

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

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## ABSTRACT

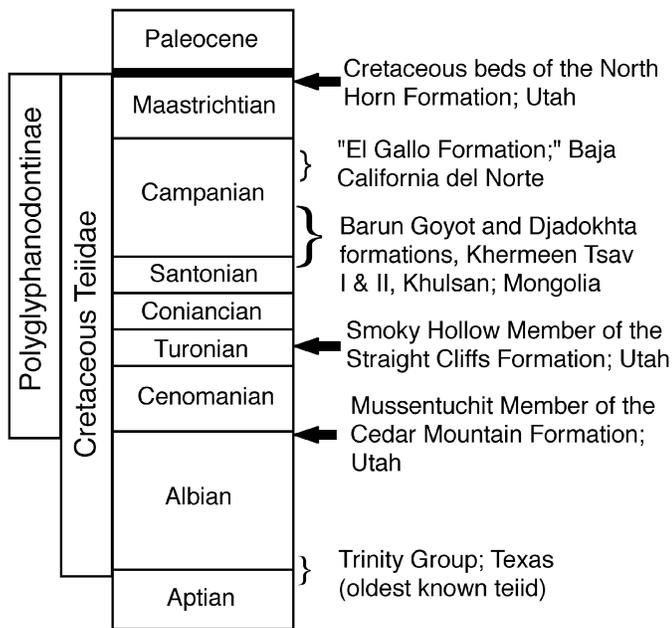
Isolated lizard teeth from the upper Albian part of the Cedar Mountain Formation and the Turonian part of the Straight Cliffs Formation, both in Utah, and from the upper Campanian "El Gallo Formation" in Baja California del Norte closely resemble described teeth of the North American Maastrichtian polyglyphanodontines *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 a 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 Anguillidae (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 occasions, more nearly complete material, even complete skeletons, have been recovered. Such is the case for most of the taxa referred to the Polyglyphanodontinae.

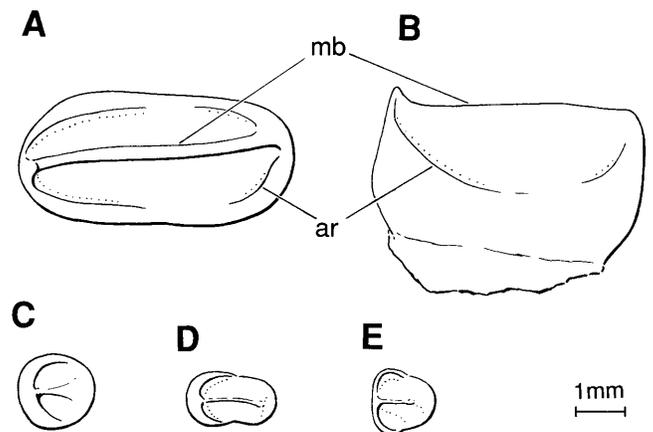
The Polyglyphanodontinae is a primitive group of teiids (Estes, 1983) which includes taxa from the Late Cretaceous (figure 1) of North America (Gilmore, 1940, 1942, 1943a) and Mongolia (Gilmore, 1943a; Sulimski, 1972, 1975, 1978). The group is diagnosed by a variety of characteristics associated with the skull: fusion of the 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 of the group. One of the 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 (for example, *Darchansaurus*, *Erdenetesaurus*, and *Macrocephalosaurus*); large, bulbous, durophagous-type teeth (for



**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).

example, *Adamisaurus*); and slightly rotated (=obliquely oriented), chisel-like, teeth with polycusate crowns (for example, *Cherminisaurus*). By contrast, teeth in the North American taxa *Polyglyphanodon* and *Paraglyphanodon* (figure 2) 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 vertebrate taxa (Cifelli, 1990a-d, 1993; Cifelli and Eaton, 1987; Cifelli and Johanson, 1994; Cifelli and Nydam, 1995; Cifelli and Madsen, 1998; Cifelli and Muizon, 1998; Cifelli and others, 1997; Cifelli and others, 1998a; Eaton and Cifelli, 1988; Gardner, 1994, 1995; Gardner and Cifelli, 1999; 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 *Poly-*



**Figure 2.** 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 toward bottom of the page and in all figures medial is toward right side of the page. Abbreviations: ar-accessory ridge, mb-main blade.

