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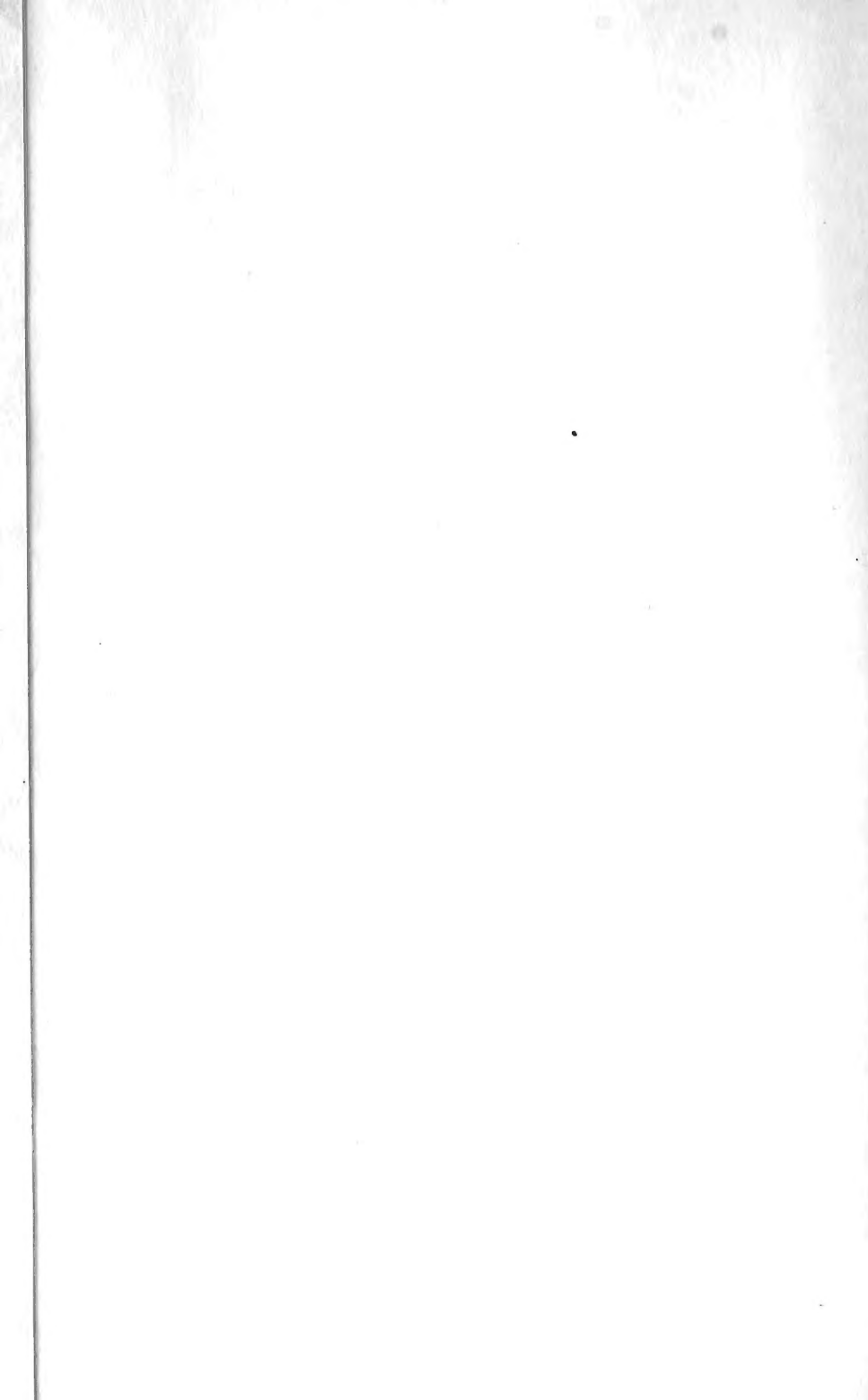
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Postilla

A THERIAN FROM THE LOWER CRETACEOUS (ALBIAN) OF TEXAS

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ABSTRACT

Mammals of metatherian-eutherian grade are represented in a collection recovered from a Wise County, Texas, locality of Lower Cretaceous (Albian) age. The form, or forms, are distinctly primitive as evidenced by the very small low protocones, large stylar cusps, and wide stylar shelf. The presence of well-developed and separate metacones at such an early date would seem to place *Deltatheridium* well off the evolutionary line of all later mammals except possibly zalambdodonts. The premolars contain both anterior and posterior cingulum cusps in addition to the protoconid and posterior accessory cusp. The lower molars have trigonids that are extremely compressed anteroposteriorly, and all but one have three talonid cusps. One lower molar apparently has but a single talonid cusp, the hypoconulid, and may have inferences as to the evolution of the therian talonid.

A new family, Pappotheriidae, is proposed which in known parts has all of the prerequisites necessary to be in or near the ancestry of all later therians.

INTRODUCTION

The oldest mammals of metatherian-eutherian grade reported to date are several isolated teeth, mostly incomplete, described by

Patterson (1956) from the Lower Cretaceous (Albian) strata at the Greenwood Canyon locality near Forestburg, Montague County, Texas. He discussed the significance of this material, but considering the condition of the specimens, did not propose formal names. Early in 1964 the Shuler Museum of Paleontology of Southern Methodist University began systematic reconnaissance of rocks of nearly the same age in northern Wise County, with the aid of National Science Foundation Grant no. GB 2092. Approximately fifty tons of material from the fossiliferous sites were processed for recovery of vertebrate microfossils. Only one site, the Butler Farm, produced any mammalian remains; from some thirty tons of these sediments eleven mammalian specimens were recovered. Of these, three were isolated teeth of multituberculates and the others were of a therian mammal similar to the forms discussed by Patterson. Although our specimens are few, they are better preserved for the most part than the material previously recovered, and they add considerably to our knowledge of these early therians.

