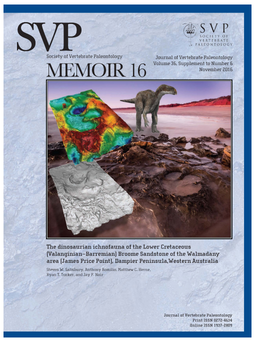

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ARTICLE

ADDITIONS TO THE LANCIAN MAMMALIAN FAUNA FROM SOUTHWEST NORTH DAKOTA

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ABSTRACT—Gaining a detailed understanding of the geographic and temporal variations between Lancian mammalian faunas within the Western Interior Basin requires specimens to be associated with precise stratigraphic data, but only a few mammal-producing localities are documented in such detail from the Hell Creek Formation of southwestern North Dakota. Recent work at two sites in southwestern North Dakota resulted in the discovery of additional mammal specimens from previously documented localities for which the stratigraphic position is precisely recorded. The most productive site is situated 12.07 m below the K/Pg boundary and produced 18 mammal specimens that are referable to at least six taxa, two of which (the multituberculate *Essonodon browni* and the marsupialiform *Glasbius twitchelli*) are first occurrences for North Dakota. Another important specimen (NDGS 1719) was collected as float approximately 1 m below a documented vertebrate locality that is positioned 2.72 m below the K/Pg boundary. This specimen is also referable to *G. twitchelli* and consists of a right dentary preserving p2–m4, making it the most complete dentary yet referred to that species. Specimen NDGS 1719 is the stratigraphically highest mammal specimen referred to a specific taxon yet reported from the Hell Creek Formation in North Dakota, and its completeness facilitates a detailed description of the dentition of *G. twitchelli*. These discoveries expand our knowledge of the Lancian fauna from southwestern North Dakota and demonstrate that further work is needed to ensure that our understanding of the Lancian fauna from North Dakota is comprehensive.

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INTRODUCTION

The Upper Cretaceous Hell Creek Formation of western North America records an important interval of time during which early mammals were diversifying and dispersing across the continent just prior to the Cretaceous-Paleogene (K/Pg) extinction event. The Late Cretaceous mammalian fauna of western North America is best documented in Montana and Wyoming where large numbers of specimens were meticulously collected with detailed geographic (Clemens, 1964, 1966, 1973; Archibald, 1982; Lofgren, 1995) and stratigraphic (Wilson, 2005, 2014) data. In contrast, these patterns in adjacent North Dakota remain less well resolved. The most detailed studies of the mammalian fauna from the Late Cretaceous of North Dakota were done using specimens collected over the past few decades in southwestern North Dakota (Bowman and Slope counties) by the Pioneer Trails Regional Museum in Bowman, North Dakota (Hunter and Pearson, 1996; Hunter and Archibald, 2002; Pearson et al., 2002). Those specimens were tied into a detailed stratigraphic framework, with the vertical distance between each locality and the contact between the Hell Creek Formation and the overlying Ludlow Formation precisely recorded (Pearson et al., 2002). The distance between each locality and the K/Pg boundary, which is not always coincident with the formation contact in that area, was also calculated using the palynology data reported by Nichols and Johnson (2002). Those studies laid the groundwork for future work on the diversity and stratigraphic distribution of mammals from the Hell Creek Formation of North Dakota.

Only a handful of mammal specimens collected from the Hell Creek Formation of North Dakota by the North Dakota Geological Survey (NDGS) are published (Hoganson et al., 1994; Murphy et al., 1995). Although those reports focused on collections from south central North Dakota, the NDGS also works extensively in the Hell Creek Formation of southwestern North Dakota. This study expands upon the work of Hunter and Archibald (2002), detailing new additions to the mammalian fauna of southwestern North Dakota collected from stratigraphically constrained localities within the upper portion of the Hell Creek Formation (Fig. 1). This study adds to the growing body of work on North Dakota's Late Cretaceous mammalian fauna, enabling future studies to conduct more accurate comparisons with other contemporaneous faunas across North America.

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York, New York; **BUNM**, University of New Mexico, Albuquerque, New Mexico; **NDGS**, North Dakota Geological Survey State Fossil Collection, Bismarck, North Dakota; **PTRM**, Pioneer Trails Regional Museum, Bowman, North Dakota; **PU**, Princeton University Collection, Yale Peabody Museum of Natural History, New Haven, Connecticut; **UCMP**, University of California Museum of Paleontology, Berkeley, California; **UW**, University of Wyoming Departmental Scientific Collections of the Department of Geology and Geophysics, Laramie, Wyoming.

MATERIALS AND METHODS

Geologic Field Methods

Specimens discussed in this study were surface collected during routine monitoring of known vertebrate fossil localities by the North Dakota Geological Survey. Even though ant hills are pervasive at most Hell Creek Formation localities in North Dakota and can concentrate microvertebrate fossils (Clemens, 1964), none of the specimens used in this study were retrieved

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*Corresponding author.

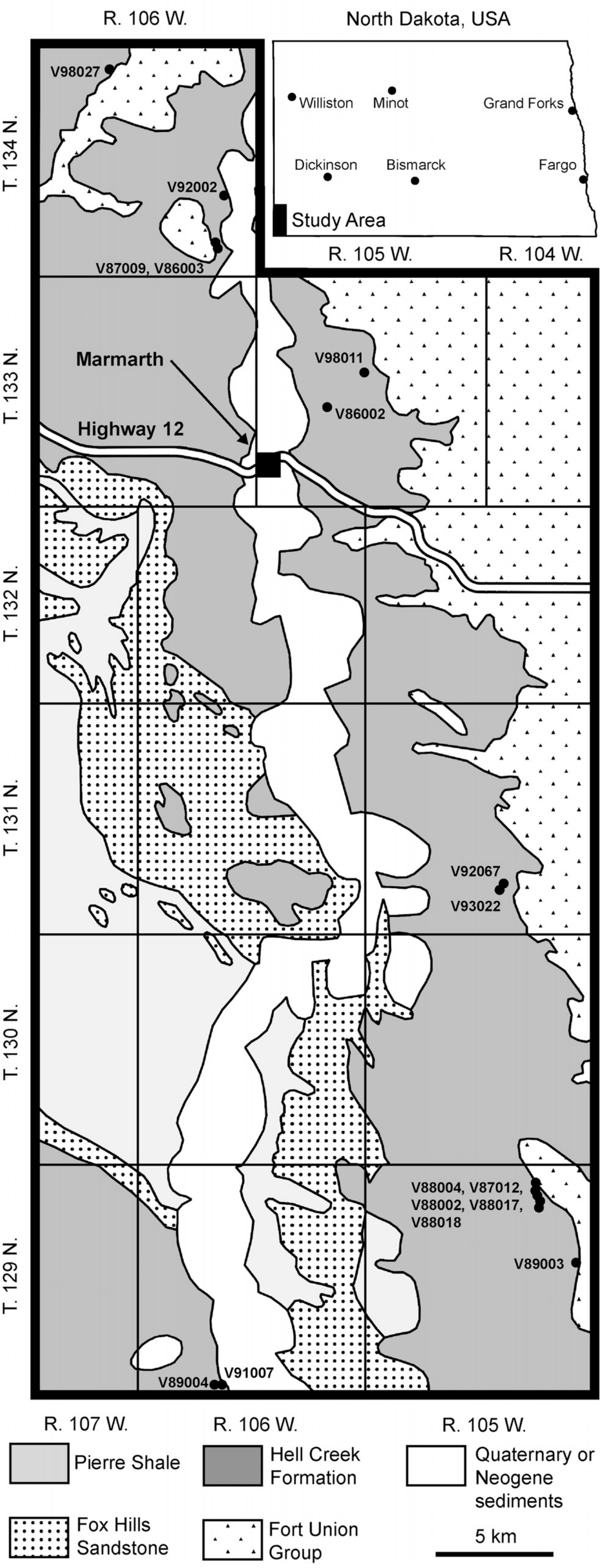

FIGURE 1. Geologic map of southwest North Dakota (western portion of Bowman County and southwestern corner of Slope County) showing the geographic positions of paleontological localities within the Hell Creek Formation where fossils of mammals were recovered. Overview of the location of the study area within North Dakota is inset in the top right. Modified from Hunter and Archibald (2002:fig. 1), with geology based on a digitized version of the map produced by Clayton (1980).

from ant hills. Fossils were first collected by members of the North Dakota Geological Survey at locality NDGS L226 (= PTRM V98027) in 1995. All of the specimens here referred to *Glasbius twitchelli* from that locality were collected during that first year. Subsequent visits to the site have produced many additional vertebrate specimens, including additional mammalian fossils, but no additional specimens of *G. twitchelli* were recovered. This locality is situated 12.07 m below the K/Pg boundary, and 10.62 m below the contact between the Hell Creek Formation and the Fort Union Group (Pearson et al., 2002). Preserved within the sandstone channel deposit is a diverse fauna that includes more than 20 taxa of fish, amphibians, lizards, turtles, crocodylians, dinosaurs, and mammals (Pearson et al., 2002:table 2; this study). Although mammals were not reported from this locality based on study of the collections held at the PTRM (Pearson et al., 2002), collection efforts by the NDGS through the years at that site produced fossils of at least six mammalian taxa represented by 18 specimens (Table 1). This makes NDGS L226 the most diverse and productive site for mammalian fossils yet reported within 30 m of the K/Pg boundary in southwestern North Dakota (Hunter and Pearson, 1996; Hunter and Archibald, 2002; Pearson et al., 2002). These new data from NDGS L226 increase the known diversity of the Late Cretaceous mammalian fauna from North Dakota (Table 2).

Specimen Preparation Methods

Specimens were cleaned using a Comco Inc. Microblaster (model MB1002–1) loaded with sodium bicarbonate.