*glyphanodon 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 elements recovered. Teeth alone are rarely used to diagnose higher taxonomic groups of lizards, 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 a 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 in *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 the 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 appropriately reflects

the diversity in the fossil record.

The goals of this paper are: (1) to describe the new taxa from the Cedar Mountain, Straight Cliffs, and "El Gallo" formations; (2) to discuss the evolutionary history of dental morphology in the Polyglyphanodontinae; and (3) to 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 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 ferrugenous* (Gilmore, 1943b) was 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 kozlowskii* and *Erdenetesaurus robinsonae* to the family.

In his comprehensive review of fossil lizards, Estes (1983) re-evaluated 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; and Sullivan and Estes, 1997) based on similarities with the modern South American tupinambine *Dracaena*.

### Abbreviations and Conventions

Abbreviations for institutions cited in the text: IGM, Instituto de Geología de la Universidad Nacional Autónoma de México, Mexico City; LACM, Los Angeles County Museum, Los Angeles; LAV, vertebrate paleontology locality, Los Angeles County Museum, Los Angeles; MNA, Museum of Northern Arizona, Flagstaff; MVZ, Museum of Vertebrate Zoology, University of California, Berkeley; OMNH, Oklahoma Museum of Natural History, University of Oklahoma, Norman; USNM, Museum of Natural History, Smithsonian Institution, Washington. Other conventions: Gr., Greek; Ma, millions of years before present; SEM, scanning electron microscopy; SVL, snout-vent-length; W/L, ratio of mediolateral width to anteroposterior length.

### MATERIALS AND METHODS

Fossils from the Cedar Mountain and Straight Cliffs Formations were collected by quarrying and underwater screenwashing 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 (for example, 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 palladium 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  $\mu$ 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 kilometers east of Moore, Emery County, Utah (figure 3) 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

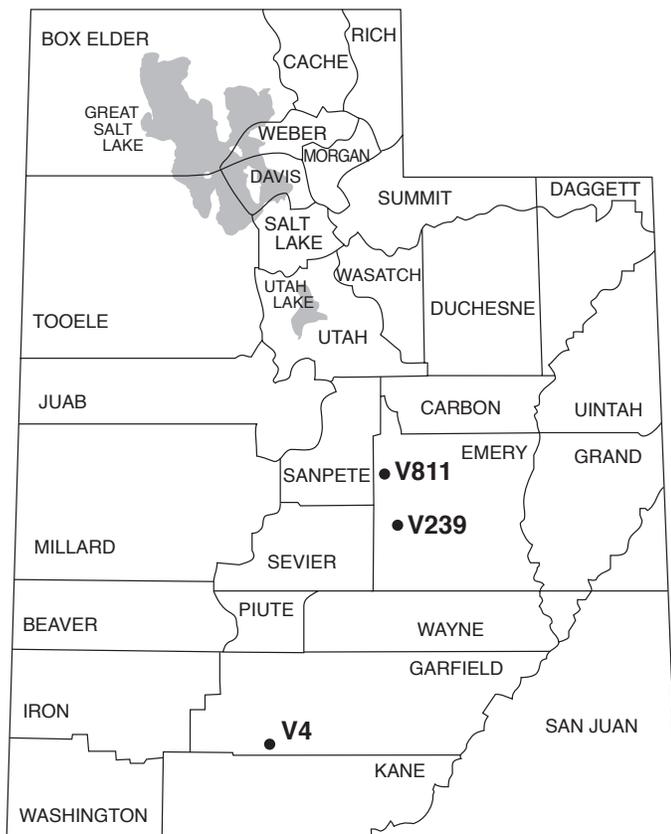
the uppermost part of the Cedar Mountain Formation, in the Uinta Basin (northeast of the localities reported here) to be Cenomanian. However, they also report that in the region of the OMNH localities the Cenomanian part of the Cedar Mountain Formation has been removed by truncation by the Dakota Sandstone. The best constrained date for the upper mudstones of the Cedar Mountain Formation is a recently reported  $^{40}\text{Ar}/^{39}\text{Ar}$  age estimate of about 98.4 million yr B.P. (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 (figure 3). 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 Members. These members were deposited in marine and terrestrial environments from the Turonian through 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; figure 3) in the Late Cretaceous (Maastrichtian) part of the North Horn Formation (Gilmore, 1946) which has yielded nearly 50 topotypic skeletons of this taxon (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 polyg-



