Origin of the tooth-replacement pattern in therian mammals: evidence from a 110 Myr old fossil

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Living placental and marsupial mammals (therians) use distinctive tooth-replacement patterns that have not yet been traced back fully to their time of divergence in the Early Cretaceous (>100 Myr ago). *Slaughteria eruptens*, a small 110 Myr old fossil mammal from Texas, USA, is near the base of that divergence. Using ultra-high-resolution X-ray CT analysis we demonstrate that *Slaughteria* preserves an unrecognized pattern of tooth replacement with simple posterior premolars replacing molariform precursors. Differing from both placentals that have a more complex posterior adult premolar, and from marsupials, in which only one premolar is replaced, *Slaughteria* provides the first direct evidence of a tooth-replacement pattern that is plausible for the common ancestor of all therians. By our interpretation *Slaughteria* has only one adult molar in place and contains two mental foramina in the jaw, thus changing characters that are critical to reconstruction of mammalian relationships and to species discrimination and interpretations of diversity for Early Cretaceous mammals.

Keywords: mammals; tooth replacement; evolution

1. INTRODUCTION

Tooth replacement in placental mammals affects most of the anterior dentition, differing markedly from marsupials in which only third premolars are replaced. In eutherians (the clade of placentals and their extinct relatives), the posterior deciduous premolars are molariform primitively and, as corroborated by Cretaceous fossils, the dp_4 at least is replaced by a semimolariform premolar (Butler 1977; Luckett 1993). Histological analysis shows that cheek teeth of modern eutherian mammals (modified in marsupials) develop and commonly erupt in sequence anteriorly and posteriorly from a locus near the ultimate premolars (Osborn 1973; Westergaard 1980, 1983; Luckett 1993; *contra* Slaughter *et al.* 1974). Some primitive Mammalia (Wible *et al.* 1995; Rougier *et al.* 1996), specifically those lacking the characteristic cutting-crushing tribosphenic molars (i.e. mammals outside the crown clades, but especially those outside Tribosphenida (Cifelli 1993; Rougier *et al.* 1998; Flynn *et al.* 1999); or Boreosphenida (Luo *et al.* 2001)), resemble reptiles in retaining alternate tooth replacement (Edmund 1960; Martin 1997; Rougier *et al.* 1998). Other groups have unique replacement patterns (e.g. multituberculates (Greenwald 1988)) or are unlike living mammals in that they replaced molar teeth (Jenkins & Schaff 1988). Assessment of the primitive tooth-replacement pattern that was common to both groups of modern mammals is based largely on conjecture from developmental studies (Osborn 1973; Westergaard 1980, 1983; Luckett 1993). Directly related to this evolutionary dilemma are the basal members of Tribosphenida (Boreosphenida), mainly Cretaceous in age (Cifelli 1993; Rougier *et al.* 1998; Flynn *et al.* 1999; Luo *et al.* 2001).

Slaughteria eruptens (Butler 1978) (figure 1) from the

Lower Cretaceous Antlers Formation, TX, is a basal tribosphenidan (Cifelli 1993; Flynn *et al.* 1999). It has been considered to be a key outgroup taxon to Theria (the group comprising the last common ancestor of modern marsupials and placentals and all its descendants (Rougier *et al.* 1998)). Of special interest in this specimen is the preservation of one tooth in the process of eruption. Previously, no replacement teeth were believed to be present within the jaw (Slaughter 1971). Butler (1978) identified the four teeth in the holotype specimen (a single portion of the left lower jaw) as two premolars and two molars, despite previous alternative suggestions (Slaughter 1971). The systematic position of *Slaughteria* was interpreted, in part, from cusp patterns of presumed molars, but because of its incompleteness, its phylogenetic position remains unresolved (Cifelli 1993; Rougier *et al.* 1998; Flynn *et al.* 1999). Here we examine replacement pattern and tooth structure using ultra-high-resolution X-ray computer tomography (CT).

