Fig. 6.   Projections on the first canonical axis for a discriminant analysis by islands. This axis explains more than half (58.8 per cent) of all information. Note the perfect correspondence of morphological gradation and geographic position for the modern samples. Only the St. Croix fossils depart from the trend. Code letters as in Figure 5.

distances on Figure 5, they depart markedly from the regression line of modern samples. Geographic and morphological distance are closely correlated in living eastern cerions. But this relationship does not guarantee any graded trend of morphology along the linear array of islands. In fact, we already have a test for clines in the results of our canonical analysis.

In our canonical analysis for islands, the most significant discriminator (the first axis) explains 58.8 per cent of all information. Figure 6 shows the array of projections. Living cerions are arranged in perfect geographic order; only the fossils of St. Croix depart from the pattern. The morphological gradation runs from egg-shaped, finely and copiously ribbed shells with very obtuse apices (Virgin Islands) to more cylindrical, apically pointed shells with fewer, stronger ribs (Hispaniola) — see the discussion of factor patterns in Section V. The direction of the cline also meets our expectations. Virgin Island shells represent the extreme expression of morphological features that characterize eastern cerions; they are also geographically furthest from any contact with non-eastern congeners. The Hispaniolan specimens, situated in closest proximity to non-eastern cerions, depart most strongly from modal eastern morphology towards the more "normal" form of the genus.

We are not addicted to speculative biogeography, and we offer no preferred hypothesis for this pattern; we do not see how museum specimens can distinguish among such alternatives as selective gradients and gene flow, and we know virtually nothing about the history of colonization. We only note that the strikingly discordant position of the St. Croix fossils may indicate a fairly recent origin for the graded series of modern forms. (The St. Croix fossils are morphologically furthest from their nearest modern relatives on Necker and Anegada.)

In the light of this pattern, we see no reason to maintain the taxonomic distinction among living eastern forms. Some common factor accounts for most of the morphological variabiity among these populations. We therefore consider all of the following names as synonyms of the first-named form, *Cerion striatellum* ("Férrusac" Guerin-Meneville), 1829: *C. monaense* Clench, 1951; *C. yumaense* Pilsbry and Vanatta, 1895 (with its four subspecies); *C. ferruginum* (Maynard, 1896 — ranked as a subspecies of *C. yumaense* by most later authors); and *C. tortuga* Pilsbry and Vanatta, 1928. We maintain, for now, *Cerion rude* (Pfeiffer), 1855 for the St. Croix fossils. The St. Croix shells depart completely from modern trends in geographic variation. Indeed, this departure serves as a strong support for taxonomic identity of recent populations — for it argues against any appreciable antiquity for the modern pattern. Moreover, the St. Croix shells, while closer to the eastern mode than to any other morphotype of *Cerion,* vary from this mode in the direction of more conventional Bahamian and Cuban forms — shells are larger, more cylindrical, and more sparsely and strongly ribbed. As another argument for the taxonomic unity of modern forms, we note that the morphological distances among islands are trifling compared with the distinction of several forms that interbreed freely throughout the Bahamas. In fact, and incredible as it may seem in the light of *Cerion*'s fantastic morphological variety, we have located no unambiguous case of sympatry without interbreeding for the entire genus (two of nine reported cases have a fair chance of validation in our opinion).

## VIII.  CONCLUSION

Studies of *Cerion* have been dominated by the conviction that no regular patterns of geographic variation exist. All leading students have invoked haphazard transport by hurricanes to support a notion of "crazy-quilt" distributions (Mayr and Rosen, 1956). We now present the first evidence for simple, graded, coherent variation over a large part of *Cerion*'s range. Moreover, S. J. Gould and D. S. Woodruff, working in the northern Bahamas during the past four years, have found strikingly consistent patterns of within-island variation on all islands visited (Abaco, Grand Bahama, New Providence, Great Exuma, and Long). The "ribby" morphotype, for example (called *C. glans* (Küster) and

about 50 synonyms on New Providence, *C. abacoense* Pilsbry and Vanatta and 3 synonyms on Abaco and Grand Bahama, etc.), always inhabits coastal areas at the edges of the Pleistocene banks; while the mottled morphotype inhabits interior coasts (with respect to the banks) and interior areas. The two morphotypes intergrade in a variety of interesting ways at their contacts. The discovery of simple and coherent patterns, both within and between islands, leads to a hope — even an expectation — that some sense will yet be made of *Cerion*.

## IX.   ACKNOWLEDGMENT

## REFERENCES

BAKER, H. B., 1924. Land and freshwater molluscs of the Dutch Leeward Islands. Occ. Pap. Mus. Zool. Univ. Mich. No. 152, 158 pp.

BARTSCH, P., 1920.   Experiments in the breeding of Cerions. Papers Dept. Marine Biol. Carnegie Inst. Wash. No. 282, 55 pp.

CLENCH, W. J., 1951.   Land shells of Mona Island, Puerto Rico. J. Conchyliologie 90: 269-276.

————, 1957.   A catalogue of the Cerionidae (Mollusca — Pulmonata). Bull. Mus. Comp. Zool. 116: 121-169.

DALL, W. H., 1905.   Fossils of the Bahama Islands, with a list of the nonmarine mollusks. *in* G. B. Shuttuck (ed.), The Bahama Islands. N. Y., MacMillan, pp. 23-47.

DE VRIES, W., 1974.   Caribbean land molluscs: notes on Cerionidae. Stud. Fauna Curaçao and other Carib. Islands 45: 81-117.

GOULD, S. J., 1969.   Character variation in two land snails from the Dutch Leeward Islands: geography, environment, and evolution. Syst. Zool. 18: 185-200.

GOULD, S. J., D. S. WOODRUFF, AND J. P. MARTIN, 1974.   Genetics and morphometrics of *Cerion* at Pongo Carpet: a new systematic approach to this enigmatic land snail. Syst. Zool. 23: 518-535.

GUÉRIN-MENEVILLE, F. E., 1829.   Iconographie du regne animal de G. Cuvier, Mollusques. Paris, Fortin.

HUMMELINCK, P. W., 1940.   Mollusks of the genera *Cerion* and *Tudora*. Stud. Fauna Curaçao, Aruba, Bonaire, and Venezuelan Islands 2: 43-82.

JACOBSON, M. K., 1968. The land Mollusca of St. Croix, Virgin Islands. Sterkiana 32: 18-28.

KÜSTER, H. D., 1847.   Die Gattungen *Pupa, Megaspira, Balea* und *Tornatellina*. Conchylien-Cabinet (2), 1, pt. 15, 194 pp.

MAYNARD, C. J., 1896.   Monograph of the genus *Strophia*. Contributions to Science, vol. 3, Newtonville, Mass.

MAYR, E., 1963. Animal species and evolution. Cambridge, Mass., Harvard Univ. Press, 797 pp.

MAYR, E., AND C. B. ROSEN, 1956. Geographic variation and hybridization in populations of Bahama snails (*Cerion*). Novitates Am. Mus. Nat. Hist. No. 1806, 48 pp.

PFEIFFER, L., 1855. Beiträge zur Molluskenfauna Westindiens. Malak. Blät. 2: 98–106.

PILSBRY, H. A., 1902. Family Cerionidae. Manual of Conchology, Second Series, Pulmonata, Vol. 14. Philadelphia, Acad. Nat. Sci., pp. 174–281.

———, 1943. Note on *Cerion striatellum*. Nautilus 57: 34–35.

PILSBRY, H. A. AND E. G. VANATTA, 1895. New species of the genus *Cerion*. Proc. Acad. Nat. Sci. Phila. 47: 206–210.

———, 1896. Catalogue of the species of *Cerion*, with descriptions of new forms. Proc. Acad. Nat. Sci. Phila. 48: 315–338.

———, 1928. Land shells of Tortuga Island, Haiti, and a new Haitian *Oleacina*. Proc. Acad, Nat. Sci. Phila. 80: 475–478.

PLATE, L., 1906. Die Artbildung bei den Cerion-Landschnecken der Bahamas. Verhandl. deutsch. zool. Ges. 16: 127–136.

———, 1907. Die Variabilität und die Artbildung nach dem Prinzip geographischer Formenketten bei den Cerion-Landschnecken der Bahama-Inseln. Arch. Rassen Gesellsch. Biol. 4: 433–470, 581–614.

SNEATH, P. H. A., AND R. R. SOKAL, 1973. Numerical Taxonomy. San Francisco, W. H. Freeman, 573 pp.

SOWERBY, G. B., 1875. Monograph of the genus *Pupa*. Conchologia Iconica, vol. 20.

VANATTA, E. G., 1923. Two new Santo Domingan land shells. Proc. Acad. Nat. Sci. Phila. 75: 359–360.

