

ARIKAREEAN (OLIGOCENE-MIOCENE) *HERPETOTHERIUM* (MARSUPIALIA, DIDELPHIDAE) FROM NEBRASKA AND FLORIDA

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North American *Herpetotherium* (Marsupialia, Didelphidae) is a small mouse-sized (<80g) opossum that ranged from the middle Eocene into the early Miocene (Uintan-Hemingfordian) of the Great Plains, Pacific Northwest, and Atlantic Southeast. New Arikareean (30-18.8Ma) *Herpetotherium* samples are described from the lower Arikaree Group of Nebraska (Dw-121 or Ridgeview Local Fauna, a locality south of Chadron, from localities of the Wildcat Ridge region, and the McCann Canyon Local Fauna) as well as from 4 localities in Florida (I-75, Brooksville 2, SB-1A, and White Springs). The samples from Dw-121 and Brooksville 2 are the first large (>25) populations of *Herpetotherium* described from the Arikareean age. Three species are recognized in the Arikareean: *H. fugax*, *H. youngi*, and *H. merriami*. Most early Arikareean samples are referred to *H. fugax* and are slightly smaller on average than older *H. fugax*. Later Arikareean *Herpetotherium* samples are referable to *H. youngi* on the basis of possessing a single central styler cusp. A large species, *H. merriami*, from the early Arikareean John Day Formation in Oregon is similar to *Herpetotherium* molars described from the early Arikareean or late Whitneyan Florida I-75 locality. Taxonomy of *Herpetotherium* has previously been based on tooth size and upper molar styler cusp morphology. *H. fugax* exhibits several configurations of styler cusp morphology, separate to fused central styler cusps, and a wide range of dental size variation. These ranges of variation are similar to those exhibited by the Chadronian species, *H. valens*.

Key Words: *Herpetotherium*; Arikareean; taxonomic review; dental variation; Florida; Nebraska.

INTRODUCTION

Herpetotherium is a small (<40-80g) mouse-sized didelphid marsupial that ranges from the late Eocene to the early Miocene of North America (Rothecker & Storer 1996). It is a common component of Arikareean (30-18.8Ma) North American Land Mammal "Age" (NALMA) micro-mammal faunas from the Great Plains, Pacific Northwest, and Atlantic Southeast. However, material usually consists of only scarce, fragmentary dental material and isolated teeth. Because of the lack of large samples, numerous described species have been based solely on stratigraphic occurrence or small differences in tooth morphology (particularly styler cusp configuration in the upper molars), as well as small differences in dental size between species. In localities that produce significant numbers (>25) of specimens it is becoming increasingly evident that *Herpetotherium* populations show a wide range of dental variation (Hough 1961; Morton & Green 1976; Setoguchi 1978; Eberle & Storer 1995).

In the most recent review of North American Tertiary marsupials, Korth (1994) reported no large samples of Arikareean *Herpetotherium* (>15) and many of those that were discussed had vague chronologic or stratigraphic resolution (Stock & Furlong 1922; J. Macdonald 1963, 1970; L. Macdonald 1972; Korth 1992). Much of the material discussed in this report from the Arikareean of Nebraska and Florida represents relatively large samples with more precise stratigraphic and biochronologic correlation. These samples provide more evidence that coexisting *Herpetotherium* populations exhibit a wide range of dental variation, both in size and morphology. I also include a review of the Florida record of pre-Pliocene (before *Didelphis* migrated from South America) marsupials.

McGrew (1937) described the first Arikareean marsupial in the Great Plains from Nebraska. At this time marsupials were well known from the late Eocene and Oligocene White River Group of Nebraska (Simpson 1928), but none from the younger Arikaree Group deposits that overlie the White River. McGrew named a new species, "*Peratherium*" *youngi*, based on a single upper molar (UC 1544) collected from the upper Arikaree

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Group lower Harrison “beds” near Agate, Nebraska. The first North American Arikareean marsupial, “*Peratherium*” *merriami* had earlier been described on the basis of a single partial skull from the John Day Formation of Oregon (Stock & Furlong 1922). The skull was collected from the lower Logan Butte volcanoclastic sediments that have been radiometrically dated (single crystal Ar/Ar) to be older than 28.8 Ma (Tedford et al., 2004). This would place *H. merriami* in the early Arikareean or possibly the late Whitneyan. The Picture Gorge Ignimbrite occurs at the top of the Logan Butte section and recent work by Robert Hunt (pers. comm., 2004) suggests that the lower part of the section is more likely Whitneyan in age. The third Arikareean “*Peratherium*”, *P. spindleri*, was named by Macdonald (1963) from the Wounded Knee faunas of South Dakota.

Korth (1992) described the only other Arikareean Nebraska *Herpetotherium* sample from the McCann Canyon LF. The McCann Canyon paper included most of the small mammals (except the carnivores) from a locality believed to be a Harrison Formation equivalent although the sediments cannot be directly correlated with the type Harrison of the Pine Ridge. Korth’s biochronologic analysis suggested an early late Arikareean age (24–22Ma, Tedford et al., 2004) for the fauna. In his paper Korth referred all later Tertiary North American didelphines to Cope’s (1873) *Herpetotherium* which followed Crochet (1977), who separated European *Peratherium* from North American “*Peratherium*” because *Herpetotherium* has a dominant central styler cusp on upper molars whereas *Peratherium* species show a dominant styler cusp B. Further, based on comparison of the lower dentition of the material from McCann Canyon, Korth formally synonymized *P. spindleri* with *H. youngi*. Korth (1992) distinguished other species of *Herpetotherium* from *H. youngi* on the basis of size differences.

In the Great Plains, Green and Martin (1976) reviewed didelphids from the Oligocene and Miocene of South Dakota. In their analysis they found styler cusp morphology of the upper molars to be variable and commented on the validity of diagnosing species on this basis. They suggested that “*P. spindleri*” and “*P. youngi*” might be synonyms of “*P. fugax*” but the samples were too small to make a conclusive assignment. Their review also included description of a few teeth of “*Peratherium* sp.” from the “Hemingfordian” NALMA Black Bear Quarry II LF from the Rosebud Formation

that was slightly smaller than older “*Peratherium*”. Later, Martin and Green (1984) described other small mammals from the fauna and extended the range of “*Peratherium*” sp. into the Hemingfordian Batesland Formation, but they did not describe this Batesland sample. In addition, they correlated the South Dakota Rosebud Formation with the “Marsland” (=“Upper Harrison” beds) of Nebraska which would place the small Rosebud marsupial sample in the late Arikareean (Tedford, et al. 1987, 2004).

Reports have listed Oligocene and Miocene marsupials from Florida, but none have discussed them in detail. Patton (1964) reported a didelphid from the I-75 LF. Wolff (1987) referred all then known Florida marsupials from four localities to “*Peratherium*.” Later, Morgan and Pratt (1988) also listed “*Peratherium*” from the late Hemingfordian Brooks Sink locality and the Barstovian NALMA “Nichols Mine” fauna (now Bird Branch LF). I assign most of the Florida marsupials to *Herpetotherium*, except for those from Brooks Sink and Bird Branch which instead appear to be closely related to marmosine opossums. A partial didelphid lower tooth reported from the Barstovian of Texas (Slaughter 1978) is very similar to the marmosine-like Florida material and may not be a herpetotheriine as reported by Korth (1994). This would therefore restrict *Herpetotherium* to Florida localities no younger than the early Hemingfordian. Here, I describe all of the above *Herpetotherium* specimens, along with newly discovered specimens from the Brooksville 2 LF (Hayes 2000), from the White Springs LF (Morgan 1989), and the SB-1A LF (Frailey 1978).

Korth (1994) most recently reviewed all Chadronian through Hemingfordian North American marsupials. He recognized two families of marsupials during this time, Didelphidae (represented by *Herpetotherium* and *Copedelphys*) and Peradectidae (represented by *Nanodelphys* and *Didelphidectes*). Most post-Duchesnean NALMA *Peratherium*, except for *P. titanelix* and *P. stvensoni* (which Korth placed in a new genus, *Copedelphys*) were allocated to *Herpetotherium* as a genus distinct from *Peratherium* following his 1992 paper. Korth recognized five species of *Herpetotherium* (*H. valens*, *H. fugax*, *H. merriami*, *H. youngi*, and *H. sp.* from the Rosebud Formation) on the basis of size and styler cusp differences. All of these species were thought to be derived from the Duchesnean *Peratherium knighti*. *P. donahoei* was synonymized with *Herpetotherium valens*, and occurs in the

Chadronian. Korth separated several of the small specimens from the Chadronian Pipestone Springs fauna as representing *H. fugax*, therefore extending the range of this species back to the middle Chadronian. *H. fugax* is the sole Orellan NALMA species. Korth did not recognize a Whitneyan NALMA species even though he had referred the probable (Emry et al. 1987) Cedar Ridge LF marsupial described by Setoguchi (1978) as “*P. cf. spindleri*” to *H. fugax*. By the Arikareean, Korth suggests *Herpetotherium* diversity increased to two or three species: (1) *H. merriami*, a relatively large species with pleisomorphic styler cusp morphology; (2) *H. youngi*, a small species with a derived single central styler cusp, and (3) *H. sp.*, a very small species from the Rosebud Formation of South Dakota. After Korth’s review, Eberle and Storer (1995) reported on *Herpetotherium* from the Chadronian Calf Creek LF, Cypress Hills Formation, Saskatchewan. Based on styler cusp variation, two species of *Herpetotherium* were thought to exist in the Calf Creek LF. The authors’ analysis showed that, even though the sample did exhibit considerable differences in styler cusp configuration and tooth size, this variation was normally and continuously distributed and therefore the material belonged to a single species, *Herpetotherium valens*.

