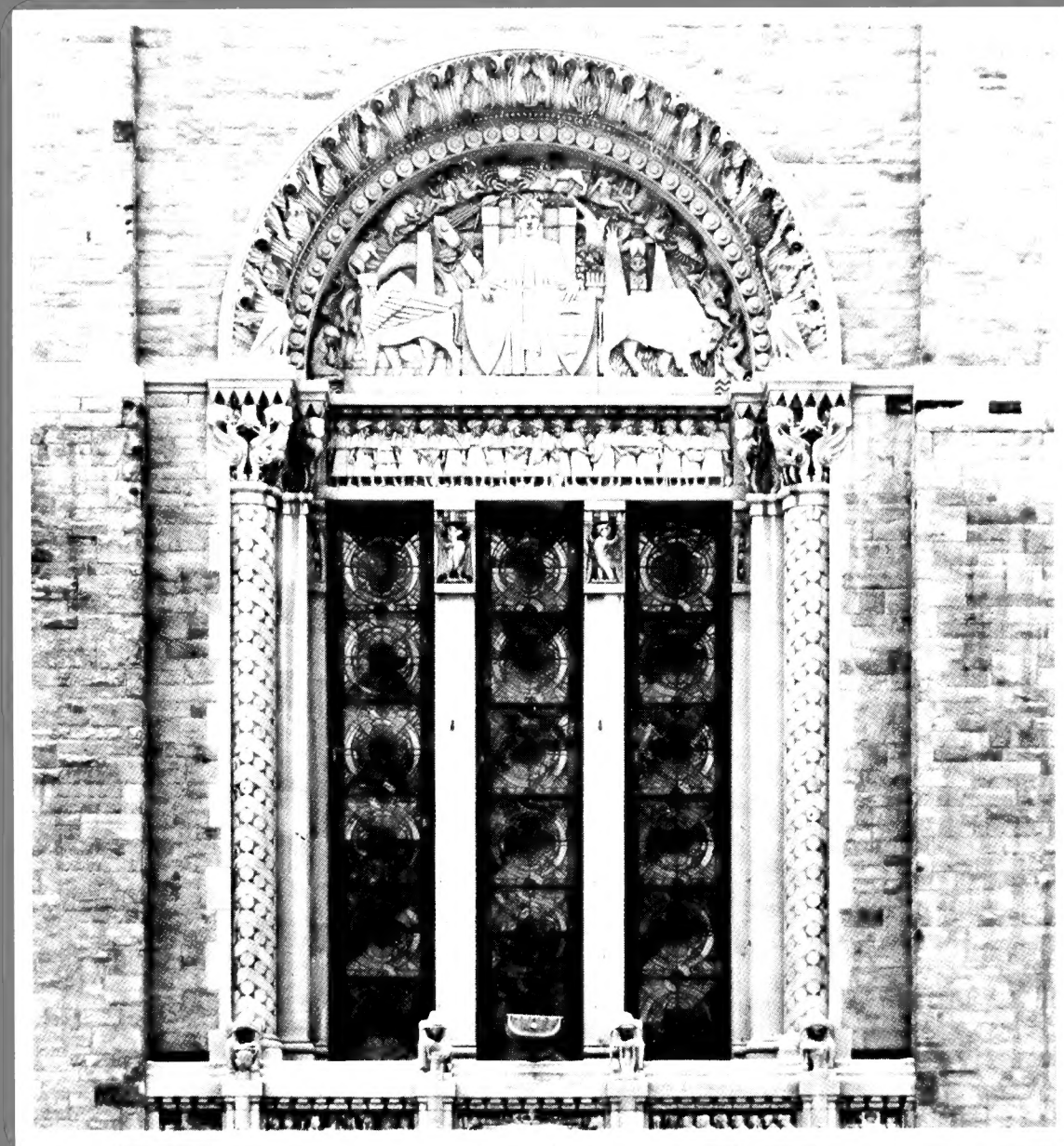


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Tertiary Mammals of Saskatchewan
Part VII
Oligocene Marsupials

Loris S. Russell

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Tertiary Mammals of Saskatchewan
Part VII: Oligocene Marsupials

Loris S. Russell



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Tertiary Mammals of Saskatchewan

Part VII: Oligocene Marsupials

Abstract

Large collections of marsupial teeth from the Lower Oligocene Cypress Hills Formation of Saskatchewan are preserved in the Saskatchewan Museum of Natural History and the Royal Ontario Museum. The majority of these specimens are referable to *Peratherium valens* (Lambe). The upper molars show much variation in the development and location of the various stylar cusps, but these differences appear to be intraspecific. *P. valens* and other Oligocene and Miocene species of *Peratherium* from North America make up a group for which subgeneric status as *Herpetotherium* is appropriate. Eocene species of *Peratherium* from North America are not separable generically from those of Europe. The genus was probably derived from a branch of the Cretaceous *Alphadon* in which dilambdodonty had already begun to develop. Upper molars previously referred to *Nanodelphys? mcgrewi* are made the basis for a new genus *Alloeodectes*, related to *Mimoperadectes* and *Nanodelphys*. Didelphid lower teeth of uncertain generic affinities are described.

Introduction

Oligocene marsupials from North America were first reported by Cope (1874) and more fully described by Cope (1884). These were from the so-called Cedar Creek beds of northeastern Colorado, part of the White River Group of that state. The first record of a Canadian occurrence was by Lambe (1908) from the Cypress Hills Formation of Saskatchewan. Additional specimens from this provenience, obtained over the years by field parties from the National Museums of Canada and the Royal Ontario Museum, were described by Russell (1972). Meanwhile, the Saskatchewan Museum of Natural History developed a semimechanical screening device, and field parties under Bruce A. McCorquodale and Albert Swanston used this equipment to obtain an impressive collection of small vertebrate remains, especially from a site in Calf Creek Valley (locality 117 of Fenley Hunter; see Russell, 1972). This collection included numerous marsupial teeth. Most of this "micro-vertebrate" material has remained undescribed

until recently. In 1972 a field party from the Royal Ontario Museum, under Gordon Gyrmov, exploited the same locality, using an electrically driven screening device developed by the writer.

The present account is based on the marsupial specimens in the Saskatchewan Museum collection, generously assigned to me by Dr John E. Storer, Curator of Earth Sciences, and those in the Royal Ontario Museum collected by Gyrmov. It is intended as a supplement and revision of the description of Cypress Hills marsupials given by me previously (Russell, 1972:6–9).

Museums in which the catalogued specimens are preserved are indicated by the following abbreviations: NMC, National Museum of Natural Sciences, National Museums of Canada; ROM, Department of Vertebrate Palaeontology, Royal Ontario Museum; SMNH, Saskatchewan Museum of Natural History.