# A NEW INTERPRETATION OF THE MAMMALIAN TEETH OF TRIBOSPHENIC PATTERN FROM THE ALBIAN OF TEXAS

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ABSTRACT. A reappraisal has been made of tribosphenic teeth from the Albian of Texas, previously described by Patterson, Slaughter and Turnbull. At least six genera are represented. *Pappotherium* and *Holoclemensia,* the most common genera; are sufficiently alike to be placed in the same family, Pappotheriidae. They have four molars as in marsupials and complex premolars as in placentals. They cannot be classified either as marsupials or placentals but are considered to belong to a separate evolutionary line (Pappotherida, new order). Two forms of smaller size, *Kermackia texana* and *Trinititherium slaughteri* gen. et sp. nov., whose lower molars are at a more primitive stage of evolution than the Pappotheriidae, are placed in a new family Kermackiidae (Aegialodontia, new order). *Slaughteria eruptens* gen. et sp. nov., the only species for which there is evidence of tooth-replacement, is placed provisionally in the same family. A new infraclass, Tribotheria, is proposed to include mammals with tribosphenic molars that are not classifiable as marsupials or placentals.

## INTRODUCTION

Patterson (1956) reported on a collection of teeth found in the Greenwood Canyon, near Forestburg in eastern Texas. Many of the molar teeth are of tribosphenic pattern. They are mid-Cretaceous (Albian), the oldest tribosphenic molars known at that time. The Greenwood Canyon fauna is intermediate in age between the late Jurassic Purbeck and Morrison faunas and the late Cretaceous Djadokhta fauna of Mongolia. During this long interval of about 50 million years, the Jurassic mammal orders were largely replaced

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by marsupials and placentals. Only the multituberculates survived into the late Cretaceous in more than small numbers.

The differentiation between marsupials and placentals is believed to have taken place during the earlier part of the Cretaceous. Both marsupials and placentals share the tribosphenic molar pattern. With only the evidence of isolated teeth, Patterson was unable to decide in which infraclass his specimens belonged or whether they represented a group from which both marsupials and placentals would arise. Accordingly, he classified them as "Therian mammals of uncertain infraclass affinities but of Metatherian-Eutherian grade."

Between 1965 and 1971, Slaughter published descriptions of important additional material. He obtained it from Butler Farm, a locality of similar age to the Greenwood Canyon locality. He named two species based on upper molars: *Pappotherium pattersoni* and *Holoclemensia texana*. The holotype of *P. pattersoni* is a fragment containing the last two molars. The holotype of *H. texana* is a penultimate molar of which the protocone shelf is lacking; Slaughter used a complete last molar as a paratype and referred a lower molar to this species. He named a third species, *Kermackia texana* from another isolated lower molar.

*Holoclemensia* differs from *Pappotherium* in the arrangement of the buccal stylar cusps of its upper molars (Fig. 1). In *Pappotherium* there is a large stylocone (Style B), about as high as the metacone. In *Holoclemensia,* the stylocone is much smaller, but there is a large conical cusp (Style C) opposite the notch between the paracone and the metacone. In the incomplete material at his disposal Patterson (1956) mistook Style C for the stylocone. Style C occurs in many late Cretaceous marsupials; it is higher than the stylocone in *Albertatherium* and *Aquiladelphis* (Fox, 1971).

Slaughter (1968b) regarded *Holoclemensia* as a marsupial, not only because of the presence of Style C, but also because the metacone is less reduced than in *Pappotherium.* In 1968a he described some partly molariform premolars, unlike those of any marsupial. In 1971, he referred to *Pappotherium* a mandible that contained a newly erupted and a partially erupted premolar together with worn molars. This specimen indicates diphyodonty of the anterior dentition, characteristic of placentals. He therefore regarded *Pappotherium* as a placental. Subsequently Fox (1975) deduced from the
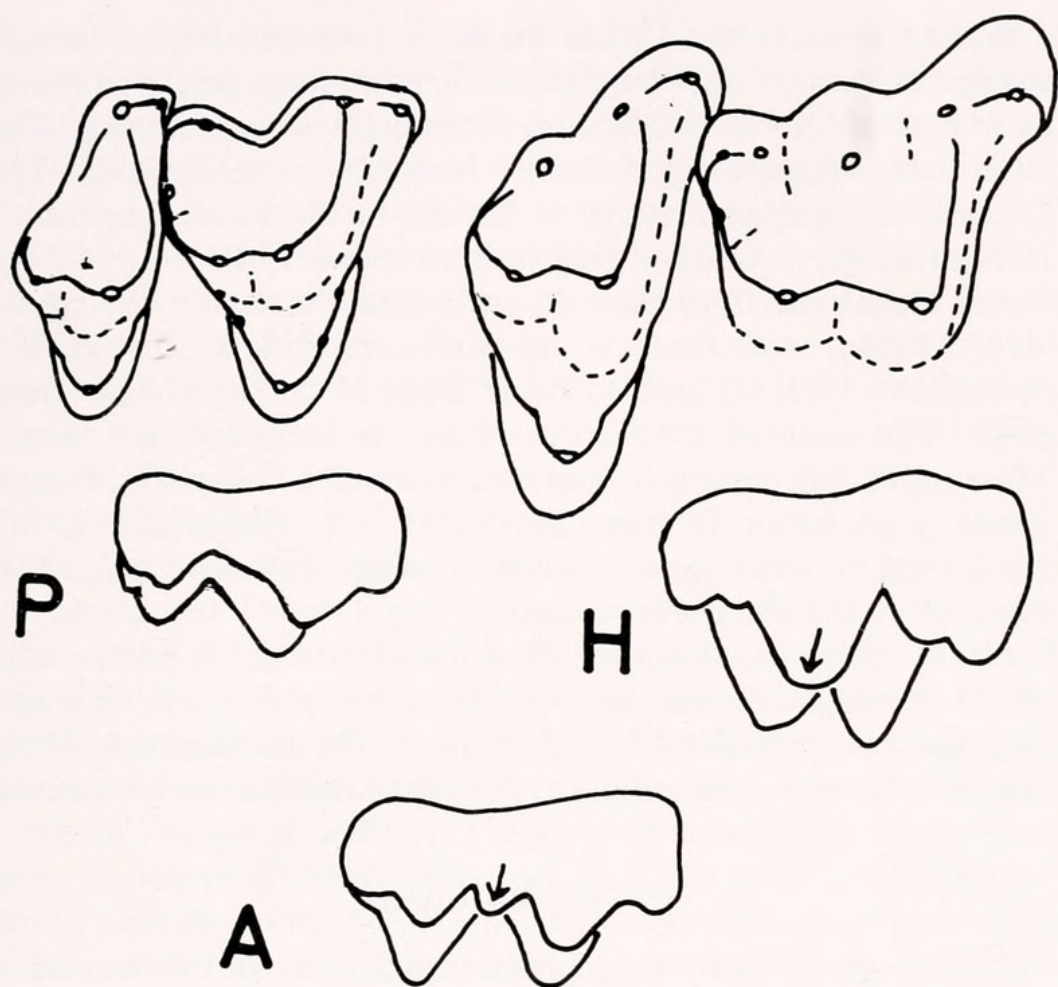
Figure 1.   P, last two upper molars of *Pappotherium pattersoni*, SMP-SMU 61725, and buccal view of penultimate molar. H, the same, *Holoclemensia texana*, SMP-SMU 62099 and 62147. A, buccal view of upper molar of *Alphadon marshi*. Stylar cusp c is indicated by an arrow.

shapes of the last two teeth that *Pappotherium* had only three molars.

Lillegraven (1969, 1974) and Hoffstetter (1970, 1972) believe that the marsupial-placental differentiation was due to isolation on different continents.  Placentals in Asia and marsupials in North America suggest that the placentals that appear in North America towards the end of the Cretaceous are immigrants from Asia.  This opinion does not accord with Slaughter's view that both infraclasses were present on the continent as early as the Albian.  It seemed desirable to reexamine the evidence provided by the Texas Albian fauna that affects a crucial stage of mammalian evolution.

During visits to the United States in 1966 and 1974 I studied specimens from Greenwood Canyon that Patterson described (1956) as well as additional material that Turnbull (1971) described. The latter was subsequently collected from the same locality. The Greenwood Canyon material is housed in the Field Museum of Natural History, Chicago (registration numbers PM —). Of the Butler Farm collection, I saw the specimens described by Slaughter (1965, 1968a) and the jaw containing premolars with molars (Slaughter, 1971). I studied other Butler Farm specimens from casts. The material from Butler Farm is housed in the Shuler Museum of Paleontology, Southern Methodist University, Dallas, Texas (registration numbers SMP-SMU —). I used a Wild M5 microscope to make camera lucida drawings, at known magnifications, of all the specimens studied.

Nearly all the specimens consist of isolated teeth. A primary aim of the investigation was to find the most probable way in which they could be combined into dentitions. The relationships of the species believed to be present in the fauna could then be considered.