The following year, Rothecker and Storer (1996) described the marsupials from a stratigraphically lower fauna in the Cypress Hills Formation. In their analysis of the marsupials from the Duchesnean Lac Pelletier lower fauna, they proposed that all pre-Duchesnean North American “*Peratherium*” that Korth did not assign to *Herpetotherium* be so assigned, because the species from the Lac Pelletier lower fauna were transitional between older Uintan *Herpetotherium* and the Chadronian *Herpetotherium valens*. The samples showed an indistinguishable morphocline from earlier *Peratherium*-like species to later species of *Herpetotherium*. Although two species of *Herpetotherium* (*H. sp.*, cf. *marsupium* and *H. sp.*, cf. *knighti*) were described, based on distinct size and minor morphology differences, styler cusp variation in position, twinning, and separation of cusps was noted for both.

MATERIALS AND METHODS

NEBRASKA LOCALITIES

Arikareean-age *Herpetotherium* described in this paper were collected from a locality in the Pine Ridge region (UNSM Dw-121= Ridgeview LF) and from sev-

eral localities in the lower Arikaree Group (including the Gering Formation) of the Wildcat Ridge region of western Nebraska (Fig. 1). As mentioned above, Korth (1992) described the marsupials from University of Nebraska State Museum localities Cr-125 and Cr-117, collectively termed the McCann Canyon LF. I am only adding additional newly collected material to the McCann Canyon LF. The other samples have not previously been described.

UNSM Dw-121. A new Arikareean *Herpetotherium* sample was recovered from a locality south of Chadron, Nebraska, discovered by Nebraska highway salvage paleontologist Bruce Bailey. This locality, designated UNSM Dw-121 (Bailey 1992, 1999, 2004) was found in fluvial sediments of the basal Arikaree Group incised into the fine-grained volcanoclastics of the White River Group along the axis of the Pine Ridge paleovalley (northern Gering paleovalley of Swinehart et al. 1985). Bailey (2004) recently listed the fauna from Dw-121 and named it the Ridgeview LF. It is one of the stratigraphically lowest localities producing microvertebrates (the other is Wagner Quarry [Hayes, 2004]) of the Arikaree Group in the Pine Ridge region. A diverse fauna has been recovered from the sediments representing at least 26 mammalian species, including the hedgehog *Ocajila* and the rodent *Geringia*. Faunal comparison suggests an early Arikareean age for the site (Bailey, 2004, Tedford et al., 2004).

The marsupials recovered from UNSM Dw-121 are represented by over 300 specimens of *Herpetotherium* and over 50 specimens of an undescribed species of *Nanodelphys*. The two are separable on the basis of size and styler cusp morphology. *Nanodelphys* is considerably smaller and all the upper molars have an ectoflexus and lack a central styler cusp unlike *Herpetotherium* which has a central styler cusp or cusps and an ectoflexus only on M3.

Gering Formation. Marsupials were collected from the “brown siltstone”, Gering Formation and other undifferentiated lower Arikaree Group deposits (= “Monroe Creek”) along the Wildcat Ridge of western Nebraska by Swisher (1982). These sediments are considered early early Arikareean, ~30-28 ma (Tedford et al. 1987, 1996, 2004) and unconformably overlie rocks of the earlier Oligocene White River Group, Brule Formation. The age is also supported by several radiometric dates (Tedford et al. 1996) taken from ash deposits within the rocks. Swisher (1982) collected at 27 localities of the Wildcat Ridge, of which eight (Swisher 1982 locali-

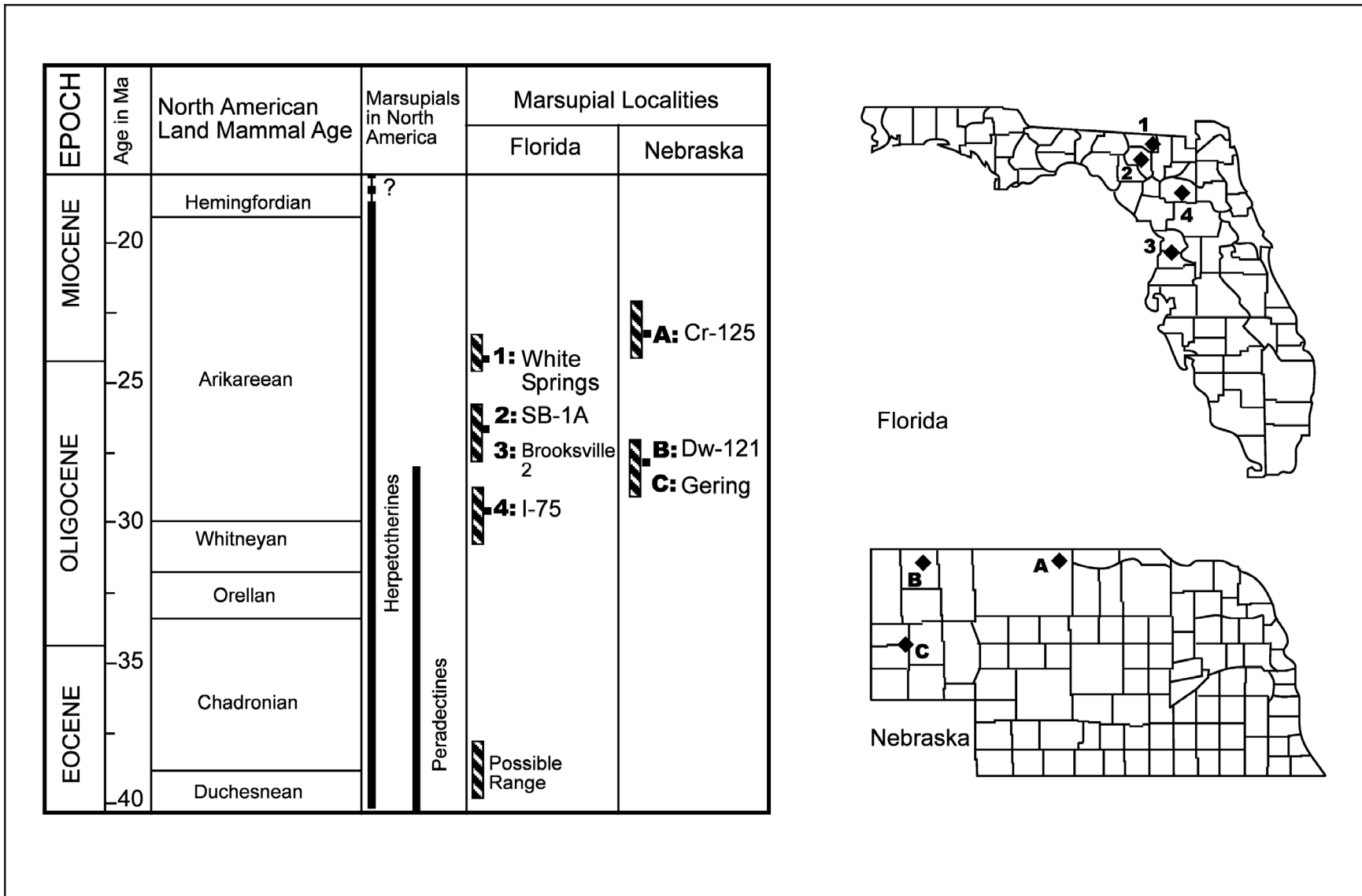


Figure 1. Age relationship and location of Nebraska and Florida *Herpetotherium* localities.

ties: 1- in the "brown siltstone", 2, 3, 11, 21, 23- in the Gering Formation, and 27- in the undifferentiated lower Arikaree). Eight localities produced some *Herpetotherium* material, predominately lower teeth and jaw fragments that he referred to "*Peratherium spindleri*."

FLORIDA LOCALITIES

Herpetotherium occurs at four localities in Florida that range in age from late Oligocene to early Miocene (Fig. 1). Prior to this report, marsupials were reported from four localities in the state: I-75, Brooks Sink, Bird Branch, and Thomas Farm. *Herpetotherium* is found in only the I-75 locality and three new localities: Brooksville 2, SB-1A, and White Springs. The Brooks Sink and Bird Branch marsupials are not herpetotheriines and will be reported on elsewhere. The well-known Hemingfordian Thomas Farm site is removed from the list because I believe that the single reported didelphid tooth (UF 97364; Wolff 1987; Marshall et al 1990) is a contaminant introduced from another locality. I recognized it as an upper molar of *Nesophontes* derived from prior screen washing of sediment from a Haitian site.

