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Description of a new species of the North American archaic pika *Hesperolagomys* (Lagomorpha: Ochotonidae) from the middle Miocene (Barstovian) of Nebraska and reassessment of the genus *Hesperolagomys*

Andrea R. Bair

ABSTRACT

Hesperolagomys niobrarensis (Lagomorpha, Ochotonidae; new species) is described from a large sample from the late Barstovian (Miocene) of Nebraska. Along with new specimens of *H. galbreathi* and *H. fluviatilis*, this sample provides a context for reassessment of taxonomy and understanding of morphological variation in *Hesperolagomys*. I introduce a new method for determining the relationship between occlusal width and wear stage in isolated lagomorph upper cheek teeth. Cranial and dental characters of *Hesperolagomys*, including presence of a premolar foramen in the maxilla, place it within Ochotonidae. The P3 of *Hesperolagomys* is unique among North American lagomorphs in possessing two persistent cement-filled lingually oriented striae, and an anteriorly-directed stria paralleling the outer curve of the tooth. *Hesperolagomys* additionally differs from *Russellagus* in smaller size and presence of a deep, persistent lingual hypostria in P4-M2. *Hesperolagomys* species differ primarily in size and in lower cheek tooth shape; ANOVAs of tooth dimensions strongly support three size groups corresponding to three species. *H. fluviatilis* (late Barstovian) is smallest in most dimensions, with p3 lacking a cement-filled anterolingual groove and lower molariform teeth with relatively narrow, asymmetrical talonids. *H. niobrarensis* (late late Barstovian) is largest in most dimensions; p3 has a weak but cement-filled anterolingual groove and lower molariform teeth have moderately wide, asymmetrical talonids. Transverse width of upper cheek teeth of *H. niobrarensis* is anomalously variable and has a statistically highly significant linear relationship with wear. *H. galbreathi* (late Clarendonian) is intermediate in size; lower molariform teeth have relatively wide and buccolingually symmetrical talonids, and p3 is short with a prominent cement-filled anterolingual groove.

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INTRODUCTION

Little is known regarding the fossil record of North American ochotonid lagomorphs. Seven species of ochotonids with rooted cheek teeth have been described from late Oligocene to late Miocene faunas: *Hesperolagomys galbreathi* (Clark et al. 1964), *?Desmatolagus schizopetrus* (Dawson 1965), *Russellagus vonhofi* (Storer 1970,1975), *Hesperolagomys fluviatilis* (Storer 1970,1975), *Gripholagomys lavocati* (Green 1972), *Cuyamalagus dawsoni* (Hutchison and Lindsay 1974), and *Oklahomalagus whisenhunti* (Dalquest et al. 1996). These species are based largely on small samples of isolated teeth and are difficult to confidently assign to species, genus, or in some cases, to family. Dentally archaic ochotonids pose a particular challenge to workers because of dramatic changes in the size and shape of the occlusal surface of upper cheek teeth with wear (Bair 2007), and with only a few isolated teeth, distinguishing ontogenetic from taxonomic differences in morphology has proven problematic.

Hesperolagomys galbreathi, the type species of the genus, was first described from deposits of the Clarendonian Esmeralda Formation in Fish Lake Valley, Nevada, by Clark et al (1964), who noted its dental similarities to both *Amphilagus fontannesi*, a late Miocene European ochotonid, and *Desmatolagus gobiensis* from the Oligocene of Asia. At the time of its initial description, *Hesperolagomys* was arguably the most ‘primitive’ late Miocene ochotonid; *Oreolagus* (possessing many ‘advanced’ dental characters including rootless cheek teeth) was the only other North American Miocene ochotonid known. Clark et al. (1964) described plesiomorphic characters of *Hesperolagomys galbreathi* including: (1) rooted cheek teeth, (2) buccal folds persisting on the occlusal surface of P4 and M1, and (3) talonids transversely narrower than trigonids in p4-m2. Apomorphic characters of *Hesperolagomys* noted by Clark et al. (1964) are the unique position and emphasis of mental foramina, and “marked anterior projections of the talonids on p4-m2.”

A slightly older species of *Hesperolagomys*, *H. fluviatilis*, was described by Storer (1970, 1975) from the Barstovian Wood Mountain Formation of south-central Saskatchewan, along with a new genus of dentally archaic North American ochotonid, *Russellagus*. Since then, *Hesperolagomys galbreathi* has been reported in Clarendonian faunas in Nebraska (Korth 1998) and Utah (Tedrow and Robison 1999), and *Hesperolagomys fluviatilis* has been reported from Barstovian localities in Nebraska (Voorhies 1990a, 1990b).

Part of a larger-scale project to document dental variation and revise the systematics and biochronology of North American Oligo-Miocene ochotonids, the purpose of this study is to describe a new species of *Hesperolagomys* from a large sample from the late Barstovian of Nebraska, and to review and revise *Hesperolagomys*. Previously undescribed topotypic specimens of *Hesperolagomys galbreathi* and *H*. *fluviatilis* and previously undescribed specimens from Nebraska allow taxonomic reassessment and more definite characterization of these taxa. Having many more specimens at my disposal than were available to previous authors, I can now document pronounced wear-related changes in the occlusal patterns of *Hesperolagomys* upper cheek teeth and can confidently distinguish *Hesperolagomys* from the commonly co-occurring ochotonid *Russellagus*. Both dental and skull morphology, along with size, distinguish the three species of *Hesperolagomys*, and advances in biochronology allow refinement of their chronologic ranges.

MATERIALS AND METHODS

Fossil Material

Fossil localities with specimens included in this study are shown in Figure 1 and range in age from late Barstovian to late Clarendonian (middle to late Miocene, Ba2 to Cl3 of Tedford et. al 2004); more detailed biochronologic information and refinement of faunal ages is below. Material examined is primarily derived from: (1) Ogallala Group (Valentine and Ash Hollow Formation) sediments of Nebraska, (2) Esmeralda Formation of Fish Lake Valley, Nevada, and (3) Wood Mountain Formation of south-central Saskatchewan. Additional published specimens previously identified as *Hesperolagomys* were directly examined when possible.

The largest sample of *Hesperolagomys* studied, representing a previously undescribed species, derives from three of the five Barstovian-age Valentine Railway Quarries (Valentine Quarry B, West Valentine Quarry, and Stewart Quarry) in the Crookston Bridge Member of the Valentine Formation in north-central Nebraska. Important specimens of *Hesperolagomys* (sp. nov.) from the previously unpublished Garner Bridge South faunal assemblage are included in this study. Specimens

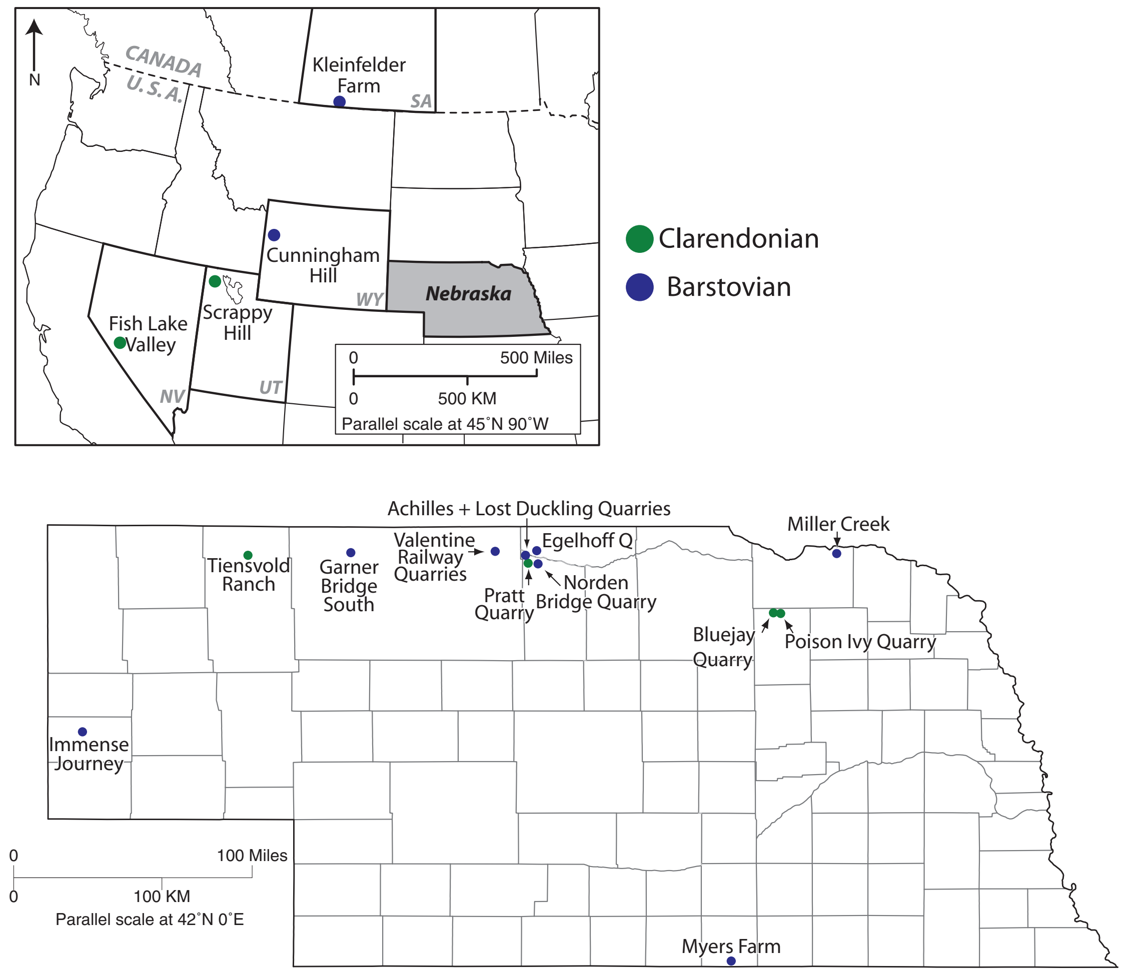

FIGURE 1. Map of western North American localities with *Hesperolagomys* included in this study; inset of detailed view of Nebraska localities.

referred to *Hesperolagomys* from the Barstovian Norden Bridge Quarry Fauna and Nebraska faunas of equivalent age from the Cornell Dam Member of the Valentine Formation (Achilles, Lost Duckling, and Egelhoff Quarries) were studied (Voorhies 1990a, 1990b).

The hypodigm and previously undescribed topotypes of *H. galbreathi* from Fish Lake Valley were included in this study. Well-preserved specimens referable to *H. galbreathi* from the Tiensvold Ranch faunal assemblage, in Ash Hollow Formation sediments in Sheridan County of northwestern Nebraska, were also studied. Other *Hesperolagomys* specimens of Clarendonian age from Nebraska included here are from Poison Ivy Quarry, northeastern Nebraska, and from Pratt and Bluejay Quarries in the Merritt Dam member of the Ash Hollow Formation of north-central Nebraska (Korth 1998). Clarendonian *Hesperolagomys* described from Scrappy Hill, Utah (Tedrow and Robison 1999), are also included in this study.

The hypodigm and previously undescribed topotypes of *Hesperolagomys fluviatilis* from the Barstovian Kleinfelder Farm locality, Wood Mountain Formation (Storer 1970, 1975) were studied. Barnosky (1986) described *Oreolagus colteri* (referred below to *Hesperolagomys* sp.) from the Barstovian Cunningham Hill Fauna, Colter Formation, western Wyoming.

Comparative Material

Specimens included in this study were compared with specimens of other lagomorphs including the extinct ochotonids *Russellagus vonhofi*, *Oreolagus nebrascensis*, *Gripholagomys lavocati*, *Amphilagus fontannesi*, *Amphilagus ulmensis*, and the extinct leporids *Palaeolagus*, *Megalagus*, *Archaeolagus*, and *Hypolagus* in the collections of

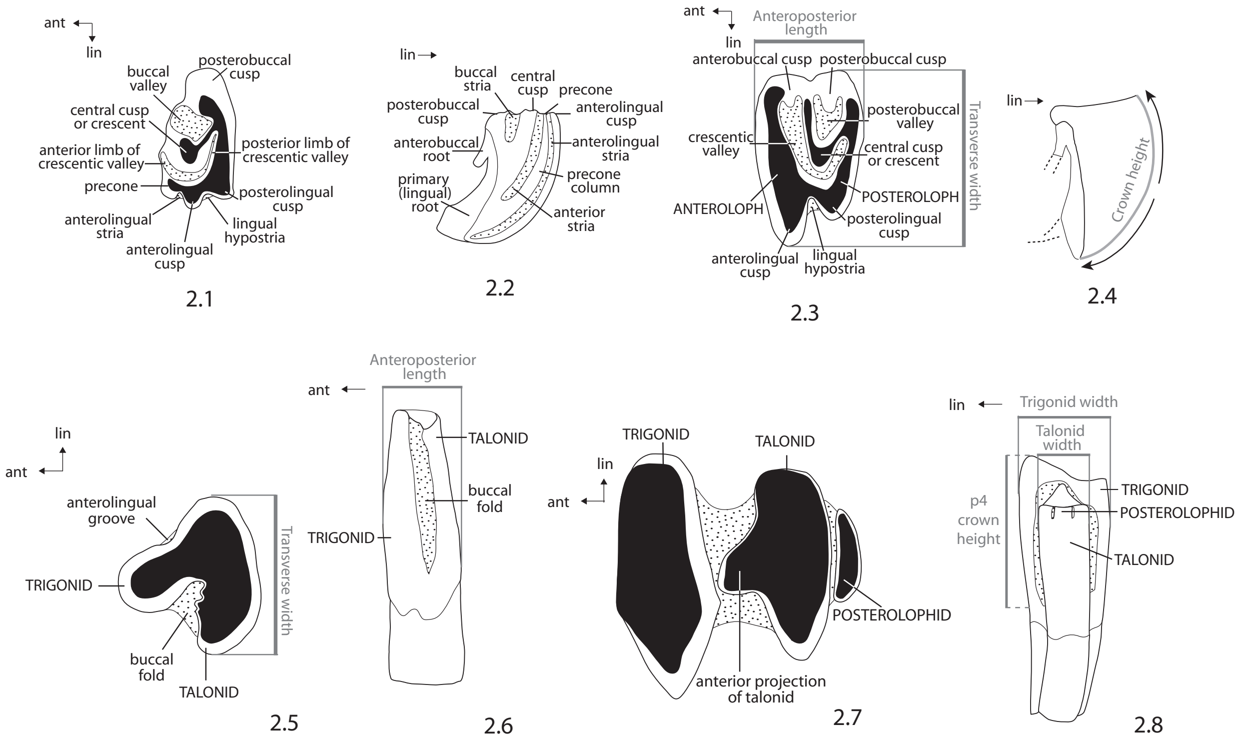

FIGURE 2. Generalized morphology of *Hesperolagomys* cheek teeth, with terminology used and measurements taken. In occlusal view (2.1, 2.3, 2.5, and 2.7), white areas indicate enamel and black shaded areas indicate dentine; in both occlusal and side views stippled areas indicate cement. Anatomical terms in black text. Major features in all capital text, minor features in lowercase text. Measured dimensions in gray text and indicated by gray bars. 2.1, occlusal view of P3. 2.2, anterior view of P3. 2.3, occlusal view of upper molariform tooth (generalized P4-M2). 2.4, anterior view of upper molariform tooth. 2.5, occlusal view of p3. 2.6, buccal view of p3. 2.7, occlusal view of lower molariform tooth (generalized p4-m2). 2.8, posterior view of lower molariform tooth.

the University of Nebraska State Museum (Division of Vertebrate Paleontology), Royal Ontario Museum, University of Michigan Museum of Paleontology, Museum of Paleontology at the South Dakota School of Mines and Technology, University of California Museum of Paleontology, and the Carnegie Museum of Natural History. Comparison was made with the published description of *Cuyamalagus dawsoni* (Hutchison and Lindsay 1974). Specimens of extant *Ochotona princeps* (adult skulls: ZM 2114, 2117, 2118, 14366; adult skeleton: ZM 2114; juvenile skull: ZM 2134), *Sylvilagus audubonii* (adult skulls: ZM 3281 and 3284) and *Sylvilagus floridanus* (adult skulls: ZM 12086, 12087, 17159; juvenile skull: ZM 26135) in the collections of the Division of Zoology, University of Nebraska State Museum, were also used for comparison.

Methods

Dental terminology used in this paper (Figure 2) is descriptive and is modified from Dawson (1958), Storer (1975), and Tobien (1974). Standard orientation of specimens is illustrated in Figure 2 and used in other figures unless otherwise noted. Measured values are in millimeters. I made most specimen measurements directly with Mitutoyo calipers (instrumental error ± 0.02 mm). Repeated measurements revealed no significant differences beyond instrumental error. Anteroposterior length and transverse width of incisors are maxima. Anteroposterior length and transverse width of upper cheek teeth were measured at the occlusal surface (Figure 2.3). Trigonid width and talonid width of p4-m1 were measured as shown in Figure 2.8. Maximum anteroposterior length of lower cheek teeth was measured as in Figure 2.6. Length and width of deciduous teeth, p3, and m3 were measured as shown in Figures 2.5 and 2.6. Dorsoventral depth of the dentary was measured at the inside of the jaw at m1.

Crown height of p4 (the lower cheek tooth with the highest crown) was measured on the trigonid from crown apex to the base of the lingual hypostria (see Figure 2.8). Hypsodonty indices for p4 were calculated as crown height divided by anteroposterior length using unworn or nearly unworn teeth (possessing a posterolophid completely isolated from the main body of the talonid). Because upper cheek teeth are strongly buccolingually curved, straight-line measurements severely underestimate crown height. I devised a new method to measure the height of the curved crown of P4s, the upper cheek teeth with the highest crowns (as shown in Figure 2.4). Scaled camera lucida line drawings or digital photographs of the lingual margin (tallest part of the crown), in anterior or posterior view (which give equivalent measures of crown height for P4s), were input into Object-Image (Vischer 2003), which was used to calculate the length of the curved line representing the crown height. I also used this technique to measure tip-to-base length of incisors.

Upper cheek teeth demonstrate considerable delay in completion of the crown and root until after occlusal wear has occurred ('incipient hypselodonty', e.g., Webb and Hulbert 1986), such that the 'complete' crown height and degree of hypsodonty cannot be measured directly from any single tooth. To obtain an estimate of the 'complete' crown height of P4 I overlaid line drawings of the lingual profiles of teeth with unworn or nearly unworn crowns and more heavily worn teeth with completed crowns, and measured the length of the curved line representing the 'complete' crown using the methodology described above for measuring crown height of P4 of individual specimens. I calculated an estimate of the hypsodonty index of P4 as the 'complete' crown height divided by the mean value of anteroposterior length.

To determine the significance of the relationship between crown height (as a proxy for stage of wear) and occlusal dimensions in P4 of *Hesperolagomys*, I tested the linear correlation of crown height with width and length of P4s from the largest (Valentine Railway Quarries) sample. For this analysis, I used only those crown height values measured directly from specimens, omitting the estimated maximum crown height values obtained by the method described above.

I calculated minimum, maximum, and mean values, standard deviation and coefficient of variation for each tooth dimension for specimens of *H. fluviatilis* from the Kleinfelder Farm locality sample and a combined Valentine Railway Quarries and Garner Bridge South sample of *Hesperolagomys*. I also tested tooth dimensions of the Valentine Railway Quarries and Garner Bridge South pooled sample to determine if distributions approximated normality using Shapiro-Wilk W tests.

One-way ANOVAs on length of P3-M2, length and width of p3, and length and trigonid width of p4-m2 were performed to evaluate the significance of size differences between species. An additional ANOVA was performed using a pooled sample of m1s and m2, as these teeth are sometimes difficult to differentiate in practice. *Hesperolagomys* sp. nov. and *H. fluviatilis* samples from the combined Valentine Railway Quarries + Garner Bridge South and Kleinfelder Farm, respectively, as described above were included, and a pooled sample of *H. galbreathi* was composed of topotypes from Fish Lake Valley and specimens from the Tiensvold Ranch locality. Preliminary analysis of specimens from the two Clarendonian localities revealed that they could not be distinguished morphologically or statistically. Pairwise comparisons were conducted using Student's *t* tests (Zar 1999; Sall et al. 2005). I also calculated estimates of power of the ANOVAs to investigate if small sample size might reduce the meaningfulness of the analyses; I varied sample size from that of the actual sample to 100 in increments of 1.

Abbreviations

Anatomical Abbreviations. **ant**, anterior; **a-p**, anteroposterior; **CH**, crown height; **L**, length; **lin**, lingual; **tr**, transverse; **tri**, trigonid; **tal**, talonid; **W**, width.

Institutional Abbreviations. **IMNH**, Idaho Museum of Natural History; **MCZ**, Harvard Museum of Comparative Zoology; **ROM**, Royal Ontario Museum; **UCMP**, University of California Museum of Paleontology; **UNSM**, University of Nebraska State Museum; **UWBM**, University of Washington-Burke Museum.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Order LAGOMORPHA Brandt, 1855
Family OCHOTONIDAE Thomas, 1897
HESPEROLAGOMYS Clark, Dawson, and Wood, 1964

Synonymies. *Hesperolagomys* Storer, 1970, 1975 (in part); *Russellagus* Storer, 1970, 1975 (in part); *Oreolagus* Barnosky, 1986 (in part); *Hesperolagomys* Voorhies, 1990b (in part); *Russellagus* Voorhies, 1990b (in part); *Hesperolagomys* Korth, 1998 (in part); *Russellagus* Korth, 1998 (in part).

Type Species. *Hesperolagomys galbreathi* (Clark et al. 1964).

Included Species. *Hesperolagomys galbreathi* (Clark et al. 1964), *H. fluviatilis* (Storer 1970, 1975), and *H. niobrarensis*, sp. nov.

Distribution. Late Barstovian through Clarendonian NALMAs; Ba2-Cl3 of Tedford et al. (2004) of the Great Plains, Great Basin, and Rocky Mountains of North America.

Emended Diagnosis. Hypsodont but rooted cheek teeth; upper cheek teeth strongly curved (lingually convex) and unilaterally hypsodont. Premolar foramen present between P3 and P4 and closer to P3. Largest mental foramen ventral to p3 or p4. Tooth formula 2(presumed)/1, 3/2, 2/3. P3-M2 with one large lingual root and two much smaller spreading buccal roots, with cement-filled crescentic valley present in nearly all stages of wear. Lingual hypostria on P4-M2 deep (persists to near the crown base) and extends buccally nearly to crescentic valley; crosses over approximately one-half to two-thirds of the occlusal surface width on M2. P3 distinct from that of other North American lagomorphs in possessing two persistent cement-filled lingually oriented striae; anterior limb of the crescentic valley in P3 opens into an anterior stria that extends nearly to the base of the crown, paralleling the outer curve of the tooth. The p3 has a deep buccal fold.

Further differing from *Russellagus* in: (1) lower incisor extending posteriorly at least to beneath middle of m1 (to beneath p4 in *Russellagus*), (2) anterior talonid projections on lower cheek teeth relatively narrow buccolingually, (3) and smaller size (cheek tooth length ~45-90% that of *Russellagus*). Differing from *Cuyamalagus* in: smaller cheek teeth, and talonid buccolingually narrower than trigonids in lower molariform teeth. Differs from *Gripholagomys* in: anteroposteriorly longer anterior projections of the talonids of lower cheek teeth and deeper lingual hypostriae on P3-M2.

Hesperolagomys niobrarensis, sp. nov.

Holotype. UNSM 123305, dentary with i-m2 and alveolus for m3, from Garner Bridge South locality, Nebraska, in Crookston Bridge Member, Valentine Formation, from deposits of late late Barstovian age (Ba2c).