Measurement Methods

All measurements were taken digitally using the following procedure. Specimens were digitally photographed in the same orientations as shown in their respective figures using a Wild Heerbrugg M8 binocular microscope with an attached Olympus D72 camera using the Olympus Steam Essentials (v. 1.6.1) software. The measurement tools built into that program were then used to draw lines onto the images and record their lengths once the final size and placement was properly adjusted. For the premolars, maximum anteroposterior length was first recorded followed by maximum labiolingual width oriented orthogonal to the length. For the molars, maximum anteroposterior length (from the anterior margin of the precingulid to the posterior margin of the hypoconulid) was measured along a line parallel to a line drawn through the apices of the metaconid and entoconid. The maximum labiolingual widths of the trigonid and talonid portions of the molars were then measured along a line orthogonal to the maximum anteroposterior length. Once all measurements for a specimen were complete, a .jpg file was saved that recorded the placement and extent of the measurement lines and a Microsoft Excel table was exported recording the measurements. Measurements were recorded to a hundredth of a micrometer but were rounded to a hundredth of a millimeter to match other published data sets.

Photography Methods

Specimens NDGS 1719, 1720, 1721, 1722, 1723, and 1724 were coated with magnesium oxide by burning a strip of magnesium metal and holding the specimen over the resulting smoke. All

TABLE 1. Mammalian fauna from locality NDGS L226 (= PTRM V98027), Hell Creek Formation, southwestern North Dakota.

NDGS 1792	Multituberculata	*Essonodon browni*	Right dentary with m1
NDGS 1789	Multituberculata	*Mesodma* sp. cf. *M. thompsoni*	Right M1
NDGS 1790	Multituberculata	*Cimolodon nitidus*	Right P4
NDGS 1791	Multituberculata	*Cimolodon nitidus*	Partial right P4
NDGS 1794	Multituberculata	indeterminate	Left p4
NDGS 1795	Multituberculata	indeterminate	Right m2
NDGS 1801	Metatheria	*Alphadon* sp.	Right M2 or M3
NDGS 1793	Metatheria	*Glasbius twitchelli*	Left maxilla with M2–3
NDGS 1720	Metatheria	*Glasbius twitchelli*	Left m2
NDGS 1721	Metatheria	*Glasbius twitchelli*	Left m2
NDGS 1722	Metatheria	*Glasbius twitchelli*	Left m3
NDGS 1723	Metatheria	*Glasbius twitchelli*	Right m3
NDGS 1724	Metatheria	*Glasbius twitchelli*	Right m3
NDGS 1798	Eutheria	*Gypsonictops* sp.	Right M2
NDGS 1800	Eutheria	*Gypsonictops* sp.	Left P4
NDGS 1796	Mammalia	indeterminate	Partial mx
NDGS 1797	Mammalia	indeterminate	Partial Mx
NDGS 1799	Mammalia	indeterminate	Two incisors

Abbreviations: **M**, upper molar; **m**, lower molar; **P**, upper premolar; **p**, lower premolar; **x**, uncertain tooth position.

specimens were then imaged 12 times at varying focal planes using a Canon 60D camera, a custom-built 4 × magnification lens, and the Stacksho camera control system. Focal stack images were montaged with Helicon Focus and final processing (e.g., removal of background) was done in Adobe Photoshop.

Tooth Terminology

This study uses the marsupialiform dental terminology outlined in Williamson et al. (2014:fig. 3), which used the dentition of *Glasbius* as the model for their terminology. Marsupialiform tooth identification follows the traditional pattern of three premolars and four molars in both the upper and lower dentition for ease of comparison with previous studies, rather than that proposed in Williamson et al. (2014:fig. 4). Tooth position abbreviations used below are P or p for premolars and M or m for molars, depending on if they are from the upper or lower dentition, respectively.

TABLE 2. Mammalian fauna of the Hell Creek Formation, southwestern North Dakota.

- Multituberculata
  - *Essonodon browni* Simpson, 1927
  - *Mesodma thompsoni* Clemens, 1964
  - *Mesodma* sp. cf. *M. thompsoni* Clemens, 1964
  - *Cimolodon nitidus* Marsh, 1889
  - *Cimolodon* sp.
  - *Meniscoessus robustus* (Marsh, 1889)
  - *Meniscoessus* sp.
  - ?*Meniscoessus* sp.
- Metatheria
  - *Alphadon marshi* Simpson, 1927
  - *Alphadon* sp.
  - *Didelphodon vorax* Marsh, 1889
  - *Didelphodon* sp.
  - ?*Didelphodon* sp.
  - *Protolambda florencae* (Clemens, 1966)
  - *Protolambda* sp. cf. *P. florencae* (Clemens, 1966)
  - *Glasbius twitchelli* Archibald, 1982
- Eutheria
  - *Altacreodus magnus* (Clemens and Russell, 1965)
  - *Gypsonictops illuminatus* Lillegraven, 1969
  - *Gypsonictops* sp.

Modified from Hunter and Archibald (2002:table 2). Updated taxonomy based on Davis (2007) and Fox (2015).

Geologic Terminology

Terminology of stratigraphic units follows that proposed by the North Dakota Geological Survey, which may differ from that employed by the United States Geological Survey. The stratigraphic positions of all localities relative to the K/Pg boundary are based on data provided by Hunter and Archibald (2002) and Pearson et al. (2002). The PTRM locality numbers and geographic positions of the two paleontological localities that are the focus of this study were provided in the field in May and July of 2015 by Dean Pearson of the PTRM.

SYSTEMATIC PALEONTOLOGY

MAMMALIA Linnaeus, 1758
MULTITUBERCULATA Cope, 1884
CIMOLOMYIDAE Marsh, 1889
ESSONODON Simpson, 1927

Name-Bearing Species—*Essonodon browni* Simpson, 1927.

Other Included Species—None.

Diagnosis—As for type and only known species.

ESSONODON BROWNI Simpson, 1927
(Fig. 2)

Holotype—AMNH 14410, an isolated right m2.

Type Locality—The holotype was collected from the Hell Creek Formation near the head of the East Fork of Crooked Creek in Garfield County, Montana (Dawson County at the time of collection; Clemens, 1964; Lofgren, 1995), but no exact location is provided.

Referred Specimens—NDGS 1792: fragment of right dentary preserving the crown of m1 and the alveoli for p4 and the incisor (Table 3).

Distribution—Restricted to the Lancian North American Land Mammal Age (Cifelli et al., 2004). Geographic distribution is the Ojo Alamo Formation (Naashoibito Member) of New Mexico, U.S.A. (locality BUNM-77-675; Lehman, 1984); the Lance Formation of Wyoming, U.S.A. (locality UCMP V84215 [= UW V-79032] and several other specimens from unknown locations; Marsh, 1892; Clemens, 1964; Archibald, 1982; Donogue et al., 2013); the Hell Creek Formation of Montana, U.S.A. (localities UCMP V73076, UCMP V73083, UCMP V73087, UCMP V76138, UCMP V77130, UCMP V80092, UCMP V86084, and UCMP V87151; the Bug Creek Anthills; and the type locality [see description above]; Simpson, 1927; Sloan and Van Valen, 1965; Archibald, 1982; Lofgren, 1995; Hutchinson and Chiappe, 1998; Hunter and Archibald, 2002), and North Dakota, U.S.A. (Slope County [PTRM V98027 = NDGS L226]; this report); and possibly the Frenchman Formation of Saskatchewan, Canada (Wounded Knee local fauna: Fox, 1989).

Emended Diagnosis—*Essonodon browni* is differentiated from all other cimolomyids as follows: "length ratios of P4 to M1, M2 to M1, and m2 to m1 very low; known portion of P4 crown very tall, probably with extremely steep anterior edge; P4 possibly lacking anteroexternal cusps; molar cusps complicated by numerous accessory ridges; crowns of M1 and m1 very low and broad; internal cusp row on M1 greater than half M1 length; m2s and M2s wider than long; m1 with small, posterolabial cuspules; M2 with only two distinct cusp rows; M1 and m1 with numerous accessory roots" (Archibald, 1982:89–90).

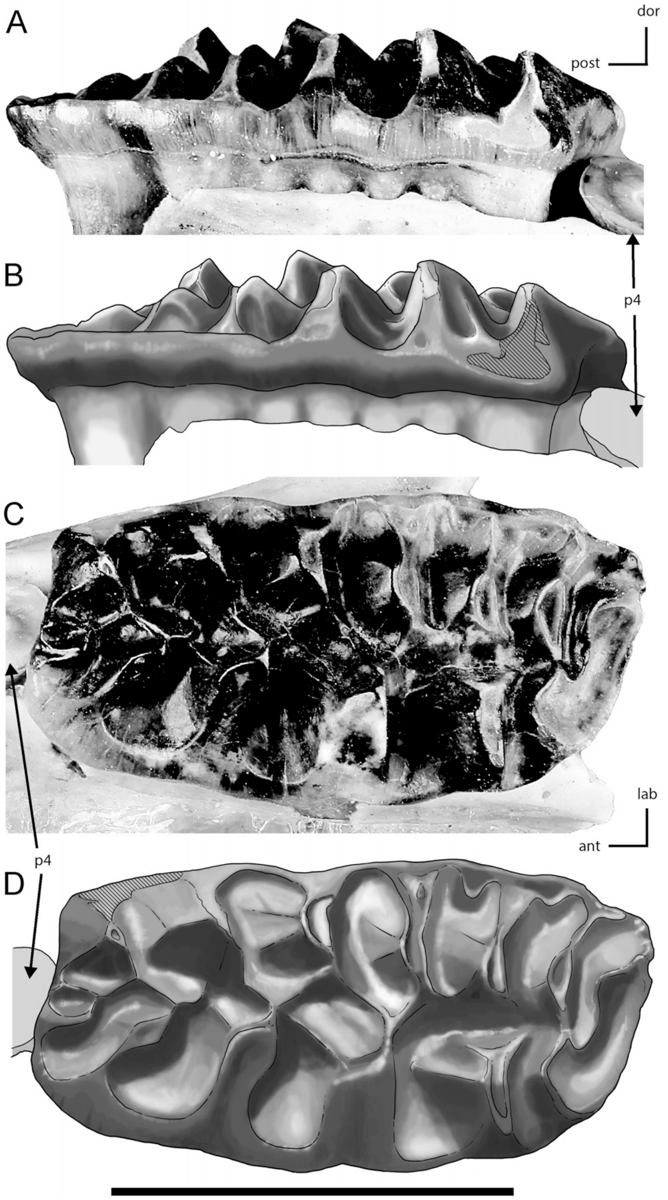

FIGURE 2. Illustrations and photographs of partial right dentary with m1 (NDGS 1792) referred to *Essonodon browni*. **A**, photograph in labial view; **B**, illustration in labial view; **C**, photograph in occlusal view; **D**, illustration in occlusal view. Crosshatching in illustrations denotes broken region. **Abbreviations**: **ant**, anterior; **dor**, dorsal; **lab**, labial; **p4**, broken root of lower fourth premolar; **post**, posterior. Scale bar equals 5 mm.