Samples of marsupials from Florida sites vary from single specimens (e.g., SB-1A) to more than fifty teeth (Brooksville 2 LF). As most of the sites are sinkhole or fissure-fill deposits, they can only be dated by biochronologic correlation. However, a few sites were collected from sediments that inter-tongue with or are superposed by marine strata which permits aging by stable isotopic means. Biochronologic analyses by Albright (1999) and Hayes (2000) have led to a better understanding of the temporal relationships between the late Oligocene and early Miocene land mammal sites in Florida.

I-75 LF. Patton (1969) recorded the I-75 LF from a small sinkhole deposit uncovered by construction of Interstate 75 just west of Gainesville, Florida (Alachua County). It is a small but diverse sample that includes taxa known previously from only Western North American localities. Patton (1969) tentatively identified its age as Whitneyan (late Oligocene) because of the presence of *Mesohippus*, a paleolagine rabbit, *Nanotragulus*, two small oreodonts, and *Paleogale*. Current evidence supports either a Whitneyan or possibly early Arikareean land mammal age for the I-75 LF (Hayes 2000).

White Springs LF. The White Springs LF was recovered from ancient shoreline sediments of the Parachula Formation exposed along the Suwannee River

lying unconformably on the Oligocene Suwannee Limestone. Morgan (1989) placed the site in the early Miocene (22-21 Ma) on the basis of correlation of the marine sediments to the upper N4 and lower N5 subtropical foraminiferal zones. However, Jones et al. (1993) obtained an $^{87}\text{Sr}/^{86}\text{Sr}$ date of $24.4 \pm 0.5-1.0$ Ma from mollusk shells at the locality. Recent faunal analysis has supported this older date (Albright 1998; Hayes 2000). Screen washing of sediment from the site White Springs 3B produced a single specimen of marsupial, the trigonid of a lower molar.

SB-1A (= Live Oak) LF. The SB-1A LF (also known as the Live Oak LF) includes *Mammacyon* cf. *obtusidens*, *Paroligobunis frazieri*, *Nothokemas waldropi*, and *Protosciurus*. Frailey (1978) described most of the larger taxa and assigned SB-1A to a "middle" Arikareean age. Frailey characterized SB-1A as an unstratified conglomeratic sequence above the Suwannee Limestone (Oligocene). The vertebrates are all terrestrial and the sediments were poorly sorted clasts of Suwannee Limestone in a matrix of clay derived from weathering of the limestone. On this basis, Frailey suggested that the fossil-bearing deposit originated as slopewash and slumping in a fissure. SB-1A produced a single marsupial specimen, a lower molar.

Brooksville 2 LF. The late Oligocene age of Brooksville dates from Patton (1967), who described four specimens that he believed showed affinities to Great Plains taxa of that time. This fauna was designated as the Brooksville 1 LF (Hayes 2000), because in 1994, fissure fills in the Suwannee Limestone at a different location near Brooksville produced an abundant and diverse assemblage of vertebrates designated the Brooksville 2 LF. This new fauna includes the largest sample of Florida marsupials. Brooksville 2 contains *Miohippus*, an entoptychine rodent, *Palaeogale*, *Megalagus*, *Agnotocastor*, and *Nanotragulus*. These taxa, in comparison to those of the Great Plains, suggest an early middle Arikareean age (Hayes 2000).

MEASUREMENTS AND TECHNOLOGY

A Gertner measuring microscope was used to measure to the nearest 0.01 mm the same dental parameters established by Korth (1994:fig. 1) to enable direct comparison with the specimens of his study. Dental terminology used is shown in Figure 2. In tables and text, a lower case letter indicates lower teeth, while an upper case letter indicates upper teeth. Cheek teeth are described as P3, M1, M2, M3, and M4, instead of M1,

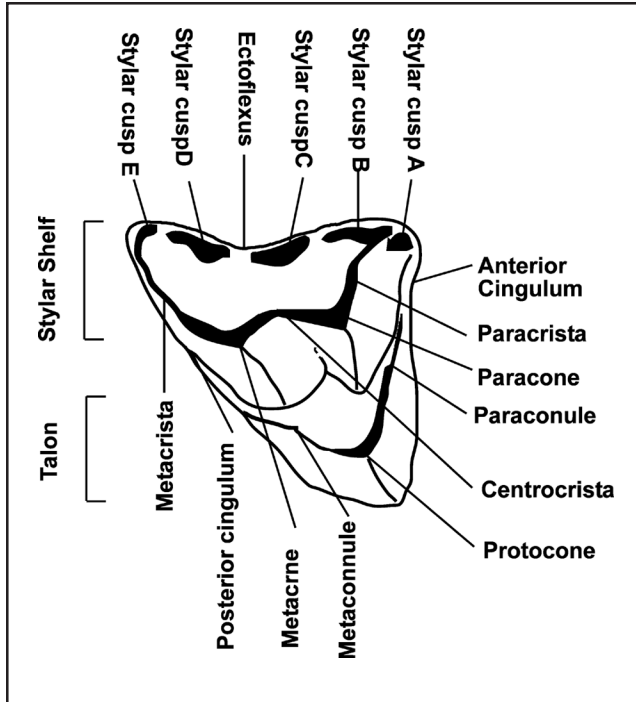


Figure 2. *Herpetotherium* dental nomenclature for a right upper molar.

M2, M3, M4, and M5 (Marshall 1990). The position of a tooth in the toothrow used in the study of variation was determined by association in a maxilla or jaw with the exception of M3 which, because of its distinct morphology, could be easily separated from other molars. All measurements are in millimeters unless otherwise stated. Quotation marks are used where informal or obsolete nomenclature is retained for purposes of discussion.

Abbreviations.—(others defined in text) ap, anterior to posterior measurement, length; apt, anterior to posterior measurement of trigonid on lower molars, length; CV, coefficient of variation; F, Fauna; LF, Local Fauna; lf, local fauna; M, mean; m# or M#, molar; N, number of specimens; OR, observed range of variation; p# or P#, premolar; S, standard deviation; SE, standard error of the mean; tr, transverse measurement, width; tra, transverse measurement of anterior trigonid width in lower molars; trp, transverse measurement of posterior talonid width in lower molars.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York; UC, University of Chicago collections, Field Museum, Chicago, Illinois; UCMP, University of California Museum of Paleontology, Berkeley, California; UF, University of Florida col-

lections, Florida Museum of Natural History, Gainesville; UNSM: University of Nebraska State Museum, Lincoln.

GENERAL UPPER MOLAR DESCRIPTION OF *HERPETOTHERIUM*

The upper molars of most species of *Herpetotherium* are characterized by a large central stylar cusp or cusps and equal, reduced, or absent stylar cusp B (Figs. 2-3). In the oldest (Uintan NALMA) species, stylar cusp B may be larger than the central cusps. *Peratherium* has a reduced central cusp and enlarged stylar cusp B (for other comparisons see Korth 1994). Lower molars differ only in size from species to species of *Herpetotherium* (Korth 1994).

Upper molars have the metacone higher than protocone. The centrocrista is 'V'-shaped. The M1 is longer than wide with slight to no flexion in the central buccal margin. The protocone is situated along the anterior margin of the molar. The metaconule and protoconule are usually present with metaconule larger and protoconule quickly worn away. An anterior cingulum runs from stylar cusp A, which can be distinct or integrated into the cingulum, and joins the preprotocrista. A narrow posterior cingulum connects with the postprotocrista and ends below the metacone. Stylar cusp B joins the paracrista but is usually distinct in unworn teeth and can be as large as the central stylar cusp/cusps in *Herpetotherium valens* and older species. The central buccal margin contains one or two distinct cusps, C and D, in varying degrees of separation or fusion with one another. Stylar cusp D is generally the largest central stylar cusp with C becoming more reduced in younger samples, and possibly completely fusing with D in the youngest samples. The position of D varies from being in line with the premetacrista to being well posterior and in line with the metacone. Stylar cusp E is minute, joins with the metacrista, and disappears quickly with wear.

The M2 is similar to the M1 in width and length and the buccal edge has a slightly more well-defined ectoflexus. Stylar cusp morphology resembles the M1. Stylar cusps C and D are centrally located and can vary in the same manner as observed on the M1.