## UPPER MOLARS

All the upper molars that I have seen are drawn in crown view in Fig. 2. Except in the holotype of *Pappotherium,* all are isolated, and their position in the series must be judged from their shape alone. Last molars, whether $M^3$ or $M^4$, are easily recognizable. Reduction of the metacone and loss of the metastyle accompany a reduction of the posterobuccal lobe of the outline. These features are widespread and almost certainly primitive among mammals with tribosphenic molars. On passing forward along the molar series, both in marsupials and placentals, the posterobuccal lobe becomes relatively larger, so that eventually it projects buccally beyond the level of the parastyle; the metacone also enlarges and the metastylar crest becomes longer. The degree of difference between adjacent molars varies considerably between genera and families and to some extent individually. The penultimate molar is preserved in the holotypes of *Pappotherium* and *Holoclemensia* (Fig. 2, d, l). In both, the posterobuccal lobe is less prominent than the parastylar region, though both possess the metastylar crest.

When measured by the relative distances of the metacone and par-
acone from the buccal edge, *Holoclemensia* has a rather less prom-
inent posterobuccal lobe, but the difference between the two genera
is not great. *Holoclemensia* also has a higher metacone than *Pap-
potherium,* a difference that is repeated on the last molar.

Of the isolated last molars, PM 1075 (Fig. 2, c), though smaller
than the holotype of *Pappotherium,* agrees with that specimen in
structure; PM 1015 (Fig. 2, b) has a less reduced posterobuccal
lobe and a larger metacone; PM 1287 (Fig. 2, p) has a smaller pro-
tocone shelf than *Pappotherium.* The posterior surface of the stylo-
cone of PM 1015 has a small cusp, indistinctly indicated on PM
1075. Whether this cusp is the equivalent of Style C is uncertain.
Style C is comparatively well developed on the last molar of *Holo-
clemensia,* but Turnbull (1971, Fig. 1) misidentified it as the meta-
style. PM 1015 and PM 1075 both differ from *Holoclemensia* and
resemble *Pappotherium* in having a concavity of the anterior out-
line lingually to the parastyle. PM 1287, with its small protocone,
is clearly distinct from both *Holoclemensia* and *Pappotherium.*

Several upper molars have the posterobuccal region less reduced
than on the penultimate molars of *Holoclemensia* and *Pappothe-
rium,* and they must be considered as examples of more anterior
molars. PM 1000 (Fig. 2, o) has a well preserved buccal stylar shelf
on which Style C is the highest cusp. This identifies the tooth as
*Holoclemensia,* but the metacone is farther from the buccal edge
than the paracone is. PM 886 (Fig. 2, m) has lost the parastylar
region, but Style C, which is preserved, is as high as the metacone.
This tooth is larger than PM 1000 and differs from it in that the
paracone and metacone are nearly equidistant from the buccal
edge. PM 1004 (Fig. 2, n), poorly preserved, agrees with PM 886
in comparable parts. There is evidence that *Holoclemensia* had two
molars anterior to the penultimate tooth and four molars with all
included (Fig. 5, H).

PM 999 (Fig. 2, h) resembles the penultimate molar of *Pap-
potherium* in the enlarged stylocone and in the metacone, which
is less high than the paracone; however, the posterobuccal lobe of
PM 999 is prominent and bears a strong metastylar crest. PM 1238
(Fig. 2, i), of which the anterior part of the stylar shelf is missing,
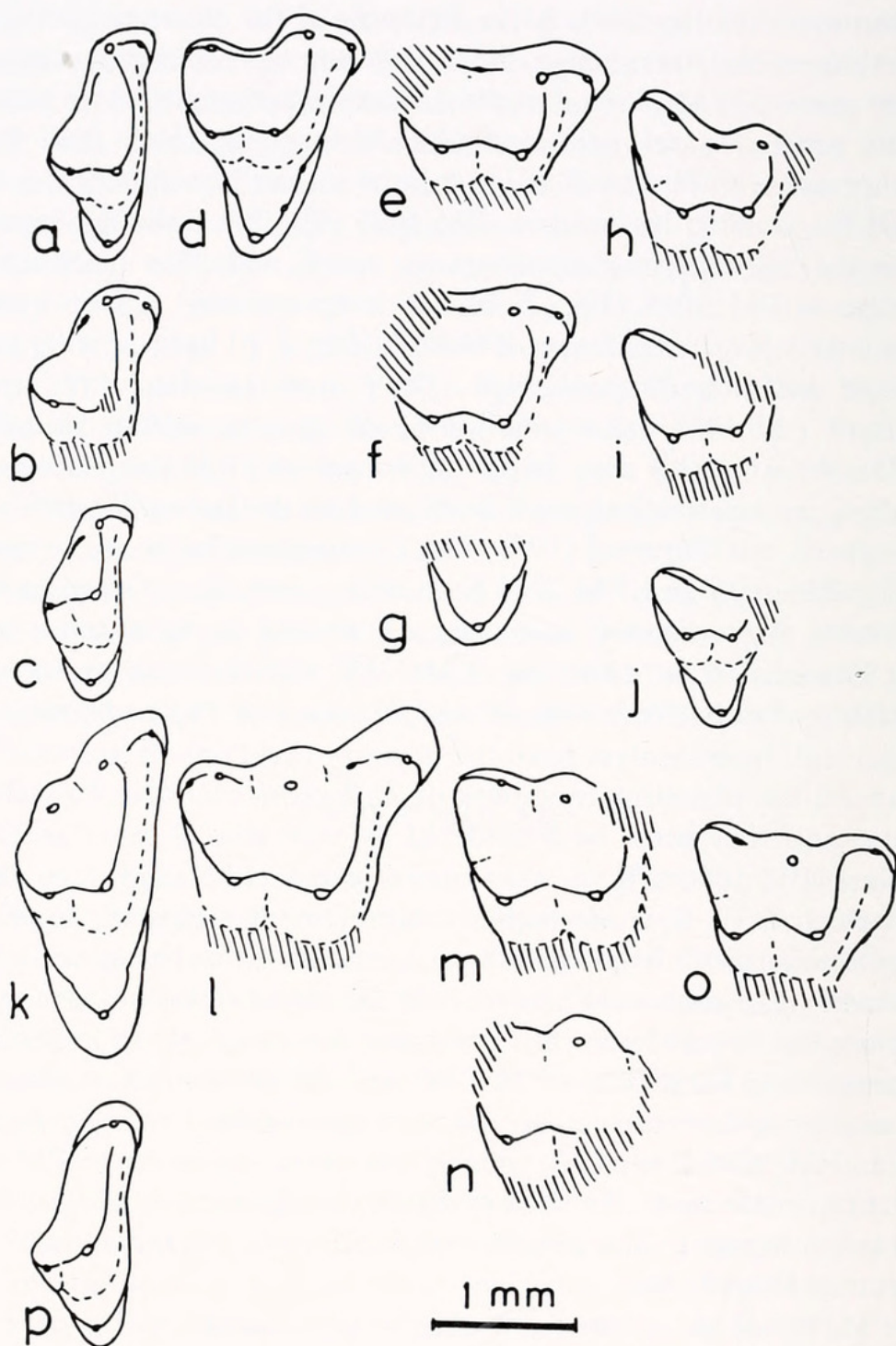agrees with PM 999 in the metacone and metastyle and is almost

Figure 2. Crown views of upper molars. a, SMP-SMU 61725 (holotype of *Pappotherium pattersoni*); b, PM 1015; c, PM 1075; d, SMP-SMU 61725 (holotype of *P. pattersoni*); e, PM 884; f, PM 1749; g, PM 1325; h, PM 999; i, PM 1238; j, SMP-SMU 62402; k, SMP-SMU 62099 (paratype of *Holoclemensia texana*); l, SMP-SMU 61947 (holotype of *H. texana*); m, PM 886; n, PM 1004; o, PM 1000; p, PM 1287. All drawn as right teeth: b, c, e, f, i, o, p have been reversed.

certainly another example of the same tooth. PM 884 and PM 1749 (Fig. 2, e, f) represent a different type of molar. The metastylar region has broken off in both specimens. As in *Pappotherium,* the stylocone is high and the metacone is lower than the paracone. These teeth are larger than PM 999 and PM 1238 (Fig. 2, h, i), and based on the incomplete crowns, the metacone and paracone were nearly equidistant from the buccal margin. On PM 999, PM 884 and PM 1749 there is a slight elevation of the marginal ridge in the region corresponding to Style C, but this elevation is very different from the enlarged Style C of *Holoclemensia.*

There are therefore two types of upper molar, with a pattern similar to *Pappotherium,* that correspond to the supposed first two molars of *Holoclemensia* — a larger, more symmetrical $M^2$ and a smaller $M^1$ with a more prominent metastylar corner. The evidence suggests that *Pappotherium* has four molars like *Holoclemensia* (Fig. 5, P).

PM 1325 (Fig. 2, g) is the lingual part of an upper molar which seems from its size to be more probably referable to *Pappotherium* than to *Holoclemensia.*

SMP-SMU 62402 (Fig. 2, j) resembles PM 999 and PM 1238 in pattern but differs from them in its smaller size. This tooth may be $M^1$ of a smaller species, of which PM 1075 might be the last molar.

## LOWER MOLARS

The allocation of lower to upper molars is particularly difficult in the case of the therians from the Albian of Texas. This difficulty arises because *Pappotherium* and *Holoclemensia* have been distinguished mainly by the buccal stylar shelf, which does not occlude with the lower teeth. The protocone, which does occlude, is missing from most upper molars.

