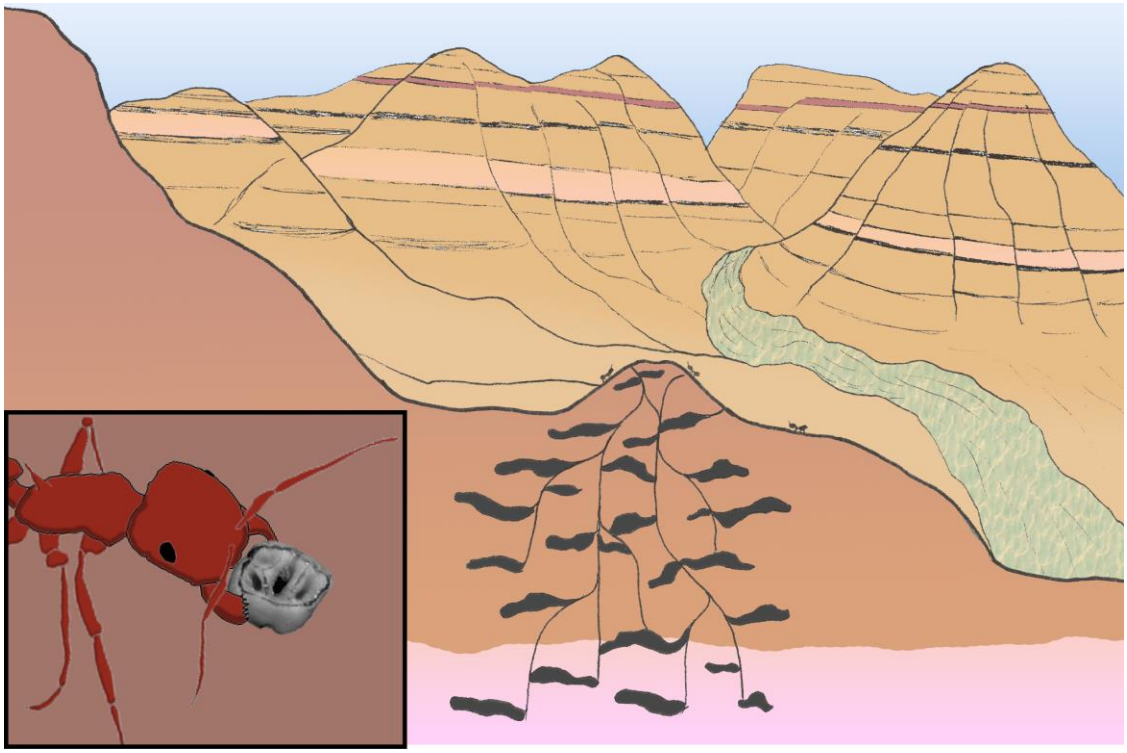
PALUDICOLA

SCIENTIFIC CONTRIBUTIONS
of the
ROCHESTER INSTITUTE OF VERTEBRATE PALEONTOLOGY



Special Issue: Fossil mammals from ant mounds situated on exposures of the Big Cottonwood Creek Member of the Chadron Formation (latest Eocene-early Oligocene), Sioux County, Nebraska—William W. Korth, Clint A. Boyd, Jeff J. Person, and Deborah K. Anderson

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FOSSIL MAMMALS FROM ANT MOUNDS SITUATED ON EXPOSURES OF THE BIG COTTONWOOD CREEK MEMBER OF THE CHADRON FORMATION (LATEST EOCENE – EARLY OLIGOCENE), SIOUX COUNTY, NEBRASKA

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ABSTRACT

For over a century the mounds of harvester ants (*Pogonomyrmex* spp.) have been targeted by paleontological field crews as sources of concentrated microvertebrate fossils that facilitate the collection of large numbers of specimens with a small investment of time. This study describes a collection of over 6,000 identifiable micromammal teeth and jaws recovered from 19 ant mounds in Sioux County, Nebraska south of Toadstool Geologic Park. All of these ant mounds are situated on rocks of the Big Cottonwood Creek Member and their stratigraphic positions span from seven meters below to five meters above the upper purplish-white layer (UPW). The large sample size and stratigraphic position of this collection allows for the documentation of the micromammal faunae of this region, investigation of patterns of faunal change across the Chadronian-Orellan boundary, and identification of the local stratigraphic position of the Chadronian-Orellan boundary.

Over 80 mammalian taxa are recognized in this collection, including ten new species and four new genera. Among the rodents nine new species, including three new genera, are described. The new genera include the cylindrodont *Siouxlindrodon* (*S. sullivani* n. sp.) and the aplodontids *Cosepeiromys* (*C. attasorus* n. sp.) and *Protansomys* (*P. gulottai* n. sp.). The additional new rodent species consist of the ischyromyid *Ischyromys brevidens* n. sp., the eomyids *Paradjidaumo patriciae* n. sp., *Yoderimys massarae* n. sp., and *Litoyoderimys grossus* n. sp., the florentiamyid *Kirkomys miriamae* n. sp., and the sciurid *Cedromus modicus* n. sp. Among the Lipotyphla, the soricid *Domnina compressa* Galbreath, 1953, is referred to a new genus *Noritrimylus* (as *N. compressus*), along with *N. dakotensis* (Repenning, 1967) and *N. metaxy* (Korth, 2020a), and a new species of oligoryctid, *Oligoryctes tenutalonidus* n. sp., is recognized.

The large sample size available in this study also improved the understanding of the morphology and distribution of several previously described taxa. Tooth positions that were previously unknown for several taxa were identified and described for the first time (e.g., *Adjidaumo intermedius*; *Eutypomys hibernodus*, *Ecclesimus tenuiceps*, *Micropternodus montrosensis*). In some cases, the number of specimens here referred to specific taxa exceeds the total number of specimens previously known for that taxon (e.g., *A. intermedius*). A single chiropteran specimen (partial dentary with m3) and three isolated omomyid primate teeth are present in the collection but cannot be confidently referred to any known species. A partial M2 is referred to the borophagine canid *Otarocyon macdonaldi*, potentially representing the earliest occurrence of borophagines in North America.

The majority of the non-lagomorph specimens identified in this study (~69 percent) are referred to taxa that elsewhere first appear in Orellan or younger faunae and Orellan taxa dominate the faunal lists of all 19 ant mounds regardless of their stratigraphic position. This prevalence of Orellan taxa results from downslope transport of Orellan specimens into the foraging range of the ant mounds, an important factor that must be considered when working with ant mound collections. To compensate for that effect the local last appearance datums of 14 Chadronian taxa (including three new species) were used to estimate the local stratigraphic position of the Chadronian-Orellan boundary instead of the local first appearance datums of Orellan taxa. It is estimated that the boundary is situated at the distinctive layer derived from volcanic ash (=UPW; ±2 meters), in close agreement with previous studies.

INTRODUCTION

Ant mounds formed by Western Harvester Ants (*Pogonomyrmex occidentalis*) were first recognized as artificially concentrated sources of microvertebrate fossils in the 19th century (Hatcher, 1896). In addition to gathering seeds and other food sources, harvester ants gather small resistant objects from their local environment and bring them back to place on the outer surfaces of the mounds. In areas with exposures of fossiliferous rocks, microvertebrate fossils can be concentrated on these mounds through the foraging behavior of the ants, allowing paleontologists to recover a large number of otherwise difficult to locate fossils in a short period of time. Originally sampled to speed the recovery of typically rare mammalian fossils from Late Cretaceous rocks in Western North America (e.g., Hatcher, 1896; Lull, 1915), the practice of targeting *P. occidentalis* ant mounds (and other species with similar habits) for microvertebrate fossils was eventually adopted by paleontologists studying a wide range of taxa from a broad span of geologic time, as well as

archaeologists searching for small bones and artifacts (e.g., Shipman and Walker, 1980; Bass and Jefferson, 2003; Schoville et al., 2009).

Along the Pine Ridge Escarpment in northwestern Nebraska these ant mounds have been sought out as a source of microvertebrate fossils from the fossiliferous rocks of the White River Group for over half a century (e.g., Hough and Alf, 1956; Alf, 1962; Tornow and Arbor, 2017). In this area each ant mound can provide hundreds of specimens, providing the sample sizes necessary to document variation in dental morphology within abundant species and to compile detailed faunal lists that include rare taxa whose presence can be difficult to document through other sampling methods.

The exposures of the White River Group along the Pine Ridge Escarpment preserve a relatively continuous depositional record across the Eocene-Oligocene boundary within the Big Cottonwood Creek Member of the Chadron Formation. Prior studies of fossils from this region have documented morphological change and taxonomic turnover through this stratigraphic interval in the artiodactyl *Leptomeryx* (Zanazzi et al., 2009). Earlier work on micromammal fossils from this area was foundational for defining the Chadronian North American Land Mammal Age (NALMA) and its subzones (e.g., Wood, 1969; Ostrander, 1985), especially the middle Chadronian (Ch3: Prothero and Emry, 2004). Thus, this geographic location is an excellent area to study faunal turnover in the micromammal fauna across the Charonian-Orellan boundary that is approximately coincident with the Eocene-Oligocene boundary.

In this study fossiliferous sediment was collected from the outer surfaces of nineteen ant mounds situated on the upper portion of the Big Cottonwood Creek Member of the Chadron Formation on the eastern margin of the Pine Ridge Escarpment. Examination of that sediment resulted in the recovery of over 6,000 identifiable micromammal teeth and jaws, facilitating a detailed study of the micromammal fauna preserved in these rocks. The large sample size utilized in this study permits the recognition of ten new species, the identification and description of tooth positions for multiple taxa that were previously unreported, and an independent estimate of the local position of the Chadronian-Orellan boundary. This work also highlights several important factors that must be considered by paleontologists when reporting on fossils recovered from ant mounds, reveals the limitations of ant mound derived collections to investigating certain research questions, and calls into question the appropriateness of comparing micromammal faunae collected using different field techniques (e.g., ant mound collection versus screen washing) in broader paleogeographic or evolutionary studies.

GEOLOGIC SETTING

The contact between the Chadron and Brule Formations along the Pine Ridge Escarpment in northwestern Nebraska was originally placed at either the base (Schultz and Stout, 1938) or the top (Schultz and Stout, 1955) of a white volcanic ash bed informally termed the upper purplish white layer (UPW). In that geographic region the Chadron Formation was subdivided into three informal units from bottom to top: Chadron A, Chadron B, and Chadron C. The middle Chadron B unit was also subdivided into four parts (lower B1 through upper B4) with the boundaries placed at the third through fifth purplish white layers (Schultz and Stout, 1955). Those researchers subdivided the Brule Formation into two formal members, the upper Whitney Member and the lower Orella Member, with the latter subdivided into four informal units: Orella A, Orella B, Orella C, and Orella D (Figure 1).

A series of revisions to the stratigraphic nomenclature proposed by Shultz and Stout (1955) were made in the 1990s. The lower-most Chadron A was removed from both the Chadron Formation and the White River Group and named the Chamberlain Pass Formation (Terry and Evans, 1994; Terry and LaGarry, 1998). The most significant change as it relates to the present study was a revision of the upper boundary of the Chadron Formation. Though previously placed at the UPW, the boundary was moved upward to the transition from silty claystones to clayey siltstones and sandstones, effectively expanding the Chadron Formation to include most of the prior contents of the Orella A (Figure 1). Those rocks previously included in the informal Orella A, Chadron C, and part of the Chadron B units were combined into the Big Cottonwood Creek Member of the Chadron Formation (Terry and LaGarry, 1998). Rocks referred to that member are identified in northwestern Nebraska and eastern Wyoming but are largely absent from all but the southwestern corner of South Dakota and are unreported in North Dakota (Terry and LaGarry, 1998).

All of the ant mounds sampled in this study rest upon rocks of the Big Cottonwood Creek Member. Detailed study of fossils previously collected in and around Toadstool Geological Park a few miles north of the present study area (Figure 2: TP) placed the stratigraphic position of the faunal transition between the Chadronian and Orellan biochrons at two meters above the UPW (±5 meters: Zanazzi et al., 2009). That same study determined that the late Chadronian (Ch4) to middle Chadronian (Ch3) subdivision transision occurred 18 meters below the UPW (±2 meters: Zanazzi et al., 2009), which is below the stratigraphic positions of all the ant mounds sampled in this study. Thus, the stratigraphic distribution of these ant mounds spans rocks that may preserve fossils deposited across the

Chadronian-Orellan boundary, with the oldest fossils contributed from a late Chadronian fauna.

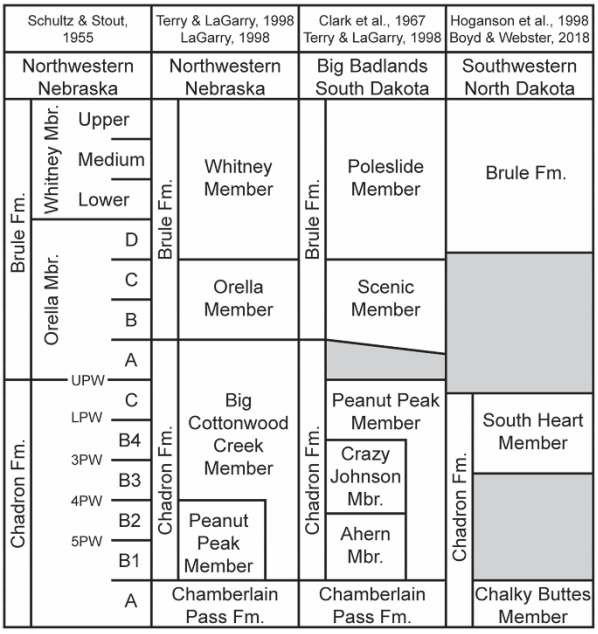

FIGURE 1. Lithostratigraphy of the White River Group in northwestern Nebraska, South Dakota, and North Dakota. The current lithostratigraphic schema for northwestern Nebraska is compared to the classic units proposed by Schultz and Stout (1955). Abbreviations: Fm., formation; LPW, lower purplish-white layer; Mbr., member; PW, purplish-white layer; UPW, upper purplish-white layer.

REVIEW OF PRIOR PALEONTOLOGICAL WORK

The specimens in this study were collected from ant mounds situated on private property (Figure 2: SA) approximately four miles southeast of Toadstool Geological Park and Campground in Sioux County, Nebraska (Figure 2: TP) and eleven miles northwest of the city of Crawford, Nebraska. The study area is part of the property referred to as the Arner Ranch in prior publications (e.g., Alf, 1962). This area along the eastern margin of the Pine Ridge Escarpment has been actively studied by paleontologists for decades and several biostratigraphically significant assemblages of microvertebrate fossils collected via screen washing, ant mound sampling, and surface collection were made from this area. Thus, discussion of the history of paleontological work in this area is pertinent to interpreting and understanding the importance of the specimens examined in this study.

Raymond M. Alf was among the first to conduct detailed sampling of microvertebrate fossils from the area surrounding Toadstool Geological Park and Campground, beginning in the late 1940's (Lofgren et al., 2019). Each summer Alf would bring groups of high school students out from The Webb School in Claremont, California for summer paleontological collection trips. During their work in the summer of 1953 the group discovered microvertebrate fossils concentrated on a *P. occidentalis* ant mound, spurring them to collect the surface of the ant mound to bring back with them for later examination (Lofgren et al., 2019). That discovery also prompted them to search for additional ant mounds with microvertebrate material over the course of the next few summers. In 1955, Jean Hough from the United States National Museum joined them in the field to examine these ant mound sites. That collaboration led to the publication of a review of the mammalian fauna Alf's crew had collected from the region (Hough and Alf, 1956). That paper describes two distinct sets of fossils, though it is not entirely clear that is the case at first glance, leading to misunderstandings in subsequent publications. The majority of the paper describes a set of fossils collected "in place" from the Chadron Formation from near the town of Orella (Figure 2: CiP). There is also a short discussion of "an interesting ant hill fauna" that includes a faunal list of mammalian taxa recovered from ant mounds "in the vicinity of the Chadron outcrops near Orella" (Hough and Alf, 1956: p. 132). Some authors have reported the ant mound collection as coming from the same location as the larger *in situ* specimens (e.g., Ostrander, 1985), but subsequent study by one of the authors of this study (CAB) of field notes and collections records related to those specimens reveals those fossils were collected from one of two localities located approximately two miles to the west (Figure 2: M1 and M2). Alf's crew also collected microvertebrates from ant mounds on the former Arner Ranch (Figure 2: AH and BH), including some which were situated in the same location as the present study area (Figure 2: SA). Subsequent publications on specimens collected from ant mounds by the Raymond Alf Museum were based on a mixture of specimens from the Meng anthills in the northwest and the Arner Ranch ant mounds (i.e., Alf, 1962; Clemens, 1964), contrary to the locality information reported in those studies. The age of the "interesting ant hill fauna" remains uncertain, reported as either middle or late Chadronian (Ch3 or Ch4; Janis et al., 2008) and likely includes reworked Orellan taxa (Guthrie and Allen, 1971). That collection is being reassessed by the current authors and will be the focus of a future report.

The Chadronia Pocket is located southeast of the present study area (Figure 2: CP). Fossils from this locality were first reported by Cook (1934, 1954) and a detailed description of the microvertebrate fauna was later published by Wood (1969). The locality consists of between twenty to thirty feet of *in situ* exposures of the Chadron Formation that display substantial lateral facies changes that make placing the site confidently within regional stratigraphy difficult (Ostrander, 1985). The Chadron Formation rocks at this locality are capped by

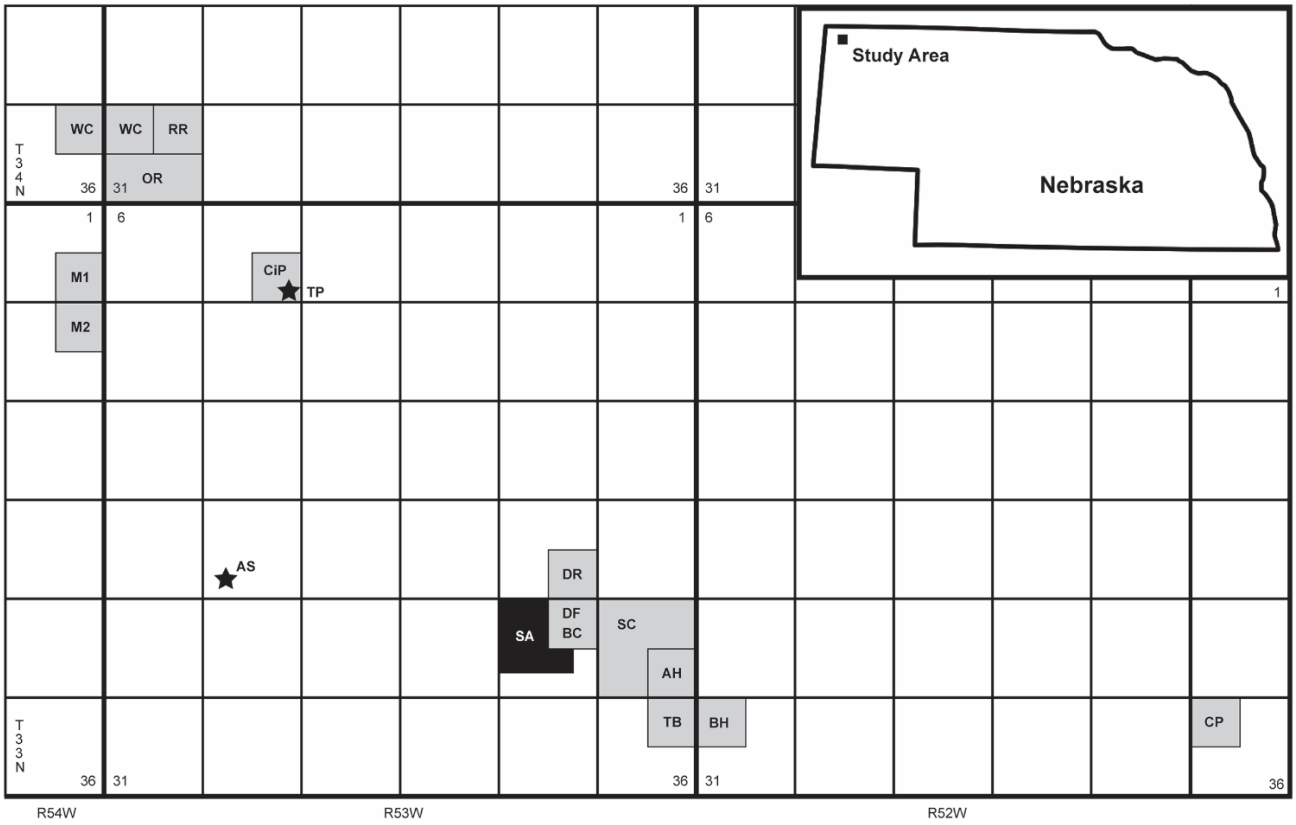

FIGURE 2. Map of the area around Toadstool Geologic Park showing the study area and the locations of previously published paleontological localities. Abbreviations: AH, Alpha Hill (unpublished RAM site); BC, Bone Cove (Ostrander, 1985); BH, Beta Hill (unpublished RAM site); CiP, Chadron in Place (Hough and Alf, 1956); CP, Chadronia Pocket (Wood, 1969); DF, Dirty Creek Flats (Ostrander, 1985); DR, Dirty Creek Ridge (Ostrander, 1985); M1, Meng Anthills site 1 (unpublished RAM site); M2, Meng Anthills site 2 (unpublished RAM site); OR, Orella Road (Tornow and Arbor, 2017); RR, Raben Ranch (Ostrander, 1985); SA, study area; SC, Sand Creek (Tornow and Arbor, 2017); TB, Twin Buttes (Ostrander, 1985); TP, Toadstool Geologic Park; WC, Whitehead Creek (Tornow and Arbor, 2017).

a layer of Quaternary alluvium between one to two feet thick that overlaps erosional remnants of the Brule Formation. The fauna from this locality was reported as late Chadronian (Ch4: Wood, 1969; Janis et al., 2008) based in part on the presence of some taxa typically restricted to Orellan faunae (e.g., *Eumys elegans*) mixed with typical Chadronian taxa (e.g., *Ischyromys veterior*). However, screen washing of *in situ* rock collected from the Chadronia Pocket did not recover any of those Orellan taxa, prompting Ostrander (1985) to argue this locality preserved a middle Chadronian fauna that was contaminated with younger fossils eroding from the overlying alluvium.

Ostrander (1985) presented faunal lists for five other Chadronian faunae collected from Chadron Formation exposures situated along the Pine Ridge Escarpment and an updated faunal list for the Chadronia Pocket. Screen washing was used at all of these localities to recover microvertebrate fossils, though loose specimens resting on the surface were also collected. The most diverse fauna reported was the Raben Ranch local fauna (Figure 2: RR), a middle Chadronian fauna (Ostrander, 1985; Janis et al., 2008) collected from the lower half of the Big Cottonwood Creek Member (Terry and LaGarry, 1998) just above the Peanut Peak Member. Magnetostratigraphic work at this site places the fossil producing horizon at the base of chron 15r, dating between 35.3 to 35.7 Ma (Prothero, 1996; Ogg, 2012), consistent with the interpretation of a middle Chadronian fauna. The abundance of fossils from this

site and the independently confirmed age data for the rocks makes this a key middle Chadronian fauna for comparing to other localities.

Two of the localities reported by Ostrander (1985) are immediately adjacent to the current study area. The Bone Cove and Dirty Creek Flats localities are situated within the NE ¼ of section 26 (T. 33N., R. 53W.: Ostrander, 1985), immediately adjacent to the ant mounds sampled in this study that are distributed throughout the remaining portions of section 26 (Figure 2: BC and DF versus SA). The faunae produced by those two localities is reported as middle Chadronian (Ch3: Ostrander, 1985; Janis et al., 2008) and positioned within the lower half of the Big Cottonwood Creek Member (Terry and LaGarry, 1998). However, given the stratigraphic data collected from within our study area, it is possible that the Bone Cove locality is situated high enough stratigraphically within the Big Cottonwood Creek Member to be above the middle Chadronian-late Chadronian transition identified by Zanazzi et al. (2009), and the broad flats that comprise the Dirty Creek Flats locality (reported as one half square mile) certainly include *in situ* rocks that span that stratigraphic interval. Thus, it is considered here that the specimens collected from those localities are from either a middle Chadronian, late Chadronian, or mixed fauna until further work can be done to confirm the stratigraphic positions of the fossil horizons at those localities.

The Dirty Creek Ridge locality is situated just to the north of the previous two localities in section 25 (Figure 2: DR) and the broadly defined Dirty Creek Flats locality extends to the flats adjacent to this locality as well. In the published stratigraphic column for Dirty Creek Ridge (Ostrander, 1985: fig. 2) a bed that may correspond with one of the purplish white layers was identified within the upper third of the section. If correctly identified, the position of that bed would correspond with the expected position of the lower purplish white layer relative to the level of the UPW in our study area, which is 10 meters below the UPW to the north at Toadstool Geological Park and Campground (Zanazzi et al., 2009), though the spacing of those two beds can vary in the region (Schultz and Stout, 1955). If correct, the fauna from this locality could be from the late Chadronian rather than middle Chadronian as previously reported (Ostrander, 1985; Janis et al., 2008). Additional stratigraphic work at this locality as well as a review of the previously collected specimens is needed before it can be confidently determined if this fauna is from the middle or late Chadronian.

The Twin Buttes locality (Figure 2: TB) is situated just over a mile southeast of the study area (Ostrander, 1985; *contra* Tornow and Arbor, 2017). Four purplish-white layers are present at this site (Vondra, 1958) with the fossil producing horizon situated at the base of the measured section and composed of a flat area of greenish silty claystone (Ostrander, 1985). Given the stratigraphic position of the producing horizon below four purplish-white layers, this fauna is either from the lower portion of the Big Cottonwood Creek Member or the underlying Peanut Peak Member of the Chadron Formation. This fauna is identified as middle Chadronian (Ostrander, 1985; Janis et al., 2008), which is consistent with the reported stratigraphic position of the fossil producing horizon.

Three additional ant mound collections were recently reported from the Pine Ridge Escarpment by Tornow and Arbor (2017): the Sand Creek, Orella Road, and Whitehead Creek localities (Figure 2: OR, SC, and WC). The ant mounds sampled at these localities are situated upon rocks of the Peanut Peak Member of the Chadron Formation, making these collections important for assessing the age of the fauna preserved in those rocks and for tracking faunal turnover between these slightly older assemblages and those previously reported from the lower portion of the Big Cottonwood Creek Member of the Chadron Formation. To date, the full faunae from these localities remains unpublished, with only the apatemyids described in detail (Tornow and Arbor, 2017), a brief summary of the taxa from the Whitehead Creek locality provided (Arbor and Tornow, 2015), and paleoenvironment of the Whitehead Creek locality analyzed, based on the locomotor guilds inferred from isolated mammalian tarsals and unguals (Mills, 2019). The stratigraphic placements of these localities make their corresponding faunae older than those at the focus of this study.

DISTRIBUTION OF STUDIED ANT MOUNDS

The geographic locations of each of the nineteen ant mounds sampled in this study were recorded by CAB using a Samsung Galaxy Tab S4 connected via Bluetooth to a Bad Elf global positioning system (GPS) and glonass receiver using the program ArcGIS Collector (Figure 3). In addition to recording the positions of the ant mounds, the positions of exposures of the upper purplish-white layer (UPW) and the contact between the Chadron and Brule Formations were also recorded throughout the study area. After returning from the field, those points were transferred to the program QGIS where they were compared to one-meter digital elevation models downloaded from the United States Geological Survey's National Map viewer (apps.nationalmap.gov/downloader) to accurately calculate the elevations of the ant mounds relative to the UPW and the Chadron-Brule Formation contact.

All of the ant mounds are situated on or adjacent to (when situated on outwash deposits) rocks of the Big Cottonwood Creek Member of the Chadron Formation. Most of these ant mounds sit on broad, relatively flat outwash surfaces adjacent to more vertically weathered

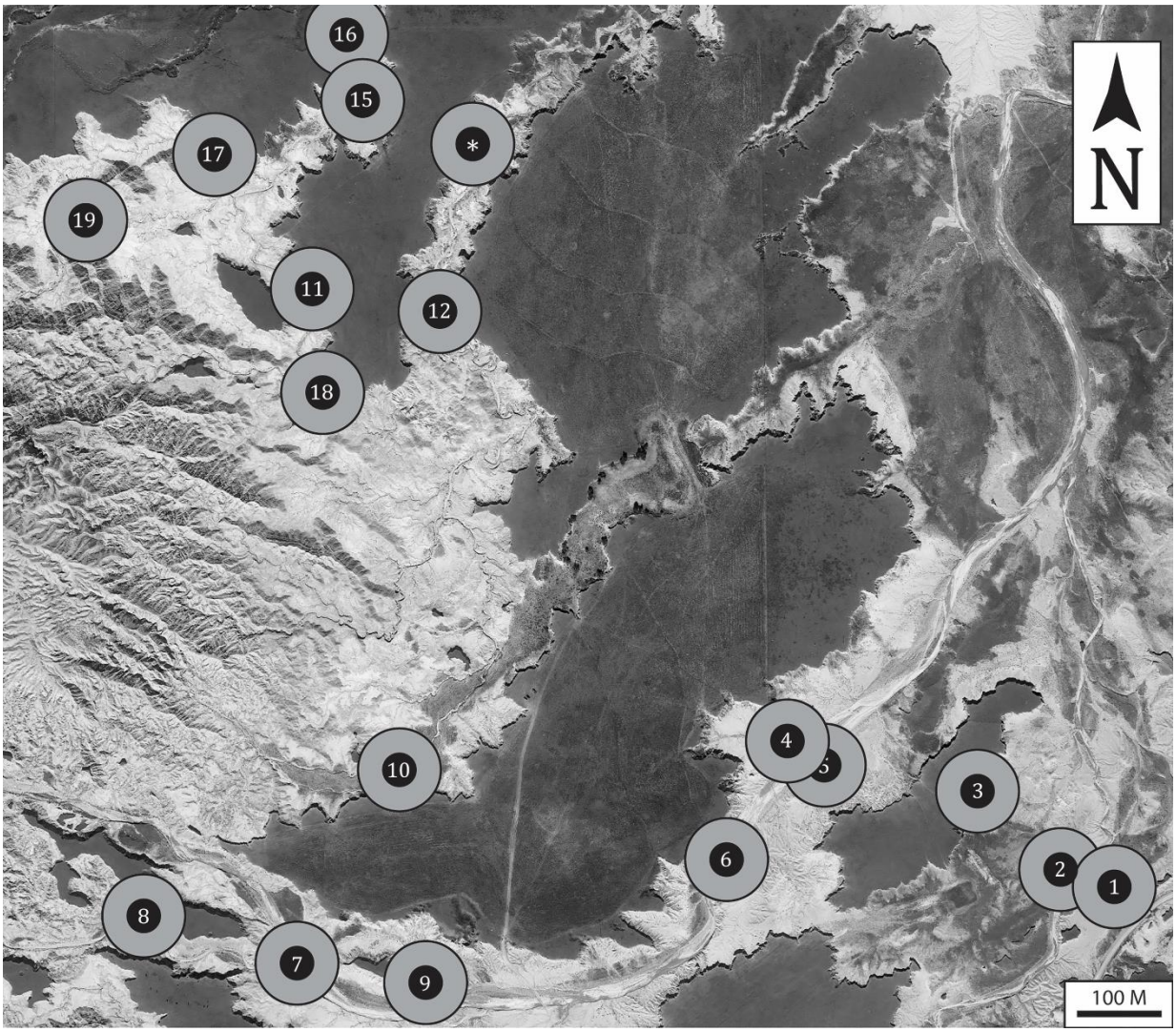

FIGURE 3. Map of the geographic positions of the nineteen ant mounds used in this study within section 26 (township 33 north, range 53 west). Abbreviations: *, ant mounds 13 and 14. Grey circles represent a 48-meter radius around each ant mound.

outcrops (e.g., ant mound 19) or sod tables capped with Quaternary alluvium (e.g., ant mound 10). The stratigraphic positions of these ant mounds can be divided into three broad groups. The first consists of ant mounds situated above the UPW (ant mounds 8, 10, 11, and 17-19) on rocks previously identified as the Orella A (Figure 1). This places them within the upper to middle portion of the uncertainty range for the Chadronian-Orellan boundary (Zanazzi et al., 2009). The second group of ant mounds is situated either directly on or up to three meters below the UPW (ant mounds 7, 9, 12, and 13-16) on rocks previously identified as the Chadron C (Figure 1). This distribution places these mounds within the lower end of the uncertainty range for the Chadronian-Orellan boundary (Zanazzi et al., 2009). The third group is situated between six and seven meters below the UPW, below the Chadronian-Orellan boundary based on the evidence documented by Zanazzi et al. (2009). All of these ant mounds are well above the reported level of the middle Chadronian-late Chadronian boundary at Toadstool Geological Park and Campground to the north of the study site (18 meters below the UPW ±2 meters: Zanazzi et al., 2009). Thus, the ants from these mounds should be sampling fossils from either late Chadronian or Orellan faunae depending on their stratigraphic positions.

METHODS

Collection Methods—All collection of fossils from the ant mounds was completed by the landowners prior to the specimens being sent to the authors for study. When ant mounds containing vertebrate fossils were located, the outer approximately half inch of sediment was removed from the mound and placed into a bag and left to sit for a period of time until any ants accidentally captured with the sediment were dead. Then the sediment was examined under a binocular microscope and the fossils were separated from the sediment. Once that work was completed, the mammalian fossils were separated from those of other taxonomic groups and sent to the authors for study. Fossils from the other taxonomic groups were sent to other researchers and will likely be the focus of future publications. Once the authors received the mammalian specimens, identifiable teeth and jaws were individually separated, cataloged, and identified (both to tooth position[s] and taxon). All specimens from the study area were donated to the Museum of Geology at the South Dakota School of Mines and Technology at the landowner's request.

Measurements—All measurements were taken with an optical micrometer to the nearest 0.01 mm (abbreviations: L, anteroposterior length; W, transverse width). Maxillary teeth designated by capital letters, dentary teeth by lower-case letters (e.g., M1 or m1).

Dental Terminology—Dental terminology for rodents follows that of Wood and Wilson (1936) and for all non-rodents follows that of Rich (1981). Incisors are denoted by I/i, C/c, canines, premolars by P/p, antemolars by A/a, and molars by M/m.

Abbreviations for Institutions—AMNH, American Museum of Natural History; CM, Carnegie Museum of Natural History; KUVP, University of Kansas, Museum of Vertebrate Paleontology; RAM, Raymond Alf Museum of Paleontology; SDSM, South Dakota School of Mines and Technology, Museum of Geology; UNSM, University of Nebraska State Museum.

SYSTEMATIC PALEONTOLOGY

Order Marsupialia Illiger, 1811

Family Herpetotheriidae Trouessart, 1879

Genus *Herpetotherium* Cope, 1873a

Herpetotherium fugax Cope, 1873a

(Figure 4; Table 1)

Referred Specimens—557 specimens (see Appendix).

Localities—Recovered from all sampled ant mounds. Big Cottonwood Creek Member of the Chadron Formation.

Discussion—This species has been previously described in detail. The collection from the Sioux County ant mounds does not differ from these previous descriptions (Scott and Jepsen, 1936; Fox, 1983; Korth, 1994a, 2018a). The dental dimensions of this collection are comparable to samples of *H. fugax* previously reported from the Orellan, averaging and ranging slightly larger than the later occurring samples from the Whitneyan and Arikareean (Table 1; Korth, 2018a: table 8).

Herpetotherium fugax, the best represented species of non-rodent from these ant mounds, is represented by over 500 specimens (see Appendix). There appears to be no difference in size or morphology in this collection between the ant mounds situated above or below the UPW (Table 1).

Herpetotherium valens (Lambe, 1908)

Referred Specimens—SDSM 156394, right M1; SDSM 156422, right m2.

Locality—Recovered from ant mound 5 below the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Measurements—M1: L = 2.48 mm; W = 2.37 mm. m2: L = 2.49 mm; W = 1.51 mm.

Discussion—The two specimens referred here to *Herpetotherium valens* are distinctly larger than any specimens of *H. fugax* from the Sioux County ant mounds and more closely comparable to those of *H. valens* (Korth, 1994a: table 3; Eberle and Storer, 1995: table 1; Kihm and Schumaker, 2015: tables 2, 3; Korth, 2018a: supplementary tables 3, 4, 5). The M1 has a small but distinct stylar cusp A, a larger cusp B, a large anteroposteriorly elongated cusp D with a minute cusp C fused to the latter anteriorly. This pattern of cusps is characteristic of *H. valens* (Green and Martin, 1976; Korth, 1994a, 2018a; Eberle and Storer, 1995; Kihm and Schumaker, 2015).

Both specimens reported here are from ant mound 5, which is situated six meters below the UPW. Elsewhere, *H. valens* is limited to the Chadronian except for several isolated molars reported from the Orellan of Sioux County (Korth, 2018a). Tabrum et al. (1996) included *H. valens* in faunal lists from two Orellan faunae in Montana, but those identifications have not been reviewed.

Genus *Copedelphys* Korth, 1994a

Copedelphys stevensoni (Cope, 1873b)

(Figure 5A-C; Table 2)

Referred Specimens—SDSM 150622, 150623, 150624, partial maxilla with M2-M3; SDSM 150625, M3; SDSM 150640, dentary with p3-m3; SDSM 156434 partial dentary with p3-m1; SDSM 150581,

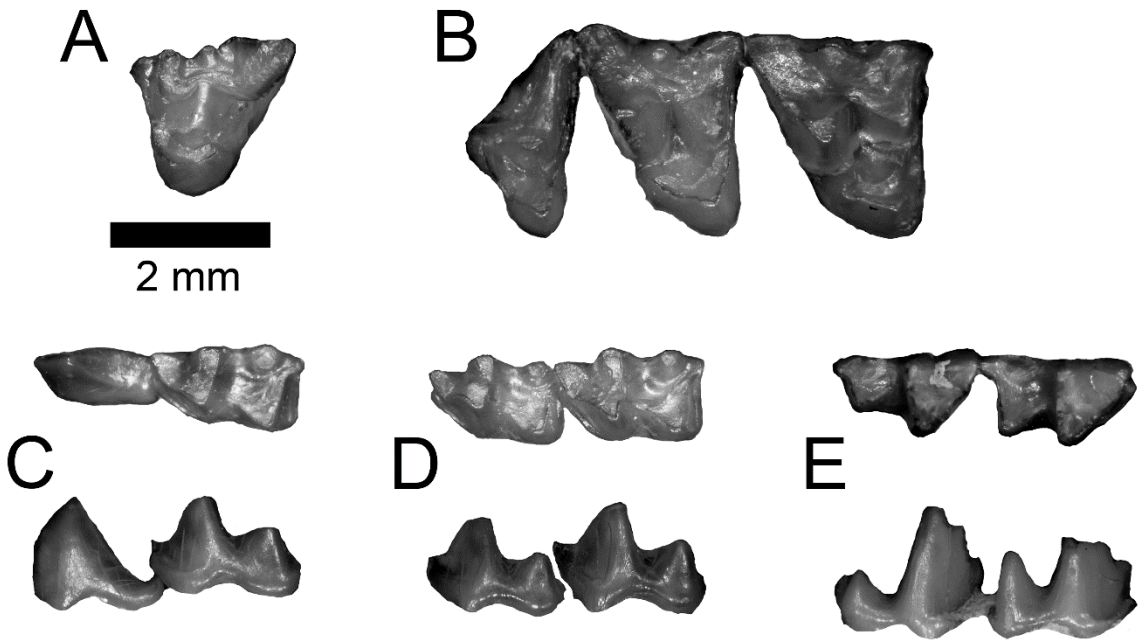

FIGURE 4. *Herpetotherium fugax* from the ant mound collection from Sioux County, Nebraska. A, SDSM 145032, left M1. B, SDSM 150439, right M2-M4. C, SDSM 150353, left p3-m1. D, SDSM 150386, left m1-m2. E, SDSM 150204, right m3-m4. Figures C-E, occlusal view above, labial view below.

