the coronoid projecting anterior farther forward than the surangular thus conforming to the condition in *Peltosaurus* as reported by Meszoely (1970). In general, the subfamily displays labial suturing in which the anterior extremities of the coronoid and surangular lie in a vertical plane except where noted. The exceptions probably indicate a derived condition which is seen in other anguid subfamilies.

The position of the anterior alveolar foramen between the dentary and the splenial reported for *Glyptosaurus* (*sensu lato*) Meszoely, 1970) is the same in all mandibles of glyptosaurines where this region is preserved and is not unlike the condition found in the Recent *Gerrhonotus*.

Fusion among the posterior mandibular elements in *Glyptosaurus* (*sensu lato*), including the surangular, angular, and prearticular as noted by Gilmore (1928), was based on his

observations of "*Glyptosaurus hillsi*" (now *Paraglyptosaurus princeps*, see above) and most likely the type of "*Glyptosaurus montanus*" (now *Helodermoides tuberculatus*, see above). Upon reexamination of the type of "*G. montanus*" (CM 1050), I find traces of sutures including the suture that separates the retroarticular process from the prearticular and the articular from the surangular. This division of mandibular elements is best seen in UNSM 4511 (fig. 21). Fusion of these elements is seen in all of the Eocene glyptosaurines, whereas non-fusion generally seems to be the case in the Oligocene genus *Helodermoides*. Reasons for fusion and non-fusion are discussed in more detail below.

The splenial in all fossil anguids is wide posteriorly and extends anteriorly to the symphysis. This condition is seen in the type of *Melanosaurus*, referred specimens of *Helodermoides*, the type of *Paraglyptosaurus*, paratype of *Eoglyptosaurus* (USNM 18317) as well as an

undescribed specimen of cf. *Xestops vagans* (CM 8701, fig. 22b).

SUMMARY: A number of characters described by Marsh (1871, 1872), Gilmore (1928), and Meszoely (1970) as being diagnostic of *Glyptosaurus* (*sensu lato*) have been shown above to be diagnostic to subfamily and tribe at best. Of these character states the only consistent ones for the subfamily Glyptosaurinae are the possession of tuberculate dermal armor and the occurrence of large ovoid patches of pterygoid teeth. For the tribe Glyptosaurini the character of hexagonal cephalic scutellation on the entire skull separates it from the Melanosaurini which have fused platelike dermal armor impressed by enlarged epidermal laminae. A number of characters are considered to have no known, or uncertain, value at the subfamilial level or below. These include (1) tooth type; (2) keeling, extent of gliding surface (amount of overlap), prominent groove between gliding surface and sculptured region of osteoderm, concentric pat-

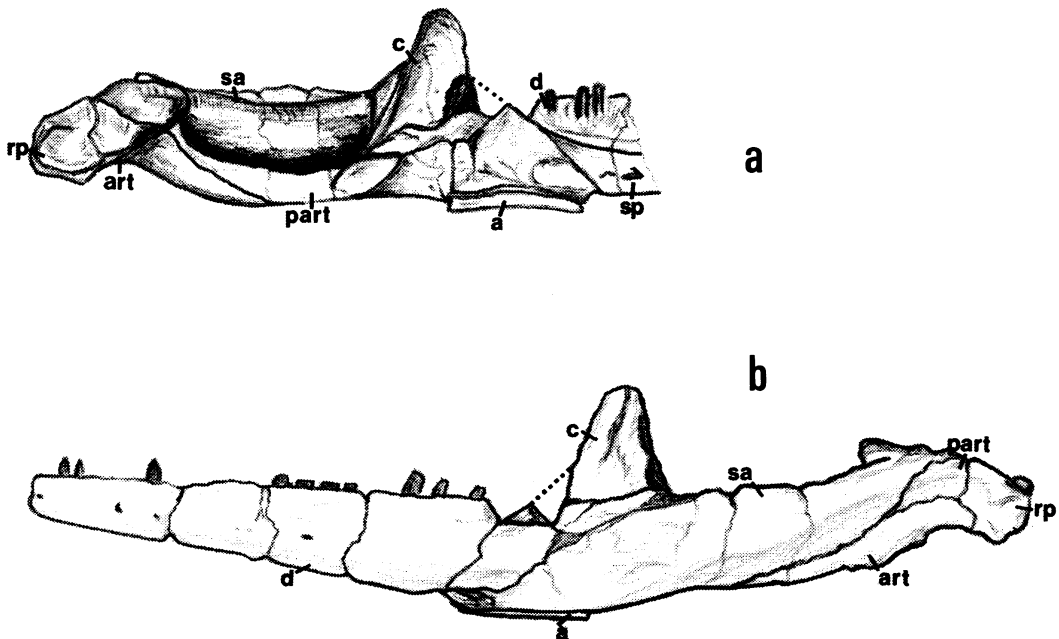


FIG. 21. Demarcation of mandibular elements in the left mandible of *Helodermoides tuberculatus* Douglass (UNSM 4511) due to non-fusion. a. Lingual view. b. Labial view.

Abbreviations: a., angular. art., articular. c., coronoid. d., dentary. part., prearticular. rp., retroarticular process. sa., surangular. sp., splenial.

tern of tubercles, lateral suturing and overall size and shape of osteoderms; (3) exclusion of postorbital bone from the orbit; (4) anterior extremities of the coronoid and surangular in a vertical plane; (5) presence of the anterior inferior alveolar foramen between the dentary and the splenial; and (6) fusion of posterior mandibular elements. Some of the above characters may be diagnostic for the family Anguidae with exceptions, these include (1) and (3). *Helodermoides* can be separated from other glyptosaurines by the absence of (6), but its utility is questionable. None of the above character

states are of value in specific identification. Characters that are presently of unknown value at all taxonomic levels include (2) (4) and (5).

However, trends can be seen when comparing the above character states among all the subfamilies of the Anguidae.

REVIEW AND RE-EVALUATION OF THE CHARACTERS OF THE ANGUID SUBFAMILIES

Meszoely (1970) revised the family Anguidae to include the four subfamilies recognized by McDowell and Bogert (1954): (1)

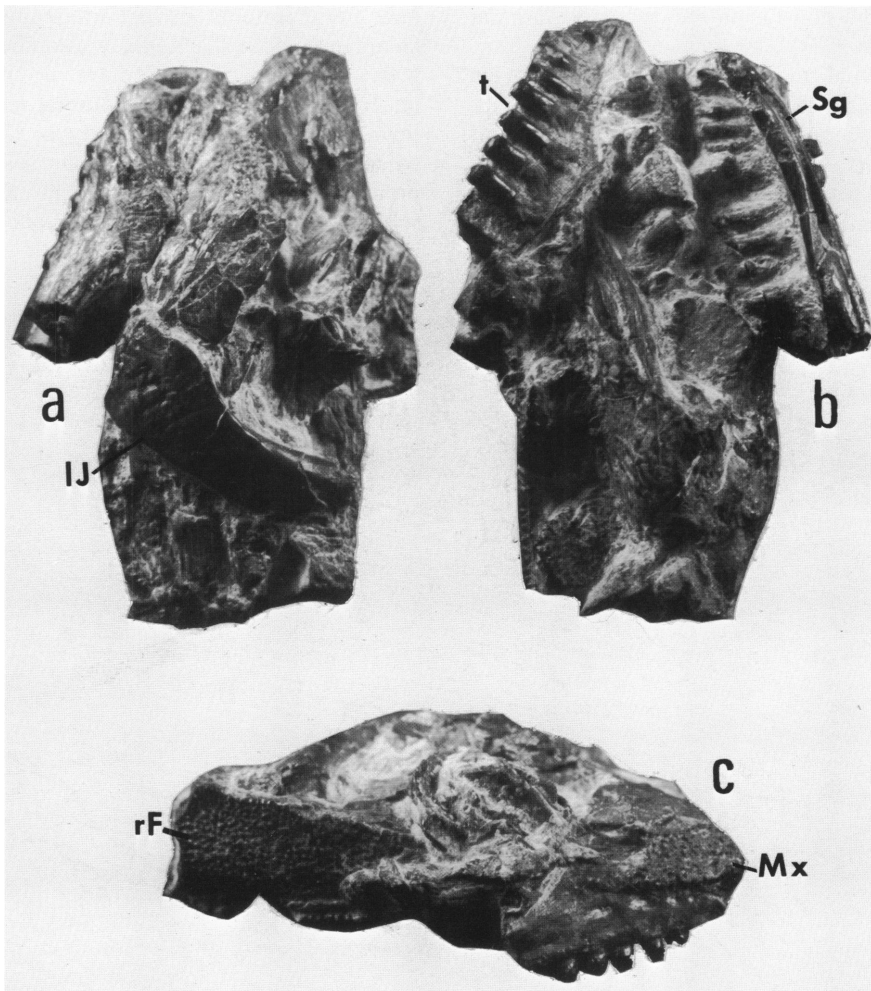


FIG. 22. cf. *Xestops vagans*, CM 8701, crushed skull. West of Manderson on Adobe Creek, Big Horn Basin (Wasatchian), Wyoming. X2.2. a. Dorsal view. b. Palatal view. c. Right lateral view.

Abbreviations: IJ., left jugal. Mx., maxilla. rF., right frontal. Sg., splenial groove. t., teeth.

Glyptosaurinae; (2) Gerrhonotinae; (3) Diploglossinae, and (4) Anguinae. The relationship of these subfamilies to one another was reviewed by Meszoely (1970) who concluded that the subfamily Anguinae was probably the most primitive, on the basis of unfused frontals¹ with relatively smooth dermal bone on

¹Meszoely (1970, p107) has characterized the frontals of *Odaxosaurus* (= *Pancelosaurus*) *piger* as being separate and thus, one would assume, that they do not become fused during later stages of ontogeny. However, Meszoely (1970, p. 105) states that there are "no significant differences" between the late Cretaceous and the late Paleocene specimens of *Odaxosaurus piger* and then illustrates a partially fused frontal, not unlike that of *Xestops stehlini* (see Meszoely, Estes and Haubold, 1978, p. 164, fig. 6a), from the late Paleocene and designates it *O. piger*. (I am assuming that the late Paleocene *O. piger* specimens are distinct from the "transitional" *Odaxosaurus jepseni* specimens of Jacques Gauthier's, that he reports from the same geologic horizon, see below). The frontal of the late Paleocene *O. piger* is fused, as the metopic suture on the dorsal side ends posteriorly at the anterior border of the interparietal scute region of the frontal. There is no indication in Meszoely's description (1970) as to the presence or absence of a metopic suture on the ventral side of the frontal. There is apparently a contradiction in his diagnosis of the frontal morphology for this species. Based on similar morphologies, it may be expected then, that the late Cretaceous representatives of *Odaxosaurus piger* also fused the frontal bones in later ontogenetic stages and thus should be properly characterized by fused frontals. In fact, this is not surprising, as all the established early Eocene glyptosaurine genera have solidly fused frontals, a character state that is shared with their common ancestor *Odaxosaurus*. The character state of fused frontals is considered by me as primitive for the subfamily Glyptosaurinae. Separate frontals, if characteristic of adult forms, are then secondarily derived as in the case of the latter genera of the Glyptosaurini (see below). As mentioned in the next footnote, there are now a number of early Eocene melanosaurinids known that show various stages in frontal fusion, thus adding to the uncertainty of establishing taxa on such a variable character state where there have been previously few specimens known.