Patterson and Slaughter have distinguished six types of lower molars, Types 1, 2, and 3 by Patterson (unworn examples illustrated in Fig. 3), Types 4, 5 and 6 by Slaughter. Combinations of some of these types seem probable.

Teeth cf Type 1 are characterized by the anteroposteriorly short trigonid, in which the paraconid is lower than the metaconid, and a comparatively wide talonid on which the hypoconid is elevated and placed nearly in line with the protoconid. In Type 1 Patterson

placed PM 1005 (Fig. 3, H) and the trigonid PM 887; to these may
be added the trigonid PM 3877. Slaughter (1965) classified three
teeth from Butler Farm as Type 5 (SMP-SMU 62131, 61727, and
61735). These differ from Type 1 in the less elevated trigonid,
which has a greater anterior tilt, and in the narrower talonid. Teeth
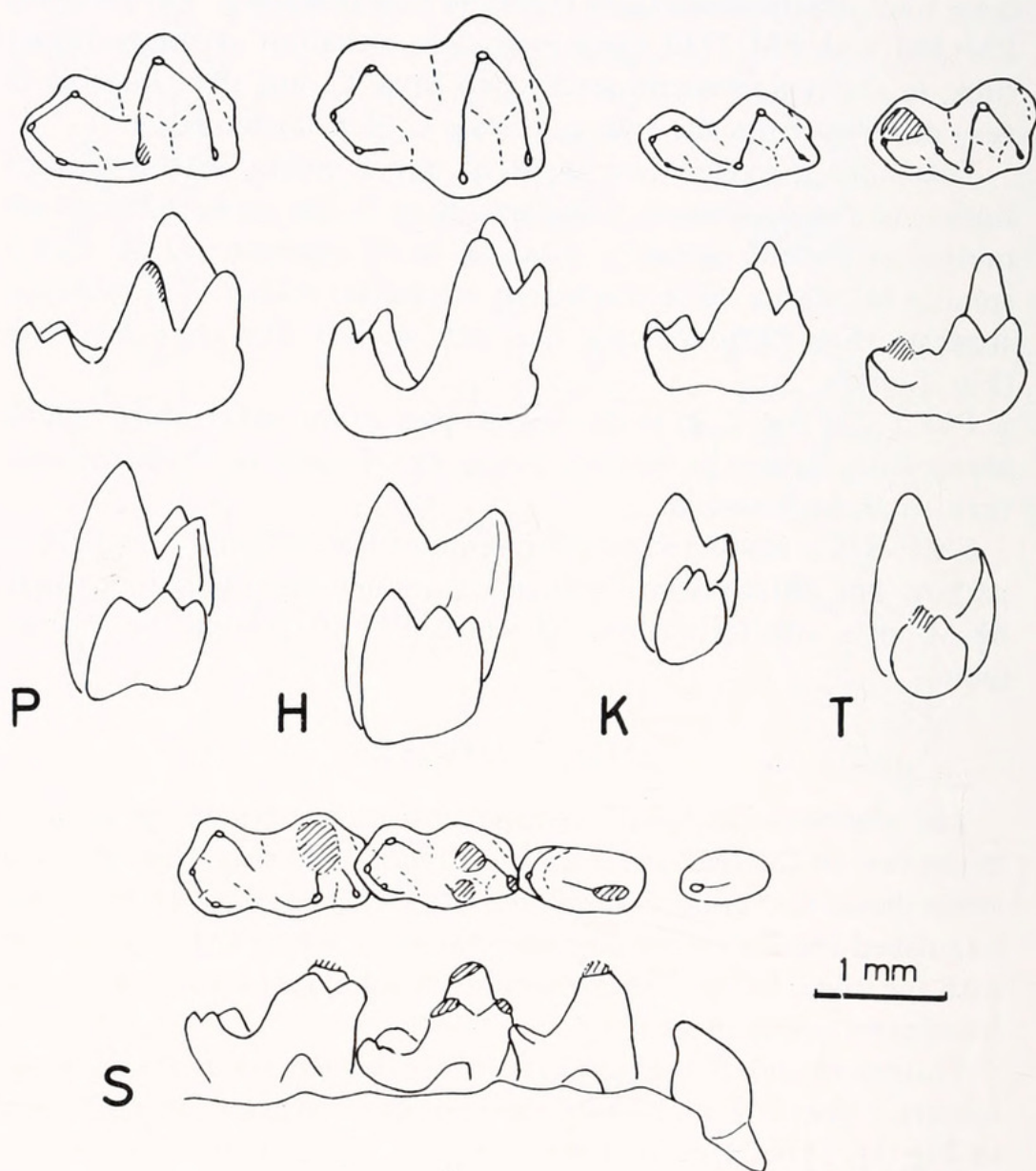


Figure 3.   P, H, K, and T, left lower molars drawn in crown, lingual and pos-
terior views. P, Type 2 (PM 965, reversed), referred to *Pappotherium*; H, Type 1
(PM 1005, reversed), referred to *Holoclemensia*; K, Type 3 (PM 1245, reversed),
*Kermackia*; T, Type 6 (SMP-SMU 61728), holotype of *Trinititherium slaughteri*.
S, SMP-SMU 61992, holotype of *Slaughteria eruptens*, crown and lingual views.

of Type 5 were referred by Slaughter (1968b) to *Holoclemensia*. SMP-SMU 61726, belonging to Slaughter's Type 4, has a relatively long and narrow talonid with a less elevated hypoconid; it has lost the tops of the trigonid cusps.

The differences between Types 1, 4, and 5 could be due to serial position in a single species — Type 4 being the last molar, Type 5 the penultimate, and Type 1 the most anterior molar of the three. A trigonid, PM 966, agrees with Type 1 in the relative height of the paraconid and metaconid, but the trigonid is narrower transversely and less compressed anteroposteriorly. Probably because of its more open trigonid, Patterson included this specimen with Type 2, but it could be a first molar standing in the same dentition as Type 1 and bringing the number of molars to four (Fig. 5, H).

Teeth of Patterson's Type 2 have a more open trigonid than those of Type 1. The metaconid is smaller; it is similar in height to the paraconid. The talonid is narrower than in Type 1. The hypoconid is comparatively low, and it is not placed so far buccally in relation to the protoconid. The talonid is preserved completely only in PM 965 (Fig. 3, P); in PM 948 the hypoconulid has been broken off. PM 930, PM 660, PM 1249, and PM 1119 are isolated trigonids. A feature of Type 2 teeth, not noted by Patterson, is the oblique crest that continues along up the posterior wall of the trigonid almost to the top; it ends in an intermediate position between the tip of the metaconid and the notch dividing that cusp from the protoconid. In teeth of Types 1 and 5, and also in PM 966, the oblique crest is confined to the lower part of the trigonid wall. Type 2 teeth are smaller than those of Types 1, 4 and 5: their trigonid widths range from 0.91 to 1.16 mm compared with 1.26 to 1.46 mm in the other types (measurements from Turnbull, 1971). No teeth of Type 2 have been reported from Butler Farm.

It is probable that Types 1, 4, and 5 are referable to *Holoclemensia* and Type 2 to *Pappotherium*. The upper molars of *Holoclemensia* are larger, and they have larger metacones which might correlate with large and buccally situated hypoconids on the lower molars. The upper molars referred to *Pappotherium* are too small to fit lower molars of Types 1, 4, and 5, but their occlusion with Type 2 lower molars is feasible. PM 930, the Type 2 tooth with the smallest and most open trigonid, would be a first molar. The largest examples of Type 2, PM 965 and PM 660, would be second

molars, corresponding to the largest upper molars. The smaller PM 948 and PM 1249 would be third or perhaps fourth molars (Fig. 5, P). It is to be noted that Crompton (1971) used a Type 4 tooth to illustrate the occlusion of *Pappotherium*.

Patterson's Type 3 was represented by only one damaged tooth (PM 922), but an unworn specimen (PM 1245; Fig. 3, K) has been recovered subsequently. It is very similar to the holotype of *Kermackia texana*, from which it differs by its higher and more pointed protoconid and metaconid. This difference is due to loss of enamel from the trigonid of the holotype. The trigonid is widely open, and the paraconid points anteriorly. The protoconid is the highest trigonid cusp, the paraconid the lowest. From the metaconid arises a strong posterior crest (named *Distal Metacristid* by Fox, 1975), continuous with the crista obliqua. The talonid is narrower than the trigonid. The hypoconid stands only slightly more buccally than the hypoconulid. The entoconid is small, and the talonid basin is open on the lingual side between the entoconid and the metaconid.

