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# New material of the marsupial (Mammalia, Metatheria) *Herpetotherium merriami* (Stock and Furlong, 1922) from the John Day Formation, late Oligocene, Oregon, USA

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**Abstract.**—Recently discovered specimens of the marsupial *Herpetotherium merriami* (Stock and Furlong, 1922) from the John Day Formation, Oregon, are described. The species was previously known only from a single (type) specimen. These additional specimens have allowed for a revised diagnosis of the species based on the presence of an additional stylar cusp on the upper molars, as well as the relative size of the stylar cusps. This new material also allows for an examination of the variability within the species and establishes a time range for the species, which extends through most of the Arikareean (late Oligocene: Ar1–Ar3: late Rupelian-Aquitanian). *Herpetotherium merriami* is distinct within the genus because it is among the larger of the species, but one of the latest occurring, whereas the general pattern of the genus is a reduction in size through time.

## Introduction

The John Day Formation of Oregon represents nearly ten million years (late Whitneyan to early Hemingfordian North American Land Mammal Ages [NALMA]: middle Oligocene to early Miocene: Rupelian to early Burdigalian) and has produced a mammalian fauna that is very diverse, including over 100 species (Hunt and Stepleton, 2004; Tedford et al., 2004; Albright et al., 2008; Fremd, 2010; Korth and Samuels, 2015). However, only a single specimen of a marsupial, which was referred to a new species, *Peratherium merriami* by Stock and Furlong (1922), has ever been described from it. At the time of its description, this was the latest-occurring Tertiary marsupial in North America. It differed from other described species mainly in its larger size. In the most recent survey of the middle Tertiary marsupials of North America (Korth, 1994), this species was transferred to the genus *Herpetotherium* Cope, 1873, but the holotype remained the only record of this species (Korth, 2008). Recently discovered specimens referable to *H. merriami* from the John Day Formation has allowed for a better analysis of the species and a more complete comparison with other described species of the genus.

*Herpetotherium* has traditionally been considered in the order Marsupialia within the family Didelphidae, and generally in the subfamily Herpetotheriinae (see citations in Korth, 2008, p. 39). However, in a recent systematic analysis based on cranial morphology, *Herpetotherium* was included in the Metatheria but viewed as a sister-group to the Marsupialia, and raised to the rank of family (Horovitz et al., 2009, fig. 5).

## Materials and methods

Dental terminology follows that of Crochet (1980) with modification for stylar cusps (Fig. 1); upper teeth are indicated by capital letters, lower teeth by lower-case letters (e.g. M1 or m1). Measurements were taken to the nearest 0.01 mm on an optical micrometer using the orientation presented in Korth (1994, fig. 1). Terminology for cranial anatomy follows that of Wible (2003). Reference to the stratigraphy of the John Day Formation and its recognized horizons are taken from Albright et al. (2008). Horizons within the John Day Formation are subdivided as Ar1 (early Arikareean) to Ar3 (early late Arikareean) following the terminology of Janis et al. (2008). Radiometric dates for each of these horizons in the John Day Formation are presented elsewhere (Fremd et al., 1994; Hunt and Stepelton, 2004; Albright, et al., 2008; Korth and Samuels, 2015).

*Repositories and institutional abbreviations*.—JODA, John Day Fossil Beds National Monument; UCMP, University of California Museum of Paleontology.

## Systematic paleontology

Order Metatheria Huxley, 1880
Faimly Herpetotheriidae Trouessart, 1879
Genus *Herpetotherium* Cope, 1873

*Type species*.—*Herpetotherium fugax* Cope, 1873.



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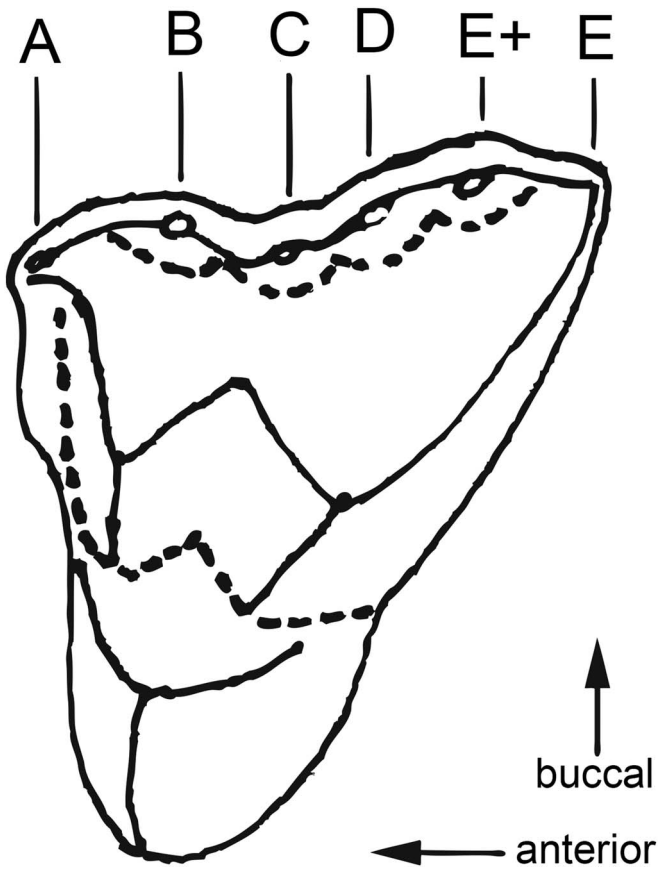


**Figure 1.** Schematic diagram of upper left molar with stylar cusps labeled.

*Referred species*.—*Herpetotherium valens* (Lambe, 1908); *H. merriami* (Stock and Furlong, 1922); *H. marsupium* (Troxell, 1923); *H. youngi* (McGrew, 1937); *H. knighti* (McGrew, 1959).

