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A NEW SPECIES OF *AELURODON* (CARNIVORA, CANIDAE) FROM THE BARSTOVIAN OF MONTANA

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ABSTRACT—*Aelurodon montanensis*, sp. nov. (Carnivora, Canidae, Borophaginae), is described from a new locality, Aelurodon Cut, near Pipestone Springs in Jefferson County, Montana. The new species is a primitive representative of the previously recognized *Aelurodon mcgrewi–A. stirtoni* clade, one of the most hypercarnivorous, relatively rare clades in the subfamily Borophaginae. It shares with this clade such derived characters as a broadened posterior cingulum of p3, initial development of a posteriorly expanded M1 internal cingulum, and similarities in dental proportions. Evolutionary trends within this clade include reduction in size, increasingly hypercarnivorous dentition with lengthened shearing blades on the upper and lower carnassials, a more trenchant talonid on m1, a reduced grinding part of upper and lower molars, and a posteriorly expanded M1 internal cingulum. Based on the stage of evolution of the new canid and on an associated metapodial fragment of *Aepycamelus*, we tentatively assign an early Barstovian age to the Aelurodon Cut locality.

INTRODUCTION

Late Tertiary deposits occur within numerous intermontane valleys of southwestern Montana. The valleys typically contain several structural basins that hold as much as 4,850 meters of Tertiary fill. The Tertiary basin-fill deposits range in age from about 55 to 4 Ma (Fields et al., 1985; Hanneman and Wideman, 1991). Fossil vertebrate localities are widely scattered throughout these intermontane valleys, causing difficulties in the establishment of a reliable biochronology for any significant length of time. Despite such difficulties, however, Tertiary faunas of Montana frequently offer a unique zoogeographic perspective. Straddling the Columbia Plateau and Great Basin to the west and the Great Plains to the east, the Montana strata are in a position to shed much light on problems arising from terrestrial faunal provincialism in western North America (Tedford et al., 1987). The new species described herein offers yet another example of this critical zoogeographic location.

In December 2001, a partial upper and lower jaw of *Aelurodon*, along with a metapodial fragment of an *Aepycamelus*, were recovered from a new locality in a cut on the north side of Interstate 90, approximately 4.8 km west of Whitehall, Montana, and about 6.4 km east of the classic Pipestone Springs locality. This is a significant discovery, not only because it is an undescribed form, but also it is the only representative of the genus *Aelurodon* in Montana. Here we report this new canid, which has a morphology transitional between *Aelurodon asthenostylus* from the Great Basin and *Aelurodon mcgrewi* from the Great Plains, and represents the northernmost distribution of the genus.

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York; **F:AM**, Frick Collection of American Museum of Natural History, New York; **MOR**, Museum of the Rockies, Montana State University, Bozeman; **MV**, vertebrate locality number designation of Museum of the Rockies, Montana State University, Bozeman and of University of Montana, Missoula; **UM**, University of Montana, Missoula; **UCMP**, University of California Museum of Paleontology, Berkeley; **UNSM**, University of Nebraska State Museum, Lincoln.