Slaughter's Type 6 is based on the jaw fragment SMP-SMU 61728. This contains a molar (Fig. 3, T), apparently the last, and the alveoli of the next anterior tooth. Type 6 resembles *Kermackia texana* in size and general proportions, but the metaconid of Type 6 is much smaller, no higher than the paraconid. As in *Kermackia*, the crista obliqua runs to the metaconid. As the crest continues up the posterior surface of the metaconid, it is much weaker and nearly vertical. The talonid basin is widely open on the lingual side as in *Kermackia*, but the entoconid is almost absent, and an additional cusp is present on the crista obliqua. The top of the hypoconid has been broken off. Two trigonids from Greenwood Canyon, PM 1065 and PM 1045, have the same structure. This form is sufficiently distinctive to deserve a name, which I propose formally as follows:

*Trinititherium,* gen. nov.

*Diagnosis.* The lower molars differ from those of *Kermackia* as follows: (1) metaconid and paraconid subequal; (2) an accessory cusp present on the crista obliqua; (3) the crest on the posterior surface of the metaconid weaker and more vertical; (4) entoconid rudimentary. Type species:

*Trinititherium slaughteri,* sp. nov.

*Diagnosis.* This is the only known species of *Trinititherium.*

Holotype, SMP-SMU 61728, from Butler Farm. Illustrated by Slaughter (1965, Fig. 4, and 1971, Pl. 1).

W. A. Clemens (personal communication) has raised the question whether *Trinititherium* might represent the posterior molar of *Kermackia.* This would imply a reduction of the metaconid towards the posterior end of the series. Such a process occurs as an aspect of carnassial specialization in Cenozoic carnivorous mammals (Butler 1947). The metaconid is also reduced in Deltatheridiidae and Stagodontidae in the late Cretaceous. In all these, there is evidence of a sectorial specialization of the paraconid which is not shown by *Trinititherium.* The metaconid is similar in height to the paraconid in *Kielantherium* and probably in *Aegialodon.* In these genera, however, the talonid is shorter and narrower than in *Trinititherium* and *Kermackia.*

Turnbull (1971) grouped together Types 1, 2, and 5 as *Holoclemensia* and Types 3, 4, and 6 as *Pappotherium.* He included in *Holoclemensia* the specimens of Type 2 that are here regarded as *Pappotherium.* He did not consider in detail the morphological features that distinguish Type 2 from Types 1 and 5. He ascribed the differences to individual variation, to position in the series, and possibly to the presence of more than one species of *Holoclemensia.* The teeth that Turnbull identified as *Pappotherium* include those of *Kermackia* and *Trinititherium,* together with Type 4, regarded here as the last molar of *Holoclemensia.* The criteria by which he distinguished *Pappotherium* from *Holoclemensia* are those which in the present paper are used to distinguish *Kermackia* and *Trinititherium* from *Pappotherium* and *Holoclemensia.* *Kermackia* had not been described when Turnbull wrote his paper, and his supposition, that all the tribosphenic molars in the collection could be referred to *Pappotherium* or *Holoclemensia,* was not unreasonable.

There remains to be considered the lower jaw with four teeth (SMP-SMU 61992; Fig. 3, S), referred by Slaughter (1971) to *Pappotherium.* Two teeth are simple, and two are molariform. The first molariform tooth is narrower than the second and has less elevated cusps. Slaughter says the first is less worn than the second molariform tooth and identifies it as a premolar. The existence of a molariform premolar at such an early date seems very unlikely. Both molariform teeth are much more worn than the two premo-

lariform teeth, one of which is in process of eruption. Slaughter's statement (1971: 137) that X-rays showed no unerupted teeth excludes the possibility that the first molariform tooth is a milk molar. The molariform teeth must be regarded as permanent molars.

$M_1$ is similar in size to that of *Kermackia;* $M_2$ is larger than $M_1$, though it is smaller than the smallest specimen of Type 2 (PM 930). On both teeth, the tops of the trigonid cusps are broken off or worn, but the metaconid was evidently higher than the forwardly projecting paraconid. On both molars the talonid is as wide as the trigonid, and the hypoconid is buccally situated in relation to the hypoconulid. The entoconid is as high as the hypoconulid on $M_2$, but lower on $M_1$. On both molars the anterior end of the crista obliqua has been obliterated through wear, and its relations to the trigonid are uncertain. However, the metaconid of $M_2$ carries a strong posterior ridge that resembles *Kermackia* and differs from Type 2. This specimen cannot be placed in any of the species so far described, and because of its importance I propose a name for it as follows:

*Slaughteria,* gen. nov.

*Diagnosis.* $M_2$ differs from lower molars of Type 2, referred to *Pappotherium,* in that (1) the metaconid is higher than the paraconid, and (2) the metaconid has a posterior ridge, probably continuous with the crista obliqua. $M_2$ differs from lower molars of *Kermackia* in that (1) the talonid is equal in width to the trigonid, and (2) the entoconid is larger than that of *Kermackia.* There is no metaconid on the lower premolars. Type species:

*Slaughteria eruptens,* spec. nov.

*Diagnosis.* This is the only known species of *Slaughteria.*

Holotype, SMP-SMU 61992, from Butler Farm. Illustrated by Slaughter, 1971, Pl. 9. It is a mandibular fragment with two molars and two premolars, the anterior premolar in process of eruption.

## PREMOLARS

The last premolar of *Slaughteria* is a two-rooted tooth with a well developed, one-cusped heel but no anterior cusp. The anterior premolar is smaller and seemingly has a single root. There are some isolated two-rooted premolars from Greenwood Canyon. PM 1247 (Fig. 4, a) is larger than the last premolar of *Slaughteria.* It has a

small posterior heel and an anterior basal cusp which is displaced towards the lingual side, indicating that the tooth is from the lower jaw. PM 1098 (Fig. 4, b) is the posterior part of a lower premolar, probably a little larger than PM 1247 and with a larger, two-cusped heel. PM 1136 (Fig. 4, c) is a much smaller tooth with no anterior
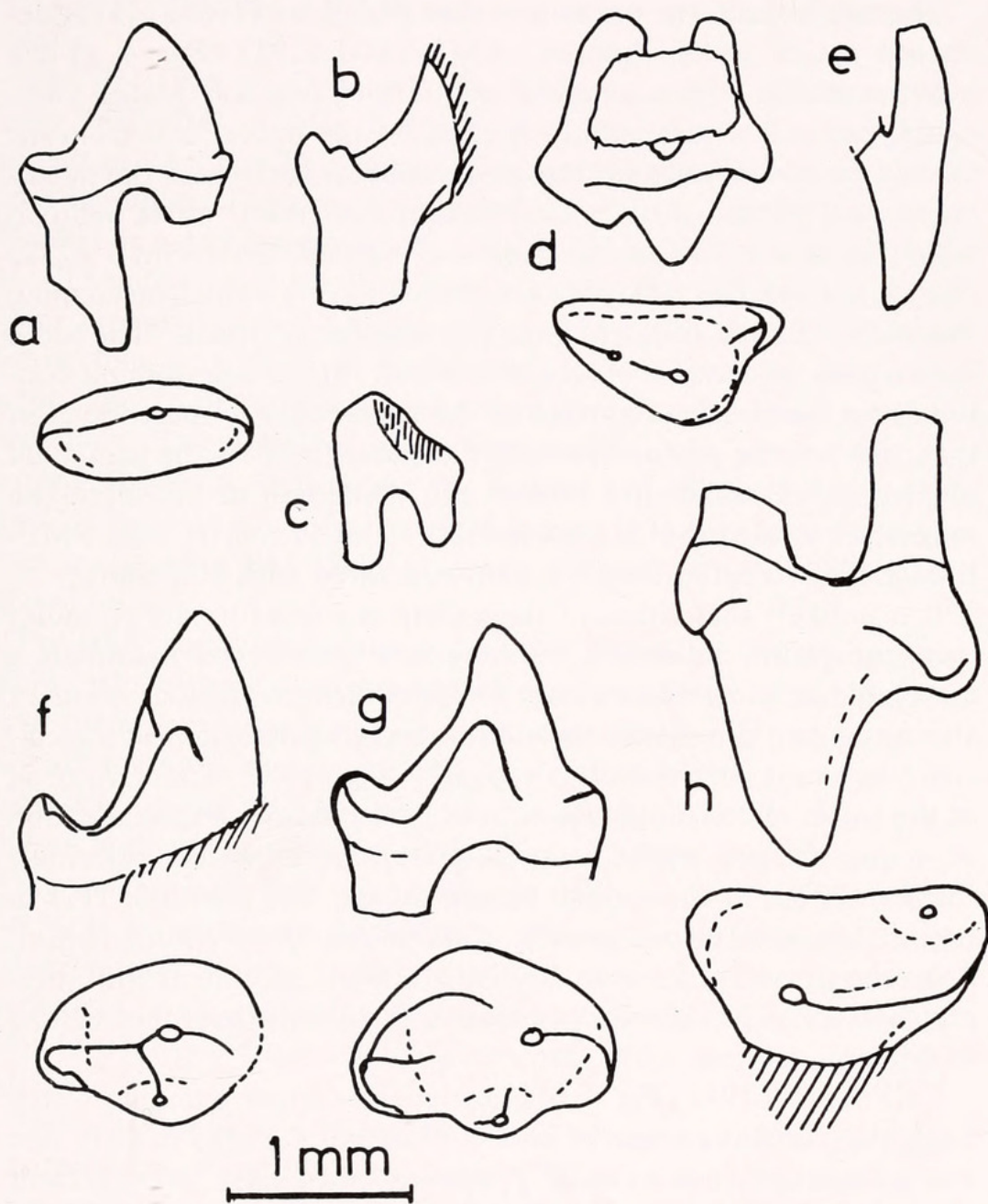


Figure 4.    Premolars and canine. a, PM 1247, lingual and crown views; b, PM 1098, lingual view; c, PM 1136, ? buccal view; d, PM 931, buccal and crown views; e, PM 1124; f, SMP-SMU 62399, lingual and crown views (from a cast); g, SMP-SMU 61947, lingual and crown views; h, SMP-SMU 61948, buccal and crown views.

cusp or posterior heel. Its anterior profile is strongly convex, and there is a posterior crest which shows wear. None of the Texas specimens resembles the Wealden specimen that Clemens (1963, Fig. 10) described. The latter is a narrow tooth with divergent roots and a low crown, having the appearance of a milk molar. SMP-SMU 61730 and 61731 (Slaughter 1965, Fig. 5) are triconodont.