*Occurrence*.—Middle Eocene (Uintan: Lutetian) to middle Miocene (Barstovian: Serravallian) of North America (39–18 Ma: Hunt and Stapleton, 2004; Albright et al., 2008).

*Herpetotherium merriami* (Stock and Furlong, 1922)
Figures 2–4

1922 *Peratherium merriami* Stock and Furlong, p. 312, figs. 1 to 5.

1994 *Herpetotherium merriami* (Stock and Furlong); Korth, p. 381, table 5.

*Holotype*.—UCMP 24240, rostrum and palate of skull (Fig. 2) with left P3-M4 and right M1-M4 and associated partial dentaries with left p3-m4 (in part) and right m1-m3.

*Emended diagnosis*.—Large species, larger than all other species except *H. valens* and *H. marsupium*; stylar cusps C and D on M1 and M2 large and fused at their bases either with distinct apices or fused into a single elongated cusp; stylar cusp E always absent; an accessory stylar cusp is present between cusp D and posterobuccal corner of the tooth (designated as cusp E+); stylar cusps B and E+ are slightly smaller than C or D on M1-M3; large, central stylar cusp on M3-M4 (cusp C); short diastema separating p1 and p2 on dentary.

*Type locality and horizon*.—Logan Butte, Lower Turtle Cove Member, John Day Formation, Crook County, Oregon (Arikareean [Ar1]: late Oligocene; see Korth and Samuels, 2015, fig. 26).

*Additional referred specimens*.—JODA 16801, partial maxilla with M1-M3; JODA 12858, 12859, M1; JODA 12848, 12853, 12860, M2; JODA 12846, 12847, 12849–12852, 12854–12857, M3; JODA 12845, M4; JODA 10348, dentary with m2-m3; JODA 12862, dentary fragment with p3; JODA 12861, dentary fragment with m1.

*Occurrence*.—JODA 12845–12862 from Lone Rock, Unit L, Kimberly Member (Ar3); JODA 10348 from Haystack Valley Member (Ar3); JODA 16801 from Unit K1, Turtle Cove Member (Ar2); all from John Day Formation, Oregon. (Arikareean: late Oligocene: late Rupelain to Aquitanian).

*Description*.—The partial cranium (UCMP 24240) is badly damaged except for the majority of the palate. Dorsally, the frontal extends from the postorbital constriction to approximately 2.5 mm anterior of the zygomatic arch (Fig. 2.1). There are no recognizable sutures with the nasals on the specimen. There is no indication of parasagittal crests on the frontal. The lacrimal forms the anterior edge of the orbit and extends anteriorly onto the rostrum. The only other bones visible in dorsal view are a small fragment of the parietal on the left side of the skull and a posterodorsal part of the maxillaries on both sides.

In lateral view (Fig. 2.2), the infraorbital foramen on the maxilla opens anteriorly and is dorsal to the anterior root of M1. The lacrimal bone extends dorsally and anteriorly onto the rosturm. There is a single minute lacrimal foramen on the lacrimal bone, just posterior to the anterior ridge of the orbital margin. There is no evidence of a second foramen on the fossil skull, but it cannot be verified due to damage to the specimen. The lacrimal does not extend posteriorly onto the orbital wall. Similarly, the palatine bone extends slightly dorsally. The anterior margin of the orbit is above the posterior margin of M2. The sphenopalatine foramen is dorsal to the anterior margin of M4 in the palatine bone. Due to damage, no other observations can be made on the lateral side of the cranium other than the relative size of the neurocranium, which is slightly larger than the anterior portion of the skull.

Ventrally, two foramina are identifiable on the palatal surface (Fig. 2.3). Anteriorly, there is a large major palatine foramen that is oval in outline and extends from the anterior margin of P3 to the anterior margin of M3 (Table 1). The minor palatine foramen is present along the posterior margin of the palate lingual to M4.

The remainder of the skull is badly damaged. The narrow basisphenoid is along the center line of the cranium and its suture with the basioccipital is recognizable. The ventral part of the bulla is present on the right side, and only the anterior-most part is preserved on the right left side.