The M3 is much wider than long with a pronounced ectoflexus (Fig. 3D). The protocone is central rather than anterior as in the M1 and M2. Stylar cusp B can be reduced or absent in younger samples, but is usually present and can be of equal height to the central cusp/cusps in unworn teeth of older species. The M3 typically exhibits only one central stylar cusp which has been

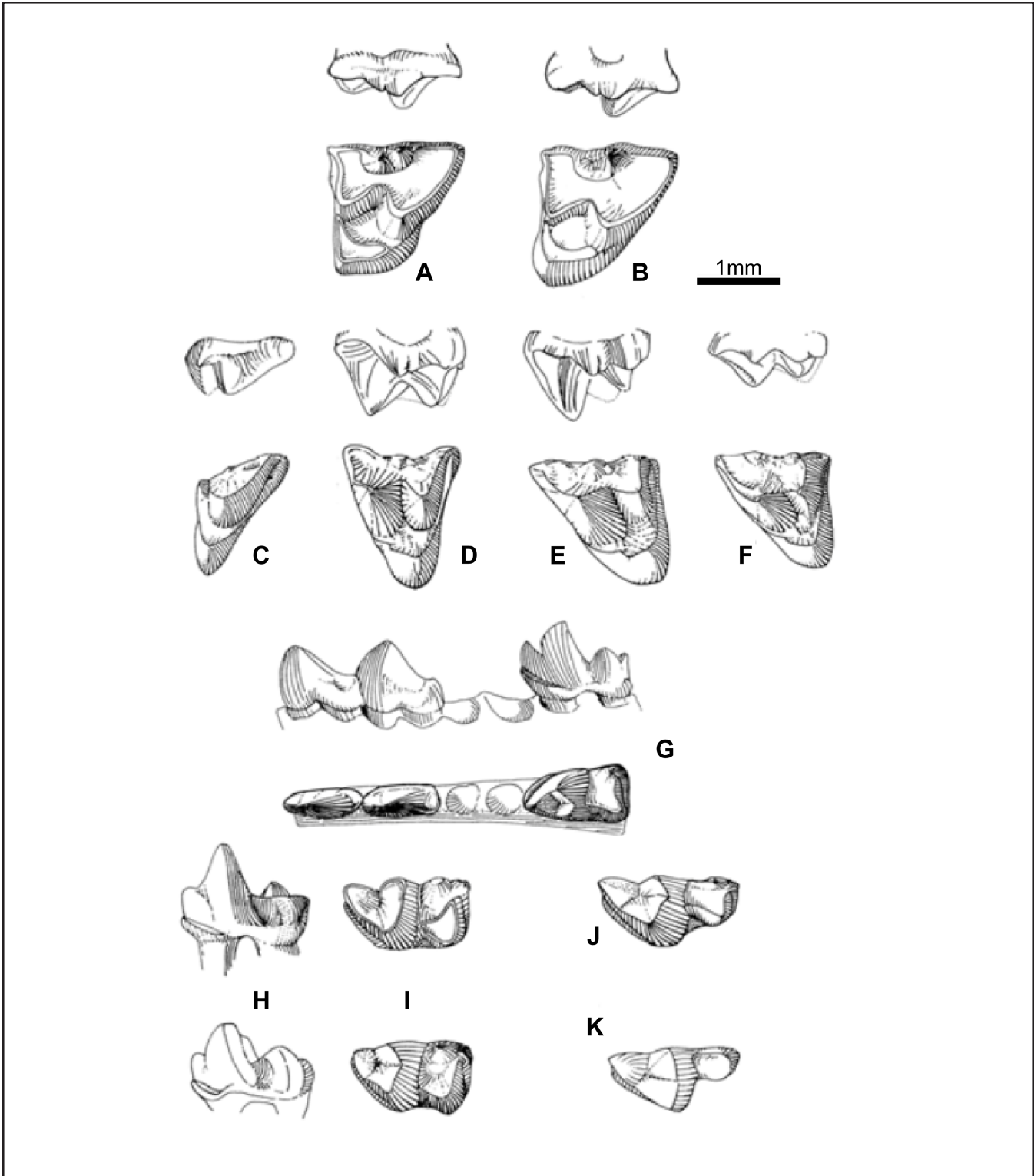


Figure 3. Teeth of *Herpetotherium* from Florida, occlusal and buccal views, scale bar = 1 mm. I-75. (A) UF 97361 L M2; (B) UF 97362 L M2. Brooksville 2: (C) UF 156255 R M4; (D) UF 156292 R M3; (E) UF 156262 R M2; (F) UF 163554 R M1; (G) UF 156294 R p2-p3, m1; (H) UF 156283 lower cheek tooth; (I) UF 156284 lower cheek tooth; (J) UF 163574 L m4; (K) UF 163572 L m4.

cusps C with D completely absent. However, both authors have noted M3s that exhibit a central styler cusp with twinned apices or even M3s with two separate central cusps that suggest that D is not absent. The new material described here also shows these variations. In teeth that have two cusps the larger is often the more posterior of the central cusps. The dominant central cusp appears to be a fusion of C with a larger D, rather than the loss of D. The M3 is therefore similar to the M1 and M2 in trends of styler cusp morphology. The process of fusion may have progressed more in the M3 of older species. This evidence, that the central cusp of *Herpetotherium* M3s and M4s may be styler cusp D and C fused together, suggests that the diagnoses of Korth (1994) and Eberle and Storer (1995) should be emended.

The M4 is very compressed anteroposteriorly, yet is almost as wide as M3 (Fig. 3C). The metacone is small at the posterior margin and not connected to the paracone by a crista. The anterior cingulum begins from styler cusp A, thickens anterolingually to paracrista, and is continuous with preprotocrista. Protocone and paracone are centrally aligned. There is a small reduced single central styler cusp that could represent C, D, or both of them fused together.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus 1758

Subclass THERIA Parker and Haswell 1897

Infraclass MARSUPIALIA Illiger 1811

Order DIDELPHIMORPHA Gill 1872

Family DIDELPHIDAE Gray 1821

Subfamily HERPETOTHERIINAE Trouessart 1879

Genus *HERPETOTHERIUM* Cope 1873

HERPETOTHERIUM FUGAX (Cope 1873)

Holotype.—AMNH 5254, R M1-M4.

Type Locality.—Cedar Creek Beds, White River Formation, Logan County, Colorado.

Revised Range.—Middle Chadronian through early Arikarean of the Great Plains, Montana, Wyoming, and Colorado.

Revised Diagnosis.—Smaller on average than *H. valens* and *H. merriami*. Similar in size to *H. youngi*. Slight decrease in average size from Chadronian to early Arikarean. Styler cusp B reduced in comparison to *H. valens* and larger than *H. youngi*. Central styler cusps variable. C and D may be separate to completely fused into a single central styler cusp.

SPECIMENS FROM DW-121 = RIDGEVIEW LF, NEBRASKA

Referred Specimens.—UNSM 77041-77360, UNSM 77041 LM2-4, 77042 RP2-M1, 77043 LM2-4, 77044 LM1-4, 77045 RM2-4, 77046 RM2-3, 77048 RM1-4, 77049 RM2-4, 77050 LP3-M1, 77051 LM2-3, 77053 RM-2, 77057 LP3-M1, 77059 LM1-2, 77061 RP3-M4, 77062 LM1-3, 77065 LM1-2, 77067 RM3-4, 77072 RM1-2; UNSM 77064, 77066, 77067, 77071, 77089-77095, 77111, 77117, 77133-77145, 77148-77150, 77152-77154, 77157-77158, 77181, 77197, 77198, 77202, 77203, 77210, 77212, 77215, 77225, 77229: 77219, 77220, 77221, 77224, 77228, M1s; UNSM 77063, 77098, 77101, 77102, 77104, 77133, 77135-77139, 77196, 77200, 77211, 77217, 77227, 77366, 77367, M2s; UNSM 77068 p3, 77070 m2-3, 77073 m2, 77074 p2-3, 77076 m1-3, 77077 m2, 77082 p2-3, UNSM 77070, 77075, 77076, 77140, 77141, 77143, 77144, 77146, 77151, 77154, 77155, 77164, 77167, 77168, 77185, 77194, 77205, 77364, m4; UNSM 77068, 77074, 77076, 77077, 77080, 77082, m1.

Description.—Dental measurements presented in Table 1. The M1 central styler cusp/cusps are always larger than styler cusp B in the DW-121 sample. There are four configurations of the central styler region. In smaller teeth, there is a single conical cusp, a complete fusion of C and D (Fig. 4F). Slightly larger teeth show a single elongated blade-like central cusp (Fig. 4I). In large teeth, C forms a distinct small cusp on the anterior slope of D (Fig. 4L). The largest teeth have C and D separate with D the dominant cusp (Fig. 4N). The most common variations are a single blade cusp or the reduced C (Table 2). Styler cusp E is occasionally present as a slight rise on the buccal edge at the metacrista.

In M2s there can be a single central cusp that is either conical (Fig. 4E) or blade-like (Fig. 4H). If two central cusps are present, D is dominant with C moved slightly lingual from the buccal margin (Fig. 4K). Styler cusp B is usually smaller than the central cusps except in large M2s. Single and reduced C are the most common configurations (Table 2).

Similar to the M1, M3 exhibits four central styler cusp morphologies based on the size of the teeth: A small single cusp (Fig. 4D). A large elongate single cusp (Fig. 4G). A twinned central cusp with a distinct furrow in the center that separates the cusp into equal parts (Fig. 4J). The fourth morphology is a doubled central cusp with D dominant and C slightly smaller and equal to B (Fig. 4M). Almost all the M3s that were relatively unworn exhibited a twinned central cusp (Table 2).