150596, 150609, 150635, 150659, 150660, partial dentary with m3-m4; SDSM 150628, 156435, m1;SDSM 150631, 150633, 150636, 150642, 150658, 150688, 156436, m2; SDSM 150639, 150641, m3; SDSM 150637, 150946, m4.

Localities—Recovered from ant mounds 1, 4, 5, 6, 7, 9, 12, 15, and 16 below the UPW; ant mound 13 on the UPW; ant mounds 8, 18, and 19 above the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Discussion—The Chadronian species of *Copedelphys*, *C. titanelix* (Matthew, 1903a) and the Orellan species *C. stevensoni* (Cope, 1873b) can be distinguished from one another by the slightly larger size of the cheek teeth of the former as well as the proportions of the lower molars (relatively wider in *C. titanelix* [Korth, 1994a, 2018a]). The size and proportions of the molars from the Sioux County ant mounds best fit the Orellan and Whitneyan samples of *C. stevensoni* (Table 2; Korth 2018a: table 14). Again, as in *H. fugax* there appears to be no difference in the samples of *C. stevensoni* from below and above the UPW in the Sioux County collection.

Family Peradectidae Crochet, 1979
Genus *Nanodelphys* McGrew, 1937
Nanodelphys hunti (Cope, 1873a)
(Figure 5D-G; Table 3)

Referred Specimens—SDSM 150569, partial maxilla with P3-M1; SDSM 150580, maxilla with M1-M4; SDSM 150656, partial maxilla with M1-M2; SDSM 150560, 150561, 150578, maxilla with M2-M4; SDSM 150556, 150558, 150566-150568, 150570-150572, 150574, 150576, 150579, partial maxilla with M2-M3; SDSM 156423, partial maxilla with M3-M4; SDSM 150559, 150577, 156433, M1; SDSM 150557, 150562, 150563, 150575, 156425, 156426, M2; SDSM 150564, 150573, 156427, M3; SDSM 150565, 156424, M4; SDSM 150610 dentary with c1, p2, m1; SDSM 150592, dentary with p2, m3; SDSM 150594, 150599, 150601, 150608, 150644, 150654, partial dentary with p3-m2; SDSM 150607, 150612, 150613, 150617, 150619, 150650, 156437, partial dentary with p3-m1; SDSM 156431, partial dentary with dp3-m1; SDSM 150621, partial dentary with m1-m3; SDSM 150588, 150616, 150618, 150652, 150604, partial dentary with m1-m2; SDSM 150591, dentary with m2-m4; SDSM 150583, 150614, 150615, 150646, 150651, 150655, 156432, partial dentary with m2-m3; SDSM 150620, 150649, 156430, partial dentary with m3-m4; SDSM 150598, 150603, 150645, 150653, m1; SDSM 150582, 150585, 150595, m2; SDSM 150589, 150600, 150647,

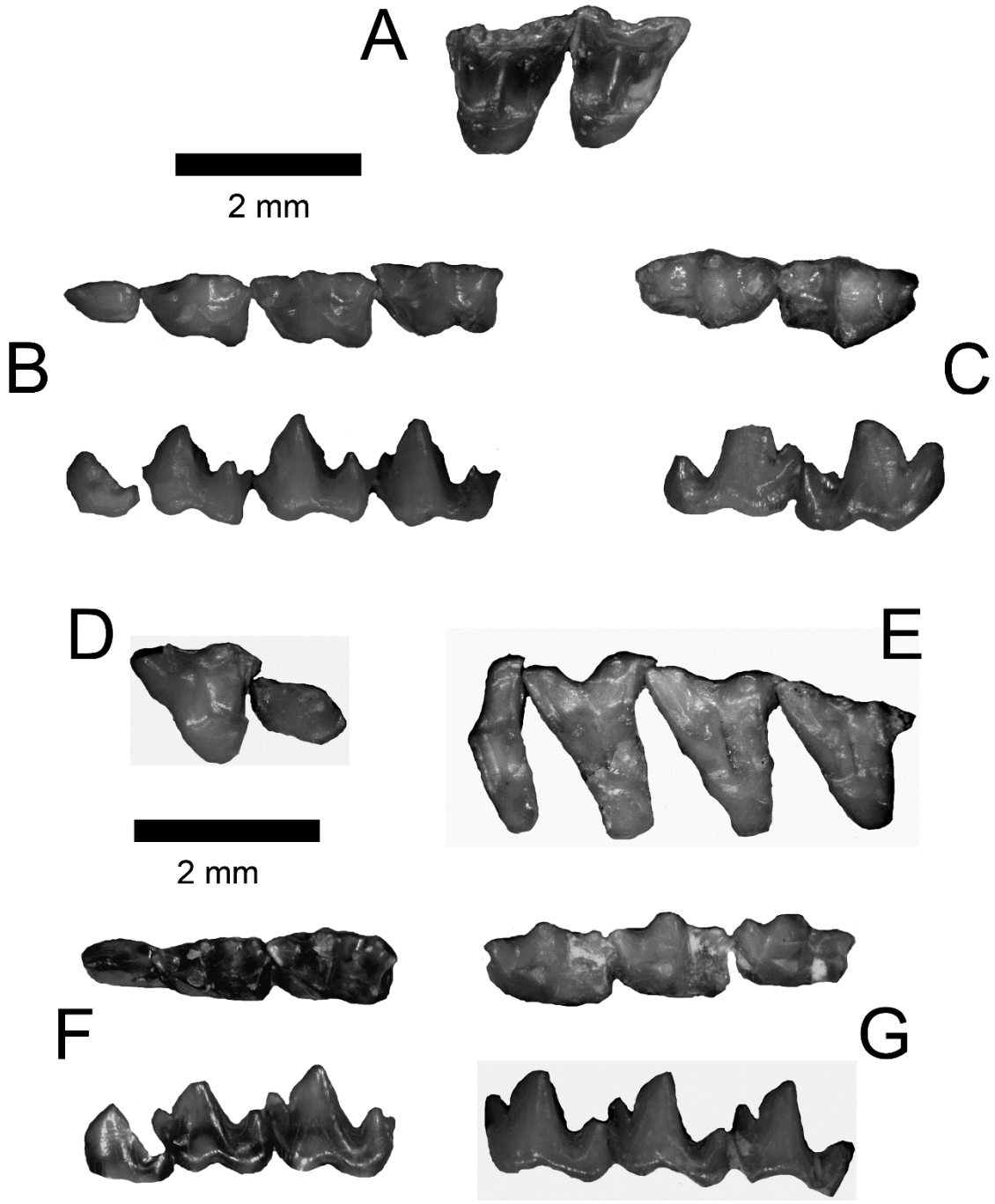

FIGURE 5. *Copedelphys* and *Nanodelphys* from the ant mound collection from Sioux County, Nebraska. A-C, *C. stevensoni*. A, SDSM 150624, right M2-M3. B, SDSM 150640, left p3-m3. C, SDSM 150660 right m3-m4. D-G, *N. hunti*. D, SDSM 150569, right P3-M1. E, SDSM 150580, right M1-M4. F, SDSM 150594, left p3-m2. G, SDSM 150591, left m2-m4. Figures B-C, F-G, occlusal view above, labial view below.

156428, 156429, m3; SDSM 150584, 150586, 150587, 150590, 150593, 150597, 150611, m4.

Localities—Recovered from ant mounds 1-7, 9, 12, and 15-16 below the UPW; ant mound 13 on the UPW; ant mounds 8, 11, and 19 above the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Discussion—The measurements and morphology of the cheek teeth of *N. hunti* from the Sioux County ant mounds best fit that of *N. hunti* from the Orellan (Table 3; Korth, 2018a: table 19). Previously, the range of *Nanodelphys* has been limited to the Orellan and later (Korth, 1994a, 2008a, 2018a). If the localities collected on the Chadron Formation are truly Chadronian, it would extend the earliest occurrence of *Nanodelphys* into the Chadronian. Once again, as with the other marsupial species from Sioux County, the specimens from the two different horizons cannot be separated from one another on the basis of size or morphology.

Order Leptictida McKenna, 1975
Family Leptictidae Gill, 1872
Genus *Leptictis* Leidy, 1868
Leptictis dakotensis (Leidy, 1868)
(Figure 6, A-H; Table 4)

Referred Specimens—SDSM 157005, dP4; SDSM 150728, 150776, 156976, P4; SDSM 150729, 150733, 150775, 156451, 156457, 156459, 156460, P5; SDSM 150731, 156974, M1; SDSM 150727, 150732, 150735, 150778, M2; SDSM 156453-156455, 156458, 156461, 156468, M1 or M2 (partial); SDSM 150730, 150777, 150957, 150958, 156456, M3; SDSM 150758, 156975, dp5; SDSM 150738, 150739, 150741, 150743, 150759, 150766, 150770, 156469, p5; SDSM 150736, 150744-150749, 150751, 150753, 150755, 150757, 150762, 150764, 150765, 150769, 150959, 156463, m1; SDSM 150760, 150761, 150767, 150772, 150773, 156462, 156465, 156538, m2; 150737, 150740, 150742, 150750, 150752, 150754, 150756, 150763, 150771, 150774, 156464, 156466, 156467, 156489, m3.

Localities— Recovered from all ant mounds except mound 2. Big Cottonwood Creek Member of the Chadron Formation.

Discussion—The last survey of the species of *Leptictis* was by Novacek (1976). He recognized nine species of *Leptictis* but questioned the inclusion of *L. thompsoni* [sic] from the late Chadronian of Montana based on molar morphology. Among the species recognized by Novacek (1976; also see Gunnell et al., 2008a) only two are similar in size to the Sioux County collection, *L. haydeni* and *L. dakotensis* (Table 4; Douglass, 1905: 223; Scott and Jepsen, 1936: 19, 20; Novacek, 1976: tables 1, 2). Since the ant mound material from Sioux County does not contain any complete dentaries or cranial material, none of the cranial characters used by Novacek (1976) to separate species can be used. Novacek (1976) noted that the P3 of *L. haydeni* (later identified as P4: Novacek, 1986) was unique in lacking a lingual cusp (=protocone), and that this cusp was present in all other species. All of the specimens of P4 from the Sioux County ant mounds (Figure 6A: n=3) have a distinct protocone and thus are referred to *L. dakotensis*. *L. dakotensis* has previously been reported from the Orellan and Whitneyan of South Dakota (Gunnell et al., 2008a).

Genus *Blacktops* Meehan and Martin, 2010
Blacktops sp.
(Figure 6I-K; Table 4)

Referred Specimens—SDSM 156976, left P4; SDSM 150734, 156493, P5(partial); SDSM 156452, left M3; SDSM 156494 left dP5(?); SDSM 156495, right dp5; SDSM 156977, right p5; SDSM 150768, 156470, m1 or m2; SDSM 156471, 156473, m3.

Localities—Recovered from ant mounds 4, 7, 9, and 16 below the UPW; ant mounds 13 and 14 on the UPW; ant mounds 10 and 19 above the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Description—The m1 or m2s (SDSM 150768, 156470) are nearly square in occlusal outline; only slightly shorter than wide (Figure 6L; Table 4). The trigonid is markedly higher than the talonid. In overall occlusal morphology, it does not differ markedly from that of other leptictids. The trigonid is anteroposteriorly compressed with a small central paraconid along the anterior edge. The protoconid is slightly larger than the metaconid and extends slightly more anteriorly; both are triangular in occlusal outline. The talonid consists of three cusps of nearly equal size, the entoconid, hypoconid and hypoconulid. The latter is the most posterior at the center of the posterior margin of the tooth. The entoconid is circular in occlusal outline and the hypoconid is triangular. A low cristid obliqua extends anteriorly from the hypoconid and ends anteriorly slightly labial to the center of the base of the trigonid.

SDSM 156495 is considered a deciduous premolar due to its thinner enamel and splayed roots. It is similar to p5s of *Leptictis* (Douglass, 1905; Scott and Jepsen, 1936; Novacek, 1976, 1986) but is longer and relatively narrower than the specimens of p5 referred to *L. dakotensis* (Table 4). Other than its proportions, the only morphological difference between it and p5 is the presence of a second cusp along the anterior margin of the tooth, labial to the protoconid.

A single specimen of p5 is referred here to *Blacktops* (SDSM 156977; Figure 6K) due to its larger size and proportions similar to that of the referred m1 or m2s (relatively wider than in *Leptictis*). Other than its size and proportions, the occlusal morphology does not

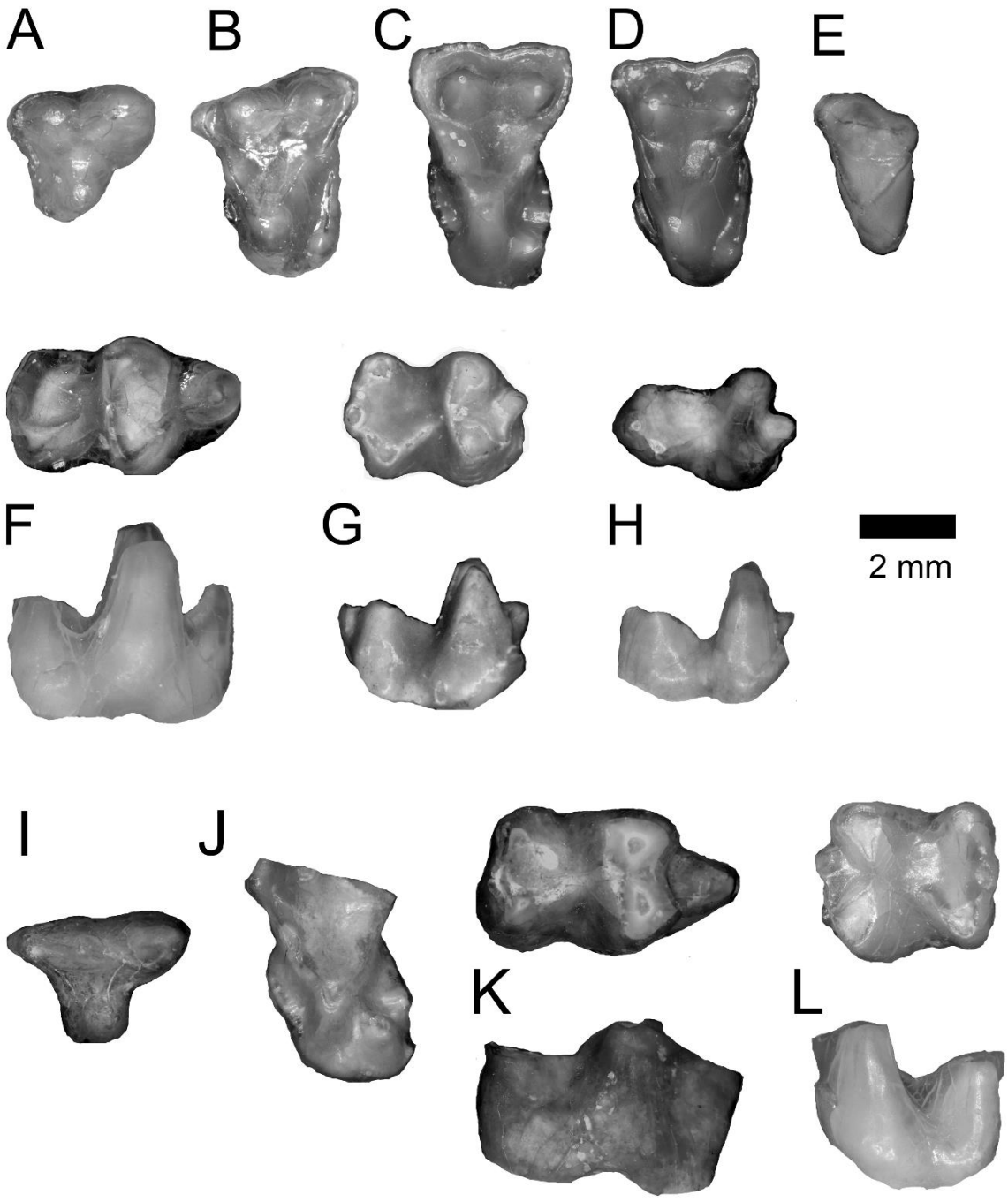

FIGURE 6. Leptictids from the ant mound collection from Sioux County, Nebraska. A-H, *Leptictis dakotensis*. A, left P4, SDSM 150776. B, SDSM 150775, left P5. C, SDSM 150731, left M1. D, SDSM 150727, left M2. E, SDSM 150957, left M3. F, 150738, right p5 (occlusal above, labial below). G, SDSM 150748, right m1 or m2 (occlusal above, labial below). H, SDSM 150750, right m3 (occlusal above, labial below). I-L, *Blacktops* sp. I, SDSM 156976, left P4. J, SDSM 150734, left P5 (partial). K, SDSM 156977, right p5 (occlusal above, labial below). L, SDSM 150768, right m1 or m2 (occlusal above, labial below). All figures to same scale.

differ from that of *Leptictis* (Douglass, 1905; Scott and Jepsen, 1936; Novacek, 1976, 1986).

Most of the upper cheek teeth are not complete, so exact measurements are not possible. The most complete specimen is a P5 (SDSM 150734: Figure 6J). The metacone is also lacking and only the base of the paracone is present. The tooth is markedly wider than long and follows the general pattern of leptictid upper cheek teeth. The lingual height of the tooth is clearly greater than the labial height but owing to breakage no definite measurements can be made. There is a broad anterior cingulum along the anterior edge of the tooth extending lingually from its center. There is a distinct paraconule that is triangular in outline just lingual to the paracone that is continuous with a high preprotocrista that reaches the apex of the protocone. The postprotocrista extends posterolabially from the apex of the protocone, forming a V-shape of the pre- and protocristae. The cingulum lingual and posterior to the protoconid is wide. A large hypocone is present posterior and slightly lingual to the protocone. A smaller secondary cusp is also present along the posterior cingulum just posterior and labial to the hypocone. The postcingulum ends labially before reaching the level of the metacone.

SDSM 156494 appears to be a dP5, again due to its thinner enamel. Only the labial half of the tooth is preserved, and the labial margin and cusps (paracone, metacone) do not differ from that of P5. Unfortunately, the lingual half of the tooth is broken away, but it is evident that the apex of the protocone is along the anterior margin of the tooth much closer to the labial cusps, giving the appearance of a much narrower tooth (transversely) than any molars or P5. However, it is more molariform than is typical for P4 with equal sized paracone and metacone and no anteriorly expanded parastyle.

A single P4 (SDSM 156976: Figure 6I) is referred because of its size (larger than the referred *Leptictis* specimens). In morphology it generally follows the pattern found in other leptictids but has only two distinct labial cusps, a central paracone and a larger, anteroposteriorly elongated metacone. There is only a minute parastyle along the anterior margin of the paracone. The protocone is circular in occlusal outline and positioned lingual to the boundary between the labial cusps. A very thin cingulum wraps around the anterior margin of the tooth and ends labially even with the apex of the paracone and lingually even with the labial margin of the protocone.

Discussion—The specimens referred to *Blacktops* are larger than those referred above to *L. dakotensis* (Table 4). Other than size, the referred lower molar is only slightly longer than wide, whereas *L. dakotensis* and other species of *Leptictis* have lower molars that are distinctly longer than wide (Douglass, 1905: 223). No lower molars were described for *Blacktops* and the only reported leptictid of similar size and proportions of the lower teeth is *Megaleptictis altidens* Meehan and Martin, 2012, from the Chadronian or Orellan of South Dakota.

An upper cheek tooth, SDSM 150734 (Figure 6J), is similar in size to the P4 and M1 of both described species of *Blacktops*, *B. longidens* and *B. latidens* (Meehan and Martin, 2010: table 1). The enlarged hypocone and the smaller accessory hypocone on SDSM 150734 is also present on the P4 and M1 of the holotypes (only known specimens) of both *Blacktops* species (Meehan and Martin, 2010: fig. 4). At present, the ant mound specimens cannot be confidently referred to either of these species with certainty. It is also possible that the two named species of *Blacktops* may be synonyms because the differences between these species are based predominantly on proportions of the cranium and both type specimens appear to have been at least partially distorted during fossilization (Meehan and Martin, 2010: fig. 1).

The SDSM specimens described here were collected from ant mounds situated both above and below the UPW, all within the Big Cottonwood Creek Member of the Chadron Formation. The holotypes and only previously known specimens of *Blacktops* are from the upper portion (Orella C) of the Orella Member of the Brule Formation, Sioux County, Nebraska (Meehan and Martin, 2010).

Order Apatotheria Scott and Jepsen, 1936
Family Apatemyidae Matthew, 1909
Genus *Sinclairella* Jepsen, 1934
Sinclairella dakotensis Jepsen, 1934
(Figures 7A-E; Table 5)

Referred Specimens—SDSM 156362, left P3; SDSM 156361, left M2; SDSM 156547, left M3; SDSM 156970, m1; SDSM 156357, 156360, 156969, m2; SDSM 156358, 156548, m3.

Localities—Recovered from ant mounds 1, 2, 6, and 9 below the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Discussion—The specimens referred here do not differ in size or morphology from those of *S. dakotensis* described elsewhere (Table 5; Scott and Jepsen, 1936: 29; West, 1973: table 6; Tornow and Arbor, 2017: tables 1, 2). The specimens differ from those of *S. simplicidens* from the Arikareean of Florida in being slightly larger and not having the simplified occlusal morphology of the upper molars characteristic of that species (Czaplewski and Morgan, 2015: table 2). The Sioux County ant mound specimens are larger than those referred to *S. nanus* from the Chadronian of North Dakota (Korth et al., 2021: table 1) and differ in lacking

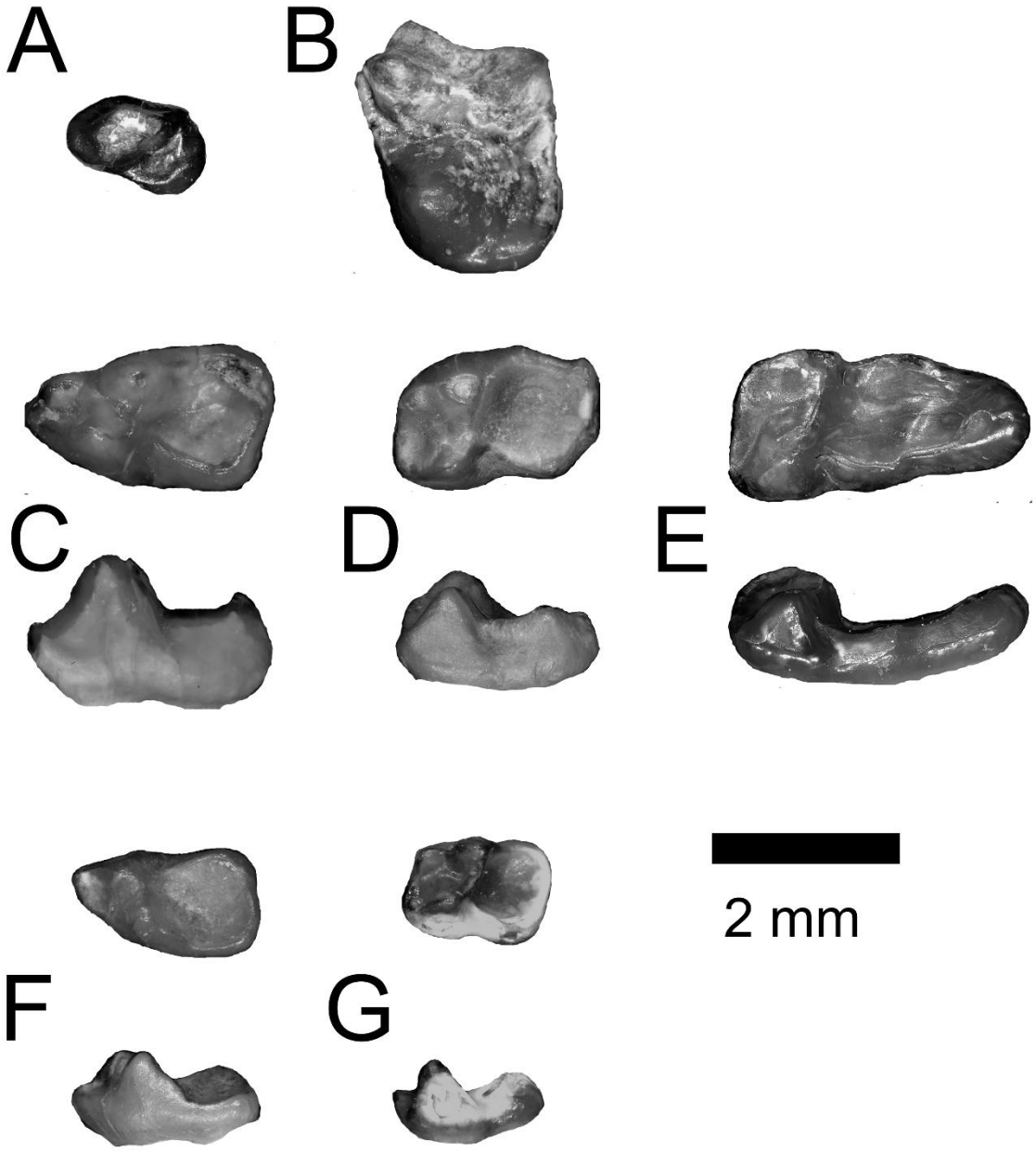

FIGURE 7. Apatemyids from the ant mound collection from Sioux County, Nebraska. A-E, *Sinclairella dakotensis*. A, SDSM 156362, left P3. B, SDSM 156361, left M2. C, SDSM 156970, left m1. D, SDSM 156357, left m2. E, SDSM 156358, left m3. F-G, *Apatemys* sp. F, SDSM 156359, right m1. G, SDSM 156971, left m2. C-E and G, occlusal view above, labial view below. F, occlusal view above, lingual view below. All figures to same scale.

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the well-developed paraconid on the lower molars (Figure 7B).

Specimens of *S. dakotensis* were only recovered from ant mounds situated below the UPW. Elsewhere, the occurrence of *S. dakotensis* has generally been limited to the Chadronian except for several specimens recently reported from the Whitneyan of South Dakota (Korth, 2020a).

Genus *Apatemys* Marsh, 1872
Apatemys sp.
(Figure 7F-G; Table 5)

Referred Specimens—SDSM 156359 left m1; SDSM 156971, 156972, m2.

Localities—Recovered from ant mounds 1, 3, and 4 below the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Description—The referred m1 is slightly longer than the referred m2s but clearly smaller than the specimens referred above to *Sinclairella* (Figure 7F; Table 5). The trigonid consists of three principal cusps, paraconid, protoconid and metaconid. The protoconid and metaconid are similar in size, the latter only being slightly smaller and positioned slightly more posteriorly. The paraconid is directly anterior to the protoconid at the anterolabial corner of the tooth. The paracristid is very weak, sloping ventrally and divided by a narrow transverse valley before rising to the apex of the paraconid. There is no evidence of an accessory cusp on the trigonid. The talonid is wider than the trigonid. The entoconid and hypoconid are minute but recognizable, the former at the posterolingual corner of the talonid, the latter at the posterolabial corner; both are obliquely compressed. The postparacristid is along the lingual side of the tooth. A continuous ridge wraps around the posterolingual corner of the tooth, continuous along the posterior margin of the talonid, then continues as the cristid obliqua that runs along the labial side of the talonid, ending at the posterolabial base of the protoconid.

The referred m2s are slightly shorter than the referred m1 but similar in width (Figure 7G; Table 5). In general morphology they follow the description of Gazin (1958). The protoconid and metaconid are the tallest of the cusps, much higher than the remainder of the tooth. As in m1, the metaconid is more posteriorly placed than the protoconid and strongly connected by the postprotocristid that is angled posterolingually. The paraconid is at the anterolingual corner of the trigonid and much lower than the metaconid. There is no distinct cristid continuous from the paraconid to the metaconid. The trigonid is anteriorly squared; the paraconid not being any more anterior than the anterolabial corner. A distinct ridge runs anteriorly and ventrally from the protoconid (preprotocristid), ending at the anterolabial corner of the trigonid. As with m1, there is no indication of an accessory cusp on the trigonid other than the paraconid. The talonid is similar to that of m1 but is approximately equal in width with the trigonid. Both the entoconid and hypoconid are barely distinguishable but present, the hypoconid being slightly larger. The talonid is rimmed by a ridge around the lingual and posterior sides (as in m1). The cristid obliqua runs slightly lingually, ending at the posterior wall of the protoconid even at the base of the apex of the cusp.

Discussion—The specimens referred here are distinctly smaller than those referred above to *Sinclairella* (Table 5). Although small in size, the paraconid and cusps of the talonid are more pronounced and the cristid obliqua ends anteriorly slightly more lingually than those on the molars of *Sinclairella*, similar to those of *Apatemys* (Jepsen, 1934; West, 1973). Tornow and Arbor (2017) referred three specimens from the Chadronian of Sioux County to *Apatemys* sp. aff. *A. downsi* Gazin, 1958, including an m1 previously referred to *Sinclairella* by Ostrander (1987). The m1 from the ant mound collections is similar in size and morphology to the specimen referred by Tornow and Arbor (2017: table 2). Similarly, the referred m2 does not differ markedly from those of species of *Apatemys* (Gazin, 1958: pls. 11, 12).

Korth (2020a) referred two lower molars from the Whitneyan Blue Ash fauna of southwestern South Dakota to *Sinclairella* sp. These two specimens are similar in size and morphology to the specimens referred here and may represent a species of *Apatemys*. The three specimens from the Sioux County ant mound collection described here are all from ant mounds situated below the UPW. With the exception of the uncertain Blue Ash specimens, the previously recognized range of *Apatemys* extends only into the Chadronian (West, 1973; Gunnell et al., 2008a; Tornow and Arbor, 2017).

Order Lipotyphla Haeckel, 1866
Family Geolabididae McKenna, 1960
Genus *Centetodon* Marsh, 1872
Centetodon marginalis (Cope, 1873b)
(Figure 8A-E; Table 6)

Referred Specimens— SDSM 150662, partial maxilla with P3-M1; SDSM 150661, maxilla with P4-M2; SDSM 150667, 156540, maxillary fragment with P4-M1; SDSM 150663, 150672, 150962, 156481, 156482, P4; SDSM 150664, 150665, 150668, 156474, 156477, 156479, M1; SDSM 156475, 156476, 156480, M2; SDSM 150955 partial dentary with c1-p2; SDSM 150953, 150956, dentary fragment with c1-p1; SDSM 150715, partial dentary with p3-m1; SDSM 150605, 150719, partial dentary with p3-p4; SDSM 150682 partial dentary with p4-m2; SDSM 150671, 150675, partial dentary with p4-m1; SDSM 150657, 150670, 150685, 150704, 150705, 150714, 150720, 150725, 150951, 150952, 156487, partial dentary with m2-m3; SDSM 150689, 150691, 150693, 150695, 150697, 150701, 150703, 150726, 150948, 150954, 156483, 156484, 156485, p4; SDSM 150674, 150683, 150686, 150690, 150698, 150699, 150707, 150708, 150710-150712, 150718, 150724, 150949, 150950, m1; SDSM 150684, 150687, 150694, m2; SDSM 150602, 150673,

150677, 150679-150681, 150696, 150713, 150716, 150721-150723, 150947, m3.

Localities—Recovered from ant mounds 1, 3-7, 9, 12, and 15-16 below the UPW; ant mound 13 on the UPW; ant mounds 8, 11, and 19 above the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Discussion—The material referred here best matches the size and morphology of *C. marginalis* that has been described in detail elsewhere (Lillegraven et al., 1981: 47-55; tables 6, 10). It is easily separable from the other species of *Centetodon* from this fauna (listed below) based on its smaller size (Table 6). Specimens of *C. marginalis* were recovered from Sioux County ant mounds situated below and above the UPW. Elsewhere this taxon is limited in occurrence to the Orellan of North Dakota, South Dakota, Nebraska, and Wyoming (Lillegraven et al., 1981: appendix 1; Gunnell et al., 2008b: 105).

Centetodon wolffi (Macdonald, 1965)
(Figure 8F-I; Table 6)

Referred Specimens—SDSM 150666, P4; SDSM 156478, M2; SDSM 150706, dentary fragment with p4; SDSM 156486, p4; SDSM 150669, 150676, 150692, 150702, 150709, m1 or m2; SDSM 150678, 150700, m3.

Localities—Recovered from ant mounds 1, 3, 6, 7, 9, and 15 below the UPW; ant mound 13 on the UPW; ant mound 10 above the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Description—The P4 (SDSM 150666: L = 2.30 mm; W = 2.36 mm) is as described by Macdonald (1965) and Lillegraven et al. (1981). There is no cingulum anterior to the parastyle, but a low labial cingulum runs the length of the buccal edge of the tooth (Figure 8F). The parastyle is a small circular cusp. The paracone is markedly higher than any other cusp and positioned at the center of the lingual side. A slightly concave centrocrista runs from the apex of the paracone to the posterolabial corner of the tooth. The protocone is markedly smaller and lower than the paracone and positioned along the lingual side of the tooth, just anterior to the position of the paracone. There is a thin cingulum that runs labially from a point anterior to the protocone along the base of the tooth for a short distance. There is a wear facet midway between the protocone and paracone for a small protoconule. A circular wear facet is posterior and slightly more lingual than the protocone (hypocone). There is no lingual cingulum but there is a low, distinct posterior cingulum that runs along the base of the tooth from the hypocone to nearly the buccal margin of the tooth. On the lingual surface of the protocone is a narrow groove that continues dorsally to the base of the lingual root.

The p4 similarly does not vary from the morphology of this tooth of other species (Figure 8G). The metaconid and protoconid are markedly higher than the talonid or the protoconid. The protoconid is slightly larger; both cusps are closely appressed to one another, the apex of the metaconid being slightly posterior to that of the protoconid. The paraconid is minute and situated anterior to the base of the metaconid. A low ridge runs from the apex of the protoconid along the anterior of the tooth, bending posteriorly along the labial side, ending at the base of the protoconid near its center. The talonlid is small; the only recognizable cusp is the hypoconid along the posterior margin of the tooth, just lingual to its centerline. A low ridge runs anteriorly from the hypoconid to the base of the trigonid, below the apex of the metaconid. A low ridge runs around the lingual border of the talonid from the hypoconid to the base of the metaconid. There is a small cuspule near the base of the tooth (much lower than the hypoconid) on the labial side anterior and labial to the hypoconid.

Since m1 and m2 are very similar in morphology and size, the five specimens from Sioux County cannot be separated from one another with confidence. The m1 and m2 of species of *Centetodon* are fully described by Lilleraven et al. (1981). The specimens from the ant mounds do not differ from their general description other than being slightly larger (Table 6). The only character cited by Lillegraven et al. (1981) as diagnostic of *C. wolffi* is a more distinct entoconid. All of the specimens from Sioux County have this larger, more distinct entoconid (Figure 8H).

The two m3s, SDSM 150678, 150700, are smaller than the anterior molars, with a slightly smaller talonid relative to the trigonid (Figure 8I). The only other feature that separates m3 from m1 and m2 is the slightly more posterior position of the hypoconulid relative to the other cusps of the talonid.

Discussion—The P4 from the Sioux County ant mounds fully fits the description of this tooth from the holotype (Macdonald, 1965; Lillegraven et al., 1981), and has its distinctive lingual groove along the lingual root. Previously, the only described lower tooth was m2 (Lillegraven et al., 1981). It differed from other species of *Centetodon* in having a relatively larger and more distinct entoconid. All of the specimens from the Sioux County ant mounds have this same degree of development.

The holotype of *C. wolffi* was originally described from the Whitneyan (Macdonald, 1965) and a partial dentary was referred from the Orellan (Lillegraven et al., 1981) both occurrences from South Dakota. Four additional isolated teeth were recently cited from the late Whitneyan Blue Ash ant mound fauna of South Dakota (Korth, 2020a). All but one of the specimens in this study come from ant mounds situated on or below the UPW.

