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MIMOPERADECTES, A NEW MARSUPIAL, AND *WORLANDIA*, A NEW DERMOPTERAN, FROM THE LOWER PART OF THE WILLWOOD FORMATION (EARLY EOCENE), BIGHORN BASIN, WYOMING

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MIMOPERADECTES, A NEW MARSUPIAL, AND *WORLANDIA*, A NEW DERMOPTERAN, FROM THE LOWER PART OF THE WILLWOOD FORMATION (EARLY EOCENE), BIGHORN BASIN, WYOMING

By

Thomas M. Bown and Kenneth D. Rose

Abstract.– Two new genera of Clarkforkian and early Wasatchian mammals add to our knowledge of the diversity of early Eocene faunas of the Bighorn Basin. The new genus *Mimoperadectes* is most closely related to the early Tertiary *Peradectes–Nanodelphys* lineage of marsupials but, in contrast to them, it has divergently developed large trigonids, enlarged molar paraconids, and relatively narrower talonids with small, posterior entoconids. *Mimoperadectes* is one of the largest early Tertiary didelphids from North America.

The new genus *Worlandia* is closely related to the plagiomenid *Planetetherium* but differs from that genus and other plagiomenids in having narrower, less exodaenodont molars; larger, more robust P_3^3 and P_4^4; lower, more bulbous paraconid on P_4; and less crenulated enamel. The most striking features of *Worlandia* are its shortened mandible with a large medial incisor, the reduction of teeth between this incisor and P_3, and the pronounced reduction in size of the molars from front to rear. These characters are shared with *Planetetherium* but are in sharp contrast to *Plagiomene*. These traits indicate that two divergent lineages of plagiomenids coexisted in the Bighorn Basin during the early Eocene. The new subfamily Worlandiinae, to accommodate *Worlandia* and *Planetetherium*, reflects this divergence.

INTRODUCTION

In 1975, the fragmentary mandibles of two new mammals, a didelphid marsupial and a plagiomenid dermopteran, were recovered by a University of Wyoming field party in rocks of the lower part of the Willwood Formation in the southeastern Bighorn Basin, Wyoming. Bown (in press) deferred naming or describing these specimens, pending the discovery of more adequate material. Additional specimens of both new taxa were obtained in 1975-78 by University of Michigan field personnel working in the Clark's Fork Basin. A few more previously unrecognized specimens of the new didelphid were discovered in the Yale Peabody Museum, Carnegie Museum, and American Museum collections.

Didelphids and plagiomenids are relatively rare elements of Wasatchian mammal faunas. Cope (1884), Jepsen (1930), and Bown (in press) have reported the only previously known Willwood marsupials. A left M_2 of a didelphid (AMNH 56307), assigned by Delson (1971, fig. 6) to *Peratherium comstocki*, is here referred to the new marsupial described below. Other occurrences of

North American early Eocene didelphids have been reported by Gazin (1952, 1962), McKenna (1960), and Savage, *et al.* (1972). Recent studies of the phylogeny and systematics of early Tertiary North American and European didelphids have been presented by Crochet (1969, 1977) and Setoguchi (1973).

Plagiomenids are known principally from Paleocene and Eocene rocks of North America, but may occur also in Europe (see Russell, *et al.*, 1973; Rose and Simons, 1977, and references therein). Willwood representatives (*Planetetherium* and *Plagiomene*) have been described by Matthew (1918), Szalay (1969), Rose (1973), and Rose and Simons (1977). *Planetetherium* has been considered until now to be closely related and possibly ancestral to *Plagiomene* (Simpson, 1929; Rose, 1973).

Abbreviations used in the text are: AMNH, American Museum of Natural History (New York); CM, Carnegie Museum (Pittsburgh); UM, University of Michigan Museum of Paleontology (Ann Arbor); UW, The Geological Museum, University of Wyoming (Laramie); YPM, Yale Peabody Museum (New Haven); L, greatest anteroposterior measurement (length); W, greatest transverse measurement (breadth); Tri, trigonid; Tal, talonid.

SYSTEMATIC PALEONTOLOGY

Infraclass METATHERIA

Superorder MARSUPIALIA

Order POLYPROTODONTA[1]

Family DIDELPHIDAE

Mimoperadectes, gen. nov.

Etymology.— Gr. *mimos*, imitator; in reference to the superficial resemblance to the early Tertiary didelphid *Peradectes.*

Type.— *Mimoperadectes labrus*, sp. nov. and only known species.

Diagnosis.— Molars as large as in *Peratherium comstocki.* Molar paraconids (except on M_1) larger than metaconids as in *Didelphodon vorax* and in contrast to *Peratherium, Peradectes, Pediomys, Alphadon,* and *Glasbius.* Paraconid less removed anteriorly from metaconid and protoconid than in *Peratherium, Peradectes,* and Cretaceous marsupials except *Didelphodon.* Metaconid posterolingual to protoconid, not more directly lingual to protoconid (as in *Peradectes* and most *Peratherium*). Trigonid both longer and wider than talonid (longer but not wider on M_1) and talonid width decreasing from M_2 to M_4. Molar entoconids low, relatively bulbous as in *Peradectes*, but separated more from metaconid than in other didelphids. Hypoconulids resemble those of *Peradectes*, less lingual than in *Peratherium*, and without entoconid–hypoconulid notch or strong entocristid.

Paracones of M^{2-3} slightly smaller or equal in size to metacones as in *Peradectes, Nanodelphys,* and most Late Cretaceous marsupials, but unlike *Peratherium.* Stylar cusp B largest (and only discrete stylar cusp on M^4); other stylar cusps small and B>E>C>D>A on M^{2-3}. Conules relatively smaller on M^{2-3} than in most *Peratherium*, resembling *Peradectes* and *Nanodelphys.*

Mimoperadectes labrus, sp. nov.

Etymology.— Gr. *labros*, gluttonous or greedy; in allusion to the large size of individuals of this species.

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[1] We follow the classification adopted by Kirsch (1977).

