New data on the dentition of the scincomorphan lizard *Polyglyphanodon sternbergi*

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Polyglyphanodon sternbergi Gilmore, 1940 is a large-bodied lizard from the Late Cretaceous of North America distinguished by its transversely oriented, interlocking teeth. Initially the teeth of *P. sternbergi* were described as smooth and blade-like, but recent discoveries of new specimens from the type locality and re-examination of the original material indicate that the chisel-like teeth of *P. sternbergi* have small, irregular serrations along the blades. These serrations are similar in size to those found on the teeth of the modern herbivorous lizard *Iguana iguana* and were likely used in a similar manner to crop vegetation, but was also capable of a degree of oral food processing due to the transverse orientation and interlocking arrangement of the dentition of *P. sternbergi*. Additionally, the presence of transversely oriented teeth with V-shaped blades in the anterior portion of the tooth row of *P. sternbergi* represents an additional shared characteristic in tooth structure between *P. sternbergi* and *Dicothodon moorensis*, *Bicuspidon numerosus*, and *Peneteius aquilonoius*; all transversely-tooth polyglyphandontine lizards from the Cretaceous of North America. It appears that the unique dentitions of *Polyglyphanodon sternbergi* (large teeth with transverse, serrated blades) and *Peneteius aquilonius* (small teeth with mammal-like specializations) present by the end of the Cretaceous were derived from a bicuspid, transversely oriented precursor tooth with a V-shaped blade.

Key words: Squamata, Polyglyphanodontinae, *Polyglyphanodon*, dentition, Cretaceous, North America.

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Introduction

Polyglyphanodon sternbergi Gilmore, 1940 is a large-bodied fossil lizard recovered from the Late Cretaceous (Maastrichtian) of Utah, U.S.A. (Gilmore 1940, 1942) and is unusual among lizards in having numerous transversely oriented and expanded, chisel-like teeth in the posterior part of its tooth rows. These transversely oriented teeth of the upper and lower tooth rows interdigitated when the jaws closed (Fig. 1). *Polyglyphanodon sternbergi* belongs to the Polyglyphanodontinae (*sensu* Estes 1983, but see competing taxonomic interpretations by Sulimski 1975 and Alifanov 1993, 2000), a group of primitive scincomorphans closely related to, or within, Teiidae. The Polyglyphanodontinae includes taxa from the Late Cretaceous of Asia (Alifanov 1993, 2000; Gilmore 1943a; Sulimski 1975; Wu et al. 1996) and North America (Estes 1983; Gilmore 1940, 1943b; Nydam 1999). The dentitions of the Asian taxa include either leaf-shaped, polycuspate teeth similar to those of modern Iguanidae (taxa described and figured by Gilmore 1943 and Sulimski 1975) or conical teeth (additional taxa recognized by Alifanov 1993). Three North American genera (*Gerontoseps*, *Socognathus*, and *Sphenosiagon*), referred by Gao and Fox (1991, 1996) to the Teiidae, were later referred to Macrocephalosauridae (= Polyglyphanodontinae, Estes 1983) by Alifanov (1993, 2000). Although synapomorphic characteristics are yet to be identified that support this taxonomy, we accept the possibility that macrocephalosaurids (*sensu* Alifanov 2000) may have been present in North America during the Late Cretaceous. Additional North American taxa referred to Polyglyphanodontinae (including *Bicuspidon*, *Dicothodon*, *Peneteius*; we exclude here the conical–weakly anteroposteriorly trifid toothed *Haptosphenus,* which was included in the Polyglyphanodontinae by Estes 1983, but tentatively transferred to Tupinabinae by Gao and Fox 1996) all share in common with *P. sternbergi*, and to the exclusion of all other polyglyphanodontine taxa, the fully transverse orientation of the cusps and blades of the teeth of the posterior portion of their tooth rows.