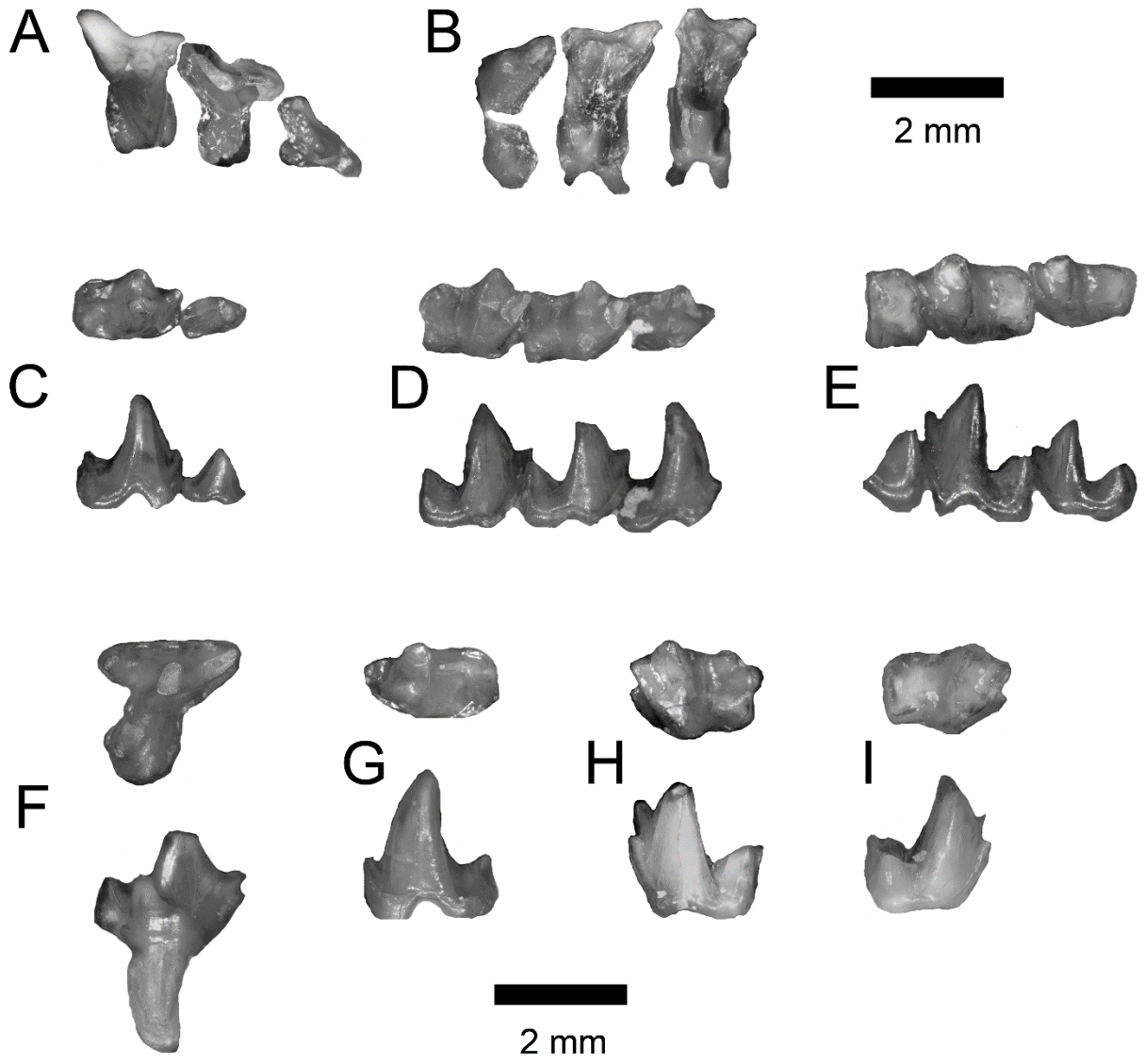

FIGURE 8. *Centetodon* from the ant mound collection from Sioux County, Nebraska. A-E, *C. marginalis*. A, SDSM 150662, right P3-M1. B, SDSM 150661, left P4(partial)-M2. C, SDSM 150719, right p3-m4. D, 150682, right p4-m2. E, SDSM 150670, left m1(partial)-m3. F-I, *C. wolffi*. F, SDSM 150666, left P4. G, SDSM 150706, left p4. H, SDSM 150702, left m1 or m2. I, SDSM 150678, right m3. Figures C-E and G-H, occlusal view above, labial view below. Figure F, occlusal view above, lingual view below. All figures to same scale.

Family Erinaceidae Fischer von Waldheim, 1817
Genus *Proterix* Matthew, 1903b
Proterix minimus Korth, 2009a
(Figure 9A-C; Table 7)

Referred Specimens—SDSM 150911, 150912, M2; SDSM 150913, dentary fragment with m1-m2; SDSM 150914, m1; SDSM 150915, m2.

Localities—Recovered from ant mounds 3, 5, and 16 below the UPW; ant mounds 8 and 19 above the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Discussion—The morphology and size of the specimens referred to *P. minimus* do not differ from the topotypic material previously described from the Blue Ash fauna of South Dakota (Table 6; Korth, 2009a: 79;

Korth, 2020a: table 1). This species is mainly distinguished from other species of the genus by its much smaller size. Three specimens of *P. minimus* cited here are from ant mounds situated below the UPW and the other two are from above the UPW, spanning almost the entire stratigraphic range sampled by these ant mounds. Elsewhere species of *Proterix* are reported to first occur in the Whitneyan (Gunnell et al., 2008b; Korth, 2009a, 2020a).

Genus *Amphechinus* Aymard, 1850
Amphechinus sp.
(Figure 9D)

Referred Specimens—SDSM 150924, M2; SDSM 156354, 156355, partial M1 or M2.

Localities—Recovered from ant mounds 3 and 4 below the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Measurements—SDSM 150924: M2, L = 2.77 mm; W = 3.13 mm.

Description—The labial cusps (paracone, metacone) are circular in occlusal outline and equal in size (Figure 9D). A narrow labial cingulum wraps around the anterior and labial side of the paracone but is lacking labial to the metacone. The paracrista extends directly anteriorly from the apex of the paracone to the anterior border of the tooth. It is continuous with the centrocrista, forming a straight anteroposteriorly directed ridge. The metacrista curves slightly labially before ending at the posterior edge of the tooth. The precingulum is thin and runs from the paracrista to the lingual edge of the tooth anterior to the protocone. The protocone is crescentic in occlusal outline. The preprotocrista runs labially and slightly anteriorly, ending anterolabially to the paracone in a small, distinct protoconule. The postprotocrista bows slightly posteriorly as it runs from the apex of the protocone, ending lingual to the base of the metacone near the labiolingual center of the tooth. A large conical hypocone is posterior to the protocone, and only slightly smaller than the protocone. A thin posterior cingulum runs along the posterior margin of the tooth from the metacrista to the posterolabial corner of the hypocone.

Discussion—Based on its larger size and generalized erinaceid morphology, SDSM 150924 appears similar to the M2 of *Amphechinus* (e.g., see Bendukidze et al., 2009: pl.1 fig. 4). The two partial upper molars referred here (SDSM 156354, 156355) are not complete enough for measurements, but are clearly larger than those referred above to *Proterix* and appear to agree with the complete upper molar referred here. In North America *Amphechinus* is known only from the Arikareean of South Dakota (Macdonald, 1970; Rich and Rasmussen, 1973). The size of the Sioux County specimens is similar to that of M1s of *A. horncloudi* (Macdonald, 1970: table 5; Rich and Rasmussen, 1973: table 3) suggesting it may be referable to this species. However, the M2 of *A. horncloudi* has never been described.

In their review of the Lipotyphla, Gunnell et al. (2008b: fig. 7.4) only questionably identified two erinaceid genera prior to the Arikareean in North America, *Proterix* and *Ocajila*. Later, Korth (2009a) named a species of the former from the Whitneyan, *P. minimus*. The Sioux County ant mound specimen, SDSM 150924, differs from the upper molars of *Proterix* in having a distinct protoconule and no metaconule, whereas those of *Proterix* have a large metaconule and a greatly reduced or no protoconule (Matthew, 1903b: fig. 1; Korth, 2009a: fig. 2A, B; Korth, 2020a: fig. 2A). SDSM 150924 is also markedly larger than the upper molars of *P. minimus* (Korth, 2009a: 79; Korth, 2020a: table 1) and smaller than the other known species of *Proterix* from the Arikareean (Gawne, 1968: table 1).

Ocajila, limited to the type species *O. makpiyahe*, is not known from any upper cheek teeth. In addition, the size of the type and only other referred specimen of *O. makpiyahe* is proportionally much smaller than SDSM 150924 (Macdonald, 1963: 167; Macdonald, 1970: table 4; Hutchison, 1972). Korth (1992a) referred an isolated m1 to *Ocajila* sp. from the early Arikareean of Nebraska that is proportionally larger than the ant mound specimen, but it cannot be referred to this genus with certainty.

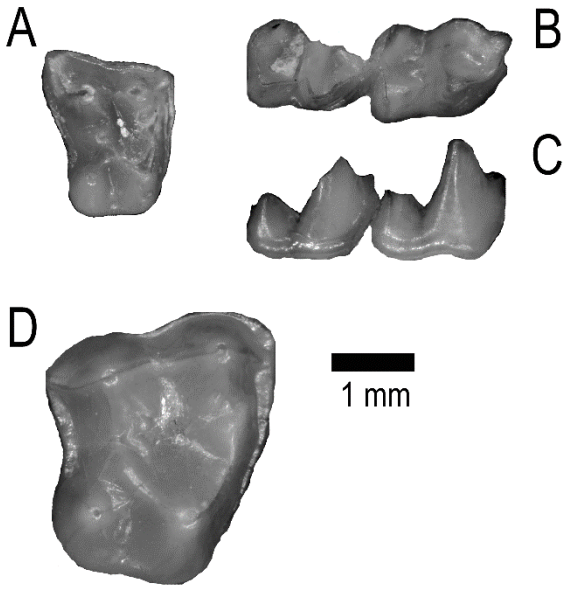

FIGURE 9. Erinaceidae from the ant mound collection from Sioux County, Nebraska. A-C, *Proterix minimus*. A, SDSM 150911, right M1. B-C, SDSM 150913, right m1-m2(partial). B, occlusal view. C, labial view. D, *Amphechinus* sp., SDSM 150924, right M2.

Family Sespedectidae Novacek, 1985
Genus *Ankylodon* Patterson and McGrew, 1937
Ankylodon sp., cf. *A. progressus* Galbreath, 1953
(Figure 10A-B)

Referred Specimens—SDSM 150916, P4; SDSM 150717, p4.

Localities—Recovered from ant mound 13 on the UPW; ant mound 8 above the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Measurements—p4: SDSM 150717, L = 1.89 mm, W = 1.30 mm; P4: SDSM 150916, L = 2.10 mm; W = 2.26 mm.

Description—P4 is nearly T-shaped but the labial border is angled anteromedial-posterolabially (Figure 10A). The paracone is the highest cusp at the center of the labial border. There is no distinct cusp on the anterolabial corner of the tooth, it appears as a short anteriorly directed arm from the base of the paracone. A distinct blade-like ridge runs from the apex of the paracone to the posterolabial corner of the tooth and is slightly curved. The protocone is at the anterolingual corner of the tooth. There is no indication of either a para- or metaconule, and the tooth is narrowest at its center. A minute hypocone is posterior to, and slightly more lingual than the protocone. An accessory minute cuspule is also present at the posterolingual corner of the tooth, posterior to, and slightly more labial than the hypocone.

The p4, SDSM 150717, is dominated by an extremely high protoconid that extends dorsally well above the remainder of the tooth (Figure 10B). A slightly smaller metaconid is fused to its lingual side, its apex reaching approximately 2/3 the height of the protoconid. The paraconid is markedly smaller and lower, essentially isolated from the other trigonid cusps. The talonid is much lower than the protoconid and slightly lower than the paraconid. There is a small, central hypoconid along the posterior margin of the tooth. A short cristid obliqua runs anteriorly and slightly lingually from it, fusing anteriorly with the base of the trigonid. A minute entoconid is just lingual to the hypoconid and is continuous with a low ridge (entocristid) that encloses the lingual side of the talonid. On the labial side, there is no cristid obliqua or lingual enclosure of the talonid, which remains open to the base of the crown.

Discussion—The specimens of *Ankylodon* from the Sioux County ant mounds are smaller (Table 7) than those of *Ankylodon* sp. from the Chadronian of Wyoming reported by Lillegraven et al. (1981: table 9) and slightly larger than the p4 of *A. annectens* from the Orellan of Colorado (Patterson and McGrew, 1937:271). They are nearest in size to the lower molars of *A. progressus*, also from the Orellan of Colorado (Galbreath, 1953: table 3). However, the latter species is only known from a dentary with m1-m3 so no teeth from Sioux County can be directly compared.

Lillegraven et al. (1981) suggested that the two Orellan species of *Ankylodon* may possibly be synonyms because of their similar size and occurrence. Due to the sparsity of specimens of all species, it is not possible to resolve this taxonomic question currently. The ant mound specimens are tentatively referred to *A. progressus* pending the discovery of additional specimens. The holotypes of both *A. progressus* and *A. annectens* are from the Orellan Cedar Creek Member, Brule Formation, Colorado. Both specimens described here are from ant mounds on or above the UPW.

Family Micropternodontidae Stirton and Rensberger, 1964
Genus *Micropternodus* Matthew, 1903a
Micropternodus borealis Matthew, 1901
(Figure 10C-F; Table 7)

Referred Specimens—SDSM 150917, 156511, P4; SDSM 156450, partial M1 or M2; SDSM 156364, 156365, p4; SDSM 150921, 150923, 156488, 157008, m1; SDSM 150920, 156512, m2; SDSM 150922, m3.

Localities—Recovered from ant mounds 4, 6, 9, and 15 below the UPW; ant mounds 13 and 14 on the UPW; ant mound 8 above the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Description—There are two P4s referred here. SDSM 150917 is broken along the labial margin of the tooth, preserving the parastyle anteriorly, and retaining only the anterolingual edge of the paracone, but SDSM 156511 is complete (Figure 10C). The labial border is dominated by a large, central paracone with a blade-like postparacrista extending to the posterolabial corner of the tooth. Anterior to the paracone is a small parastyle at the anterolabial corner of the tooth, at the base of the crown. Conules are lacking and the protocone is a sharp triangle in shape. The large hypocone is nearly as large as the protocone and positioned posterior to it and slightly more lingually.

The only upper molar, SDSM 156450, is missing the labial half of the tooth. The remaining protocone and hypocone are similar to that of the referred P4 and agree with the descriptions of other species with a strongly V-shaped protocone and only slightly smaller but similarly shaped hypocone (White, 1954; Stirton and Rensberger, 1964).

The two p4s are dominated by the very high protoconid (labial height range 2.69-2.94 mm) and an extremely low talonid. The protoconid is conical with a minute paraconid along its anterior slope near the base of the crown. The metaconid is slightly larger than the paraconid and situated on the posterolingual slope of the protoconid at about half its height. The talonid is small and low. There is a single cusp along the posterior

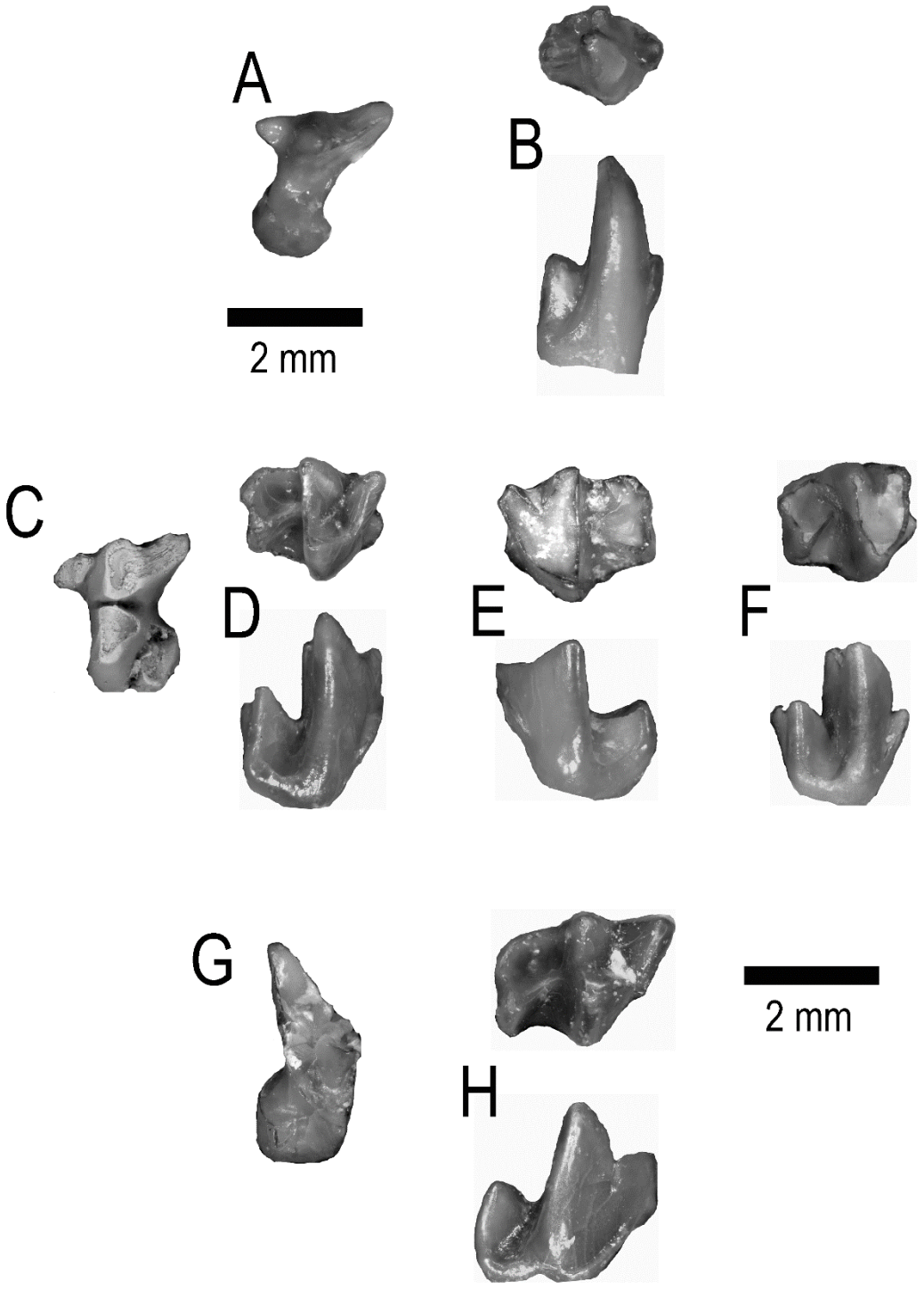

FIGURE 10. *Ankylodon* and *Micropternodus* from the ant mound collection from Sioux County, NE. A-B, *A.* sp., cf. *A. progressus*. A, SDSM 150916, left P4. B, SDSM 150717, right p4. C-F, *M. borealis*. C, SDSM 156511, left P4. D, SDSM 150923, right m1 or m2. E, SDSM 150920, left m2. F, SDSM 150922, right m3. G-H, *M.* sp., cf. *M. montrosensis*. G, SDSM 150918, P4(partial). H, SDSM 150960, right m1 or m2. Figures B, D-F and H, occlusal view above, labial view below.

margin of the tooth, just lingual to its center (?hypoconulid). There is a short labial cingulid that runs along the base of the tooth from the posterior edge of the base of the protoconid to the base of the talonid cusp.

Of the isolated specimens of m1 or m2, SDSM 150921 is heavily worn and SDSM 150923 (Figure 10D) is almost completely unworn to the base of the crown and SDSM 156488 moderately worn. The trigonid is markedly higher than the talonid on the unworn and moderately worn specimens (trigonid height measured labially = 2.69 mm and 2.75 mm). The paracristid and protocristid form a V-shape, uniting the cusps of the trigonid. All three trigonid cusps are equal in height. The trigonid basin is broadly open lingually. A short anterior cingulid originates on the anterior face of the tooth at approximately half its height and extends ventrally and slightly labially but does not reach the base of the crown. The talonid is a completely enclosed basin and is narrower than the trigonid. A low ridge runs along the labial side of the tooth between the bases of the protoconid and hypoconid. A small hypoconulid is at the center of the posterior margin. Just lingual to it is a minute entoconid. At the posterolabial corner of the talonid is a slightly larger hypoconid that is triangular in occlusal outline. The cristid obliqua extends from the anterolingual corner of the hypoconid and ends at the base of the posterior wall of the trigonid near its center.

The only confidently identified m2 is SDSM 150920 (Figure 10E) because it is retained in a fragment of the dentary with surrounding alveoli for m1 and m3. It is slightly more worn than SDSM 150923 but otherwise nearly identical in morphology.

The only m3 is SDSM 150922 (Figure 10F). It is only minimally worn so the height of the trigonid can be measured (2.29 mm). It differs only slightly from m1 or m2 in morphology. The talonid is smaller relative to the trigonid, the entoconid is more reduced, and the hypoconulid is relatively larger (nearly the size of the hypoconid) and positioned slightly more posteriorly.

Discussion—The Sioux County ant mound material referred here is comparable in size to both *M. borealis* and *M. morgani* Stirton and Rensberger, 1964 (Table 6; Ostrander, 1983: table 1). However, the height of the trigonid on the m1 or m2 of the Sioux County specimens is markedly lower than in *M. morgani* (3.6-3.7 mm) and comparable to that of *M. borealis* and *M. strophensis* (=3.1 mm; Stirton and Rensberger, 1964: 77). This is also true for the height of m3. One of the characters used by Stirton and Rensberger (1964) to distinguish the two Chadronian species was the presence of a low ridge (cingulid) on the labial side of m1 and m2 of *M. borealis* (lacking on *M. strophensis*). All of the Sioux County lower molars have this cingulid.

The holotypes of both *M. strophensis* and *M. borealis* are from the Chadronian of Montana (Matthew, 1901; White, 1954; Gunnell et al., 2008b). The Sioux County specimens are nearly all from ant mounds situated on or below the UPW, except for one specimen (SDSM 150921) from an ant mound above the UPW.

Micropternodus sp., cf. *M. montrosensis* Ostrander, 1983
(Figure 10G-H; Table 7)

Referred Specimens—SDSM 150918, P4 (partial); SDSM 150960, m1 or m2; SDSM 150919, m3.

Localities—Recovered from ant mound 1 below the UPW; ant mound 13 on the UPW; ant mound 17 above the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Description—The only P4, SDSM 150918, is partially broken; the anterolabial corner of the tooth is missing along with the majority of the paracone (Figure 10G). The paracone appears to be large and in the center of the labial half of the tooth. The metasyle is a minute cusp in the posterolabial corner of the tooth. The centrocrista (=paraconal blade) is mostly broken away but there is evidence of it along the posterior margin of the tooth, extending lingually from the metastyle. The protocone is V-shaped with a small paraconule and metaconule near the center of the tooth along the preprotocrista and postprotocrista, respectively. The hypocone is slightly larger than the protocone and extends slightly more lingually. It has a more rounded surface than the protocone and is continuous with a broad talon.

The only m1 or m2, SDSM 150960, is slightly wider than long (Figure 10H; Table 6). The labial height of the trigonid is 3.21 mm. On the measurable specimen of *M. borealis* the ratio of the height to the length is 1.26, whereas on the specimen referred here this ratio is 1.18, just slightly lower. In overall morphology it differs little from that of *M. borealis* (described above). On SDSM 150960, the entoconid is more greatly reduced and confluent with the hypoconulid, which is relatively smaller than that in *M. strophensis*. The only other difference in SDSM 150960 and the *M. borealis* molars is the anterior cingulid that extends along the base of the crown around the labial side, ultimately ending at the base of the hypoconid.

The referred m3, SDSM 150919, is heavily worn, so no measurement of the crown-height can be made. In overall morphology, it is similar to the m1 or m2, but the talonid appears to be relatively smaller and there is no basal cingulid along the anterior or labial side of the tooth.

Discussion—In size, the specimens referred here are most similar to those of *M. montrosensis* (Table 6). However, both of the lower molars from the Sioux County ant mounds are slightly wider than long,

whereas the length is much greater than the width in all other samples (Stirton and Rensberger, 1964: 77; Ostrander, 1983: table 1). The upper cheek teeth of *M. montrosensis* have not been previously reported. The Sioux County P4 specimen (SDSM 150918) is referred here to *M.* cf. *montrosensis* based on its larger size and its *Micropternodus*-like morphology. Ostrander (1983) described this species based on material from the Chadron Formation exposures in Sioux County, Nebraska.

Family Soricidae Fischer von Waldheim, 1817
Subfamily Heterosoricinae Viret and Zapfe, 1951
Genus *Domnina* Cope, 1873b
Domnina gradata Cope, 1873b
(Figure 11A-D; Table 8)

Referred Specimens—SDSM 150783, maxilla with A4-M2; SDSM 156509, maxilla fragment with A4-M1; SDSM 150781, 150784-150786, 150789, 150791, 150867, partial maxilla with M1-M2; SDSM 150779, 150782, 150861, 150863, 150895, 150929, 156439, A4; SDSM 150780, 150787, 150788, 156440, M1; SDSM 150790, 150862, 150864, 156438, M2; SDSM 150816, dentary fragment with i1, a1-a3; SDSM 150802, dentary fragment with i1, m1; SDSM 150815, dentary with a4-m2; SDSM 150808, 150827, partial dentary with a4-m1; SDSM 150793, 150794, 150797, 150809, 156441, 156442, dentary with m1-m3; SDSM 150792, 150796, 150798-150801, 150803, 150805, 150806, 150812, 150823, 150835, 150850, 150927, partial dentary with m1-m2; SDSM 150795, 150807, 150810, 150811, 150817, 156445, partial dentary with m2-m3; SDSM 150814, 150819-150822, 150826, 150828, 150830, 150837, 150839, 150841, 150846, 150847, 150849, 150857, 150860, 150928, 150931, 150932, 150934, 150935, 156443, 156444, m1; SDSM 150804, 150813, 150818, 150824, 150825, 150832, 150836, 150838, 150840, 150844, 150845, 150853, 150856, 150858, 150859, 150925, 150926, 150930, m2; SDSM 150829, 150831, 150833, 150834, 150842, 150843, 150851, 150852, 150854, 150855, 150933, 156449, m3.

Localities—Recovered from ant mound 1, 3-7, 9, 12, 15, and 16 below the UPW; ant mound 13 on the UPW; ant mounds 8, 11, 17, 18, and 19 above the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Discussion—The dentary and dentition of *Domnina gradata* have been described elsewhere in great detail (Patterson and McGrew, 1937; Repenning, 1967), so no additional description is offered here. In size, the teeth referred here are equivalent to those previously described for *D. gradata* (Table 8: Patterson and McGrew, 1937:256), clearly smaller than those of *D. sagittariensis* (Kihm and Schumaker 2008: table 2) and *D. dakotensis* (Macdonald, 1970: table 7), and larger than *D. thompsoni* (Simpson, 1941:2; Kihm and Schumaker 2008: table 3). Although the dental dimensions of *D. greeni* are similar to those of *D. gradata* (Macdonald, 1963: 168), the former is diagnosed as having the cingulid on the lower molars limited to the anterior margin, contrasting with the morphology present in this collection. The Sioux County collection also lacks the additional antemolar of *D. thompsoni*.

Domnina gradata is the best represented lipotyphlan from the Sioux County ant mounds both below and above the UPW, being represented by over 100 specimens and from nearly all localities. Elsewhere, *D. gradata* is limited to the Orellan (Patterson and McGrew, 1937; Repenning, 1967; Gunnell et al., 2008b). Ostrander (1987) referred several specimens from the Chadronian Raben Ranch fauna of Sioux County to *D. gradata.* However, based on the measurements he presented (Ostrander, 1987: table 4), all of the widths of the lower molars slightly exceed those of the large collection from Sioux County described here (Table 8). One of the upper molars cited by Ostrander (1987: SDSM 9830) is narrower than any from the current collection, suggesting that Raben Ranch samples another species.

Genus *Noritrimylus* n. gen.

Type Species—*Noritrimylus compressus* (Galbreath, 1953)

Included Species—*Noritrimylus dakotensis* (Repenning, 1967); *Noritrimylus metaxy* (Korth, 2020a) and the type species.

Diagnosis—Characters shared with *Pseudotrimylus* Gureev, 1971: cusps on cheek teeth blunt and rounded; lower molars lack posterior cingulid (hypocristid continuous from hypoconid to entoconid); no entocristid on lower molars; depth of dentary greatest below m1 and narrows posteriorly (narrowest just posterior to m3); little or no pigmentation of teeth (apices same color as bases of cusps). Primitive characters of *Noritrimylus* not present in *Pseudotrimylus*: mental foramen ventral to m1 (ventral to m2 in *Pseudotrimylus*); four antemolars in dentary (three in *Pseudotrimylus*); posterior most antemolar (a4) largest (anterior most [a1] largest in *Pseudotrimylus*).

Range—Possibly Chadronian (latest Eocene) to Arikareean (latest Oligocene), South Dakota, Nebraska, and Colorado.

Etymology—Greek, *noris*, early; *tri*, three; *mylos*, grinder or molar.

Historical Review—Galbreath (1953) named a new species of soricid, *Domnina compressa* from the Orellan of Colorado based on a single dentary, KUVP 8154, with m1-m3 and no antemolars or alveoli anterior to m1. Later Repenning (1967), in his review of the

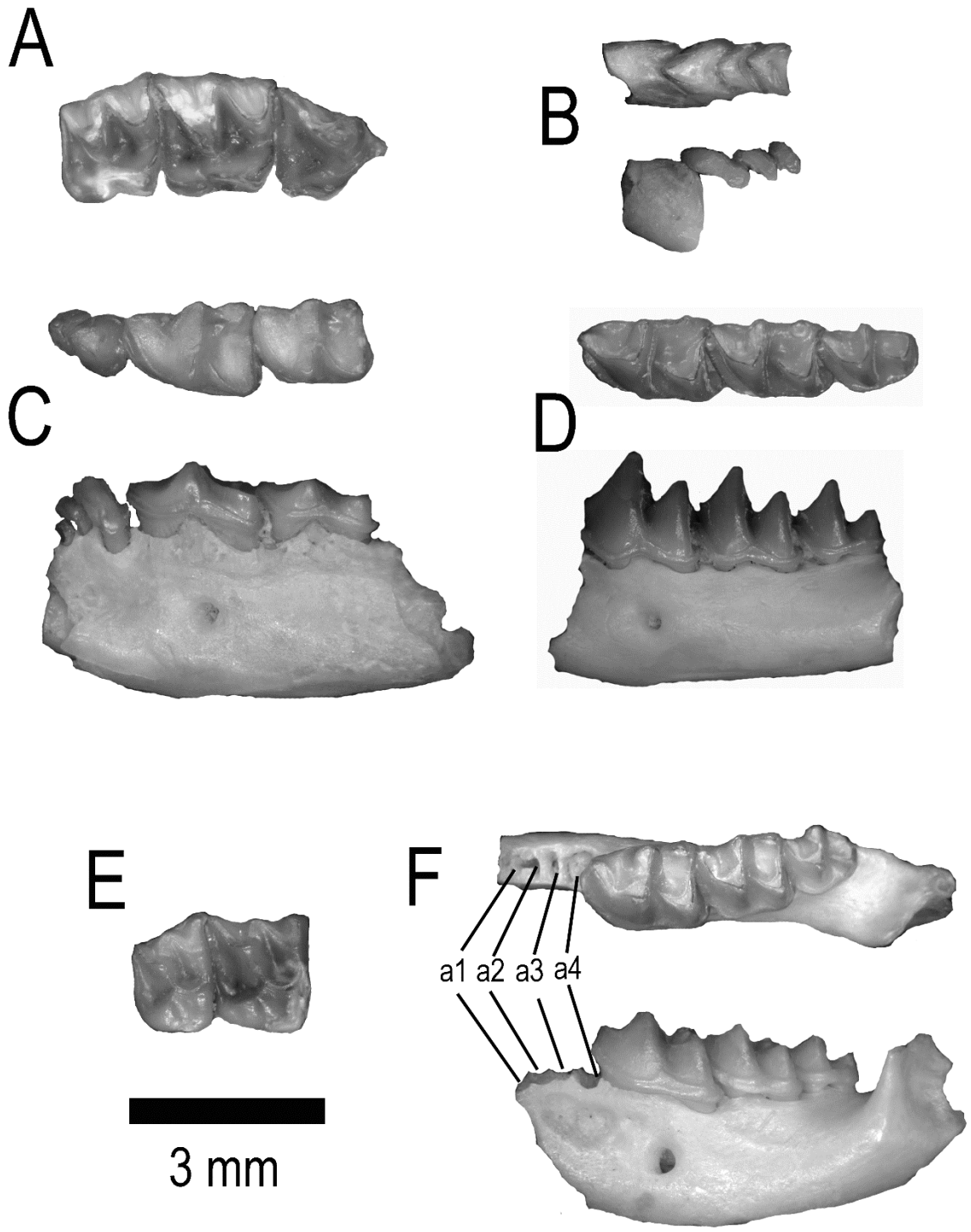

FIGURE 11. Soricidae from the ant mound collection from Sioux County, Nebraska. A-D, *Domnina gradata*. A, SDSM 150783, right P4-M2. B, SDSM 150816, partial dentary with i1,a1-a3. C, SDSM 150815, dentary with left a2(root)-m2. D, SDSM 150793, dentary with left m1-m3. E-F, *Nototrimylus compressus*. E, SDSM 150866, right M1-M2. F, SDSM 150869 (holotype), left dentary with m1-m3 with alveoli for antemolars. Figures B-D and F, occlusal view above, labial view below.

Soricidae of the world, cited a second specimen of "*D.*" *compressus* from the Orellan of Sioux Co, Nebraska, FMNH UM 400 (similarly missing the antemolar dentition) and transferred the species to *Trimylus* Roger, 1885. He named two new species of the genus, *T. dakotensis* from the Arikareean of South Dakota and *T. mawbyi* from the Barstovian of Oregon. He also included *Heterosorex roperi* Wilson, 1960, from the Hemingfordian of Colorado in *Trimylus*. Later, Gureev (1971) proposed a new generic name *Pseudotrimylus* for *T. roperi*. Hutchison (1972) referred a specimen that had been previously referred to the erinaceid *Ocajila makpiyahe* from the Arikareean Sharps Formation of South Dakota by Macdonald (1970) to *Trimylus* sp.

Engesser (1975) noted that the generic name *Trimylus* was invalid and shortly thereafter reviewed the taxonomic history of this group of soricids (Engesser, 1979) and transferred all species previously included in *Trimylus* by Repenning (1967) to *Pseudotrimylus* and suggested the earlier occurring species were likely referable to a new genus but retained them in *Pseudotrimylus* provisionally.

More recently, Martin and Lim (2004) named a new species *P. blacki* (mislabeled in their figure as *P. nebraskensis*) from Hemingfordian of Nebraska. In their review of North American soricids, Gunnell et al. (2008b) listed four species of *Pseudotrimylus* that did not include *P. blacki*. Finally, Korth (2020a) named *P. metaxy* from the late Whitneyan of South Dakota.

Discussion—Engesser (1979: table 1) presented extensive comparisons between *Pseudotrimylus* and other North American and Eurasian heterosoricines: *Domnina*, *Heterosorex* Gaillard, 1915, *Ingentisorex* Hutchison, 1966, and *Paradomnina* Hutchison, 1966 (also see Engesser, 1975). The only other recognized North American heterosoricine is *Wilsonsorex* Martin, 1978, from the Arikareean of South Dakota, and Arikareean and Hemindfordian of Colorado. *Wilsonsorex* differs from *Pseudotrimylus* in having "…upper molars with distinct paraconule and metaconules, divided mesostyle, lingual cusps anteroposteriorly compressed into V-shape…" (Gunnell et al., 2008b: 113).

Engesser (1979) also noted several differences between the later occurring *P. roperi* and other earlier occurring species referred to *Pseudotrimylus*. These earlier species are referred here to the new genus *Noritrimylus* and are distinct from *P. roperi* and *P. mawbyi* in several characters: 1) mental foramen ventral to m1 (ventral to m2 in *Pseudotrimylus*); 2) four antemolars present in dentary (three in *Pseudotrimylus*); and 3) posterior most antemolar (a4) largest (anterior most [a1] largest in *Pseudotrimylus*).

The species referred here to *Noritrimylus* were previously referred to *Pseudotrimylus* and range from the Orellan to the Arikareean (Oligocene), whereas *P. roperi* and *P. mawbyi*, both retained in *Pseudotrimylus* are known from the Hemingfordian and Barstovian (Miocene).

Noritrimylus compressus (Galbreath, 1953)
(Figure 11E-F; Tables 9, 10)

Domnina compressa Galbreath, 1953
Heterosorex compressus (Galbreath); Mawby, 1960
Trimylus compressus (Galbreath); Repenning, 1967
Pseudotrimylus compressus (Galbreath); Engesser, 1979

Type Specimen—KUVP 8154, right dentary with m1-m3 (Galbreath, 1953: 46).

Referred Specimens—SDSM 150865, M1; SDSM 150866, 156447, partial maxilla with M1-M2; SDSM 150868-150870, 150881, dentary with m1-m3; SDSM 150873-150875, 150877, 150878, 150883, 150884, dentary with m1-m2; SDSM 150889, dentary with m1-m2; SDSM 150879, partial dentary with m2-m3; SDSM 150886-150888, 156508, m1; SDSM 150871, 150872, 150876, 150880, 150882, 150885, 156448, m2; SDSM 150848, m3.

Localities—Recovered from ant mounds 1, 3-6, 9, 15, and 16 below the UPW; ant mound 13 on the UPW; ant mounds 8, 10, 11, and 19 above the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Emended Diagnosis–Small species, near size of *Noritrimylus metaxy*, smaller than *Noritrimylus dakotensis*; lower molars decrease in size from m1 to m3 more dramatically than in other species.

Description—The only morphology of the maxilla preserved is the base of the zygomatic arch that originates lateral to the boundary between M1 and M2. The cusps of the molars are blunt and bulbous. M1 is squared in occlusal outline (Figure 11E). The paracone and metacone are crescentic, forming a 'W-shaped' ectoloph (dilambdodonty). The parastyle, mesostyle, and metastyle are distinct cuspules. The mesostyle forms a 'U-shape' at the center of the ectoloph. A minute labial cingulum extends for the entire length of the tooth. There is no indication of a para- or metaconule. The protocone is also 'U-shaped' with the pre- and postprotocristae fusing with the center of the lingual edge of the paracone and metacone, respectively. The hypocone is round and positioned slightly more lingually than the protocone. The talon is a broad basin that is enclosed by a lingual cingulum that is continuous with a posterior cingulum that ends labially posterolingual to the metastyle.

M2 is smaller than M1 and more anteroposteriorly shortened (Figure 11E). The labial margin slopes posterolingually, making the posterior width shorter

than the anterior width. Other than proportions, the remainder of the morphology of M2 is similar to that of M1.

The dentary is deepest ventral to m1, slopes dorsally posteriorly, and is narrowest just posterior to m3 (Figure 11F). The mental foramen is relatively large and ventral to the center of m1. A shallow anteriorly oriented depression in the dentary originates anterior to the mental foramen and extends anteriorly and slightly dorsally to a point ventral to the most anterior antemolar. The ascending ramus rises just posterior to m3. Unfortunately, none of the available specimens preserves the mandibular condyle. The masseteric fossa is deep and limited to the ascending ramus.