Comments—The presence of the row of posterolabial cuspules on m1 is diagnostic for *Essonodon browni* (Fig. 2B; Archibald, 1982), as is the presence of numerous accessory roots on the m1 (Fig. 2A; Archibald, 1982). The morphology of m1 was extensively described by Archibald (1982), eliminating the need for a similar effort here.

METATHERIA Huxley, 1880
MARSUPIALIFORMES Vullo and Gheerbrant, 2009
GLASBIIDAE Clemens, 1966
GLASBIUS Clemens, 1966

Name-Bearing Species—*Glasbius intricatus* Clemens, 1966.

Other Included Species—*Glasbius twitchelli* Archibald, 1982.

Emended Diagnosis—The following differential diagnosis is modified from Archibald (1982) based on observation of the specimens here referred to *Glasbius*: principal cusps on upper molars low relative to trigon basin; metacone higher than paracone and metaconule larger than paraconule; stylar shelf broad; stylar cusp B large on M1–4; D higher than B on M1–2, smaller than B on M3, absent on M4; A and E small; C small or absent; m2 longer than other molars; talonid (including labial cingulum) wider than trigonid, except on m4; width of trigonids of m3 > m2 > m1; cristid obliqua contacts trigonid on back of protoconid; trigonid short anteroposteriorly, paraconid and metaconid closely approximated on m3–4; difference in height of trigonid over talonid not great and decreases from m1 to m4; lingual side of crown higher than labial, except on m1–2 where protoconid is subequal to metaconid; basal cingulum on anterior, labial, and posterior sides of m1–4 with variously developed cusps on some molars; M4/m4 much smaller than preceding molars; p1–3 double-rooted. *Glasbius* may also be differentiated from most other North American metatherians by the anteroposterior axis of p1 rotated at 30–45° to long axis of dentary, although this is only confirmed in *Glasbius twitchelli* and the discovery of more complete specimens of *Glasbius intricatus* may reveal this trait to be an apomorphy of *G. twitchelli* (see comments below).

GLASBIUS TWITCHELLI Archibald, 1982
(Figs. 3, 4)

Holotype—UCMP 115853, an isolated right M3.

Type Locality—UCMP V73087 (Hell Creek Formation, Garfield County, Montana).

Referred Specimens from This Study—NDGS 1719, partial right dentary with alveoli for lower canine and p1, crowns of p2–m4 present; NDGS 1720, left m2 in situ within a small piece of the dentary; NDGS 1721, isolated left m2; NDGS 1722, left m3 in situ within a small piece of the dentary; NDGS 1723, isolated right m3; NDGS 1724, isolated right m3; NDGS 1793, partial maxilla with M2–3.

Distribution—Restricted to the Lancian North American Land Mammal Age (Cifelli et al., 2004). Geographic distribution is the Frenchman Formation of Saskatchewan, Canada (Wounded Knee local fauna; Fox, 1989); the Lance Formation of Wyoming, U.S.A. (locality UCMP V5621; Clemens 1966; see Discussion section); and the Hell Creek Formation of Montana, U.S.A. (localities UCMP V65127, UCMP V70201, UCMP V72212, UCMP V72215, UCMP V73077, UCMP V73078, UCMP V73087, UCMP V73097, UCMP V74116, UCMP V80092, UCMP V86083, UCMP V86084, UCMP V87035,

TABLE 3. Comparisons between published measurements of m1 of *Essonodon browni* (a single specimen was reported in each study) and the referred specimen from North Dakota (NDGS 1792). All measurements are in mm.

Dimension	This study Hell Creek Fm. North Dakota	Archibald (1982) Hell Creek Fm. Montana	Lehman (1984) Kirtland Shale New Mexico	Archibald (1982) Lance Fm. Wyoming
Length	7.71	7.90#	6.8	7.12
Width	3.98	4.15	3.4	3.83

Abbreviations: **Fm.**, Formation; #, approximate measurement.

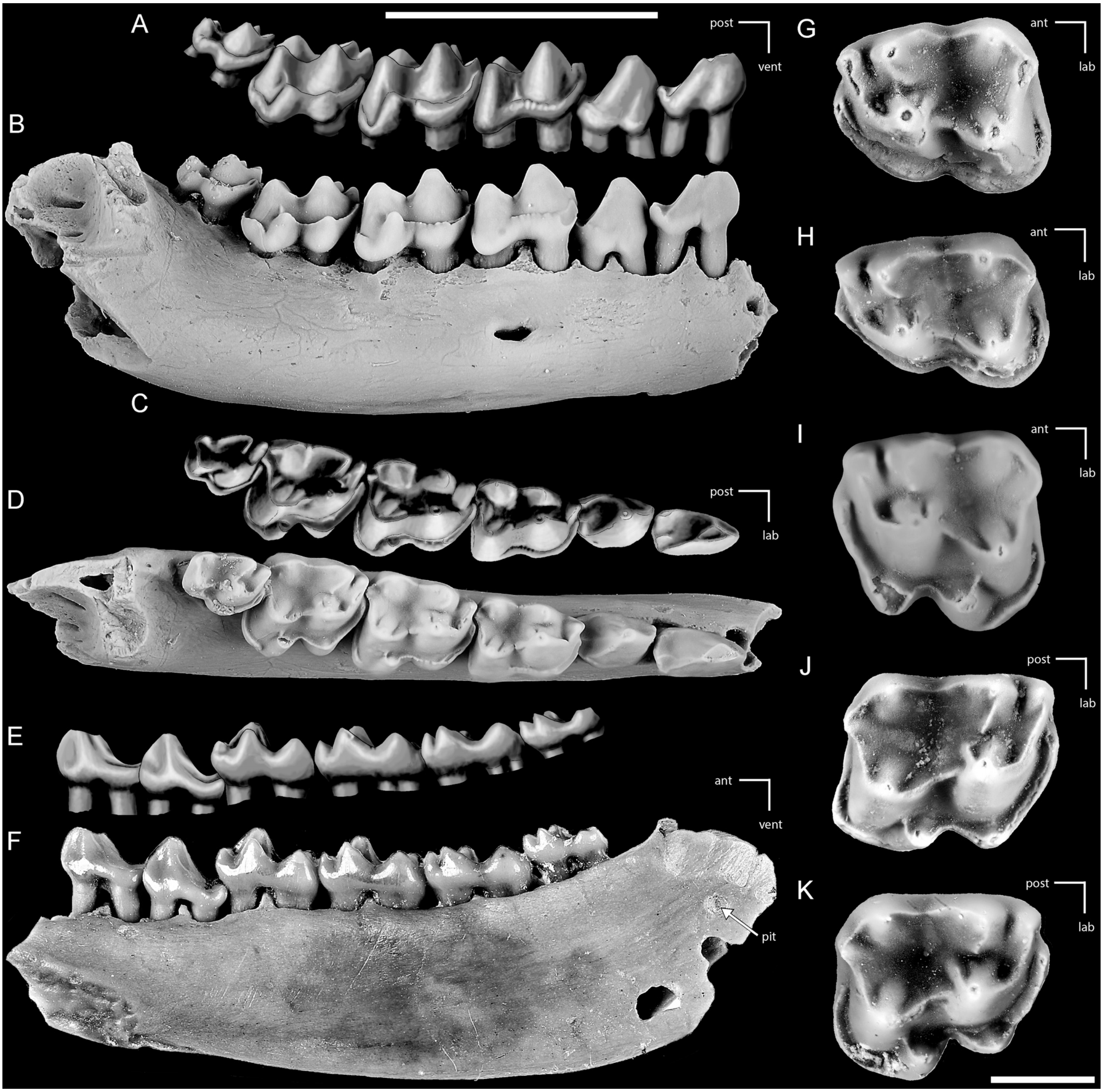

FIGURE 3. Illustrations and photographs of specimens from North Dakota referred to *Glasbius twitchelli*. **A**, illustration of the dentition (p2–m4) of NDGS 1719 in labial view; **B**, photograph of NDGS 1719 (right dentary with p2–m4) in labial view (view is oriented slightly more ventral than in **A**); **C**, illustration of the dentition (p2–m4) of NDGS 1719 in occlusal view; **D**, photograph of NDGS 1719 (right dentary with p2–m4) in occlusal view; **E**, illustration of the dentition (p2–m4) of NDGS 1719 in lingual view; **F**, photograph of NDGS 1719 (right dentary with p2–m4) in lingual view; **G**, photograph of NDGS 1720 (left m2) in occlusal view; **H**, photograph of NDGS 1721 (left m2) in occlusal view; **I**, photograph of NDGS 1722 (left m3) in occlusal view; **J**, photograph of NDGS 1723 (right m3) in occlusal view; **K**, photograph of NDGS 1724 (right m3) in occlusal view. In **B**, **D**, **G**, **H**, **I**, **J**, and **K**, specimens were coated with magnesium oxide prior to photographing (see Materials and Methods). **Abbreviations**: **ant**, anterior; **lab**, labial; **pit**, possible feeding trace; **post**, posterior; **vent**, ventral. Scale bars equal 5 mm (**A**–**F**) and 1 mm (**G**–**K**).

UCMP V87037, UCMP V87038, UCMP V87072, and UCMP V87074; Sloan and Van Valen, 1965; Archibald, 1982; Lofgren, 1995; Hutchinson and Chiappe, 1998; Hunter and Archibald, 2002), and North Dakota, U.S.A. (Bowman County [PTRM V88002 = NDGS L10173] and Slope County [PTRM V98027 = NDGS L226]; this report).