Systematic Description

Order Marsupialia Family Didelphidae

Genus *Peratherium* Aymard, 1850

TYPE SPECIES

Didelphis elegans Aymard, 1846

GENERIC CHARACTERS

Small didelphids with dentition closely resembling that of *Didelphis*. M^1 to M^3 broadly and obliquely triangular, dilambdodont (i.e., with W-shaped ectoloph); paracone smaller than metacone, but distinct; metaconule usually present; protoconule vestigial or absent; stylar cusp A reduced or absent; cusp B small to relatively large; anteriorly placed; cusp C or D moderate to large. M^4 much narrower anteroposteriorly than the more anterior molars, narrowly dilambdodont; paracone larger than metacone; buccal margin very oblique; stylar cusp B moderate, cusp C relatively large, cusp D absent. P_4 larger than P_3 . M_1 to M_3 with talonid wider than trigonid; hypoconulid close to, or at, posterolingual angle of crown, almost directly posterior to entoconid. M_4 with trigonid wider than talonid; hypoconulid about midway between hypoconid and entoconid, and produced posterad.

REMARKS

The genus *Herpetotherium* was proposed by Cope (1873, 1874), type species *H. fugax*, from the Lower Oligocene of Colorado. Most subsequent authors, including Cope (1884:789), regarded this genus as a synonym of *Peratherium*; exceptions were Troxell (1923) and Hough (1961). The latter author defined *Herpetotherium* mainly on the basis of an uninflected or only slightly inflected mandibular angle. This is a very doubtful character in fossils that usually have been subjected to crushing. Crochet (1977) restricted *Peratherium* to the European species, implying that all of the North American species referred to *Peratherium* could be separated under *Herpetotherium*. Krishtalka and Stucky (1983a), in contrast, retained the Eocene species from North America in *Peratherium*, separating *Herpetotherium* on the basis of "the distinctive anterior dentition". For reasons discussed below, *Herpetotherium* is here regarded as a subgenus of *Peratherium*, restricted at present to the post-Eocene species.

Peratherium valens (Lambe)

Didelphys valens Lambe, 1908:22, 23, pl. 8, figs. 1-7.

TYPE

NMC 6249, right M^1 or M^2 .

SPECIFIC CHARACTERS

Molar teeth relatively large for the genus. Stylar cusp A reduced to an anterad-projecting spur, or absent. Stylar cusp B relatively small, usually at buccal end of preparacrista; may be at anterobuccal angle of crown or posterior to this. No distinct stylar cusp opposite paracone. Large stylar cusp adjacent to mesostylar position, corresponding either to cusp C or cusp D. Lower molars with trigonid slightly inclined anterad; hypoconulid on M_1 to M_3 set in slightly from directly behind entoconid; on M_4 , medially situated and projecting posterad.

DESCRIPTION

The Cypress Hills specimens assigned to this species show great variability in the upper molars, especially in the stylar shelf and its marginal cusps. Four representative examples are described; other variations are dealt with in a more general description.

The type specimen of the species, NMC 6249 (see Russell, 1972, fig. 1A), displays the particular development of the stylar cusps that is commonest in the combined collections. Among the new specimens, SMNH P661.401 (Fig. 1A) resembles the type closely, although it is a left, rather than right, upper molar, probably M^2 . The outline of the crown is relatively narrow anteroposteriorly, and the buccal margin is more nearly at right angles to the anterior margin than is usual. As a result, the posterobuccal angle of the crown is directed more posterad than buccad. The buccal margin is moderately concave in front of midlength, slightly convex behind. There is no cusp A or even an anterobuccal spur; this corner is actually rounded. Cusp B is close behind, moderately prominent but with no distinct marginal bulge; it is at the end of a long, slightly recurved preparacrista. There is no cusp on the buccal flank of the paracone (cusp C), but there is a very prominent cusp D located posterior to the premetacrista, with a faint suggestion of a cusplule on its anterior flank. The metaconule, unlike the other cusps, has been worn to a facette, but evidently it was a distinct prominence at the buccal end of the short postprotocrista. There is a faint suggestion of a protoconule.

SMNH P1585.642 (Fig. 1B), a left M^2 , is slightly broader anteroposteriorly. Cusp D is without any satellite cusplule,

and is located a little more anterior, opposite the end of the premetacrista. There are no conules at the abrupt ends of the protocristae. The lingual margin of the crown is more broadly rounded than that of P661.401.

Other upper molars that show structure similar to that described above are SMNH P661.399, P1585.620, P1585.642, P1585.654, P1585.661, P1585.665, P1585.671, P1585.677, P1585.684, P1585.687, P1585.692, P1585.697, P1585.698, P1585.706, P1585.710, P1585.716, P1585.728, P1585.733, P1585.735. Some variation may be seen in the degree of concavity of the buccal margin anterior to cusp D, and in the location of cusp D, which varies from near the mesostyle position to a point opposite the metacone. Some specimens have a short cingulum on the anterior face of the crown, adjacent to cusp B.

A few other upper molars are similar to P661.401 but show a more complex cusp D, with a small cusplike spur on its anterior flank; examples are seen in P661.403, P1585.641, P1585.676, P1585.682, P1585.686, and P1585.709. On P1585.738 and ROM 23227 (Fig. 1C), cusp D has a double apex, the more posterior in the normal cusp D position, the anterior opposite the juncture of postparacrista and premetacrista (mesostyle position).

The most important variation in the stylar cusp structure described above, and one that is represented by almost as many specimens, is that in which stylar cusp A is present. This may be merely an anterad projection from the anterobuccal angle of the crown, or in its extreme development, a curved spur with a cusplike vertical prominence. An example is P1585.704 (Fig. 1D), presumably a right M³. The crown is relatively narrow anteroposteriorly, as in the type of the species and in P661.401, described above. One difference is the concave, rather than straight or convex, posterior portion of the buccal margin. Cusp D is in line with the premetacrista, but the anterobuccal angle of the crown is formed by the anterad-projecting, closely attached cusp A, which has its own vertical apex, although less prominent than cusp B. Extending linguad from cusp A, but not confluent with it, is a distinct cingulum, which reaches a point opposite the paracone apex. There is a conular prominence at the buccal end of the postprotocrista but none on the preprotocrista.

A more usual form of cusp A is seen on SMNH P1585.736 (Fig. 1E), a right M¹ or M² with unworn cusps. Cusp A is a rounded, anterad-projecting spur from the large cusp B, but without an apex of its own. There is a short but prominent anterior cingulum as in P1585.704. The most conspicuous feature of P1585.736 is its cusp D, which is almost as prominent as the metacone and projects posterobuccad as well as vertically. There is a distinct metaconule on the postprotocrista.

Other specimens that have a cusp-A spur along with a simple cusp D are SMNH P661.400, P1585.659, P1585.691, P1585.696, P1585.699, P1585.702, P1585.705, P1585.707,

P1585.712, P1585.714, P1585.715, P1585.717, P1585.718, P1585.719, P1585.721, P1585.722, P1585.737, and ROM 23228.