No antemolars are preserved in any specimens; however, one specimen, SDSM 150869, preserves the alveoli for the incisor and all the antemolars (Figure 11F). The root of i1 extends posteriorly to below the posterior margin of m1. Based on the alveolus it was laterally compressed with a much greater dorsoventral than labiolingual cross-section. There are four additional distinct alveoli anterior to m1. Of these, the most posterior (a4) has an alveolus that is oval in outline, whereas the more anterior alveoli are compressed into transverse slits in the dorsal margin of the dentary. The a4 is larger than any of the anterior antemolars, which appear to be of equal size based on the alveoli.

The lower molars dramatically decrease in size from m1 to m3 (length of m3 averaging 60 percent length of m1). As with the upper molars, the cusps have blunt apices (Figure 11F). The trigonid and talonid of m1 are nearly equal in width. The paraconid is at the center of the anterior margin. The paracristid is continuous from the apex of the protoconid to the apex of the paraconid with a slight flexure at its center. The protoconid is triangular in occlusal outline. The metaconid is nearly as high as the protoconid and positioned directly lingual to it. The protocristid runs directly lingually from the apex of the protoconid to the apex of the metaconid. The cusps of the talonid are lower than the trigonid, the entoconid being the tallest. The hypoconid is crescentic on occlusal outline. The cristid obliqua runs anterolingually from the anterolingual corner of the hypoconid to the center of the base of the trigonid. The postcristid runs directly lingually from the posterolingual corner of the hypoconid to the entoconid at the posterolingual corner of the talonid. The entoconid is circular in occlusal outline. The only indication of an entocristid is a minute ridge running along the anterolingual slope of the entoconid. There is a minute swelling at the base of the entoconid on its posterior side (?hypoconulid). A distinct cingulid is present along the base of the crown, originating ventral to the paraconid and wrapping around the labial base for the length of the tooth, then extending around the posterolabial corner of the tooth, ending near the center of the posterior margin of the tooth.

The length of m2 averages 76 percent that of m1 but is similar in occlusal morphology. Other than size, m2 differs from m1 in having a higher and more lingually placed paraconid and only variably has a minute hypoconulid that is relatively smaller than in m1, if present.

The m3 is much smaller than m2, averaging 79 percent of m2 length and only 60 percent that of m1 (Table 9). The trigonid of m3 is similar to that of m2 but the talonid is greatly reduced in size. The entoconid is relatively lower than in m1 and m2. A very low ridge extends anteriorly from the entoconid (entocristid) on some specimens. There is never a hypoconulid.

Discussion—The material from the Sioux County ant mounds is the largest collection of any species referred to *Pseudotrimylus* or *Noritrimylus* ever reported. It allows for a better understanding of the morphology of the latter. Previously, no specimens of *N. compressus* cited have retained all of the antemolars or the alveoli (Galbreath, 1953; Repenning, 1967). It is evident from the specimen of *N. compressus* reported here, SDSM 150869 (Figure 11F), and that of *N. metaxy* (Korth, 2020a: fig. 5D) that there are clearly four antemolars present in contrast to three in *P. roperi* and *P. mawbyi* (Repenning, 1967).

The specimen Hutchison (1972) referred to *Trimylus* sp. from the Arikareean of South Dakota appears referable to *N. dakotensis* but was not examined directly in this study. Martin and Lim (2004) named *Pseudotrimylus blacki* based on a single dentary with m1-m3 (UNSM 20047) from the Hemingfordian of Nebraska. It was diagnosed as being distinct from *P. roperi* based on the proportions of m1 (relatively longer) and m3 (relatively shorter). However, the dimensions of the molars of the holotype and only known specimen of *P. blacki* are well within the range of those of the topotypic collection of *P. roperi* from Colorado (Wilson, 1960: 32; Martin and Lim, 2004: 207). It appears likely that *P. blacki* is a junior synonym of *P. roperi*.

Family Proscalopidae Reed, 1961
Genus *Oligoscalops* Reed, 1961
Oligoscalops galbreathi (Reed, 1956)
(Figure 12A-F; Table 11)

Referred Specimens—SDSM 150896, 150901, P4; SDSM 156502, 156505, M1; SDSM 150898, 150900, 156497, 156499-156501, 156504, M2; SDSM 150897, M3; SDSM 150908, 150909 partial dentary with m2-m3; SDSM 150903, 150905, 150907, 150910, 156446, m1; SDSM 150904, 156506, m2; SDSM 150902, m3.

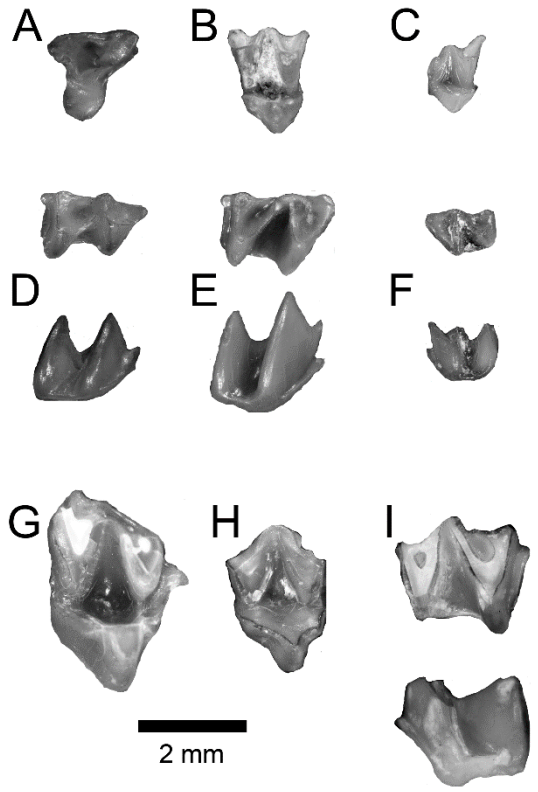

FIGURE 12. Proscalopidae from the ant mound collection from Sioux County, Nebraska. A-F, *Oliogscalops galbreathi*. A, SDSM 150896, right P4. B, SDSM 150898, right M2. C, SDSM 150897, right M3. D, SDSM 150903, right m1. E, SDSM 150904, right m2. F, SDSM 150902, left m3. G-I, *Proscalops* sp. G, SDSM 150899, right M1 (partial). H, SDSM 150894, right M2 (partial). I, SDSM 150906, left m2. Figures D-F and I, occlusal view above, labial view below.

Localities—Recovered from ant mounds 3, 4, 6, 7, 9, and 15 below the UPW; ant mound 13 on the UPW; ant mound 8 above the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Discussion—This species has been previously described and diagnosed in detail (Reed, 1956; Reed, 1961; Hutchison, 1972; Barnosky, 1981; Gunnell et al., 2008b). The specimens referred here do not differ in morphology or size from the previously described material (Table 10; Reed, 1961: 475). The specimens from the Sioux County ant mounds were collected from mounds below and above the UPW. Gunnell et al. (2008b: 100) listed this species as occurring in localities ranging from latest Chadronian to Orellan of Colorado and late Chadronian of South Dakota.

Genus *Proscalops* Matthew, 1901
Proscalops sp.
(Figures 12G-I)

Referred Specimens—SDSM 150899, 156498 M1; SDSM 150894, 156503, partial M2; SDSM 156507, left m1; SDSM 150906, left m2.

Measurements—M1: SDSM 150899, L = 2.68 mm; SDSM 156498, L = 3.08 mm; W = 3.11 mm. M2: SDSM 150894, W = 2.74 mm; SDSM 156503, W = 2.63 mm. m1: SDSM 156507, L = 2.52 mm; W = 1.81 mm. m2: SDSM 150906, L = 2.56 mm; W = 1.99 mm.

Localities—Recovered from ant mounds 1 and 3 below the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Discussion—Most of the specimens referred to *Proscalops* from the Sioux County ant mounds are incomplete; only an M1 (SDSM 156498) and an m1 (SDSM 156507) are complete. However, they are clearly larger than the specimens referred to *Oligoscalops* (Table 10) and are much higher crowned. They are similar in size to other species of *Proscalops* (Reed, 1961: 476-477; Bjork, 1975: table 1) but lack any diagnostic features of the individual species. Gunnell et al. (2008b: fig. 7.7) figured the occurrence of *Proscalops* as ranging from the late Chadronian to the late Hemingfordian. All of the Sioux County specimens are from ant mounds below the UPW.

Family Apternodontidae Matthew, 1910
Genus *Apternodus* Matthew, 1903a
Apternodus sp., cf. *A. major* Asher et al., 2002
(Figure 13H)

Referred Specimen—SDSM 156363, right M2.

Locality—Recovered from ant mound 16 below the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Measurements—L = 2.04 mm; W = 4.76 mm.

Discussion—The single upper molar has the morphology characteristic of *Apternodus* (Figure 13H): markedly wider than long, a single zalambdodont paracone near its center, and wider anteriorly than posteriorly, typical of M2 (Asher et al., 2002). In terms of size, the Sioux County specimen is much larger than specimens referred below to the zalambdodont *Oligoryctes*, and best matches the size of *A. major* known from the Chadronian of eastern Wyoming (Asher et al., 2002: table 2). The occurrence of the Sioux County specimen from an ant mound below the UPW matches the known record for this species from elsewhere (Asher et al., 2002; Gunnell et al., 2008b).

Family Oligoryctidae Asher et al., 2002
Genus *Oligoryctes* Hough, 1956
Oligoryctes tenutalonidus n. sp.
(Figure 13A-E; Table 11)

Type Specimen—SDSM 150890, dentary with m1-m3 (Figure 13A, B).

Referred Specimens—SDSM 156356, partial dentary with p3(partial)-m2; SDSM 150892, SDSM 150891, partial dentary with m1-m2; SDSM 150606, dentary fragment with m2-m3; SDSM 150648, dentary fragment with m3.

Localities—Recovered from ant mounds 3, 4, 7, and 15 below the UPW; ant mound 13 on the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Diagnosis—Smallest species of the genus; m1 and m2 longer than wide (approximately equal in length and width in other species); trigonid widths of m1-m3 subequal in size, as in *O. altitalonidus*; accessory mental foramen variably present ventral to p4-m1 boundary on dentary.

Etymology—Latin, *tenues*, thin; *talus*, ankle: in reference to the proportionally narrower molars.

Description—The dentary is dorsoventrally thin and narrows slightly anteriorly from ventral to p4 (Figure 13C, E). Two mental foramina are present on one specimen, SDSM 150892 (Figure 13C). The larger, more anterior foramen is ventral to the roots for p4; the second is only slightly smaller and ventral to the boundary between p4 and m1. However, there is no indication of this second foramen on the other specimens that preserve this part of the dentary (SDSM 150891, 156356; Figure 13E). SDSM 150891 retains the anterior margin of the ascending ramus which originates just posterior to the posterior margin of the m3.

Only the base of p3 is preserved on SDSM 156356 (Figure 13D, E). It is two-rooted and much smaller than p4 with a minute cingulid that wraps around the labial and posterior borders of the tooth. The talonid is minute and dominated by a central anteroposterior ridge.

The p4 is only present on SDSM 156356 (Figure 13E). It is similar to m1 and m2 in being narrower than long, trigonid markedly higher than the talonid, and having a much reduced talonid. A cingulid is restricted to the anterior and labial base of the tooth. All other features are as in m1 and m2.

The m1 and m2 are nearly identical in size and morphology, the trigonid being slightly more anteroposteriorly compressed on m2 (Figure 13A, D). The protoconid is the tallest of the trigonid cusps. The metaconid is directly lingual to it connected by the protocristid, forming a high posterior wall of the trigonid. The paraconid is the lowest of the trigonid cusps at the anterolingual corner of the tooth and is anteroposteriorly compressed. An anterior cingulid originates anteriorly ventral and slightly labial to the paraconid. The cingulid wraps around the anterolablial corner of the tooth at its base and continues along the posterior border of the tooth, forming the labial portion of the talonid, ending at the posterolingual corner of the tooth. A short posteriorly directed lophid runs from the base of the metaconid to the posterior margin of the tooth, ending in a minute cusp (hypoconid?).

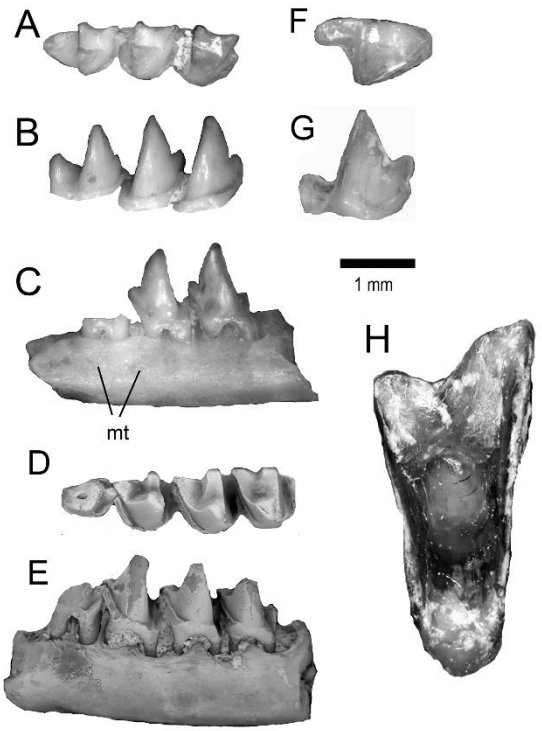

FIGURE 13. *Oligoryctes* and *Apternodus* from the ant mound collection from Sioux County, Nebraska. A-E, *Oligoryctes tenutalonidus*. A-B, SDSM 150890 (holotype), right m1-m3. A, occlusal view. B, labial view. C, SDSM 150892, labial view of dentary with partial dentary with p4(roots)-m2. D-E, SDSM 156356, left p3(partial)-M2. D, occlusal view. E, labial view of dentary. F, G, *O.* sp., cf. *O. cameronensis* SDSM 150893, right m3. F, occlusal view. G, labial view. H, *Apternodus* sp. SDSM 156363, right M2, occlusal view. All specimens to same scale.

The m3 is similar in width to m1 and m2 with a similar trigonid (Figure 13A, B). The talonid extends posteriorly for approximately the same length as the trigonid making the tooth longer than m1 and m2 (Table 11). There is a distinct hypoconid at the center of the posterior margin of the talonid that extends well dorsal to the remainder of the talonid and reaches the height of the paraconid, but not the metaconid and protoconid. The same anteroposterior lophid present on m1 and m2 is continuous with the anterolablial corner of the hypoconid and encloses a narrow transversely compressed basin between it and the lingual side of the talonid where a lophid runs posteriorly from the posterolingual base of the metaconid to the anterolabial corner of the hypoconid.

Discussion—*O. tenutalonidus* is distinctly smaller than other recognized species of the genus (*O. altitalonidus* and *O. comeronensis*;Table 11). It also differs in the proportions of the cheek teeth; the m1 and m2 of other species of *Oligoryctes* are approximately equal in length and width (Asher et al., 2002: table 2)

but those of *O. tenutalonidus* are distinctly narrower, the length averaging 120 percent the width. All of the specimens referred to *O. enutalonidus* from Sioux County are from ant mounds situated on or below the UPW.

Oligoryctes sp., cf. *O. cameronensis* Hough, 1956
(Figure 13F-G)

Referred Specimen—SDSM 150893, dentary fragment with m3; SDSM 156978, right M1 (partial).

Locality—Recovered from ant mounds 4 and 9 below the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Measurements—m3: L = 1.55 mm, W = 1.77 mm; M1: L = 1.39 mm.

Discussion—An m3 of *Oligoryctes* from the Sioux County ant mounds is distinctly larger than those referred to *O. tenutalonidus* (Table 11). It is tentatively referred to the larger of the known species of *Oligoryctes*, *O. cameronensis* (Asher et al., 2002: table 2). Similarly, a partial M1 (SDSM 156978) is larger than those reported for *O. altitalonidus* and similar to those of *O. cameronensis* and thus is also larger than should be expected for *O. tenutalonidus*. However, this tooth is only partially preserved. *O. cameronensis* is previously reported from the Chadronian (Gunnell et al., 2008b), which is consistent with the recovery of these specimens below the UPW in this study.

Order Primates Linneaus, 1758
Family Omomyidae Trouessart, 1879
Genus and species uncertain
(Figure 14)

Referred Specimens—SDSM 156331, right M1 or M2; SDSM 156330, left M3; SDSM 154953, left m3.

Localities—Recovered from ant mounds 2, 4, and 15 below the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Measurements—SDSM 156331, M1 or M2: L = 3.47 mm; W = 4.68 mm; SDSM 156330, M3: L = 3.05 mm; W = 4.31 mm; SDSM 154953, m3 L =4.40 mm; W = 2.89 mm.

Description—The M1 or M2, SDSM 156331 (Figure 14A), has a small chip of the enamel missing in the anterolabial corner, which may have produced an anteroposterior measurement slightly less than its actual size (see above measurements). The tooth is markedly wider than long and longer labially than lingually. Only the posterolingual half of the paracone remains but it appears conical in shape and is higher and larger than the metacone. The centrocrista extends posteriorly and slightly labially from the paracone to the center line of the tooth, where it then is redirected posteriorly and slightly lingually until it reaches the apex of the metacone. A short postmetacrista extends directly posteriorly from the metacone to the posterior margin of the tooth where it meets the postcingulum. The postcingulum originates at the posterolabial corner of the tooth and continues along the base of the posterior border. The lingual end of the postcingulum curves slightly, then rises in the direction of the apex of the protocone but does not extend more than half the height of the protocone. There is no cusp or broadening of the cingulum that would indicate a hypocone. The protocone is the tallest of the cusps and is positioned along the centerline of the tooth labial to its lingual boundary. The preprotocrista and postprotocrista form a V-shape with the protocone at the lingual apex. Both cristae slope downward as they extend labially. The postprotocrista ends at the posterolingual base of the metacone; there is no indication of a metaconule. The preprotocrista ends labially in a small paraconule that forms a small V-shape at the anterolingual base of the paracone. There is a low, narrow precingulum that originates at the base of the protocone and runs labially but its labial extent cannot be determined because of breakage.

The referred M3, SDSM 156330 (Figure 14B) is similar in morphology to the anterior molar but is slightly smaller and wider anteriorly than posteriorly. The anterior half of the tooth is similar to that of the anterior molar. There is no ectocingulum, but the precingulum echoes that of the referred M1 or M2. The posterior half of the tooth is narrower and the metacone more reduced relative to the paracone than in the anterior molar. The preprotocrista extends from the protocone to the precingulum at a point well lingual to the base of the paracone with no indication of a paraconule. As with the preprotocrista, the postprotocrista runs to the posterior boundary of the tooth lingual to the metacone. However, there is a small metaconule from which a short ridge extends posterolingually to the edge of the tooth. The pre- and postcingulum are as in the anterior molar, very low along the base of the crown and ending at the labial corners of the tooth.

The trigonid of m3 is much higher than the talonid and anteroposteriorly compressed (Figure 14C). The paraconid is closely appressed to the metaconid but the apex of the former has been chipped away. The metaconid and protoconid are similar in size. The metaconid is slightly higher and slightly more anteriorly placed than the protoconid. The trigonid valley is completely enclosed by the paracristid anteriorly and the protocristid posteriorly. The talonid is elongated posteriorly. The cristid obliqua is low and joins the posterior wall of the trigonid posterior to the apex of the protoconid. The entoconid is the smallest of the talonid cusps, transversely compressed, and anterolingual to the hypoconulid. The hypoconid is ‘V-shaped,’ slightly

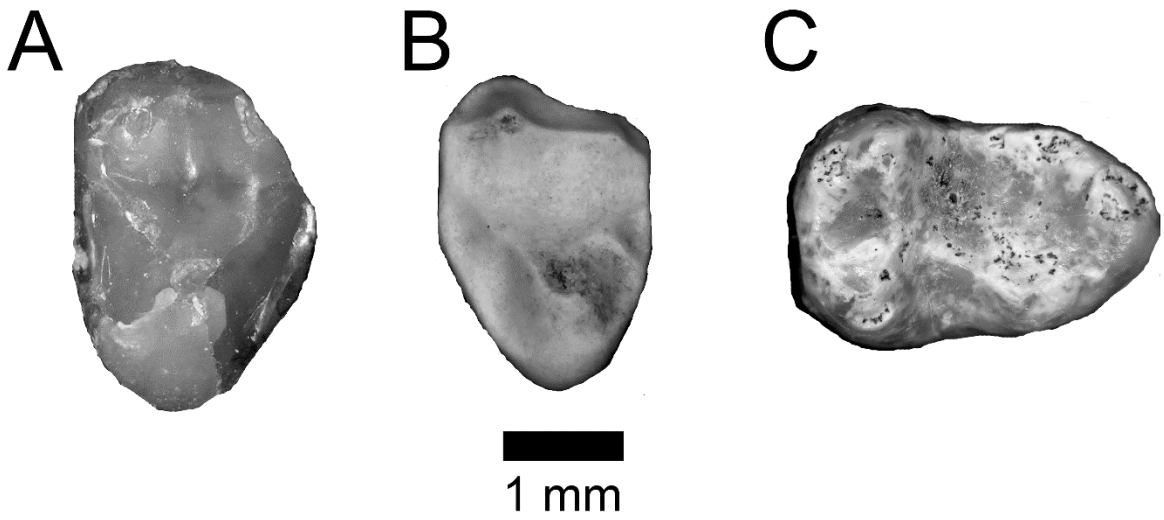

FIGURE 14. Primate indeterminate from the ant mound collection from Sioux County, Nebraska. A, SDSM 156331, right M1 or M2. B, SDSM 156330, left M3. C, SDSM 154953, left m3.

larger than the entoconid and on the labial margin of the talonid directly across from the entoconid. The hypoconulid is the largest of the talonid cusps and positioned at the center of the posterior margin of the tooth.

Discussion—The two upper molars referred here generally follow the morphology of omomyines with uninflated acute cusps, weak cingulae, and lack of a hypocone or protocone fold (Szalay, 1976; Gunnell et al., 2008c). Ostrander (1987) reported the occurrence of four specimens of a primate from the Chadronian of Sioux County that he referred to "*Chumashius* sp. Indet." He noted that the single referred upper molar differed from the original referred specimens in the lack of pre- and postcingula and a reduced lingual cingulum. The specimens referred here have narrow pre- and postcingulae along the anterior and posterior sides of the tooth but none on the lingual side.

The m3 referred here (SDSM 154953a; Figure 14C) is comparable in size to the referred upper molars and has a generalized omomyid-like morphology (see Szalay, 1976; Gunnell et al., 2008c, for comparisons). As with the upper molars, it is too large to belong to the same species as the specimens described by Ostrander (1987). It is similar to m3 of *Chumashius* (Stock, 1933: figs. 1a, 2a, 3a) but, once again, the ant mound specimen is 30 to 40 percent larger (Szalay, 1976: table 16; Ostrander, 1987: table 12).

In terms of size, the ant mound specimens most nearly approach those of the large omomyines such as *Macrotarsius* Clark, 1941, *Hemiacodon* Marsh, 1872, and *Ekgmowechashala* Macdonald, 1963 (Clark, 1941: 562; Macdonald, 1963: 67; 1970: table 9; Szalay, 1976: tables 18, 23, 27) but differ from the first two genera in lacking crested or crenulated enamel of the cheek teeth and the distinct mesostyle and broad stylar shelf of *Macrotarsius* and the distinct hypocones of the upper molars of *Hemiacodon* (Szalay, 1976:fig. 81). The trigonid on m3 of *Macrotarsius* (Clark, 1941: fig. 1; Szalay, 1976:fig. 78) is widely open, unlike the ant mound m3. None of the specimens referred here have the rugose "dendritic system of grooves" (Szalay, 1976: 355) of the enamel surface of the molars of *Ekgmowechashala*.

The simplified molar morphology of the Sioux County ant mound specimens best matches that of the Eocene *Chumashius* and *Uintanius* but the specimens are markedly larger (Stock, 1933: fig. 1; Szalay, 1976: figs. 70, 116, 118, table 24). At present these three specimens of primate teeth cannot be assigned to a known genus with confidence and the record is too poor to propose naming it as a new taxon at this time.

Order Chiroptera Blumenbach, 1779
Family ?Verspertilionidae Gray, 1821
Genus and species uncertain
(Figure 15)

Referred Specimen—SDSM 150961, left dentary fragment with m3.

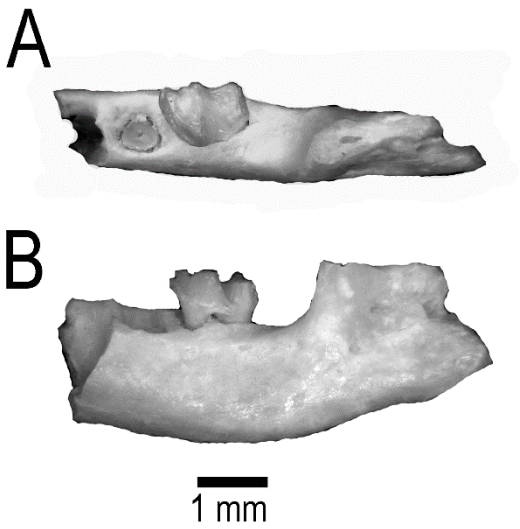

FIGURE 15. Chiropteran genus and species uncertain from the ant mound collection from Sioux County, Nebraska, SDSM 150961, left partial dentary with m3. A, occlusal view. B, labial view.

Locality—Recovered from ant mound 15 below the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Measurements—m3: L = 1.06 mm; W = 0.73 mm.

Description—The dentary is slender (maximum depth = 1.4 mm ventral to m3), and the ventral margin is essentially a straight line (Figure 15B). The anterior margin of the ascending ramus originates well posterior to m3. There is a shallow depression posterior to the vertical anterior margin for the muscular attachment.

The alveolus for m2 is larger than the length of m3 (approximate length = 1.55 mm). The m3 is moderately worn, so the trigonid is only slightly higher than the talonid (Figure 15A). The trigonid is an anteroposteriorly compressed V-shape with a protoconid slightly larger than the paraconid and metaconid, the lingual cusps are oval in occlusal outline. The talonid is squared posteriorly with a crescentic hypoconid in the posterolabial corner and an anteroposteriorly compressed entoconid on the posterolingual corner. The postcristid runs directly lingually from the posterolingual corner of the hypoconid to the posterolabial corner of the entoconid, giving the tooth a squared posterior margin. A low lophid runs anteriorly from the entoconid (entocristid) to the base of the metaconid along the lingual margin of the tooth. A small but distinct cingulid runs from the base of the paraconid along the anterolabial base of the tooth and ends ventrally below the apex of the protoconid labially.

Discussion—This specimen is similar in size to the previously described chiropteran *Chadronycteris rabenae* Ostrander, 1983, known from the Chadron Formation of Sioux County. However, *C. rabenae* is known only from a maxilla so no direct comparison can be made with SDSM 150961. The length of m3 of SDSM 150961 is similar to that of the M3 of the holotype of *C. rabenae* (L = 0.79 mm [Ostrander, 1983: table 2]; or L = 1 mm [Czaplewski et al., 2019: table 1]). The m3 referred here is clearly myotodont (postcristid continuous with entoconid) and cannot be referred to the *Quinetia frigidaria*, which has been reported from the Whitneyan of North Dakota (Czaplewski et al., 2019). However, a partial lower molar from the same locality as the type of *Q. frigidaria* has the myotodont morphology of the talonid similar to that of the Sioux County specimen (Czaplewski et al., 2019). Similarly, the questionable occurrence of the otherwise European *Stehlinia* Revilliod, 1919, from the Chadronian of Nebraska, based on a lower premolar (Ostrander, 1987) also has the nyctalodont morphology (Czaplewski et al., 2008: fig. 12.1B). Although it cannot be verified at this time, it is likely that the m3 identified here is referable to the only known bat from this area, *Chadronycteris*. SDSM 150961 is from an ant mound below the UPW in the Chadron Formation, slightly higher stratigraphically than the holotype of *C. rabenae* from the Raben Ranch locality that is in the lower portion of the Big Cottonwood Creek Member below the lower purplish white layer (Terry and LaGarry, 1998).

Order Rodentia Bowdich, 1821
Family Ischyromyidae Alston, 1876
Genus *Ischyromys* Leidy, 1856
Ischyromys brevidens n. sp.
(Figure 16; Tables 12, 13)

Syntype Specimens—SDSM 155929, right P4; SDSM 156085, right p4 (Figures 16B, G).

Referred Specimens—585 isolated cheek teeth (see Appendix).

Localities—Recovered from all sampled ant mounds; syntypes are both from ant mound 4. Big Cottonwood Creek Member of the Chadron Formation.

Diagnosis—Molars similar in size and hypsodonty to those of *I. typus* and *I. veterior*; conules on upper molars absent; P4 always shorter than wide with no lingual groove separating hypocone from protocone and shorter than upper molars and has a small and poorly developed parastyle and anterior cingulum; ectolophid poorly developed on p4 (markedly lower on crown than other cusps and lophs).

Etymology—Latin, *brevis*, short; and *dens*, tooth. In reference to the shortened and simplified premolars of the species.

Description—The molars referred here do not differ markedly from those described for other species and are discussed below in the following section. P4 is wider than long on all specimens but the protoloph and

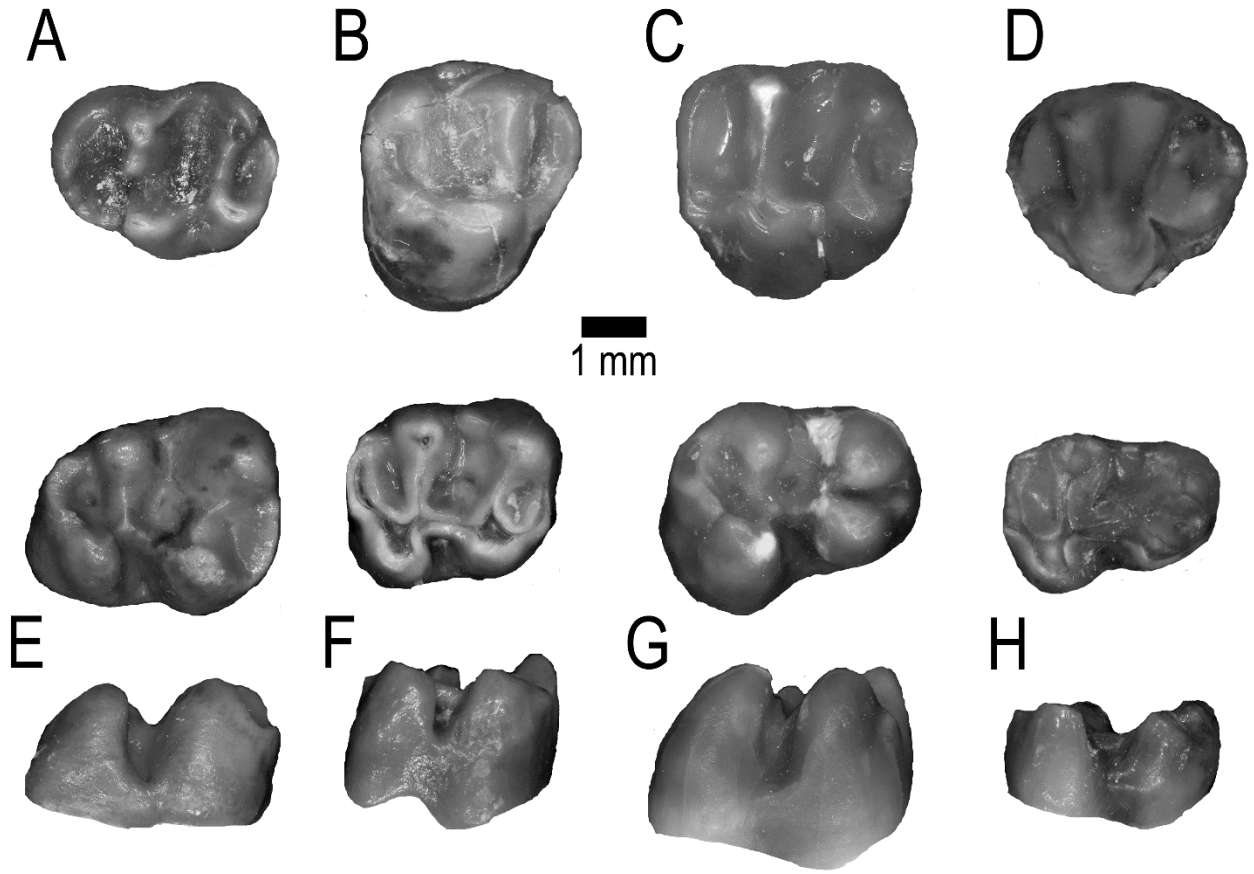

FIGURE 16. *Ischyromys brevidens* from the ant mound collection from Sioux County, Nebraska. A, SDSM 155809, left dP4. B, SDSM 155929, right P4 (syntype). C, SDSM 155777, left M1 or M2. D, SDSM 155791, left M3. E, SDSM 156038, right m3. F, SDSM 156040, right m1 or m2. G, SDSM 156085, right p4 (syntype). H, SDSM 156066, right dp4. E-H, occlusal view above, labial view below. All specimens to same scale.

metaloph are complete from the protocone to the lingual cusps (Figure 16B). The metaconule is a slight swelling on the metaloph rather than a distinct cusp. There is a hypocone present on all specimens, but it is smaller than the protocone and situated on the posterolabial corner of the tooth with little or no lingual groove separating it from the protocone.

The deciduous premolars can be distinguished from the permanent premolars by their thinner enamel, proportions, and splayed roots. DP4 is more molariform than P4 and longer than wide (P4 wider than long; Table 12). The anterolabial corner of dP4 is expanded anteriorly with a distinct transversely elongated parastyle along the anterior border of the tooth, limited to the labial half (Figure16A). A distinct basin separates it from the protoloph. The paracone and metacone are small, similar in size and anteroposteriorly compressed. The protoloph and metaloph are nearly parallel to one another and run almost directly transversely from the labial cusps. Variably, there is a slight swelling at the center of the metaloph and protoloph indicating conules, but there is never a distinct cusp. The protoloph joins the anterolabial corner of the protocone and the metaloph joins the anterolabial corner of the hypocone. The protocone is the largest cusp, is crescentic in outline, and makes up slightly more than half of the lingual border of the tooth. The hypocone is only slightly smaller than the protocone and directly posterior to it in the posterolingual corner of the tooth. It is more anteroposteriorly compressed than the protocone. The posterior cingulum runs lingually from the posterolabial corner of the hypocone, then bends anteriorly at the posterolabial corner of the tooth to fuse with the metacone.

On unworn or little-worn p4s the ectolophid is extremely thin and low, not reaching the occlusal surface until moderate to heavy wear (Figure 16G). The hypolophid is continuous to the ectolophid on 74 percent of the specimens. On the remaining specimens it is directed slightly posteriorly and joins the center of the

posterior cingulid. On a few unworn specimens of p4, there is a slight swelling at the center of the hypolophid indicating a poorly developed conulid.

As with dP4, dp4 is narrower than the permanent premolar, giving it a more elongated occlusal outline that tapers more dramatically at the anterior end (Figure 16H). Dp4 is approximately triangular in occlusal outline: widest posteriorly, narrowest anteriorly. The metaconid and protoconid are of equal size but small. The metaconid is always more anteriorly placed than the protoconid, more so than in p4. A small, circular trigonid basin is formed by a continuous anterior cingulid that extends around the anterior edge of the tooth from the anterolabial corner of the metaconid to the center of the anterior margin of the protoconid and posteriorly by a complete metalophulid II. A low metastylid crest runs posteriorly from the metaconid along the lingual border of the tooth, ending at the base of the entoconid. A small mesostylid is variably present at its center. Lingually the ectolophid is a short and very narrow lophid that extends directly posteriorly from the posterolingual corner of the protoconid to the anterolingual corner of the hypoconid. The entoconid is circular in occlusal outline and situated along the lingual border of the tooth well anterior to the position of the hypoconid. This orients the hypolophid in a posterolabial direction more slanted than in the molars or p4. The hypoconid is similar to that of p4, but the posterior cingulid bows more posteriorly and forms a much wider basin between it and the hypolophid. The posterior cingulid ends at the posterolingual corner of the tooth, separated from the entoconid by a deep valley.

The lower molars do not differ markedly from those of other species (Figures 16E, F; see Wood, 1937; Black, 1968; Rankin et al., 2020).

Comparisons—The ant mound specimens of *Ischyromys brevidens* are larger than those of *I. blacki* (Russell, 1972: 29; Storer, 1978: 7) and *I. junctus* (Wood, 1974: tables 6, 7). The upper molars of *I. blacki* and *I. junctus* also have a distinct metaconule and the metaloph is incomplete until a very late stage of wear (Black, 1968: figs. 15-16; Wood 1974: figs. 10C, D; Rankin, et al., 2020: fig. 5). The upper cheek teeth of *I. brevidens* have a complete metaloph on upper molars with no metaconule. The posterior cingulid is continuous with entoconid on lower molars of *I. junctus* but not on *I. brevidens* specimens. The P4 of *I. junctus* is also more molariform than in the ant mound specimens (Storer, 1978: fig. 1B).

I. brevidens differs from *I. douglassi* in being slightly smaller (Black, 1968: tables 1, 2), having m1-m2 longer than wide (wider than long in *I. douglassi*), metaconule not distinct on upper molars, hypolophid always complete on lower molars (variable in *I. douglassi*), m3 not as elongated relative to the anterior molars, and lack of accessory cusps on lower cheek teeth (Rankin et al., 2020). P4 of *I. brevidens* is similar in morphology to that of *I. douglassi* (not expanded anteroposteriorly, no valley between protocone and hypocone) but lacks the metaconule present in P4s of *I. douglassi* (Black, 1968: figs. 10-12, 16-17; Rankin et al. 2020: figs. 3, 5, 6).

The molars of *Ischyromys brevidens* are only slightly larger than those of *I. veterior* in size (Wood, 1974; Black, 1968: tables 1, 2) but have the same degree of lophodonty and proportions of the lower molars (slightly longer than wide). However, P4s of *I. veterior* are longer and more molariform than those of *I. brevidens* (Black 1968: figs. 13-15).

Ischyromys brevidens specimens are similar in morphology (crown height, degree of lophodonty, proportions of lower molars) and size to those of *I. typus* from the Orellan to Whitneyan of Sioux County described elsewhere (Wood, 1937: 89; Howe 1966: table 2, 3; Black, 1968: tables 1, 2; Heaton 1996: fig. 4) as well as samples of *I. typus* from the Orellan of North Dakota, Colorado, and the Big Badlands of South Dakota (Heaton 1996: figs. 5, 6, 7) but differ in the morphology of P4 (shorter than wide) and p4 (ectolophid weak or absent).