Diagnosis—*Glasbius twitchelli* differs from *Glasbius intricatus* as follows: "Stylar cusp C absent on all molars except for slight swelling on anterior margin of cusp D of M1; buccal (basal) cingulum of unworn m2 bears cusp below and anterior to hypoconid; m3 has similar cusp plus additional buccal (basal) cusp below protoconid. Molars are slightly larger than their counterparts in *G. intricatus*" (Archibald, 1982:138).

Comments—No single specimen preserves portions of both the upper and lower dentition of *Glasbius twitchelli*. As a result, different levels of confidence are associated with referrals of new specimens to that taxon. Specimen NDGS 1793 preserves the M3, facilitating direct comparison with published illustrations and descriptions of the holotype M3 (UCMP 115853; Archibald, 1982:figs. 45e, f), allowing confident referral of that specimen to *Glasbius twitchelli*. The referrals in this study of specimens preserving portions of the lower dentition to *G. twitchelli* (NDGS 1719–1724) are based on comparisons with illustrations and descriptions of other specimens previously referred to *G. twitchelli*, especially those in the original description (Archibald, 1982). Although these latter referrals are not based on direct comparison with the holotype, the consistent co-occurrence of these upper and lower dental morphologies in the same localities makes it unlikely that they represent separate genera.

Specimen AMNH 58759, a partial dentary preserving p2–m3 and the alveolus for p1, was tentatively referred to *G. intricatus* by Clemens (1966). It was the only specimen that preserved portions of the lower premolar dentition for that taxon. Archibald (1982) argued that AMNH 58759 should not be referred to *G. intricatus* in part because p3 was shorter anteroposteriorly and narrower labiolingually than p2, the opposite condition to that seen in the one specimen confidently referred to *G. twitchelli* that preserves the crowns of p2 and p3 (UCMP 117570). In NDGS 1719, the p3 is labiolingually wider than p2, but it is slightly shorter anteroposteriorly (Table 4). These observations demonstrate that the relative sizes of p2 and p3 are variable in *G. twitchelli* (Table 5) and should not be a feature used to either refer or exclude specimens from *Glasbius*. Archibald (1982) also used the fact that the p1 alveoli are not rotated relative to the long axis of the dentary as evidence that AMNH 58759 should not be referred to *Glasbius*. However, that unique orientation of the p1 alveoli is only observed in specimens of *G. twitchelli* and is unknown for *G. intricatus*, so it may be that this feature differentiates these two species rather than diagnosing *Glasbius* as proposed by Archibald (1982). However, several other differences between AMNH 58759 and other specimens referred to *G. intricatus* remain that may support the removal of this specimen from that taxon (Clemens, 1966; Archibald, 1982). Until a more detailed examination of AMNH 58759 is conducted, its taxonomic affinities should be regarded as uncertain as proposed by Archibald (1982).

Specimen UCMP 52045, an isolated m3 from the Lance Formation of Wyoming (locality UCMP V5621), was part of the original hypodigm of *G. intricatus* (Clemens, 1966:fig. 18). Archibald (1982) reassigned some specimens previously referred by Clemens (1966) to *G. intricatus* to *G. twitchelli* (e.g., PU 17286), but no mention is made regarding the taxonomic status of UCMP 52045 in that or any other publication after the original referral by Clemens (1966). That specimen displays prominent posterior and anterior buccal cingulid cusps that are diagnostic for *G. twitchelli*, and the overall morphology of UCMP 52045 closely matches that of the m3s here referred to *G. twitchelli* (Fig. 3). Thus, UCMP 52045 is here transferred to *G. twitchelli*, making it the first occurrence of that species from the Lance Formation of Wyoming. No other specimens were referred to *Glasbius* from locality UCMP V5621, so there remains no overlap of the two species of *Glasbius* from a single locality, although the geographic distributions of these taxa are now much closer based on this referral. It remains uncertain if these two species were contemporaneous, if the slight differences between them may be the result of anagenetic change within the lineage, or if larger sample sizes will eventually demonstrate that the two currently recognized species actually represent the extreme endpoints of the range of tokogenetic variation present within a single species. Collection of additional specimens with detailed geographic and stratigraphic data is needed to properly address those possibilities. Although information on the stratigraphic distribution of *Glasbius* from the Hell Creek Formation of Montana and North Dakota is available (e.g., Wilson, 2005, 2014; this study), comparable information is not yet available for the Lance Formation of Wyoming.

Description—Although Archibald (1982) provided a general overview of the dentition of *Glasbius twitchelli*, his description largely focused on the differences between *G. intricatus* and *G. twitchelli*, referring readers to the description of *G. intricatus* by Clemens (1966) for a more detailed description of the dentition. Specimen NDGS 1719 preserves nearly the entire postcanine dentary dentition, missing only the crown of p1, making it the preferred basis for the first detailed description of the lower dentition of *G. twitchelli*. When differences are noted between the morphology of NDGS 1719 and either the isolated lower teeth above referred to *Glasbius twitchelli* or previously published descriptions, that variation is discussed and the relevant specimens or references are cited. This allows for tokogenetic variation in *G. twitchelli* to be discussed, although given the small number of specimens examined, the full extent of such variation likely remains unsampled. Regardless, this information will help to prevent erroneous identification of additional specimens in the future and contribute to our understanding of the evolution of this relatively poorly known taxon. The maxillary dentition preserved in NDGS 1793 is also described in detail, with comparisons made with previously published descriptions. Dental measurements for all of the North Dakota specimens of *G. twitchelli*, along with previously published dental measurements for both *G. twitchelli* and *Glasbius intricatus*, are given in Tables 4, 5, and 6.

The total preserved length of the dentary in NDGS 1719 is 14.23 mm. The anterior-most and posterior-most portions are missing, including much of the mandibular ramus. A small portion of the anteroventral corner of the masseteric fossa is preserved. Anterior to that fossa, the base of the anteroposteriorly compressed and labiolingually thickened coronoid crest is

TABLE 4. Measurements of specimens preserving the lower dentition here referred to *Glasbius twitchelli* from the Hell Creek Formation of North Dakota. All measurements are in mm.

	p2		p3		m1			m2			m3			m4		
Specimen	L	W	L	W	L	Wtri	Wta	L	Wtri	Wta	L	Wtri	Wta	L	Wtri	Wta
NDGS 1719	1.62	0.84	1.51	1.00	2.02	1.23	1.57	2.13	1.50	1.91	1.97	1.71	1.88	1.55	1.14	0.88
NDGS 1720	—	—	—	—	—	—	—	2.05	1.54	1.76	—	—	—	—	—	—
NDGS 1721	—	—	—	—	—	—	—	2.02	1.50	1.68	—	—	—	—	—	—
NDGS 1722	—	—	—	—	—	—	—	—	—	—	2.03	1.77	1.99	—	—	—
NDGS 1723	—	—	—	—	—	—	—	—	—	—	2.11	1.59	1.87	—	—	—
NDGS 1724	—	—	—	—	—	—	—	—	—	—	2.09	1.64	1.63	—	—	—

Abbreviations: **L**, length; **m**, lower molar; **p**, lower premolar; **Wta**, width of talonid; **Wtri**, width of trigonid.

TABLE 5. Comparisons between published measurements of the lower dentition of *Glasbius* and the specimens here referred from North Dakota. All measurements are in mm.

		This study *Glasbius twitchelli* Hell Creek Fm. North Dakota				Archibald (1982) *Glasbius twitchelli* Hell Creek Fm. Montana				Fox (1989) *Glasbius twitchelli* Frenchman Fm. Saskatchewan				Lofgren (1995) *Glasbius twitchelli* Hell Creek Fm. Montana				Clemens (1966) *Glasbius intricatus* Lance Fm. Wyoming			
Tooth	Dimension	N	Min	Max	Mean	N	Min	Max	Mean	N	Min	Max	Mean	N	Min	Max	Mean	N	Min	Max	Mean
p1	Length	—	—	—	—	1	—	—	0.98	—	—	—	—	—	—	—	—	—	—	—	—
	Width	—	—	—	—	1	—	—	0.52	—	—	—	—	—	—	—	—	—	—	—	—
p2	Length	1	—	—	1.62	2	1.47	1.49	1.48	—	—	—	—	—	—	—	—	—	—	—	—
	Width	1	—	—	0.84	2	0.73	0.75	0.74	—	—	—	—	—	—	—	—	—	—	—	—
p3	Length	1	—	—	1.51	2	1.40	1.68	1.54	—	—	—	—	1	—	—	1.53	—	—	—	—
	Width	1	—	—	1.00	2	0.70	0.92	0.81	—	—	—	—	1	—	—	0.97	—	—	—	—
m1	Length	1	—	—	2.02	3	1.95	2.04	2.00	—	—	—	—	—	—	—	—	1	—	—	1.80
	Wtri	1	—	—	1.23	3	1.00	1.10	1.04	—	—	—	—	—	—	—	—	1	—	—	1.05
	Wta	1	—	—	1.57	3	1.20	1.34	1.25	—	—	—	—	—	—	—	—	1	—	—	1.15
m2	Length	3	2.02	2.13	2.07	4	2.13	2.26	2.20	1	—	—	2.10	3	1.98	2.29	2.15	4	1.90	1.95	1.93
	Wtri	3	1.50	1.54	1.51	4	1.24	1.44	1.34	1	—	—	1.30	3	1.25	1.41	1.35	4	1.10	1.20	1.16
	Wta	3	1.68	1.91	1.78	5	1.51	1.73	1.61	1	—	—	1.60	3	1.51	1.76	1.66	4	1.30	1.40	1.34
m3	Length	4	1.97	2.11	2.05	3	2.08	2.20	2.12	—	—	—	—	3	2.10	2.10	2.10	6	1.70	2.05	1.83
	Wtri	4	1.59	1.77	1.68	3	1.42	1.53	1.48	—	—	—	—	3	1.60	1.78	1.69	6	1.20	1.55	1.38
	Wta	4	1.63	1.99	1.84	4	1.52	1.75	1.65	—	—	—	—	3	1.75	2.02	1.91	6	1.30	1.70	1.47
m4	Length	1	—	—	1.55	1	—	—	1.56	—	—	—	—	1	—	—	1.55	2	1.20	1.40	1.30
	Wtri	1	—	—	1.14	1	—	—	1.10	—	—	—	—	1	—	—	1.21	2	0.80	1.00	0.90
	Wta	1	—	—	0.88	1	—	—	1.06	—	—	—	—	1	—	—	1.06	2	0.65	0.85	0.75
mx	Length	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	Wtri	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	Wta	—	—	—	—	—	—	—	—	—	—	—	—	4	1.83	1.91	1.87	—	—	—	—