AGE AND OCCURRENCE

In Texas the southern portion of the Trinity Group (Comanchean Series) is divided into three formations which are in ascending order: the Basement sands (Travis Peak equivalent) at the base of which usually occurs a conglomerate of quartz pebbles; the Glen Rose Formation, which is composed of limestone and clay of marine origin; and the Paluxy Formation, which is composed of compact whitish clayey sand with a few clay and sand lenses. The Glen Rose pinches out near the middle of Wise County; north and west of that point it is impossible to differentiate between the Basement and Paluxy sands, and the entire section is referred to simply as the Trinity. The closest outcrop of the Glen Rose to the Butler Farm locality is slightly more than one mile to the west and some 150 feet lower topographically. As the dip of the Cretaceous rocks in the area is about 40 feet per mile to the southeast, the Butler Farm local fauna is doubtless of Paluxian age even though it cannot be referred to the Paluxy Formation by definition.

The locality is in a shallow gully 250 yards northeast of U.S. Highway 81, three miles northwest of Decatur, Texas, Wise County, on the farm of Mr. Lee Butler.

The fossils occur in the basal few inches of a shallow channel fill. This channel was cut into a compact white sandy clay and was about 70 feet wide at its base. The fossiliferous zone fills the small irregularities at the bottom of the channel. It has a maximum thickness of four inches and is no more than a film in most places. Although the zone may be traced almost throughout the basal width of the channel, it is of quarryable thickness only at a few places. Above this zone the channel fill is made of alternating lenses of sand and clay and is capped by dense red sandstone. The total overburden at the quarry site averaged six feet.

ASSOCIATED FAUNA

By far the most numerous by-product of the washing are ganoid scales and teeth of a lepidotid. The other fishes represented include *Ceratodus,* possibly *Caturus,* and a hybodont shark. Fragments of turtles, teeth and tooth fragments of camptosaurs, carnosaurs, and crocodiles; bones of frogs, salamanders, lizards; and a few coprolites represent the tetrapods.

<center>SUBCLASS **THERIA** Parker and Haswell 1897</center>

<center>INFRACLASS and ORDER, *incertae sedis*</center>

<center>PAPPOTHERIIDAE Slaughter, n. fam.</center>

Diagnosis. Paracone and metacone well developed and separate; base of paracone extends to the lingual half of the crown; well-developed stylocone; low protocone connected to the parastyle and base of the metacone by crests. Lower molars have a cingulum cusp on the anterior face of the anteroposteriorly compressed trigonid and three talonid cusps.

<center>*Pappotherium pattersoni* n. gen., n. sp.</center>

Etymology. Greek: *pappos,* grandfather or ancestor beyond plus *therium,* mammal. The specific dedication is made with pleasure to Dr. Bryan Patterson whose work stimulated the original exploration.

Holotype. SMP-SMU[1] no. 61725 (fig. 1). Right maxillary fragment containing the last two molars (fig. 1).

Type locality. In a shallow gully 250 yards northeast of U. S. Highway 81, three miles northwest of Decatur, Wise County, Texas, on the farm of Mr. Lee Butler.

Horizon. 100 feet below the top of the Trinity Group; probably of Paluxian age.

Diagnosis. Same as for Pappotheriidae plus the presence of a well-developed and separate parastyle, extra cusp on the crest connecting the metacone to the metastylar area, and presence of small but distinct conules.

<center>DESCRIPTION</center>

Next-to-last molar. The base of the paracone extends well onto the lingual half of the tooth.

The lingual aspect of the paracone is conical but the buccal side is less convex, giving the cusp a more or less half-cone cross-section. The metacone is separated from the paracone and has

[1] SMP-SMU Shuler Museum of Paleontology, Southern Methodist University.

a crest joining its apex to the metastylar area. About halfway
between the metacone and the metastyle, basal swelling and eleva-
tion of the crest creates an additional cusp. The paracone has
a crest running down its anterobuccal side; the crest extends
buccally from the paracone's base to join the stylocone at its
apex. The stylocone is large, about the size of the metacone.
The parastyle is almost the same size as the stylocone and sepa-
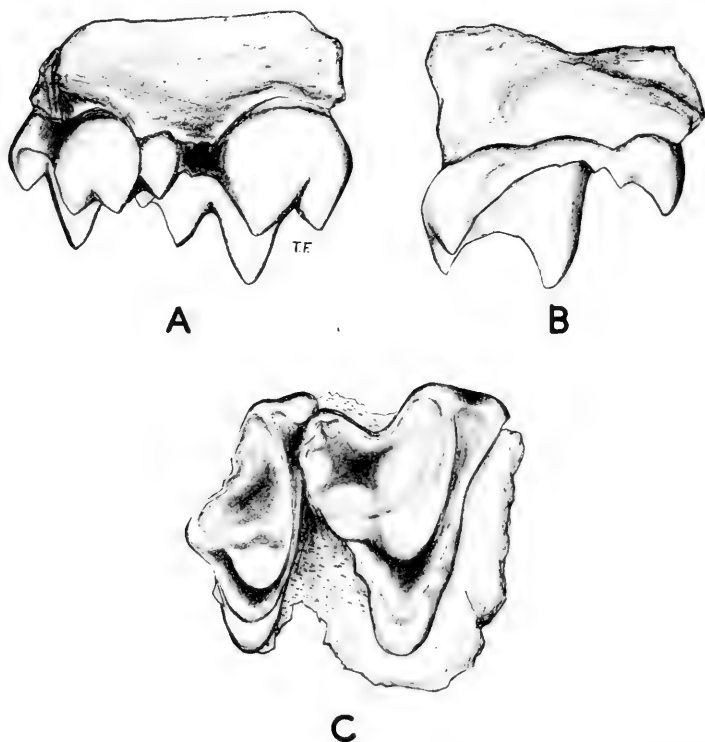
Fig. 1. *Pappotherium pattersoni*, n. gen., n. sp. Holotype: SMP-SMU
no. 71725. A. External aspect of right M.²⁻³ B. Anterior aspect of M². C.
Right M²⁻³, occlusal view. ×20.

