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CT reconstructions and relationships of the Early Cretaceous tribosphenidan mammal, *Slaughteria eruptens* (Trinity Group Texas, USA)

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ABSTRACT

Among the nine taxa of tribosphenidan (boreosphenidan) mammals named from the Early Cretaceous Trinity Group of Texas and Oklahoma, *Slaughteria eruptens* provides unique information about the evolution of tooth replacement. High-resolution CT scans and SEM imagery elucidate the jaw anatomy of *S. eruptens*. Associated upper and lower dentitions from Asian Cretaceous mammals provide the basis for a statistical model to quantify the tooth size relationships of the often cited Trinity Group mammals *Pappotherium pattersoni* and *Holoclemensia texana*, which were named based upon upper molar teeth. Two groups of Trinity mammals are evident based on lower molar size. Most large teeth are referable to *H. texana*. The lower m1 of *S. eruptens* fits neatly into the size range predicted for lower molars of *P. pattersoni*, and it shares compatible tooth cusp relationships. *Slaughteria eruptens* is regarded most parsimoniously as a junior synonym of *P. pattersoni*. *Pappotherium pattersoni* thus shares the alternate premolar replacement pattern of more primitive therian mammals and basal eutherians, but lacks any hint of a submolariform last premolar, as typifies Eutheria. Other small therian mammal teeth from the Trinity Group should be evaluated as possible deciduous teeth.

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Davis (2011) has reinterpreted the teeth in -*Slaughteria eruptans* based upon a fresh analysis of the same CT data used by Kobayashi et al. (2002). He posits that the partly calcified portion of an unrecognized replacement premolar (p5) exists below ultimate tooth preserved in the jaw, which he interprets as dp5. He supports this new interpretation with the statement (Davis, 2011; page 380): "The crown of the dp5 is more worn than the dp4 (in accord with observations by Slaughter, 1971, and contra Kobayashi et al., 2002)."

We offer these observations: in *Slaughteria* the crown of the 3rd tooth (our interpreted dp4) is heavily worn through the enamel to expose the dentine on the protoconid, metaconid, and hypoconulid. The 4th tooth (our m1) shows wear on the paraconid, (unlike the 3rd tooth) and on the hypoconid (neither exposes dentine), and has essentially no wear on the metaconid and entoconid cusps. The protoconid of the 4th tooth is broken off and missing. Interpretation of wear on the posterior face of the trigonid is a matter of opinion. The 3rd tooth has a much more open trigonid and is proportionately narrow and low crowned, as fitting a deciduous tooth. The 4th tooth does not share this morphology. A mental foramen is present in the jaw beneath the anterior of the 4th tooth, a position usually associated with m1 in other Early Cretaceous tribosphenidans, not the ultimate premolar. The conjectured structure below the 4th tooth which Kobayashi et al. (2002) interpreted as fragments and Davis (2011) interprets as primordial p5 is posteriorly open and resembles neither the cap nor bell stage of a developing tooth. The "partial calcification" disjoining the cusps of the undisputed replacement tooth (below the 3rd tooth in the jaw) that Davis cites is an artifact of low resolution CT data. Thus, while we recognize that new data could provide a real test, we stand by the interpretation of the dentition postulated in Kobayashi et al. (2002).

INTRODUCTION

One of the most interesting events in mammalian evolution is the divergence between marsupials and placentals. Putative earliest eutherian and metatherian taxa have been named from the Early Cretaceous Liaoning Beds of China (Ji et al. 2002; Luo et al. 2003). In North America, Early Cretaceous mammals are known mainly from fragmentary dental remains. Among these, an apparent diversity of tribosphenidan (sensu McKenna and Bell 1997; or boreosphenidan sensu Luo et al. 2001) mammals provides provocative glimpses into the morphotypes that, it is argued, preceded the origin of the modern marsupial and placental clades (Jacobs et al. 1989; Kobayashi et al. 2002). Nine tribosphenidan mammals (*Pappotherium pattersoni*, *Holoclemensia texana*, *Kermackia texana*, *Slaughteria eruptens*, *Trinititherium slaughteri*, *Comanchea hilli*, *Adinodon pattersoni, Atokatheridium boreni*, *Oklatheridium szalayi*) have been named from the Late Aptian-Early Albian Trinity Group of Texas and Oklahoma, each based on one or a few upper or lower teeth with equivocal association of teeth from the opposing jaw (Slaughter 1965, 1968a, 1971; Butler 1978; Jacobs et al. 1989; Hershkovitz 1995; Kielan-Jaworowska and Cifelli 2001; Davis et al. 2008). A fresh opportunity to examine relationships among these taxa is provided by new information about one of them, *Slaughteria eruptens*. Analysis of high resolution X-ray CT data revealed that the holotype (a lower jaw) of *S. eruptens* (SMU 61992) houses an unerupted replacement premolar below what had been presumed to be a molar (Figures 1 and 2; Kobayashi et al. 2002). The four erupted teeth in *S. eruptens* are now interpreted as two permanent premolars, plus dp4 and m1 (Kobayashi et al. 2002). *Slaughteria eruptens* demonstrates that the premolar eruption sequence for this primitive tribosphenic mammal was p3->p2->p4 (Kobayashi et al. 2002; Kielan-Jaworowska et al. 2004; Luo et al. 2004).