The submolariform premolars that Slaughter (1968a, 1971) described are of greater interest. SMP-SMU 61947 (Fig. 4, g) is a lower premolar with a small talonid, a low, lingually placed paraconid, and a low metaconid. A crest on the buccal side from the talonid cusp continues up the posterobuccal surface of the protoconid. In addition, there is a median talonid crest (=crista obliqua) which terminates at the base of the trigonid. SMP-SMU 62399 (Fig. 4, f) resembles SMP-SMU 61947 in having a small metaconid, but it differs from that specimen in a number of details. The tooth is narrower and the protoconid is taller. The crista obliqua continues up the posterior surface of the protoconid to meet the crest that connects the protoconid with the metaconid. As the paraconid of SMP-SMU 62399 has broken off, the length of the tooth can only be estimated, but it was probably a little shorter than SMP-SMU 61947 (length about 1.4 mm, compared with 1.55 mm).

It is unlikely that either of these teeth is a penultimate premolar (conventionally called $P_3$). Among late Cretaceous mammals a metaconid is known on $P_3$ only in *Gypsonictops*. In that genus $P_3$ also has a partly molariform talonid, and its possession of a metaconid can be ascribed to the unusually high level of molarization of the tooth. Such molarization is almost certainly a specialization of *Gypsonictops*, unlikely to be present in ancestral placentals (Butler 1977). A metaconid occurs on the last premolar ($P_4$) in several late Cretaceous genera: *Zalambdalestes, Protungulatum, Procerberus* and *Batodon*. Both the Albian specimens are interpreted as $P_4$. The differences between them show that they belong to different species.

SMP-SMU 61948 (Fig. 4, h) is a triangular upper premolar which Slaughter (1968a) compared with a placental $P^3$. The lingual lobe was broken off, but a small protocone must have been present originally. The paracone is a tall cusp, similar in height to the protoconid of SMP-SMU 62399. There is no metacone. This tooth resembles $P^3$ of *Asioryctes*, but whether it is a $P^3$ or a $P^4$ is uncer-

tain. In *Asioryctes,* as in *Kennalestes* and *Zalambdalestes,* the paracone of $P^3$ is higher than that of $P^4$ and subequal to the protoconid of $P_4$. However, $P^3$ may have been secondarily enlarged (Butler 1977). There is no metaconid on the lower premolars of *Kennalestes* and *Asioryctes,* and comparison with these genera may be misleading. In Cretaceous marsupials, such as *Alphadon,* the last upper premolar is the largest, and this is true also of *Deltatheridium.*

PM 931 (Fig. 4, d) is an upper premolar which differs greatly from SMP-SMU 61948. It has a metacone on the shearing crest, but no protocone. This last cusp is represented only by an indistinct cingulum. The strongly developed shearing crest suggests that PM 931 is a last premolar that functioned against the trigonid of $M_1$. The absence of the protocone suggests that the corresponding lower premolar lacked a metaconid, and therefore that PM 931 did not occlude with either of the known complex lower premolars. It is too large to fit the lower dentition of *Slaughteria.* There are only two roots. The posterior one is flattened in cross section and arranged obliquely, to support the lingual as well as the posterior apex of the crown. A similar arrangement is known in symmetrodont molars, but PM 931 is much too large to be referred to *Spalacotheroides.*

Probably some of the submolariform premolars belong to species of which the molars are already known. Only in *Slaughteria* have premolars been found in association with molars, and there the last premolar has no metaconid. In *Slaughteria,* the length of the last premolar is 65 per cent of that of $M_2$. The two lower premolars with metaconids are as long as or longer than the molars of *Kermackia* and *Trinititherium,* and they are therefore probably too large to belong to these forms. Moreover in *Kermackia* and *Trinititherium* the crista obliqua on the molars runs directly to the metaconid. The possibility that the submolariform premolars belong to *Pappotherium* or *Holoclemensia* must therefore be considered.

The crista obliqua of SMP-SMU 62399 resembles that of Type 2 (supposedly *Pappotherium*) molars in meeting the protoconid-metaconid crest, whereas that of SMP-SMU 61947 fades out near the base of the trigonid as on *Holoclemensia* molars. In the late Cretaceous marsupials, *Alphadon* and *Pediomys,* the last lower

premolar is about three-quarters as long as the longest molar, and in the placental *Kennalestes* the proportion is about 80 per cent. SMP-SMU 61947 is 80 per cent as long as PM 1005, interpreted as $M_2$ of *Holoclemensia;* the somewhat shorter SMP-SMU 62399 would bear about the same proportion to PM 965, the largest supposed *Pappotherium* molar. Size as well as structure is therefore consistent with the reference of SMP-SMU 61947 to *Holoclemensia* and SMP-SMU 62399 to *Pappotherium.*

The upper premolar SMP-SMU 61948 would fit either of the two complex lower premolars. It possesses a strongly developed stylar cusp on the buccal edge, anterior to the metastyle. This cusp might be considered serially homologous with Style C of the molars. For this reason I refer SMP-SMU 61948, tentatively, to *Holoclemensia* as a $P^4$ or $P^3$.

PM 931 (Fig. 4, d) is too small and its shearing crest too longitudinal to have functioned against the trigonid of PM 966, the supposed $M_1$ of *Holoclemensia.* The absence of the protocone on the premolar suggests that this cusp was relatively small on the molars. Perhaps this tooth belongs to the same species as the last molar PM 1287 (Fig. 2, p) in which the protocone is small.

The mandible PM 583 (Patterson 1956, Figs. 10, 11) contains alveoli for four two-rooted premolars. The posterior alveoli are of a size to fit *Kermackia* molars and are probably too large for premolars of that genus. The last pair of alveoli, however, could have held either of the premolars with metaconids, and the simple premolar PM 1247 would fit the alveoli for $P_3$. There is a possibility that this mandible belongs to either *Holoclemensia* or *Pappotheium.* The remarkably large canine alveolus differentiates this specimen from SMP-SMU 62400 (Slaughter 1971, Pl. 10), a fragment containing a small, procumbent canine. PM 1124 (Fig. 4, e) is an upright two-rooted canine of small size, probably from the upper jaw. The mandible PM 583 contains alveoli for four lower incisors. Slaughter (1971, Pl. 10) described a rather large, spatulate upper incisor.

## DISCUSSION

### Number of Genera Represented

The material from the Albian of Texas consists almost entirely of isolated teeth. Until more complete specimens are discovered,

any interpretations or conclusions must remain highly speculative. Differences in the molars, premolars, canines and incisors indicate that a number of distinct taxa are present, at least on the generic level. In attempting to allocate the various sorts of teeth, I have avoided the introduction of additional taxa as far as possible. The minimum number of taxa necessary to include the known molars seems to be the following six:

1. *Holoclemensia,* the largest form, is represented by several upper and lower molars; complex upper and lower premolars are allocated to this form.

2. *Pappotherium,* a somewhat smaller form, is represented again by several upper and lower (Type 2) molars; a complex lower premolar is referred to it.

*Holoclemensia* and *Pappotherium* are the most common members of the fauna, but *Pappotherium* seems to be relatively more common at Greenwood Canyon than at Butler Farm. The toothless mandible may belong to either genus.

3. *Slaughteria* is represented by a single mandibular specimen, which is the only one to show associated molar and premolar teeth; it is smaller than *Pappotherium.*

4. *Kermackia* is a small form known only by three lower molars.

5. *Trinititherium,* similar in size to *Kermackia,* is known by one complete lower molar and two trigonids. The small upper molar SMP-SMU 62402, and the last molar PM 1075 may belong to either *Kermackia* or *Trinititherium.*

6. The last upper molar PM 1287 and the upper premolar PM 931 do not appear to belong to any of the foregoing and probably represent one or two additional species.