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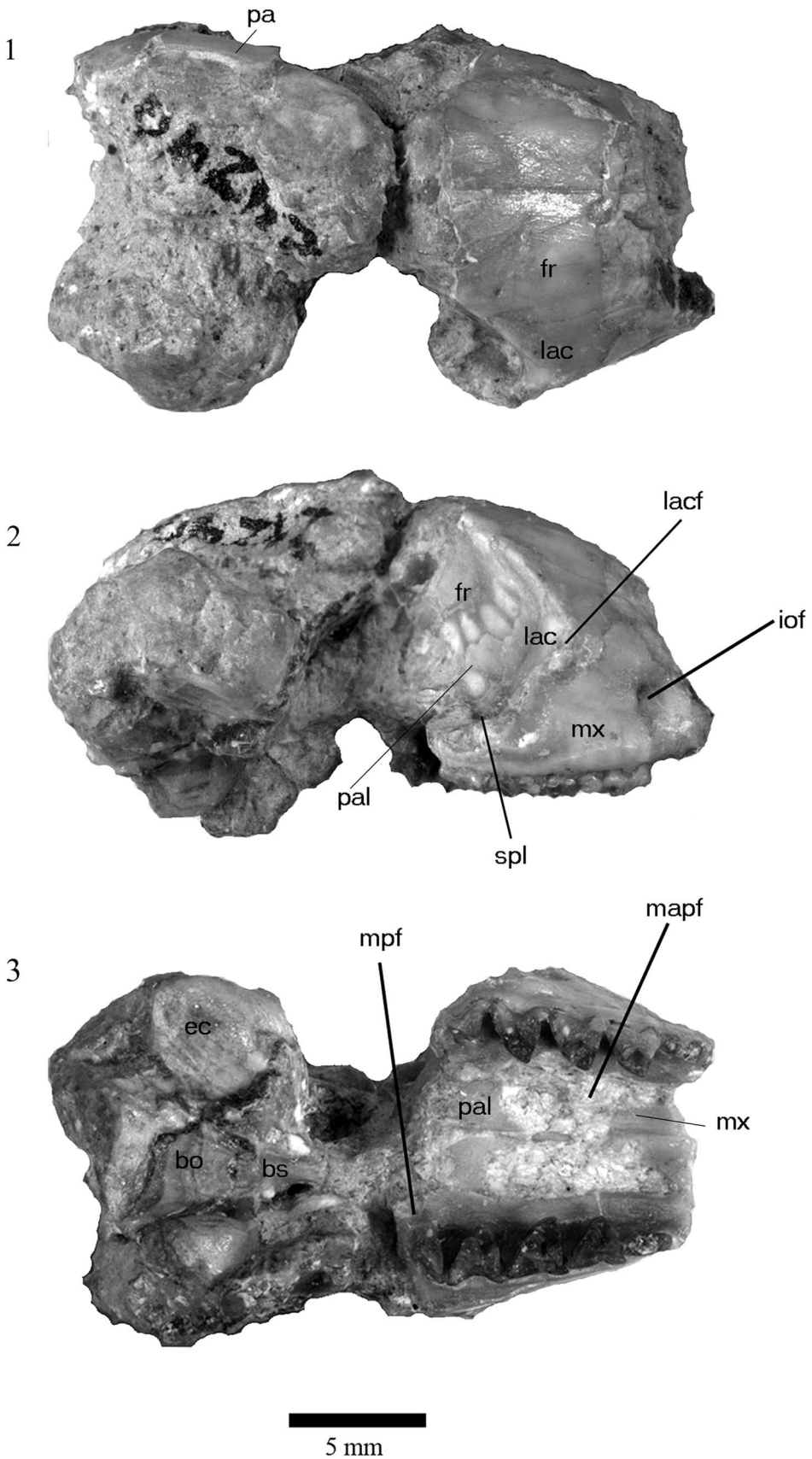


**Figure 2.** Cranium of holotype of *Herpetotherium merriami*, UCMP 24240, from the John Day Formation, Oregon. (**1**), dorsal view; (**2**) right lateral view; (**3**) ventral view (anterior to right). Abbreviations: **fr**, frontal bone; **iof**, infraorbital foramen; **lac**, lacrimal bone; **lacf**, lacrimal foramen; **mapf**, major palatine foramen; **mpf**, minor palatine foramen; **mx**, maxilla; **pa**, parietal; **pal**, palatine bone; **spl**, sphenopalatine foramen.

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Both dentaries are preserved in the holotype, but the anterior portion is broken away from both rami (Stock and Furlong, 1922, fig. 3). One specimen (JODA 10348; Fig. 3) preserves the alveoli for all of the premolars. It is evident from these that all three premolars are two-rooted, similar in size, and that there is a small diastema between p1 and p2 (Fig. 3). There is a larger mental foramen on the dentary below the diastema between p1 and p2 and a second smaller foramen below m1.