The initial descriptions of *Polyglyphanodon sternbergi* (see Gilmore 1940, 1942) were significant in that they were based on the several nearly complete skeletons collected during United States National Museum investigations (1937–1938) of the Late Cretaceous part of the North Horn Formation, central Utah. *Polyglyphanodon sternbergi* remains the only Cretaceous-aged lizard from North America known by the complete skull and skeleton. Of particular interest are the unusual chisel-like posterior teeth that Gilmore (1942: 243) described as having a "smooth, sharp-edged crown". Likewise, Gilmore's illustration detailing tooth shape (1942: fig. 22) matches this description and shows the apex of a chisel-like tooth as a straight, smooth blade. Estes (1983) followed

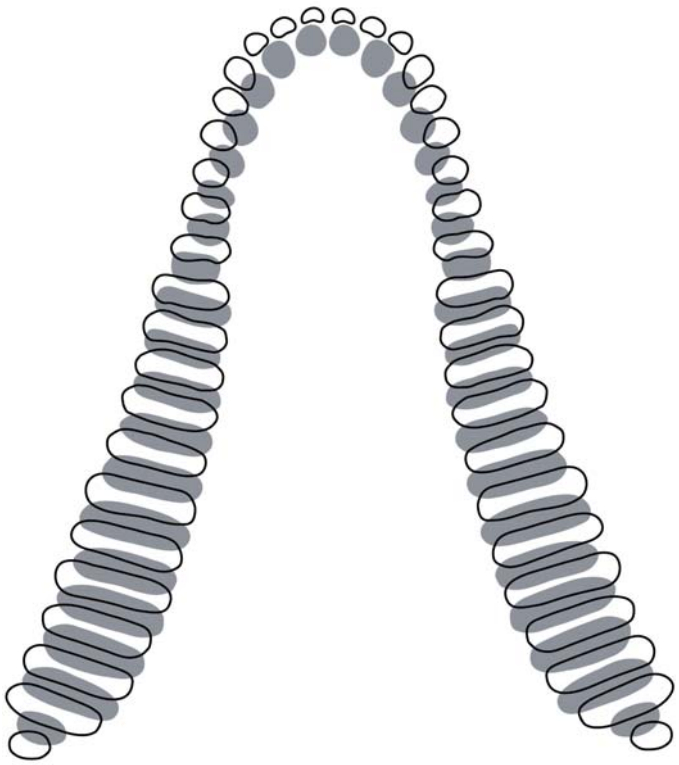

Fig. 1. Diagrammatic representation of the interdigitating upper (black outline) and lower (grey shading) tooth rows of *Polyglyphanodon sternbergi* Gilmore, 1940 based on illustrations by Gilmore (1940, 1942) and observations by RLN.

Gilmore's description and added to it the presence of a medial cusp, whereas Gilmore (1942: 243) had specifically reported a lack of this feature. Estes (1983) also noted the presence of *P. sternbergi* from the Campanian of Baja California, Mexico, but did not figure the specimens. Based on several differences in tooth morphology from *P. sternbergi*, Nydam (1999) erected the new species *P. bajaensis* for the material from Baja California. Nydam (1999) also figured teeth from a newly collected, disarticulated skull showing that the blades of the teeth of *P. sternbergi* are not straight, but actually weakly sinusoidal in occlusal view. Otherwise, the teeth on this new specimen agreed with Gilmore's characterization of the horizontal blade as smooth and otherwise unremarkable.

An additional new specimen of *P. sternbergi*, together with reexamination of some of Gilmore's original jaw material have revealed the presence of previously unreported morphological characteristics of the teeth in this taxon. These additional characters necessitate the revision of aspects of Gilmore's (1942) description of the teeth of *P. sternbergi* and provide important additional evidence for interpretation of the feeding specializations and evolutionary relationships of this unusual lizard.

Institutional abbreviations.—OMNH, Oklahoma Museum of Natural History, Norman, Oklahoma, U.S.A.; USNM, United States National Museum, Washington, D.C., U.S.A.