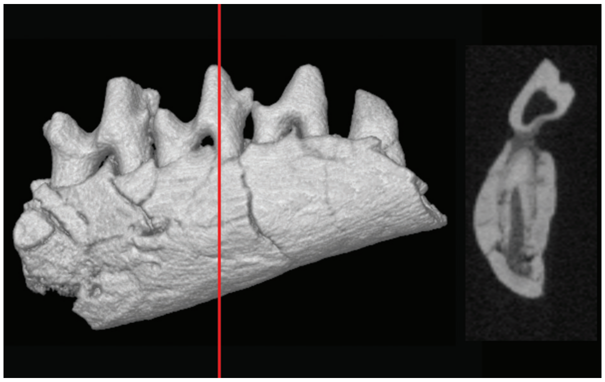

FIGURE 1. *Slaughteria eruptens*, SMU 61992, in right lateral view, QuickTime animation from CT reconstruction with vertical slices proceeding anterior to posterior. Replacement premolar within jaw is highlighted. Jaw length equals 5.42 mm.

We utilize current visualization techniques to document the anatomy of *S. eruptens* in high-resolution interactive 3D imagery and reconstructions based on CT data and new digital SEM photography. Using molar morphology and size relation-

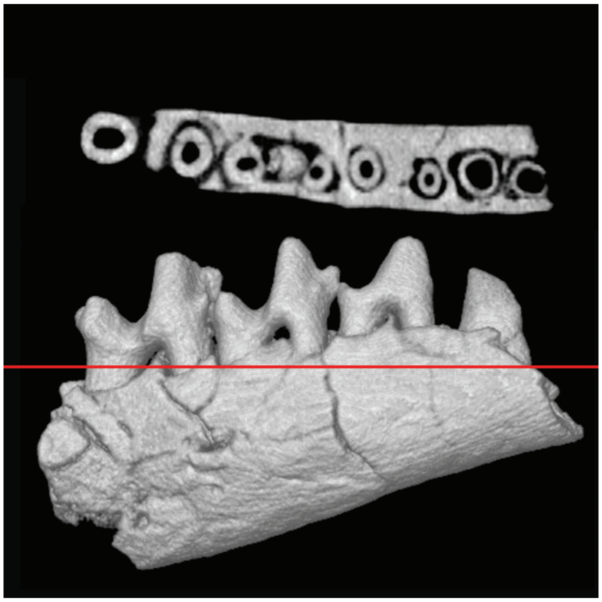

FIGURE 2. *Slaughteria eruptens*, SMU 61992, in right lateral view, QuickTime animation from CT reconstruction with horizontal slices proceeding dorsal to ventral. Replacement premolar within jaw is highlighted. Jaw length equals 5.42 mm.

ships developed from other Cretaceous tribosphenidan mammals, we quantitatively evaluate this taxon's relationship to other Trinity tribosphenidan taxa that are named from upper molars. Of the well-represented Trinity Group mammal taxa that are based upon upper molars, those that are compatible with the tooth structure of *S. eruptens* are *Pappotherium pattersoni* and *Holoclemensia texana*. These three are the Trinity Group therian mammals most commonly cited in phylogeny reconstructions and studies of molar occlusal function (e.g., Crompton 1971; Flynn et al. 1999; Luo et al. 2002)

MATERIAL AND METHODS

The left mandible of *Slaughteria eruptens* was scanned at the High-Resolution X-ray Computed Tomography Facility of the University of Texas at Austin. Scanning methods are described in Kobayashi et al. (2002). Three-dimensional reconstructions and sections were made using LightWave 9.3. *Slaughteria eruptens* has four erupted teeth, two premolars, a deciduous premolar, and a molar. Scanning electron microscopy was done at SMU using the VPSEM Leo-Zeiss 1450VPSE. Size estimates for lower molars of *Pappotherium pattersoni* and *Holoclemensia texana* are based on statistical relationships established from published measurements obtained from associated skulls and lower jaws of a series of Cretaceous therian mammals. Single specimens from each of nine Asian Cretaceous tribosphenidan species were used to predict (based on regression coefficients) the lower first (m1) and second (m2) molar anteroposterior lengths (dependent), from corresponding upper molar anteroposterior lengths (independent) (*Asiatherium reshetovi*, PIN 3907, Szalay and Trofimov 1996; *Asioryctes nemegetensis*, ZPAL MgM-I/56, Kielan-Jaworowska 1981; *Baurunlestes butleri*, PIN 3142-701, Kielan-Jaworowska and Trofimov 1980; *Deltatheridium pretituberculare tardum*, ZPAL MgM-I/91, Kielan-Jaworowska 1975; *Kennalestes gobiensis*, ZPAL MgM-I/3, Kielan-Jaworowska 1968; *Uchkudukodon (Daulestes) nessovi*, ZIN 79066, McKenna et al. 2000, Archibald and Averinov 2006; *Ukhaatherium nessovi*, PSS-MAE 102, Novacek et al. 1997; *Zalambdalestes grangeri*, ZPAL MgM-I/14, *Zalambdalestes lechei*, ZPAL MgM-I/13, Kielan-Jaworowska 1968). Different subsets of taxa were used in the M1/m1 and M2/m2 regressions because of missing data. PIN = Institute of Paleontology, Russian Academy of Sciences, Moscow; PM = Field Museum of Natural History, Chicago; PSS-MAE = Paleontological and Stratigraphy Section (Geological Institute), Mongolian Academy of Sciences, Ulaanbaatar; SMU = Shuler Museum of Paleontology, Southern Methodist University, Dallas; ZPAL MgM = Institute of Paleobiology, Polish Academy of Sciences, Warsaw; ZIN = Zoological Institute, Russian Academy of Sciences, Saint Petersburg.