A smaller group of upper molars has the cusp-A spur more or less developed, together with a small but distinct stylar cusplike spur anterior to cusp D. A good example is SMNH P1585.667 (Fig. 1F), a left M¹. On this, the cusp-A spur has a small but distinct apex. Anterior to cusp D along the stylar rim is a smaller, ovoid cusp, adjacent to the juncture of postparacrista and premetacrista (mesostyle position). The postprotocrista ends abruptly, without a distinct metaconule. Other specimens showing a similar combination of cusp structure are SMNH P1585.690, P1585.713, P1585.720, P1585.732, P1585.737, ROM 23229 and 23231. On ROM 23232, the anterior cusplike spur is very distinct and is followed behind by a smaller cusplike spur on the anterior ridge of cusp D.

The remaining upper molars to be noted here are distinguished by having the main stylar cusp located at or in front of the juncture of postparacrista and premetacrista. It is thus by definition cusp C, and will be referred to as such here. I suspect, however, that the cusps referred to here as cusps C and D are the same cusp, differing only in a slightly more anterior or posterior position.

As in the case of the upper molars showing stylar cusp D, described above, those with the so-called cusp C are divisible according to the presence or absence of cusp A. In the latter category a good example is ROM 23226 (Fig. 1G), a right M³, in which the buccal margin is biconcave, with a deep concavity in front of cusp C and a less pronounced concavity behind. This gives the two buccal angles the appearance of a pair of horns. Cusp B is terminal at the anterobuccal angle, forming a rounded bulge. There is nothing that can be identified as cusp A, but there is a short cingulum extending linguad from the side of cusp B. Cusp C is conspicuous, conoid rather than ovoid in shape, and without any subsidiary cusplike spur. It is exactly in the mesostyle position, at the junction of postparacrista and premetacrista.

A number of other specimens show the same combination of cusp C with a terminal cusp B. In most of these the buccal margin is deeply concave or biconcave. A few have a cusp C with two small apices rather than a single apex. Specimens with cusp C but no cusp A are SMNH P661.394, P661.395, P1585.623, P1585.633, P1585.643, P1585.648, P1585.651, P1585.653, P1585.657, P1585.668, P1585.670, P1585.672, P1585.673, P1585.675, P1585.683, P1585.688, P1585.689, P1585.701, P1585.723, P1585.727, and P1585.729.

The combination of cusp C with a distinct cusp-A spur is shown by SMNH P1585.621 (Fig. 1H), a right M³. It is relatively narrow anteroposteriorly, and has a deep concavity between the two convex extremities. Cusp C is rounded, and has a suggestion of a subsidiary cusplike spur on its anterior flank. Cusp B is almost as large, and is situated at the slightly

recurved end of the preparacrista. It is separated from cusp A by a slight sulcus. Cusp A is spurlike, with a small vertical apex. It continues linguad into a short but prominent cingulum. The postprotocrista terminates abruptly, without a distinct metaconule. There is a suggestion of a protoconule at the end of the preprotocrista.

Other specimens have both cusp C and cusp A or the cusp-A spur: SMNH P1585.624, P1585.636, P1585.650, P1585.652, P1585.662, P1585.685, P1585.693, P1585.700, P1585.708, P1585.711, ROM 23233. These teeth vary mainly in the presence or absence of subsidiary cuspules on cusp C, and in the degree of concavity of the buccal margin.

Examples of M^4 are not as numerous as the natural ratio of one in four would suggest. SMNH P1585.675 (Fig. 1I), a right M^4 , is a narrow tooth, with an oblique, sinuous buccal margin, convex in front, concave behind. Cusp A is not distinct and cusp B is low and poorly defined. Cusp C is at the mesostyle position, opposite, but well spaced from, the juncture of postparacrista and premetacrista; it is a large, rounded cusp. The paracone is the largest cusp; it is irregularly rounded and situated on the anterior rim of the crown at about midwidth. The metacone is smaller and more conoid; it is on the posterior crown margin, well lingual to the posterior angle of the crown. The protocone is low and V-shaped; the postprotocrista is worn, but may have borne a metaconule. Other examples of M^4 are SMNH P661.396, P1585.627, P1585.629, P1585.658, P1585.663, P1585.675, P1585.689, P1585.723, and P1585.729. Most of these show stylar cusp C slightly in advance of the mesostyle position, and cusp B, where preserved, terminal, without the cusp-A spur.

Lower molars are represented in the combined collections by more than a hundred specimens that are well enough preserved to show the cusp structure. As an example, SMNH P661.406 (Fig. 1J) may be described. It is a right molar, probably M_2 , but possibly M_3 . In the outline of the crown, the buccal and lingual margins are almost parallel and the posterior margin transverse, but the anterior margin is oblique, trending anterolinguad. The trigonid is much higher than the talonid, and the tallest cusp is the protoconid. The somewhat lower metaconid lies directly lingual, and the two cusps form the flat, almost vertical posterior wall of the trigonid. The paraconid is a much lower cusp, partly because it is directed more anterolinguad than dorsad. The talonid is shallowly basined. The hypoconid, at the posterobuccal angle, is like a lower version of the protoconid. Its anterior crest, the cristid obliqua, joins the rear wall of the trigonid below the apex of the protoconid. The entoconid is slightly higher than the hypoconid, and lies on the lingual margin of the crown in line with the paraconid and metaconid. The hypoconulid is a little buccad of this line, and projects posterad, forming the posterior extremity of the crown. As its lingual side

is convex and its buccal side concave, it has a distinct hook shape. The narrow cingulum extends almost continuously from below the paraconid around the buccal side of the crown and turns linguad at the hypoconid to reach the hypoconulid.

Numerous specimens of M_2 and M_3 in the combined collections show similar structure. Good examples are SMNH P661.415, P1585.744, P1585.746, P1585.751, P1585.759, P1585.761, P1585.772, P1585.829, P1585.830, P1585.849, P1585.850, P1585.852, ROM 23236, 23237, 23238, 23239, and 23240.

The M_1 differs from the M_2 in that the trigonid is much narrower than the talonid, and the paraconid is directed more anterad than linguad. As a result, the tooth is proportionately longer and narrower than M_2 . The talonids of both teeth are similar in shape, and in size and position of the cusps. Good examples of M_1 are SMNH P661.412 (Fig. 1K, L), and P1585.856.

In M_4 the talonid is distinctly narrower than the trigonid, and its buccal margin oblique, so that the hypoconid is closer to the hypoconulid than on M_3 . Examples of M_4 in the collections are SMNH P661.404 (Fig. 1M), P661.405, P1585.825, P1585.826, and ROM 23242.