Discussion—In his review of *Ischyromys*, Heaton (1996) recognized five species of the genus: *I. typus* Leidy, 1856, *I. veterior* Matthew, 1903a, *I. douglassi* Black, 1968, *I. junctus* Russell, 1972, and *I. blacki* Wood, 1974, as well as possibly three additional unnamed species. He followed Black (1968) in including all other previously named species as synonyms of these recognized species. More recently, Anderson (2008) listed seven species of *Ischyromys* including *I. parvidens* Miller and Gidley, 1920, and *I. plicatus* Troxell, 1922, without discussion, both of which had been listed previously as synonyms of other species (Black, 1968; Heaton, 1996). The synonymies of Black (1968) and Heaton (1996) are followed here.

In crown-height, degree of lophodonty, size, and proportions of the lower molars, *Ischyromys brevidens* is closest to *I. veterior* and *I. typus*. However, both of these species have higher, complete ectolophids on p4 and an anteriorly expanded P4 (longer than M1) with a distinct lingual valley separating the hypocone and protocone (Wood, 1937: pl. XXVII, fig. 1a; Howe, 1966: text-fig. 2). P4 of *I. brevidens* is always wider than long with no separation of the protocone from the hypocone, and an ectolophid on p4 that is markedly lower than the other lophids and even incomplete on some specimens. The only other species with similar proportions of the P4 is *I. douglassi* but it differs markedly from *I. brevidens* in other features (see above comparative description).

Heaton (1996) suggested that there was an unnamed species of *Ischyromys* from the lower part of the Orella Member in Sioux County (Orella A and B)

that was smaller than *I. typus*. The mean and range of the length of the m1 and m2 of *I. brevidens* more nearly matches that of *I. typus* rather than this smaller unrecognized species (Heaton, 1996: fig. 4), so this is not the same species as Heaton's collection. Specimens of *I. brevidens* are known from all localities in the ant mound collection and there is no difference in the dental dimensions from the different horizons (Tables 12, 13).

The deciduous premolars make up approximately half of the isolated teeth referred here to *Ischyromys* (see Appendix). This unusual accumulation by ants clearly shows a preference for the deciduous teeth over the larger and bulkier permanent teeth.

Family Cylindrodontidae Miller and Gidley, 1918
Genus *Siouxlindrodon* n. gen.

Type Species—*Siouxlindrodon sullivani* n. sp.

Diagnosis—Cheek teeth unilaterally subhypsodont (uppers lingually; lowers labially) and lophate; all lophs (-ids) high and thin, cusps subdued into lophs; ectoloph on upper molars continuous for length of tooth, mesostyle absent or minute; protoloph and metaloph high, thin, and continuous to protocone; endolophid on lower molars continuous for length of tooth, enclosing central basin lingually; ectolophid generally incomplete, shorter and markedly lower than endolophid; metalophulid II on lower molars long, complete, and parallel to hypolophid; hypolophid lacking on p4 and variably present on m3.

Discussion—*Siouxlindrodon* can be easily distinguished from *Cylindrodon* in having a lower crown-height of the cheek teeth (subhypsodont), but *Siouxlindrodon* has greater crown-height than the earlier Eocene genera *Tuscahomys* Dawson and Beard, 2007; *Mysops* Leidy, 1871, and *Pareumys* Peterson, 1919. *Siouxlindrodon* differs from all jaywilsonomyine cylindrodonts in lacking a prominent hypocone and having a complete metaloph connected to the protocone on the upper molars and having a complete metalophulid II on the lower molars (Wood, 1974; Walsh and Storer, 2008).

The most unique features of *Siouxlindrodon* are the degree of lophodonty (lophs higher and thinner than other genera) and the enclosed central basins of the teeth (uppers blocked labially [=ectoloph], the lowers blocked lingually [=metaconid crest or endolophid]). It is not known if *Siouxlindrodon* lacks a P3 as in *Cylindrodon* (present in all other cylindrodonts).

Siouxlindrodon sullivani n. sp.
(Figure 17; Table 14)

Syntypes— SDSM 155559, left M1 or M2 (Figure 17B); SDSM 155576, left m1 or m2 (Figure 17E).

Referred Specimens—SDSM 155550, 155551, 155560, 155564, P4; SDSM 155547-155549, 155553-155556, 155558, 155561-155563, M1 or M2; SDSM 155552, 155557, M3; SDSM 155567, 155574, 155575, p4; SDSM 155568-155571, 155577-155587, m1 or m2; SDSM 155565, 155566, 155572, m3.

Localities—Recovered from ant mounds 1-6 below the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Diagnosis—As for genus.

Etymology—Patronym for Joseph Sullivan of the Buffalo Geological Society.

Description—The cusps of all cheek teeth are nearly indistinguishable from the lophs (-ids). There is very little swelling of any of the cusps. The upper cheek teeth are markedly higher lingually than labially, the labial height averaging approximately 70 percent of the lingual height on P4-M2, and over 80 percent on M3s (Table 14).

P4 is ovate in occlusal outline, wider than long and there is little definition of any cusps (Figure 17A). The entire tooth is enclosed by a high, thin, continuous cingulum that is highest at center of the lingual side (apex of protocone) and sometimes dips slightly below the paracone and metacone along the labial margin. The protoloph and metaloph are high and thin with no indication of conules and continuous across the tooth. They are nearly parallel, converging only slightly lingually but never meeting. The central basin is the deepest, the anterior and posterior basins are much shallower. There is a hint of a hypocone in the form of a slight swelling along the posterolingual corner of the tooth.

M1 and M2 cannot be separated from one another, and all referred specimens are isolated teeth. These teeth are nearly identical in morphology to P4 but are slightly larger and relatively longer (anteroposteriorly) than P4 (Figure 17B). Other than size and proportions, M1 and M2 are nearly identical to P4.

Besides the slightly smaller size, M3 is distinguishable from M1 and M2 by its more nearly circular occlusal outline and shortened metaloph (Figure 17C). The basin posterior to the metaloph is smaller than the anterior basin between the protoloph and anterior cingulum. In one specimen, SDSM 155557, the metaloph is very short, directed posterolingually from the metacone, and joins the posterior cingulum lingual to the center of the posterior margin of the tooth.

The lower cheek teeth are also unilaterally hypsodont, the lingual height of p4-m2 averages approximately 60 percent of the labial height. In the two m3s this ratio is 73 and 77 percent. As in the upper cheek teeth, p4 is smaller than the molars (Table 14). On the two unworn specimens (SDSM 155567, 155574) the metaconid and protoconid are distinct cusps (Figure 17D). In the worn specimen (SDSM 155575) there is a

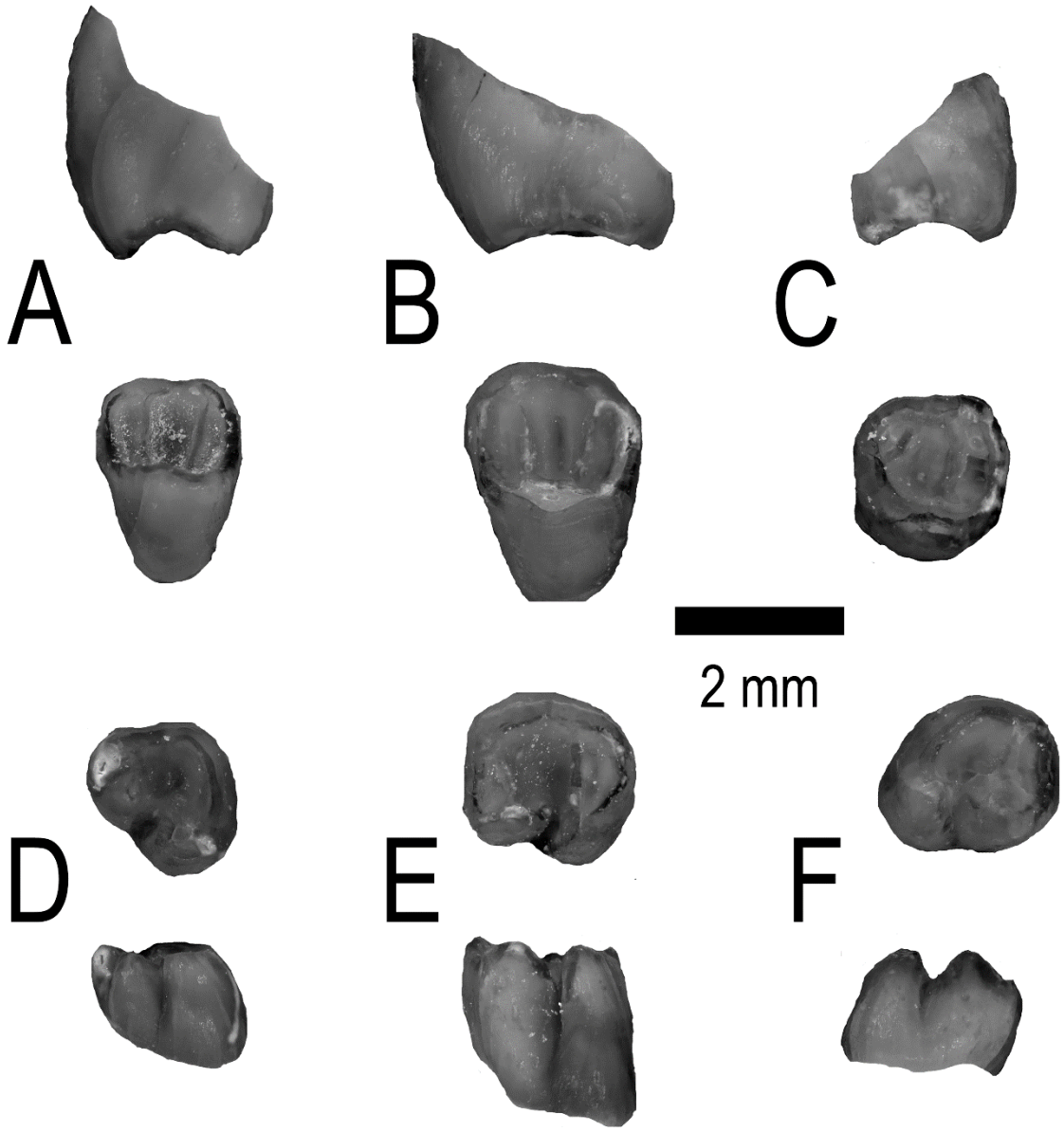

FIGURE 17. *Siouxlindrodon sullivani* from the ant mound collection from Sioux County, Nebraska. A, SDSM 155551, left P4. B, SDSM 155559, left M1 or M2 (syntype). C, SDSM 155557, right M3. D, SDSM 155574, left p4. E, SDSM 155576, left m1 or m2 (syntype). F, SDSM 155565, right m3. D-F, occlusal view above, labial view below. All figures to same scale.

single wear facet at the anterior end of the tooth with no distinguishable cusps. SDSM 155567 has a minute anterostylid at the base of the anterior margin of the tooth that is not present in the other little-worn specimen. The hypoconid is an anteroposteriorly compressed ridge at the posterolabial corner of the tooth. A thin metalophid runs from the posterior side of the metaconid to the protoconid enclosing a minute trigonid basin. The lingual and posterior sides of the tooth are enclosed by a continuous cingulid that runs from the metaconid around the lingual and posterior sides of the tooth, ending in the hypoconid. There are no distinguishable cusps, the entoconid is merely a bend in the continuous cingulid. The ectolophid is markedly lower than any of the cusps or the cingulid but is continuous for a short distance from the posterior side of the protoconid to the anterolingual corner of the

hypoconid with a minor labial bend just anterior to the hypoconid.

The m1 cannot be distinguished from m2. In overall morphology m1 or m2 is similar to that of p4 except that the trigonid is relatively wider, but not as wide as the talonid (Figure 17E). The cusps are barely distinguishable as minor swellings at the corners of the teeth. The trigonid basin is wider than in p4 and the anterolophid runs directly across the anterior margin from the metaconid to the anterolabial corner of the protoconid with a slight flexure at the anterolabial corner of the tooth. The metalophid II is slightly bowed posteriorly but encloses the posterior side of the trigonid. On the syntype (SDSM 155576; Figure 17E), there is a slight swelling of the anterior cingulid (metalophulid I) at its center. As in the upper molars, the tooth is enclosed by a high rim that wraps around it from the anterior side of the protoconid to the posterior side of the hypoconid. The hypolophid is complete across the entire tooth. The central basin, as in the upper molars, is the deepest and most persistent. The ectolophid is either incomplete between the protoconid and hypoconid or very low on the crown, making it essentially noncontinuous between the two labial cusps. As in the upper molars, sometimes there is a slight dip in the enclosing cingulid on the lingual side between the entoconid and metaconid.

The m3 is similar in size to m1 or m2 but is the most variable in morphology. It differs from the anterior molars in being narrower posteriorly than anteriorly (Figure 17F). The hypolophid is extremely variable; it can be complete across the entire tooth as in SDSM 155572, absent as in SDSM 155565, or a low, rounded cusp centered between the entoconid and hypoconid as in SDSM 155566.

Discussion—The crown-height, lophodonty and enclosure of the central basin of the cheek teeth of *Siouxlindrodon* are a unique combination of features among cylindrodonts. The Whitneyan *Lophicylindrodon* Korth and Tabrum, 2017, has the same degree of lophodonty but differs in not having as great a degree of unilateral hypsodonty, more discernible cusps, and lack of a metalophulid II on lower molars. *Siouxlindrodon* is limited to ant mound localities situated more than five meters below the UPW.

Cylindrodon Douglass, 1902
Cylindrodon nebraskensis Hough and Alf, 1956
(Figure 18A)

Referred Specimens—SDSM 155588, 155589, M1 or M2; SDSM 156734, M3; SDSM 156735, m1 or m2.

Locality—Recovered from ant mounds 3 and 7 below the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Occlusal Measurements—M1 or M2: SDSM 155588; L = 1.98 mm, W = 1.90 mm, lingual height = 4.0 mm. SDSM 155589; L = 2.24 mm, W = 1.89 mm, lingual height = 5.4 mm. M3: SDSM 156734; L = 1.98 mm, W = 2.28, lingual height = 4.20 mm. m1 or m2: SDSM 156735; L = 1.91 mm, W = 1.95 mm, labial height = 3.91 mm.

Discussion—These specimens are distinct from all of the other cylindrodonts from the Sioux County ant mound collection in their larger size, presence of an accessory anteroposterior loph between the metaloph and posterior cingulum on the M1 or M2, and much higher crowns; all diagnostic for *Cylindrodon*. The size of the specimens best fits that of *C. nebraskensis* (Ostrander, 1983: table 3; Korth, 1992a: table 1; Emry and Korth, 1996: table 1). Elsewhere this species is limited to the Chadronian (Korth, 1994c; Walsh and Storer, 2008) and all specimens referred here to this taxon are from ant mounds situated below the UPW.

Genus and Species Indeterminate (small)
(Figure 18C, D)

Referred Specimens—SDSM 155573, left m1 or m2; SDSM 156546, right M3.

Localities—Recovered from ant mounds 4 and 6 below the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Measurements—SDSM 155573: m1 or m2, L = 2.00 mm; W = 2.12 mm; SDSM 15646: M3, L = 1.39 mm; W = 1.45 mm.

Description—The lower molar is heavily worn so the original crown height cannot be measured (Figure 18D), however the labial height is only 10 percent higher than the lingual height, much lower than in the *Siouxlindrodon* specimens. Due to the degree of wear the morphology of the trigonid is obscured. The ectolophid is complete from anterolingual corner of the hypoconid to the posterolingual corner of the protoconid wear facet. The hypolophid is only a short spur extending lingually from the anterolingual corner of the hypoconid. There are two distinct cusps along the lingual side of the tooth. The metaconid is large and slopes labially into the center of the tooth. The entoconid is similar in size, at the posterolingual corner of the tooth, and extends only a short distance anterolabially into the center of the tooth. The posterior cingulid extends lingually from the posterolingual corner of the hypoconid but ends before meeting the more posterior lingual cusp.

The M3 is relatively smaller than the referred lower molar and may not represent the same species. It is nearly circular in occlusal outline (Figure 18C). The

lingual crown height (0.82 mm) is only slightly greater than the labial height (0.51 mm). The only distinct cusps are the paracone and protocone. The protoloph is continuous from the protocone to the paracone. The anterior cingulum runs nearly the width of the tooth, ending lingually at the lingual side of the protocone. The protocone is only slightly higher than the cingulum and is a transversely compressed crescent. A central mesoloph runs directly lingual from the center of the protocone and ends before reaching the lingual margin. The posterior cingulum is continuous with the protocone and wraps around the posterior half of the tooth, then bends anteriorly at the posterolabial corner of the tooth and is continuous with the paracone. A short lophule extends from the posterolabial corner of the tooth a short distance in an anterolingual direction.

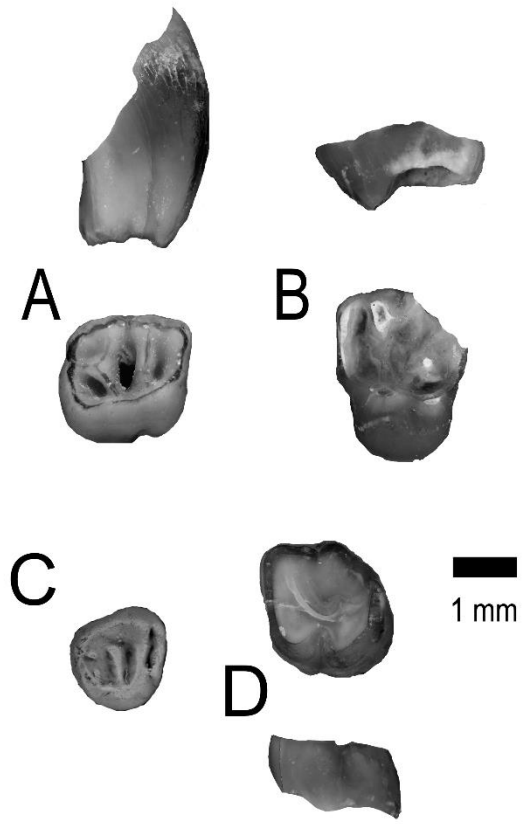

FIGURE 18. Cylindrodonts from the ant mound collection from Sioux County, Nebraska. A, *Cylindrodon nebraskensis*, SDSM 155588, right M1 or M2. B, Gen. et sp. indet (large), SDSM 155751, left M1 or M2. C, D, Gen. et sp. indet, (small). C, SDSM 156546, right M3. D, SDSM 155573, left m1 or m2 (occlusal view above labial view below). A, B, anterior view above, occlusal view below. All figures to same scale.

Discussion—It is most likely that these two specimens represent different species based on their differing size and crown height. The lower molar, SDSM 155573, is similar in size to *Siouxlindrodon* but lacks a hypolophid and may be slightly lower crowned and appears to have a complete ectolophid. No other cylindrodonts completely lack a hypolophid on lower molars; however, a shortened hypolophid extending labially from the entoconid is present is some species of the earlier Eocene genera *Tuscahomys* and *Mysops* (Anemone et al., 2012). The M3, SDSM 156546, is smaller and lower crowned than the referred lower molar and is closest to species of the earlier Eocene *Mysops* in size, crown height, and morphology (Wilson, 1938: fig 6; Anemone et al., 2012: fig. 6B). The occurrence of this specimen in the Chadron Formation also postdates the otherwise latest occurrence of *Mysops* in the Uintan (Walsh and Storer, 2008: fig. 20.4).

Genus and Species Indeterminate (large)
(Figure 18B)

Referred Specimen—SDSM 155751, left M1 or M2.

Localities—Recovered from ant mound 4 below the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Measurements—L = 2.97 mm; W = 3.87 mm; labial crown-height = 0.81 mm; lingual crown-height = 1.86 mm.

Description—This specimen is markedly larger than any other of the cylindrodonts in the fauna. The lingual height of the crown is greater than the labial height but the difference is not as extreme as in *Siouxlindrodon* or other mesodont cylindrodonts. The anterolabial corner of the tooth is broken away (Figure 18B). The tooth is much wider than long with distinct bulbous cusps. The anterior cingulum runs from the anterolabial corner of the tooth along the anterior margin for more than half the width of the tooth, then turns posteriorly to join the apex of the protocone. The paracone is anteroposteriorly compressed and transversely elongated. The protoloph is continuous from the paracone to the apex of the protocone. The protoconule is a minute swelling along the protoloph, just lingual to the paracone. There is a distinct ectoloph running posteriorly from the center of the paracone that curves labially, and ends in what remains of an apparently relatively large mesostyle. Although the posterolabial corner of the tooth is missing, it appears that the metacone is equal in size to the paracone. A large, rounded metaconule is weakly continuous with the lingual side of the metacone via a short, curved loph. There is no connection between the metaconule and the protocone or posterior cingulum. A small transversely compressed hypocone is present on the posterolingual slope of the protocone. The posterior cingulum extends from the apex of the protocone, through the hypocone and is continuous along what remains of the posterior

margin of the tooth, joining the metacone at its posterolingual corner.

Discussion—The large size of this specimen and the large isolated metaconule most nearly approaches the morphology of upper molars of *Jaywilsonomys* Ferrusquia and Wood, 1969, suggesting that it may be referable to the Jawilsonomyinae. However, the tooth is much lower crowned than those of *Jaywilsonomys* and even the earliest member of the subfamily *Pareumys* Peterson, 1919 (see Wilson, 1940; Black, 1970, 1974; Walsh and Storer, 2008). The partial ectoloph is elsewhere only known among cylindrodonts only in *Ardynomys* Matthew and Granger, 1925 (Wood, 1974: fig. 22C) and is of a similar size but the metaloph is continuous to the protocone in *Ardynomys*, unlike SDSM 155751. This specimen likely represents a new, later occurring, more brachydont cylindrodont. Owing to the poor record it will not be named here. The occurrence of this specimen from an ant mound more than five meters below the UPW is consistent with the record of most other later occurring cylindrodonts.

Family Aplodontidae Brandt, 1855
Subfamily Prosciurinae Wilson, 1949
Genus *Altasciurus* Korth and Tabrum, 2017
Altasciurus relictus (Cope, 1873b)
(Figures 19A-E; Tables 15, 16)

Paramys relictus Cope, 1873b
Scirus relictus (Cope) Cope, 1875
Prosciurus relictus (Cope) Osborn and Matthew, 1909
Prosciurus parvus Korth, 1989a
Altasciurus relictus (Cope) Korth and Tabrum, 2017

Referred Specimens—439 specimens (see Appendix).

Localities—Recovered from all ant mounds sampled in this study. Big Cottonwood Creek Member of the Chadron Formation.

Discussion—The dentition of *A. relictus* has been described previously in detail (Wood, 1937; Galbreath, 1953; Rensberger and Li, 1986; Korth and Tabrum, 2017) and need not be repeated here. Korth (1989a) named *Prosciurus parvus* from the Orellan of Sioux County distinguishing it from *"P." relictus* by its smaller size, lack of a protocone crest, relative size of the protoconule on upper molars, and length of the hypolophid on the lower molars. However, with the large collection from the ant mounds it appears that there is no distinct size difference (Tables 15, 16) and that the differences between these species (presence of protocone crest and relative size of protoconule) appear to be variable. It is evident that the presence of a protocone crest on the upper molars is variable; in the ant mound collection approximately 30 percent of the specimens have this feature, whereas in a large collection of *A. relictus* from the Whitneyan of Montana this feature occurs in approximately 50 percent of the specimens (Korth and Tabrum, 2017). The size of the protoconule also seems to be within the observed range in the ant mound collection and the length of hypolophid varies in the ant mound collection as well.

Specimens of *A. relictus* were recovered from all ant mounds sampled in this study. There is no significant difference in the measurements of the specimens recovered from different stratigraphic intervals (Tables 15, 16).

Altasciurus clausulus (Korth, 2009b)
(Figures 19F-K; Table 17)

Prosciurus clausulus Korth, 2009b
Altasciurus clausulus (Korth) Korth and Tabrum, 2017

Referred Specimens—SDSM 152264, right maxilla with P4-M2; SDSM 155162, right maxilla with P4-M1; SDSM 152263, left maxilla with M1-M3; SDSM 152252, 152277, 155035, 155060, 155080, P4; SDSM 152267, 154973, 154975, 155057, 155077, 155119, 155142, 155143, 156991, M1 or M2; SDSM 155003, 155111, 155149, M3; SDSM 155219, 155394, left dp4; SDSM 152513, 155266, 155277, p4; SDSM 155233, 155394; 155724, 155726, m1; SDSM 155205, 155330, 155339, 155366, m2.

Localities—Recovered from ant mounds 1, 3, 4, 6, 7, 9, 12, and 15 below the UPW; ant mound 13 on the UPW; ant mounds 8, 10, 11, 18, and 19 above the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Description and Discussion—This species is previously known only from the Whitneyan Blue Ash fauna of South Dakota (Korth, 2009b). The ant mound specimens have the diagnostic morphology of *A. clausulus* of a "bulge" anterior to the protocone instead of protocone crest. Since there are two partial maxillae from the ant mound collection that contain both P4 and M1 (SDSM 155162, 152264; Figure 19G) the relative size of P4 to M1 can be observed. In both specimens, P4 is longer than M1 but M1 is wider, similar to the condition of *A. relictus*.

Previously, m1 was not separated from m2 because of the lack of specimens (only two known: Korth, 2009b: table 1). However, with the large collection from these ant mounds it appears that m1 can be separated from m2; the former having an anterior width much less than posterior width, and on m2 the anterior and posterior widths are nearly equal (Table 17). The referred m1s also do not have a hypolophid complete to the ectolophid as in m2 (Figure 19J), again, a character also seen in *A. relictus*. All other morphologies are as in the Blue Ash collection (Korth, 2009b).

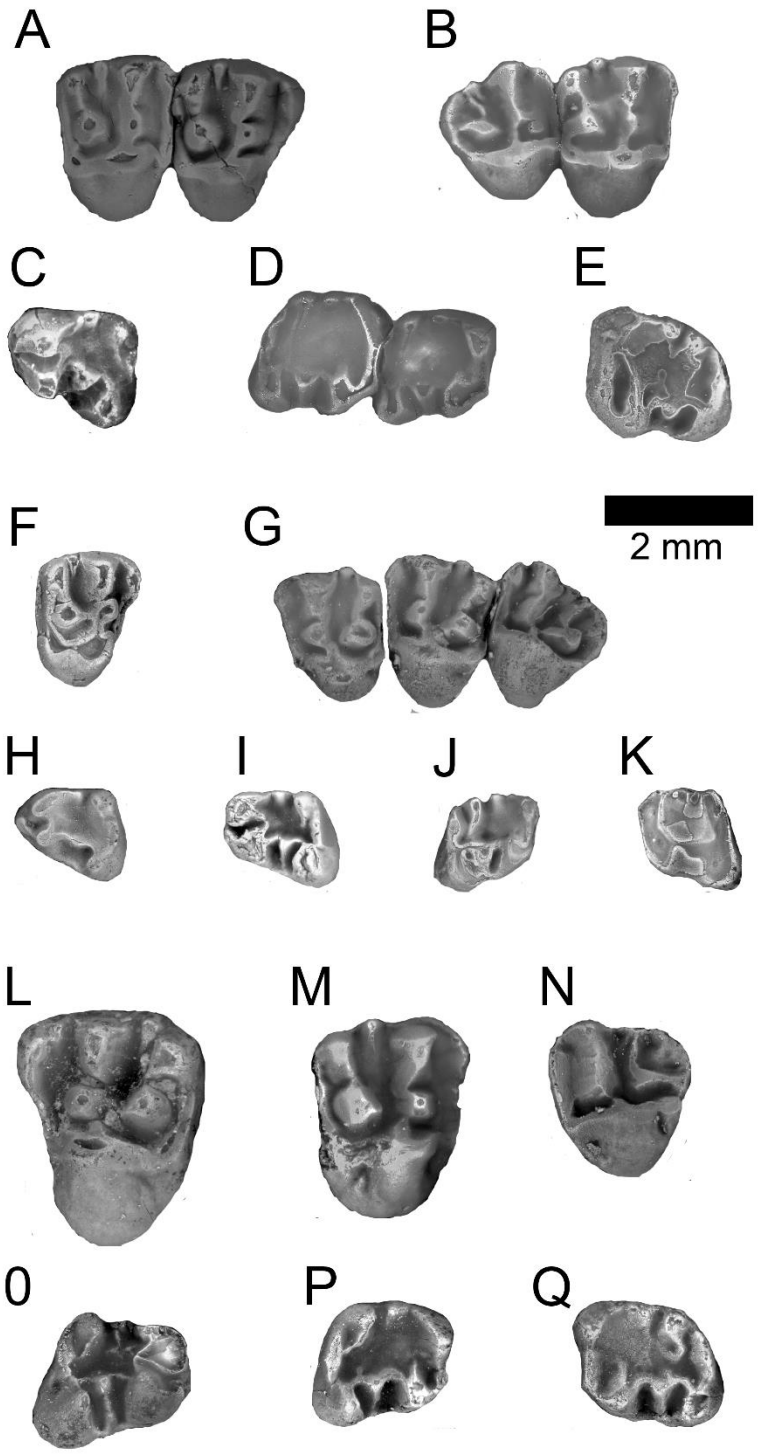

FIGURE 19. *Altasciurus* from the ant mound collection from Sioux County, Nebraska. A-E, *A. relictus*. A, SDSM 152280, right P4-M1. B, SDSM 154989, right M2-M3. C, SDSM 152434, left p4. D, SDSM 155721, right m1-m2. E, SDSM 155173, right m3. F-K, *A. clausulus*. F, SDSM 152252, right P4, G, SDSM 152263, left M1-M3. H, SDSM 155394, left dp4. I, left p4. J, SDSM 155233, right m1. K, SDSM 155726, left m1. L-Q, *A. albiclivus*. L, SDSM 155160, left P4. M, SDSM 155033, right M1 or M2. N, SDSM 154974, left M3. O, SDSM 155340, right p4. P, SDSM 155320, right m1. Q, SDSM 155187, left m3. All figures to same scale.

The age of the Blue Ash collection is Whitneyan, whereas the material in the current study is from ant mounds both below and above the UPW, predating the Blue Ash collection.

Altasciurus albiclivus (Korth, 1994b)
(Figure 19L-Q; Table 17)

Prosciurus albiclivus Korth, 1994b
Altasciurus albiclivus (Korth) Korth and Tabrum, 2017

Referred Specimens—SDSM 155204, dP4; SDSM 155023, 155106, 155160, P4; SDSM 155029, 155033, 155078, 155083, 155097, 155098, 155138, 155717, M1 or M2; SDSM 137311, 154971, 154974, 155022, 155031, 155043, 155065, 155084, 155109, M3; SDSM 152480, 155340, 155722, 155728, 155732, p4; SDSM 155258, 155312, 155320, 155322, 155357, 155753, m1; SDSM 155174, 155195, 155251, 155284, 155327, 155333, 155360, m2; SDSM 155187, 155263, 155361, m3.

Localities—Recovered from ant mounds 1, 3-7, 9, 15, and 16 below the UPW; ant mounds 13 and 14 on the UPW; ant mounds 8, 10, 18, and 19 above the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Discussion—The specimens referred here to *A. albiclivus* are distinctly larger than those of *A. relictus* (Table 17). All of the upper molars lack a protocone crest and the P4 averages slightly larger than M1 (Figures 19L, M), both diagnostic features of *A. clausulus* (Korth, 1994b). *A. albiclivus* has previously been reported from the Orellan of Sioux County, Nebraska as well as the Orellan of Montana. Specimens here referred to this taxon were recovered from ant mounds situated below and above the UPW.

Altasciurus sp. indet.
(Figure 27A)

Referred Specimen—SDSM 155348, right m3.

Locality—Recovered from ant mound 3 below the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Measurements— L = 2.84 mm; AW = 2.16 mm.

Description and Discussion—This tooth can be identified as an m3 based on its elongated talonid. The trigonid is widely open lingually due to the short metalophulid II. The hypolophid is nearly complete with a slight break at its center but otherwise continuous from the entoconid to the ectolophid. The ectolophid is complete with an anteroposteriorly flattened mesoconid that extends labially nearly to the labial edge of the tooth. The posterolingual corner of the tooth is broken away. The hypoconid is obliquely compressed and continuous with the posterior cingulid that typically bows posteriorly.

SDSM 155348 is referable to *Altasciurus* and distinguished from *Prosciurus* by its complete hypolophid (Korth, 1989a; Korth and Tabrum, 2017). It is much larger than the specimens referred above to *A. albiclivus* (Table 17), the largest known species of the genus. It is from an ant mound situated below the UPW.

Genus *Campestrallomys* Korth, 1989a
Campestrallomys siouxensis Korth, 1989a
(Figure 20A-E; Table 18)

Referred Specimens—SDSM 155465, 155469, dP4; SDSM 155385, 155471, 155472, P4; SDSM 155371, 155372, 155466, 155470, 155474, M1 or M2; SDSM 155467, 155468, 155473, 155475, M3; SDSM 155482, 155740, m1 or m2; SDSM 155478, 155481, 155483, m3.

Localities—Recovered from ant mounds 1- 7, 9, 15, and 16 below the UPW; ant mound 14 on the UPW; ant mound 19 above the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Description and Discussion—The only cheek tooth not previously described for *Campesterallomys siouxensis* is m3. The isolated specimens of m3 referred here are done so because of the presence of multiple metastylids and their appropriate size. As in *C. dawsonae*, the m3 is longer than m2 and the trigonid is open posteriorly owing to a shortened metalophulid II (Macdonald, 1963: fig. 9; Korth, 1989a: fig. 4F). On the most complete specimen, SDSM 155483 (Figure 20E), the entoconid has a slight labial extension into the talonid basin for less than half the width of the tooth. This is lacking in the holotype of *C. dawsonae*.

The presence of the ectoloph on the upper cheek teeth, multiple metastylids, and lack of a hypolophid on the lower molars allows these specimens to be referred to *Campestrallomys* (Korth, 1989a). The relative size of P4 (smaller than M1 or M2) and more distinct conules on the upper molars (Figure 20C) allow confident referral to *C. siouxensis*.

The type and only other referred specimens of *C. siouxensis* are from the Brown Siltstone beds, Brule Formation (Korth, 1989a) that has a determined age of earliest Arikareean (Swinehart et al., 1985; Tedford et al., 1996, 2004). The specimens of this species described here are from ant mounds situated both below and above the UPW in the Big Cottonwood Creek Member of the Chadron Formation (Chadronian-Orellan), making them older than the previously known material.

Campestrallomys sp.
(Figure 20F)

Referred Specimen—SDSM 155477, right M2.

Locality—Recovered from ant mound 3 below the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Measurements—L = 2.61 mm; W = 3.27 mm.

Description and Discussion—SDSM 155477 is distinctly larger than specimens referred to either species of *Campestrallomys* (Macdonald, 1970: table 11; Korth, 1989a: table 3). Other than its size, it is nearly identical in morphology to the upper molars of *C. dawsonae* and *C. siouxensis* (Figure 20F; Korth, 1989a: figs. 4C, E). The conules are more distinct, as in *C. siouxensis*, and there is a second minute metaconule on labial slope of the larger metaconule. The only other distinct feature of this specimen is that the metaloph is not complete between the metacone and metaconule. Due to its markedly larger size and more distinct conules, this specimen appears to represent a new species. However, because it is represented by a single specimen only, it will not be named here. The recovery of this specimen from an ant mound more than five meters below the UPW means that it predates the previously known earliest occurrence of this genus, as is the case with the specimens referred above to *C. siouxensis* (Korth, 1989a).

Genus *Pelycomys* Galbreath, 1953
Pelycomys spp. indet.
(Figures 20G-K; Tables 19, 20)

Referred Specimens—SDSM 155749, left P4; SDSM 152479, 155699, left M1 or M2; SDSM 155748, left p4; SDSM 152475, 155700, m1 or m2; SDSM 152499, right m3.

Localities—Recovered from ant mounds 3, 4, 5, 9, and 16 below the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Description—The cusps of the P4, SDSM 155749, are round and blunted. Minute irregularities are present in the central basin of the tooth (Figure 20G). The parastyle is small and transversely elongated in the anterolabial corner of the tooth and extends lingually for approximately half the width of the tooth. A short anterior cingulum connects the anterolingual end of the parastyle to the anterolabial corner of the protocone. The metacone and paracone are rounded and of approximately equal size. The mesostyle is small and appears to have a short lophule connecting its posterolingual corner to the posterolabial corner of the paracone. The protoloph is continuous from the protocone to the paracone without a distinct protoconule. The apex of the protocone is not centered and is in the anterolingual corner of the tooth. The metaloph has four minute swellings (metaconules) and is continuous from the lingual side of the metacone to the posterolabial side of the protocone. The posterolabial half of the metacone is broken off. The posterior cingulum runs from the protocone along the posterior margin of the tooth until it reaches the broken area of the metacone. The hypocone is a slight swelling along the posterior cingulum at its posterolingual corner.

The referred upper molars, SDSM 152479 and 155699 are similar to those described for *P. brulanus* (Korth, 1986). As with the P4, there is minor wrinkling in the basins of the less worn tooth (SDSM 155699; Figure 20H). It differs little from the upper molars of *P. brulanus*. The protoconule is small and the metaconule is doubled, the more lingual being markedly larger. The protoloph is continuous to the protocone, whereas the metaloph ends in the larger metaconule. The only slight difference in the ant mound specimens from those referred to *P. brulanus* is that there is no distinct protocone crest; instead, there is a minor swelling on the anterolabial corner of the protocone on the unworn specimen.

There are no complete p4s of any species of *Pelycomys*, only a partial one described for *P. placidus* (Galbreath, 1953). SDSM 155748 is a complete p4, but moderately worn (Figure 20I). There is no wrinkling of the enamel in the central basin. The trigonid is narrower than the talonid. The trigonid is open anteriorly and closed posteriorly by the metalophulid II. A distinct metastylid is present near the center of the lingual side of the tooth and continuous with the metaconid via the metaconid crest. The ectolophid is complete from the circular protoconid to the anterolingual corner of the hypoconid. There is a relatively large, round mesoconid at the center of the ectolophid. The entoconid is isolated from both the metastylid and the posterior cingulid by narrow valleys. The hypolophid is complete from the entoconid to the ectolophid but is greatly reduced in size on its labial half. A short anteroposterior loph connects the center of the hypolophid to the center of the posterior cingulid.

The two specimens identified as m1 or m2 are both incomplete, they are assigned to this taxon because of their appropriate size, presence of a complete hypolophid, and metastylid continuous with the metaconid along the metastylid crest. The enamel in the basins of these teeth is smooth (Figure 20J). The only difference between them is that the trigonid basin on SDSM 155700 is narrowly open posteriorly near its center. Otherwise, all morphologies are consistent with those previously described for *P. placidus*.