Abbreviations: **Fm.**, Formation; **m**, lower molar; **Max**, maximum observed value; **Min**, minimum observed value; **N**, number of measurements; **p**, lower premolar; **Wta**, width of talonid; **Wtri**, width of trigonid.

present. The alveoli for m4 are positioned on the anterior surface near the base of that crest, which results in the reduced m4 (relative to the other molars) being situated higher than much of the rest of the dentition. The lateral surface is broadly dorsoventrally convex and bears two mental foramina. The anterior-most mental foramen is small and rounded, situated slightly below the alveolar margin at the level of the alveoli for p1, as seen in UCMP 117570 (Archibald, 1982:fig. 46b). The posterior-most mental foramen is larger and anteroposteriorly elongate, situated at about mid-height of the dentary and positioned below the posterior alveolus for m1. In other specimens referred to *Glasbius*, the posterior-most mental foramen is positioned below the anterior alveolus for m1, underneath the trigonid (Clemens, 1966; Archibald, 1982), although the published figures show that there is some variability in the exact position of that foramen and the position described here for NDGS 1719 is likely just an extension of that variation. The ventral surface is deeply convex labiolingually and is slightly convex anteroposteriorly. The anteroventral portion of the medial surface bears the rugose dentary symphysis, which extends up to mid-height and terminates approximately level with the posterior alveolus for p2, consistent with other specimens of *G. twitchelli* (Archibald, 1982). The surface of the dentary symphysis is oriented ventrolingually, with the dorsal margin demarcated by a moderately developed ridge. Posterior to the dentary symphysis the medial surface is slightly convex, but it transitions to slightly concave starting below m3. A slight, crescentic ridge is present on the medial surface at the base of the coronoid crest, and above that ridge the coronoid crest deflects slightly labially and the surface is slightly concave. An ovate hole is present near the posteroventral corner of the medial surface. Posterodorsal to that hole, a rounded indentation is present along the broken posterior margin, and directly dorsal to that, a small, circular pit is present (Fig. 3F). Neither the hole nor the rounded indentation represents natural foramina because their margins are formed by irregular, broken bone. Given the presence of the rounded pit just dorsal to these broken areas, these features may represent feeding traces from an unidentified carnivore.

The canine and p1 are not preserved in NDGS 1719, nor are they represented in the other specimens referred to *Glasbius twitchelli* from North Dakota. Both alveoli for p1 are preserved, and they indicate that the anteroposterior axis of p1 was rotated between 45° and 50° from the long axis of the dentary, a feature seen in other specimens referred to *Glasbius twitchelli* and proposed to be diagnostic for *Glasbius* by Archibald (1982), although see comments above. The p2 is also double-rooted. In occlusal view, the p2 is 'triangular-shaped,' being pointed anteriorly and broadly convex posteriorly with distinct posterolabial and posterolingual facing portions (Fig. 3D). The anterolabial surface of the p3 fits against the posterolingual margin of the p2. A slight ridge extends along the anterior edge of the crown from the base to the apex. The apex of the tooth bears a triangular, dorsally flattened wear facet. The posterior surface of the tooth bears three slight ridges. The most pronounced extends from the apex to the posterolabial corner of the crown, forming the labial margin of a broad, posterolingually facing basin. The anterolingual margin of that basin is formed by a broad, lingually convex swelling situated about halfway along the lingual margin of the crown that extends from the base of the crown to the apex. A slight swelling extends along the base of the crown from that lingual convexity to the posterolingual corner. The second ridge extends down to a very small cusp situated at the posterolingual corner of the crown. That ridge is difficult to identify unless the light is positioned on the specimen just right, making it the least developed of the three posterior ridges. The final ridge at first extends just lingual to the posterolabial ridge before angling lingually and terminating at a small, triangular cusp that forms the highest point along the posterior margin of the crown (Fig. 3B), separating a small, posterolabially facing basin from the rest of the posterior margin of the crown. A slight, irregularly denticulate ridge extends along the posterior margin of the crown from the end of the posterolabial ridge to the end of the faint posterolingual ridge. The labial surface of the crown is very gently anteroposteriorly convex, and a slight swelling is present along the base that is most pronounced posteriorly. The anterolingual surface of the tooth is very slightly anteroposteriorly concave.

The p3 is generally similar in morphology to the p2, but distinct differences are present that differentiate these teeth. The wear facet at the apex of the crown is smaller, circular, and faces dorsally and slightly posteriorly. The anterior ridge extends down from the apex of the crown, but curves anterolingually. As a result, the anterior-most point of the crown is situated level with the posterolingual corner of the p2 and the labial surface of the tooth is much more broadly convex, extending around the anterior margin of the crown (Fig. 3D). The anterolingual concavity is still present, but the ventral margin is more clearly demarcated by a slight ridge. The anterolingual concavity is separated from the posterolingual basin by a broad, dorsoventrally oriented, convex swelling that extends the entire height of the crown. Unlike on the p2, only two posterior ridges are well developed, with the posterolingual ridge reduced and nearly absent. The posterolabial ridge runs down to the posterolabial corner of the crown and forms the labial border of the posterolingual basin. The second posterior ridge is shifted lingually relative to its position in the p2, running nearly exactly down the midline of the posterior surface of the tooth and terminating at the highest point along the posterior margin of the crown. A small cusp is still present in the posterolingual corner of the crown, and the ridge that extends along the posterior margin of the crown is slightly better developed, extending around past the posterolingual cusp to near the base of the lingual swelling, creating a clearer margin of the posterolingual basin. The posterior end of the crown extends ventral to an anteriorly projecting portion of the m1, and a facet was likely present along the posterior margin to fit against the m1, although this cannot be determined with certainty as long as the teeth remain in position.

In the only other specimen referred to *G. twitchelli* that preserves the crowns of p2 and p3 (UCMP 117570), the p3 is larger than the p2 (Archibald, 1982:table 27). Although the crown of p3 is labiolingually wider than p2 in NDGS 1719, the p3 is anteroposteriorly shorter than p2, demonstrating that variation exists in the relative sizes of the premolars in this taxon. However, the p3 may not be fully erupted given that the posterior end of p3 is still situated ventral to the anterior border of m1. It is possible that the fully erupted p3 would be subequal to or anteroposteriorly longer than p2. Otherwise, the premolar morphology of NDGS 1719 agrees with the description of UCMP 117570 provided by Archibald (1982), although more of the finer morphological details are apparent in NDGS 1719 because the premolars are not abraded as in the UCMP specimen.

The trigonid of m1 is smaller than the talonid, both in anteroposterior length and labiolingual width (Fig. 3D). The metaconid is slightly shorter than the protoconid, although the paraconid is much shorter than both. The paraconid forms the anterior-most apex of the crown in occlusal view (Fig. 3D). The paracristid extends from the labial margin of the paraconid to the anterior margin of the protoconid, enclosing the anterolabial margin of the trigonid basin. At approximately mid-length, the paracristid is deeply indented by the paracristid notch, and at this point the direction of the paracristid changes from anteriorly oriented as it extends from the protoconid to anterolingually oriented as it meets the paraconid. No connection exists between the paraconid and the metaconid, so the trigonid basin is open lingually. A slight swelling is present along the lingual margin of the base of the paraconid. A slight ridge does extend from the posterolingual corner of the protoconid, likely representing a poorly developed postprotocristid, but it ends well before reaching the metaconid. Therefore, there is no connection between the metaconid and the protoconid, but the fact that these two cusps are better developed than the paraconid results in the posterior margin of the trigonid basin being slightly enclosed by the bases of those conids, leaving only a broad groove (the metacristid notch) connecting the trigonid and talonid basins. A slight ridge, the cristid obliqua, extends from the posterior margin of the protoconid posterolabially towards the hypoconid, decreasing in height until it is almost gone at mid-length, then increasing in height until it reaches the anterior margin of the hypoconid. Thus, the labial wall of the talonid basin is slightly enclosed. Similarly, a postmetacristid extends from the posterior margin of the metaconid along the lingual margin of the crown, progressively decreasing in height until it meets the preentocristid that extends from the anterior margin of the entoconid, enclosing the lingual margin of the talonid basin. A postentocristid extends from the posterolabial margin of the entoconid a short distance until it reaches the anterolingual margin of the posteriorly projected hypoconulid, which is less developed than any of the five conids of the molar. A narrow groove is situated between the hypoconulid and the entoconid, extending from the anterior margin of the postentocristid into the talonid basin. Another ridge, the posthypocristid, extends from the anterolabial margin of the hypoconulid, angling anterolabially for a short distance and then curving labially, connecting to the posterolingual corner of the hypoconid. The posterior projection formed by the hypoconulid fits into a small notch (the hypoconulid notch) between the paraconid and the anterolingual end of the precingulid of the m2, with the distinct, posterolabially concave curve of the posthypocristid fitting against the curve of the precingulid of the m2. The anterolingual surface of the hypoconid bears a broad swelling, creating narrow grooves to either side that extend down from the hypoconid into the talonid basin (Fig. 3D). A tiny cusp is also present about halfway up the posterolabial surface of the entoconid, situated anterolabial to the postentocristid. The entoconid is the same height or slightly taller than the hypoconid, and both are shorter than the paraconid, metaconid, and protoconid. A slight swelling is present at the base of the crown along the posterior margin, terminating along the posterior margin of the hypoconid and not extending around to the labial margin of the crown. A buccal cingulid is present at the base of the crown along the anterolabial margin that consists of a sharp ridge that arises from the base of the hypoconid and extends around the protoconid, becoming less pronounced anteriorly. At the anterolabial corner of the protoconid, this ridge moves to a lower position on the crown before extending anterolingually to form a moderately developed precingulid. The precingulid terminates just labial to the anterior-most extension of the paraconid. There are no pronounced cusps along the cingulid at the base of either the hypoconid or the protoconid on the m1.

