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UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

**NEW RECORDS OF EARLY, MEDIAL, AND LATE CRETACEOUS LIZARDS
AND THE EVOLUTION OF THE CRETACEOUS LIZARD FAUNA
OF NORTH AMERICA**

A Dissertation

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

degree of

DOCTOR OF PHILOSOPHY

By

RANDALL LAWRENCE NYDAM

Norman, Oklahoma

2000

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AND THE EVOLUTION OF THE CRETACEOUS LIZARD FAUNA
OF NORTH AMERICA**

A Dissertation APPROVED for the
DEPARTMENT OF ZOOLOGY

BY

Ricci
Charles H. Ricci
Richard S. Ford
John D. Smith

PREFACE

This dissertation has been prepared as five chapters. Each of the five chapters has been or will be submitted for publication in either a refereed edited volume or a refereed journal for publication. The first chapter is formatted as a chapter for the book *Vertebrate Paleontology in Utah*, edited by David D. Gillette, Miscellaneous Publication 99-1 of the Utah Geological Survey, Salt Lake City. Chapters two through five are formatted for submission to the *Journal of Vertebrate Paleontology*; chapter 2 as a Rapid Communication (a format for expedited publication of reports of outstanding new discoveries, concepts, or interpretations) and chapters 3-5 as articles.

ACKNOWLEDGMENTS

The work for this dissertation began in the summer of 1992, prior to my enrollment at the University of Oklahoma, when I first joined Dr. Cifelli in Utah for several weeks of fieldwork in the Cedar Mountain Formation. It is to Dr. Richard Lawrence Cifelli that I owe a great debt of gratitude as I complete this dissertation program. Not only did he serve as my advisor for this project, but he also went out of his way on numerous occasions to assist me during my development as a vertebrate paleontologist. There is insufficient space to mention all of the ways in which he helped and guided, but some include financial assistance for laboratory and field work; patient instruction of many concepts of paleontological science, paleontological field work, and professional relationships. He also provided me several opportunities to lead my own expeditions in Utah and Oklahoma.

The other members of my advisory committee also deserve recognition. Dr. Nicholas J. Czaplewski has an encyclopedic knowledge of vertebrate osteology and an unending reserve of patience and good humor. Nick is by far one of the best and most genuine persons that I have met during my several years in academia. Dr. Laurie J. Vitt is an accomplished herpetologist and an excellent source of discussion and debate and provided me with many useful critiques of my work. Dr. Gary D. Schnell is the consummate editor and made time in what can only be described as very full schedule to review my work and suggest many useful revisions. Dr. Charles W. Harper provided a number of educational comments on systematics.

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I would like to finish by recognizing those people who were and are my most valued supporters. My wife Kathy and our two children, Cory and Samantha, are the

focus and balance to my life. It is through their love, encouragement, and patience that I have been able to accomplish all that I have. I am certain that I would not have finished this work were it not for Kathy's amazing patience and encouragement to continue when it seemed that to do so was futile. Also, my parents, Russell and Joy Nydam, have always been staunch supporters of my abilities and their belief in me has been a constant source of strength. I can't thank them enough for all they have done. Paul and Diane Thomas, my father and mother in-law have also been very supportive over the years and have become a valued part of my life.

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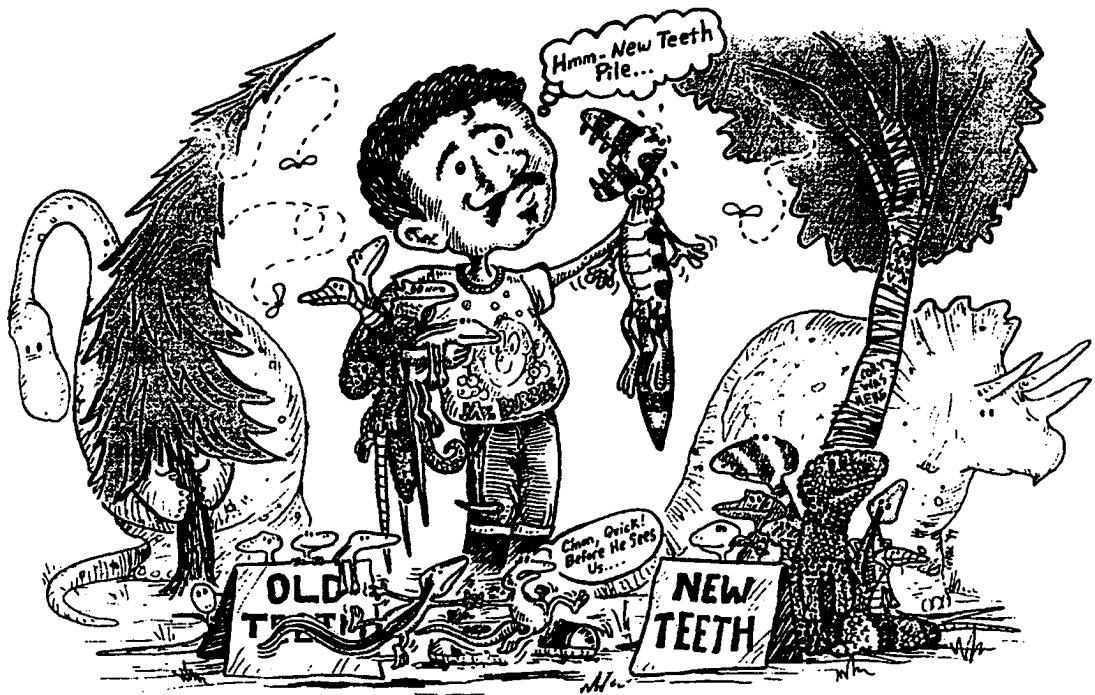
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ABSTRACT

The record of Mesozoic lizards has, for many years, consisted of records of primitive lizards from the Late Jurassic and derived lizards from the Late Cretaceous. The intervening time period has almost no record of lizards, with the exception of a brief report of lizards from the Early Cretaceous of Texas. This investigation includes lizards recovered from microvertebrate faunas of the Early Cretaceous (Albian-Cenomanian) Antlers and Cloverly formations of Oklahoma, and, Montana and Wyoming (respectively), the medial Cretaceous (Albian-Cenomanian) Cedar Mountain Formation of Utah, the Late Cretaceous (Turonian) Straight Cliffs Formation of Utah, the Late Cretaceous (Campanian) "El Gallo Formation" of Baja California del Norte, and the Late Cretaceous (Maastrichtian) Hell Creek Formation of Montana. The lizards of the Antlers and Cloverly formations are taxonomically and morphologically similar to the primitive lizard fauna (i.e., paramacellodid dominated) of the Late Jurassic indicating a nearly 30 million year period of relative stasis. The lizards of the Cedar Mountain Formation are taxonomically and morphologically similar to the derived lizard faunas of the Late Cretaceous. This fauna includes the earliest global occurrences of Monstersauria (helodermatid-like platynotans), Polyglyphanodontinae, and possibly Cordylidae and Scincidae as well as the latest global record of paramacellodids. Additional records of polyglyphanodontine lizards with *Polyglyphanodon*-like teeth from the Turonian of Utah, the Campanian of Mexico, and the Maastrichtian of Montana indicate that there was a lineage of *Polyglyphanodon*-like polyglyphanodontines endemic to North America. These taxa are distinct in tooth morphology from the Asian polyglyphanodontine lizards, from which they must have diverged at least by the end of the Early Cretaceous.

The relatively rapid shift in the North American lizard fauna during between the Early and medial Cretaceous coincides with the diversification of angiosperms. However, a derived lizard fauna in Asia, similar in composition to the lizard faunas of the medial and Late Cretaceous of North America, is antecedent to the diversification of angiosperms. The sudden appearance of derived lizard taxa in the medial and Late Cretaceous of North America is likely due to the dispersal of taxa from Asia to North America during the Early Cretaceous and Late Cretaceous.



POLYGLYPHANODONTINAE (SQUAMATA:TEIIDAE) FROM THE MEDIAL AND
LATE CRETACEOUS: NEW RECORDS FROM UTAH, U.S.A. AND BAJA
CALIFORNIA DEL NORTE, MEXICO.

Randall L. Nydam, Oklahoma Museum of Natural History and Department of Zoology,
University of Oklahoma, Norman, Oklahoma 73019.

Contact numbers: (405)325-4712 (phone); (405)325-7600 (fax); rlnydam@ou.edu (e-mail)

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ABSTRACT

Isolated lizard teeth from the upper Albian part of the Cedar Mountain Formation and the Turonian part of the Straight Cliffs Formation, both in Utah, and from the upper Campanian "El Gallo Formation" in Baja California del Norte closely resemble described teeth of the North American Maastrichtian polyglyphanodontines *Polyglyphanodon* (1 species) and *Paraglyphanodon* (2 species), but differ from the Asian Genera (Santonian-Campanian; Mongolia) in being transversely oriented and medially expanded. Apart from these generalized similarities, the new teeth are distinctive from the three described North American taxa. A new genus and two new species are named for the teeth from Utah and a second species of *Polyglyphanodon* is erected for the teeth from Baja California del Norte. The new fossils extend the record of the Polyglyphanodontinae back to the medial Cretaceous and indicate that the unusual tooth morphology found in *Polyglyphanodon* and *Paraglyphanodon* (1) was not derived from Late Cretaceous Mongolian polyglyphanodontines, (2) is much more archaic than previously believed, and (3) represents a stable pattern that underwent little apparent change during the mid- and Late Cretaceous. The extended record of North American polyglyphanodontine lizards with this characteristic tooth morphology and the temporally limited record of Asian polyglyphanodontines with vastly different tooth morphologies, indicates that the North American and Asian Polyglyphanodontinae diverged early in their history, perhaps as a result of an Early Cretaceous faunal exchange between the continents, and existed as separately evolving groups during the latter half of the Cretaceous. Although there is no direct evidence as to what the diet of these lizards may have been, the stable tooth morphology of the North American polyglyphanodontines was possibly associated with omnivory and/or herbivory.

INTRODUCTION

Introductory Remarks

The Cretaceous Period is an important time in the evolution of lizards, as indicated by, but not restricted to, the fossil record of North American and Asian lizards. It is during this period that many of the modern lizard families first appear in the fossil record. These geologically oldest occurrences include the Anguidae (Gilmore, 1928), Cordylidae, (Gao, 1994), Gekkonidae (Alifanov, 1992), Helodermatidae (Estes, 1964), Iguanidae (Gao and Fox, 1996), Scincidae (Estes, 1964), Teiidae (Marsh, 1892; Gilmore, 1940), Xantusiidae (Miller, 1997), and Varanidae (Gilmore, 1928). Many Cretaceous lizard taxa are represented by isolated jaws and vertebrae, which complicates their taxonomic identification. On rare occasion, more nearly complete material, even complete skeletons, have been recovered. Such is the case for most of the taxa referred to the Polyglyphanodontinae.

The Polyglyphanodontinae are a primitive group of teiids (Estes, 1983) which includes taxa from the Late Cretaceous (Fig. 1) of North America (Gilmore, 1940, 1942, 1943a) and Mongolia (Gilmore, 1943a) and (Sulimski, 1972, 1975, 1978). The group is diagnosed by a variety of characteristics associated with the skull; fusion of supratemporal and squamosal, contact of vomers and pterygoids, and a large and extensive postorbital (Estes, 1983). Most taxa in this group are large lizards with massive skulls, which may account for the unusually good fossil record for this group. One of the most unique features of the Polyglyphanodontinae is the diverse array of tooth patterns exhibited in the different taxa (see Estes, 1983 for a review and figures of the known tooth types). Tooth morphologies found in the Mongolian taxa include the following: leaf-shaped, polycusate teeth (e.g. *Darchansaurus*, *Erdenetesaurus*, and *Macrocephalosaurus*); large, bulbous, durophagous-type teeth (e.g. *Adamisaurus*); and slightly rotated (=obliquely oriented), chisel-like, teeth with polycusate crowns (e.g. *Cherminisaurus*). By contrast, teeth in the North American taxa *Polyglyphanodon* and *Paraglyphanodon* are transversely oriented and

medially expanded with chisel-like crowns. In addition to medial expansion, the teeth of *P. utahensis* are also anteroposteriorly expanded on the lateral side.

Work by crews of the Oklahoma Museum of Natural History and the Museum of Northern Arizona in rocks of the medial and Upper Cretaceous of Utah has resulted in the recovery of fossils of numerous vertebrates taxa (Cifelli, 1990a-d, 1993; Cifelli and Eaton, 1987; Cifelli and Johanson, 1994; Cifelli and Nydam, 1995; Cifelli and Madsen, in press; Cifelli and others, 1997; Cifelli and others, 1998a; Eaton and Cifelli, 1988; Gardner, 1994, 1995, Gardner and Cifelli, in press; Kirkland and Parrish, 1995; Nydam, 1995, 1997).

Among the polyglyphanodontine specimens collected was an incomplete topotypic skeleton of *Polyglyphanodon sternbergi* from the North Horn Formation (Maastrichtian). Also collected were geologically older isolated teeth of a new genus from the upper Albian part of the Cedar Mountain Formation and the Turonian part of the Straight Cliffs Formation. In addition, a fossil jaw fragment and isolated teeth collected by crews of the Los Angeles County Museum from the "El Gallo Formation" in Baja California del Norte resemble those of *Polyglyphanodon sternbergi*, but are referable to a new species in the genus.

Most Cretaceous lizards, especially those from North America, are diagnosed, primarily, on the basis of jaw and dental characteristics, largely because these are typically the only fossils available. Teeth alone are rarely used to diagnose lizard taxa, which is understandable because in many lizard groups teeth can be similar and, when isolated, difficult to distinguish without clarification from associated skeletal material. However, transversely oriented teeth, like those reported herein, are rare in lizards and all occurrences are restricted to the Teiidae. The only other taxa besides *Polyglyphanodon* and *Paraglyphanodon* described as having transverse tooth orientation are *Peneteius* from the Maastrichtian of Montana (Estes, 1969) and the extant South American teiids *Teius* and *Dicrodon* (Presch, 1974). Transversely oriented teeth that are also medially expanded are only known to occur *Polyglyphanodon* and *Paraglyphanodon*. Although modified differently in specimens from each horizon, the new taxa described herein share this

transversely oriented, medially expanded tooth pattern, indicating that they belong to the Polyglyphanodontinae extending the North American record of this group over 30 million years back to the medial Cretaceous. The new material presented here also indicates that during this 30+ million year record tooth morphology in North American polyglyphanodontines remained relatively stable. I believe taxonomic assignment for the taxa described herein is justified because formally naming these new lizards would appropriately reflect the diversity in the fossil record.

The goals of this paper include: (1) to describe the new taxa from the Cedar Mountain, Straight Cliffs, and "El Gallo" formations; (2) discuss the evolutionary history of dental morphology in the Polyglyphanodontinae; and (3) examine aspects of polyglyphanodontine biogeography and biology in light of the new fossils.

Previous Work

Polyglyphanodontine lizards were first described by Gilmore (1940, 1942, 1943a) from the Upper Cretaceous North Horn Formation, Emery County, Utah. These taxa include *Polyglyphanodon sternbergi*, a species of large lizard known from nearly 50 topotypic skeletons, some nearly complete (Gilmore, 1940, 1942); and *Paraglyphanodon utahensis* and *P. gazini*, two species of smaller lizards each known from fragmentary cranial material (Gilmore, 1940, 1943a). Based on these two genera, Gilmore (1942) erected the family Polyglyphanodontidae which he allied with the Iguanidae. Hoffstetter (1955) and later Estes (1964, 1969) subsequently argued that *Polyglyphanodon* and *Paraglyphanodon* are more closely allied with the Teiidae.

Asian polyglyphanodontines are only known from the upper Cretaceous of Mongolia (Gilmore, 1943b; Sulimski, 1972, 1975). As with their North American counterparts, the Asian taxa were originally referred to various families.

Macrocephalosaurus ferrugineus (Gilmore, 1943b) was originally placed in the Agamidae

as was *Adamisaurus magnidentatus* (Sulimski, 1972). Later, Sulimski (1978) erected *Adamisaurus* as the type genus of the monotypic scincomorph family Adamisauridae. Sulimski (1975) then referred *M. ferrugenous* and the newly discovered taxa *M. chulsanensis*, *M. gilmorei*, and *Darchansaurus estesi* to his newly erected Macrocephalosauridae. In addition, Sulimski (1975), following the example of Hoffstetter (1955) and Estes, (1964, 1969), transferred the Polyglyphanodontidae (sensu Gilmore, 1942) to the Scincomorpha and assigned the Mongolian taxa *Cherminisaurus kozłowskii* and *Erdenetesaurus robinsonae* to the family.

In his comprehensive review of fossil lizards, Estes (1983) reevaluated the relationships of all of the taxa listed above. He considered *Adamisaurus*, *Cherminisaurus*, *Darchansaurus*, *Erdenetesaurus*, *Macrocephalosaurus*, *Paraglyphanodon*, *Polyglyphanodon*, and the aberrant taxon *Haptosphenus placodon* to all be closely related and included these genera within a new teiid subfamily, the Polyglyphanodontinae. The Polyglyphanodontinae has remained relatively unchanged since its establishment, however, two recent studies deserve comment. In examining the phylogenetic position of the Upper Cretaceous teiid *Prototeius*, from the Marshalltown Formation in New Jersey, Denton and O'Neil (1995) concluded that the Polyglyphanodontinae is paraphyletic. However, their results are difficult to evaluate since their phylogenetic analysis included only three of the eight known polyglyphanodontine genera. More recently, Gao and Fox (1996), questioned the placement of *Haptosphenus* in the Polyglyphanodontinae and suggested that it may be more closely allied with the teiid subfamily Tupinambinae (sensu Estes and others, 1988; sensu Sullivan and Estes, 1997) based on similarities with the modern South American tupinambinine *Dracaena*.

Abbreviations and Conventions

Abbreviations for institutions cited in the text: Gr., Greek; IGM, Instituto de

Geología de la Universidad Nacional Autonoma de Mexico, Mexico City; LACM, Los Angeles County Museum, Los Angeles; MNA, Museum of Northern Arizona, Flagstaff; OMNH, Oklahoma Museum of Natural History, University of Oklahoma, Norman; USNM, Museum of Natural History, Smithsonian Institution, Washington. Other conventions: W/L, ratio of mediolateral width to anteroposterior length; Ma, millions of years before present; SEM, scanning electron microscopy; SVL, snout-vent-length.

MATERIALS AND METHODS

Fossils from the Cedar Mountain and Straight Cliffs formations were collected by quarrying and underwater screen washing following the methods described by Cifelli and others (1996a). The classification used in this report follows that of Estes (1983). Comparative material used in this study includes *Dicrodon guttatum* (MVZ 85401) and *Teius teyou* (MVZ 92989). Measurements of the greatest mediolateral width and anteroposterior length, as well as the ratio of the two measures (e.g., W/L values), are used to demonstrate the size and relative shapes of the teeth reported herein.

For SEM figures specimens were secured to aluminum mounts and sputter coated with gold paladium in an Hummer VI Sputtering System (Anatech, Ltd.) at 10 mA for 90 seconds under a vacuum of approximately 57 mtorr. Micrographs were taken with an ETEC Autoscan scanning electron microscope at 20 kV, 15 mm working distance, using a 100 μ m final aperture. Images were recorded on Polaroid 660 positive/negative film.

GEOLOGICAL SETTING

The isolated polyglyphanodontine teeth (OMNH 29771 and 32629) from the Cedar Mountain Formation were recovered from OMNH locality V239, 7 km east of Moore, Emery County, Utah (Fig. 2) during the 1992 field season. Locality V239 is in the Mussentuchit Member (sensu Kirkland and others, 1997), or uppermost beds, of the Cedar Mountain Formation. This part of the formation is a variegated, terrestrial deposit

composed primarily of bentonitic mudstones with interbedded channel sands, caliche, and cherts (Stokes, 1944; Tschudy and others, 1984). The Mussentuchit Member lies unconformably above the caliche-covered slopes of the Ruby Ranch Member (Kirkland and others, 1997) of the Cedar Mountain Formation and unconformably below the Dakota Sandstone. Tschudy and others (1984: p. 10-11) stated that palynomorphs from the Cedar Mountain Formation "eliminates the possibility of Cenomanian age" and shows the age to be "clearly of late or latest Albian." More recent work by Molenaar and Cobban (1991) on regional Cretaceous deposits in Utah indicates the age of the uppermost part of the Cedar Mountain Formation, in the Uinta Basin to the northeast to be Cenomanian. However, they also report that in the region of the OMNH localities the Cenomanian part of the Cedar Mountain Formation has been removed by truncation of the Dakota Sandstone. The best constrained date for the upper mudstones of the Cedar Mountain Formation is a recently reported $^{40}\text{Ar}/^{39}\text{Ar}$ date of about 98.4 Ma (latest Albian) of a volcanic ash from a fossil-bearing locality that is laterally equivalent and geographically close to V239 (Cifelli and others, 1997). For a review of the paleontology of the Cedar Mountain Formation see Cifelli and others (1998a)

The polyglyphanodontine tooth (OMNH 25386) from the Straight Cliffs Formation was recovered in 1990 from OMNH locality V4 (=MNA locality 1003-1) Garfield County, Utah (Fig. 1). The Straight Cliffs Formation lies between the underlying Tropic Shale and the overlying Wahweap Formation in the Kaiparowits Plateau region of southern Utah. Peterson (1969) divided the Straight Cliffs Formation into four members; in ascending stratigraphic order these are the Tibbett Canyon, Smoky Hollow, John Henry, and Drip Tank. These members were deposited in marine and terrestrial environments from the Turonian to the Campanian. Locality V4 is in the Smoky Hollow Member, which consists primarily of terrigenous rocks interpreted to be Turonian in age based on laterally equivalent invertebrate horizons (Peterson, 1969) and palynological evidence (Orlansky, 1971). At the level of locality OMNH V4, the depositional environment of the Smoky Hollow Member is

interpreted as primarily fluvial/floodplain (Peterson, 1969). For a complete review of the Straight Cliffs Formation, see Eaton (1991).

Based on the taxonomic diversity and number of vertebrate fossils recovered from both the Cedar Mountain and Straight Cliffs formations, the rarity of fossils of the polyglyphanodontine taxa described below likely reflects the scarcity of these lizards in their respective paleoenvironments.

The partial skeleton of *Polyglyphanodon sternbergi* was collected in 1994 from the type locality (=OMNH V811; Fig. 1) in the Late Cretaceous (Maastrichtian) part of the North Horn Formation (Gilmore, 1946) which has yielded nearly 50 topotypic skeletons (Estes, 1983). The North Horn Formation consists of predominantly terrigenous deposits which span the K/T boundary in the Wasatch Plateau (Spieker, 1960). For a review of the paleontology of the North Horn Formation see Cifelli and others (1998b).

Jaw fragments and broken limb elements of a polyglyphanodontine from Baja California del Norte were collected by crews from the LACM working in the "El Gallo Formation" in 1970 and 1973. This unit has not yet been formally described and can only be referred to informally. The "El Gallo Formation" is believed to represent an upper Cretaceous (late Campanian) terrestrial deposit (see Lillegraven, 1972). Other vertebrates associated with the polyglyphanodontine material include a small diversity of mammals, amphibians, and fish (Lillegraven, 1972, 1976; Clemens and others, 1979) as well as dinosaurs and turtles (McLeod, personal communication). All of the fossils collected in the "El Gallo Formation" were originally curated into the collections at the LACM, but are now housed in the collections at the IGU.

SYSTEMATIC PALEONTOLOGY

Order Squamata Oppel 1811

Family Teiidae Gray 1827

Subfamily Polyglyphanodontinae Estes 1983

Genus *Polyglyphanodon* Gilmore 1940

Prior to this paper *Polyglyphanodon* was known only by the type species, *P. sternbergi*. *Polyglyphanodon* is diagnosed by numerous cranial characters (Estes, 1983), the most distinguishing of which is the transversely-widened anteroposteriorly-compressed (=high W/L value) teeth of the posterior part of the tooth row (Gilmore, 1942, Estes, 1983; my Figs. 5E, F and 6A, B).

Polyglyphanodon bajaensis new species, Fig. 3

Etymology— Named for Baja California, where the taxon was discovered.

Holotype— IGM 6965 (=LACM 58008; Fig. 3C), posterior tooth.

Hypodigm— IGM 6965 (holotype), posterior tooth; IGM 6963 (=LACM 57869; Fig. 3A), anterior right dentary fragment with two teeth and a broken base of a third tooth; IGM 6964 (=LACM 57877; Fig. 3B), posterior tooth; IGM 6966 (=LACM 58011; Fig. 3D), posteriormost tooth.

Horizon and Locality— Middle one-third of the upper Campanian "El Gallo Formation," Baja California del Norte, Mexico. LACM localities LAV-7170 (IGM 6963, 6965, 6966) and LAV-7172 (IGM 6964). Both localities are near the village of El Rosario (see Lillegraven, 1972: fig. 1).

Diagnosis— Differs from *Polyglyphanodon sternbergi* in having posterior teeth that are bicuspid with a cusp on the medial side of the tooth as well as on the on the lateral side, lateral and medial cusps connected by a central U-shaped main blade and well defined anterior and posterior accessory blades. The main and accessory blades border shallow basins on the anterior and posterior sides of the tooth crown. The anterior teeth differ from *P. sternbergi* in that they are oval in occlusal view and weakly expanded medially.

Description— Positions for each tooth in *Polyglyphanodon bajaensis* can be inferred by comparison to teeth preserved in jaws of *P. sternbergi*, *Paraglyphanodon*

gazini, and the extant teiids *Teius teyou* and *Dicrodon guttatum*. The two teeth on IGM 6963 are identified as anterior teeth with the broken base the anteriormost position. In occlusal view these teeth are ovoid with the medial side wider than the lateral. These teeth are also small (tooth next to broken base: 0.83 mm wide, 0.71 mm long, W/L 1.17; more posterior tooth: 0.98 mm wide, 1.19 mm long, W/L 1.21). Both lack the bi-concave medial surface seen in the anterior teeth of *P. sternbergi*. IGM 6965 and IGM 6964, identified as teeth from the posterior part of the tooth row, resemble teeth from the posterior tooth row of *P. sternbergi* in being medially expanded and anteroposteriorly compressed. These teeth differ, however, from posterior teeth of *P. sternbergi* in being bicuspid and possessing well-defined accessory blades, anterior and posterior basins, and a wide, shallow U-shaped main blade. The main blade on IGM 6965 is unusual in that it bifurcates in the center of the tooth, forming a small, oval basin in the middle of the blade. I cannot determine whether this is a diagnostic or pathologic condition. IGM 6964 is the only specimen from locality LAV 7172 and is the largest (2.62 mm wide, 1.86 mm long, W/L 1.41) of the four teeth from Baja California del Norte. This tooth differs from IGM 6965 (2.50 mm wide, 1.43 mm long, W/L 1.75) in having a smaller W/L value and one side (medial?) of the tooth more anteroposteriorly expanded than the other. A small bicuspid tooth, IGM 6966, is symmetrical rather than medially expanded (1.07 wide, 1.07 long, W/L 1.0). This tooth also has well-defined lateral and medial cusps, anterior and posterior accessory blades, and a narrow, U-shaped, main blade. Based on comparison with the teeth of *P. sternbergi* (Gilmore, 1940: fig. 19) I tentatively assign this tooth a posteriormost position in the tooth row.

Remarks— The specimens described here were originally referred to *Polyglyphanodon sternbergi* as unnumbered and undescribed IGM specimens by Estes (1983). The similarities in tooth morphology between *Polyglyphanodon bajaensis* and the teeth of *P. sternbergi* support, in part, Estes (1983) placement of this taxon in the genus *Polyglyphanodon*, but not his assignment to the species *P. sternbergi*. The specimens are

referred to *Polyglyphanodon* based on dental characteristics shared with *P. sternbergi*; conical anterior teeth, posterior teeth greatly anteroposteriorly compressed (resulting in a high W/L value), a predominantly horizontal main blade on posterior teeth, and posteriormost tooth bicuspid though not transversely expanded (variable, see below).

Dicothodon new genus

Type species—*Dicothodon moorensis* new species.

Etymology—*Di*, Gr., two; *kothos*, Gr, cup; *odous*, Gr., tooth; in reference to the basins on either side of the V-shaped blade on the occlusal surface of the tooth.

Diagnosis—Teeth differ from *Polyglyphanodon* and *Paraglyphanodon* in having the medial and lateral cusps connected by a V-shaped main blade rather than a U-shaped main blade (e.g., *Polyglyphanodon bajaensis*) or horizontal ridge (e.g., *P. sternbergi*, *Paraglyphanodon*), and medial part of crown expanded anteroposteriorly in relation to the lateral part giving the tooth an egg-like oval shape in occlusal view.

Remarks— The material described below is too limited to permit a phylogenetic analysis and it is, therefore, impossible to eliminate the possibility that the new teeth represent a convergent evolution of this unusual tooth pattern. This interpretation could be supported by the same morphological evidence used to place the Utah taxa in a new genus, the V-shaped main blade as well as the strongly developed accessory blades. However, it is less parsimonious that such striking similarities in such an unusual and rare tooth morphology among these taxa could be explained in any other way than by phylogenetic relatedness.

Dicothodon moorensis new species, Figs. 4A, B; 5A, B, C

Etymology—Named for the town of Moore, Utah, which is close to the holotype locality.

Holotype—OMNH 29771, dentary fragment with one complete tooth and the

broken base of another tooth.

Hypodigm—OMNH 29771 (holotype; Figs. 4A, B; 5A, B) and OMNH 32629, isolated tooth (Fig. 5C).

Horizon and Locality—Upper Albian Mussentuchit Member, Cedar Mountain Formation. OMNH locality V239.

Diagnosis—Same as for the genus.

Description— Of the two teeth recovered, OMNH 29771 is the only one which is complete and is still attached to a fragment of the dentary. The tooth is medially expanded, anteroposteriorly compressed, and moderate in size (1.65 mm wide and 1.25 mm long W/L 1.32). The tooth-jaw contact in OMNH 29771 is similar to that seen in *Polyglyphanodon sternbergi* in superficially appearing to be acrodont. However, broken surfaces on the anterior and posterior sides of the jaw fragment show that the implantation was subpleurodont (sensu Gao and Fox, 1996). Below the constricted base of the crown, the tooth is obscured by heavy deposits of cementum, which also appears to fill the sulcus dentalis and the space between the teeth. The body of the tooth is bulbous, widens medially, and is constricted, below the crown. There are two cusps on the tooth, one labial and one lingual. The labial cusp is taller and narrower than the lingual cusp, and bears two weak sulci on its lateral surface. These sulci run vertically down either side of the cusp and terminate above the waist. A main, V-shaped blade runs between the two cusps. The medial arm of the blade is short and set at about a 20° angle between the lingual cusp and the base of the "V." The lateral arm of the blade is longer and set at about a 45° angle between the labial cusp and the base of the "V." The anterior and posterior sides of the crown have well-defined ridges, which will henceforth be referred to as accessory blades. These accessory blades originate at the apices of the cusps, are lunate (semicircular) in mesiodistal view, run around the crown, below the level of the V-shaped blade, defining the outer borders of the occlusal surface of the tooth. The accessory blades and the V-shaped blade border small lunate basins on anterior and posterior sides of the tooth. One of these basins is smaller

than the other and may represent the posterior side of the tooth, assuming that this taxon follows the same pattern as seen in *Polyglyphanodon sternbergi* (see below).

The referred tooth, OMNH 32629, differs slightly from OMNH 29771. These differences include a reduced degree of widening of the medial part of the tooth crown, a more acute angle in the V-shaped blade, the lateral and medial arms of the V-shaped blade are equal in length, cusps are equal in height, and the basins on either side of the V-shaped blade are lower down on the crown with steeper sides (the basins do not appear to be deeper than those on OMNH 29771). The accessory blades in OMNH 32629 are eroded, but it is evident that they were not as tall as those on OMNH 29771. Lastly, OMNH 32629 (1.77 mm wide, 1.24 mm length, L/W 1.43) either came from a slightly larger individual than OMNH 29771 or represents a different position in the tooth row of a similar sized animal. Most of these differences are minor, and when compared to tooth sets of *Polyglyphanodon sternbergi* and the extant teiids, *Dicrodon* and *Teius*, the observed variation appears to be intraspecific in nature, and, as mentioned above, is likely related to either positional differences along the jaw or ontogenetic variation.

Dicothodon sp., Figs 4C,D; 5D

Referred Specimen—OMNH 25386, isolated tooth.

Horizon and Locality—Smoky Hollow Member of the Straight Cliffs Formation, Garfield County, Utah; late Turonian. OMNH locality V4.

Description— OMNH 25386, is an isolated tooth which is broken such that most of one cusp and about half of one of the basins is missing. This tooth resembles the teeth described above for *Dicothodon moorensis* as follows: the tooth is transversely oriented, medially expanded, and anteroposteriorly compressed; there is a lateral and medial cusp connected by a main V-shaped blade; and there are anterior and posterior accessory blades that border lunate basins. Aside from these similarities in general morphology, OMNH 25386 shows features that may distinguish it from *D. moorensis*. Though not completely

preserved, the broken cusp on OMNH 25386 appears to have been the same width as the better preserved cusp giving the tooth a symmetrical shape in occlusal view. Also, OMNH 25386 is smaller (width 1.43 mm vs. 1.65 mm; length 1.03 mm vs. 1.25 mm) than both OMNH 29771 and OMNH 32629. The more complete of the accessory blades on OMNH 25386 differs from those of *D. moorensis* in having a nearly horizontal central portion that abruptly becomes vertical directed on the medial and lateral ends resulting in a more rectangular (as opposed to lunate) shaped blade and a basin that is more constrained to the center of the tooth. Lastly, the better preserved cusp on OMNH 25386 has a prominent, apical wear facet. The pattern of tooth attachment and amount of cementum cannot be determined in OMNH 25386 as no jaw material is known for the taxon.

Remarks— The V-shaped and accessory blades as well as the associated basins clearly show that OMNH 25386 belongs in the new genus *Dicothodon*. Although differences in size, age, and accessory blade structure may indicate the specimen from the Straight Cliffs formation is a new taxon. However, I have refrained from designating a new species because better material is needed to eliminate the possibility of these differences being due to positional differences in the tooth row or ontogeny.

COMPARISONS

OMNH 33460 is an incomplete topotypic skeleton consisting of associated cranial (braincase, quadrate, mandible) and post cranial (broken humerus, ulna, broken radius, broken femur, assorted phalanges, and an articulated series of four distal caudal vertebrae). The osteology of *Polyglyphanodon sternbergi* is well documented from the numerous skeletons previously collected and now housed at the USNM (Gilmore, 1942; Estes, 1983). Although previously described by Gilmore (1942) I will briefly discuss the morphology of the teeth (Fig. 5E, F; 6A, B, C) of *P. sternbergi* because the new taxa are based on comparative differences with these elements. Also, additional features of the teeth of *P. sternbergi*, based on examination of teeth on OMNH 33460, are discussed.

Anterior teeth (Fig. 6C) in the maxilla and dentary of *Polyglyphanodon sternbergi* are different from those of most teiids (e.g., *Tupinambis*, Rieppel, 1980; fig. 7A) in not being recurved. Instead, the anterior teeth in *P. sternbergi* are blocky, unrecurved, and have a conical outline in lateral view. The lateral surface of these teeth is strongly convex and the medial surface is weakly concave with a low vertical ridge that extends about half way down the crown from the apex. This vertical ridge separates the medial surface of the anterior teeth into two concave lingual surfaces in much the same way the main blade on the teeth of the posterior tooth row separates two semicircular surfaces.

The posterior part of the tooth rows in *P. sternbergi* consists of a series of transversely oriented, parallel, chisel-like teeth (Gilmore, 1942; my Fig. 6A, B). These teeth are larger (3.75 mm wide, 1.62 mm long; topotypic tooth from OMNH 33460; Figs. 5E, F) and show more extreme medial expansion and anteroposterior compression (W/L 2.31, same tooth) than those described above for the new taxa. The posterior have a small lateral cusp, but no medial cusp. The horizontal main blade between the medial and lateral sides of the tooth traces a weak, sigmoidal curve in occlusal view (contra Gilmore, 1942). To either side (anterior and posterior) of the main blade are low, semicircular, accessory ridges that define the periphery of the occlusal surface. There are no basins between the main blade and accessory ridges in most of the teeth of the posterior tooth row (the anterior and posterior faces of the crown are steep, lunate shaped surfaces), however, the second to last tooth in the right mandible of OMNH 33460 (Fig. 4E, F) has incipient basins medially and laterally. The posterior surface on the chisel-like teeth are smaller than the anterior one. The last tooth in the maxilla and dentary of *P. sternbergi*, is described by Gilmore (1942) as conical (i.e., not expanded transversely) with a small vertical ridge on the center of the medial surface. However, in his figures (Gilmore, 1942: figs. 19 and 21) only the last maxillary tooth has this morphology. The last dentary tooth remains slightly expanded transversely, and thus resembles the anteriormost chisel-like tooth in the tooth row. Likewise, the last dentary tooth in OMNH 33460 is nearly identical to the five anterior teeth

in being conical and having a weakly concave medial surface. Apparently the morphology of the last tooth in the tooth row of *P. sternbergi* varies between being unicuspid to transversely expanded and chisel-like.

Dicothodon moorensis, *Dicothodon* sp., *Polyglyphanodon bajaensis*, and *P. sternbergi* all possess teeth that are transversely oriented, medially expanded, and bear a main, central ridge or blade and semicircular accessory structures (blades or low ridges) that define the perimeter of the occlusal surface. Variations in this design separate the new taxa from one another and from *P. sternbergi* (see above).

The primary difference between the new taxa and *P. sternbergi* is size of the teeth. As seen by comparison of the scale bars in Fig. 5, teeth of *P. sternbergi* are up to twice as large as those of the new taxa. Teeth of the two species of *Dicothodon* further differ from those of *P. sternbergi* in having a V-shaped, main blade instead of the horizontal ridge seen in the teeth of *P. sternbergi*. The shallow, U-shaped main blade of *P. bajaensis* can also differentiate teeth in this species from those of *P. sternbergi*. Accessory structures on the teeth of *P. sternbergi* are low ridges and not well developed blades seen on the teeth of the new taxa. In teeth of *Dicothodon* and *P. bajaensis*, there are small basins between these accessory blades and the main blades (both V- and U-shaped). The symmetrical, bicuspid tooth (IGM 6966), here referred to *P. bajaensis*, is nearly identical to the last tooth in the maxillary tooth row of *P. sternbergi* (see Gilmore, 1942: fig. 19).

Gilmore (1940, 1943a) described two other lizards, *Paraglyphanodon gazini* and *P. utahensis*, from the holotype locality of *Polyglyphanodon sternbergi*. Although smaller, the teeth of *Paraglyphanodon gazini* (Fig. 6D) are nearly identical to those of *Polyglyphanodon sternbergi*. The other taxon found in the North Horn Formation is *Paraglyphanodon utahensis* (Fig. 6E). This lizard has teeth that are triangular in occlusal view as opposed to transversely expanded. Except for size, the morphological comparisons between the new taxa and *Paraglyphanodon gazini* are that same as with *Polyglyphanodon sternbergi*. However, none of the new taxa compare favorably, in dental morphology, with

Paraglyphanodon utahensis, except for the shared presence of a transversely oriented ridge in the center of the teeth.

The disparity of size and similarity in tooth structure, in addition to the direct association of these three taxa of lizards from the North Horn Formation (all from the same locality), led Estes (1969, 1983) to suggest that the two species of *Paraglyphanodon* represent ontogenetically younger specimens of *Polyglyphanodon sternbergi*, rather than distinct taxa. A figure of *Paraglyphanodon gazini* (Gilmore, 1943a: fig. 7) shows the enlarged orbits and reduced tooth row (= reduced snout length) associated with juvenile lizards (and most vertebrates). Although speculation on the ontogenetic relationships of these taxa is shared by others (e.g., Cifelli and others, 1998b), such a relationship has not yet been convincingly demonstrated. Because of the uncertain status of the relationship between *Polyglyphanodon sternbergi* and the two species of *Paraglyphanodon*, comparisons between the latter and the new taxa may not bear the same weight as comparisons with former.

DISCUSSION

History of the Cretaceous Teiidae

The earliest record of the Teiidae are two dentary fragments from the Aptian-Albian of Texas (Winkler and others, 1990). New teiid jaws from the uppermost Albian Cedar Mountain Formation in the collections of the OMNH (two as yet undescribed taxa and *Dicothodon moorensis*) represent three distinct grades of tooth morphology, suggesting that diversification of the family was well underway by the medial Cretaceous. The Upper Cretaceous fossil record of the Teiidae includes numerous morphologically and taxonomically diverse taxa from North America and Asia (Marsh, 1892; Gilmore, 1940, 1943a, 1943b; Estes, 1964, 1969, 1983; Sulimski, 1972, 1975; Gao and Fox, 1991, 1996; Denton and O'Neil, 1995). In North America, Cretaceous teiids are known to occur from

Baja California (this report) to New Jersey (Denton and O'Neil, 1995). Most records, however, are from the extensively worked deposits of west central North America (Marsh, 1892; Gilmore, 1940, 1943a, 1943b; Estes, 1964, 1969, 1983; Gao and Fox, 1991, 1996). Asia teiids are restricted to the polyglyphanodontines of the upper Cretaceous of Mongolia (Sulimski, 1972, 1975). To some degree the high diversity of teiids (including the Polyglyphanodontinae) during the Late Cretaceous can be explained by a bias towards collecting in horizons of this age. However, recent work in Lower Cretaceous deposits (Winkler and others, 1990; Kirkland and others, 1997; Cifelli and others, 1998a) has not revealed a similar diversity for older teiids. The polyglyphanodontines parallel other teiids in having had their greatest diversity during the Late Cretaceous. All teiids in the northern hemisphere appear to have gone extinct at the end of the Cretaceous.

Dental Evolution in the Polyglyphanodontinae

Throughout the Cretaceous the majority of the specimens that make up the fossil record of the Teiidae are jaws and jaw fragments. It is in these jaws that many of the characteristics used to diagnose the Teiidae are found; Meckelian fossa widely open to the symphysis to accommodate hypertrophied splenial, replacement teeth develop in subcircular replacement pits at the base of the teeth, and heavy deposits of cementum at tooth bases (Estes and others, 1988; Gao and Fox, 1991, 1996). For many of the Cretaceous teiid taxa, it is the morphology of the teeth in these jaws that are considered diagnostic at the genus and/or species level (Estes, 1983; Gao and Fox, 1991, 1996). As a group, the Teiidae are unusual in the high diversity of tooth types represented in the various taxa, a diversity that was even greater during the Cretaceous.

The oldest known teiid (Aptian-Albian of Texas) has unicuspid, conical teeth (Winkler and others, 1990). Based on these specimens and the iterative occurrence of this morphology in numerous Late Cretaceous teiids, Gao and Fox (1991) proposed that this

was the primitive tooth pattern for teiids. This is further supported by widespread occurrence of this simple tooth pattern in Gekkonidae and Pygopodidae (outgroups to the Teiidae; Estes and others, 1988). By the medial and Late Cretaceous teiids exhibit a wide array of tooth morphologies. Three dental patterns are evident among the Late Cretaceous non-polyglyphanodontine teiids: (1) "ancestral-type" with unicuspid and conical teeth (e.g., *Socognathus*, *Sphenosiagon*, and *Gerontoseps*); (2) "normal-type" with anteroposteriorly oriented teeth with bi- or tricuspid crowns (e. g., *Chamops*, *Leptochamops*, *Glyptogenys*, and *Meniscognathus*); or (3) "transverse-type" with transversely-oriented, bicuspid crown (e.g., *Peneteius*, undescribed taxon from the Cedar Mountain Formation). *Peneteius* and *Polyglyphanodon sternbergi* share a transverse orientation, however, the teeth of *Peneteius* are otherwise distinct and this taxon is not considered a polyglyphanodontine (Estes, 1969, 1983; personal observation). As with the Mesozoic teiids, the "normal-type" tooth pattern is also the most common tooth pattern of modern teiids, with the exception of *Dicrodon* and *Teius* which have transversely oriented teeth. An evolutionary pattern of teiid tooth types in the Cretaceous is not clear; all three morphotypes listed above can occur at the same horizon (Estes, 1983; Gao and Fox, 191, 1996). Unlike the rest of the Cretaceous Teiidae, the Polyglyphanodontinae exhibit even more diverse and unusual dental patterns.

The Mongolian polyglyphanodontines exhibit three tooth patterns: (1) leaf-shaped, polycusate teeth (e.g., *Darchansaurus*, *Erdenetesaurus*, and *Macrocephalosaurus*); large, bulbous, conical teeth (e.g., *Adamisaurus*); and obliquely oriented, polycusate, blade-like teeth (e.g., *Cherminisaurus*). The most common tooth pattern of the Mongolian taxa is the leaf-shaped, polycusate morphology found in a majority of the taxa. This pattern is similar to that found in modern herbivorous lizards such as those in the family Iguanidae (sensu Frost and Etheridge, 1989). The conical teeth of *Adamisaurus* are the closest in form to the presumed primitive teiid tooth pattern. However, it is quite possible that this tooth morphology was secondarily derived in association with the development of a durophagous diet (see below). The most unusual dentition of the Mongolian polyglyphanodontines

occurs in *Cherminsauros* (Sulimski, 1975, fig. 14A) which has horizontal, polycusate, and diagonally rotated teeth. The pattern of dental evolution within the Mongolian Polyglyphanodontinae remains uncertain.

The North American Polyglyphanodontines all have chisel-like teeth which are transversely oriented, medially expanded, and anteroposteriorly compressed (except for *Paraglyphanodon utahensis*). The age of *Dicothodon moorensis* demonstrates that this morphology was established by the end of the Early Cretaceous. The iteration of this morphology in *Dicothodon* sp., *Polyglyphanodon bajaensis*, and *P. sternbergi* shows that this morphology underwent only minor changes throughout the rest of the Cretaceous with the main difference between the North American taxa being the shape of the main blade (see above). Without a phylogenetic analysis it is not certain that these differences represent an evolutionary trend in the North American polyglyphanodontines towards more chisel-like teeth.

In his evaluation of the relationships between the taxa from North America and Mongolia, Estes (1983, p. 80) interpreted the obliquely oriented teeth in *Cherminsauros* (Campanian; Mongolia) as "demonstrating a trend towards transverse orientation of teeth that culminated in the Maastrichtian North American *Polyglyphanodon* and *Paraglyphanodon*," implying that the tooth morphology of *Cherminsauros* is ancestral to that of *P. sternbergi*. The discovery of the new North American polyglyphanodontine taxa requires that this scenario be re-examined. *Dicothodon moorensis* (upper Albian) and *Dicothodon* sp. (Turonian) are the geologically oldest polyglyphanodontine lizards and both taxa exhibit tooth morphologies similar to that of *Polyglyphanodon*. As such, *Dicothodon* would be a more likely ancestor of *Polyglyphanodon* than *Cherminsauros*. Following the same criteria used by Estes (1983), the age and tooth morphology of *Dicothodon* could be interpreted to imply that *Cherminsauros* represents a transitional form in the evolution of the Mongolian taxa from the older North American Taxa. However, both Estes' scenario and the reverse just described have some difficulties. First, the oldest taxon

is not necessarily the most primitive and a phylogenetic analysis is required to establish character polarity and identify evolutionary trends; as mentioned already, the new material described here is insufficient for such an analysis. Second, the teeth of both the Mongolian and the North American taxa appear to be "derived" with respect to the supposed primitive teiid dental condition (see above) as well as with respect to each other indicating that the time of divergence between the Mongolian and North American lineages predates the age of the oldest known specimen, *Dicothodon moorensis*. The best approach at this point would be to recognize both the Asian and North American taxa as representing two groups of polyglyphanodontine lizards that diverged from each other some time prior to the medial Cretaceous...Following the convention of placing the point of origin of a group at the location of the oldest known specimen (Humphries, 1992), the polyglyphanodontines appear to have originated in North America, but without a better understanding of the Early Cretaceous of Asia broad statements such as this remain speculative.

Recent work examining the fossil record of the late Early and medial Cretaceous of North America indicates that a faunal exchange (predominantly from east to west) between Asia and North America was active during the time between the Barremian and Cenomanian (Kirkland and others, 1997). Assuming that the present record reflects the actual temporal and geographic distribution of the Polyglyphanodontinae, this group would represent only the second record (the first being the Cretaceous shark *Baibisha*; Cifelli and others, this volume) of a west to east dispersal of a group during this Early Cretaceous faunal exchange.

Dietary Interpretations of the Polyglyphanodontinae

In modern lizards it is possible to associate the dental patterns of some taxa with their diet, particularly if the diet is specialized. Examples of this include the carnivorous varanoids (trenchant, laterally compressed, recurved teeth), herbivorous iguanids (leaf-shaped, polycusate teeth), and molluscivores (massive, bulbous teeth). These correlations

are easy to make because we can observe the habits of modern taxa. However, for fossil lizards, dietary interpretation requires deducing the possible diets represented by a particular dental pattern. For generalized teeth this is difficult, but for specialized teeth, like those found in the Polyglyphanodontinae, reasonable conclusions about diet are possible.