TABLE 1

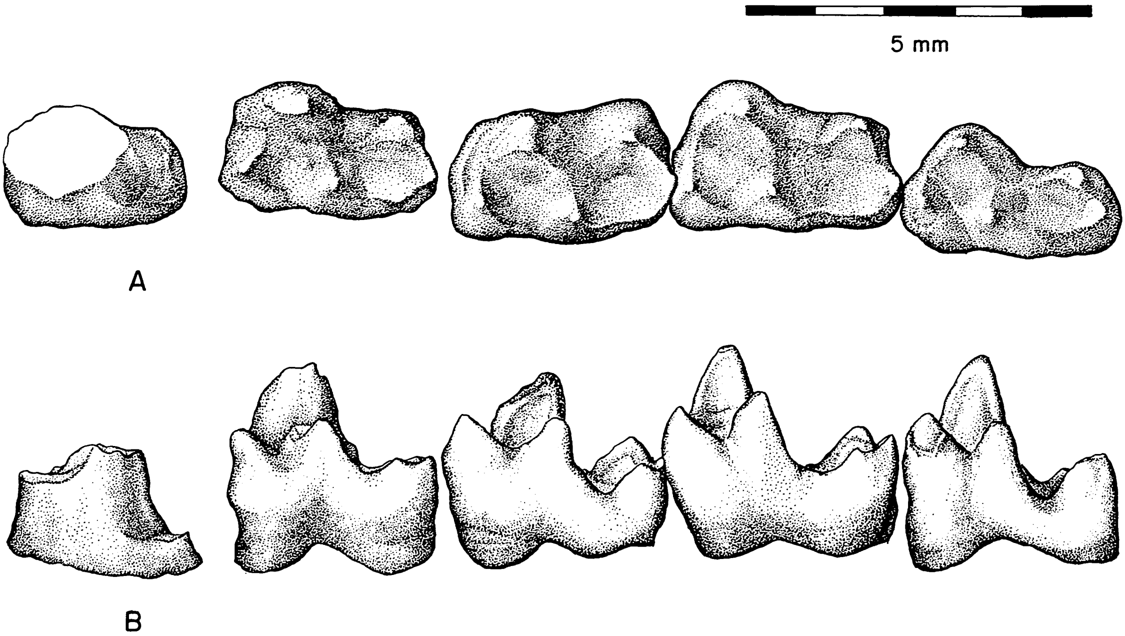
MEASUREMENTS (mm) OF SPECIMENS OF
Mimoperadectes labrus, gen. et sp. nov.

	UM 66144 (Type)	UM 66656 (UM Loc. SC-64)	YPM 35149 (YPM 278-75)	YPM 26522 (YPM Loc. 206)	YPM 25335 (YPM Loc. 295)	YPM 23108 (YPM Loc. 93)	UW 9826 (UW Loc. V-73125)	AM 56307 (Reculusa Blowout, Powder River Basin)	CM 12240 ("Graybull beds, Bighorn Basin")
P_3L	2.70		2.35	2.88					
P_3W	1.45		1.30	1.54					
M_1L	2.97		2.80	3.21					
M_1TriL	1.95		1.75	2.00					
M_1TalL	1.02		1.05	1.21					
M_1TriW	1.76		1.50	1.70					
M_1TalW	1.59		1.40	1.58					1.85
M_2L	3.07		3.00	2.84	–		2.66	3.20	3.05
M_2TriL	1.95		1.85	1.83	–		1.60	2.00	1.95
M_2TalL	1.12	1.20	1.15	1.01	–		1.06	1.20	1.10
M_2TriW		–	1.55	1.89	–		1.56	1.90	2.00
M_2TalW	1.83	1.50	1.45	–	1.78		1.57	1.70	2.10
M_3L	3.20	3.25	2.75	–	–	3.26	2.58		3.55
M_3TriL	1.90	1.80	1.75	–	1.85	1.75	1.55		1.75
M_3TalL	1.30	1.45	1.00	–	–	1.51	1.03		1.80
M_3TriW	1.77	1.75	1.65	–	2.00	–	1.55		2.00
M_3TalW	1.71	1.70	1.45	–	1.64	–	1.38		2.00
M_4L	3.05			3.12	–		2.80		3.30
M_4TriL	1.80			1.86	–		1.65		1.80
M_4TalL	1.25			1.26	–		1.15		1.50
M_4TriW	1.84			1.77	1.76		1.58		1.95
M_4TalW	1.40			1.37	–		1.12		1.55
M^1L	2.84								
M^1W	–								
M^2L	3.09								
M^2W	3.47								
M^3L	2.94								
M^3W	3.66								
M^4L	2.36								
M^4W	3.26								

EXPLANATION OF PLATE 1

Mimoperadectes labrus, holotype, UM 66144. (Scale in mm)

Figure 1 – left mandible with part of M_1 and M_{3-4}.
Figure 2 – right mandible with P_3, M_{1-3}.



TEXT-FIG. 1 – Composite right lower dentition of *Mimoperadectes labrus*, P_3-M_4. Based on UM 66144 (holotype), UW 9826, and YPM 26522. A: Crown view. B: Lingual view.

Holotype.– UM 66144, mandible with left M_{3-4}, broken P_3 and M_1, and alveoli or roots for canine, P_{1-2}, and M_2, and right P_3-M_3 with roots or alveoli for canine and P_{1-2}; associated maxillary fragments preserving left M^{1-4} and right M^3 (Pl. 1, figs. 1-2; Pl. 2, fig. 1; text-figs. 1, 2); possibly associated bone fragments, including a claw and a proximal ulnar (?) fragment; found by K. D. Rose.

Locality.– UM Locality SC-69, lower part of Willwood Formation, early Eocene (very early Wasatchian), SW¼ Section 3, T55N, R100W, Park County, Wyoming.