MORPHOLOGY AND RELATIONSHIPS OF *SLAUGHTERIA ERUPTENS*

A single replacement tooth sits in the jaw below a molariform deciduous precursor as is clear in the reconstructions from CT data of *S. eruptens* (Figures 1 and 2). External morphology is presented in a QuickTime VR model from CT data (Figure 3) and in a movie constructed from SEM photos of the jaw (Figure 4).

One reinterpreted salient character of *S. eruptens* is the lack of molarization of the posterior premolars, in contrast to eutherian mammals (Kielan-Jaworowska et al. 2004). Slaughter (1968b) referred what he identified as submolariform premolars from the Trinity Group to Eutheria and later, by inference, to *Pappotherium*, which he considered a eutherian (Slaughter 1981). A submolariform lower premolar figured by Slaughter (1968b) differs in morphology from the dp4 *S. eruptens*. It either derives from a different taxon than *S. eruptens*, or may represent a deciduous premolar ante-

FIGURE 3. *Slaughteria eruptens*, SMU 61992, 3D QuickTime VR reconstruction of external morphology from CT data. Jaw length equals 5.42 mm.

rior to the dp4 position of *S. eruptens* or another taxon.

Molar length has been used as a character in phylogenetic reconstructions of Cretaceous eutherian mammals (Archibald and Averianov 2006). The length of the newly interpreted lower m1 of *S. eruptens* closely matches first molars of *Eomaia scansoria* (Ji et al. 2002) and *Prokennalestes minor* (Kielan-Jaworowska and Dashzeveg 1989).

Proposed Taxonomic Associations

Pairing of isolated upper and lower teeth of Trinity Group tribosphenidan mammals has been attempted since Patterson (1956) described, but did not name the first sample of these teeth. Despite new collections, little consensus has resulted (Slaughter 1965, 1971; Turnbull 1971; Butler 1978). Upper teeth of Trinity Group tribosphenidans are differentiated primarily on morphology of the stylar shelf and protocone. The first tribosphenidan taxa named from the Trinity Group (*Pappotherium pattersoni* Slaughter 1965 and *Holoclemensia texana* Slaughter 1968a) were based on upper molar teeth. These two mammals differ notably in size as well as stylar cusp development. Other Trinity Group tribosphenidan taxa that were named, based upon upper teeth, include *Comanchea hilli* (Jacobs et al. 1989), *Atokatheridium boreni* (Kielan-Jaworowska and Cifelli 2001), and *Oklatheridium szalayi* (Davis et al. 2008). The four remaining taxa are named from lower teeth or jaws.

FIGURE 4. *Slaughteria eruptens*, SMU 61992, QuickTime animation of jaw from medial to occlusal views based on SEM images.

Patterson (1956) recognized three distinct morphologies of therian lower molars (structural types 1-3) (Table 1). Based upon additional material, Slaughter (1965) added three more morphotypes (4-6) to Patterson's previous three. Several of these morphotypes were described originally from single teeth. In his first paper on the subject, Slaughter (1965) noted that his type 6 lower molar (one molar in a jaw fragment; SMU 61728) was of the size expected to match the uppers of *P. pattersoni*. This specimen was subsequently designated the type of a new genus and species *Trinititherium slaughteri* (Butler 1978). Slaughter (1971) described a left lower mammalian jaw with four teeth (SMU 61992), and tentatively allocated it to *P. pattersoni* based upon size and probable occlusal relationships. He did not comment on its relationship to the morphotypes of Patterson (1956) or Slaughter (1965). Turnbull (1971) assigned all the teeth of Patterson's types 1 and 2 and Slaughter's type 5 to *Holoclemensia*. One small tooth (PM 922) formed the basis for Patterson's (1956) morphotype 3. This tooth, along with Slaughter's types 4 and 6 (6 would become the type of *T. slaughteri*), and some more recent discoveries, were referred by Turnbull (1971) to *Pappotherium*. In contrast, Butler (1978) associated Patterson's type 2 lower molars with *Pappotherium* (and types 1, 4, 5 with *Holoclemensia*), but he argued that molariform teeth in the jaw SMU 61992 differed from other type 2 molars and named the lower jaw *Slaughteria eruptens*. Butler (1978) also believed that type 3 teeth (including PM 922) resembled *Kermackia texana* (Slaughter 1971), a taxon described from lower teeth nearly simultaneously with Turnbull's