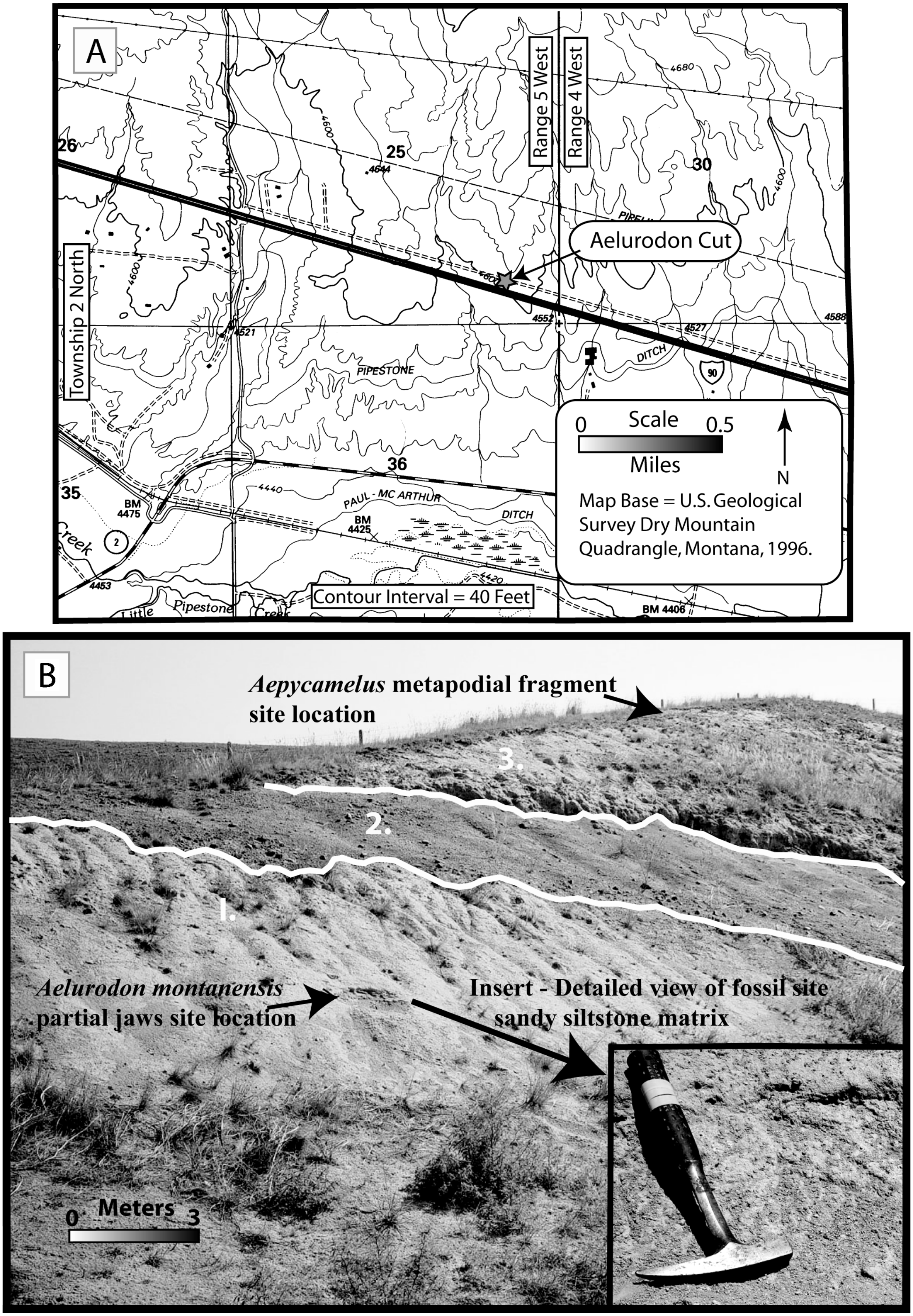
SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1785
Order CARNIVORA Bowdich, 1821
Family CANIDAE Fischer de Waldheim, 1817
Subfamily BOROPHAGINAE Simpson, 1945
Tribe BOROPHAGINI Simpson, 1945
Subtribe AELURODONTINA Wang, Tedford, and Taylor, 1999
AELURODON Leidy, 1858
AELURODON MONTANENSIS, sp. nov.

Holotype—MOR 1724, associated fragments of a skull and mandible consisting of maxillary fragments with left I2 (?), C, P1 root, P2–P3, P4 broken, and M1; isolated right P4 and M1; partial left and right rami with left c, p1–p2 broken, p3–m2; and right c, p1 root, p2–m2, and m3 root. The isolated right P4 and M1 were recovered more than 15 m east of and stratigraphically at least 3 m above the majority of the specimens, although every other indication (size, state of wear, preservation) give the appearance of all the material belonging to a single individual.

Type Locality—Aelurodon Cut, MOR MV320, is a road cut located on the north side of Interstate 90, in the SE¼ of section 25, T. 2 N., R. 5 W. (UTM coordinates 409,878 m East; 5,082,311 m North, Zone 12, NAD 27 Conus), approximately 4.8 km west of Whitehall, Jefferson County, Montana (Fig. 1).

Stratigraphy and Age—The Pipestone Springs area has long been known for its Chadronian vertebrate fauna (see Tabrum et al., 2001 for recent summary and references). Faunas of younger age are previously unknown in the immediate vicinity of Aelurodon Cut. However, Kuenzi (1966) documented some late Tertiary vertebrate sites near Whitehall (see Nichols et al., 2001 for late Tertiary vertebrate localities in southwestern Montana). The spatially closest late Tertiary sites located by Kuenzi lie approximately 3.2 km south and 3.2 km to the southwest of Aelurodon Cut (UM localities MV 6305 and MV 6306, respectively). Fossil material from UM locality MV 6305 consisted of an equid tooth fragment, and UM locality MV 6306 yielded tooth and bone fragments. These two sites were grouped by Kuenzi with other late Tertiary vertebrate locales


A
Range 5 West
Range 4 West
Township 2 North
Aelurodon Cut
PIPESTONE
PAUL - MC ARTHUR
DITCH
Scale
0
0.5
Miles
N
Map Base = U.S. Geological Survey Dry Mountain Quadrangle, Montana, 1996.
Contour Interval = 40 Feet
B
Aepycamelus metapodial fragment site location
3.
2.
1.
Aelurodon montanensis partial jaws site location
Insert - Detailed view of fossil site sandy siltstone matrix
0
Meters
3

near Whitehall, and collectively they became the basis for an age assignment of Barstovian to Hemphillian for the Parrot Bench Formation.