The little known melanosaurinid, *Xestops vagans*, from the Bridgerian of North America, has been thought by some (Meszoely, 1970 and Meszoely, Estes and Haubold, 1978) to be the most "primitive" glyptosaurine because it approaches the frontal condition of *Odaxosaurus piger* in both retaining separate frontals and the primitive epidermal scalation pattern; a pattern that is shared by all the melanosaurinids. *Xestops vagans*, in addition, is very small when compared with other melanosaurinids, and that in itself, may indicate that the type was based on a juvenile or

which are impressed frontoparietal scales separated by frontal and interparietal scale impressions, as well as the Cretaceous occurrence of *Odaxosaurus*, included in the Anguinae by Meszoely (1970). These scale impressions are, however, seen in all the subfamilies (but is absent in the tribe Glyptosaurini of the Glyptosaurinae) and is the only character that points to the primitive condition in the Anguinae; it is a condition which has been believed to be shared with the ancestral autarchoglossan, as this pattern of epidermal scutellation is widely distributed in the Scincomorpha. However, a number of important characters compiled by Meszoely (1970) show more conclusively that the Glyptosaurinae should be considered the most primitive of the anguid subfamilies and that the Anguinae is the most derived.

The following characters are used in the analysis of the primitive and derived states in the Anguid subfamilies. These states include: (A) dermal armor morphology; (B) thickness of dermal armor; (C) mandible length (associated with this is a number of characters that I believe are integral components of one character system; this character system includes the number of teeth and mental foramina and the position of the anterior supra-angular foramen, anterior inferior alveolar foramen and the mylohyoid foramen); (D) presence or absence of limbs; (E) presence or absence of premaxillary fenestrae; (F) nature of the postorbital and postfrontal association; and (G) nature of the palatal teeth.

A classification based on weighted character states as proposed by Hecht and Edwards (1976) and Hecht (1977) is difficult to achieve when dealing with fossil and Recent anguids due to the lack of comparable elements in the

sub-adult lizard. It is my belief that this may be the case or that if *Xestops* is representative of an adult form, the separate frontal condition is secondarily derived and consequently is pedomorphic with respect to the earlier Eocene glyptosaurine genera, or for that matter, ancestral *Odaxosaurus*. The fact that the European *Xestops stehlini* has fused frontals (Meszoely, Estes and Haubold, 1978) supports the conclusion that *Xestops* cannot be considered the most primitive glyptosaurine based on the character states of unfused frontals, primitive epidermal scale impressions and small size, as these states all appear at one point or another in other melanosaurinids.

fossil forms. However, decisions on the primitive and derived nature of some states can be reached based on our knowledge of these states in other reptilian groups.

Taking the above character states and assigning them relative weights, a method used by Yatkola (1976), 0 = primitive state, 1 = a derived intermediate state and 2 = the most derived state, the following analysis results and is summarized in table 2.

The primitive condition for character A (dermal armor sculpture) is non-tuberculate, 0, as seen in all anguids, save the glyptosaurines, and the scincomorphs. The tuberculate condition seen in the glyptosaurines is derived and is assigned the weight 2. The intermediate condition as seen in *Odaxosaurus jepseni* is designated 1.

The primitive condition for character B (dermal armor thickness) is robust dermal armor (see McDowell and Bogert, 1954, p. 45), and is designated 0. Reduction in thickness is designated by 1. Thin dermal armor is given the weight 2.

Character C (mandible length and associated character systems) is considered primitive when the mandible is elongate and tooth counts are high along with a high number of mental foramina, 0. Reduction in mandibular length is designated 1. Further reduction is designated by 2.

Character D (limbs) is considered primitive when they are well developed, 0. Limb reduction is indicated by 1. Limb loss is 2.

Character E (premaxillary fenestrae) is primitive when absent, 0. This character is absent in most other lizard families and is a derived character where it occurs. The presence of premaxillary fenestrae is derived, 2.

Character F (nature of the postfrontal and postorbital association) is primitive when the postorbital and the postfrontal are distinct and the former does not participate in orbit formation. Fusion of these bones into one element or participation of the postorbital in orbit formation or both, is considered to be derived, 2.

The last character, G, is considered primitive when palatal teeth occur in extensive ovoid patches on both the palatines and pterygoids. Reduction of palatal teeth is assigned 1. Total loss is indicated by 2.

As seen in table 2, the Glyptosaurinae is the most primitive subfamily of the Anguidae, being derived only in the possession of tuberculate dermal armor.

The Gerrhonotinae is more derived in reduction of dermal armor (character B), reduction in limbs (character D), postorbital entering orbit formation (character F) and loss of palatine teeth (character G).

The Diploglossinae is further derived in the possession of relatively thin dermal armor in the form of cycloid osteoderms (character B), reduction in mandible (character C), reduced or absent limbs (character D), presence of premaxillary fenestrae (character E), fusion of postorbital and postfrontal with postorbital en-

TABLE 2
Taxonomic Distribution of Anguid Character States^a

Character	Glyptosaurinae	Gerrhonotinae	Diploglossinae	Anguinae	<i>Odaxosaurus</i>
A = dermal armor sculpture	2	0	0	0	0-1
B = dermal armor thickness	0	1	2	1-2	0-1
C = mandibular length, etc.	0	0	1	1-2	1
D = limbs	0	1	1-2	1-2	(?)
E = premaxillary fenestrae	0	0	2	2	2(?)
F = prefrontal/postfrontal	0-1	1	1	0	(?)
G = palatal teeth	0	1	2	1-2	0
Total score	2-3	4	9-10	6-10	1-3+(?)

^aThe low score seen in the genus *Odaxosaurus* suggests that this form should be removed from the subfamily Anguinae because it displays a number of primitive character states not seen in the other members of this subfamily (see text). *Odaxosaurus* may best be regarded as Anguidae: *incertae sedis*.

tering in some forms (character F), and palatal teeth absent (character G).

The Anguinae is similar to the Diploglossinae, and is derived, when *Odaxosaurus* is excluded, in having thin dermal armor (character B), short mandible length (character C), reduction or absence of limbs (character D), presence of premaxillary fenestrae (character E), reduction or absence of palatal teeth (character G).

Odaxosaurus, included in the Anguinae by Mesozoely (1970), displays a number of primitive states that makes inclusion in the Anguinae difficult. It is more primitive than members of the Diploglossinae and the Anguinae in characters B, C, and G. Comparing the total scores of these weighted character states (table 2) shows that *Odaxosaurus* is more similar to Glyptosaurinae and Gerrhonotinae than to the

Diploglossinae and Anguinae. On the basis of this analysis, then, I here exclude *Odaxosaurus* from the Anguinae and place it as Anguidae: *incertae sedis*. If *Odaxosaurus* is excluded from the Anguinae, the cladogram of the subfamilies of the Anguidae is as given in (fig. 23).

Mesozoely, Estes and Haubold (1978) suggested some possible phylogenetic relationships of *Odaxosaurus* and its presumed close relative *Machaerosaurus* Gilmore (1928). Nevertheless, their relationship to established subfamilial groupings is uncertain at present and may remain unsettled until more complete material is available.

Odaxosaurus has been principally known from the Cretaceous species *O. piger* (= *Peltosaurus? piger* Gilmore, 1928, and = *Pan-celosaurus piger* Meszoely, 1970). Recently,

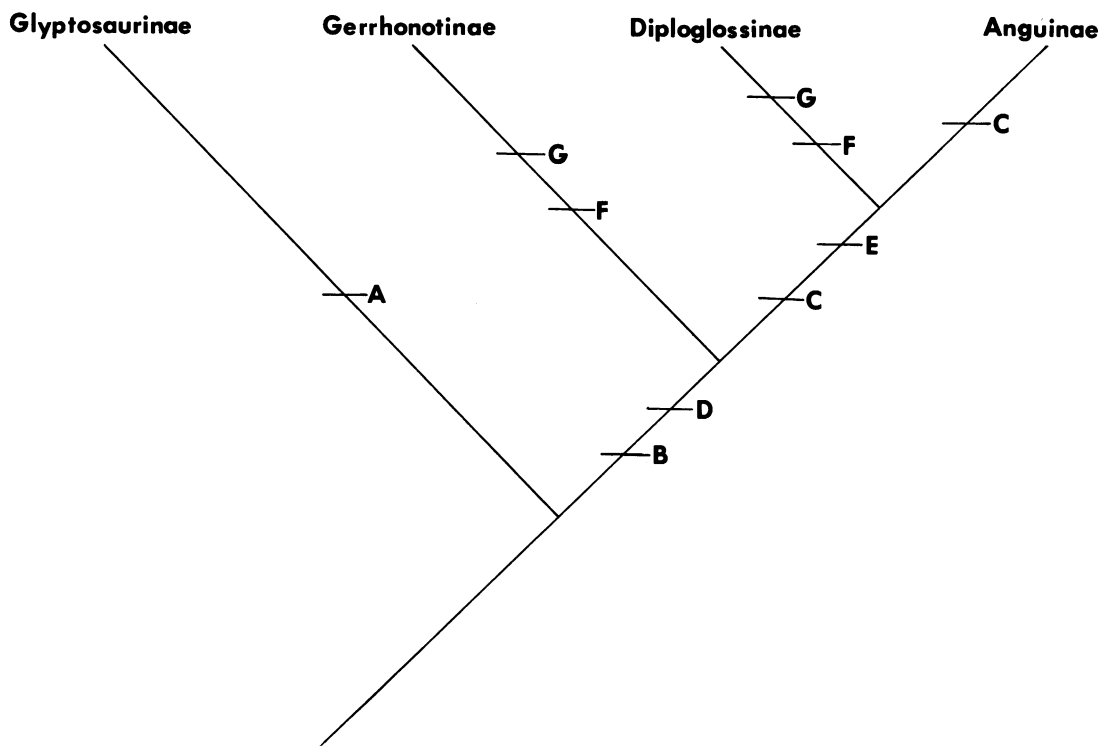


FIG. 23. Cladogram of the subfamilies of the Anguillidae. Character A. dermal armor sculpture; Character B. Dermal armor thickness; Character C. Mandibular length and associated character systems; Character D. Limbs; Character E. Premaxillary fenestrae; Character F. Postfrontal-postorbital association; and Character G. Palatal teeth (see text for discussion).