Discussion.—The sample from Dw-121 is the sec-

Table 1. Dental measurements of *Herpetotherium fugax* from Dw-121, Nebraska. Individual measurements in all tables that do not have catalog numbers directly above them are taken from a single dentary/maxillary fragment with more than one tooth whose catalog number can be found above the first measurement of the specimen.

		UNSM77082	UNSM77074	UNSM77079				
p2	a-p	1.39	1.37	1.43				
	tr	0.56	0.61	0.55				
					UNSM77080	UNSM77068		
p3	a-p	1.31	1.27	1.30	1.37			
	tr	0.65	0.68	0.62	0.68			
		N	M	OR	R	SD	SE	CV
m1	a-p	8	1.66	1.53-1.78	0.25	0.09	0.03	5.4
	tr	8	0.97	0.88-1.05	0.17	0.04	0.02	4.1
		UNSM77070	UNSM77077	UNSM77073				
m2	a-p	1.77	1.62	1.73				
	tr	1.02	1.04	1.07				
		UNSM77076		UNSM77075				
m3	a-p	1.66	1.53	1.79				
	tr	1.10	0.94	1.14				
		N	M	OR	R	SD	SE	CV
m4	a-p	19	1.77	1.49-1.97	0.48	0.12	0.03	6.8
	tr	19	1.00	0.90-1.14	0.24	0.07	0.02	7.0
		UNSM77042	UNSM77057	UNSM77050				
P3	a-p	1.59	1.46	1.86				
	tr	0.80	0.82	0.92				
		N	M	OR	R	SD	SE	CV
M1	a-p	27	1.7	1.45-1.93	0.48	0.11	0.02	6.4
	tr	27	1.58	1.39-1.81	0.42	0.09	0.02	5.7
M2	a-p	15	1.74	1.48-1.87	0.39	0.12	0.03	6.9
	tr	15	1.85	1.52-2.11	0.59	0.15	0.04	8.1
M3	a-p	55	1.8	1.58-2.01	0.43	0.11	0.01	6.1
	tr	55	2.11	1.92-2.36	0.44	0.11	0.01	5.2
M4	a-p	7	1.02	0.87-1.14	0.27	0.10	0.04	9.8
	tr	7	1.95	1.79-2.07	0.28	0.10	0.04	5.1

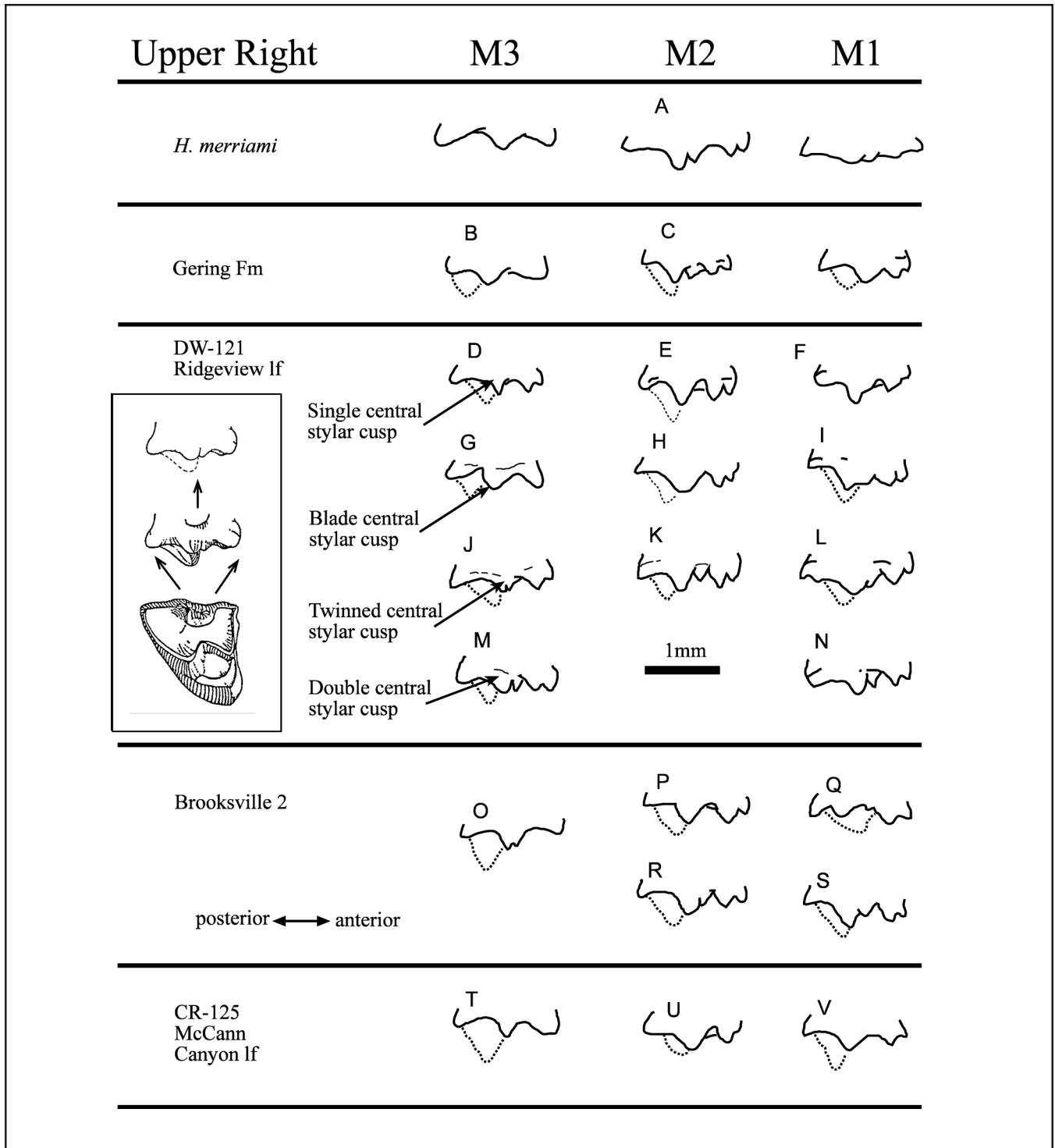


Figure 4. Variation in Arikareean *Herpetotherium* stylar cusp arrangement, x12. Buccal view shown. Left molars have been reversed in view. (A) *H. merriami*, UCMP 24240 R M1-M3. "Gering": (B) UNSM 81321 R M3; (C) UNSM 11576, R M1-M2. Dw-121: (D) UNSM 77210 R M3; (E) UNSM 77121 L M2; (F) UNSM 77099 L M1; (G) UNSM 77133 R M3; (H) UNSM 77204 L M2; (I) 77101 R M1; (J) UNSM 77135 L M3; (K) UNSM 77190 R M2; (L) UNSM 77134 L M1; (M) UNSM 77145 R M3; (N) UNSM 77100 R M1. Brooksville 2: (O) UF 156242 R M3; (P) UF 163555 R M2; (Q) UF 163555 R M1; (R) UF 156262 R M2; (S), UF 156291 L M1. Cr-125 (McCann Canyon): (T) UNSM 4197 R M3; (U) UNSM 24200 L M2; (V) UNSM 77172 R M1.

Table 2. Variation of central stylar cusp in upper molars from Dw-121, Nebraska. Each box indicates the number of teeth showing the particular variation. Variation states defined in text and Figure 4.

	Single	Blade	Side	Double
M1	3	8	8	2
M2	7	3	8	1
M3	7	3	0	10

described by Korth (1994) and Eberle and Storer (1995) in their diagnoses of *Herpetotherium* as representing the second largest sample of *Herpetotherium* (N= 300+) known from a single locality (the first is the aforementioned Calf Creek LF). The Dw-121 teeth are on average slightly smaller than those of Whitneyan and older *Herpetotherium* (Fig. 5). The Dw-121 sample has a continuous distribution of stylar cusp characters and size similar to *Herpetotherium valens* from the Calf Creek LF sample (Eberle & Storer 1995). In general, the teeth show that stylar cusp variation is a function of size. The smaller teeth have a single central cusp and the largest teeth exhibit two distinct cusps, those of intermediate sizes exhibit partial fusion of the central cusps. Although there is not a clear distinction between size groups, all the variations overlap. The retention of variable single to double central stylar cusps in comparison to *Herpetotherium youngi*, which was diagnosed by Korth (1994) as having a single central cusp, suggests the early Arikareean samples from Nebraska should be assigned to *Herpetotherium fugax*.

Because the fluvial sediments at Dw-121 incise the White River Group, the question arises as to the possibility of reworking of older *Herpetotherium* material into the sample. However, based on the associated taxa and the preservation of the specimens, there is no evidence of reworking of material from the underlying Brule Formation (Bailey 1992).

SPECIMENS FROM BROOKSVILLE 2 LF, FLORIDA

Referred Specimens.—UF 156251-156293 isolated cheek teeth; UF 156294 Rp2, p3, m2; UF 156295 RM1-4; UF 156296-156304 isolated cheek teeth; UF 163551-163560 isolated teeth (Fig. 3C-K).