Based upon previous geologic mapping (Kuenzi, 1966; Hanneman, 1989), it seems likely that the strata of Aelurodon Cut fall near the base of Kuenzi's Parrot Bench Formation, which was later reassigned to the Sixmile Creek Formation (Kuenzi and Fields, 1971), and has recently been informally mapped as Cenozoic Sequence 4 (approximately 16 to 4 Ma) (Hanneman and Wideman, 1991).

Lacking an associated fauna (but see below for comments on a metapodial fragment of *Aepycamelus*), the only independent source of chronologic information is from the stage of evolution of the single canid taxon. As discussed below, *Aelurodon montanensis* is more primitive than *Aelurodon mcgrewi* Wang, Tedford, and Taylor, 1999. *A. mcgrewi* is currently known from a limited sample in the late Barstovian of Nebraska. The Montana form is apparently on the primitive side of *A. mcgrewi* in its less hypercarnivorous dentition with less reduced grinding part of the cheek teeth, along with less reduced M1 internal cingulum and m1 metaconid. The Montana form is also rather large (especially the large lower carnassial), which is consistent with a general trend within the *A. mcgrewi*–*A. stirtoni* clade that becomes progressively smaller in size and more hypercarnivorous. On the other hand, the new Montana form is more derived than *A. asthenostylus* (Henshaw, 1942), the most basal species of *Aelurodon*, in its larger size and more derived dentition. Biostratigraphically, *A. asthenostylus* is known from the early through early late Barstovian of southern Great Basins (Barstow Formation, California) and northern Great Plains (Pawnee Creek Formation, Colorado and Hay Springs Creek and Driftwood Creek of Nebraska). *A. mcgrewi*, on the other hand, is confined to the late Barstovian of Nebraska (Crookston Bridge and Devil's Gulch members of the Valentine Formation and equivalent rocks) (Wang et al., 1999). The intermediate morphology of the new Montana materials between those of *A. asthenostylus* and *A. mcgrewi* thus indicates an age that predates the earliest known samples of *A. mcgrewi*, i.e., an early Barstovian age probably around 15 to 16 Ma.

A single fragment of distal metapodial (MOR 1729) of an *Aepycamelus* sp. was found in the same locality (Fig. 1B). Lacking distal condyles, this specimen preserves the segment where the medial and lateral digits are incompletely fused (Fig. 2). The size of this metapodial is similar to those of adult individuals (epiphysis fully fused) from the early Barstovian of the northern Great Plains (e.g., those from the Olcott Formation of Nebraska). *Aepycamelus* is also found in early Barstovian beds in the Madison Valley (about 48 km east of Aelurodon Cut), the Boulder Valley (about 20 km east of Aelurodon Cut), and the New Chicago site (approximately 80 km northwest of Aelurodon Cut, near Drummond, Montana) (*Procamelus* of Douglass, 1909). To the south in the Lemhi Valley, Idaho, the Bannock Pass locality (F:AM Lemhi Valley locality) (early Barstovian) in Lemhi County has also yielded an *Aepycamelus* metapodial (e.g., F:AM 50750) of similar size to MOR 1729. Collectively, the Montana and Idaho materials form the early Barstovian Flint Creek Fauna of Tedford et al. (1987).

FIGURE 2. Anterior view of a metapodial fragment of *Aepycamelus*, MOR 1729, from Aelurodon Cut, Montana. Scale is in mm.

Diagnosis—Differs from *Aelurodon asthenostylus* in its larger size, a more reduced M1 relative to P4, a narrower m1 talonid, a more reduced m1–m2 metaconid, and a shorter m2 relative to m1; and from the *Aelurodon ferox*–*A. taxoides* clade in its relatively small non-carnassial premolars and less reduced M1 internal cingulum. *A. montanensis* shares with the *A. mcgrewi*–*A. stirtoni* clade such derived features as a widened p3 posterior cingulum, initial development of a posteriorly expanded M1 internal cingulum, and a relatively large P4. Within the *A. mcgrewi*–*A. stirtoni* clade, *A. montanensis* is easily distinguishable from *A. stirtoni* in its larger size, presence of both m1 and m2 metaconids, and less reduced M1 talon; and *A. montanensis* differs from *A. mcgrewi* in its larger P4 protocone, longer m1, larger m1 metaconid, larger m2, and smaller p1–4.

Etymology—Referring to its occurrence in Montana.