however, Jacques Gauthier reported (personal commun.) that the species *Odaxosaurus jepseni* (= *Peltosaurus jepseni* Gilmore, 1942; synonymized with *Pancelosaurus piger* by Meszoely, 1970) is distinct from the Cretaceous *O. piger*, and may represent an intermediate form between the latter and the "primitive" glyptosaurine *Xestops*. *Odaxosaurus jepseni* first appears in the upper Paleocene Polecat Bench Formation and has since been reported from the lower Eocene Bitter Creek Formation. *O. jepseni* is distinguished from *O. piger* primarily in showing a weakly developed tuberculation on the osteoderms and thus shows similarities to the glyptosaurines. However, this late Paleocene species appears too late in time to be considered the direct ancestor to *Xestops* and hence, the Glyptosaurinae. Indications are that large anguids, probably glyptosaurines, have already been established by the middle Paleocene based on the fossil material (AMNH 5187, see above) from the Nacimiento Formation of New Mexico. The tuberculate sculpture seen on *O. jepseni* may indicate that this species was ancestral to the Glyptosaurinae or that the tuberculation is an independent parallel acquisition.

If *O. jepseni* can be interpreted as being a "protoglyptosaurine" the uncertain position of *O. piger* still remains unchanged. The question of the presence or absence of premaxillary fenestrae continues to be a problem when considering subfamilial ranking for this genus. The premaxillary fenestrae have been considered to be present in *O. piger* (Meszoely, 1970) based on a referred maxilla that appears to have a bifid anterior process, suggesting the presence of premaxillary fenestrae as seen in the Recent Diploglossinae and Anguinae. The presence or absence in *O. jepseni* is unknown. This character is absent in all known glyptosaurines in which this region is preserved. Its absence is considered primitive by me in both Glyptosaurinae and Gerrhonotinae and its presence is derived in the Diploglossinae and Anguinae. It may be that the presence of premaxillary fenestrae is primitive in the Anguidae and that its loss in Glyptosaurinae and Gerrhonotinae is derived. However, in view of the fact that the presence of premaxillary fenestrae occur with the other derived character states seen in the Diploglossinae and Anguinae seems to indicate

that they too may be derived in the Anguidae, but their presence in *O. piger* at a very early date, if confirmed, would suggest that this species may be already on the line away from glyptosaurines. The question of their presence in the late Paleocene *O. jepseni* then remains a problem. If *O. jepseni* is classified as a glyptosaurine by virtue of its tuberculate dermal sculpture, then a new generic name for this species would probably be in order. In any case, additional material is necessary to clarify the relationships of *O. piger* to the other anguid subfamilies, even if *O. jepseni* is accepted as the earliest glyptosaurine.

PRIMITIVE AND DERIVED CHARACTERS OF THE GLYPTOSAURINAE: It has been pointed out by Olson (1971) that our knowledge and understanding of the ancestors of lizards is based on very incomplete material. Lepidosaurians of the late Triassic and late Jurassic times show that there had already been considerable radiation and diversification of the early squamates (Hoffstetter, 1962*b*, 1964, 1965, 1966) with the Jurassic lepidosaurians being intermediate between the more archaic late Triassic and the essentially modern Cretaceous forms. Estes (1964) and Hoffstetter (1966) have indicated that many of the modern lizard families were well established by the Late Cretaceous, one of which was the Anguidae. Limbless anguids have been reported by Meszoely and Haubold (1975) and Meszoely and Ford (1976) as early as the middle Eocene, indicating that the antiquity of the Anguinae may be indeed greater than what has been recently thought.

Here I present a discussion of what I believe are the best characters used in determining phylogenetic relationships within the Glyptosaurinae with particular attention given to the tribe Glyptosaurini. It is my intention to point out what character states are viewed as primitive and derived and to analyze their appearance in the stratigraphic record, from the lower Eocene through the middle Oligocene.

DERMAL ARMOR: PRIMITIVE VERSUS THE ADVANCED CONDITION: A thorough study of the primitive condition of dermal armor and its overlying epidermal scales is beyond the scope of this study. However, based on some recent studies on dermal armor morphology a hypothetical phylogeny can be suggested.

As indicated in the above classification of the genera of the Glyptosaurinae, two distinct groups are recognized here. The tribe Glyptosaurini comprises those glyptosaurines that possess unfused, hexagonal dermal armor on the entire skull. By contrast the tribe Melanosaurini has relatively smooth fused dermal bone on the frontal and parietal region of the skull, on which the impression of frequently enlarged epidermal laminae may be visible. Both of these tribes possess hexagonal osteoderms on the cheek region of the skull behind the jugal and below the supratemporal arch. Where the muzzle region of these lizards is preserved, the dermal armor for the Melanosaurini forms distinct enlarged shieldlike osteoderms unlike the smaller hexagonal dermal armor exhibited in this region in the Glyptosaurini.

Camp (1923) reviewed the problem of dermal bone in relation to the overlying epidermal scales among the lizard families. He concluded that four primitive features of squamation in lizards are "(1) uniform granular scales on all parts of the body; (2) imbricated scales, when present, with a wide free margin; (3) transverse rows of ventral scales not in correspondence with each pair of ribs; (4) osteoderms composed of many small, diffuse granules. All of these features are represented in the *Ascalabota*."

Of importance in regard to determining the primitive and advanced conditions seen in the Glyptosaurinae are characters 1, 2, and 4. Character 3 cannot be determined from fossil material. Of these three remaining characters, character 2 is seen in all anguids. Character 1 is more closely approached by the Glyptosaurini than by the Melanosaurini. Although the granular condition of the individual osteoderm, character 4, is unknown, it may be that the tubercles seen in the Glyptosaurinae represent individual granules that fuse into larger units that form a hexagonal osteoderm. If this were the case, further fusion would result in the broader dermal plates seen on the frontals and parietals of the Melanosaurini, making the Glyptosaurini, on the face of it, the more primitive tribe of the Glyptosaurinae according to Camp's character states.

As we have seen, recent work of Meszoely

(1970) and Meszoely, Estes and Haubold (1978) suggested that *Odaxosaurus* (*Pancelosaurus* of Meszoely, 1970) represents the primitive anguid and in their view probably gave rise to the most "primitive" glyptosaurine *Xestops* and other Glyptosaurinae, in contrast to McDowell and Bogert (1954, p. 45) who suggested that glyptosaurus (*sensu lato*) "are the most primitive of the Anguinomorpha, showing none of the specializations of later groups but retaining a heavy dermal armor of osteoderms as in the scincomorphs and usually retaining a distinct suture between the frontals."

Although McDowell and Bogert (1954) placed *Melanosaurus* in the Xenosauridae, they believed it was the most primitive member of that family, and their phylogeny (McDowell and Bogert, 1954, fig. 43) of the "Anguinomorpha" shows that the "Melanosaurinae" was derived from their "Glyptosaurinae" indicating that the latter was indeed a more primitive group. In addition, they believed (McDowell and Bogert, 1954, p. 114) the Glyptosaurinae to be derived from the Gerrhonotinae (which was based on their inclusion of *Peltosaurus* in the Gerrhonotinae), and that the Diploglossinae was an early offshoot of this latter subfamily. Despite their statements concerning the primitive nature of the glyptosaurus, they believed (McDowell and Bogert, 1954, p. 115) that *Glyptosaurus* (*sensu lato*) was advanced in: (1) disintegration of the typically large and rectangular head osteoderms; (2) widening of the frontals, and (3) increase in size. Their reconstructed phylogeny of the "Anguinomorpha" seems thus to be in contradiction to their earlier statement that the "glyptosaurus" were the most primitive anguimorphs. This apparent contradiction is probably due to the fact that they were unable to recognize the possible paedomorphic character states among the lizards in question.

Recent studies outside the reptiles and the order Squamata as well as within the Reptilia, has led to some very interesting implications as to the primitive condition of dermal armor and lend support for the recognition of paedomorphic trends in the Glyptosaurinae.

Tarlo (1967), in his studies of the heterostracans, suggests that the primitive condition of the dermal armor in this group is represented

by the presence of individual tesserae, whereby tubercles form a concentric ring around a central tubercle (ossification center). As these tubercles grow out from the center of the osteoderm, these circles abut against each other thus forming hexagonal packing units that can be seen to fuse into larger shields among the heterostracans. Tarlo (1967) believed that the "ability to develop tesserae is a primitive feature which is never entirely lost. The potential to form such structures in the skin is retained throughout the vertebrates, if not all."

The pattern of tubercles seen in the Heterostraci is similar, if not identical with that of the Glyptosaurini. If it could be shown, by paleohistological analysis of the osteoderms, that the individual tubercles are in fact minute ossification centers and not just superficial sculpture structures which has been the thought to date, if it were not for the reverse stratigraphic sequence then Tarlo's theory would suggest that the Glyptosaurini are the more primitive tribe, with the Melanosaurini being more derived by virtue of the larger dermal bone units. Nevertheless both tribes would be considered primitive over the non-tuberculated forms in this view. However, a reversion to a tuberculated pattern as seen in the Glyptosaurinae would seem to indicate a pedomorphic trend in the reacquisition of this primitive character state, as there is no other known widespread occurrence of tuberculate dermal armor among the lizards.