The only m3, SDSM 152499, is assigned to this taxon because of its comparable size, posteriorly closed trigonid and complete hypolophid, but is incomplete. The enamel in the basin is smooth as in *P. placidus* (Figure 20K). The posterior cingulid ends just before

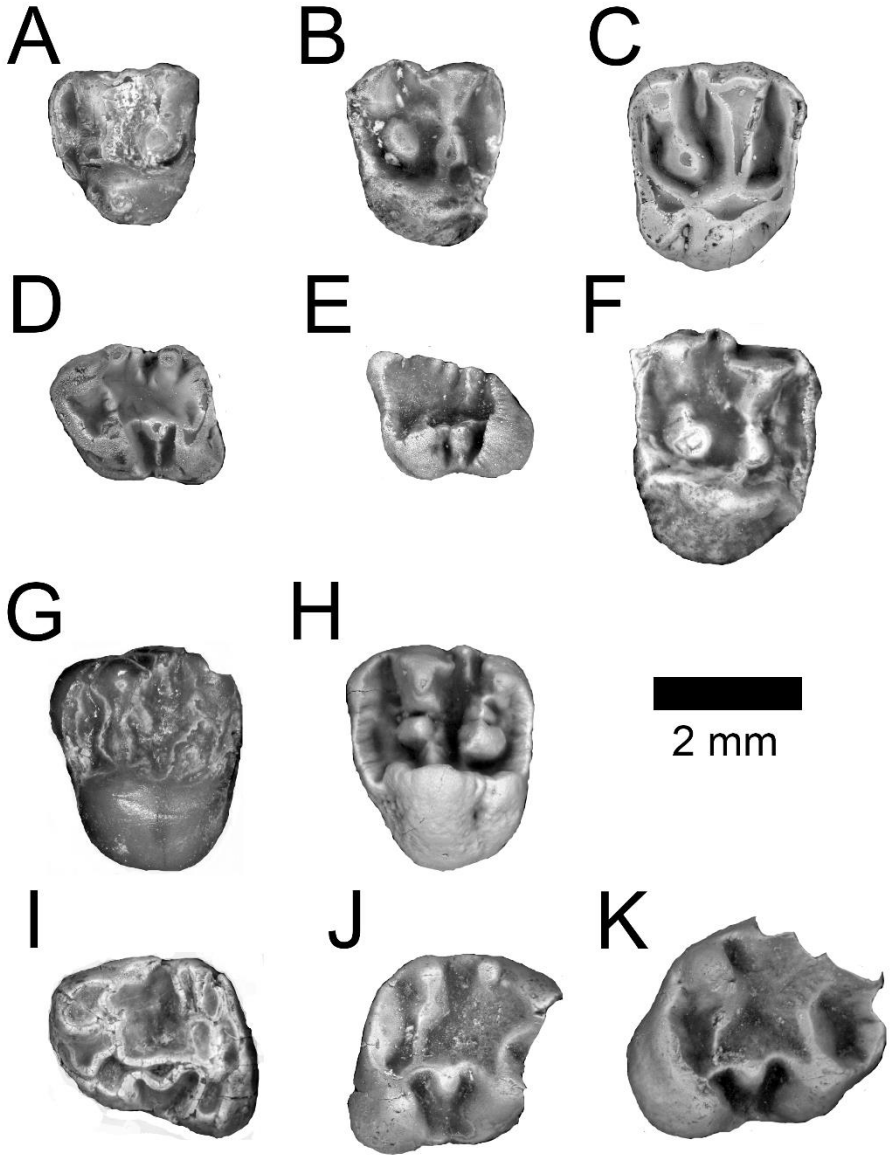

FIGURE 20. *Campestrallomys* and *Pelycomys* from the ant mound collection from Sioux County, Nebraska. A-E, *C. siouxensis*. A, SDSM 155465, left dP4. B, SDSM right 155472, P4. C, SDSM 155372, right M1 or M2. D, SDSM 155740, left m1 or m2. E, SDSM 155483, left m3. F, *Campestrallomys* sp. SDSM 155477, right M1 or M2. G-K, *Pelycomys* sp. G, SDSM 155749, left P4. H, SDSM155699, left M1 or M2. I, SDSM 155748, left p4. J, SDSM 152475, right m1 or m2 (partial). K, SDSM 152499, right m3 (partial). All figures to same scale.

reaching the posterior side of the entoconid. The hypolophid is much lower in its labial half and has a slight flexure. All other morphologies are as in *P. placidus* (Galbreath, 1953).

Discussion—Galbreath (1953) named two species of *Pelycomys* from northeastern Colorado, the Chadronian *P. rugosus* and the Orellan *P. placidus*. He distinguished the two species based on size (*P. rugosus* slightly larger) and irregularities in the enamel of the teeth (present in *P. rugosus*, absent in *P. placidus*). The only other species of the genus is *P. brulanus* Korth, 1986, from the Orellan of Sioux County, Nebraska that

was similar in size to *P. placidus* but had the irregularities in the enamel of the molars as in *P. rugosus*. It differed from both of the Colorado species in having the metasylid on the lower molars separated from the posterior end of the metaconid crest, whereas the metastylid was continuous with the metaconid crest in both of the Colorado species. This feature appears to be variable in the specimens in the ant mound collection as does the presence of crenulations. The measurements of the ant mound specimens also overlaps those of all of the known species as well (Tables, 19, 20; Galbreath, 1953: tables 7, 8; Korth, 1986: 547). Owing to these variations in the ant mound collection, a definite species identification cannot be made. Alternatively, there may be more than one species represented but due to the scarcity of specimens and the incompleteness of several of them, this cannot be determined. Specimens of *Pelycomys* were only recovered in this study from ant mounds situated below the UPW.

Genus *Oropyctis* Korth, 1989a
Oropyctis sp., cf. *O. pediasius* Korth, 1989a
(Figures 21A-C; Table 20)

Referred Specimens—SDSM 155460, 155696, 156492, p4; SDSM 155697, 155698, m1 or m2; SDSM 152477, right m3.

Localities—Recovered from ant mounds 1, 4, 6, and 9 below the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Description—The three p4s referred here are done so based on similar size to the referred lower molars, and similarity to the unerupted p4 of the holotype (Korth, 1989a: fig. 3A). They are much narrower anteriorly than posteriorly. There is no indication of crenulations or wrinkling of the enamel (Figure 21A). The metaconid and protoconid are closely spaced; the trigonid is open anteriorly and closed posteriorly. There is a distinct anteroconid on SDSM 155696 at the base of the center of the anterior margin. The trigonid is much narrower on SDSM 155460 and 156492 and the anterostylid is minute or absent. There is a short metaconid crest extending posteriorly from the apex of the metaconid that ends in a distinct metastylid that is separated from the entoconid by a deep valley. The ectolophid is complete from the posterolingual corner of the protoconid to the anterolingual corner of the hypoconid. The mesoconid is relatively large and anteroposteriorly elongated at the center of the ectolophid. The entoconid is isolated and there is a hypolophid extending labially from it. On SDSM 155696 and SDSM 156492 it ends near the center of the talonid basin, whereas in SDSM 155460 it is continuous labially to the ectolophid, just posterior to the mesoconid. However, the labial half of the hypolophid is markedly lower than the lingual half on this specimen. The posterior cingulid runs from the posterolingual corner of the hypoconid to a point posterior to the apex of the entoconid but is not continuous with it. The hypoconulid is a distinct anteroposteriorly compressed cusp on the posterior cingulid just lingual to the hypoconid.

Both lower molars have the distinct flexure in the metaconid crest diagnostic of the genus (Figure 21B). In general morphology the specimens are similar to those described for the holotype (Korth, 1989a). The only differences are that the hypolophid appears continuous to the ectolophid on both specimens, however both are more heavily worn than the holotype. Also, there is an anterior extension of the anterolabial corner of the hypoconid on both specimens that ends in a small labial cuspule. As with the referred premolars, the enamel in the basins of the teeth is smooth.

The referred m3, SDSM 155968 (Figure 21C), is similar in size to the referred anterior molars. The flexure in the metalophid crest is not as pronounced as in m1 and m2, similar to the type specimen. The only difference between the ant mound m3 and that of the holotype is that the trigonid basin is more nearly closed posteriorly and the hypolophid is slightly longer but not continuous with the ectolophid.

Discussion—The specimens referred here are similar to those of the holotype of *O. pediasius* but are slightly larger (Table 20; Korth, 1989a: table 3). The referred p4s from the ant mounds are slightly shorter than the referred molars. Korth (1989a) diagnosed the genus (and species) as having a p4 longer than m1 or m2. However, the of the p4 measurements of holotype are questionable due to the fact that it is still within the crypt and cannot be measured precisely. The holotype of *O. pediasius* is from the Whitneyan of Sioux County, Nebraska, whereas the specimens referred here are from ant mounds situated below the UPW.

Oropyctis sp.
(Figures 21D, E)

Referred Specimen—SDSM 155479, left m1; SDSM 155676, dentary fragment with right m3.

Locality—Recovered from ant mound 1 below the UPW; ant mound 8 above the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Measurements—m1: L = 2.07 mm; W = 1.94 mm. m3: L = 2.01 mm; W = 1.70 mm.

Description—The referred m1 is markedly smaller than those referred above to *O.* cf. *pediasius* (Table 20) but has the distinct morphology of the genus (Figure 21D). It is identified as an m1 because the trigonid is markedly narrower than the talonid, not subequal as in m2s. The metaconid and protoconid are closely spaced making the trigonid basin small. It is blocked anteriorly by the short anterior cingulid and posteriorly by a short metalophulid II. There is a distinct

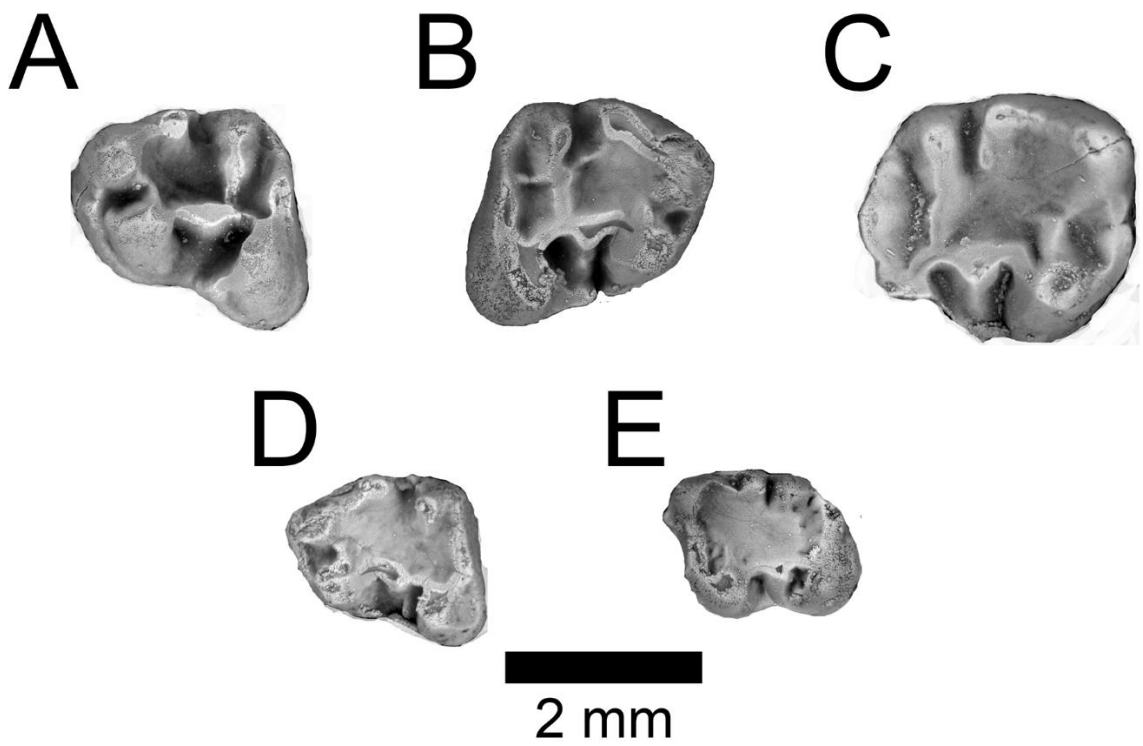

FIGURE 21. *Oropyctis* from the ant mound collection from Sioux County, Nebraska. A-C, *O.* sp., cf. *O. pediasius*. A, SDSM 155460, left p4. B, SDSM 155967, right m1 or m2. C, SDSM 152477, right m3. D-E, *Oropyctis* sp. D, SDSM 155479, left m1. E, SDSM 155676, left m3. All figures to same scale.

metastylid near the center of the lingual margin of the tooth that is connected to the metaconid via a metalophid crest that bows slightly labially at its center. The ectolophid is complete from the posterolingual corner of the protoconid to the anterolingual corner of the hypoconid and is directed slightly in a posterolabial direction. At its center is a small, circular mesostylid. The hypoconid is slightly anteroposteriorly compressed. The posterior cingulid runs from the posterolingual corner of the hypoconid along the posterior margin of the tooth ending lingually posterior to the apex of the entoconid. The hypoconulid is a transversely elongated swelling near the center of the posterior cingulid. The entoconid is conical with no indication of a hypolophid. Just anterior to the entoconid is a minute cuspule along the lingual side of the tooth, just posterior to the valley separating the mesostylid from the entoconid.

The m3 is slightly longer than wide (Table 20). The metaconid is at the anterolingual corner of the tooth and anteroposteriorly flattened (Figure 21E). The anterior cingulid runs along the anterior margin of the tooth ending lingually in the anterolingual corner of protoconid. The protoconid is approximately circular in occlusal outline. The very short metalophulid II extends lingually only slightly from the posterolingual corner of the protoconid. The mesoconid is small and positioned midway between the protoconid and hypoconid along a low, thin ectolophid that joins the hypoconid at its anterolingual corner. The hypoconid is slightly anteroposteriorly compressed with a low lophid extending anteriorly from its anterolabial corner. There is a distinct metaconid crest extending posteriorly from the metaconid. The crest bows labially at its center, fusing posteriorly with a relatively large metastylid. The entoconid is approximately the same size as the protoconid. A low, short, broad lophid extends labially (=partial hypolophid). The posterolophid is broad and extends directly lingually from the hypoconid along the posterior margin of the tooth, then tapers to a very thin lophid ending at the posterolingual corner of the entoconid.

Discussion—The m3 (SDSM 155676) is very similar in morphology to that of the holotype of *O. pediasius* (UNSM 56397: Korth, 1989a: fig. 3A) differing only in having a relatively larger metastylid and being markedly smaller in overall size. The distinctive flexure in the metaconid crest on the specimens referred here is only present elsewhere in

Oropyctis among early aplodontines, making the Sioux County specimens referable to this genus. The referred m1 is also similar to the m3 in being smaller and it also lacks the low hypolophid present in m1 of *O. pediasius* (Korth, 1989a: fig. 3A) and m1 and m2 of the specimens referred above to *O.* cf. *pediasius*.

Because the sizes of these two specimens are only approximately 60 percent that of the holotype of *O. pediasius* and the above material referred to *O.* cf. *pediasius* (Table 20), suggests that they are not referable to either of these species. One of these specimens was recovered on an ant mound situated below the UPW, while the other comes from above the UPW. The type and only other known specimen of *O. pediasius* is from the Whitneyan Whitney Member of the Brule Formation, also from Sioux County (Korth, 1989a).

Genus *Haplomys* Miller and Gidley, 1918
Haplomys galbreathi Tedrow and Korth, 1997
(Figure 22A-D; Tables 19, 20)

Referred Specimens—SDSM 155687, left P4; SDSM 155686, left M1; SDSM 152481, dentary fragment with right m1-m2; SDSM 155678, 155679, 155680, 155682, 155685, m1; SDSM 155677, m2; SDSM 155681, 155683, 155684, m3.

Localities—Recovered from ant mounds 1, 3, 4, 6, and 7 below the UPW; ant mound 8 above the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Description—The lower cheek teeth have been described in detail elsewhere (Tedrow and Korth, 1997). The only variation appears to be the length of the hypolophid on the referred m1s. The isolated first and second lower molars were separated based on proportions, m1 being slightly longer than wide and m2 wider than long (Table 20; Tedrow and Korth, 1997: table 2). On the holotype, the hypolophid on m1 extends more posteriorly, fusing with the posterior cingulid at its center, whereas the hypolophid is complete to the ectolophid on m2 (Tedrow and Korth, 1997: fig. 3A). On all of the referred isolated m1s the hypolophid is as in m2 but in the dentary fragment that contains both m1 and m2, the hypolophid of m1 is shorter as in the holotype (Figure 22D).

The two upper cheek teeth are referred to this species based on comparable size with the lowers and distinctive morphologies of *Haplomys*. The parastyle on P4 is large, rounded anteriorly and flattened posteriorly (Figure 22A). Due to breakage some enamel has been lost on the anterior side of the cusp. It extends lingually for less than half the width of the tooth, ending at a point even with the lingual side of the paracone. It is separated from the paracone by a deep transverse valley. A minute stylar cusp is present on the anterior edge of the tooth lingual to the parastyle, just anterior to the protoconule (anterostyle). The paracone and metacone are slightly convex labially and of equal size. The ectoloph extends labially between the cusps with a distinct mesostyle. The protoloph is continuous from the posterolingual corner of the paracone to the center of the labial side of the protocone. The protoconule is large, nearly rectangular in occlusal outline, and is attached to the protoloph along its posterior margin. The protocone is large, centered along the lingual edge of the tooth, and flattened on its labial side. The metaloph mirrors the protoloph in having a large metaconule that is attached to the metaloph along its anterior side. However, the metaconule is more rounded on its posterior side and the metaloph is not continuous with the hypocone, ending in a small spur on the anterolingual side of the metaconule. A distinct cingulum runs both anteriorly and posteriorly from the apex of the protocone. On the anterior side it bends, then runs labially along the anterior margin of the tooth, ending at the anterostyle. There is no indication of a protocone crest. The posterior cingulum also bends labially at the posterolingual corner of the tooth and runs along the posterior side of the tooth until it joins the posterolabial corner of the metacone.

The M1 or M2, SDSM 155686 (Figure 22B), is comparable in size to the referred P4. The tooth is complete except for a small chip on the posterolabial corner of the metacone. The paracone and metacone, as in P4, are slightly concave labially and of equal size. A low but distinct ectoloph runs from the anterolabial corner of the tooth across both cusps, bending labially at its center ending labially in a minute mesostyle. There is no parastyle. The anterior cingulum runs from the anterolabial corner of the tooth along the anterior margin and ends lingually at a point even with the apex of the protocone near the base of the crown. The protoloph and metaloph are as in P4 except that the two lophs fuse at a point just labial to the protocone. The protoconule is more rounded on the molar than on P4. There is a distinct protocone crest extending anteriorly and slightly labially from the apex of the protocone. The cingula are as in P4.

Discussion—The specimens of lower molars referred here are similar in size and morphology to the holotype of *Haplomys galbreathi* (Tedrow and Korth, 1997: fig. 3A, table 2). The P4 and upper molar are referred to this species based on comparable size with the lowers and similarities to the morphologies of those of the type species of *Haplomys*, *H. liolophus* (Rensberger, 1975: fig. 2C). The upper cheek teeth of *H. galbreathi* are smaller and slightly less lophate than those of *H. liolophus*; the same differences cited between the lower teeth of these species (Tedrow and Korth, 1997).

Haplomys galbreathi was previously only known from a single specimen from the Orellan of South Dakota (Tedrow and Korth, 1997). The referred

specimens from Sioux County are from ant mounds situated both below and above the UPW.

Genus *Costepeiromys* n. gen.

Type Species—*Costepeiromys attasorus* n. sp.

Diagnosis—Cheek teeth brachydont, as in *Prosciurus* Matthew, 1903a, and *Altasciurus* Korth and Tabrum, 2017; minute irregularities (lophules) in the enamel of the basins of all cheek teeth; trigonid open posteriorly on lower molars; hypolophid complete on lower molars with distinct S-curve on m3; partial ectolophid on M3.

Range—Late Chadronian to early Orellan (latest Eocene-earliest Oligocene) of Nebraska.

Etymology—Latin, *costa*, ridge; and *Epeiormys*, genus with cheek teeth that have similar crenulations of enamel.

Comparisons—The generally prosciurine morphology of the cheek teeth clearly separate *Costepeiromys* from the more advanced meniscomyine and aplodontine aplodontids based on the low crown height, cuspate nature, degree of lophodonty, and proportions of m3 (largest of the lower molars). Among prosciurines the lower molars of *Costepeiromys* are most similar to those *Altasciurus* in having: 1) trigonids open posteriorly; 2) complete hypolophids; 3) and isolated metastylids (Korth and Tabrum, 2017). They differ from those of *Altasciurus* in having the distinct crenulations of the enamel (smooth in *Altasciurus*). The upper molars of *Altasciurus* do not have an ectoloph as in *Costepeiromys* and the protoconule of the upper molar of the former is on the anterior side of the protoloph, not centered as in *Costepeiromys*.

Besides the crenulations of the molars, *Costepeiromys* differs from *Prosciurus* in having hypolophids complete to the ectolophid on the lower molars and an ectoloph on the upper molars, neither of which are present in *Prosciurus* (Korth and Tabrum, 2017; Korth et al., 2019a). *Ninamys* Vianey-Liaud et al., 2013, has the partial ectoloph on the upper molars as in *Costepeiromys* but the trigonid basins of the lower molars of *Ninamys* are closed or nearly so, whereas in *Costepeiromys* they are open. The lower molars of *Ninamys* also average wider than long; in *Costepeiromys* they are longer than wide, proportioned as in *Altasciurus* (Korth and Tabrum, 2017). *Pseudallomys* (Korth, 1992b) has crenulated enamel of the cheek teeth; however, the crenulations are much higher and radiate from the center of the tooth unlike the minute irregular wrinkles in the teeth of *Costepeiromys* (see below discussion of *Pseudallomys*).

Pelycomys has complete hypolophids on the lower molars as in *Costepeiromys* but the trigonid basins are closed posteriorly (Galbreath, 1953; Korth, 1986) and there is no partial ectoloph on the upper molars (Korth, 1986). The Chadronian species of *Pelycomys*, *P. rugosus* and *P. brulanus*, have crenulations of the enamel on the molars but the Orellan species, *P. placidus*, does not (Galbreath, 1953). Although *Epeiromys* has similar wrinkling of enamel as in *Costepeiromys*, the former completely lacks a hypolophid on the lower molars and the metastylid is markedly smaller without a labial extension (Korth, 1989a; 2014; 2020b). *Costepeiromys* differs from *Leptoromys* (Tedrow and Korth, 1997) in lacking the multiple metastylids and doubled hypolophid on the lower molars.

Costepeiromys attasorus n. sp.
(Figures 22E-H; Tables 19, 21)

Type Specimen—SDSM 155705 left m2 (Figure 22G).

Referred Specimens—SDSM 155711, 155763, m1; SDSM 155706-155710, m3; SDSM 155712, 155713, M3.

Localities—Recovered from ant mounds 1, 3, 5, 6 (holotype), and 9 below the UPW; ant mound 19 above the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Diagnosis—As for genus.

Etymology—Latin, *Atta*, genus of ants; *sorus* heap or pile; in reference to the ant mound source of the specimens.

Description—All referred cheek teeth have minute irregularities in the enamel of the basins. This wrinkling is most similar to that of *Epeiromys* (Korth, 1989a, 2020b) but does not display a pattern of radiating lophules as in *Hesperopetes* (Emry and Korth, 2007). The m1 can be separated from m2 by the larger size of the latter (Figures 22F, G). Both m1 and m2 are slightly longer than wide and narrower anteriorly than posteriorly. The metaconid is anteroposteriorly compressed at the anterolingual corner of the tooth. The anterior cingulid is relatively high and extends from the apex of the metaconid along the anterior margin of the tooth, then bends slightly posteriorly to join the anterior margin of the protoconid. There is a minute anterostylid near the labial end of the anterior cingulid, just anterolingual to the protoconid. The trigonid basin is blocked posteriorly by a short metalophulid II that does not reach the base of the metaconid, leaving the trigonid basin open posterolingually. A metastylid is present near the center of the lingual edge of the tooth. It is separated from the posterior end of the metalophid crest by a distinct valley. The metastylid varies in size from small to large. There is always a short lophulid that extends directly labially from it. The ectolophid is complete from the posterolingual corner of the protoconid to the anterolingual corner of the hypoconid. The mesoconid is smaller than the major labial cusps at the center of the

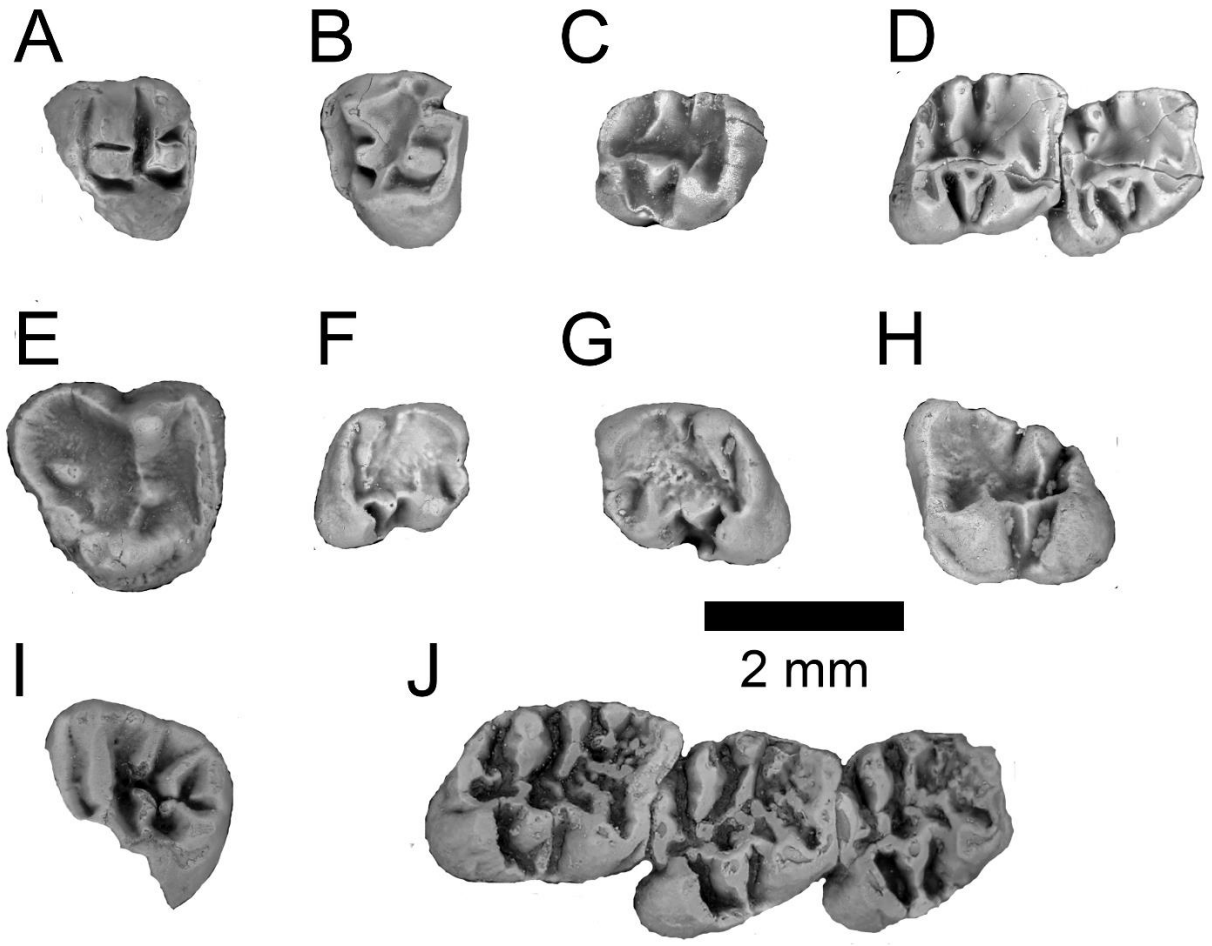

FIGURE 22. Aplodontid rodents from the ant mound collection from Sioux County, Nebraska. A-D, *Haplomys galbreathi*. A, SDSM 155687, left P4. B, SDSM 155686, left M1 or M2. C, SDSM 155681, right m3. D, SDSM 152481, right m1-m2. E-H, *Costepeiromys attasorus*. E, SDSM 155712, left M3. F, SDSM 155763, right m1. G, SDSM 155705, left m2 (holotype). H. SDSM 155709, left m3. I, *Pseudallomys* sp., SDSM 155750 left M3 (partial). J, *P. nexodens*, CM 11898, right m1-m3 (holotype). All figures to same scale.

ectolophid and is nearly flat lingually and rounded labially. The labial side of the mesoconid slopes labially, nearly reaching the margin of the tooth. The entoconid is slightly anteroposteriorly compressed. The hypolophid extends labially from the entoconid and bows slightly posteriorly, ultimately joining the ectolophid at the posterolingual corner of the mesoconid. On the smallest specimen, SDSM 155763, the hypolophid ends just lingual to the ectolophid. The hypoconid is compressed anterolingually to posterolabially. The posterior cingulid runs from the posterolingual corner of the hypoconid along the posterior margin of the tooth and ends lingually just posterior to the entoconid. The hypoconulid is a transversely elongated swelling at the center of the posterior cingulid.

The majority of the referred specimens are m3s. They differ from the m1 or m2 in being longer and wider and having the posterior width less than the anterior width. The nature of the crenulations of the enamel are the same as in the anterior molars (Figure 22H). Other than size and proportions, the major difference between m3 and the more anterior molars is the general elongation of the talonid with the posterior cingulid

bowing posteriorly. The hypolophid is always complete with a distinct S-curve before joining the ectolophid. The trigonid basin is slightly more open on m3 than the anterior molars.

The two M3s are referred here based on their comparable size to the lowers as well as the presence of their crenulated enamel. M3 is approximately triangular in occlusal outline. The anterior cingulum runs the entire width of the tooth along the anterior margin, well separated from the protoloph (Figure 22E). The protocone is crescentic and at the anterolingual corner of the tooth. A small protocone crest extends from its anterolabial corner into the valley between the protoloph and anterior cingulum. The paracone is circular in occlusal outline and slightly smaller than the protocone. The protoloph runs from the lingual side of the paracone and joins the protocone at the center of its labial side. There is a small but distinct protoconule at the center of the protoloph. A distinct ectoloph extends posteriorly from the paracone along the labial border of the tooth with a distinct lingual bend at its center and ends in a small mesostyle at the center of the labial border of the tooth. The tooth is slightly expanded posteriorly at its posterolabial corner but there is no indication of a metacone. The posterior cingulum runs from the posterolabial corner of the protocone along the posterior border of the tooth ultimately reaching the posterolabial corner of the tooth. On both M3s there is a distinct, isolated metaconule. It is relatively larger on SDSM 155713 than on SDSM 155712. The remnant of a metalophid is present on both specimens as a short loph extending posterolabially from the protocone. It joins the metaconule only on the more worn specimen (SDSM 155713).

Discussion—Although the specimens of *Costepeiromys attasorus* are similar in size to those referred to *Altasciurus relictus* from the ant mounds (Tables 15, 16, 19, 21), and have a generally similar morphology of the cheek teeth, those of *C. attasorus* have the crenulated enamel and partial ectoloph on the upper molars not present in *Altasciurus. C. attasorus* is predominantly from ant mounds situated below the UPW, with only one specimen (SDSM 15576) recovered from above the UPW.

Genus *Pseudallomys* Korth, 1992b
Pseudallomys sp.
(Figure 22I)

Referred Specimen—SDSM 155750, partial M3.

Locality—Recovered from ant mound 6 below the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Measurements—M3: L = 2.13; m1: L = 1.90 mm; W = 1.97 mm.

Description—The M3, SDSM 155750, is partially broken (anterolingal corner missing). It is triangular in occlusal outline (Figure 22I). The only recognizable major cusp is the paracone in the anterolabial corner of the tooth. A protoloph runs directly lingually from it with no indication of a protoconule. The anterior cingulum is a thin loph running along the anterior margin of the tooth paralleling the protoloph. The crown is filled with high crenulated ridges posterior to the protoloph extending toward the center of the tooth from the labial, posterior and lingual margins. A ridge runs anteroposteriorly along the labial margin from the paracone that wraps around the remainder of the tooth, and ends at the posterolabial corner of the protocone. There is no indication of a mesostyle.

Discussion—The referred M3 (SDSM 155750) is of similar size to the lower molars of the holotype of *P. nexodens* (Korth, 1992b) but no direct comparisons can be made because no upper molars have been previously described for that species. The referral of this upper molar from the ant mound collection is done based on its comparable size to the lower molars of the holotype (Korth, 1992b: table 1) and the pronounced crenulations in the enamel, markedly higher than in the specimens referred below to *Ansomys.* It is also distinct from M3s of *Ansomys* by lacking the mesostyle that is "…squared labial flexure and shaped overall like the cross section of a flat-brimmed hat…" (Hopkins, 2004: 734) diagnostic of *Ansomys* (see Qiu, 1987:pl. 1, fig. 10; Qiu and Sun, 1988: fig. 10; Hopkins, 2004: fig. 5.4).

Hopkins (2004) referred *P. nexodens* to the genus *Ansomys*; however, based on her amended diagnosis of the genus there are only three diagnostic characters of the lower molars for *Ansomys*: 1) accessory lophules present in basins; 2): cusps anteroposteriorly flattened and transversely elongated; and 3) presence of a crest-like metaconid. Of these only the first is true for *P. nexodens.* Also, *Ansomys* is characterized by m3 being smaller than m2 unlike *P. nexodens* where m3 is the largest of the lower molars. In the cladistic matrix presented by Hopkins (2004), 39 percent of characters she used are not applicable to *P. nexodens* owing to the fact that it was only known from a single dentary with m1-m3 (Korth, 1992b) so all morphologies of p4 or the upper dentition could not be scored. The majority of the characters cited by Hopkins (2004: 734) as unique for "*A.*" *nexodens* are more primitive and *Prosciurus*-like or are more typical of prosciurines and distinct from *Ansomys*. These features include: 1) m3 longer than m2; 2) hypolophid on m1-m2 meets ectolophid posterior to mesoconid; 3) two distinct metasylids on lower molars; and, 4) basal anterolabial cingulid present on lower molars (Figure 22J). Also, there are posteriorly oriented lophules extending from anterior cingulid on the molars of *P. nexodens* that are not present on any of the species of *Ansomys* (Rensberger and Li, 1986: fig. 1; Qiu,

1987:pl. 2; Qiu and Sun, 1988: fig. 2; Hopkins, 2004: fig. 5, 6). In an abstract, Meyer et al. (2008) reported the first upper cheek teeth of *Pseudallomys* from two localities in Saskatchewan. Based on the morphology of the upper molars (e.g., lack of "hat shaped" mesostyle, nature of lophules) they were able to demonstrate that *Pseudallomys* was clearly distinct from *Ansomys*.

The Sioux County specimen is from an ant mound situated more than five meters below the UPW, whereas the type specimen of *P. nexodens* is from the Orellan of Montana (Korth, 1992b). The specimens of *Pseudallomys* reported from Saskatchewan represent two species, one Orellan and one Whitneyan (Meyer et al., 2008).

Subfamily Ansomyinae Qiu, 1987
Genus *Ansomys* Qiu, 1987
Ansomys cyanotephrus Korth, 2007a
(Figures 23A, B; Table 21)

Referred Specimen—SDSM 155690, right m2; SDSM 152448, 152482, 155691, m3.

Localities—Recovered from ant mounds 3, 6, and 7 below the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Description—The m2, SDSM 155690, is slightly wider than long and wider posteriorly than anteriorly (Figure 23B). The anterior cingulid extends along the anterior margin of the tooth from the metaconid in the anterolingual corner to the anterolingual corner of the protoconid. The metaconid is flattened posteriorly and rounded anteriorly. The protoconid is crescentic; the posterior arm extends directly lingually from its posterolingual corner for approximately half the width of the tooth. The metalophid crest extends posterior from the apex of the metaconid for half the length of the tooth where there is a distinct mesostylid that has a lophid extending lingually and slightly posteriorly into the center of the basin. A minute second mesostylid is posterior to the larger one, and much lower. The hypolophid is complete from the entoconid to the mesoconid but has two flexures near its center. The ectolophid is complete from the protoconid to the hypoconid with a large, triangular mesoconid at its center. The hypoconid is anteroposteriorly compressed and continuous with the posterior cingulid that extends the width of the posterior margin of the tooth, ending lingually posterior and slightly labial to the entoconid.

The m3s are rectangular in occlusal outline, longer than wide, and narrower posteriorly than anteriorly (Figure 23A). The metaconid is anteroposteriorly compressed. The center of the talonid is filled with a series of lophulids. The hypolophid is continuous from the entoconid to the posterior side of the mesoconid with a slight flexure at its center. There is a single metastylid attached anteriorly to the metaconid via a metaconid crest. A lophid extends labially from the metastylid that is continuous with the posterior arm of the protoconid and has a distinct flexure at its center. There are variable minute lophules in the basin of the tooth that run anteroposteriorly. In SDSM 155691 (the least worn specimen) there are two, one running from hypolophid just labial to the entoconid that connects with the posterior cingulid and a second that runs posteriorly from the flexure in the posterior arm of the protoconid and joins the anterolabial corner of the entoconid. On SDSM 152482 there is a distinct accessory metastylid anterior to the central metastylid, as well as the accessory lophules present in SDSM 155691. SDSM 152448 is the most worn specimen and much of the occlusal morphology has been worn away. However, the posteriorly directed lophulid from the hypoconid is present, but not complete to the posterior cingulid.

Discussion—All specimens referred here are similar to m2 or m3 of *Ansomys* (Qiu, 1987:pl. 2, fig. 11-14; Qiu and Sun, 1988: fig. 2; Hopkins, 2004: fig. 6.1: Korth, 2007a: fig. 1G). The Sioux County ant mounds specimens of *Ansomys* are most similar to *A. cyanotephrus* described from the Whitneyan Blue Ash fauna of Sioux County but are slightly larger (Table 20; Korth, 2007a: table 1). All of the specimens here referred to this taxon are from below the UPW.

Genus *Protansomys* n. gen.

Type Species—*Protansomys gulottai* n. sp.