Descriptions—MOR 1724 (Table 1; Figs. 3, 4) is preserved in sandy siltstones that are light brown in color. The specimen

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FIGURE 1. **A**, Location site map of Aelurodon Cut. Whitehall, Montana lies about 4.8 km east of Aelurodon Cut, and the classic Pipestone Springs locality is approximately 6.4 km west of Aelurodon Cut. **B**, Photograph of Aelurodon Cut taken looking north from Interstate 90. The *Aelurodon montanensis* partial jaws were found within a semi-indurated, very light brown colored (10 YR 7/3 Munsell color notation) sandy siltstone unit (labeled as 1). Floating subangular to subrounded pebbles of granite, quartz, and andesite occur within this unit. Approximately 3 meters stratigraphically above the *Aelurodon montanensis* excavation area, the sandy siltstone of unit 1 is overlain by a relatively thin, approximately 2.5 meter thick unit of coarse-grain sand, pebbles, and cobbles (labeled as 2). The sand/pebble/cobble zone is overlain by a very light brown colored (10 YR 7/3 Munsell color notation) micaceous, semi-indurated fine-grained sandstone that grades upward into a sandy siltstone (labeled as 3). This unit also contains floating subangular to subrounded pebbles of granite, quartz, and andesite. The basal micaceous sandstone is intensely burrowed in some areas. The *Aepycamelus* metapodial fragment was found within the upper sandy siltstone of this unit, approximately 4 meters stratigraphically above the top of the sand/pebble/cobble zone.