rated from it by a distinct notch. There is a U-shaped and crenu-
late indentation in the buccal edge of the tooth between the
stylocone and the metastylar area. The metastylar area is some-
what lower than the paracone-metacone and the anterior buccal
styles. At the extreme posterobuccal point of the tooth there is

a weakly-developed blade-like cusp or style. A ledge-like cingulum runs along the anterior face of the paracone and merges with the protoconal basin. The anterior edge of this cingulum connects the apices of the protocone and parastyle. On this ridge, about halfway between the protocone and the line of the paracone, there is a small but very distinct cuspule (protoconule) and just buccal to this there is a smaller cuspule. There is a single cuspule on the posterolingual edge of the tooth in the position of a metaconule. The exact pattern of the roots cannot be ascertained without damage to the specimen, but small portions of the alveoli piercing the maxillary fragment indicate there are three roots: one between the paracone and the buccal edge, one posterior to this and just slightly more lingual, and a third apparently supporting the protocone, but the alveolus of this third root does not pierce the bone.

Last upper molar. The paracone is the largest cusp and its apex is almost at the center of the tooth. However, the lingual face of the paracone slopes less steeply, reducing the area of the protoconal basin. A smaller but distinct metacone is on about the same anteroposterior line and is separated from the paracone by a V-shaped notch. A crest connects the anterobuccal base of the paracone to the apex of the stylocone which in turn is separated from the parastyle by a notch. The stylocone and parastyle are developed about as in the penultimate molar, but the parastyle is more inclined lingually and rather hook-like. The metastylar area is reduced and·a low ridge forming the posterobuccal edge of the tooth connects the metacone to the base of the stylocone. Midway on this ridge is a tiny but visible cuspule. Like that of the penultimate molar, the protocone is connected to the parastyle by a low ledge-like cingulum. A single conule is present on the protocone-metacone crest, and none is visible on the protocone-parastyle crest.

Associated therian material. There are several other specimens of eutherian-metatherian grade collected from the same level at the Butler Farm locality that are believed to belong to the same animal or at least to animals very closely related. As a matter of fact, all were recovered only a few feet apart and some could even represent the same individual.

Lower molars. The trigonids in all of the specimens are

anteroposteriorly compressed, being less than one half of the tooth's total length. Indeed, the trigonid of one (no. 61726) is barely more than one third of the tooth's total length. There are three types of these teeth, although one may be a molariform premolar.
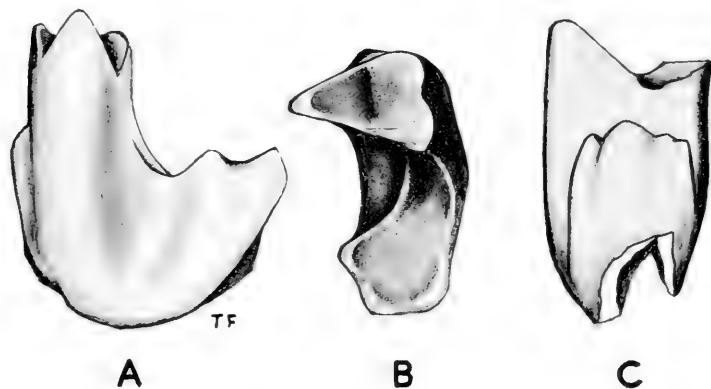

Fig. 2.   Trinity lower molar. Type 4. SMP-SMU 61726. A. Buccal view. B. Occlusal view. C. Posterior view. ×20.

Type 4[2] (no. 61726, fig. 2). The trigonid is extremely compressed anteroposteriorly and the narrow talonid curves curiously in a wide arc from the lingual side of the trigonid. The protoconid is the largest cusp and its apex is connected to the bases of the metaconid and paraconid by crests in broad V-shaped notches. The metaconid is slightly larger than the paraconid, but both are on the lingual edge of the tooth, instead of the paraconid being more central on the anterior face as in many similar teeth of later mammals. On the anterior face a cingulum originating near the base of the crown at the buccal edge projects diagonally upward; it terminates in a small cusp about one third of the way up the crown and near the transverse center. The three talonid cusps (hypoconid, hypoconulid and entoconid) are of equal size; the hypoconulid is equidistant from the others. There is a ridge connecting the entoconid to the base of the trigonid on the lingual side and another (the *crista obliqua*) connecting the hypoconid to the posterior face of the trigonid just lingual to the notch

[2] Types 1, 2, and 3 were described by Patterson (1956).

between the protoconid and the metaconid, forming a narrow, closed talonid basin.