Polyglyphanodon sternbergi is immediately distinguishable by its large size and unusual dentition. This dental morphology is unusual for lizards as well as other vertebrate groups. Lizards with specialized diets (i.e., herbivory, vertebrate carnivory, durophagy) commonly have the most derived and distinguishable teeth. Good examples of this are extant taxa such as the herbivorous iguanid *Iguana iguana*, the carnivorous varanid *Varanus komodoensis*, and the durophagous teiid *Dracaena guianensis*. In some cases, similarity in diet may result in highly similar tooth morphologies in otherwise unrelated taxa. Such is the case with the extant taxa *Iguana iguana* and the skink *Corucia zebrata*. These animals have nearly identical leaf-shaped, polycuspate teeth (Montanucci, 1968; personal observation) and both are herbivores (Rand, 1990; Parker, 1983). Since these two lizards are not closely related they must have independently/convergently evolved similar diets and dentition. Unfortunately, determining the diet of *P. sternbergi* and the new taxa is not at straight forward as these examples.

The transverse orientation and medial expansion, characteristic of the teeth of the North American polyglyphanodontines, also occurs in *Trilophosaurus*, a primitive archosaur from the Triassic (Gregory, 1945; Demar and Bolt, 1981). Demar and Bolt (1981) identify the chisel-like teeth, alternating occlusion, and weak wear facets on some teeth, in addition to the evidence of a horny beak, as evidence that *Trilophosaurus* was an herbivore, supporting an earlier conclusion of Gregory (1945). Gilmore's reconstruction (1942) of *Polyglyphanodon sternbergi* shows an interlocking or alternating pattern of maxillary and dentary teeth similar to that of *Trilophosaurus*. This tooth morphology and jaw reconstruction was similarly interpreted by him to "indicate quite conclusively that *Polyglyphanodon* was herbivorous in diet" (Gilmore, 1942: p. 265). One line of evidence

that supports the possibility of *P. sternbergi* having been herbivorous, is its large size. Based on the energetic requirements of lizards and energy available from plant material, Pough (1973) determined that in order for a lizard to be able to sustain itself through herbivory it would need to be relatively large; about 15 cm SVL, minimum. The SVL of *P. sternbergi* is approximately 45 cm (from Gilmore, 1942), well over the minimum needed to effectively exploit plant material as a food source.

Gao and Fox (1996: 44) described *Polyglyphanodon sternbergi* as having "greatly expanded crushing teeth" implying a durophagous diet. A durophagous diet involves an animal crushing hard food items with teeth that are usually broad and flat which results in various degrees of apical wear on the teeth. There are no reports of apical wear on the chisel-like teeth of any of the material of *P. sternbergi* described by Gilmore (1942) and no wear is evident on the teeth of OMNH 33460. However, a jaw fragment with two teeth of a polyglyphanodontine (OMNH 27683) was recovered from the Cretaceous part of the North Horn Formation. Both of the teeth have wear facets indicating abrasive occlusion of teeth. The specimen (possibly one of the species of *Paraglyphanodon*) is currently involved in a study of the possible ontogenetic relationships of *Polyglyphanodon* and *Paraglyphanodon* (Nydam and Caldwell, unpublished data). The chisel-like shape of the teeth of *Polyglyphanodon sternbergi* and the manner in which they are securely cemented to the jaw suggest that they were used to process a tough food item that could be sliced, most likely a tough vegetation. As such, I tentatively accept Gilmore's (1942) interpretation of an herbivorous diet for *Polyglyphanodon sternbergi*. The interpretation of the diets of the polyglyphanodontine lizards from Mongolia are less ambiguous.

Three of the Mongolian taxa, *Macrocephalosaurus*, *Darchansaurus*, and *Erdenetesaurus*, possess teeth that are similar in structure to modern herbivorous lizards such as *Iguana iguana* and *Corucia zebrata* (*M. ferrugineus* may be an exception because the teeth of the specimen are worn and denticles may or not have been present; Sulimski, 1975; Estes, 1983). Estes' (1983) conclusion that these lizards were either herbivores or

omnivores is reasonable, though I speculate that the close similarities in dental pattern to the Iguanidae makes a stronger case for herbivory. *Adamisaurus* (Sulimski, 1972) has teeth of durophagus design (large, bluntly conical), similar to those found in the molluscivorous modern skink *Tiliqua*, with a reduced tooth count similar to that of the extant durophagous amphisbaenid, *Amphisbaena ritleyi* (Pregill, 1984). *Adamisaurus* was most likely durophagous and may have been a molluscovore. The teeth of *Cherminisaurus* are unusual and there is no modern analogue with which to compare and infer a possible diet. However, the presence of multiple small cusps on the teeth of *Cherminisaurus* imply possible herbivory.

The diets of the *Dicathodon moorensis*, *Dicathodon* sp., and *Polyglyptodon bajaensis* are the most difficult to interpret. Although similar to the teeth of *P. sternbergi*, the differences in the shape of the main blade and the presence of accessory ridges preclude an automatic assignment of herbivory to these taxa. The material is too limited to determine the SVL of the animals so their possible energetic requirements are also indeterminate. In *Trilophosaurus*, Demar and Bolt (1981) believed that the juveniles were carnivorous because of the presence of sharp cusps on the teeth. The teeth of *Dicathodon moorensis*, *Dicathodon* sp., and *P. bajaensis* are more cuspid than those of *P. sternbergi*, but, these cusps are not tall and sharp as would be expected for a carnivore or insectivore. Comparison with modern, analogous taxa does not clarify the situation. *Teius* and *Dicrodon* (Fig. 7) are the only modern lizards that have bicuspid, transversely oriented teeth (although lacking the medial expansion seen in the fossil taxa). Of the two, only *Dicrodon holmbergi* is completely herbivorous (Holmberg, 1957). *Dicrodon guttatum* is primarily insectivorous, but is known to take flowers when available (J. Dixon, personal communication). *Teius oculatus* (Alcosta and others, 1991) and *T. teyou* (Milstead, 1961) are reported to be insectivorous. Based on this information, there is no iterative dietary trend, or adaptation, associated with the transversely oriented teeth of *Teius* and *Dicrodon*. Although only speculative, the cuspid morphology of the teeth in the new taxa, in addition

to the similarities in morphology to the possibly herbivorous *P. sternbergi*, it is likely that *Dicothodon moorensis*, *Dicothodon* sp., and *Polyglyphanodon bajaensis* were omnivores.

CONCLUSION

The discovery of the Albian *Dicothodon moorensis* and Turonian *Dicothodon* sp. of Utah, and the Campanian *Polyglyphanodon bajaensis* in Baja California del Norte, considerably extend the record of the Polyglyphanodontinae in North America. More importantly, these new taxa demonstrate that the unique morphology of transversely oriented, medially expanded teeth became established much earlier than previously believed. This morphology was also very stable, showing only minor changes over a history of more than 30 million years.

Contrary to previous interpretations, it now appears that the transversely oriented, medially expanded teeth found in the North American polyglyphanodontines did not evolve from any of the known Asian polyglyphanodontine taxa. Instead, the taxa in Mongolian and North American most likely represent a divergence within the Polyglyphanodontinae sometime during the Early Cretaceous. The differences in tooth morphologies between the Asian and North American polyglyphanodontine taxa, as well as the apparent endemism of these taxa, suggest that after diverging these groups remained separated throughout the medial and Late Cretaceous. Although the morphologies are different, teeth in taxa from both continents appear to be adapted for herbivory.

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FIGURE LEGENDS

Figure 1—Geologic time scale showing the relative ages of the rock units which are known to produce polyglyphanodontine material as well as the oldest record of a teiid. The left side of the time scale shows the known ranges for the Teiidae and the teiid subfamily, Polyglyphanodontinae during the Cretaceous. All teiids went extinct in Asia and North America at the K/T boundary (Estes, 1983).

Figure 2—OMNH localities in Utah from which fossils of polyglyphanodontine lizards have been recovered. V4, Smoky Hollow Member of the Straight Cliffs Formation, Garfield County; V239, Mussentuchit Member of the Cedar Mountain Formation, Emery County; V811 (=type locality for *Polyglyphanodon sternbergi*, *Paraglyphanodon gazini*, and *P. uthaensis*), North Horn Formation, Emery County.

Figure 3—Occlusal views of teeth of *Polyglyphanodon bajaensis* n. sp. from the "El Gallo Formation," Baja California del Norte, Mexico. A, IGM 6963, anterior dentary fragment; B, IGM 6964, posterior tooth; C, IGM 6965, transverse tooth, holotype; D, IGM 6966, posteriormost tooth. Scale bar =1 mm.

Figure 4—*Dicothodon* new genus from the Cretaceous of Utah. A and B, OMNH 29771, holotype of *Dicothodon moorensis* n. sp., from the Cedar Mountain Formation, Emery County, mesiodistal and occlusal views, respectively. C and D, OMNH 25386, *Dicothodon* sp. from the Straight Cliffs Formation, Garfield County, mesiodistal and occlusal views, respectively. Abbreviations: ab-accessory blade, mf-Meckelian fossa, vb-V-shaped main blade.

Figure 5—Polyglyphanodontine teeth from Utah. A-B, OMNH 29771, *Dicothodon moorensis*, mesiodistal and oblique lingual views, respectively; C, OMNH 32629, *D.*

moorensis, occlusal view; D, OMNH 25386 *Dicothodon* sp., occlusal view; E and F, OMNH 33460 *Polyglyphanodon sternbergi* Gilmore 1940, North Horn Formation, Emery County, Utah, 2nd to last left dentary tooth from topotypic skeleton (lateral cusp broken off), anterior and occlusal views, respectively. All scale bars =1 mm.

Figure 6—Teeth of polyglyphanodontines from the North Horn Formation. A-C based on OMNH 33460. A and B, posterior tooth of *Polyglyphanodon sternbergi*, occlusal and anterior views, respectively. C, occlusal view of anterior tooth of *P. sternbergi*. D, occlusal view of right dentary tooth of *Paraglyphanodon gazini*, redrawn from Gilmore (1943a). E, occlusal view of right dentary tooth of *P. utahensis*, redrawn from Gilmore (1940). All occlusal views are oriented with anterior towards bottom of the page and in all figures medial is towards right side of the page. Abbreviations: ar-accessory ridge, mb-main blade.

Figure 7—Transversely oriented bicuspid teeth of extant teiids. A and B, *Dicrodon guttatum*, coastal Peru, MVZ 85401, posterior tooth from right maxilla, posterior and occlusal views, respectively. B and C, *Teius teyou*, southcentral South America, posterior tooth from left maxilla, anterior and occlusal views, respectively.

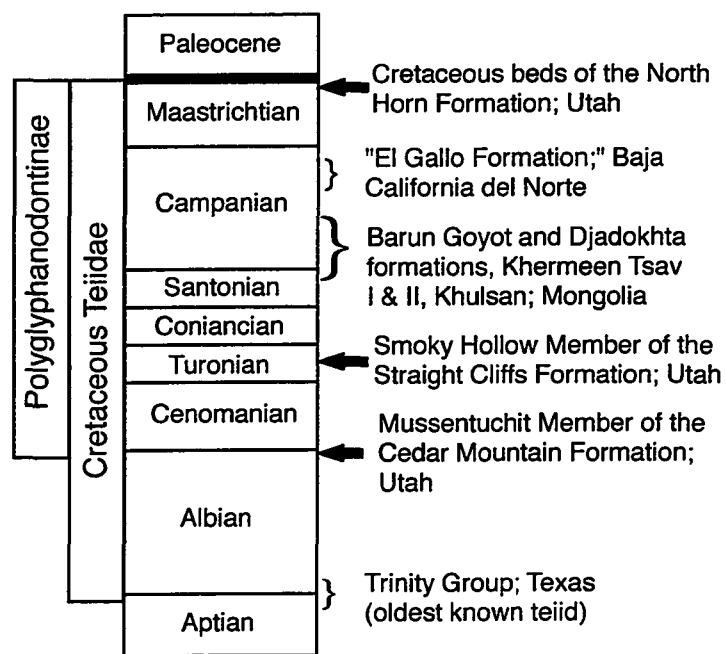


Figure 1

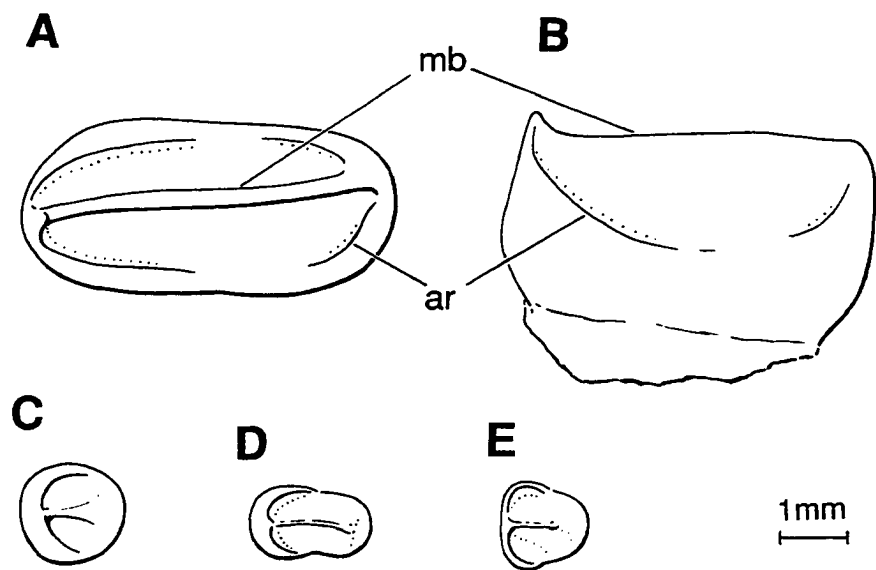


Figure 2

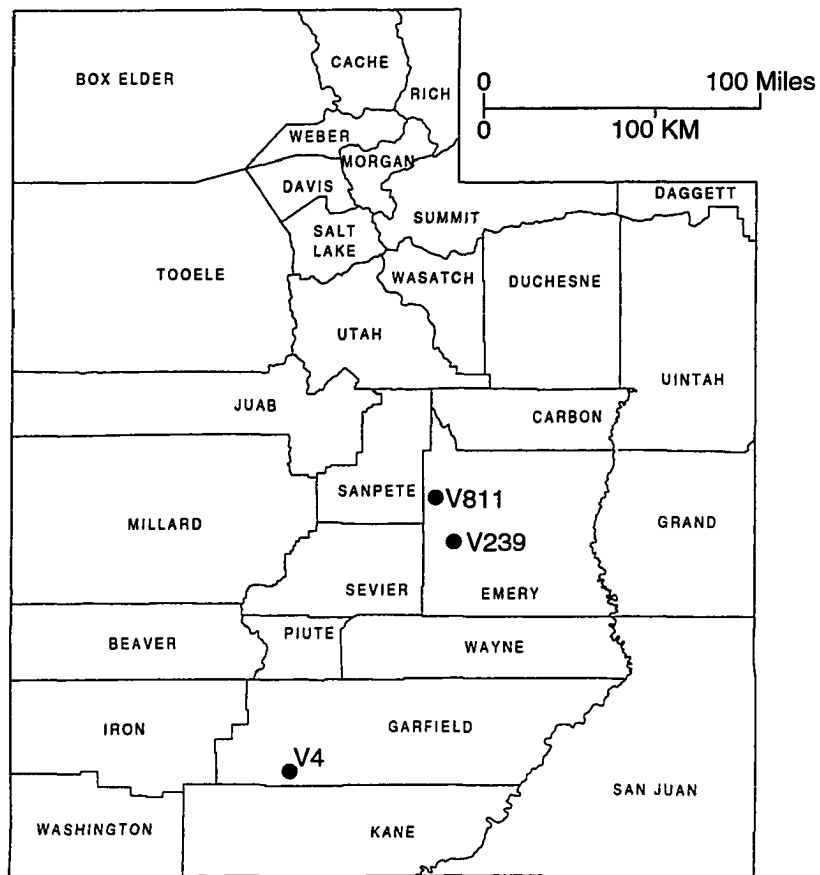


Figure 3

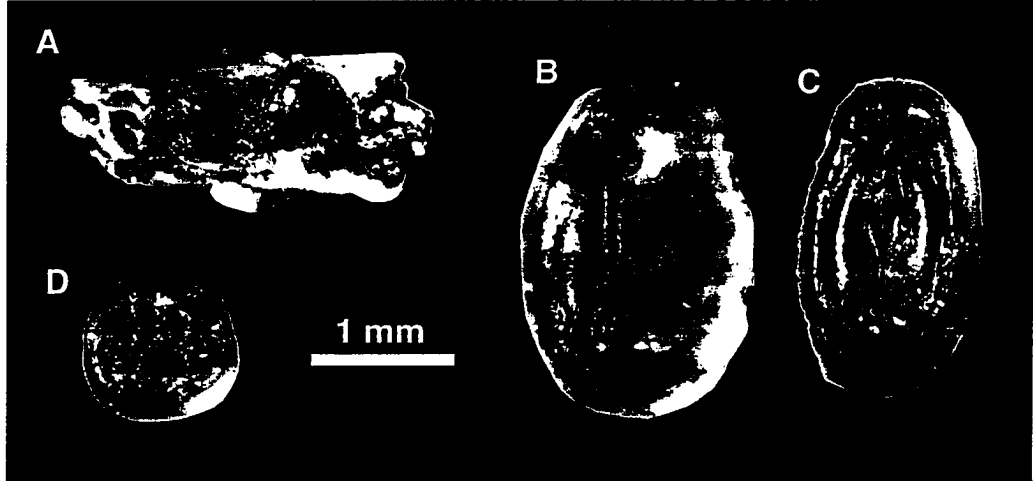


Figure 4

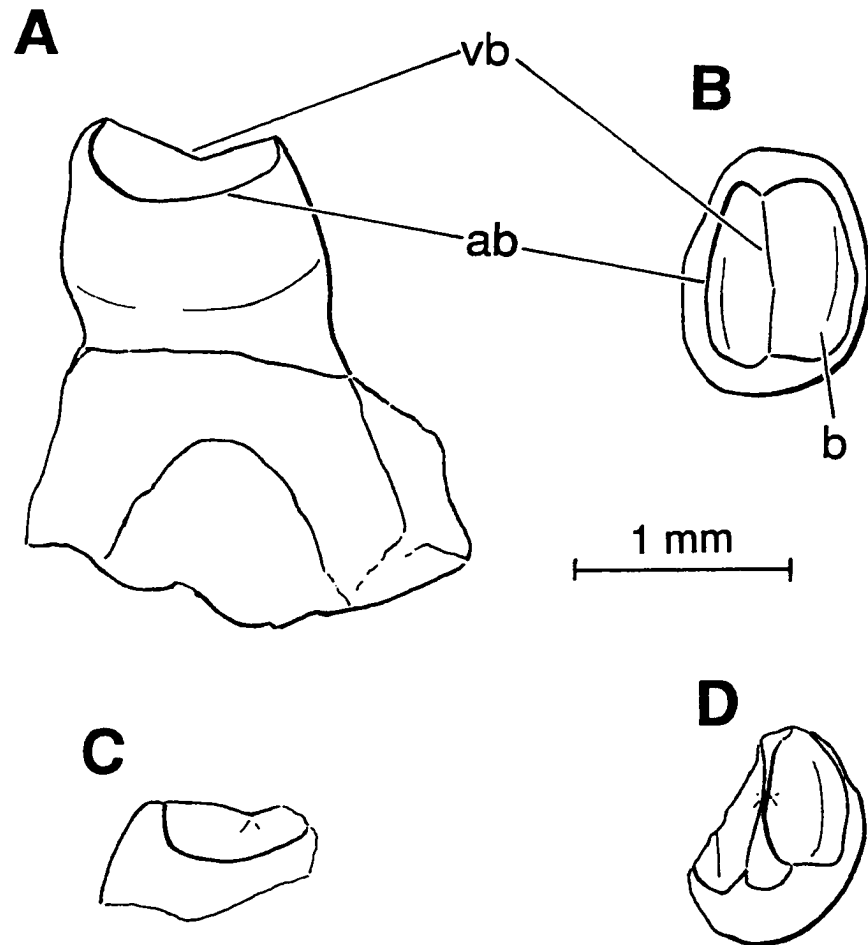


Figure 5

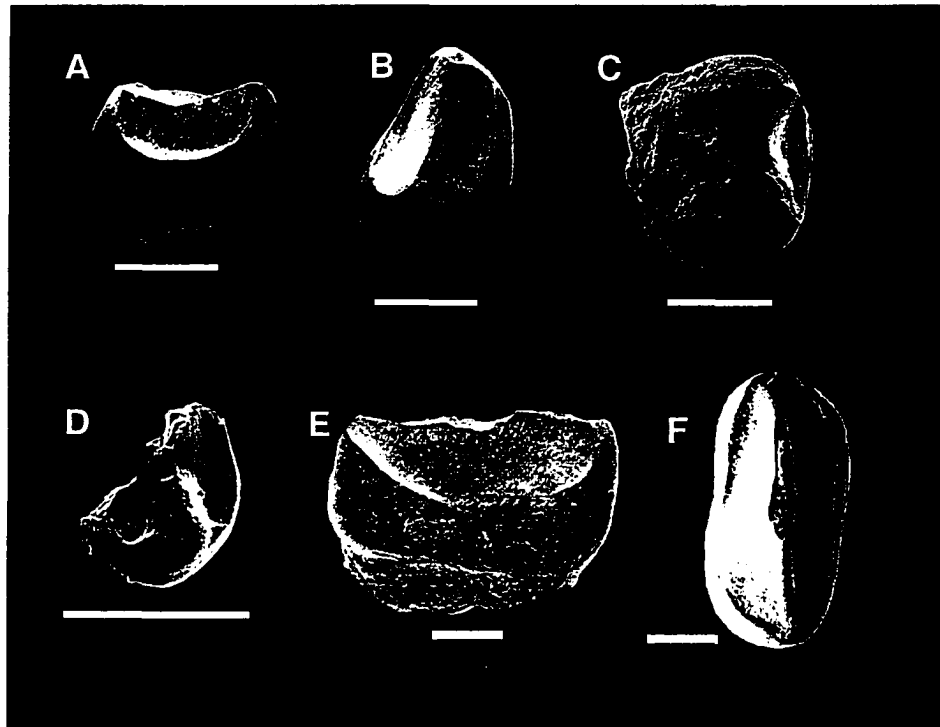


Figure 6

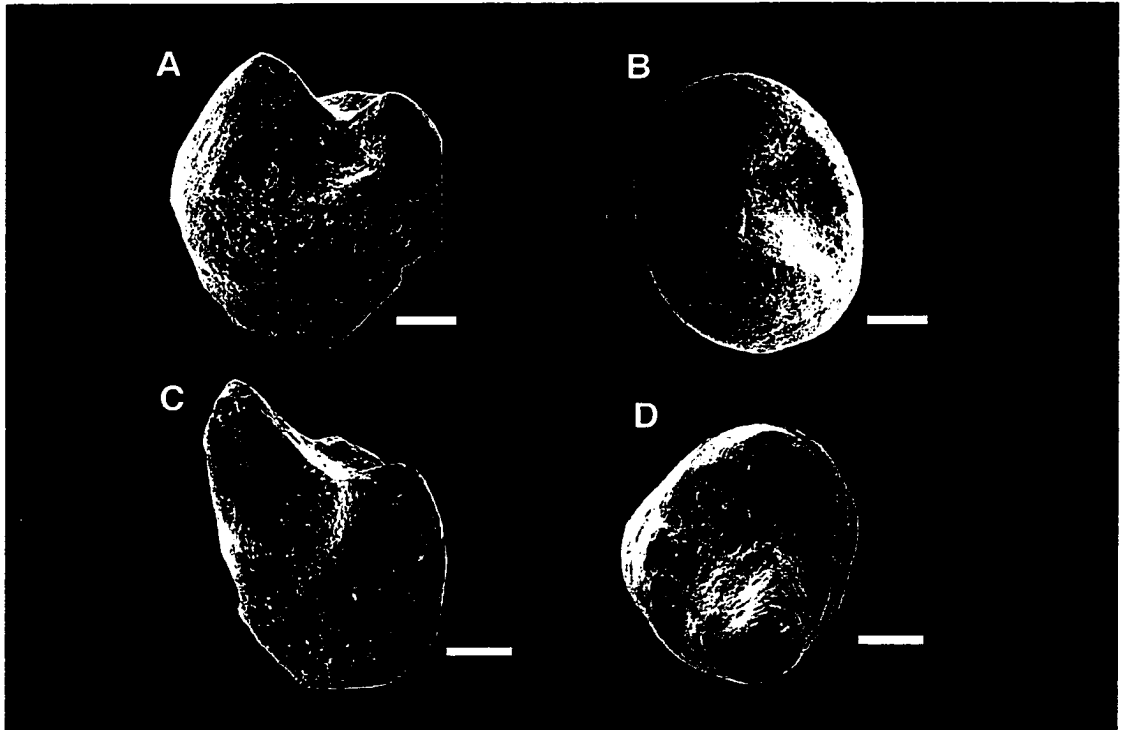


Figure 7

A NEW TAXON OF HELODERMATID-LIKE LIZARD FROM THE ALBIAN-
CENOMANIAN OF UTAH

RANDALL L. NYDAM

Oklahoma Museum of Natural History, University of Oklahoma, Norman, Oklahoma
73072 and Department of Zoology, University of Oklahoma, Norman, Oklahoma 73019

Contact numbers: phone (405) 325-4712; FAX (405) 325-7699; email rlnydam@ou.edu

Suggested running head: NYDAM—HELODERMATID-LIKE LIZARD

ABSTRACT—A new platynotan lizard, Primaderma nesso*vi* gen. et sp. nov., from the Mussentuchit Local Fauna, Cedar Mountain Formation (Albian-Cenomanian) of Utah is unique in having a premaxillary process of the maxilla that forms a vertical flange and fine serrations on anterior and posterior edges of the maxillary teeth. Primaderma is the oldest-known terrestrial platynotan and phylogenetic analysis indicates that it is a member of Monstersauria, a clade of helodermatid-like platynotans. The teeth of Primaderma show several derived platynotan characteristics, but do not possess venom grooves. The distribution of this trait in fossil taxa is reassessed. Although a North American origin of helodermatid-like platynotans is likely, it is possible that Primaderma represents another example of an Asian influence on the North American Cretaceous fauna. As with similar taxa, Primaderma was likely highly predaceous, presumably taking vertebrate prey and it appears that helodermatid-like lizards have changed very little since the Albian-Cenomanian.

INTRODUCTION

Among extant platynotan (sensu Gao and Norell, 1998) lizards (Varanus, Lanthanotus, Heloderma), the helodermatids are immediately distinguished by their heavy dermal armor, their venomous bite, and the predominance of vertebrate prey in their diets (Pregill et al., 1986). The fossil record of helodermatid-like platynotans (i.e., blunt snouted, typically with osteoderms fused to the skull) extends back to the Late Cretaceous with stereotypical helodermatids known from North America and Europe (Gilmore, 1928; Hoffstetter, 1957; Estes, 1964, 1983a; Stevens, 1977; Gao and Fox, 1996). Previous workers have referred these taxa to the family Helodermatidae based on their short, stout heads, rounded muzzles, and teeth with venom grooves (Yatkola, 1976; Estes, 1983a). Cladistic analysis by Pregill et al. (1986) supports these hypotheses and confirms the evolutionary relationships of the North American (Paraderma bogerti, Lowesaurus matthewi, Heloderma texana, H. suspectum, H. horridum) and European (Eurheloderma gallicum) taxa. A more recent analysis by Norell and Gao (1997) suggests that the Asian taxa Gobiderma pulchrum and Estesia mongoliensis should be included with the North American and European taxa in a new clade of helodermatid-like lizards, the Monstersauria. The oldest of these taxa is Late Cretaceous, but the diversity of taxa by that time suggests that the lineage is even older.

A maxilla of a helodermatid-like lizard from the Cedar Mountain Formation in Utah (Cifelli and Nydam, 1995) extends the record of these lizards back to near Albian-Cenomanian boundary in North America and confirms the existence of helodermatid-like lizards prior to the Campanian. Because what is now known as the Mussentuchit Local

Fauna of the Cedar Mountain Formation (Cifelli et al., 1999) was still being extensively studied at the time and the chance for recovery of more complete material was believed to be likely, the initial report on this specimen did not include formal taxonomic treatment. More material referable to the lizard reported by Cifelli and Nydam (1995) has been recovered, and it is now clear that this lizard from the Mussentuchit Local Fauna is a new taxon and is sufficiently well represented to allow evaluation of its phylogenetic relationship with respect to other platynotan taxa.

Abbreviations for institutions: KU, University of Kansas, Museum of Natural History, Lawrence, Kansas; OMNH, Oklahoma Museum of Natural History, University of Oklahoma, Norman, Oklahoma; UALVP, University of Alberta, Laboratory for Vertebrate Paleontology, Edmonton, Alberta; UCMP, University of California Museum of Paleontology, Berkeley, California.

GEOLOGICAL SETTING

The specimens of the new taxon were recovered from four different microvertebrate-producing localities (Fig. 1) within the Mussentuchit Member (mudstone unit at the top of the Cedar Mountain Formation; see Kirkland et al., 1997). All of these localities are found approximately 10-20 m below the unconformable (contra Kirkland et al., 1997) contact with the overlying Dakota Sandstone. The Mussentuchit Member is a terrestrial deposit composed primarily of bentonitic mudstones with interbedded channel sands (Kirkland et al., 1997) and varies considerably in thickness throughout the study area. This unit lies unconformably above the caliche-covered slopes of the Ruby Ranch

Member (Kirkland et al., 1997) of the Cedar Mountain Formation, with which it was previously grouped as a single mudstone unit (Stokes, 1944; Tschudy et al., 1984).

Based on palynomorph data Tschudy et al. (1984) determined that the age of the upper mudstones of the Cedar Mountain Formation to be late Albian. However, Molenaar and Cobban (1991) gave the age of the uppermost part of the Cedar Mountain Formation (in the Uinta Basin to the northeast of the OMNH localities) as Cenomanian. They also reported that, in the region to the southwest of their study area (where the OMNH localities reported herein are located), the Cenomanian part of the Cedar Mountain Formation has been removed by truncation of the Dakota Sandstone. The most constrained date for the upper mudstones of the Cedar Mountain Formation is a recently reported (Cifelli et al., 1997) $^{40}\text{Ar}/^{39}\text{Ar}$ determination of 98.39 ± 0.07 Ma, based on a mean of four volcanic-ash samples. Two of these samples are from the locality (V695) that yielded two of the specimens reported herein. The same ash (not yet dated) appears to directly overly the fossil horizon at another site (V868), which has yielded three specimens. This places the age of the locality near the Albian-Cenomanian boundary (Early Cretaceous-Late Cretaceous). For a review of the paleontology of the Cedar Mountain Formation, see Cifelli et al. (1999).

SYSTEMATIC PALEONTOLOGY

SQUAMATA Oppel 1811

ANGUIMORPHA Fürbringer 1900

PLATYNOTA Camp 1923

MONSTERSAURIA Norell and Gao 1997

PRIMADERMA gen. nov.

Type and Only Known Species—P. nessovi sp. nov.

Etymology—From primus (Latin for first or early), in reference to this taxon being oldest helodermatid-like lizard, and, derma (Latin for skin), a common suffix used for names of helodermatid-like lizards.

Diagnosis—As for type and only known species.

PRIMADERMA NESSOVI, sp. nov.

Diagnosis—Distinguished from other known monstersaurian taxa by presence of a small, dorsally inflected premaxillary process of maxilla and fine serrations on anterior and posterior edges of marginal teeth of maxilla.

Holotype—OMNH 26742, broken right maxilla with four teeth and vacant spaces for four others.

Hypodigm—The holotype, and OMNH 27750, partial left dentary with one complete and two broken teeth; OMNH 27022, a partial parietal; OMNH 28444, a cervical vertebra; OMNH 34399, a dorsal vertebra.

Referred Material—Isolated jaw fragments, OMNH 22071, OMNH 22122, and OMNH 34311.

Localities and Horizon—Type locality OMNH V695 (type specimen and OMNH 27750, 28444, and 34399); other localities include V235 (OMNH 34311), V696 (OMNH

27022), and V868 (OMNH 22071 and 22122). All localities in upper part of Mussentuchit Member of Cedar Mountain Formation (Albian-Cenomanian), Emery County, Utah, USA.

Etymology—In recognition of late Lev A. Nessov and his many contributions to paleoherpetology.

Description—The maxilla (OMNH 26742, Fig. 2) was first described by Cifelli and Nydam (1995). The following is an updated review of that account. The specimen is a large (20 mm long) right maxilla with four teeth and eight tooth positions. The first tooth position is anterior of the first preserved tooth. The posterior part of the element is missing. The preserved part of the maxilla curves medially at its anterior end in much the same way as in Paraderma and Heloderma (Pregill et al. 1986), indicating that the snout was blunt and rounded. The exterior surface of the maxilla is covered with osteoderms that are fused to the jaw. These osteoderms are not as thick as those found on Heloderma, but do compare closely to those of Paraderma in that both taxa have a similar pattern of fragmentation and pitting, with the more ventrally placed osteoderms being more completely fragmented. The osteoderms of Primaderma are slightly thinner than those of Paraderma, but are definitely not plate-like as in anguids (e.g., Odaxosaurus, Gerrhonotus). Above the parapet, on the external surface of the maxilla, there are seven labial foramina, all of which open anteriorly. At each tooth position, the parapet of the maxilla has a rounded, ventral projection that participates in anchoring the tooth to the jaw. These projections are more fully developed in Primaderma than they are in either Paraderma or Heloderma. The nasal process of the maxilla of Primaderma is similar to that of Heloderma and Paraderma in that it rises moderately steeply above the third tooth

position and curves medially to form a dorsolateral contribution to the roof of the snout. The posteroventral surface of the preserved portion of the nasal process bears two articulation facets, which were interpreted by Cifelli and Nydam (1995) as the squamous articulation with the prefrontal bone. Unlike Heloderma, the medial edge of the nasal process is grooved, indicating an abutting contact with the nasal bone (Cifelli and Nydam, 1995). The holotype maxilla of Paraderma (UCMP 54261; personal observation) has a similar groove on the medial edge of the nasal process, although most of this process is missing on the specimen. However, it appears that Primaderma and, possibly, Paraderma had unretracted nares. Some skulls of Heloderma also show contact of the maxilla and nasal (e.g., KU 23006; the two elements abut on the right side, but do not contact on the left side leaving a slit filled with dense connective tissue). The premaxillary process of the maxilla in Primaderma forms a small, upturned projection with an anteromedially directed vertical facet for articulation with the premaxilla. The tooth-bearing surface of the maxilla is steep, much as in Heloderma and Varanus. The supradental shelf widens medially above the second and third tooth positions to form a palatal process that is smaller than that of modern platynotans. Posterior to the third tooth position the shelf is reduced and does not extend medially much beyond the base of the teeth. Anterior to the palatal process and just posterior to the premaxillary process there is a semicircular recess in the supradental shelf. This recess represents the maxillary contribution to the maxilla-premaxillary aperture and is similar to that of modern Varanus. No such aperture exists in Heloderma or Lanthanotus and the condition of Paraderma cannot be evaluated since this area of the maxilla is broken. Posterior to the recess for the maxilla-premaxillary aperture in Primaderma, above the nutrient

foramen for the second tooth, is a small triangular facet interpreted here to represent the contact with the vomer. Immediately posterior to this facet, above the anterior part of the third tooth position, is a shallow recess for the maxillary contribution to the opening for the Jacobson's organ (fenestra vomeronasalis externa). Posterior to this recess is a long facet (extending to level of the middle of the fifth tooth position) for a second contact with the vomer. This second contact between the maxilla and the vomer would create a closed posterior border to the opening for Jacobson's organ which is referred to as the neochoanate condition (Estes et al., 1988). This condition is also found in Varanus, but not in Heloderma, Lanthanotus, or Paraderma. In the latter three genera the vomer does not come into contact with the maxilla posterior to the fenestra vomeronasalis externa, and the fenestra is confluent with the internal narial opening (paleochoanate condition).

Another articulation facet on the maxilla of Primaderma is present on the dorsal surface, above the recess for Jacobson's organ, and is directly anterior to the single opening of the anterior interior alveolar foramen. This shallow facet represents the articulation with a lateral portion of the septomaxilla. A similar, yet more robust expansion without a recessed medial edge is seen in Heloderma, where it also forms the lateral border of the fenestra vomeronasalis externa. In Heloderma the relationship of the maxilla and septomaxilla is similar to that of Primaderma, except that in Heloderma the septomaxilla covers the maxilla to a lesser extent and the floor of the capsule for a large Jacobson's organ is formed to a greater extent by the medial expansion of the supradental shelf of the maxilla.

The exact number of teeth on the maxilla of Primaderma is not known. To estimate the tooth count of Primaderma it was compared to modern Heloderma

suspectum, H. horridum, Varanus komodoensis, V. salvator, V. tristis, and V. sp. In each specimen tooth position relative to landmarks on the maxilla was noted and compared (Table 1). Primaderma was most similar to Heloderma suspectum the relative position of its teeth. Based on this comparison it seems likely that Primaderma had a similar tooth count to Heloderma; between 9 and 13 teeth. No venom grooves (see discussion below) are present on the maxillary teeth.

OMNH 27750 (Fig. 3) is an incomplete left dentary preserving eight tooth positions, but only a single, nearly complete tooth. The anteriormost and posteriormost ends of the dentary are missing, and the preserved element is approximately 12 mm long. Overall, the dentary is a gracile (more lightly built than those of Heloderma, Paraderma, and Estesia), ventrally convex element that curves medially at its anterior end. The Meckelian canal is widely open ventromedially along the posterior portion of the dentary, is constricted abruptly near the midpoint of the tooth row, and opens ventrally as a narrow slit anteriorly. The abrupt constriction appears to indicate the anterior extent of the splenial. Because the dentary is missing the posteriormost portion the condition of the intramandibular septum (fused/free, notched/ unnotched) cannot be determined. The external surface of the dentary free of ornamentation, but has four inferior alveolar foramina, which open anteriorly along the superior edge, parallel to the tooth row. The tooth-bearing surface of the dentary is narrow, shallow (when compared to the maxilla), and lacks a subdental gutter or a subdental shelf. The preserved articulation surface for the splenial is represented by a smooth facet under the two posteriormost tooth positions. This facet is very much like that in Heloderma in which the splenial and dentary have a loose articulation with at least limited movement of the elements relative to each other

(Estes et al., 1988).

The teeth of Primaderma are typical of platynotans: they are subpleurodont, having plicidentine infolding, lack resorption pits, and are separated by empty spaces (indicative of an alternating pattern of tooth replacement). The anteriormost maxillary tooth is generally similar in shape to the teeth of Heloderma in that it is recurved, pointed, and round in cross section. Posteriorly, each succeeding tooth in the maxilla becomes increasingly laterally compressed such that the fourth tooth is trenchant. Of the four preserved teeth on the maxilla, the anterior edges of the second, third and fourth, as well as the posterior edge of the fourth, are all distinctly offset from the main body of the tooth and all of these edges bear minute serrations (Fig. 2D) similar to those described for Paleosaniwa canadensis (Estes, 1964). These offset blades are better developed but otherwise similar to those of the best preserved tooth known for Paraderma, a complete dentary tooth (UALVP 29845; Gao and Fox, 1996). No serrations are known for the teeth of Paraderma.

The bases of the teeth of Primaderma are similar to those of other platynotans in that they are dilated and have plicidentine infolding. The dilated portion of the tooth bases of Primaderma and Heloderma are tapered with a consistent slope to the edges whereas the bases of the teeth of Paraderma are swollen with relatively steep edges.

A single tooth in the middle of the tooth row on the dentary of Primaderma is nearly complete. This tooth is gracile and blade-like, with offset anterior and posterior carinae. The anterior and posterior edges of the tooth are worn and the minute serrations seen in the maxillary teeth cannot be seen on this tooth. An unusual feature of this tooth—a prominent, dorsomedial wear facet at the tip—indicates that this tooth

maloccluded with a maxillary tooth. The dentary tooth is flanked by the broken bases of four other teeth. Each of these tooth bases shows the well-developed infolding of plicidentine. There is no evidence of venom grooves in the one preserved dentary tooth of Primaderma (see discussion below).

The broken parietal (OMNH 27022, Fig. 4) is covered dorsally with fused osteoderms that show a similar pattern of pitting and fragmentation to that seen on the maxilla (Fig. 2). The anterior border is missing, and it is impossible to evaluate the condition of the frontoparietal suture or whether there was a pineal foramen. There is evidence, however, for the mode of attachment of the temporal musculature. A small flange extends laterally from the parietal table anterior to the left supratemporal process; a similar flange in Heloderma is associated with ventral attachment of the temporal muscles. Platynotan taxa with dorsal attachment of the temporal musculature (such as Varanus) do not possess such a flange on the parietal. The posterior part of the parietal of Primaderma has an attachment surface (for the M. spinalis capitus), which is visible dorsally instead of being obscured by a posterior expansion of the parietal table. This condition is similar to that in Heloderma texana, Eurheloderma gallicum, Varanus salvator, and Parasaniwa wyomingensis, but is unlike the condition in Heloderma suspectum.

The supratemporal processes of the parietal are broken distally; however, enough remains to determine that they were taller than wide, and separated by an angle of about 60°. In Heloderma the supratemporal processes are very flat and have little more than a slight ventral swelling as opposed to the deep construction apparent in Primaderma. The right supratemporal process is the most complete and shows that the articulation with the

supratemporal was medial instead of dorsomedial, as in Heloderma. The dorsal surface of the supratemporal processes is flat coming off the parietal table, but it is not possible to determine whether this condition persisted (as in Heloderma) or became a crest (as in Estesia; see below). On the ventral surface of the parietal, anterior to the angle between the supratemporal processes, is a posteroventrally oriented projection. Although broken, this projection obviously incorporated the parietal fossa and marks the articulation with the supraoccipital. Such a ventral projection is known in Parasaniwa, but not in Heloderma or Varanus. It is not possible to determine the extent of contact between the supratemporal and the parietal.

Vertebrae (Fig. 5) —Two vertebrae, OMNH 28444 (7.13 mm ventral length from condyle to cotyle rim) and OMNH 34399 (6.56 mm), are referred to Primaderma nessovi based on their large size and platynotan affinities. The centra of both vertebrae are short, triangular in ventral outline, and dorsoventrally flattened. The ventral surface of the centrum on OMNH 28444 is weakly convex and bears a low sagittal ridge flanked on either side by shallow, anterolateral depressions. The condyles are unflanged to weakly flanged, dorsoventrally flattened, and directed almost completely dorsally, as they are in Heloderma. The cotyles are dorsoventrally flattened and anteroventrally oriented. The neural arches of both vertebrae are broken, each preserving a different aspect of the morphology of this structure. Most of the neural arch in OMNH 34399 is missing. What remain are the dorsally oriented prezygapophyses, which extend anteriorly to the rim of the cotyle. In OMNH 28444 the neural arch is present, but the postzygapophyses are missing. The arch is tall with vertically oriented pedicles, and the entire structure is offset anteriorly such that the dorsomedially oriented prezygapophyses extend well

anterior to the rim of the cotyle. The diapophyses and parapophyses are joined to form narrow synapophyses posterior to which there are concave depressions on the pedicles. Anteriorly there is a neural crest on OMNH 28444 that is similar to that of cervical vertebrae in Heloderma in forming a low, sagittal ridge. The posterior part of the neural spine is broken, leaving only the base of the narrow neural process, and the height of the process cannot be determined. There is no zygosphenes present on OMNH 28444 and it is presumed that the zygantrum is correspondingly absent. The neural canal of OMNH 28444 is arch-shaped with a horizontal floor that bears a low, sagittal ridge. The prezygapophyses on both vertebrae are deeply faceted to receive the postzygapophyses of the preceding vertebra.

The sagittal ridge on the centrum and the morphology of the neural arch (not projected anterior of the cotyle) of OMNH 28444 are similar to an anterior cervical vertebra of Heloderma suspectum, whereas the morphology of OMNH 34399 is similar to a typical dorsal vertebra of H. suspectum.

Three isolated jaw fragments (OMNH 22071, 22122, and 34311, Fig. 6) are identified as platynotan by the single plicidentine tooth base found on each specimen. All of these fragments come from animals with jaws much smaller than the holotype maxilla, but roughly the same size as the referred dentary (Fig. 3).

Taken together, the jaw fragments and dentary may represent a second taxon of platynotan in the fauna. However, the jaw fragments are tentatively referred to Primaderma (though they are not formally included in the hypodigm) based on the absence of apomorphic characters. Should future studies show that these jaw fragments do represent a taxon distinct from Primaderma nessovi, the diagnosis given above would

not be affected.

PHYLOGENETIC ANALYSIS

Phylogenetic analysis was performed using the computer program Phylogenetic Analysis Using Parsimony (PAUP) version 4.0b1 (Swofford, 1998). Trees generated from PAUP analyses were imported into MacClade 3.07 (Maddison and Maddison, 1997) for analysis of character evolution and distribution. The data set has been used several times for the phylogenetic analyses (each with subsequent modifications) to evaluate platynotan lizards (Pregill et al., 1986; Norell et al., 1992; Norell and Gao, 1997; Gao and Norell, 1998). As used here the data set (Appendix 1) is nearly identical to that employed by Gao and Norell (1998) and consists of 105 osteological and myological characters, of which 83 can be scored for fossil taxa. All discussions of characters use a standard shorthand such that 11-2 refers to character 11, state 2. The scoring of taxa (Appendix 2) is nearly identical to that of Gao and Norell (1998) with only minor changes that are described below.

Primaderma could be scored for 18 characters (Appendix 1), two of which require explanation. Character 10 was scored as state 0 (prefrontal not entering the external narial opening), following the logic of Gao and Norell (1998) in scoring Necrosaurus; both taxa have articulation facets on the maxilla for the nasal and prefrontal bones, indicating that the prefrontal could not have entered the external narial opening. Character 78 (neural spine shape and height) was conservatively scored as unknown because the height of the neural spine on OMNH 28444 cannot be determined, although the base indicates that it was narrow. Parviraptor was scored for 31 characters (Appendix

1) based on the published descriptions and figures of Evans (1994, 1996a).

Some changes were made in the scoring of characters for those taxa used by Gao and Norell (1998). In Paraderma, venom grooves are here considered absent instead of present. This is based on my examination of Paraderma specimens (UCMP 54261, holotype maxilla; UALVP 29845, referred dentary) and my conservative definition of what constitutes a venom groove (see below). This scoring is contrary to the interpretations of Pregill et al. (1986), Gao and Fox (1996), Norell and Gao (1997), and Gao and Norell (1998). The scoring of character 37 (muzzle shape) in Varanus was changed to polymorphic (37-0&1) to reflect the presence of a rounded muzzle in V. komodoensis.

In an attempt to improve the resolution of their cladograms, Gao and Norell (1998) sequentially removed numerous taxa based on amounts of missing data. My test of these taxa shows that Palaeosaniwa and Eosaniwa introduce the most uncertainty in the analysis and result in consensus trees with large basal polytomies and I have removed them from my analysis. The inclusion or exclusion of Restes, Bainguais, Exostinus, Parasaniwa, Paraderma, Eurheloderma, and Lowesaurus has little effect on the topology of the resulting consensus tree, as these taxa are all members of crown-group polytomies. Because Primaderma appears to be most closely allied to Monstersauria and because of the need to consider all the relevant taxa, Paraderma, Eurheloderma, and Lowesaurus were retained in the analyses. Restes, Exostinus, Parasaniwa, and Bainguais do not affect the position of Primaderma in resulting trees, but they were removed from the analysis to decrease the number of equally-parsimonious trees (49,498 vs. 60). The Late Cretaceous helodermatid Labrodioctes (Gao and Fox, 1996) was not used in the analyses because it

can only be scored for 6% of characters.

As in the analyses of Gao and Norell (1998), Iguania, Scincomorpha, and Gekkota were placed as sequential outgroups to polarize the character states of ingroup taxa, and all characters were designated as unordered. A change was made in the composition of the data set so that the parsimony assumption for taxa with multistate characters more accurately reflects the character distribution of such taxa in the data set. In PAUP, polymorphic taxa (taxa with multiple character states present) are coded, for example, as “0&1”, whereas taxa in which the states are uncertain are coded as “0/1.” All multistate taxa in this analysis have been coded as polymorphic. This difference has resulted in greater tree lengths, higher consistency indices (CI), and lower retention indices (RI) than the trees reported by Gao and Norell (1998), but the topologies of the resulting consensus trees are not affected. All analyses were run using the Heuristic search option in PAUP. The analysis of the position of Primaderma resulted in 60 equally parsimonious trees of length 328 (CI = 0.634, RI = 0.778). A strict consensus of these trees (Fig. 7) shows the same Monstersauria of Gao and Norell (1998), with a basal polytomy that includes Gobiderma, Primaderma, Paraderma, and a crown polytomy of monstersaurian taxa (Eurheloderma, Lowesaurus, Heloderma, and Estesia). Parviraptor is placed as the sister taxon to Platynota, a position that supports Evans’ (1994) observation that this taxon shares traits with both platynotans and more primitive anguimorphs. It is not clear why the relative positions of the outgroup taxa Scincomorpha and Gekkota are the opposite of what is shown Estes et al. (1988: fig. 6).