The dentition of *Herpetotherium* has been described elsewhere in detail (Stock and Furlong, 1922; Green and Martin, 1976; Korth, 1994; Eberle and Storer, 1995). Only the features distinctive to *H. merriami* will be described herein. On the upper molars there is a smaller cusp posterior to D, but anterior to the position of cusp E (posterobuccal corner of the tooth) that is designated here as cusp E+ that is also unique to *H. merriami*. The distinguishing features of the stylar cusps of *H. merriami* are mainly on M1 and M2 (Fig. 4). Stylar cusp D is always the largest cusp and positioned posterior to the center of the buccal border. Cusps B and E+ are slightly smaller; B anterior to the center of the buccal margin of the tooth and E+ posterior to cusp D, but not at the posterior edge of the tooth; cusp E is always lacking. Cusp C varies in occurrence. It is either nearly equal to cusp D and fused with it at the base (Fig. 4.1), or completely fused into a large elongated cusp (Fig. 4.2, 4.4). On a single specimen, JODA 12858, stylar cusp C is replaced by two minute cusps anterior to cups D (Fig. 4.3). Korth (1994) erroneously stated that cusp C on M1 of the holotype was much smaller than cusp D and on its anterior slope, similar to the condition in other species of the genus. However, on both M1 and M2 of the holotype (Fig. 4.1; Stock and Furlong, 1922, fig. 4), these cusps are subequal in size and do not totally fuse into a single cusp as in M3.

The only distinctive character of the lower dentition is the size of p1 (based on alveolus); nearly equal p2 (Fig. 3).

**Table 1.** Cranial and dentary measurements of *Herpetotherium merriami*. Measurements in mm; *, indicates estimated measurement. Abbreviation: **mapf**, major palatine foramen.

| | UCMP 24240 | JODA 10348 |
|---|---|---|
| Height of cranium at M3 | 6.67 | |
| Maximum width of maxilla | 12.92* | |
| Maximum width at parietals | 14.52* | |
| Palatal width at M1 | 5.55 | |
| Palatal width at M4 | 6.6 | |
| Length of mapf | 6.67 | |
| Length M1-M4 (left) | 7.74 | |
| Length M1-M4 (right) | 7.97 | |
| Depth of dentary at m2 (left) | 3.1 | |
| Depth of dentary at m2 (right) | 3.5 | 3.7 |
| Alveolar length m1-m4 (left) | 7.62 | |
| Alveolar length m1-m4 (right) | 7.79 | 7.85 |
| Alveolar length p1-p3 | | 6.23 |

*Remarks*.—Although the size range of the cheek teeth of *Herpetotherium merriami* overlaps with those of *H. fugax* (smaller measurements) and *H. valens* (larger measurements), the means of nearly all dental measurements are in between those of these other species (Table 2; Figs. 5, 6). It is markedly smaller than the Duchesnean to early Chadronian *H. marsupium* (Krishtalka and Stucky, 1983; Rothecker and Storer, 1996; Kihm and Schumaker, 2015). Morphologically, *H. merriami* is