Hypodigm. Type; topotypes: (all UNSM numbers) 123306, partial dentary with p4-m3, alveolus for p3; 123307, partial maxilla with P3-P4, alveolus for P2. From **Valentine Railway Quarries**, by locality: **West Valentine Quarry:** 122500, partial maxilla with P3-P4; 122509, 122719, partial maxillae with P4; 123348, edentulous partial maxillary; 122996, upper anterior incisors; 122516-122526, 122543-122545, 122830, P3s; 122630, 122634-122641, 122643-122662, 122673, 122745-122751, P4s; 122700-122701, 122703-122710, 122714, 122718, 122774, 122801-122808, M1s; 122809-122814, 122817, 122819-122820, 122823, M2s; 122512, partial dentary with p3-m3; 122501, partial dentary with p4-m3 and alveolus for p3; 122502, partial dentary with p4-m2 and alveolus for m3; 122503-122504, 122510, and 122513-122514, partial dentaries with m1-m2; 122515, partial dentary with m1; 122511, partial dentary with m2; 122993, partial right lower incisor; 122838, 122859, p3s; 122878, 122881, 122891-122907, 122943, 122945, 122951, p4s; 122908, 122940-122942, 122944, 122946, 122952-122953, 122986, m1s; 122983-122985, 122987-122992, m2s. **Stewart Quarry:** 123021-123030, P3s; 123052-123068, 123081, P4s; 123082-123088, 123103, M1s; 123097, 123099, M2s; 123104, partial upper cheek tooth; 123003, partial dentary with p4; 123140-123145, p4s; 123162-123163, m1; 123177, m2. **Valentine Quarry 'B':** 123186, partial maxilla with P4; 123300, p4.

Referred Specimen from Nebraska. UNSM 45206, m1, from Myers Farm.

Etymology. *niobrarensis*; after 'Niobrara', for the abundant Miocene fossiliferous deposits exposed along the Niobrara River and tributaries in northern Nebraska deposits, from which specimens of this species were first recognized.

Diagnosis. Larger than other species of *Hesperolagomys*. Talonid moderately wide compared to trigonid in lower molariform teeth, intermediate between that of *H. fluviatilis* and *H. galbreathi* (talonid width/trigonid width of p4 ≈1.41). Additionally distinguished from *H. fluviatilis* by presence of anterolingual groove on p3. Also differs from *H. galbreathi* in possessing a weaker (but cement-filled) anterolingual groove on p3 and more asymmetric talonid on lower molariform teeth.

Geologic Age and Distribution. Late late Barstovian (informally designated Ba2c) of Nebraska (see discussion in Biochronology section below).

DESCRIPTION

Skull

Four partial maxillae of *H. niobrarensis* provide new information on skull structure. The specimens show an overall similarity to *Oreolagus* and *Ochotona* in features of the anterior zygoma and maxilla but differ notably in having rooted upper cheek teeth that occupy a relatively greater occlusal area. The specimen from Garner Bridge South and two of the three from the Valentine Railway Quarries (Figure 3.1, 3.2, 3.3) each have a small premolar foramen located medial to and just posterior of P3 (the relevant portion of the palate is not preserved in the other Valentine Railway Quarries specimen); the presence of this character indicates affinity with the Ochotonidae (Dawson 2008; McKenna 1982; but see also discussion below). As seen in ventral view, the anterior zygomatic root extends from a point anterior to P3 to a line between P4 and M1, leaving the shafts of M1 and M2 free of the zygoma (Figure 3.1-3.4). The preserved portion of the anterior zygoma has a shallow concavity on the lateral surface nearly identical to that in *Oreolagus*, and much shallower and less well defined than the zygomasserteric fossa in *Ochotona princeps*.

Upper Dentition

Upper Incisors. Two anterior upper incisors (one shown in Figure 3.5) are referred to *H. niobrarensis*, primarily because they closely resemble specimens of *H. galbreathi* described by Clark et al. (1964) in both size and morphology, with a longitudinal groove on the anterior surface displaced slightly medially of center. Both incisors are slightly anteroposteriorly longer (Table 1A) than those of *H. galbreathi* in Clark et al. (1964), and both lack the posterior portion and are slightly damaged at the wear facet. The teeth are similar in size and morphology to those of *Ochotona princeps* but the groove on the anterior surface is slightly shallower and less angular, and the tooth is more compressed laterally. Both *Hesperolagomys* and *Ochotona* anterior upper incisors have elongate wear facets and sharp tips compared with those of *Sylvilagus* and *Lepus,* which have shorter facets and less acuminate tips.

P2. P2 is not known, but an alveolus for this tooth suggests that it had a single (lingual) root and was much smaller than the other upper cheek teeth (Figure 3.3;Table 1A).

P3. P3 in anatomical position in UNSM 123307 (Figure 3.1) and its alveolus in UNSM 123348 (Fig. 3.3) allow confident identification of this tooth in *Hesperolagomys* for the first time. 26 P3s are known for *H. niobrarensis*, allowing documentation of variation and wear stages (Figure 4). Two buccal roots are present; the anterior one is shifted lingually compared with its position in more posterior cheek teeth, such that the tooth is nonmolariform and anteroposteriorly shorter buccally than lingually. The disposition of stria and overall gracile structure of P3 is unique to *Hesperolagomys*. In anterior view (see Figure 4.1-4.3; 4.5), two cement-filled striae are present: an anterolingual stria close to and paralleling the curvature of the lingual margin, and a more centrally-located anterior stria, also paralleling the outer curvature of the tooth and extending nearly to the base of the crown. A third and shorter stria is often but not always cement-filled, and merges with the anterior stria (Figure 4.3). In lingual view (Figure 4.2), two cement-filled striae (the anterolingual stria and a more posteriorly-located lingual hypostria) extend to near the base of the crown (more easily seen in isolated specimens). In occlusal view, the anterior stria corresponds to the anterior limb of the crescentic valley, and the cement-filled anterolingual stria and lingual hypostria separate the lingual edge of P3 into three subequal rounded lingual lobes (see Figure 2.1, 2.2 for a schematic view of these relationships). The cement-filled crescentic valley is separated from the anterolingual stria by only a narrow bridge of dentine and enamel. The crescent forms the anterior edge of the central part of the tooth.

Isolated teeth demonstrate a slight curvature in the anteroposterior plane, concave to posterior (illustrated in Figure 4.2). In the youngest individuals (Figure 4.1) the crown base is still forming, and the enamel-dentine junction extends beyond perpendicular relative to the slightly worn occlusal surface. Three distinct cement-filled striae are visible in anterior view (e.g., Figure 4.1 and 4.2). The lingual most is the anterolingual stria, separated from the anterior stria by the precone column; in these specimens, the buccal stria is completely separated from the cement of the anterior stria (but see Figure 4.3 for a slight connection). The anterolingual and anterior striae nearly merge towards the crown apex. In occlusal view, the precone is topographically lower than the rest of the lingual quarter of the tooth, but is worn and connected to the lingual cusps by a thin portion of dentine. A small rounded area of the crescent is worn through to dentine, with the anterior portion topographically lower and unworn. The anterior limb of the crescentic valley projects nearly directly anteriorly into the anterior stria from the posterobuccally-directed posterior limb. The buccal valley is large and primarily unworn, separating the crescent from a small peninsula of exposed dentine on the posterobuccal corner, with a large anterobuccal area topographically lower and unworn.

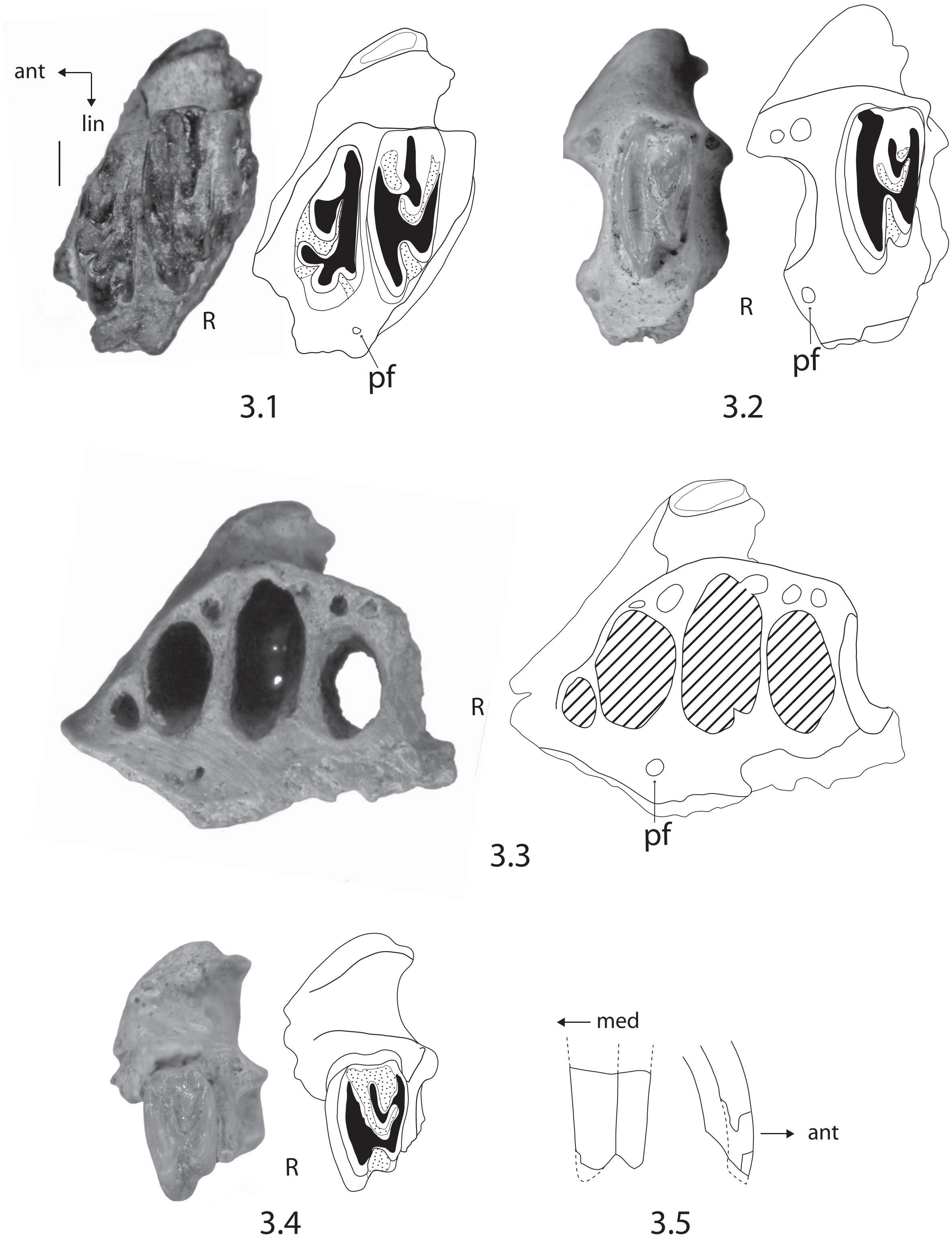

FIGURE 3. Maxillaries and upper incisor of *H. niobrarensis*. Scale bars equal 1 mm. 3.1, UNSM 123307, partial maxillary with P3-P4, from Garner Bridge South. 3.2-3.5, specimens from Valentine Railway Quarries. 3.2, UNSM 122509, partial maxillary with P4. 3.3, UNSM 123348, edentulous maxillary with alveoli for P2-M1. 3.4, UNSM 123186, partial maxilla with P4. 3.5, 122996 (in part), partial upper anterior incisor; anterior view to left, medial view to right. Abbreviation: **pf,** premolar foramen.

TABLE 1. Summary statistics of tooth dimensions of *H. niobrarensis* from combined Valentine Railway Quarries and Garner Bridge South samples. A, upper teeth; B, lower teeth. Abbreviations: $\bar{x}$, mean (for samples N=1, $\bar{x}$ refers to single measurement value); SD, standard deviation; N, number of specimens; CV, coefficient of variation; MIN, minimum value; MAX, maximum value.

1A.

	Ant I		P2 (alveolus)		P3		P4		M1		M2	
	L	W	L	W	L	W	L	W	L	W	L	W
$\bar{x}$	1.11	1.60	0.70	0.99	1.41	2.94	1.63	3.43	1.42	3.03	1.42	2.72
SD	-	-	-	-	0.10	0.61	0.09	0.55	0.07	0.45	0.07	0.2
MIN	1.09	1.59	-	-	1.17	2.00	1.33	2.62	1.27	2.23	1.32	2.36
MAX	1.13	1.60	-	-	1.55	4.22	1.81	4.78	1.57	3.92	1.53	3.01
N	2	2	1	1	17	17	47	46	24	24	8	8
CV	-	-	-	-	7.4	20.8	5.4	16.0	4.7	14.9	5.1	7.7

1B.

	i		p3		p4			m1			m2			m3	
	L	W	L	W	L	tri W	tal W	L	tri W	tal W	L	tri W	tal W	L	W
$\bar{x}$	1.44	1.46	1.34	1.48	1.90	2.15	1.52	1.69	2.01	1.37	1.80	1.94	1.42	0.61	1.05
SD	-	-	0.14	0.11	0.09	0.132	0.11	0.08	0.13	0.10	0.08	0.12	0.09	-	-
MIN	1.38	1.43	1.13	1.32	1.70	1.80	1.25	1.58	1.75	1.17	1.64	1.71	1.20	0.57	0.92
MAX	1.49	1.48	1.46	1.59	2.08	2.32	1.83	1.81	2.19	1.59	1.91	2.15	1.59	0.65	1.17
N	2	2	4	4	34	34	33	18	18	18	20	20	20	2	2
CV	-	-	10.7	7.7	4.8	5.8	7.2	4.7	6.5	7.6	4.6	6.3	6.7	-	-

In a somewhat older individual, (Figure 4.2) crown formation is complete, occlusal width is greater, and areas of dentine exposed at the posterobuccal corner and in the crescent are expanded. The precone is worn to the same topographic level as other lingual cusps. In the illustrated specimen, cement of the buccal and anterior striae are separated, but a depression connects the striae. With increasing wear stage (Figure. 4.3-4.4), transverse width at the occlusal surface increases while length stays relatively constant. The crescent, posterobuccal cusp, and precone become transversely elongated, and greater areas of dentine are exposed. The precone becomes more buccally-directed, and cement-filled valleys are diminished.

The most worn well-preserved P3 of *H. niobrarensis* (122517: Figure 4.5) has a crown height of approximately one half that of the least worn specimen and is approximately twice as wide at the occlusal surface as the least worn examples. Both lingual striae persist nearly to crown base, although the lingual hypostria is relatively shallow and lacks cement at the occlusal surface. The crescentic valley is present in P3 even in highly worn specimens. Several additional specimens lack the buccal edge and posterobuccal root; this area between the buccal roots appears to be the thinnest part of the crown and prone to breakage at advanced stages of wear.

Most notable morphologic variation in P3 appears to be related to stage of wear; however, the separation or connection of cement in the buccal and anterior striae varies independent of wear. Mean size of P3 of *H. niobrarensis* is: length, 1.41 mm; width, 2.94 mm (Table 1A).

P4. P4s of *H. niobrarensis* at similar stages of wear strongly resemble the two P4s included in the original hypodigm of *H. galbreathi*, differing primarily in their larger size. P4 is the largest and tallest crowned upper cheek tooth of *Hesperolagomys*, characterized by an anteroposteriorly-oriented buccal margin, anteroloph wider than posteroloph, and a persistent (extending to or nearly to crown base) cement-filled lingual hypostria that is shallower than that of M1 and M2 (compare Figures 5, 6, and 7). The tooth is strongly curved buccolingually, but is nearly straight in the anteroposterior plane (Fig-

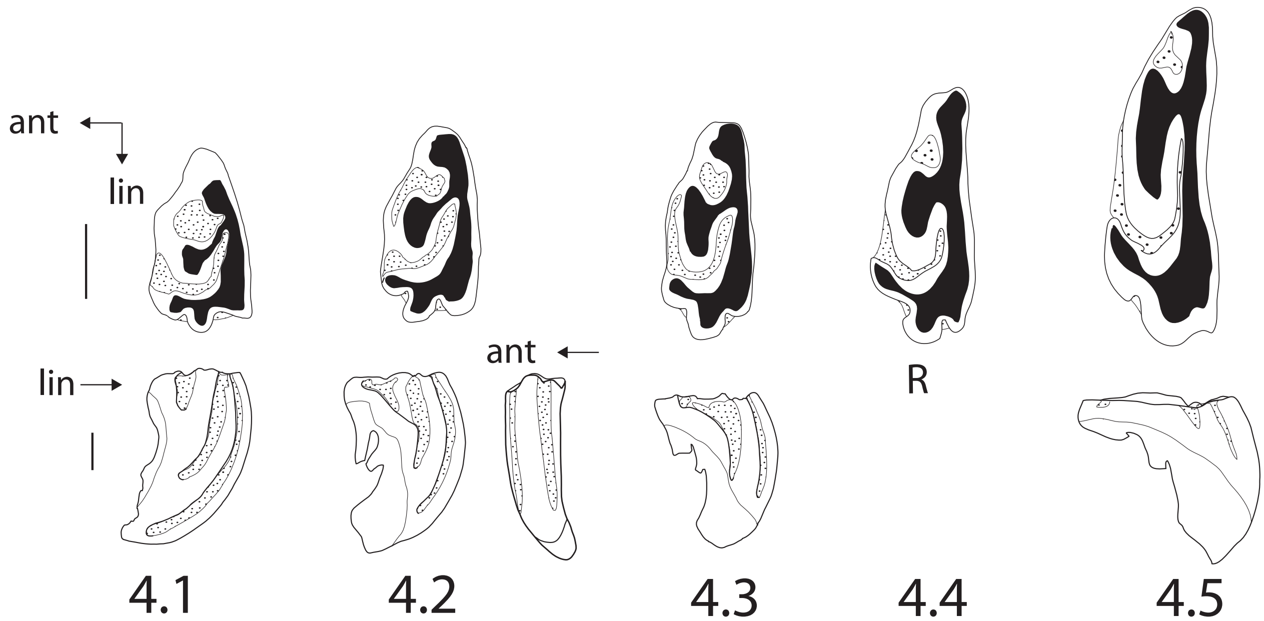

FIGURE 4. P3s of *H. niobrarensis* from Valentine Railway Quarries (arranged in order of increasing wear stage, from left to right). Scale bar equals 1 mm. Occlusal view above, anterior view below. 4.1, UNSM 122519. 4.2, UNSM 122523. 4.3, UNSM 122544. 4.4, UNSM 122500 (anterior view not available). 4.5, UNSM 122517.

ure 5.3). The crown is incompletely formed, exhibiting incipient hypselodonty (wear occurring before completion of the crown base). A broad range of wear stages is represented among the more than 60 specimens available, demonstrating dramatic changes in occlusal morphology and width through wear.

A nearly unworn P4 (Figure 5.1) is characterized by a very tall crown, a large open crown base in which enamel formation is incomplete, absence of wear at the buccal margin of the occlusal surface, extensive cement filling large valleys, a topographically tall and barely worn crescent with a thin line of dentine exposed, and a narrow occlusal width. The buccal and crescentic valleys have confluent cement, and the buccal cusps are low. At this stage, the lingual hypostria is anteroposteriorly elongate and buccolingually narrow at the occlusal surface.

P4s exhibiting progressively more wear (e.g., Figure 5.2-5.3) have completely formed crowns and less cement in valleys. The occlusal surface widens through wear, crown elements are buccolingually stretched, and the lingual hypostria becomes absolutely wider. Further wear (e.g., Figure 5.4-5.5) produces further buccal reduction in cement and buccolingual stretching of elements at the occlusal surface. The lingual hypostria curves posteriorly towards the crown base; as the occlusal surface intersects the crown closer to the base, the lingual portion of the anteroloph expands at the expense of the posteroloph, and the anterior wall of the tooth becomes more curved. The lingual hypostria terminates in a slightly rounded point buccally. At its maximum (Figure 5.5) the lingual hypostria extends across no more than one third of the occlusal width of the tooth.

The most worn well-preserved P4 is UNSM 122643 (Figure 5.6), which has only a small portion of enamel remaining on the posterior wall of the tooth, shows extreme buccolingual stretching of the occlusal surface (width nearly 2.5 times that of the youngest individual), with only the extreme buccal portions of both limbs of the crescentic valley retaining enamel, and the lingual hypostria very shallow but still containing some cement.

Mean size of P4 of *H. niobrarensis* is: length, 1.63 mm; width, 3.43 mm (Table 1A). The composite 'complete' specimen (Figure 5.7) has an estimated crown height of 11.69 mm and an estimated hypsodonty index of 7.17.