2. MATERIAL AND METHODS

The specimen (Southern Methodist University (SMU) 61992) was scanned at the High-Resolution X-ray CT Facility of the University of Texas at Austin. Fifty-four parasagittal sections were obtained with a 180 kV microfocal X-ray source and with 36 μ m intervals. Consecutive sections were rendered into digital animations to produce three-dimensional reconstructions and sections in different orientations using VOXBLAST v.2.2 (VayTek, Inc.). The four erupted teeth of *Slaughteria* are referred to as t_1 , t_2 , t_3 and t_4 , from anterior to posterior (figure 1).

3. DISCUSSION

Computer tomography images (figure 1) reveal an unrecognized, simple-crowned replacement premolar situated lingually beneath the first molariform tooth (t_3) and

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Figure 1. Stereographs of three-dimensional CT reconstruction of the holotype of *S. eruptens* (SMU 61992). Left dentary in lateral (a) and occlusal (b) views. Stereographs of three-dimensional reconstruction of teeth without bony elements in medial view (c) and t_{3r} in medial (left), occlusal (middle) and lateral (right) views (d). mf, mental foramen. Scale bar represents 2 mm.

show that a mental foramen is present on the lateral surface of the ramus between t_3 and t_4 . This foramen (not previously recognized in *Slaughteria*) is a derived character not found in more primitive mammals. For example, a posterior mental foramen is not present in *Kielantherium* (Dashzeveg & Kielan-Jaworowska 1984), a taxon considered by many to be more primitive than *Slaughteria*. All erupted teeth are double-rooted. The t_1 is partly erupted, with the posterior cusp (previously hidden) below the alveolar level, and its roots are not fully formed.

The crowns of t_1 and t_2 have a premolariform shape, with a high main cusp and a small posterior heel cusp. Unlike t_1 , t_2 is missing part of the main cusp and has some wear on the posterior border. On t_1 , the main cusp has a sharp apex and there is a smaller posterior cusp. This cusp is more labially positioned than in t_2 , the crown is narrower relatively (t_1 , $L \times W = 0.90 \text{ mm} \times 0.40 \text{ mm}$; t_2 , $L \times W = 1.00 \text{ mm} \times 0.54 \text{ mm}$) and its roots are larger. The axes of roots of t_1 are angled, whereas the axes in t_2 are parallel.

The trigonid and talonid basins on t_3 and t_4 are well developed, similar to other Cretaceous tribosphenidan mammals (figure 1b). The t_3 is smaller ($t_3 = 1.24 \text{ mm} \times 0.64 \text{ mm}$; $t_4 = 1.44 \text{ mm} \times 0.80 \text{ mm}$ in total length and talonid width, respectively). The trigonid in t_3 is more open (larger angle between the paraconid–protoconid–metaconid) than in t_4 , with a more labially placed paraconid. The anterior root of t_3 is shorter than the posterior root, possibly because of resorption, whereas they are approximately equal in t_4 .

Computer tomography images show a cone-shaped replacement tooth (t_{3r}) with a posterior cusp between the roots of t_3 (figures 1c and 2). The t_{3r} is a replacement tooth for a molariform deciduous premolar (t_3) because:

- (i) its morphology conforms to that of a simpler permanent premolar;
- (ii) it is in a crypt;
- (iii) it is positioned lingually to t_3 (Luckett 1993);
- (iv) it shows a thickening of calcified tissue (enamel and dentine) occlusally; and
- (v) the anterior root of t_3 is reduced, indicating resorption.

The root and crown base of the replacement tooth are not formed, yet a connection between the main and posterior cusp is partially completed (figure 1d). The crown of t_{3r} is transversely compressed, with a large main cusp and a small labially displaced posterior cusp (as in the erupting t_1).

There is no wear on t_1 and little on t_2 , but both molariform teeth are worn and t_3 clearly is more worn than t_4 . Heavy wear occurs on the all trigonid cusps of t_3 , especially the protoconid and metaconid, as well as on the hypoconid, entoconid area and cristid obliqua area of the talonid. Evaluations of the relative height of talonid cusps of t_3 (Rougier *et al.* 1998) are obscured because the entire area of the entoconid is obliterated and dentine is exposed through wear on the hypoconid. Wear is shown on t_4 , especially on the paraconid and hypoconid, but the metaconid and entoconid are little worn (protoconid broken off). The t_3 was in use significantly before any other erupted tooth.