## The Family **Pappotheriidae**

As interpreted here, *Pappotherium* and *Holoclemensia* are much alike in the organization of their molar series. Both have four molars, of which the second is the largest, and in the upper jaw, $M^3$ is reduced posterobuccally. $M^1$ of *Holoclemensia* is more symmetrical than in *Pappotherium,* and $M^3$ less so, but such differences are to be found frequently in closely related genera of mammals.

There is a wide stylar shelf in both genera. The trigonid is elevated, and it has a well developed, trenchant paraconid. The talonid is narrower than the trigonid. The lower molars have no cingu-

lum except on the anterior surface of the protoconid. The last lower premolar has a metaconid and, at least in *Holoclemensia,* the last upper premolar has a protocone.

The large Style C of *Holoclemensia* is represented in some specimens of *Pappotherium* by a minor elevation of the buccal marginal ridge. The metacone of *Holoclemensia* is larger in comparison with the paracone than in *Pappotherium.* The lower molars of *Holoclemensia* have a more compressed trigonid, a higher metaconid, and a more buccally situated hypoconid. The crista obliqua in *Holoclemensia* fades out at the base of the trigonid, whereas in *Pappotherium* it continues up the trigonid wall. These differences seem insufficient to place the two genera in separate families, and I propose to include them both in the Pappotheriidae Slaughter 1965.

## Relationship of Pappotheriidae to Marsupials and Placentals

The Pappotheriidae agree with the primitive marsupial *Alphadon* in the possession of four molars and in the wide stylar shelf of the upper molars. *Holoclemensia* resembles *Alphadon* in having a distinct Style C, but in *Alphadon* this is smaller than the stylocone (Style B), and it varies in size between the species. In *Alphadon* $M^3$ is the largest molar, and its posterobuccal apex and metastylar blade are not reduced. A further difference appears to be that the protocone shelf of *Alphadon* is better differentiated with more strongly developed conules. In *Alphadon* the metacone is as tall or taller than the paracone; *Holoclemensia,* with its larger metacone, approaches *Alphadon* in this respect more closely than *Pappotherium* does.

The lower molars of Pappotheriidae resemble *Alphadon* in the trenchant paraconid and in the connection of the crista obliqua to the middle of the posterior trigonid wall. However, in the marsupials the talonid is as wide as the trigonid, sometimes wider. The hypoconulid is in a lingual position, close to the entoconid, and a cingulum, arising from the hypoconulid, passes behind the hypoconid. In pappotheriids the trigonid, especially in *Holoclemensia,* is more elevated. *Holoclemensia* also differs from *Alphadon* in that the trigonid is more compressed on $M_2$-$M_4$. The metaconid is higher than the paraconid, and the hypoconid is higher in comparison with the entoconid on $M_2$ and $M_3$. *Pappotherium* (i.e. Type 2)
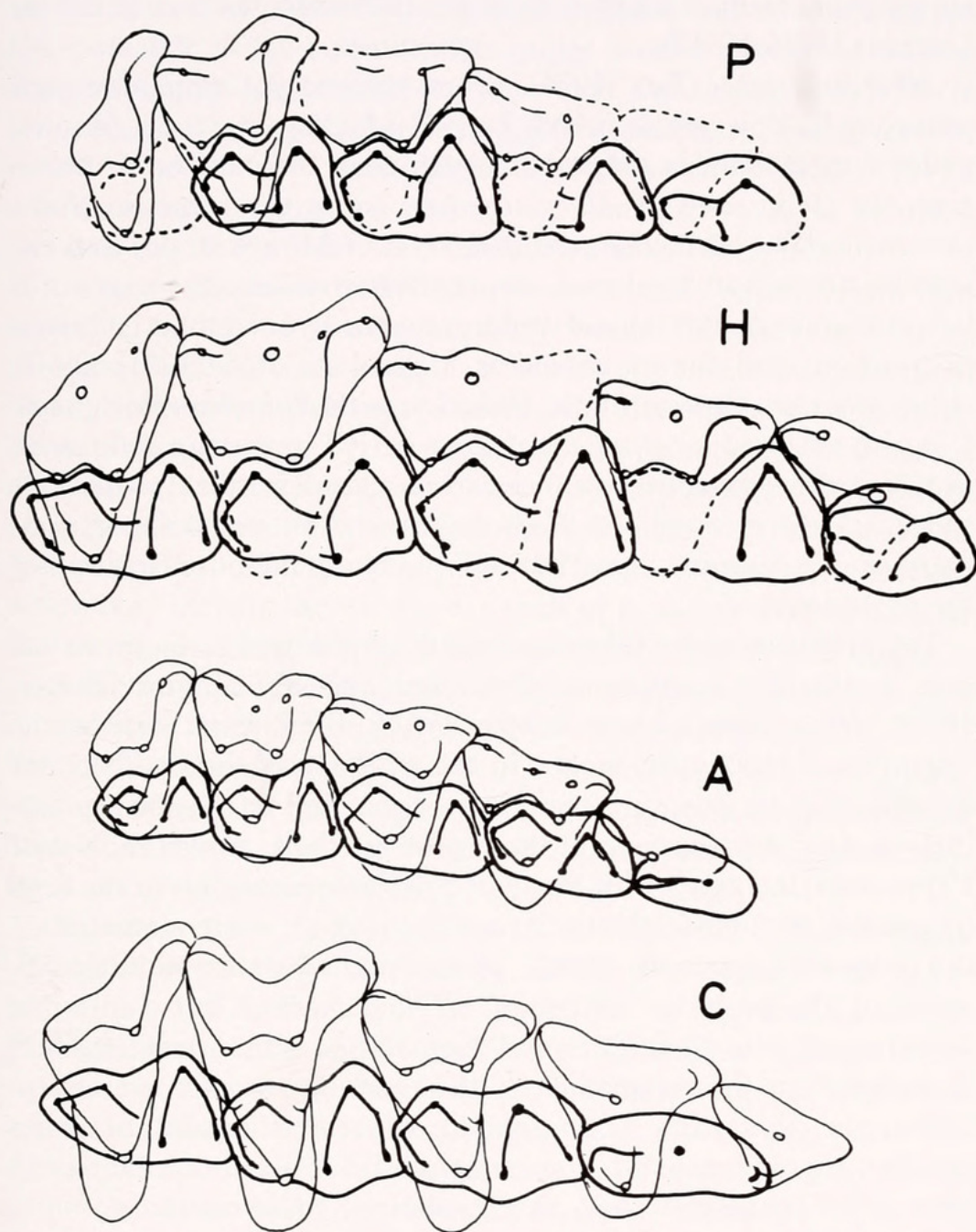
Figure 5.    Reconstructions of cheek teeth in occlusion. P. *Pappotherium patter-soni;* H, *Holoclemensia texana;* A, *Alphadon marshi* (a marsupial); C, *Cimolestes incisus* (a placental).

Specimens used in the reconstruction of *Pappotherium:* M$^1$, PM 999; M$^2$, PM 894; M$^3$ and M$^4$, the holotype; P$_4$, SMP-SMU 62399; M$_1$, PM 930; M$_2$, PM 965; M$_3$, PM 948.

Specimens used in the reconstruction of *Holoclemensia:* P$^4$, SMP-SMU 61948; M$^1$, PM 1000; M$^2$, PM 886; M$^3$, the holotype; M$^4$, the paratype; P$_4$, SMP-SMU 61947; M$_1$, PM 966; M$_2$, PM 1005; M$_3$, SMP-SMU 61727; M$_4$, SMP-SMU 61726.

agrees more with *Alphadon* in these characters, as was noted by Clemens (1966:16–17).

*Albertatherium* (Fox 1971), from the early Campanian, approaches *Holoclemensia* in that Style C is higher than the stylocone, and the metaconid is somewhat higher than the paraconid. However, the stylar shelf of *Albertatherium* is narrower than in *Holoclemensia*. The metacone and metastyle of $M^3$ are larger, and the conules are better developed. On the lower molars, the trigonid is less compressed; the talonid wider; and the hypoconulid is lingual in position, and the entoconid is higher. As Fox (1971) noted, *Albertatherium* does not link *Alphadon* with *Holoclemensia*. Style C is also enlarged in *Aquiladelphis,* an early Campanian pediomyid in which the stylocone is reduced to two small cusps. In other respects this form resembles *Holoclemensia* even less than *Albertatherium;* for example, the crista obliqua meets the posterior wall of the protoconid.