MEASUREMENTS

The following measurements were made in accordance with the procedure described and illustrated by Clemens (1966:4). In the case of upper molars, the length (anteroposterior diameter) was measured parallel to the paracone-metacone axis, and the width at right angles to this axis. For the lower molars, the length was measured parallel to, and the width perpendicular to, the paraconid-entoconid axis.

	Length	Width
SMNH P1585.736, right M^1	2.1	2.7
SMNH P1585.667, left M^1	2.1	2.0
SMNH P661.401, left M^2	1.8	2.3
SMNH P1585.642, left M^2	2.2	2.7
SMNH P1585.704, right M^3	2.0	2.7
ROM 23226, right M^3	2.3	2.9
SMNH P1585.621, right M^3	2.0	2.6
SMNH P1585.675, right M^4	1.4	2.4
SMNH P661.412, right M_1	2.1	1.5
SMNH P661.406, right M_2	2.3	1.4
SMNH P661.404, left M_4	2.4	1.3

RELATIONSHIPS

The marked variation in the upper molars, especially in the relative development of the stylar cusp, might suggest that more than one species is represented in the *Peratherium* material from the Cypress Hills Formation. However, I have been unable to sort the various differences into consistent groups; there seems to be a random combination

of all of the variables. For this reason I tentatively retain all of the *Peratherium* specimens in the single species *P. valens*. The finding of upper dentitions in associated sequence might help to support or refute this assignment.

Among the species of *Peratherium* described from Oligocene formations of the western United States, there is a close resemblance of the upper molars of *P. fugax* (Cope, 1873, 1874) (see Fig. 3A, B herewith) to those of *P. valens* in which cusp B is subterminal, cusp C small or absent, and cusp D relatively large. There appears to be some variation in these characters in *P. fugax* also (Green and Martin, 1976:159). *P. youngi* McGrew, 1937, from the Lower Miocene, is similar in structure to *P. fugax*, and it is possible, as hinted by Green and Martin, that the two species are not distinct. All three species, *P. fugax*, *P. youngi*, and *P. valens*, are similar in size. The same cusp arrangement persists in the upper molars of *Peratherium* sp. described by Green and Martin from the Rosebud Formation (Lower Miocene).

The lower molars of the Oligocene and Miocene species of *Peratherium* also have features in common that are absent or less developed in the earlier species. Most conspicuous of these is the anterad projection of the paraconid, which makes the triangular outline of the trigonid very asymmetrical. Another feature contributing to trigonid asymmetry is the transverse orientation of the posterior trigonid wall; in most Eocene species it is slightly oblique. The cristid obliqua, which extends from hypoconid to trigonid, usually ends below the protoconid apex.

It seems that by Oligocene time, the species of *Peratherium* in North America had become a variable but cohesive group in which the styler shelf of the upper molars is reduced anteriorly and cusp B is distinctly smaller than cusp D. It is to this group that the writer would apply the name *Herpetotherium* in the subgeneric sense.*

The species of *Peratherium* from the Eocene of North America are mostly known from lower dentitions (Simpson, 1928; Krishtalka and Stucky, 1983a, b). The best-known upper dentition is that of *P. knighti* McGrew, 1959, originally described from the Middle Eocene (Bridger Formation) of Wyoming. In this (Fig. 3C), M¹ to M³ have an almost complete complement of styler cusps: cusp A is a prominent parastylar spur, cusp B is relatively large and nearly opposite the apex of the paracone, cusp C is smaller

and situated opposite the juncture of paracone and metacone crests, and cusp D, a little larger than C, is located opposite the apex of the metacone. This description would serve almost as well for various European species of *Peratherium*, as described and illustrated by Crochet (1977, 1979, 1980).

McGrew did not describe the lower dentition associated with the type of *P. knighti*, but Krishtalka and Stucky (1983b) figured lower molars from the type locality, as well as those of *Entomacodon minutus* Marsh, 1872, and *Peratherium morrisi* Gazin, 1962, which they referred to *P. knighti*. In these teeth the paraconid is moderately produced anterad, and the posterior margin of the trigonid is slightly oblique. As in the Oligocene species, the cristid obliqua terminates below the protoconid apex.

Setoguchi (1975) referred upper and lower teeth from the Upper Eocene (Tepee Trail Formation) of Wyoming to *Peratherium* cf. *knighti*. The upper molars have well-developed cusps B, C, and D, but differ from the typical *P. knighti* in having a shallow marginal reentrant just posterior to cusp B, which is more anteriorly situated. A DP₃ associated by Setoguchi has an anterad-projecting paraconid and a transverse posterior trigonid wall, as in the molars of Oligocene species.

Lillegraven (1976) assigned upper and lower dentitions from the Upper Eocene of California to *Peratherium* cf. *knighti*. In the upper molars, cusps B, C, and D are well developed, much as on those described by Setoguchi. In some specimens the reentrant posterior to cusp B is a deep groove. The lower molars are like the DP₃ described by Setoguchi, with anterad-projecting paraconid, but with a slightly oblique posterior trigonid wall.

From the Middle Eocene Bridger Formation, Troxell (1923) described *Herpetotherium marsupium*, referred by most authors to *Peratherium*. Krishtalka and Stucky (1983a) have extended the range from Lower to uppermost Eocene. According to those authors, styler cusps B and D are small and subequal, cusp A smaller, and cusp C minute. The published illustrations of the lower dentitions show a moderately produced paraconid, with a convex anterior trigonid wall, and a posterior trigonid wall that is transverse, rather than oblique. Unlike most species of *Peratherium*, the cristid obliqua ends below the protoconid-metaconid notch.

Peratherium innominatum Simpson, 1928, was also described from the Bridger Formation and also on the lower dentition. Krishtalka and Stucky (1983a) have extended the range from Lower to uppermost Eocene. From the figures and descriptions of those authors, the upper molars have a very small cusp A, a relatively large cusp B, and smaller, more or less equal cusps C and D. In the lower molars the paraconid projects strongly anterad, and the posterior trigonid wall is slightly oblique.

Three species of *Peratherium* have been described from

*Since this paper was accepted for publication, R. C. Fox has published the description of well-preserved upper and lower dentitions of *Herpetotherium fugax* (Canadian Journal of Earth Sciences, vol. 20, 1983:1565–1578). The cheek teeth closely resemble some of those here described for *Peratherium valens*. The lower incisor series shows the “distinctive anterior dentition” referred to by Krishtalka and Stucky (1983a). The mandibular symphysis is compressed, and the I₂ lies dorsolateral, rather than lateral, to the I₁. On this basis Fox recognizes *Herpetotherium* as a distinct genus. It is hoped that future discoveries will show whether or not this arrangement of the lower incisors is present in *Peratherium valens* and other Oligocene and Miocene didelphids.

the Lower Eocene of Wyoming. *Peratherium comstocki* Cope is said to be from the Willwood Formation of the Bighorn Basin, but was recorded by Cope (1884:269) as coming from "the badlands of the Wind River, Wyoming". Krishtalka and Stucky (1983a) report it also from the Bridger Formation. From the illustrations provided by those authors, it appears that the upper molars have strong stylar cusps, with A moderately produced, and the posterior wall of the trigonid somewhat oblique. *Peratherium edwardi* Gazin, 1952, from the Knight Formation has the paraconid more produced, but the trigonid wall is also slightly oblique. The third Lower Eocene species is *Peratherium macgrewi* Bown, 1979, from the Willwood Formation of the Bighorn Basin. The upper molars (Fig. 3D) have distinct stylar cusps B, C, and D, as well as a parastylar A. As in *P. knighti*, this is like the stylar condition in species of *Peratherium* from the European Eocene (Fig. 3F, G).