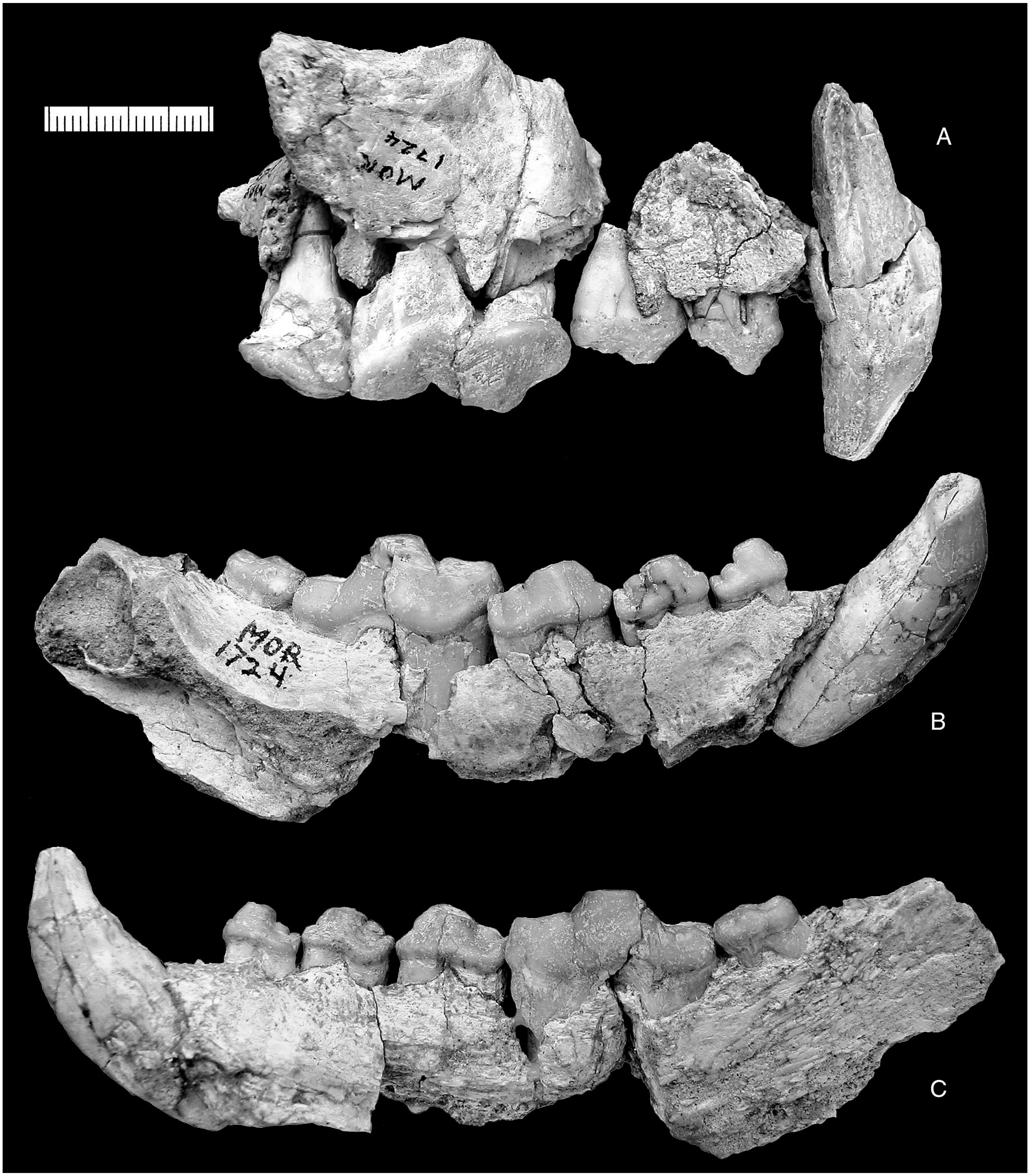

FIGURE 3. Upper and lower jaws of *Aelurodon montanensis*, MOR 1724, holotype from Aelurodon Cut, Jefferson County, Montana. **A**, lateral view of composite upper jaw made up of left C–P3 (reversed) and right P4–M1; **B**, lateral view of right ramus; and **C**, medial view of right ramus with c–m2. Scale is in mm.

FIGURE 4. Stereo photographs of upper and lower teeth of *Aelurodon montanensis*, MOR 1724, holotype from Aelurodon Cut, Jefferson County, Montana. **A**, composite upper teeth made up of left C–P3 (reversed) and right P4–M1; and **B**, right c, p2–m2. Scale is in mm.

shows signs of extensive weathering, particularly on the medial surface of the right ramus and the lateral surface of the left ramus. Of the upper jaw, only maxillary fragments around the roots of left P2–P3 and right P4–M1 are preserved. The lower jaw is similarly weathered, although the preserved bone fragments are continuous enough to permit confident restorations of the original positions of all lower teeth. There are two mental foramina, the anterior one is below the anterior root of p2, the posterior one below the posterior root of p3. The lower halves of both horizontal rami are broken, leaving the roots of most cheek teeth exposed.

Upper Teeth—An isolated incisor is present among the upper teeth. It is judged to be an I2 because of its relatively straight root, in contrast to a more procumbent root on the lower incisors. Its crown is worn flat, and except for a triangular outline, the crown pattern is no longer recognizable. Both left and right upper canines are present, the left one being better preserved (Fig. 3A). A distinct ridge is present along the posterior face of the tooth.

The upper cheek teeth are moderately worn and cusp patterns are well preserved (Figs. 3A, 4A). The right P1 is broken off at the base and only a single root is preserved. There is no diastema in front or behind the P1, and the P2–P3 are imbricated to fit a short jaw. The double-rooted P2 has an anteriorly located main cusp with an anterior ridge. An anterior accessory cusp is delineated from the anterior ridge by a small notch. There are two posterior accessory cusps, a large one immediately behind the main cusp and a small one following the large accessory cusp. The small posterior accessory cusp is distinct from the posterior cingulum. Except for its larger size, the P3 is similar to P2, but has a stronger posterior cingulum. The P4s suffered fractures on both left and right sides. It is a robust tooth with a wide shearing blade. The protocone is extremely reduced, to be merely a small anteromedial corner of the tooth.