The m2 is similar in many aspects to the m1, but there are a few major differences between the two tooth positions that need to be detailed. Rather than fully describing the morphology of the m2, the focus here is on highlighting how the morphology of the m2 differs from that described for the m1. The trigonid of m2 is more anteroposteriorly shortened than in m1, largely as a result of the paraconid being situated closer to the metaconid (Fig. 3D). As a result, the paracristid is more strongly lingually angled along its entire length. The metaconid and protoconid are more widely separated than in m1 and are shorter than those of m1, although both are still taller than the paraconid and the metaconid remains slightly shorter than the protoconid. The result of this restructuring of the trigonid is that the metacristid notch is slightly deeper, and the lingually extending groove from the trigonid between the metaconid and the paraconid is shallower, making the connection between the trigonid and talonid basins as well developed as the opening of the trigonid basin to the lingual margin of the crown. A slight, posterolabially curved ridge, the premetacristid, is also present on the labial surface of the metaconid that extends a short distance towards the postprotocristid, although the two do not connect. The postcingulid is more pronounced, extending farther around the posterolabial corner of the hypoconid, although it still does not connect to the buccal cingulid. The buccal cingulid is also better developed and is continuous with the precingulid around the protoconid. A prominent cusp is present near the posterior end of the buccal cingulid situated anterolabial to the hypoconid (Fig. 3D). The presence of this posterior buccal cingulum cusp on m2 differentiates *Glasbius twitchelli* from *Glasbius intricatus* (Archibald, 1982). A sharp ridge emerges from the anterolabial surface of the hypoconid, curves along the labial margin of the posterior buccal cingulum cusp, continues along the margin of the buccal cingulum and the precingulum, and ends at the anterolingual extent of the precingulid.

Specimens NDGS 1720 (Fig. 3G) and NDGS 1721 (Fig. 3H) differ from this description in a few particulars. In both specimens, a faint ridge arises from the lingual surface of the protoconid, anterior to the postprotocristid, and extends lingually either all the way to the side of the curved premetacristid (NDGS 1720; Fig. 3G) or nearly so (NDGS 1721; Fig. 3H). There is no trace of that ridge in NDGS 1719 (Fig. 3D). In NDGS 1720, the small accessory cusp on the posterolabial surface of the entoconid is lacking. In both NDGS 1720 and 1721, the cristid obliqua does not extend all the way to the apex of the protoconid (Figs. 3G, H), unlike in NDGS 1719 (Fig. 3D).

The m3 is most similar in morphology to the m2, and many of the differences seen between the m2 and the m1 are accentuated in the m3. The trigonid is further reduced in anteroposterior

TABLE 6. Comparisons between published measurements of the upper molars of *Glasbius* and the referred specimen from North Dakota (NDGS 1793). All measurements are in mm.

		This study *Glasbius twitchelli* Hell Creek Fm. North Dakota				Archibald (1982) *Glasbius twitchelli* Hell Creek Fm. Montana				Lofgren (1995) *Glasbius twitchelli* Hell Creek Fm. Montana				Clemens (1966) *Glasbius intricatus* Lance Fm. Wyoming			
Tooth	Dimension	N	Min	Max	Mean	N	Min	Max	Mean	N	Min	Max	Mean	N	Min	Max	Mean
M1	Length	—	—	—	—	2	2.01	2.08	2.05	—	—	—	—	3	1.85	1.90	1.88
	Width	—	—	—	—	2	2.16	2.19	2.18	—	—	—	—	3	1.80	2.00	1.91
M2	Length	1	—	—	2.11	5	2.05	2.11	2.07	3	2.08	2.18	2.14	2	2.00	2.00	2.00
	Width	1	—	—	2.20	5	2.13	2.45	2.31	3	2.31	2.53	2.42	2	2.00	2.20	2.10
M3	Length	1	—	—	1.98	5	1.68	1.89	1.77	2	1.78	1.93	1.86	4	1.65	1.75	1.71
	Width	1	—	—	2.38	5	1.80	2.15	1.97	2	2.14	2.35	2.25	4	2.00	2.15	2.08
M4	Length	—	—	—	—	2	0.91	1.24	1.08	—	—	—	—	—	—	—	—
	Width	—	—	—	—	2	1.32	1.50	1.41	—	—	—	—	—	—	—	—

Width measurements are maximum widths. **Abbreviations**: **Fm.**, Formation; **M**, upper molar; **Max**, maximum observed value; **Min**, minimum observed value; **N**, number of measurements.

FIGURE 4. Partial left maxilla with M2–3 (NDGS 1793) referred to *Glasbius twitchelli*. Photograph is in occlusal view. **Abbreviations**: **ant**, anterior; **lab**, labial. Scale bar equals 1 mm.

length, with the metaconid and paraconid closely appressed and separated by a narrow groove. As a result, the trigonid basin is limited to a small, deep pocket situated anterolingual to the protoconid and the connection between that basin and the talonid basin is better developed than the connection to the lingual margin of the crown, which is nearly closed. This progressive shortening of the trigonid from m1 to m2 to m3 is largely the result of a gradual anterior shift of the metaconid relative to the protoconid, enlarging the anterolingual corner of the talonid while compressing the posterolingual corner of the trigonid. The paraconid and metaconid are shortened to the point that they are only slightly taller than the entoconid and hypoconid, although the metaconid remains taller than the paraconid. Unlike in m1 and m2, the protoconid and metaconid are subequal in height, although they are even more widely separated than in m2. The protoconid is also shifted slightly more posteriorly relative to the metaconid. The premetacristid is better developed, but it still only reaches about halfway to the protoconid and does not connect with the postprotocristid, which is about equally developed between m1, m2, and m3. The postcingulid is better developed and wraps fully around the posterolabial corner of the hypoconid, terminating at the posterior margin of the posterior buccal cingulum cusp. The connected buccal cingulid and precingulid are as well developed as in m2, but in m3 a second prominent cusp is present at the junction between the buccal cingulid and the precingulid situated anterolabial to the protoconid. The presence of both posterior and anterior buccal cingulid cusps on the m3 differentiates *Glasbius twitchelli* from *Glasbius intricatus* (Archibald, 1982). The anterior buccal cingulid cusp is slightly less well developed than the posterior buccal cingulid cusp.

Variations in the morphology of m3 include the lack of an accessory cusp on the entoconid in NDGS 1722 and 1724 (Figs. 3I and K, respectively) and the lack of the slight groove where preentocristid meets postmetacristid in NDGS 1723 and 1724 (Figs. 3J and K, respectively). The most pronounced differences between the m3s from North Dakota involve the cingulids and their associated cusps. In NDGS 1723, the postcingulid reduces in size as it extends anterolabially around the base of the hypoconid, making the posterolabial corner of the crown more sharply angled than in any of the other specimens (Fig. 3J). In that specimen, the posterior buccal cingulid cusp is also situated more anterolingually than in other specimens and is slightly less pronounced. Finally, the anterior buccal cingulid cusp of NDGS 1723 is less well developed than in other specimens. As a result of these differences, the labiolingual widths of the talonid and trigonid on NDGS 1723 are nearly equal (Table 4). In NDGS 1722, the anterior buccal cingulid cusp projects farther labially than in any other specimen, creating a more pointed anterolabial corner of the crown (Fig. 3I).

The m4 of *Glasbius twitchelli* is highly reduced relative to the other molars, requiring a full description. The trigonid remains anteroposteriorly shorter than the talonid, but in m4 the trigonid is labiolingually wider than the talonid (Fig. 3D). The paraconid remains shorter than the subequal metaconid and protoconid, and a narrow groove separates the paraconid and metaconid. The paracristid curves strongly anterolingually from the anterior margin of the protoconid to the posterolabial margin of the paraconid. The premetacristid extends from the posterolabial surface of the metaconid and the postprotocristid extends from posterolingual corner of the protoconid, curving anterolingually. Unlike in m1, m2, and m3, these two cristids contact each other, forming a continuous ridge from the metaconid to the protoconid that bears a small groove at mid-length where the two meet. The postmetacristid and preentocristid are slight ridges that connect along the lingual margin of the crown, connecting the metaconid and entoconid, respectively. The hypoconulid is reduced and tightly appressed to the posterolabial margin of the entoconid, with a faint postentocristid connecting them. There is no small cusp on the posterolabial surface of the entoconid, unlike in m1, m2, and m3. The hypoconid is a short, broad, rounded structure that dominates the posterolabial corner of the crown, connecting to the hypoconulid via the posthypocristid. The cristid obliqua extends from the anterior margin of the hypoconid, angling anterolingually and reducing in height until it reaches the posterolingual corner of the protoconid where it terminates without connecting to the protoconid. Thus, the talonid basin is slightly open labially. There is no postcingulid. The buccal cingulid arises from the anterolabial margin of the hypoconid and becomes better developed as it wraps around the protoconid. The buccal cingulid and precingulid are continuous, as in m2 and m3, and the precingulid terminates anteriorly labial to the anterior-most extent of the paraconid, forming a shallow notch that the hypoconulid of m3 fits into. A fine ridge extends along the margin of much of the buccal cingulum and the precingulid. The well-developed cingulid around the anterolabial portion of the crown of m4 is largely responsible for the trigonid being labiolingually wider than the talonid.

A small fragment of the maxilla is preserved in NDGS 1793 (Fig. 4; Table 6). Three alveoli are present for both the M2 and M3, with a single alveolus situated lingually and two situated labially for each tooth. The base of the zygomatic arch overhangs the labial margin of M3, and the posterior margin of M3 is roughly level with the posterior margin of the base of the zygomatic arch. The floor of the orbit dorsal to the molars was smooth and gently sloped dorsolabially.