Type 5 (no. 61727, fig. 3). The talonid of this specimen is more like Patterson's type 1, but the trigonid is more compressed anteroposteriorly, being less than one half of the tooth's total length. Although the apex of the protoconid is broken away, it obviously is the largest of the trigonid cusps. The paraconid is much smaller than the metaconid and placed in a more antero-medial position. The paraconid is worn completely to its base on a horizontal plane much like Patterson's Greenwood Canyon specimen PM 922[3]. Another tooth (no. 61735) has the posterior portion of the talonid broken away but the character of the trigonid, especially the size of the paraconid and its more antero-medial position place it with lower molar Type 5. The talonid is broader than that of Type 4 and all three talonid cusps are better developed. The entoconid and hypoconulid are of equal size but the hypoconid is a little larger and placed slightly farther from the hypoconulid. The *crista obliqua* connects the hypoconid to the trigonid in the same fashion and in the same place as in Type 4. However, the talonid basin is wider and more functional. The two roots are round and of approximately equal size.

Type 6 (no. 61728, fig. 4) is most nearly the size one might expect for lower molars of *Pappotherium*. It is quite unlike the other lower molars in detail. The differences are so great that we must conclude that it belonged to a different animal if indeed it is a molar. One alternative may be that it is a molariform pre-molar, although I am inclined to dismiss the possibility. If this is the case, however, it is contrary to the usual view that the talonid becomes molarized first. The trigonid is compressed antero-posteriorly. The protoconid is much higher relative to the meta-conid and paraconid, which are the same size and at the extreme lingual border of the tooth. The talonid is of similar size and shape as Type 4 in occlusal outline but differs in several details. There is but a single talonid cusp visible, apparently the hypoconulid. The hypoconid area is slightly worn but the *crista obliqua* is directed to that corner of the tooth. This crest does not join the base of the trigonid near the transverse center, however, as it does on the other specimens. Rather it rises to join the trigonid high on the

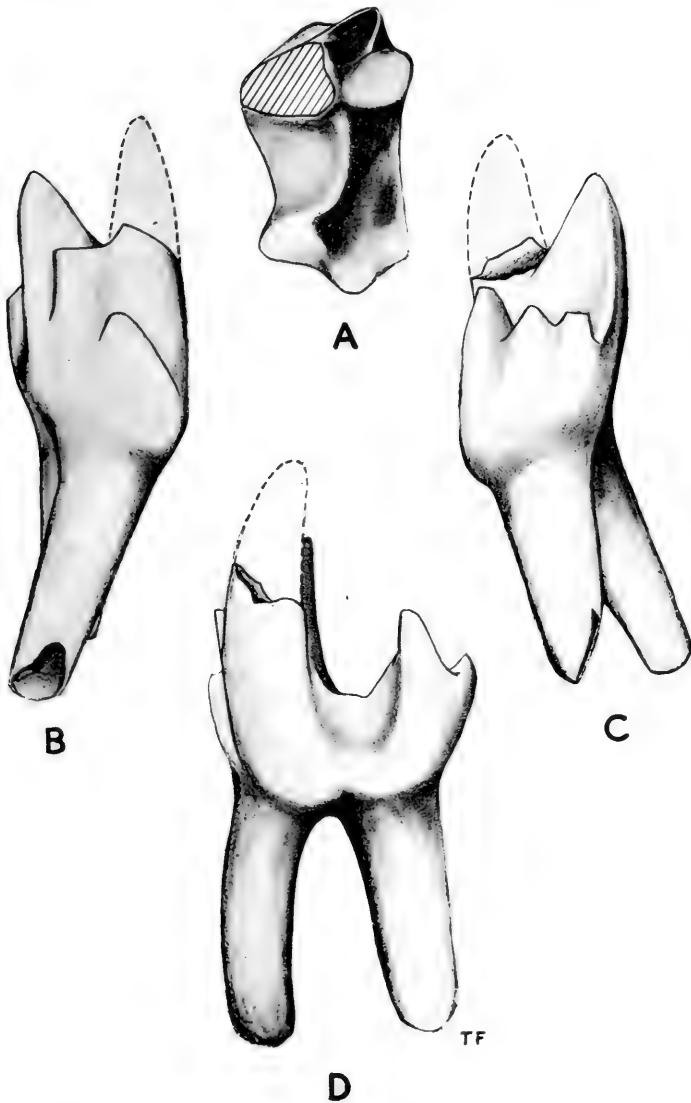[3] PM numbers are those of the Chicago Natural History Museum.

Fig. 3.   Trinity lower molar. Type 5. SMP-SMU no. 61727. A. Occlusal view. B. Anterior view. C. Posterior view. D. Buccal view. ×20.

extreme lingual edge—continuing as a ridge onto the apex of the metacone. The enamel slopes toward both sides from this crest. Although the hypoconid area is slightly worn and difficult to inter-
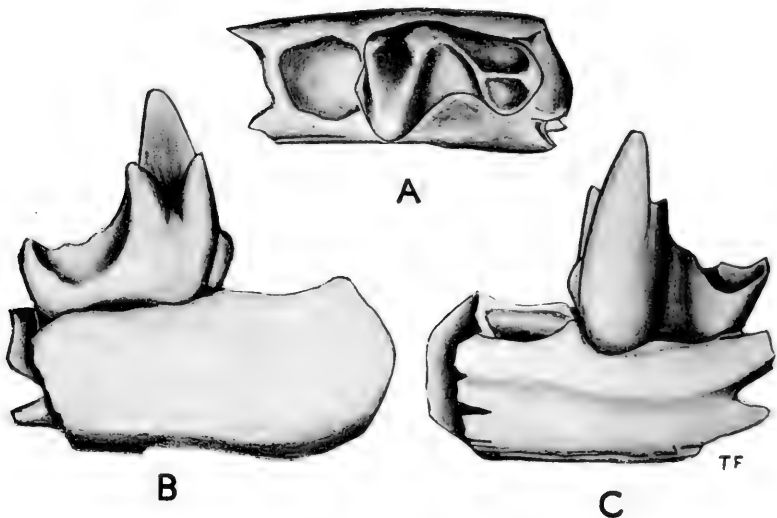
Fig. 4. Trinity lower molar. Type 6. SMP-SMU no. 61728. **A.** Occlusal view. B. Lingual view. C. Buccal view. ×20.