M1. M1 is smaller and slightly shorter-crowned than P4, such that it experiences substantial but slightly less dramatic changes in occlusal size and shape with wear (Figure 6.1-6.5). Other differences from P4 are: (1) an expanded lingual hypostria, which extends relatively and absolutely farther buccally across the occlusal surface to at least one

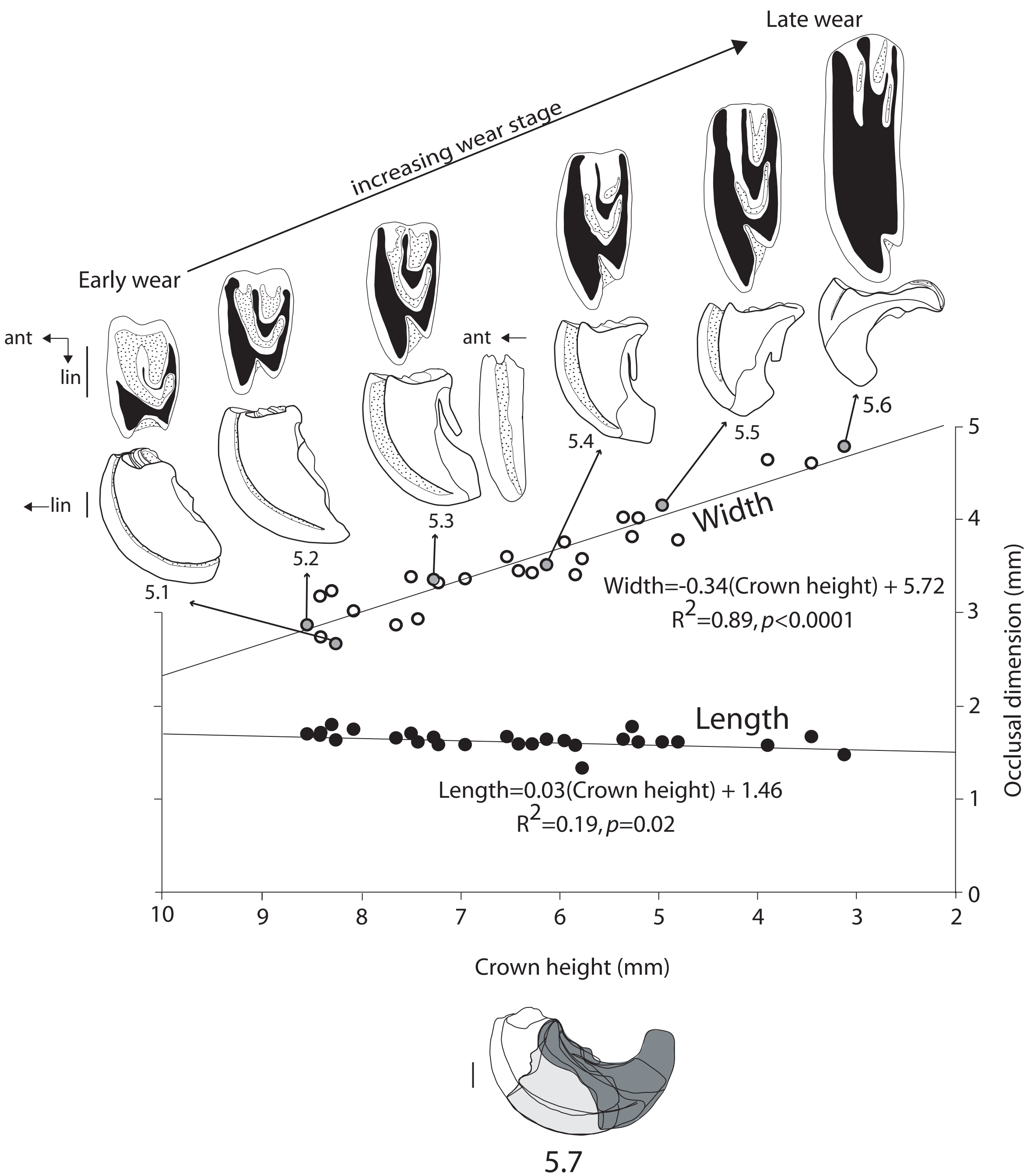

FIGURE 5. *H. niobrarensis* P4s from Valentine Railway Quarries (modified from Bair 2007). Wear series superimposed on plot showing correlation between crown height and occlusal dimensions, from left to right. Scale bar equals 1 mm; occlusal view above, posterior view below. 5.1, UNSM 122643. 5.2, UNSM 122648. 5.3, UNSM 122637. 5.4, UNSM 122645. 5.5, UNSM 122653. 5.6, UNSM 122939. 5.7. 'composite' P4 constructed by overlay of posterior view of 5.1, 5.4, and 5.6. Lines on plot show linear regressions; upper white circles for occlusal width, lower black circles for occlusal length. Gray width circles mark location on plot of specimens 5.1-5.6.

third its width, and terminates very near the crescentic valley in a squared-off groove, (2) buccal cusps are more prominent in M1 (such that cement is more rapidly lost from the buccal valleys, and may never have been confluent as in P4), and (3) lingual portion of the crescentic valley retains cement even through the latest stages of wear. In the most worn M2s, (Figure 6.5), the crescentic

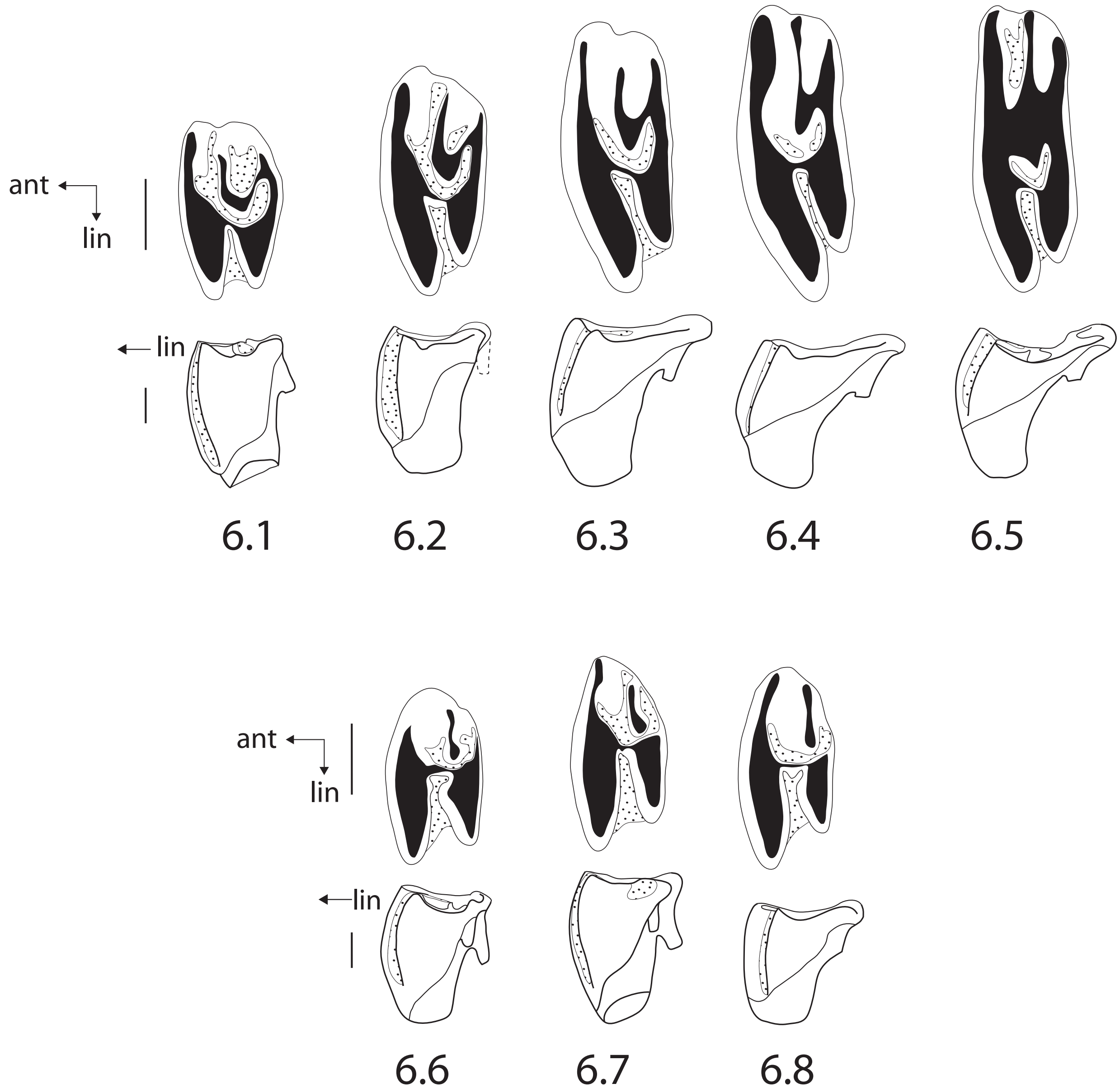

FIGURE 6. *H. niobrarensis* M1s and M2s from Valentine Railway Quarries. Teeth are arranged in order of increasing wear stage, from left to right. Standard orientations as in Fig. 2. Each lettered pair shows occlusal view (above) and posterior view (below). Scale bars for occlusal and posterior views next to 6.1 also indicate scale for all other specimens. 6.1-6.5, M1s. 6.1, UNSM 122519. 6.2, UNSM 122523. 6.3, UNSM 122707. 6.4, UNSM 122718. 6.5, UNSM 122704. 6.6-6.8, M2s. 6.6, UNSM 123097. 6.7, UNSM 12286. 6.8, UNSM 122811.

valley can become separated into lingual and buccal portions, separated by dentine. Mean size of M1 of *H. niobrarensis* is: length, 1.42 mm; width, 3.03 mm (Table 1A).

M2. M2s of *Hesperolagomys* are not currently known in anatomical position in maxillary fragments with other cheek teeth; however, eight upper cheek teeth of *H. niobrarensis* are distinct from previously described upper cheek teeth of *Hesperolagomys* and are here identified as M2s. In comparison with M1, in M2 the posterobuccal portion of the crown is reduced, such that the medial edge of the crown tapers anteroposteriorly, and the anteroloph is much wider than the posteroloph. The most noticeable characteristic of the occlusal surface is the expanded hypostria, which extends across approximately 80% the width of the occlusal surface and is separated from the crescentic valley by a very thin strip of dentine. Crown elements

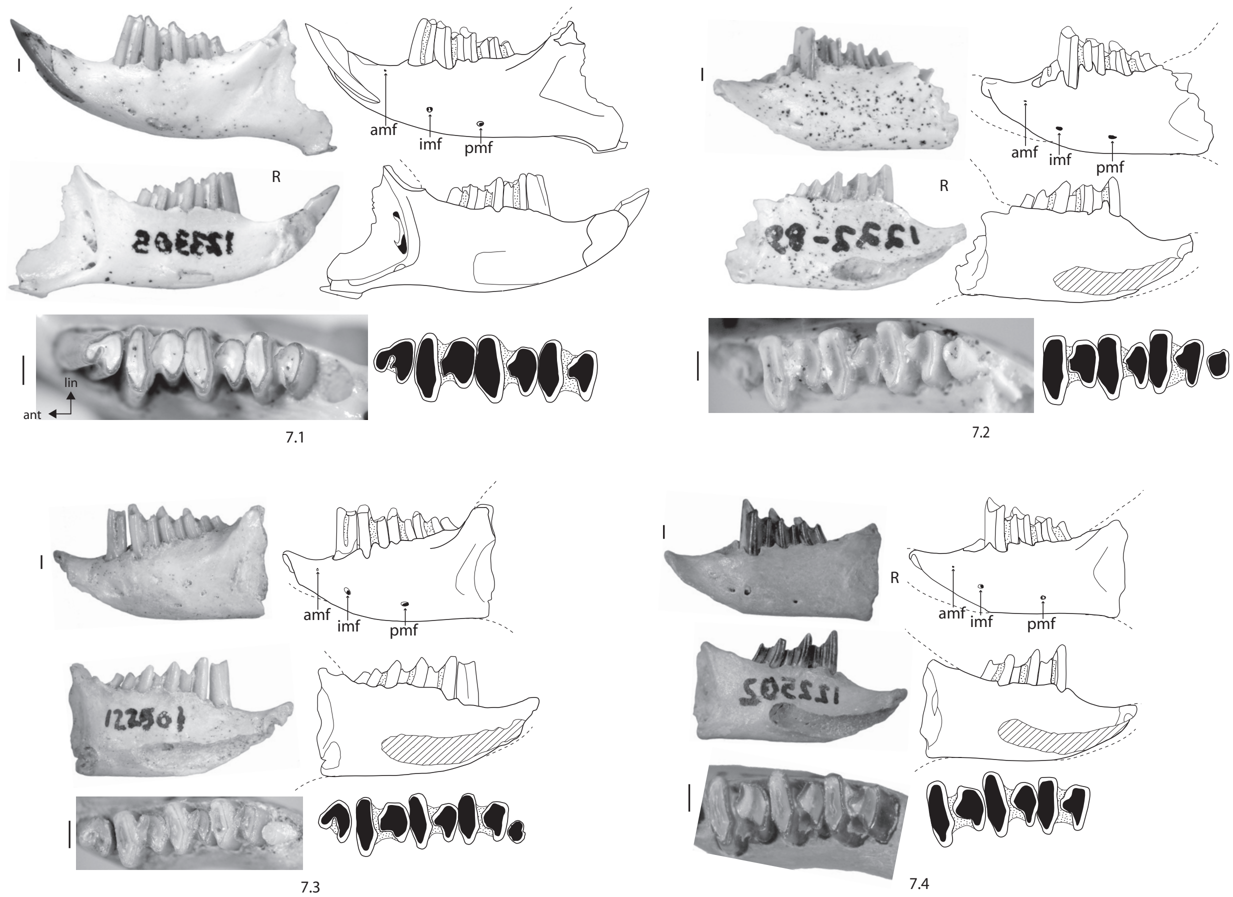

FIGURE 7. *H. niobrarensis* dentaries. Standard orientations as in Figure 2; scale bar equals 1 mm. For each specimen, lateral view above, medial view in middle, occlusal view of tooth row below. Abbreviations: **amf**, anterior mental foramen; **imf**, intermediate mental foramen; **pmf**, posterior mental foramen. 7.1, 7.2 from Garner Bridge South; 7.3, 7.4 from Valentine Railway Quarries. 7.1, UNSM 123305, holotype, dentary with p3-m2. 7.2, UNSM 123306, dentary with p4-m3. 7.3, UNSM 122501, dentary with p3-m3. 7.4, UNSM 122505, dentary with p4-m2.

buccal to the crescentic valley are much reduced in comparison with their size in P4 and M1. The lingual root is more strongly posteriorly curved than P4 and M1.

Three M2s are illustrated in Figure 6.6-6.8 and illustrate variation. Based on available specimens, M2 appears to have less dramatic changes to occlusal morphology with wear than more anterior cheek teeth. The wear series reveals that though wear M2 increases in transverse width at the occlusal surface, and the lingual hypostria extends over progressively more of the occlusal surface as the crescentic valley is reduced. Figure 6.6 and 6.7 are M2s at a similar stage of wear, but showing some differences not associated with ontogeny: variation in anteroloph width compared with posteroloph width (although anteroloph always wider, the extent to which this is the case varies), the buccal termination of the lingual hypostria is either squared off (6.7) or may expand into a bifurcation (as in 6.6 and 6.8). Mean size of M2 of *H. niobrarensis* is: length, 1.42 mm; width, 2.72 mm (Table 1A).

Dentary

The holotype of *H. niobrarensis* (UNSM 123305: Figure 7.1) is the most complete dentary available, lacking only the dorsal portion of the ascending ramus and m3. It closely resembles previously described jaws of *H. galbreathi* overall shape (Clark et al. 1964). The number and relative size of mental foramina are consistent with those in the type specimen of *H. galbreathi* in Clark et al. (1964), but their position differs somewhat. The largest mental foramen is on the lateral surface ventral to the border of p3-p4, slightly posterior of

TABLE 2. Lower jaw measurements (in mm). Abbreviations: AL, alveolar length; Dm1, dentary depth at level of m1; >, minimum value; ~, approximate value. * Values from Clark, Dawson, and Wood (1964).

Taxon	Locality	Age	Specimen no.	Dm1	AL	p3-m3	L p4-m2	Diastema L
**H. galbreathi*	FLV	Cl2	MCZ 17890	5.3	8.1	4.9	-	-
H. galbreathi	FLV	Cl2	UCMP 14980	5.83	-	5.47	-	-
H. galbreathi	TR	Cl2	UNSM 123312	-	-	-	3.68	12.40
H. galbreathi	TR	Cl2	UNSM 123313	5.51	7.51	-	-	-
H. niobrarensis	GBS	Ba2c	UNSM 123306	5.95	8.20	5.64	>3.30	-
H. niobrarensis	GBS	Ba2c	UNSM 123305	5.65	8.19	5.44	-	~12.94
H. niobrarensis	VRQ	Ba2c	UNSM 122515	5.68	-	-	-	-
H. niobrarensis	VRQ	Ba2c	UNSM 122513	5.34	-	-	-	-
H. niobrarensis	VRQ	Ba2c	UNSM 122502	5.41	8.80	5.80	>3.66	-
H. niobrarensis	VRQ	Ba2c	UNSM 122501	6.27	9.27	5.99	>4.21	-
H. fluviatilis	KF	Ba2a	ROM 52642	4.91	7.67	5.08	>2.59	-

its position in the type specimen of *H. galbreathi* (in line with and beneath p3). A depression with two smaller foramina is beneath the talonid of m1, very similar to the condition of the type specimen of *H. galbreathi* (below m1-m2). The smallest and anterior-most foramen is anterior to p3, positioned more anterodorsally than the anterior-most foramen in *H. galbreathi* and just ventral to p3.

The posterior portion of the horizontal ramus is more completely preserved than for other known species of *Hesperolagomys*. The ventral border is concave beneath the anterior margin of the masseteric fossa. The preserved portion of the masseteric fossa resembles that of *Ochotona*. The incisor capsule forms a bulge on the medial wall, and a small portion is damaged, revealing the incisor extending posteriorly to approximately the middle of m1. The roots of p4, partially visible through a small area of damage to the lateral wall of the dentary, are displaced laterally from the incisor.

Additional dentaries of *H. niobrarensis* (Figure 7.2-7.4; Table 2) closely resemble the holotype in morphology but vary somewhat in size, in the size and position of the anterior-most mental foramina, and in the relative depth of the jaw. The anterior-most foramen is more ventrally located in the three additional figured specimens than in the type. The type specimen is shallower at m1 than other figured specimens, but is not anomalous compared with values for all referred specimens (Table 2).

Lower Dentition

Lower Incisor. The lower incisor in UNSM 123305 (Figure 7.1) is slightly larger than but otherwise similar in cross-sectional morphology to type material of *H. galbreathi* (Table 1B; Clark et al. 1964, table 2). The wear facet has a rounded triangular shape, in which the medial edge comes to a sharp point whereas the lateral edge is more rounded, similar to that of *Ochotona princeps*. An isolated left lower incisor, UNSM 122993, lacks both ends but cross-sectional morphology and size is nearly identical to that of the type. Mean size of *H. niobrarensis* lower incisor is: length, 1.44 mm; width, 1.46 mm (Table 1B).

p3. The p3 in the type specimen has a shallower cement-filled anterolingual groove than in the type specimen of *H. galbreathi* and additionally differs in having a small anterior-facing projection in the thin enamel of the anterobuccal wall of the talonid (Figure 7.1). Three other specimens exhibit wear-related and individual differences from the holotype. The least worn (Figure 8.1) is similar in occlusal pattern to p3 in the type specimen and likewise has a minor inflection of the anterobuccal talonid wall. The remaining p3s (Figures 7.3, 8.2) are shorter-crowned, and in both the anterolingual wall is slightly concave and bears traces of cement (not visible in figures). The enamel is thicker at the occlusal surface, and the trigonid is more anteriorly oriented in both worn specimens. Mean size of *H. niobrarensis* p3 is: length, 1.34 mm; width, 1.48 mm (Table 1B).

Lower Molariform Teeth. Teeth in the holotype, in referred dentaries, and isolated lower molariform teeth are like those of the type specimen of *H. galbreathi* in having trigonids transversely wider and anteroposteriorly shorter than talonids, and in the buccolingually narrow anterior projections of talo-

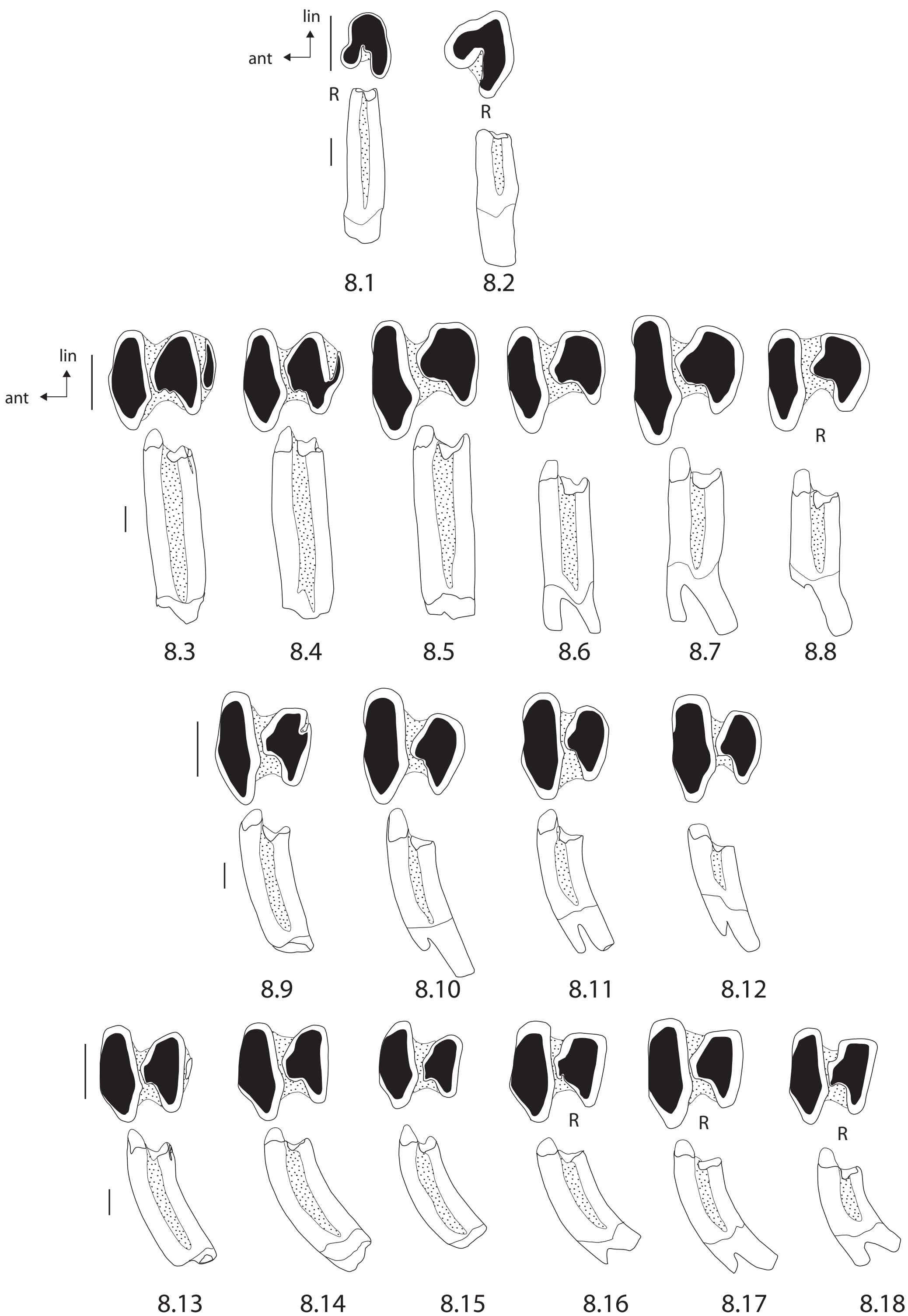

FIGURE 8. Lower cheek teeth of *H. niobrarensis* from Valentine Railway Quarries. Teeth are arranged in order of increasing wear stage, from left right. Standard orientations as in Figure 2. Each lettered pair shows occlusal view (above) and buccal view (below) except in 8.9, with lingual view below. Scale bars equal 1 mm; bars for occlusal and side views next to first specimen in each row also indicate scale for other specimens in that row. All UNSM numbers. 8.1-8.2, p3s. 8.1, 122859. 8.2, 122838. 8.3-8.8, p4s. 8.3, 122878. 8.4, 122907. 8.5, 123300. 8.6, 122900. 8.7, 122886. 8.8, 122892. 8.9-8.12, m1s. 8.9, 122942. 8.10, 122941. 8.11, 122986. 8.12, 123162. 8.13-8.18, m2s. 8.13, 122989. 8.14, 122992. 8.15, 122987. 8.16, 122988. 8.17, 122991, 8.18, 123177.

nids (Clark et al. 1964). Lower molariform teeth can be distinguished in the majority of cases by their relative size and anteroposterior curvature, with p4 the largest and straightest tooth (with no anteroposterior curvature), m1 the smallest and intermediate in curvature, and m2 intermediate in most dimensions and with the strongest curvature. In early stages of wear, all three teeth have small posterolophids isolated from the main body of the talonid by cement (Figure 8.3, 8.9, and 8.13). Clark et al. (1964) noted the presence of completely isolated posterolophids on p4 and m1 of a referred partial jaw of a young individual of *H. galbreathi* (UCMP 29626; originally tentatively identified by Hall 1930, figure 29, as *Sylvilagus*? sp.).

p4. An extensive sample of p4s illustrates how the occlusal pattern of this tooth varies with increasing wear, particularly in the shape of the lingual edge of the anterior projection of the talonid. In earliest wear stages (Figure 8.3), the anterior projection of the talonid has a nearly straight lingual edge merging smoothly into the main body of the talonid; the buccal edge is concave and crenulated. A relatively large posterolophid is completely isolated at the occlusal surface from the main body of the talonid, and is a short ovoid shape (appearing buccolingually wider than in *H. galbreathi* as figured in Hall (1930, figure 29). In slightly more worn teeth (Figure 8.4) the posterolophids are buccally connected to the main body, but are still separated lingually by cement. In specimens at slightly more advanced stages of wear (Figure 8.5-8.6) posterolophids have been obliterated, filling out the tooth in the posterolingual corner. In these specimens, the lingual wall of the anterior projection of the talonid has become slightly concave; the buccal edge of the anterior project of the talonid shows little change with wear and remains concave and is often crenulated. The most worn p4s (Figure 8.7-8.8) show a slight reduction of the posterolingual corner of the talonid; the posterior talonid wall is more curved, and the lingual wall of the anterior projection is more concave, such that the talonid is more buccolingually symmetrical than in earlier wear. Mean size of p4 of *H. niobrarensis* is: length, 1.90 mm; trigonid width, 2.15 mm; talonid width, 1.52 mm (Table 1B). The ratio of trigonid width to talonid width in p4 is on average ≈1.41. The tallest-crowned p4 has a crown height of 5.18 mm, resulting in a hypsodonty index of 2.96.

m1. The m1 of *H. niobrarensis* is more curved anteroposteriorly than p4 and has a shorter talonid, similar to that of the talonid of p4 in early stages of wear (before the posterolophid is fully incorporated into the main body). No completely unworn m1 is known but a slightly worn example (Figure 8.9) has a minor cement-filled posterolingual groove marking the point of attachment of a small posterolophid. The anterior projection of the talonid varies with wear (Figure 8.10-8.12) but perhaps less so than in p4, the lingual wall of the anterior projection of the talonid being nearly always straight or slightly convex. Mean size of Valentine Railway Quarries + Garner Bridge South combined sample of m1 of *H. niobrarensis* is: length, 1.69 mm; trigonid width, 2.01 mm; talonid width, 1.37 mm (Table 1B).