Peratherium, or an obvious relative, has not been reported from the Paleocene of North America or Europe. *Thylacodon* Matthew and Granger, 1921, from the Lower Paleocene of New Mexico, is regarded here as representing the *Peradectes* branch of the Didelphinae (tribe Peradectini of Crochet, 1979). This raises the question of the origin of *Peratherium* and its relatives (tribe Didelphini), didelphines characterized by dilambdodont upper molars. Before I had access to the excellent work of Crochet on the European species of *Peratherium*, I was impressed by the reduction in width of the anterior stylar shelf and the small size of cusp B in the North American species. As a result, I postulated (Russell, 1976) that the ancestors of *Peratherium* and a number of other polyprotodont marsupials might be found among the Pediomyinae of the Late Cretaceous of North America. It is now evident that the pediomyine-like condition of the stylar cusps in *Peratherium* spp. is a secondary development, characteristic of the post-Eocene species of that genus in North America (Fig. 3A, B). Eocene species of both North America and Europe are more like *Alphadon* in this respect, with well-developed cusp B, but, like their descendants, also with the dilambdodont ectoloph. This seems to exclude *Pedimys* from an ancestral relationship with any of the didelphines, leaving *Alphadon* as the most likely progenitor. Nearly all known species of *Alphadon* have the straight ectoloph and the conoid paracone and metacone, but there are exceptions, such as the two upper molars described and figured by Clemens (1966:13, fig. 12) as *Alphadon* cf. *rhaister*. In these, both paracone and metacone show moderately lambdoidal crests. An even more dilambdodontal ectoloph is seen in the upper dentition of *Alphadon marshi* Simpson as figured by Lillegraven (1969, fig. 15:3a) (see Fig. 3E herewith). There seems to be no difficulty in deriving the Didelphini, as well as the Peradectini, from the genus *Alphadon*.

Crochet's (1977, 1980) restriction of the genus *Peratherium* to the European species, and placing of all North American species in *Herpetotherium*, is not followed here. As noted, Lower and Middle Eocene species from North America have upper molars (Fig. 3C, D) that are almost identical with those of European *Peratherium* spp. (Fig. 3F, G, H). By late Eocene time, the *Herpetotherium* type of molar structure (cf. *P. knighti*) was beginning to appear in North America, but did not reach full development until the Early Oligocene. For these reasons, I regard *Herpetotherium* as a subgenus of *Peratherium* known at present only from the Oligocene and Miocene of North America.

Pending the discovery of *Peratherium*-like didelphids in the Paleocene faunas, speculation on the phylogeny of the Tertiary didelphines is somewhat premature. However, a reasonable assumption would be that transitional forms between *Alphadon* and *Peratherium* were present in the North American Paleocene, and that they entered Europe during that epoch or in early Eocene time, when the mammalian faunas of the two continents were closely intermingled. With continental separation in Middle Eocene time, the two didelphine lines diverged, leading to the European forms with a strong stylar cusp B (Fig. 3G, H), and the North American representatives with reduced cusp B and enlarged cusp D (Fig. 3A, B).

Didelphids disappeared from the fossil record of both Europe and North America during Miocene time. The didelphids of South America, which are still flourishing, present another problem in didelphid phylogeny. In both upper and lower molars, these southern didelphids show more resemblance to the mid-Tertiary *Peratherium* of Europe than to those of North America (*Herpetotherium*). But palaeogeographic evidence indicates that the link between South America and Holarctica must have been by way of North America, and that the last pre-Quaternary connection was broken at about the close of Cretaceous time. I am forced to conclude, therefore, that the South American didelphines originated from *Alphadon*-like forms that entered South America in very late Cretaceous time and subsequently evolved more in parallel with the European species of *Peratherium* than with those of North America. The living *Didelphis virginiana* of North America, which shows the European resemblances clearly, must be assumed to have entered North America as an offshoot of the South American *D. marsupialis* when the Central American land bridge was reestablished in early Pleistocene time.

Genus *Alloeodectes* gen. nov.

TYPE SPECIES

Nanodelphys? mcgrewi Russell, 1972

GENERIC CHARACTERS

Upper molars broadly trianguloid, with greatly produced

posterobuccal angle; posterolingual margin concave; buccal margin shallowly excavated. Paracone and metacone conoid, about equal in height, aligned fore-and-aft, without ectoloph. Protoconule and metaconule small to absent. Styler shelf about the same width from front to rear; styler cusps low, cusp B the most prominent and close to parastyle, cusps C and D small to absent.

ETYMOLOGY

Greek: ἀλλοίος, different; δήκτης, biter; with reference to the peculiar molar structure, and in analogy with *Peradectes*, etc.

REMARKS

This genus is known at present only from upper molars. It is referred to the Didelphidae because of the triangular crown, the simple protocone without trace of hypocone, and the wide styler shelf with cuspules. The conoid paracone and metacone, without any ectoloph, dilambdodont or otherwise, place it in Crochet's tribe Peradectini and close to *Mimoperadectes* and *Nanodelphys*.

Alloeodectes mcgrewi (Russell)

Nanodelphys? mcgrewi Russell, 1972

TYPE

ROM 1814, left upper molar, probably M².

SPECIFIC CHARACTERS

As for the genus. Length of M² approximately 4.7 mm, width approximately 4.6 mm.

REMARKS

Three upper molars in the SMNH collection [P661.463 (Fig. 2A), P661.464, P1585.902] clearly represent this species, and confirm the generic diagnosis given above. They are more worn than the type specimen, but resemble it closely. It is curious that among the large number of marsupial lower molars in the combined collections, there is nothing of the appropriate size to be associated with these distinctive upper molars. Such lower molars, in addition to their distinctive size, should have the paraconid portion of the trigonid moderately produced and the anterior margin distinctly convex.