Material

During the summer of 1999 the authors recovered an additional partial skeleton of *Polyglyphanodon sternbergi* (OMNH 61334) from the type locality. Although the rostral portion of the skull was eroding from the outcrop, several portions of jaw material with well-preserved teeth were recovered. We also obtained a loan from the USNM of some of the original material (upper and lower jaws of USNM 15559) collected in 1937 by G. Pearce and G. Sternberg. Examination of these materials with a binocular light microscope and scanning electron microscope has revealed features of the teeth of *P. sternbergi* that have not previously been described.

Description of new dental features

Close examination of the apex of the transverse blade on the posterior, chisel-like teeth of OMNH 61334 (Fig. 2A) and USNM 15559 (Figs. 2B, 3) shows that the entire horizontal length of the blades of these teeth are lined with minute, irregular serrations. Unlike the uniform, closely spaced denticles typical of the serrated teeth of carnivorous reptiles (e.g., phytosaurs, theropod dinosaurs, large-bodied varanid lizards), the serrations on the teeth of *P. sternbergi* are not symmetrical in size and are separated by wide spaces that are not uniform in width or depth. This gives the edge of the teeth an irregular, rough-edged appearance. Although superficially these serrated blades appear to be broken edges of enamel, higher magnification clearly shows a clean, sharp edge with swelling of the tooth enamel forming each serration (Fig. $2A_3$, A_4).

The anteriormost portion of the tooth row of *P. sternbergi* consists of spatulate teeth with broad labial surfaces and lack serrations (Fig. 3; see also Gilmore 1942: fig. 22). The chisel-like teeth of the posterior portion of the tooth row have similarly broad labial surfaces with the labial cusp taller than the lingual cusp. Gilmore (1942: 243) described the "incipient median ridge" of the anteriormost teeth becoming "progressively more prominent" in successively posterior teeth until it "suddenly extends laterally into a sharp cutting edge…" that characterizes the chisel-like teeth. What Gilmore did not describe (and it certainly could not have seemed important at the time) was the shape of this expanding transverse ridge. The anteriormost three teeth of the transverse-toothed portion of the tooth row are progressively narrower in their medial-lateral width. As a result the transverse ridge forms the longer medial arm of a shallow V-shaped, not horizontal, blade (Figs. 3). The long arm of this "V" bears serrations identical to those found on the chisel-like teeth (Fig. $3A_2$, arrow 1), whereas the next tooth with a V-shaped ridge lacks serrations (Fig. $3A_2$, arrow 2). Interestingly, the intervening tooth lacks any ridge and the empty tooth space