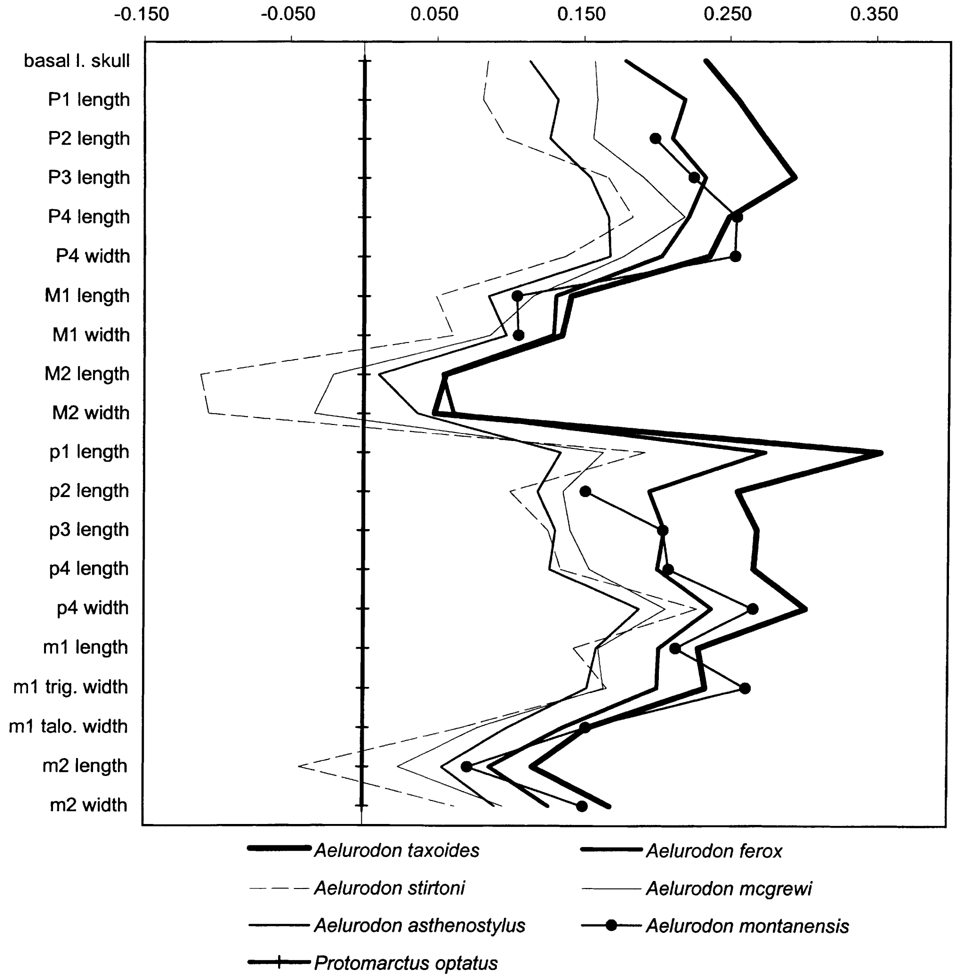

FIGURE 5. Log-ratio diagram for dental measurements of *Aelurodon* using *Protomarctus optatus* as a standard for comparison (straight line at zero) (see Simpson, 1941 for the method of the log-ratio plots). See text for explanations and Table 1 for actual measurements.

TABLE 1. Dental measurements (in mm) of selected specimens of *Aelurodon montanensis*, sp. nov., *Aelurodon mcgrewi*, and *Aelurodon stirtoni*. F:AM 22410, holotype of *A. mcgrewi*, from south of Norden, Devil's Gulch Member, Valentine Formation (late Barstovian), Brown County, Nebraska; AMNH 8307 from Republican River beds (late Barstovian), Red Willow County, Nebraska; UCMP 33474, holotype of *A. stirtoni*, from Fence Line Locality, Burge Member, Valentine Formation (late Barstovian), Cherry County, Nebraska; and UNSM 25789 from Swallow Quarry, Burge Member, Valentine Formation (late Barstovian), Cherry County, Nebraska. See Wang et al. (1999:appendix III) for definitions of measurements and summary statistics of *Aelurodon*.

	A. montanensis	*A. mcgrewi*		*A. stirtoni*	
	MOR 1724	AMNH 8307	F:AM 22410	UCMP 33474	UNSM 25789
P2 length	13.0	11.6	12.1	—	10.4
P3 length	15.9	15.0	15.0	13.7	13.6
P4 length	28.5	26.8	27.0	25.1	24.2
P4 width	13.9	12.0	11.2	9.5	11.0
M1 length	15.6	15.6	16.7	14.1	13.2
M1 width	18.6	18.2	17.2	16.7	16.1
p2 length	10.3	10.9	10.8	—	8.8
p3 length	13.4	12.7	12.6	—	10.1
p4 length	16.8	16.6	16.5	—	13.0
p4 width	10.1	10.6	9.7	—	8.7
m1 length	29.0	27.5	27.2	—	25.0
m1 trigonid width	12.6	11.8	10.5	—	9.6
m1 talonid width	10.3	10.5	—	—	8.1
m2 length	11.6	11.2	10.1	—	9.1
m2 width	8.7	8.2	8.2	—	7.0