It is not surprising that the position of Primaderma cannot be better resolved considering that this taxon is missing 82% of the total characters or 77% of those

characters that can be scored for fossils. Gao and Norell (1998) identified seven synapomorphies (34-1, 36-1, 54-1, 72-2, 73-2, 78-1) that diagnose Monstersauria, and my analysis supports these characters. Primaderma and Lowesaurus can only be scored for two of these characters (72-2, 73-2) and Paraderma for three (72-2, 73-2, 78-1).

DISCUSSION

Monstersaurian evolution

Primaderma is not only the oldest well-documented platynotan, but it also shows that several derived platynotan characteristics evolved much earlier than previously thought. Most notably, the teeth of Primaderma are unmistakably platynotan in shape and structure. Also, Primaderma has the monstersaurian traits of reduced tooth count and fused, fragmented osteoderms on the skull. Primaderma is primitive with respect to the crown group Monstersauria in having: a broad contact of the nasal and maxilla (this condition cannot be confidently scored in Paraderma) and a prefrontal not entering the external narial opening. Gobiderma is described as having a similar construction of its external nares (Borsuk-Bialynicka, 1984). The distributions of these character states indicate that the retracted nares of Monstersauria and Varanoidea (sensu Gao and Norell, 1998) evolved independently in each clade. The rounded muzzle of Primaderma is also present in all monstersaurian taxa above the level of Gobiderma. Rounded muzzles have independently evolved in Cherminotus, Lanthanotus, and Varanus komodoensis). Unlike other Monstersauria which have short heads, Estesia is more like Varanus komodoensis in having the combination of a rounded muzzle and an elongated snout (which appears to have arisen independently in this taxon with respect to Monstersauria). Primaderma and

Paraderma are primitive with respect to Heloderma, Eurheloderma, Lowesaurus, and Estesia in lacking venom grooves (see discussion below) on their marginal teeth (unknown in Gobiderma). Specialization of the teeth to aid in the delivery of venom appears during the Late Cretaceous in Asian monstersaurs (Estesia), but does not unequivocally appear in North American taxa until the Oligocene (Lowesaurus).

Primaderma clearly indicates that monstersaurs had a presence in North America much earlier than previously thought. Prior to this record the oldest confirmed North American monstersaur is Paraderma from the Lancian (Maastrichtian), but Labrodioctes (Gao and Fox, 1996) from the Campanian (Judithian), may also be a monstersaur. The age of Labrodioctes is approximately the same age as the Mongolian monstersaurs Gobiderma and Estesia. The presence of a monstersaur so early in North America would appear support to Estes' (1983b) hypothesis that helodermatid (=monstersaurian) lizards originated in North America. Additionally, Parviraptor is now known from the Late Jurassic of North America (Evans, 1996b, Evans and Chure, 1998). If Parviraptor is the sister taxon to Platynota, as is indicated by phylogenetic analysis (Fig. 7), it is possible that monstersaurs may have evolved from this lineage in North America. However, Alifanov (1993) reports, but does not describe or figure, a necrosaurid lizard from the Aptian-Albian of Mongolia. Although necrosaurs are more closely allied with varanid lizards (Fig. 7), this does, at least, indicates an early presence of platynotan lizards in Asia. An Early Cretaceous corridor between Asia and North America almost certainly existed prior to the Albian-Cenomanian boundary (Currie, 1992; Kirkland et al., 1997; Cifelli et al., 1999) and it is quite possible that this permitted the early establishment of monstersaurs in North America. Lizard material from North America and Asia that

predates Primaderma is very limited and interpretations based on these materials are tentative. It is interesting, however, to note that in the phylogeny presented here (Fig. 7), the position of Estesia suggests that this taxon may be derived from North American monstersaurs.

Venom grooves

Whether or not Cretaceous helodermatid-like taxa possess venom grooves in their teeth has been largely a matter of interpretation, with arguments both for (Pregill et al., 1986; Gao and Fox, 1996) and against (Cifelli and Nydam, 1995) such an interpretation. One for the disagreement is that the “venom grooves” in Paraderma are not the same as the venom grooves in Heloderma. What is needed is a clear definition of what constitutes a venom groove and then to assess which taxa possess such structures and which do not.

The definition of a venom groove given here is based on the condition found in the modern taxa Heloderma horridum and H. suspectum, which are the only lizards that are known to deliver venom with the aid of a specialized dental structure. As such, a venom groove is a narrow slit or infolding in the tooth, at least as deep as it is wide, that runs nearly the entire length of the tooth. Such a structure can be on the anterior, posterior, or both surfaces of the tooth (it is rare to find more than one per tooth in Heloderma). Based on this definition, the monstersaurian taxa that have venom grooves are Eurheloderma, Heloderma, Estesia, and Lowesaurus.

Although presence of venom grooves in the teeth of Paraderma have been proposed (Estes, 1964; Pregill et al., 1986; Gao and Fox, 1996), personal examination of the jaws of this taxon show no unequivocal support for this interpretation. An enlarged

infolding on the anterior surface of the bases of the maxillary teeth of Paraderma (particularly on the second tooth) was proposed as an example of an incipient venom grooves (Estes, 1964; 1983a; Pregill et al., 1986). My examination of the holotype maxilla of Paraderma bogerti confirms the existence of this infolding, but since the teeth are all broken, it is not possible to determine if this groove extended to the tip of the tooth. This condition in Paraderma is similar to that seen in the bases of the teeth of Varanus salvator, and V. komodoensis. Examination of these taxa clearly shows that the basal infoldings in the teeth are variable in height with taller, more pronounced grooves separated by shorter, shallower grooves, but none of the teeth have venom grooves. If the teeth in either of these taxa were to be broken near the base, the larger infoldings would look the same as the incipient venom groove in the maxilla of Paraderma. As such, the presence or absence of venom grooves in the teeth of Paraderma cannot be confirmed based on the holotype maxilla. The referred dentary of Paraderma (UALVP 29845) has a single complete tooth that has been interpreted to have a “clearly defined venom groove” (Gao and Fox, 1996:82). In fact, this tooth is nearly identical to those of both the maxilla and dentary of Primaderma in that it is laterally compressed and has offset blades on both the anterior and posterior sides. The distinction between the main body of the tooth and the anterior blade is slightly more pronounced than in Primaderma, but it is not at all like the venom grooves seen in the teeth of the monstrosaurian taxa noted above.

An alternative interpretation of the function of the teeth of Paraderma and Primaderma is that the blade-like shape is better suited for cutting flesh similar to the blade-like, serrated teeth of Varanus komodoensis. Indeed, the fine serrations on the tooth edges support this interpretation for Primaderma. Serrations are unknown in

Paraderma since the edges of the complete dentary tooth are worn and the known maxillary teeth do not preserve the crowns. Borsuk-Bialynicka (1984:46) describes the teeth of Gobiderma as being “bilaterally flattened,” suggesting that they too are blade-like. In comparison, the teeth of Heloderma are more cylindrical and the venom groove is prominent and unmistakable. Such is also the case for Estesia (Norell et al., 1992). Bogert and del Campo (1956) reported the presence of cutting edges on the teeth of Heloderma horridum, and they are also present on H. suspectum (UMMZ 173550). However, these blades are considerably smaller than those of Primaderma and Paraderma, and they do not disrupt the conical shape of the tooth nor add to the distinctiveness of the venom groove. Cutting blades do not occur on H. texana (Stevens, 1977:fig. 1).

Ecological Implications of Primaderma

Diet—Cifelli and Nydam (1995) reported that Primaderma is notable in being a very early example of the evolution within Platynota of the capability to take relatively large, possibly vertebrate, prey items. The same predatory habits can be inferred for many other platynotan taxa based on the structure of their jaws and teeth, and the relationships of these taxa suggests that such predatory habits are a basal platynotan characteristic. Although the teeth of Parviraptor are short, they are also recurved and sharply pointed and the lower jaw has an intramandibular hinge (Evans, 1994), which suggests the possibility of vertebrate prey, but falls short of the specializations seen in platynotans. It is clear by the existence of Primaderma that the predatory habits inferred for many platynotan taxa were well established by the Albian-Cenomanian.

Environment—Although members of the same clade, the Asian and North American monstersaurs of the Cretaceous lived in notably different environments. In North America, Primaderma and Paraderma are found in rock units interpreted as representing mesic/semimesic environments (Pregill et al., 1986; Nelson and Crooks, 1987; Gao and Fox, 1996). It is only recently that North American taxa such as Heloderma texana and H. suspectum became adapted to live in the harsh, xeric conditions of southwestern North America, while H. horridum still occupies more mesic habitats (Stevens, 1977; Bogert and del Campo, 1956). Conversely, the Asian Cretaceous platynotans, such as the monstersaurs, Estesia and Gobiderma, as well as the other varanid-like lizards (e.g., Telmasaurus, Cherminotus, Paravaranus), lived in more arid environments dominated by large dune complexes with intermittent periods of lacustrine deposition (Eberth, 1993; Jerzykiewicz et al., 1993; Loope et al., 1998). This wide diversity of habitats occupied by platynotans during the Late Cretaceous is similar to the diversity seen today in modern platynotans, particularly in the widespread distribution of species of Varanus. It appears that the long evolutionary history of platynotans is due in part to their capability to adapt to a wide variety of environmental conditions.

CONCLUSION

The new taxon, Primaderma nessovi, is the oldest member of Platynota and extends the absolute minimum age of this group to the Albian-Cenomanian boundary. Although the oldest, Primaderma possesses many highly derived features including stereotypical platynotan teeth, alternate tooth replacement, and reduced tooth count, indicating that these characteristics had evolved much earlier than previously thought. In

addition to these derived traits, Primaderma also has primitively unretracted nares. The teeth of this taxon are blade-like and serrated, but lack the well-defined venom grooves found on the teeth of most monstersaurian taxa. Even in light of the lack of venom grooves on it's teeth, phylogenetic analysis places Primaderma in Monstersauria, but in an unresolved polytomy within that clade. The presence of Primaderma in Utah supports a North American origin for Monstersauria, but limited evidence also suggests a possible Asian origin of the group. It is clear, however, that Primaderma belongs to a lineage of lizards that are apparently highly predacious and have undergone little gross morphological change, particularly those taxa from North America, in their nearly 100-million-year history.

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Table 1. Comparison of tooth position relative to landmarks on the maxilla between

Primaderma nessovi, gen. et sp. nov. and modern platynotans Heloderma and Varanus.

ANP, anterior edge of nasal process; XNP, apex of nasal process; ACP, anterior border of contact with prefrontal; AJO, aperture for Jacobson's organ. Numbers indicate tooth position, as counted from anterior to posterior, medial to landmark.

<u>Taxon</u>	<u>ANP</u>	<u>XNP</u>	<u>ACP</u>	<u>AJO</u>
<u>Primaderma nesso</u> <u>vi</u>	4	6	6	2
<u>Heloderma suspectum</u>	4	6	5/6	3
<u>H. horridum</u>	4	7	6	4
<u>Varanus komodensis</u>	6	9	9/11	4/3
<u>V. salvator</u>	7/6	10/9	8	4/5
<u>V. tristis</u>	5	7	7/6	4

Appendix 1. Descriptions of characters and character states of 90 characters used in phylogenetic analyses of Primaderma nesso gen. et sp. nov. Data set modified from that of Gao and Norell (1998), which was in turn modified from Norell and Gao (1997) and Pregill et al. (1986). See Gao and Norell (1998) for extended explanation of character states. 0—primitive character state, 1, 2, 3—differently derived character states.

1. Premaxillary-maxillary aperture absent (0), or present (1).
2. Nasal bones paired with extensive suture along midline (0), or paired with limited contact 1/2 or less length of element (1), or fused (2).
3. Nasal and prefrontal bones in broad contact (0), or separated by contact of frontal with maxilla (1), or separated by a gap (2).
4. Nasal and maxillary bones in broad contact (0), or entirely or largely separated by gap (1), or separated by prefrontal (2).
5. Nasal process of maxilla located at anterior (0), or middle (1), or posterior part of maxilla (2).
6. Frontals are paired in adult stage (0), or fused (1).
7. Lateral border of frontals more or less parallel-sided (0), or constricted between orbits and hourglass-shaped (1), or trapezoidal (2).
8. Subolfactory processes of frontals poorly defined (0), or well developed as lateral wall of olfactory tract (1).
9. Subolfactory process of frontals with no ventomedial contact (0), or with extensive contact along midline (1), or closely approach or contact anteromedially (2), or closely approach or contact posteromedially (3).

10. Prefrontal not entering external narial opening (0), entering the opening owing to strong anterior extension of prefrontal (1), or entering opening owing to strong retraction of nares (2).
11. Prefrontal does not (0), or does contact postfrontal above orbit (1).
12. Jugal/squamosal contact on supratemporal arch absent (0), or present (1).
13. Jugal well developed and angulated (0), strongly reduced with little or no angulation (1).
14. Posteroventral process of jugal well developed (0), nearly or entirely lost (1).
15. Postorbital arch complete (0), or broken (1).
16. Dilation of postorbital branch of jugal absent (0), or present (1).
17. Dermal ornamentation of postorbital branch of jugal absent (0), or present (1).
18. Ectopterygoid laterally concealed by maxilla and jugal (0), or exposed on ventral edge of skull (1).
19. Both postfrontal and postorbital (0), or only postfrontal enter the orbit (1).
20. Postorbital/postfrontal fusion absent (0), or present (1).
21. Canthal crest on temporal arch absent (0), or present (1).
22. Parietal foramen present (0), or absent (1).
23. Descensus parietalis presents a lateral flange of the parietal table (0), as ventral crest beneath the table (1), or as strongly elongated ventral process extending to or just medial to the epipterygoid (2).
24. Supratemporal arch present (0), or absent (1).
25. Supratemporal fenestra wide open (0), narrowed and elongated (1), strongly reduced and nearly closed (2), or entirely lost (3).

26. Origin of temporal musculature on dorsolateral aspect (0), or ventral aspect of parietal table (1).
27. Hypoglossal foramen not enlarged (0), or enlarged and confluent with vaginal foramen (1).
28. Posterior opening of vidian canal located at prootic/basisphenoid suture (0), or penetrates basisphenoid only (1).
29. Facial foramen in recessus vena jugularis single (0), or double (1).
30. Entocarotid fossa within recessus vena jugularis well developed (0), strongly reduced (1), or essentially lost (2).
31. Basioccipital/basisphenoid suture obtusely angulate and laterally diagonal (0), or roughly a straight-line suture in keeping with anterior shifting of spheno-occipital tubercle(1).
32. Distinct medial projection anteroventral to mesopterygoid fossa absent (0), or present to enhance basiptyergoid process/pterygoid articulation (1).
33. Supratemporal process of parietal in dorsal aspect flat (0), or narrow with sharp crest (1) [scoring Estesia changed to unknown, Scincomorpha and Varanus changed to 0&1 based on personal observation of characters].
34. Anterior extension of supratemporal does not (0), or does reach level of apex of parietal notch (1).
35. Tympanic crest of quadrate large (0), or crest strongly reduced (1).
36. Pterygoid lappet of quadrate absent (0), or present (1).

37. Muzzle tapered, narrowing anteriorly (0), or blunt and rounded (1) [scoring for Varanus changed to 0&1 to reflect snouts of larger Varanus species such as V. komodoensis].
38. Posterior lacrimal foramen single (0), or double (1).
39. Premaxillary teeth large (0), or abruptly smaller than maxillary teeth (1).
40. Plicidentine infolding of teeth absent (0), or present (1).
41. Marginal teeth are not (0), or are widely spaced with expanded tooth bases (1).
42. Replacement teeth developed entirely or partially in resorption pits (0), or developed posteriorly with presence of resorption pits (1).
43. Maxillary tooth row extends extensively suborbital (0), or slightly suborbital with not more than three tooth positions (1), or entirely antorbital (2).
44. Maxillary teeth number more than 13 (0), 10-13 (1), or 9 or less (2).
45. Venom groove on marginal teeth absent (0), or present (1) [coding for Paraderma has been changed from present (1) to absent (0) based on my more conservative definition of what constitutes a venom groove].
46. Incisive process of premaxilla as a single spine (0), or bipartite (1).
47. Vomer short or slightly elongated (0), or strongly elongated to nearly twice the length of palatine, reaching level of posterior end of tooth row (1).
48. Aperture of Jacobson's organ confluent with internal narial opening (0), or separate from the narial opening by vomer-maxillary contact (1).
49. Posterior extension of choana ends far anterior (0), or ends close to or at posterior end of maxillary tooth row (1).
50. Palatal shelves of vomer wide (0), or narrow (1).

51. Palatine longer than wide (0), or equally wide as long (1).
52. Palatine teeth present (0), or absent (1).
53. Pterygoid teeth present (0), or absent (1).
54. Anterolateral process of pterygoid short and fits into a notch of ectopterygoid (0), or extended dorsally on ectopterygoid to contact jugal (1).
55. Ectopterygoid in palatal view does not contact palatine anteriorly (0), or does, excluding maxilla from suborbital fenestra (1).
56. Posterolateral end of dentary having no notch or one notch only (0), or presence of both a coronoid and a surangular notch (1), or notches strongly reduced or lost owing to development of intramandibular hinge (2).
57. Surangular in lateral view strongly tapered anteriorly (0), weakly tapered (1), or blunt in keeping with development of intramandibular hinge (2).
58. Surangular does not extend anteriorly beyond (0), or slightly beyond (1), or well beyond coronoid eminence (2).
59. Anterior extension of splenial far beyond midpoint of tooth row (0), retracted to or posterior to midpoint of tooth row (1).
60. Posterior extension of splenial beyond coronoid eminence (0), or terminates anterior to or below the eminence (1).
61. Splenial-dentary suture firm (0), or loose, with much connective tissue between the two bones (1).
62. Intramandibular septum within Meckelian canal absent (0), or present as oblique or vertical septum (1).

63. Anterior process of coronoid is not (0), or is elongate and extensively exposed dorsally (1).
64. Subdental shelf normally developed (0), or lost in keeping with fusion of dentary tube (1).
65. Ventral border of subdental shelf does not (0), or does notch to form dorsal and anterior border of anterior inferior alveolar foramen (1).
66. Meckelian canal open medially for the entire length (0), or open ventrally anterior to anterior inferior alveolar foramen (1), or completely closed as a dentary tube (2).
67. Strong reduction of mandibular fossa absent (0), or present (1).
68. Medial exposure of angular bone small (0), or extensive (1).
69. Retroarticular process not widened (0), or widened (1).
70. Retroarticular process not (0), or strongly twisted (1).
71. Retroarticular process posteriorly directed (0), or deflected medially (1).
72. Cephalic osteoderms absent (0), present as tin and plate-like tesserae (1), or fragmented and thickened as subconical mounds (2).
73. Dermal rugosities absent (0), present with vermiculate sculpture (1), or present with conspicuously pitted surfaces (2).
74. Ossified palpebrals absent (0), or present (1).
75. Lacrimal duct single (0), or double (1).
76. Number of cervical vertebrae 8 or less (0), 9 (1), 10 or more (2).
77. Cervical intercentrum intervertebral or fixed under anterior part of following centrum (0), sutured to posterior part of preceding centrum (1), or fused to posterior part of preceding centrum (2).

78. Neural spines low and broad (0), or narrow and tall (1) [scoring for Estesia changed to unknown; see text for details].
79. Precondylar constriction of vertebrae absent (0), or present (1).
80. Number of presacral vertebrae fewer than 26 (0), or 26 or more (1).
81. Autotomy on caudal vertebrae present (0), or absent (1).
82. Peduncles on cervical and caudal vertebrae absent (0), or present (1).
83. Caudal chevrons contact centrum condyle (0), suture to centrum only (1), or fuse to centrum (2).
84. Epicoracoid contacts suprascapula and mesoscapula (0), or not (1).
85. Posterior coracoid emargination absent (0), or present (1).
86. Interclavicle T-shaped or anchor-shaped without anterior process (0), or cruciform with prominent anterior process (1), vestigial or entirely lost in adults (2).
87. Mesosternum present (0), or absent (1).
88. Rib attachments on sternum more than three pairs (0), or three pairs (1), or two or fewer pairs (2).
89. Strong elongation of symphyseal process of pubis absent (0), or present (1).
90. Body osteoderms absent (0), present dorsally (1), or present both dorsally and ventrally (2).
91. M. episterno-cleido-mastoideus inserts mainly on paroccipital process (0), or has extensive insertion on parietal (1).
92. M. constrictor colli does not (0), or does extensively cover first ceratobranchials (1).
93. Origin of 3b-layer of MAME profundus from supratemporal and parietal (0), or supratemporal only (1).

94. *M. geniomyoideus* absent (0), present but completely superficial to *m. genioglossus medialis* (1), or insertion at least partly invades deep to *m. genioglossus medialis* (2).
95. *M. genioglossus lateralis* single bundle and not inserted into hyobranchial skeleton (0), or subdivided into separate bundles and inserted in hyobranchialis (1).
96. Insertion of *m. levator pterygoidii* extends posteriorly beyond columellar fossa of pterygoid (0), or restricted anteriorly (1).
97. Anterior head of *m. pseudotemporalis profundus* absent (0), or present but not expanded (1), present and expanded (2), or lost by fusion (3).
98. Bodenaponeurosis with broad base extending onto lateral edge of mandibular fossa (0), or narrow base attached only to caudomesial edge of coronoid (1).
99. Hemibacula (mineralized horns of hemipenis) absent (0), or present (1).
100. Foretongue not notched or cleft for less than 10% of length (0), cleft for 10-20% of length (1), or deeply cleft more than 20% up to over 50% of length (2).
101. Carotid duct present (0), or absent (1).
102. Gland of Gabe absent (0), or present (1).
103. Cochlear duct not robust (0), or robust and broad, limbus elongate and heavy (1).
104. Ulnar nerve superficial (0), or deep in the forearm (1).
105. Second epibranchial present (0), or absent (1).

Appendix 2. Data set used in phylogenetic analysis of Primaderma nessovi, gen. et sp. nov. (modified from data set used by Gao and Norell, [1998]). See text for discussion of modifications and scoring.

Characters													
Taxa	1												
	1	2	3	4	5	6	7	8	9	0	1	2	3
Scincomorpha	0&1	0	1	0	1	0&1	0	0	0	0	0	0&1	0
Iguania	0&1	0	0	0	0	1	1	0	0	0	0	1	0
Gekkota	0	0	0&1	0	1	0&1	0	1	1	0	0	0	1
<u>Carusia</u>	0	0	1	0	0	1	1	1	0	0	0	1	0
<u>Exostinus</u>	?	?	?	?	0	1	1	1	0	?	0	?	0
<u>Restes</u>	?	?	?	?	0	1	1	1	0	?	0	?	0
<u>Necrosaurus</u>	?	0	?	0	1	1	1	1	0	0	?	?	?
<u>Paravaranus</u>	?	2	2	1	2	1	0	0	0	2	0	?	1
<u>Bainguis</u>	?	?	?	?	?	0	0	1	0	0	?	?	1
<u>Proplatynotia</u>	0	0	1	0	2	0	0	1	0	0	0	?	1
<u>Parviderma</u>	?	0	1	0	?	1	1	1	0	0	0	?	?
<u>Gobiderma</u>	0	0	0	0	1	0	0	1	0	0	0	0	0
<u>Saniwides</u>	0	0	1	?	2	0	0	1	0	0	0	0	1
<u>Paraderma</u>	?	?	?	?	1	?	?	?	?	?	?	?	?
<u>Parasaniwa</u>	?	?	?	?	1	1	1	1	0	?	?	?	?
<u>Eosaniwa</u>	?	?	?	?	?	?	?	?	?	?	?	?	?
<u>Cherminotus</u>	0	0	2	1	2	0	0	1	3	2	1	0	1
<u>Eurheloderma</u>	?	?	?	?	1	?	?	?	?	?	?	?	?
<u>Lowesaurus</u>	?	?	?	?	1	0	2	1	2	?	?	0	0
<u>Heloderma</u>	0	0	2	1	1	0	2	1	2	2	1	0	0

	1												
	1	2	3	4	5	6	7	8	9	0	1	2	3
<u>Saniwa</u>	1	2	2	1	2	0	0	1	3	2	0	0	1
<u>Telmasaurus</u>	?	?	?	?	2	0	0	1	3	?	0	0	1
<u>Varanus</u>	1	2	2	1	2	0	0	1	3	2	0	0	1
<u>Estesia</u>	0	0	2	1	2	0	0	1	0	2	1	0	0
<u>Xenosaurus</u>	0	1	0	0	0	1	1	1	0	0	0	1	0
<u>Shinisaurus</u>	0	1	0	2	0	1	1	1	0	1	0	1	0
<u>Gerrhonotus</u>	0	0&1	0&1	0	1	1	1	1	0	0	0	0	0
<u>Diploglossus</u>	1	0&1	1	0	1	0	0	1	0	0	0	0	0
<u>Ophisaurus</u>	1	0	0	0	1	0	2	1	0	0	0&1	0	1
<u>Anguis</u>	1	0	0	0	1	0	0	1	0	0	0	0	1
<u>Anniella</u>	0	0	0	0	1	0	0	1	1	0	1	0	1
<u>Palaeosaniwa</u>	?	?	?	?	?	?	?	?	?	?	?	?	?
<u>Primaderma</u>	?	?	?	0	1	?	?	?	?	?	?	?	?
<u>Parviraptor</u>	?	?	?	0	0	?	0	1	2	?	?	?	?

	2												
	4	5	6	7	8	9	0	1	2	3	4	5	6
Scincomorpha	0	0	0	0	0	0	0&1	0	0	1	0	0	0&1
Iguania	0	0	0	0	0	0	0	0	0	0	0	0	0
Gekkota	1	1	0	0	0	9	0	9	1	0	1	3	1
<u>Carusia</u>	0	0	0	1	0	0	1	0	0	1	0	0	1
<u>Exostinus</u>	0	0	1	1	?	?	?	?	0	0	?	?	1
<u>Restes</u>	0	0	1	1	?	?	?	?	?	?	?	?	?
<u>Necrosaurus</u>	?	?	?	?	?	0	1	?	0	0	?	?	0
<u>Paravaranus</u>	1	0	0	0	0	0	?	0	0	0	0	0	0
<u>Bainguis</u>	1	?	?	?	?	1	?	?	?	?	?	?	0
<u>Proplatynotia</u>	1	0	0	0	?	0	0	?	0	0	0	0	0
<u>Parviderma</u>	?	?	?	?	?	0	?	?	0	0	?	?	0
<u>Gobiderma</u>	0	0	0	0	0	0	0	0	0	0	0	1	1
<u>Saniwides</u>	1	0	0	0	0	0	1	0	0	0	0	0	0
<u>Paraderma</u>	?	?	?	?	?	?	?	?	0	0	?	?	1
<u>Parasaniwa</u>	?	?	?	?	?	?	?	?	0	0	?	?	0
<u>Eosaniwa</u>	?	?	?	?	?	?	?	?	?	?	?	?	?
<u>Cherminotus</u>	1	?	0	0	0	?	?	9	0	0	1	3	0
<u>Eurheloderma</u>	?	?	?	?	?	?	?	?	1	0	?	?	1
<u>Lowesaurus</u>	0	0	0	0	?	?	?	?	1	0	?	?	1
<u>Heloderma</u>	0	0	0	0	0	0	1	9	1	0	1	3	1
<u>Saniwa</u>	1	0	0	0	0	0	0	0	0	0	0	0	0
<u>Telmasaurus</u>	1	0	0	0	0	0	0&1	0	0&1	0	0	0	0
<u>Varanus</u>	1	1	0	0	1	0	1	0	0	0	0	0	0

	2													
	4	5	6	7	8	9	0	1	2	3	4	5	6	
<u>Estesia</u>	1	0	0	0	0	0	1	0	1	0	0	1	1	
<u>Xenosaurus</u>	0	0	1	1	1	0	1	1	0	0	0	0	1	
<u>Shinisaurus</u>	0	0	1	1	1	0	1	1	0	0	0	0	0	
<u>Gerrhonotus</u>	0	0	0	0	0	0	0	0	0	0	0	1	1	
<u>Diploglossus</u>	0	0	0	0	0	0&1	0&1	0	0	0	0	1	1	
<u>Ophisaurus</u>	1	0	0	0	1	1	0	0	0	0	0	2	1	
<u>Anguis</u>	1	0	0	0	0	1	0&1	0	0&1	0	0	2	1	
<u>Anniella</u>	1	1	0	0	1	1	0	9	0	2	1	3	0	
<u>Palaeosaniwa</u>	?	?	?	?	?	?	?	?	?	?	?	?	?	
<u>Primaderma</u>	?	?	?	?	?	?	?	?	?	0	?	?	1	
<u>Parviraptor</u>	?	?	?	?	?	?	?	?	0	?	?	?	1	

	3												
	7	8	9	0	1	2	3	4	5	6	7	8	9
<u>Scincomorpha</u>	0	0&1	0	0	0&1	0	0	0&1	0	0&1	0	0	0
<u>Iguania</u>	0	0	0	0	0	0	0	0&1	0	0	0	0	0
<u>Gekkota</u>	0	0	0	0	0	0	0	0	0	0	0&1	0	0
<u>Carusia</u>	0	0	0	0	0	0	0	0	0	0	0	0	0
<u>Exostinus</u>	?	?	?	?	?	?	?	?	?	?	?	?	?
<u>Restes</u>	?	?	?	?	?	?	?	?	?	?	?	?	?
<u>Necrosaurus</u>	?	?	?	?	?	?	1	?	?	?	0	?	?
<u>Paravaranus</u>	0	?	?	0	0	1	1	?	?	?	0	0	?
<u>Bainguis</u>	?	?	?	?	?	?	?	?	1	?	?	?	?
<u>Proplatynotia</u>	?	?	?	0	0	?	?	?	?	?	0	0	1
<u>Parviderma</u>	?	?	?	?	?	1	?	?	?	?	?	?	?
<u>Gobiderma</u>	0	0	?	0	0	1	0	1	0	1	0	0	1
<u>Saniwides</u>	0	?	?	0	0	1	1	?	1	0	0	0	1
<u>Paraderma</u>	?	?	?	?	?	?	?	?	?	?	1	?	1
<u>Parasaniwa</u>	?	?	?	?	?	?	?	?	?	?	?	?	?
<u>Eosaniwa</u>	?	?	?	?	?	?	?	?	?	?	0	?	?
<u>Cherminotus</u>	1	?	?	2	0	1	1	?	1	0	1	?	?
<u>Eurheloderma</u>	?	?	?	?	?	1	0	?	?	?	1	?	?
<u>Lowesaurus</u>	?	?	?	?	?	?	?	?	?	?	1	?	?
<u>Heloderma</u>	0	0	0	2	0	1	0	1	0	1	1	0	1
<u>Saniwa</u>	1	1	1	?	0	1	1	?	1	0	0	1	1
<u>Telmasaurus</u>	0	?	?	2	0	1	1	0	1	0	?	1	?
<u>Varanus</u>	1	1	1	2	1	1	1	0&1	1	0	0	0&1	1

	3												
	7	8	9	0	1	2	3	4	5	6	7	8	9
<u>Estesia</u>	0	0	0	0	0	1	1	?	0	1	1	0	1
<u>Xenosaurus</u>	0	0	0	1	0	1	0	1	0	0	0	0	0
<u>Shinisaurus</u>	0	0	0	1	0	1	0	1	0	0	0	0	0
<u>Gerrhonotus</u>	0	0	0	0	0	0	0	0	0	0	0	0	1
<u>Diploglossus</u>	0	0	0	0	0	0	0	0	0	0	0	0	1
<u>Ophisaurus</u>	0	0	0	1	0	1	0	0	1	0	0	0	1
<u>Anguis</u>	0	0	0	1	0	1	0	0	1	0	0	0	1
<u>Anniella</u>	0	0	0	2	0	1	0	1	1	0	0	0	1
<u>Palaeosaniwa</u>	?	?	?	?	?	?	?	?	?	?	?	?	?
<u>Primaderma</u>	?	?	?	?	?	?	?	?	?	?	1	?	?
<u>Parviraptor</u>	?	?	?	?	?	?	1	0	?	?	0	?	?

	4					5							
	0	1	2	3	4	5	6	7	8	9	0	1	2
<u>Scincomorpha</u>	0	0	0	0	0	0	0	0	0	0	0	0	1
<u>Iguania</u>	0	0	0	0	0	0	0	0	0	0	0	0	0
<u>Gekkota</u>	0	0	0	0	0	0	0	0&1	0	0&1	0	0	1
<u>Carusia</u>	0	0	0	0	0	0	1	0	0	0	0	0	1
<u>Exostinus</u>	0	0	0	0	0	0	?	?	?	?	?	?	?
<u>Restes</u>	0	0	0	0	0	0	?	?	?	?	?	?	?
<u>Necrosaurus</u>	1	1	1	?	0&1	0	?	?	?	?	?	?	0
<u>Paravaranus</u>	?	1	1	1	?	0	?	1	?	2	1	1	?
<u>Bainguis</u>	?	?	?	?	?	?	?	?	?	0	?	?	?
<u>Proplatynotia</u>	?	1	1	1	1	0	1	1	1	1	1	?	0
<u>Parviderma</u>	1	1	1	?	?	?	?	?	?	?	?	?	0
<u>Gobiderma</u>	1	1	1	1	1	?	1	1	1	2	1	1	0
<u>Saniwides</u>	1	1	1	1	1	0	1	1	?	1	1	1	0
<u>Paraderma</u>	1	1	1	?	1	?	?	?	?	?	?	?	?
<u>Parasaniwa</u>	1	1	1	?	1	0	?	?	?	?	?	?	?
<u>Eosaniwa</u>	?	?	?	0	0	0	?	1	?	1	1	?	0
<u>Cherminotus</u>	1	1	1	2	2	0	1	1	?	2	1	1	?
<u>Eurheloderma</u>	1	1	1	2	1	1	?	?	?	?	?	?	?
<u>Lowesaurus</u>	1	1	1	2	1	1	?	?	?	?	?	?	?
<u>Heloderma</u>	1	1	1	2	2	1	1	1	0	2	1	1	0
<u>Saniwa</u>	1	1	1	1	1	0	1	1	1	1	1	1	0
<u>Telmasaurus</u>	1	1	1	?	?	?	?	?	?	?	?	1	0
<u>Varanus</u>	1	1	1	2	1	0	1	1	1	2	1	1	1

	4										5		
	0	1	2	3	4	5	6	7	8	9	0	1	2
<u>Estesia</u>	1	1	1	2	1	1	1	1	1	2	1	1	?
<u>Xenosaurus</u>	0	0	0	0	0	0	1	0	0	0	0	0	1
<u>Shinisaurus</u>	0	0	0	0	0	0	1	0	0	0	0	0	1
<u>Gerrhonotus</u>	0	0	0	0	0	0	1	0	1	0	0	0	1
<u>Diploglossus</u>	0	0	0	0	0	0	1	0	1	0	0	0	1
<u>Ophisaurus</u>	0	0	0	0	0&1	0	1	0	1	0	0	0	0
<u>Anguis</u>	0	0	0	1	2	0	1	0	1	0	0	0	1
<u>Anniella</u>	0	0	0	2	2	0	0	1	1	1	0	0	1
<u>Palaeosaniwa</u>	1	1	1	?	1	0	?	?	?	?	?	?	?
<u>Primaderma</u>	1	1	1	?	?	0	?	?	1	?	?	?	?
<u>Parviraptor</u>	0	0	0	0	0	0	?	0	0	0	?	1	1

	6												
	3	4	5	6	7	8	9	0	1	2	3	4	5
<u>Scincomorpha</u>	0&1	0	0	0	0	0&1	0	0	0	0	0&1	0	0
<u>Iguania</u>	0	0	0	0	0	0	0	0&1	0	0	0	0	0
<u>Gekkota</u>	1	0	0&1	0	0	0	1	0	0	0	1	1	9
<u>Carusia</u>	0	0	0	1	1	1	0	0	0	1	0	0	0
<u>Exostinus</u>	?	?	?	?	1	1	0	?	?	1	0	0	0
<u>Restes</u>	?	?	?	?	?	?	?	?	?	?	?	?	?
<u>Necrosaurus</u>	0	?	0	?	?	?	1	?	?	1	?	2	0
<u>Paravaranus</u>	0	?	?	?	?	?	0	1	?	?	?	2	?
<u>Bainguis</u>	?	?	?	?	?	?	0	?	?	?	?	2	?
<u>Proplatynotia</u>	0	?	1	?	2	2	1	1	1	?	1	2	0
<u>Parviderma</u>	0	?	?	2	2	2	?	1	1	?	1	2	0
<u>Gobiderma</u>	0	1	1	2	2	2	1	1	1	?	1	2	0
<u>Saniwides</u>	0	?	1	2	2	2	1	1	1	?	1	2	0
<u>Paraderma</u>	?	?	?	2	2	?	1	?	?	1	?	2	0
<u>Parasaniwa</u>	0	?	?	2	2	2	1	?	?	1	?	2	0
<u>Eosaniwa</u>	0	?	?	?	0	2	?	?	?	?	1	?	?
<u>Cherminotus</u>	0	?	1	2	2	2	1	1	1	?	1	2	?
<u>Eurheloderma</u>	0	?	?	2	2	2	1	?	?	1	?	2	0
<u>Lowesaurus</u>	?	?	?	?	?	?	?	?	?	1	?	?	?
<u>Heloderma</u>	0&1	1	1	2	2	2	1	1	1	1	1	2	0
<u>Saniwa</u>	0	?	1	2	2	2	1	1	1	?	1	2	?
<u>Telmasaurus</u>	0	?	1	?	?	?	?	?	?	?	?	?	?
<u>Varanus</u>	1	0&1	1	2	2	2	1	1	1	1	1	2	0

	6													
	3	4	5	6	7	8	9	0	1	2	3	4	5	
<u>Estesia</u>	?	1	1	2	2	2	?	?	?	?	1	2	?	
<u>Xenosaurus</u>	1	0	0	1	1	1	0	0	0	1	0	0	0	
<u>Shinisaurus</u>	0	0	0	1	1	1	0	0	0	1	0	0	0	
<u>Gerrhonotus</u>	0&1	0	0	1	0	2	0	0	0	1	0	2	1	
<u>Diploglossus</u>	1	0	0	1	0	2	0&1	0	0	1	0	2	0	
<u>Ophisaurus</u>	0	1	0	1	0	2	0	0	0	1	0	2	1	
<u>Anguis</u>	0&1	1	0	1	0	2	1	0	0	1	0	2	1	
<u>Anniella</u>	1	1	1	1	0	2	1	0	0	1	0	2	1	
<u>Palaeosaniwa</u>	?	?	?	?	?	?	1	?	?	1	?	2	0	
<u>Primaderma</u>	?	?	?	?	?	?	1	?	?	1	?	2	0	
<u>Parviraptor</u>	0	0	1	?	?	?	?	?	?	1	?	2	?	

	7												
	6	7	8	9	0	1	2	3	4	5	6	7	8
Scincomorpha	0	0	0	0	0	0	0&1	0&1	0&1	0	0	0	0
Iguania	0	0	0	0	0	0	0	0	0	0	0	0	0
Gekkota	2	0	0	1	0	1	0	0	0	0	0	0	0
<u>Carusia</u>	1	1	0	0	0	0	2	1	1	0	?	?	?
<u>Exostinus</u>	1	?	?	?	?	?	2	1	?	?	?	?	?
<u>Restes</u>	?	?	?	?	?	?	2	1	?	?	?	?	?
<u>Necrosaurus</u>	1	?	?	?	?	?	1	0	1	?	?	1	0
<u>Paravaranus</u>	?	1	?	?	?	?	?	?	?	?	?	?	?
<u>Bainguis</u>	?	?	?	?	?	?	1	0	1	?	?	?	?
<u>Proplatynotia</u>	1	1	1	0	0	?	1	0	?	?	?	?	?
<u>Parviderma</u>	1	1	1	?	?	?	1	1	1	?	?	?	?
<u>Gobiderma</u>	1	1	1	0	0	1	2	2	?	?	?	?	1
<u>Saniwides</u>	1	1	1	0	0	1	?	?	?	?	?	?	?
<u>Paraderma</u>	1	?	?	?	?	?	2	2	?	?	?	?	1
<u>Parasaniwa</u>	1	?	?	?	?	?	1	2	?	?	?	?	?
<u>Eosaniwa</u>	?	?	?	0	0	1	?	?	?	?	?	?	?
<u>Cherminotus</u>	1	1	1	0	0	?	?	?	?	?	?	?	?
<u>Eurheloderma</u>	1	?	?	?	?	?	2	2	?	?	?	?	1
<u>Lowesaurus</u>	?	?	?	?	?	?	2	2	?	?	?	?	?
<u>Heloderma</u>	1	1	1	0	0	1	2	2	0	1	0	1	1
<u>Saniwa</u>	1	1	1	0	0	1	?	?	1	?	0	1	0
<u>Telmasaurus</u>	?	?	?	?	?	?	?	?	?	?	?	?	?
<u>Varanus</u>	1	1	1	0	0	1	1	2	1	1	1	1	0

	7												
	6	7	8	9	0	1	2	3	4	5	6	7	8
<u>Estesia</u>	1	1	?	0	0	?	?	?	?	?	?	?	1
<u>Xenosaurus</u>	1	1	0	0	0	1	2	1	1	0	0	2	0
<u>Shinisaurus</u>	1	1	0	0	0	1	2	1	1	0	0	2	0
<u>Gerrhonotus</u>	1	1	0	1	1	1	1	0&1	1	0	0	2	0
<u>Diploglossus</u>	1	1	0	1	1	1	1	0	1	0	0	2	0
<u>Ophisaurus</u>	1	1	0	1	1	1	1	0	1	0	0	2	0
<u>Anguis</u>	1	1	0	1	1	1	1	0	1	0	0	2	0
<u>Anniella</u>	1	1	0	1	1	1	0	0	1	0	2	2	0
<u>Palaeosaniwa</u>	1	?	?	?	?	?	?	?	?	?	?	?	0
<u>Primaderma</u>	1	?	?	?	?	?	2	?	?	?	?	1	?
<u>Parviraptor</u>	1	?	?	?	?	?	?	?	?	?	?	?	0

	8					9							
	9	0	1	2	3	4	5	6	7	8	9	0	1
<u>Scincomorpha</u>	0	0	0	0	0&1	0	0	0&1	0	0	1	0&1	?
<u>Iguania</u>	0	0	0&1	0	0	0&1	0&1	0	0	0	0	0	0
<u>Gekkota</u>	0	0	0	0	0	0&1	0&1	1	0	0&1	0	0	?
<u>Carusia</u>	0	?	?	0	?	?	0	1	?	?	?	?	?
<u>Exostinus</u>	?	?	?	?	?	?	?	?	?	?	?	?	?
<u>Restes</u>	?	?	?	?	?	?	?	?	?	?	?	?	?
<u>Necrosaurus</u>	0	?	?	1	1	?	?	?	?	?	?	?	?
<u>Paravaranus</u>	?	?	?	?	?	?	?	?	?	?	?	?	?
<u>Bainguis</u>	?	?	?	?	?	?	?	?	?	?	?	2	?
<u>Proplatynotia</u>	?	?	?	?	?	?	?	?	?	?	?	?	?
<u>Parviderma</u>	?	?	?	?	?	?	?	?	?	?	?	?	?
<u>Gobiderma</u>	0	?	?	?	0	?	?	?	?	?	?	?	?
<u>Saniwides</u>	?	?	?	?	?	?	?	?	?	?	?	?	?
<u>Paraderma</u>	0	?	?	0	?	?	?	?	?	?	?	?	?
<u>Parasaniwa</u>	0	?	?	?	?	?	?	?	?	?	?	?	?
<u>Eosaniwa</u>	0	?	?	1	?	?	?	?	?	?	?	?	?
<u>Cherminotus</u>	?	?	?	?	?	?	?	?	?	?	?	?	?
<u>Eurheloderma</u>	0	?	?	?	?	?	?	?	?	?	?	?	?
<u>Lowesaurus</u>	?	?	?	?	?	?	?	?	?	?	?	?	?
<u>Heloderma</u>	0	1	1	0	0	1	0	9	1	1	0	1	1
<u>Saniwa</u>	1	?	1	1	1	?	0	1	?	?	?	?	?
<u>Telmasaurus</u>	?	?	?	?	?	?	?	?	?	?	?	?	?
<u>Varanus</u>	1	1	1	1	1	1	1	0&1	1	2	0	0&1	1

	8										9		
	9	0	1	2	3	4	5	6	7	8	9	0	1
<u>Estesia</u>	?	?	?	0	?	?	?	?	?	?	?	?	?
<u>Xenosaurus</u>	0	1	1	0	0	0	0	0	0	0	0	1	0
<u>Shinisaurus</u>	0	0	0	0	0	0	0	1	?	0	0	1	0
<u>Gerrhonotus</u>	0	1	0	0	2	0	0	1	0	1	1	2	0
<u>Diploglossus</u>	0	1	0	0	2	0	0	1	0	1	1	2	0
<u>Ophisaurus</u>	0	1	0	0	2	0	0	0&2	0	1	1	2	0
<u>Anguis</u>	0	1	0	0	2	0	0	2	0	1	1	2	0
<u>Anniella</u>	0	1	0	0	2	9	9	2	1	9	1	2	0
<u>Palaeosaniwa</u>	1	?	?	?	?	?	?	?	?	?	?	?	?
<u>Primaderma</u>	?	?	?	?	?	?	?	?	?	?	?	?	?
<u>Parviraptor</u>	0	?	0	?	?	?	?	?	?	?	?	?	?

	10												
	2	3	4	5	6	7	8	9	0	1	2	3	4
Scincomorpha	0	0	0	0	0	1	0	0	0&1	0	0	0	0&1
Iguania	0	0	0	0	0	0	0	0	0	0	0	0	0
Gekkota	0&1	0	0	0	0	0&1	0	0	0	0	0	0	0
<u>Carusia</u>	?	?	?	?	?	?	?	?	?	?	?	?	?
<u>Exostinus</u>	?	?	?	?	?	?	?	?	?	?	?	?	?
<u>Restes</u>	?	?	?	?	?	?	?	?	?	?	?	?	?
<u>Necrosaurus</u>	?	?	?	?	?	?	?	?	?	?	?	?	?
<u>Paravaranus</u>	?	?	?	?	?	?	?	?	?	?	?	?	?
<u>Bainguis</u>	?	?	?	?	?	?	?	?	?	?	?	?	?
<u>Proplatynotia</u>	?	?	?	?	?	?	?	?	?	?	?	?	?
<u>Parviderma</u>	?	?	?	?	?	?	?	?	?	?	?	?	?
<u>Gobiderma</u>	?	?	?	?	?	?	?	?	?	?	?	?	?
<u>Saniwides</u>	?	?	?	?	?	?	?	?	?	?	?	?	?
<u>Paraderma</u>	?	?	?	?	?	?	?	?	?	?	?	?	?
<u>Parasaniwa</u>	?	?	?	?	?	?	?	?	?	?	?	?	?
<u>Eosaniwa</u>	?	?	?	?	?	?	?	?	?	?	?	?	?
<u>Cherminotus</u>	?	?	?	?	?	?	?	?	?	?	?	?	?
<u>Eurheloderma</u>	?	?	?	?	?	?	?	?	?	?	?	?	?
<u>Lowesaurus</u>	?	?	?	?	?	?	?	?	?	?	?	?	?
<u>Heloderma</u>	0	1	2	1	0&1	1	1	0	2	1	1	1	1
<u>Saniwa</u>	?	?	?	?	?	?	?	?	?	?	?	?	?
<u>Telmasaurus</u>	?	?	?	?	?	?	?	?	?	?	?	?	?
<u>Varanus</u>	1	1	2	1	1	2	0&1	1	2	1	1	1	1

	10												
	2	3	4	5	6	7	8	9	0	1	2	3	4
<u>Estesia</u>	?	?	?	?	?	?	?	?	?	?	?	?	?
<u>Xenosaurus</u>	0	0	1	1	0	1	1	0	1	0	0	0	0
<u>Shinisaurus</u>	?	0	1	0	0	1	0	0	1	0	0	0	0
<u>Gerrhonotus</u>	0	0	1	0	0	0	0	0	1	0	0	0	0
<u>Diploglossus</u>	0	0	1	0	1	1	0	0	1	0	0	0	0
<u>Ophisaurus</u>	0	0	1	0	0	2	0	0	1	0	0	0	0
<u>Anguis</u>	0	0	1	0	0	2	0	0	1	0	0	0	0
<u>Anniella</u>	0	0	1	0	0	3	1	0	1	?	0	?	0
<u>Palaeosaniwa</u>	?	?	?	?	?	?	?	?	?	?	?	?	?
<u>Primaderma</u>	?	?	?	?	?	?	?	?	?	?	?	?	?
<u>Parviraptor</u>	?	?	?	?	?	?	?	?	?	?	?	?	?