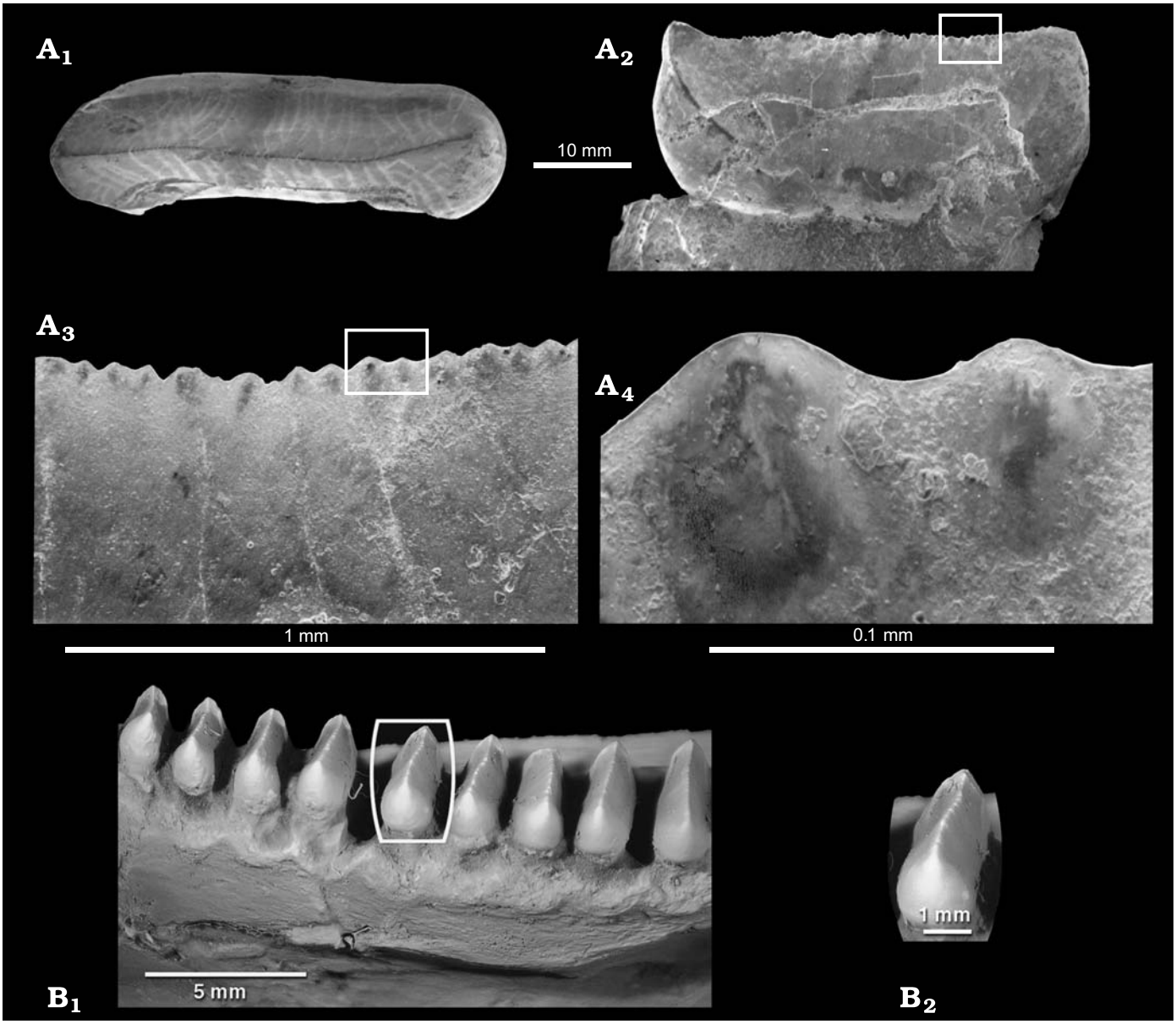

Fig. 2. *Polyglyphanodon sternbergi* Gilmore, 1940. SEM of tooth from: **A**. OMNH 61334; in occlusal (A_1), distal (A_2) views; detail of box in A_2 (A_3); detail of box in A_3 (A_4). **B**. Right dentary of UMNH 15559; posterior part in oblique lingual view (B_1) with detail of chisel-like tooth with serrations of transverse blade (B_2).

leaves open the possibility that two spatulate teeth were present between the two teeth with V-shaped ridges.

Gilmore (1942: 243) described the tooth attachment of *P. sternbergi* as "…anchylosed to the jaw bones in shallow pits that are here regarded as subacrodont in character of implantation". A portion of articulated upper and lower jaws from OMNH 61334 (Fig. 3) generally confirms Gilmore's interpretation of tooth implantation. However, this specimen (as well as USNM 15559) shows that there are differences in the implantation of teeth in the upper and lower tooth rows. The upper teeth are ankylosed to the jaw, but do not exhibit the "shallow pits" described by Gilmore, whereas the lower teeth are set in what is best described as three-sided "sockets". These "sockets" are likely what Gilmore (1942) was referring to as "shallow pits" (Fig. 4). The cementum at the bases of the lower (dentary) teeth is thick and fluted (where exposed lingually), whereas the cementum at the bases of the upper (maxillary) teeth is thinner and lacks fluting (Fig. $4A_2$). This mode of implantation appears to be a modified form of subpleurodonty.