pret, there appears to be a ridge connecting the hypoconulid to the *crista obliqua.* The enamel also slopes lingually from this ridge. The heel of the talon presumably is formed, on the buccal side, by the recurving of the *crista obliqua* around the posterobuccal edge of the tooth to join with the hypoconulid. The lingual side of the heel is a ridge connected to the hypoconulid and extending to the entoconid area before fading, without forming an entoconid. Presumably there was no hypoconid or if one was present it was smaller than the hypoconulid. Although it does not terminate with a well-defined cusp, there is a diagonal cingulum on the anterior face of the trigonid almost identical to all of the other lower molars from Greenwood Canyon and Butler Farm.

Premolars. Specimen (no. 61730, fig. 5B) tentatively identified as either P_3 or P_4, has a tall, compressed, blade-like main cusp (protoconid), one cusp to the anterior and two to the posterior. The anterior cusp is distinct but very low, centered at the anterior base of the main cusp. There is a small but distinct posterior cingulum cusp which sends out small ledge-like ridges downward and forward on both sides of the crown. Between these "ledges" and on the posterior slope of the protoconid rises a large com-

pressed accessory cusp almost as high as the main cusp. The crown as a whole is posteriorly inclined, reminiscent of the P⁴ in *Smilodon*. The tooth is supported by two round roots of equal size which are also posteriorly inclined towards their tips.

Specimen no. 61731 (fig. 5A) is believed to be either P² or P³. The paracone is not as tall relative to the tooth's antero-posterior diameter and its edges are sharpened by a thin enamel keel. Low, narrow, and rounded cingula encircle the anterior and posterior portions of the crown almost meeting at the tooth's mid-length. A low conical cusp rises at the anterior base of the proto-conid just inside the cingulum. At the extreme posterior end of the tooth the cingulum itself protrudes into a cusp of equal size. Anterior to this, and on the posterior slope of the main cusp, is another large blade-like cusp. The roots are straight and slightly compressed transversely, the anterior roots having the greatest anteroposterior diameter. Both lower premolars are quite unlike any I have seen in Mesozoic therians. They are very similar to
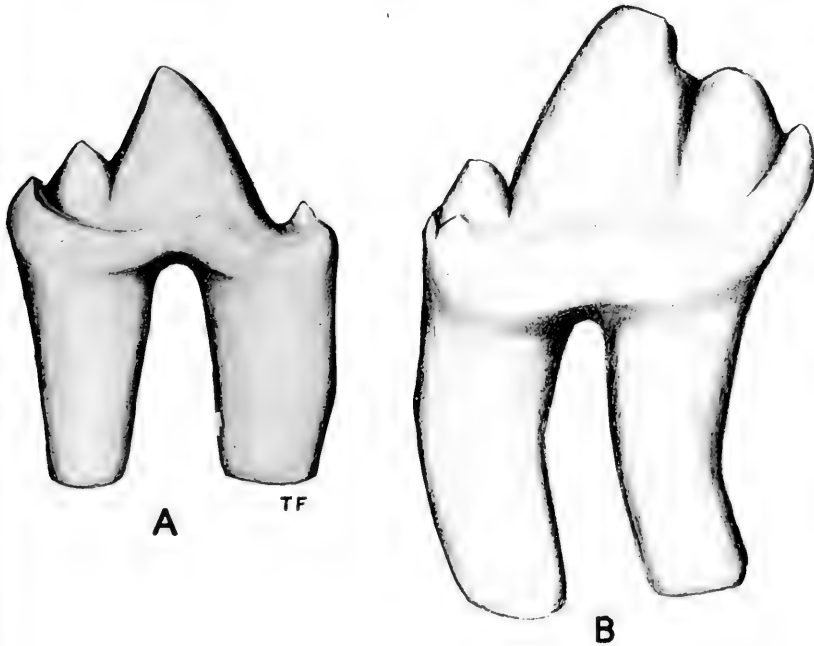

Fig. 5.   Trinity premolars. A. SMP-SMU 61731; buccal view. B. SMP-SMU 61730; buccal view. ×20.

the premolars of many later carnivores. As a matter of fact, the premolars of modern dogs match these almost exactly except for size.

MEASUREMENTS OF THERIAN TEETH

SMP-SMU no. 61725. Transverse diameter of penultimate molar–1.7 mm; anteroposterior diameter of penultimate molar–1.3 mm; transverse diameter of last molar–1.7 mm; anteroposterior diameter of last molar–0.8 mm.

SMP-SMU no. 61726 (lower molar). Anteroposterior diameter of tooth–1.8 mm; anteroposterior diameter of trigonid–0.7 mm; transverse diameter of trigonid -1.2 mm; transverse diameter of talonid–0.8 mm.

SMP-SMU no. 61727 (lower molar). Anteroposterior diameter of tooth–1.8 mm; anteroposterior diameter of trigonid–0.8 mm; transverse diameter of trigonid–1.2 mm; transverse diameter of talonid–1.1 mm.

.SMP-SMU no. 61735 (broken lower molar). Anteroposterior diameter of trigonid–0.9 mm; transverse diameter of trigonid–1.3 mm.

SMP-SMU no. 61728 (presumably lower molar). Anteroposterior diameter of tooth–1.2 mm; anteroposterior diameter of trigonid–0.6 mm; transverse diameter of trigonid–0.8 mm; transverse diameter of talonid–0.5 mm.