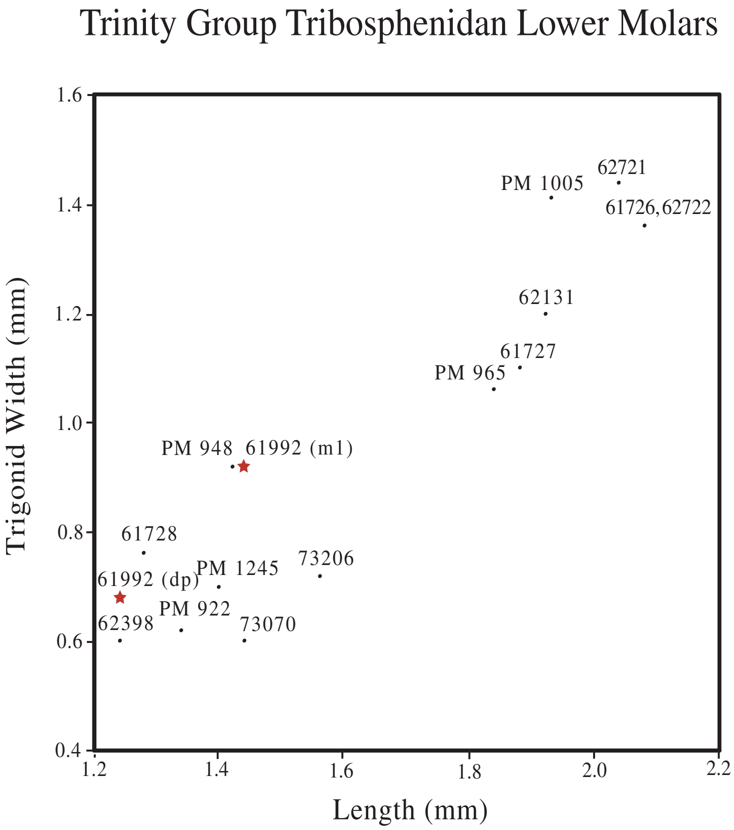

FIGURE 5. Scatter plot of lower molar trigonid width versus tooth length (in mm) of Trinity Group tribosphenidan mammals. SMU specimens designated by catalog numbers only. PM 948, 965 = type 2 teeth (Patterson, 1956); PM 922 = type 3 tooth (Patterson, 1956). We refer: SMU 62721, 61776, 61726, 62131, 61727, PM 1005 = *Holoclemensia texana*; SMU 61992 (stars) = dp4 and m1 of *Slaughteria eruptens* (holotype); SMU 61728 = *Trinititherium slaughteri* (holotype); SMU 62398 = *Kermackia texana* (holotype); SMU 73070, 73206 = *Comanchea hilli*.

(1971) paper. *Slaughteria eruptens* was regarded by Butler (1978) as smaller than teeth that he referred to *Pappotherium*.

Thus, *P. pattersoni,* which is based upon upper molars, has been variously associated with lower molars of morphotypes 2, 3, 4, or 6 (two of which are now designated as separate taxa), and *S. eruptens* has been regarded as associated lowers of *P. pattersoni* or recognized as a distinct taxon (Table 1). The only area of real agreement in previous studies is that types 1 and 5 teeth are *Holoclemensia* (Turnbull 1971; Butler 1978).

Tooth size alone clearly differentiates at least two groups of lower molars from the Trinity Group (Figure 5, Table 1; Jacobs et al. 1989; Kobayashi et al. 2002).

Tooth Size Correspondence

Our objective is to constrain quantitatively the size of the lower molars that are compatible with the holotype and unequivocally referred upper molars of *P. pattersoni.* We also test the associations that have been made of isolated lower teeth with the holotype and unequivocal upper molars of *H. texana*. Within mammalian species, it is well established that cheek teeth exhibit patterns of size correlation (correlation fields of Kurten 1953). Adjacent and occluding pairs of teeth typically exhibit the strongest correlations, especially within fields such as premolars or molars (Kurten 1953; Van Valen 1962; Gould and Garwood 1969, Gingerich and Winkler 1979; Szuma 2000). A model for estimating opposing tooth sizes in Early Cretaceous mammals is limited by the lack of population size samples of skulls with associated dentitions. However, given the limited range of tooth morphologies found in Cretaceous mammals with tribosphenic molars and their similar dental formulae, it is possible to predict that corresponding pairs of occluding upper and lower molars (especially M/m1 M/m2) across a range of species will also be constrained to strong size correlation in order to maintain

TABLE 1. Summary of proposed morphotypes and taxonomic assignments by author of Trinity Group tribosphenidan lower molars.

Patterson (1956)	**Slaughter (1965)**
Type 1	Type 4
Type 2	Type 5
Type 3	Type 6 = size of *Pappotherium pattersoni*
Slaughter (1971)	**Turnbull (1971)**
SMU 61992 = *Pappotherium pattersoni*	Types 1, 2, 5 = *Holoclemensia*
	Types 3, 4, 5 = *Pappotherium*
Butler (1978)	
Type 3 = *Kermackia texana*	
Type 2 = *Pappotherium pattersoni*	
Type 1, 4, 5 = *Holoclemensia*	
Type 6 = *Trinititherium slaughteri*	
SMU 61992 = *Slaughteria eruptens*	

occlusal relationships. Assuming robust length correlations between occluding molar teeth, an estimate of lower molar length based upon a given upper molar length can be made using regression analysis. Archibald and Averianov (2006) use differences in upper M1/lower m1 length ratios as phylogenetic character states in analyzing Asian Cretaceous mammals. Such varying proportions could confound the assumptions in the following regression analysis. However, systematic differences in upper/lower molar length ratios would be apparent in the following analysis in scatter plots and measures of length relationships (see below).