Description.—Dental measurements presented in Table 3. Stylar cusp B joins the paracrista but is distinct

and can be almost as large as C in unworn teeth. Stylar cusp E joins with the metacrista. Stylar cusp D is the largest stylar cusp, usually fused with C, but on some specimens C is distinguishable from D as a cusplule or furrow on the anterior slope (Fig. 4S). The position of D varies from being in line with the pre-metacrista to being posterior and in line with the metacone.

The M2 has stylar cusp B distinct but connected to the paracrista. Stylar cusp A is a minute cusp beside B and forms a small lateral flange, which thickens lingually into the anterior cingulum. Stylar cusp D is centrally located and the largest cusp with C occasionally forming a cusplule on the anterior slope (Fig. 4R).

Stylar cusp B is present but reduced on the M3. The central dominant cusp is usually twinned with a furrow at the apex that equally divides the cusp (Fig. 4O). Stylar cusp E is absent or quickly reduced with light wear.

Discussion.—The Brooksville 2 sample is the largest sample of marsupials in Florida. The size of the upper molars falls within the smaller measurements for *Herpetotherium fugax* and encompasses the measurements for *Herpetotherium youngi* (Tables 1, 3; Fig. 5). The sizes of the lower teeth are similar to *H. youngi* and *H. fugax*. The Brooksville 2 sample does show a greater degree of size variation than Dw-121, particularly the M2 and M3, and the CV values were higher than 10 for the M2 and M4 (Table 3). This could indicate that the Florida species is highly dimorphic in the posterior molars in comparison to Dw-121, that more than one species is present in the fauna, or that there was significant time in the deposition of the site to accumulate a greater range of non-coexisting *Herpetotherium* populations that occupied the diverse Florida landscape of the time in comparison to the Great Plains (Hayes 2000).

Varying stylar cusps in comparison to *Herpetotherium youngi* suggests that Brooksville 2, like the early Arikareean samples from Nebraska, be assigned to *Herpetotherium fugax*. Brooksville 2 does generally show a greater degree of fusion between cusps C and D relative to the Dw-121 sample. There were few teeth found that have the two cusps completely separated. The early “medial” Arikareean Brooksville 2 marsupials show transitional features between *H. fugax* and the “later” Arikareean *H. youngi*.

There was one exception to the general *Herpetotherium* stylar cusp morphology. UF 163554 is an M1 with a posteriorly placed cusp D, a very small

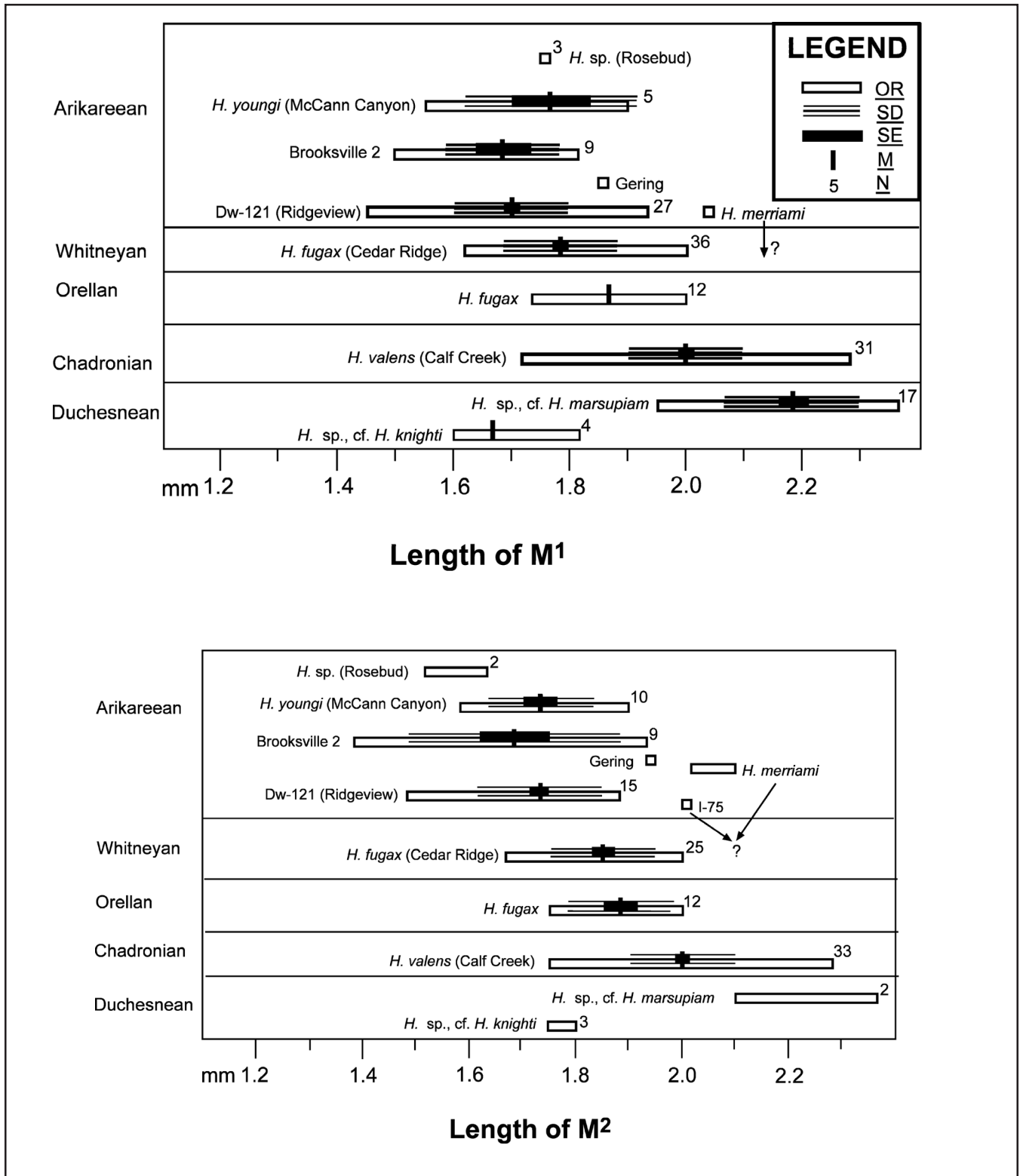


Figure 5. Comparison of *Herpetotherium* upper molar measurements from Duchesnean through Arikareean NALMAs. Compiled from author's measurements; Stock and Furlong 1922 (*H. merriami*); Green and Martin 1976 (*H. sp.*- Rosebud); Setoguchi 1978 (*H. fugax*- Cedar Ridge); Korth 1994, 1992 (*H. fugax*, *H. youngi*-McCann Canyon); Eberle and Storer 1995 (*H. valens*- Calf Creek); Rothecker and Storer 1996 (*H. sp., cf. H. marsupium*, *H. sp., cf. H. knighti*).

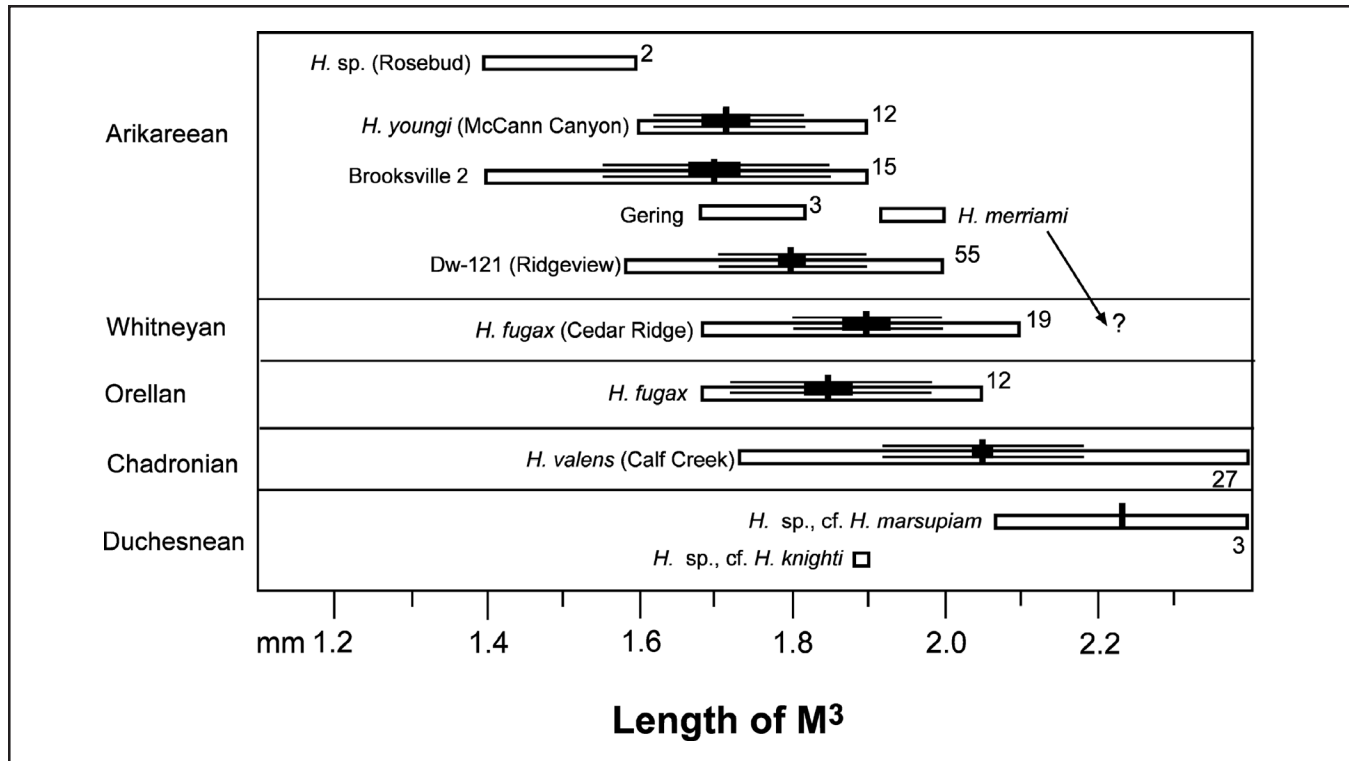


Figure 5. (cont.)