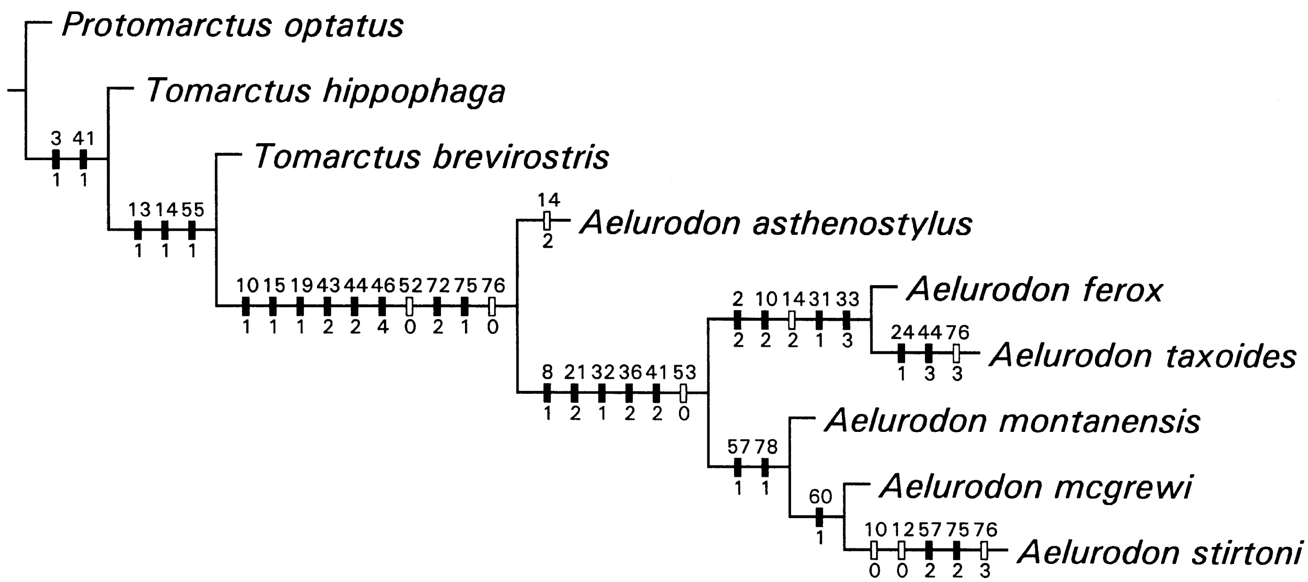

FIGURE 6. Cladistic relationship of *Aelurodon* species, using *Protomarctus* and *Tomarctus* as outgroups. Character numbers, character descriptions, and data matrix (Appendix 1) follow those in Wang et al. (1999) except noted below. PAUP (Swofford, 1993) analysis is performed on the Aelurodontina clade only. With the addition of *A. montanensis*, sp. nov., we have added two new character states to reflect the morphological status of the new species: character 57(1), posterior expansion of M1 lingual cingulum to form a concave posterior border, is an intermediate state between states 0 and 2 [equal to 57(1) of Wang et al. 1999]; character 78 is a new character and state 78(1) represents an enlargement of the posterior cingulum of p3 (the original stratigraphic character 78 of Wang et al. 1999 is here substituted by the new morphological character).

A large parastyle is present but well worn. There is no connecting ridge between the protocone and parastyle. Instead, a gentle ridge leads from the apex of the paracone toward the protocone, a feature of the genus *Aelurodon* (Baskin, 1980). The M1 is reduced in size relative to that of the P4 (Table 1; Fig. 4A). Although both the paracone and metacone are worn, it is clear that the paracone is much larger and probably was taller than the metacone. The protocone is reduced to a small crest, followed posteriorly by an indistinct metaconule. The internal cingulum (hypocone) is quite well developed and is prominently displaced posteriorly. The internal cingulum is also more elevated than the protocone and metaconule. A labial cingulum is only vaguely present on the M1. No M2 is preserved.

Lower Teeth—No lower incisors are preserved. Both lower canines are preserved but well worn (Figs. 3B, 4B). There is a slight bulge on the anterolingual aspect of the tooth (Fig. 3C). Both p1s are lost. A 3 mm diastema is present between c and p1, but no diastema is present behind the p1. The p2–p4 gradually increase in size and height, in contrast to the abrupt enlargement of the p4 in Borophagina (*Carpocyon*, *Epicyon*, and *Borophagus*). Unlike the upper premolars that have two posterior accessory cusps, the p2–p4 have one distinct posterior accessory cusp and a posterior cingular cusp (arising from an elevated posterior cingulum). The lower carnassial (m1) has a long shearing blade and a short talonid (Fig. 4B). The trigonid is almost entirely made up of paraconid and protoconid, and the metaconid is reduced to a tiny bulge in the posterolingual aspect of the protoconid. The talonid is narrower than the trigonid, and is quite trenchant with a dominant hypoconid and a small, low entoconid at the lingual edge of the talonid. A transverse cristid is present on the lingual face of the hypoconid and labial face of the entoconid, such that the two cristids enclose a small, shallow talonid basin in the anterolingual aspect of the talonid and partition a small triangular platform behind. As in the m1, the m2 trigonid is wider than its talonid. The trigonid lacks a paraconid. The protoconid is nearly twice the size of the metaconid. Similarly, the talonid is trenchant with a large hypoconid and a low, narrow entoconid crest. The m3 is broken off at the base.

Comparison and Discussion—*Aelurodon montanensis* shows a combination of size and dental morphology that clearly indicates its membership in *Aelurodon* (as revised by Wang et al., 1999). Derived characters of *Aelurodon* present in *A. montanensis* include large premolars with well-developed anterior and posterior accessory cusps, strong P4 parastyle, reduced P4 protocone, reduced M1–M2, anteriorly reduced M1 lingual cingulum, m1 talonid narrowed, shortened m2, and reduced m1–m2 metaconids.