Discussion

Feeding mechanism.—Interpretation of the function of the serrations on the chisel-like teeth of *P. sternbergi* is considered here under the assumption of an herbivorous diet for this

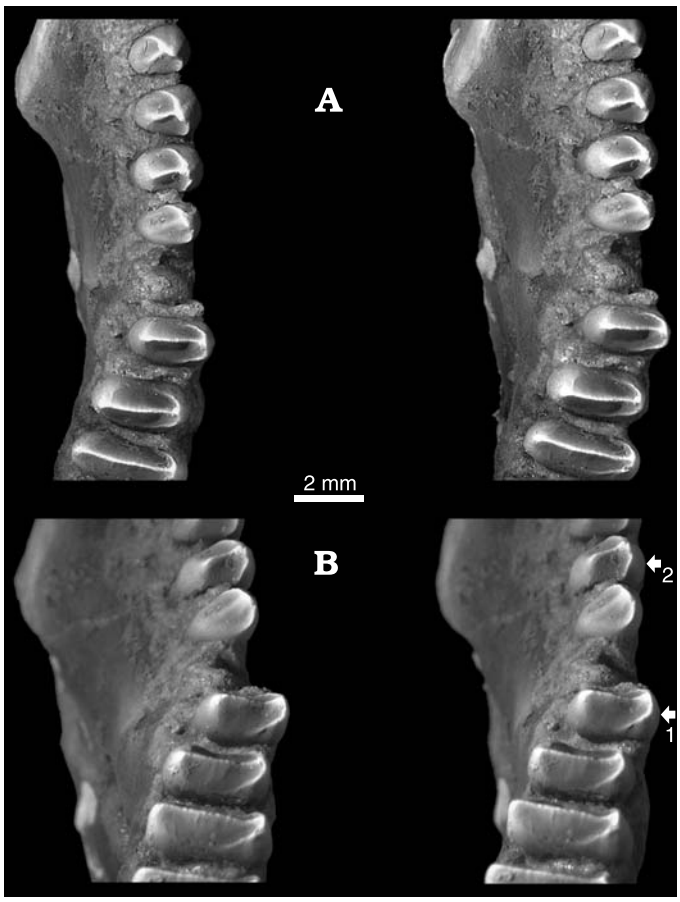

Fig. 3. Right dentary of UMNH 15559, *Polyglyphanodon sternbergi* Gilmore, 1940. Stereopair of occlusal view (**A**) and superocaudal view (**B**) of anterior portion of tooth row of right dentary; note the V-shaped transverse blade with serrations of the tooth just posterior to the empty tooth space (arrow 1) and the lack of serrations on the anterior teeth including one with an expanded ridge (arrow 2).

taxon. Gilmore (1942) originally proposed an herbivorous diet based on dental similarities between *P. sternbergi* and the presumed herbivorous fossil reptile *Trilophosaurus*. Nydam (1999) later argued that the large body size of *P. sternbergi* was consistent with that believed required of modern herbivorous lizards. The presence of serrations on the teeth of herbivorous lizards is well known, particularly within Iguanidae (*sensu* Frost and Etheridge 1989; also see review of iguanid dentition by Montanucci 1968). Serrations are typical of the leaf-shaped teeth of iguanids and are generally uniform in size and vary in number per tooth, depending on species. The serrations on the chisel-like teeth of *P. sternbergi* are most similar to those described for the teeth of *Iguana iguana* (Montanucci 1968: fig. 2D) in that both taxa posses numerous small, variably sized, serrations per tooth. However, the serrations on the teeth of *P. sternbergi* differ from those of *I. iguana*, and other iguanids, in being widely spaced versus closely spaced with narrow, nearly straight-sided grooves between each cuspule.