**Figure 3.** 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. utahaensis*), North Horn Formation, Emery County.

lyphanodontine 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 (S. A. 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 IGM.

## SYSTEMATIC PALEONTOLOGY

### Order Squamata Opperl 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 figures 5E,F and 6A,B herein).

### *Polyglyphanodon bajaensis* new species, figure 4

#### Holotype

IGM 6965 (=LACM 58008; figure 4C), posterior tooth.

#### Hypodigm

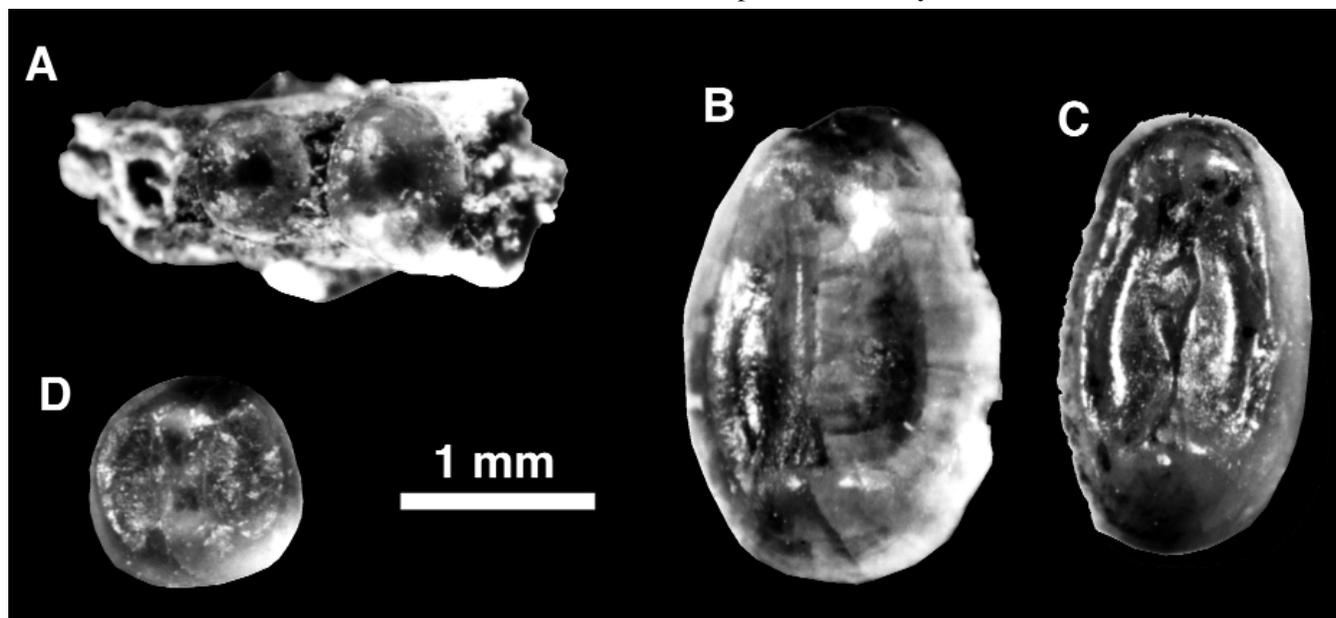
IGM 6965 (holotype), posterior tooth; IGM 6963 (=LACM 57869; figure 4A), anterior right dentary fragment with two teeth and a broken base of a third tooth; IGM 6964 (=LACM 57877; figure 4B), posterior tooth; IGM 6966 (=LACM 58011; figure 4D), posteriormost tooth.