anteriorly placed cusp C, and an enlarged cusp B that is equal in size to D (Fig. 3F). This styler cusp configuration is closest to the oldest *Herpetotherium* species except for the smaller cusp C. With only a single tooth showing this condition, it is probably an aberrant condition or as stated above a less probable indication that a second but similar species is present.

HERPETOTHERIUM YOUNGI (McGrew 1937)

Holotype.—UC 1544, L M2.

Revised Range.—Middle to latest Arikareean of South Dakota and Nebraska.

Revised Diagnosis.—Similar in size to early Arikareean and Whitneyan *Herpetotherium fugax*. Smaller than *Herpetotherium valens* and *Herpetotherium merriami*. Styler cusp B on all molars reduced in comparison to *H. fugax*. Single central styler cusp on upper molars (total fusion of C and D). Older species have varying degrees of central styler cusp separation.

Referred Specimens from Cr-125 and Cr-117.—UNSM 24200 LM2-3; UNSM 24186, 24187, 24189, 24191, 24195 jaws with lower cheek teeth; UNSM 24188, 24190, isolated lower cheek teeth. UNSM 24197

RM3, 24201 RM3, and UNSM 24202 RM1. Additional material: UNSM 4197 RM3, UNSM 24800 jaw with lower cheek teeth, UNSM 77172 RM1, 77173, LM1, UNSM 77179 LM2.

Description.—Upper molars with a single conical central styler cusp (Fig. 4T-V). Styler cusp B is smaller than the central cusp on M1 and M2 in lightly worn teeth and disappears with moderate wear. Styler cusp B on M3 is incorporated into the paracrista and almost equal to the central cusp in height in the little worn teeth, but not as massive. Styler cusp E is absent on all molars.

Discussion.—In size, although slightly larger on average than early Arikareean *Herpetotherium* (Fig. 5), which is perhaps due to the small sample, the material from the McCann Canyon LF as well as the other material referred to *Herpetotherium youngi* by Korth (1994) falls well within the range of the Dw-121 and Brooksville 2 *Herpetotherium*. It also is similar in size to the Cedar Ridge *Herpetotherium* (Setoguchi 1978) that Korth (1994) referred to *Herpetotherium fugax* (Fig. 5).

The new material from the McCann Canyon LF provides additional evidence that younger *Herpetotherium* has a fused cusp C and D as the cen-

Table 3. Dental measurements of *Herpetotherium fugax* from Brooksville 2 LF, Florida.

		UF 156294	UF 163552			
p2	a-p	1.18	1.21			
	tr	0.52	0.53			
		UF 156294	UF 163553			
p3	a-p	1.12	1.13			
	tr	0.57	0.53			
		UF 156282	UF 156284	UF 156286		
m1	a-p	1.73	1.75	1.66		
	apt	0.65	0.7	0.65		
	tra	0.92	0.93	0.97		
	trp	0.96	1.03	1.07		
		UF 156279	UF 156294	UF 156287		
m2	a-p	1.81	1.56	1.70		
	apt	0.80	0.84	0.77		
	tra	0.89	0.86	0.95		
	trp	0.90	0.96	1.00		
		UF 156283	UF 156288			
m3	a-p	1.83	1.85			
	apt	0.90	1.01			
	tra	1.15	1.06			
	trp	0.99	0.91			
		N	M	OR	SD	CV
M1	a-p	9	1.68	1.51-1.81	0.11	6.5
	tr	9	1.52	1.22-1.78	0.16	10.5
M2	a-p	9	1.69	1.38-1.91	0.19	11.2
	tr	9	1.88	1.62-2.14	0.19	10.1
M3	a-p	15	1.70	1.40-1.90	0.14	8.2
	tr	15	2.10	1.75-2.29	0.21	10.0
M4	a-p	4	1.08	0.93-1.24	0.14	12.9
	tr	4	1.96	1.83-2.12	0.12	6.1

tral sharp stylar cusp. *Herpetotherium youngi* was diagnosed (Korth 1994) as a species with a single central cusp on all upper molars. The validity of *H. youngi* on this basis is questionable since the sample of upper molars available for comparison is so small, however the diagnosis cannot be ruled out. I therefore retain *H. youngi* as a later Arikareean species separable from *Herpetotherium fugax* because it has a single central cusp and a reduced cusp B. *Herpetotherium* sp. from the Rosebud (Morton and Green 1976) also has a dominant single central stylar cusp and it falls within the size range for *H. youngi* for the M1, but has a smaller M2 and M3 than *H. youngi*. Again, this might be due to limited sample size of both *H. youngi* and *Herpetotherium* sp. Additional material might show that the Rosebud *Herpetotherium* could be referred to *H. youngi*.

HERPETOTHERIUM CF. *MERRIAMII* (Stock and Furlong 1922)

Referred Specimens.—UF 97361 LM2, UF 97362 LM2, both from the I-75 LF, Alachua County, Florida.

Description.—Both specimens from this locality appear to be left M2s. Measurements for UF 97361 are: a-p=1.98, tr=1.91; for UF97362: a-p=2.02, tr=2.11. There is a very slight flexion at stylar cusp C and an otherwise straight buccal margin. Stylar cusps C and D fused at the base, but distinguishable as separate cusps with D more dominant and C forming a small cuspule on the anterior slope of D. Stylar cusp E is a minute cusp that joins the metacrista. Stylar cusp B is connected to paracrista. Stylar cusp A forms a minute flange anterior to B. There is a barely visible anterior cingulum beginning at the base of the preprotocrista and ending before the paracone. The protocone is on the anterior margin.

Discussion.—The size of these teeth is larger than those of *Herpetotherium youngi*, but falls within the size range for *Herpetotherium valens* and *Herpetotherium merriami* (Figs. 3A-B, 5). *H. merriami* has a relatively large M1 and M2 (entirely outside the range of size variation) in comparison to other Arikareean *Herpetotherium* teeth, yet the M3 length falls within the upper measurements for Dw-121 (Fig. 5). This apparent reduction of the M3 may be a general characteristic of *H. merriami* and therefore useful for diagnosis of the species if more material is recovered from the John Day region. The cusp arrangement of the I-75 specimens is also similar to *H. valens* and *H. merriami*. Korth (1994) notes that *H. valens* has a larger cusp B than *H. merriami* and differentiates the two species on

that basis. Eberle and Storer (1995) agreed that *H. valens* is similar in size to *H. merriami* with a larger more strongly developed stylar cusp B than other *Herpetotherium* species. Based on age, the I-75 teeth are closer to *H. merriami*. However, the degree of wear on these specimens makes it difficult to accurately assess the size of stylar cusp B and only a tentative referral can be made based on size differences. *H. merriami* and the I-75 species may represent coastal variants of *Herpetotherium* outside of the Great Plains.

HERPETOTHERIUM sp.

“BROWN SILTSTONE”, GERING FORMATION, AND UNDIFFERENTIATED LOWER ARIKAREE GROUP, NEBRASKA

Referred Specimens.—UNSM 81321 LM3-4, 11576 LM1-2, 14951 Rm1-3, 11684 R m1,m3, 14947 Lm1-3, 11593 Rm3-4, 11632 Rm3-4, 11652 RM1-4, 11685 Rp2-m3, 11505 Lm2, 11584 RM3-4, 11576 RM1-2.

Description.—The two M1s that are not completely worn have a single elongate central stylar cusp. Stylar cusp B is distinct and smaller than the central cusp. Stylar cusp E is either not present or worn away. The M2 that is relatively unworn has two separate central cusps with C larger than B and slightly offset from the buccal margin (Fig. 4C). All M3s were considerably worn and had a single elongate central stylar cusp (Fig. 4B). Lower molars are typical of *Herpetotherium*.

