Modern mammal origins: Evolutionary grades in the Early Cretaceous of North America

(vertebrate paleontology/dental function/marsupial)

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ABSTRACT Major groups of modern mammals have their origins in the Mesozoic Era, yet the mammalian fossil record is generally poor for that time interval. Fundamental morphological changes that led to modern mammals are often represented by small samples of isolated teeth. Fortunately, functional wear facets on teeth allow prediction of the morphology of occluding teeth that may be unrepresented by fossils. A major step in mammalian evolution occurred in the Early Cretaceous with the evolution of tribosphenic molars, which characterize marsupials and placentals, the two most abundant and diverse extant groups of mammals. A tooth from the Early Cretaceous (110 million years before present) of Texas tests previous predictions (based on lower molars) of the morphology of upper molars in early tribosphenic dentitions. The lingual cusp (protocone) is primitively without shear facets, as expected, but the cheek side of the tooth is derived (advanced) in having distinctive cusps along the margin. The tooth, although distressingly inadequate to define many features of the organism, demonstrates unexpected morphological diversity at a strategic stage of mammalian evolution and falsifies previous claims of the earliest occurrence of true marsupials.

All living mammals, except the egg-laying monotremes, are either marsupials (metatherians) or placentals (eutherians). The two have distinguishing dental features recognized in the fossil record that show them to be closely related, diverging from a common ancestor in the Cretaceous. The fundamental dental feature that unites marsupials and placentals is the addition of an inner (lingual) cusp (protocone) to a primitive triangular upper tooth. The protocone occludes into the heel (talonid) of a lower molar forming the "tribosphenic" condition. Both shearing and crushing functions are accommodated by tribosphenic molars. Evolutionary emphasis of one function over the other has contributed to ecological diversity in modern mammals and the extreme morphological diversity of their teeth.

Marsupials are readily distinguished in the Late Cretaceous by morphological features of the molars and the mode of premolar replacement. Prior to the Late Cretaceous, recognition of the modern groups of mammals is equivocal, although both marsupials and placentals have been reported. The North American Early Cretaceous mammal fauna is known primarily from Texas. This study evaluates that fauna to determine its role in the evolution of modern mammals. We proceed from a consideration of the predicted morphology of upper teeth in early tribosphenic mammals, to a description of an upper tooth from Texas, then to a reevaluation of "marsupial" characters and their value in the Early Cretaceous, and finally provide evidence of the premolar dental formula in the Texas Early Cretaceous.

Wear Facets

Fossil evidence showing structural transformation to the tribosphenic grade is based primarily on a single heavily worn lower molar, named *Aegialodon dawsoni*, from the Early Cretaceous of England (1). An additional lower tooth and a jaw fragment with four teeth from Mongolia, *Kielantherium gobiensis*, is similar to *Aegialodon* (2–4). These resemble two lower teeth from Texas (*Kermackia* and *Trinititherium*). Thus, until now, a fundamental stage in the evolution of the tribosphenic molar was represented by a total of four lower teeth and one jaw fragment, but no upper teeth, from three continents.

Crompton (5) reconstructed a hypothetical upper molar of *Aegialodon* as having a wear facet on the anterior face of the protocone because of a matching facet seen on the medial surface of the cristid obliqua in the holotype lower molar. The upper tooth, as reconstructed, is relatively long with strong parastyle and stylocone, and without a metaconule.

An upper tooth from the Early Cretaceous of Texas (110 million years before present) is similar to Crompton's reconstruction in lacking a shearing facet on the posterior face of the protocone but is more primitive in lacking a facet on the anterior surface as well. The styler region, however, is more derived than predicted for *Aegialodon*.

Wear on the Texas tooth (Figs. 1 and 2) occurs as abrasion on the apices of cusps. Facets 1a and 1b (5), along the anterior of the tooth, demonstrate the homology and position of the stylocone. Facet 2a is defined along the posterior margin. Embrasure facets 3a and 4a (but not 3b and 4b) are present, resulting from hypoconid shear between paracone and metacone. The protocone is corroded but is rounded and shows no shear facets 5 or 6. It functioned primarily as a crushing pestle against the heel of the lower tooth.

Corresponding lower molars are predicted to have a large hypoconid, small hypoconulid, and no entoconid. The cristid obliqua would extend from hypoconid to metaconid, as in *Trinititherium* and *Kermackia*. The latter has a distinct entoconid, and the former has well-developed facet 5. The long postmetacrista of the Texas specimen suggests the trigonid is a more open triangle than in *Trinititherium*. *Trinititherium* and *Kermackia* are from Butler Farm [Southern Methodist University (SMU) locality 20, Wise County, Texas: Albian], 130 km north of where the upper molar was discovered.