#### 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, figure 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 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.



**Figure 4.** Occlusal views of teeth of *Polyglyphanodon bajaensis* new species, 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.

## 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 in 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 6964 and IGM 6965, identified as teeth from the posterior part of the tooth row, resemble posterior teeth 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 which is predominantly horizontal, but turns towards the apices on medial and lateral sides of the teeth. 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 mm wide, 1.07 mm 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: figure 19) I tentatively assign this tooth a posteriormost position in the tooth row.

## Remarks

The *Polyglyphanodon bajaensis* material was 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's (1983) placement of this taxon in the genus *Polyglyphanodon*, but not his assignment to *P. sternbergi*. The specimens are referred to *Polyglyphanodon* based on dental characteristics shared with *P. sternbergi*: conical anterior teeth, posterior teeth great-

ly 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 in *P. sternbergi*, 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 (for example, *Polyglyphanodon bajaensis*) or horizontal ridge (for example, *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 other than by phylogenetic relatedness.

## *Dicothodon moorensis* new species, figures 5A, B; 6A, B, C

### Etymology

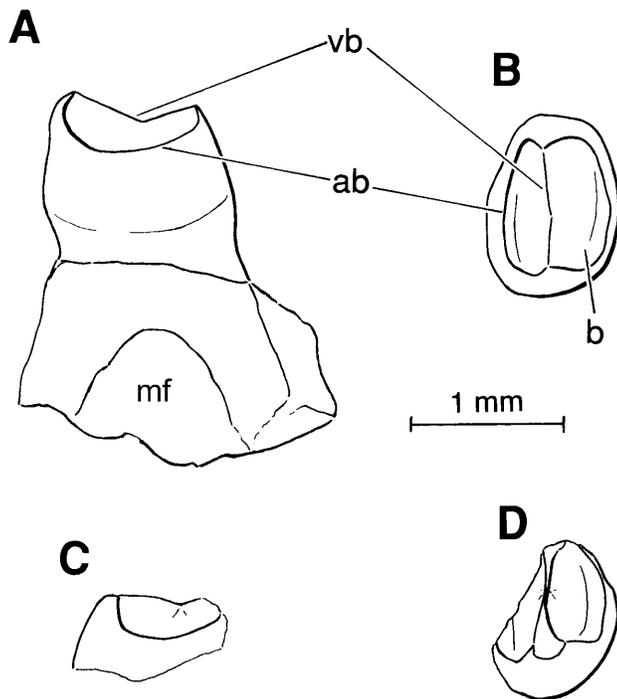
Named for the town of Moore, Utah, which is close to the holotype locality.

### Holotype

OMNH 29771, dentary fragment with one complete tooth and the broken base of another tooth.

### Hypodigm

OMNH 29771 (holotype; figures 5A, B; 6A, B) and OMNH 32629, isolated tooth (figure 6C).



**Figure 5.** *Dicothodon* new genus from the Cretaceous of Utah. A and B, OMNH 29771, holotype of *Dicothodon moorensis* new species, 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.

### 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, only OMNH 29771 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 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 base. 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 and 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 second 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 equal in length, cusps equal in height, and the basins on either side of the V-shaped blade lower down on the crown and 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 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 the differences between the two specimens are minor and, when compared to tooth sets of *Polyglyphanodon sternbergi* and the extant teiids, *Dicrodon* and *Teius*, appear to be related to either positional differences along the jaw or ontogenetic variation.