It seems clear that the serrations on the teeth of *P. sternbergi* functioned in a similar fashion to those of *I. iguana* and other herbivorous lizards (*sensu* Throckmorton 1976) by improving the capability of the teeth to crop vegetation. As described by Throckmorton (1976; personal observation of RLN) *I. iguana* uses its serrated teeth, in conjunction with lateral pulling of the head, to cut leaves from a plant. The removed plant material is then manipulated by the tongue to the rear of the mouth and swallowed without further oral processing (Throckmorton 1976). In cropping leaves *I. iguana* employs a scissors-like mechanism (Throckmorton 1976) of the tooth rows, characterized by the lower tooth row closing closely inside the upper tooth row and the point of contact between the teeth and the food item moving forward as the jaws close more completely. Although serrated, the posterior teeth of *P. sternbergi* certainly did not close in a scissors-like fashion, but instead interdigitated as the tooth rows came together (Figs. 1, 4). Based on the presence of the taller labial cusps, slightly wider labial sides (and the normal, scissors-like relationship of the anteriormost teeth), the dentition of *P. sternbergi* was capable of cropping vegetation along the entire tooth row. Unique to this taxon, however, is that in addition to cropping, as the teeth closed, the serrated blades of the posterior teeth would have cut and/or torn the plant material caught within the interdigitating tooth rows. Whereas modern iguanids tend to pack their gut with cropped, but otherwise whole leaves (Durtsche 1999), *P. sternbergi* was capable of processing plant material to a greater degree as a result of this interdigitating tooth-tooth relationship of serrated blades. The benefit of this additional processing in *P. sternbergi* is the presumed increased efficiency in digesting plant material that has undergone some degree of mechanical processing prior to being subjected to chemical processing in the gut. Based on the lack of wear on most of the known teeth of *P. sternbergi* it is unlikely that plant material was thoroughly "chewed" and likely underwent only the mechanical processing associated with being caught between the tooth rows one–two times prior to swallowing.

A similar type of oral food processing based on interdigitation of transversely oriented teeth has also been postulated for *Peneteius aquilonius* Estes, 1969, a small-bodied polyglyphanodontine lizard that evolved several mammal-like specializations (e.g., complex multicuspid teeth; differential,

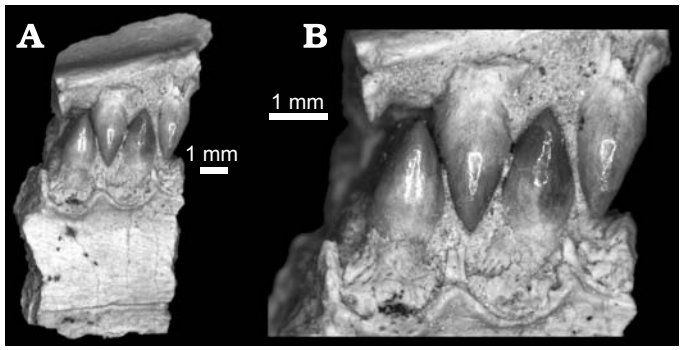

Fig. 4. Articulated upper and lower jaw fragments of OMNH 61334, *Polyglyphanodon sternbergi* Gilmore, 1940. In lingual view (**A**) and close-up of lingual view (**B**).

but complimentary upper and lower dental morphologies) to more successfully orally process arthropods (Nydam et al. 2000).

Evolutionary implications.—Based on the presence in North America of polyglyphanodontine lizards with fully transversely oriented teeth as far back as Albian–Cenomanian boundary, Nydam (1999) and Nydam and Cifelli (2002) disputed the hypothesis (*sensu* Estes 1983) that *Cherminsaurus kozlowskii* Sulimski, 1975 represents a transitional taxon (based on dental morphology) between the Santonian–Campanian-aged Asian polyglyphanodontine taxa and the Maastrichtian-aged *P. sternbergi*. The North American specimens appear to represent a lineage characterized by unique similarities in tooth orientation and morphological characteristics; they also predate *C. kozlowskii*. However, the discovery reported herein of serrations on the teeth of *P. sternbergi* and numerous cusps ("tubers" of Sulimski 1975) on the teeth of *C. kozlowskii* requires comment with respect to their potential relationships. Comparison of the cusps on the teeth of *C. kozlowskii* and the serrations on the teeth of *P. sternbergi* show few similarities. The cusps on the teeth of *C. kozlowskii* (see Sulimski 1975: pl. XXVII; Estes 1983: fig. 18 O) are few in number (4–7 per tooth), large and closely spaced, whereas the serrations on the teeth of *P. sternbergi* (Fig. 2) are numerous, minute and widely spaced. Additionally, the teeth of *C. kozlowskii* are more spatulate than chisel-like, with horizontal ridge offset to the labial side of the tooth crown; not central as in *P. sternbergi*. The modified subpleurodont implantation described herein for the dentary teeth of *P. sternbergi* is more similar to the subpleurodont tooth implantation described for *C. kozlowskii* (see Sulimski 1975), but as some type of pleurodont implantation is shared by nearly all non-acrodontan lizards it does not provide evidence relevant to the relationship of these two taxa. In light of the apparent long history of transversely toothed polyglyphanodontine lizards in North America (*sensu* Nydam and Cifelli 2002) we find no compelling reason to consider the cusps on the teeth of *C. kozlowskii* and the serrations on the teeth of *P. sternbergi* as more than roughly analogous features.