UNSM 45206 from Myers Farm, Nebraska, is an m1 of *Hesperolagomys* referred to *H. niobrarensis*. This specimen is in an extremely early stage of wear, as evidenced by a very small posterolophid completely isolated from the talonid and topographically well below the occlusal surface. Occlusal morphology closely resembles little worn m1s of *H. niobrarensis* (e.g., Figure 8.10). Measured dimensions of this specimen are well within the range of values of the Valentine Railway Quarries and Garner Bridge South combined sample.

m2. Second lower molars of *H. niobrarensis* can be distinguished from p4 and m1 by their strong anteroposterior curvature, and, in occlusal view, by nearly straight posterior talonid walls with squared posterobuccal corners. An m2 in an early stage of wear (Figure 8.13) has a very small, completely isolated posterolophid. Little variation in the talonid shape is notable through wear, although the most worn m2 (Figure 8.18) has a more concave lingual wall of the anterior projection than other specimens (Figure 8.13-8.17). Mean size of Valentine Railway Quarries and Garner Bridge South combined sample for m2 of *H. niobrarensis* is: length, 1.80 mm; trigonid width, 1.94 mm; talonid width, 1.42 mm (Table 1B).

m3. The lower third molar is present in only two dentaries (Figure 7.2, 7.3). This tooth is small and relatively simple, consisting of an oval column of enamel filled by dentine; its long axis is oriented buccolingually and the crown and root curve to mediad and posterior. Mean size of m3 of *H. niobrarensis* is: length, 0.61 mm; width, 1.05 mm (Table 1B).

REMARKS

The three lower molariform teeth (p4, m1, and m2) of *H. niobrarensis* show subtle but consistent differences in size and morphology that allow them to be distinguished from each other in most cases.

The p4 is larger in average length, trigonid width, and talonid width, and the talonid has a rounded posterior wall. The m1 is on average smaller in all three measured dimensions, and has an anteroposteriorly short talonid with an only slightly rounded posterior wall. The m2 is intermediate in length and trigonid width between p4 and m1, and has a somewhat wider talonid in which the posterior wall forms a nearly straight transverse surface and a squared posterobuccal corner. Lower molariform teeth also differ in the degree of curvature in the anteroposterior plane: p4 is relatively straight, m1 curves slightly posteriorly, and m2 is most strongly curved; however, in practice isolated specimens of m1 and m2 may be difficult to distinguish on the basis of anteroposterior curvature alone.

Although Voorhies (1990a) included *Hesperolagomys fluviatilis* in a list of mammalian species from the Valentine Railway Quarries, morphological and size differences reported here support the distinction of this *Hesperolagomys* sample as a new species related to but more derived than *H. fluviatilis*. Research to be reported elsewhere suggests that *H. niobrarensis* is likely more widespread in other Nebraska faunas of latest Barstovian age.

Hesperolagomys galbreathi
Clark, Dawson, and Wood 1964

Synonymies. *Hesperolagomys* cf. *H. galbreathi* Korth 1998: p. 336; figure 13C; *Russellagus* cf. *R. vonhofi* Korth 1998:p. 336-338.

Holotype. MCZ 17890, partial dentary with broken incisor, p3-m2, and alveolus of m3 (Clark et al. 1964) from Fish Lake Valley, Nevada (UCMP Fish Lake Valley 1 locality).

Distribution. Medial Clarendonian (Cl2) of Nevada (Clark et al. 1964), medial to late Clarendonian (Cl2-Cl3) of Nebraska (Korth 1998; this paper), and Clarendonian of northwestern Utah (Tedrow and Robison 1999).

Emended Diagnosis. Differs from other species of *Hesperolagomys* in possessing lower molariform teeth with relatively wide and buccolingually symmetrical talonids (p4 trigonid width/talonid width≈1.35), and anteroposteriorly short p3 with a prominent cement-filled anterolingual groove. Additionally distinct from *H. niobrarensis* in smaller size (cheek tooth lengths average 6-25% less).

Hypodigm

Original Hypodigm. (Revised from Clark et al. 1964) Type; MCZ 17891, partial dentary with p3-m2; MCZ 17892, partial dentary with talonid of p4 to m2; UCMP 29626, partial dentary with p4-m1; MCZ 17893-19894, upper incisors; MCZ 17895-17899, isolated upper cheek teeth; MCZ 7651-7652, isolated lower cheek teeth; UCMP 29833, dP4.

Previously Undescribed Topotypes. (All UCMP numbers) 149484, partial maxillary with P3-P4; 149485, upper anterior incisor; 149486, P3; 149487-149488, P4; 149489, M2; 149480, fragmentary dentary with p4-m2; 75269, lower incisor; 149481, p4; 149482, m1; 149483, m2.

Referred Specimens.

Nebraska (all UNSM numbers, by locality): Bluejay Quarry: 123346, m1. Poison Ivy Quarry: 123350, P4. Pratt Quarry: 101709, P3; 101776, P3. Tiensvold Ranch: 123311, partial maxillary with P3-M1; 123312, partial dentary with incisor, p3-p4; 123313, partial dentary with p3-m3.

Utah: IMNH 15871, M2; IMNH 15869, ?p4; IMNH 15870, m1; from Salt Lake Formation (Tedrow and Robison 1999).

DESCRIPTION

Skull

Two partial maxillaries with adult cheek teeth (Figure 9.1, 9.2) strongly resemble those described for *H. niobrarensis* in most characters. Both possess a distinct premolar foramen medial to P3-P4; in the topotypic maxillary (Figure 9.1) it is in line with the posterior wall of P3, whereas in the Nebraska specimen (Figure 9.2) it lies between P3 and P4.

Upper dentition

Anterior Incisor. A topotypic specimen (Fig. 9.3; Table 3) lacks the tip but is otherwise very similar in both size and shape to those described by Clark et al. (1964), with a longitudinal groove on the anterior surface displaced slightly medially of center. The tooth is slightly anteroposteriorly longer than those of *H. niobrarensis* (1.04 mm vs. 1.11 mm).

P2. P2 is unknown, but an alveolus for the tooth is preserved in UNSM 123311 and is consistent with the single (lingual) root and small size as observed for P2 of *H. niobrarensis.* The dimensions of the alveolus suggest that the tooth was approximately as long as but wider than that of *H. niobrarensis* (Figure 9.2; Table 3).

P3. Two P3s are known from the type locality, one in a maxilla (Figure 9.1) and one isolated (Figure

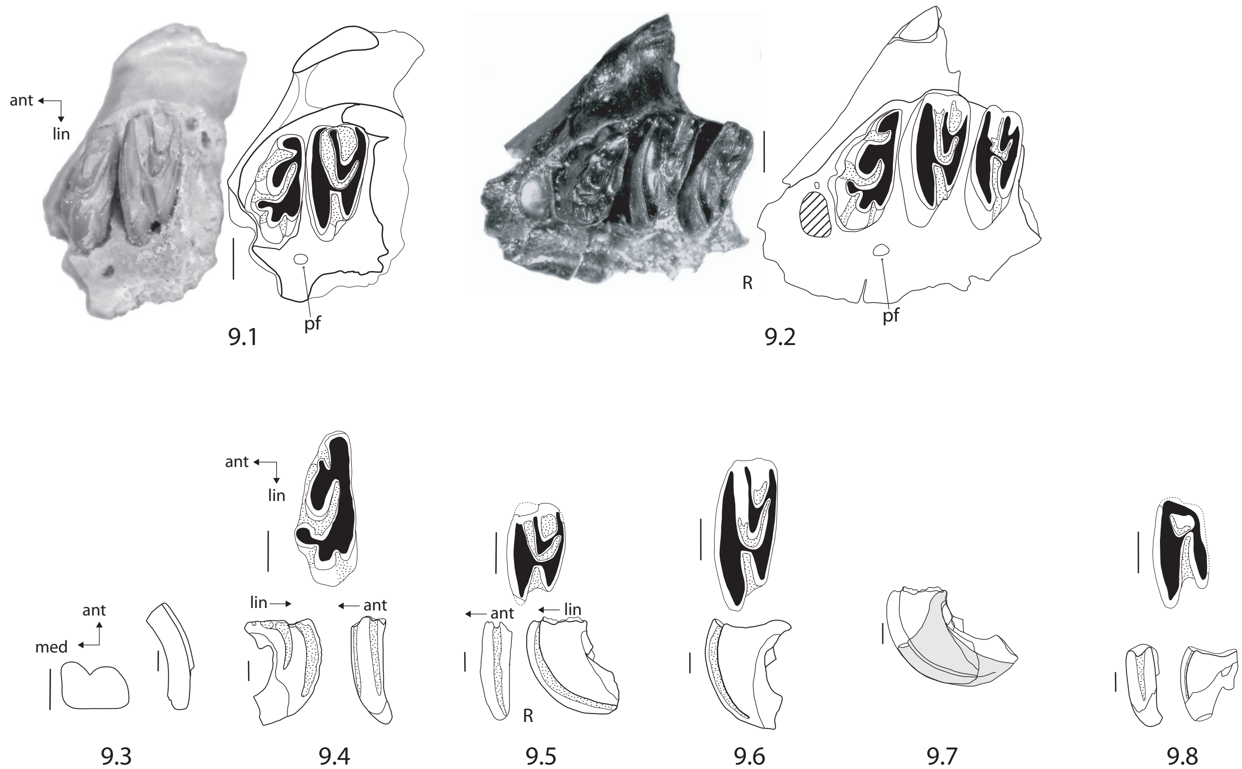

FIGURE 9. Maxillae and isolated upper teeth of *Hesperolagomys galbreathi*. Scale bar equals 1 mm. Standard orientations as in Figure 2. 'R' indicates line drawing/photo is reversed. Side views of individual teeth are shown at approximately half the scale of occlusal views. 9.1, UCMP 149484, Fish Lake Valley (topotypic) maxilla with P3-P4. 9.2, UNSM 123311, referred maxilla with P3-M1 from Tiensvold Ranch, Nebraska. 9.3, UCMP 149485, topotypic upper incisor in cross-sectional (left) and lateral (right) views. 9.4, UCMP 149486, topotypic P3 in occlusal (above), anterior (below and left), and lingual (below and right) views. 9.5, UCMP 149487, topotypic P4 in occlusal (above), lingual (below and left), and posterior (below and right) views. 9.6, UCMP 149488, topotypic P4 in occlusal (above) and posterior (below) views. 9.7, posterior view of reconstructed composite P4. 9.8, UCMP 149489, topotypic M2 in occlusal (above), anterior (below left), and lingual (below and right) views. Abbreviation: **pf**, premolar foramen.

9.4); morphology in both is consistent with specimens of *H. niobrarensis* at similar stages of wear. The P3 in UMPC 149484 (Figure 9.1) is lightly worn, appearing very similar to the *H. niobrarensis* specimen illustrated in Figure 4.2 in morphology and in stage of wear. The cement of the anterior stria is broad near the occlusal surface and is confluent with a shallower cement-filled buccal stria.

The isolated topotypic P3 is slightly more worn than P3 in the maxilla; occlusal features appear buccolingually stretched, and the precone curves more buccad in occlusal view. Cement in the anterior stria extends further buccad near the occlusal surface in this specimen than in the P3 in the maxilla. P3 in the referred Tiensvold Ranch locality maxilla (Figure 9.2) is nearly identical in size and morphology, and likely represents a similar stage of wear as the isolated topotype.

Two incomplete specimens from Pratt Quarry, UNSM 101709 (identified by Korth 1998, as P2 of *Hesperolagomys*) and 101776 (identified by Korth 1998, figure 13C, as P3 of *Russellagus*) are both identified instead as P3s of *Hesperolagomys galbreathi* based on morphology and size (Table 3) consistent with specimens described above. P2 of *H. galbreathi*, judging from the alveolus in the maxilla described above, is much smaller than either of the Pratt Quarry specimens; P3 of *Russellagus* is larger and with a distinct morphology (Bair 2006).

P4. Two P4s of different wear stages were included in the original hypodigm of *H. galbreathi*; previously unpublished specimens are consistent with most aspects of morphology with specimens of *H. niobrarensis* at similar stages of wear, and indistinguishable in size from published specimens of *H. galbreathi*. P4 of *H. galbreathi* appears to differ somewhat from P4 of *H. niobrarensis* in the nature

TABLE 3. *H. galbreathi* tooth dimensions (in mm).

Tooth position	Specimen number	Locality	a-p length	tr width
Ant I	UCMP 149485	Fish Lake Valley	1.04	1.60
P2 (alveolus)	UNSM 123311	Tiensvold Ranch	0.73	1.27
P3	UCMP 149484	Fish Lake Valley	1.29	1.51
	UCMP 149486	Fish Lake Valley	1.35	3.15
	UNSM 123311	Tiensvold Ranch	1.28	2.82
	UNSM 101709	Pratt Quarry	1.29	-
	UNSM 101776	Pratt Quarry	1.33	-
P4	UCMP 149484	Fish Lake Valley	1.51	3.00
	UCMP 149487	Fish Lake Valley	1.50	2.72
	UCMP 149488	Fish Lake Valley	1.46	3.74
	UNSM 123311	Tiensvold Ranch	1.30	3.39
	UNSM 123350	Poison Ivy Quarry	1.65	2.72
M1	UNSM 123311	Tiensvold Ranch	1.21	3.11
M2	UCMP 149489	Fish Lake Valley	1.24	-
i	UCMP 75269	Fish Lake Valley	1.32	1.40
	UNSM 123312	Tiensvold Ranch	1.27	1.39
p3	UNSM 123312	Tiensvold Ranch	0.79	1.32
	UNSM 123313	Tiensvold Ranch	1.05	1.35
m3	UNSM 123313	Tiensvold Ranch	0.65	0.89

Tooth position	Specimen number	Locality	a-p length	tri width	tal width
p4	UCMP 149480	Fish Lake Valley	1.92	2.03	1.49
	UCMP 149481	Fish Lake Valley	1.77	2.00	1.51
	UNSM 123312	Tiensvold Ranch	1.78	1.99	1.44
	UNSM 123313	Tiensvold Ranch	1.73	2.02	1.47
m1	UCMP 149480	Fish Lake Valley	1.54	1.86	1.31
	UCMP 149482	Fish Lake Valley	1.58	1.83	1.33
	UNSM 123313	Tiensvold Ranch	1.52	1.89	1.27
	UNSM 123346	Bluejay Quarry	1.60	1.79	1.24
m2	UCMP 149483	Fish Lake Valley	1.65	1.91	1.50
	UNSM 149480	Tiensvold Ranch	1.74	1.88	1.48
	UNSM 149483	Tiensvold Ranch	1.61	1.68	1.41
	UNSM 123313	Tiensvold Ranch	1.75	1.87	1.40

of the lingual hypostria. In all known specimens of *H. galbreathi*, the lingual hypostria nearly contacts the lingual wall of the crescentic valley, terminates buccally in a broad (anteroposteriorly long) squared-off groove, and is oriented nearly bucco-lingually. In contrast, the lingual hypostria in P4 of *H. niobrarensis* is separated from the crescentic valley by a wider bridge of dentine, terminates in a slightly rounded point buccally, and is oriented more posteriorly (compare Figures 9.1, 9.2, 9.5, and 9.6 with 5.2-5.5). As evidenced by specimens at various stages of wear, this difference remains present throughout the stages of wear known for both taxa.

The least worn unpublished specimen, with crown base incompletely formed (Figure 9.5), is morphologically nearly identical to MCZ 17896 as described and figured by Clark et al. (1964, figure 3C, D). The enamel border to the buccal valley is more prominent than that seen in P4 in the maxilla (Figure 9.1), such that cement of the buccal valley is separate from cement in the anterobuccal portion of the crescentic valley. A composite 'complete' P4 reconstructed from two topotypes (Figure 9.7), although not fully representing the unworn crown, gives an estimated crown height of 9.61 mm and an estimated minimum hypsodonty index of 6.49.

UNSM 123350, from Poison Ivy Quarry, Nebraska, is a P4 referred to *H. galbreathi.* This specimen is nearly unworn, with an occlusal pattern very similar to that in Figure 4.2 (*H. niobrarensis*); it is somewhat larger in size than other known P4s of *H. galbreathi* (Table 3).

M1. In size and shape, M1 in UNSM 123311 (Figure 9.2, Table 3) closely resembles MCZ 17898, described as a probable M1 by Clark et al. (1964, figure 3A, B), as well as M1s of *H. niobrarensis*, confirming its identity as such. M1 length in the referred specimen is 1.21 mm, less than for previously known values of P4 (Table 3). Clark et al. (1964, table 2) report the length of MCZ 17898 as 1.3 mm, overlapping with length of P4 in UNSM 123311 but less than the value reported for P4s in the original hypodigm (length of 1.5 mm for MCZ 17895 and 17896; Clark et al. 1964, table 2).

As for M1s of *H. niobrarensis*, M1s of *H. galbreathi* can consistently be distinguished from P4s by: (1) greater occlusal extent of the lingual hypostria (covering at least one third of the occlusal surface and nearly meeting the crescentic valley); (2) anteroloph and posteroloph subequal in width; (3) buccal edge of crown angled slightly posteriorly (posterobuccal cusp shifted lingually in comparison with anterobuccal cusp); and (4) slight curvature of the tooth in the anteroposterior plane, concave to posterior.

M2. UCMP 149489 (Figure 9.8) is consistent in morphology with M2s described for *H. niobrarensis* and is here identified as an M2. Although the crown is damaged on the posterobuccal edge, the anterobuccal root is preserved and allows estimation of occlusal width. M2 length is 1.24 mm, less than that of P4 and close to that of M1 (Table 3).

A more complete M2 of *H. galbreathi* is represented by IMHN 15971, an isolated tooth from the Clarendonian of northwestern Utah, tentatively identified as an M1 or M2 of *Hesperolagomys* cf. *H. galbreathi* by Tedrow and Robison (1999). This specimen is very similar in shape and size to UCMP 149489, possessing a "deep and persistent internal hypostria which nearly reaches the crescentic valley" (Tedrow and Robison 1999, figure 3d-e, pg. 483) and a reduced posterobuccal cusp; length is 1.31 mm (Tedrow and Robison 1999, table 2).

Deciduous Upper Premolar. A single upper deciduous P4 is known, UCMP 29633 (see description in Clark et al. 1964; Wood 1936; and Hall 1930, figure 1). In occlusal view dP4 shares features with permanent upper dentition of *Hesperolagomys*, including a prominent 'J'-shaped crescentic valley, lingual hypostria extending buccolingually across approximately one fourth of the occlusal surface and nearly meeting the crescentic valley, deep buccal valley, and poorly developed buccal cusps. However, it is very small and has a much shorter crown compared with permanent upper teeth.

Dentary

The holotypic jaw was fully described and illustrated by Clark et al. (1964). Three previously undescribed specimens, one from the type locality and two from the Tiensvold Ranch locality, closely resemble the holotype in size and require only brief additional comments regarding the disposition and relative size of major mental foramina and the posterior extent of the incisor.

The preserved portion of a topotypic jaw fragment (UCMP 149480: Figure 10.1) contains a small circular depression with a single mental foramen ventral to the trigonid of m1 and close to the ventral margin of the jaw, slightly more anteriorly placed than the depression with two small foramina in the type specimen (below m1-m2) but interpreted as a corresponding structure. The incisor is missing but the capsule indicates that it extended posteriorly to beneath m1, as in the type specimen. An additional dentary fragment (UCMP 149481: Figure 10.2) possess a larger foramen in line with the center of p4, also slightly more anteriad than the corresponding large foramen in the type specimen, which lies beneath p3.

In both specimens from the Tiensvold Ranch locality (Figure 11.1, 11.2), the roots of p3-m1 are displaced laterally from the incisor, and the incisor capsule makes a prominent bulge on the medial side of the jaw, as in the type specimen. The more complete specimen (UNSM 122313: Figure 11.1)

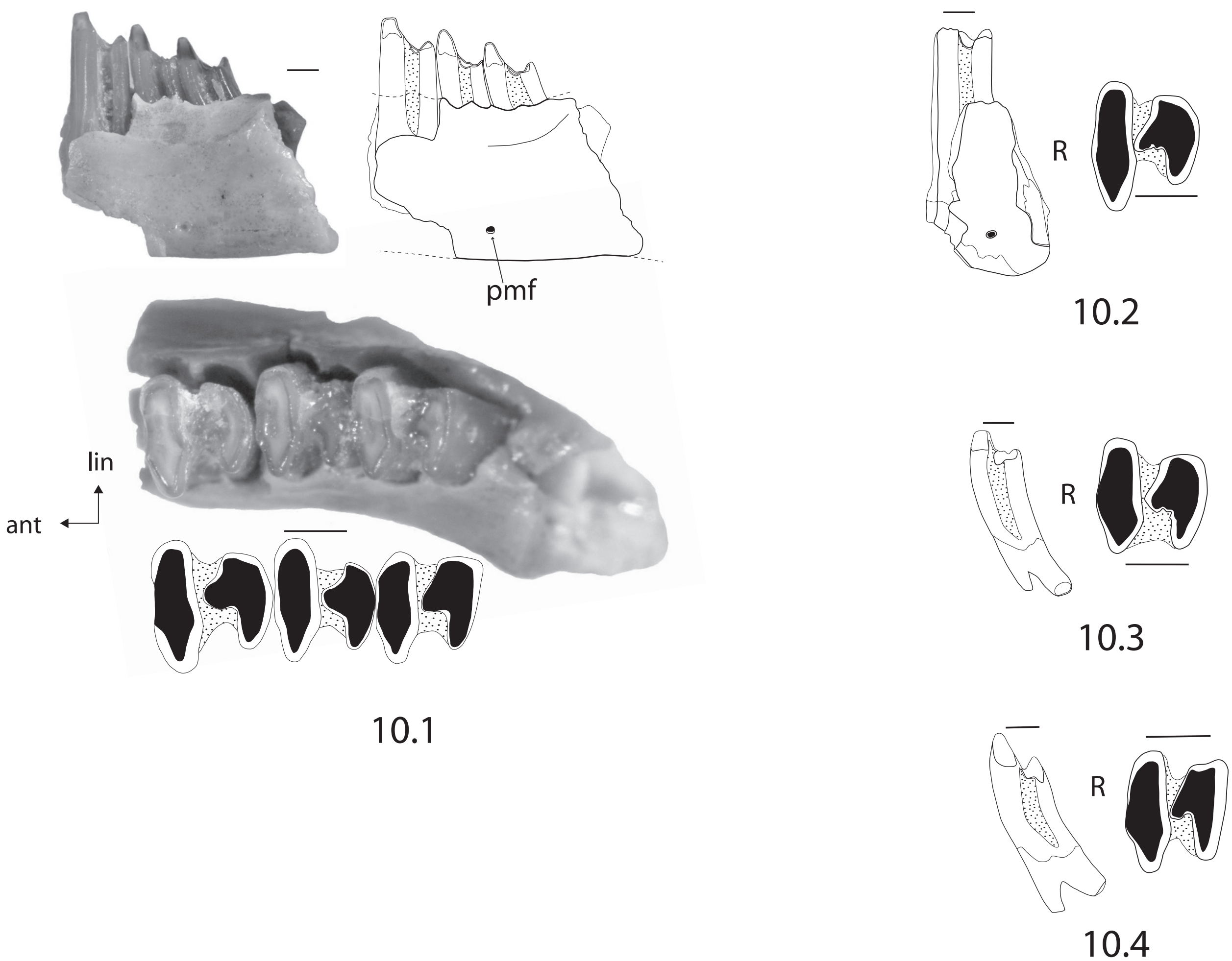

FIGURE 10. Topotypic dentary fragments and lower teeth of *H. galbreathi* from Fish Lake Valley. Standard orientations as in Figure 2; scale bar equals 1 mm. 'R' indicates line drawing is reversed. 10.1, UCMP 149480, partial dentary with p4-m2 in lateral view (above), occlusal view (below). 10.2, UCMP 149481, dentary fragment with p4 in lateral (right) and occlusal view of p4 (left). 10.3, UCMP 149482, m1 in buccal view (left), occlusal view (right). 10.4, UCMP 149483, m2 in buccal view (left), occlusal view (right). Abbreviation: **pmf**, posterior mental foramen.

has all three major mental foramina preserved: the largest is the middle foramen located beneath the talonid of p3, a smaller foramen is in line with the talonid of m1 and closer to the ventral border of the dentary, and the smallest is anterior to p3 and more dorsally positioned than the posterior foramina. The medial wall of the incisor capsule is broken to reveal the cavity, which extends posteriorly to beneath the talonid of m1. Except for the slightly more anterior placement and single opening of the most posterior mental foramen, this specimen matches the holotype. UNSM 122312 (Figure 11.2) is less complete and preserves only the anterior-most foramen located anterior to p3; the incisor is exposed and extends posteriorly to beneath the position of the talonid of m1.