SMP-SMU no. 61730 (lower P_3 or P_4). Anteroposterior diameter–2.4 mm; transverse diameter–0.7 mm.

SMP-SMU no. 61731 (upper P^2 or P^3). Anteroposterior diameter–2.2 mm; transverse diameter–0.8 mm.

DISCUSSION

Patterson's Greenwood Canyon specimens are similar to the Butler Farm material but differ significantly in several respects. The broken upper molars from Greenwood Canyon were discussed as two possible types. One type, represented by specimens no. PM 884 and no. PM 999, has paracones and metacones developed and positioned like those of *Pappotherium;* the paracone is connected to the stylocone in the same manner. However, the parastyle is small, low and poorly demarcated from the stylocone, whereas the parastyle in *Pappotherium* is almost as large as the

stylocone and separated by a deep V-shaped notch. Patterson's second type as represented by PM 886, has the parastylar area missing. There is a large stylar cusp just posterior to the position of the stylocone in all other Trinity therian specimens and the crest projecting bucally from the paracone is not directed to this cusp. If this cusp is the stylocone, this tooth differs from *Pappotherium* and Patterson's Type 1 in that its paracone is connected to the parastyle and not to the stylocone. Or, if the paracone is connected to a stylocone that is broken away, it differs by the presence of a well-developed additional stylar cusp in a mesostylar position.

Another notable difference between the Greenwood Canyon specimens and those from Butler Farm is the form of the roots of the lower molars. In both specimens from Greenwood Canyon which have the roots preserved, the anterior root has a wider transverse diameter than its anteroposterior diameter, and the posterior root has a larger anteroposterior diameter than its transverse diameter. In both Butler Farm lower molars which still have their roots, both anterior and posterior roots are round and of almost equal size.

There were two types of last upper molars described by Patterson from Greenwood Canyon. This tooth in *Pappotherium* is most like Patterson's PM 1075. The primary difference is that the paracone and metacone in our specimen are taller and better separated.

Although the new material does not eliminate the possibility of the metacone originating on the posterior slope of the paracone, as seemed to be demonstrated by *Deltatheridium* and *Palaeoryctes,* the appearance of a form or forms with the metacone well separated from the paracone at such an early date certainly does place *Deltatheridium* well off the main evolutionary line and rather strongly suggests that there has been considerable secondary reduction of the metacone in some cases. At this point it is not certain that the addition of a protocone preceded the origin of a well-developed metacone. Butler's (1941) diagrammatic drawings of possible lineages showing the secondary reduction of the metacone, includes a hypothetical intermediate between a hypothetical primitive pantothere and all later therian forms. *Pappotherium* fits these requirements perfectly. Butler also proposed the division

of all teeth previously referred to as tritubercular (or tribosphenic, when both uppers and lowers were being discussed) into three groups: (1) zalambdodonts—having upper molars with the paracone on the lingual half of the tooth; the metacone rudimentary or lacking; well-developed stylar cusps; and lower molars with small talonids and two or less talonid cusps; (2) dilambdodonts—having paracone and metacone separate and in a slightly more buccal position, but with the stylar shelf still fairly wide, and with buccal styles not so well developed; lower molars with trigonid high relative to the talonid, and the talonid with three cusps; (3) trituberculates—having paracone and metacone buccal in position; conules well developed; buccal styles rudimentary or absent; lower molars with three talonid cusps. Patterson took objection to this division stating that it merely confused the issue in that there were intermediates that could not be easily placed into such groups. The newly-recovered Butler Farm material seems to support Patterson's stand. *Pappotherium* is something of a paradox when one attempts to place it into one of Butler's divisions. The buccal styles are extremely well developed and the paracone extends lingually of the tooth's mid-width; these are zalambdodont features. However, the molars of *Pappotherium* contain small but distinct conules which in Butler's grouping do not occur in zalambdodonts. Also the associated lower molars have high trigonids, but the talonid is more than one-half the tooth's total length and has three well-developed cusps (seemingly a trait of the other two groups).

As the teeth of *Pappotherium* contain all of the major cusps found in later therian mammals (except the hypocone), any major group of later Mesozoic therians could easily be derived from such an animal by the reduction of, elimination of, or repositioning of cusps that were already present. As a matter of fact, the lower molar holotype (YPM 11775)[1] of the primitive Upper Cretaceous insectivore, *Cimolestes incisus* Marsh (fig. 6), is strikingly similar to some of the new Texas material, especially type 5. The position and form of the cingulum on the anterior face of the trigonid is almost identical. Also, the arrangement and relative size of the talonid cusps are very similar although those of *Cimolestes* are somewhat lower. The trigonid of the later form is less compressed