At the time that this species was first described, the best comparison was with *Nanodelphys* McGrew, 1937. It was obvious that the relationship was not close, but I hesitated to define a new genus on the basis of one tooth, however distinctive. With the additional material confirming the constancy of the peculiar features, recognition of a new genus seems appropriate. Closest relationships appear to be with *Mimoperadectes labrus* (Bown and Rose, 1979), from the Lower Eocene Willwood Formation. This species was

not known at the time that the present species was first described. The resemblances are in the concave posterior margin of M² and M³, and the relatively simple form and position of the cusps. However, the posterobuccal angle (parastyle) of the crown is very little, if any, produced in *Mimoperadectes*, so that the outline is very different from that of *Alloeodectes mcgrewi*. The lower molars of *M. labrus*, as described and illustrated by Bown and Rose, probably are very similar, except in smaller size, to the so-far-undiscovered lower molars of *Alloeodectes mcgrewi*.

Shotwell (1968:17) described and figured an incomplete left upper molar that he referred to the Didelphidae. This may represent *Alloeodectes*, as suggested by the large size and by the concavity of the posterior margin, which indicates a produced posterobuccal angle that is now missing. Shotwell's specimen is from the Barstovian (Upper Miocene) of southeastern Oregon.

MEASUREMENTS

	Length	Width
SMNH P661.464, left M ^{1?}	4.98	4.12
ROM 1814, left M ² (type)	4.72	4.58
SMNH P661.463, left M ² (fig. 2A)	4.76	5.02
SMNH P1585.902, left M ^{3?}	4.72	5.25

Genus *Nanodelphys* McGrew 1937

REMARKS

The genus *Nanodelphys* was based by McGrew (1937) on small molars from the Oligocene of Nebraska. The distinctive features are the subequal paracone and metacone, oriented anteroposteriorly and conoid in form, the uniformly wide styler shelf (except on M⁴), and the presence of styler cusps A, B, D, and E, of which B is the largest. On the basis of these characters, *Nanodelphys* clearly belongs in Crochet's (1979) tribe Peradectini.

Cf. *Nanodelphys minutus* McGrew 1937

REMARKS

A very small M² or M³ (ROM 6242) was described by Russell (1972:8) under the above designation. It corresponds in size and shape to the upper molars described by McGrew (1937, 1939) but differs in having only styler cusp C. This would seem to exclude it from *N. minutus*, in which styler cusp C is well developed (see Setoguchi, 1975; Lillegraven, 1976). The Cypress Hills specimen resembles, except for the smaller size, some of the upper molars described above under *Peratherium valens*, e.g., SMNH P1585.621 (Fig. 1H), in which the buccal margin is deeply concave, and styler cusp C is present.

Lower Molars of Uncertain Affinities

Two lower molars, seemingly didelphid, in the SMNH collection, do not seem referable to *Peratherium*, and may represent species of *Nanodelphys* or undescribed didelphid genera. An account of these follows.

SMNH 1585.980 (Fig. 2B, C) is probably a left M_3 . The paraconid is broken away, but evidently was moderately directed anterad. The cristid obliqua almost reaches a point below the protoconid-metaconid notch. The talonid basin is closed posteriorly by the crest joining hypoconid and entoconid. The hypoconulid lies outside this crest, almost directly behind the entoconid and at the lingual end of the posterior cingulum. Length of crown, as preserved, is 1.8 mm and its width is 1.3 mm.

The second aberrant lower molar is SMNH P661.408 (Fig. 2D, E), probably a right M_2 . It has a small chip off the hypoconid but is otherwise complete. The paraconid and metaconid are well worn, but the protoconid is still high. The talonid is unusual in that the cristid obliqua, ending below the protoconid-metaconid notch, is joined there by a low curving crest from the crown margin between entoconid and hypoconulid. The talonid basin is closed by the crest from the crown margin between hypoconid to hypoconulid. The hypoconulid is close to, but not directly behind, the entoconid. Length of crown is 2.3 mm, and its width is 1.4 mm.

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Literature Cited

- AYMARD, A.
1846 Essai monographique sur un nouveau genre de mammifère fossile trouvé dans la Haute-Loire, et nommé Entelodon, suivi d'un aperçu sur les gîtes fossilifères du département. *Annales de la Société d'Agriculture, Sciences, Arts et Commerce du Puy* 12:248.
1850 Concernant les restes de mammifères fossiles recueillis dans le calcaire miocène des environs du Puy. *Annales de la Société d'Agriculture, Sciences, Arts et Commerce du Puy* 14:83.
- BOWN, T. M.
1979 Geology and mammalian paleontology of the Sand Creek Facies, Lower Willwood Formation (Lower Eocene), Washakie County, Wyoming. *Geological Survey of Wyoming, Memoir* 2:52–56.
- BOWN, T. M., and K. D. ROSE
1979 *Mimoperadectes*, a new marsupial, and *Worlandia*, a new dermopteran, from the lower part of the Willwood Formation (Early Eocene), Bighorn Basin, Wyoming. *University of Michigan, Contributions from the Museum of Paleontology* 25:89–104, figs. 1–5, pls. 1, 2.
- CLEMENS, W. A.
1966 Fossil mammals of the type Lance Formation, Wyoming; Part II, Marsupialia. *University of California Publications in Geological Sciences* 62:1–122, figs. 1–77.
- COPE, E. D.
1873 Third notice of extinct vertebrata from the Tertiary of the Plains. *Palaeontological Bulletin* 16:1–8.
1874 Report on the vertebrate paleontology of Colorado. *United States Geological and Geographical Survey of the Territories, Annual Report for 1873*:427–533, pls. 1–7.
1884 The Vertebrata of the Tertiary formations of the West, Book I. Report of the United States Geological Survey of the Territories 3:1–1009, pls. 1–131.
- CROCHET, J.-Y.
1977 Les Didelphidae (Marsupicarnivora, Marsupialia) holarctiques tertiaires. *Académie des Sciences, Comptes Rendus Hebdomadaires des Séances, sér. D*, 284:357–360, pl. 1.
1979 Diversité systématique des Didelphidae (Marsupialia) Européens tertiaires. *Géobios* 12:365–378, figs. 1–16.
1980 Les marsupiaux du Tertiaire d'Europe. Paris, Editions de la Fondation Singer-Polignac. 279 pp., figs. 1–241, pls. 1–2.
- GAZIN, C. L.
1952 The Lower Eocene Knight Formation of western Wyoming and its mammalian faunas. *Smithsonian Miscellaneous Collections* 117:1–82, figs. 1–6, pls. 1–11.
1962 A further study of the Lower Eocene mammalian faunas of southwestern Wyoming. *Smithsonian Miscellaneous Collections* 144:1–98, figs. 1, 2, pls. 1–14.
- GREEN, M., and J. E. MARTIN
1976 *Peratherium* (Marsupialia) from the Oligocene and Miocene of South Dakota. In Churcher, C. S., ed., *Athlon, essays in honour of Loris Shano Russell*. Life Sciences Miscellaneous Publications. Toronto, Royal Ontario Museum, pp. 155–168, figs. 1–6.
- HOUGH, J. R.
1961 Review of Oligocene didelphid marsupials. *Journal of Paleontology* 35:218–228, figs. 1, 2.
- KRISHTALKA, L., and R. K. STUCKY
1983a Revision of the Wind River faunas, Early Eocene of Central Wyoming; Part 3, Marsupialia. *Annals of Carnegie Museum* 52:205–227, figs. 1–5.
1983b Paleocene and Eocene marsupials of North America. *Annals of Carnegie Museum* 52:229–263, figs. 1–8.
- LAMBE, L. M.
1908 The Vertebrata of the Oligocene of the Cypress Hills, Saskatchewan. *Geological Survey of Canada, Contributions to Canadian Palaeontology*, 3(4):1–64, figs. 1–13, pls. 1–8.
- LILLEGRAVEN, J. A.
1969 Latest Cretaceous mammals of upper part of Edmonton Formation of Alberta, Canada, and review of marsupial-placental dichotomy in mammalian evolution. *University of Kansas Paleontological Contributions, Article 50 (Vertebrata 12)*:1–122, figs. 1–53.
1976 Didelphids (Marsupialia) and *Uintasorex* (?Primates) from the later Eocene sediments of San Diego, California. *Transactions of the San Diego Society of Natural History* 18:85–122, pls. 1–11.
- MATTHEW, W. D., and W. GRANGER
1921 New genera of Paleocene mammals. *American Museum Novitates* 13:1–7.
- MARSH, O. C.
1872 Preliminary description of new Tertiary mammals. *American Journal of Science, Ser. 3*, 4:202–224.
- MCGREW, P. O.
1937 New marsupials from the Tertiary of Nebraska. *Journal of Geology* 45:448–455, figs. 1–4.
1939 *Nanodelphys*, an Oligocene didelphine. *Publications of the Field Museum of Natural History, Geological Series* 6:393–400, fig. 114.
1959 The geology and paleontology of the Elk Mountain and Tabernacle Butte area, Wyoming. *Bulletin of the American Museum of Natural History* 117:117–176, figs. 1–27, pls. 50–57.
- RUSSELL, L. S.
1972 Tertiary mammals of Saskatchewan: Part II: The Oligocene fauna, non-ungulate orders. *Royal Ontario Museum Life Sciences Contributions* 84:1–97, figs. 1–17.
1976 The palaeogeographic significance of the polyprotodont marsupials. 25th International Geological Congress, Abstracts, vol. 1, sec. 7C, pp. 333–334.