Within the genus, *Aelurodon montanensis* is easily distinguished from the most primitive species of the genus *A. asthenostylus* in its relatively larger size, reduced M1 relative to P4, narrower m1 talonid, more reduced m1–m2 metaconids, and shorter m2 relative to m1. The Montana form shows more derived conditions in all of these features, based on the phylogenetic analysis by Wang et al. (1999).

Among advanced species of *Aelurodon*, *A. montanensis* does not seem to fall into the *A. ferox*–*A. taxoides* lineage. Although its lower carnassial is quite large (comparable to those of *A. ferox* from the Burge Quarry of Nebraska), its premolars do not show corresponding enlargement, as is characteristic of the *A. ferox*–*A. taxoides* lineage (Wang et al., 1999). On the other hand, the Montana form shares certain features with the *A. mcgrewi*–*A. stirtoni* clade. These include a widening of the p3 posterior cingulum resulting in a lingual bulge just above the posterior root of the tooth. This feature is present in most individuals of the *A. mcgrewi*–*A. stirtoni* clade. Although it may be subtly expressed in certain individuals of the *A. mcgrewi*–*A. stirtoni* clade, it is entirely absent in the *A. ferox*–*A. taxoides* clade. It is interesting to note, however, that the origin of the lingual bulge may be traced to a California population of *A. asthenostylus* (e.g., F:AM 27195, 27170, 27161 of the Barstow Formation), in contrast to its absence in individuals from the Great Plains (Pawnee Creek Formation, Colorado). Another feature that suggests a close relationship between *A. montanen-*

sis and the *A. mcgrewi–A. stirtoni* clade is a posteriorly expanded M1 internal cingulum, a character that is markedly developed in *A. stirtoni* but less so in *A. mcgrewi*. Finally, dental dimensions as revealed in log-ratio diagrams (Fig. 5) also resemble those of the *A. mcgrewi–A. stirtoni* clade in its relatively wide p4 and m1 trigonid.

Within the *Aelurodon mcgrewi–A. stirtoni* clade, *A. montanensis* can easily be excluded from the more derived *A. stirtoni* (Webb, 1969) by its larger size, presence of both m1 and m2 metaconids, and less reduced M1 talon. However, the Montana form also differs from *A. mcgrewi* (e.g., AMNH 8307, F:AM 22410, 61778) in a number of features: less reduced P4 protocone, less reduced M1 internal cingulum, longer m1 (opposite to trend toward *A. stirtoni*), less reduced m1 metaconid, less reduced m2, and p1–p4 less enlarged. Such differences are pronounced enough to prevent assignment to any known species of *Aelurodon*. Combining its primitive morphology and large size, recognition of a new species is warranted.

Given the above observation, it is clear that the new Montana species occupies a basal position within the *A. mcgrewi–A. stirtoni* clade. A cladistic analysis also shows such a relationship, although some of the more subtle features discussed above are not easily coded in the data matrix (Fig. 6). *Aelurodon montanensis* appears to offer a starting point for this clade. Morphological trends within this clade include reduction in size and increasingly more trenchant cheek teeth, ultimately making this clade the most hypercarnivorous borophagines (Table 1; Fig. 5).

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Benjamin Wideman was the first to locate two teeth of *Aelurodon montanensis*, and Charles Wideman and Ralph Nichols recovered the remaining partial jaws of *Aelurodon montanensis* as well as the *Aepycamelus* metapodial fragment. Howell Thomas of the Natural History Museum of Los Angeles County prepared the specimens described herein. We thank P. David Polly and an anonymous reviewer for critical comments and editorial suggestions.

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APPENDIX 1

Data matrix for Aelurodontina is as follows. Characters and states follow Wang et al. (1999) except as noted in Figure 6.

P. optatus	01030010000100011001000000000000200000000000030100111000001000000100120000010?
T. hippophaga	011300100001000110010000000000002000000010000301001110000010000001001200000100
T. brevirostris	011300100001110110010000000000002000000010000301001101000100000001001200000100
A. asthenostylus	0113001?0101121110110000000000002000000010220401001010100010000001001202001000
A. montanensis	0??????????????????????00?????0???00200002022040100100010 1?????00010012 02001001
A. mcgrewi	011300110101111110112000000000012002000020220401001000101011000001001202001001
A. stirtoni	011300110000111110112000000000012002000020220401001000102011000001001202002301
A. ferox	021300110201121110112000000000113002000020220401001000100010000001001202001000
A. taxoides	021300110201121110112001000000113002000020230401001000100010000001001202001300