Westphal (1976) has also shown that the unfused hexagonal osteoderm is primitive for placodont reptiles, and makes a few important observations that may have a direct bearing on the relationship of bony dermal armor to the overlying epidermal scale in all reptilian vertebrates. Westphal has noted that dermal armor evolves to serve three functions for placodonts. These are: (1) stability; (2) mobility; and (3) streamlining. Stability is achieved by either deviation from the primitive hexagonal outline to form rhombic osteoderms; by the non-correspondence of epidermal scales; or by the development of interconnected mineralized fibers between individual osteoderms. Mobility is achieved by the development of gliding surfaces between individual osteoderms; osteoderm elongation; or by the alignment of osteoderms

in rows. Streamlining is achieved by the formation of keels. All these characteristics are also present in the Glyptosaurinae to one extent or another, and are of the utmost importance in determining the functional morphology and phylogenetic relationships of the genera with this subfamily.

The theory that a non-tuberculate shieldlike dermal armor with large epidermal laminae impressions upon it in the lizards is primitive for anguids has been based in part on the fact of its presence in the oldest known fossil anguid *Odaxosaurus* (*Pancelosaurus* of Meszoely, 1970; see Meszoely Estes and Haubold, 1978) as well as the fact that enlarged epidermal shields (often impressed on a relatively smooth osteodermal layer when the latter is present) are widely distributed in autarchoglossans, being absent only in *Xenosaurus*, *Heloderma*, the Glyptosaurini, and advanced varanoids. If the tuberculate nature of glyptosaurine osteoderms and the possession of small, discrete, unfused hexagonal dermal armor is thought of as being primitive rather than a derived character state, the problem of the nearly identical morphology of the epidermal scale impressions on the dermal bone in anguids, as compared with the condition in the scincomorphs, would then have to be explained as a parallel character and would not be of extreme importance in linking these groups of squamates, which seems unlikely. Rather, it appears that the primitive hexagonal dermal bone unit, as seen in the glyptosaurines, with its tuberculate morphology, is a derived character state within the Anguidae and is interpreted to have arisen through the evolutionary process of neoteny, resulting in a pedomorphic subfamily.

The dermal armor shield, that lies under the epidermal frontal scales seen in both Oligocene and Recent specimens of the scincomorph *Eumeces* (personal observ.) is made up of a network of small, partially fused, hexagonal osteoderms. A complex of larger hexagonal osteoderms is seen in the Helodermatidae (i.e., *Heloderma*) and, of course, this similar morphology is present in the Glyptosaurini.

The epidermal scale impressions seen in the earliest anguid, *Odaxosaurus*, probably had no bearing on the neotenic break-up of the dermal

armor in the Glyptosaurini, into discrete hexagonal units. More likely, this break-up was induced in the dermal armor with the overlying epidermal scale thus changing their morphology to conform on a one-to-one relationship with the individual osteoderm. Meszoely (1970, p. 141) stated that *Arpadosaurus* (fig. 20) represents a structural intermediate between *Melanosaurus* and *Glyptosaurus* (*sensu lato*) that it "is conceivable that further subdivision of the osteoscutal crust (frontal and parietal dermal armor) could have led to the situation encountered in *Glyptosaurus*, in which numerous polygonal osteoscutal plates cover the frontal and other cranial bones." I cannot agree with this suggestion as the epidermal impressions in *Arpadosaurus* are too irregular in shape to derive the uniform hexagonal pattern seen in the Glyptosaurini.

The tribe Melanosaurini is more conservative in terms of neoteny and retains the more primitive anguid characters seen in *Odaxosaurus*. On the other hand, the tribe Glyptosaurini underwent what appears to have been an accelerated neoteny that resulted in a highly specialized lizard in terms of its skull morphology. A phylogeny of the evolution of the dermal armor, without regard to the epidermal sculation patterns, is presented for the Scincomorpha and the Anguimorpha (fig. 24).

Besides the dermal armor morphology seen within the two tribes of the Glyptosaurinae, one would expect to see the more primitive conditions in genera that possess the least amount of skeletal fusion. However, among the Melanosaurini, based on frontal morphology, the most primitive genus is questionable, as noted above, due to the fact that the genera belonging to this tribe are conservative in the retention of the primitive anguid frontal morphology seen in *Odaxosaurus piger*. Likewise, the fused frontal condition seen in the early Eocene genera *Eoglyptosaurus* and *Paraglyptosaurus* is also considered to be primitive for the Glyptosaurini, but these genera are derived in their dermal armor morphology.

Glyptosaurus and *Helodermoides* possess separate frontals and are considered to be representative of a primitive condition, but are secondarily derived from the fused condition seen

in *Eoglyptosaurus* and *Paraglyptosaurus*. Stratigraphically, the primitive paired frontal state in the later two glyptosaurinid genera appears later in time (upper Wasatchian-Orellan), whereas the fused frontal condition is well represented in the lower Wasatchian genera of both tribes.

Glyptosaurus has a less bulbous tooth type (associated with unfused frontals) when compared with *Eoglyptosaurus* and *Paraglyptosaurus*, which are stratigraphically lower or coeval to *Glyptosaurus* and *Helodermoides*, which are even later in time, and are structurally the most primitive glyptosaurinids in: (1) increased number of rows of osteoderms between the orbits of the frontals (the lower Eocene-middle Eocene glyptosaurinids have typically five rows of hexagonal osteoderms running anteroposteriorly between the orbits, whereas *Helodermoides tuberculatus* has six to seven rows in this region); (2) non-fusion of posterior mandibular elements; (3) non-fusion of dermal armor to underlying bone (a trend can be seen in the type of *G. sylvestris* (fig. 3a); and (4) sharp, subconical, recurved teeth, with very weak striations when present. *Helodermoides* is more derived than *Glyptosaurus* and other glyptosaurines in: (1) gigantism; (2) loss of the tubercular concentric ring pattern on the osteoderms (which is absent in the Melanosaurini); and (3) closure of the supratemporal fenestrae.

Paraglyptosaurus is more derived than *Eoglyptosaurus* being more robust than the latter, in having large bulbous crushing teeth and curved maxilla. In the tribe Melanosaurini, *Arpadosaurus* is more derived than *Melanosaurus* in having a similar robust tooth type, but *Melanosaurus* is more derived than *Arpadosaurus* in the absence of a sutural scar from the recent fusion of the frontal dermal armor shields. *Peltosaurus* seems to have been derived from *Xestops* (Meszoely, 1970; Meszoely, Estes and Haubold, 1978).

PAEDOMORPHOSIS AND FUNCTIONAL MORPHOLOGY OF THE GLYPTOSAURINI AND THE PHYLOGENETIC IMPLICATIONS: The Glyptosaurini and the Melanosaurini are very similar in regard to their adaptations. This similarity has resulted from a common ancestor, but divergent morphologic trends of the Glyptosaurini

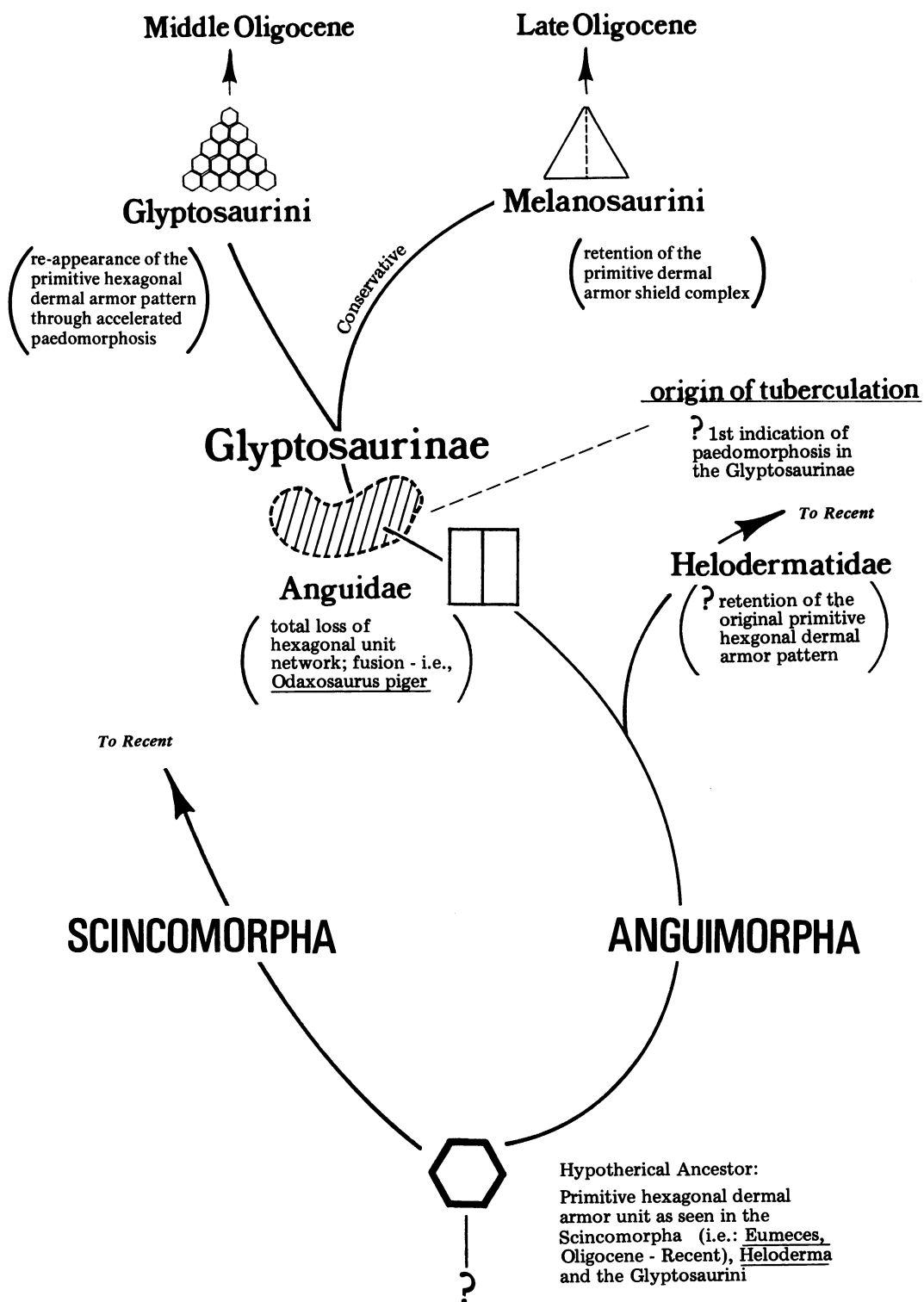


FIG. 24. Proposed evolutionary sequence of the development of the dermal armor morphology in the Glyptosaurini due to pedomorphism. The dermal armor sculpture for the frontal bone(s) are schematically illustrated for the primitive anguid (*Odaxosaurus*) as well as the morphotypes for the Glyptosaurini and Melanosaurini. Figures not drawn to scale.

that include (1) non-fusion of cephalic hexagonal osteoderms; (2) non-fusion of dermal armor to the underlying bone; (3) non-fusion of the frontals; (4) eventual acquisition of the sharp, subconical, slightly recurved tooth type; (5) the general absence of frontal constriction above the orbit; and (6) primitive head shape in *Helodermoides*, suggests that this tribe represents a lineage that progressively shows paedomorphic trends. The loss of the tuberculate concentric pattern seen in the youngest glyptosaurinid *Helodermoides* as well as the absence of this pattern in the hexagonal cheek osteoderms in the Melanosaurini and the apparent trend toward an increase in size, may be regarded as parallel development among the two tribes of the Glyptosaurinae.