Two regression models (see Materials and Methods), one for upper versus lower first molars (M1/m1; Figure 6) and one for second molars (M2/m2; Figure 7), are used to estimate the length of lower molars (dependent variable) expected from the lengths of upper molars in the types and referred specimens of *P. pattersoni* and *H. texana* (natural logs are used to equalize variance among the species sizes). Using these regression equations, the lengths of penultimate lower molar predicted from the type (SMU 61725) upper penultimate molar of *P. pattersoni* are 1.49 mm (M1/m1 model; $\ln m1L = 0.016 + 1.100(\ln M1L)$) and 1.33 mm (M2/m2 model; $\ln m2L = -0.186 + 1.336(\ln M2L)$. The two predicted lengths for *P. pattersoni* lower molars bracket the length of the last tooth preserved in *S. eruptens* (m1; L = 1.44 mm). A well-preserved left upper molar (molar position uncertain) that can be referred unquestionably to *P. pattersoni* (SMU 73069) is smaller than the holotype specimen (L = 1.28 mm x W = 1.4 mm). Using this upper molar in the regression model for M1/m1 predicts a corresponding lower molar length of 1.33 mm for *P. pattersoni*. If the M2/m2 model is employed, the predicted lower molar length for SMU 73069 is 1.15 mm.

Using the length of the holotype (SMU 61997) upper molar of *H. texana*, a lower molar length of 1.85 mm (M1/m1 model) or 1.71 mm (M2/m2 model) is predicted. Most of the lower molars that have been and are here referred to *H. texana* (Slaughter 1971; Butler 1978; Jacobs et al. 1989; Kobayashi et al. 2002; but see Turnbull 1971) are longer than 1.85 mm (Figure 5). The largest lower molars of Trinity Group tribosphenidans (including Patterson's 1956 type 1 teeth) can be distinguished clearly from the smaller teeth on morphological grounds. These are most parsimoniously referred to *H. texana*. All other known lower molars are distinctly smaller with a single exception - PM 965 is only slightly shorter and narrower than any of the specimens here referred to *H. texana*, and it matches the latter's predicted lower molar size (Figure 8). This tooth was separated by Patterson (1956) from larger "type 1" teeth and allocated to his "type 2," along with PM 948 among others (Figure 9). Despite the arguments of Turnbull (1971), PM 965 does not share characters here associated with lower molars of *H. texana*, e.g., a relatively large metaconid, a relatively small paraconid, and an enlarged hypoconid. We agree with Patterson

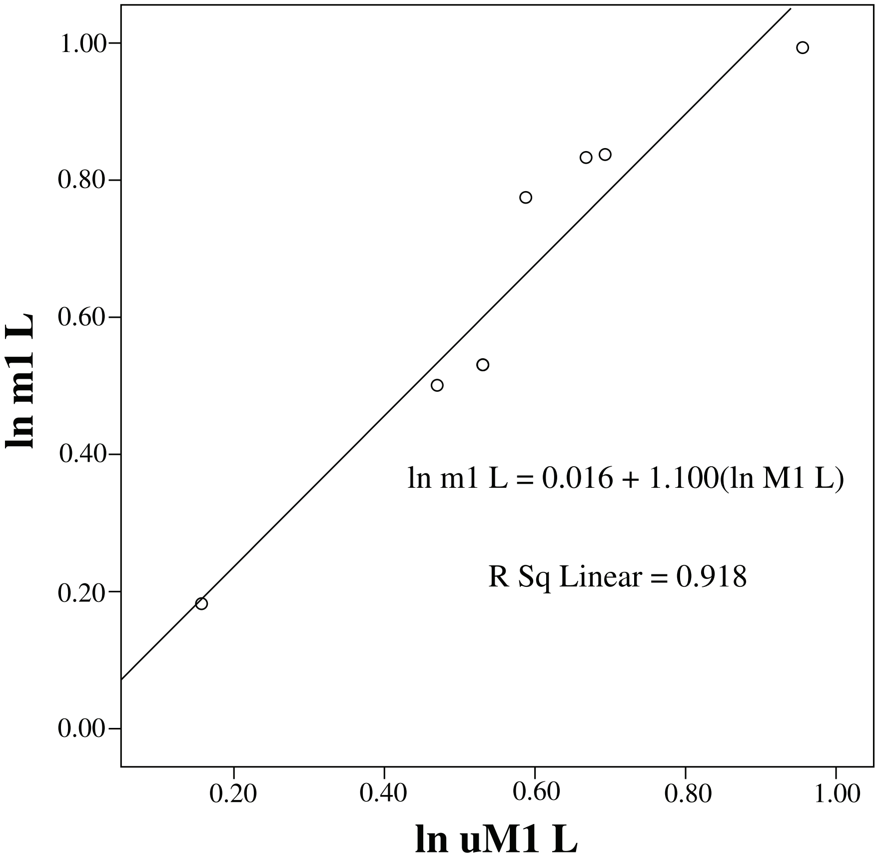

FIGURE 6. Scatter plot with regression model of ln lower m1 length versus ln upper M1 length using associated dentitions of Asian Cretaceous mammals.