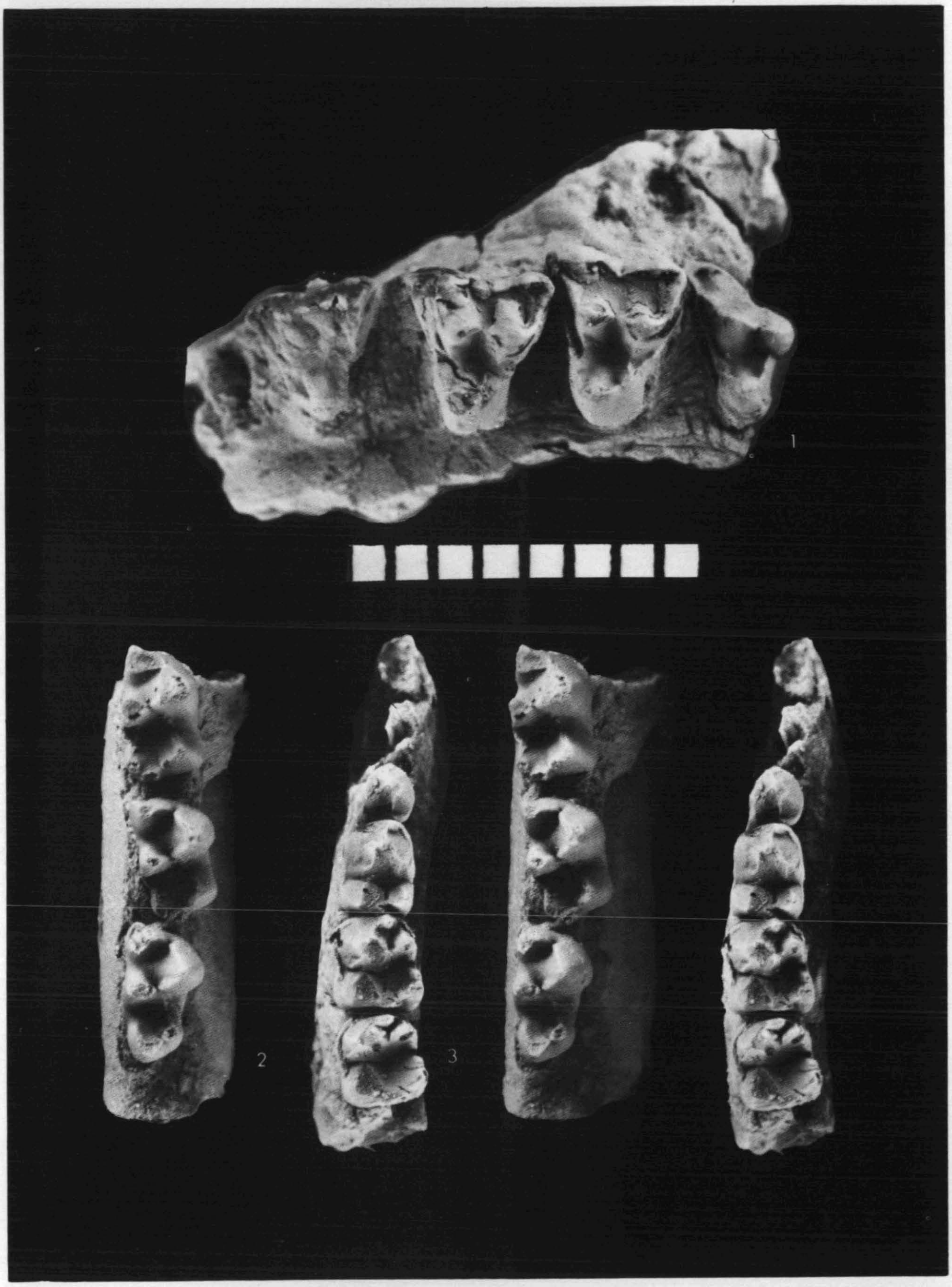
Hypodigm.– The type and UW 9826 (Pl. 2, fig. 2), UM 66656, YPM 26522, 23108, 25335, 35149, all from lower part of Willwood Formation; CM 12240, "early Eocene, Graybull, Bighorn Basin"; AMNH 56307, Reculusa Blowout, Wasatch Formation (so-called), Powder River Basin, Wyoming.

Diagnosis.– Only known species; measurements given in Table 1.

Description.– The type specimen preserves the posterior border of the canine alveolus and, on the left side, two roots each for P_1 and P_2. As indicated by its alveolus, the canine was very large. P_2 was about as large as P_3, and P_1 was somewhat smaller.

P_3 is preserved, though incomplete, in two specimens. In the type, P_3 has not fully erupted. A cristid connects the back of the protoconid with the posterior margin of the unbasined heel. Judging from YPM 26522, the undamaged P_3 was considerably taller than M_1. P_3 has no cingulids.

M_{1-4} are relatively long, narrow teeth with trigonids that are typically longer and broader than the talonids. The protoconid is the dominant cusp and the paraconid is larger than the metaconid on M_{1-4} and taller as well on M_2 and M_4. The paraconid is more erect (not tilted so anteriorly) than in *Peradectes, Peratherium*, and most Late Cretaceous marsupials. Moreover, the metaconid is situated posterolingual to the protoconid rather than directly lingual to it, causing the protoconid (in lingual view) to appear more nearly midway between the metaconid and paraconid than in *Peradectes* or *Peratherium*.



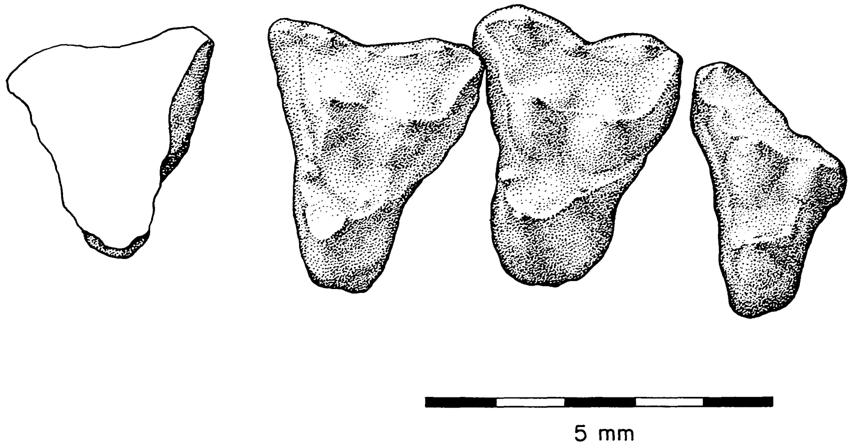
EXPLANATION OF PLATE 2

(Scale in mm)

Figure 1 – ***Mimoperadectes labrus***, holotype, UM 66144, left maxilla with M^{2-4}.