The occlusal surface of the M2 is worn, both by occlusion with the lower dentition during life and possibly by additional postmortem abrasion. As a result, the anterolabial portion of the crown is difficult to interpret and the relative sizes of the B and D stylar cusps and the paracone and metacone, and the presence or absence of the A stylar cusp cannot be determined. In other specimens of *G. twitchelli*, stylar cusp D and metacone are the taller two cusps and a small stylar cusp A is present (Archibald, 1982). The labial margin of the M2 is sinuous in occlusal view, exhibiting a moderate invagination, the ectoflexus, between stylar cusps B and D. These cusps were the largest along the labial margin of the tooth. There is no evidence of a C cusp, which is typically absent in all but the M1 of *G. twitchelli* (Archibald, 1982). A small stylar cusp E is present posterior and slightly lingual to stylar cusp D. A broad swelling is present between stylar cusp D and the metacone, although it does not fully connect these two structures. A low centrocrista extends from the posterior surface of the paracone to the anterior surface of the metacone. The presence or absence of a preparacrista is uncertain owing to wear. A prominent postmetacrista extends from the posterolabial corner of the metacone, curving labially and running along the posterolabial corner of the crown. The metacingulum is positioned posterior and ventral to the postmetacrista. The protocone is situated in the anterolingual corner of the crown and is nearly as tall as the metacone. A pronounced postprotocrista extends from the posterior margin of the protocone, curving posterolabially to form the posterolingual border of the trigon basin, eventually connecting to a ridge that forms the posterior margin of the metacingulum. Along the postprotocrista in the posterolingual corner of the crown, a well-developed metaconule is present. A faint internal conular crista extends labially from the anterolabial corner of the metaconule into the trigon basin before being lost. The preprotocrista extends labially from the anterolabial corner of the protocone, connecting to the paraconule that is situated about halfway between the protocone and paracone. The paraconule is situated slightly more anteriorly than both of those cones. A slight internal conular crista extends from the paraconule to the lingual surface of the paracone. The more pronounced preparaconule crista extends from the anterolabial corner of the paraconule along the anterolabial margin of the tooth, and may have contacted stylar cusp A, although wear makes this impossible to tell for certain. A precingulum is present along the anterior margin of the crown, extending from the lingual margin of the tooth to a point level with the paraconule. As a result, the anterior margin of the crown is slightly concave in occlusal view, with the inflexion point positioned at the labial end of the precingulum.

Grossly, the shape of the M3 in occlusal view differs from that of M2 in that the posterolabial corner does not extend as far labially, resulting in the labial margin being sloped posterolingually. A small stylar cusp A is present in the anterolabial corner of the crown. A small ridge extends posteriorly from the posterolabial corner of stylar cusp A, but it ends before reaching stylar cusp B. Stylar cusps B and D are well developed and approximately equal in height, although stylar cusp B may be slightly taller. A ridge extends from the anterior margin of stylar cusp D anteriorly towards stylar cusp B, but it ends approximately halfway between the two cusps. A very small cusp is present anterolabial to stylar cusp D. That cusp is unlikely to be a reduced stylar cusp C because it is right along the labial margin, and stylar cusp C in *G. intricatus* is positioned between and slightly lingual to stylar cusps B and D. Rather, this tiny cusp is in the same position as one of the small cuspules reported on the M3 of *G. intricatus* (Clemens, 1966:fig. 15b) but lacking in other referred specimens of *G. twitchelli* (Archibald, 1982). There is no trace of a labial cingulum between stylar cusps B and D, unlike in *G. intricatus* (Clemens, 1966), although a marked ectoflexus is present between these cusps. A small, anteroposteriorly elongated, labiolingually narrow basin is present with stylar cusp B, the stylar cusp D, the paracone, and the metacone situated in the four corners. Stylar cusp E is situated posterolingual to stylar cusp D, and a narrow cleft separates the two cusps.

On the M3 the paracone is subequal to the metacone, and a sharply defined centrocrista connects the two. The paracone is positioned close to the lingual margin of stylar cusp B, with only a slight valley separating the two. An anteroposteriorly narrow, labiolingually elongate shelf is present anterior to the protocone, extending from lingual margin of stylar cusp A to the anterolabial margin of the paraconule. A similar shelf may have been present on the M2, but wear impedes identification of this feature in the latter tooth. The metacone is situated between and lingual to stylar cusps D and E. The postmetacrista extends from the posterolabial corner of the metacone to the posterolingual corner of stylar cusp E, forming the posterolabial corner of the crown. The metacingulum is positioned posterior to the metacone along the ventral margin of the crown. The protocone is situated in the anterolingual corner of the crown, slightly more posteriorly than the paracone and stylar cusp B. A pronounced postprotocrista extends from the posterior margin of the protocone, curving posterolabially along the margin of the crown, eventually extending down to form the posterior margin of the metacingulum. The metaconule is situated along the postprotocrista, lingual and slightly anterior to the metacone. A small internal conular crista extends labially from the metaconule, connecting to the swollen base of the metacone, separating the shelf of the metacingulum from the trigon basin. A similar setup may be present in M2, but wear makes this impossible to determine. The paraconule is situated approximately halfway between and slightly anterior to both the paracone and the protocone. The preprotocrista connects the paraconule and the protocone, and an internal conular crista connects the paraconule and the paracone. As a result, the trigon basin is completely enclosed by the paracone, metacone, metaconule, protocone, paraconule, and their respective cristas. The preparaconule crista extends from the anterolabial corner of the paraconule, continuing labially along the anterior margin of the crown, and ending anterior to, but not connected to, stylar cusp A. That crest forms the anterior margin of the elongate shelf present anterior to the paracone. The precingulum is present anterior to the protocone, extending from the lingual margin to a point level with the paraconule, giving the anterior margin a concave shape in occlusal view. The labial end of the metacingulum on M2 contacted the anterior margin of M3 just labial to the end of the precingulum within that concavity, and contact between these two teeth is limited to the posterolabial corner of the M2.

DISCUSSION

From Whence Came a Lancian 'Alien'

The temporal and geographic distributions of *Glasbius* are restricted to the Lancian North American Land Mammal Age of the Western Interior Basin of North America, making it a unique occurrence for that interval (Cifelli et al., 2004). *Glasbius* is classified as an 'alien' component of the Lancian fauna (Weil and Clemens, 1998; Clemens, 2002), as opposed to most Lancian taxa that are classified as 'residents' because representatives of their respective lineages are present in slightly older Judithian or 'Edmontonian' faunas of the Western Interior Basin. In fact, *Glasbius* is a relatively late-appearing component of the Lancian fauna. In Garfield County, Montana, where microvertebrates from the Hell Creek Formation have been extensively studied, specimens of *Glasbius twitchelli* are only known from localities positioned within the upper 30 m of the formation (Wilson, 2014). That restriction to the upper portion of the Hell Creek Formation is consistent with reports from other geographic areas, including the present study (Fig. 5). Once present, *G. twitchelli* is one of the most abundant taxa sampled from microvertebrate localities in Garfield County, which is also consistent with data collected from NDGS L226 (= PTRM V98027), where *Glasbius twitchelli* is the most abundant mammalian taxon. For these reasons, the first appearance of *Glasbius*, along with a few other late-appearing mammalian taxa (e.g., *Essonodon*), is considered by some authors to denote the beginning of an informal 'Lancian 2' mammalian faunal subdivision (Wilson, 2014). These facts raise questions about where the *Glasbius* lineage emigrated from and why. Addressing these questions requires knowledge of the taxonomic affinities and systematic relationships of *Glasbius* relative to other Cretaceous and Paleogene marsupialiforms.

Three main alternative hypotheses exist regarding the systematic relationships of *Glasbius*: (1) closely allied with the pediomyids (e.g., Davis, 2007); (2) closely allied with the South

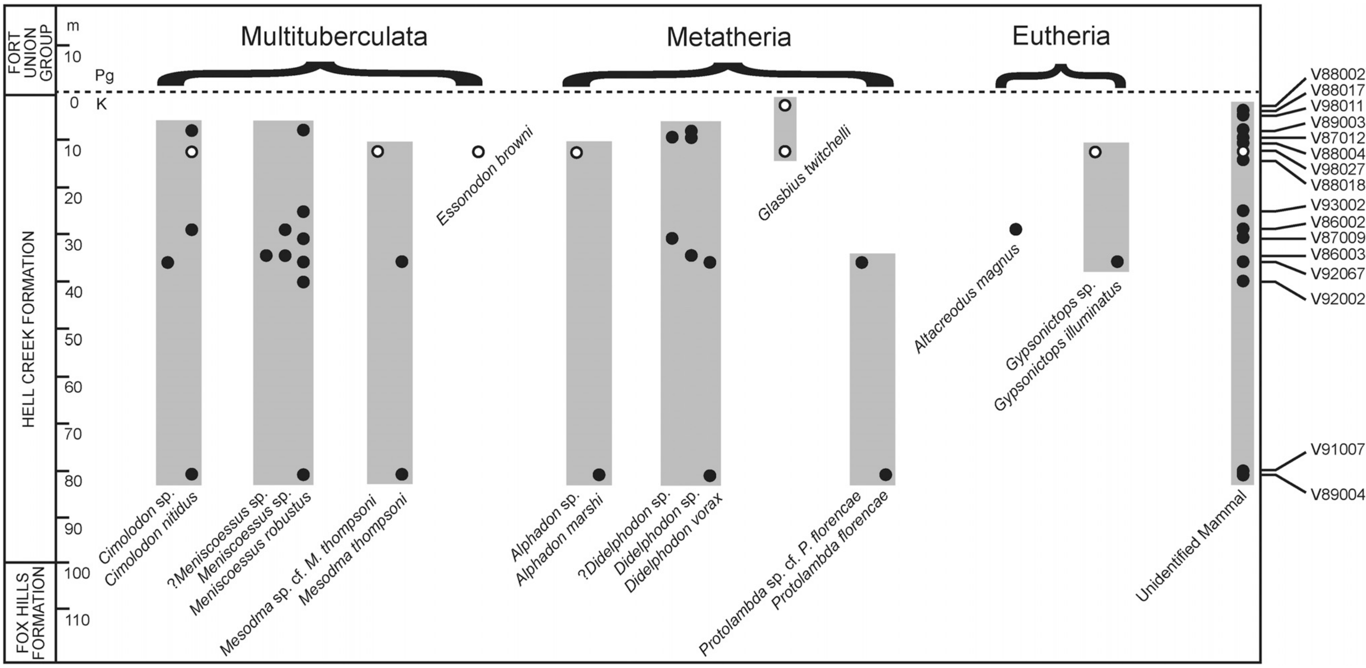

FIGURE 5. Chart of stratigraphic ranges of mammalian taxa in the Hell Creek Formation of southwestern North Dakota. All localities that produced fossils of mammals reported by Hunter and Archibald (2002) are included, along with the two new localities discussed in this study. Solid black circles represent previously reported occurrences. White circles represent new occurrences reported in this study. The symbol (*) denotes vertebrate localities with mammalian fossils first reported in this study. Note that the stratigraphic positions are measured from the K/Pg boundary, which is not always concurrent with the contact between the Hell Creek Formation and Fort Union Group in the study area (Pearson et al., 2002). Modified from Hunter and Archibald (2002:fig. 5).