	10
	5
Scincomorpha	0
Iguania	0
Gekkota	0
<u>Carusia</u>	?
<u>Exostinus</u>	?
<u>Restes</u>	?
<u>Necrosaurus</u>	?
<u>Paravaranus</u>	?
<u>Bainguis</u>	?
<u>Proplatynotia</u>	?
<u>Parviderma</u>	?
<u>Gobiderma</u>	?
<u>Saniwides</u>	?
<u>Paraderma</u>	?
<u>Parasaniwa</u>	?
<u>Eosaniwa</u>	?
<u>Cherminotus</u>	?
<u>Eurheloderma</u>	?
<u>Lowesaurus</u>	?
<u>Heloderma</u>	0
<u>Saniwa</u>	?
<u>Telmasaurus</u>	?
<u>Varanus</u>	1

	10
	5
<u>Estesia</u>	?
<u>Xenosaurus</u>	1
<u>Shinisaurus</u>	1
<u>Gerrhonotus</u>	0
<u>Diploglossus</u>	1
<u>Ophisaurus</u>	1
<u>Anguis</u>	1
<u>Anniella</u>	1
<u>Palaeosaniwa</u>	?
<u>Primaderma</u>	?
<u>Parviraptor</u>	?

FIGURE LEGENDS

FIGURE 1. OMNH localities in Cedar Mountain Formation of Emery County, Utah, which have yielded specimens of Primaderma nessovi, gen. et sp. nov. **A**, V695 (type locality); **B**, V235; **C**, V696; **D**, V868.

FIGURE 2. Holotype maxilla (OMNH 26742) of Primaderma nessovi, gen. et sp. nov. **A-C**, stereopair images of **A**, external; **B**, internal, and **C**, oblique dorsolateral views. **D**, detail of posteriormost tooth, note serrations along edges. **NF**, nasal articulation facet, **PFF**, prefrontal articulation facet, **PMP**, premaxillary process.

FIGURE 3. Stereopair image of OMNH 27750, referred dentary of Primaderma nessovi, gen. et sp. nov., medial view. **AS**, anterior extent of splenial facet.

FIGURE 4. Stereopair images of OMNH 27022, referred parietal, Primaderma nessovi, gen. et sp. nov. **A**, dorsal; and **B**, ventral views. **AM**, ventral origin of adductor musculature.

FIGURE 5. Stereopair images of OMNH 28444 (**A-C**) and OMNH 34399 (**D-F**), referred vertebrae of Primaderma nessovi, gen. et sp. nov. **A** and **D**, dorsal view; **B** and **E**, ventral view; and **C** and **F**, lateral view. Anterior is towards bottom of the page.

FIGURE 6. Isolated jaw fragments referred to Primaderma nessovi, gen. et sp. nov. **A**, OMNH 22701; **B**, OMNH 22122; and **C**, OMNH 34311.

FIGURE 7. Strict consensus tree of 60 equally most-parsimonious trees from phylogenetic analysis of Primaderma nessovi gen. et sp. nov

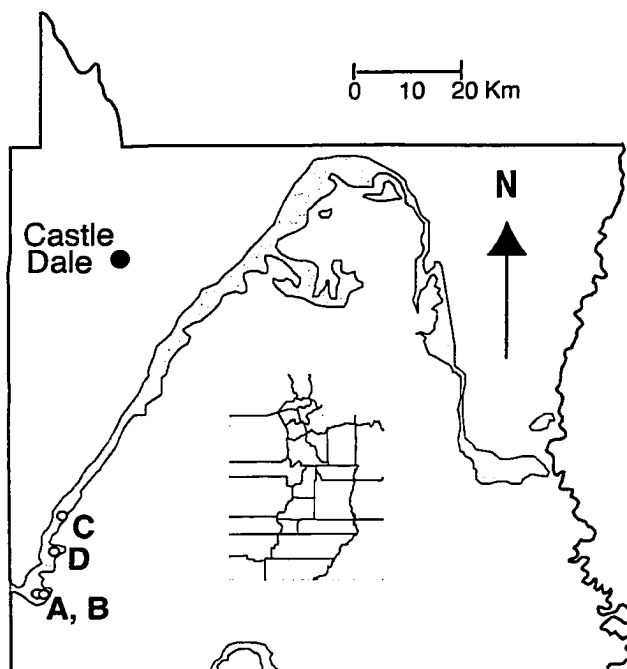


Figure 1

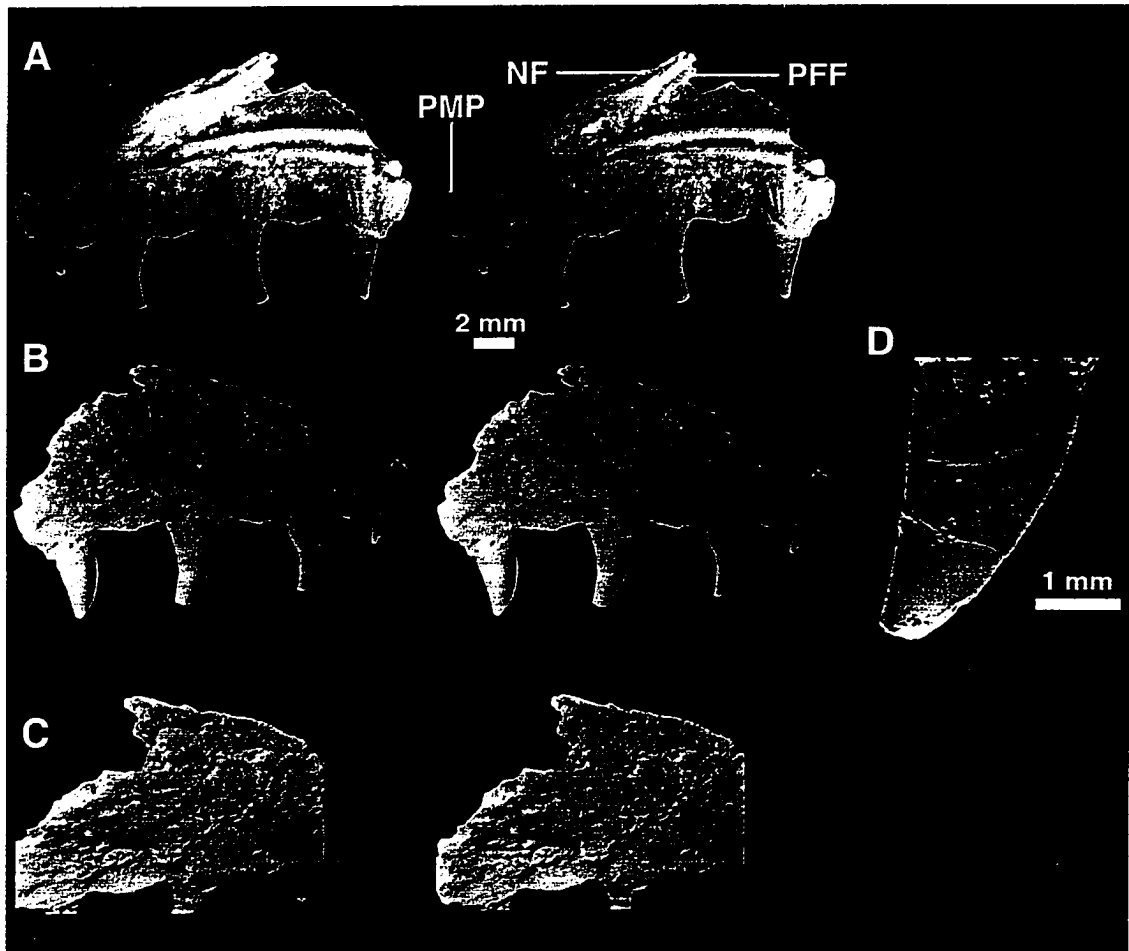


Figure 2

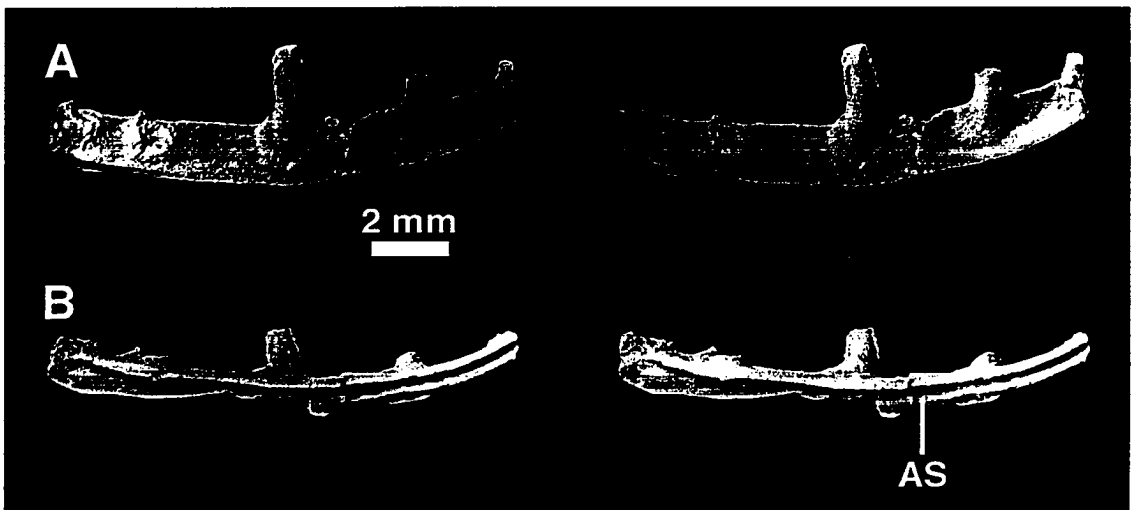


Figure 3

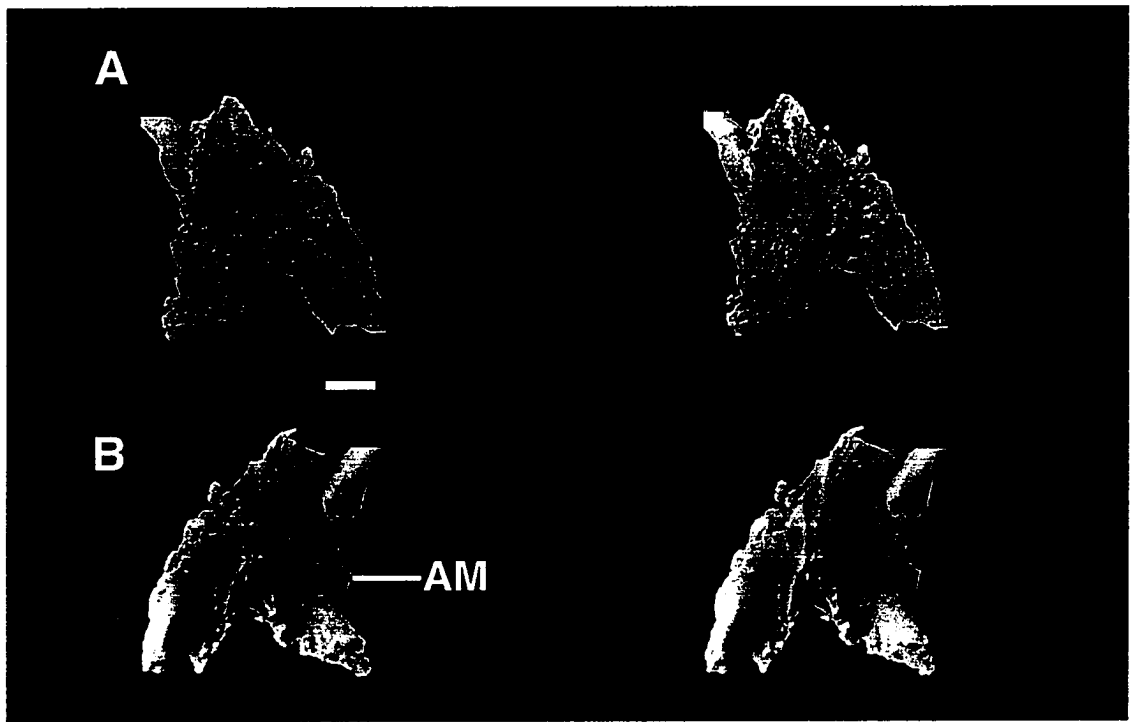


Figure 4

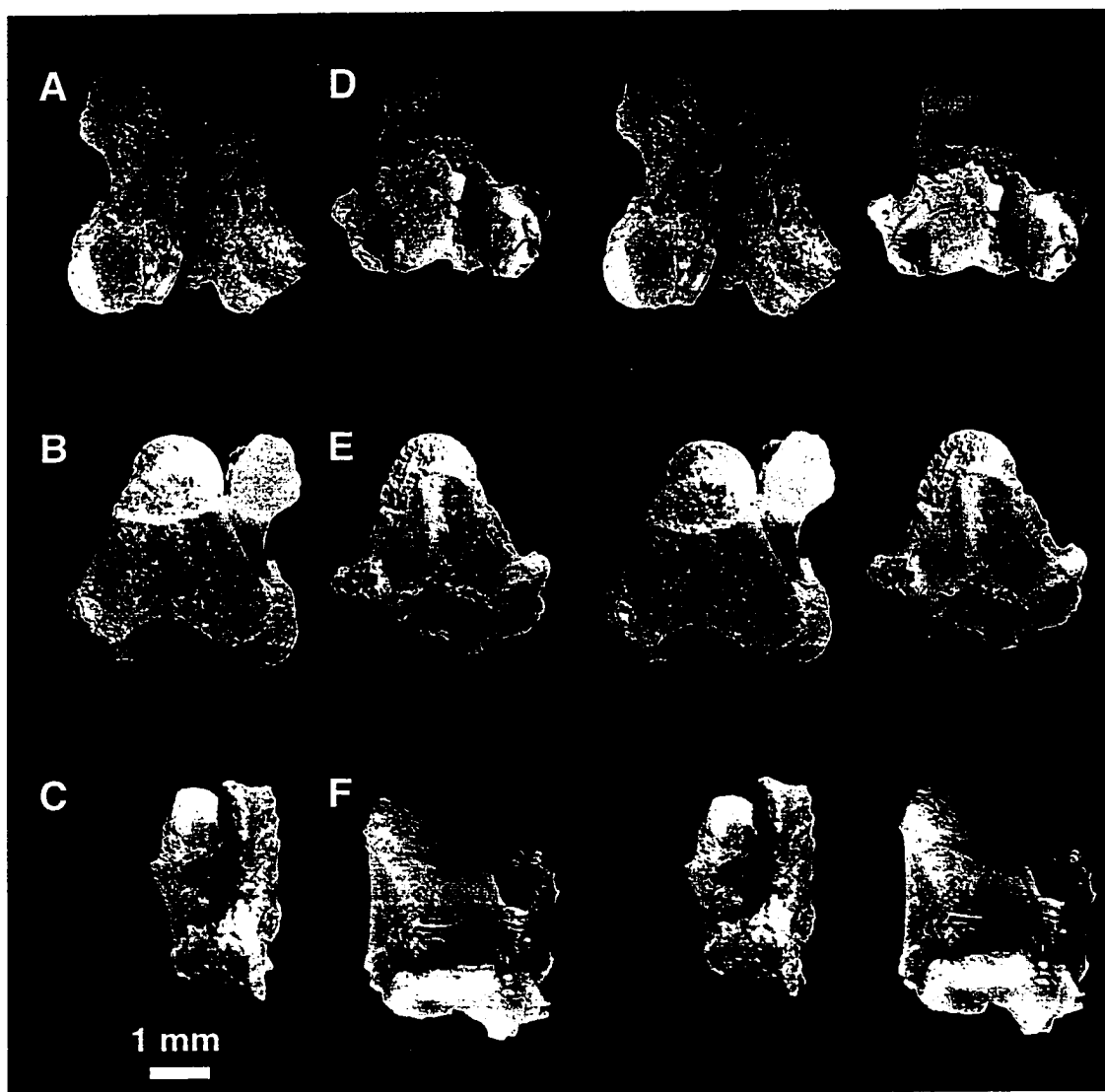


Figure 5

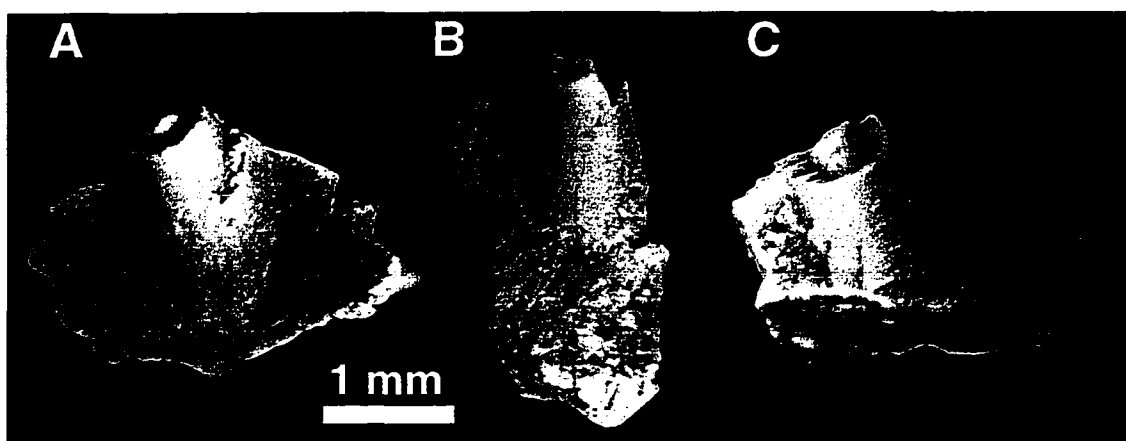


Figure 6

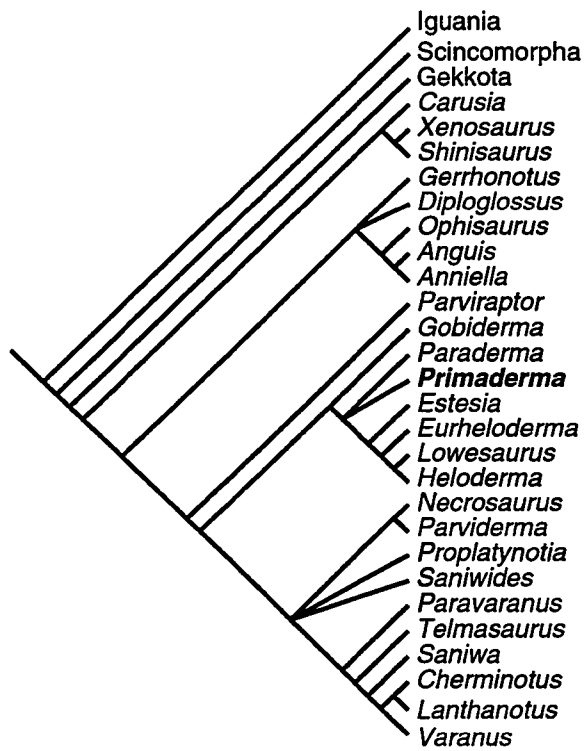


Figure 7

THE MAMMAL-LIKE TEETH OF THE LATE CRETACEOUS LIZARD *PENETEIUS*
AQUILONIUS ESTES 1969 (SQUAMATA, TEIIDAE)

RANDALL L. NYDAM¹, JACQUES A. GAUTHIER², AND JOHN J. CHIMENT³

¹Sam Noble Oklahoma Museum of Natural History, 2401 Chautauqua Ave., Norman,
Oklahoma, 73072; and Department of Zoology, University of Oklahoma, Norman,
Oklahoma 73019

²Department of Geology and Geophysics and Peabody Museum, Yale University, New
Haven, Connecticut, 06520

³Department of Geological Sciences, Cornell University, Ithaca, New York, 14853

Contact info for RLN: voice: (405) 325-4712, FAX: (405) 325-7699, e-mail:
rlnydam@ou.edu.

Suggested running head—NYDAM ET AL.--PENETEIUS TEETH

The teeth of lizards are generally considered to be structurally simple, especially when compared to the complex dentitions of mammals. This simplicity in tooth morphology underscores the relatively simple feeding processes of lizards as opposed to the complex mastication processes in mammals (Smith, 1993). Described herein are new specimens of the Late Cretaceous lizard Peneteius aquilonius. These teeth and jaw fragments show many specializations similar to those found in the molars of tribosphenic mammals. Most notably, the posterior teeth of Peneteius aquilonius are molariform and the upper teeth are shaped quite differently than the lower teeth. These dental specializations provided Peneteius aquilonius with a mechanism for efficient oral food processing. Unlike some crocodilians with “mammal-like” teeth (Clark et al., 1989; Wu et al., 1995) in which food was processed by proal movement of the lower jaw, Peneteius aquilonius appears to have processed food by cutting and crushing in a manner similar to that of an insectivorous mammal.

Institutional abbreviations—MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; UCMP, Museum of Paleontology, University of California, Berkeley, California.

SYSTEMATIC PALEONTOLOGY

REPTILIA LAURENTI. 1768

SQUAMATA Oppel, 1811

TEIIDAE Gray, 1827

PENETEIUS AQUILONIUS Estes, 1969

Holotype—MCZ 3612, left dentary.

Hypodigm—MCZ 3612 (holotype), UCMP 123325 (broken left maxilla), and UCMP 124744 (right dentary).

Referred Specimens—UCMP 124745, maxilla fragment; UCMP 124746, dentary fragment; and UCMP 124747, dentary fragment.

Localities and Horizon—Bug Creek Anthills (type locality) and UCMP locality V73087 (Flat Creek 5), McCone County, Montana; Hell Creek Formation; Upper Cretaceous (Maastrichtian).

Revised Diagnosis—Teiid lizard that differs from all other known lizard taxa in having teeth in posterior one-half of upper and lower tooth rows that are of dramatically different shape. The posterior teeth of dentary have large bases and anteroposteriorly-compressed, transversely-bicuspid crowns with cusps connected by transversely-oriented, U-shaped ridge. Teeth of maxilla have large bases and multicuspid crowns with up to six cusps arranged in three parallel, transversely oriented pairs. Central pair of cusps largest and tallest and connected by sharp, transversely oriented, V-shaped blade. Anterior and posterior cusp pairs smaller, lower, and joined by U-shaped blade.

Description—The dentary of Peneteius aquilonius (Figs. 1A-C) is the most completely preserved element. It is heavily built with a narrow, shallow subdental gutter and tall, robust subdental shelf. Posterior to the seventh tooth position the subdental gutter is completely filled with the expanded bases of the molariform teeth. Meckel's canal is widely open ventromedially in the posterior part of the jaw and turns ventrally and narrows anteriorly, remaining open to the symphysis. The symphysial facet is smooth and directed ventromedially. There are 15 preserved tooth positions on the most complete dentary (UCMP 124744), with 14 subpleurodont teeth that are heavily cemented to the jaw. The total number of teeth is not known, but it is unlikely that more than one or two additional teeth would have been present in UCMP 124744. The anterior teeth are small, conical, and slightly recurved. These teeth have replacement pits at the bases of the first, third, fifth, and seventh tooth positions. The posterior teeth (Fig. 2E) are molariform, transversely oriented,

bicuspid, widely spaced, and become larger posteriorly. The cusps, when unworn, are tall and bluntly pointed. As noted by Estes (1969), the taller labial cusp is offset somewhat posteriorly in relation to the shorter lingual cusp. The cusps are connected by a shallow, U-shaped, transverse ridge, which gives the teeth a forklike appearance. Below the cusps the tooth widens substantially to form shoulderlike expansions on the anterior and posterior sides. These shoulderlike expansions are sloped such that the labial side is shorter than the lingual side. The posterior shoulders on most of the molariform dentary teeth show more wear than do the anterior shoulders. Only specimens of the dentary have teeth with this morphology.

The specimens of maxillae (Figs. 1D-F, 2A-D) are referred to *Teiidae* based on the subpleurodont attachment of the teeth (sensu Estes et al., 1988). Referral to *Peneteius aquilonius* is based on the shared transverse tooth orientation, and the exact, complimentary fit between the upper and lower teeth. No other taxon from the Hell Creek Formation shows the tooth morphology seen in *Peneteius aquilonius*. The maxillae specimens are both incomplete and preserve only the posterior tooth-bearing portion of the element. This portion of the maxillary tooth row has a moderately thick supradental shelf and a wide, shallow supradental gutter. Like the corresponding dentary teeth, the posterior maxillary teeth are molariform and transversely oriented. The bases of the teeth are wide and asymmetrical (labial side is wider than lingual side) in occlusal view. However, the crown morphology of the posterior maxillary teeth is very different from that of the dentary teeth. The crown of each tooth has up to six cusps arrayed in transversely oriented pairs. The central pair of cusps (referred to here as primary cusps) is tall, robust, directed slightly posteriorly, and is connected by a sharp, V-shaped blade. These cusps are more stoutly built than the cusps on the dentary teeth, and the V-shaped blade is much more formidable than the corresponding U-shaped ridge of the dentary teeth. On the anterior and posterior sides of the maxillary teeth are pairs of small accessory cusps. These cusps do not extend

to the tip of the crown and in each pair the labial cusp is taller and more fully developed than the lingual cusp. A shallow, U-shaped blade connects each pair of accessory cusps, completing what is here referred to as the accessory occlusal crest. The anterior accessory occlusal crest is transversely wider than the posterior accessory occlusal crests on all teeth. In occlusal view, the V-shaped and two U-shaped blades form a parallel series of transverse blades tipped by sharp cusps. Only specimens of the maxilla have teeth of this morphology. None of the specimens of Peneteius aquilonius shows any indications (replacement pits, empty tooth spaces) of tooth replacement posterior to the seventh tooth position.

The complex combination of dental features in Peneteius aquilonius has not been found in other lizards and represents a marked divergence from the typical lizard dental pattern of identical, or nearly identical, teeth in the upper and lower marginal tooth rows. Many lizards, particularly those of Teiidae, but also Iguanidae, are known to have heterodont dentitions, but in all of these cases the differences in tooth shape are between the shapes of the anterior (typically conical and recurved) and posterior (typically multicuspid and/or massively blunt) teeth (Edmund, 1969; Presch, 1974). The distinctly different shapes of the upper and lower molariform teeth, as well as the reduced rate/suppression of these teeth, in Peneteius aquilonius is similar to, though not as extreme or complicated as, the molars of tribosphenic mammals (Crompton and Hiiemäe, 1969:fig. 1).

Another similarity with mammals is the relatively precise and “snug” fit of the upper and lower molariform teeth of Peneteius aquilonius. The transverse orientation of the primary cusps and wide spacing of the teeth indicate an alternating occlusal pattern (Fig. 3). When the jaws were closed the primary cusps on the upper and lower teeth would fit into the spaces between the opposing teeth. The ventrolaterally sloped accessory occlusal crests on the upper teeth fit over the corresponding dorsomedially sloping, shoulderlike expansions of the lower teeth. When in full contact the molariform teeth would be “locked” in place by the fit of their complementary shapes. This tooth-to-tooth

relationship in Peneteius is more derived than the simple alternating blades found in the large lizard Polyglyphanodon (see Gilmore, 1942), but is still not as complicated as the fit between upper and lower molars of a tribosphenic mammal (Crompton and Hiiemäe, 1969:fig. 2).

As with that found in mammals (Crompton and Hiiemäe, 1969, 1970; Hiiemäe and Crompton, 1985; Crompton, 1989), the oral food processing in Peneteius aquilonius could be compromised by the effects of the polyphyodont tooth-replacement pattern that is common to lizards. Processing could not occur at empty tooth spaces leading to reduced wear of the two opposing teeth. Also, new teeth would be unworn, causing them to occlude rather than interdigitate, which in turn could prevent the worn neighboring teeth from closing far enough. Peneteius aquilonius avoided these problems through the suppression of replacement of the molariform teeth. As mentioned above, the posterior teeth of Peneteius aquilonius show no signs of replacement. In addition, some of the posterior teeth show advanced stages of wear (Fig. 2D), indicating that they had been in use for long periods of time. In contrast, the most complete jaw (UCMP 124744, dentary) has replacement pits at the bases of the first, third, fifth, and seventh teeth, indicating a more rapid progression of tooth-replacement waves (Edmund, 1969) in the front of at least the dentary tooth row.

The shapes of the molariform teeth in Peneteius aquilonius indicate that it had an oral food processing mechanism unique to lizards. When Peneteius aquilonius closed its jaws (Fig. 3), the primary cusps of the lower teeth would have moved into the spaces between the upper teeth (and vice versa). A food item would initially be punctured and/or crushed by these primary cusps and the U-shaped ridges of the lower teeth would have braced the food item while it was cut by the V-shaped blades of the upper teeth. Further processing of a food item occurred when the accessory occlusal crests of the upper teeth closed down onto the shoulderlike expansions of the lower teeth. If Peneteius aquilonius “chewed” its food (bit each item multiple times), as has been reported for many lizard taxa

(Frazzetta, 1962; Smith, 1984; Throckmorton and Clarke, 1981), the molariform teeth would have effectively processed the food item.

Some taxa of acrodont lizards (e.g., Uromastyx, Agama) exhibit tooth-to-tooth occlusion and have teeth permanently affixed to the top of the jawbone. In these taxa the permanency of the teeth is due to the suppression of the Zahnreihe (Cooper, et al., 1970), with non-chamaeleontids retaining replacement of the anterior caniniform teeth. In these dentitions, teeth are added to the posterior part of the tooth row as the animal grows (Cooper, et al., 1970). This is also the most likely scenario for Peneteius aquilonius, as indicated by the relatively sharper cusps of the sequentially more posterior teeth (e.g., UCMP 123325) and increasing overall size of more posterior teeth.

Peneteius aquilonius differs from the acrodontans, however, in having different and more complex tooth-to-tooth relationships. Acrodontans occlude their teeth to shear food (Cooper et al., 1970; Cooper and Poole, 1973; Throckmorton, 1976). This creates polished wear surfaces on the teeth and in many cases the anteriormost marginal teeth are worn completely away and the jaw bone is incorporated into the occlusal surface (Cooper, et al., 1970; Cooper and Poole, 1973). Sphenodontians are similar to acrodontans in that they show significant tooth-tooth occlusion. The primary difference is that sphenodontians occlude the lower tooth row between maxillary and palatal tooth rows with heavy wear resulting from the unilateral propalinal movement of the lower jaw (Gorniak et al., 1982). The wear surfaces on the teeth of Peneteius aquilonius are pitted and rough (Figs. 2D, E) indicating wear from tooth-to-food abrasion. Also, the wear on the teeth is relatively light with only a dulling of the cusps and blades, but retention of the overall shape of the teeth. This indicates that Peneteius aquilonius had a relatively refined control of tooth position during chewing such that teeth were not damaged from the malocclusion of a misaligned bite.

Mammals overcame the detrimental affects of tooth-to-tooth occlusion and now have a system in which occlusion is used to maintain sharp shearing surfaces. This was

accomplished in part through the evolution of tight genetic controls of tooth shape in higher mammals such that upper and lower teeth are precise complements of each other. Early mammaliaforms (e.g., triconodonts) were more similar to acrodontans in having occlusion that quickly obliterated many crown features (Crompton and Jenkins, 1968). In addition, mammals have a unique feedback system to control tooth position, which is based on mechanoreceptors in the periodontal ligaments that signal malocclusion, allowing for immediate adjustment of bite forces (Lund, 1976; Crompton, 1989). Lizards lack the basic necessities (ligamentous tooth attachment, mechanoreceptors) for such a feedback system.

Intuitively, it would seem that the kinetic nature of the lizard skull, particularly the streptostylic jaw joint, would prevent the repeated and precise interdigitation of the molariform teeth of Peneteius aquilonius. However, acrodontans are able to maintain a degree of occlusal precision in the presence of a streptostylic jaw joint (Cooper and Poole, 1973; Robinson, 1976; Throckmorton, 1976; Throckmorton and Clarke, 1981). This is achieved through a combination of precise control of the muscles of mastication and the manner in which the teeth “lock” together upon contact (Cooper et al., 1970). The locking together of the teeth also results in the extreme tooth wear found in acrodontans. The lack of tooth-to-tooth wear in Peneteius aquilonius suggests that this taxon had an even more precise control of its muscles of mastication or it had a more firmly anchored quadrate similar to that in Iguana iguana (Throckmorton, 1976). Without more complete material this remains speculative.

Because the unique tooth morphology of Peneteius aquilonius has no close modern analogue among lizards, it is not immediately obvious what its diet may have been. The only modern lizards possessing a loosely similar dentition are the teiids Dicrodon and Teius. Their tooth rows are similarly divided into anterior conical, recurved teeth and posterior molariform, transversely-bicuspid teeth. Unlike Peneteius aquilonius, the upper and lower tooth rows of Dicrodon and Teius are identical and tooth replacement is continual. Diet studies of some species of Teius (Milstead, 1961; Acosta et al., 1991) have

supported the interpretation (Presch, 1974) that these lizards are insectivorous. Dicrodon holmbergi is supposedly an obligate frugivore (Holmberg, 1957), but other species of Dicrodon are insectivorous (Schmidt, 1957). Peneteius aquilonius has an estimated snout-vent-length (SVL) of roughly 80 mm (based on dentary size; Goldberg and Nydam, 1999, Nydam and Goldberg, work in progress), well below the 150 mm minimum SVL beyond which lizards can specialize in herbivory (Pough, 1973). The relatively small size of the animal and the similarity in the presumed function of the molariform teeth of Peneteius aquilonius to that of the molars of insectivorous mammals suggests an insectivorous diet for Peneteius aquilonius. Indeed, the evolution of the mammalian molar is believed to be associated with an insectivorous diet (Crompton and Hiiemäe, 1969), and it is reasonable to assume that a similar diet was associated with the convergent acquisition of the many mammal-like features seen in the teeth of Peneteius aquilonius.

New Peneteius material from the Campanian of Utah and Texas, including Manangyasaurus saueri (McCord, 1998), which represents a new species of Peneteius (Nydam, work in progress), indicate that Peneteius had a much longer and wider, temporal and geographic ranges, respectively. The evolutionary implications of the Campanian specimens will be discussed in more detail in a later work.

In summary, Peneteius aquilonius has teeth with a more complicated structure than is known for any other lizard. Peneteius aquilonius is also the first known example of a lizard that has the mammal-like dental features of differential, but complementary morphology and retarded replacement of the upper and lower posterior, molariform teeth. These dental features appear to have given Peneteius aquilonius the ability to more efficiently process food orally.

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FIGURE LEGENDS

FIGURE 1. New specimens of dentary and maxilla of Peneteius aquilonius. **A**, lingual view, **B**, occlusal view, and **C**, labial view of UCMP 124744, right dentary. **D**, lingual view, and **E**, occlusal view, and **F**, labial view of UCMP 123325, broken left maxilla. Scale bar is 1 mm.

FIGURE 2. SEM images of teeth of Peneteius aquilonius. **A-B**, UCMP 123325, broken maxilla; **A**, occlusal view; **B**, detail of second tooth. **C**, Occlusal view of UCMP 124745; **D**, oblique lingual view of heavily worn maxillary tooth on UCMP 124747 (note multidirectional wear striations on surface of crown); **E**, occlusal view of dentary teeth on UCMP 124746. 1-mm scale bar for **A** and 0.5-mm scale bar for **B-E**.

FIGURE 3. Diagrammatic sketch of oral food processing by teeth of Peneteius aquilonius as seen from lingual side of jaw. **A**, Initial contact between food item (hashed) and primary cusps of upper and lower molariform teeth; **B-C**, processing of food item by primary cusps as they close into spaces between opposing teeth and beginning of processing by accessory occlusal structures; **D**, end of processing by primary cusps and final processing by accessory occlusal structures at end of bite. **E**. Diagrammatic view of occlusal relationships of maxillary (bold) and dentary teeth of Peneteius aquilonius based on new specimens (lateral toward top of page). Note alternating positions of primary cusps and slight medial offset of dentary teeth.

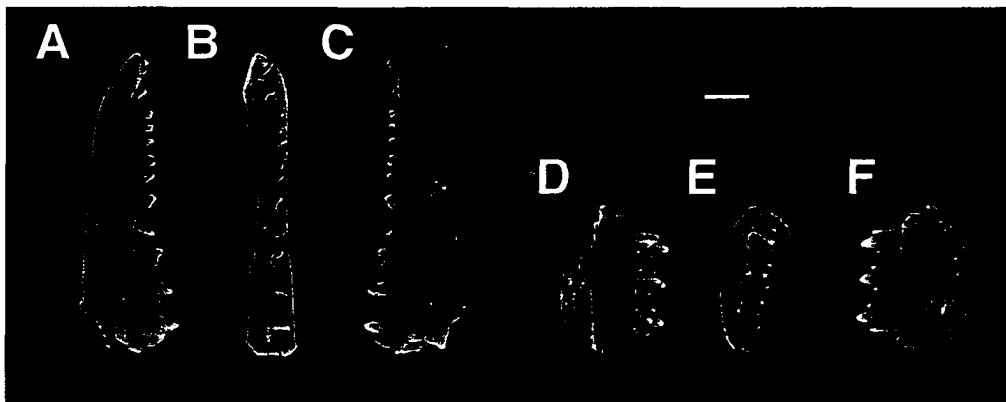


Figure 1

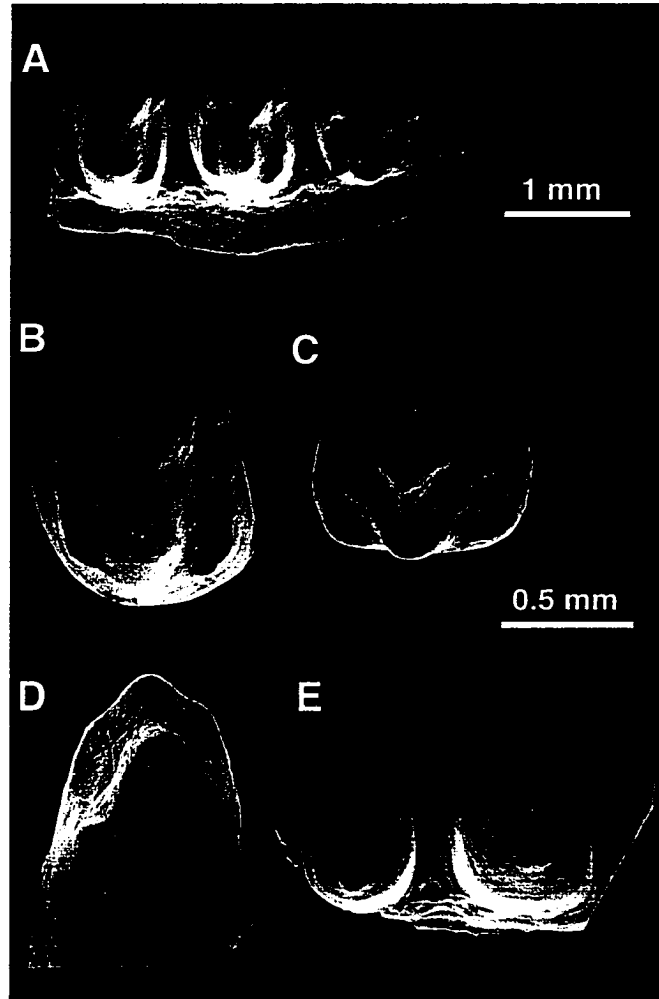


Figure 2

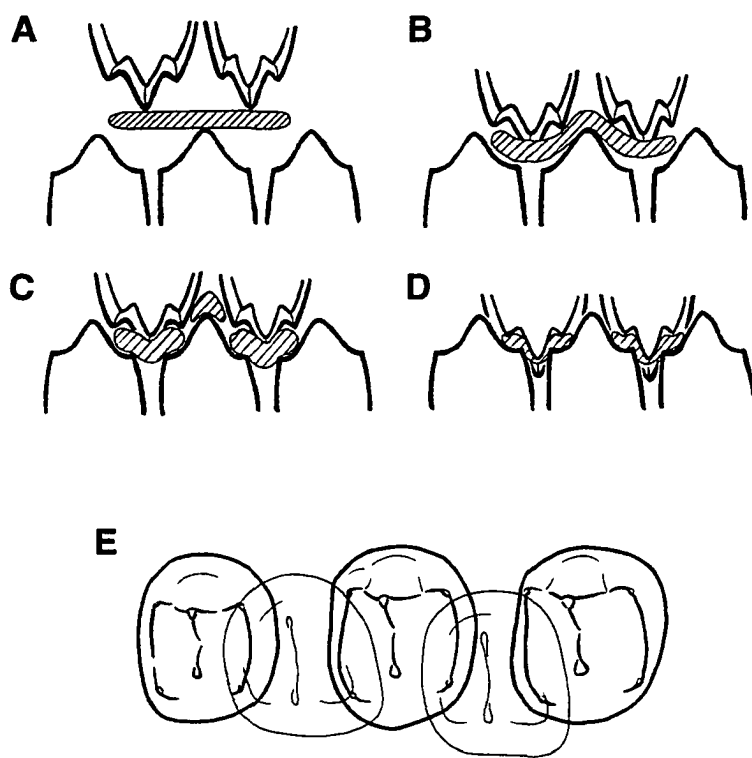


Figure 3

A NEW TEIID LIZARD FROM THE MEDIAL CRETACEOUS OF UTAH

RANDALL L. NYDAM AND RICHARD L. CIFELLI

**Sam Noble Oklahoma Museum of Natural History, 2401 Chautauqua Ave., Norman,
Oklahoma, 73072; and Department of Zoology, University of Oklahoma, Norman,
Oklahoma 73019**

**Contact information for RLN: voice: (405) 325-4712, FAX: (405) 325-7699, e-mail:
rlnydam@ou.edu.**

Suggested running head—NYDAM AND CIFELLI—NEW CRETACEOUS TEIID

ABSTRACT--A new taxon of teiid lizard, recovered from the Cedar Mountain Formation (Albian-Cenomanian) of Emery County, Utah, is the oldest reasonably well represented teiid known. This new taxon has a heterodont dentition with conical anterior teeth and transversely oriented bicuspid posterior teeth that are distinct from those of Peneteius (Late Cretaceous) and Teius and Dicrodon (Recent). It also shows ontogenetic variation in tooth shape, in which the posterior teeth become more massive and have more transversely expanded crowns, as the individual grows older. Further comparisons and analysis indicate (1) that North American Cretaceous Polyglyphanodontinae (characterized by teeth with transversely-oriented crests) achieved their unusual dental specializations independently from those of analogous modern taxa; (2) that their transverse tooth-cresting resulted from addition of a medial cusp (rather than crown rotation, as previously hypothesized and which apparently is the case for living taxa); (3) and that the species from the Cedar Mountain Formation represents a sister-taxon to remaining North American Polyglyphanodontinae (Polyglyphanodon, Paraglyphanodon, Dicothodon, Peneteius). The new taxon thus represents an example of the morphologically antecedent dental specializations that culminated in the strikingly modified and unique dentition of Polyglyphanodon sternbergi.

INTRODUCTION

With a single exception, the fossil record of teiid lizards from the Mesozoic of North America is restricted to the Late Cretaceous. These Late Cretaceous records represent a wide array of taxa in which differences in tooth morphology have figured prominently in interpretation of phylogenetic relationships (Estes, 1983). Within the Late Cretaceous, fossil teiids are known primarily from the Campanian and Maastrichtian (Estes, 1983; Gao and Fox, 1996), with very few occurrences from older rocks. Polyglyphanodontine teiids have been reported from the Turonian and Albian-Cenomanian of Utah (Nydam, 1999), and the oldest record of the family Teiidae consists of two jaws from the Aptian of Texas (Winkler et al., 1990). In each of these cases the specimens are incomplete (broken jaws, teeth) and rare in their respective faunas.

Herein we report on a new taxon of teiid lizard from the Cedar Mountain Formation (Albian-Cenomanian) of Utah. This new teiid is the most common lizard in the newly described Mussentuchit local fauna (Cifelli et al., 1999) and is represented by numerous specimens, including complete jaws and elements from juvenile individuals. Hence, it is of special interest in being relatively well-represented, with the available sample permitting some assessment of variation within the tooth row, ontogenetic changes, and intraspecific variation. Furthermore, despite its age, the new teiid appears to be derived in having a dentition that is heterodont, with posterior teeth that are transversely developed and complex, unlike the simple, unicuspid teeth found in the somewhat older teiids from Texas. In these respects, it is relevant to consider the new taxon in the context of teiids known from later in the Cretaceous, most notably the Polyglyphanodontinae, which are also found in Asia and which are thus of biogeographic

interest (Gilmore, 1940, 1943a, 1943b; Sulimski, 1972, 1975, 1978; Estes, 1983; Nydam, 1999).

All specimens described herein are deposited at the Sam Noble Oklahoma Museum of Natural History (OMNH). Numbers preceded by a “V” are OMNH vertebrate fossil localities. Detailed information on these localities is on file at OMNH and is available to qualified investigators upon request. Other abbreviations: MCZ, Museum of Comparative Zoology, Harvard University; MVZ, Museum of Vertebrate Zoology, University of California, Berkeley; UCMP, University of California, Berkeley.

GEOLOGICAL SETTING

The Cedar Mountain Formation is comprised of variegated, terrigenous rocks that are exposed in central and eastern Utah, continuing on into western Colorado in the form of its lateral equivalent, the Burro Canyon Formation (Stokes, 1944, 1952; Tschudy et al., 1984; Kirkland et al., 1997; Currie, 1998). The mudstones initially described as the Cedar Mountain Formation by Stokes (1944) are now, under an expanded definition (Stokes, 1952), considered to represent the upper part of the unit. Recent lithological and paleontological studies have resulted in the formal recognition of four new members (Kirkland, et al., 1997), for a total of five named members within the formation.

Dinosaurs are known from a number of horizons within the Cedar Mountain Formation, which may span the Barremian to lower Cenomanian (Kirkland et al., 1999). However, microvertebrates are known only from the uppermost, or Mussentuchit Member. Major exposures for this member lie principally on the west side of the San Rafael Swell, a prominent anticline in the region. The Mussentuchit Member is 25 m thick at its type

locality, but is variable in thickness throughout the region. It is composed of highly smectitic gray-green mudstones with interbedded channel sandstones (Kirkland, 1987; Cifelli, et al., 1999). The environment of deposition of the Mussentuchit Member is interpreted as having been overbank, or crevasse splay, deposits associated with multiple flood events in a meandering river system (Nelson and Crooks, 1987). Microvertebrate localities occur in a narrow stratigraphic interval in the upper part of the unit, 10-20 m below the contact with the overlying Dakota Formation. Multiple, concordant radiometric determinations from two of the localities (in direct association with the fossil horizon at V695, the principal site) yield an age of 98.39 ± 0.07 Ma for the fauna (Cifelli et al., 1997), placing it at the Albian-Cenomanian (Early-Late Cretaceous) boundary (Gradstein et al., 1995).

SYSTEMATIC PALEONTOLOGY

REPTILIA

SQUAMATA

TEIIDAE Gray, 1827

BICUSPIDON, gen. nov.

Etymology—L., bi, two; cuspis, cusp; dens, tooth (Brown, 1956). Name in reference to bicuspid morphology of posterior, molariform teeth of upper and lower jaws.

Type and Only Species—Bicuspidon numerosus, sp. nov.

Distribution—Mussentuchit Member of Cedar Mountain Formation (medial Cretaceous), Emery County, Utah.

Diagnosis—as for type and only known species.

BICUSPIDON NUMEROSUS, sp. nov.

(Figs. 2, 3, 5A)

Etymology—L., numerosus, plentiful. Name in reference to common occurrence of taxon in Mussentuchit local fauna.

Holotype—OMNH 26743, a nearly complete left maxilla missing only posteriormost portion of element.