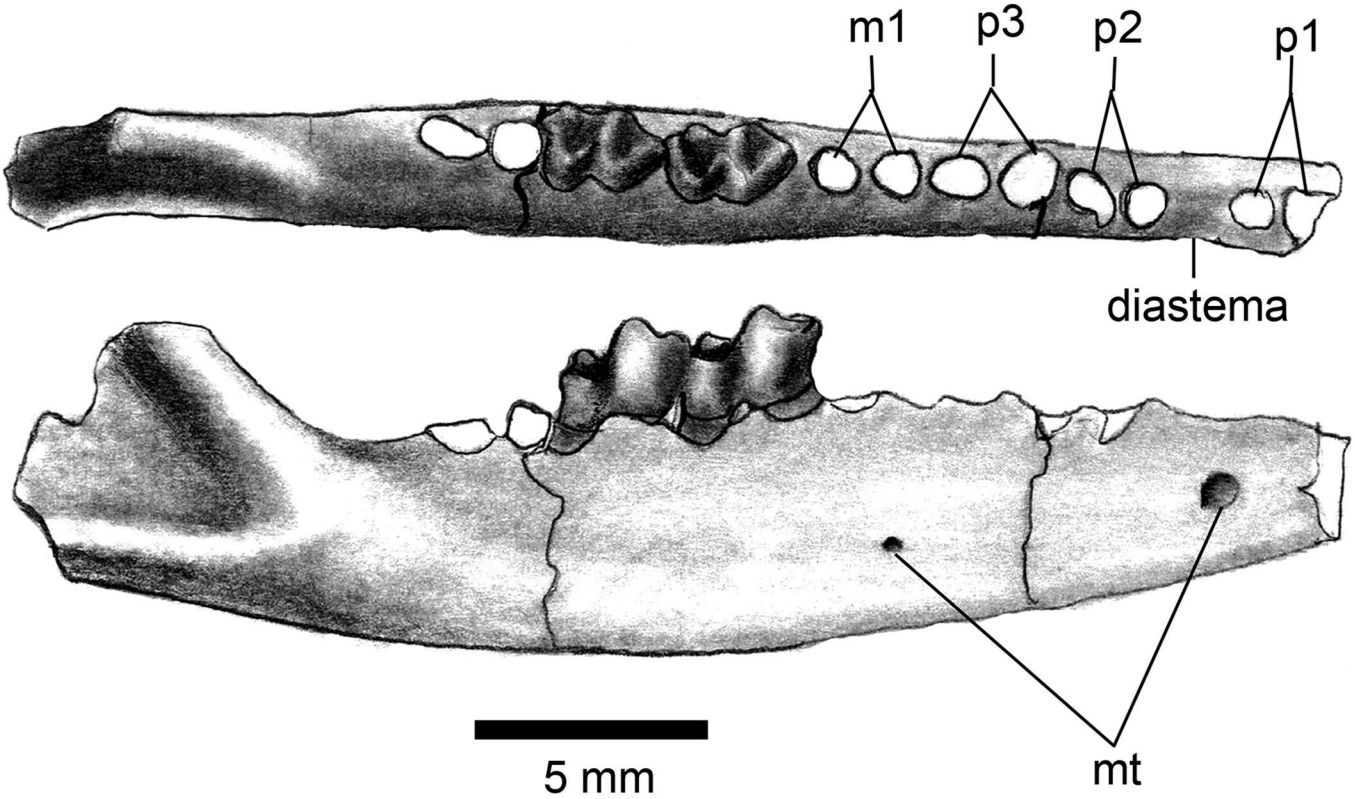


**Figure 3.** Dentary of *Herpetotherium merriami*, JODA 10348, right with m2-m3; anterior to right; occlusal view (upper); lateral view (lower); abbreviaton: **mt**, mental foramen.

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distinguishable in the size and arrangement of the stylar cusps on the upper molars. In overall size, the stylar cusps of *H. merriami* are comparatively much larger than in any other species (see comparative figures in Green and Martin, 1976; Korth, 1994; Eberle and Storer, 1995; Hayes, 2005; Kihm and Schumaker, 2015). On M1 and M2 of *H. merriami* stylar cusp D is not central and is the largest cusp; cusp C is of nearly equal size and twinned with D (Fig. 4.1) or fused together into a large continuous cusp (Fig. 4.2). The presence of an accessory stylar cusp, E+, is not known in any other species of the genus. Traditionally, stylar cusp E is in the posterobuccal corner of the tooth (= metastylid of eutherian mammals), whereas cusp E+ is midway between the traditional stylar cusps D and the posterobuccal corner of the tooth (Fig. 1; Crochet, 1980, fig. 2). Stylar cusps B and E+ are always present, but slightly smaller than C and D. In both *H. fugax* and *H. valens*, the arrangement of stylar cusps is variable and the cusps often vary in size. On M1 of these species cusp C, if present, is always small and on the anterior slope of cusp D, whereas in *H. merriami* cusps C and D nearly equal in size as distinct cusps (= twinned or double cusps of Hayes, 2005), or fused into a single elongated cusp (= blade of Hayes, 2005). This type of arrangement is present but rare in the other species (Eberle and Storer, 1995; Hayes, 2005, table 2) and always present on specimens of *H. merriami*. On M3 of *H. merriami* there is a main, large central cusp (cusp C) and slightly smaller cusps B and E+ (Fig. 4.1). On M3 of *H. valens*, cusp C is always doubled and the cusps are of different sizes (Eberle and Storer, 1995, fig. 3D–G) and in *H. fugax* the central cusp is frequently double or fused into an elongated cusp (Hayes, 2005, table 2). The Arikareean *H. youngi* differs from *H. merriami* in its much smaller size (Figs. 5, 6) and in the reduction in the number of stylar cusps (often only cusp C present on M1 or M2; Korth, 1992, 1994).

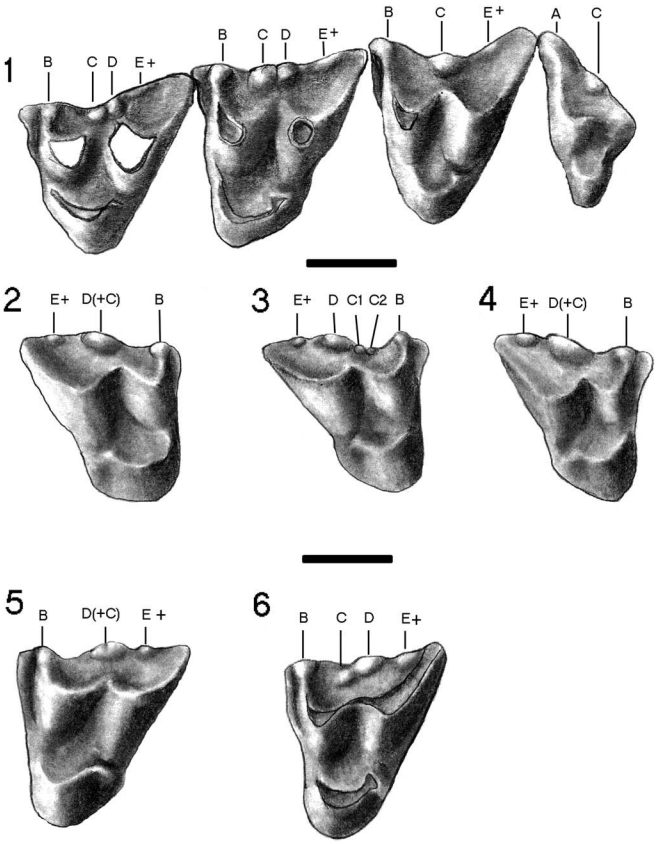


**Figure 4.** Upper dentition of *Herpetotherium merriami* from the John Day Formation, Oregon. (**1**) UCMP 24240 (holotype), left M1-M4. (**2**) JODA 12859, right M1. (**3**) JODA 12858, right M1. (**4**) JODA 12860, right M2. (**5**) JODA 12851, left M2. (**6**) 12852, left M2. Bar scales = 1 mm.