(1956) that this tooth is distinct from type 1 teeth that are referred here to *H. texana*, although it is larger than any other lower tooth of type 2. Lower molars referred to *H. texana* are morphologically distinct from the molar (m1) of *S. eruptens*. The smaller lower molar length predicted for *H. texana* by the model may indicate a different upper/lower molar size relationship in this taxon, or that the holotype is a small individual.

The last tooth (= m1) preserved in *S. eruptens* is compatible with the size of lower tooth predicted from the type upper molar of *P. pattersoni*. Furthermore, the m1 of *S. eruptens* matches one type 2 tooth (PM 948; Figures 5, 9) nearly exactly in size. However, the m1 of *S. eruptens* shows weaker development of an anterolingual accessory cusp on the base of the paraconid, a character originally associated with type 2 teeth (PM 948 and 965; Patterson 1956). Development of this “antero-internal” cuspule (Patterson, 1956) or “mesial” cuspule (Kermack et al. 1965) may be lacking on first lower molars (Turnbull, 1971), or may be of taxonomic significance. Its presence in *Aegialodon* (Kermack et al. 1965) suggests that the cuspule is a primitive character state. The protoconid of m1 in *S. eruptens* is broken, and it is difficult to assess its size relative to the metaconid (type 2 teeth were, in part, differentiated from those of type 1 by a relatively smaller protoconid). Talonid cusp size and arrangement differ between the teeth assigned here to *H. texana* and all the smaller Trinity Group tribosphenidans. Wear on the hypoconid of *S. eruptens* m1 makes its size relative to other talonid cusps unclear, but it is evident that the hypoconid was not so enlarged nor the entoconid relatively so small as in molars referred to *H. texana*.

There is clearly a group of lower molars from the Trinity Group (Figure 5) that are smaller than the m1 of *S. eruptens* and other teeth of similar morphotype (e.g., PM 948; Figure 9). Small lower molars that are referred to *Trinititherium, Kermackia,* and *Comanchea* differ morphologically from the dp4 of *S. eruptens*, which fits in their size class. Those lowers referred to *Comanchea hilli* trend along a somewhat narrower width to length relationship than the others (Figure 5).

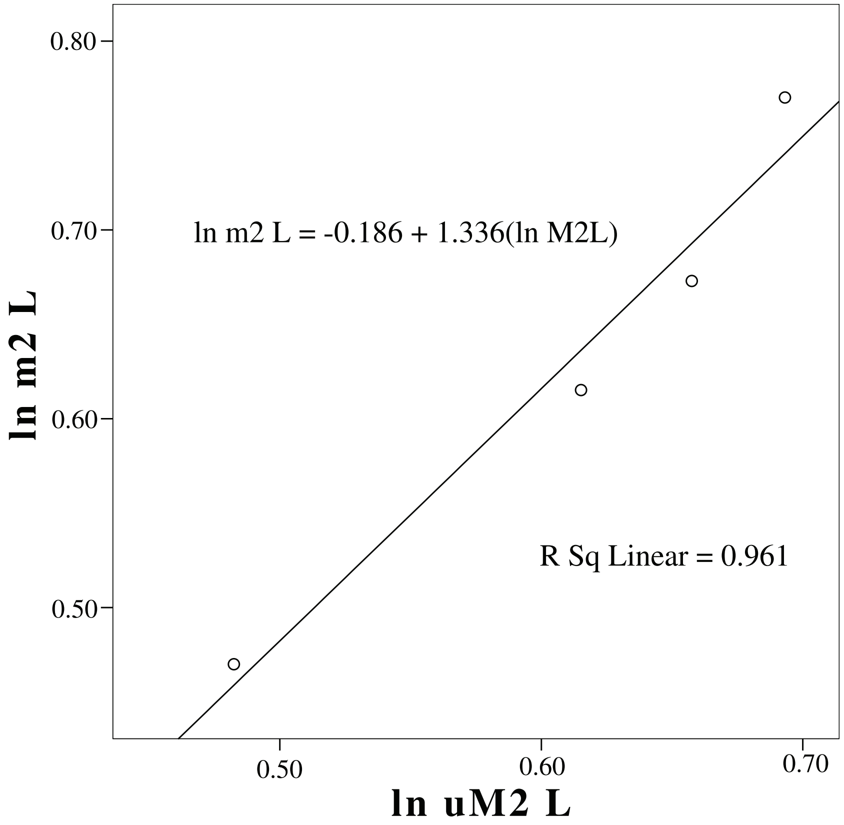

FIGURE 7. Scatter plot with regression model of ln lower m2 length versus ln upper M2 length using associated dentitions of Asian Cretaceous mammals.

Deciduous Teeth. Recognition of a deciduous tooth in *S. eruptens* affords an insight not previously available; the diagnosable morphology of a molariform deciduous premolar in Trinity Group tribosphenidan mammals. Important characters, in addition to small size and narrowness, include the relatively low, anteroposteriorly elongate trigonid with a small paraconid rotated to the midline of the tooth. These characters were noted in other deciduous teeth of Cretaceous mammals (Butler 1977). Several teeth from the Trinity Group fit this description including PM 922 (Figure 10; Patterson's 1956, "type 3") and *Kermackia texana,* and invite further examination of the status of these specimens to identify them as permanent or replacement teeth. More than one taxon of smaller therians exist within the Trinity Group, but how many remains open to question. It is also not clear whether any "molarized" premolars from the Trinity Group (Slaughter, 1968b) represent permanent teeth.