The primitive eutherian molar pattern is believed to be preserved best in the late Cretaceous *Cimolestes* and *Kennalestes* (Butler, 1977). *Holoclemensia* and *Pappotherium* differ from these in the retention of the fourth molar, in the wide stylar shelf with better developed styles posterior to the stylocone, and in the correspondingly weaker development of the protocone shelf. Lower molars of Pappotheriidae agree with those of primitive placentals in the high trigonid and comparatively narrow talonid, in the connection of the crista obliqua to the middle of the trigonid wall, and in the absence of the posterior cingulum. *Holoclemensia,* not *Pappotherium,* agrees with *Cimolestes* and *Kennalestes* in that the metaconid is higher than the paraconid. If the tooth has been correctly referred, the possession of a premolar protocone would constitute another resemblance of *Holoclemensia* to placentals. However, there is no metaconid on $P_4$ in *Cimolestes* or *Kennalestes.*

Fox (1975) noted a resemblance in the outlines of the last two upper molars between *Holoclemensia* and the late Cretaceous *Deltatheroides,* which has four molars. He concluded that *Holoclemensia* must have four molars. Because the penultimate molar of *Pappotherium* shows less reduction in the metastyle, Fox inferred that only three molars were present in that genus. I find his argument unconvincing; the relationship between the shapes of teeth and their numerical position is too inconstant for such deductions

to be made. Late Cretaceous didelphids have four molars, and yet the metastyle of their penultimate molar is more developed than in *Pappotherium*. *Deltatheroides,* in which the metastyle of $M^3$ is reduced, can be regarded as being in the process of losing its $M^4$, which is absent in *Deltatheridium* (Kielan-Jaworowska 1975); *Holoclemensia* might by analogy be considered to be evolving towards the three-molar state characteristic of placentals.

It seems impossible to fit *Holoclemensia* and *Pappotherium* into a simple metatherian-eutherian framework. They have a mixture of characters which indicate that they belong to neither infraclass. Though *Holoclemensia* approaches primitive marsupials in some ways, *Pappotherium* is more like them in others; *Holoclemensia* also shows some resemblances to primitive placentals. No doubt some of the characters that pappotheriids share with marsupials or placentals are plesiomorphs inherited from a common ancestor, which may include the wide stylar shelf of primitive marsupials and the narrow talonid of primitive placentals. The fourth molar is probably another plesiomorphous character lost in placentals but retained in Deltatheridiidae (Butler & Kielan-Jaworowska, 1973; Kielan-Jaworowska, 1975) as well as in marsupials. Other shared characters may be due to parallel evolution, such as the enlarged Style C. The metaconid of $P_4$ may also have evolved independently, for it occurs in some placentals but not in others.

Placentals have been reported from Khovboor in Mongolia (Beliajeva et al., 1974; Dashzeveg, 1975) in a deposit that is believed to be of Aptian age. The fauna, still undescribed, is said to contain forerunners of the much later Djadokhta fauna. If the Aptian age of these specimens is correct, the divergence of placentals and marsupials must already have taken place at that time. The Albian Pappotheriidae would in that case be too late to be the common ancestors of the two infraclasses. Clemens (1971: 174) states that "The evidence . . . does not exclude the possibility that when the tribosphenic grade of dental evolution was attained an adaptive radiation occurred producing lineages in addition to those ancestral to marsupials and placentals." The Pappotheriidae may well have belonged to one such lineage.

During much of the Cretaceous the land surface was more than usually fragmented by epicontinental seas (Lillegraven, 1974; Telford, 1974). North America was divided, from middle Albian time

onwards, into eastern and western land-masses by the Interior Seaway. The northern part of the Atlantic was closed: the seaway between Greenland and Canada developed only in the Campanian (Martin, 1973). Europe was separated from Asia by the Turgai Strait. In mid-Cretaceous time, eastern North America and Europe thus formed a single continent from which the mammals from Texas are the only known representatives of their class. Following Lillegraven (1974) one may imagine a wide dispersal, in the early Cretaceous, of an ancestral group with tribosphenic molars, of which *Aegialodon,* from the English Wealden, is the only known example. Subsequently isolated on different land-masses, the ancestral group gave rise to the placentals in Asia and the marsupials in western North America (or as Telford (1974) suggests, in South America). Possibly the Pappotheriidae represent another lineage that evolved on the Euramerican continent, but subsequently became extinct. A molar from the Campanian of Champ-Garimond, France (Ledoux et al., 1966; Butler, 1977) might conceivably be a pappotheriid derivative, but it is more advanced, and it might equally well be a placental immigrant from Asia.

## Kermackiidae, *Fam. nov.*

*Kermackia* and *Trinititherium* are distinguished from *Pappotherium* and *Holoclemensia* by the continuation of the crista obliqua to the tip of the metaconid, so that on the posterior surface of that cusp it forms a ridge (the distal metacristid of Fox, 1975). The talonid is narrow, its basin is widely open lingually, and the entoconid is small or rudimentary. These genera are at a lower level of molar evolution than the Pappotheriidae. In the latter the connection of the crista obliqua to the trigonid has shifted to a more buccal position, the talonid is wider, and the entoconid is larger. Dashzeveg (1975) noted the resemblance of *Kermackia* to *Aegialodon* and *Kielantherium,* which belong to the family Aegialodontidae Kermack (1957). However, these differ from *Kermackia* in having the talonid reduced in length as well as in width. Because of this difference I propose the family Kermackiidae to include *Kermackia* and *Trinititherium.* The Kermackiidae resemble the Aegialodontidae in retaining the distal metacristid but differ from them in that the talonid is equal in length to the trigonid. The

Aegialodontidae, Kermackiidae and Pappotheriidae represent three stages in the evolution of the talonid (Fig. 6).

*Slaughteria,* which probably possesses a distal metacristid, has a wide talonid, and (on $M_2$, but not on $M_1$) a fully developed entoconid like the Pappotheriidae. It may represent another family, but, as some doubt remains over the details of the molar pattern, I prefer to place *Slaughteria* provisionally in the Kermackiidae. To judge from the relative size of the penultimate premolar, the number of premolars may bave been reduced. *Slaughteria* is the only Albian therian for which there is evidence of tooth replacement, and on this character, Slaughter (1971) placed it in the Eutheria. However, diphyodonty occurs in pantotheres (Butler & Krebs, 1973), and it must be considered a plesiomorphous character, re-
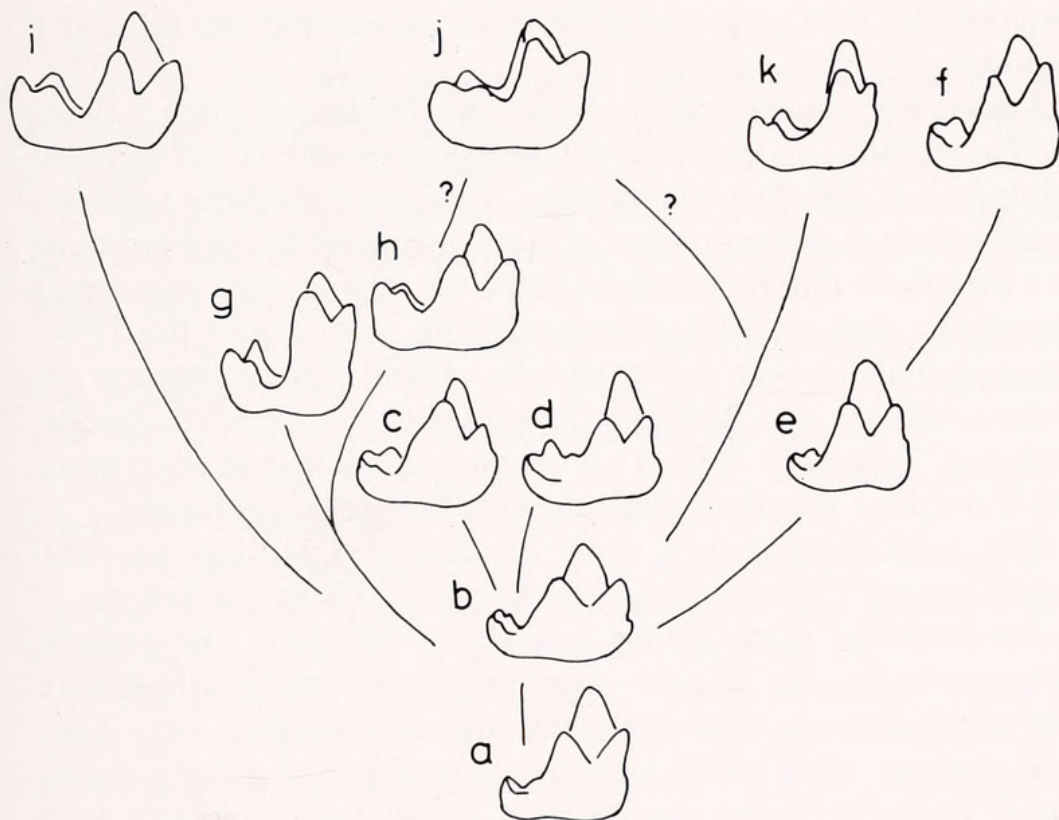


Figure 6.  Left lower molars in lingual view, to illustrate possible evolutionary radiation in the early Cretaceous. a, *Peramus* (Pantotheria); b, *Aegialodon;* e,*Kielantherium* (Aegialodontidae); c, *Kermackia;* d, *Trininitherium* (Kermackiidae); f, *Deltatheridium* (Deltatheridiidae); g, *Holoclemensia;* h, *Pappotherium* (Pappotheriidae); i, *Alphadon* (Metatheria); j, Champ-Garimond molar; k, *Kennalestes* (Eutheria).