Hayes (2005) noted that in M1 and M2 of larger specimens of *H. fugax*, cusps C and D were more likely separate, and on smaller specimens, they were either completely or partially fused. On *H. merriami*, the larger specimens have two distinct central cusps, but on smaller individuals these are fused. However, when this fusion occurs in *H. merriami* the result is a very elongated stylar cusp that is similar in length to the two individual stylar cusps, not a single smaller cusp C as in *H. fugax* or *H. youngi*.

The specimens from the lower horizons of the John Day Formation (Ar1–2), the holotype and JODA 16801, are the largest and have subequal stylar cusps C and D on M1 and M2. The remaining specimens (from higher in the section; Ar3) have the elongated and completely fused stylar cusps and are smaller in overall size of the tooth (Table 1). This follows Hayes' (2005) observation of the smaller individuals having fewer stylar cusps, and follows the trend in *H. fugax* that there is a slight reduction in size through time (Korth, 1994, fig. 2; Hayes, 2005, fig. 5).

In the dentary of *H. fugax*, p1 is markedly smaller than p2 and p3, but in *H. merriami* p1 is nearly equal to the length of p2 (Fig. 3; Fox, 1983, fig. 1b; Korth, 1994, fig. 8.1). Both species have a small diastema between p1 and p2.

The skull of *H. merriami* differs from that of Recent didelphids such as *Monodelphis* (Fig. 2; also see Wible, 2003).

**Table 2.** Dental measurements of *Herpetotherium merriami*. Measurements in mm. Abbreviations: L, anteroposterior length; W, transverse width; N, number of specimens; M, mean; OR, range of measurements; SD, standard deviation; CV, coefficient of variation.

| | M1L | M1W | M2L | M2W | M3L | M3W | M4L | M4W |
|---|---|---|---|---|---|---|---|---|
| N | 4 | 4 | 11 | 12 | 8 | 8 | 3 | 3 |
| M | 1.98 | 1.87 | 1.92 | 2.11 | 1.90 | 2.29 | 1.16 | 2.12 |
| OR | 1.78–2.05 | 1.80–1.97 | 1.80–2.15 | 1.96–2.24 | 1.81–2.05 | 2.18–2.35 | 0.92–1.37 | 2.05–2.27 |
| SD | 0.13 | 0.07 | 0.14 | 0.11 | 0.09 | 0.07 | | |
| CV | 6.62 | 3.81 | 7.07 | 5.17 | 4.54 | 2.88 | | |
| | p3L | p3W | m1L | m1W | m2L | m2W | m3L | m3W |
| N | 2 | 2 | 3 | 3 | 3 | 3 | 3 | 3 |
| M | 1.52 | 0.72 | 1.87 | 1.07 | 1.98 | 1.23 | 2.06 | 1.34 |
| OR | 1.36–1.67 | — | 1.67–1.98 | 1.02–1.15 | 1.67–2.16 | 1.22–1.24 | 1.91–2.18 | 1.23–1.45 |
| SD | — | — | 0.18 | 0.07 | 0.27 | 0.01 | 0.14 | 0.11 |
| CV | — | — | 9.40 | 6.78 | 13.52 | 0.94 | 6.72 | 8.21 |

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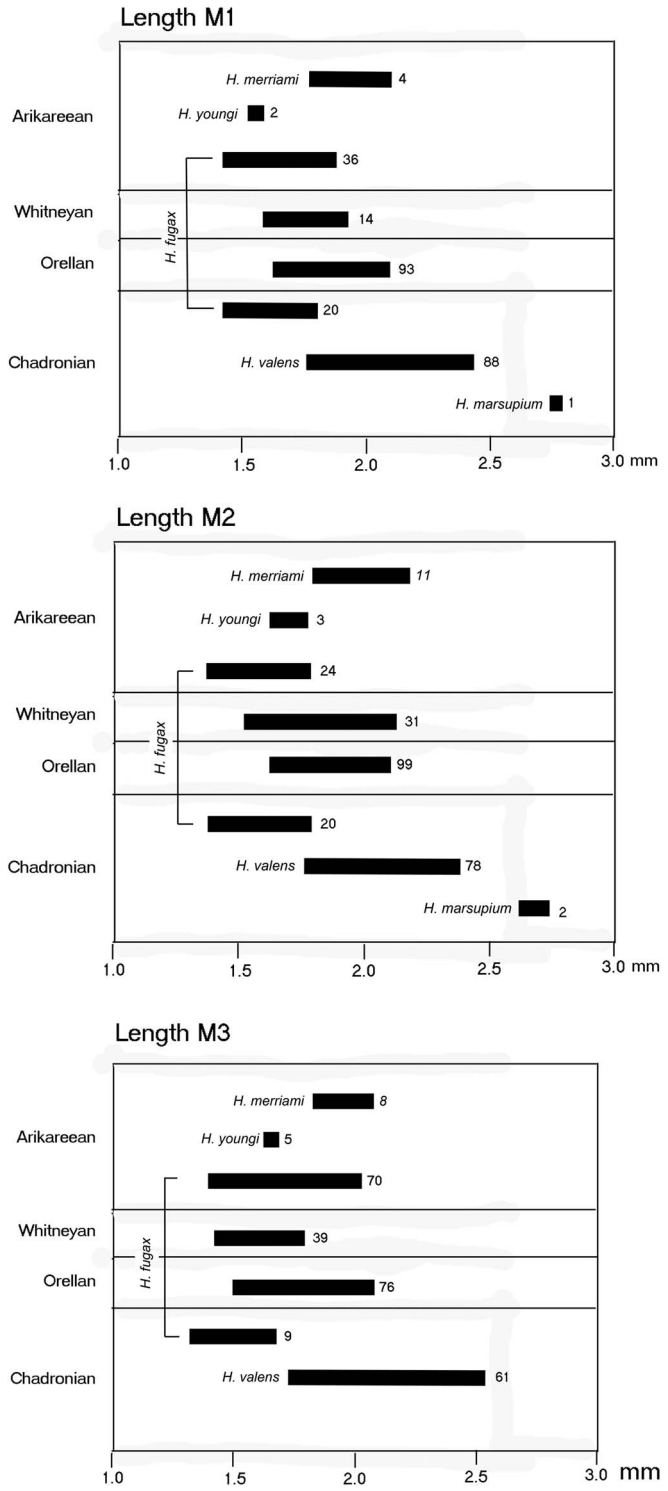