American taxon *Caroloameghinia*, which is often placed within or near the Peradectidae (e.g., Marshall et al., 1990); and (3) closely allied with the South American clade Polydolopimorphia (e.g., Chornogubsky and Goin, 2015). Archibald (1982) noted similarities between the lower dentition of *Glasbius* and pediomyids. Specifically, the cristid obliqua contacts the posterior margin of the trigonid below the apex of the protoconid, rather than that contact being more lingually positioned as seen in other taxa (e.g., *Alphadon*; Archibald, 1982). Rougier et al. (1998) recovered *Glasbius* as the sister taxon to *Pediomys* in their phylogenetic analysis of basal marsupialiform relationships. These facts prompted Davis (2007) to include *Glasbius* in his analysis of the relationships of pediomyid marsupialiforms, where it was recovered within a polytomy with Pediomyidae and the North American taxon *Aquiladelphis*. That result led Davis (2007) to speculate that *Glasbius* may be an offshoot of the *Aquiladelphis* lineage, which is present in North American faunas from the Santonian through the Campanian (Fox, 1971; Rigby and Wolberg, 1987; Rowe et al., 1992; Davis et al., 2016).

Alternatively, several studies noted similarities between *Glasbius* and several clades of South American marsupialiforms. The original description of *Glasbius intricatus* noted similarities to the bunodont marsupialiform *Caroloameghinia* but suggested that those similarities represented convergence and not evidence of a close phyletic relationship (Clemens, 1966). Later studies (e.g., Marshall et al., 1990; Lofgren, 1995) placed *Glasbius* within either the family Caroloameghiniidae or the subfamily Caroloameghiniinae (depending on what rank each study assigned that clade) and placed that clade within or in a close relationship with the Peradectidae (e.g., Crochet and Sigé, 1993; Lofgren, 1995; Goin et al., 1998, 2010; Case et al., 2005).

Case et al. (2005) placed *Glasbius* and two other North American taxa, *Ectocentrocristus* and *Hatcheritherium*, in an unresolved position within the otherwise exclusively South American marsupialiform order Polydolopimorphia. Beck et al. (2008) argued against the inclusion of those three taxa within Polydolopimorphia on the grounds that their inclusion greatly increased the amount of dental homoplasy inferred within the clade, but they did not suggest an alternative placement for *Glasbius*. Goin et al. (2009) conducted a phylogenetic analysis that focused on South America marsupialiforms, but they included *Glasbius* as the only North American taxon in the analysis (aside from outgroup taxon *Alphadon*) owing to the previously proposed relationship with the Polydolopimorphia. The results of that analysis agreed with the suggestion of Beck et al. (2008) in placing *Glasbius* in a polytomy with Polydolopimorphia and *Microbiotherium*. Clemens (1966) had also mentioned similarities between the dentition of *Glasbius* and South American microbiotheriines but again did not infer a phyletic relationship. The South American taxon *Chulpasia* was suggested to be closely related to *Glasbius* by Crochet and Sigé (1993), and an updated analysis of the Goin et al. (2009) data set that included *Chulpasia* recovered that taxon within the polytomy containing *Glasbius, Microbiotherium*, and Polydolopimorphia (Chornogubsky and Goin, 2015). Finally, the largest phylogenetic data set yet employed to analyze the relationships of Cretaceous and Paleogene marsupialiforms recovered *Glasbius* as the sister taxon to *Roberthoffstetteria*, the only representative of the Polydolopimorphia included in the analysis (Williamson et al., 2012, 2014).

Although on the surface these alternative hypotheses seem difficult to reconcile, a deeper examination shows that the perceived disagreements between the alternative placements are likely related to the different sets of taxa included in these analyses. No single phylogenetic analysis has densely sampled members of the Polydolopimorphia, the Caroloameghiniinae, and the Pediomyidae. The data set of Davis (2007) includes only North

American taxa and does not contain any taxa traditionally referred to the Peradectidae, which are often thought to be closely allied to the Caroloameghiniinae (e.g., Crochet and Sigé, 1993; Lofgren, 1995; Goin et al., 1998). If we only compare taxa that are included in the analyses of Davis (2007:fig. 24) and Williamson et al. (2014:fig. 6), *Glasbius* is situated just outside of Pediomyidae in both trees (although the taxonomic contents of the Pediomyidae do differ between analyses). Only four taxa are shared between the data sets of Chornogubsky and Goin (2015: fig. 4) and Williamson et al. (2014:fig. 6), but their relative positions are the same, with *Glasbius* and *Roberthoffstetteria* being most closely related, *Pucadelphys* the next most closely related, and *Alphadon* situated basal to all three. Thus, the perceived differences in the systematic relationships of *Glasbius* between these three analyses are largely a result of taxon sampling. In fact, these three hypotheses are not necessarily mutually exclusive, which is demonstrated by examining the strict consensus topology from Williamson et al. (2014). That topology is congruent with hypothesis 3 in that *Glasbius* is the sister taxon to the Polydolopimorphia (represented by *Roberthoffstetteria*). It is relatively consistent with hypothesis 1 in that *Glasbius* is situated within a large polytomy just outside of a clade composed of a paraphyletic 'Peradectidae' + Pediomyidae, similar to its position in the analysis of Davis (2007). Finally, if the Caroloameghiniinae is closely related to peradectids, then placement of *Glasbius* just below a paraphyletic 'Peradectidae' would make that taxon somewhat closely related to the Caroloameghiniinae, as suggested by hypothesis 2. Overall, it appears likely that *Glasbius* shared a close relationship with some taxa present in the Paleocene of South America, although the exact details remain unresolved.

So where did the 'alien' *Glasbius* emigrate from during the Lancian? Interpretation of the ancestral area of the *Glasbius* lineage requires a well-resolved phylogenetic hypothesis that includes all pertinent taxa from North and South America, which is currently lacking and is beyond the scope of this study. As a result, it is difficult to determine if *Glasbius* was an endemic North American lineage that dispersed into South America during the late Maastrichtian or early Paleocene, or if *Glasbius* was part of a lineage endemic to South America (as the result of an earlier, unrecognized dispersal from North America) that then emigrated back to North America in the late Maastrichtian. The phylogenetic hypotheses of Davis (2007) and Williamson et al. (2014) would suggest the former, whereas that of Chornogusky and Goin (2015) supports the latter, although this again is largely a factor of the taxon sampling employed by each analysis. However, if the *Glasbius* lineage did originate in South America, it would be expected that marsupialiforms would be present in Late Cretaceous faunas from South America. Several South American mammalian faunas are known from the Campanian through Maastrichtian (Kielan-Jaworowska et al., 2004), but no marsupialiforms are reported from those localities. The fauna from Laguna Umayo, which includes possible marsupialiforms and was thought to be Maastrichtian in age (Jaillard et al., 1993), is now interpreted as either latest Paleocene or earliest Eocene (Sigé et al., 2004).

The well-supported origination of Marsupialiformes within North America, the current lack of evidence for marsupialiforms in South American until the earliest Paleocene, and the inferred dispersal of at least one other marsupialiform lineage from North America to South America during either the latest Cretaceous or earliest Paleocene (e.g., Williamson et al., 2014) make it most parsimonious to conclude that the *Glasbius* lineage was endemic to North America and later dispersed to South America. This hypothesis is preferred until either a more expansive analysis of basal marsupialiform relationships is available that facilitates resolution of the ancestral area of the *Glasbius* lineage or new fossils referable to this lineage are discovered that add clarity to this situation.

Appearance of the Late Lancian *Glasbius* Habitat

Regardless of where the *Glasbius* lineage came from, the question of what factors changed between the early and late Lancian that resulted in the appearance and eventual abundance of *Glasbius* within the late Lancian (or 'Lancian 2') fauna remains. In southwestern North Dakota, where detailed stratigraphic information is available for both mammalian faunas (Hunter and Archibald, 2002; Pearson et al., 2002; this study) and fossil leaf localities (Johnson, 2002), the stratigraphic positions of the local first appearances of *Glasbius* occur within the Hell Creek III (HC III) megaflora zone. The HC III megaflora is marked by a substantial increase in diversity (Johnson, 2002), and leaf margin analysis indicates that the climate had warmed considerably during the transition from the older HC II megaflora to the HC III megaflora (Johnson and Hickey, 1990). These factors reveal that the late Lancian environment was significantly different from the early Lancian environment.

Principal components analysis of the tooth morphology of *Glasbius* grouped that taxon with the extant, frugivorous marsupial *Caluromys* (Gordon, 2003). That result implies a similar frugivorous diet in both taxa, supporting claims also made by other studies (e.g., Wing and Tiffney, 1987; Kielan-Jaworowska et al., 2004). The first appearance of *Glasbius* may then be at least in part constrained by the environmental changes that occurred during the late Lancian. Those changes may have either allowed the preferred habitat of *Glasbius* to expand out of its ancestral area and across the Western Interior Basin of North America or increased the abundance and distribution of its preferred food source. Although this hypothesis fits well with currently available data, thorough vetting will require more detailed studies of the composition and stratigraphic distribution of the three distinct megaflorae of the Hell Creek Formation in areas where mammalian faunas are well sampled and stratigraphically constrained (e.g., Garfield County, Montana).

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