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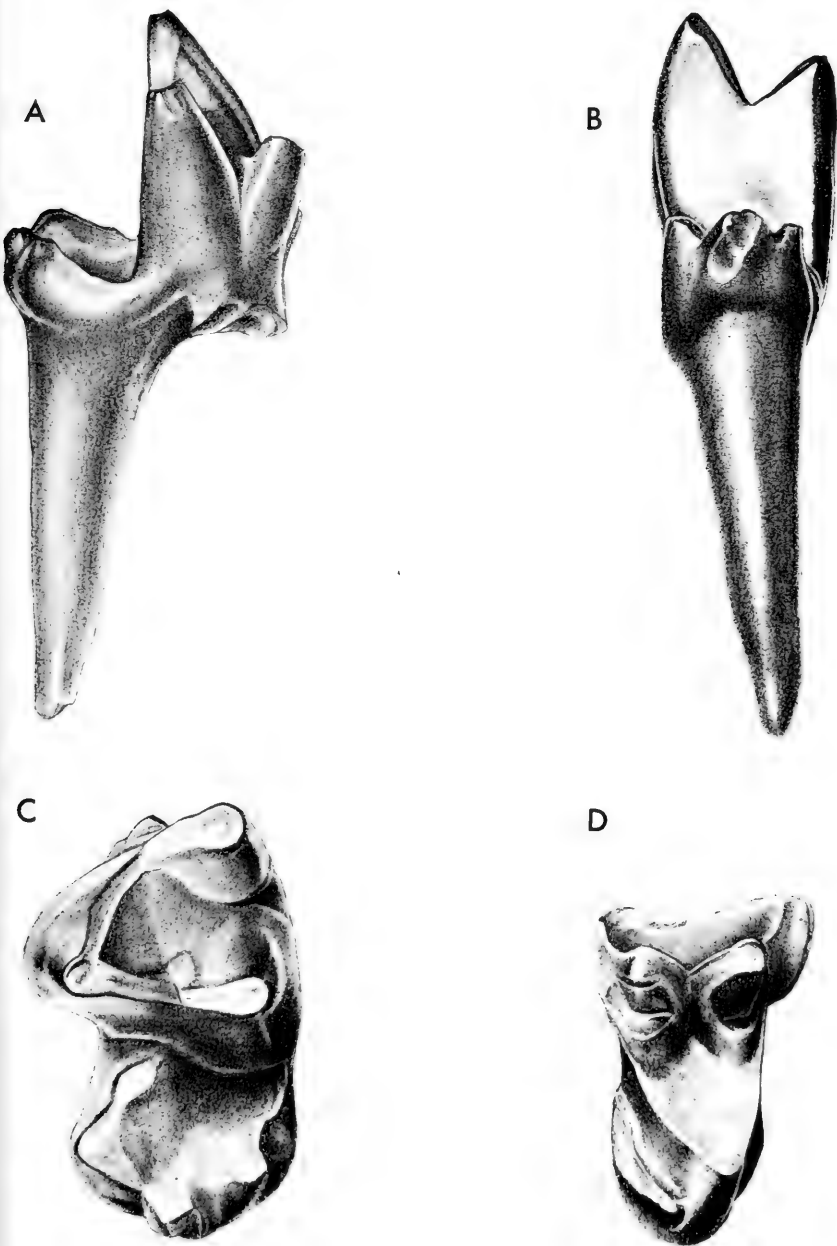[1] YPM numbers are those of the Yale Peabody Museum.

Fig. 6.   A. *Cimolestes incisus* Marsh. YPM 11775. Lower molar holotype. Lingual view. ×11.5. B. *C. incisus*. Posterior view. ×11.4 C. *C. incisus*. Occlusal view. ×17 D. *Gypsonictops hypoconus* Marsh. YPM 13662. Upper molar holotype. Occlusal view. ×14.7.

anteroposteriorly, however. Comparisons of the upper molar holo-
type of *Gypsonictops hypoconus* Marsh (fig. 6, YPM 13662) and
material of *Cimolestes* from the Upper Cretaceous Lance Forma-
tion reveal the following differences from the holotype of *Pappo-
therium,* all of which can be considered slightly more advanced:
stylar shelf is much reduced and buccal styles are not so well devel-
oped; the crests connecting the metacone to the metastyle and the
paracone to the styloconal area are much weaker; protoconule and
metaconule are larger and V-shaped due to their bridging part of
the protoconal basin connecting them to the lingual faces of the
paracone and metacone. The apex of the protocone follows the
buccal displacement of the paracone and metacone in both
Gypsonictops and *Cimolestes.* This is accomplished without reduc-
tion of the tooth's transverse width by a drastic steepening of the
lingual face of the tooth. A distinct hypocone has developed on
this broadened surface in *Gypsonictops.*

· Butler Farm specimen no. 61728 may have some bearing on
which of the talonid cusps was the first to arise. It is still unknown
whether it is a molar of a different animal or a molariform pre-
molar of the same animal. If it is indeed a premolar, it creates a
rather interesting problem. One might expect the talonid to become
molarized before the trigonid, but in this specimen all three
trigonid cusps are developed while there probably is but one
talonid cusp, certainly no more than two. Even so, the metaconid
and paraconid are much smaller, relative to the protocone, than
in the typical molars from both Greenwood Canyon and Butler
Farm. If this specimen is a molar (and I am inclined to believe
that it is), the identification of the single talonid cusp is of con-
siderable importance. Osborn (1907) considered the single talonid
cusp in pantotheres as the hypoconid; Gregory (1916, 1934) pre-
ferred an entoconid interpretation; Simpson (1929) did not decide
between the entoconid and the hypoconulid but apparently did not
believe it to be the hypoconid; Butler (1939) favored the hypo-
conulid; and Patterson (1956) felt that the Greenwood material
supported either Osborn or Butler—that is, either the hypoconid
or the hypoconulid. The single cusp present on this Butler Farm
specimen is clearly the hypoconulid. There is a ledge-like cingulum
directed from the apex of this cusp anterolingually lending the
talonid the same essential shape it would have if an entoconid

were present. It is probable that the entoconid arose from a similar crest. There remains the possibility that there was a hypoconid at the end of the *crista obliqua*. If so, only the entoconid would be eliminated as the first talonid cusp. A very close examination of the broken or worn surface, however, discloses no change of dentine banding or anything else suggesting there was a cusp on the crest. Apparently the *crista obliqua* simply looped around the hypoconid area and joined the hypoconulid in a fashion similar to the crest extending from the hypoconulid to the entoconid area. I interpret this specimen as evidence of the hypoconulid being the original talonid cusp.