### *Dicothodon* sp., figures 5C,D; 6D

#### 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*: a more symmetrical shape in occlusal and a smaller size (width 1.43 mm vs. 1.65 mm; length 1.03 mm vs. 1.25 mm) than both OMNH 29771 and OMNH 32629. Also, 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 vertically 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.

### Remarks

The V-shaped and accessory blades as well as the associated basins clearly show that OMNH 25386 belongs in the new genus *Dicothodon*. However, 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 ontogeny or positional differences in the tooth row.

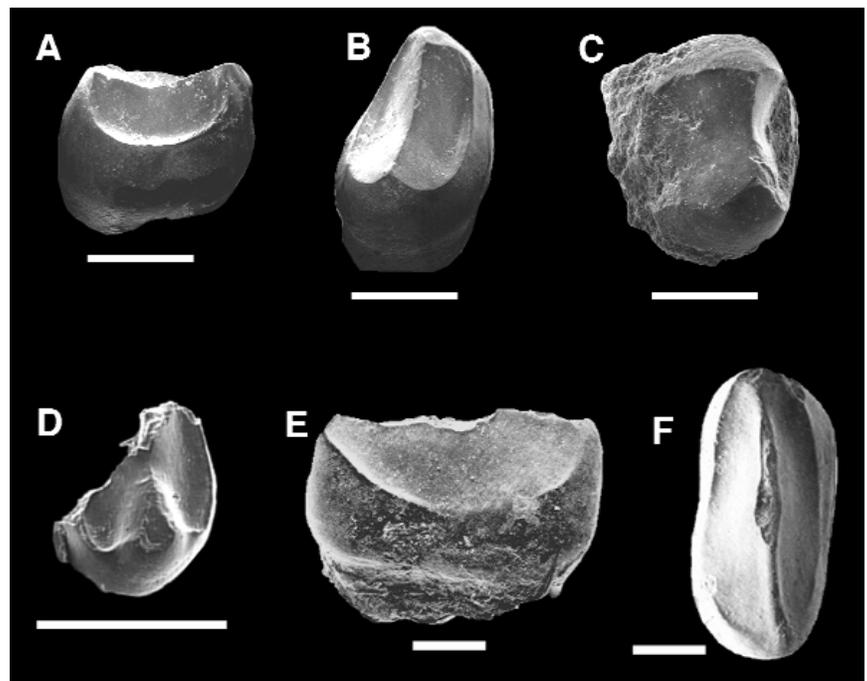
### Comparisons

OMNH 33460 is an incomplete topotypic skeleton of *Polyglyphanodon sternbergi* 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) material. 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 (figures 2A, B, C, and 6E, F) 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 below.

Anterior teeth (figure 2C) in the maxilla and dentary of *Polyglyphanodon sternbergi* differ from those of most teiids (for example, *Tupinambis*, Rieppel, 1980; figure 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 maxillary and dentary tooth rows in *P. sternbergi* consists of a series of transversely oriented, parallel, chisel-like teeth (Gilmore, 1942; figure 2A, B herein). These teeth are larger (3.75 mm wide, 1.62 mm long; topotypic tooth from OMNH 33460; figures 6E, 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 teeth 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



**Figure 6.** *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.

occlusal view (contra Gilmore, 1942). To either side (anterior and posterior) of the main blade are low, semi-circular, 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 (figure 5E, F) has incipient basins medially and laterally not evident in the other teeth of the same jaw. 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* was described by Gilmore (1942) as conical (that is, not expanded transversely) with a small vertical ridge on the center of the medial surface. However, in his figures (Gilmore, 1942: figures 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 figure 6, 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* also differentiates teeth in this species from those of *P. sternbergi*. Accessory structures on the teeth of *P. sternbergi* are low ridges and not the 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) of *P. bajaensis* is nearly identical to the last tooth in the maxillary tooth row of *P. sternbergi* (see Gilmore, 1942: figure 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* (figure 2D) are nearly identical to those of *Polyglyphanodon sternbergi*. The other taxon found in the North Horn Formation is *Paraglyphanodon utahensis* (figure 2E). 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 much the 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. This could be supported by a figure of *Paraglyphanodon gazini* (Gilmore, 1943a, figure 7) that 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 (for example, 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; Estes, 1964, 1969, 1983; Gao and Fox, 1991, 1996). Asian teiids are restricted to the polyglyphanodontines from the Upper Cretaceous of Mongolia (Sulimski, 1972, 1975). To some degree the high diversity of teiids (including 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