Diagnosis—Cheek teeth similar to those of *Ansomys* (see Hopkins, 2004) but differ in: smaller size; cheek teeth less complex (fewer accessory lophules) and less lophate; ectoloph complete on upper molars and extends labially at center to meet mesostyle but mesostyle not anteroposteriorly elongated; metaconid not as anteroposteriorly compressed on lower molars; minute metastylid on posterolingual corner of metaconid of m1 and m2 (not present in *Ansomys*).

Range—Late Chadronian to early Orellan (latest Eocene-earliest Oligocene) of Nebraska.

Etymology—Greek, *protos*, first; and *Ansomys*, a related rodent.

Protansomys gulottai n. sp.
(Figures 23C, D; Tables 19, 21)

Holotype—SDSM 152447, left dentary fragment with m1-m2;

Referred Specimens—SDSM 155688, right M1 or M2; SDSM 155689, right m1 or m2.

Localities—Recovered from ant mound 1 (holotype) below the UPW; and mound 8 above the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Diagnosis—As for genus.

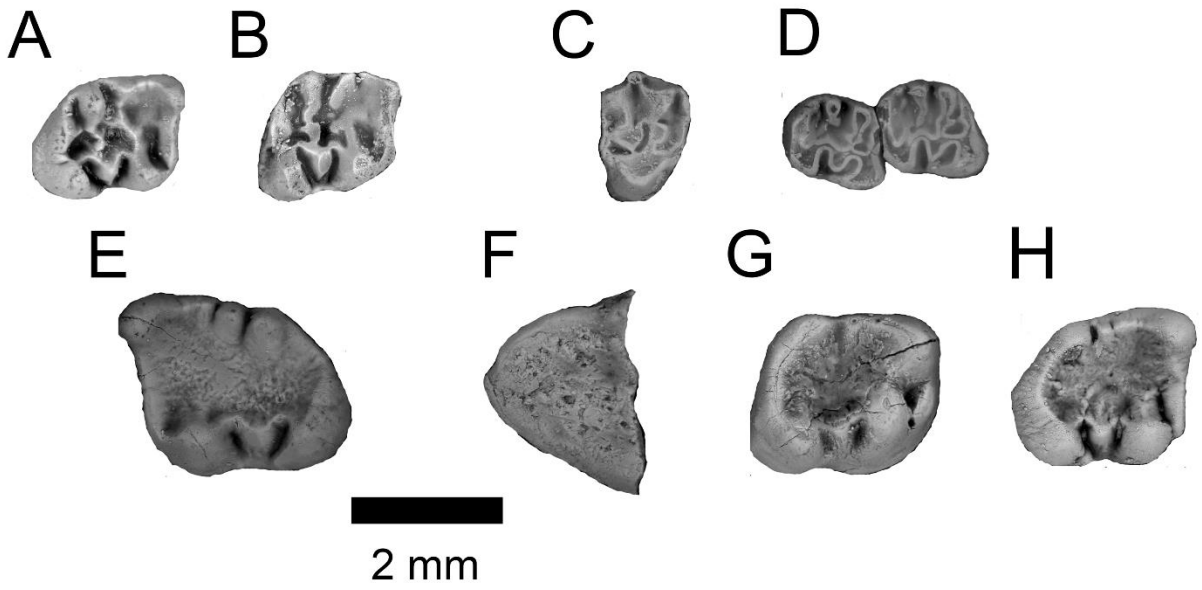

FIGURE 23. Additional aplodontids, *Epeiromys* and *Hesperopetes* from the ant mound collection from Sioux County, Nebraska. A-B, *Ansomys*. A, SDSM 155691, right m3. B, SDSM 155690, right m2. C-D, *Protansomys gulottai*. C, SDSM 155688, right M1 or M2. D, SDSM 152447, left m1-m2 (holotype). E, *Epeiromys* sp., SDSM 155702, left m3. F, G, *Hesperopetes* sp. F, SDSM 155704, right M3 (partial). G, SDSM 155703 right m1 or m2. H, SDSM 15645, right m3. All figures to same scale.

Etymology—Patronym for Marco Gulotta Sr. who brought these specimens to our attention and put in numerous hours of work to separate the fossils from the associated sediment after they were recovered from the ant mounds.

Description—The single referred upper molar, SDSM 155688 (Figure 23C), is wider than long and equivalent in size to the type and referred lower molars. The tooth is moderately worn and roughly triangular in occlusal outline. The anterior cingulum runs from the anterolabial corner of the tooth, where it meets the anterolabial corner of the paracone, along the anterior margin of the tooth to a point even with the labial extent of the protocone, then bends posteriorly joining the protocone. The paracone and metacone are equal in size and slightly concave labially. The ectoloph is continuous across the entire labial length of the tooth. It bends lingually at both the paracone and metacone but extends labially at its anterior and posterior ends as well as at its center between the labial cusps where it meets the labial edge of the tooth and forms a distinct, round mesostyle. The protoconule and metaconule are only slightly smaller than the labial cusps, the metastyle being the larger of the two. The protoloph extends lingually from the posterolingual corner of the paracone to the labial side of the protocone, just anterior to its center. The protoconule is on the anterior side of the protoloph; rounded anteriorly and flattened posteriorly. The metaconule is similarly positioned on the metaloph and rounded posteriorly rather than anteriorly. It is also connected to the labial side of the protocone but more weakly than the protoconule. There is an accessory loph between the protoloph and metaloph. It extends anteriorly from the metaconule, then curves labially where it meets the end of a similar loph extending posterolabial from the protoconule. The protocone is the largest of the cusps and is flattened labially and rounded lingually. The posterior cingulum extends posteriorly from the posterolabial corner of the protocone and runs along the posterior margin of the tooth until it joins the posterolabial corner of the metacone.

The m1 is similar in size to m2 but narrower anteriorly than the latter (Figure 23D, Table 21). The metaconid is anteroposteriorly compressed in the anterolingual corner of the tooth. The trigonid basin is markedly smaller on m1 than m2 with the metaconid and protoconid more closely spaced. The trigonid is open posteriorly on both molars but more narrowly on m1. There is a small but distinct anterior metastylid at the anterolingual corner of the tooth that is continuous with the metaconid crest from the metaconid. A much larger, central metastylid is at the center of the lingual border of the tooth. It is separated from both the anterior metastylid and hypoconid by deep valleys. The

protoconid is crescentic. The ectolophid extends posteriorly from its posterolingual corner of the protoconid, then bends labially where it joins the anterolingual corner of a large semicircular mesoconid, then extends directly posteriorly to join the anterolingual corner of the hypoconid. The hypoconid is transversely elongated. The anterolabial corner has a short anteriorly directed spur that ends before reaching the labial end of the mesoconid. The entoconid is isolated. The hypolophid extends labially and slightly anteriorly from it, joining the ectolophid at the posterolingual corner of the mesoconid. There is a minute swelling near the center of the hypolophid that is more pronounced on m2 than m1. There are a few low, rounded lophules in the talonid basin of both molars, extending labially and anterolabially from the metastylid. The posterior cingulid runs from the posterolingual corner of the hypoconid along the posterior margin of the tooth, ending posterior to the entoconid. On both molars there is a low, minute lophulid running anteroposteriorly between the hyolophid and posterior cingulid. The referred m2 differs from m2 of the holotype in that the accessory lophulids are slightly more prominent but not as high as the major lophids.

Discussion—The specimens referred to *Protansomys gulottai* are much smaller than those referred above to *Ansomys* and *Pseudallomys* (Tables 19, 21). The upper molar is referred here based on its similar size to the lower cheek teeth and *Ansomys*-like morphology. The most distinctive character of this species (and genus) is the ectoloph on the upper molar that has the distinct mesostyle but lacks the flattened labial surface diagnostic of *Ansomys* (Hopkins, 2004). The lower molars are similar to those of *Ansomys* in overall morphology but have more weakly developed accessory lophulids in the basins and an accessory metastylid. The lophulids on the molars of *Protansomys* are clearly much lower than those in the cheek teeth of *Pseudallomys*. *Protansomys* appears to be the most primitive ansomyine. It is known only from ant mounds situated below and above the UPW.

Family uncertain
Genus *Epeiromys* Korth, 1989a
Epeiromys sp.
(Figure 23E; Table 21)

Referred Specimens—SDSM 155701, 155702, right m3.

Localities—Recovered from ant mounds 1 and 5 below the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Discussion—The two m3s are similar in morphology to those of *Epeiromys* with minute, irregular crenulations in the basins, posteriorly open trigonid basin, and lack of a hypolophid (Figure 24E; Korth, 1989a). In size (Table 21), the smaller of the two specimens, SDSM 155701, is closest to that of the type of *E. spanius* from the Orellan of Sioux County, Nebraska (Korth, 1989a: table 3) and the larger specimen, SDSM 155702, is closest to that of *Epeiromys* sp. from the Whitneyan of South Dakota (Korth, 2020b: table 1). The specimens referred here to *Epeiromys* sp. differ from those referred above to *Costepeiromys* in their larger size and lack of a hypolophid.

Both specimens of *Epeiromys* in the ant mound collection are from below the UPW, all other recognized specimens of this genus are late Orellan to late Whitneyan in age (Korth, 2020b).

Family Sciuridae Fischer de Waldheim, 1817
Genus *Protosciurus* Black, 1963
Protosciurus mengi Black, 1963
(Figure 24A-F; Table 22)

Referred Specimens—SDSM 152496, 155485, 155488, 155744, P4; SDSM 152486, 152494, 155367, 155489-155491, M1 or M2; SDSM 152488, 152492, 155484, 155486, 155487, M3; SDSM 155495, p4; SDSM 152498, 155492, m1 or m2; SDSM 152502, 152509, 155480, 155501, m3.

Localities—Recovered from ant mounds 1, 3-7, 9, 15, and 16 below the UPW; ant mound 13 on the UPW; ant mounds 10 and 19 above UPW. Big Cottonwood Creek Member of the Chadron Formation.

Discussion—The cheek teeth referred to *Protosciurus mengi* do not differ in size or morphology from those described from elsewhere (Black, 1963; Korth, 1987, 2009c). Previously this species has only been identified from the Orellan (Black, 1963; Goodwin, 2008). The specimens referred here are from ant mounds situated both below and above the UPW.

Genus *Douglassciurus* Korth and Emry, 2001
Douglassciurus bjorki Korth, 2014
(Figures 24G-L; Table 23)

Referred Specimens—SDSM 152491, dP4; SDSM 152478, 152484, 152490, M1 or M2; SDSM 152483, 152487, 152489, 152493, 152495, M3; SDSM 155494, 155742, p4; SDSM 152504-152506, 152510, 152512, 155461, 155462, 155743, m1 or m2; SDSM 152501, 152507, 152511, 155498-155500, 155723, 155754, m3.

Localities—Recovered from ant mounds 1-6, 9, 15, and 16 below the UPW; ant mounds 8, 10, 11, 18, and 19 above the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Description and Discussion—The dentition of *Douglassciurus bjorki* has been described in detail elsewhere (Korth, 2014). The specimens from the Sioux County ant mounds do not differ in morphology or size

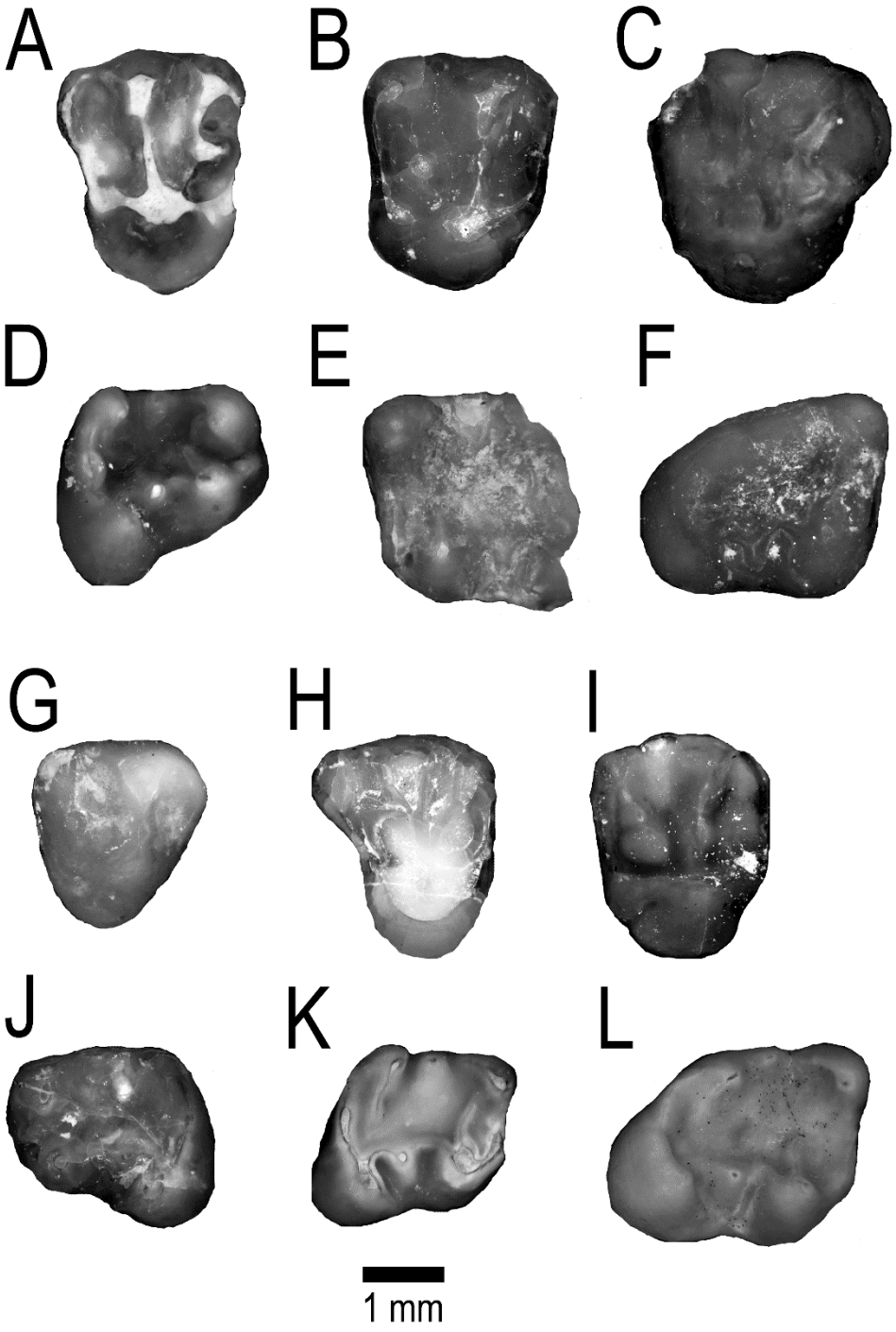

FIGURE 24. *Protosciurus* and *Douglassciurus* from the ant mound collection from Sioux County, Nebraska. A-F, *Protosciurus mengi*. A, SDSM 155488, left P4. B, SDSM 155489, right M1 or M2. C, SDSM 155487, left M3. D, SDSM 155495, right p4. E, SDSM 155492, left m1 or m2 (partial). F, SDSM 155501, right m3. G-L, *Douglassciurus bjorki*. G, SDSM 152491, right dP4. H, SDSM 152489, left P4, I, SDSM 152484, right M1 or M2. J, SDSM 155494, left p4. K, SDSM 152506, right m1 or m2. L, SDSM 152501, right m3. All figures to same scale.

from the original collection of topotypic specimens (Table 23; Korth, 2014: table 5). The only tooth not previously described for this species is dP4. A single specimen from the ant mound collection appears to be referable to *D. bjorki* because of its similar size and morphology to the previously reported P4s (SDSM 152491: Figure 24G). The specimen is heavily worn but most of the occlusal morphology is observable. The tooth is nearly triangular in occlusal outline. The anterolabial corner is expanded anteriorly along the labial border but narrows lingually, ending at the anterolabial corner of the protoconid. The paracone is slightly larger than the metacone. The ectoloph runs posteriorly from the paracone, ending at a small, central mesostyle, similar to that of upper molars. The protoloph is continuous from the paracone to the anterolabial corner of the protocone. The metaloph curves anterolingually from the metacone, ending at the posterolabial corner of the protocone. A low, central metaconule is present at the center of the metaloph. The hypocone is posterior and slightly lingual to the apex of the protocone. A posterior cingulum extends labially from the hypocone along the posterior margin of the tooth, ending posterior to the apex of the metacone.

Specimens of *D. bjorki* were recovered from ant mounds situated below and above the UPW in Sioux County. However, the only previous records of this species were limited to the late Whitneyan of southwestern South Dakota (Korth, 2009c, 2014), making the Sioux County occurrence the earliest to date.

Genus *Cedromus* Wilson, 1949
Cedromus modicus n. sp.
(Figure 25; Table 24)

Cedromus cf. *C. wilsoni* Korth and Emry, 1991

Holotype—UNSM 56406, right dentary with p4-m3 (Figure 25I, J).

Referred Specimens—SDSM 152245, 152246, 152250, 155428, 155430, dP4; SDSM 155407, 155422, 155425, 155429, 155431, 155434, P4; SDSM 152242, 152243, 152247-152249, 152251, 152485, 155405, 155408, 155410-155412, 155415-155420, 155423, 155426, 155432, 155433, M1 or M2; SDSM 152241, 152244, 155406, 155409, 155413, 155414, 155421, 155424, 155427, M3; SDSM 152470, 155448, dp4; 152467, 152472, 152476, 155446, 155447, 155449, 155450, 155459, 155464, p4; SDSM 152469, 155463, 155493, m1 or m2; SDSM 152468, 152474, 155496, 155497, 155502, m3.

Localities—Holotype from the Orella Member, Brule Formation, Sioux County, Nebraska; referred specimens recovered from ant mounds 1, 3-7, 9, 15, and 16 below the UPW; ant mound 13 on the UPW; ant mounds 8, 10, and 17-19 above the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Diagnosis—Intermediate size (larger than *C. wilsoni* Korth and Emry, 1991, smaller than all other species); ectoloph complete from paracone to metacone on upper molars; hypolophid on lower molars not complete to ectolophid, commonly fusing with posterior cingulid.

Etymology—Latin, *modicus*, moderate or medium.

Description—P4 is slightly smaller than the referred M1s. The parastyle is expanded slightly anteriorly at the anterolabial corner of the tooth and forms a crescentic cusp (Figure 25B). The anterior cingulum extends lingually to the anterolabial corner of the protocone. Labially, the parastyle is connected to the anterolabial corner of the paracone, which encloses a narrow valley between the protoloph and the anterior cingulum. The paracone is a transversely elongated oval that is continuous via the protoloph to the center of the labial border of the protocone. There is no indication of a protoconule. There is a small mesostyle at the center of the labial edge of the tooth that is continuous to both the paracone and metacone by slightly curved ridges that run from it to the apices of both labial cusps (=ectoloph). The metacone is smaller than the paracone and circular in occlusal outline. The metaloph runs from the anterolingual corner of the metacone and joins the anterolabial corner of the metaconule. The metaconule is nearly circular in outline and slightly larger than the metacone. On the least worn specimens the metaloph is only weakly connected to the protocone on one (SDSM 155429) and not connected on the other (SDSM 155425). The protocone is the largest cusp at the center of the lingual border of the tooth. The posterior cingulum extends from the posterolabial corner of the protocone along the posterior margin of the tooth to the posterior slope of the metacone. Only on one specimen (SDSM 155425) is there a minute swelling on the posterior cingulum that can be interpreted as a hypocone.

Five specimens have been referred to dP4 based on their similarity to P4 in morphology but slightly smaller size and thinner enamel. Besides the thickness of the enamel, dP4 is also proportioned differently than P4 in that it is nearly equal in length and width, whereas P4 is distinctively wider than long (Table 24). The parastyle and anterior cingulum on dP4 are expanded slightly anteriorly and separated farther from the protoloph than in P4. DP4 is nearly triangular in occlusal outline with the protocone at the anterolingual corner of the tooth, rather than near the center of the lingual edge (Figure 25A). On two specimens (SDSM 155428, 155430) the metaconule is doubled and there is a minute protoconule present.

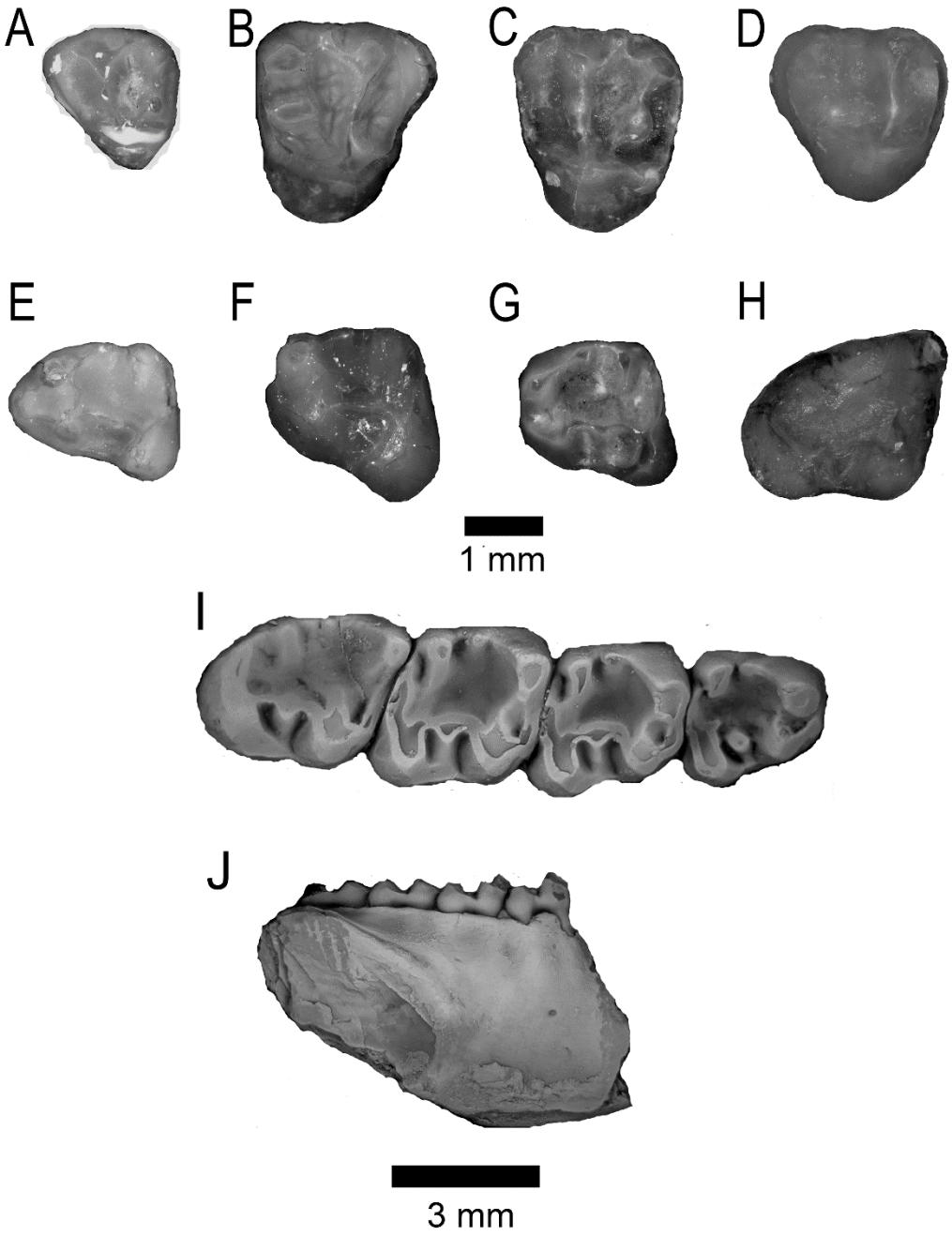

FIGURE 25. *Cedromus modicus* from the ant mound collection from Sioux County, Nebraska. A, SDSM 152246, left dP4. B, SDSM 155425, right P4. C, SDSM 152242, left M1 or M2. D, SDSM 155413, right M3. E, SDSM 155448, left dp4. F, SDSM 152467, left p4. G, SDSM 152469, left m1 or m2. H, SDSM 155496, right m3. I, J, UNSM 56406 (holotype). I, roght p4-m3. J, lateral view of dentary. A-I to same scale (above); J to different scale (below).

M1 and M2 cannot be separated from one another, and all molars are isolated teeth. In overall morphology M1 and M2 are similar to P4 but are slightly larger and do not have the anteriorly expanded parastyle (Figure 25C). There is a small anteroposteriorly compressed parastyle at the anterolabial corner of the tooth. The only other differences between the molars and P4 is that there is a minute protoconule on all specimens, the metacone is relatively larger, the metaconule is variably connected to the protocone (if so, by a minute loph), and a distinct hypocone is present as a swelling along the posterior cingulum posterior and slightly labial to the apex of the protocone.

M3 is nearly triangular in occlusal outline and approximately equal in length and width (Figure 25D). The anterior cingulum and metaloph are similar to that of M1-M2 with the variable presence of a minute protoconule. The posterior half of the tooth is expanded labially and reduced lingually. The ectoloph is continuous from the paracone to the mesostyle then follows the labial border of the tooth, continuous with the labial and posterior cingula, wrapping around the posterior and lingual borders of the tooth, then joining the hypocone on its posterolabial corner. The metaconule varies from a small circular cusp weakly connected to the posterior cingulum to completely absent.

The p4 is only slightly longer than wide with the trigonid much narrower than the talonid (Figures 25F, I). The trigonid consists of equal sized and closely placed metaconid and protoconid. The metaconid is placed just slightly more anteriorly than the protoconid. The trigonid basin is small and closed posteriorly by the metalophulid II, and narrowly open anteriorly. A minute anterostylid is present on some specimens at the anterior base of the crown, well below the trigonid basin. Also present on some specimens is a short lophid extending anterolingually from the protoconid but it never reaches the metaconid. The metaconid crest runs posteriorly from the apex of the metaconid for approximately half the length of the tooth along its lingual side ending in a distinct metastylid. The ectolophid is continuous from the center of the posterior side of the protoconid to the anterolingual corner of the hypoconid. The mesoconid is only a slight swelling near the center of the ectolophid. The hypoconid is elongated and slightly obliquely oriented (anterolabial-posterolingual). A short lophid runs anteriorly from its anterolabial corner but never completely reaches the labial side of the mesoconid. The entoconid is transversely elongated and a hypolophid extends labially from it. The hypolophid is always present but is variable in length from reaching the ectolophid to turning posteriorly and joining the posterior cingulid along its lingual half. The posterior cingulid extends from the hypoconid along the posterior border of the tooth and nearly reaches the posterolingual corner but is separated from the entoconid by a narrow valley.

As with the upper molars, m1 cannot be separated from m2. Typically, m1 and m2 are similar to p4 but are widened anteriorly and average slightly wider than long with the trigonid being only slightly narrower than the talonid (Figure 25G). The trigonid is small and closed posteriorly by the metalophulid II and anteriorly by the anterior cingulid. The lingual side of the tooth is as in p4 with a metastylid and continuous metastylid crest from the apex of the metaconid. The remainder of the morphology of m1-m2 is similar to that of p4. The hypolophid parallels the posterior cingulid and is complete to the ectolophid only on the most worn specimen (SDSM 155463). There is also a more pronounced labial extension of the mesoconid on the molars than on p4.

The m3 is typically more elongated posteriorly than m1 or m2. As in the latter, the trigonid is closed or nearly closed by the metalophid II (Figures 25H, I). There is a distinct metastylid and metastylid crest also as in the anterior molars. The hypolophid is variable in length but never reaches the hypoconid or ectolophid. All other features are as in m1 or m2.

Discussion—*Cedromus modicus* can be distinguished from all other species by size: smaller than *C. wardi* Wilson, 1949, and *C. woodi* Korth, 2015, and larger than *C. wilsoni* (Table 24; Wilson, 1949: 32; Galbreath, 1953: table 9; Korth and Emry, 1991: tables 1, 2; Korth, 2015: table 1). It also differs from *C. wilsoni* and is similar to *C. wardi* in having a complete ectoloph on the upper molars but an incomplete hypolophid on the lower molars (Figure 25; Korth and Emry, 1991: figs. 6.1, 6.2). Other than size, *C. modicus* has the metastylid continuous with the metaconid crest as in *C. wilsoni*, whereas in *C. wardi* and *C. woodi* the metastylid is narrowly separated from the posterior end of the metaconid crest (Wilson, 1949: pl. 1, fig. 1A; Korth and Emry, 1991: fig. 5.2; Korth, 2015: fig. 1). The hypolophid on the m1-m2 of *C. modicus* is more variable, sometimes fusing posteriorly with the posterior cingulid unlike all other species, but never reaching the ectolophid as it does in *C. wilsoni*.

The holotype of *C. modicus* was originally identified as *Cedromus* sp., cf. *C. wardi* (Korth and Emry, 1991:fig. 5.2) and was distinguished from *C. wardi* by its smaller size and morphology of the hypolophid on the lower molars. The specimens referred here are from ant mounds situated both below and above the UPW, whereas the holotype is from the Orella Member of the Brule Formation (Orellan) also from Sioux County, Nebraska.

Oligospermophilus Korth, 1987
Oligospermophilus douglassi (Korth, 1981)
(Figure 26; Table 24)

?*Protosciurus douglassi* Korth, 1981
Oligospermophilus douglassi (Korth) Korth, 1987

Referred Specimens—SDSM 155370, 155381, P4; SDSM 155383, right dP4; SDSM 152259, 152514, 152519, 155369, 155374-155377, 155380, 155382, 155384, 155386-155388, 155476, 155734, 155735, 155745, M1 or M2; SDSM 152517, 155368, 155373, 155378, 155379, 156544, M3; SDSM 155391, 155395, 155398, 155399, 155403, 155436-155438, 155746, 155747, 155454, 155457, 155458, p4; SDSM 152473, 152497, 152515, 152516, 155392, 155393, 155397, 155400-155402, 155404, 155435, 155440-155443, 155445, 155451–155453, 155455, 155456, 155736-155739, 156543, 157009, m1 or m2; SDSM 152518, 155396, 155439, 155444, m3.

Localities—Recovered from ant mounds 1-7, 9, 15, and 16 below the UPW; ant mound 13 on the UPW; ant mound 8, 10, and 17-19 above the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Description—The dentary, p4-m2, and upper cheek teeth of *O. douglassi* have been described elsewhere in detail (Korth, 1981, 1987). The only variation in the upper cheek teeth in the ant mound collection is that there is a minute protoconule on approximately half of the specimens of P4, M1 and M2 (Figure 26B, C). Previously described upper dentitions lack a protoconule (Korth, 1987: fig. 3). On several specimens the minute metaconule is doubled. A minute protocone crest is also variably present on several specimens.

On the lower cheek teeth, the most variable feature is the length of the hypolophid. On most m1 and m2s it is as figured for the holotype (Korth, 1981: fig. 1) but on a few the hypolophid curves posteriorly and joins the posterolophid on its lingual half or is a shorter spur into the talonid basin (Figure 26F). The m3 is slightly larger than m1 or m2 (Table 24) and elongated posteriorly. The metaconid is more anteroposteriorly compressed, the hypolophid shorter, and the posterior cingulid bowed posteriorly, giving the tooth a rounded posterior outline. On three of the four referred specimens the trigonid basin is blocked posteriorly by the metalophulid II as in the anterior molars but remains slightly open on one specimen (SDSM 155444). The hypolophid is shorter on m3 than in m1 or m2.

Discussion—This is the largest collection of *Oligospermophilus douglassi* reported, being known previously from fewer than ten specimens (Korth, 1987). This species has been previously reported from both Chadronian and Orellan of Sioux County as well as possibly from the Whitneyan of South Dakota (Korth, 1981, 1987).

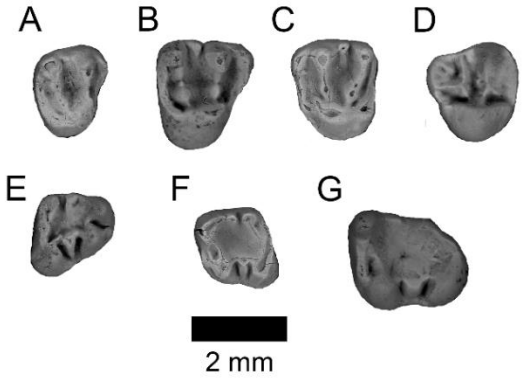

FIGURE 26. *Oligospermophilus douglassi* from the ant mound collection from Sioux County, Nebraska. A, SDSM 15383, right dP4. B, SDSM 155381, right P4. C, ,SDSM 152514, left M1 or M2. D, SDSM 155368, right M3. E, SDSM 155395, right p4. F, SDSM 155397, left m1 or m2. G, SDSM 155439, left m3. All figures to same scale.

Genus *Hesperopetes* Emry and Korth, 2007
Hesperopetes sp.
(Figures 23F, G)

Referred Specimens—SDSM 155704, right M3 (partial); SDSM 155703, right m1 or m2; SDSM 156545, right m3.

Measurements—SDSM 155704: m1 or m2, L = 2.48 mm, W = 2.06 mm; SDSM 156545, m3: L = 2.30 mm; W = 1.98 mm; SDSM 155704: M3, W = 2.17 mm.

Localities—Recovered from ant mound 6 below the UPW; ant mound 13 on the UPW; ant mound 18 above the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Discussion—All specimens have the minute radiating crenulation in the basins typical of this species (Emry and Korth, 2007). The m1 or m2, SDSM 155704 (Figure 23G) also has a minute, posteriorly closed trigonid and an entoconid that is reduced and incorporated into the posterolingual corner of the tooth, typical of *Hesperopetes*. The only distinction is that the ant mound lower molar is slightly longer than wide, whereas all lower molars previously reported of *Hesperopetes* are wider than long (Emry and Korth, 2007: table 1; Korth, 2014: table 7). The referred m3, SDSM 156545, is also longer than wide. The partial M3 retains only the posterior half of the tooth (Figure 23F) but has the distinct radiating lophules of the genus. In size, the specimens are closest to those of *H. jamesi* but slightly larger. The M3 from the ant mounds is smaller than the single specimen of M3 previously reported from the Orellan of Nebraska (Korth, 2017).

Specimens here referred to *Hesperopetes* were recovered from ant mounds situated below and above the UPW. Previously, *H. thoringtoni* was the only species of the genus reported from the Chadronian. However, the specimens referred here to *Hesperopetes* sp. are larger than those previously referred to *H. thoringtoni* (Emry and Korth, 2007: table 1).

Family Eutypomyidae Miller and Gidley, 1918
Genus *Eutypomys* Matthew, 1905
Eutypomys sp., cf. *E. hibernodus* Korth, 2000
(Figure 27B, C)

Referred Specimen—SDSM 156329, left p4.

Locality—Recovered from ant mound 14 on the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Measurements—L = 3.77 mm; W = 3.29 mm; ht (crown height) = 1.89 mm.

Discussion—The single p4 has the occlusal morphology of *Eutypomys* with a complex of lophulids that form a series of minute fossettids characteristic of the genus (Matthew, 1905; Wood, 1937; Korth, 1994c, 2000; Flynn and Jacobs, 2008). In size, it is larger than that of any other reported species (Wood, 1937: 232; Korth, 2016: table 1). The large species, *E. magnus* described by Wood (1937), is of similar size but has been shown to be referable to a different genus (Korth et al., 2019a). Even though the ant mound specimen is slightly worn, the crown proportional height (ht/W = 0.57) is greater than that of the lower molars of the Chadronian and later species of *Eutypomys* (Korth, 2016: table 2; Korth et al., 2019a: 16). Based on its size, crown height, and complexity of the occlusal surface, this specimen best fits *E. hibernodus*. The p4 of *E. hibernodus* has not been previously reported but the similarity in size and occlusal pattern to the molars of that taxon is unmistakable (Figure 27; Korth, 2000: fig. 1).

The Sioux County specimen is from an ant mound situated on the UPW. The only previously reported specimens of *E. hibernodus* are from the Orellan of North Dakota (Korth, 2000). The lack of additional specimens of *Eutypomys* or larger castorids in the ant mound collection is not surprising due to the size of the individual teeth, clearly larger than those typically accumulated by *P. occidentalis*.

Family Eomyidae Winge, 1887
Genus *Metanoiamys* Chiment and Korth, 1996
Metanoiamys paradoxus Emry and Korth, 2012
(Figure 28A)

Referred Specimens—SDSM 152401, right maxilla with P4-M2; SDSM 155692, left M1 or M2.

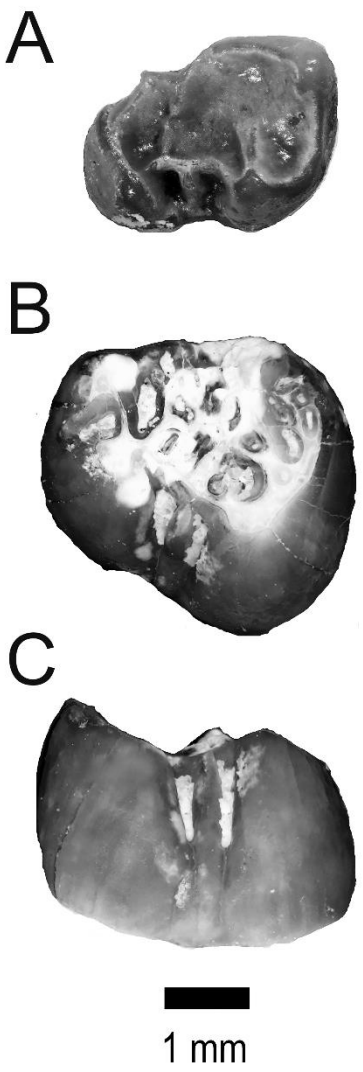

FIGURE 27. *Altasciurus* sp. and *Eutypomys* from the ant mound collection from Sioux County, Nebraska. A, *Altasciurus* sp., SDSM 155348, occlusal view, right m3. B, C, *E.* cf. *E. hibernodus*, SDSM 156329, left p4. B, occlusal view. C, labial view.

Localities—Recovered from ant mounds 7 and 16 below the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Measurements—SDSM 152401: P4, L = 0.92 mm; W = 1.06 mm; M1, L = 0.98 mm; W 1.17 mm; M2, L = 0.97 mm; W = 1.21 mm. SDSM 155692: M1 or M2: L = 1.01 mm; W = 1.14 mm.