Figure 2 – ***Mimoperadectes labrus***, UW 9826, right mandible with M_{2-4}.

Figure 3 – ***Worlandia inusitata***, holotype, UM 68381, left mandible with incisor root and P_2-M_1.



TEXT-FIG. 2 – Left upper dentition of *Mimoperadectes labrus*, M^{2-4}. Holotype, UM 66144.

The cristid obliqua is short and usually terminates before reaching the back of the trigonid. The entocristid is faint when developed at all, and the entoconid is a relatively low, bulbous cusp situated well posterior to the metaconid. The entoconid is not tall, trenchant, and soricid-like as it is in *Peradectes* and, especially, in *Peratherium*.

The hypoconulids of M_{1-3} are cuspidate, project posterolabially, and are closely appressed to the entoconids, as in *Peradectes*. The M_4 entoconid is very small (*e.g.*, YPM 26522, CM 12240) or is connate with the hypoconulid (*e.g.*, holotype and UW 9826).

Cingulids are not well developed on the molars. A weak ectocingulid is present across the hypoflexid on M_{1-3} of the type, on M_{2-3} in YPM 25335, and on M_3 in YPM 23108. A small postcingulid is variably developed behind the hypoconid on M_{1-3}.

Upper molars (text-fig. 2; Pl. 2, fig. 1) are known only in the type specimen (the crown of M^1 is missing). The paracones of M^{2-3} are nearly as large as the metacones and these cusps have about the same size relationship as in *Peradectes elegans* and *P. chesteri* (Bown, in press). On M^4 the paracone is much larger than the metacone.

The paracone of M^2 is joined to stylar cusp B by a faint, anteriorly convex preparacrista. The parastylar shelf is much narrower on M^2 than is the metastylar shelf; on M^3 both shelves are broad, and on M^4 the parastylar shelf is very broad and the metastylar shelf is considerably reduced. The M^{3-4} preparacristae are longer and straighter than on M^2 and are oriented anterobuccally. A small but acute accessory cusp is present on the preparacrista between the paracone and the anterobuccal border of the M^4 parastylar shelf.

Cusp B is the largest of the stylar cusps on all molars (the only one of M^4) and is succeeded in size by cusps E, C, D, and A, respectively. Cusp C is somewhat smaller than in most specimens of *Peradectes* and *Peratherium* and is situated just anterior to the ectoflexus.

M^3 has small conules with pre- and post- paraconule and metaconule cristae. These were probably present on M^2, but this cannot be confirmed because of damage to the tooth. No conules are present on M^4 and the upper molars lack shelf-like cingula.

Discussion.– *Mimoperadectes* is perhaps most easily confused with the partly contemporaneous *Peratherium comstocki* (including *Peratherium edwardi* Gazin), another large didelphid. The type of *P. comstocki* (AMNH 4252), a damaged left M_{2-3}, and USNM 19206, a left M^{3-4}, show that *P. comstocki* and *Mimoperadectes labrus* differ in the following characters: (1) the paraconid is smaller than the metaconid and is tilted anteriorly in *Peratherium comstocki* to a greater degree than in *Mimoperadectes*; (2) the hypoconulids are much larger and more shelf-like in *P. comstocki*, and the entoconids are taller, more acute, and closer to the trigonid than in *Mimoperadectes*; (3) *M. labrus* has no hypoconulid–entoconid notch as occurs in *Peratherium comstocki*; (4) the trigonids are relatively larger than the talonids in *Mimoperadectes*; and (5) the paracone is much more reduced relative to the metacone in *Peratherium comstocki*.

A combination of several diagnostic features, *e.g.*, subequal paracones and metacones, small conules, relatively small stylar cusp C, and the positions and development of the entoconid and hypoconulid, argues for the closer affinity of *Mimoperadectes* to the *Peradectes–Nanodelphys*[1] lineage than to *Peratherium*. *Mimoperadectes* is the largest of the *Peradectes*-like didelphids and therefore complements its lineage in much the same way that *Peratherium comstocki* and *Peratherium marsupium* represent early, large-bodied members of the *Peratherium* group.

Mimoperadectes differs from *Peradectes* in its much larger size and in the construction of the trigonid. The paraconid size and position give *M. labrus* a superficial resemblance to the late Cretaceous stagodontid *Didelphodon vorax*. *D. vorax*, however, has so enlarged the paraconid that it is about subequal in height with the protoconid (Matthew, 1916; Clemens, 1966). In *Mimoperadectes*, the paraconid, although relatively large, is clearly smaller than the protoconid. Clemens (1966: 81) believed that enlargement of the paraconid was a progressive trend in the stagodontids, and this may have been true in *Mimoperadectes* as well. The presence of a relatively low and anteriorly inclined paraconid is already well established in the Late Cretaceous didelphid *Alphadon* and it appears most likely that this paraconid structure is primitive for known Tertiary didelphids.