The Asian scincomorphan *Adamisaurus magnidentatus* Sulimski, 1972, the sole member of the family Adamisauridae (Sulimski 1978; Alifanov 2000; but synonymized with Polyglyphanodontinae by Estes 1983), was described by Sulimski (1972, 1978) as having massive, conical teeth and then later described by Alifanov (2000: 376, fig. 18.6) as having teeth with transversely expanded bases. Although they share with *Polyglyphanodon* a transverse expansion of at least the tooth bases, the teeth of *Admisaurus* do not otherwise bear any additional similarities to the teeth of *Polyglyphanodon*, but the teeth figured by Alifanov (2000: fig. 18.6B) are similar to those figured by Gilmore (1940: fig. 2) for *Paraglyphanodon utahensis* in that the apices of the teeth are offset to the lateral sides of the teeth. However, the photograph of the palatal view of the same specimen (Sulimski 1978: pl. 13-3) shows the apices to be more centrally placed on the teeth. Alifanov (2000) retained family level separation of the Adamisauridae (*sensu* Sulimski 1978) and Polyglyphanodontidae (*sensu* Sulimski 1975) due to "many differences" between the representative taxa. We have followed herein the systematic conventions of Estes (1983; see also the discussion of Gao and Fox 1991) pending a formal presentation and description of evidence to the contrary.

Peneteius aquilonius (particularly the maxillary teeth; Nydam et al. 2000) and *Polyglyphanodon sternbergi* share the presence of a transversely oriented, central blade on the teeth of the posterior portion of the tooth row. Whereas this blade is horizontal and serrated in *Polyglyphanodon sternbergi*, it is smooth and V-shaped in *Peneteius aquilonius*. A similar V-shaped, transverse blade is also found in *Dicothodon* and other known polyglyphanodontine taxa from North America (Nydam 1999). The presence of a V-shaped transverse blade in the teeth between the anteriormost spatulate and posterior chisel-like tooth series in *P. sternbergi*, while certainly a transitional feature, may also be indicative of the evolutionary relationships of this taxon to the other North American polyglyphanodontines and closely related taxa (*sensu* Nydam and Cifelli 2002). A V-shaped transverse blade is one of the diagnostic features of *Dicothodon moorensis* Nydam, 1999, a polyglyphanodontine lizard from the Albian–Cenomanian boundary of Utah (Nydam 1999). Similarly V- or U-shaped transverse blades are also found on *Polyglyphanodon bajaensis* Nydam, 1999 from the Campanian of Mexico (Nydam 1999; currently under revision by Nydam and others), new specimens of *Dicothodon* from the Turonian of Utah, *Peneteius aquilonius* from the Maastrichtian of Montana (Estes 1969; Nydam et al. 2000) and *Manangysaurus saureri* McCord, 1998 from the Campanian of Utah (taxon currently under revision by Nydam and others). In addition to other homologous dental features that unite these taxa (see Nydam and Cifelli 2002), the iterative presence of V-shaped transverse blades indicates that this is a historical feature of the North American polyglyphanodontine taxa (excluding the problematic *Haptosphenus*). Indeed, it appears that dental adaptations of *P. sternbergi* for an herbivorous diet (as well as the mammal-like feeding specializations of *Peneteius aquilonius*) evolved within the phylogenetic constraints of the transversely oriented dentition characteristic of the North American polyglyphanodontine taxa.

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