Crown pattern and surface wear show that t_2 , and the erupting t_1 , are part of the permanent premolar dentition. This assignment is further supported by the lack of a crypt or a replacement tooth beneath t_2 in the CT images and the fact that t_2 is larger than t_1 , a presumed replacement tooth. The total premolar count of *Slaughteria* is unclear, but there is no evidence that any of the Texas Early Cretaceous therians had less than four (Jacobs *et al.* 1989). Further, interpretation of a metatherian dental pattern (of three premolars with replacement of only the last) for *Slaughteria* cannot be supported because the erupting t_1 is a relatively large complex tooth (unlike p_1 of metatherians), and no Texas Early Cretaceous mammal, including *Slaughteria*, possesses any synapomorphies of the Metatheria (Jacobs *et al.* 1989). Arguments about the primitive premolar count for therians notwithstanding (see Butler & Clemens 2001), we follow developmental studies and evidence from therian sister taxa in interpreting t_3 as the ultimate deciduous premolar (dp_4 ; Luckett 1993; Martin 1997). This interpretation depends upon t_4 being the first lower molar (m_1) and not a deciduous tooth itself. CT images below t_4 show only a cavity between its roots and indistinct fragments due to crushing. No replacement tooth is visible. The position of the posterior mental foramen in Theria is variable, but in two of the most comparable Cretaceous mammals it is under m_1 , suggesting that t_4 is a molar. These are *Montanalestes*, an early eutherian-like mammal (Cifelli 1999) and *Kokopellia*, an early metatherian-like mammal (Cifelli & de Muizon 1997). The angle formed by the trigonid cusps of t_4 is significantly more acute with a more lingually placed paraconid versus t_3 , which are typical differences between permanent and deciduous teeth (Butler 1977). Wear patterns demonstrate that t_3 erupted before t_4 , which is expected if they are dp_4 – m_1 . Assuming *Slaughteria* possessed four pre-

Figure 2. Three-dimensional CT reconstructions of *S. eruptens*. Horizontal cross-sections (a–d), showing a replacement tooth (t_{3r}) beneath t_3 and with a transverse cross-section, showing the medial position of the replacement tooth (t_{3r}) with respect to the erupted tooth (t_3) (e). Scale bar represents 2 mm.

molars (Luckett 1993; Martin 1997), if t_4 were interpreted as the ultimate deciduous premolar it would require that the erupting t_1 be dp_1 , a tooth that erupts before, not after,

other permanent premolars (e.g. t_2 in *Slaughteria*) in extant mammals (Slaughter *et al.* 1974).

Based upon the above assertions, the erupted teeth of *Slaughteria* are p_2 – p_3 – dp_4 – m_1 and the eruption sequence of known teeth is judged to be: (dp_3 ?)– dp_4 – m_1 / p_3 – p_2 – p_4 (following the convention of Slaughter *et al.* (1974), ‘/’ separates teeth with an equivocal eruption order). In contrast to most modern mammals, eruption of dp_3 before dp_4 in *Slaughteria* was possible, but not confirmed, because of the appearance of p_3 before p_4 . In either case, retention of a fully molarized dp_4 as the last functional deciduous cheek tooth is shared with many modern eutherians (Slaughter *et al.* 1974) and with the Late Cretaceous eutherians *Asioryctes* and *Kennalestes* from Mongolia (Luckett 1993). One possible anomaly of *Slaughteria* relative to extant mammals is that p_3 is not typically the first replacement premolar to appear (Slaughter *et al.* 1974). Modern mammals exhibit significant variability in eruption patterns and eruption sequences do not always correspond to developmental sequence (Slaughter *et al.* 1974; Luckett 1993). However, the fact that t_2 (= p_3) is the first functional replacement premolar might support the proposal of Luckett (1993) that dp_3 was the first tooth to differentiate during development in ancestral therian mammals. *Slaughteria* also shares this eruption sequence (p_3 – p_2 – p_4) with a Jurassic dryolestid (a sister group of therians (Martin 1997)) and with a Late Cretaceous eutherian from Asia (McKenna *et al.* 2000). This premolar eruption pattern may be primitive for mammals that include clades outside of Theria (i.e. Cladotheria (Luo *et al.* 2001)).