Simpson (1929) pointed out that primitive marsupials usually have the entoconid and hypoconulid much closer together than the hypoconid is to the hypoconulid (almost twinned in some cases). whereas insectivores usually have all the talonid cusps more or less equidistant. There are a few rare exceptions where insectivores have the twinning character, but I know of no primitive marsupials that have their talonid cusps ,equidistant. Patterson's specimens from Greenwood Canyon all are of the equidistant variety, but he said that it may not be meaningful as this specialized development may not have taken place as early as the Albian. Butler Farm specimen no. 61726 has all three talonid cusps of equal size and equidistant, but specimen no. 61727 has a hypoconid larger than the other two cusps and not set aside as much as in the usual marsupial; nevertheless there is an undoubted tendency in that direction. Some placentals have developed the character to the same extent as the fossil; however, this could be interpreted several ways: (1) that only one type of mammal is represented and there is a tendency towards the twinning in some teeth while others remain more primitive (thus *Pappotherium* may not be the common ancestor of the two infraclasses, but a primtive marsupial); (2) that there are at least two animals present representing placentals *and* marsupials (or at least pro-placentals and pro-marsupials) very near the radiation from a still unknown common ancestor; or (3) that the twinning character of the hypoconulid and entoconid is primitive and a reversal of (1) is the case. The last possibility seems unlikely considering the posterocentral position of the hypoconulid in Type 6.

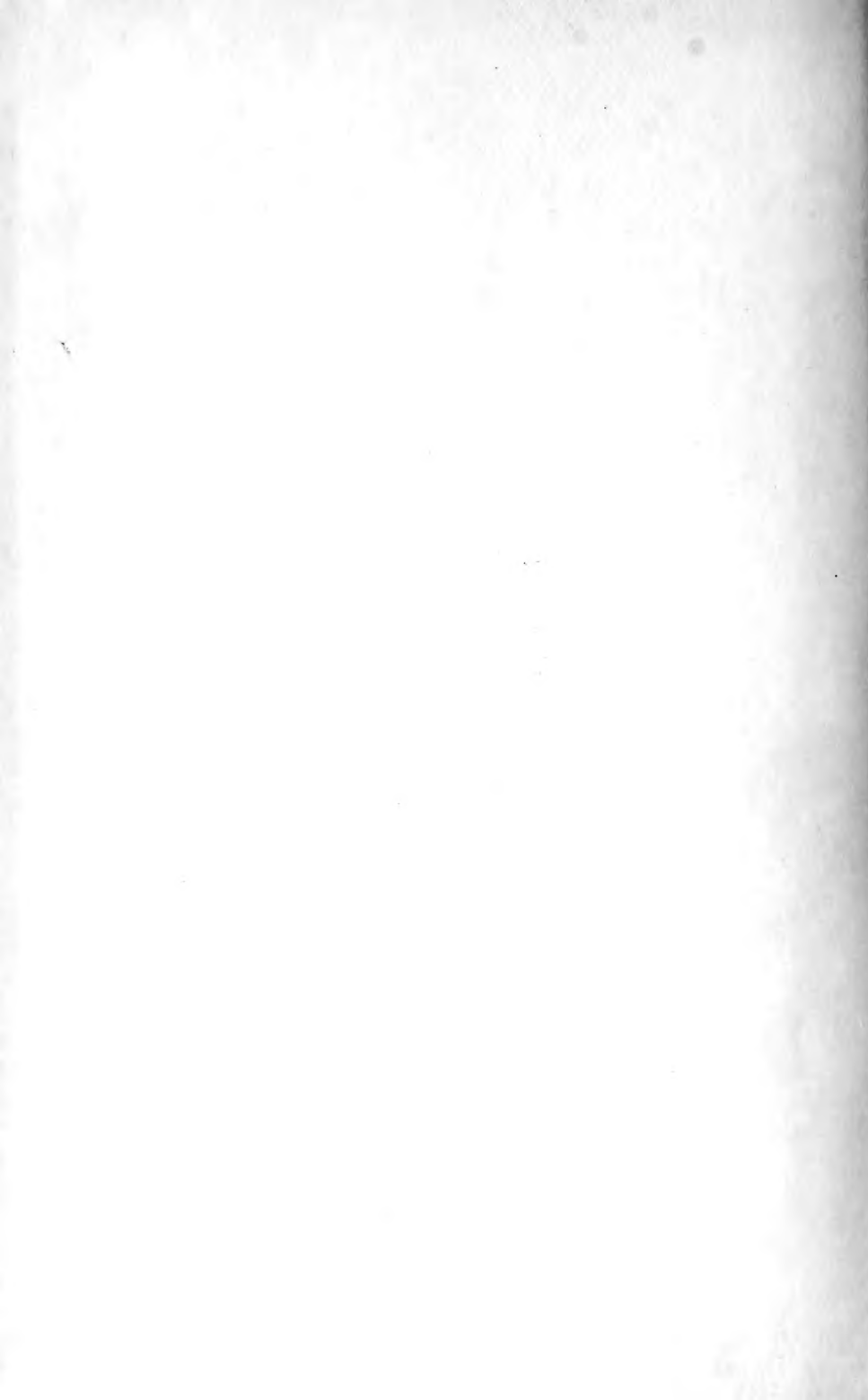In any case, *Pappotherium* and Patterson's forms from Green-

wood Canyon are the earliest known mammals of metatherian-eutherian grade and apparently are very near the point of divergence of placentals and marsupials from a common ancestor—either just before, just after, or during that event.

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