Discussion.—The “Gering” marsupials are represented by neither large samples nor relatively unworn specimens of upper molars, so an accurate determination of species is not possible. Although most of the teeth preserve only a single central cusp, the morphology of UNSM 11576 (a relatively large M2 with doubled central cusps) suggests that variation similar to other *Herpetotherium* populations is present in the Gering marsupials. However, the possibility of reworking from older White River sediments cannot be excluded. Except for the M2 mentioned above, the teeth fall within the size range of the Dw-121 sample (Table 4, Fig. 5).

SB-1A LF, FLORIDA

Referred Specimen.—UF 97363 L m4.

Description.—The left m4 from SB-1A shows typical *Herpetotherium* characteristics. The cusp of the protoconid is broken off. The base of the valley formed by the protoconid and metaconid is higher than the one formed by the protoconid and paraconid. There is a very strong anterior cingulid present. The talonid is much reduced and quite narrow compared to the trigonid. The

Table 4. Dental measurements of *Herpetotherium* sp. from the "brown siltstone", Gering Formation, and undifferentiated lower Arikaree Group (= "Monroe Creek Fm"), Wildcat Ridge, Nebraska.

		UNSM14947	UNSM11685	UNSM14951	
m1	a-p	1.80	1.70	1.70	
	tr	0.94	0.98	1.04	
m2	a-p	1.96	1.86	2.00	
	tr	1.10	1.15	1.18	
m3	a-p	2.00	1.76	1.98	
	tr	1.10	1.14	2.11	
		UNSM11652	UNSM11584	UNSM11576	UNSM81321
M1	a-p	1.86	-	1.86	-
	tr	1.56	-	1.56	-
M2	a-p	1.94	-	-	-
	tr	1.96	-	1.80	-
M3	a-p	1.68	1.82	-	1.82
	tr	2.10	2.12	-	2.12
M4	a-p	1.12	0.98	-	-
	tr	1.06	2.16	-	-

hypoflexid is not pronounced, instead there is a wide shelf formed that begins at the base of the protoconid and curves to the base of the hypoconid and merges into the talonid. The cristid obliqua is low and joins the trigonid wall at the base of the metacone. The hypoconulid extends posteriorly from a worn entoconid. The tooth measures: a-p=1.67, tra=1.01, trp=0.62, and apt=0.78.

Discussion.—The SB-1A tooth is comparable in size to *Herpetotherium youngi* and the Brooksville 2 sample. This tooth does compare well with a m4 of *H. youngi* figured in Green and Martin (1976:fig. 3e). Older species such as *Herpetotherium valens* appear to have a more pronounced hypoflexid in the m4.

WHITE SPRINGS LOCAL FAUNA, FLORIDA

Referred Specimen.—UF 125547 Left trigonid.

Description.—Trigonid morphology is typical of *Herpetotherium*. Protoconid is the largest cusp, followed by the metaconid, and then the paraconid. There is a strong anterior cingulid. The valley formed between protoconid and metaconid higher than that separating the paraconid from the other cusps. The trigonid measures: a-p=0.91, tr=0.75.

Discussion.—The White Springs tooth is similar in morphology to those from Brooksville 2, but is smaller and more transversely compressed. It is also smaller transversely than measurements reported by Korth (1992) for *Herpetotherium youngi*. In size it is similar

to the Rosebud *Herpetotherium* sp. (Morton & Green 1976). Since White Springs is the youngest Florida site, this could be indicative of the general trend in *Herpetotherium* of size reduction for younger samples (Fig. 5).

CONCLUSIONS

Eberle and Storer (1995) demonstrated that a single species of *Herpetotherium*, *H. valens*, from the Chadronian Calf Creek Fauna, exhibits a wide range of upper molar styler cusp variation as well as a wide range of dental size. Early Arikareean *Herpetotherium* is also highly variable in dental morphology and size and this variation is continuously distributed in large samples. While size ranges are high in comparison to many mammals they are not outside the ranges of other marsupials such as *Didelphis* (Hough 1961) and although modern didelphid species appear to have consistent styler cusp morphology that is suitable for Linnaean diagnosis, individual variation in the position of styler cusps on the molars (anteriorly or more posteriorly located) is known in marmosine opossums (Case 1991).

Recognition that *Herpetotherium* might have a considerable amount of dental variation is not new. In her much criticized review (Green & Morton 1976; Korth 1994) of Oligocene and Miocene didelphids, Hough (1961) discussed the large degree of size variation in modern didelphids due to sexual dimorphism and individual variation. She suggested this as the probable rea-

son for the taxonomic confusion of “*Peratherium*.” This agreed with Scott (1941) who had earlier suggested that all large “*Peratherium*” from the Oligocene were assignable to “*Peratherium*” *fugax* and the large degree of size separation was due to sexual and individual variation. However, later in her paper, Hough dismissed this proposal by Scott as an “impossibility” (Hough 1961: 220) simply based on the large numbers of specimens. In their review of Great Plains didelphids, Green and Morton (1976) again noted the high degree of variation found in South Dakota samples and proposed that all *Herpetotherium* after the Chadronian might be assignable to *Herpetotherium fugax*.

In Korth’s (1994) review of *Herpetotherium*, his taxonomic classification of species was based in part on size. Comparison of size relationships in *Herpetotherium* (Fig. 5) shows that while a case can be made for a morphocline in average size reduction, there is considerable overlap in observed ranges. Arikareean *Herpetotherium*, with the exception of *H. merriami* and *H. cf. merriami* from I-75, is similar in size to the marsupials from the Whitneyan Cedar Ridge LF (Setoguchi 1978), which Korth referred to *H. fugax* as well as other reported Orellan *H. fugax*. While the degree of size separation between *H. valens* and *H. fugax* may be suitable for species distinction, the separation in dental size for most Arikareean *Herpetotherium* and *H. fugax* is not as pronounced. The early Arikareean samples show that they may be a distinct group from the older samples. The standard errors are distinct for the early Arikareean samples in comparison to the Orellan and Whitneyan populations. Later Arikareean samples referred to *H. youngi* even show a slight increase in average size in comparison to early Arikareean samples (Fig. 5).

Korth (1994) also followed the trend in moving away from stratospecies, or species defined on the basis of superposed stratigraphic occurrence, by organizing *Herpetotherium* species on the basis of stylar cusp morphology, but at the time there were few reported large samples. The material from Calf Creek (Eberle & Storer 1996) and the material described here show that coexistent *Herpetotherium* populations have highly variable stylar cusp morphology. In early Arikareean samples, such as the largest sample described here (Dw-121, Nebraska), the upper molars show variation in central stylar cusp configuration that range from having a single central stylar cusp to teeth possessing two clearly distinct central stylar cusps (Fig. 4). In part, this relationship appears to be a function of size of the molar, with the smaller teeth possessing the more fused central cusps.

Large samples also allow consideration of worn and unworn molar states which can give a more accurate picture of stylar cusp size relationships. In the Brooksville 2 and DW-121 marsupials, the unworn stylar cusp B is often as large as the central stylar cusp or cusps (Fig. 5). Korth (1994) and Eberle and Storer (1995) both used the relative size of B in relation to the central cusps as a diagnostic feature. Comparison of the Arikareean unworn teeth to unworn teeth of older species is needed to determine the applicability of this character.

Because of the small sample size, it remains to be seen if *Herpetotherium youngi* is a valid species diagnosed on the basis of possessing a single fused central cusp and reduced stylar cusp B. At present, there is no evidence that suggests that *H. youngi* has variable stylar cusp morphology. Larger samples of middle to late Arikareean *Herpetotherium* are needed to conclusively determine this. *H. youngi* is therefore tentatively retained as a species with a single pointed stylar cusp and a reduced stylar cusp B in comparison to older *Herpetotherium* species.

Several taxonomic alternatives present themselves in describing the Nebraska and Florida Arikareean *Herpetotherium* samples. Resurrect *Herpetotherium spindleri* as an early Arikareean species that differs only in slight average size, but has considerable size range overlap (Fig. 5), from *Herpetotherium fugax* (as suggested by Setoguchi 1978). *Herpetotherium spindleri* would not be separable on the basis of size from later Arikareean *H. youngi* but does have a variable stylar cusp condition in contrast to a single central stylar cusp and a large cusp B. The alternative (as suggested in part by Green and Morton, 1976, discussed above) is to refer *Herpetotherium* of similar size and variable stylar cusp morphology after the Chadronian to *H. fugax*, recognizing that younger well-sampled Arikareean populations have a smaller average size than Orellan and Whitneyan *H. fugax*. This solution to the problem, favored here due to the demonstrated high degree of variability between and within *Herpetotherium* populations, retains *H. youngi* as a later Arikareean species without variable cusps. *H. merriami* is enigmatic, it may be a larger northwestern Pacific Arikareean species, or there is the possibility that *H. merriami*, from the lower section of Logan Butte (Stock and Furlong, 1922), is late Whitneyan in age (Hunt, pers. comm. 2004) and agrees in size and morphology to the relatively large Whitneyan *Herpetotherium* species in Florida from I-75. This would essentially solve the problem of *H. merriami* in that it

would fall close to, and within (for some measurements), the size range of *H. fugax* in the Whitneyan and Orellan and it could be referred to this species.

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