SETOGUCHI, T.

- 1975 Paleontology and geology of the Badwater Creek area, central Wyoming: Part 11: Late Eocene Marsupials. *Annals of Carnegie Museum* 45:263–275, figs. 1–14.

SHOTWELL, J. A.

- 1968 Miocene mammals of southeast Oregon. University of Oregon, Museum of Natural History, Bulletin 14: 1–67, figs. 1–33.

SIMPSON, G. G.

- 1928 American Eocene didelphids. *American Museum Novitates* 307:1–7, figs. 1–5.

TROXELL, E. L.

- 1923 A new marsupial. *American Journal of Science, Ser. 5*, 5:507–510, figs. 1–4.

Fig. 1 All $\times 8$.

- A. *Peratherium valens* (Lambe), SMNH P661.401, left upper molar, probably M², occlusal view.
B. *Peratherium valens* (Lambe), SMNH P1585.642, left M², occlusal view.
C. *Peratherium valens* (Lambe), ROM 23227, right M², occlusal view.
D. *Peratherium valens* (Lambe), SMNH P1585.704, right M³, occlusal view.
E. *Peratherium valens* (Lambe), SMNH P1585.736, right M¹ or M², occlusal view.
F. *Peratherium valens* (Lambe), SMNH P1585.667, left M¹, occlusal view.
G. *Peratherium valens* (Lambe), ROM 23226, right M³, occlusal view.

- H. *Peratherium valens* (Lambe), SMNH P1585.621, right M³, occlusal view.
I. *Peratherium valens* (Lambe), SMNH P1585.675, right M⁴, occlusal view.
J. *Peratherium valens* (Lambe), SMNH P661.406, right lower molar, probably M₂, occlusal view.
K. *Peratherium valens* (Lambe), SMNH P661.412, right M₁, occlusal view.
L. Same specimen, buccal view.
M. *Peratherium valens* (Lambe), SMNH P661.404, left M₄, occlusal view.





Fig. 2 All $\times 8$.

- A. *Alloeodectes mcgrewi* (Russell), SMNH P661.463, left M^2 or M^3 , occlusal view.
- B. Didelphid, SMNH P1585.980, left M_3 , occlusal view.

- C. Same specimen, buccal view.
- D. Didelphid, SMNH P661.408, right M_2 , occlusal view.
- E. Same specimen, buccal view.