Lower Dentition

Lower Incisor. A lower left incisor lacks both ends, but is similar in cross-sectional morphology and dimensions to type material (Table 3; Clark et al. 1964, table 2) and to lower incisors described for *H. niobrarensis*. The incisor in UNSM 122312 (Figure 11.2, 11.3) is better preserved and is nearly identical to UCMP 75269 in size and cross-sectional shape.

p3. The p3s in the Tiensvold Ranch jaws (Figure 11.1, 11.2) resemble that in the type specimen (Clark et al. 1964, figure 4B) in overall shape and size (Table 3), and in possessing a deep, cement-filled buccal fold separating the trigonid and talonid, and a shallower, wide cement-filled anterolingual

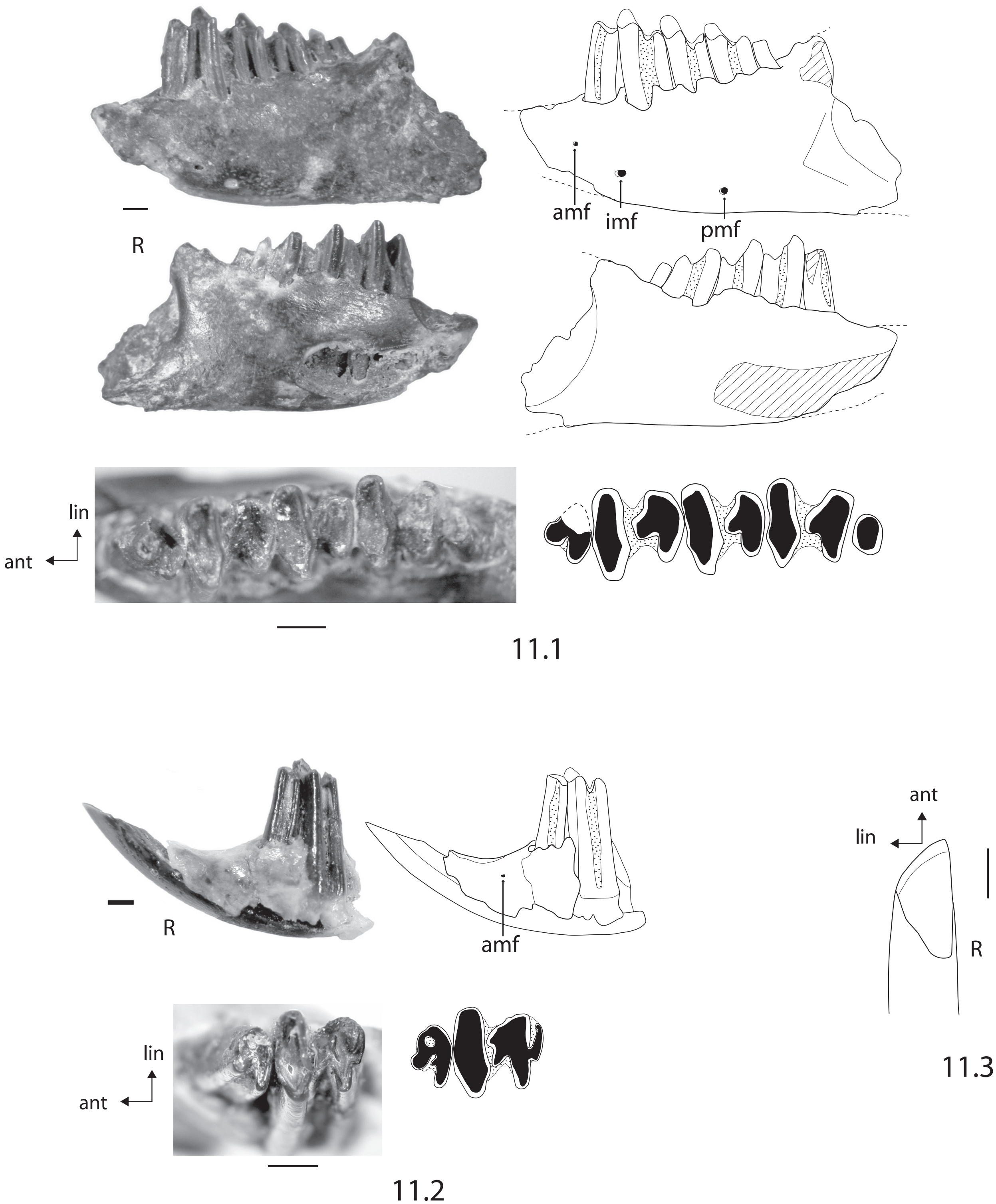

FIGURE 11. Referred dentaries of *H. galbreathi* from Tiensvold Ranch, Nebraska. Standard orientations as in Figure 2; scale bar equals 1 mm. 11.1, UNSM 123313, dentary with p3-m2 in lateral (above), medial (middle), and occlusal (below) views. 11.2, UNSM 123312, partial dentary with i-p4 in lateral (above) and occlusal (below) views. 11.3. UNSM 123312, dorsal view of incisor facet.

'groove'. Both teeth taper markedly from the crown apex to base. The less worn specimen (Figure 11.2) additionally has a small cement-filled enamel lake at the connection between trigonid and talonid, a feature unique to this specimen, in which the trigonid is also anteroposteriorly shorter and more buccally directed than in the type specimen. The p3 in UNSM 123313 lacks the buccal portion of the crown at the occlusal surface and is slightly shorter-crowned (older) than 123312, and has neither the enamel islet nor the crenulation of the anterior wall of the talonid present in the latter. The trigonid is slightly more anteriorly directed than in 123312, resembling the type specimen in this respect. The p3 of *H. galbreathi* does not expand anteriorly towards crown base as much as in p3 of *H. niobrarensis*, so maximum length is less in *H. galbreathi*.

p4-m2. Teeth in the topotypic dentary fragment, in referred dentaries, and isolated lower molariform teeth are like those of the type specimen and in specimens described for *H. niobrarensis* in having trigonids transversely wider and anteroposteriorly shorter than talonids, and in the buccolingually narrow anterior projections of talonids (Clark et al. 1964). The lower molariform teeth can be distinguished on the basis of relative size and anteroposterior curvature, as noted for *H. niobrarensis*. In contrast to lower molariform teeth of *H. niobrarensis*, those of *H. galbreathi* have relatively wide and buccolingually more symmetrical talonids. Some wear-related variation in the shape of the anterior projection of the talonid is apparent between the type specimen, topotypes, and referred material.

Lower cheek teeth of the type specimen have buccolingually narrow and nearly symmetrical anterior projections of the talonid, with the main body of the talonid connected to the anterior projection lingually and buccally by concave enamel surfaces (Clark et al. 1964, figure 4). Clark et al. (1964) also referred a partial jaw to *Hesperolagomys* (UCMP 29626; originally tentatively identified by Hall 1930, figure 29, as *Sylvilagus*? sp.) and identified it as a young individual as evidenced by completely isolated posterolophids on p4 and m1. This specimen has anterior projections of the talonids of p4 and m1 that are more buccolingually asymmetrical than in the more mature type specimen and have straight anterolingual talonid walls. In the topotypic dentary (UCMP 149480: Figure 10.1), interpreted here as intermediate between the above two specimens in ontogenetic age, the m1 talonid is buccolingually narrow and nearly symmetrical with concave enamel walls on both lingual and buccal sides of the anterior projection. In contrast, the buccal enamel wall connecting the projection to the main body of the talonid in m2 is straight, while in p4 the anterobuccal wall is convex and the anterolingual wall is concave; in both teeth the talonid is asymmetrical, with an expanded anterobuccal corner in comparison with the anterolingual corner. Lower cheek teeth of UCMP 149481 (Figure 10.2) and UNSM 123313 (Figure 11.1), and isolated lower cheek teeth UCMP 149482 (Figure 10.3) and 149483 (Figure 10.4) have wider, asymmetrical anterior projections of the talonid and more closely resemble p4 and m2 of UCMP 149480 than the narrower, symmetrical anterior projection of m1 of that specimen or the lower molariform teeth of the type specimen.

The p4 in UNSM 123312 (Figure 11.2) from the Tiensvold Ranch locality is in an early stage of wear as evidenced by a posterolophid in the process of merging with the main body of the talonid and has a distinctly different talonid morphology. The lingual side of the posterolophid is still separated by cement, but the buccal side is marked only by a minor enamel groove. Rather than a coherent single projection, the anterior portion of the talonid is composed of two rounded anteriorly-directed points separated by a small central groove; the anterobuccal enamel wall is sharply convex and attaches near the center of the talonid, whereas the anterolingual wall is nearly straight and aligned with the main body of the talonid. UNSM 123346 from Bluejay Quarry (Nebraska) is an m1 referred to *H. galbreathi*; this specimen is slightly smaller in measured dimensions than other m1s (Table 3), but has postmortem enamel loss, which may account for the discrepancy since it closely resembles topotypic specimens in occlusal morphology (Figure 10.1 and 10.4).

m3. The m3 is present only in UNSM 123313 (Figure 11.1; Table 3) and does not differ notably from that of *H. niobrarensis* in size or morphology.

REMARKS

Specimens referred to *Hesperolagomys* cf. *H. galbreathi* from the Black Butte Fauna, Oregon (Shotwell, 1970), do not belong to this taxon; they are referable to *Russellagus vonhofi* and will be discussed in a future publication on *Russellagus*. Other referred specimens of Clarendonian age from Utah and Nebraska are consistent with *H. galbreathi*.

HESPEROLAGOMYS FLUVIATILIS Storer, 1970

Synonymies. *Russellagus vonhofi* Storer 1970, 1975 (in part): p. 116-121; figure 83M, N; 85B; *Hesperolagomys fluviatilis* Voorhies 1990b (in part): p. A79, 323-324, 400, 487; *Russellagus vonhofi* Voorhies 1990b (in part) p. A79-80, 324, 487.

Holotype. ROM 7320, left m1, from Kleinfelder Farm locality, Wood Mountain Formation, south-central Saskatchewan, early late Barstovian (Ba2a) (Storer 1970, 1975).

Emended Diagnosis. Differs from other species of *Hesperolagomys* in: (1) p3 relatively anteroposteriorly long and lacking a cement-filled anterolingual groove; (2) lower molariform teeth with relatively narrow talonids (p4 trigonid width/talonid width≈1.50); (3) smaller than both *H. niobrarensis* (cheek tooth length 10-20% less) and *H. galbreathi* (cheek tooth length 1-10% less) in most measured dimensions. Also differs from *H. galbreathi* in possessing more asymmetric talonids on lower molariform teeth.

Geologic age and distribution. Early late Barstovian (Ba2a) of Saskatchewan (Storer 1970, 1975); medial late Barstovian (Ba2b) of Nebraska (Voorhies 1990a, 1990b; this paper).

Hypodigm

Original Hypodigm (revised from Storer 1975). Type; (all ROM numbers) 7385, 7386, P3s; 7342, 7399, 7412, P4s; 7345, 7352, M1; 7343, 7346, 7348, 7350-7351, 7353, 7354, M2s; 7302, 7304, 7305, 7306, p3s; 7314, 7319, 7321, 7322, 7324, 7338, 7416, p4s; 7313, 7315, 7318, 7320, 7321, 7326, 7330, 7331, 7336, 7337, 7418, m1s; 7310, 7311, 7312, 7315, 7317, 7325, 7327, 7333, 7335, m2s; 7323, 7328, lower molariform teeth; 7303, 7329, trigonids of lower molariform teeth; 7340, dP4.

Specimens Formerly Included in *Russellagus vonhofi* Hypodigm. ROM 7385, 7386, P3s; 7399, P4; 7349, M2;

Previously Undescribed Topotypes. (ROM numbers): 52635, P4**;** 52637, M1; 52636, M2; 52642, partial dentary with p4-m2 and alveolus for m3; 52638, p4**;** 52641, m1; 52639, m2. (UNSM numbers): 123357, m1; 123355, m2.

Referred Specimens from Nebraska (all UNSM numbers, by locality).

Achilles Quarry: 83031, P4; 83029, m1; 83032, m2.

Egelhoff Quarry: 90001, M1; 90000, m2.

Immense Journey: 123328, P4; 123331 and 123332, M2.

Lost Duckling Quarry: 83141, m2.

Miller Creek: 123314, fragmentary maxillary with P4 and M1.

Norden Bridge Quarry: 83738, P3.

DESCRIPTION

Skull

Cranial material for this taxon is fragmentary and consistent with characters described for other taxa.

Upper Dentition

Several upper cheek teeth in the original descriptions of *H. fluviatilis* and *Russellagus vonhofi* of Storer (1975) are here reinterpreted in light of new information on upper cheek tooth morphology of *H. niobrarensis* and *H. galbreathi*, as described above. Upper cheek teeth of *H. fluviatilis* closely resemble those of *H. niobrarensis* in morphology but are slightly smaller (Table 4).

P3. Two teeth originally described as P2s of *Russellagus* (ROM 7385 and 7386) by Storer (1975) are here identified as P3s of *H. fluviatilis* on the basis of a nearly perfect match in occlusal morphology with P3 of *H. galbreathi* and *H. niobrarensis* (compare P3s in Figures 4, 9.1, 9.2, 9.4, and 12.1 in this paper with figure 83F of Storer 1975). ROM 7386 (Figure 12.1) represents a moderately young individual, while ROM 7385 (Storer 1975, figure 83F) is an older individual with a crown approximately half as tall, and with crown elements buccolingually 'stretched' compared to the younger tooth. Mean P3 length for *H. fluviatilis* is 1.14 mm; mean width is 2.78 mm (Table 4A).

UNSM 83738 from Norden Bridge Quarry, initially referred to *R. vonhofi* by Voorhies (1990b) on the basis of its close resemblance to specimens considered to be *Russellagus* P2s by Storer (1975), is here identified as a P3 of *Hesperolagomys*; this specimen was not available for measurement at the time of this study but is referred to *H. fluviatilis* as the size of dimensions of other *Hesperolagomys* specimens support the presence of this taxon at Norden Bridge Quarry (see below).

P4. The numerous specimens now available for *H. galbreathi* and *H. niobrarensis* allow upper cheek teeth of *H. fluviatilis* to be unambiguously distinguished. P4 of *H. fluviatilis* is more similar in morphology to that of *H. niobrarensis* in the rounded point of the buccal edge of the lingual hypostria,

TABLE 4. Summary statistics of tooth dimensions of *H. fluviatilis* from Kleinfelder Farm locality. A, upper teeth; B, lower teeth. Abbreviations: $\bar{x}$, mean (for samples N=1, $\bar{x}$ refers to single measurement value); SD, standard deviation; N, number of specimens; CV, coefficient of variation; MIN, minimum value; MAX, maximum value.

4A.

	P3		P4		M1		M2		dP4	
	L	W	L	W	L	W	L	W	L	W
$\bar{x}$	1.14	2.78	1.44	3.31	1.28	2.23	1.21	2.20	1.22	1.85
SD	0.08	0.23	0.09	0.54	0.10	0.14	0.06	0.23	-	-
MIN	1.08	2.57	1.30	2.51	1.21	2.13	1.12	1.89	-	-
MAX	1.19	2.98	1.50	3.74	1.35	2.33	1.28	2.54	-	-
N	2	2	4	4	2	2	6	6	1	1
CV	6.9	10.4	6.6	16.5	7.5	6.1	5.3	10.6	-	-

4B.

	p3		p4			m1			m2		
	L	W	L	tri W	tal W	L	tri W	tal W	L	tri W	tal W
$\bar{x}$	1.48	1.37	1.62	1.84	1.24	1.66	1.84	1.26	1.56	1.66	1.19
SD	0.08	0.25	0.05	0.13	0.04	0.13	0.15	0.11	0.13	0.14	0.09
MIN	1.39	1.12	1.53	1.68	1.19	1.50	1.59	1.10	1.35	1.39	1.08
MAX	1.53	1.61	1.67	2.02	1.32	1.85	2.04	1.44	1.80	1.86	1.37
N	3	3	8	8	7	11	11	11	11	11	10
CV	5.1	17.9	3.1	7.0	3.3	8.1	9.3	10.0	8.6	7.7	7.9

contrasting with the squared-off edge of the feature in *H. galbreathi* (Figure 12.2 through 12.5). Changes in occlusal morphology through wear differ little from that documented for the tooth in the other species. Two teeth identified as probable P4s and figured as paratypes of *H. fluviatilis* by Storer (1975, figures 81L-M and 82C-E) are here identified as M1s as discussed below. ROM 7351 and 7354, also listed as P4s by Storer (1975) are identified here as M2s. Three upper cheek teeth (ROM 7399, 7342, 7412), determined here to be P4s of *H. fluviatilis*, were assigned to *Russellagus vonhofi* by Storer (1975). These, along with four newly described specimens, demonstrate occlusal changes associated with wear in this tooth.

A moderate wear stage is shown by ROM 7399 with nearly complete crown base (Storer 1975, figures. 83M-N and 85B; Figure 12.2, this paper), in which the cement-filled posterobuccal and crescentic valleys are reduced in size, and the lingual hypostria has closed basally. A slightly older individual is represented by ROM 7412 (Figure 12.3), in which crown formation is complete, and the crown is approximately half as tall as in ROM 7399; the occlusal pattern appears stretched buccolingually and cement has nearly been obliterated from the posterobuccal valley. ROM 52635 (Figure 12.4) is slightly more worn but has a similar occlusal pattern. The oldest available P4 is ROM 7342 (Figure 12.5) in which buccolingual 'stretching' has proceeded still further, and the crescentic valley has become separated into two portions still containing cement: an anterobuccal portion approximately the same size as the buccal valley, and a lingual 'v'-shaped portion. Mean values for dimensions of P4 of *H. fluviatilis* from Kleinfelder Farm: length, 1.44 mm; width, 3.31 mm (Table 4A).

Three P4s from additional Ba2b Nebraska localities are referred to *H. fluviatilis* on the basis of their very similar morphology and occlusal dimensions. UNSM 83031 from Achilles Quarry appears to represent a very early stage of wear of P4 (comparable with Figure 12.2), with only a narrow sliver of dentine exposed in the central crescent, prominent cement in the buccal valleys, and an incompletely formed crown base. UNSM 123314 from Miller Creek and UNSM 123328 from Immense Journey Quarry are slightly more worn. Occlusal dimensions of these referred specimens (Table 5)

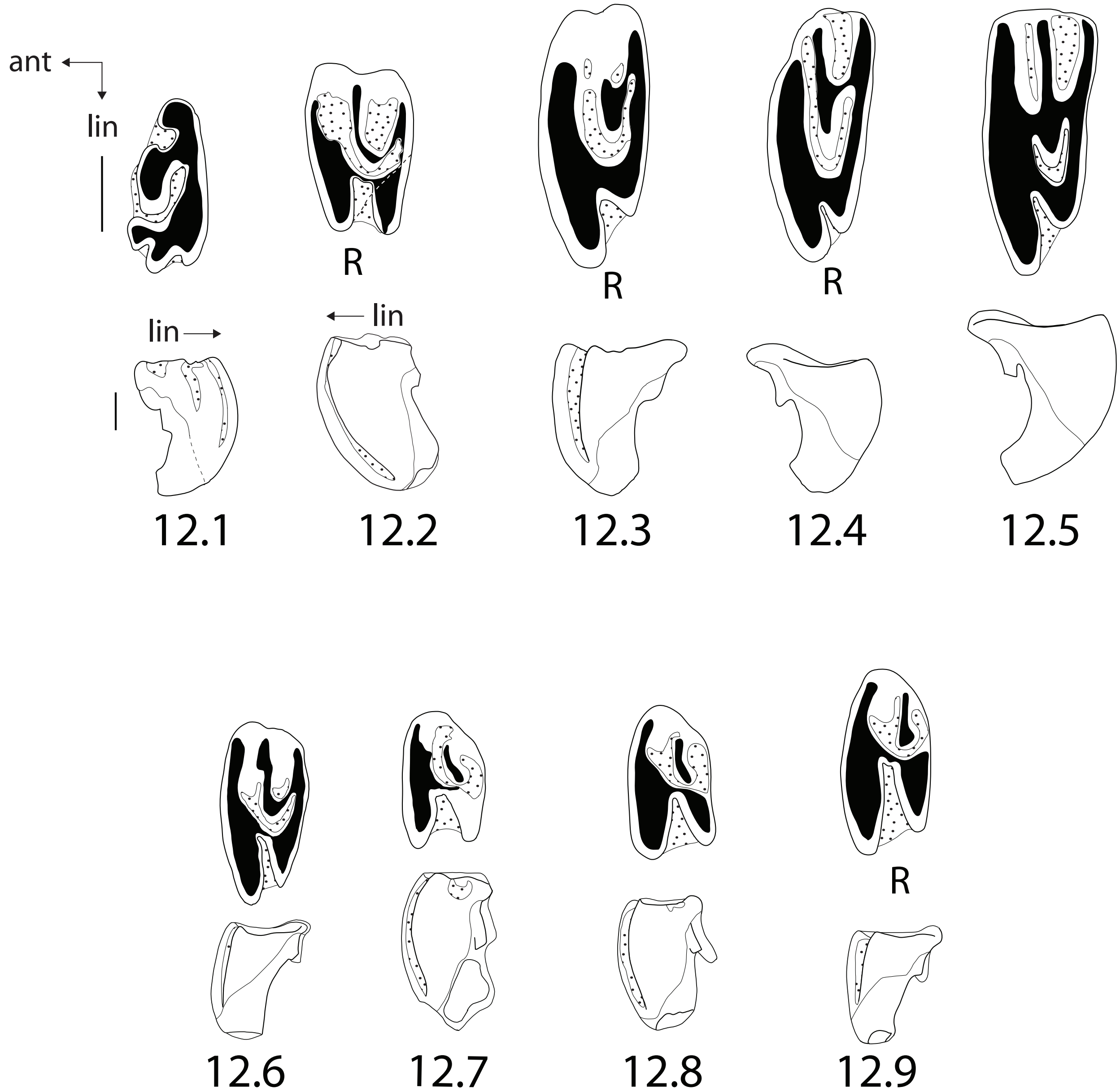

FIGURE 12. Topotypic upper cheek teeth of *H. fluviatilis* from Kleinfelder Farm. Standard orientations as in Figure 2. Each lettered pair shows occlusal view (above) and anterior view (below) unless otherwise indicated. 'R' indicates line drawing is reversed. Scale bars (equal to 1 mm) for occlusal and side views next to 12.1 also indicate scale for all other specimens. 12.1, ROM 7386, P3. 12.2, UNSM 83031, P4. 12.3, ROM 7412, P4; lower drawing is posterior view. 12.4, ROM 52635, P4; lower drawing is posterior view. 12.5, ROM 7342, P4. 12.6, ROM 52637, M1. 12.7, ROM 7346, M2. 12.8, ROM 52636. 12.9, ROM 7353, M2.

are within the range for P4s in the hypodigm of *H. fluviatilis*.