Referred Specimens (Listed by Locality) —V235: OMNH 25565, tooth; 25567, tooth; 25568, tooth; 25569, tooth; 34312, jaw fragment. V238: OMNH 26331, tooth. V239: OMNH 26215, jaw fragment; 26216, jaw fragment; 26228, lot of five isolated teeth; 26229, jaw fragment; 32446, tooth. V240: OMNH 26289, jaw fragment. V695: OMNH 26745, tooth; 26747, jaw fragment; 26750, jaw fragment; 26813, lot of three isolated teeth; 26815, tooth; 26817, tooth; 27707, broken left maxilla; 27708, broken left dentary; 27709, broken right dentary; 27710, maxilla fragment; 27712, broken left dentary; 27728, jaw fragment; 27736, jaw fragment; 27737, jaw fragment; 27757, jaw fragment with three teeth and replacement tooth crown in replacement pit; 27759, tooth; 27760, tooth; 27881, tooth; 27882, tooth; 27886, jaw fragment; 27887, jaw fragment; 27900, right dentary with 18 tooth positions; jaw fragment; 27925, jaw fragment; 28069, broken left dentary with articulated splenial; 28070, broken left dentary; 28073, broken

right dentary; 28113, jaw fragment; 28118, broken right maxilla; 28128, broken right dentary; 28129, tooth; 28531, lot of 15 isolated teeth; 28688, jaw fragment; 28689, lot of 5 isolated teeth; 29632, jaw fragment. V794: OMNH 28020, lot of 3 isolated teeth; 29633, jaw fragment; 30462, lot of 4 isolated teeth; 34561, left dentary. V801: OMNH 27969, jaw fragment; 27992 lot of 2 isolated teeth. V868: OMNH 22111, jaw fragment; 22112, jaw fragment; 22113, tooth; 22114, jaw fragment; 22117, jaw fragment; 22143, broken left maxilla; 22144, jaw fragment; 22145, jaw fragment; 22146, jaw fragment; 22147, jaw fragment; 32638, jaw fragment; 32432, tooth; 33435, tooth; 33436, tooth; 33437, tooth; 33918, jaw fragment.

Localities and Horizon—OMNH localities V235, V238, V239, V240, V694, V695 (type locality), V794, V801, V868 (Fig. 1). All localities are 10-20 m below upper contact of Mussentuchit Member of Cedar Mountain Formation and Dakota Formation, Emery County, Utah.

Diagnosis—Similar to fossil teiids Peneteius, Dicothodon, Polyglyphanodon, and Paraglyphanodon, and extant teiids Dicrodon and Teius, in having transversely oriented, bicuspid teeth in posterior part of marginal tooth rows. Differs from Peneteius in having pleurodont rather than subacrodont teeth and in having dentary teeth without shoulder-like expansions below crowns and more sharply pointed cusp apices, and maxillary teeth with only two cusps. Differs from Dicothodon in not having anterior and posterior accessory blades and associated basins. Differs from Polyglyphanodon and Paraglyphanodon in having medial and lateral cusps connected by V-shaped blade, as opposed to horizontal blade, and in that teeth not greatly expanded mediolaterally. Differs from Teius and Dicrodon in having well-defined, straight sided, V-shaped blade

between the cusps and in having cusps with flat, not rounded, internal surfaces.

Description

Maxilla—OMNH 26743 (holotype, Fig. 2A-C, F) is a small (8.97 mm long) left maxilla missing only its posteriormost tip. The nasal process occupies the anterior two-thirds of the maxilla, is triangular in lateral view, turns medial anteriorly, and is vertical posterior to the dorsal apex. The external surface is unornamented, though it has a rough texture. A single exterior superior alveolar foramen is present above the eleventh tooth position. The premaxillary process of the maxilla is forked, with the lateral prong directed anteromedially and the medial prong directed dorsolaterally. The medial prong has a dorsal ridge that is continuous with the anterior edge of the nasal process and that defines the ventral, lateral, and part of the medial borders of the external naris. The supradental shelf is mediolaterally wide along the entire length of the maxilla, dorsoventrally narrow, and weakly arched. The anterior edge of the supradental shelf turns dorsally to become the medial edge of the medial prong of the premaxillary process. The tooth row is also weakly arched, but the dorsal apex of the arch is more anterior than that of the supradental shelf. There are 13 tooth positions and 11 teeth are present. Based on the shape of the tooth in the last preserved tooth position (see below), the tooth row is probably complete or, if not, is or missing only a single tooth.

Mandible—Numerous specimens of Bicuspidon consist of dentary fragments, but there is only one complete dentary (OMNH 27900; Fig. 2D, E). One specimen, OMNH 28069, preserves part of the splenial articulated with the dentary. None of the postdentary bones are known. The dentary is heavily built in larger individuals but is

more gracile in smaller individuals (e.g., OMNH 27900, tooth row 7.4 mm long). The subdental shelf is tall and the subdental gutter is deep and well developed anteriorly, but it is narrow and filled by the bases of the large, molariform teeth in the posterior portion of the tooth row. Meckel's groove is large and open to the symphysis (presumably to accommodate a hypertrophied splenial). It is directed ventrally in the anterior part of the dentary, turning medially toward the posterior end of the element. The symphysis is small and simple. Based on OMNH 28069, in which the splenial is preserved, the dentary is convex laterally and the splenial is weakly concave medially, giving the mandible a moderate concavo-convex shape. The splenial has both mylohyoid and anterior inferior alveolar foramina that open ventromedially below the more molariform teeth that lie posterior to the midpoint of the tooth row. There are 18 tooth positions on the only complete dentary that, if all teeth were present, would be occupied by nine conical and nine bicuspid teeth. Although poorly preserved, OMNH 27900 retains most of the articulation facets for the postdentary bones. There is a small, triangular facet on the dorsolateral surface of the dentary for the anterolateral process of the coronoid. The facet indicates that this process extended anteriorly to the posteriormost tooth position. A similar facet on the medial side of the element, posterior to the posteriormost tooth position, represents the articulation with the anteromedial process of the coronoid.

Teeth—The teeth of Bicuspidon (Figs. 2, 3) are, like those of many of the Teiidae, heterodont. All of the teeth in the dentary and maxilla are subpleurodont and cemented to the jaw with a heavy deposits of cementum (a teiid synapomorphy, Estes et al., 1988). Some specimens have empty tooth positions or deep, subcircular replacement pits at the bases of the teeth. This type of replacement pit is also a diagnostic characteristic of

Teiidae (Estes et al., 1988). Specimen OMNH 27757 not only preserves one of these replacement pits, but also the crown of a replacement tooth within the replacement pit (Fig. 2G). The anterior portion of the tooth row (first five to seven teeth) has conical, recurved teeth, with those of the maxilla being more recurved and caniniform than those of the dentary. In the two maxillae that preserve the anterior portion of the element (holotype OMNH 26743 and OMNH 28818) the third and fourth tooth positions are occupied by caniniform teeth that are significantly larger than the preceding teeth (3rd tooth position of OMNH 26743 is empty). The fifth tooth is dramatically smaller than the caniniform teeth and creates a step in the tooth row similar to that seen in some modern teiids (Estes, 1969: fig. 3). At tooth position 5 in the maxilla and by at least tooth position 9 or 10 of the dentary there is also a change from a conical, recurved tooth shape to a conical, unrecurved tooth shape. The size of these unrecurved teeth increases posteriorly from the fifth position, with each successive tooth being larger and more widely separated from adjacent teeth. The crowns of some of these bicuspid teeth (particularly those posterior to 8th tooth position in the maxilla and 12th position in dentary) are slightly compressed anteroposteriorly, giving the tooth a “pinched” appearance. This “pinching” of the crown is similar to, though not nearly as strongly developed, as that seen in the teeth of Peneteius aquilonius (see Estes, 1969: fig. 1). The most striking feature of these unrecurved teeth is the structure of the crowns.

Beginning with the 7th maxillary and approximately 10th dentary tooth positions, and continuing posteriorly, the tooth crowns of Bicuspidon become transversely bicuspid, with the appearance of a small medial cusp that is connected to the lateral cusp by a sharp, V-shaped, transverse ridge. On each successive posterior tooth (except at very end

of tooth row) this cusp becomes larger and more anteroposteriorly expanded, such that the last five to six tooth positions of the maxilla (Fig. 2F) and dentary (Fig. 2D) have transversely oriented, bicuspid crowns with widely spaced lateral and medial cusps. The posteriormost two tooth positions in the dentary (not preserved on any of the maxillae) are more like the anteriormost bicuspid teeth in that the medial cusp is small and not greatly separated from the lateral cusp. The larger lateral cusp is flanked on both the anterior and posterior sides by offset ridges, or carinae, that wrap dorsomedially around the tooth, but do not contact the medial cusp. Smaller carinae also descend from the medial cusp turning dorsolaterally towards the carinae of the medial cusp. The carinae from each cusp do not meet. The medial surface of the lateral cusp is divided into two flat facets by the transverse ridge. On some teeth these facets are weakly crenulated (Fig. 3A), whereas other teeth are missing the crenulations due to abrasive wear (Fig. 3B).

DISCUSSION

Variation in tooth shape

Bicuspidon is represented by numerous specimens, ranging from isolated teeth to complete jaws of varying sizes. Assuming that the smaller specimens represent younger individuals, and not sexual dimorphism (see below), the sample shows that tooth shape changed ontogenetically. The jaws of smaller, presumably juvenile, Bicuspidon have posterior bicuspid teeth that are conical in overall shape, with a small, triangular medial cusp that is offset from the body of the tooth well below the apex of the larger lateral cusp. In larger specimens (presumably from older individuals), the teeth retain an overall conical shape, but the crown morphology changes. The medial cusp becomes

correspondingly larger and taller until it is nearly the size of the lateral cusp. Although it increases in size, the medial cusp is never wider or taller than the lateral cusp. In addition to becoming larger, the medial cusp of some, but not all, of the posterior teeth expands anteroposteriorly to form a weakly trifid blade (Fig. 3B). The distance between the lateral and medial cusps also increases with increasing jaw size (Fig. 4), such that the teeth of the largest specimens have a wide occlusal surface broadly similar in appearance to that of Dicothodon (Nydam, 1999:figs. 5 and 6). Because of the lack of specimens preserving the anteriormost teeth, it is not clear what (if any) ontogenetic changes occur among the anterior teeth of Bicuspidon.

Many lizards are known to have ontogenetic variation in tooth form (Lönnerberg, 1903; Presch, 1974b; Estes and Williams, 1984; Dessem, 1985). This change in shape is usually from smaller teeth in juveniles to larger, more blunt teeth in adults (Estes and Williams, 1984). Within Teiidae, ontogenetic variation of the dentition is best documented for Tupinambis teguixen, T. nigropunctatus (see Dessem, 1985), and Ameiva exul albogutta (see Estes and Williams, 1984). In all of these taxa, as the animal ages, the teeth in the posterior portion of the tooth row enlarge, and accessory cusps are typically reduced and/or lost. Hence, Bicuspidon differs from T. teguixen, T. nigropunctatus, and A. exul albogutta in that many of the posterior teeth become more complex ontogenetically, with the development of a trifid medial cusp. However, Bicuspidon is similar to most lizards with ontogenetic variation in tooth shape in that the posterior teeth do become more massive, or molariform, as the animal grows. As pointed out by Estes and Williams (1984) and Dessem (1985), there is not always an obvious dietary change associated with ontogenetic changes in tooth shape in lizards. Because the

teeth of Bicuspidon are so unusual for a lizard and because teiids tend to be dietary generalists, an interpretation of the diet of Bicuspidon is not attempted here.

Another possible explanation for differences in tooth shape with increasing size is sexual dimorphism. Sexual dimorphism is common to lizards within Iguania (e.g., Fitch, 1977), but has also been noted for teiids, particularly in relation to sexual selection (Anderson and Vitt, 1990). Unfortunately, although numerous, the specimens of Bicuspidon numerosus are too fragmentary to obtain a sufficient number of repeatable, comparative measurements to statistically determine the presence of sexual dimorphism.

Relationships of Bicuspidon

Bicuspidon clearly is related to Teiidae, with which it shares a hypertrophied splenial, subcircular, basal tooth replacement pits, and heavy cementum at tooth bases, characters that have been identified as teiid synapomorphies (Estes, et al., 1988 and references therein). The heterodont dentition of Bicuspidon, with transverse development of posterior teeth, is an obvious similarity to Teius and Dicrodon, the only two Recent genera that exhibit this condition and, notably, to North America Cretaceous teiids placed in the subfamily Polyglyphanodontinae. Polyglyphanodon itself is a large lizard with strongly modified cheekteeth from the Maastrichtian of Utah. Gilmore (1943b) initially placed Polyglyphanodon in the new family Polyglyphanodontidae within the Ascalobata (polyphyletic combination of taxa now separated into Iguania and Gekkota). Teiid affinities for the genus were suggested by Hoffstetter (1955) and corroborated by Estes (1983) on the basis of four osteological synapomorphies: quadrate process of pterygoid expanded, absence of pterygoid teeth, divergent process on autotomous vertebrae, and

medially expanded teeth. Estes (1983) also noted that the structure of the maxilla, retroarticular process, and construction of the lower jaw of Polyglyphanodon is very similar to that of Teius and Dicrodon.

Estes (1983) placed Polyglyphanodon and the other North American and Asian polyglyphanodontines in the teiid subfamily Polyglyphanodontinae based the presence of osteological characters in these taxa that are primitive to the rest of the Teiidae (e.g., presence of a parietal foramen, 27-29 presacral vertebrae, arrangement of scapular fenestrae, caudal vertebrae with short, non-divergent processes on either side of the autotomy septa anteriorly, posterior process absent on posterior caudals).

Polyglyphanodon has since been reported from the Campanian of Baja California (Estes, 1983; Nydam, 1999). Other North American taxa included in the subfamily include Paraglyphanodon (generally considered a variant of Polyglyphanodon; Estes, 1969, 1983) from the Maastrichtian of Utah (Gilmore, 1940; 1942; 1943b), Dicothodon from the Albian-Cemomanian and Turonian of Utah (Nydam, 1999); and Peneteius from the Campanian of Utah and the Maastrichtian of Montana (Estes, 1964). Manangyasaurus saueri, described from the Campanian of Utah (McCord, 1999), is based on an upper dentition clearly referable to Peneteius, though specifically distinct from P. aquilonius, the type species (see Nydam et al., in press). In addition, a diverse array of taxa from the Campanian of Mongolia have been referred to the Polyglyphanodontinae, based largely on cranial characteristics (see Estes, 1983). Notably, the dentitions of the Asian taxa vary widely and, in general they are quite distinct from those of North American taxa.

A review of the relevant literature (Gilmore, 1942; Sulimski, 1975, 1978) indicates that polyglyphanodontines possess nearly all of the 8 cranial synapomorphies

(3-9, 11) of the 14 teiid synapomorphies listed by Estes et al. (1988) that can be determined from the figures and descriptions. Of these the presence or absence of synapomorphy 6 (origin of adductor musculature on dorsal surface of parietal) is indeterminate for Darchansaurus, Adamisaurus and Erdenetesaurus and is absent in Polyglyphanodon. Also, Polyglyphanodon has suppressed tooth replacement (Gilmore, 1942; Nydam, 1999) and it therefore does not exhibit deep, subcircular replacement pits (synapomorphy 7 of Estes et al., 1988) as is found in all of the other taxa. The presence of elongate vomers that approach the pterygoids is indeterminate in Erdenetesaurus and absent in Adamisaurus, but is present all of the other taxa. Based on the possession of these synapomorphies, inclusion of the polyglyphanodontine lizards in Teiidae (sensu Estes et al., 1988) and the absence of some of these synapomorphies in some taxa is likely due to either reversals or secondary specializations.

Although monophyly of Teiidae is well supported (Estes, et al., 1988), few analyses have been aimed at resolving relationships within the group. A significant obstacle to interpretation is that, with the exception of Polyglyphanodon itself, North American taxa are known by little more than jaw fragments or teeth. Clearly, any hypothesis of relationships for these taxa must be regarded as highly tentative. The only existing data set that is appropriate in this context is that of Denton and O'Neil (1995), which includes 30 characters for fossil and modern Teiidae. In order to evaluate the suspected affinities of Bicuspidon with respect to Polyglyphanodontinae and living teiids, we performed phylogenetic analysis using a modified version of the data presented by Denton and O'Neil (1995). We made some significant revisions in scoring of taxa; brief explanations follow.

Character 18, presence or absence of a heterodont dentition, has been rescored to reflect the fact that the dentitions of Callopietes, Cnemidophorus, Kentropyx, and Teius are not homodont but heterodont. In all of these taxa, the anterior teeth are conical, whereas those at the back of the jaw are multicusped, as is typical of the heterodonty found in nearly all Recent Teiidae. Dracaena is more problematic: it has large, conical anterior teeth and massive crushing teeth posteriorly, in association with its durophagous diet. Despite the fact that multiple cusps are not present posteriorly, dramatic differences separate these teeth from those at the front of the jaw. We consider Dracaena also to be heterodont.

Similarly, we have modified scoring for character 19, medial expansion of the posterior dentition. Teius and Dicrodon are the only modern lizards that exhibit this unusual pattern. For the fossil taxon Cherminisaurus (Mongolia), the state cannot be determined. Its teeth are completely different: they are obliquely rather than transversely placed in the jaw, and there is no basis for establishing homology with what is seen in other taxa. The only basis for scoring this character as present in Cherminisaurus (Denton and O'Neil, 1995) would appear to be an assumed model of character change, in which this taxon is viewed as having teeth that are transitional between the anteroposteriorly aligned crowns of Macrocephalosaurinae (Asia) and North American Polyglyphanodontinae (sensu Estes, 1983). Lacking a morphological basis for this assumption, we prefer to establish a new state, "oblique," for teeth of Cherminisaurus. By assuming the character to be undirected, this coding leaves open the possibility for either hypothesis (the state in Cherminisaurus being transitional or something quite different).

Note that the distinctive pattern of North American polyglyphanodontine teeth was established at least 20 Ma prior to the appearance of Cherminsauros.

A further revision in coding for Cherminsauros is needed for character 26, mode of tooth attachment. Based on published figures (Sulimski, 1975:fig. 14A3, pl. XXIV-2a), the teeth of Cherminsauros are not “pseudothecodont” (Denton and O’Neil, 1995), but clearly subpleurodont (state 1), with substantial exposure of the medial sides of the teeth below the level of the lateral parapet of the jaw.

Character 29 refers to the shape of the anterior teeth of the maxilla. The anterior teeth of Teius and Dicrodon are typical of teiids in being simple and conical, grading posteriorly (by middle of tooth row) into bicuspid teeth (state 2 rather than 1 as originally coded).

The last character, 30, codes for the presence or absence of medial striae on the teeth. Such striae are present not only in Chamops and Prototeius, as indicated by Denton and O’Neil (1995), but also in living Dracaena. Significantly, they are also present in the oldest known teiid unnamed), from the Aptian of Texas (Winkler et al., 1990), as well as on teeth of relevant outgroup taxa such as paramacellodids, cordylids, and scincids. Given this distribution, we follow Gao and Fox (1996) in considering the presence (not absence) of medial tooth striae as primitive for Teiidae. In addition to making the foregoing emendations, we have rooted the analysis with Gekkonidae as the outgroup, which was scored based on the character analysis of Estes et al. (1988) and observation of a skeleton of Uroplatus fimbriatus (Nydham comparative collection). All characters with more than two character states were treated as unordered.

McCord (1998) added two characters to those evaluated by Denton and O'Neil (1995). However, coding of states was ambiguous and, thus, we did not include these characters in our analysis.

We were able to score Bicuspidon for 9 of the 30 characters (Table 1) from the modified data set of Denton and O'Neil (1995). In addition to Bicuspidon, we also included Peneteius, another Cretaceous teiid with transversely oriented teeth (Estes, 1969; Nydam et al., in press). Dicothodon was not included in our analysis as it is only known from three teeth. Peneteius was scored based on specimens MCZ 3612, UCMP 123325, UCMP 124744 UCMP 124745, UCMP 124746, and UCMP 124747 (Nydam et al., in press). A heuristic analysis was performed with the program PAUP 4.0b4a (Swofford, 2000). This resulted in 2 equally parsimonious trees of length 55, consistency index of 0.66, and a retention index of 0.83. Bicuspidon is placed as the sister taxon to the dichotomous clade containing Polyglyphanodon and Peneteius in both of the trees produced in the analysis (Fig. 4). Using MacClade (Maddison and Maddison, 1992) tooth shape and orientation was traced on the resulting trees in order to determine the possible evolutionary patterns of these traits (see below).

Interestingly, the Asian polyglyphanodontines Cherminsauros and Macrocephalosaurus either 1) form a clade that is the sister taxon to the clade containing Bicuspidon, Polyglyphanodon, and Peneteius, or, 2) are successive sister taxa to the clade containing Prototeius and Chamops. The low CI value for the trees produced by this analysis reflects the large amount of missing data for most of the fossil taxa and indicates that any interpretations based on these results should be considered as tentative.

Though the trees are not robust, there are some interesting evolutionary patterns suggested by the two equally parsimonious trees. The position of Bicuspidon as a member of, or closely related sister taxon to, the North American polyglyphanodontines provides additional evidence that transversely toothed teiids were present in North America by end of the Early Cretaceous. Also, Teius and Dicrodon are placed well within the clade of Recent teiid taxa, suggesting that the transverse orientation of their teeth is convergent with and not homologous to the transverse teeth of the fossil taxa from North America (contra Estes, 1969; 1983). Another interesting result of the analysis is the reconstruction of the relationship of the fossil and extant teiid taxa. The fossil taxa comprise a sister clade to the clade made up of the Recent teiid taxa suggesting that the two groups diverged prior to the medial Cretaceous and that care should be taken when referring fossil taxa to the teiine tribes of Presch (1974a).

The irregular placement of Cherminsauros and Macrocephalosaurus is likely the result of missing data in some of the fossil taxa. Certainly there is a need for more work to help resolve the interrelationships of the known polyglyphanodontine and teiinine (taxonomy following Estes [1983]) taxa from the Cretaceous.

Below we present a discussion of the evolution of tooth types among Teiidae based on morphological and ontogenetic considerations. Given the paucity of data relevant to phylogenetic relationship, and the fact that these data are based mainly on tooth morphology, we reiterate that interpretation is limited and regarded as tentative.

Ancestral tooth shape and cusp homology in Teiidae

The most common tooth arrangement found in modern teiids (as well as other

groups such as Iguania) is a heterodont tooth row with anterior conical, recurved teeth and posterior teeth that have two or three anteroposteriorly-arranged cusps. The only exceptions being the massive teeth of Dracaena and the transversely bicuspid teeth of Dicrodon and Teius (Presch, 1974b). The number and relative sizes of these teeth vary (Presch, 1974b; Estes and Williams, 1984; Dessem, 1985), but in general they are very similar from taxon to taxon. When tooth shape and orientation is mapped onto the cladograms generated by the phylogenetic analysis (Fig. 5), the tooth type of the most recent common ancestor of the Recent and Cretaceous taxa is anteroposteriorly oriented and multicuspid. Based on this distribution of tooth types transversely oriented teeth arose independently in Teiidae two times; once in Polyglyphanodon, Peneteius, and Bicuspidon and again in Teius and Dicrodon. Examination of the tooth rows of Teius teyou (MVZ 92989), Dicrodon guttulatum (MVZ 58401), and Bicuspidon numerosus (OMNH 26742) gives an indication of the different mechanism by which this transformation occurred in these taxa. In both the upper and lower tooth rows of T. teyou and D. guttulatum, the anterior teeth are conical and slightly recurved. At the 10th-12th maxillary and 12th dentary tooth position of the T. teyou specimen, as well as the 7th maxillary and 6th dentary tooth positions of D. guttulatum specimen, the teeth become bicuspid, with the appearance of a small cusp on the anteriomedial surface of the tooth crown (Fig. 6A,B). In succeeding teeth, this second cusp becomes progressively more medially situated, so that it is completely medial within two to five tooth positions in the specimens studied, suggesting that the transversely bicuspid tooth form in Teius and Dicrodon developed by the progression of an anterior accessory cusp (typically the second cusp to appear in multicuspid teiids) to a medial position.

Estes (1983) used a similar model, though not explicitly based on the modern taxa, to explain the evolution of transversely oriented teeth in Polyglyphanodon. He concluded that the oblique angle of the teeth of Cherminsauros represents a transitional stage between the anteroposteriorly directed teeth found in most Asian polyglyphanodontines (Macrocephalosaurus, Erdenetesaurus, Darchansaurus) and the fully transverse teeth of Polyglyphanodon and Paraglyphanodon. The morphology of the teeth of Bicuspidon suggests an alternative hypothesis.

The medial cusp on the posterior teeth of Bicuspidon appears to represent a neomorph, not homologous to the anterior cusp of modern Teiidae and, thus, not arising through simple tooth rotation. In Bicuspidon, the secondary cusp is uniformly medial in position on all of the teeth in which it is present (Fig. 6C). Both Polyglyphanodon and Peneteius share with Bicuspidon teeth that are uniformly transverse in orientation (Gilmore, 1942; Nydam et al., in press). This contrasts with the condition described above for T. teyou and D. guttalatum, in which the secondary cusp appears anteriorly in those teeth at the front of the jaw, but is increasingly medial on succeeding teeth. The consistent medial position of the second cusp on the teeth of Bicuspidon, Polyglyphanodon, and Peneteius suggests that this second cusp initially developed in this position and was not derived from rotation of an anteroposteriorly-oriented tooth. Therefore, the transverse teeth of Bicuspidon, Polyglyphanodon, and Peneteius, and Dicrodon and Teius, as well as the obliquely oriented teeth of Cherminsauros, almost certainly represent three independent evolutionary events.

Comparison with similar taxa

As indicated by the phylogenetic analysis, Bicuspidon is closely related to North American Cretaceous Polyglyphanodontinae, with which it shares transverse development of the posterior teeth. Previously described members of this group include Polyglyphanodon and (dubiously distinct) Paraglyphanodon (Gilmore, 1940, 1942, 1943b; Nydam, 1999), Peneteius (Estes, 1969; McCord, 1998; Nydam et al., in press), and Dicothodon (Nydam, 1999). One of the similarities among the teeth, in addition to transverse orientation, is the shared possession of a central blade connecting the medial and lateral sides of the teeth, as well as the anterior and posterior accessory structures of the teeth. The distribution of these features on the known Cretaceous taxa suggests the existence of two different evolutionary paths for the North American polyglyphanodontine taxa. The V-shaped central blade seen in Bicuspidon is also found in the low-crowned, massive teeth of Dicothodon (Nydam, 1999:figs.5 and 6A-D), which also have semicircular accessory blades that border anterior and posterior basins. Compared to Bicuspidon, the tooth morphology of Dicothodon (medial expansion, larger size) appears to be derived and part of a trend of increasing tooth size, which has its next intermediate step in Polyglyphanodon bajaensis (Nydam, 1999:fig. 4) and that culminates in P. sternbergi (Gilmore, 1942:figs. 19-22; Nydam, 1999:fig. 6E,F). Dicothodon moorensis and Bicuspidon numerosus are contemporary taxa, both having been recovered from the Mussentuchit Member of the Cedar Mountain Formation, which indicates that the establishment of medially bicuspid teeth predates the Albian-Cenomanian.

The second pattern is one of increasing tooth complexity as seen in the teeth of Peneteius. The maxillary teeth of Peneteius also have a V-shaped blade (Nydam, et al., in

press), but they are not like the low-crowned, massive teeth, characteristic of Dicothodon and Polyglyphanodon. Instead, the teeth of Peneteius are specialized relative to those of Bicuspidon in having complicated accessory cusps and differential morphology of the upper and lower teeth. These features comprise a sophisticated masticatory system, unique among lizards, that is remarkably analogous to specializations of the mammalian dentition (Nydam et al., in press).

The Asian polyglyphanodontines have dentitions strikingly different from those of the North American taxa (Fig. 6). Asian taxa have been grouped with North American polyglyphanodontines on the basis of shared, derived features in their cranial osteology (Estes, 1983). Estes (1988) also indicated that the skull morphology in the Asian taxa is distinct, and that they are more similar to each other than any are to Polyglyphanodon. Furthermore, the dentitions of the Asian taxa do not fit the model of dental evolution for the North American taxa. Indeed, if the obliquely oriented teeth of Cherminsauros originated through rotation of an anteroposteriorly oriented tooth (e.g., Macrocephalosaurus, Erdenetesaurus), then a specialization roughly similar to that seen in North American polyglyphanodontines is implied. Given the relative antiquity of these new teiids from North America, the common ancestor of the North American and Asian polyglyphanodontines almost certainly existed in the Early Cretaceous and, perhaps, had simple (e.g., conical) teeth. Based on the differences in dental structure, it would appear that the North American and Asian polyglyphanodontine taxa represent lineages that remained isolated following their probable Early Cretaceous split.

CONCLUSIONS

Bicuspidon numerosus is important in that it is the oldest well-represented teiid known and provides further evidence about the evolution of Teiidae prior to the Campanian. Bicuspidon also represents a very early example of a teiid with a heterodont dentition and complex, multicusped posterior teeth. Expression of these features was evidently present early in the history of Teiidae. Bicuspidon is an early member of, or a sister taxon to, a North American lineage of Polyglyphanodontinae that is distinct from the taxa from the Late Cretaceous of Asia. The dental modifications seen in Bicuspidon are characteristic of the North American polyglyphanodontines and are morphologically, as well as temporally antecedent to the highly specialized, chisel-like teeth of latest Cretaceous Polyglyphanodon sternbergi. Development of transversely expanded, complex posterior teeth apparently arose independently in Polyglyphanodontinae and Recent teiids, suggesting that this represents an iterative pattern in the history of these lizards that may, in part, help to explain the great diversity of tooth types among Recent members of the family.

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TABLE 1. Data set used in phylogenetic analysis. See Appendix 1 and Denton and O'Neil (1995) for description of characters and character states. Abbreviations for polymorphic character scoring as follows: p = 0 & 1; P = 1 & 2. See text for discussion and explanation of changes in scoring for some taxa (9 = not applicable).

TAXA	CHARACTERS																				
	1										2										3
	12345	67890	12345	67890	12345	67890	12345	67890													
<u>Ameiva</u>	11111	01111	11111	11100	11101	10000															
<u>Cnemidophorus</u>	11111	01111	11111	11100	11101	10000															
<u>Kentropyx</u>	11111	01111	11111	11100	11101	10000															
<u>Teius</u>	11100	01111	11111	11110	11101	20000															
<u>Dicrodon</u>	11100	01111	11111	11110	11001	20000															
<u>Callopistes</u>	11100	11101	10111	11100	11111	00000															
<u>Tupinambis</u>	11110	11101	10111	11100	10111	10100															
<u>Dracaena</u>	10110	11111	10111	01100	10111	20101															
<u>Crocodilurus</u>	11110	11101	10110	01100	10111	10100															
<u>Prototeius</u>	00000	00100	00000	02101	01000	00001															
<u>Chamops</u>	100??	00100	00100	02101	00000	0000p															
<u>Polyglyphanodon</u>	00000	00000	00010	00111	00001	21000															
<u>Macrocephalosaurus</u>	00000	00000	00010	00101	00001	10000															
<u>Cherminsauros</u>	00000	00000	00000	00121	00001	10000															
<u>Peneteius</u>	?????	?????	?????	??11?	?10??	P1?00															
<u>Bicuspidon</u>	?0????	?????	?????	??11?	?10??	10?0p															
Gekkonidae	p1000	00900	00010	10000	11110	10000															

Appendix 1. Characters and character states used in phylogenetic analysis. See Denton and O'Neil (1995) for further discussion of characters.

1. Ontogenetic fusion of frontals: (0) paired; (1) fused. 2. Narial buttress/mesial process of maxillary narial border: (0) present; (1) absent. 3. Retracted nares: (0) absent; (1) retracted on dorsal maxilla. 4. Vomer-premaxilla contact: (0) contact; (1) vomers isolated from premaxilla by mesiopalatal extensions of maxilla. 5. Ectopterygoid contribution to suborbital fenestra: (0) much; (1) little. 6. Anteromedial edge of supratemporal fenestra: (0) formed by postfrontal and/or postorbital; (1) formed by anterolateral extensions of parietal. 7. Temporal bones: (0) robust, insert extensively on parietal; (1) much reduced with limited along length of anterior parietal. 8. Postorbital contribution to posterior border of orbit: (0) forms about one-half of posterior border, is primarily an orbital bone with strong ventral process; (1) forms less than one-half of border, is primarily a temporal bone with a weak ventral process. 9. Postfrontal fusion: (0) separate or absent; (1) fused to postorbital. 10. Adductor origin: (0) extends only along posterior 2/3 to 1/2 of parietal dorsolateral surface; (1) extends along nearly the entire dorsolateral surface. 11. Pterygoid lappet of quadrate: (0) absent; (1) pronounced projecting mesioventral lappet forms extensive sliding contact with the posterior pterygoid. 12. Medially expanded quadrate: (0) present; (1) absent. 13. Articular condyle of quadrate: (0) extends along entire ventral surface of quadrate; (1) extends along lateral 2/3 of quadrate only. 14. Parietal length-to-width ration (exclusive of supratemporal processes): (0) parietal longer than wide; (1) parietal width equal to or wider than long. 15. Parietal downgrowths: (0) absent; (1) pointed ventral downgrowths

extend to (or just medial to) ectopterygoid. 16. Parietal foramen: (0) present; (1) absent.

17. Parietal fossa: (0) near caudal edge of parietal, closed posteriorly with processus ascendens of supraoccipital locked firmly into place; (1) located caudally, open posterior margin; (2) anteriorly displaced an end of groove incising ventral surface of parietal. 18. Heterodont dentition with differentiation along the tooth row: (0) absent; (1) present. 19. Medially expanded posterior dentition: (0) absent; (1) present. 20. Dorsal extension of coronoid process of dentary: (0) absent or with only small dorsal extension; (1) large, extends dorsally onto anterolateral surface of coronoid. 21. Coronoid lateral process as lappet on dentary: (0) absent or covered by posterior dentary; (1) present. 22. Meckelian fossa (= Meckel's groove): (0) widely open to symphysis; (1) restricted anteriorly so that ventral edge is visible medially. 23. Intramandibular septum posterior extension: (0) posterior extension of intramandibular septum present a ridge along roof of dentary, separating coronoid medial process from surangular; (1) absent, surangular directly abutting coronoid medial process. 24. Retroarticular process dorsal surface: (0) sulcus or pit present; (1) absent. 25. Retroarticular flange (prearticular crest): (0) crest present but little or not development of medially directed flange; (1) well developed flange present. 26. Subpleurodont dentition: (0) tooth attachment to base and parapet, shallow sulcus dentalis (= subdental gutter); (1) well developed sulcus dentalis, attachment predominantly basal with extensive deposits of cementum; (2) cementum completely surrounding tooth bases and filling sulcus dentalis producing "pseudothecodont" condition. 27. Posterior tooth replacement: (0) continuous throughout post-embryonic ontogeny and adulthood; (1) posterior dentition permanent in adults. 28. Premaxillary

teeth: (0) simple, unicuspate; (1) bicuspate, tricuspate. **29.** Anterior maxillary teeth: (0) simple, unicuspate; (1) complex. **30.** Longitudinally striate teeth: (0) absent; (1) present.

FIGURE LEGENDS

FIGURE 1. Map of localities from which Bicuspidon numerosus, gen. et sp. nov., have been recovered. Localities are along west flank of San Rafael Swell in Emery County, Utah. Star indicates type locality.

FIGURE 2. Bicuspidon numerosus, gen. et sp. nov. A, medial; B, oblique medial; and C, occlusal views of holotype left maxilla (OMNH 26743). D, occlusal; and E, medial view of hypodigm right dentary (OMNH 27900). F, stereopair occlusal views of holotype left maxilla (OMNH 26743). G, Stereopair of OMNH 34244. H, oblique medial view of jaw fragment (OMNH 27757) with deep, subcircular replacement pit with replacement crown. Scale bars 1 mm.

FIGURE 3. SEM images of teeth of Bicuspidon numerosus, gen. et sp. nov. A, medial view of juvenile posterior tooth (OMNH 26743); B, medial view of adult tooth (OMNH 27896); C, stereopair of occlusal view of juvenile tooth (OMNH 26228); D; stereopair of occlusal view of adult tooth (OMNH 27992). Scale bars 0.5 mm.

FIGURE 4. Two equally most parsimonious trees from phylogenetic analysis of position of Bicuspidon numerosus, gen. et sp. nov. Cretaceous taxa are shaded. See text for details and explanation.

FIGURE 5. Comparison of tooth rows (in occlusal view) of A, right dentary of Teius teyou (MVZ 92989, B, left dentary of Dicrodon guttulatum (MVZ 58401), and C,

holotype left maxilla of Bicuspidon numerosus, gen. et sp. nov. (OMNH 26743).

Arrows indicate anteriormost bicuspid tooth. Note anterior position of secondary (smaller) cusp in teeth of T. teyou and D. guttatum as compared to medial position of secondary cusp of B. numerosus. Scale bars 1 mm.

FIGURE 6. Distribution of tooth shape and orientation on trees generated from phylogenetic analysis of Bicuspidon numerosus, gen. et sp. nov. See text for discussion.

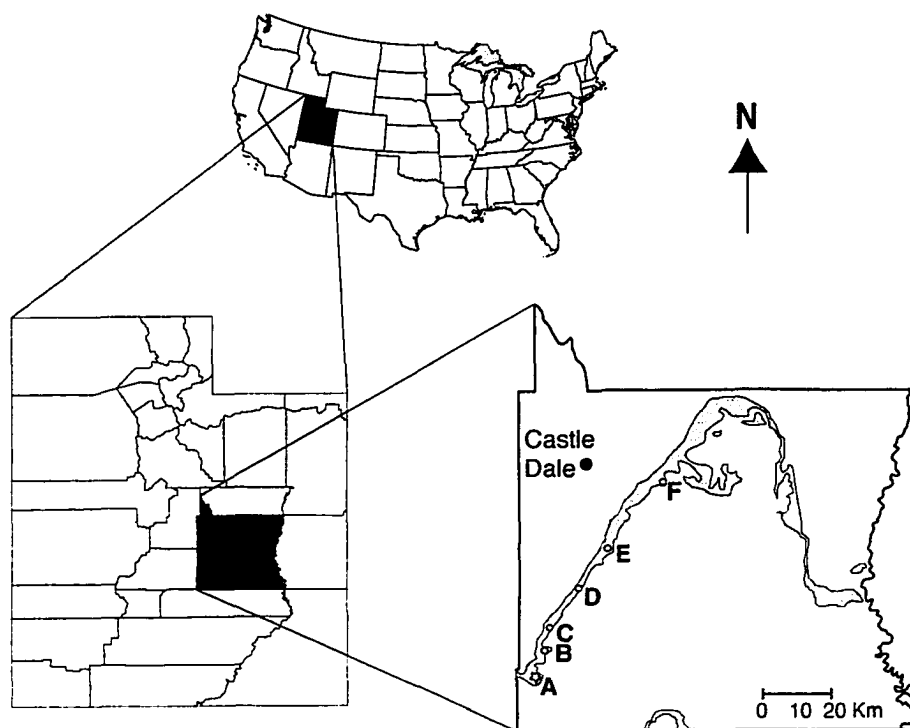


Figure 1

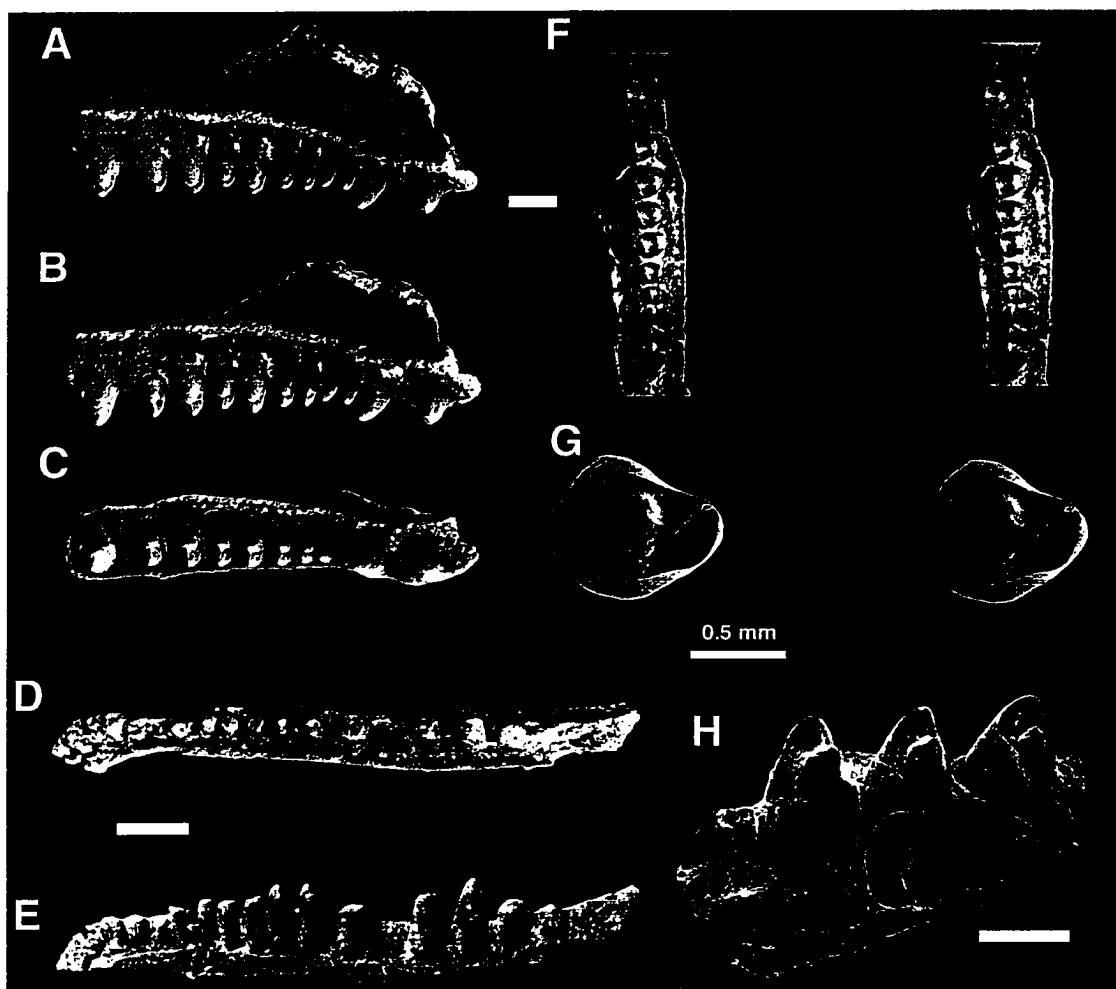


Figure 2

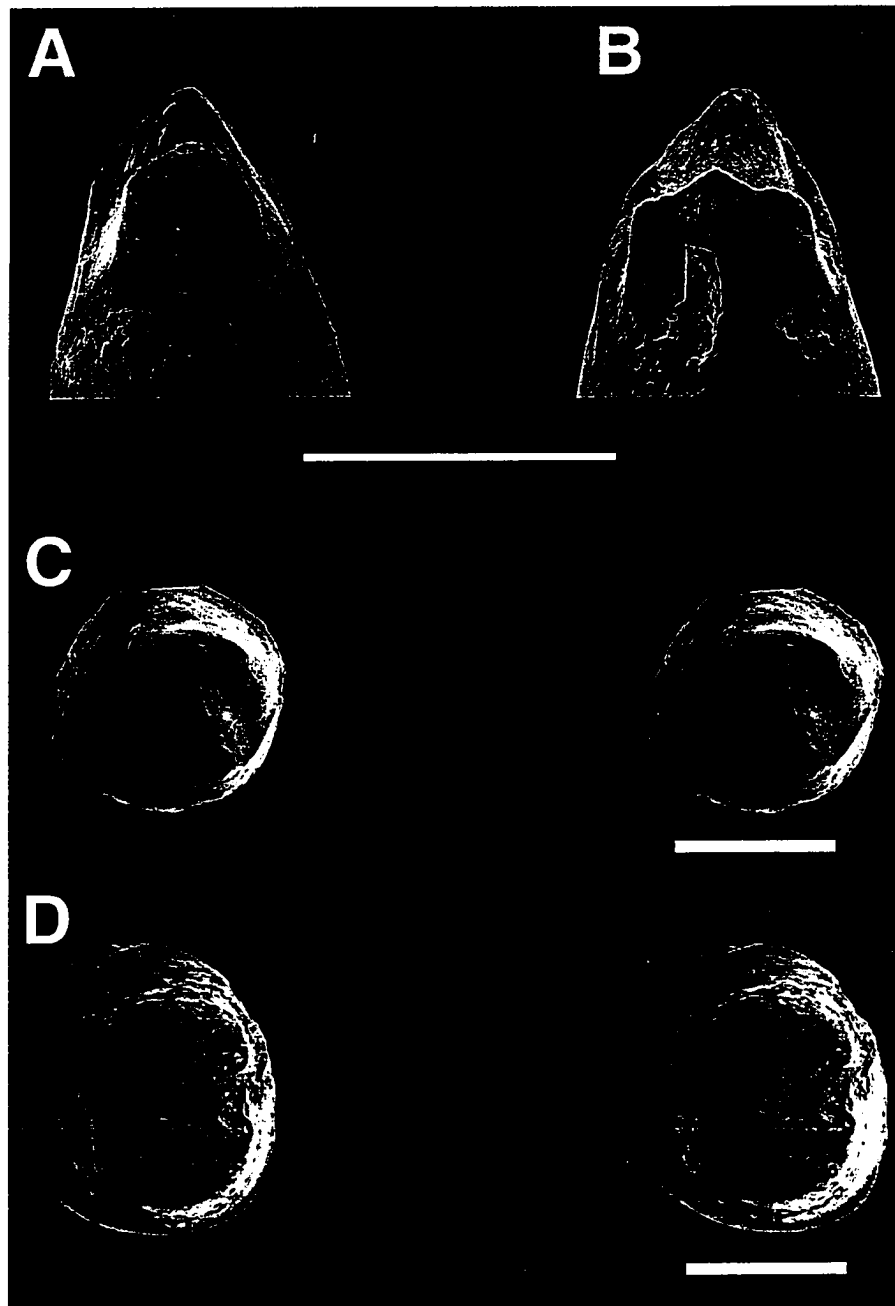


Figure 3

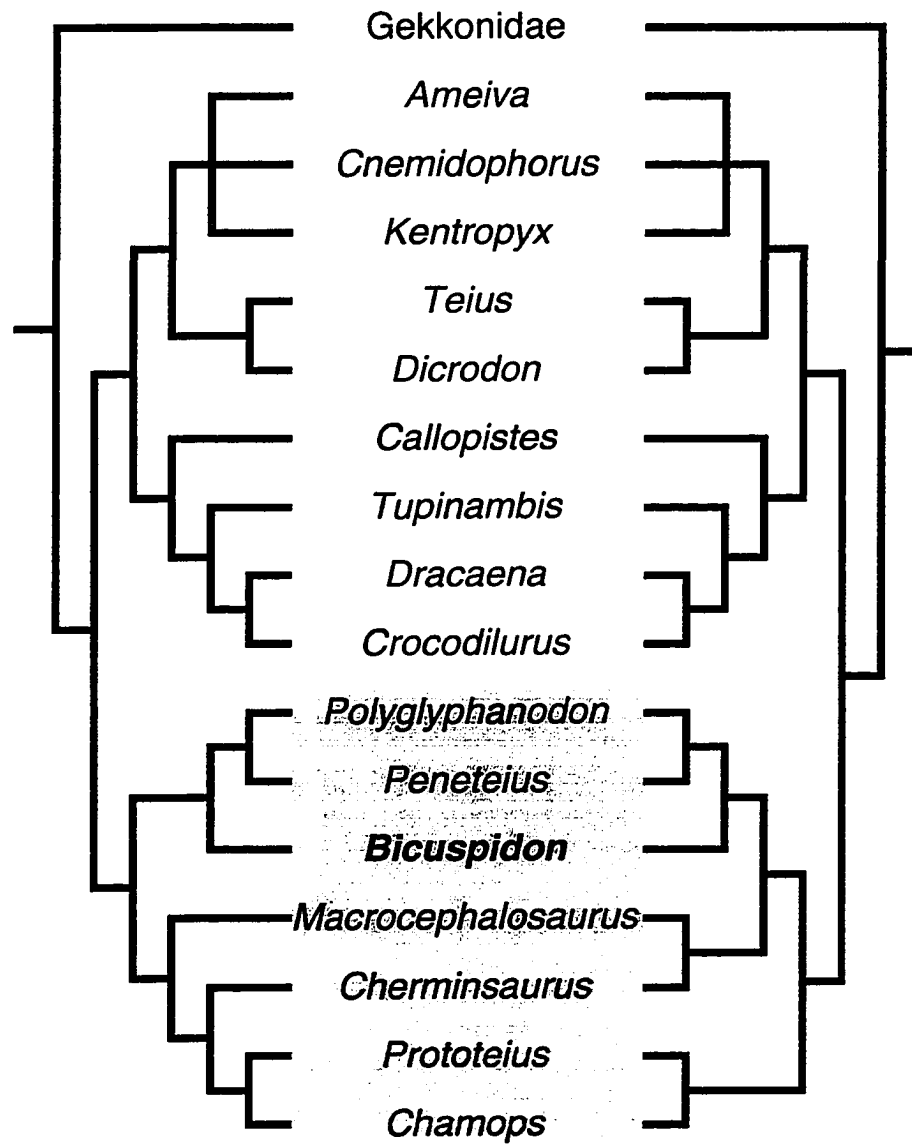


Figure 4

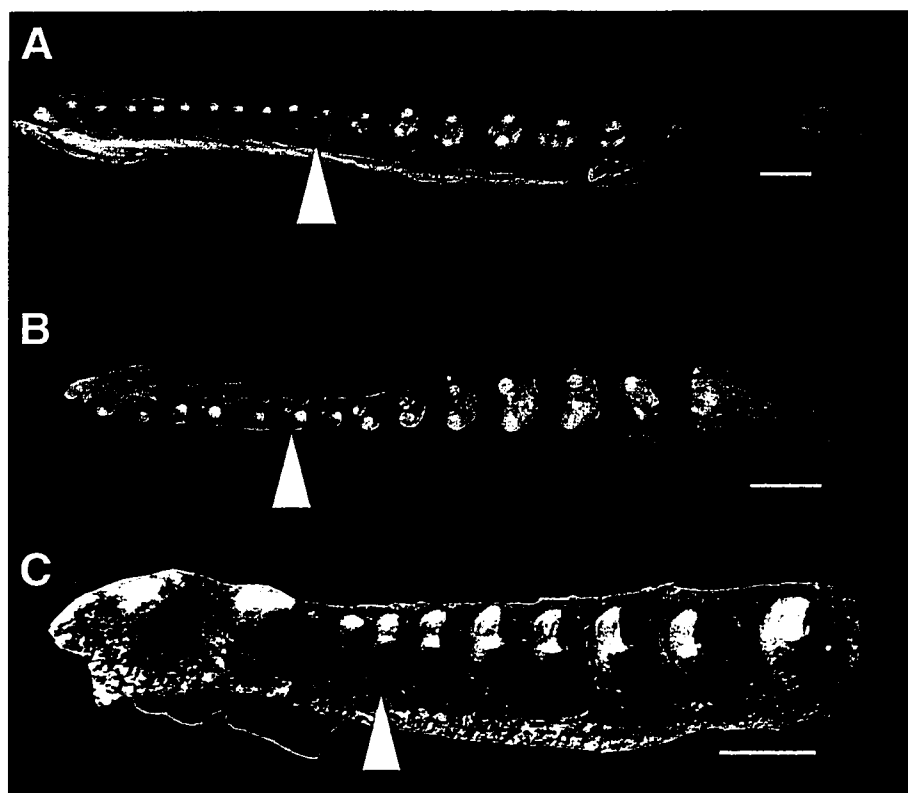
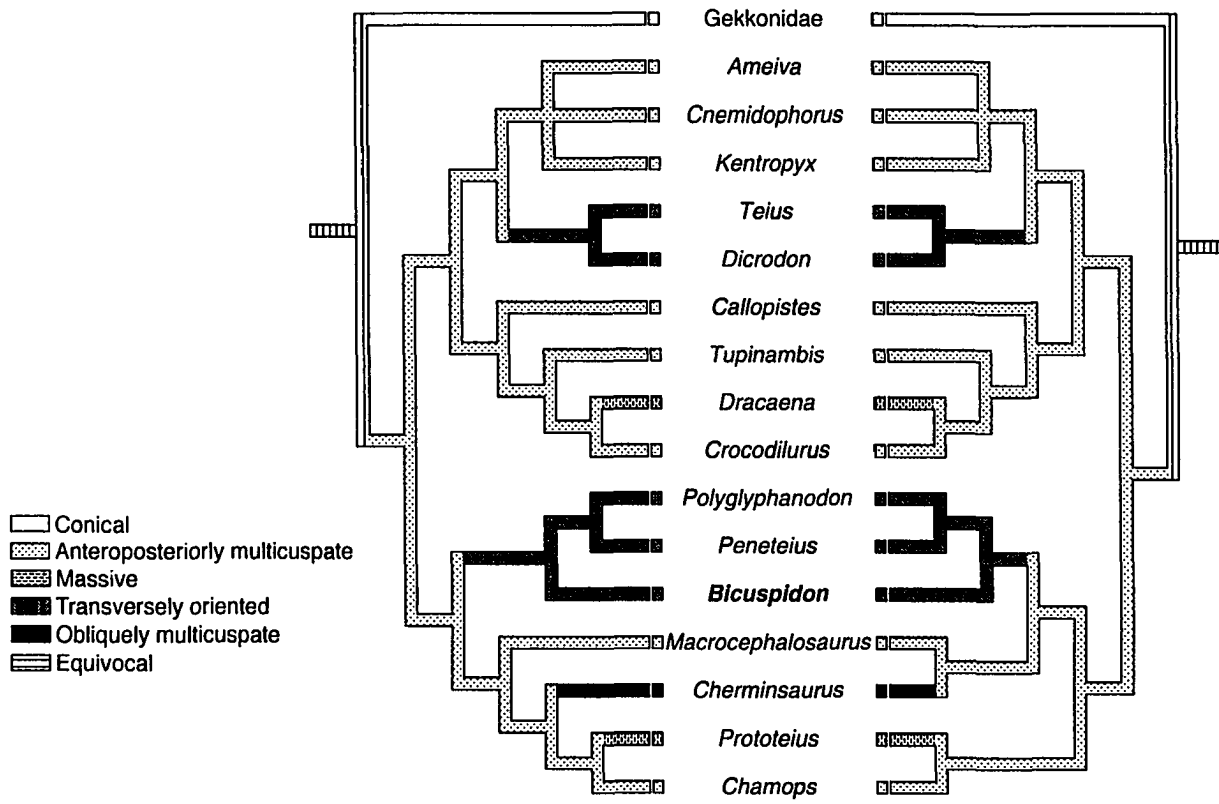


Figure 5

Figure 6



**LIZARDS FROM THE LOWER CRETACEOUS (APTIAN-ALBIAN) ANTLERS AND
CLOVERLY FORMATIONS**

Randall L. Nydam and Richard L. Cifelli

**Sam Noble Oklahoma Museum of Natural History, University of Oklahoma, Norman,
Oklahoma, 73072; and Department of Zoology, University of Oklahoma, Norman,
Oklahoma, 73019**

Contact info: voice: (405) 325-4712, FAX: (405) 325-7699, e-mail: rlnydam@ou.edu.