CONCLUSIONS

Size relationships help distinguish small and large groups of lower molars in Trinity Group tribosphenidan mammals, some of which can be associated with the upper molars of the type specimens of *Pappotherium pattersoni* and *Holoclemensia texana*, respectively.

Holoclemensia texana is distinctly larger and the lower molars referred to this taxon share a coherent suite of characters including enlarged metaconid, small anteriorly tilted paraconid, and robust hypoconid. They lack the "mesial" or "antero-lingual" cuspule beneath the paraconid.

A single lower molar (PM 965) is nearly the size of the smallest *H. texana* molars, but differs in the relative size of its paraconid, metaconid, and hypoconid. It also differs in possession of a distinct anterolingual cingular cusp on the paraconid (as does PM 948). PM 965 is not *H. texana* and may represent a new genus or a new species of *Pappotherium*.

The first molar of *Slaughteria eruptens* fits the size predicted for lowers of *P. pattersoni*, and is compatible in structure with the upper molars of the

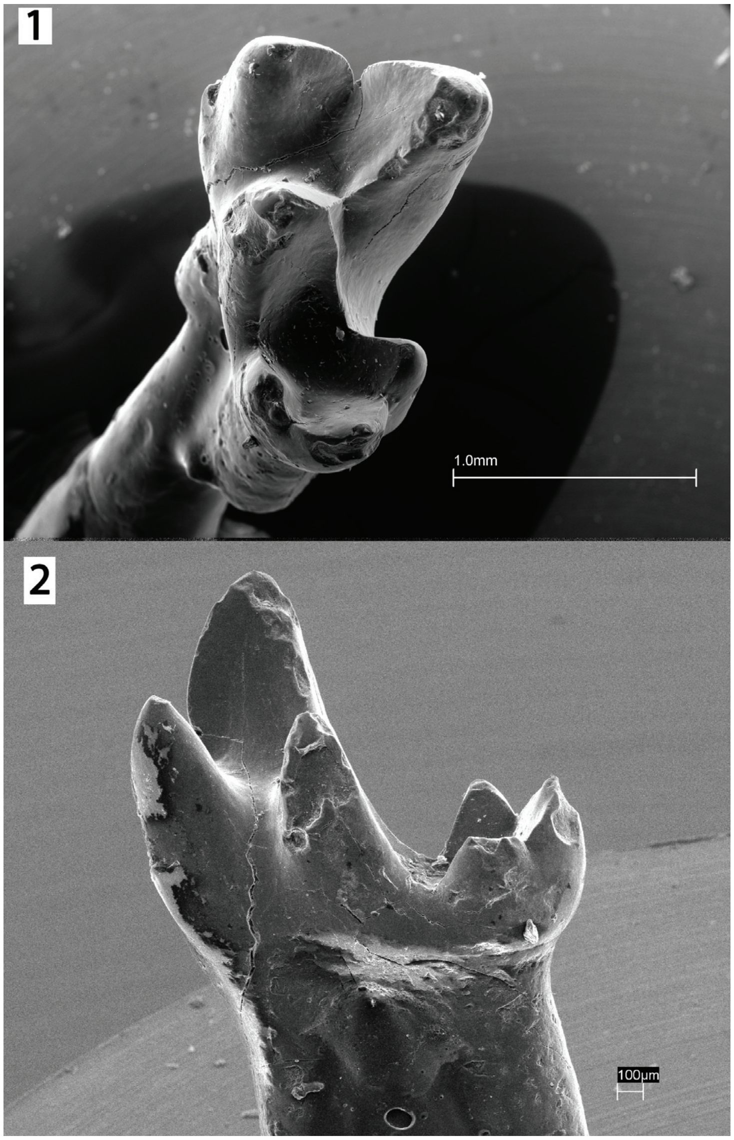

FIGURE 8. SEM images of large type 2 (Patterson, 1956) right lower molar PM 965; 8.1) occlusal view, anterior is up, 8.2) medial view.

latter. It is distinctly different from smaller, more primitive, lower teeth that are referred to other genera (*Trinititherium*, *Kermackia, Comanchea*). These more primitive teeth are less compatible with the upper molar structure of *P. pattersoni*, although they should be evaluated as possible deciduous teeth. Morphological variation associated with sequential molar position and variation within a tooth position cannot be adequately constrained in most Trinity Group mammals. Despite the potential to underestimate species diversity without cognizance of variation, size, and structure unite *S. eruptens* and *P. pattersoni*. It is most parsimonious to regard *S. eruptens* as a junior synonym of *P. pattersoni*, pending discovery of more complete specimens.

Pappotherium pattersoni Slaughter 1965

Type: SMU 61725
Slaughteria eruptens Butler 1978, syn. n.
SMU 61992

Pappotherium pattersoni thus shares with the trechnotherian clade and early eutherians the replacement of multiple deciduous precursor premolars and the alternate premolar eruption sequence of p3->p2->p4, but differs from eutherians in the lack of molarization of the lower premolars.