The tribe Glyptosaurini, by virtue of its characteristic hexagonal dermal armor covering the entire skull, displays a number of character states documented through time, that offers a look at one of the best evolutionary sequences within a lineage that strongly suggests paedomorphosis. I will first summarize these additional paedomorphic character states. They are as follows:

1. Non-fusion of cephalic hexagonal osteoderms. As I have stated above, I believe that fusion of individual osteoderms to form larger dermal units is normally a derived character. This theory is further supported by the fact that a number of specimens of *Helodermoides* display osteoderms that have apparently fused to adjacent ones. *Arpadosaurus* (fig. 20a) displays a sutural scar along the midline of the frontal dermal armor that apparently indicates that primitively the condition was to develop separate dermal armor shields that covered each frontal.¹ The fact that the cheek region of *Ar-*

padosaurus bears the typical hexagonal osteoderms as in the Glyptosaurini and that these were present in *Xestops* species and *Melanosaurus* also supports the theory that these smaller hexagonal dermal armor units are primitive. However, the stratigraphic sequence in the fusion of osteoderms is the reverse of what would be expected if the condition of the small hexagonal dermal armor units are a primary primitive state. The fact that the number of rows of dermal armor units on the frontals between the orbits of the Glyptosaurini is the greatest in *Helodermoides*, the youngest genus stratigraphically, suggests that this break-up into smaller units is paedomorphic.

2. Non-fusion of dermal armor to the underlying bone. Members of both tribes show that there is a general tendency for the fusion of the dermal armor to the underlying bone particularly on the frontal and parietal. Fusion of dermal armor on *Helodermoides* to the frontal and parietal is rarely the case (fig. 25) and when fusion appears to occur in this genus, it is the result of post-diagenetic causes. *Glyptosaurus* displays an intermediate state of fusion of dermal armor to underlying bone as do some specimens of *Paraglyptosaurus* (notably the parietal of USNM 6004, (fig. 4c). The two known specimens of *Eoglyptosaurus* show fusion as do all known specimens of the Melanosaurini. Again it appears that *Helodermoides*, and to a lesser degree *Glyptosaurus*, may be regarded, along with the other members of the Glyptosaurini, as paedomorphic.

3. Non-fusion of the frontals. The primitive condition in lizards and reptiles in general is the retention of separate (paired) frontal bones. The frontals are characteristically separate in *Helodermoides* and *Glyptosaurus*, and usually in *Xestops* as well, although fusion of frontals has been reported in the European *Xestops stehlini* (Meszoely, Estes and Haubold, 1978). As previously mentioned, frontal fusion occurs in the earliest glyptosaurinids (*Eoglyptosaurus* and *Paraglyptosaurus* of the lower Wasatchian)

¹Jacques Gauthier has recently shown me a number of *Melanosaurus-Arpadosaurus*-like forms from the Willwood Formation (Wasatchian), that show various stages of frontal fusion. The specimens also lack well defined epidermal scutellation impressions, as seen in the type of *Arpadosaurus*; rather, exhibit different degrees of impressions. This may indicate that frontal fusion may occur later in ontogeny in *Melanosaurus* and *Arpadosaurus* and that the distinctiveness of the epidermal scales impressions may not, in this case, be taxonomically useful in designating genera. I suspect that the apparent variation of scale impressions could be correlated, generally, to the size of the individual; the larger melanosaurinid being more apt to

display well-defined epidermal scale impressions on the skull roofing dermal armor. Preservation of the specimen itself is undoubtedly a factor in observing this feature. The type *Melanosaurus* does display very faint epidermal scale impressions near the interparietal region of the frontal (personal observ.).

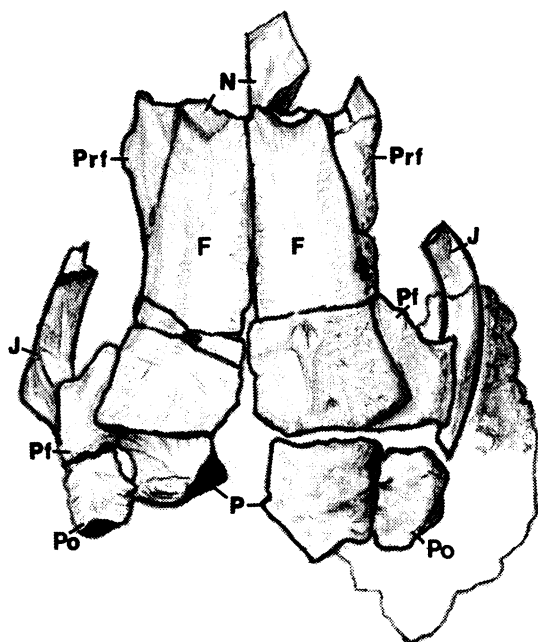


FIG. 25. Dorsal view of skull of *Helodermoides tuberculatus* Douglass (UNSM 4511) showing the absence of dermal armor due to non-fusion of osteoderms to the frontal and parietal bones.

Abbreviations: F., frontal. J., jugal. N., nasal. P., parietal. Pf., postfrontal. Po., postorbital. Prf., prefrontal.

as is with the Melanosaurini save for *Xestops vagans*. The oldest known occurrence of the separate frontal condition is in a specimen of *Glyptosaurus sylvestris* from the Upper Wasatchian (Gardner Butte Member) (fig. 4a and b). Again this reversal to a primitive condition seems best interpreted as a paedomorphic trend.

4. Acquisition of the sharp, subconical, slightly recurved tooth type. Romer (1956) recognized that the primitive tooth type seen in earlier lepidosaurs is that of the simple, conical, pointed, somewhat recurved and essentially isodont type. This is the type seen only in the Oligocene glyptosaurine, *Helodermoides tuberculatus*. All other glyptosaurines display variations of the obtuse tooth type, where the teeth are somewhat swollen, more robust, and with striations confined to the crown. Various degrees of this obtuse tooth type are seen in all

the glyptosaurines and the earliest anguid, *Odaxosaurus*, making it virtually impossible to assign any particular dentary or maxillary fragment to a specific genus.

Despite the fact that the majority of the specimens of *Helodermoides* exhibit the "primitive" toothed condition some large specimens, i.e., UNSM 12100, display traces of striations confined to the crowns of the teeth as well as exhibiting a blunter condition, but not so extreme as that seen in the earlier Eocene genera, and is probably the result of attaining a large size. This later acquisition of the sharp tooth type is viewed as secondarily primitive and is paedomorphic.

5. Constriction of frontals. The constriction of frontals is best seen among living lizards. In the Glyptosaurinae it appears in both tribes, but seems to be more pronounced in the Melanosaurini, with the exception of *Xestops*. In the Glyptosaurini, slight constriction is seen in the fused frontal genera *Eoglyptosaurus* and *Paraglyptosaurus* and appears to be more pronounced in the Asian *Helodermoides mongoliensis*. *Helodermoides tuberculatus* differs strongly from its Asian cousin in this regard. Again the character of constricted frontals in lizards is normally viewed as being derived, and is widely distributed among the oldest known glyptosaurines. The later form, *Helodermoides tuberculatus*, displays a seemingly wider, primitive frontal with no evidence of frontal constriction and therefore appears to be paedomorphic.

6. Primitive head shape. The skull of *Helodermoides tuberculatus* when compared to the skull of *Eoglyptosaurus donohoei* appears to be more primitive in that the former is "highly vaulted," having a short face in comparison to the latter. Romer (1956) considered this shorter face type as the primitive reptilian skull type, and is viewed here as another indication of paedomorphosis.

Three other character states, not attributable to a neotenic process in the Glyptosaurinae include the apparent trend toward gigantism, the loss of the concentric ring patterns of tubercles on individual osteoderms and the closure of the supratemporal fenestrae.

McDowell and Bogert (1954) regarded the

apparent increase in size, or gigantism, in *Glyptosaurus* (*sensu lato*) as a derived condition. The Glyptosaurinae, as a whole, are represented by a number of large forms, and are larger than any members of the Recent subfamilies, only approached by a few species of *Diploglossus* and *Ophisaurus*. Most of the glyptosaurines were large, having skull lengths of about 100 mm. in *Helodermoides tuberculatus*, 100 mm. in *Paraglyptosaurus*, 80 mm. in *Eoglyptosaurus* and probably 80 to 100 mm. in *Glyptosaurus*. The known species among the Melanosaurini are not as large as those in the Glyptosaurini, and probably reached a maximum skull length of 90 mm. based on known material. Some of the oldest melanosaurinids display a large size and these include only *Melanosaurus* and *Arpadosaurus*. *Xestops* and *Peltosaurus* are typically small, not much larger than some large species of *Gerrhonotus*, around 37 mm. in skull length.

The loss of a tuberculate concentric pattern would be viewed by Tarlo (1967) as an advanced character state because this would suggest the prior fusion of the individual hexagonal dermal armor units and the obliteration of suture between these units exhibiting only a continuous surface with relatively evenly spaced tubercles. The concentric pattern is primitively absent in the Melanosaurini, as might be expected, by virtue of the frontal and parietal dermal armor morphology in this group. The concentric pattern is seen in the oldest known members of the Glyptosaurini, *Eoglyptosaurus* and *Paraglyptosaurus*, as well as in the genus *Glyptosaurus* and is considered primitive by me for that tribe but derived for the subfamily. The condition is again later lost in *Helodermoides*. This loss is viewed as an advanced character state obtained independently in the Glyptosaurini as a result of parallelism as the nearest ancestral group, the Melanosaurini already show that this character is lost, or more appropriately, never acquired.