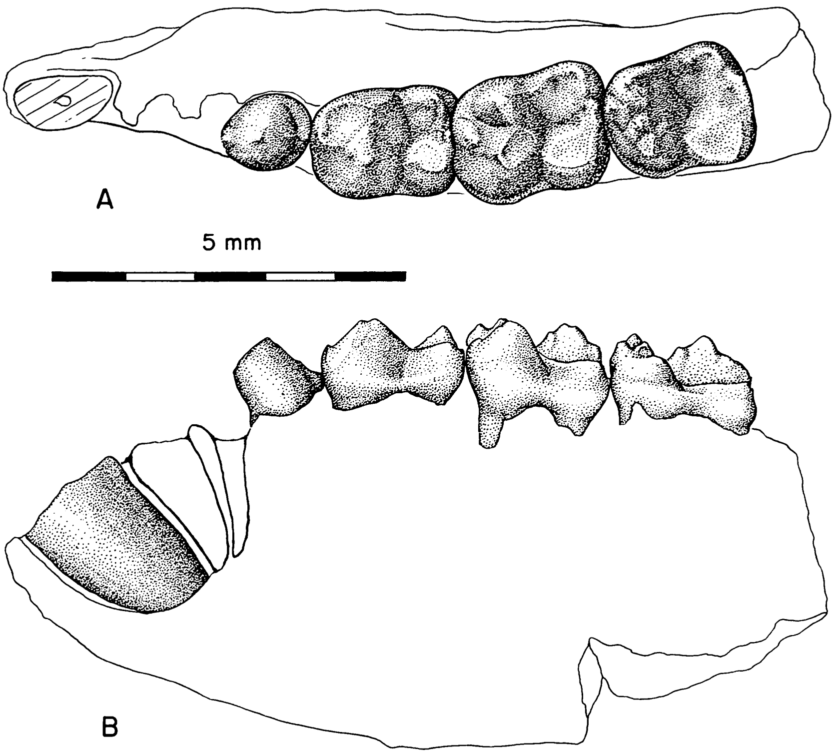
It is unlikely that *Mimoperadectes* is a descendant of Tiffanian *Peradectes elegans*, and derivation from an unknown late Paleocene form is more likely. *P. elegans* has a trenchant M_{1-2} entocristid and entoconid, and the latter is relatively close to the metaconid, in contrast to both *Alphadon* and *Mimoperadectes*. This construction in *Peradectes* is probably derived with respect to the constructions in *Alphadon* and *Mimoperadectes*.

Mimoperadectes is clearly divergent from both *Alphadon* and *Peradectes* in the development of long and broad trigonids, narrow talonids, enlarged paraconids, less lingual hypoconulids, and small, bulbous entoconids. These developments are clearly specializations that could have been derived from teeth of a generalized didelphid such as *Alphadon* (Clemens, 1966), but that would be unexpected in an immediate ancestor of *Peradectes*.

Occurrence.– Four of the Willwood specimens are tied to measured sections of the Willwood Formation in the central Bighorn Basin, where they occur at localities between about 145 and 295 meters above the top of the Polecat Bench Formation (of Jepsen, 1940; Schankler, written communication, 1977). The highest of these records is within the upper part of the local range zone for the common adapid primate *Pelycodus mckennai* (Gingerich and Simons, 1977). Two specimens were collected from Willwood localities in the Clark's Fork Basin at approximately 400 meters (holotype) and 790 meters (UM 66656) above the base of the Willwood Formation. The holotype is from near the bottom, and UM 66656 from near the top of the early Wasatchian ("Gray Bull") part of the local section. The latter occurrence is well into the local range zone of *Pelycodus trigonodus*, a descendant of *P. mckennai*. The holotype is from the lower part of the local range zone of *P. ralstoni*, the oldest known species of *Pelycodus* (Gingerich and Simons, 1977).

Stratigraphic sections and faunal studies precisely correlating Willwood rocks of the Clark's Fork and central Bighorn Basins remain to be accomplished. This correlation will be complicated by the fact that the Willwood Formation is thicker in the Clark's Fork Basin than in the central Bighorn Basin (Bown, in press).

[1] *Nanodelphys* may be a junior synonym of *Peradectes* (Bown, in press).



TEXT-FIG. 3 – Holotype of *Worlandia inusitata*, UM 68381. Left mandible with incisor root, P_2-M_1. A: Crown view. B: Buccal view.

Infraclass EUTHERIA

Order DERMOPTERA

Family PLAGIOMENIDAE

Subfamily WORLANDIINAE, nov.

Type genus.– *Worlandia*, gen. nov.

Included genera.– *Worlandia* and *Planetetherium*.

Distribution.– Clarkforkian and early Wasatchian (early Eocene), Wyoming and Montana.

Diagnosis.– Small plagiomenids with short mandibles. Teeth anterior to P_3 reduced in number and size, except for enlarged medial incisor. Molars decrease in size from M_1^1 to M_3^3.

Worlandia, gen. nov.

Etymology.– For Worland, Wyoming, town nearest to locality of the first known specimen.

Type.– *Worlandia inusitata*, sp. nov. and only known species.

Diagnosis.– Small plagiomenid, smaller than *Plagiomene, Elpidophorus,* and *Planetetherium*. Lower jaw short as in *Planetetherium*, with nine teeth in contrast to eleven in *Plagiomene*. Medial incisor large and procumbent. P_2 small and single-rooted in contrast to *Plagiomene*. P_3 semimolariform, robust, and differing from that in *Planetetherium* and *Plagiomene* in greater breadth, relatively

TABLE 2

MEASUREMENTS (mm) OF SPECIMENS OF
Worlandia inusitata, gen. et sp. nov.