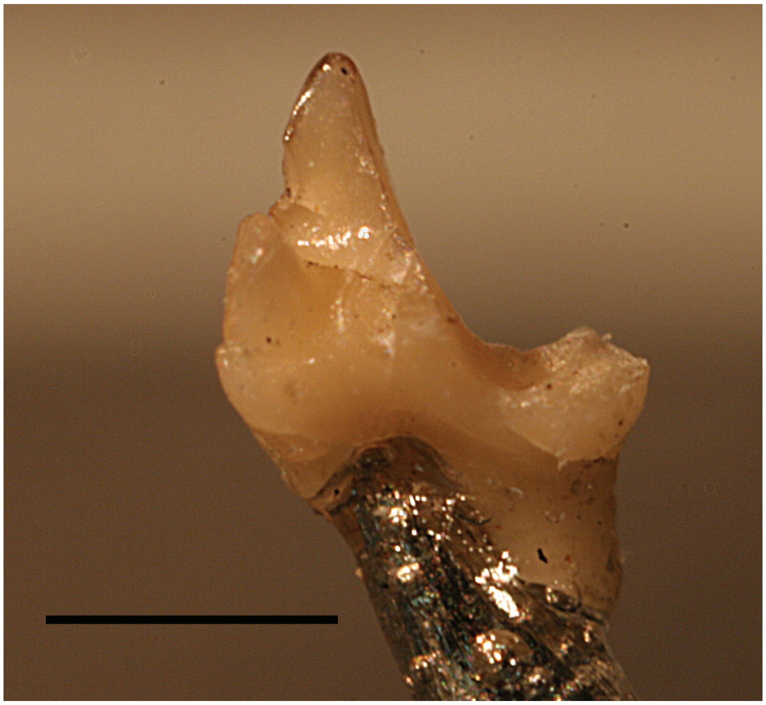

FIGURE 9. Type 2 tooth (Patterson, 1956), right lower molar, PM 948, medial view. Tooth length equals 1.42 mm, Scale bar equals 1 mm.

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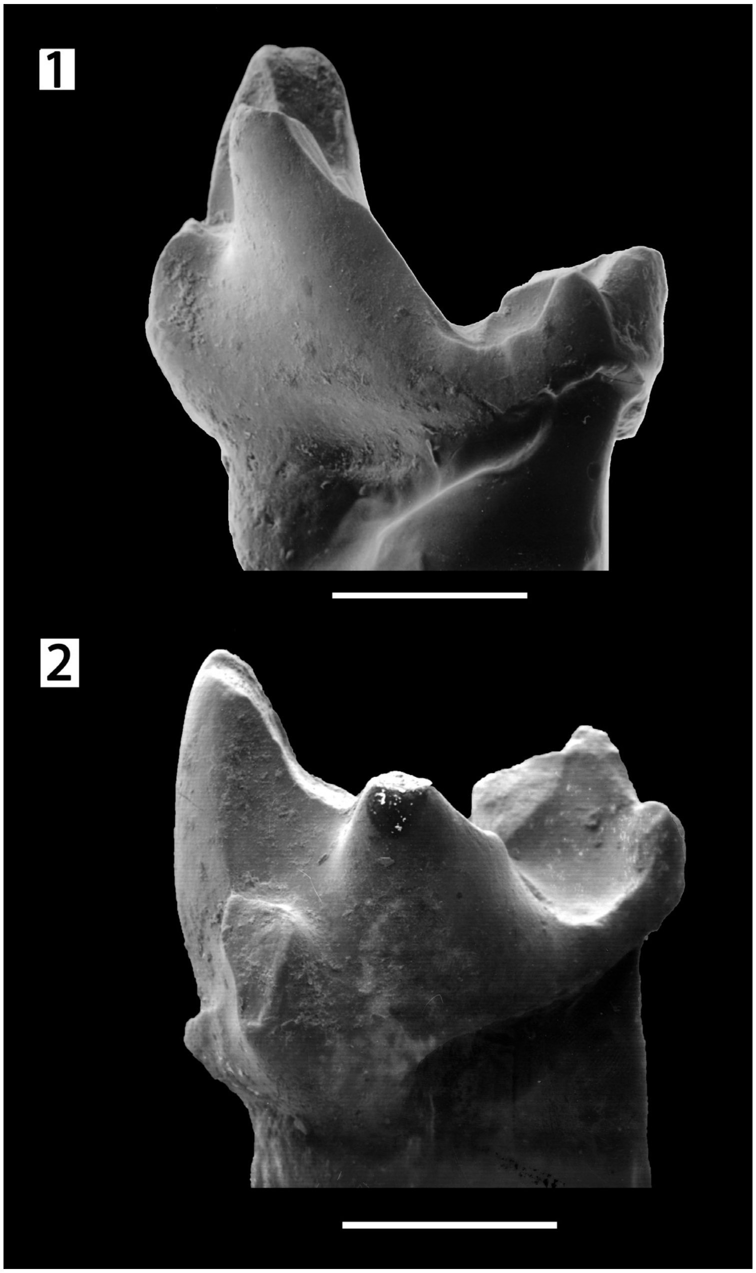

FIGURE 10. Type 3 tooth (Patterson, 1956), right lower molar, PM 922; 10.1) medial view, 10.2) oblique posteromedial view of occlusal surface. Scale bars equals 0.5 mm; SEMs courtesy of Dr. W. Turnbull.

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