The loss of the concentric pattern in tuberculate dermal armor probably results from the increasing number of tubercles per dermal unit. It is possible to conjecture that even a more advanced condition would be a continuation of tubercle crowding, resulting then in a pit and

ridge condition to the individual tubercles to adjacent tubercles. This osteoderm morphology is seen in Recent *Heloderma* and a similar type in the Cretaceous *Odaxosaurus*, although the latter is represented by diminutive dermal sculpture.

The closure of the supratemporal fenestrae in the glyptosaurinid *Helodermoides* is a derived character, appearing only in this glyptosaurine genus. Supratemporal fenestrae are open in *Peltosaurus* and *Eoglyptosaurus* and apparently were open in *Paraglyptosaurus*, *Glyptosaurus*, *Melanosaurus*, *Arpadosaurus*, and *Xestops* based on parietal shape in relation to the squamosal bones. This closure may have occurred in response to the paedomorphic head shape in *Helodermoides*. This character state is viewed, however, as being derived, not as paedomorphic.

DISCUSSION: Unlike most fossil animal groups, the Glyptosaurinae seem to present a number of characters, that when viewed in the proper context, seem to indicate a well-documented case for the occurrence of paedomorphosis through time. While many of the characters may seem interrelated, possibly forming a "complex" or "character suite" such as the de-ossification of the skull, linked with the separation of the dermal armor from the underlying bone, linked with frontal separation, etc., I believe, however, that this lizard subfamily and particularly the tribe Glyptosaurini, offers one of the best documented evolutionary sequences of neoteny in a fossil vertebrate group.

Neoteny has also been noted in lizards by Stephenson (1960) and Kluge (1967) as the mechanism for the separation of the parietal in some of the Gekkonidae genera. However, Moffat (1973), has rejected the use of these and other paired skull bones in her taxonomy, as there is sufficient doubt that one can emphatically state whether the paired condition is truly primitive or that it is secondarily derived as we have seen in the above discussion of the Melanosaurini. I believe, however, that there is sufficient evidence to support the theory of frontal separation as being paedomorphic in the Glyptosaurini.

Reasons for apparent neoteny within a lineage may at best be speculative. However, as

Gould (1977, p. 344) pointed out that in “neoteny, K- selected trends are ‘rescued’ from over specialization,” which he believes is due primarily to “the linking of retarded somatic development with the delay in maturation.” Maturation among the Glyptosaurinae is best observed in the fusion of the epiphyses to the long bones. I have observed within the glyptosaurines, where the long bones are preserved (usually humeri), that the epiphyses are not fused to these bones. Only in the very largest specimens of *Helodermoides* is there any indication of epiphyses fused to the long bones (i.e., UNSM 12100) and thus, suggesting at the very least, sexual maturity. Although sexual maturity, within a fossil group cannot be proven with certainty, it probably occurred, in the case of the Glyptosaurini, before epiphysial fusion.

At the outset of the Eocene there were a number of glyptosaurine genera (*Xestops*, *Melanosaurus*, *Arpadosaurus*, *Eoglyptosaurus*, and *Paraglyptosaurus*) that virtually all have

similar skull morphology including dentition. Neoteny, used as a divergent strategy, changed the functional morphology of the skull in the tribe Glyptosaurini to that of a more flexible type.

SUMMARY

A number of characters exhibited in the Glyptosaurini, found in particular in the genus *Helodermoides*, seem to be primitive but may best be viewed as secondarily derived. The degenerate nature of this group points to the possibility that the lineage may be pedomorphic based on the primitive characters and their late appearance in the geologic record. These characters are: (1) non-fusion of cephalic hexagonal osteoderms; (2) non-fusion of dermal armor to the underlying bone; (3) non-fusion of the frontals; (4) acquisition of the sharp, subconical, slightly recurved teeth; (5) general absence of frontal constriction above the orbit; and (6) primitive head shape.

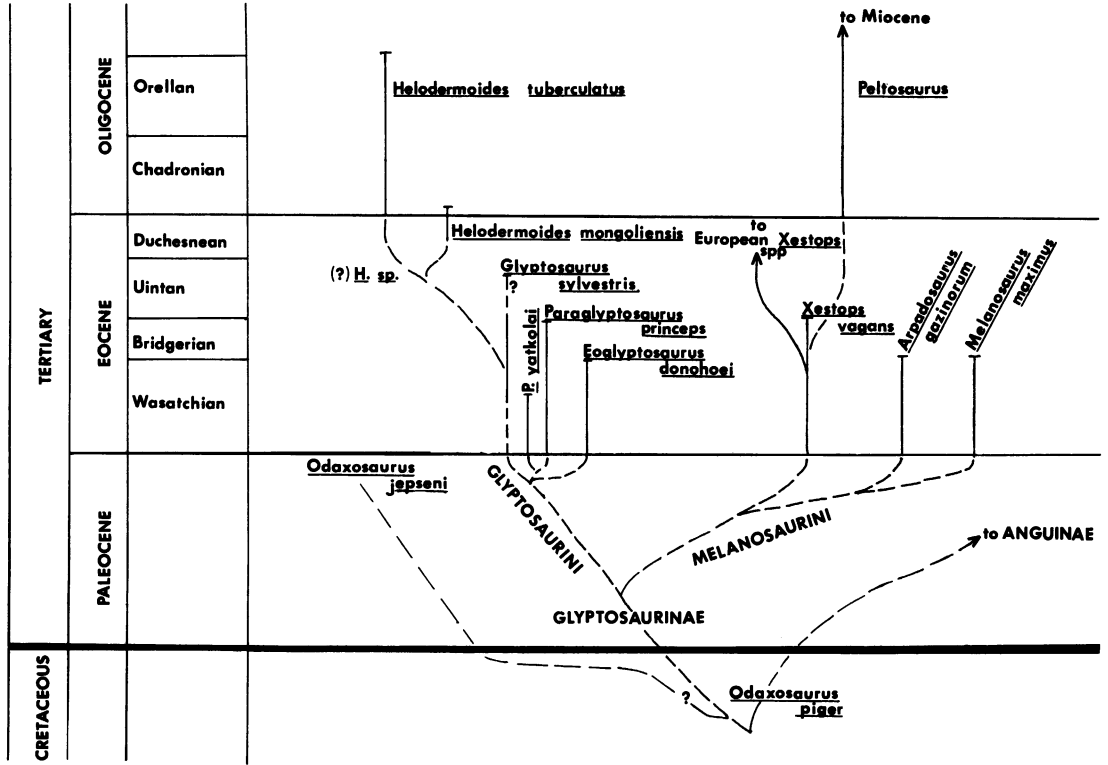


FIG. 26. Phylogeny of the Glyptosaurinae.

The Glyptosaurini are divergent from the Melanosaurini in their increase in size through time. The loss of the concentric ring pattern of tubercles in the youngest member of the Glyptosaurini, *Helodermoides*, may be regarded as a derived character as well as the closure of the supratemporal fenestrae.

Given the fact that the geologic record shows the increasing number of primitive characters among the tribe Glyptosaurini through time, the phylogeny presented in figure 26 best indicates the paedomorphic nature of this tribe and its relation to the other fossil anguids in the tribe Melanosaurini.

PALEOECOLOGY AND EXTINCTION

Little has been written about the paleoecological relationships of the glyptosaurines. I have already briefly covered some aspects of *Helodermoides tuberculatus* in regard to morphology and extinction (Sullivan, in press); there are, however, additional aspects that may be noted here.

EOCENE GLYPTOSAURINES

Representatives of both tribes of the Glyptosaurinae are well established at the outset of the Eocene Epoch. Members of the tribe Melanosaurini represented in the lower Eocene deposits of North America include *Xestops*, *Melanosaurus*, and *Arpadosaurus*, whereas the Glyptosaurini is represented by *Eoglyptosaurus*, *Glyptosaurus* and *Paraglyptosaurus*.

The Eocene glyptosaurines are known to have a simple obtuse tooth type that varies in degree of robustness in different genera. This character state is best seen in *Paraglyptosaurus* and *Arpadosaurus*, and the teeth are particularly robust in the posterior region of the dentary and the maxilla. The other Eocene glyptosaurines have moderately obtuse teeth. In some specimens of *Paraglyptosaurus princeps*, notably AMNH 1619 (fig. 5c and d), the dentary and maxilla seem to display a heterodont condition. The obtuse tooth type seems to be partly correlated to body size. However, the appearance of the obtuse blunt crushing type in small species is not uncommon, as in an undescribed specimen of cf. *Xestops* (CM 8701) (see fig. 22b).

The Eocene in North America was a time of equable tropical conditions (Wolfe, 1975). It was during this time that these early obtuse toothed glyptosaurines flourished, probably in response to the diverse prey items. The tooth morphology of these early glyptosaurines sug-

gests, based on lizard dentition studies by Hottel (1955), a diet consisting primarily of land molluscs which occurred frequently throughout the Eocene and Oligocene of North America. The fused frontal bones and the dermal armor in the early Eocene Glyptosaurini and the presence of the extensive coossified dermal armor complex coupled with the shieldlike epidermal scales seen in the Melanosaurini may be correlated with the presence of this obtuse crushing tooth type. The robustness of the mandible and the curvature of the maxilla in the glyptosaurines with fused frontals seems to be the direct result of the accommodation of their huge crushing teeth, which with the highly fused skull appears to have been adapted for ingestion of hard carapaces or shells. The apparent paedomorphic trend away from the fused frontal and large obtuse tooth type, seen in *Glyptosaurus* and later in *Helodermoides*, is probably a strategy to diversify the diet in response to climatic changes that may have effected available prey items.

OLIGOCENE GLYPTOSAURINES

By contrast, the late Eocene was marked by a cooling trend that continued through the Oligocene (Wolfe, 1975). This Oligocene deterioration resulted in a more arid and less equable climate (Wolfe, 1971). It was in this later temperate environment that *Helodermoides tuberculatus* and *Peltosaurus* thrived.

Peltosaurus is currently recognized by two species: *P. abbotti* and *P. granulosus* (see Meszely, 1970). It is the only representative of the Melanosaurini found in post-Eocene deposits and is confined to the Oligocene of North America (Holman, personal commun., 1977). *Helodermoides tuberculatus* is the sole representative of the tribe Glyptosaurini in the North

American Oligocene. While *Peltosaurus* does not seem all that different from its presumed ancestor *Xestops* (Meszoely, Estes and Haubold, 1978), *Helodermoides tuberculatus* appears to be more divergent from its Eocene ancestor *Glyptosaurus*.