Systematics of the Texas Specimen

Order Aegialodontia (7)

Family *Incertae sedis*

Comanchea hilli, new genus and species

Etymology. The generic name refers to the Comanche Series of Texas, from which the holotype was collected; the species is after Robert T. Hill, who studied and named the Comanche Series.

FIG. 1. *Comanchea hilli*, left upper molariform tooth, occlusal view, anterior to left, is shown with a length of 1.26 mm and a width of 1.30 mm. Note large stylar cusps C and D (also see Fig. 2) but reduced stylocone (cusp B), parastyle (cusp A), and metastyle (cusp E). Postprotocone crista is damaged (diagonal lines). Part of parastylar region may be missing. (Bar is 0.5 mm.)

Type and Only Specimen. Southern Methodist University 71848, a left upper molariform tooth (Fig. 1).

Locality and Horizon. SMU locality 157, Erath County, Texas: Paluxy Formation, Albian.

Diagnosis. The suite of characters listed in Table 1 and compared to *Holoclemensia* and *Pappotherium* (8, 9). It is clearly derived over most Jurassic and Early Cretaceous therians in having a protocone but is more primitive than *Holoclemensia* and *Pappotherium* in lacking anterior and posterior wear facets on the cusp. Its primitive protocone is not unexpected; however, the enlarged stylar cusps C and D and reduced parastyle, stylocone, and metastyle are a derived set of features on the buccal side of the tooth not expected in the Texas Cretaceous. In comparison with other relevant taxa (10), *Comanchea* has a straight buccal margin, a derived feature that also occurs in *Falepetrus* and *Picopsis*. It is more similar to *Deltatheridium*, *Potamotelses*, and *Picopsis* than to *Pappotherium* and *Holoclemensia* in small size of the stylocone, parastyle, and metastyle. Lack of a shearing protocone clearly separates *Comanchea* from Cretaceous tribosphenic mammals known from upper molars. Derived characters 9 and 10 (Table 1) preclude *Comanchea* from the morphological ancestry of later tribotheres including marsupials.

The Earliest Marsupials

The most controversial report of an early marsupial is *Holoclemensia* from the Early Cretaceous of Texas (8, 9). The features used to recognize *Holoclemensia* as a marsupial are those that supposedly distinguish isolated molars of unquestioned Late Cretaceous marsupials: presence of a central buccal cusp (stylar cusp C) on upper molars and close approximation of the lingual and medial talonid cusps (twinning of the entoconid–hypoconulid). Additional support for marsupial allocation relies on the qualitative assessment of a relatively large metacone.

The buccal shelf of tribosphenic mammals is primitively broad with variable development of cusps and little functional occlusal relationship with lower teeth. Fortunately, stylar

FIG. 2. Wear facets (5, 6) of *Comanchea hilli*. (A) Occlusal view (stylar cusps labeled A–E). (B) Anterior view. (C) Posterior view. Light stipple, abrasion on cusp apices; dark stipple, wear facets 1a and 1b (merged together in the specimen); dashed-line hatched area, wear facet 2a; hatched area, wear facets 3 (anterior) and 4 (posterior). (Bar is 0.5 mm.)

cusp B (stylocone) occludes with the posterior margin of the trigonid forming wear facet 1a (5). Therefore, identification of the wear facet facilitates identification of cusp B. In *Comanchea* wear facet 1a (Fig. 2) extends to a low swelling, representing cusp B. The succeeding stylar cusp is associated with the paracone and is, therefore, cusp C. Further, no shearing surface connects cusp C and the paracone in *Comanchea*. *Comanchea* is certainly not a marsupial because of the morphology of the protocone, the height of the paracone as compared to the metacone, and the weak paraconule. However, it is similar to marsupials in having a broad stylar shelf with a C cusp. The C cusp is independently derived in *Comanchea* and marsupials because a C cusp is primitively absent in marsupials (10–12).

The metacone of *Comanchea* is as well developed as in *Holoclemensia*, and neither is like that of true marsupials. *Pappotherium* is smaller than *Holoclemensia* and the relative size of the metacone has never been quantitatively compared between the two, although that in *Holoclemensia* is purported to be larger (7, 13). In all three cases, the metacone bears a strong wear facet from occlusion with a large hypoconid, a character that is probably primitive for all mammals

Table 1. Comparison of *Comanchea*, *Holoclemensia*, and *Pappotherium*

Character	<i>Comanchea</i>	<i>Holoclemensia</i>	<i>Pappotherium</i>
1. Broad stylar shelf	+	+	+
2. Low protocone	+	+	+
3. Paracone larger than metacone	+	+	+
4. Metaconule present	?	+	+
5. Large stylar cusp C	+	+	—
6. Wide metastylar area	+	—	+
7. Small paraconule	+	+	+
8. Reduced parastyle	?	—	—
9. Reduced metastyle	+	—	—
10. Reduced stylocone	+	—	—
11. Large stylar cusp D	+	—	—
12. Straight buccal margin	+	—	—
13. Broad trigon basin	+	—	—
14. Anteroposterior elongate protocone apex	+	—	—
15. Convex anterior border	+	—	—
16. Lingual angle	52°	NA	43°