**Figure 5.** Comparison of lengths of upper molars of species of *Herpetotherium* from the late Paleogene of North America. Vertical axis does not represent actual time span of each provincial age. Numbers to the right of range bars are the number of specimens measured. Data for *H. marsupium* from Kihm and Schumaker (2015); for *H. valens* from Eberle and Storer (1995) and Kihm and Schumaker (2015); for *H. fugax* from Setoguchi (1978), Korth (1994, 2015) and Hayes (2005); for *H. youngi* from Korth (1992).

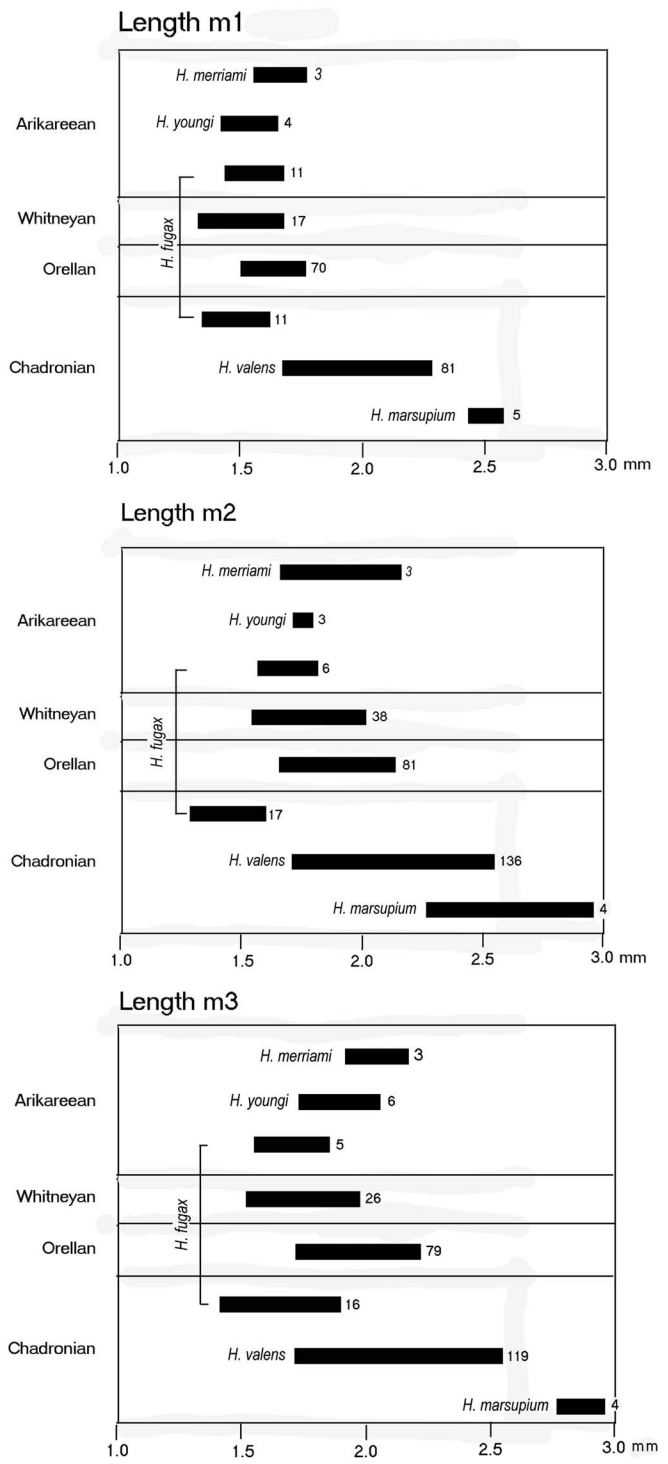


**Figure 6.** Comparison of lengths of lower molars of species of *Herpetotherium* from the late Paleogene of North America. Vertical axis does not represent actual time span of each provincial age. Numbers to the right of range bars is the number of specimens measured. Data for *H. marsupium* from Kihm and Schumaker (2015); for *H. valens* from Eberle and Storer (1995) and Kihm and Schumaker (2015); for *H. fugax* from Setoguchi (1978), Korth (1994, 2015) and Hayes (2005); for *H. youngi* from Korth (1992).