M1. Three isolated teeth closely resemble the morphology of M1 described for *H. niobrarensis* and *H. galbreathi* and are identified as M1s of *H. fluviatilis*. One of these, ROM 7352, was identified tentatively by Storer (1975, figures 81M and 82E) as P4 of *H. fluviatilis*. In this specimen, the lingual hypostria covers nearly half of the occlusal surface, much greater than that observed for P4, and only a thin portion of dentine separates the crescentic valley from the lingual hypostria. ROM 52637 (Figure 12.6) is buccolingually wider with a shorter crown and represents a slightly older wear stage. Mean values for dimensions of M1 of *H. fluviatilis* from Kleinfelder Farm are: length, 1.28 mm; width, 2.23 mm (Table 4A).

TABLE 5. Cheek tooth dimensions (in mm) of *H. fluviatilis* specimens from Nebraska localities. All UNSM numbers.

Tooth position	Specimen number	Locality	a-p length	tr width
P4	83031	Achilles Quarry	1.33	2.06
	123328	Immense Journey	1.43	2.90
	123314	Miller Creek	1.40	2.52
M1	90001	Egelhoff Quarry	1.02	2.05
	123314	Miller Creek	1.28	2.72
M2	123331	Immense Journey	1.29	3.03
	123332	Immense Journey	1.28	2.34
p3	83737	Norden Bridge Quarry	1.50	1.67

Tooth position	Specimen number	Locality	a-p length	tri width	tal width
m1	83029	Achilles Quarry	1.29	1.40	0.92
m2	83032	Achilles Quarry	1.55	1.78	1.20
	83141	Lost Duckling Quarry	1.56	1.72	1.14
	90000	Egelhoff Quarry	1.54	1.72	1.24

An M1 (in UNSM 123314) from Miller Creek, Nebraska, supports referral of this specimen (a maxilla fragment) to *H. fluviatilis.* The M1 is lacking the buccal cusps and the buccal portion of the crescentic valley due to minor damage at the occlusal surface, but is similar to other M1 specimens in size (compare Tables 4 and 5) and lingual occlusal features, closely resembling the specimen in Figure 12.6 in these features and in stage of wear.

An upper cheek tooth from Egelhoff Quarry (Nebraska), UNSM 90001, is tentatively referred to *H. fluviatilis* as an M1. This specimen shows a strong resemblance to other M1s (such as Figure 12.6) in occlusal morphology but it is anomalously small in occlusal dimensions (Table 5); some damage to the enamel at the anterolingual corner of the tooth is evident, and may account for the size difference.

M2. M2s of *H. fluviatilis* fall within the range of morphological variation expressed in the Valentine Railway Quarries *H. niobrarensis* sample (Figure 6.6-6.8); they differ significantly only in size, having a shorter length (Table 4). ROM 7346 (Figure 12.7) was originally tentatively identified by Storer (1975, figure 81P) as a M1 or M2, and is more confidently identified here as a little-worn M2. In this specimen, the posterior limb of the crescentic valley terminates in a cingulum, offset topographically below the rest of the crown by approximately 0.5 mm. The lingual hypostria is anteroposteriorly long and extends across between one half and one third the buccolingual extent of the occlusal surface. ROM 52636 (Figure 12.8) is slightly more worn than 7346, still retaining the posterior cingulum but the lingual hypostria extends over approximately one half the width of the occlusal surface and is anteroposteriorly narrower. ROM 7348 (Storer 1975, figure 81K, M) is very similar to 52636 but has less enamel exposed in the posterior part of the crescentic valley. ROM 7353 (Figure 12.9) and ROM 7343 (not figured) are next oldest in the wear series, with the cingulum no longer present (the posterior limb of the crescentic valley now is narrowly separated from the posterior enamel wall of the tooth and topographically at the same level). The lingual hypostria dominates the occlusal surface, extending more than one half the width of the tooth. Mean values of dimensions for M2 of *H. fluviatilis* from Kleinfelder Farm are: length, 1.21 mm; width, 2.20 mm (Table 4A).

Two M2s from Immense Journey Quarry (Nebraska), UNSM 123331 and 123332, are referred to *H. fluviatilis*. UNSM 123331 is more worn than other *H. fluviatilis* specimens, most closely resembling a worn *H. niobrarensis* specimen (Figure 6.8) in occlusal morphology. UNSM 123332 is lacking the buccal-most portion, but is very similar to the *H. fluviatilis* specimen in Figure 12.9.

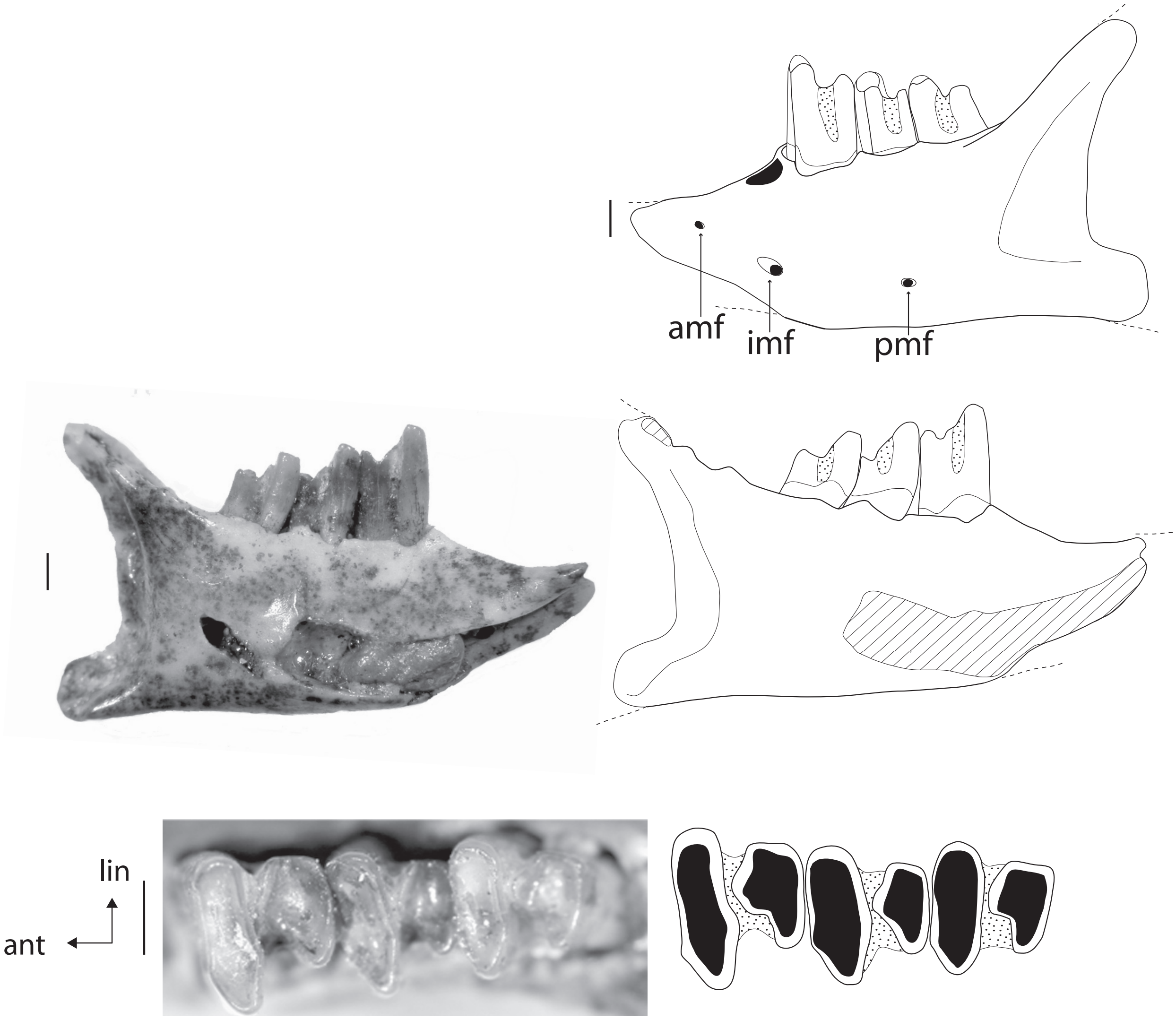

FIGURE 13. Topotypic dentary of *H. fluviatilis* from Kleinfelder Farm, ROM 52642. Lateral view, above. Medial view, middle. Occlusal view of cheek teeth, below. Scale bar equals 1 mm; orientation as in Figure 2. Abbreviations: **amf**, anterior mental foramen; **imf**, intermediate mental foramen; **pmf**, posterior mental foramen.

Deciduous Upper Premolar. I agree with Storer's interpretation of ROM 7340 as a dP4 of *H. fluviatilis* (1975, figure 81H, I). The tooth is much smaller than P4 (Table 3) and has a very short crown with the lingual edge broadening dorsolingually. The occlusal pattern is nearly identical to that of UCMP 29633 (dP4 of *H. galbreathi*, Hall, 1930, figure 1). Except for its short crown and small size it could be confused with a P4 in very early wear stages (e.g., UNSM 83031, Figure 12.2).

Dentary

A previously undescribed lower jaw of *H. fluviatilis* from the type locality (ROM 52642: Figure 13) has similar proportions to other known dentaries but is quite small as compared to those of *H. niobrarensis* and slightly smaller than *H. galbreathi* (Table 2). Two large mental foramina nearly equal in size are present, one beneath p3 and the other beneath m1. A smaller foramen anterior to p3 is poorly preserved but is positioned similarly to that in specimens of *H. galbreathi*. The incisor capsule extends posteriorly to beneath m1. The ventral border of the horizontal ramus is fairly straight between the level of the ascending ramus and p4.

Lower Dentition

p3. Three p3s from Kleinfelder Farm (Figure 14.1-14.3) are very similar in shape to those of *H. galbreathi* but lack the characteristic anterolingual

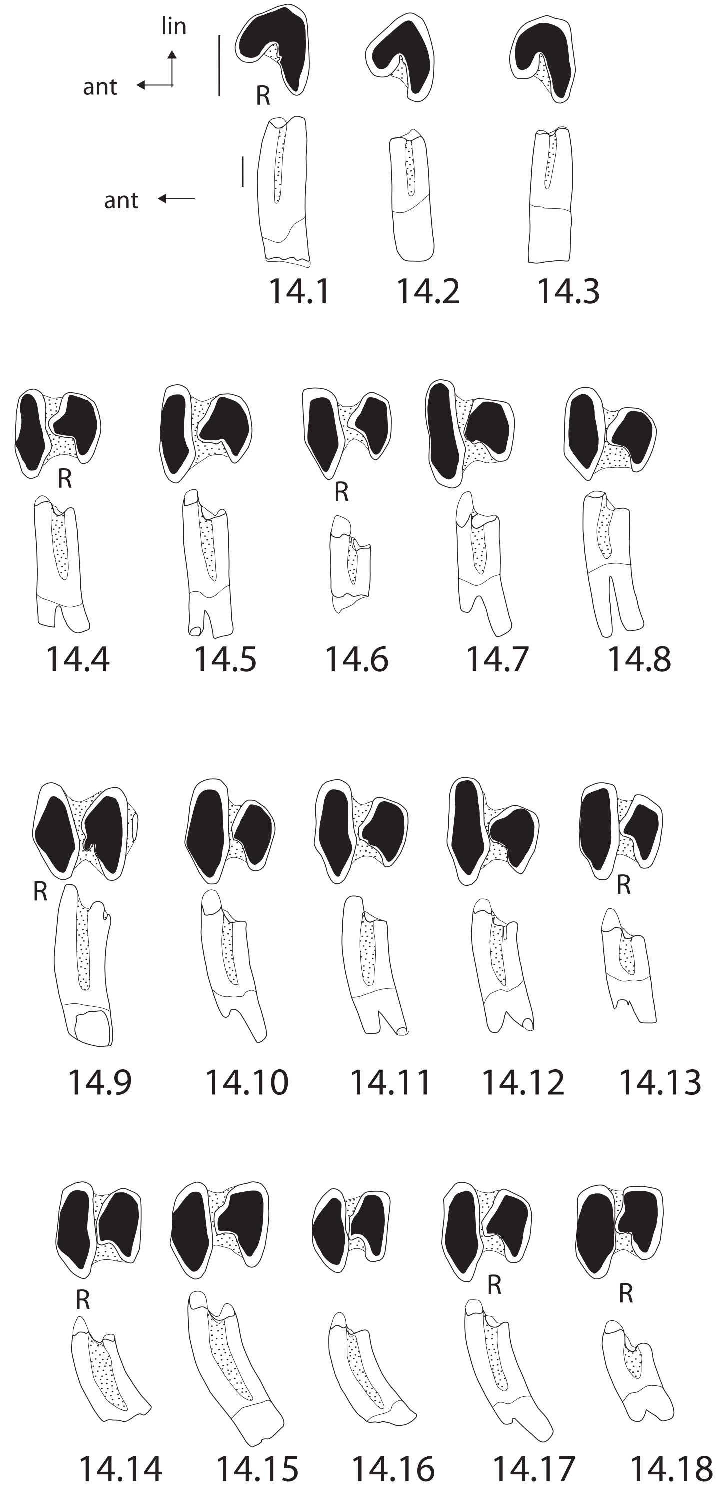

FIGURE 14. Topotypic lower cheek teeth of *H. fluviatilis* from Kleinfelder Farm. Teeth are arranged in order of interpreted wear stage, from left to right. Standard orientations as in Figure 2. Each lettered pair shows occlusal view (above) and buccal view (below) except in 14.9 with lingual view below. Scale bars (equal to 1 mm) for occlusal and side views next to first specimen in each row also indicate scale for all other specimens in the row. 14.1-14.3, p3s. 14.1, ROM 7305. 14.2, ROM 7303. 14.3, ROM 7304. 14.4-14.8, p4s. 14.4, ROM 52638. 14.5, ROM 7314. 14.6, ROM 7338. 14.7, ROM 7324. 14.8, ROM 7321. 14.9-14.13, M1s. 14.9, ROM 7337; side view is from lingual. 14.10, ROM 7336. 14.11, ROM 7318. 14.12, ROM 7313. 14.13, ROM 52641. 14.14-14.18, m2s. 14.14, ROM 7311. 14.15, ROM 7327. 14.16, ROM 7312. 14.17, ROM 7335. 14.18, ROM 7333.

groove. All specimens are relatively low crowned and with thick enamel at occlusal surface; both features are interpreted as representing advanced wear stages as noted in p3 for the other Hesperolagomys species. Mean size of p3 of *H. fluviatilis* is: length, 1.48 mm; width, 1.37 mm (Table 4B).

Lower Molariform Teeth. As in other *Hesperolagomys* species, lower molariform teeth can be differentiated by the length of the talonid (shorter in m1 than in p4 and m2), the nature of the posterior talonid wall (rounded in p4 and m1, transversely oriented and straight in m2), and in curvature in the anteroposterior plane (p4 is straight, m1 moderately curved, and m2 more strongly curved). p4-m2 in the dentary (ROM 52642: Figure 13) have short crowns and lack posterolophids, indicating they are at least somewhat worn. Each has a similarly-shaped talonid, with a wide, buccolingually asymmetrical anterior projection characterized by a concave buccal wall and lingual wall varying from slightly concave (p4 to m1), to straight or slightly convex (m2).

No p4s in early stages of wear (with posterolophids) are known. Most p4s of *H. fluviatilis* have talonids with a concave lingual wall and a slightly concave to straight buccal wall (e.g., Figure 14.5-14.8); the specimen with the tallest crown (ROM 52638: Figure 14.4) has a more concave lingual wall than other specimens. No clear trends in changing morphology of the lingual wall of the anterior projection are apparent within the wear stages represented. Mean dimensions for p4 of *H. fluviatilis* is: length, 1.62 mm; trigonid width, 1.84 mm; talonid width, 1.24 mm (Table 4B). Talonids are relatively narrow, such that the ratio of trigonid width to talonid width is ≈1.50.

A tall-crowned, little-worn m1 (Figure 14.9) has a small posterolophid separate from the talonid. The anterior projection is divided into two small anteriorly facing projections, similar to but smaller than in *H. galbreathi* at a similar stage of wear (Figure 10.3); the lingual wall of the anterior projection is straight. A slightly more worn specimen (Figure 14.10) lacks a posterolophid but also has a relatively tall crown and a straight lingual wall. Other specimens, exhibiting more advanced stages of wear, (e.g., Figure 14.11-14.13) have a slightly concave lingual wall. Mean size of m1 of *H. fluviatilis* from Kleinfelder Farm is: length, 1.66 mm; trigonid width, 1.84 mm; talonid width, 1.26 mm (Table 4B).

UNSM 83029 from Achilles Quarry, Nebraska, is tentatively referred to *H. fluviatilis* as a p4 or m1; it is very strongly worn, with little crown remaining and is slightly damaged on the posterolingual edge of the talonid. It is similar in occlusal morphology to known specimens and has strong roots as observed in other lower (permanent) molariform teeth, but is anomalously small (Table 5).

No specimens of m2 with a posterolophid are known. A relatively unworn specimen (Figure 14.14) has crown base still forming and a straight lingual margin, as in tall-crowned m1s (e.g., Figure 14.15-14.16). Teeth in more advanced stages of wear (e.g., Figure 14.17), have a similarly shaped, slightly concave lingual margin. The most worn m2 (Figure 14.18) also has a concave lingual margin, but the main body of the talonid extends farther anteriorly on the lingual side than observed in other specimens, such that the talonid length on the lingual side is nearly two times that on the buccal side, and the talonid appears more asymmetrical than in other specimens. Mean size of m2 of *H. fluviatilis* from Kleinfelder Farm is: length, 1.56 mm; trigonid width, 1.66 mm; talonid width, 1.19 mm (Table 4B).

Three specimens from Nebraska localities (Table 5) are referred to *H. fluviatilis* as m2s: UNSM 83032 from Achilles Quarry, UNSM 90000 from Egelhoff Quarry, and UNSM 83141 from Lost Duckling Quarry. UNSM 83032 and UNSM 90000 are very tall-crowned, representing an early stage of wear, closely resembling that figured in Figure 14.15. UNSM 83141 is highly worn with little crown remaining; its occlusal morphology is similar to that of Figure 14.18.

REMARKS

Storer (1975:111) recognized that the "shape and strength" of the anterior projection of the talonid of p4-m2 was an important characteristic differentiating *H. galbreathi* and *H. fluviatilis*, with that of *H. fluviatilis* being "always stronger" than that of *H. galbreathi*. Voorhies (1990b) also noted a consistent morphologic difference between *Hesperolagomys* lower molariform teeth of Clarendonian age (*H. galbreathi*) and those of Barstovian age (referred by Voorhies 1990b, to *H. fluviatilis*). He emphasized the buccolingual symmetry of the talonid and the narrow protrusion "bounded both lingually and buccally by a concave enamel wall" in *H. galbreathi*, contrasting with the wider anterior projection and asymmetry of the talonid of *H. fluviatilis* created by the straight or convex anterolingual wall, and suggested that "…the compressed, pointed anterior talonid extensions in *H. galbreathi* are actually more, not less, prominent than those of *H. fluviatilis*" (Voorhies 1990b:A323)

Based on observations of the more numerous specimens now available for comparison, I find that the talonid of lower molariform teeth of *H. galbreathi* is distinct from that of other species in two respects: (1) the anterior projection is narrower and more clearly separated from the main body of the talonid, as both anterolingual and anterobuccal walls of the projection attach medial to the outer walls of the main body; and (2) the main body of the talonid is buccolingually more symmetrical. In *H. fluviatilis* and *H. niobrarensis*, it is more difficult to demarcate the anterior projection from the main body of the talonid because the anterolingual wall attaches more laterally, confluent with the lingual wall of the talonid; additionally, the main body of the talonid is asymmetrical, extending more anteriad on the lingual side than on the buccal side. Specimens described here illustrate the degree to which variation in the shape of the talonid can be attributed to stage of wear. In all three species, the anterolingual wall of the talonid is straight in very early wear, becoming much more concave in later wear. In earlier wear stages of p4 of *H. galbreathi*, the anterior projection appears more asymmetrical than in later wear, as the lingual side is straight and does not mirror the buccal side, but the talonid is never as anterolingually expanded as it is in *H. fluviatilis*.

Hesperolagomys sp.

Synonymies. *Oreolagus colteri* Barnosky 1986 (in part); *Hesperolagomys* sp. (Kraatz and Barnosky 2004).

Referred specimens from Wyoming. (all UWBM numbers) 62702, P3; 62704 and 62720, M1s; 62698, M2.

Geologic Age and Distribution. Medial late and/or late late Barstovian (Ba2b-c) of Wyoming.

Description. UWBM 62698 (Barnosky 1986:plate IIIB), the type specimen of *O. colteri*, is strikingly similar to M2s of *Hesperolagomys* and is here reinterpreted as such. The Cunningham Hill specimen is nearly identical in occlusal morphology to ROM 7343 (Storer 1975, figure 81O) and to ROM 7353 (Figure 11.9, this paper). Length reported for this specimen (1.2 mm) is less than for specimens included in *H. niobrarensis* but overlaps *H. fluviatilis* in size (see Tables 1 and 4).

Two specimens originally placed in the hypodigm of *Oreolagus colteri* by Barnosky (1986:plate IIIA, D, and G) as P4s or M1s are here interpreted as M1s of *Hesperolagomys*. Both are incomplete buccally, but clearly have wide lingual hypostriae nearly meeting the crescentic valley, a characteristic of *Hesperolagomys*. Occlusal lengths of these specimens (1.5 and 1.4 mm) reported by Barnosky (1986:table 2) fall within the range for *H. niobrarensis* but are larger than those known for specimens of *H. fluviatilis* from Saskatchewan and Nebraska

UWBM 62702 from the Wyoming Colter Formation is here identified as a partial P3 of *Hesperolagomys*. Although the tooth lacks the buccal margin at the crown apex, an accurate measure of length was possible (1.13 mm), which places it within the size range of both Barstovian species, *H. fluviatilis* and *H. niobrarensis*.

Remarks. Confusion over the identity of ochotonid remains from Cunningham Hill highlights the similarity of occlusal features of some upper molariform teeth of *Hesperolagomys* and *Oreolagus*. *Hesperolagomys* is rare among lagomorphs in possessing both a deep lingual hypostria and persistent crescentic valley in (rooted) upper molariform teeth. P4-M1 of *Oreolagus* also always possess deep lingual hypostriae, but only in some species is a crescentic valley variably present (Dawson 1965), or early wear stages known only for some species. Incomplete preservation of buccal roots in the Cunningham Hill specimens apparently let to their misidentification as *Oreolagus*. As shown above, however, upper molariform teeth of *Hesperolagomys* can also be distinguished from those of *Oreolagus* by the presence of persistent buccal cusps in the former and lack of enamel-covered buccal cusps in the latter. Since the few available specimens from Cunningham Hill overlap with both *H. fluviatilis* and *H. niobrarensis* in size, no definite referral to species level is attempted here.