	UM 68381 (Type)	UM 65122 (UM Loc. SC-23)	UM 68387 (UM Loc. SC-188)	UM 68388 (UM Loc. SC-188)	UM 68389 (UM Loc. SC-188)	UM 68391 (UM Loc. SC-188)	UW 10158 (YPM Loc. 158)	UM 69600 (UM Loc. SC-188)
P_2L	1.20							
P_2W	1.10							
P_3L	2.00		2.15			2.00	2.15	
P_3WTri	1.50		1.50			1.50	1.56	
P_3WTal	1.50		1.48			1.50	1.65	
P_4L	2.20	2.05					2.24	
P_4WTri	1.70	1.38					1.79	
P_4WTal	1.80	1.51					2.00	
M_1L	2.00	2.00		2.10	2.00		2.14	
M_1WTri	1.65	1.43		1.70	1.80		1.58	
M_1WTal	1.70	1.50		1.80	1.90		1.70	
Inc. root, L	2.00							
Inc. root, W	1.30							
Mand. Depth (at M_1, buccal)	4.80a	4.10a					4.50	
Upper C, L								0.90
Upper C, W								0.70
P^1L								0.95
P^1W								0.70
P^2L								1.85
P^2W								1.35
P^3L								1.90
P^3W								2.90
P^4L								1.95
P^4W								2.80
M^1L								1.75
M^1W								2.40
M^2L								1.60
M^2W								2.10
M^3L								1.30
M^3W								1.60

larger protoconid, and often smaller paraconid; heel with larger hypoconid and entoconid than in *Planetetherium*. Differs from other known plagiomenids in having P_4 slightly larger than molars and P^3 and P^4 markedly larger than molars. P_4 completely molariform, with small, bulbous paraconid more median in position than in *Plagiomene* and *Planetetherium*. Protoconids of P_3 and P_4 high and directed somewhat posteriorly. Molars low-crowned, less broad than in *Planetetherium*; enamel smooth to moderately crenulated. Lower cheek teeth less exodaenodont than in *Elpidophorus, Plagiomene,* and *Planetetherium*.

Upper dental formula ?-1-4-3. Premolars morphologically similar to those of *Plagiomene*; P^3 and P^4 fully molariform, larger than molars (especially in transverse dimension). $M_1^1 > M_2^2 > M_3^3$ as in *Planetetherium*, but unlike *Plagiomene* and *Elpidophorus*.

Worlandia inusitata, sp. nov.

Etymology.— L. *inusitata*, rare, uncommon.

Holotype.— UM 68381 (Pl. 2, fig. 3; text-fig. 3), fragment of left ramus preserving P_2-M_1, root of medial incisor, and alveoli for two single-rooted teeth between that incisor and P_2; collected by David W. Krause.

Locality.— UM locality SC-188, lower part of Willwood Formation, early Eocene (Clarkforkian), SE¼ Section 1, T56N, R102W, Park County, Wyoming.

Hypodigm.— The type and UW 10158, UM 65122, 68387-68392, 69600; all from lower part of Willwood Formation, Bighorn Basin, Wyoming.

Diagnosis.— Only known species; measurements given in Table 2.

Description.— The front of the horizontal ramus is preserved in the type specimen and alveoli for the terminal cheek teeth are preserved in UW 10158. The intervening teeth are present, in composite, in the type and referred specimens and demonstrate that the most anterior fully molarized tooth is P_4. Thus, it can be shown that the lower jaw of *Worlandia* contained nine teeth on each side.

The most anterior tooth, the medial incisor, is large and has a procumbent, laterally compressed root. Between the incisor and P_2 are two small alveoli that housed two single-rooted teeth. The anterior alveolus is somewhat anteriorly inclined but the posterior alveolus is vertically oriented. Judging from occlusal relationships with the upper teeth, these most likely held the canine and P_1.

P_2 is a small, single-rooted, premolariform tooth that is oval in occlusal aspect. P_3 is very distinctive. The tooth is rectangular and semimolariform and resembles most closely its counterpart in *Planetetherium*, but it is considerably more robust. The trigonid is dominated by the large protoconid and has a small, low paraconid situated anterolingual to the protoconid. A faint metaconid occurs low on the lingual side of the protoconid in some specimens (UM 68387, 68391), but the cusp is obliterated after moderate wear and cannot be detected on the P_3 of remaining specimens. The postvallid surface of the P_3 trigonid is broad and is typically heavily worn. In UW 10158, the wear is so deep that the enamel has been perforated. The talonid is shorter than the trigonid but is equally wide. The entoconid and hypoconid are prominent, bulbous cusps that are very broad at their bases. There is no hypoconulid. In UW 10158, P_3 lacks cingulids but in the holotype it bears a faint ectocingulid across the hypoflexid.

P_4 is rectangular and fully molariform and differs from M_1 principally in the more anterolabial displacement of its paraconid. It is the largest cheek tooth, slightly larger than the molars, and a little longer and much broader than P_3. As in other plagiomenids, the lingual cusps of the molariform teeth are taller than the buccal cusps, and the trigonids are not much taller than the talonids. The protoconids of P_3 and P_4 are high and project slightly posteriorly. The metaconid of P_4 is somewhat more acute and is situated slightly anterolingual to the protoconid; in the molars the metaconid is more closely appressed to the paraconid. Again, these are features characteristic of plagiomenids. The hypoconid in P_4 and M_1 is broad and low, whereas the entoconid is conspicuously taller and more acute. The entoconulid is well developed (stronger on M_1 than on P_4), and the hypoconulid is prominent and is larger and more posteriorly situated on M_1 than on P_4. The hypoconulid is closer to the entoconid than to the hypoconid. A discrete irregular transverse valley separates the trigonid and talonid, as is typical in plagiomenids. In most of these features, *Worlandia* most closely resembles *Planetetherium*.

The enamel is moderately crenulated in unworn specimens but rapidly wears smooth, unlike *Planetetherium* and *Plagiomene*.

The ectocingulid is variably developed on P_4 and M_1, but is typically stronger on M_1 where it may persist to the front of the tooth as a precingulid. These cingulids are developed about as in *Planetetherium* and are less prominent than in *Plagiomene*.

M_{2-3} are represented only by alveoli in UW 10158, where they are filled and obscured by a very hard hematitic matrix. Radiographs of this specimen reveal four alveoli behind the last preserved tooth, confirming the latter as M_1 and demonstrating that the molars decrease in size posteriorly as in *Planetetherium* and most erinaceids.