In *Monodelphis*, the lacrimal foramen is doubled and only single in *H. merriami*. The infraorbital foramen on *H. merriami* is dorsal to the anterior root of M1, just slightly more posterior than in *Monodelphis* where it is dorsal to the posterior root of P3 (Wible, 2003, fig. 2), and the lacrimal bone extends more dorsally and anteriorly in *H. merriami* than in *Monodelphis*.

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The lacrimal in *H. merriami* does not extend posteriorly onto the orbital wall as in *Monodelphis* (Wible, 2003, fig. 4). Similarly, the palatine bone does not extend as far dorsally as in *Monodelphis*. Stock and Furlong (1922) noted that the anterior margin of the orbit was above the posterior margin of M2 in *H. merriami* and *H. fugax*, and that of the Recent *Marmosa* was above the anterior margin of M1. In *Monodelphis*, the anterior margin of the orbit is dorsal to the anterior edge of M2 (Wible, 2003, fig. 2). In both instances, the position of the anterior margin of the orbit is more posterior in *Herpetotherium* than in Recent genera. The sphenopalatine foramen is dorsal to the anterior margin of M4 in the palatine bone in *H. merriami*, slightly more posterior than in *Monodelphis* where it is dorsal to M3. The major palatine foramen in *H. merriami* extends from the anterior margin of P3 to the anterior margin of M3; longer and more anterior than in *Monodelphis* where it extends from the anterior margin of M1 to the posterior margin of M2, and the minor palatine foramen is slightly more anterior than in *Monodelphis* (Wible, 2003, fig. 5). In all of these features that differ from *Monodelphis*, it appears that the cranium of *H. merriami* has a slightly more elongated and less transverse rostrum.

Hayes (2005, fig. 3A, B) referred two isolated M2s from the Arikareean of Florida to "*Herpetotherium* cf. *merriami*". These specimens are similar in size to those of *H. merriami* from Oregon, but stylar cusp C is markedly smaller than cusp D and on its anterior slope, a characteristic of *H. fugax*. Due to the variability of these cusps and the small sample from Florida, these specimens cannot be definitely referred to *H. merriami*.

## Discussion

*Herpetotherium merriami*, known through most of the Arikareean (latest Oligocene: Ar1–Ar3), is one of the last occurring marsupials in North America before the immigration of Recent didelphids from South America in the Pleistocene (McKenna and Bell, 1997; Korth, 2008). The Miocene record of marsupials in North America is limited to several specimens of an indeterminate species of *Herpetotherium* from the Hemingfordian of South Dakota (Green and Martin, 1976) and a single isolated tooth from the Barstovian of Texas (Slaughter, 1978). This also follows the trend in the reduction of marsupial species in North America beginning in the Chadronian, when as many as seven species and five genera are present (Kihm and Schumaker, 2015), to the early Arikareean, from which only four species and two genera are recognized (Korth, 1994, 2008; Hayes, 2005).

Within *Herpetotherium*, there is a general reduction in size through time, from the larger early Chadronian *H. marsupium* and *H. valens*, to the smaller *H. fugax* in the Orellan through the early Arikareean, to the smaller Miocene specimens (Figs. 5, 6; Korth, 1994, fig. 2; Hayes, 2005, figs. 5, 6). However, *H. merriami* does not follow this pattern and is similar in size to the larger, earlier Chadronian species.

In terms of morphological change through time in *Herpetotherium*, with the reduction in overall size, there is also a reduction in the number of stylar cusps on the upper molars, especially in populations of *H. fugax*, which spans the longest time interval (Hayes, 2005), and in the Arikareean *H. youngi* (Korth, 1992, 1994). Again, *H. merriami* is the exception. It has stylar cusps that are not only maintained or increased in number (presence of cusp E+), but also in the size of the stylar cusps relative to the size of the molars. This unique nature of the size and morphology of the cheek teeth of *H. merriami*, separate from the trends in other species, may be attributed to its relative geologic isolation from the other known species of the genus that are predominantly from the Rocky Mountains, Great Plains, and Florida.

## Conclusions

*Herpetotherium merriami* was previously known only from the holotype. With the addition of more than 20 specimens from the type area described here, its range of variation and consistency of morphology can be better examined. *Herpetotherium merriami* is distinct from other species of the genus by its large size, the consistent presence of stylar cusp E+ on M1–M3, and the enlargement and fusion of stylar cusps C and D on M1 and M2. Its large size and more complex pattern of stylar cusps on the upper molars is a reversal in the trend through the Tertiary of a reduction in size and simplification (reduction in number) of stylar cusps.

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