As mentioned above, the majority of Cretaceous specimens that make up the fossil record of the Teiidae are jaws and jaw fragments. Many of the characteristics used to diagnose the Teiidae are found in these jaws; for example, Meckelian fossa widely open to the symphysis to accommodate a 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, the morphology of the teeth in these jaws is 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 (theoretical 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 (for example, *Gerontoseps*, *Socognathus*, *Sphenosiagon*, and

*Stypodontosaurus*); (2) "normal-type" with anteroposteriorly oriented teeth with bi- or tricuspid crowns (e.g., *Chamops*, *Glyptogenys*, *Haptosphenus*, *Leptochamops*, and *Meniscognathus*); or (3) "transverse-type" with transversely oriented, bicuspid crown (for example, *Peneteius*, undescribed taxon from the Cedar Mountain Formation). *Peneteius* and *Polyglyphanodon sternbergi* share a transverse orientation, however, the teeth of *Peneteius* are otherwise distinct; expanded medially (Estes, 1969) and multicuspidate (Nydham and others, unpublished data). *Peneteius* 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 as all three morphotypes listed above are known to occur at the same horizon (Estes, 1983; Gao and Fox, 1991, 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, polycuspidate teeth (for example, *Darchansaurus*, *Erdenetesaurus*, and *Macrocephalosaurus*); large, bulbous, conical teeth (for example, *Adamisaurus*); and obliquely oriented, polycuspidate, blade-like teeth (for example, *Cherminisaurus*). The most common tooth pattern of the Mongolian taxa is the leaf-shaped, polycuspidate morphology found in a majority of the taxa. This pattern is similar to that found in modern herbivorous lizards such as 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 *Cherminisaurus* (Sulimski, 1975, figure 14A) which has horizontal, polycuspidate, 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 tooth pattern in *Dicothodon* sp., *Polyglyphanodon bajaensis*, and *P. sternbergi* shows that this morphology underwent only minor changes (i.e., shape of main blade

and extent of accessory blades) throughout the rest of the Cretaceous. Without a phylogenetic analysis it is not certain that these differences actually represent the apparent 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 its reverse 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 *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 vertebrate record (the first being the Cretaceous shark *Baibisha*; Cifelli and others, this volume) of a west-to-east dispersal during the 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. Lizards with specialized diets (for example, 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, polycusate 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. Because we can observe the habits of modern taxa we can determine the correlations between diet and morphology (at least in many of the specialized taxa) and use these correlations as modern analogs to aid in interpreting the diets of fossil lizards, assuming we find similar patterns.

*Polyglyphanodon sternbergi* is immediately distinguishable by its large size and unusual dentition. The transverse orientation and medial expansion, characteristic of the teeth of the North American polyglyphanodontines, also occur 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 likely presence 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*. He interpreted this tooth morphology and jaw reconstruction to "indicate quite conclusively that *Polyglyphanodon* was herbivorous in diet" (Gilmore, 1942, p. 265). One line of evidence that supports the