STATISTICAL ANALYSIS

ANOVA

Although the analysis of variance is robust with respect to the assumption of normality (Zar 1999), I performed Shapiro-Wilk W tests on the distributions of cheek tooth dimensions of Valentine Railway Quarries samples for which $N \geq 10$ (limited to length of P3, P4, and M1; length and talonid width of p4, m1, and m2). Results were all consistent with populations with normally distributed values, although the value for length of P3 was $p=0.0501$. I did not test very small samples for conformity to a normal distribution, but no evidence suggests they are inconsistent with this assumption.

ANOVAs of the tooth dimensions (Table 6) strongly support recognition of three size groups of *Hesperolagomys* corresponding to the three spe-

TABLE 6. Summary of results of pairwise comparisons of one-way ANOVAs of tooth dimensions by species at α=0.05. Items in bold indicate significant comparisons.

Tooth position	Dimension	Comparison	p-value for t-test
P3	length	**niobrarensis vs. fluviatilis**	**<0.001**
		niobrarensis vs. galbreathi	**0.048**
		fluviatilis vs. galbreathi	**0.035**
P4	length	**niobrarensis vs. fluviatilis**	**<0.001**
		niobrarensis vs. galbreathi	**<0.001**
		fluviatilis vs. galbreathi	0.895
M1	length	**niobrarensis vs. fluviatilis**	**0.013**
		niobrarensis vs. galbreathi	0.007
		fluviatilis vs. galbreathi	0.421
M2	length	**niobrarensis vs. fluviatilis**	**<0.001**
		niobrarensis vs. galbreathi	**0.030**
		fluviatilis vs. galbreathi	0.679
p3	length	niobrarensis vs. fluviatilis	0.222
		niobrarensis vs. galbreathi	**0.011**
		fluviatilis vs. galbreathi	0.004
	width	niobrarensis vs. fluviatilis	0.283
		niobrarensis vs. galbreathi	0.238
		fluviatilis vs. galbreathi	0.803
p4	length	**niobrarensis vs. fluviatilis**	**<0.001**
		niobrarensis vs. galbreathi	0.032
		fluviatilis vs. galbreathi	**<0.001**
	tri width	**niobrarensis vs. fluviatilis**	**<0.001**
		niobrarensis vs. galbreathi	**0.034**
		fluviatilis vs. galbreathi	**0.022**
m1	length	niobrarensis vs. fluviatilis	0.385

cies qualitatively described above. Mean values of cheek tooth dimensions differ significantly between samples of the Barstovian species, *H. niobrarensis* and *H. fluviatilis*, for all teeth except p3 and m1. *H. galbreathi* differs significantly from *H. fluviatilis* in the lengths of P3 and the lower premolars (p3, p4) but not other teeth. Measured dimensions of all *H. niobrarensis* teeth, excepting p3 width, m1 trigonid width, and length and trigonid width of m2, differ significantly from those of *H. galbreathi*. Tooth dimensions of *H. fluviatilis* and *H. galbreathi* showing significant differences are length of P3, length p3, and length and trigonid width p4. Although sample sizes in most cases were quite small, the lowest power estimate (for p3) was 0.895, indicating that there is a 10.5% chance of committing a Type II error in the analysis. Other power estimates were 0.9 or greater.

Differences between species in length of most teeth are consistent with scaling, such that *H. galbreathi* length and width values are intermediate between *H. fluviatilis* (smaller) and *H. niobrarensis* (larger) (Figures 15, 16, and 17). Only p3 of *H. fluviatilis* deviates from this pattern, being both relatively and absolutely longer than that of the other species (Figure 16).

Table 6 (continued).

Tooth position	Dimension	Comparison	p-value for t-test
m1	length	**niobrarensis vs. galbreathi**	**0.026**
		fluviatilis vs. galbreathi	0.095
	tri width	**niobrarensis vs. fluviatilis**	**0.002**
		niobrarensis vs. galbreathi	0.085
		fluviatilis vs. galbreathi	0.781
m2	length	**niobrarensis vs. fluviatilis**	**<0.001**
		niobrarensis vs. galbreathi	0.110
		fluviatilis vs. galbreathi	**0.040**
	tri width	**niobrarensis vs. fluviatilis**	**<0.001**
		niobrarensis vs. galbreathi	0.103
		fluviatilis vs. galbreathi	0.067
m1+m2	**length**	**niobrarensis vs. fluviatilis**	**<0.001**
		niobrarensis vs. galbreathi	0.013
		fluviatilis vs. galbreathi	0.774
	tri width	**niobrarensis vs. fluviatilis**	**<0.001**
		niobrarensis vs. galbreathi	**0.028**
		fluviatilis vs. galbreathi	0.173

Variation in Transverse Width of Upper Cheek Teeth

Coefficients of variation for check tooth dimensions of *H. niobrarensis* and *H. fluviatilis* (Tables 1 and 4) are mostly within the range expected (CV=4 to 10) for a single species (Simpson et al. 1960). Upper cheek tooth widths, however, especially of the tall-crowned premolars, have much higher CV values.

Many workers have noted the extreme change in transverse width with increased wear in unilaterally hypsodont lagomorph upper cheek teeth (e.g., Wood 1940; Sych 1975; Tobien 1975, 1978; Gawne 1978), but only Gawne (1978) attempted to quantify the relationship between occlusal width and crown height and explore its taxonomic implications. Using crown heights and widths in tooth rows of a large sample of previously unstudied Chadronian leporids from Wyoming, she was able to demonstrate that a number of named 'species' of *Megalagus* and *Montanolagus* are better interpreted as wear stages of the single species *Megalagus brachyodon* (Gawne 1978).

Because Gawne's technique utilized measurements from complete tooth rows (rare in the samples studied here), I developed a similar approach using isolated teeth. Results for P4, the tallest-crowned and most abundantly represented upper cheek tooth in the Valentine Railway Quarries sample, are shown in Figure 5. As crown height decreases with increasing wear, occlusal width increases in a statistically highly significant (negative) linear relationship (R^2=0.89, p<0.0001). Occlusal length in P4 shows a statistically significant (positive) linear relationship with crown height, but at a much lower level of significance (R^2=0.19, p=0.02). Thus, as wear proceeds, the occlusal surface of P4 nearly doubles in width while decreasing only slightly. Larger samples representing the spectrum of wear stages of other species of T*esperolagomys* are needed to test if the linear function determined for P4 of *H. niobrarensis* width through wear is species-specific. As described above, buccolingual 'stretching' of *Hesperolagomys* upper cheek teeth has led to their misidentification as *Russellagus*, a larger ochotonid, by previous authors.

Size-related Bias in Recovery of Isolated Teeth

Ochotonid jaws are large enough (greater than one centimeter in length) to be collected during routine surface prospecting but isolated teeth

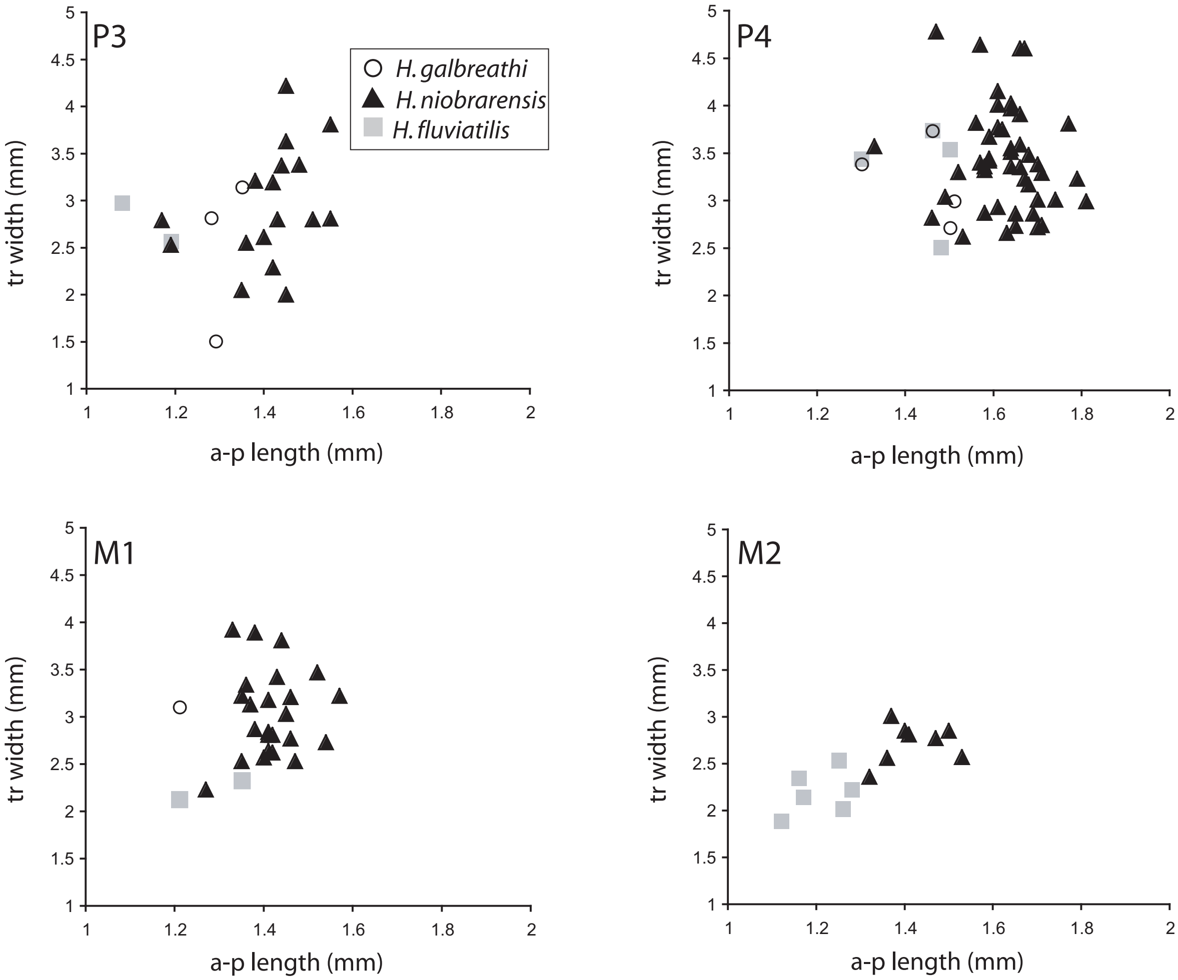

FIGURE 15. Bivariate plots of occlusal dimensions of upper cheek teeth of *Hesperolagomys* by species.

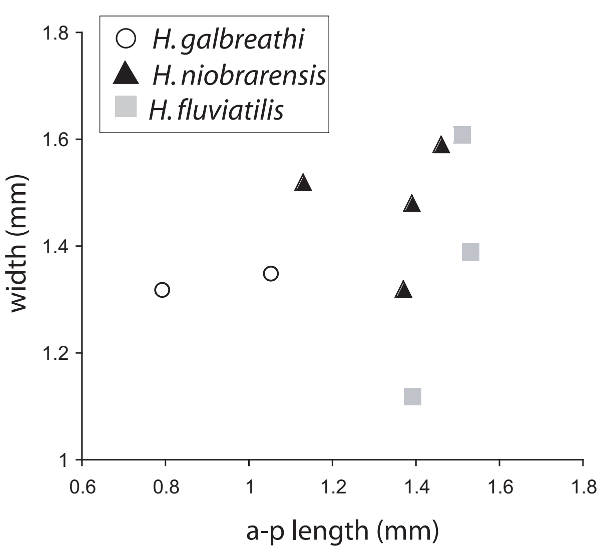

FIGURE 16. Bivariate plot of maximum dimensions of p3 of *Hesperolagomys* by species.

are rarely recovered by this method. The large samples of individual teeth studied here were obtained almost entirely by the sieving of large volumes of unconsolidated sediment using 0.16 inch (1.6 mm) mesh screens (Voorhies and Timperley 1997; B.E. Bailey, personal commun., 2005). To address how the method of collection might have influenced the composition of the studied sample, I counted the identifiable specimens for each tooth position in the Valentine Railway Quarries collection (see Thomas 1969). These counts, plotted against a measure of mean maximum diameter for each tooth position (width for upper cheek teeth and p3, trigonid width for p4-m2), are shown in Figure 18. Upper (larger) cheek teeth outnumber lowers and the largest upper (P4) and lower (p4) teeth are both disproportionally abundant. The smallest upper (M2) and lower (p3) teeth are correspondingly less abundant. Teeth poorly represented in the sample, notably p3, are close to or smaller than

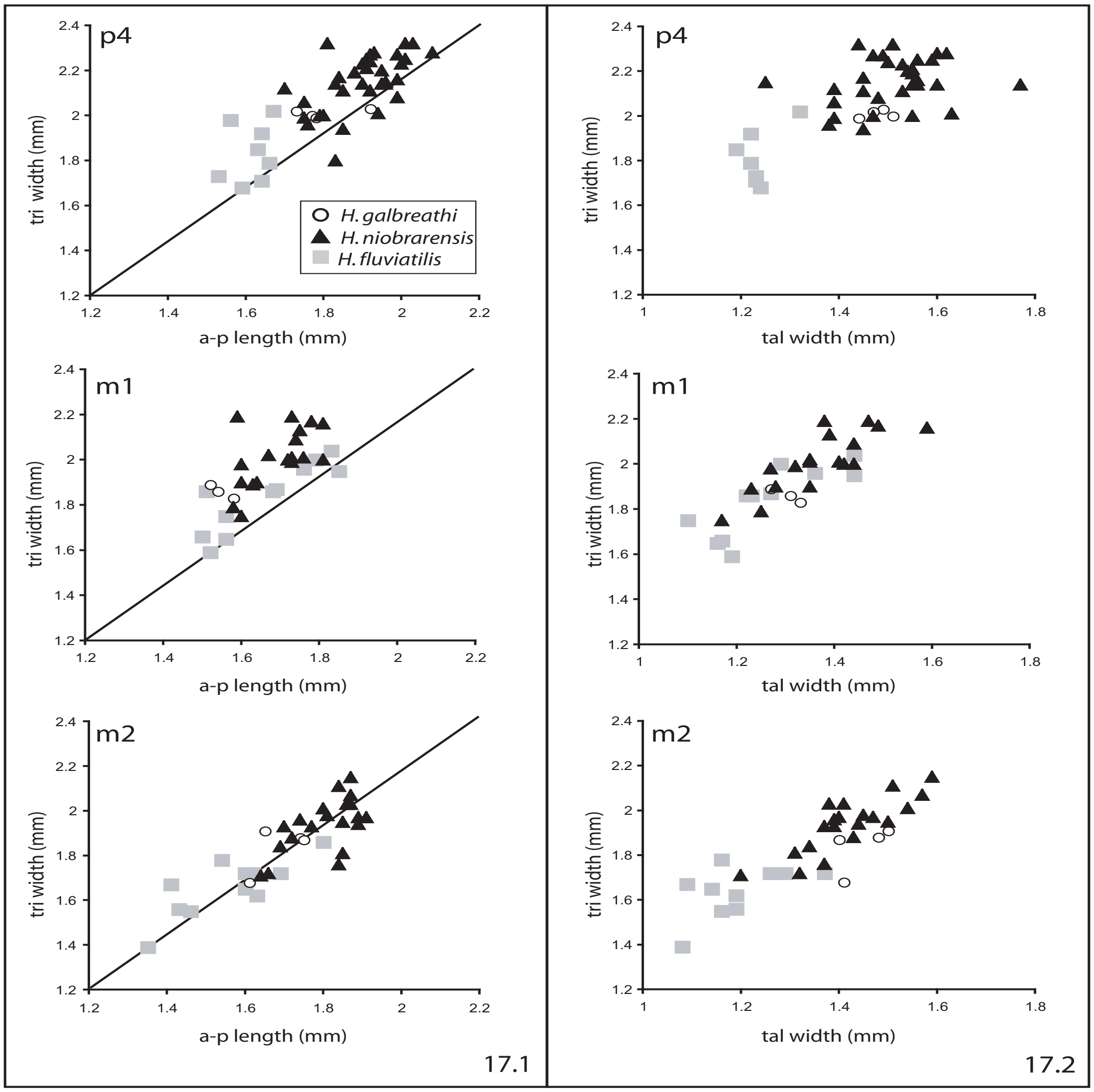

FIGURE 17. Bivariate plots of maximum dimensions of lower cheek teeth of *Hesperolagomys* by species. 17.1, trigonid width vs. anteroposterior length; solid line marks 1:1 ratio of length:tri width. 17.2, trigonid width vs. talonid width. Note scale difference on x-axis between 17.1 and 17.2.

1.6 mm in mean maximum diameter. The cylindrical shape of the latter tooth especially appears to allow it to elude recovery by passing through the screens. The lack of P2s in the Valentine Railway Quarries and other *Hesperolagomys* samples probably also results from size bias, the tooth being barely 1 mm in width.

BIOCHRONOLOGIC CONTEXT

Faunal assemblages included in this study are arranged biochronologically in Figure 19. Ages are after Tedford et al. (2004); Nebraska faunal age relationships after Voorhies (1990a; 1990b). Further informal subdivisions of the late Barstovian (Ba2a, Ba2b, and Ba2c) based on previously identified biozones are described below. "Primary faunas" are previously published and/or have well-defined external age control.

Barstovian. The oldest faunal assemblage included in this study is the Kleinfelder Farm locality, Wood Mountain Fauna. Storer (1975) recognized elements of the Wood Mountain Fauna in common with the early Barstovian Lower Snake Creek Fauna of western Nebraska as well as with the somewhat younger Norden Bridge Fauna (lowermost Valentine Formation, Niobrara River valley, north-central Nebraska), and considered the Wood Mountain Fauna to be "just older than the Norden

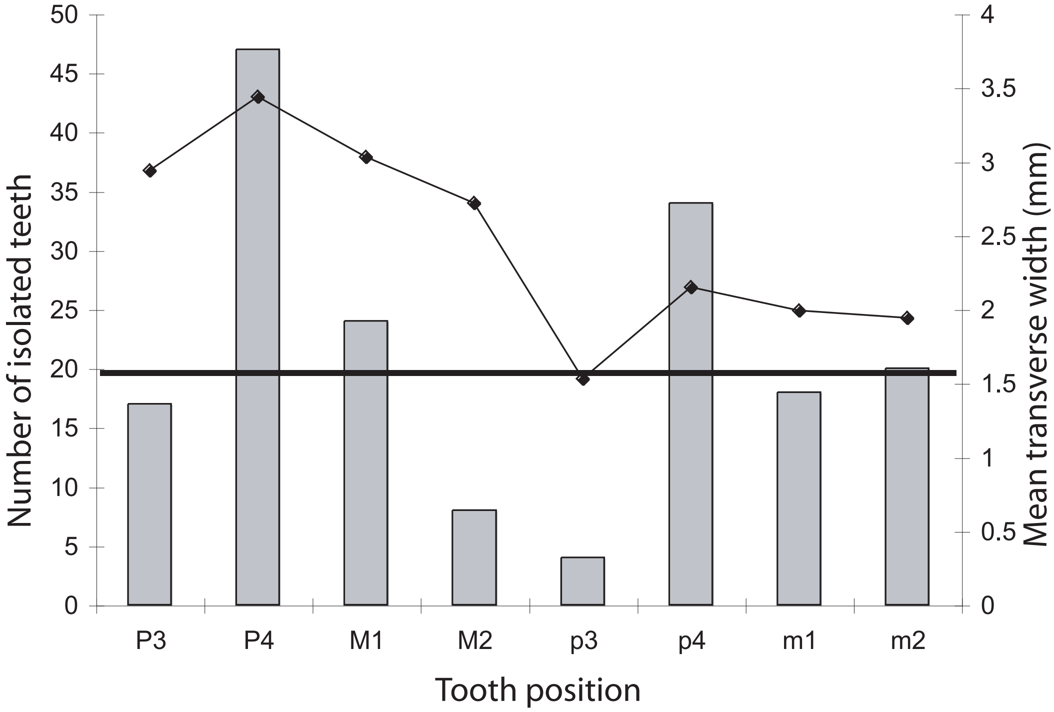

FIGURE 18. Distribution of isolated cheek teeth of *H. niobrarensis* from Valentine Railway Quarries by tooth position. Bars correspond to number of isolated teeth (scale to left); diamonds with connecting line correspond to the mean value of the maximum measurement for each tooth position (in all cases, width). Solid, straight line at 1.6 mm is reference to screen size used for obtaining specimens.

Bridge local fauna" (p. 127). Tedford et al. (2004) further noted a close resemblance of the Wood Mountain Fauna to the Keota Fauna of the upper Pawnee Creek Formation in northeastern Colorado (14-14.5 Ma). The Wood Mountain Fauna is here considered earliest late Barstovian in age (informally designated Ba2a, Figure 19). This interval is sparsely represented in northeastern Nebraska by the Miller Creek Fauna (Voorhies 1990a).

The Norden Bridge Quarry Fauna and Nebraska faunas of equivalent age from the Cornell Dam Member of the Valentine Formation (Achilles, Lost Duckling, and Egelhoff Quarries; Voorhies 1990a, 1990b), are slightly younger than the Wood Mountain and Keota Faunas by as much as 1 Ma, based on ages of 13.5-13.6 Ma on the Hurlbut Ash within the Cornell Dam Member (Tedford et al. 2004). The Norden Bridge Quarry Fauna, as well as the faunal assemblage from Immense Journey Quarry (southwestern Nebraska) also dates to this interval (Voorhies et al. 1987), here informally designated as Ba2b in age (Figure 19).

The Valentine Railway Quarries Fauna in the Crookston Bridge Member of the Valentine Formation represent the youngest informal division of the late Barstovian used here, Ba2c (Figure 19). In north-central Nebraska, the Crookston Bridge Member lies in superposition above the Cornell Dam Member of the Valentine Formation, and the Valentine Railway Quarries Fauna is constrained below by the 13.5-13.6 Ma Hurlbut Ash and above by the ~12.2 Ma Swallow Ash in the lower part of the overlying Ash Hollow Formation (Tedford et al. 2004). Vertebrate fossils from individual Valentine Railway Quarries are derived from the same paleochannel deposits within the Crookston Bridge Member (Voorhies and Timperley 1997). The faunal assemblages from Garner Bridge South locality and Myers Farm are considered equivalent in age to the Valentine Railway Quarries (B.E. Bailey personal commun., 2002; Voorhies 1990a respectively). The Cunningham Hill Fauna, Colter Formation, western Wyoming, has rodent and horse taxa in common with both the Norden Bridge and Valentine Railway Quarries Faunas (Barnosky 1986) and cannot be further constrained from Ba2b and/or Ba2c in age.