As noted above, *Helodermoides tuberculatus* is characterized by separate frontals; closure of the supertemporal fenestra; highly vaulted skull; sharp, conical, somewhat recurved teeth; and overall lack of coossification of dermal armor. It is clear, based on tooth type, that *Helodermoides tuberculatus* did not feed on molluscs as did its Eocene predecessors. Rather, *Helodermoides tuberculatus* was carnivorous and probably preyed upon small mammals such as rodents and insectivores or may have been a scavenger, feeding on carrion. Fusion of frontals and dermal armor with the overlying epidermal shields, as seen in the Eocene mollusc-eating glyptosaurines, is unnecessary for this type of diet so that we see, through neoteny, a reduction of coossification and change in skull morphology through time.

DISTRIBUTION AND PALEOBIOGEOGRAPHY

Anguid lizards are presently known from North and South America, Europe, western North Africa, eastern Asia and southeast Asia. Fossil anguids are known from both Europe, Asia, and North America. Until recently, the European and North American fossil anguid lizard faunas were recognized as different genera. However, Depéret (1917), Gilmore (1928), Kuhn (1940), and McDowell and Bogert (1954) have suggested that the genus *Glyptosaurus* and its European relative *Placosaurus* may be synonymous. This then implies a migration route between the Old and the New World in order for this lizard to be present in both regions. Although the synonymy of *Placosaurus* and North American forms may never be resolved, as noted above, evidence for migration of both the melanosaurinids and glyptosaurinids is unquestionable. The recent recognition of *Xestops* in Europe (Meszoely, Estes and Haubold, 1978) suggests a rapid dispersion of this primitive glyptosaurine genus and probably others.

McKenna (1975) has presented evidence of an early Eocene land continuity between North America and Europe (the De Geer Route) which connects these two land masses through the Arctic Circle. Recent discoveries of vertebrate fossils from the Eureka Sound Formation of Ellesmere Island (Dawson et al., 1976) support this theory of a major migration route during Wasatchian times. The presence of anguids in the fauna, most probably glyptosaurines (Estes and Hutchison, 1978), indicates that this was also the route followed by these lizards.

Meszoely, Estes and Haubold (1978, p. 165) have suggested a North American origin for the Glyptosaurinae based on the numerous specimens found on that continent. My study lends support to this theory. Despite the known occurrence of the tribe Glyptosaurini in Europe and Asia it seems to have been more diversified in North America and its members are more common in the Eocene deposits than those of the Melanosaurini.

EXTINCTION

Causes for extinction are virtually always expressed as the inability to adapt to changing environments. This is the most acceptable hypothesis for the mass extinction of the diverse genera of glyptosaurines by the end of the Bridgerian in North America. Glyptosaurines were present through the late Eocene of Europe (Hoffstetter, 1962b; Meszoely, Estes and Haubold, 1978). There is no record of Oligocene glyptosaurines outside North America, and the only genera present during this time were *Helodermoides* and *Peltosaurus*. The extinction of six North American glyptosaurine genera by the end of the Bridgerian (save for the possible occurrence of *Glyptosaurus* in the Uintan) is striking. It appears that this major extinction of these glyptosaurines coincides with the climatic fluctuations that occurred in the late Eocene times. The later extinction of the Oligocene *Helodermoides* and *Peltosaurus* may possibly have been the result of continued climatic fluctuations.

Osteoderms reported by Estes and Tihen (1964) from the Valentine Formation (upper

Miocene) have served to extend the range of the subfamily Glyptosaurinae to that time. I and Richard Estes (personal commun.) are now of the opinion that these osteoscutes may be referable to the gerrhonotine *Gerrhonotus mungerorum* of the lower Pliocene (Wilson,

1968). The last positive occurrence of *Peltosaurus* and *Helodermoides* is from the Whiteneyan and Orellan deposits, respectively. However, these osteoderms may indeed belong to some member of the Glyptosaurinae.

SUMMARY

1. *Glyptosaurus* (*sensu lato*) Marsh, 1871 is interpreted as including four genera: *Glyptosaurus* (*sensu stricto*) Marsh, 1871, *Helodermoides* Douglass 1903, *Paraglyptosaurus*, new genus and *Eoglyptosaurus*, new genus.

2. *Glyptosaurus* (*sensu stricto*) is represented by the single species *G. sylvestris*, with *G. nodosus* placed into its synonymy.

3. *Helodermoides tuberculatus* Douglass, 1903 is resurrected and includes as its synonyms *Glyptosaurus montanus* Douglass, 1903 and *Glyptosaurus giganteus* Gilmore, 1928.

4. *Paraglyptosaurus princeps*, new genus (Marsh, 1872) includes as synonyms *Glyptosaurus rugosus* Marsh 1872 and *Glyptosaurus hillsi* Gilmore, 1928.

5. *Glyptosaurus donohoei* White, 1952 is placed in a new genus *Eoglyptosaurus*.

6. The following taxa are recognized as being *nomina dubia*: the European Eocene *Placosaurus rugosus* 1852 and *Placosaurus waltheri* (Weigelt, 1929), and *Placotherium waltheri* (Weigelt, 1929); the North American *Glyptosaurus sphenodon* Marsh, 1872 and *G. obtusidens* Loomis, 1907.

7. Two tribes are recognized in the subfamily Glyptosaurinae based on dermal armor morphology. The Glyptosaurini, which includes *Glyptosaurus*, *Helodermoides*, *Paraglyptosaurus*, and *Eoglyptosaurus*, possess cephalic dermal armor in the form of discrete hexagonal osteoderms. The Melanosaurini, which include *Xestops*, *Melanosaurus*, *Arpadosaurus*, and *Peltosaurus*, possess dermal armor in the form of flattened coossified dermal shields over the frontal and parietal as well as smaller shield units that cover the muzzle region of the skull; both groups have identical body armor in the form of overlapping rectangular osteoderms.

8. The Glyptosaurinae is viewed as the most primitive of the four anguid subfamilies based on characters noted by McDowell and Bogert (1954) and Meszoely (1970).

9. The Gerrhonotinae show a number of character states similar to the Glyptosaurinae but are slightly more derived.

10. The Diploglossinae and the Anguinae are the most derived based on the characters noted by Meszoely (1970).

11. *Odaxosaurus* (*Pancelosaurus* of Meszoely, 1970) is removed from the subfamily Anguinae because of its many primitive character states and designated as Anguidae: *incertae sedis*.

12. The appearance of tuberculate dermal armor in the Glyptosaurinae may indicate the first appearance of a paedomorphic character based on the primitive nature of this structure as suggested by Tarlo (1967).

13. Based on studies by Camp (1923), McDowell and Bogert (1954), Tarlo (1967), and Westphal (1976) the hexagonal dermal armor seen in the tribe Glyptosaurini is derived because of its late appearance in the Anguidae, and may be a paedomorphic reversal to more primitive lizard scale-osteoderm relationship.

14. The tribe Melanosaurini has larger dermal armor shields with enlarged epidermal shields impressed upon them, as in other anguids (save for the Glyptosaurini) and the scincomorphs, and thus is viewed as the more conservative tribe in retaining this squamation condition.

15. Of the Glyptosaurini, *Helodermoides* is the youngest and yet the most primitive genus; *Glyptosaurus* is stratigraphically older and not so primitive, but is younger and more primitive than *Paraglyptosaurus* and *Eoglyptosaurus*.

This reverse stratigraphic appearance of the primitive characters suggests that the tribe Glyptosaurini shows a trend toward increasing paedomorphism through time.

16. Of the Melanosaurini, *Peltosaurus* appears to be the most derived member. *Arpadosaurus* is more derived than *Melanosaurus* and *Xestops* in the development of heterodont dentition. *Melanosaurus* or *Xestops* can be considered equally primitive.

17. The major extinction of the obtuse-

toothed glyptosaurines that occurred at the end of the Bridgerian Age in North America presumably was the result of the climatic shift from the equable tropical climate to the less equable arid warm temperate climate. The extinction of the Oligocene glyptosaurines was probably the result of continuing climatic deterioration. The occurrence of osteoderms from the Valentine Formation (upper Miocene) of Nebraska is interpreted to belong to the gerrhonotine lizard *Gerrhonotus mungerorum*.

LITERATURE CITED

- Boulenger, M. G. A.
1918. Les Lézards Helodermatides de l'Éocène Supérieur de la France. *Compt. Rend. des Séances de l'Acad. des Sci., Paris*, vol. 166, pp. 889-893.
- Camp, Charles L.
1923. Classification of the lizards. *Bull. Amer. Mus. Nat. Hist.*, vol. 48, no. 11, pp. 289-481.
- Chow, Minchen.
1957. Remarks on *Placosaurus* (or *Glyptosaurus*) of China. *Vert. Palis.* vol. 1, no. 2, pp. 155-157.
- Clark, John, J. R. Beerbower, and K. K. Kietzke
1967. Oligocene sedimentation, stratigraphy, paleoecology, and paleoclimatology in the Big Badlands of South Dakota. *Fieldiana, Geol. Mem.*, vol. 5, pp. 1-158.
- Cope, Edward D.
1877. Report on extinct vertebrates obtained in New Mexico by parties of the expedition of 1874. *U.S. Geol. Surv. West of 100th Meridian, Wheeler Rept.*, vol. 4, pp. 1-370.
- Dawson, Mary R., Robert M. West, Wann Langston, Jr., and J. Howard Hutchison
1976. Paleogene terrestrial vertebrates: Northemmost occurrence, Ellesmere Island, Canada. *Science*, vol. 192, no. 4241, pp. 781-782.
- Depéret, C.
1917. Monographie de la faune de mammifères fossiles du Ludien inférieur d'Euzet-les-Bains (Gard). *Ann. d'Univ. Lyon n.s.*, vol. 1, no. 40, pp. viii-288, pl. 1-25.
- Douglass, Earl
1903. New vertebrates from the Montana Tertiary. *Ann. Carnegie Mus.*, vol. 2, pp. 145-199.
1908. Some Oligocene lizards. *Ibid.*, vol. 4, pp. 278-281.
- Emry, Robert J.
1973. Stratigraphy and preliminary biostratigraphy of the Flagstaff Rim Area, Natrona County, Wyoming. *Smithsonian Contrib. Paleobiol.*, vol. 18, pp. 11-43.
- Estes, Richard
1964. Fossil vertebrates from the Late Cretaceous Lance Formation Eastern, Wyoming. *Univ. California Publ. Geol. Sci.*, vol. 49, pp. 1-187.
- Estes, Richard, and J. Howard Hutchison
1978. Eocene lower vertebrates from Ellesmere Island. *In* Abstracts with programs of the Geol. Soc. Amer. Vol. 10, no. 7, p. 398, August (abstr.).
- Estes, Richard, and Joseph Tihen
1964. Lower vertebrate from the Valentine Formation of Nebraska. *Amer. Midland Nat.*, vol. 72, no. 2, pp. 495-515.
- Gervais, Paul
1859. *Zoologie et paléontologie française*, 2nd ed. [N.p.], Paris. 544 pp., figs, atlas, 84 pls.
- Gilmore, Charles W.
1928. Fossil lizards of North America. *Mem. Natl. Acad. Sci.*, vol. 22, no. 3, pp. v-201.
1938. Description of new and little known fossil lizards from North America. *Proc. U.S. Natl. Mus.*, vol. 87, pp. 11-26.
1942. Paleocene faunas of the Polecat Bench Formation, Park County, Wyoming. Part II: Lizards. *Proc. Amer. Philos. Soc.*, 85:159-167.
1943. Fossil lizards of Mongolia. *Bull. Amer. Mus. Nat. Hist.*, vol. 87, pp. 361-384.
- Gould, Stephen Jay
1977. *Ontogeny and phylogeny*. Harvard Univ. Press, Cambridge, 487 + ix pp.
- Hecht, Max K.
1977. *Phylogenetic inference and methodology*