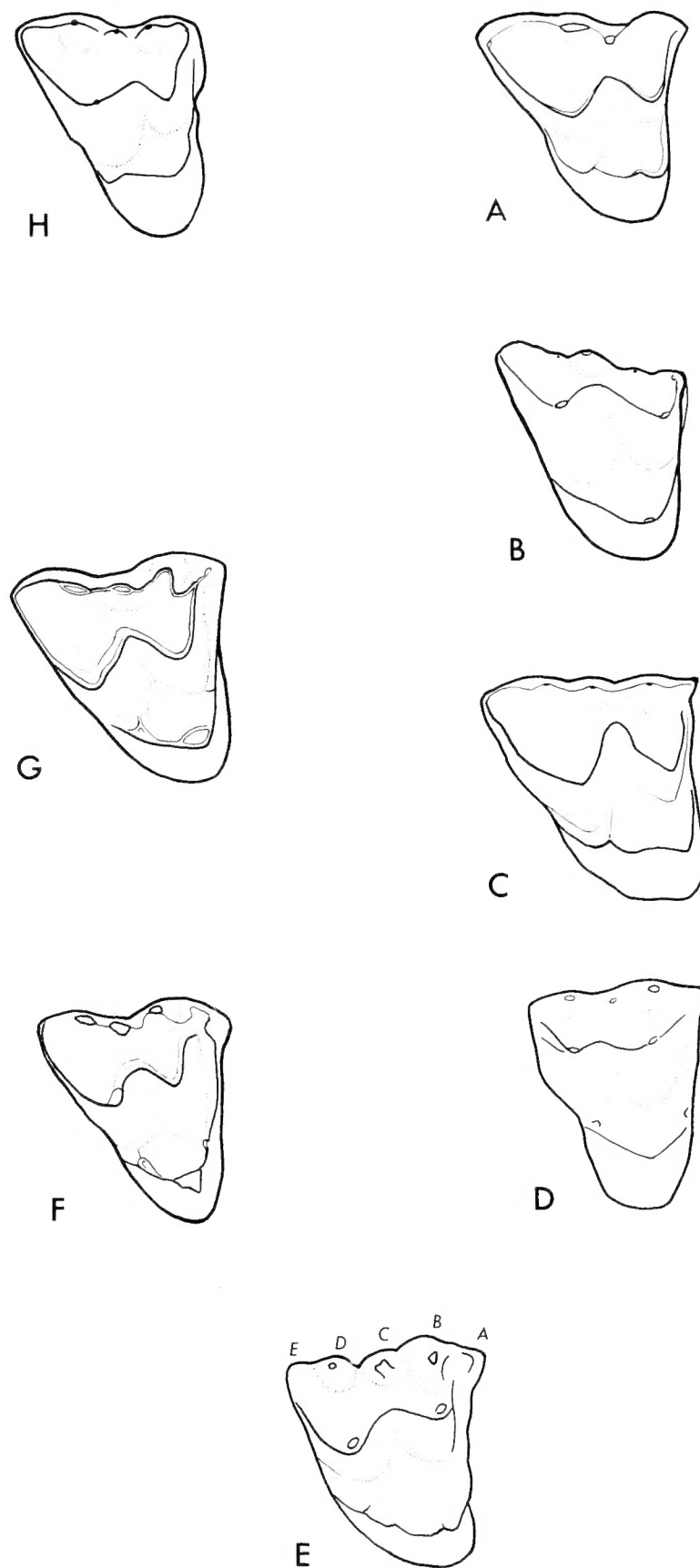


Fig. 3 Diagrammatic representation of crown pattern in M^2 of Cretaceous and Tertiary didelphids, showing variations in the stylar cusps.

A. *Peratherium (Herpetotherium) fugax* (Cope), left, M^2 reversed, Middle Oligocene, South Dakota, U.S.A., $\times 14$ (after Green and Martin, 1976).

B. *Peratherium valens* (Lambe), right M^2 (type), Lower Oligocene, Saskatchewan, Canada, $\times 12.5$ (after Russell, 1972).

C. *Peratherium knighti* McGrew, left M^2 reversed, Middle Eocene, Wyoming, U.S.A., $\times 13$ (after McGrew, 1959).

D. *Peratherium macgrewi* Bown, left M^2 reversed, Lower Eocene, Wyoming, U.S.A., $\times 15$ (after Bown, 1979).

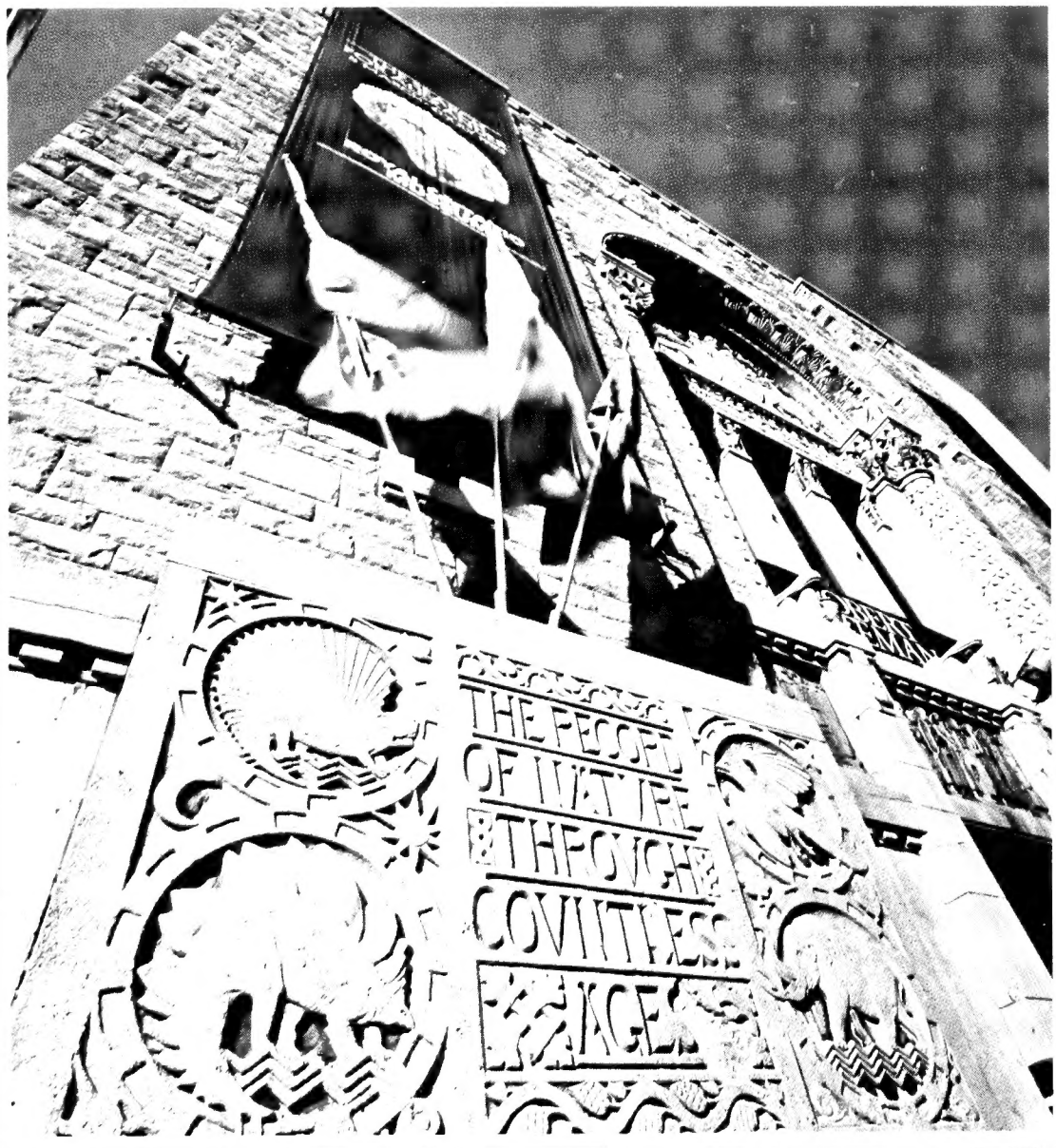
E. *Alphadon marshi* Simpson, left M^2 reversed, Upper Creta-

ceous, Alberta, Canada, $\times 8$ (after Lillegraven, 1969). [Italic letters have been added to show the stylar-cusp notation used in this paper.]

F. *Peratherium matronensis* Crochet, right M^2 , Lower Eocene, Marne, France, $\times 13$ (after Crochet, 1980).

G. *Peratherium sudrei* Crochet, left M^2 reversed, Upper Eocene, Gard, France, $\times 13$ (after Crochet, 1980).

H. *Peratherium antiquum* (Blainville), right M^2 , Upper Oligocene, Tarn-et-Garonne, France, $\times 9$ (after Crochet, 1980).



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