Clarendonian. Tedford et al. (2004) reported an Ar-Ar age date of 11.58±0.05 Ma for a tuff just

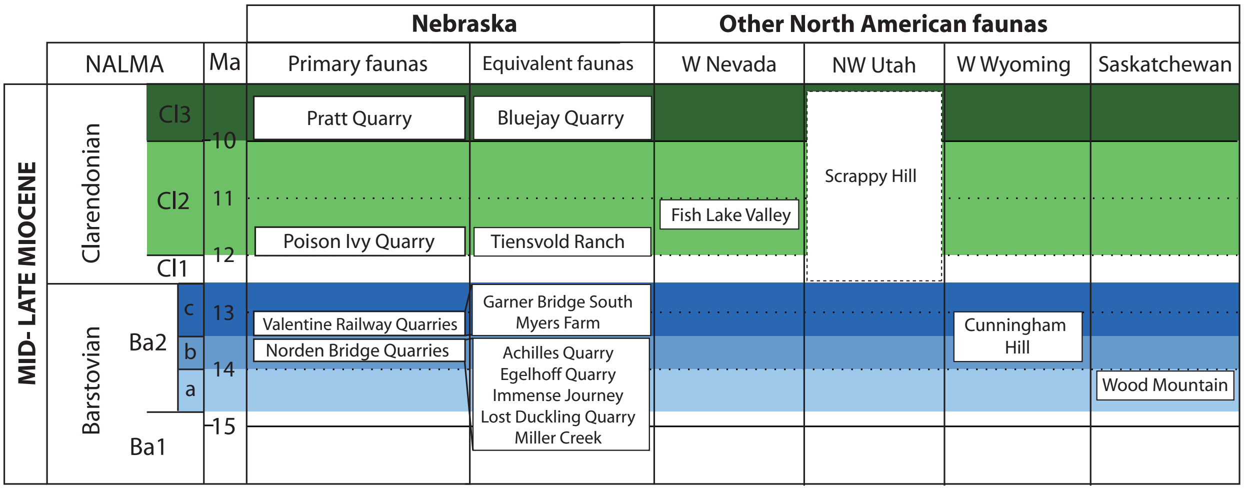

FIGURE 19. Biochronologic position and correlation of faunas included in this study. Ages after Tedford et al. (2005) and Voorhies (1990a, 1990b). 'Ba2a', 'Ba2b', and 'Ba2c' are informal subdivisions of the late Barstovian based on previously recognized distinctions between Norden Bridge Quarry Fauna (Ba2b), the Valentine Railway Quarries Fauna (Ba2c), and the Wood Mountain Fauna (Ba2a). "Primary faunas" refer to published faunas and/or faunal assemblages that are relatively diverse and well-constrained in age; "equivalent faunas" are unpublished, considered correlative to the primary faunas, or less diverse and/or constrained in age. Dashed outline for 'Scrappy Hill' faunal assemblage indicates that the age is not refined within the Clarendonian NALMA.

beneath the small mammal locality of Fish Lake Valley, placing it within the first half of Cl2. Tedrow and Robison (1999) referred specimens from the Scrappy Hill faunal assemblage in the Salt Lake Formation, northwest Utah, to *H. galbreathi*; the presence of *H. galbreathi* was used by the authors to infer an approximate correlation with the Fish Lake Valley Fauna.

The faunal assemblage from Tiensvold Ranch locality, collected from Ash Hollow Formation sediments in Sheridan County of northwestern Nebraska, is undescribed but a faunal list was compiled by Bair and Voorhies (1998) under the name 'Gordon Fish Site' (fish are the most abundant fossil vertebrate known from the locality). All large mammalian species present at Tiensvold Ranch are present in the Minnechaduza Fauna described by Webb (1969, p.18-19) indicating an early Cl2 age, constrained by age dates of the Swallow Ash at ~12.2 Ma below and Davis Ash at 11.6 Ma above (Tedford et al. 2004). The faunal assemblage collected directly below the volcanic ash bed at Poison Ivy Quarry, northeastern Nebraska, is dated to 11.93 Ma by Perkins (1998), also early Cl2 in age (Figure 19). The geologically youngest specimens of *Hesperolagomys* studied are from the late Clarendonian Pratt and Bluejay Quarries in the Merritt Dam member of the Ash Hollow Formation of north-central Nebraska (Cl3 of Tedford et al. 2004).

DISCUSSION AND CONCLUSIONS

Hesperolagomys was originally described as an ochotonid by Clark et al. (1964), who noted its dental similarities to both *Amphilagus fontannesi*, a late Miocene European ochotonid, and *Desmatolagus gobiensis* from the Oligocene of Asia. Whereas most subsequent authors have accepted this interpretation, Storer (1984) challenged it, suggesting that the genus should belong to the Leporidae (see also McKenna and Bell 1997, p. 109; for an additional alternate view, see Erbajeva (1988; 1994). The basis for Storer's suggestion appears to be his assertion that undescribed maxillary fragments assigned to *Hesperolagomys* lack a premolar foramen. Absence of this feature, if confirmed by published descriptions, would clearly necessitate radical reassessment of the affinities of the genus because a premolar foramen has been regarded as diagnostic of the Ochotonidae by major students of lagomorph evolution beginning with Bohlin (1942) and followed by Dawson (1967; see also Dawson 2008) and McKenna (1982).

All of the *Hesperolagomys* maxillae reported here, including one from the type locality of Fish Lake Valley, have a distinct premolar foramen, confirming that the genus belongs in the Ochotonidae.

TABLE 7. Summary of major differences between *Hesperolagomys* species.

Character	*H. fluviatilis*	*H. niobrarensis*	*H. galbreathi*
Age range	Ba2a-b	Ba2c	Cl2-3
Size (in most dimensions)	small	large	intermediate
p3 size	large	intermediate	small
Anterolingual groove on p3	absent	weak but cement-filled	strong and cement-filled
Lower molariform talonid shape	asymmetrical	asymmetrical	symmetrical
p4 trigonid width/talonid width	relatively narrow	intermediate	relatively wide

Other diagnostic ochotonid features (Bohlin 1942) of *Hesperolagomys* were also confirmed in the present study: (1) bases of upper cheek teeth curving into the zygoma (not extending into orbit); (2) in lower molariform teeth, trigonid and talonid not united lingually with wear; (3) M3 absent; (4) P3 nonmolariform; (5) m3 lacking talonid; (6) mental foramen posterior to its 'usual' position in leporids. An additional characteristic considered diagnostic of Ochotonidae by McKenna (1982), lower incisor extending posteriorly at least to p4, is also confirmed for all three *Hesperolagomys* species studied here. In summary, there is no longer any reason to doubt that *Hesperolagomys* is an ochotonid.

Characteristics of *Hesperolagomys*

Clark et al. (1964) described *Hesperolagomys* as "unusually primitive" compared to other Miocene ochotonids, possessing plesiomorphic characters including: (1) rooted cheek teeth; (2) buccal folds persisting on the occlusal surface of P4 and M1; and (3) talonids transversely narrower than trigonids in p4-m2. Additionally, the posterior extent of the lower incisor to beneath m1 is plesiomorphic. Apomorphic characters of *Hesperolagomys* noted by Clark et al. (1964) are the unique position and emphasis of mental foramina, and "marked anterior projections of the talonids on p4-m2." Additional apomorphies are P3 with two persistent cement-filled lingual striae, and P4-M2 with persistent crescentic valleys and deep persistent lingual hypostriae.

At the time of its initial description, *Hesperolagomys* was arguably the most 'primitive' late Miocene ochotonid; *Oreolagus* (possessing many 'advanced' dental characters including rootless cheek teeth) was the only other North American Miocene ochotonid known. A greater diversity of 'primitive' North American forms have now been described, including *Gripholagomys*, *Russellagus*, and ?*Desmatolagus schizopetrus,* but the relationship of *Hesperolagomys* to other ochotonid taxa has not been defined. Clark et al. (1964) suggested that *Hesperolagomys* might be derived from *Desmatolagus*, either from North American or Asian forms. Storer (1975) noted that *Hesperolagomys* and *Russellagus* are clearly related, but show distinct morphological differences. Working with only small samples of primarily isolated teeth, Storer successfully described pertinent characteristics of *Russellagus vonhofi* and *H. fluviatilis*, but was unable to correctly identify some isolated teeth due to the remarkable morphological similarity between some wear stages of teeth of the two taxa. Martin (1976) suggested a close relationship between the more poorly known taxon *Gripholagomys* and *Hesperolagomys*. Revision of *Russellagus* and *Gripholagomys* by the author (in progress) should elucidate the nature of their relationship to *Hesperolagomys* and other North American taxa.

Characteristics and Relationships of *Hesperolagomys* Species

Major differences between *Hesperolagomys* species are summarized in Table 7. Size of most dimensions is important in distinguishing the species, with *H. fluviatilis* smallest, *H. galbreathi* intermediate, and *H. niobrarensis* largest. *H. galbreathi* overlaps with both *H. fluviatilis* and *H. niobrarensis* in some dimensions and is difficult to distinguish from the older taxa on size only; most elements of *H. fluviatilis* are distinguishable from those of *H. niobrarensis* on the basis of size alone. Lower third premolar of *H. fluviatilis* is anteroposteriorly longer than that of the other species, both absolutely and relatively.

Morphological characters differing between species are primarily those of lower cheek tooth shape. The trigonid of p3 of *H. fluviatilis* extends more anteriad than in other species, in which it extends more lingually; p3 of *H. fluviatilis* also lacks an anterolingual groove, present in *H. niobrarensis* and *H. galbreathi*. The talonid of lower molariform

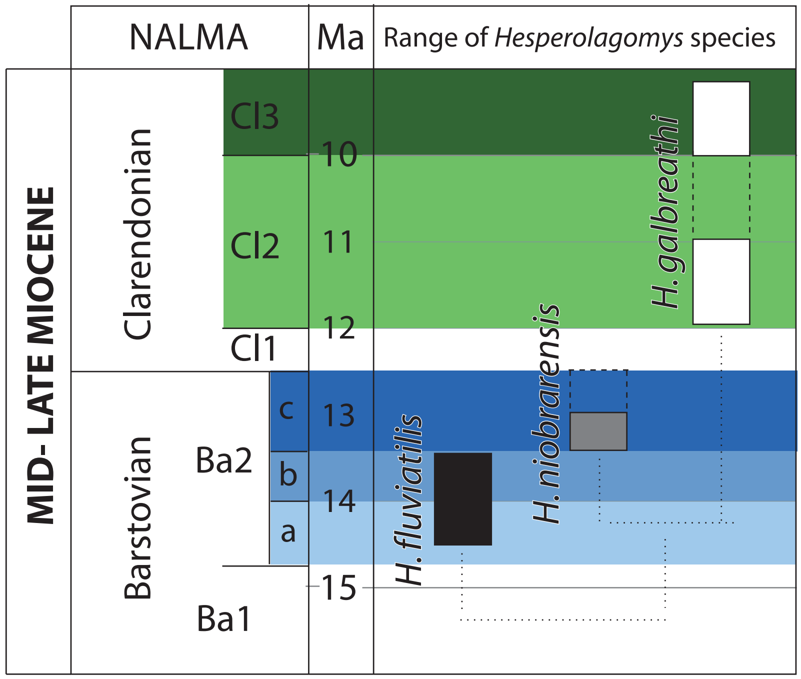

FIGURE 20. Biochronologic age ranges and hypothesized phylogenetic relationship of *Hesperolagomys* species. Filled boxes indicate known biochronologic ranges; dashed line indicates suspected extensions to known ranges. Dotted line indicates inferred sister group relationship between *H. fluviatilis* and (*H. niobrarensis* + *H. galbreathi*).

teeth of *H. galbreathi* is consistently more buccolingually symmetrical than those of *H. fluviatilis* and *H. niobrarensis*; although the occlusal morphology of the talonid does change with wear, those of *H. fluviatilis* and *H. niobrarensis* are more asymmetrical and can be distinguished from *H. galbreathi* in all but the earliest stages of wear.

Hypotheses of relationships between *Hesperolagomys* species were not specifically tested in this study, but new information presented here indicates that *H. galbreathi* is likely more closely related to *H. niobrarensis* than to *H. fluviatilis* (depicted in Figure 20). With this hypothesis, the presence of an anterolingual groove and more lingually directed trigonid on p3 are synapomorphies of *H. niobrarensis* and *H. galbreathi*. The greater buccolingual symmetry of the talonid of lower molariform teeth of *H. galbreathi* is an autapomorphy. *H. fluviatilis* thus possess the plesiomorphic state for the characters ‘presence of anterolingual groove on p3’ (absent) and ‘shape of trigonid of p3’ (anteroposteriorly long).

Age ranges of *Hesperolagomys* species are shown in Figure 20. The first appearance of *Hesperolagomys* is with *H. fluviatilis* near the beginning of the late Barstovian (Ba2ba), reinforcing the view of Tedford et al. (2004). *H. fluviatilis* apparently persisted until near the middle of the late Barstovian (Ba2b). *H. niobrarensis* (sp. nov.) is restricted to the late late Barstovian (Ba2c) and is currently known only from Nebraska. All known *Hesperolagomys* specimens of medial and late Clarendonian age (Cl2-3) are consistent with *H. galbreathi*. At this time, no ochotonid specimens of early Clarendonian (Cl1) age are known; in Nebraska, at least, their absence from the Burge and equivalent faunas appears to reflect poor recovery of small mammal fossils as compared with their much greater diversity in Barstovian faunas (e.g., Voorhies 1990a, Tables 2 and 3). The last appearance of *Hesperolagomys* is near the end of the Clarendonian, apparently disappearing as part of an extinction event extirpating many taxa characteristic of the medial Miocene (Tedford et al. 2004).

The cause of the extinction of *Hesperolagomys* and other dentally archaic ochotonids at the end of the Clarendonian is unknown. Bair (2007) used a geometric model of wear in curved mammal teeth to demonstrate that the upper cheek teeth of *Hesperolagomys* and other dentally archaic ochotonids were constrained from attaining greater crown height while maintaining their unilateral hypsodonty and curved shape, and suggested that these constraints may account for the Miocene transition in dominance from dentally archaic ochotonids to dentally "advanced" leporids. Potts et al. (1992) suggest that ochotonids were among mammalian taxa which "successfully colonized the closed habitat of the savanna mosaic but did not radiate significantly into the more open environments during the Miocene." Preliminary analysis suggests that Clarendonian *Hesperolagomys* may have been restricted to relatively closed, mesic settings such as those near ponds or lakes (e.g., Fish Lake Valley, Nevada; fossil fish-rich deposits of Tiensvold Ranch, Nebraska). While these hypotheses are compelling and internally consistent, further work testing both is necessary.

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SUPPLEMENTARY DATA

SUPPLEMENTARY DATA TABLE 1. Tooth dimensions (in mm) of *H. niobrarensis* from Valentine Railway Quarries (all UNSM numbers) (note: incisors and m3 not included here).

Tooth position	Specimen number	a-p length	tr width
P3	122500	1.45	3.63
	122516	1.55	2.81
	122517	1.45	4.22
	122518	1.35	2.05
	122519	1.36	2.55
	122520	1.17	2.79
	122522	1.42	3.19
	122523	1.19	2.53
	122543	1.40	2.61
	122544	1.48	3.38
	123021	1.42	2.29
	123023	1.51	2.80
	123024	1.43	2.80
	123026	1.38	3.21
	123027	1.45	2.00
	123028	1.55	3.81

Tooth position	Specimen number	a-p length	tr width	CH
P4	122500	1.57	4.64	3.92
	122509	1.67	3.23	-
	122634	1.67	4.60	3.48
	122635	1.79	3.23	8.33
	122636	1.74	3.01	8.11
	122637	1.64	3.51	6.16
	122638	1.81	2.99	-
	122639	1.63	2.66	8.29
	122640	1.64	3.97	-
	122641	1.62	3.75	5.98
	122643	1.47	4.78	3.15
	122644	1.58	3.36	6.98
	122645	1.66	3.35	7.30
	122646	1.61	2.93	7.46
	122647	1.64	4.02	5.38
	122648	1.61	4.15	4.99
	122649	1.66	3.59	6.56
	122650	1.65	2.86	7.68
	122651	1.71	2.74	8.44

	122652	1.61	4.01	5.23
	122653	1.69	2.86	8.58
	122654	1.58	3.32	7.25
	122655	1.70	3.01	-
	122656	1.59	3.44	6.44
	122657	1.70	3.38	7.53
	122658	1.59	3.42	6.30
	122659	1.70	2.72	-
	122661	1.68	3.17	8.45
	122662	1.66	3.91	-
	122673	1.64	3.55	-
	122709	1.66	4.60	-
	122719	1.65	2.73	-
	122747	1.54	-	-
	123052	1.49	3.04	-
	123053	1.53	2.62	-
	123054	1.57	3.40	5.87
	123055	1.33	3.57	5.80
	123056	1.64	3.36	-
	123057	1.71	3.29	-
	123058	1.46	2.82	-
	123059	1.52	3.30	-
	123062	1.68	3.48	-
	123063	1.58	2.87	-
	123065	1.77	3.81	5.29
	123066	1.59	3.67	-
	123068	1.61	3.77	4.83
Tooth position	**Specimen number**	**a-p length**	**tr width**	
M1	122700	1.41	2.81	
	122701	1.38	3.89	
	122703	1.47	2.53	
	122704	1.33	3.92	
	122705	1.35	2.53	
	122706	1.35	3.22	
	122707	1.36	3.34	
	122708	1.41	3.18	
	122718	1.27	2.23	
	122774	1.40	2.57	
	122801	1.46	2.77	
	122802	1.54	2.73	

	122803	1.37	3.13		
	122804	1.38	2.87		
	122805	1.43	3.42		
	122806	1.41	2.84		
	122807	1.44	3.81		
	122808	1.46	3.21		
	123082	1.42	2.81		
	123083	1.42	2.62		
	123085	1.41	2.64		
	123086	1.45	3.03		
	123087	1.52	3.47		
	123088	1.57	3.22		
Tooth position	**Specimen number**	**a-p length**	**tr width**		
M2	122809	1.36	2.56		
	122810	1.53	2.57		
	122811	1.37	3.01		
	122812	1.40	2.85		
	122813	1.47	2.77		
	122814	1.41	2.81		
	123097	1.32	2.36		
	123099	1.50	2.85		
Tooth position	**Specimen number**	**a-p length**	**tr width**		
p3	122512	1.13	1.52		
	122838	1.46	1.59		
	122859	1.39	1.48		
Tooth position	**Specimen number**	**a-p length**	**tri width**	**tal width**	**CH**
p4	122501	1.88	2.19	1.55	-
	122502	1.92	2.27	1.49	-
	122512	1.99	2.08	1.48	-
	122878	1.96	2.15	1.25	5.96
	122881	2.00	2.23	1.83	-
	122891	1.94	2.01	1.63	-
	122892	1.75	1.99	1.39	3.48
	122893	1.90	2.14	1.60	-
	122894	1.85	1.94	1.45	-
	122895	1.75	2.06	1.39	-
	122896	1.79	2.00	1.47	-
	122897	1.91	2.25	1.59	-
	122898	1.96	2.14	1.55	3.63

	122899	1.95	2.14	1.77	-
	122900	1.92	2.11	1.53	-
	122901	1.93	2.28	1.60	-
	122902	1.76	1.96	1.38	-
	122903	1.99	2.16	1.56	-
	122904	1.92	2.24	1.50	4.86
	122905	1.83	2.14	1.56	-
	122906	2.01	2.25	1.56	-
	122907	2.08	2.28	1.62	6.33
	122943	1.90	2.23	1.53	-
	122945	1.99	2.27	1.47	-
	122951	2.01	2.32	1.44	-
	123003	1.91	2.21	1.55	-
	123140	1.84	2.17	1.45	3.31
	123141	1.85	2.11	1.45	5.00
	123142	1.95	2.20	1.54	5.74
	123143	1.83	1.80	-	-
	123144	1.80	2.00	1.55	3.76
	123300	2.03	2.32	1.51	5.87

Tooth position	**Specimen number**	**a-p length**	**tri width**	**tal width**
m1	122503	1.75	2.13	1.39
	122504	1.73	2.01	1.41
	122510	1.60	1.75	1.17
	122513	1.67	2.02	1.35
	122514	1.63	1.89	1.23
	122515	1.73	2.19	1.38
	122908	1.81	2.16	1.59
	122940	1.60	1.98	1.27
	122941	1.72	2.00	1.42
	122942	1.74	2.09	1.44
	122944	1.81	2.00	1.44
	122946	1.64	1.90	1.35
	122953	1.78	2.17	1.49
	122986	1.60	1.90	1.28
	123162	1.73	1.99	1.32
	123163	1.58	1.79	1.25

Tooth position	**Specimen number**	**a-p length**	**tri width**	**tal width**
m2	122501	1.85	1.95	1.50
	122502	1.80	2.01	1.54
	122503	1.81	1.98	1.45

122504	1.84	1.76	1.37
122510	1.64	1.71	1.20
122511	1.77	1.93	1.39
122513	1.89	1.97	1.40
122514	1.85	1.81	1.31
122983	1.84	2.11	1.51
122984	1.72	1.88	1.43
122985	1.89	1.94	1.44
122987	1.70	1.93	1.37
122988	1.86	2.03	1.38
122989	1.74	1.96	1.39
122990	1.91	1.97	1.47
122991	1.87	2.03	1.41
122992	1.87	2.07	1.57
123177	1.66	1.72	1.32

SUPPLEMENTARY DATA TABLE 2. Tooth dimensions (in mm) of *H. niobrarensis* from Garner Bridge South locality (all UNSM numbers) (note: m3 not included here).

Tooth position	Specimen number	a-p length	tr width	
P3	123307	1.44	3.37	
P4	123307	1.56	3.82	
p3	123305	1.37	1.32	
Tooth position	**Specimen number**	**a-p length**	**tri width**	**tal width**
p4	123305	1.70	2.12	1.39
123306	1.81	2.32	1.51	
m1	123305	1.76	2.01	1.35
123306	1.59	2.19	1.47	
m2	123305	1.69	1.84	1.34
123306	1.87	2.15	1.59	

SUPPLEMENTARY DATA TABLE 3. Tooth dimensions (in mm) of *H. fluviatilis* from Kleinfelder Farm locality.

Tooth position	Specimen number	a-p length	tr width
P3	ROM 7385	1.08	2.98
	ROM 7386	1.19	2.57
P4	ROM 7342	1.46	3.74
	ROM 7399	1.48	2.51
	ROM 7412	1.50	3.54
	ROM 52635	1.30	3.44
M1	ROM 7345	1.35	2.33
	ROM 7352	1.21	2.13
M2	ROM 7343	1.16	2.35

Tooth position	Specimen number	a-p length	tr width
P3	ROM 7385	1.08	2.98
	ROM 7346	1.26	2.02
	ROM 7348	1.28	2.23
	ROM 7350	1.17	2.15
	ROM 7353	1.25	2.54
	ROM 52636	1.12	1.89
p3	ROM 7302	1.39	1.12
	ROM 7304	1.51	1.61
	ROM 7305	1.53	1.39

Tooth position	Specimen number	a-p length	tri width	tal width
p4	ROM 7314	1.64	1.71	1.23
	ROM 7319	1.64	1.92	1.22
	ROM 7322	1.67	2.02	1.32
	ROM 7324	1.63	1.85	1.19
	ROM 7338	1.53	1.73	1.23
	ROM 7416	1.66	1.79	1.22
	ROM 52638	1.59	1.68	1.24
	ROM 52642	1.56	1.98	-
m1	ROM 7313	1.50	1.66	1.17
	ROM 7315	1.69	1.87	1.27
	ROM 7318	1.56	1.75	1.10
	ROM 730	1.68	1.86	1.22
	ROM 7321	1.52	1.59	1.19
	ROM 7326	1.56	1.65	1.16
	ROM 7330	1.85	1.95	1.44
	ROM 7331	1.79	2.00	1.29
	ROM 7332	1.83	2.04	1.44
	ROM 7337	1.76	1.96	1.36
	UNSM 123357	1.51	1.86	1.23
m2	ROM 7310	1.41	1.67	1.09
	ROM 7311	1.62	1.72	1.29
	ROM 7312	1.46	1.55	1.16
	ROM 7317	1.43	1.56	1.19
	ROM 7325	1.63	1.62	1.19
	ROM 7327	1.69	1.72	1.37
	ROM 7334	1.80	1.86	-
	ROM 7335	1.54	1.78	1.16
	ROM 52639	1.35	1.39	1.08
	ROM 52642	1.60	1.65	1.14

Tooth position	Specimen number	a-p length	tr width	
P3	ROM 7385	1.08	2.98	
	UNSM 123355	1.60	1.72	1.26