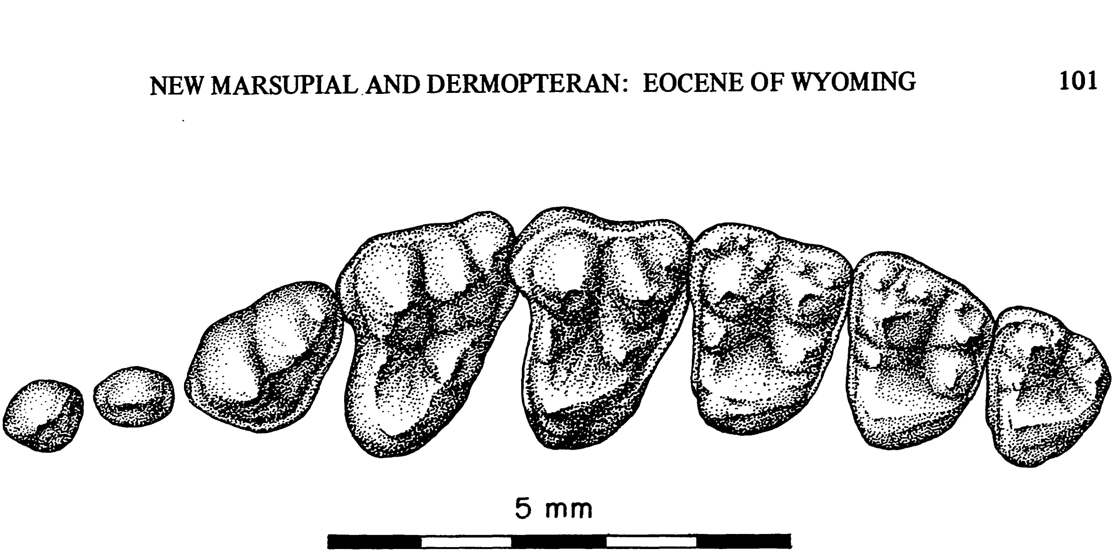
The upper dentition of *Worlandia* is known from a nearly complete palate (UM 69600, text-fig. 4) preserving the canine through M^3 on both sides. The crowns of right P^3 and left P^1 are damaged. Like the lower teeth, the uppers bear close resemblance to those of *Planetetherium*, differing mainly in having a molariform P^3 as in *Plagiomene*, in having P^3 and P^4 larger than the molars, and in showing more pronounced reduction in size from M^1 to M^3.

The upper canine is a diminutive pointed tooth, about the same size and morphology as the single-rooted P^1. P^{2-4} are similar morphologically to their counterparts in *Plagiomene*. P^2 is three-rooted, with prominent paracone and metacone, the former larger and higher than the latter. A lingual projection is supported by a large lingual root, but no protocone is present. There is a short anterior cingulum and a small metastyle. P^3 is fully molariform, as in *Plagiomene*, but unlike *Planetetherium*. Like P^2, its paracone is larger than its metacone and these two cusps are more closely appressed than in P^4 or the molars. Both conules are present on P^3, the metaconule somewhat larger than the paraconule, and there is a prominent metastyle. P^4 is similar to the molars but is larger, especially transversely, and lacks distinct stylar cusps except for the metastyle.

M^1 and M^2 resemble those of *Planetetherium* and *Plagiomene* in having a pair of stylar cusps labial to both the paracone and the metacone. The pair labial to the metacone is reduced in M^2, and all stylar cusps are faint on M^3.

Wear patterns in *Worlandia* are essentially identical with those of *Planetetherium* and are not appreciably different from those of *Plagiomene* (see Rose and Simons, 1977). Shearing (Phase I) facets are well developed and, as in *Plagiomene*, facet 6 is extensive on lower molars, covering the labial face of the entoconulid and hypoconulid, as well as the entoconid. Facets 1 and 5 (on the back of the trigonid) are confluent and often cause perforation of the postvallid surface near the protoconid. On the upper molars, facets 1-4 are multiple, extending onto the conule cristae, as in *Plagiomene*. Facets 3 and 4 also extend labially onto the stylar cusps. These adaptations enhance shearing capabilities and appear to be associated with herbivorous habits. Phase II wear (facet 9) is well developed, as is characteristic of more herbivorously adapted mammals. Heavy abrasive wear is common, leaving the tips of the cusps fenestrated. The hypoconid is particularly susceptible to such wear and, in some specimens, is marked by a large crescentic perforation in the enamel.

Discussion.– *Worlandia* is the smallest North American plagiomenid, near the size of Uintan *Thylacaelurus*. It is the only plagiomenid besides *Plagiomene* in which the number of teeth in the lower jaw is known. The retention of only nine teeth in a relatively short jaw contrasts sharply with the eleven teeth and long jaw in *Plagiomene*. This difference led us to restudy the holotype and referred



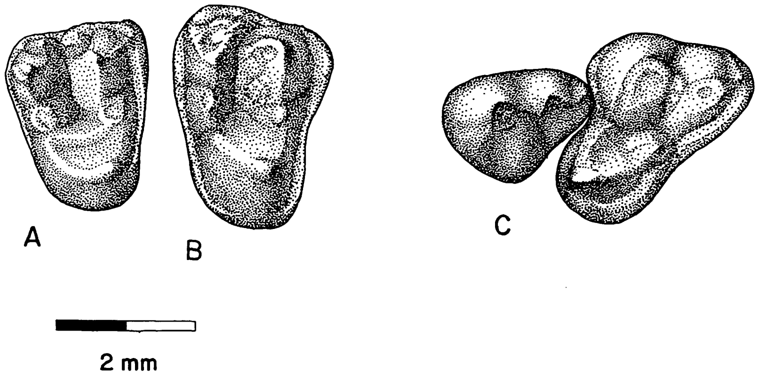
TEXT-FIG. 4 – Left upper dentition of *Worlandia inusitata*, canine–M^3, UM 69600. P^1 (reversed) from right side.

specimens of *Planetetherium*, the most similar genus to *Worlandia. Planetetherium* had earlier been regarded as a close relative and possible ancestor of *Plagiomene* (Simpson, 1929; Rose, 1973).