- as applied to the vertebrate record. *Evol. Biol.*, vol. 9, pp. 335-363.
- Hecht, Max K., and J. L. Edwards
1976. The determination of parallel or monophyletic relationships: The proteid salamanders—a test case. *Amer. Nat.*, vol. 110, no. 974, pp. 653-677.
- Hills, R. C.
1888. The recently discovered Tertiary beds of the Huerfano River Basin, Colorado. *Proc. Colorado Sci. Soc.*, vol. 3, pp. 148-164.
1889. Additional notes on the Huerfano beds. *Ibid.*, vol. 3, pp. 217-223.
- Hoffstetter, Robert
1962a. Observations sur les Ostéodermes et la classification des Anguïdés actuels et fossiles (reptiles, sauriens). *Bull. Mus. Nat. d'Hist. Nat.* 2nd ser., vol. 34, no. 2, pp. 149-157.
1962b. Revue des récentes acquisitions concernant l'histoire et la systématique des squamates. *Colloque Internat. Centre Nat. Recherche Sci.; Problèmes Actuels Paléotol.* (Évol. Vertébrés), vol. 104, pp. 243-278.
1964. Les sauria du Jurassique supérieur et spécialement les gekkota de Bavière et de Mandchourie. *Senck. Biol.*, vol. 45, no. 3/5, pp. 281-324.
1965. Les sauria (=Lacertilia) du Jurassique supérieur du Montsec (Espagne). *Bull. Soc. Geol. France*, vol. 7, pp. 549-557.
1966. Coup d'oeil sur les sauriens (=Lacertilien) des couches de purbeck (Jurassique supérieur d'Angleterre). *Colloque Internat. Centre Nat. Recherche Sci.; Problèmes Actuels Paléotol.* (Évol. Vertébrés), vol. 163, pp. 349-371.
- Hotton, Nicholas III
1955. A survey of adaptive relationships of dentition to diet in the North American Iguanidae. *Amer. Midland Nat.*, vol. 53, no. 1, pp. 88-114.
- Kluge, A.
1967. Higher taxonomic categories of gekkonid lizards and their evolution. *Bull. Amer. Mus. Nat. Hist.*, vol. 135, art. 1, pp. 1-59.
- Kuhn, Oskar
1940. Die Placosauriden und Anguinen aus dem Mittleren Eozän des Geiseltales. *Nova Acta Leopoldina*, vol. 8, no. 53, pp. 461-486.
- Leenhardt, F.
1906. À propos des edentés fossiles de France. *Bull. Soc. Geol. France*, vol. 4, p. 176.
- Loomis, F. B.
1907. Origin of the Wasatch deposits. *Amer. Jour. Sci.*, vol. 23, pp. 356-364.
- Love, J. D.
1960. Cenozoic sedimentation and crustal movement in Wyoming. *Amer. Jour. Sci.*, vol. 258, no. A, pp. 204-214.
- Love, J. D., Paul O. McGrew, and H. D. Thomas
1963. Relationship of latest Cretaceous and Tertiary deposition and deformation to oil and gas in Wyoming. *Contrib. Geol. Surv. Wyoming*, vol. 21, pp. 196-208.
- Marsh, Othniel Charles
1871. Notice of some new fossil reptiles from the Cretaceous and Tertiary formations. *Amer. Jour. Sci.*, vol. 1, no. 3, pp. 447-459.
1872. Preliminary description of new Tertiary reptiles, part 1. *Ibid.*, vol. 4, no. 3, pp. 298-309.
- McDowell, S. B., and C. M. Bogert
1954. The systematic position of *Lanthanotus* and the affinities to the anguimorphophan lizards. *Bull. Amer. Mus. Nat. Hist.*, vol. 105, pp. 1-142.
- McKenna, Malcolm C.
1975. Fossil mammals and early Atlantic land continuity. *Ann. Missouri Bot. Garden*, vol. 62, pp. 335-353.
- Mesozoely, Charles A. M.
1970. North American fossil anguoid lizards. *Bull. Mus. Comp. Zool.*, vol. 139, no. 2, pp. 87-149.
- Mesozoely, Charles A. M., Richard Estes, and Hartmut Haubold
1978. Eocene anguoid lizards of Europe and a revision of the genus *Xestops*. *Herpetologica*, vol. 36, pp. 156-166.
- Mesozoely, Charles A. M., and Richard L. E. Ford
1976. Eocene glass-lizard *Ophisaurus* (Anguidae) from the British Islands. *Copeia*, vol. 2, pp. 407-408.
- Mesozoely, Charles A. M., and Hartmut Haubold
1975. The status of the Middle Eocene Geiselthal limbless anguoid lizards. *Ibid.*, vol. 1, pp. 36-43.
- Moffat, Lynette A.
1973. The concept of primitiveness and its bearing on the phylogenetic classification of the Gekkota. *Proc. Linn. Soc. N.S.W.*, vol. 97, pt. 4, no. 32, pp. 275-301.
- Olson, Everett C.
1971. Vertebrate paleozoology. New York, John Wiley & Sons, 893 + xv pp.
- Radinsky, Leonard B.
1964. Notes on Eocene and Oligocene fossil lo-

- calities in Inner Mongolia. Amer. Mus. Novitates, no. 2180, pp. 1-11.
- Robinson, Peter
1972. Tertiary history. In William W. Mallory (ed.), Geologic atlas of the Rocky Mountain region. Rocky Mountain Assoc. of Geol., Denver, Colorado, pages 233-243.
- Romer, Alfred S.
1956. Osteology of the reptiles. Univ. Chicago Press, Chicago. 772 + xxi pp.
- Savage, Donald E.
1975. Cenozoic—the primate episode. Contrib. Primatol., vol. 5, pp. 2-27.
- Schatzinger, Richard A.
1975. Later Eocene (Unitan) lizards from the greater San Diego Area, California. Unpublished master's thesis. San Diego State Univ. 212 pp.
- Schultz, C. Bertrand, and T. M. Stout
1955. Classification of Oligocene sediments in Nebraska. Bull. Univ. Nebraska State Mus., vol. 4, no. 2, pp. 16-52.
- Stephenson, N. G.
1960. The comparative osteology of Australian geckos and its bearing on their morphological status. Jour. Linn. Soc., Zool., vol. 44, pp. 278-299.
- Strahm, Michael H., and Albert Schwartz
1977. Osteoderms in the anguid lizard subfamily Diploglossinae and their taxonomic importance. Biotropica, vol. 9, no. 1, pp. 58-72.
- Sullivan, Robert M.
[In Press] Dermal armor pathology in the tail of a specimen of *Helodermoides tuberculatus* (Reptilia, Anguidae, Glyptosaurinae). Herpetologica
- Tarlo, L. B. Halstead
1967. The tessellated pattern of dermal armor in the Heterostraci. Jour. Linnean Soc. (Zool.), vol. 47, no. 311, pp. 45-54.
- Weigelt, J.
1929a. *Loricotherium waltheri* nov. gen. nov. sp. ein altweltliches gurteltier aus der mitteleuropäischen braunkohle des Geiseltals. Jahrb. Hallesch. Verband., vol. 8, no. 1, pp. 5-31.
- 1929b. *Loricotherium waltheri* ist doch kein gurteltier, sondern eine gurtlelechte. *Ibid.*, vol. 8, no. 2, pp. 187-191.
- Westphal, F.
1976. The dermal armour of some Triassic placodont reptiles. In Morphology and biology of reptiles, Bellairs, A d'A. and C. Barry Cox, (eds.), Linnean Soc. London Acad. Press, Linn. Soc. Symposium ser. #3, pp. 31-41.
- White, Theodore E.
1952. Preliminary analysis of the vertebrate fossil fauna of the Boysen Reservoir area. Proc. U.S. Natl. Mus., vol. 102, no. 3296, pp. 185-207.
- Wilson, Richard L.
1968. Systematics and faunal analysis of a lower Pliocene vertebrate assemblage from Trego County, Kansas: Contrib. Mus. Paleontology Univ. Mich., vol. 22, no. 7, p. 75-126.
- Wolfe, Jack A.
1971. Tertiary climatic fluctuations and methods of analysis of Tertiary floras. Paleogeog., Paleoclimatol., Paleoecol., vol. 9, pp. 27-57.
1975. Some aspects of plant geography of the Northern Hemisphere during the Late Cretaceous and Tertiary. Ann. Missouri Bot. Garden, vol. 62, pp. 264-279.
- Wood, H. E., Ralph W. Chaney, John Clark, Edwin H. Colbert, Glenn L. Jepsen, John B. Reeside, Jr., and Chester Stock
1941. Nomenclature and correlation of the North American Continental Tertiary. Bull. Geol. Soc. Amer., vol. 52, pp. 1-48.
- Yatkola, Daniel A.
1976. Fossil *Heloderma* (Reptilia, Helodermatidae). Occasional Papers Mus. Natl. Hist. Kansas, vol. 51, pp. 1-14.