**Suggested running head—NYDAM AND CIFELLI—EARLY CRETACEOUS
LIZARDS**

ABSTRACT--Recent discoveries from the Aptian-Albian Antlers (Oklahoma) and Cloverly (Montana, Wyoming) formations provide significant additions to the Early Cretaceous record of lizards in North America. The lizards from the Antlers Formation include two teiids, an anguimorph, and a series of fragmentary jaws with paramacellodid or paramacellodid-like teeth. The lizards from the Cloverly Formation include a new species of Paramacellodus and many indeterminate jaw fragments. The apparent lack of shared lizard taxa between the two units calls into question their temporal equivalence, which is based on similarity of dinosaur taxa. Although apparently distinct, the lizard faunas of both units are very similar to that of the Late Jurassic Morrison Formation in being composed primarily of paramacellodid or paramacellodid-like taxa. It appears that there was a period of relative stasis in the evolution of lizards in North America between the Late Jurassic and Early Cretaceous paralleling a similar trend in Europe. Reported lizards from the Aptian-Albian of Mongolia show a taxonomic diversity much different than that of Oklahoma, Montana, and Wyoming, but more like that of the Late Cretaceous of North America, suggesting that the establishment of taxonomic groups common to the Late Cretaceous and Tertiary occurred earlier in Asia than in North America.

INTRODUCTION

The record of lizards from the Mesozoic of North America is patchy. The earliest lizards on the continent are from the Upper Jurassic Morrison Formation, where a limited number of taxa are represented by a some partial skeletons and other, more fragmentary material. The Late Jurassic fauna includes paramacellodids (primitive scincomorphs with possible ties to Cordylidae) and primitive anguimorphans (Prothero and Estes, 1980; Evans, 1996, 1998a; Evans and Chure, 1998b, 1999), as well as the primitive lizard Schilleria (Evans and Chure, 1998a, 1999). This fauna is very similar to those of the Late Jurassic and Early Cretaceous of Europe (Evans, 1993, 1995, 1998). To date, the only records of Early Cretaceous lizards from North America are: 1) numerous indeterminate scincomorphs (many similar to paramacellodids in tooth structure), and two teiids from the Aptian-Albian of Texas (Winkler et al., 1990); and 2) primitive lizards and a possible scincomorph from Mexico (Reynoso, 1995, 1996, 1998). In contrast, lizards from the somewhat younger Albian-Cenomanian of Utah include a number of more modern taxa, such as derived teiids and helodermatid-like platynotans (Cifelli and Nydam, 1995; Nydam, 1995, 1999, in press), as well as several cordyliforms currently under study by one of us (RLN). Similarly, the lizards from the Late Cretaceous (primarily Campanian-Maastrichtian) encompass an even wider variety of modern families, including Anguidae, Helodermatidae (=Monstersauria of Norell and Gao, 1997), Scincidae, Teiidae, Xantusiidae, Xenosauridae, Cordylidae, and Varanidae (Estes, 1983; Gao and Fox, 1996).

The lack of information on lizards from Early Cretaceous is unfortunate as this was an important transitional interval in the evolution of the terrestrial biota. It is during this time period that angiosperms diversified dramatically and became established as the

dominant component of the terrestrial flora (Retallack and Dilcher, 1986; Friis and Crepet, 1987; Lupia et al., 1999) and a faunal-interchange event evidently occurred between Asia and North America. Both the floral and faunal events may have affected the evolution or, at least, the composition of lizard taxa in North America from the Late Jurassic through the Late Cretaceous (Cifelli et al., 1997b and references therein).

Our goal here is to partially occlude this gap in the fossil record by reporting on Lower Cretaceous (Aptian-Albian) lizards of the Antlers and Cloverly formations of Oklahoma and Montana/Wyoming, respectively. These new specimens are significant to the record of Early Cretaceous lizards from North America, not only as additions to a poorly understood time period, but also because they expand the geographic record of lizards into the more northern latitudes of Montana and Wyoming. Due to the fragmentary nature of the material, many of the “taxa” are recognized here only as distinct, unnamed morphotypes, but other specimens are sufficiently complete to permit formal description of new paramacellodid and teiid taxa.

We make comparisons with other Early Cretaceous lizard faunas from North America, Europe, and Asia to evaluate whether there is a pattern of cosmopolitanism in the Aptian-Albian similar to that suggested for lizards of the Late Jurassic-basal Cretaceous (1998; Evans and Chure, 1998b). Additionally, we make comparisons to both older (Late Jurassic) and younger (Late Cretaceous) lizard faunas, primarily from North America, to evaluate how the new lizards from the Aptian-Albian fit into the transition from the more primitive to the more derived faunas, respectively.

ABBREVIATIONS

OMNH, Oklahoma Museum of Natural History, Norman; SMU, Southern Methodist University, Dallas; UALVP, Laboratory of Vertebrate Paleontology, Department of Biological Sciences, University of Alberta, Edmonton.

GEOLOGICAL AND PALEONTOLOGICAL SETTING

Antlers Formation

The Antlers Formation is exposed as a narrow band of terrigenous deposits in the southeastern region of Oklahoma and northern Texas. This unit is laterally equivalent to units of the Trinity Group of Texas (Thurmond, 1974; Winkler, et al., 1990). The Antlers Formation in Oklahoma is comprised of packed sands and clays derived from the Wichita-Arbuckle-Ouachita mountain systems and deposited in a subtropical-semiarid environment near the northwestern shore of the East Texas Embayment, a northerly extensive ancestral Gulf of Mexico (Hobday et al., 1981). The depositional settings recognized in the Antlers Formation include fluvial, deltaic, and strandplain systems (Hobday, et al., 1981; Winkler, et al., 1990). The formation thickens to the southwest at which point there is a nomenclature change associated with the presence of the intertonguing marine deposits of the Glen Rose Formation. The terrestrial deposits of the more northerly Antlers Formation become the Twin Mountains and Paluxy formations, which bracket the Glen Rose Formation above (Paluxy) and below (Twin Mountains). Together these three units are referred to as the Trinity Group of Texas (Thurmond, 1971; Hobday, et al., 1981; Jacobs et al., 1991).

OMNH locality V706 (the primary fossil-producing locality) is located in the Antlers Formation, Atoka County, Oklahoma on the property of the Howard McLeod Correctional Center, 23 km west-southwest of Antlers, Oklahoma. The sediment at this site is composed primarily of red and gray/green clays with intermittent lenses of packed sands and numerous carbonate concretions. There are two fossiliferous horizons at this locality. The upper horizon is characterized by numerous skeletons of the ornithomimid dinosaur Tenontosaurus sp., together with less common remains of the small theropod dinosaur Deinonychus antirrhopus (see Brinkman et al., 1998). These taxa also co-occur in the Cloverly Formation of Montana, in what is believed to be a predator-prey association (Maxwell and Ostrom, 1995). The microvertebrate horizon at locality V706 lies 1-1.5 m below the dinosaur-bearing horizon. No large bone or articulated material has been found in the microvertebrate level. Locality V706 is interpreted as representing an overbank deposit associated with a meandering fluvial system (Cifelli et al., 1997a). The microvertebrate material was likely deposited as part of a flood event, whereas the dinosaur material appears to have been buried after a period of subaerial exposure.

Various studies (summarized by Winkler et al. [1990] and Jacobs and Winkler [1998]) have estimated the age of the Antlers Formation to be Aptian-Albian. Jacobs and Winkler (1998) gave an age of 121-107 Ma for the mammal-yielding part of the Trinity Group of Texas based on correlation of marine invertebrates. Stable carbon-isotope analysis of plant remains from the localities of both Texas and Oklahoma tentatively supports correlation of the lower-mid Antlers Formation with the middle Trinity Group (Rennison, 1996). A review of the correlations between the Texas and Oklahoma localities by Brinkman et al. (1998) led them to conclude that locality V706 was in the

lower Albian part of the section; higher than the microvertebrate producing Paluxy Church locality in Texas (Winkler et al., 1990). The vertebrate fauna of the Trinity Group-Antlers Formation has been treated as paracontemporaneous with the Cloverly Formation of Montana and Wyoming, the Arundel Clays of Maryland, and the Wealdon/Purbeck deposits in England (Stovall and Langston, 1950; Ostrom, 1970; Thurmond, 1971, 1974; Gardner, 1999). More recently, Jacobs and Winkler (1998) discussed the comparisons of the archosaur and mammal remains from the Trinity/Antlers in more detail.

Cloverly Formation

The Cloverly Formation is composed of a series of terrestrial deposits that outcrop in scattered areas of Montana and Wyoming, with extensive and fossiliferous exposures along the eastern periphery of the Bighorn Basin, west of the Bighorn Mountains (Ostrom, 1970). The stratigraphy of the Cloverly Formation has been the subject of numerous studies, the most relevant of which have been summarized by Ostrom in his monographic treatment of the stratigraphy and paleontology of the formation. Ostrom divided the Upper Mesozoic rocks of the region into eight distinctive units, of which Units IV-VII represent four divisions of the Cloverly Formation. Unit IV, the basal member, is a non-fossiliferous, discontinuous, massive conglomeratic sandstone. Unit V (= Little Sheep Mudstone) is an unstratified, calcareous claystone, high in bentonite, with laterally discontinuous channel sands and numerous surface concretions. Unit VI is a laterally discontinuous, coarse-grained, cross-bedded channel sandstone representing multiple stream channels in the region. Unit VII is a steeply-sloped series of brightly

colored (red, maroon, brown, purple, green) mudstones with interbedded channel sands and polished stones or “gastroliths.” This unit is the most continuous and easily identifiable of the members of the Cloverly Formation. Vertebrate fossils, particularly dinosaurs, are common to units V and VII, but have also been found in Unit VI (Ostrom, 1969, 1970; Sues, 1980; Maxwell, 1993; Maxwell and Ostrom, 1995; Maxwell et al., 1997; Cifelli et al., 1998). Most of the fossils are dinosaurs (Ostrom, 1969, 1970; Sues, 1980; Maxwell, 1996), but crocodilians, turtles (Ostrom, 1970), amphibians (Gardner, 1999), and mammals (Jenkins and Schaff, 1988; Cifelli et al., 1998; Cifelli, 1999) are also known. Lizards have never been described from the Cloverly Formation.

The depositional environments of all of the units of the Cloverly Formation are terrestrial fluvial systems (Ostrom, 1970). Sedimentologic studies of the Cloverly Formation suggests climatic shift from an arid/semi-arid environment (Unit V) to a more tropical-semitropical environment (Unit VII) (Forster, 1984). Unit VII is overlain in most of the region by the Sykes Mountain Formation (Ostrom, 1970). This massive sandstone unit represents the southward transgression of the Arctic sea (Haun and Kent, 1965), which continued to migrate south until it joined the northward transgressing sea from the Gulf of Mexico.

SYSTEMATIC PALEONTOLOGY—Antlers Formation

SQUAMATA Oppel 1811

SCINCOMORPHA Camp 1923

Cf. PARAMACELLODIDAE Estes 1983

ATOKASAURUS gen. nov.

Etymology—Atoka, in reference to Atoka County, Oklahoma, where the specimen was recovered; sauros (Greek, “lizard”) is a commonly-used suffix for genera of fossil lizards.

Type and Only Known Species—Atokasaurus metarsiodon, sp. nov.

Known Distribution—Antlers Formation (Lower Cretaceous), Oklahoma.

Diagnosis—As for the type and only known species.

ATOKASAURUS METARSIODON, sp. nov.

(Fig. 2A)

Etymology—Metarsios (Greek, high up), odous (Greek, tooth), in reference to the implantation of teeth above the subdental gutter.

Holotype and Only Specimen—OMNH 60535, broken right dentary with one tooth.

Locality and Horizon—OMNH locality V706, Howard McLeod Correctional Center, 23 km west of Antlers, Atoka County, Oklahoma; middle Antlers Formation, Early Cretaceous (Aptian-Albian).

Diagnosis—Differs from other known Paramacellodidae in the following combination of character states. Base of teeth with more pronounced, medially swollen

base and crown more deeply medially concave than in Paramacellodus and Becklesius, giving the medial side of the tooth a strongly sigmoidal outline in mesiodistal view. Crown of tooth has no medial striae aside from the two main striae descending from the medial cuspule and is only weakly rotated posteromedially.

Description—OMNH 60535 (Fig. 2A) is the midsection of a right dentary preserving spaces for seven teeth, but only one complete tooth is present in the posteriormost tooth position. The tooth is pleurodont, with only its apical one-third extending above the lateral parapet. The body of the tooth is anteroposteriorly compressed. The bases of the teeth are closely spaced, and it appears that they would have abutted one another if they were all present. The base of the preserved tooth terminates well above the floor of the subdental gutter, as do the bases of the broken teeth, though not to as great an extent as the complete tooth. This condition, in which the posterior dentary teeth are set higher on the parapet than those at more anterior positions, is common among lizards. There is a small nutrient foramen at the base of each tooth position in the cementum below the base of the tooth. The single complete tooth is very much like those of other paramacellodids such as Becklesius, Paramacellodus, and Saurillodon (sensu Estes [1983]; but see Winkler [1990] and Gao and Fox [1997] for discussions of the phylogenetic status of Paramacellodidae) in that the base of the tooth is swollen medially and the crown is medially concave, though these features are accentuated in Atokasaurus. On the apex of the crown there is a prominent medial cuspule (sensu Estes, 1983) formed by the convergence of two large, medial striae. Anterior and posterior carinae are present along the lateral borders of the crown. These

carinae come together to form a chisel-shaped tooth with a moderately squared-off crown. The apex of the crown points medially.

The tooth is weakly rotated posteriorly such that the anterior carina is medial to the posterior carina. This rotation is less pronounced in Atokasaurus than in other paramacellodids for which it has been described. The subdental gutter is narrow but well developed. The subdental shelf is tall (approximately three-fourths tooth height) anteriorly and tapers posteriorly. This tapering of the subdental shelf is typical of many scincomorphans and is due to the articulation of the splenial with the dentary under the posterior portion of the tooth row.

SCINCOMORPHA Camp 1923

TEIIDAE Gray 1827

PTILOTODON, gen. nov.

Etymology—Ptilotos (Greek, winged), odous (Greek, tooth), in reference to the wing-like expansions on the crowns of the teeth.

Type and Only Known Species—Ptilotodon wilsoni, sp. nov.

Known Distribution—Antlers Formation (Lower Cretaceous), Oklahoma.

Diagnosis—As for the type and only known species.

PTILOTODON WILSONI, sp. nov.

(Fig. 2B)

Etymology—In recognition of Jack Wilson, the discoverer of the locality from which the type specimen was recovered.

Holotype and Only Known Specimen—OMNH 60764, broken right dentary with four teeth.

Locality and Horizon—OMNH locality V706, Howard McLeod Correctional Center, 23 km west of Antlers, Atoka County, Oklahoma (Fig. 1); middle Antlers Formation, Early Cretaceous (Aptian-Albian).

Diagnosis—Differs from Late Cretaceous teiids in being a much smaller lizard, in having teeth with anterior and posterior expansions of crown that are not developed into accessory cusps.

Description—OMNH 60764 (Fig. 2B) is a broken right dentary preserving six tooth positions and four complete teeth. The ventral surface of the subdental shelf bears a notch for the apparent articulation with the splenial, but this notch is shallow and terminates before reaching the anteriormost preserved tooth. The exact size of the Meckel's groove is unknown, as the lateral and ventral walls are not preserved. The subdental shelf is narrow and tapers posteriorly. The subdental gutter is narrow and shallow. The lateral surface of the dentary is convex, and three inferior alveolar foramina are present. There are four widely spaced teeth preserved on OMNH 60764. The teeth are subpleurodont (one-half to two-thirds of each tooth is exposed above lateral parapet) and have posteromedially placed, subcircular replacement pits at the bases of the first and third teeth (similar to some specimens of *Chamops segnis*). The crowns of the teeth have well-developed anterior and posterior expansions that are offset from the shaft of the

tooth. These expansions are similar to those seen on many teiids from the Late Cretaceous of North America, but most closely resemble those on the posterior teeth of Leptochamops. Unlike Leptochamops, however, there is no development of accessory cusps. The teeth in OMNH 60764 become more massively built posteriorly.

Comments—Referral to Teiidae is based on the presence of thick cementum at the bases of the teeth, together with deep, subcircular replacement pits at the tooth bases (Estes et al., 1988). Estes et al. (1988:162) noted that posterior placement of these replacement pits is known to occur in some Recent teiids and is also seen in some specimens of C. segnis (e.g., UALVP 29721, 29820). The only other teiid material described from the Early Cretaceous consists of two specimens (SMU 72282, right dentary and SMU 72283, left dentary) from the Paluxy Church locality in the Twin Mountains Formation of the Trinity Group, Texas (Winkler, et al., 1990). Unlike Ptilotodon wilsoni, the teeth of SMU 72282 and 72283 are conical, with those of SMU 72283 being more massive and having medial striae on the crowns (Winkler et al., 1990:figs. 6C, 8A). The Paluxy Church locality is stratigraphically lower than V706 (Brinkman et al., 1998).

Other lizards from the Antlers Formation

Locality V706 has yielded a number of fragmentary specimens of lizards that are not immediately referable to any known taxa, nor are they complete enough to justify the erection of new taxa. These specimens are described below as a series of morphotypes.

OMNH 60538 (Fig. 3A) is a jaw fragment (possibly maxilla) with two teeth. The teeth are pleurodont, narrow, closely spaced, and have chisel-like crowns. Unlike many

of the other taxa from the Antlers Formation, the teeth of this specimen do not have medially swollen bases or medially concave crowns. Instead, the medial surface of the teeth is straight. The bases of the teeth are attached to the jaw with very little cementum, and, the cementum that is present is perforated by numerous small foramina. The supradental gutter (assuming OMNH 60538 is a maxillary fragment) is shallow, and the supradental shelf is short and lightly built. There is a large canal dorsolateral to the teeth for the neurovascular bundle. The jaw is not well preserved, and the crowns of the teeth are slightly eroded and likely missing some detailed structure.

OMNH 60765 (Fig. 3B) is a small fragment from either a dentary or maxilla. The single preserved tooth is pleurodont, has a medially swollen base, a slightly medially concave crown with very fine striae on the medial surface, and an apex that is offset posteriorly, giving the tooth a false “recurved” appearance. At the apex, there is a weakly-developed medial cuspule. A large replacement pit is present at the base of the tooth.

OMNH 60763 (Fig. 3C) is a posterior fragment of a right maxilla with two teeth. The teeth are pleurodont, simple, bluntly conical, closely spaced, unrecurved. There is a large central replacement pit at the base of one of the teeth. A small but prominent supradental shelf borders a wide, shallow supradental gutter.

OMNH 60763, 60538, and 60763 have similar, simple teeth that may represent different portions of the tooth row of the same taxon. The tooth shape is similar to that described for the paramacellodid Pseudosaurillus (Estes, 1983), but the specimens are too incomplete to make further comparisons. However, such a simple and unremarkable tooth shape is not a diagnostic characteristic, as it is also common to a number of lizards

including geckos, phrynosomatids, and cordylids. The size of the teeth relative to the size of the jaw is greater than typically found in gekkonids, and the presence of a supradental shelf near the back of the maxilla all but eliminates the possibility that OMNH 60763 is an iguanian. Based on the presence of a moderate amount of cementum, direct tooth replacement, and the small supradental shelf, it is most likely that this taxon is a scincomorphan.

OMNH 34206 (Fig. 4A) is a jaw fragment with a single tooth. The size of the specimen indicates that it would be the smallest known lizard in the fauna from the Antlers Formation of Oklahoma. The tooth has well-defined anterior and posterior carinae that converge at a posteriorly displaced apex, giving the tooth a false “recurved” appearance. The medial surface of the crown is slightly concave and has numerous well-developed striations. A medial cuspule is present at the apex of the tooth. The specimen shows similarities in tooth structure to the paramacellodid Becklesius, but is too incomplete to be certain of its affinities.

OMNH 32585 (Fig. 4B) is a partial right dentary with four teeth and spaces for three more. The teeth are pleurodont, have narrow, parallel-sided tooth shafts, and pointed tips. The slight recurvature of the teeth is accentuated by the false-recurve of the tooth apices. These false “recurved” tips are very similar to that of OMNH 34206. The enamel of the crowns of the teeth of OMNH 32585 is eroded, and detailed structures such as striae or carinae are not preserved and cannot be evaluated. There are resorption pits at the bases of the first (anteriormost) and third teeth, indicating direct tooth replacement. These resorption pits are slightly posterior to the center of their respective teeth, a position similar to that found in other lizards from the Antlers Formation (see below).

The subdental shelf of OMNH 32585 is tall, and the subdental gutter is narrow and shallow. Posteriorly, the Meckel's groove is wide, opens ventromedially, and turns to open ventrally as a narrow slit anteriorly. There is a shallow groove on the ventral surface of subdental shelf for the articulation of the splenial. There is also a corresponding facet on the medial side of the lateral border of the Meckel's groove. Both the groove and the taper of the facet indicating that the splenial was to the third preserved tooth (counting from anterior to posterior). The exterior surface of OMNH 32585 is smooth, convex, and pierced by three inferior alveolar foramina.

OMNH 32585 has teeth that are similar in overall shape to that of OMNH 34206 and it is possible that these two specimens represent the same taxon, likely a paramacellodid lizard similar in tooth structure to Becklesius. More complete materials are required for a more confident taxonomic referral.

OMNH 61206 (Fig. 4C) is a broken left dentary with four teeth and two empty tooth positions. The specimen is robust, indicating that the dentary was heavily built. The subdental shelf is tall and deeply notched on its ventral edge for articulation with the splenial. The notch for the splenial is medial to a narrow Meckel's groove. The lateral wall of the Meckel's groove is thick and robust. Anterior to the notch for the splenial, the subdental shelf increases in height and the Meckel's groove narrows considerably. The lateral surface of the specimen is moderately convex and pierced by two inferior alveolar foramina. Of the four teeth preserved in OMNH 61206, only the anteriormost is complete. It is tall, is weakly recurved, and has a conical crown with two weak carinae. The crown has been broken on the second tooth, but is otherwise similar to the first. The third and fourth teeth are more massive and their crowns have been worn flat.

Attachment is subpleurodont, cementum is heavily deposited around the bases of the teeth, and replacement was direct, as indicated by the deep, subcircular resorption pit at the base of the third tooth. The bases of the teeth are sufficiently wide that teeth in positions 1 and 2 nearly fill the subdental gutter and teeth in positions 3 and 4 do fill the subdental gutter.

The robust structure of OMNH 61206 indicates that this specimen represents the anterior portion of a dentary. The heavy cementum, direct tooth replacement via subcircular replacement pits, and anterior extension of the splenial are all synapomorphies of Teiidae (Estes et al., 1988). OMNH 61206 appears to be similar to SMU 72282, a teiid from the Twin Mountains Formation (Winkler et al., 1990). Direct comparison of the specimens must await completion of a study of the lizards from the Trinity Group of Texas currently being undertaken by P. A. Murry.

OMNH 60537 (Fig. 4D-E) is a fragment of a dentary with a single tooth. The base of the subpleurodont tooth is firmly attached to the jaw by a thick band of cementum that extends medially to fill the narrow, shallow subdental gutter. A deep groove runs anteroposteriorly along the ventral surface of the subdental shelf. This groove is presumably for a firm “tongue-in-groove” articulation between the splenial and dentary. A similar groove is found in various scincomorphan taxa from the Late Cretaceous (Gao and Fox, 1996). The tooth is conical in lateral view, and weakly recurved, with a mediolaterally compressed crown and moderately swollen base medially. Two carinae outline the crown and there is also a medially deflected cuspule. No medial striae are present on the crown.

The presence of heavy cementum around the base of a subpleurodont tooth on OMNH 60537 is typical of Teiidae, but the specimen is fragmentary and has no other diagnostic characteristics preserved for referral to that family. It is possible that OMNH 60537 is a posterior tooth from the same taxon as OMNH 61206. Indeed, the more massive shape of the tooth of OMNH 60537 in relationship to the teeth of OMNH 61206 is consistent with the differences between posterior and anterior teeth of many teiids. A jaw containing both tooth types is needed to confirm referral of both these specimens to the same taxon.

OMNH 60541 (Fig. 4F) is a small fragment of jaw with a single tooth. The tooth is subpleurodont and has a widely flared base. The crown of the tooth is strongly recurved and is mediolaterally compressed, with prominent anterior and posterior keels. The element is too fragmentary to evaluate the conditions of the subdental gutter and subdental shelf. A large foramen is present on the ventromedial surface of the jaw below the tooth.

The tooth structure of this specimen is similar to that described for Parviraptor gilmorei (Evans, 1996), an advanced anguimorph from the Upper Jurassic Morrison Formation of Colorado. Dorsetisaurus, another anguimorph known from the Morrison Formation, also has blade-like recurved teeth (Prothero and Estes, 1980; Evans, 1996; Evans and Chure, 1998b). However, the teeth of Dorsetisaurus have more strongly developed anterior and posterior keels and a lesser degree of recurvature than is found OMNH 60541 (see Evans and Chure, 1998b; Milner and Evans, 1998). OMNH 60541 is too incomplete for a precise identification, but it is probable that this specimen represents an anguimorph in the lizard fauna of the Antlers Formation.

OMNH 60595 (Fig. 5) is a broken right frontal preserving the anterior portion of the element. The frontal is heavily built, and has an irregular pattern of pits and grooves on the dorsal surface. This sculpturing is similar to that figured for Paramacellodus sp. cf. P. oweni, from the Morrison Formation (Evans and Chure, 1998). The crista cranii is weakly developed posteriorly and thickens considerably anteriorly, giving rise to an anteroventrally directed descending process. No part of the crista cranii approaches the midline of the skull.

OMNH 32613 (Fig. 6A) is a broken osteoderm that appears to have had parallel sides. The dorsal surface of the osteoderm has the same pattern of sculpturing as the frontal described above. OMNH 32613 also has a prominent central keel and an overall arched shape.

OMNH 60766 (Fig. 6B) is a broken lizard scute with a distinctive “step” common to overlapping osteoderms. This osteoderm is longer than wide and ornamented with a pattern similar to, but more weakly developed, than that of the frontal and osteoderm described above. The distal end of OMNH 60766 appears to have been perforated by a large hole at the bottom of a concavity. It is not clear whether this is part of the structure of the element or a pathological condition. OMNH 60766, 32613, and 60595 may well be from the same taxon, based on the similarity in the dorsal sculpturing of all three specimens. The large size difference between OMNH 60766 and 32613 is either ontogenetic or taxonomic (indicating two taxa rather than one). The pattern of ornamentation on the specimens is similar to that described for paramacellodid lizards (Estes, 1983; Evans and Chure, 1998a). Although it is very likely that the two

osteoderms and frontal belong to one of the taxa represented by the paramacellodid-like jaws described above, it is not possible to make a confident association at this time.

OMNH 60802 (Fig. 6C) and OMNH 61132 (Fig. 6D) are two osteoderms representing another taxon. Both of these specimens have weak sculpturing and a tall, offset ridge that runs the length of the element. These two osteoderms are almost certainly from a different taxon than is represented by OMNH 32613 and OMNH 60766. Similar osteoderms from the Berriasian of Morocco have been referred to Paramacellodus (Broschinski and Sigogneau-Russell, 1996), but, referral of these osteoderms to any of the jaws described above cannot be made at this time.

The presence of osteoderms in the Jurassic anguimorph Parviraptor has been suggested, but none can be unquestionably associated with any of the known skeletons (Evans, 1994a, 1996), and no osteoderms are known to be associated with Parviraptor material from North America. It also is possible that OMNH 32613 could belong to any of the scincomorph taxa known from the Antlers Formation.

SYSTEMATIC PALEONTOLOGY—Cloverly Formation

As with the Antlers Formation, the lizards from the Cloverly Formation are represented by only a few fragmentary jaw elements. Referral of these specimens to any taxonomic group is based on limited morphological comparisons (primarily dental) and should be considered tentative. Notable exceptions are two specimens of Paramacellodus sp. that were found in situ as opposed to specimens recovered from screen wash concentrate.

SQUAMATA Oppel, 1811

SCINCOMORPHA Camp, 1923

PARAMACELLODIDAE Estes, 1983

PARAMACELLODUS Hoffstetter, 1967

PARAMACELLODUS KEEBLERORUM, sp. nov.

(Fig. 7)

Etymology—For the Keebler family, owners of the land on which the type locality is situated.

Holotype—OMNH 60576, left maxilla.

Paratype—OMNH 61133, left maxilla.

Locality and Horizon—OMNH locality V1156, 12 km NNE of Edgar, Carbon County, Montana; basal unit VII, Cloverly Formation (Aptian-Albian, Lower Cretaceous).

Diagnosis—Differs from other species of Paramacellodus in having teeth with a well-developed cuspule on anterior carina forming an anterior “step” on the tooth crown. Also, the dorsal edge of the nasal process of maxilla forms a narrow, posterodorsally-oriented projection, and overall anteroposterior length of the nasal process of maxilla is shorter than in other Paramacellodus.

Description—OMNH 60576 (Fig. 7A-C) is a poorly preserved left maxilla in a block of ironstone that was recovered from the same locality as OMNH 61133. The

medial surface is exposed and six teeth are present. The teeth are narrow and tall, with well-developed anterior and posterior carinae of unequal length. The difference in carina lengths gives the teeth a false “recurved” appearance. The anterior carina of the teeth (Fig. 7D) is offset from the crown, creating a “step” along the anterior margin. The apex of each tooth is displaced posteriorly, and there is a small medial cuspule below the apex. The medial surface has weak striae and is weakly medially concave. In occlusal view the crown is rotated slightly such that the anterior carina is medial to the posterior carina. The supradental shelf appears to be heavily built, but it is poorly preserved and difficult to evaluate. There are robust limb bones associated with the maxilla, but they are too fragmentary to provide taxonomically useful information.

OMNH 61133 (Fig. 7D) is a left maxilla preserved in ironstone, with only the exterior surface exposed. The maxilla is tall and nearly flat, with a slight laterally convex surface. The anterior margin of the nasal process rises steeply near the anterior edge of the element forming the semicircular ventral and posterior borders of the external naris. Above the border for the external naris, the angle of the anterior margin of the nasal process decreases, only to increase again along the anterior border of a narrow dorsal projection on the dorsal edge of the nasal process. The posterior border of the nasal process is concave posteriorly. The prefrontal and lacrimal are not exposed. There are three teeth exposed below the lateral parapet of the maxilla. The crowns are tall, sharply pointed and rotated slightly, such that the posterior carina is lateral to the anterior carina. A small anterior “step” is present on the anterior carina of each tooth. There are six superior alveolar foramina that open along the exterior surface of the maxilla. There is no noticeable sculpturing of the exterior surface of the maxilla. The specimen is

preserved in a block in association with some larger, indeterminate elements and osteoderms. The pit and ridge structure of the osteoderms and the relatively larger size of the miscellaneous bones indicate this additional material belongs to a small crocodilian.

Comments—The anterior “step” on the anterior carina of the tooth has not been described before for Paramacellodus, but is found in numerous other lizard taxa. Similar tooth structure can be found in the teeth of lizards from the families Anguidae, Cordylidae, Gymnophthalmidae, Scincidae, and Teiidae. The “step” in the tooth of P. keeblerorum is distinct in that it is the first time this, or any accessory structure (excluding a medial cuspule), has been reported for the teeth of a paramacellodid lizard.

Other lizards from the Cloverly Formation

A number of fragmentary lizard remains were recovered from OMNH localities V62 (Unit V of the Cloverly Formation); approximately 17 km NNE of Lovell, Bighorn County, Wyoming and V1075 (base of Unit VII); approximately 36 km ESE of Pryor, Bighorn County, Montana. As with those from the Antlers Formation, these specimens cannot be referred with confidence to any taxon and are treated here as morphotypes.

OMNH 23256 (Fig. 8A) is an anterior portion of a right dentary from V62. There are three closely spaced, pleurodont, and slightly procumbent teeth preserved on the specimen. Only the middle tooth has a complete crown. The crown is sharply pointed and has well defined anterior and posterior carinae. There are no medial striae on the crown of the tooth, but there is a well-developed medial cuspule. Overall, the tooth has a slight false “recurved” appearance and is rotated such that the anterior carina is more

medial than the posterior carina. The other two teeth are missing their crowns, but they do exhibit the same rotation of the tooth shafts. The height of the subdental shelf is 1/2 tooth height (approximate) and it borders a narrow, shallow subdental gutter. The Meckel's groove is narrow and opens ventrally, indicating that the specimen is likely from the anterior portion of the dentary and that the splenial did not extend to the symphysis.

OMNH 23255 (Fig. 8B) is an anterior fragment of a right maxilla from V62. The specimen preserves two pleurodont teeth that are tall, narrow, and have medially swollen bases and medially concave crowns with sharp, delicate carinae. The tips of the teeth are eroded and the nature of the apex is unknown. There are deep replacement pits at the bases of the teeth.

OMNH 30717 (Fig. 8C) was recovered from V1075 and is too incomplete to determine if it is part of a maxilla or a dentary. The specimen preserves four teeth; these teeth become progressively wider and more robust posteriorly. The bases of the teeth are swollen medially and the crowns are compressed mediolaterally and chisel-shaped. The anterior and posterior carinae on the tooth crowns are prominent and converge at a posteriorly displaced apex, giving the teeth a false "recurved" appearance. The anterior and posterior carinae meet at the apices to form medially directed cuspules and the medial surfaces of the tooth crowns are smooth. Each cuspule becomes progressively smaller on successively posterior tooth such that the posteriormost tooth has only a small swelling on the medial surface of the apex. The teeth are rotated slightly such that in occlusal view the anterior carina is displaced medially relative to the posterior carina. The second-most-anterior tooth has a small replacement pit located centrally at its base.

The shape of the teeth is generally similar to Paramacellodus, but the change in tooth size and shape along the tooth row is more dramatic than is known for paramacellodid lizards.

OMNH 60849 (Fig. 8D) is a posterior portion of a left dentary of a small lizard from V1075. There are two preserved teeth, which are pleurodont, but only the anterior tooth is complete. This tooth is slender and sharply pointed with well-developed carinae on the anterior and posterior margins of the crown, joining at a posteriorly displaced apex (false recurve). There is also a slight, but real recurvature of the tooth. The medial surface of the crown of the complete tooth is weakly concave. The bases of both teeth have weak medial expansions. The subdental shelf is robust, but is not very tall (less than one-half tooth height) and tapers posteriorly. This posteriorly decreasing height of the subdental shelf is consistent with this specimen being from the posterior portion of a dentary. The subdental gutter is shallow and wide and the Meckel's groove appears to have opened ventromedially, but most of the lateral wall is missing. There are two inferior alveolar foramina on the smooth, convex lateral surface of the specimen.

OMNH 60850 (Fig. 8E) is an indeterminate jaw fragment from V1075, preserving a single, subpleurodont tooth with a medially swollen base. The tooth is tall and has a well-developed, false "recurved" appearance. Below the apex is a prominent medial cuspule. There are no striae on the medial surface of the tooth. A large replacement pit is present at the base of the tooth and is slightly posterior of center.

The above five specimens all bear similarities to paramacellodid lizards (particularly Paramacellodus) in having relatively simple teeth that are falsely recurved shapes and medial cuspules (sensu Estes, 1983) on the crowns. It is likely, though not certain, that these specimens are from a single taxon of paramacellodid or

paramacellodid-like lizard. This, of course, assumes that there is some degree of heterodonty in tooth shape and size along the tooth row of this lizard, a condition not known for paramacellodids, but is common to many other taxa of lizards.

OMNH 30715 (Fig. 9A) is a jaw fragment (possibly from a maxilla) recovered from V62. It preserves a single, subpleurodont, heavily built tooth, with a blunt, rounded crown. The base of the tooth is long anteroposteriorly and wide mediolaterally. In anterior view the medial outline of the tooth is weakly concave. The lateral border of the tooth is more strongly convex and the tooth is inset from the lateral parapet. The crown of the tooth has large, dull anterior and posterior carinae that meet at the center of the tip of the tooth (no false “recurved” appearance) to form a small, medially directed cuspsule. In medial view the crown of the tooth is markedly narrower than the base, giving the crown a “pinched” appearance. The empty tooth spaces on either side of the tooth indicate that the teeth were closely spaced. The tooth on OMNH 30715 is distinct from the teeth of other lizards from the Cloverly Formation, described above, in being more massive and symmetrical, and, in having a tapered crown with a dull apex and more heavily built carinae. The closest similarity is to the possible teiid, OMNH 60537 (Fig. 4D), from the Antlers Formation of Oklahoma and a teiid, SMU 72283 (Winkler et al., 1990), from the Twin Mountains Formation of Texas. However, unlike OMNH 60537, OMNH 30715 lacks the heavy ring of cementum around the base of the tooth. It differs from SMU 72283 in not possessing striae on the medial surface of the tooth crown. Although the subpleurodont tooth implantation is shared with Teiidae, the specimen is, like OMNH 60537, too fragmentary to be referred confidently to the family.

OMNH 30716 (Fig. 9B) is a posterior portion of a left maxilla from V62. It preserves two short, conical, and slightly recurved teeth. The teeth have mediolaterally compressed crowns and the bases are medially expanded, but not swollen. The crowns of the teeth are tapered and bluntly tipped, but have no carinae. The cementum around the bases of the teeth forms heavily perforated rings. The supradental shelf is broken medially, but is thin. The posterior end of the dorsal process of the maxilla extends dorsolaterally away from the tooth row, and the internal surface of this process is lightly striated for what is presumed to have been the jugal-maxillary contact. The posterior opening of the interior superior alveolar foramen opens posteriorly above the posteriormost tooth. The external surface of the facial process is smooth and is perforated by a single superior alveolar foramen along the posterior edge (broken) of the specimen.

OMNH 23249 (Fig. 9C) is an indeterminate (maxilla or dentary) jaw fragment from V62. It preserves three pleurodont, blunt, chisel-like teeth. The anteriormost and posteriormost teeth are significantly larger, both in height and width, than the middle tooth. The medial and lateral margins of the teeth are straight in anterior view. The crowns are smooth with no carinae or striae. The shafts of the teeth are wider laterally than they are medially, giving the teeth a wedge-like appearance in occlusal view. A small excavation at the base of one of the outside teeth appears to represent an early stage in the development of a basal replacement pit, and may indicate that this taxon had direct tooth replacement. The blunt, chisel-like teeth of OMNH 23249 are uncommon in lizards.

These last three specimens are unlike the other lizards from the Cloverly Formation in being distinctly different from paramacellodids in tooth structure. Although all three specimens differ to some degree in tooth shape, they all have very distinct, heavily built, blunt teeth, which may indicate that they all belong to the same taxon. These specimens are somewhat similar in tooth shape to the teiid Haptosphenus placodon from the Late Cretaceous (Lancian) of North America, which also has massive teeth. However, none of the above specimens can be referred to Teiidae and it is likely that the similarity is coincidental or possibly convergent due to dietary similarities.

DISCUSSION

Fragmentary as these materials are, they add substantially to the known diversity of Early Cretaceous lizards from North America and provide a basis for a few preliminary, qualitative comparisons with older and younger assemblages. We tentatively recognize a minimum of five taxa (two named, three morphotypes) of lizards from the Antlers Formation and three taxa (one named, two morphotypes) from the Cloverly Formation. Of these, the five morphotypes we have recognized are based primarily on observed differences in tooth shapes. With the exception of the possible teiids and the anguimorphan, the variation in tooth shape is centered around a single theme of paramacellodid-like teeth (false “recurved” crown, medial cuspule, and moderately developed carinae). Indeed, based on tooth shapes, the majority of the lizards from both formations are either paramacellodids similar to those found in the Jurassic of Europe (Seiffert, 1973; Estes, 1983) and North America (Prothero and Estes, 1980; Evans and Chure, 1999), or they are taxa with similarly simple paramacellodid-like teeth. This

tooth shape is common not only to paramacellodid lizards of the Late Jurassic and Early Cretaceous (Estes, 1983), but is also found in many taxa of extant Cordylidae and some Scincidae (RLN personal observation). Reference to either Cordylidae or Scincidae is possible, as both are present in Late Cretaceous faunas of North America (Gao and Fox, 1996), but it seems more likely that the specimens represent paramacellodids based on the widespread distribution of Paramacellodidae during the Late Jurassic and Early Cretaceous. Although limited in taxonomic information, these specimens add significantly to our knowledge of Early Cretaceous lizards and comparisons can be made other to other lizard paleofaunas.

In comparing the lizard material from the Antlers Formation with that of the Cloverly Formation, we find no conclusive evidence that any one taxon is shared between the two faunas. This apparent lack of shared taxa is somewhat surprising, in view of the fact that the two units are generally considered to be paracontemporaneous (Ostrom, 1970; Jacobs et al., 1991; Jacobs and Winkler, 1998) and the two faunas share the theropod Deinonychus antirrhopus (see Brinkman, et al., 1998), as well as the ornithopod Tenontosaurus (Cifelli et al., 1997a), though it is not yet clear if the ornithopods are the same species. The apparent difference in the lizard assemblages may be, in part, due to the fragmentary nature of the material. However, geographical, environmental, and temporal differences also may be factors.

In contrast to the paracontemporaneous ages of the Cloverly and Antlers formations as estimated by Jacobs et al. (1991), Jacobs and Winkler (1998), and Brinkman (1998), the lizards from the sampled horizons of the Cloverly Formation may be older than those sampled for the Antlers Formation. Some support for this hypothesis

is found in the comparison of the new specimens with the lizards of the Twin Mountains Formation of the Trinity Group, Texas. Although the lizard fossils from both formations are fragmentary, the samples are sufficient to permit some general comments on the comparison of the two assemblages. The teiid Ptilotodon wilsoni of the Antlers Formation is derived relative the teiids of the Twin Mountains Formation with respect to tooth shape. Ptilotodon has teeth with anterior and posterior accessory structures whereas the teiids from the Twin Mountains Formation have simple, conical teeth. In contrast to the lack of shared taxa between the Antlers and Cloverly formations, it is possible that the latter shares two taxa with the Twin Mountains Formation. OMNH 23256 (Fig. 8A) is very similar in tooth structure to SMU 72286 (Winkler et al., 1990:fig. 8C), as are OMNH 30716 (Fig. 8G) and SMU 72284 (Winkler et al., 1990:fig. 8B). It is conceivable, though not demonstrable, that this similarity implies similarity in age, and that the Cloverly Formation may correspond better to the Twin Mountains Formation than to the Antlers Formation. Such a correlation would mean that the Cloverly Formation is stratigraphically lower than the Antlers Formation. This contrasts with evidence suggested by distribution of species of the ornithopod Tenontosaurus (Head, 1998). However, the differences could be ecological or biogeographical in nature. The geographically widespread mammal Gobiconodon, known from both Asia and the Cloverly Formation, is lacking in the Trinity Group, as are nodosaur dinosaurs, which are present from the Jurassic onward in the western interior of North America, but do not appear in Texas until the Cenomanian (Jacobs and Winkler, 1998).