Only a few specimens of *Planetetherium* include the anterior portion of the mandible, and none of these are well preserved. The holotype of *P. mirabile* (AMNH 22162) has three small alveoli in front of P_3 and what may be a single large alveolus immediately anterior to these. The back of the symphyseal scar on the anteromedial aspect of the jaw indicates that the latter is probably the most anterior tooth and that the mandible is almost as short as that of *Worlandia*. X-ray photographs of the specimen show that the most anterior of the three small alveoli is anteriorly inclined (as in *Worlandia*), the second is weakly inclined, and the third (probably for a single-rooted P_2) is vertical. Thus it is probable that *Planetetherium*, like *Worlandia*, possessed only nine teeth and that the first three of these, anterior to P_3, were also considerably reduced. The presence of an enlarged anterior tooth in *Planetetherium*, however, is less certain.

In addition to the palatal dentition described above, upper teeth of *Worlandia inusitata* are represented by UM 68392 (incomplete left P^4) and UM 69603 (right maxilla with P^{1-2}). Two other specimens are referred here to the Worlandiinae, although their allocation to this species is less certain. UM 66542 (right P^4 and M^1 or ^{2}, text-fig. 5A,B) was initially identified as *Planetetherium mirabile* (Rose and Simons, 1977: 232) but may belong to *Worlandia inusitata*. PU 18299 (left maxilla with P^{2-3}, text-fig. 5C) has a molariform P^3 as in *Worlandia*. Both specimens come from late Clarkforkian sites, stratigraphically higher than SC-188, the locality of the holotype mandible and the referred palate. They are morphologically very close to *Worlandia*, but both are slightly larger.

That *Worlandia* is clearly referable to the Plagiomenidae is shown by the mutual possession of several derived characters: (1) highly molarized posterior premolars (especially P^{3-4} and P_4); (2) lingual cusps of molariform teeth higher than buccal cusps; (3) paraconid and metaconid of molars closely appressed, paraconid adjacent to hypoconulid of immediately anterior tooth, and metaconid slightly anterolingual to protoconid; (4) entoconid anterolingual to hypoconid; (5) shelf-like hypoconulid; (6) short cristid obliqua; (7) prominent entoconulid (weak in *Elpidophorus*); (8) irregular but discrete valley separating trigonid and talonid; (9) wear facet 6 large, extending onto entoconulid and hypoconulid; wear facets 1 and 5 confluent; facets 1-4 multiple on upper teeth; wear tending to result in extensive fenestration of enamel (these features less well developed in *Elpidophorus*); (10) upper molars with multiple stylar cusps.



TEXT-FIG. 5 – Upper teeth of a worlandiine plagiomenid, possibly *Worlandia inusitata*. A: Right M^1 or M^2, UM 66542. B: Right P^4, UM 66542. C: Left maxilla with P^{2-3}, PU 18299.

Worlandia also shares the following additional characters with *Planetetherium* but not with other plagiomenids: (1) short mandible with teeth reduced in number and size between P_3 and medial incisor (probably only nine lower teeth in each side, medial incisor greatly enlarged); (2) relatively broad, low-crowned cheek teeth with bulbous (not acute or trenchant) cusps; (3) molars decrease in size from M_1^1 to M_3^3.

These features indicate a close relationship between *Worlandia* and *Planetetherium* and also demonstrate that at least two lineages of plagiomenids coexisted in the Bighorn Basin during part of the early Eocene. In the light of this new evidence, we propose the following classification of North American plagiomenids:

Family Plagiomenidae Matthew, 1918

Subfamily Plagiomeninae Matthew, 1918

Plagiomene Matthew, 1918. early Wasatchian (early Eocene)

Elpidophorus Simpson, 1927. Torrejonian–Tiffanian (middle–late Paleocene)

Subfamily Worlandiinae, nov.

Worlandia, gen. nov. Clarkforkian–early Wasatchian (early Eocene)

Planetetherium Simpson, 1928. Clarkforkian (early Eocene)

?Plagiomenidae

Subfamily Thylacaelurinae Van Valen, 1967

Thylacaelurus Russell, 1954. Uintan (late Eocene)

Paleocene *Elpidophorus* is the oldest known plagiomenid (Rose, 1975) and is best placed in the Plagiomeninae because of its long jaw, moderately high-crowned teeth, and acute cusps. Nothing now known about the dentition of *Elpidophorus* precludes it from being near the ancestry of both *Plagiomene* and the Worlandiinae. *Planetetherium* can no longer be considered a plausible ancestor of *Plagiomene* because of the features cited above. The Uintan *Thylacaelurus* (Russell, 1954; Krishtalka and Setoguchi, 1977) is poorly known and its relationships to other plagiomenids are unclear; indeed, its allocation to the Plagiomenidae is uncertain. If correctly referred to this family it may represent yet another line, for which Van Valen (1967) has proposed subfamily status.

The discovery of *Worlandia* and its bearing on relationships among plagiomenids are further indications that we are only beginning to appreciate the diversity of this unusual family.

Occurrence.– *Worlandia* is known from several specimens from the Clark's Fork Basin. All are from localities in the Willwood Formation within strata that yield a Clarkforkian fauna. Most come from UM SC-188, also yielding *Plesiadapis cookei*, a primate characteristic of the early Clarkforkian. One specimen (UM 65122) is from a locality stratigraphically above this zone and about 50 meters below the lowest known Wasatchian faunas. UW 10158, the only Wasatchian specimen, is from near Yale locality 158, located between the 250 and 400 meter levels of the Willwood Formation in the central Bighorn Basin (the locality is not yet tied to a measured section). Wasatchian faunas occur within about 20 meters of the base of the Willwood Formation in this area (Bown, in press).

Plagiomenids were elements of northern early Tertiary faunas. They have been found at several sites in Wyoming, Montana, Alberta, and Ellesmere Island (Rose and Simons, 1977; Russell, 1967; West, *et al.*, 1977). Except for a few isolated teeth of *Thylacaelurus* from the Badwater area of central Wyoming (Krishtalka and Setoguchi, 1977), there is no published record of the Plagiomenidae from south of the Bighorn Basin in northern Wyoming.

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