Characters (8?) 9–15 are apomorphies for *Comanchea*. NA, not available; +, character present; —, character not present; ?, character uncertain.

that possess a true metacone. As a metacone developed, so did a prominent hypoconid. Therefore, the talonid in tribosphenic mammals is primitively asymmetrical with the hypoconid the dominant cusp.

Fig. 3 demonstrates the asymmetry of talonid cusps in Texas Early Cretaceous mammals. Specimens referred to *Holoclemensia* are comparable in talonid asymmetry to Asian *Deltatheridium*. No specimens referred to *Holoclemensia* have entoconid–hypoconulid as close together as in the undisputed Late Cretaceous marsupial *Alphadon*. Some Texas specimens that have not been considered marsupial have the cusps relatively as close as *Holoclemensia*. In *Slaughteria*, cusps are closer together, but tooth replacement is unlike metatherians (13). *Holoclemensia* is not a marsupial based on the degree of twinning in referred lower molars. There is no clear evidence of marsupials before early in the Late Cretaceous (15).

Premolar Number

The primitive eutherian dental formula probably included five premolars (4, 16). One edentulous jaw fragment (Fig. 4) is the only specimen sufficiently complete to indicate the number of premolars in an Early Cretaceous therian from Texas. It preserves 12 alveoli. The first is for a canine; the last is distinctly wider than those preceding it, indicating a morphological break in the tooth row such as would occur between premolars and molars. Five double-rooted premolars were present, demonstrating that the species represented by this specimen had a primitive number of premolars. The jaw is similar in size and morphology to a previously described fragment referred tentatively to *Holoclemensia* or *Pappotherium* (7, 17).

Conclusions

The Texas Early Cretaceous fauna contains six named genera of tribosphenic mammals, all that are known from North America. They present clear evidence of morphological diversification by 110 million years before present, soon after the origin of the tribosphenic molar. The Texas Cretaceous fauna includes two distinct grades of tribosphenic mammals coexisting simultaneously: aegialodonts, represented by *Co-*

FIG. 3. Asymmetry of talonid in Cretaceous mammals from Texas. Natural logarithms (ln) of the distance (mm) between hypoconid–hypoconulid versus entoconid–hypoconulid. (Inset) Occlusal surface of a *Holoclemensia* lower molar. Isometry is the 45° line. *Alphadon* and *Deltatheridium* are included for comparison. Samples: A, *Slaughteria* (SMU 61992, SMU locality 20), measurements from two molariform teeth in the holotype; B, *Kermackia* (SMU 62398, SMU locality 20); C, *Trinititherium* (SMU 61728, SMU locality 20), estimated; D, *Holoclemensia* (SMU 62131; ref. 13); E, *Holoclemensia* (SMU 61726; ref. 6); F, *Holoclemensia* (SMU 61727; ref. 6); G, *Deltatheridium* second molariform (cast of MgM-1/91, Khormeen Tsav II, Mongolia; ref. 14); H, unallocated (SMU 62722, SMU locality 20); I, *Alphadon* M/2 (SMU 62733, Bug Creek Anthills, SMU locality 19); J, unallocated (SMU 62721, Greenwood Canyon, Montague County, Texas, SMU locality 21, Albian). Molar position along the tooth row has not been considered a significant variable with respect to twinning (7, 13).

manchea, *Kermackia*, and *Trinititherium*; and pappotherids (*sensu* 6), represented by *Pappotherium*, *Holoclemensia*, and *Slaughteria*. The pappotherids were derived in developing shear on the protocone and, thereby, took a separate evolutionary direction from derived aegialodonts exemplified by *Comanchea*. At least one therian of the Texas Cretaceous had five premolars, the primitive number for eutherians, more than in modern grade marsupials (three) or placentals (four).

The morphological diversity of Cretaceous tribosphenic mammals demonstrates that a twofold division into marsupials and placentals is simplistic and that other groups of

FIG. 4. SMU 62006, right dentary from SMU locality 138, Twin Mountains Formation, Hood County, Texas: Aptian, is shown. Alveolar width increases markedly between the last two alveoli.

comparable grade, now extinct, evolved in an initial radiation (10). Unfortunately, the fragmentary nature of Early Cretaceous samples and lack of synapomorphies with later mammals complicates cladistic analysis. Nevertheless, no known Early Cretaceous genus shows any special resemblance to marsupials.

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