Phylogenetic reconstructions and diagnoses that have employed *Slaughteria* (e.g. Fox 1980; Rougier *et al.* 1998; Cifelli 1999; Flynn *et al.* 1999) include the following characters that may be incorrectly scored: the presence of a second mental foramen in the dentary, relative size of first two molariform teeth, morphology of ‘ m_1 ’ (= dp_4 ; trigonid openness, relative size of trigonid cusps, size of talonid versus trigonid, size and position of talonid cusps) and shape of anterior cingulid cusps. For example, *Slaughteria* would advance to a more derived position in the analysis of mammalian relationships presented by Rougier *et al.* (1998) based on the presence of a second mental foramen. Reinterpretation also invites consideration of the diagnoses of other Early Cretaceous therians from Texas. Figure 3 shows that the t_4 of *Slaughteria* (= m_1) is in the size range of lower molar teeth ascribed to *Pappotherium* (*contra* Butler 1978), an Early Cretaceous mammal described originally from upper teeth (Slaughter 1965). Other criteria used to distinguish these taxa (relative size of paraconid versus metaconid and possession of a posterior ridge on the metaconid (Butler 1978) are, at best, open to interpretation. It is possible that *Slaughteria* is a juvenile of *Pappotherium*. Other tribosphenic mammal teeth from the Texas Early Cretaceous overlap t_3 (dp_4) of *Slaughteria* in size (*Trinititherium*; Butler 1978) and one of these also exhibits tooth characters of its lower ‘molar’ that are consistent with deciduous premolars (*Kermackia*; Slaughter 1971). In samples of isolated teeth, factors of preservation and recovery being equal, molariform deciduous teeth should be recovered in the ratio to true molars in which they exist in each species, a prediction that could

Figure 3. Size comparison of lower molar teeth of Early Cretaceous tribosphenic mammals from the Antlers Formation and correlative Trinity Group units, TX. Abbreviations: C1, *Comanchea* (SMU 73070, right m_3); C2, *Comanchea* (SMU 73206, left m_3); H1, *Holoclemensia* (SMU 61727, left m_3); H2, *Holoclemensia* (SMU 62131, left m_3); H3, *Holoclemensia* (SMU 61726, left m_4); K, *Kermackia* (SMU 62398, right m_3); P1, *Pappotherium* (PM 948, m_3 or m_4); P2, *Pappotherium* (PM 965, m_2); S1, *Slaughteria* (SMU 61992, left t_3); S2, *Slaughteria* (SMU 61992, left t_4); T, *Trinititherium* (SMU 61728, left m_3). PM, Field Museum of Natural History, Chicago. Measurements of PM 948 and PM 965 are from Turnbull (1971).

bias taxonomic diversity and morphological disparity estimates if deciduous teeth are not recognized as such.

Tooth-eruption patterns in *Slaughteria* corroborate interpretations based on morphology of its primitive status relative to modern clades of therian mammals. We suggest that the pattern of dental replacement present in *Slaughteria* is the primitive condition for Theria. More closely resembling the condition in eutherian mammals, *Slaughteria* also demonstrates that the metatherian pattern of tooth replacement (known since the Late Cretaceous (Cifelli *et al.* 1996; Cifelli & de Muizon 1998)) is more derived among modern mammals. *Slaughteria* is more primitive than either group because it does not share with eutherians the derived condition of semimolarized permanent posterior premolars (Butler 1977; Luckett 1993). Simple posterior premolars are the plesiomorphic condition inherited from more primitive mammals (demonstrated in Dryolestidae (Martin 1997)). *Slaughteria* is the closest sister taxon to the evolutionary divergence of modern mammal clades for which the tooth-replacement pattern is known. It demonstrates that a sequence of simple posterior premolars replacing molariform antecedents was present 110 Myr ago (Jacobs *et al.* 1991; Jacobs & Winkler 1998) and provides a plausible model of tooth replacement from which both clades of modern therian mammals could be derived.

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