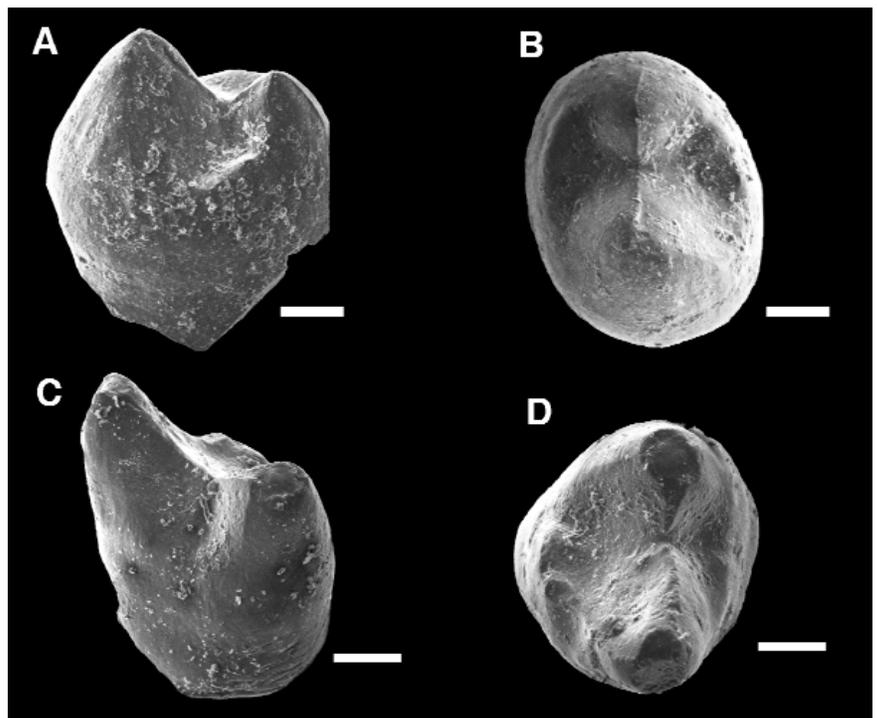
possibility of *P. sternbergi* having been herbivorous is its large size. Based on the energetic requirements of lizards and energy available from plant material, Pough (1973) determined that in order for a lizard to be able to sustain itself through herbivory it would need to have a minimum SVL of 15 cm. 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, p. 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 of a polyglyphanodontine with two teeth (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* (Nydham 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 tough food items that could be sliced, most likely 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*. *Macrocephalosaurus ferrugineus* is difficult to interpret because the teeth of the specimen are worn and denticles may or not have been present (Sulimski, 1975; Estes, 1983). Estes's (1983) conclusion that these lizards were either herbivores or omnivores is reasonable, though I speculate that the close similarity in dental pattern to the Iguanidae makes a stronger case for herbivory. *Adamisaurus* (Sulimski, 1972) has teeth of duroph-

agus design (large, bluntly conical), similar to those found in the molluscivorous modern skink *Tiliqua*. The teeth of *Adamisaurus* also have a reduced tooth count similar to that of the extant durophagous amphisbaenid, *Amphisbaena ridleyi* (Pregill, 1984). *Adamisaurus* was most likely durophagous and may have been a molluscivore. 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 *Dicothodon moorensis*, *Dicothodon* sp., and *Polyglyphanodon 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 *Dicothodon moorensis*, *Dicothodon* sp., and *P. bajaensis* are more cusped than those of *P. sternbergi*, but these cusps are not tall and sharp as would be expected for a carnivore or insectivore, or as seen in *Trilophosaurus* (Demar and Bolt, 1981: figure 6). Comparison with modern, transversely bicuspid teeth (*Dicrodon* and *Teius*, figure 7)



**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*, south-central South America, posterior tooth from left maxilla, anterior and occlusal views, respectively.

does not clarify the situation. Of the two genera, *Dicrodon holmbergi* is the only completely herbivorous species (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 cusped morphology of the teeth in the new polyglyphanodontine taxa, in addition to the similarities in morphology to the possibly herbivorous *P. sternbergi*, make it likely that *Dicothodon moorensis*, *Dicothodon* sp., and *Polyglyphanodon bajaensis* were omnivores. More complete material may help clarify this interpretation.

### CONCLUSIONS

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 Mongolia 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 to their respective continents, suggest that after diverging these groups remained separated throughout the medial and Late Cretaceous. Although the morphologies are different, tooth patterns in taxa from both continents appear to be adapted for omnivory/herbivory.

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