Another North American Aptian-Albian locality that has yielded lepidosaurs is Tepexi de Rodríguez, Mexico (Reynoso, 1995, 1996, 1997, 1998). Unlike the localities

from the United States, the material from Mexico represents primarily sphenodontians, but also includes a primitive lizard and a possible paramacellodid. The presence of sphenodontians is unusual and is the youngest Cretaceous record of the group for North America. The lizard material from Mexico has yet to be figured or comprehensively described, so detailed comparisons to the specimens from the Antlers and Cloverly formations are not possible.

The lepidosauromorphs from the Upper Jurassic Morrison Formation (see Prothero and Estes, 1980; Callison, 1987; Evans, 1993, 1996; Chure et al., 1998; Evans and Chure, 1998b, 1999; Fraser and Wu, 1998) include paramacellodids (Paramacellodus and Saurillodon), as well as anguimorphans (Dorsetisaurus and Parviraptor), an enigmatic basal lizard (Schilleria), and abundant sphenodontians. A significant difference between the Late Jurassic and Early Cretaceous lepidosauromorphs of North America is the loss of sphenodontians as a major component of the fauna. However, the lizard assemblages are morphologically and taxonomically similar, the major differences being an apparent decline, or relative rarity, of anguimorphs, and the addition of a modest diversity of teiids with relatively simple teeth.

Other, worldwide Jurassic through earliest Cretaceous lizard faunas have been reported from numerous regions. Jurassic faunas are known from Portugal, England, Germany, France, Japan and China (see Evans, 1993 and references therein). Like the lepidosaurians of the Morrison Formation, the faunas of England, Portugal, and Japan are composed primarily of sphenodontians, scincomorphs (primarily paramacellodids) and anguimorphs (Seiffert, 1973; Ensom et al., 1991; Evans, 1993, 1994a, 1998, Evans and Manabe, 1979). The German lizard fauna is similar except for the presence of a possible

gekkotan (Evans, 1993, 1994b). The lizards from China and France are of uncertain affinities, and some of the referred French specimens are actually of a sphenodontian (Evans, 1993). Earliest Cretaceous lepidosaurian faunas have been reported from England, Spain, Japan (see Evans, 1998 and references therein), and Morocco (Richter, 1994; Broschinski and Sigogneau-Russell, 1996). As with the Jurassic, these faunas are composed primarily of sphenodontians, scincomorphs and anguimorphs, but an early snake has been reported from Spain (Rage and Annette, 1994). The lizard faunas from the Jurassic-earliest Cretaceous of Europe and Asia are similar in morphologic (predominately simple-toothed) and taxonomic composition (predominately paramacellodid or paramacellodid-like) with those from the Antlers and Cloverly formations in that nearly all the faunas share the presence of paramacellodids or paramacellodid-like taxa as the major component of the fauna. There is no evidence that any of the taxa (at the species level) from the Antlers and Cloverly formations are the same as European or Asian taxa.

Outside of North America there are Aptian-Albian lizard localities in Brazil, Algeria, Uzbekistan, and Mongolia, all of which have been reviewed by Evans (1998). From Brazil there is only the taxon Olidalacerta brasiliensis, which is of uncertain affinities below the level of Squamata (Evans and Yabumoto, 1998). The only squamate known from Algeria is an early snake (Hoffstetter, 1960). Another snake and an early amphisbaenian have been found in Uzbekistan (Nessov, 1988). The earliest record of snakes in North America is from the Albian-Cenomanian (Gardner and Cifelli, 1999).

The most detailed and appropriate (in a temporal sense) comparisons can be made with the fauna of Mongolia because numerous lizard taxa have been reported from the

Khobur ("Hobur," Nessov, 1993) locality, presumed to be of Aptian-Albian age. This unusual fauna is comprised of a diverse mix of primitive (Paramacellodidae, Dorsetisauridae) and derived taxa (Gekkonidae, Scincidae, Xantusiidae, Priscagamidae, Xenosauridae, Necrosauridae) (Alifanov, 1992; 1993). Paramacellodidae and Dorsetisauridae are common to the Late Jurassic and Early Cretaceous, whereas the Gekkonidae, Scincidae, Xantusiidae, Priscagamidae, Xenosauridae, and Necrosauridae are not present prior to the Late Cretaceous in North America. Whether or not all of the taxonomic assignments for the lizards of Khobur are accepted, the fauna certainly exhibits a much greater diversity, both morphologically and taxonomically, than is seen in any of the other Aptian-Albian lizard faunas known, particularly those of North America. Such diversity is not seen until later in the Cretaceous in North America, with the earliest approximation being from the Albian-Cenomanian Cedar Mountain Formation (Cifelli and Nydam, 1995; Cifelli et al., 1997b, 1999; Nydam, 1995, in press). It is not until the Late Cretaceous that many of the same groups seen in Khobur appear in North America (Estes, 1983; Gao and Fox, 1996).

CONCLUSIONS

The lizards from the Antlers and Cloverly formations provide important additions to our understanding of Early Cretaceous lizards and permit some initial observations of the evolution of lizards during this time period. Two fundamental changes occur in the lepidosauromorph fauna of North America prior to and after the Aptian-Albian. Between the Late Jurassic and Early Cretaceous, sphenodontians all but completely disappear, while the lizards show little change (morphologically if not taxonomically). Between the

Early and Late Cretaceous the lizard fauna itself shifts from a paramacellodid (or paramacellodid-like taxa)-dominated fauna (similar to many Late Jurassic-Early Cretaceous lizard faunas), to a fauna rich in both morphologic and taxonomic diversity, with many modern families making their initial appearances. The timing of this change in North America does not correspond to a similar change seen in Asia. The lizards from Khobur, Mongolia, indicate that a similar shift occurred prior to, rather than after, the Aptian-Albian. The possibilities of biogeographic interchange or other factors on global distribution of modern lizard groups underscore the importance of this interval and the need for greater representation in the medial Cretaceous.

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FIGURE LEGENDS

FIGURE 1. Location map of Early Cretaceous lizard localities of Cloverly (A-C) and Antlers (D) Formations. A, OMNH locality V1156. B, OMNH locality V1075. C, OMNH locality V62. D, OMNH locality V706.

FIGURE 2. New lizard taxa from Antlers Formation, Atoka County, Oklahoma. A, OMNH 60535, holotype left dentary of Atokasaurus metarsiodon, gen. et sp. nov. in medial view. B, OMNH 60764, holotype right dentary of Ptilododon wilsoni, gen. et sp. nov. in medial view. Scale bars 1 mm.

FIGURE 3. Lizard specimens from Antlers Formation, Atoka County, Oklahoma. A, OMNH 60538, broken maxilla (?) in medial view. B, OMNH 60765, jaw fragment in medial view; C, OMNH 60763, posterior right maxilla in medial view. Scale bars 1 mm.

FIGURE 4. Lizard specimens from Antlers Formation, Atoka County, Oklahoma. A, scanning electron micrograph of OMNH 34206, jaw fragment in medial view. B, OMNH 32585, right dentary in medial view. C, OMNH 61206, left dentary in medial view. D-E, OMNH 60537, left (?) dentary fragment in medial (D) and posterior (E) views (arrow indicates groove for articulation with splenial). F, OMNH 60541, jaw fragment in medial view. Scale bars 1 mm unless otherwise indicated.

FIGURE 5. OMNH 60595, Paramacellodidae incertae sedis, broken right frontal in A, ventral; B, lateral; and C, dorsal views. Scale bar 1 mm.

FIGURE 6. Cf. *Paramacellodidae* osteoderms from Antlers Formation, Atoka County, Oklahoma. **A**, OMNH 32613, **B**, OMNH 60766; **C**, OMNH 60802; **D**, 61132. Scale bars 1 mm.

FIGURE 7. *Paramacellodus keeblerorum*, sp. nov. from Cloverly Formation of Montana. **A-C**, OMNH 60576, holotype left maxilla; **A**, medial view with box around tooth detailed in **C**. **B**, silhouette of holotype maxilla of *Paramacellodus keeblerorum*, sp. nov., in white and associated limb bone (crocodilian?) in gray. **C**, detail of tooth from OMNH 60573 arrow indicates anterior “step” on anterior carina of tooth. **D**, OMNH 61133, paratype left maxilla in lateral view. Scale bars: **A-B**, 1 cm; **C-D**, 1 mm.

FIGURE 8. Additional lizard specimens from Cloverly Formation of Montana and Wyoming. **A**, OMNH 23256, broken right dentary in medial view. **B**, OMNH 23255, maxilla (?) fragment in medial view. **C**, OMNH 30717, jaw fragment in medial view (arrow indicates resorption pit at base of tooth). **D**, OMNH 60849, broken left dentary in medial view. **E**, OMNH 60850, jaw fragment in medial view. All scale bars 1 mm.

FIGURE 9. Additional lizards from Cloverly Formation of Montana and Wyoming. **A**, OMNH 30715, maxilla (?) fragment in medial view. **B**, OMNH 30716, right maxilla fragment in medial view; **C**, OMNH 23249, jaw fragment in medial view. All scale bars 1 mm.

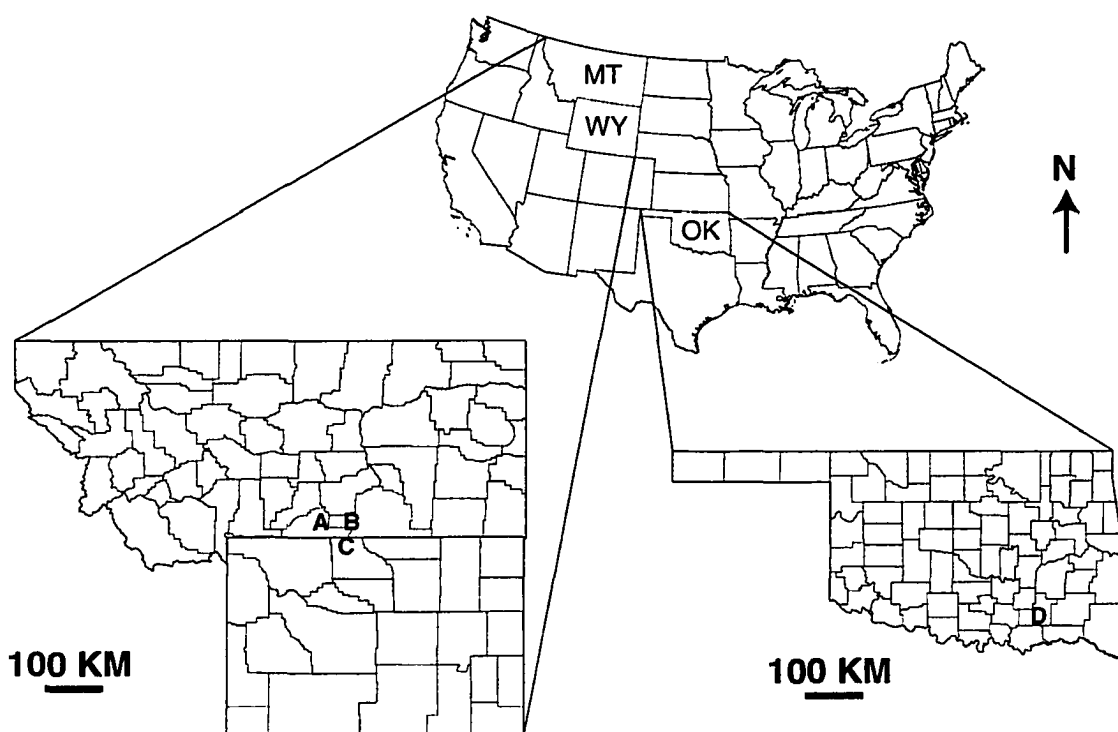


Figure 1

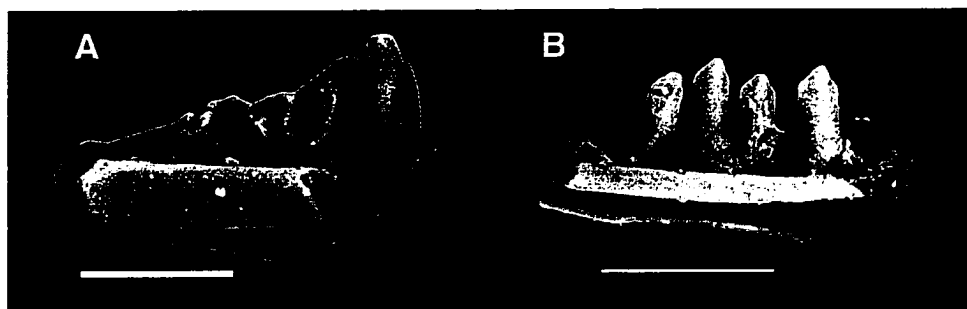


Figure 2

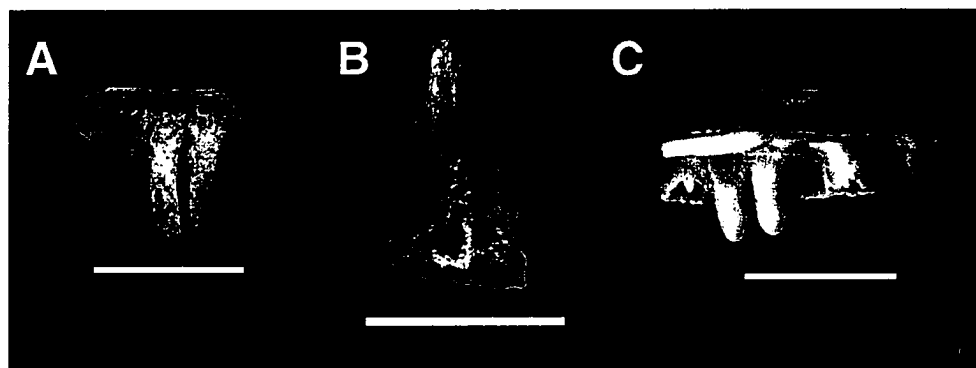


Figure 3

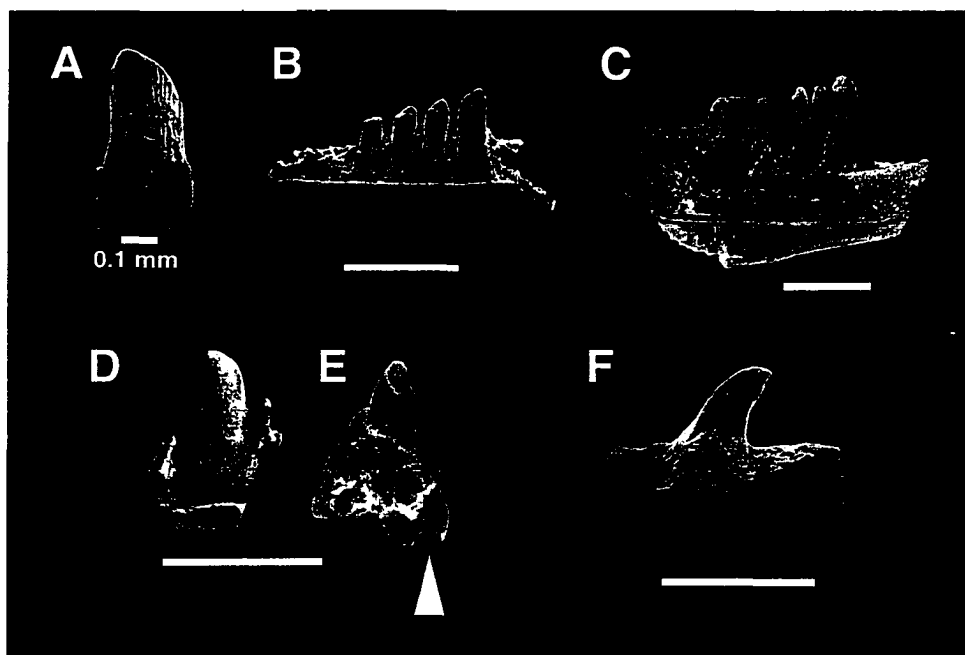


Figure 4

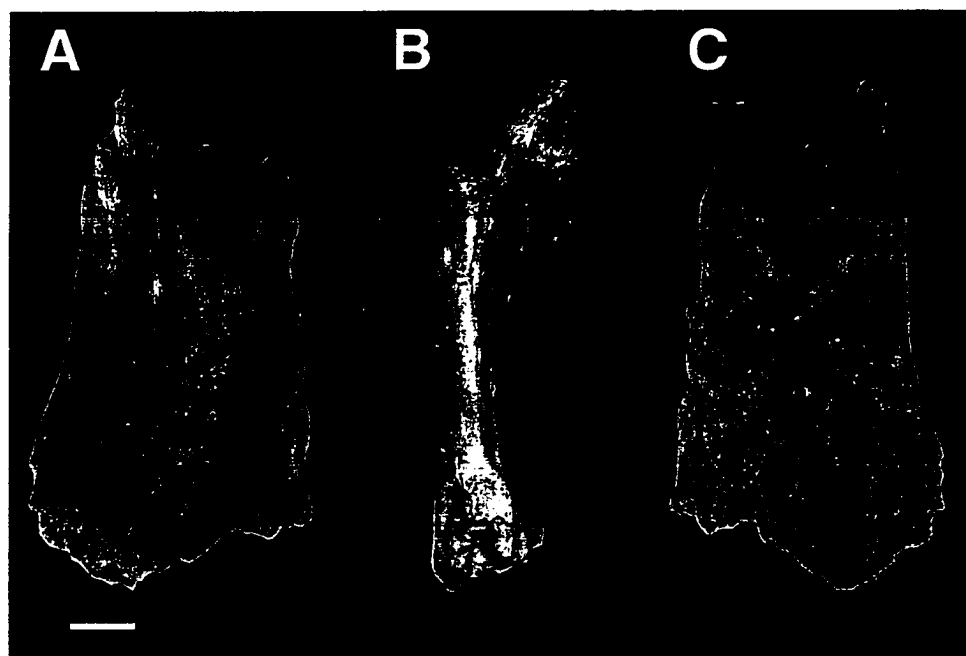


Figure 5

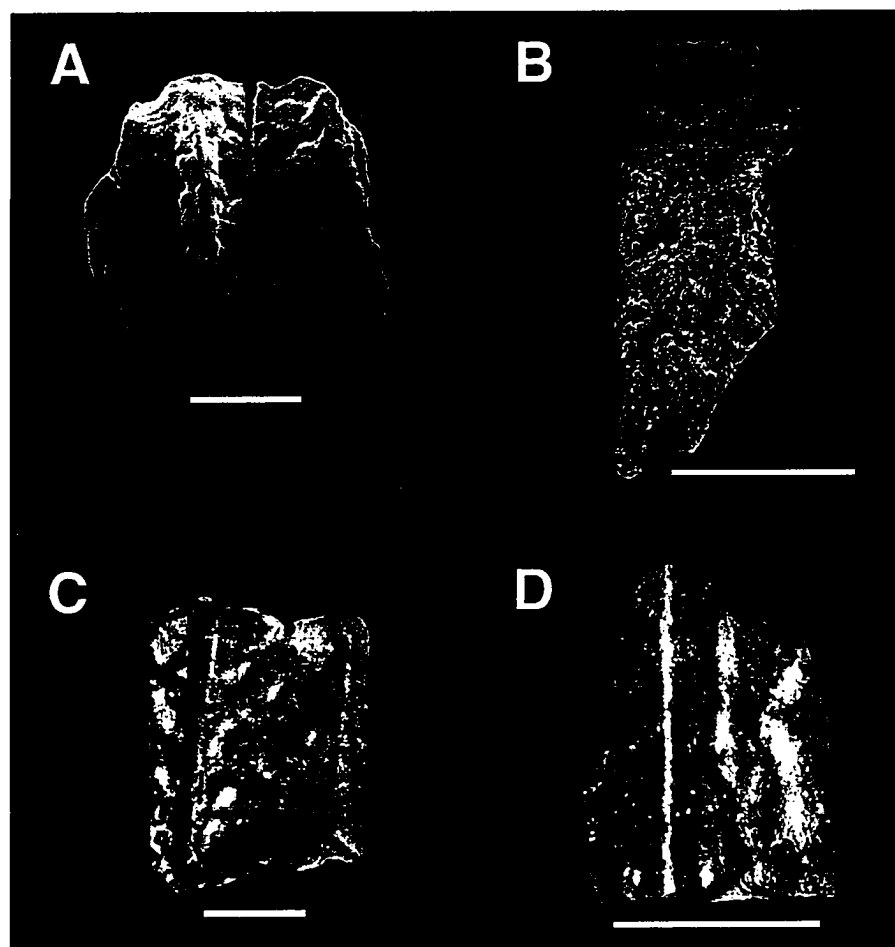


Figure 6

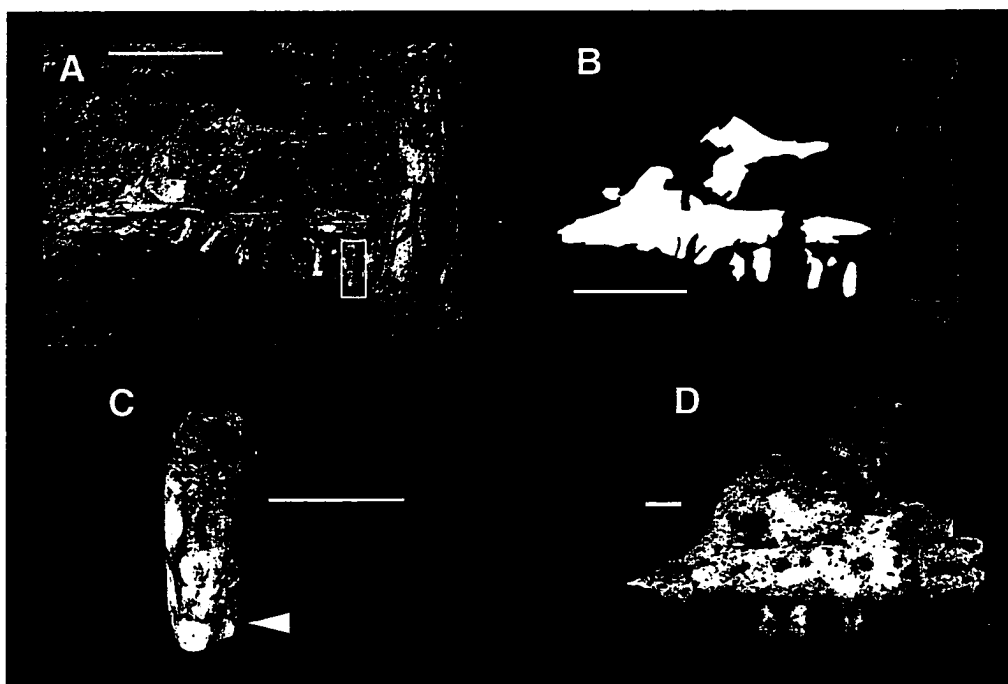


Figure 7

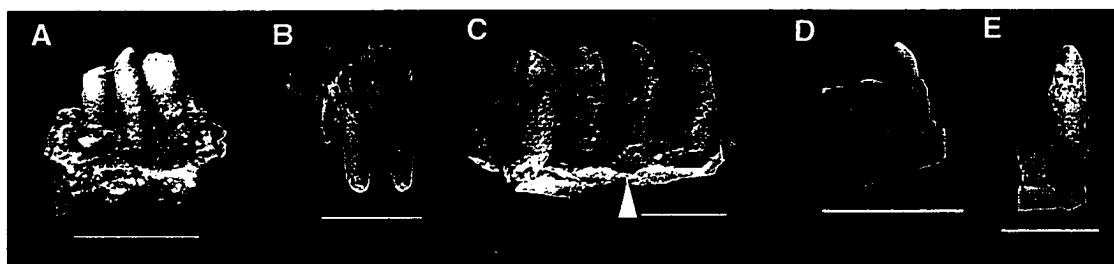


Figure 8



Figure 9

LIZARDS OF THE MUSSENTUCHIT LOCAL FAUNA (ALBIAN-CENOMANIAN)
AND COMMENTS ON THE EVOLUTION OF THE CRETACEOUS LIZARD
FAUNA
OF NORTH AMERICA

RANDALL L. NYDAM

Sam Noble Oklahoma Museum of Natural History, 2401 Chautauqua Ave., Norman,
Oklahoma, 73072; and Department of Zoology, University of Oklahoma, Norman,
Oklahoma, 73019

Contact information: phone, (405) 325-4712; FAX, (405) 325-7699; email,
rlnydam@ou.edu.

Suggested running head—NYDAM—CRETACEOUS LIZARDS

ABSTRACT—A diverse fauna of lizards has been recovered from the medial Cretaceous Cedar Mountain Formation of central Utah. These lizards are a component of the now recognized Mussentuchit local fauna and, like many of the other vertebrate groups within this fauna, show striking similarities to their North American Late Cretaceous (Campanian-Maastrichtian) counterparts. Unlike the Late Cretaceous lizard faunas, the lizards from the Mussentuchit local fauna also include at least one paramacellodid, a group common to Late Jurassic and Early Cretaceous lizard faunas of North America. Comparison with other Cretaceous lizard faunas from both North America and Asia indicate that the changes in the North American lizard fauna represented by the lizards of the Mussentuchit local fauna are more likely the result of the introduction of taxa from Asia during the Early Cretaceous. Supposedly herbivorous taxa are found among the Polyglyphanodontine lizards from the Late Cretaceous of North American and Asia, but the general changes in the Cretaceous lizard fauna of North America cannot be convincingly shown to be linked to the concurrent angiosperm radiation. A later influx of Asian lizard taxa prior to the Campanian may explain the relatively sudden appearance of additional groups of lizards in the early Campanian of North America.

INTRODUCTION

The North American record of Mesozoic lepidosauromorphans includes intermittent fossil horizons from the Late Jurassic through the K/T boundary. Within this time frame two basic faunal arrangements have been identified. The first is an older, more primitive fauna composed primarily of sphenodontians, paramacellodid scincomorphs, and primitive anguimorphans from the Jurassic (Kimmeridgian) Morrison Formation (Prothero and Estes, 1980; Evans, 1993, 1996; Evans and Chure, 1998a, 1998b, 1999; Fraser and Wu, 1998). The composition of this fauna remained relatively stable through the Early Cretaceous (Aptian-Albian), as indicated by lepidosaurians from: the Trinity Group of Texas (Winkler et al., 1990); Cantera Tlayua, Mexico (Reynoso, 1995, 1996, 1997, 1998); and the Antlers and Cloverly formations of Oklahoma and Montana/Wyoming, respectively (Nydam and Cifelli, submitted A). The most notable changes after the Kimmeridgian and before the Aptian-Albian are the reduction in the presence of both sphenodontians (restricted to Cantera Tlayua, Reynoso, 1997) and anguimorphans (possibly present in Antlers Formation; Nydam and Cifelli, submitted A) and the appearance of the earliest representatives of Teiidae (Winkler, et al., 1990; Nydam and Cifelli, submitted B). In both the Kimmeridgian and Aptian-Albian faunas, however, the major taxonomic component consists of paramacellodid or paramacellodid-like scincomorphan lizards (Nydam and Cifelli, submitted A).

Following the Aptian-Albian, there is a 30+ million year period for which little is known about the North American lizard fauna. The second faunal arrangement of the Mesozoic is the younger (Campanian-Maastrichtian), more derived lepidosaurian fauna, which is composed of a wide diversity of taxa referable to numerous modern groups,

including Anguidae, Cordylidae, Monstersauria (clade of platynotans that includes Helodermatidae, Norell and Gao [1997]), Iguanidae, Scincidae, Teiidae, Xenosauridae, Xantusiidae, and Varanidae (Estes, 1983b; Gao and Fox, 1996). Of these groups, the greatest diversity is found in the Teiidae, both polyglyphanodontine (Gilmore, 1940, 1943a) and non-polyglyphanodontine ("chamosiine teiids" of Denton and O'Neill, 1995) taxa. Anguids (particularly Odaxosaurus) also are commonly recovered from most Late Cretaceous localities (Estes, 1964, 1969; Sullivan, 1981; 1983b; Rowe et al., 1992; Gao and Fox, 1996). Between the Campanian and the Maastrichtian there was little in the way of taxonomic changes in the lizard fauna (sphenodontians are not found in North America after Aptian-Albian), but there was an apparent loss of diversity. There are 37 taxa (named and unnamed) of lizard that have been reported from Campanian-aged strata in North America (Estes, 1983; Gao and Fox, 1996; Rowe et al., 1992; Denton and O'Neil, 1995; McCord; 1998; Eaton et al., 1999; Nydam, 1999) versus 20 taxa from Maastrichtian-aged strata (Estes, 1983; Gao and Fox, 1996). A similar loss of diversity in lizards between the Campanian and Maastrichtian has been identified for the lizards of Mongolia (Alifanov, 1993a) suggesting that the trend was a global. Lehman (1997) suggested that at least during the Campanian there also were latitudinal differences in the lizard fauna, as indicated by a greater diversity of lizard taxa in more southerly deposits. However, additions to the record of lizards from the Campanian of Canada (Gao and Fox, 1996) indicate that the latitudinal trend may be opposite of that proposed by Lehman (1997).

Comparison of these two faunal arrangements shows a major shift in the composition of lepidosaurian taxa between the Aptian-Albian and the Campanian-

Maastrichtian. However, the fossil record of lizards from North America between these horizons is sparse, giving little indication of the specifics (e.g., timing, pace) of this change. Some evidence suggests that changes had begun in at least two lineages, polyglyphanodontine teiids and helodermatid-like platynotans, by the Albian-Cenomanian (Nydham, 1999, 2000). However, it is not clear when other lineages appeared and whether this was a rapid or gradual transition between the primitive and derived faunas.

Herein I describe the lizards of the Mussentuchit local fauna from the Cedar Mountain Formation (Albian-Cenomanian), Emery County, Utah. This fauna is important in that it is temporally intermediate between the Late Jurassic and Late Cretaceous faunas, and has been well sampled (Cifelli et al., 1999). I make comparisons to both older and younger lizard faunas of North America to examine how the Mussentuchit lizards fit into the transition between the primitive and derived faunas. I also examine the relationship of the Mussentuchit lizards to the temporally relevant lizard faunas of Asia, which have been previously considered to be a possible source of the taxonomic diversity of lizards from the Late Cretaceous of North America (Estes, 1983a, 1983b).

ABBREVIATION USED IN TEXT

OMNH, Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma.

GEOLOGIC SETTING

The Cedar Mountain Formation is comprised of variegated, terrigenous rocks that

are exposed in central and eastern Utah, continuing on into western Colorado as the laterally equivalent Burro Canyon Formation (Stokes, 1944, 1952; Tschudy et al., 1984; Kirkland et al., 1997; Currie, 1998). The lower member of the Cedar Mountain Formation is the massive, but discontinuous, sand-pebble Buckhorn Conglomerate (Stokes, 1944, 1952). The upper mudstones of the Cedar Mountain Formation have been subdivided into four additional members based on lithological and paleontological differences (Kirkland et al., 1997). Microvertebrate-producing localities (Fig. 1) are known only from the uppermost, or Mussentuchit Member, of which major exposures lie principally on the west-side of the San Rafael Swell, a prominent anticline in the region. The Mussentuchit Member is 126 m thick at its type locality (Stokes, 1952), but is variable in thickness throughout the region. It is composed of highly smectitic gray-green mudstones with interbedded channel sandstones (Kirkland, 1987; Cifelli et al., 1999). The environment of deposition of the Mussentuchit Member is interpreted as having been overbank, or crevasse splay, deposits associated with multiple flood events in a meandering river system (Nelson and Crooks, 1987). Microvertebrate localities occur in a narrow stratigraphic interval in the upper part of the unit, 10-20 m below the contact with the overlying Dakota Formation. Multiple, concordant radiometric determinations from two of the localities (in direct association with the fossil horizon at each) yield an age of 98.39 ± 0.07 Ma for the fauna (Cifelli et al., 1997), placing the fauna at the Albian-Cenomanian (Early-Late Cretaceous) boundary (sensu Gradstein et al., 1995). This horizon has also been referred to as the medial Cretaceous (Cifelli and Muizon, 1997; Cifelli and Madsen, 1998, 1999; Cifelli, et al., 1999), a convention that is followed herein.

SYSTEMATIC PALEONTOLOGY

SQUAMATA Oppel, 1811

SCINCOMORPHA Camp, 1923

SCINCOIDEA Oppel, 1811

PARAMACELLODIDAE Estes, 1983

cf. PSEUDOSAURILLUS Hoffstetter, 1967

cf. PSEUDOSAURILLUS sp.

(Fig. 2)

Referred Specimen—OMNH 27711, broken right maxilla.

Locality and Horizon—OMNH locality V695; 10-20 m below upper contact of Mussentuchit Member of the Cedar Mountain Formation and Dakota Formation, Emery County, Utah.

Description—OMNH 27711 is the posterior portion of a right maxilla, preserving 10 teeth. The exterior surface of the element is smooth and unornamented. There are three superior alveolar foramina above the lateral parapet. The anterior two foramina open anterolaterally and the posterior foramen opens posterolaterally. Internally, the posterior interior alveolar foramen opens posteriorly above the sixth preserved tooth position. The facet for the maxillary process of the jugal is a narrow slit restricted by the dorsally swollen supradental shelf to the lateral edge of this shelf. The supradental shelf

is well developed and wide, but not very deep. The supradental gutter, which is narrow and shallow, does not extend posterior to the posterior interior alveolar foramen. The teeth are homodont, columnar, closely spaced, and strongly pleurodont (only very tips of teeth extend beyond lateral parapet). The tips of the teeth are rounded and very weakly recurved. However, the crowns are not preserved well enough to determine if the medial surfaces were striate. Deep replacement pits at the bases of the teeth indicate that tooth replacement was direct.

Comments—Pseudosaurillus was first described from the Purbeck Limestone Formation of England (Hoffstetter, 1967) and placed in the Paramacellodidae by Estes (1983b) based on similarities to Paramacellodus and Becklesius in general form. Evans and Chure (1998a) noted that the teeth of Pseudosaurillus are similar to those of Paramacellodus in having medial facetting of the apex. The teeth of OMNH 27711 are poorly preserved and no facetting or striae can be seen, but they otherwise fit the same description as for Pseudosaurillus in that they are narrow, cylindrical, closely spaced, and low crowned. In the absence of more diagnostic material, I tentatively assign this specimen to Paramacellodidae as cf. Pseudosaurillus. If correct, this assignment would extend the range of this genus from the Berriasian to the Albian-Cenomanian.

SCINCOIDEA Oppel, 1811

Family indet.

DIMEKODONTOSAURUS, gen. nov.

Etymology—"Di" (Greek), double; "mekos" (Greek), length; "odous" (Greek) tooth; and "sauros" (Greek) lizard. In reference to distinct difference in height between anteriormost and posteriormost teeth in comparison to those teeth in middle of tooth row.

Type and Only Known Species—Dimekodontosaurus madseni, sp. Nov.

Diagnosis—As for type and only known species.

DIMEKODONTOSAURUS MADSENI, gen. et sp. nov.

(Fig. 3)

Etymology—In recognition of Scott Madsen who skillfully prepared the type of this many other lizards from the Cedar Mountain Formation.

Holotype—OMNH 34560, left dentary.

Referred Specimens—OMNH 22105- 22106, 28257, jaw fragments; 28733, dentary fragment; 28814, partial left maxilla; 29634, partial left dentary; 30207, partial right dentary; 32625-32627, 32634- 32635, 33431, 33449, jaw fragments; 34558, broken right maxilla; 61243, osteoderm; 61244, osteoderm; 61806, jaw fragment.

Localities and Horizon—OMNH localities V239, V240, V695 (type locality), and V868; 10-20 m below upper contact of Mussentuchit Member of Cedar Mountain Formation and Dakota Formation, Emery County, Utah.

Diagnosis—Differs from other known cordyliform scincomorphs in having distinctly different sizes of teeth along tooth row such that anterior and posterior teeth are much taller than teeth in middle part of tooth row.

Description—OMNH 34560 (Figs. 3A-C) is a complete left dentary of

Dimekodontosaurus madseni with 27 tooth positions and 23 teeth preserved. The symphysis forms a broad surface, extending only under the anteriormost two tooth positions. The subdental gutter is narrow and shallow, and runs the length of the tooth row. The subdental shelf is tall anteriorly, but narrows substantially posteriorly and turns sharply posterodorsally beneath the posteriormost three tooth positions. Based on articulation scars, an anteromedial process from the coronoid extended anteriorly beneath the posteriormost three tooth positions, separating the splenial from the subdental shelf. The articulation facet for the splenial on the dentary indicates that the splenial extended anteriorly to end beneath the 9th or 10th tooth positions, leaving a narrow, slit-like symphyseal foramen between the splenial and the symphysis. A lateral lappet of the coronoid onto the dentary is absent as indicated by the lack of a facet on the external edge of the posterior portion of the dentary. The very tip of the posterodorsal process of the dentary is broken, and it is not possible to determine if there was a lateral lappet of the dentary onto the coronoid. Within the Meckel's canal, below the 19th and 20th tooth positions, is the posteriorly directed opening of the posterior inferior alveolar foramen. Posterior to this foramen is a remnant of the surangular still articulated to the surface of the internal lateral wall of the dentary. Along the dorsal edge of this articulation is a small ridge that extends from the roof of the Meckel's canal and posteriorly to the end of the tooth row. Just posterior to the opening of the posterior inferior alveolar foramen this ridge forms a prominent and narrow septum, tapers to short ridge, and becomes a prominent septum again for the rest of its length. The dorsomedial edge of the surangular abuts against this ridge. The exterior surface of the dentary is strongly convex.

The teeth all have a medially directed cuspule (sensu Estes, 1983b) at the apex and striae on the lingual surface of the crowns. There are two well-developed lingual striae that extend from the medial cuspule. The anterior and posterior carinae of each tooth meet at the apex to form an inward pointing “V” in occlusal view. With the exception of the posteriormost two teeth, the crowns of the teeth are rotated posteriorly such that medial cuspule is directed approximately 30° posteromedially. The last two teeth have almost no rotation of the crown. The anterior 10 teeth (first 12 tooth positions) of the dentary are tall, narrow, recurved, and have sharp anterior and posterior carinae. The 14th tooth is slightly shorter than the 12th tooth (tooth 13 is missing) and has a much wider base than the anterior teeth. Teeth in positions 15-22 are all blocky teeth that are distinctly shorter than either the anterior teeth or the teeth in the last five tooth positions. Teeth in positions 23-25 are much taller and more massive than the preceding seven teeth. Teeth in positions 26 and 27 are not as massive and are much shorter, but owing to the upward curvature of the tooth bearing portion of the dentary, their crowns are at the same height as the preceding three teeth. There are basal replacement pits at tooth positions 9, 11, and 27, and are missing teeth in positions 1, 10, and 13. The replacement pit at tooth position 27 contains the crown of a developing replacement tooth.

OMNH 32625 and 32626 (Figs. 3D, E) are isolated jaw fragments of Dimekodontosaurus madseni that exhibit anterior and posterior tooth morphologies, respectively. OMNH 28814 (Fig. 4A) is a partial left maxilla, preserving most of the posterior maxillary tooth row. The teeth of OMNH 28814 are subpleurodont to pleurodont, moderately spaced with bases that are wider than the crowns. The tooth crowns are without medial striae, and have no distinct carinae, but do have medially

directed cuspules on the apices. None of the tooth crowns are rotated. Of the six teeth preserved in OMNH 28814, the third (counting from anteriormost tooth) is distinctly larger than the other five. The fourth tooth has a large replacement pit at its base. This specimen can only be tentatively referred to D. madseni because of the lack of lingual striae and anterior and posterior carinae on the teeth.

OMNH 34558 (Fig. 4B) is a broken right maxilla preserving two teeth from the posterior portion of the maxillary tooth row. Its teeth are subpleurodont, and the posteriormost tooth is distinctly larger than the preceding one. A broken tooth base anterior of the small tooth indicates this tooth also was relatively small. Neither of the complete teeth have discernable striae, but well defined, delicate, anterior and posterior carinae are present on the crowns. Both tooth crowns are similar to those of the dentary in having sharp apices that form inward pointing “V’s” in occlusal view. Also like the teeth of the dentary, the crown of the smaller tooth is rotated nearly 30°, but the large tooth is rotated nearly 60°. There is a small replacement pit at the base of the smaller tooth. As with OMNH 28814, OMNH 34558 can only be tentatively referred to D. madseni because of the lack of lingual striae on the teeth.

OMNH 61243 and 61244 (Figs. 5A, B) are imbricating osteoderms. They are heavily built with a central ridge and are sculptured with a pattern of small pits.

Comments—The dentary of D. madseni is almost certainly that of a scincomorph with cordyliiform affinities, as indicated (*sensu* Estes et al., 1988) by the large anteromedial process of the coronoid that articulated below the posterior portion of the tooth row and the lack of an anterolateral process of the coronoid. The morphology of the teeth, particularly the striae, cuspule, and carinae of the crowns, are very much like

that of the teeth of some taxa of paramacellodids and modern cordylids. However, no known paramacellodid (see figures in Estes [1983b] and Evans and Chure [1998a, 1999]) or cordylid (Edmund, 1969) has a dentition with the heterodonty, particularly with respect to tooth height, is found in D.madseni. Without more complete materials it is not possible to make a familial assignment for D.madseni. Sakurasaurus shokawensis from the Early Cretaceous of Japan (Evans and Manabe, 1999) is a scincomorphan with heterodonty similar to that of Dimekodontosaurus in that the anterior teeth are gracile and recurved and the posterior teeth are blunt and striated. However, all of the teeth in the dentary of Sakurasaurus are the same height. The reduced height of the teeth in the middle of the tooth row in the dentary is not known to occur in any other known scincoids, but a similar condition is found in the maxillae of some Recent teioids, lacertids, and iguanids (Estes et al., 1988). A similar condition has been described maxillary tooth row of the Late Cretaceous iguanian Cnephasaurus (Gao and Fox, 1996). Such a taxonomically widespread occurrence of this feature suggests that it may represent a feeding specialization (see Gao and Fox, 1996) that arose several different times in different lineages.

The osteoderms are referred to Dimekodontosaurus based on their similarity to the osteoderms of other paramacellodid and cordylid scincomorphs. Also, of the other taxa in the fauna that could have possibly been armored, only Dimekodontosaurus appears to have been large enough to possess osteoderms of the size of OMNH 61243 and 61244.

CF. SCINCOMORPHA Camp, 1923

Family indet.

BOTHRIAGENYS n. gen.

Etymology—"Bothrion" diminutive for "bothros" (Greek), trench; "genys" (Greek), jaw. In reference to narrow Meckel's groove along length of dentary.

Type and only Species—Bothriagenys mysterion.

Distribution—Mussentuchit Member of Cedar Mountain Formation (medial Cretaceous), Emery County, Utah.

Diagnosis—as for type and only known species.

BOTHRIAGENYS MYSTERION, sp. nov.

(Fig. 6)

Etymology—"Mysterion" (Greek), mystery. In reference to uncertain familial affinities of new taxon.

Holotype—OMNH 28119, left dentary.

Hypodigm—Holotype and OMNH 22118, dentary fragment.

Locality and Horizon—OMNH localities V695 (OMNH 22119) and V868 (OMNH 22118); 10-20 m below upper contact of the Mussentuchit Member of Cedar Mountain Formation and Dakota Formation, Emery County, Utah.

Diagnosis—Meckel's groove moderately wide at posterior end of dentary, but

open as only a narrow slit for most of length of dentary; teeth tall, narrow, conical, closely spaced, with crowns weakly medially striate, and with short carinae that wrap ventromedially around crown. Differs from scincids (e.g., Eumeces), cordylids (e.g., Cordylus), in a more posterior narrowing of Meckel's groove. Differs from Penemabuya (the most similar fossil taxon) in having more fully developed carinae on tooth crown, teeth that are set higher on lateral parapet of dentary, and an anterior end of dentary that points anteriorly rather than anterodorsally.

Description—OMNH 28119 (Fig. 6) is a left dentary that is lightly built, with 16 tooth spaces, only the last two of which have complete teeth. Comparison to lizards with similar dentary morphology indicates that only the last three to four teeth are missing. The exterior surface is smooth with five inferior alveolar foramina opening below the lateral parapet. The subdental gutter is narrow but well developed along the entire tooth row. The subdental shelf is well developed and maintains a uniform height along tooth row except at the last two tooth positions, where it narrows in concert with the widening of the Meckel's groove. The Meckel's groove is open ventrally as a narrow slit along most of the preserved portion of the dentary and widens only at the posteriormost part of the element, where it turns somewhat medial. The anterior extent of the splenial would have terminated posterior to the midpoint of the tooth row. The teeth appear to have been homodont, as indicated by the uniform shape and size of the tooth bases, but this cannot be confirmed without more complete material. The posteriormost two teeth are conical, narrow, and tall, with bases slightly compressed anteroposteriorly, and crowns slightly laterally compressed and shallowly medially concave. The medial surfaces of the crowns are weakly striate and bordered by two short carinae that wrap ventromedially around the

crown. Deep replacement pits at the bases of the teeth indicate direct replacement.

Comments—The presence of a well-developed subdental gutter and shelf in OMNH 28119 suggests that it is closely allied to scincomorphans (sensu Gao and Fox, 1996:74). I consider the presence of an open Meckel's groove as further support for such an affiliation. Among scincomorphans, a reduced anterior extent of the splenial and slit-like opening of the Meckel's canal is not found in any known paramacellodid taxa (Estes, 1983b), but is present in some taxa of Cordylidae and Scincidae (Estes et al., 1988). Of these last two families there are no features preserved on the specimens of Bothriagenys that diagnose the genus or clearly indicate to which family it might belong. Pending the recovery of more diagnostic material, Bothriagenys can only tentatively be referred to Scincomorpha (sensu Estes et al., 1988).

TEIIDAE Gray, 1827

HARMODONTOSAURUS, gen. nov.

Etymology—G., "Harmos" (Greek), shoulder; "odous" (Greek), tooth; "sauros" (Greek), lizard. "Shoulder-toothed lizard" in reference to shoulder-like anterior expansion of teeth.

Type and Only Species—Harmodontosaurus emeryensis sp. nov.

Distribution—Mussentuchit Member of Cedar Mountain Formation (medial Cretaceous), Emery County, Utah.

Diagnosis—as for type and only species.

HARMODONTOSAURUS EMERYENSIS, sp. nov.

(Figs. 7A, B)

Etymology—species name is in reference to Emery County, Utah, where holotype was found.

Holotype—OMNH 33889, right dentary broken posteriorly.

Referred Specimens—OMNH 22109, partial left maxilla; 27753, 28067, partial right dentaries; 28068, 32627, 60195, jaw fragments.

Locality and Horizon—OMNH localities V868 (type locality), V240, and V695, 10-20 m below upper contact of Mussentuchit Member of Cedar Mountain Formation and Dakota Formation, Emery County, Utah.

Diagnosis—Differs from other known Cretaceous teiids (Gao and Fox, 1991; 1996) in following combination of characters: anterior teeth gracile, posterior teeth comparatively much more robust, teeth more closely spaced, and approximately 1/2 of tooth height below lateral parapet.

Description—The holotype dentary, OMNH 33889, of Harmodontosaurus emeryensis (Fig. 7A) is heavily built with 15 tooth spaces and 14 teeth in the preserved portion of the dentary. The mandibular symphysis is large and extends posteriorly to the seventh tooth position. The subdental gutter is narrow and runs the length of the tooth row. The subdental shelf narrows posteriorly and is well developed, weakly dorsally concave, and deep anteriorly. The splenial is not preserved with any of the dentaries, but it is clear from the attachment scars on the ventral surfaces of the subdental shelves of

OMNH 28067, 27753, and 33889 that the splenial extended anteriorly to just short of the symphysis, leaving a short symphyseal foramen. In accordance with the hypertrophied splenial, the Meckel's groove is widely open ventromedially in the posterior portion of the dentary and narrows anteriorly to a ventrally directed slit that is open to the symphysis. The exterior surface of the dentary is smooth, deeply convex, and bears five small inferior alveolar foramina. It is not possible to determine the exact tooth count of the element, but comparison with other teiids indicates that only one to three teeth are missing from the holotype specimen. The anterior teeth bear sharp anterior and posterior carinae and are columnar, procumbent, and weakly recurved. At about the eighth tooth position successive posterior teeth become substantially more massive and widely spaced, such that the four preserved tooth positions are occupied by heavily built, conical teeth with wide bases. These posterior teeth also have more robustly built anterior and posterior carinae, with the anterior carina forming a shoulder-like process (Fig. 7B). Starting at the sixth tooth position, all successively posterior teeth have swollen tooth shafts that extend medially such as to obscure the subdental gutter in occlusal view. The anterior and posterior carinae on all teeth join at a posteromedially directed apex, forming a similarly directed "V." Harmodontosaurus lacks the medial striae on the crowns of its teeth. Replacement pits form as subcircular pits at the bases of the teeth.

Comments—Harmodontosaurus emeryensis is most similar in tooth structure to the Judithian teiid Socognathus unicuspis from the Oldman Formation of Alberta (Gao and Fox, 1991, 1996). Both of these taxa have posteriorly rotated crowns and a well-developed posteromedially directed apex. Unlike Socognathus, the teeth of Harmodontosaurus show a greater disparity in size between the front and back of the

tooth row, with the posterior teeth nearly twice the size of the anterior teeth, whereas in Socognathus the posterior teeth are roughly only half again as large as the anterior teeth.

POLYGLYPHANODONTINAE Estes, 1983

DICOTHODON Nydam, 1999

DICOTHODON MOORENSIS Nydam, 1999

(Figs. 7C)

Description and Comments—The teeth are bicuspid, bulbous, transversely oriented in the jaw, and oval shaped in occlusal view. The crowns of the teeth are distinct in having a central, transverse V-shaped blade, as well as anterior and posterior semicircular accessory blades that border small basins on either side of the V-shaped blade. Dicothodon moorensis is a rare taxon in the Mussentuchit local fauna. A full description and discussion of the taxon has already been published (Nydam, 1999).

CF. POLYGLYPHANODONTINAE

BICUSPIDON Nydam and Cifelli, submitted

BICUSPIDON NUMEROSUS Nydam and Cifelli, submitted B

(Fig. 7D)

Description and Comments—Bicuspidon numerosus is a small teiid with conical, recurved anterior teeth and with transversely bicuspid, unrecurved posterior teeth. There

is a short, transverse, V-shaped blade between the medial and lateral cusps of the posterior teeth (Nydham and Cifelli, submitted B). This taxon is the most common lizard in the Mussentuchit local fauna and likely is a sister taxon to the North American lineage of polyglyphanodontine teiids (Nydham and Cifelli, submitted B).

SCINCOMORPHA Camp, 1923

Family, Genus, and Species indet.

(Fig. 8A, B)

Referred Specimens—OMNH 22107, 22108 jaw fragments; 22109, partial left maxilla; 22110, jaw fragment; 27405, broken right maxilla; 27408, partial left maxilla; 28905, left maxilla missing nasal process; 30208, broken right maxilla; 32626, jaw fragment; 33455, jaw fragment.

Localities and Horizon—OMNH localities V235 (OMNH 32628), V695 (OMNH 27405, 30208), V868 (OMNH 22105-22110, 32626, 33455); 10-20 m below upper contact of Mussentuchit Member of Cedar Mountain Formation and Dakota Formation, Emery County, Utah.

Description—The left maxilla, OMNH 28905 (Figs. 8A, B), has 21-22 tooth spaces (wear at posterior end makes exact count difficult), with 10 teeth having crowns that extend past the parapet. The tooth row is bowed dorsally. Although this bowing in part can be attributed to the preservation of the element, some bowing was present during life and is considered here to be characteristic of the maxillary tooth row. The dorsal part of the nasal process is missing, but the remaining portion shows that it extended

posteriorly to about the 18th tooth position. The facet for the maxillary process of the jugal opens dorsolaterally posterior to the posterior interior alveolar foramen. The preserved exterior surface is smooth and has eight superior alveolar foramina along the parapet above the tooth row. The anteriormost of these foramina is the largest and opens anterolaterally just below the anterior edge of the nasal process. The second through fourth foramina are smaller and open anterolaterally, but gradually become more medially directed with the more posterior positions. The fifth through eighth foramina open posterolaterally, with the last three closely spaced and posterior to the posterior edge of the nasal process. Internally the anterior interior alveolar foramen opens anteriorly at the base of the nasal process above the third tooth position, and the posterior interior alveolar foramen opens posteriorly above the 12th tooth position (Fig. 8B). The supradental shelf is narrow where preserved and borders a weak supradental gutter. The teeth are homodont, pleurodont, columnar, weakly recurved anteriorly, and have tapering tips and striated medial surfaces. In occlusal view the crowns have a posteromedially pointing “V,” indicative of posterior rotation of the tooth crowns. Tooth replacement was direct, as evidenced by the replacement pits at the bases of some teeth.

OMNH 30208 (Fig. 8C) is an anterior portion of a right maxilla and preserves the anterior portion of the nasal process. The nasal process ascends at a posterodorsal angle. The anterior edge of the nasal process comprises the lateral border of the narial opening. There is a long, narrow facet along the medial edge of the nasal process above the narial opening for an abutting contact with the nasal. The anterior extent of the nasal-maxillary contact indicates that the narial opening was small. The premaxillary process of the maxilla is forked, and it possesses an anterior process that articulated with the premaxilla

and a medial process that presumably approached or contacted the corresponding process from the other maxilla. The exact extent of the medial process is unknown since all specimens are incomplete. OMNH 22110 (not figured) is a partial right dentary, preserving the medial portion of the tooth row. The teeth are identical to those of the maxillary specimens. The subdental shelf is short, the subdental gutter is shallow and narrow, and the exterior surface is smooth and convex.

Comments—Although too incomplete for formal diagnosis, the specimens listed above are very similar in tooth and jaw morphology and distinct from any of the other lizards recovered from the Cedar Mountain Formation. As such, they have been placed together in an unnamed taxon. The teeth and the small external narial opening are very much like those in cordylids and paramacellodids. Based on these characteristics, the specimens are referred to Scincomorpha, but no characteristics are preserved that indicate a familial affinity.

ANGUIMORPHA Fürbringer, 1900

PLATYNOTA Camp, 1923

MONSTERSAURIA, Norell and Gao 1997

PRIMADERMA Nydam, 2000

PRIMADERMA NESSOVI Nydam, 2000

(Figs. 9A)

Description and Comments—Primaderma nessovi is a helodermatid-like

platynotan with widely spaced plicidentine teeth and with fragmented osteoderms fused to the skull. For a complete description and detailed discussion of Primaderma nessovi, see Cifelli and Nydam (1995) and Nydam (2000).

Cf. ANGUIMORPHA Fürbringer, 1900

Family incertae sedis

Gen. et sp. indet.

(Figs. 9B)

Specimens—OMNH 29785, Jaw fragment; OMNH 33441, jaw fragment.

Locality and Horizon—MNA 1072 (OMNH 29785); 10-20 m below upper contact of Mussentuchit Member of Cedar Mountain Formation and Dakota Formation, Emery County, Utah.

Description—OMNH 29785 (Fig. 9B) is a jaw fragment with two teeth that are closely spaced and recurved. A small nutrient foramen is present on the medial surface of the base of each tooth, though it is somewhat eroded on the anteriormost tooth. The tips of the crowns are missing, so it is not possible to determine if the teeth were trenchant. Since the bases have no infolding, the jaw fragments do not belong to Primaderma nessovi.

Comments—Gao and Fox (1996) identified a medial nutrient foramen at the base of the teeth as an indicator of anguimorphan affinities. However, this characteristic is not identified as one of the 22 synapomorphies of Anguimorpha by Estes et al. (1988). The close spacing of the teeth and the way in which the teeth are recurved suggest close

affinity to Anguidae. The crowns are missing on all teeth, so tooth shape is not available as a comparative character. Comparison to other anguimorphans of the Late Jurassic and Early Cretaceous provides little additional clarification of the relationships of this taxon. The lack of any bony buildup around the bases of the teeth indicates that this taxon is likely not closely related to Parviraptor. The bases of the teeth generally are similar to those of Dorsetisaurus, but both represent only a generalized anguimorphan trait and without tooth crowns or more complete skeletal material it is not possible to determine more precisely the taxonomic affinities of these specimens.

SERPENTES Linnaeus, 1758

ANILIIDAE Stejneger, 1907

CONIOPHIS Marsh, 1892

CONIOPHIS sp.

Vertebrae of the primitive snake Coniophis have been reported from the Mussentuchit local fauna (Gardner and Cifelli, 1999). They represent the oldest record of a snake from North America. Gardner and Cifelli (1999) provided detailed illustrations and discussion of this taxon.

DISCUSSION

Comparison to Other Cretaceous Lizard Faunas

The lizards of the Mussentuchit local fauna make up one of the oldest well-sampled lizard faunas in North America and emphasize an important time period (medial

Cretaceous) between the distinctly different lizard faunas of the Late Jurassic-Early Cretaceous and the Late Cretaceous. As such, the lizards of the Mussentuchit local fauna fill an important gap in the fossil record of lizards and provide an opportunity to examine changes in the North American lizard fauna during the Early and medial Cretaceous, especially the shift from the primitive lizard fauna of the Late Jurassic-Early Cretaceous to the more modern-type lizard fauna of the Late Cretaceous.

North American Early Cretaceous—The lizards of the Early Cretaceous (Aptian-Albian) of North America consist primarily of primitive taxa referable to Paramacellodidae (Winkler, et al., 1990; Reynoso, 1995, 1996, 1997, 1998; Nydam and Cifelli, submitted A), but also include the earliest records of teiids (Winkler, et al., 1990; Nydam and Cifelli, submitted A). Paramacellodid lizards are common constituents of the Jurassic and basal Cretaceous lizard assemblages from North America, Europe, Europe, and many parts of Asia (Prothero and Estes, 1980; Evans, 1993, 1998). The systematic validity of Paramacellodidae has been questioned, with some suggesting that that the family may be a junior synonym of Cordylidae (Estes, 1983b; Gao and Fox, 1996). However, phylogenetic analysis of Paramacellodus (Evans and Chure, 1998a) indicates that it is the sister taxon of the Scincoidea (Cordylidae + Scincidae). The teiids from the Early Cretaceous are considered to be primitive based on their relatively simple dentitions (Winkler et al., 1990). However, at least one of the teiids has some modification of its teeth, though the teeth are not modified to the degree seen in most of the Late Cretaceous teiids (Nydam and Cifelli, submitted A).

At least one paramacellodid lizard (cf. Pseudosaurillus) has been tentatively identified as part of the Mussentuchit local fauna. In addition, some of the specimens of

the indeterminant taxa (e.g., OMNH 28905 and 30208) are very paramacellodid-like, though too incomplete for diagnosis. In comparison to the rest of the lizards from the Mussentuchit local fauna, however, the paramacellodid and paramacellodid-like taxa are rare. Dimekodontosaurus madseni is problematic in that it may represent either a paramacellodid or a cordylid. If it is a paramacellodid, it would represent the most derived (with respect to dentition) example of this primitive family. However, if it is a cordylid, it would be the oldest and have one of the most derived dentitions of this family. Either way, D. madseni has a specialized dentition that makes it unique among the Scincoidea. Among the teiids of the Mussentuchit local fauna, none of the taxa share the primitive tooth structure found in three of the four taxa identified from the Early Cretaceous. The fourth taxon of Early Cretaceous teiid, Ptilododon (Fig. 10Q; also see Nydam and Cifelli, submitted A) is more derived in that it has delicate teeth with small anteroposterior expansions of the crown. None of the teiids from the Mussentuchit local fauna have this type of tooth design. Overall the lizard component of the Mussentuchit local fauna includes some primitive taxa, but most of the taxa are quite distinct from the known lizard fauna of the Early Cretaceous.

North American Late Cretaceous—Nearly all taxa of lizard faunas of the Late Cretaceous have been referred to modern families (Estes, 1983b; Rowe, et al., 1992; Gao and Fox, 1996). The most common and diverse lizards of the Late Cretaceous are the teiids. These consist of both non-polyglyphanodontine taxa (i.e., Chamops, Leptochamops, Meniscognathus, Haptosphenus, Stypodontosaurus, Sphenosiagon, Glyptogenys, Socognathus, Gerontoseps; Estes, 1964, 1969, 1983b; Gao and Fox, 1996; Sankey, 1997; Figs. 10S, T, U) and polyglyphanodontine taxa (i.e., Polyglyphanodon,

Paraglyphanodon, Peneteius, Dicothodon; Gilmore, 1940, 1943a; Estes, 1969; McCord, 1998; Nydam, 1999; Figs. 10M, N, O). Other modern groups represented in the Late Cretaceous lizard faunas of North America include Platynota (Helodermatidae and Varanidae; Estes, 1964, 1983b; Gao and Fox, 1996; Figs. 10C, D), Anguidae (Estes, 1964, 1969, 1983b; Sullivan, 1981; Gao and Fox, 1996; Fig. 10H), Iguanidae (Gao and Fox, 1996; Fig. 10CC), Scincidae (Estes, 1964, 1983b; Rowe et al., 1992; Gao and Fox, 1996; Figs. 10K), Xenosauridae (Estes, 1964, 1969, 1983b; Gao and Fox, 1996; Fig. 10I), and Xantusiidae (Gao and Fox, 1996; Fig. 10L).

Although no taxa were figured, Eaton et al. (1999) described a series of vertebrate faunas, which include numerous lizards from the Cenomanian, Turonian, Coniacian-Santonian, and Campanian of southern Utah. These are important records in that little is known of the lizards from North America during the Cenomanian-Santonian.

Interestingly, Eaton et al. (1999) described the Cenomanian vertebrate fauna from the Dakota Formation as generally consisting of more primitive taxa in comparison to the Turonian-Santonian faunas, as well as with the well-known faunas of the Campanian-Maastrichtian. Among the seven types of lizards they listed from the Dakota Formation, the paramacellodid "Saurilodon" (which is assumed to equal Saurillodon [Seiffert, 1973] from which Fig. 10BB was redrawn because Cenomanian specimen has not been figured) represents an approximately 45-million-year extension of the record of this taxon. The other notable record of a lizard listed by Eaton et al. (1999) is the presence of Dorsetisaurus (Fig. 10E) in the Turonian fauna of the Smoky Hollow Member of the Straight Cliffs Formation, an extension of approximately 60 million years of the record of this taxon. Eaton et al. (1999) concluded that the lizards from the Turonian-Campanian

are very similar in composition to those from other Late Cretaceous (Campanian-Maastrichtian) vertebrate faunas from North America. This includes the presence of cordylids, polyglyphanodontines, teiinines, scincids, xantusiids (Contogenys is listed as a skink by Eaton et al., 1999, but was shown to be a xantusiid by Gao and Fox, 1996), and varanoids.

The diversity of the lizards of the Mussentuchit local fauna is much like that of the lizard faunas of the Late Cretaceous. Most notably, Harmodontosaurus, Dicothodon, and Bicuspidon represent the earliest examples of non-polyglyphanodontine and polyglyphanodontine teiids, and Primaderma represents the earliest monstersaurian platynotan (Cifelli and Nydam, 1995; Nydam, 2000). Additionally, Bothriagenys appears to be a scincomorphan allied to either Cordylidae or Scincidae. Should Dimekodontosaurus prove to be a cordylid, it would be another example of a modern taxon in the fauna. Interestingly, of the three teiids known from the Mussentuchit local fauna, two (Bicuspidon, Dicothodon) are allied with the subfamily Polyglyphanodontinae (sensu Estes, 1983b) and one (Harmodontosaurus) with the subfamily Teiinae (sensu Estes, 1983b; = Chamopsiinae of Denton and O'Neil, 1995 with respect to Cretaceous taxa). In the Late Cretaceous, teiinines exhibited a greater taxonomic diversity (Estes, 1983a; Gao and Fox, 1996) and were more widespread (Estes, 1983b; Rowe et al., 1992; Gao and Fox, 1996) than polyglyphanodontine teiids (Estes, 1983b; Nydam, 1999).

The similarities between the lizards of the medial and Late Cretaceous of North America indicate that many elements of the basic taxonomic structure found in Late Cretaceous lizard faunas had become established between the Aptian-Albian and the Albian-Cenomanian (Fig. 11). However, the formation of the Late Cretaceous lizard

fauna appears to have been multi-step process, since representatives of the Iguania, Xenosauridae, and Varanidae do not have their first records in North America until the Campanian (Fig. 11; see also Estes, 1983b; Gao and Fox, 1996).

Asian Early Cretaceous—The fossil record of lizards from the Early Cretaceous of Asia, particularly Mongolia, stands in stark contrast to that from the Early Cretaceous of North America. In addition to the primitive scincomorph family Paramacellodidae and the primitive anguimorph family Dorsetisauridae, the lizards from Khobur, Mongolia also include Gekkonidae, Scincidae, Necrosauridae, Hoplocercidae, Priscagamidae (probable iguanians allied with Agamidae; Borsuk-Bialynicka, 1984), Xenosauridae, Macrocephalosauridae (= Polyglyphanodontinae, Estes, 1983b), and possibly Xantusiidae (Alifanov 1992, 1993a, 1993b). The age of this fauna is ?Aptian-Albian (Alifanov, 1992, 1993a), but the lizard taxa exhibit greater diversity than similarly aged lizard faunas in North America (Winkler et al., 1990; Nydam and Cifelli, submitted A) or Europe (Evans, 1995, 1998). Comparison of the Early Cretaceous Khobur lizards to those of the medial Cretaceous Mussentuchit local fauna shows a number of similarities. These include the presence of paramacellodids, polyglyphanodontines (= Macrocephalosauridae of Alifanov, 1993b), and platynotans. These similarities are much like those found between the lizards of the medial and Late Cretaceous within North America. Indeed, five of the groups reported from Khobur (Polyglyphanodontinae, Xenosauridae, Xantusiidae, Necrosauridae, and Scincidae) have also been reported from the Late Cretaceous of North America (Estes, 1983b; Gao and Fox, 1996).

Asian Late Cretaceous—The lizards of the Late Cretaceous of Asia are, like their North American counterparts, very diverse, with agamids, iguanids, gekkonids,

teiinines, polyglyphanodontines, anguids, monstersaurs, and varanids (Alifanov, 1993a, 1993b; Borsuk-Bialynicka, 1984, 1985, 1991, 1996; Borsuk-Bialynicka and Moody, 1984; Borsuk-Bialynicka and Alifanov, 1991; Estes, 1983b; Gilmore, 1943b; Gao and Hou, 1995a, b; Gao and Norell, 1998; Nessov, 1998; Sulimski, 1972, 1975, 1984). Although some of these groups also are found in the Cretaceous of North America (Polyglyphanodontinae, Varanidae, Iguanidae, Teiinae, Monstersauria), the individual taxa are distinct from those in North America. This is most evident between the polyglyphanodontines of Asia and North America (see Nydam, 1999 for further discussion of polyglyphanodontine biogeography).

Biogeographical Implications

Between the Late Jurassic and the Early Cretaceous the lizard fauna of North America appears to have remained relatively stable (Evans, 1998; Nydam and Cifelli, submitted A), exhibiting a composition dominated by primitive paramacellodids that defines nearly all of the global faunas during the Late Jurassic-basal Cretaceous (Evans, 1993, 1995, 1998; Evans and Chure, 1998b). There were some changes, however, during this time period: sphenodontians are reduced from being common and widespread to a single occurrence in Mexico (Reynoso, 1995, 1997), anguimorphans show an apparent loss in diversity (Nydam and Cifelli, submitted A), and teiids appear in North America (Winkler et al., 1990; Nydam and Cifelli, submitted A). In the 8-10 million years from the Early (Aptian-Albian) through the medial (Albian-Cenomanian) Cretaceous, there was a dramatic change in the taxonomic composition of the North American lizard fauna (Fig. 11).

Based on the lizards present in the Mussentuchit local fauna, polyglyphanodontine and teiine teiids, monstersaurs, and possibly advanced scincomorphs (?Scincidae, ?Cordylidae) were added to the North American fauna. Paramacellodids were apparently reduced to a minor constituent. Additionally, the presence of the two polyglyphanodontines Bicuspidon and Dicothodon (Nydham, 1999; Nydam and Cifelli, submitted B) shows that this group had already undergone some diversification. Also, Primaderma indicates that platynotans had become derived by the time of its appearance in the Mussentuchit local fauna. Although it is possible that these taxa all evolved in situ in North America, the 13 million years from the Aptian-Albian to the Albian-Cenomanian requires relatively rapid evolution within several lineages. An equally plausible, if not more parsimonious, hypothesis is that these represent taxa introduced from an already derived fauna, such as that described from Mongolia. The existence of a Asian-American corridor late in the Early Cretaceous is supported by numerous similarities between Asia and North America in the dinosaur and mammal faunas (Jenkins and Schaff, 1988; Currie, 1992; Cifelli et al., 1997, 1999; Kirkland et al., 1997), as well as by geological evidence (Cifelli et al., 1997 and references therein). The lizard fauna from the Early Cretaceous of Mongolia (reviewed above) is both temporally antecedent and taxonomically similar to the Mussentuchit local fauna, suggesting that the Early Cretaceous Asian lizard fauna could have served as source for at least some of taxa in the medial Cretaceous lizard fauna of North America.

Based on the current record, which is admittedly limited both geographically and stratigraphically (e.g., a single fauna for Aptian-Albian of Mongolia and a single fauna for Albian-Cenomanian of North American), an Asian-North American interchange may

have occurred more than once during the early Late Cretaceous. The initial exchange, which took place after Aptian-Albian and before the Albian-Cenomanian, appears to have been responsible for the introduction of at least three groups of lizards (based on taxa in Mussentuchit local fauna) to North America—the Scincidae, Cordylidae, and Monstersauria. The earliest North American occurrence of Xantusiidae and Necrosauridae is in the Turonian (Eaton et al., 1999) indicating a second dispersal from Asia. The Iguania, Xenosauridae, and Varanidae, which all have their earliest North America occurrence in the Campanian (Fig. 11; see also Estes, 1983a, 1983b; Gao and Fox, 1996), are known from the Santonian of Asia (Borsuk-Bialynicka, 1991; Gao and Hou, 1995a, b), suggesting dispersal during the latest Santonian-earliest Campanian.

Based on the faunal comparisons, there almost certainly was an Asian influence on the North American Cretaceous lizard fauna. However, during at least the Late Cretaceous, South America was another potential source for changes in the North American lizard fauna. The sauropod dinosaur Alamosaurus, from the Maastrichtian of New Mexico, Texas, Utah, and Wyoming is very similar to South American titanosaurs and is believed to represent immigration from that continent to North America (Kues et al., 1980; Lehman, 1987). In addition, Estes and Baéz (1985 and references therein) reviewed the evidence (distribution of lower vertebrate taxa) of an interchange between North and South America and concluded that a limited exchange, possibly over an island chain, existed during the Late Cretaceous. Alifanov (1993b) proposed the existence of a pre-Cretaceous link between North and South America as a solution to the problematic distribution of lizards during the Cretaceous and Paleogene. The lack of fossil taxa from the Mesozoic of South America (only record is an inguanian from Brazil [Estes and

Price, 1973]) makes it difficult to evaluate the possible influences of the South American fauna on that of North America. It is likely, however, that teiids entered South America from North America sometime prior to the end of the Cretaceous (Estes, 1983a). The concept of South America as a source for North American iguanians (*sensu* Estes, 1983a) has recently been challenged by new records of iguanians from the Late Cretaceous of Asia (Gao and Hou, 1995a, b). Additional work on the Mesozoic lizard fauna of South America is needed to help establish its possible role in the evolution of the North American lizard fauna.

Angiosperm Interactions

The change in the North American lizard fauna from the Early Cretaceous to the medial Cretaceous coincides with the global diversification of angiosperms. Indeed, a moderately diverse assemblage of angiosperms has been reported for the Cedar Mountain Formation, including one of the earliest records of angiosperm wood (Thayne et al., 1983; Tschudy et al., 1984). During the Early Cretaceous (Aptian-Albian) angiosperms were relatively simple in both flowering and fruiting structures (Friis and Crepet, 1987), and comprised only a modest part of the terrestrial flora (Crane and Lidgard, 1990). Based on palynological and macrofossil evidence (Crane and Lidgard, 1990; Lupia et al., 1999), angiosperms had become a more prominent part of the terrestrial flora by the Albian-Cenomanian, but flowering and fruiting structures remained relatively primitive until the latest Santonian-earliest Campanian (Friis and Crepet, 1987:figs. 6.6, 6.7). The timing of the diversification of angiosperms coincides with the change in the North American lizard fauna after the Aptian-Albian and before the Albian-Cenomanian raising

the possibility that the two events were linked. Vertebrate-angiosperm co-evolution has been studied with respect to herbivorous dinosaurs (Swain, 1976; Wing, 1987), but these studies were based on herbivorous dinosaurs. However, most lizards are insectivorous (Zug, 1993) and herbivory (i.e., folivory and not opportunistic feeding on flowers and fruits) in lizards is rare (Sokol, 1967; King, 1996). For lizards to be successful herbivores requires specific physiological and environmental conditions (Pough, 1973; Zimmerman and Tracy, 1989). Based on the close association of insects and flowering plants it would seem obvious that as angiosperm diversity increased so did that of insects. There is very little evidence on the prehistoric relationships of plants and insects and a review of the fossil record of both (albeit very poor for insects) actually shows a drop in insect diversity when angiosperms show an increase (Labandeira and Sepkoski, 1993). However, based on molecular data there appears to be a link between the diversity of beetles and the Cretaceous increase in angiosperm diversity (Farrel, 1998). Assuming a parallel increase in angiosperm and insect diversity, it would be reasonable to expect a concomitant increase in lizard diversity. In contrast to the North American record, the diverse lizard fauna from the ?Aptian-Albian of Mongolia predates the radiation of angiosperms, indicating that the diversity of that fauna was most likely not tied to angiosperm evolution. Therefore, if the Asian fauna was the source for the derived lizard families that appear in the North American during the Cretaceous, then increasing angiosperm diversity was likely not major influence on the changes in the North American lizard fauna. Additionally, well represented sequences of faunas and associated floras during the critical period (mid-Cretaceous: Albian-Santonian) of

transition are lacking, making it impossible to investigate simultaneous changes in vertebrate and angiosperm diversity.

If the presence of angiosperms did not play a major role, however, these plants represented a new resource that may have been exploited by the polyglyphanodontine teiids. The North American polyglyphanodontine teiids (Bicuspidon, Dicothodon, and Polyglyphanodon) show a temporally progressive trend toward larger body size and increasingly medially expanded teeth (Nydam, 1999; Nydam and Cifelli, submitted B) that culminated in the large, probably herbivorous taxon Polyglyphanodon sternbergi from the Maastrichtian of Utah (Gilmore, 1942). An analogous scenario was also part of the evolutionary history of the Asian polyglyphanodontine taxa. Macrocephalosaurus, Darchansaurus, Erdenetesaurus, and Cherminisaurus all possess large, polycusate teeth very similar to those teeth found in the herbivorous family Iguanidae (Gilmore, 1943b; Sulimski, 1975). The similarities in tooth structures between the Asian Polyglyphanodontinae and the Iguanidae indicate that the Asian polyglyphanodontine taxa were probably herbivorous, or at least omnivorous (Estes, 1983a; Nydam, 1999).

CONCLUSIONS

The lizards from the medial Cretaceous (Albian-Cenomanian) Mussentuchit local fauna of central Utah represent a diverse fauna composed of both primitive and derived taxa. As such, this lizard fauna is both temporally and taxonomically intermediate between those of the Early (Aptian-Albian) and Late (Campanian-Maastrichtian) Cretaceous. Although closer in age to the lizard fauna of the Early Cretaceous, the lizards of the Mussentuchit local fauna show greater taxonomic similarity to lizard faunas

of the Late Cretaceous. This relatively rapid change in the North American lizard fauna is likely the result of an influx of Asian taxa sometime after the Aptian-Albian and before the Albian-Cenomanian. This permitted lizards (e.g., helodermatid-like platynotans, polyglyphanodontine teiids, and possibly scincids and xantusiids) from the more derived faunas of Asia to become established in North America. A Late Cretaceous faunal exchange may have led to the establishment of Iguanidae, Xenosauridae, and Varanidae in the early Campanian of North America. Although angiosperm evolution and diversification is coincident with the Early-medial Cretaceous changes in the North American lizard fauna, it appears that interaction between lizards and angiosperms was limited to the evolution of a few herbivorous lizards in the Late Cretaceous of North America and Asia.

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FIGURE LEGENDS

Figure 1. Locality map of lizard-producing localities from Mussentuchit Member of Cedar Mountain Formation (gray stippling) in Emery County, Utah.

Figure 2. OMNH 27711, broken right maxilla of cf. Pseudosaurillos sp. Scale bar 1 mm.

Figure 3. Dimekodontosaurus mussentuchitensis, gen. et sp. nov. A-C, OMNH 34560, holotype left dentary. A, medial view (arrow indicates scar for articulation of anteromedial flange of coronoid). B, detail of anterior portion of tooth row. C, detail of posterior portion of tooth row. D, scanning electron micrograph of representative anterior teeth on OMNH 32625. E, scanning electron micrograph of representative posterior teeth on OMNH 32626. Scale bars 1 mm unless otherwise noted.

Figure 4. Maxilla specimens referred to Dimekodontosaurus mussentuchitensis, gen. et sp. nov. A, medial view of OMNH 28814, broken left maxilla B, medial view of OMNH 34558, broken right maxilla. Scale bars 1 mm.

Figure 5. Osteoderms referred to Dimekodontosaurus mussentuchitensis, gen. et sp. nov. A, dorsal view of OMNH 61243 B, dorsal view of OMNH 61244. Scale bars 1 mm.

Figure 6. OMNH 28119, holotype left dentary of Bothriagenys mysterion, gen. et sp. nov. A, medial view. B, detail of teeth. C, sketch of specimen. Note narrow opening of Meckel's groove. Scale bars 1 mm.

Figure 7. Teiidae of Mussentuchit local fauna. **A**, OMNH 33889, holotype right dentary of Harmodontosaurus emeryensis, gen. et sp. nov. **B**, detail of second to last tooth of holotype dentary of Harmodontosaurus emeryensis, gen. et sp. nov. **C**, OMNH 29771, holotype tooth of Dicothodon moorensis; arrow indicates shoulder-like anterior process of crown. **D**, OMNH 26743, holotype left maxilla of Bicuspidon numerosus. Scale bars 1 mm.

Figure 8. Indeterminant Scincomorpha of Mussentuchit local fauna. **A**, lateral and **B**, medial views of OMNH 28905. **C**, lateral view of OMNH 30208, partial right maxilla. **Abbreviations:** AAF, anterior interior alveolar foramen, PAF, posterior interior alveolar foramen. Scale bars 1 mm.

Figure 9. Anguimorpha of Mussentuchit local fauna. **A**, medial view of OMNH 26742, holotype right maxilla of Primaderma nessovi. **B**, medial view of OMNH 29785, indeterminant anguimorphan (arrow indicates nutrient foramen at base of tooth).

Figure 10. Diagramatic illustration of lizard tooth morphotypes from Late Jurassic (Kimmeridgian) through end of Cretaceous (Maastrichtian) of North America; notice relatively simple tooth types during Kimmeridgian and Aptian-Albian and dramatic increase not only in taxa, but also in complexity of tooth morphology starting at Albian-Cenomanian. Position of tooth types should not be interpreted as indicating direct evolutionary lineages, but as record of representatives of groups listed to right. All taxa

listed left-to-right, top-to-bottom. **A**, Parviraptor; **B**, Primaderma; **C**, Labrodioctes; **D**, Paraderma; **E**, Dorsetisaurus; **F**, indeterminant anguimorphan; **G**, indeterminant anguimorphan; **H**, Odaxosaurus; **I**, Exostinus; **J**, Bothriagenys; **K**, Orthrioscincus, Penemabuya, Aocnodoromeus; **L**, Contogenys; **M**, Bicuspidon, Dicothodon; **N**, Polyglyphanodon, Peneteius; **O**, Polyglyphanodon, Peneteius; **P**, indeterminant teiid of Winkler et al. (1990), indeterminate teiid of Nydam and Cifelli (submitted A); **Q**, Ptilotodon; **R**, Harmondontosaurus; **S**, Chamops, **T**, Sphenosiagon, Leptochamops, Gerontoseps, Glyptogenys; **U**, Chamops, Leptochamops, Haptosphenus, Stypodontosaurus, Meniscognathus; **V**, Dimekodontosaurus; **W**, ?Cordylidae; **X**, Paramacellodus; **Y**, indeterminate paramacellodid-like taxa; **Z**, Paramacellodus; **AA**, cf. Pseudosaurillus; **BB**, cf. Saurillodon; **CC**, indeterminant inguanians. **XX** indicates published, but not figured, record of representative of group not referred to a known genus. **A** after Evans (1994; European taxon, complete teeth not known for North American Parviraptor); **B** after Nydam (2000); **C**, **D**, **H**, **I**, **K**, **L**, **T**, **U**, and **W**, and **CC** after Gao and Fox (1996); **S** and Leptochamops of **T** and **U** after Estes (1964); **E** and **X** after Evans and Chure (1999); **F**, **Y**, and **Z** after Nydam and Cifelli (submitted B); **G**, **J**, **R**, **V**, and **AA** from specimens reported herein; **M** after Nydam (1999) and Nydam and Cifelli (submitted B); **N** and **O** after Nydam (1999) and Nydam et al. (in press); **P** from Winkler et al. (1990) and Nydam and Cifelli, (submitted A). Taxa shown for Cenomanian-Santonian are based on lists of Eaton et al. (1999). For clarity and size constraints, figures not drawn to scale, and not all published taxa have been included (no taxon that affects patterns seen here was excluded).

Figure 11. Distributions of lizard taxa during Mesozoic in North America and Asia.

Bars above group names represent known temporal distributions based on references cited herein. Gray bars at end of Albian, end of Turonian, and beginning of Campanian denote likely times of influx of Asian taxa into American fauna. Asterisk (*) denotes lineages possibly introduced from Asia upon opening of land bridge. Double asterisks (**) indicates lineages possibly introduced from Asia during late Santonian-early Campanian. Arrows represents fossil record for group beyond Cretaceous-Tertiary boundary. Cladogram adapted from Estes et al. (1988), with addition of Polyglyphanodontinae and Dorsetisauridae following Estes (1983b), Paramacellodidae following Evans and Chure (1998a), and Parviraptor following Nydam (2000). Helodermatidae of Estes et al. (1988) considered here to be conceptually equivalent to Monstersauria of Norell and Gao (1997) and Gao and Norell (1998).

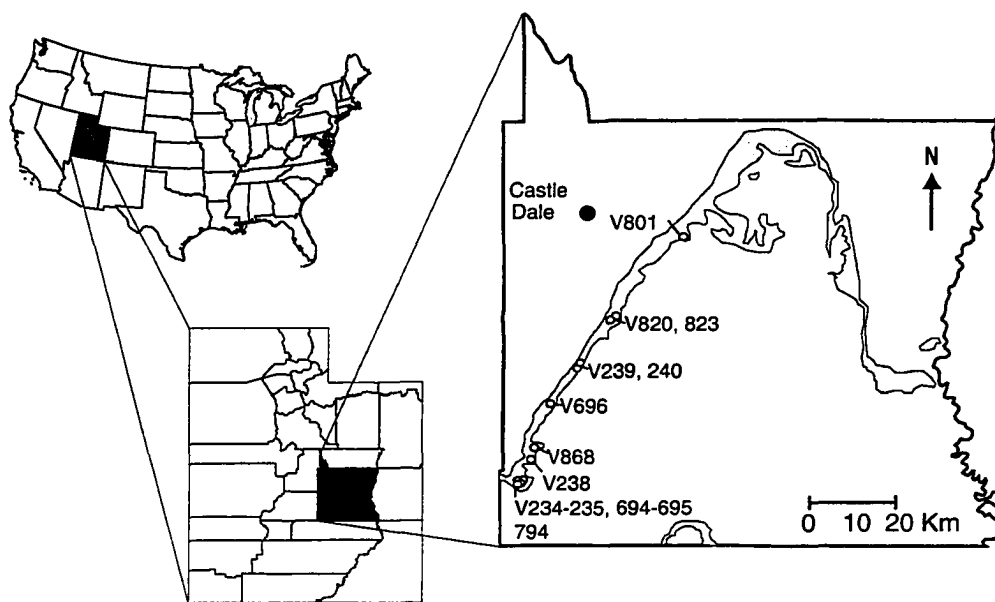


Figure 1



Figure 2

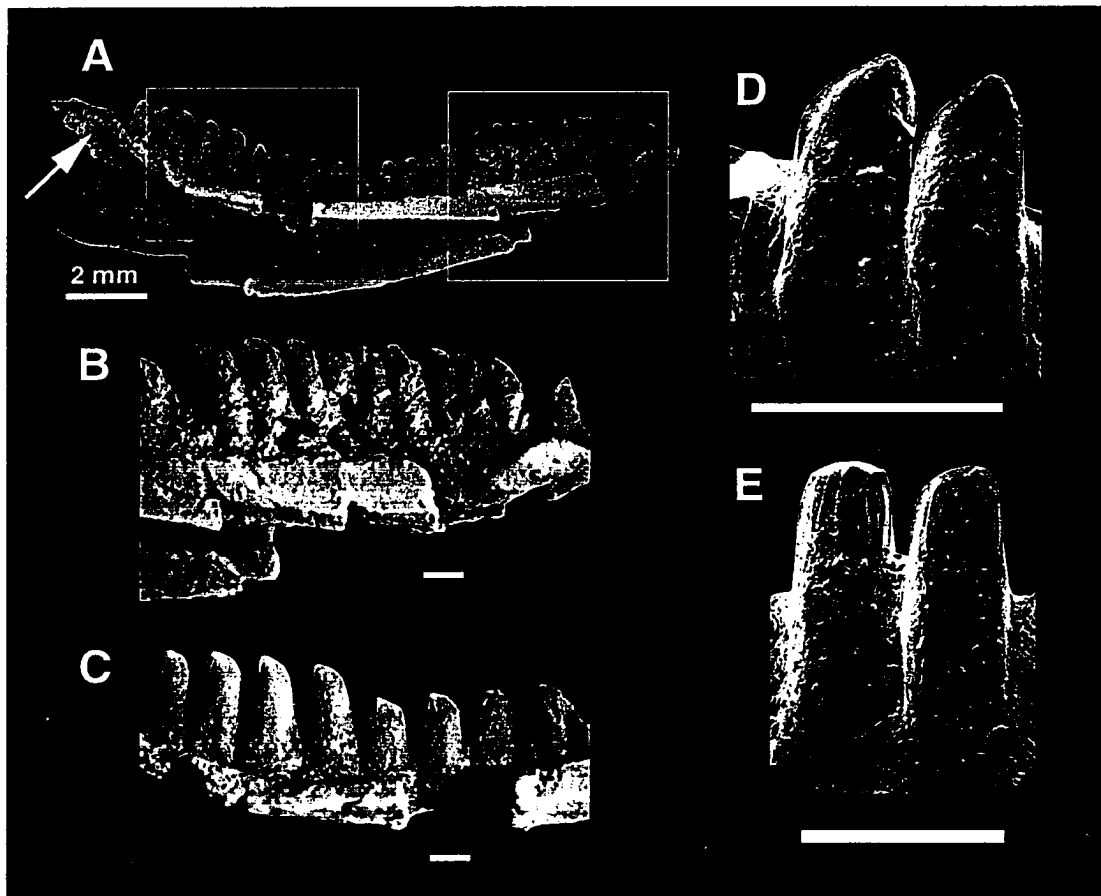


Figure 3

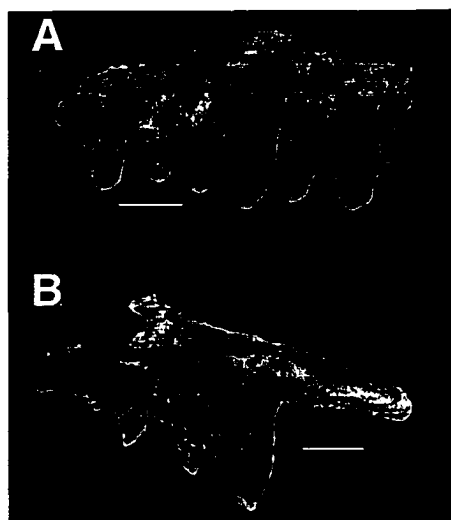


Figure 4



Figure 5

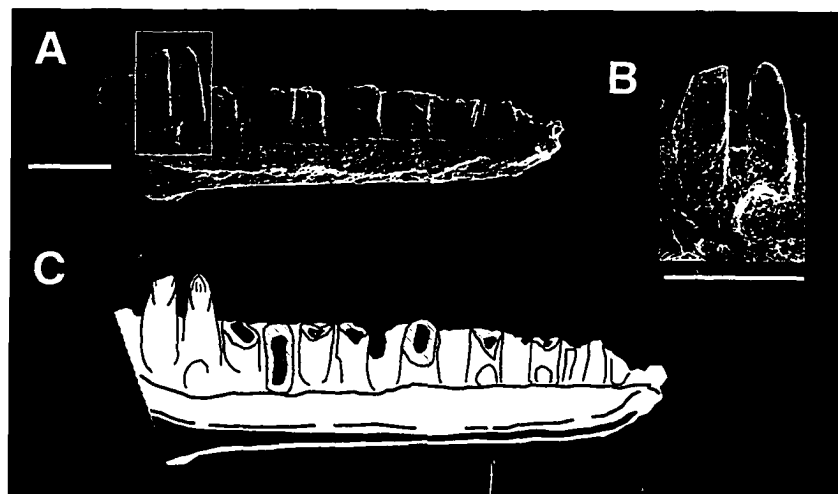


Figure 6

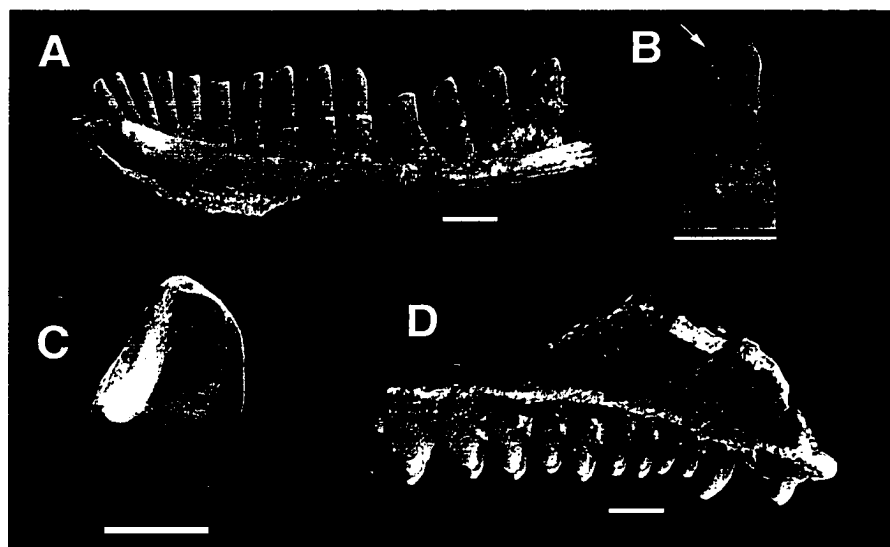


Figure 7

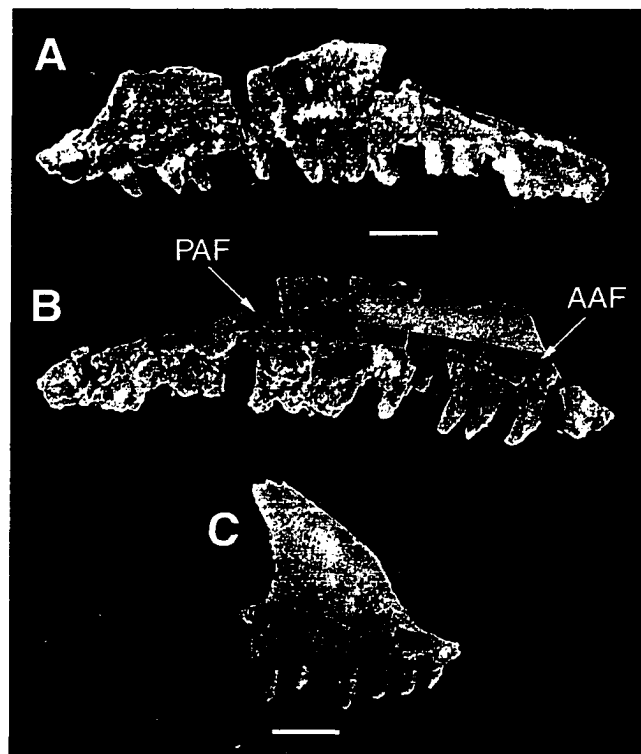


Figure 8

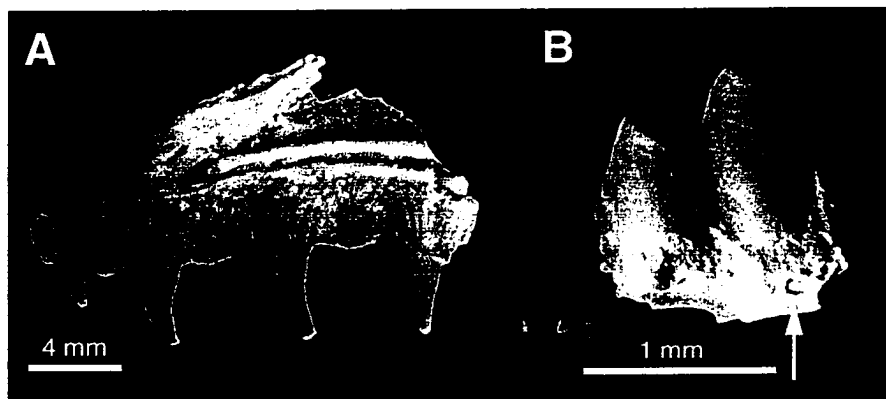


Figure 9

Figure 10

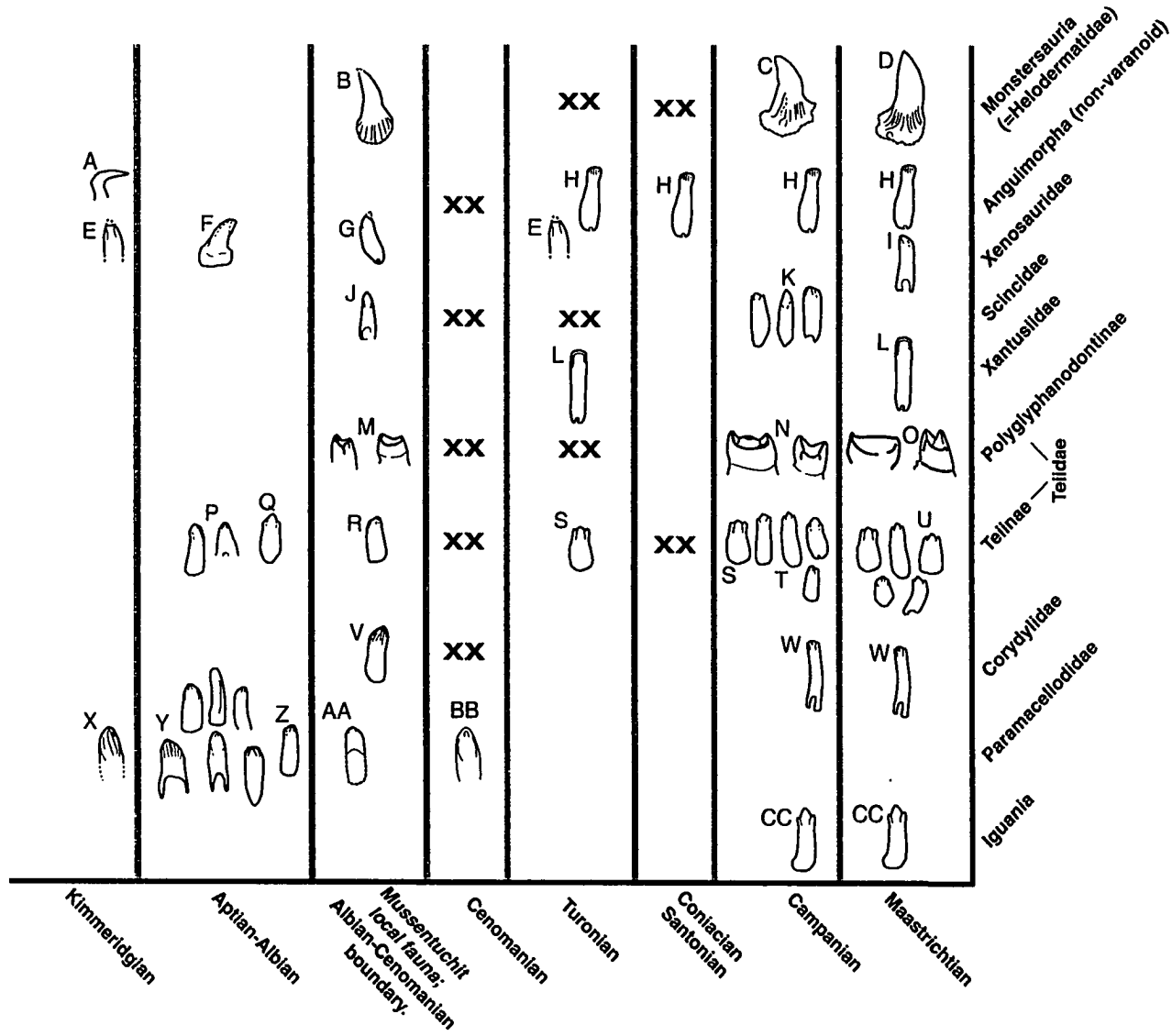


Figure 11