Discussion—The Sioux County ant mound specimens match the morphology and size of the topotypic specimens of *Metanoiamys paradoxus* from the Chadronian Flagstaff Rim, Wyoming (Emry and Korth, 2012: table 2). One of the major features that Emry and Korth (2012) used to distinguish *M. paradoxus* from other species of the genus was the lack of P3 based on the lack of a wear facet on the anterior

side of P4, but did not have any maxillae with P4 to verify this. SDSM 152401 is a maxilla with P4-M2 and retains a portion of the maxilla anterior to P4 where there is no P3 or alveolus, hence verifying the character. The only difference in the Sioux County specimen from the topotypic material is that the entoloph on P4 is complete on the Sioux County specimen (Figure 28A) and incomplete in the topotypic specimens. However, both referred specimens of P4 from Flagstaff Rim are virtually unworn (Emry and Korth, 2012: fig. 4A) whereas the Sioux County specimen has a greater amount of wear, which has allowed for the fusion of the entoloph with the protocone (Figure 28A).

M. paradoxus was only recovered from ant mounds situated below the UPW in this study. Previously, the Chadronian occurrence of *M. paradoxus* from Wyoming was the latest occurrence (Flynn, 2008a; Emry and Korth, 2012) but these specimens may be slightly younger depending on the exact position of the Chadronian/Orellan boundary relative to the UPW and if any of these specimens were transported downslope.

Genus *Adjidaumo* Hay, 1899
Adjidaumo minimus (Matthew, 1903a)
(Figures 28B, C; Table 25)

Gymnoptychus minimus Matthew, 1903a
Adjidaumo minimus (Matthew); Burke, 1934

Referred Specimens—SDSM 151128, left maxilla with P4-M3; SDSM 137299, 151145, maxilla with P4-M2; SDSM 151052 left partial maxilla with P4-M1; SDSM 151129, left P4; SDSM 151151, dentary with p4-m2; 152361, dentary with i1, p4-m2; SDSM 137238, 152376, partial dentary with p4-m1; SDSM 152358, partial right dentary with m2-m3; SDSM 154916, right partial dentary with i1, p4; SDSM 137317, right dentary with m1-m2; SDSM 152377, 154909, m1 or m2.

Localities—Recovered from ant mounds 1, 3, 7, and 16 below the UPW; ant mounds 8 and 10 above the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Discussion—The cheek teeth of *Adjidaumo minimus* have been described in detail elsewhere (Matthew, 1903a; Black, 1965; Korth et al., 2015). The only difference between the Sioux County collection and those from some other localities is that they are slightly smaller (Table 25; Black, 1965: 25; Korth et al., 2015: table 2) but not significantly so, more comparable to the collection reported from North Dakota (Korth et al., 2019a: table 5A).

The cheek teeth of the Duchesnean *A. craigi* Storer, 1987, are similar in size to those of *A. minimus* from Sioux County but are less lophate, have more poorly developed mesolophs (-ids), incomplete ectolophids, and a more pronounced anterior cingulum on P4 (Storer, 1987: fig. 4L-O, table 4). The specimens referred here to *Adjidaumo minimus* differ from those referred below to *A. intermedius* from the Sioux County ant mound in being smaller (Tables 25, 26) and lower crowned with less well developed lophs (-ids).

Only two specimens of *A. minimus* (SDSM 137317, 154916) were recovered from ant mounds situated above the UPW while the remainder were recovered from below the UPW. *A. minimus* was originally limited to the Chadronian (Matthew, 1903a; Wood, 1937; Galbreath, 1953; Black, 1963; Korth et al., 2015) but recently has been reported from both the Orellan of Montana (Korth, 2019) and Whitneyan of North Dakota (Korth et al., 2019a).

Adjidaumo intermedius Korth, 1989a
(Figure 28D-G; Table 26)

Referred Specimens—133 specimens (see Appendix).

Localities—Recovered from ant mounds 1, 3-7, 9, 12, 15, and 16 below the UPW; ant mounds 13 and 14 on the UPW; ant mounds 8, 10, 11, 18, and 19 above the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Description—P4 is similar to that of other species with four major cusps, narrower anteriorly than posteriorly, a short posterior cingulum, and a variable anterior cingulum ranging from completely absent to a distinct anterostyle with a slight labial extension (Figure 28E). A minute mesoloph is variably present but never long.

DP4 is retained only in a single specimen, SDSM 151107 (Figure 25D). In overall morphology it is similar to that of P4 but has thinner enamel, is proportionally narrower anteriorly, has a short mesoloph, and a well pronounced anterior cingulum on the labial half of the tooth. The length of the mesoloph and anterior cingulum are greater than in any of the referred P4s.

On specimens that preserve both M1 and M2, the M1 is slightly larger and proportionally longer (nearly square in occlusal outline; Figures 28D, E). However, isolated M1s and M2s cannot be separated with confidence so are included in the table as M1 (Table 26). On both M1 and M2 the general morphology is similar to that of other species (see Wahlert, 1978: fig. 7C; Korth et al., 2015: fig. 4). The only difference appears to be the mesoloph is slightly longer and higher than in *A. minimus*.

M3 is markedly smaller than M1 and M2 and nearly oval in occlusal outline (Figure 28D). The protocone is near the posterolingual corner of the tooth and obliquely compressed (anterolingual-posterolabial). The posterior width of the tooth is less than the anterior width and the metacone is smaller than the paracone. A

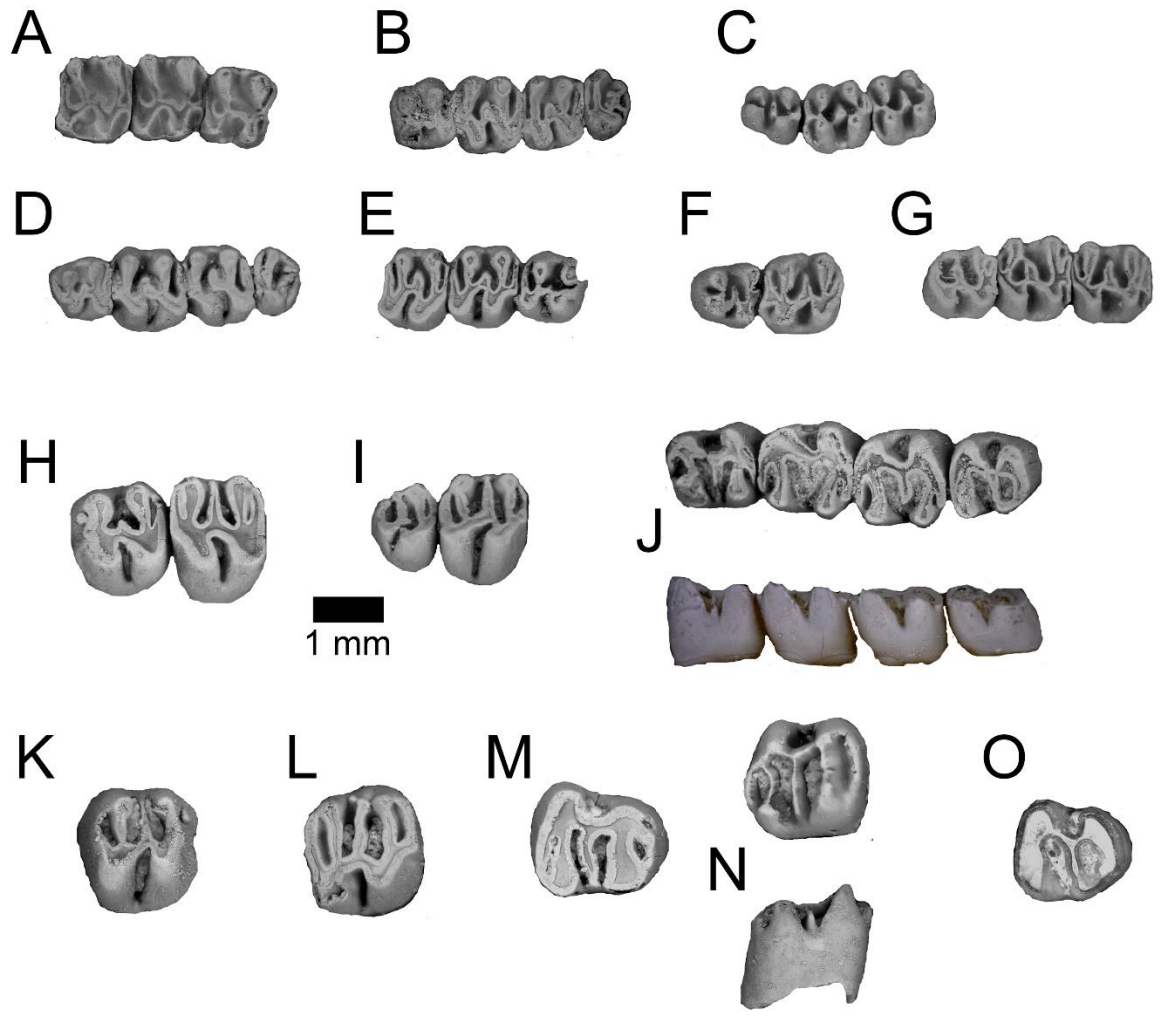

FIGURE 28. *Metanoiamys* and *Adjidaumo* and *Paradjidaumo* from the ant mound collection from Sioux County, Nebraska. A, *Metanoiamys paradoxus*, SDSM 152401, right P4-M2. B, C, *A. minimus*. B, SDSM 151128, left P4-M3. C, SDSM 151151, left p4-m2. D-G, *A. intermedius*. D, SDSM 151107, left dP4-M3. E, SDSM 152392, right P4-M2. F, SDSM 151104, left p4-m1. G, SDSM 151148, right m1-m3. H-J, *P. patriciae*. H, SDSM 150970, left P4-M1. I, SDSM 150965, right M2-M3. J, SDSM 150984, left p4-m3 (occlusal view above, lingual view below; holotype). K-O, *Paradjidaumo* cf. *validus*. K, SDSM 154686, right P4. L, SDSM 154949, right M1 or M2. M, 154437, left p4. N, SDSM 154323, right m1 or m2 (occlusal view above, lingual view below). O, SDSM 154534, right m3. All figures to same scale.

minute paraconule is present on the two unworn specimens (SDSM 151107, 152381) and a metaconule is present on only one (SDSM 152381). The protoloph and metaloph converge at the anterolabial end of the elongated hypocone. One specimen (SDSM 152381) has a minute hypocone along the posterior margin of the tooth, labial to the protocone.

The p4 is smaller than the molars and narrower anteriorly than posteriorly (Figure 28F). The only variations appear to be the presence of a short anterior cingulid extending from the anterior slope of the protoconid on a few of the specimens, and the length of the posterior cingulid. The holotype (Korth, 1989a: fig. 4B) has a longer posterior cingulid than any of the referred specimens, where it varies from a small swelling at the center of the hypolophid to a short spur extending slightly lingually.

The m1 and m2 have a slightly more prominent mesolophid than in *A. minimus* sometimes crossing the entire width of the tooth but otherwise are very similar to those of both *A. minimus* and *A. minutus* (Figures 28F, G). The m3 has not been previously described for this species. It is the smallest of the molars and is reduced posteriorly, typical of the genus. The anterior half of the tooth is as in m1 and m2 with the anterior cingulid slightly more closely positioned to the metalophid. The

hypoconid is smaller than the protoconid, making the posterior width of the tooth narrower than the width of the trigonid. The posterior cingulid wraps around the posterior margin of the tooth ending in a variable but small entoconid. There is no indication of a hypolophid.

Discussion—Previously, only the dentary and p4-m2 of *Adjidaumo intermedius* have been described and was limited to a hypodigm of only four specimens from the Orella Member of the Brule Formation of Sioux County (Korth, 1989a). The specimens referred here best fit *A. intermedius* in being larger than *A. minimus* and smaller than *A. minutus* (Table 26; Black, 1965: 25; Korth et al., 2015: table 2; Korth et al., 2019a: tables A5-A8). The mesolophs (-ids) on the cheek teeth are also longer and higher than in *A. minimus*. Specimens referable to *A. intermedius* are known from nearly all ant mounds situated below and above the UPW.

Genus *Paradjidaumo* Burke, 1934
Paradjidaumo patriciae n. sp.
(Figures 28H-J; Table 27)

Type Specimen—SDSM 150984, right dentary with partial i1, p4-m3 (Figure 28J).

Referred Specimens—749 specimens (see Appendix).

Localities—Recovered from all sampled ant mounds; holotype from ant mound 6 below the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Diagnosis—Small species, near size of *P. disjunctus*, larger than *P. nanus* and *P. obritschorum*, smaller than all other species; p4 longer than m1 (average Lp4/Lm1 = 1.04), similar to that of *P. trilophus*, shorter than *P. validus* and *P. hansonorum*, longer than in other species; crown height of m1 and m2 low (average ht/W = 0.30), less than all other species except *P. disjunctus* and *P. nanus*; anterior cingulid on lower molars always continuous with protoconid.

Etymology—Patronym for Patricia Monaco for all of her contributions to the field of vertebrate paleontology and specifically for her interest in microvertebrate fossils collected from ant mounds.

Description—The cheek teeth are mesodont in crown height with relatively high lophs (-ids), reduced cusps and long mesolophs (-ids), diagnostic of the genus (Burke, 1934; Wood, 1937; Korth, 1981, 2013; Flynn, 2008a). The features that separate this species from others are overall size, crown height, proportional length of p4, and connection of the anterior cingulid to the protolophid on the lower molars.

In terms of size, the cheek teeth most closely approach those of *P. disjunctus* (Korth, 2013: table 4), are larger than *P. nanus* (Korth and Emry, 2013a: table 2) and smaller than all other species (Wood, 1937: 224, 245; Wilson, 1949: 42; Black, 1965: 28, 30; Korth, 1980: table 2; Korth, 2013: tables 2, 6, 7, 8). The crown height index was measured on m1 and m2 and is based on the height of the tooth on the lingual side between the major cusps divided by the maximum width of the tooth (Korth, 2013: 111). This index for the ant mound collection averages 0.30 for m1 or m2 (range = 0.19-0.45), lower than all other species except *P. disjunctus* and *P. nanus* (Korth, 2013: table 1). The relative length of p4 versus that of m1 for the ant mound collection is 1.04 (range = 0.96-1.16), nearest that of *P. trilophus* and *P. spokanensis*, shorter than in *P. validus* and *P. hansonorum* but longer than all other species (Korth, 2013: table 5).

Of the more than 100 referred p4s, fewer than 10 specimens have a remnant of an anterior cingulid. In most, it is a minute cuspule. In a few a short lophid extends lingually but never reaches the lingual border of the protoconid.

The anterior cingulid on the lower molars of the ant mound collection is always attached at the labial end to the anterolabial side of the protoconid (Figure 28J). This is generally the case for most species of *Paradjidaumo* but is not continuous on *P. disjunctus* (Korth, 2013).

Discussion—*Paradjidaumo patriciae* is referable to this genus because of its mesodonty and "omega" pattern of the cheek teeth, diagnostic of the genus (Burke, 1934). *P. patriciae* differs from: 1) *P. trilophus* in slightly being smaller, with lower-crowned molars (Korth, 1980, 2013); 2) from *P. disjunctus* with higher-crowned cheek teeth and continuous anterior cingulid and p4 relatively longer versus m1 (Korth, 2013); 3) from *P. nanus* in being larger, with higher-crowned cheek teeth, continuous anterior cingulid on the molars, and p4 relatively longer versus m1 (Korth and Emry, 2013a); 4) similar size and crown-height to *P. hansonorum* but p4 relatively shorter (versus m1) with continuous anterior cingulid on m1-m2 in little-worn specimens (Storer, 1978; Korth and Emry, 2013a); 5) markedly smaller with slightly lower crowned molars than *P. spokanensis* (White, 1954; Korth, 2013); 6) markedly smaller and lower crowned molars than *P. validus* with p4 relatively shorter versus m1 (Korth, 1980); 7) differs from *P. obritschorum* in being larger with lower crowned m1-m2, and a proportionally longer p4 versus m1 (Korth et al., 2019b); 8) differs from *P. reynoldsi* and *P. alberti* (referred to the subgenus *Macroadjidaumo*) in being larger with lower crowned molars, m1 and m2 wider than long (longer than wide in *P. reynoldsi* and *P. alberti*), and p4 relatively longer versus m1 (Russell, 1954; Kelly, 1992, 2010; Korth, 2013). *P. patriciae* differs from *Orelladjidaumo* in having upper teeth wider relative to length with no pronounced unilateral hypsodonty of the latter (Korth, 1989a; Korth and Tabrum, 2017).

Specimens of *P. patriciae* have been recovered from all ant mounds sampled in this study. There is no

difference in the morphology or size of the specimens from ant mounds situated at different stratigraphic levels (Table 27).

Paradjidaumo sp., cf. *P. validus* Korth, 1980
(Figure 28K-O; Table 28)

Referred Specimens—SDSM 150992, 154624, 154686, P4; SDSM 154949, 154958, 154706, M1 or M2; SDSM 154437, left p4; SDSM 154323, 154348, 154481, 154747, 154850, m1 or m2; SDSM 154534, right m3.

Localities—Recovered from ant mounds 3, 4, 6, 9, and 12 below the UPW; ant mound 14 on the UPW; ant mounds 8, 10, and 17 above the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Description—Specimens from the Sioux County collection of this species were separated from those of *P. patriciae* based on their larger size and slightly higher crowned lower molars. P4 differs from those of other species in having the protoloph as wide as the metaloph (protoloph narrower in other species). Only one of the three referred P4s, SDSM 154686, is little worn (Figure 28K). On this specimen there is no anterior cingulum but there is a distinct parastyle anterior to the center of the paracone and the posterior cingulum runs labially from the posterolabial corner of the hypocone, curves slightly anteriorly, then the labial end fuses anteriorly with the base of the metacone even with the apex of that cusp. The mesoloph extends the full width of the tooth on all specimens. The only referred upper molar, SDSM 154706, does not differ markedly from those referred to *P. patriciae* except in its larger size (Figure 28L). The mesoloph extends to the labial border of the tooth where it fuses with the paracone.

The referred p4, SDSM 154437, is distinctively larger than any referred to *P. patriciae* (Tables 27, 28). As in the holotype of *P. validus* (Korth, 1980: text-fig. 2A), there is an anterior cingulid running lingually from the anterior margin of the protoconid. Unlike the holotype, however, it extends to the center of the anterior margin of the metaconid, enclosing a small, ovate trigonid basin (Figure 28M). The posterior cingulid is short and fuses lingually with the entoconid.

The m1 or m2 differs little from those of other species (Figure 28N). The anterior cingulid is always fused with the protoconid even on unworn specimens and the mesolophid always extends to the lingual margin of the tooth. The posterior cingulid differs from that of the holotype (Korth, 1980: text-fig. 2A) in being relatively longer and never fusing with the posterolabial corner of the entoconid. Instead, the posterior cingulid is free lingually on little to moderately worn specimens and relatively longer as in other species. The crown height index of the referred molars averages 0.33 (range 0.29-0.39), slightly lower than in the holotype (Korth, 2013: table 1).

The referral of an m3, SDSM 154534 (Figure 28O), is done so based on its similar size and crown height to the anterior molars. In occlusal outline, it is flattened anteriorly and rounded posteriorly. The hypolophid is slightly narrower than the trigonid. The tooth is moderately worn so most of the trigonid basin is worn away leaving only a small oval basin near the anterolingual corner of the tooth. There is no evidence of a mesolophid. The hypolophid runs posterolingually from the posterior end of the endolophid to the center of the entoconid. There is a slight swelling of the hypolophid near its labial end before joining the entoconid. The hypoconid is continuous with a broad, posteriorly convex posterolophid that tapers lingually, ending in a minute connection with the posterolabial corner of the entoconid. There is a slight swelling of the wear facet on the anterior side of the posterolophid just before reaching the entoconid.

Discussion—Previously, only two specimens of *Paradjidaumo validus* have been identified (Korth, 1980, 1989a). Other than its larger size, this species was diagnosed as having a distinct anterior cingulid on p4, an anteroposterior oriented lophid connecting the mesolophid with the hypolophid on m2, a relatively elongated p4, reduced posterior cingulids on the molars, and higher crowned cheek teeth (Korth, 1980, 2013).

The ant mound specimens are distinct from those referred above to *P. patriciae* from the Sioux County ant mounds based on their much larger size, higher crown height of the lower molars, and protoloph equal to the metaloph on P4. However, they differ from the holotype of *P. validus* in lacking the accessory transverse lophule (or its remnant) on m1 or m2 and having longer and lingually free posterior cingulids (Figure 28N; Korth, 1980: fig. 2A). In addition, the lower molars appear to be slightly lower crowned than in the holotype. However, the ratios of the holotype and that of the ant mound collection overlap (type = 0.32-0.38; ant mound specimens = 0.29-0.39).

The holotype and original referred specimen are from Sioux County, both from the Orella Member (Korth, 1980; 1989a). Specimens in this study were recovered from ant mounds situated below and above the UPW2.

Genus *Centimanomys* Galbreath, 1955
Centimanomys major Galbreath, 1955
(Figure 29; Table 29)

Referred Specimens—SDSM 154921 left dP4; SDSM 154918, right M1 or M2; SDSM 155774, right dp4; SDSM 152429, 154920, 154923, m1; SDSM 154917, 154919, 154924, m2; SDSM 152428, 154922, m3.

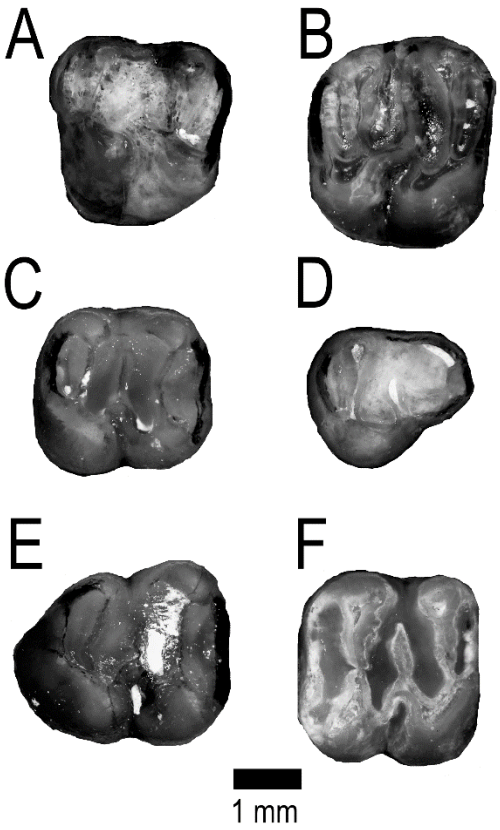

FIGURE 29. *Centimanomys major* from the ant mound collection from Sioux County, Nebraska. A, SDSM 154921, left dP4. B, SDSM 154918, right M1 or M2. C, SDSM 152429, 152429, right m1. D, SDSM 155774, right dp4. E, SDSM 154922, right m3. F, SDSM 154917, left m2. All figures to same scale.

Localities—Recovered from ant mounds 3, 4, and 6 below the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Description—All the upper cheek teeth are quadrate and low crowned; the lingual half is only slightly higher crowned. The overall occlusal pattern is typical of eomyids. The lophs on the referred M1 or M2, SDSM 154918 (Figure 29B) are thin and long, the cusps relatively small. There are five distinct transverse lophs; anterior cingulum, protoloph, mesoloph, metaloph, and posterior cingulum. The labial cusps (paracone and metacone) are of similar size to one another; relatively small and slightly anteroposteriorly compressed and at the labial margin of the tooth. The lingual cusps are obliquely compressed (posterolabial-anterolingual). The anterior cingulum originates at the anterolabial corner of the protocone and appears to extend labially to the anterolabial margin of the tooth. A small chip of enamel has broken away from the anterolabial corner of the tooth, so the labial end of the anterior cingulum is not complete. The protoloph runs from the lingual center of the paracone to the anterolabial corner of the protocone, just posterior to the origin of the anterior cingulum. There is no indication of a protoconule. The metaloph is similarly arranged, running parallel to the protoloph from the metacone to the anterolabial corner of the hypocone. The endoloph originates at the posterolabial corner of the protocone, extends posterolabially, then is redirected posterolingually, joining the anterolabial corner of the hypocone. The mesoloph arises from the center of the endoloph (its most labial point) and extends to the labial edge of the tooth. The labial end of the mesoloph is connected to the posterolabial corner of the paracone by a slightly curved anteroposteriorly oriented loph (?partial ectoloph). The posterior cingulum runs labially from the posterolabial corner of the hypocone along the posterior margin of the tooth, ultimately joining the posterolabial corner of the metacone.

SDSM 154921 is identified as a dP4 of this species because of its similar size and morphology to the referred upper molar but thinner enamel (Figure 29A). The differences in occlusal morphology relative to the molar are: anterior cingulum shorter (only about half the width of the tooth) and ending labially before reaching the paracone; mesoloph shorter, extending only halfway to the labial border of the tooth; cusps of the protoloph (protocone, paracone) slightly smaller than the cusps of the metaloph; and endoloph ends at the lingual base of the mesoloph (not continuous to protocone). A partial ectoloph runs posteriorly from the paracone and ends posteriorly at a small mesostyle at the center of the labial border.

A single specimen, SDSM 155774 (Figure 29D), is identified as a dp4. As with dP4, it has thinner enamel than the referred molars and is slightly smaller relative to the molars. It is markedly narrower anteriorly than posteriorly. The trigonid is small and circular in outline, blocked posteriorly by a short metalophulid II and open anteriorly as a narrow valley. The metaconid is slightly larger than the protoconid and obliquely compressed, whereas the protoconid is triangular in occlusal outline. There is a distinct ridge running posteriorly from the metaconid along the lingual edge of the tooth (metastylid crest) that ends just anterior to the entoconid. Labially the ectoloph is short and runs diagonally from the protoconid to the anterolingual corner of the hypoconid with a slight lingual bend at its center at the base of the mesolophid. The mesolophid crosses slightly more than half the talonid and does not reach the lingual border of the tooth. The hypoconid is an obliquely compressed (anterolingual-posterolabial) crescent. The hypolophid extends labially from the entoconid but angles posterolabially, joining the hypoconid at its posterolingual point where there is a minute cuspule (?hypoconulid). The posterior cingulid wraps around the

posterior margin of the tooth, ending at the posterolabial corner of the entoconid.

The m1 can be separated from m2 by the proportions of the teeth; m1 is longer than wide and m2 is wider than long (Table 29). The m1 and m2 of *Centimanomys* have been described in detail elsewhere (Galbreath, 1955; Martin and Ostrander, 1986; Korth, 2012).

As for m1 and m2, m3 is similar to that previously described for this species (Figure 29E; Galbreath, 1955; Martin and Ostrander, 1986). It is narrower posteriorly than anteriorly. The anterior half of the tooth is like that of the anterior molars except the mesolophid ends at the posterolabial base of the metaconid rather than extending to the lingual margin of the tooth. The hypoconid and entoconid are smaller than the trigonid cusps. The hypolophid is strongly convex posteriorly, ending labially at the posterolingual corner of the hypoconid. The posterior cingulid is as in the anterior molars but is strongly bowed posteriorly.

Discussion—No upper cheek teeth have previously been referred to *Centimanomys*. The two specimens referred here are done so based on their general eomyid-like morphology, low crown height, elongated transverse lophs, reduced cusps, and comparable size to the referred lower molars. The specimens from Sioux County are similar in size to those of all specimens previously referred to *C. major* (=*C. galbreathi* Martin and Ostrander, 1986) and are smaller than those of *C. gigantus* (Table 29; Korth, 2012: table 1). Besides size, the ant mound specimens differ from *C. gigantus* in lacking the low anteroposterior lophid in the talonid of p4 and m1 of the holotype of that species (Korth 2012: fig. 2B).

All previously reported specimens of *Centimanomys* have been from the Chadronian of northeastern Colorado (Wood, 1980; Korth, 1994c, 2012; Flynn, 2008a). All specimens referred here to *C. major* were recovered from ant mounds below the UPW, consistent with the previously known record.

Aulolithomys Black, 1965
Aulolithomys vexilliames Korth and Emry, 1997
(Figures 30A-D)

Referred Specimens—SDSM 154946, left P4; SDSM 154939, right M1 or M2; SDSM 155693, right p4; SDSM 154950, 154957, m1 or m2.

Localities—Recovered from ant mounds 6 and 15 below the UPW; ant mound 11 above the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Measurements—P4: SDSM 154946, L = 1.22 mm, W = 1.45 mm; M1 or M2: SDSM 154939, L = 1.36 mm, W = 1.39 mm; p4: SDSM 155693, L = 1.07 mm, W = 1.03 mm; m1 or m2: SDSM 154950, L = 1.37 mm, W = 1.58 mm; SDSM 154957, L = 1.14 mm; W = 1.38 mm.

Discussion—The morphology of the cheek teeth of *Aulolithomys vexilliames* have been described in detail elsewhere (Korth and Emry, 1997). The specimens referred here from the Sioux County ant mounds do not differ in morphology from the topotypic material from the Chadronian of Wyoming. One specimen of m1 or m2, SDSM 154950, has a slightly greater width than any in the topotypic collection (Korth and Emry, 1997: table 1) but not significantly so.

Aulolithomys sp., cf. *A. bounites* Black, 1965
(Figures 30E-I; Table 30)

Referred Specimens—SDSM 154948, P4; SDSM 152427, 154947, 154952, 154954, 154955, 154956, M1 or M2; SDSM 154938, 154940, 154941, 154944, p4; SDSM 154931, 154932, 154934, 154935, 154936, 154937, 154943, 154945, 154951, 155694, m1 or m2; SDSM 154933, 154942, m3.

Localities—Recovered from ant mounds 2-6, 12, and 16 below the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Description—P4 is square in occlusal outline and similar to that previously described for the Texas specimen (Figure 30E; Wood, 1974: fig. 32A). The only difference is that the Sioux County specimen has a slightly longer anterior cingulum but it is still limited to the anterolabial corner of the tooth and there is no indication of a mesoloph or mesocone. The anterior arm of the hypocone meets the posterior arm of the protocone near the center line of the tooth.

M1 or M2, again, are similar to that of the specimen from Texas (Figure 30F; Wood, 1974: fig. 32A) but differ in the presence of a distinct mesoloph. The mesoloph is short on the ant mound specimens, never approaching the labial margin of the tooth.

The only difference between the p4 of the ant mound specimens and those previously described for *A. bounites* (Black, 1965) is that the trigonid is not always closed anteriorly, remaining open on some of the specimens (Figure 30G). The lower molars do not differ from those described elsewhere other than by size.

Discussion—The specimens from the Sioux County ant mounds do not differ significantly in morphology from those previously described from Montana or Texas (Black, 1965; Wood, 1974). In size, the ant mound fossils best match the Texas collection (Table 30; Wood, 1974: tables 13, 14), and are slightly smaller than the topotypic material from Montana (Black, 1965: 38) but markedly larger than the specimens from Sioux County referred above to *A. vexilliames* (Table 30). All specimens referred here to *A.* cf. *bounites* are from ant mounds on the Chadron Formation.

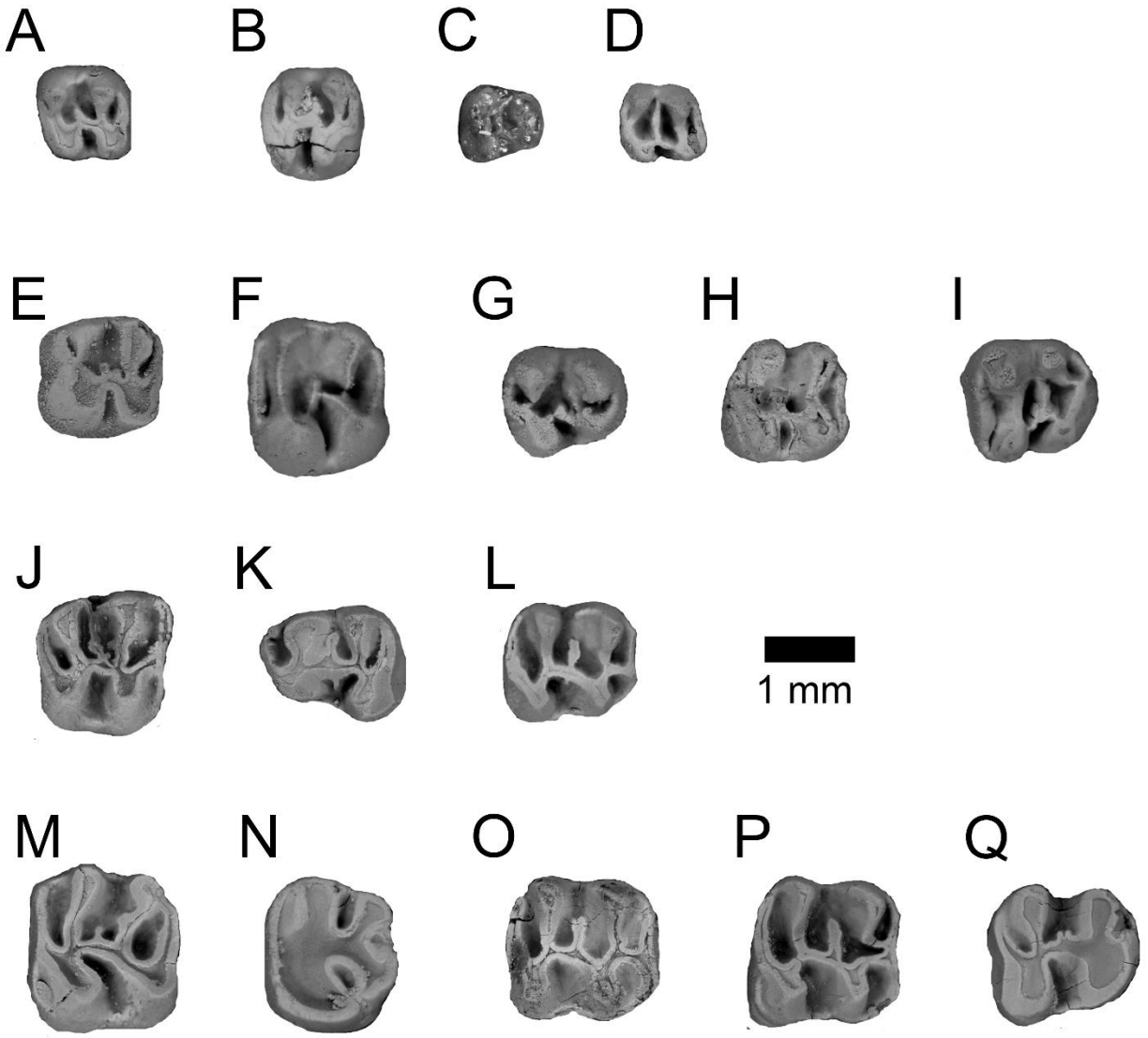

FIGURE 30. *Aulolithomys*, *Yoderimys*, and *Litoyoderimys* from the ant mound collection from Sioux County, Nebraska. A-D, *A. vexilliames*. A, SDSM154946, left P4. B, SDSM 154939, right M1 or M2. C, SDSM 155693, right p4. D, SDSM 154957, right m1 or m2. E-I, *A. bounites*. E, SDSM 154948, left P4. F, SDSM 154952, left M1 or M2. G. SDSM 154938, right p4. H. SDSM 154935, right m1 or m2. I, SDSM 154942, left m3. J-L, *Yoderimys massarae*. J, SDSM 154961, right M1 or M2 (syntype). K, SDSM 154967, left p4 (syntype). L, SDSM 154968, right m1 or m2. M-N, *Litoyderimys grossus*. M, SDSM 154959, left M1 or M2. N, SDSM 154962, left M3. O, SDSM 154966, right m1 or m2. P, SDSM 154970, right m1 or m2 (syntype). Q, SDSM 154969, right p4 (syntype). All figures to same scale.

Subfamily Yoderimyinae Wood, 1955
Genus *Yoderimys* Wood, 1955
Yoderimys massarae n. sp.
(Figures 30J-K; Table 31)

Syntype Specimens—SDSM 154961, right M1 (Figure 30J); SDSM 154967, left p4 (Figure 30K).

Referred Specimens—SDSM 152430, 154960, 154963, 154964, 154965, M1 or M2; SDSM 154968, right m1 or m2.

Diagnosis—Near size of *Yoderimys bumpi*, smaller than all other species; cheek teeth less lophate than other species; ectoloph on upper molars more weakly developed (variably complete) with unmodified metacone; prominent anterior cingulid on p4 continuous with protoconid.

Etymology—Matronym for J. A. Massare; provost of Rochester Institute of Vertebrate Paleontology.

Localities—Recovered from ant mounds 1, 3, 4, and 6 below the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Description—The only upper dentitions known are M1 or M2s, and no distinction can be made between them. They are nearly square in occlusal outline (Figure 30J) being only slightly wider than long and are generally similar to those described for other species (Wood, 1955; Emry and Korth, 1993). The degree of lophodonty is slightly less than other species of the genus. The labial half of the anterior cingulum originates at the labial border of the tooth anterior to the paracone, then extends lingually ending at the anterior arm of the protocone. The anterior cingulum then continues along the base of the crown around the anterolingual base of the tooth, ending at the anterolingual margin of the protocone. The labial cusps (paracone, metacone) are small, anteroposteriorly compressed labial ends of the protoloph and metaloph, respectively. The protocone is directly lingual to the paracone and is flattened obliquely (anterolabial-posterolingual). The protoloph runs directly lingually from the paracone and joins the labial end of the posterior arm of the protocone near the center of the tooth. A low ectoloph runs directly posteriorly from the posterior margin of the paracone to the center of the labial edge of the tooth. On SDSM 154960, it ends at this point but is continuous with the mesoloph. On all other specimens the ectoloph has a sharp labial bend and is continuous to the anterior margin of the metacone. The mesoloph is always continuous with the ectoloph. The endoloph is short, near the center of the tooth, and runs directly posteriorly from the posterolabial arm of the protocone to the anterolabial arm of the hypocone. A minute mesocone is present at the junction of the endoloph and mesoloph. The metaloph parallels the protoloph from the metacone to the anterolabial corner of the hypocone. The hypocone is crescentic in occlusal outline. A minute labial cingulum is present at the base of the crown between the protocone and hypocone. The posterior cingulum arises from the posterolabial arm of the hypocone and runs lingually along the posterior margin of the tooth to the posterolabial corner, ending near the posterior base of the metacone.

The isolated p4, SDSM 154967 (Figure 30K), is referred to this species because of its *Yoderimys*-like morphology and similar size to the referred lower and upper molars. The p4 is narrowest anteriorly, tapering nearly to a point. The metalophid is slightly narrower than the hypolophid. There is a minute cuspid low on the crown directly anterior to the apex of the metaconid. Labial to it is a slightly larger swelling (anterostylid) that is continuous with the anterior cingulid that rises labially and slightly posteriorly and ultimately joins the anterolingual corner of the apex of the protoconid. The protoconid is crescentic and positioned slightly more anterior than the metaconid. The metalophulid II runs from the posterior margin of the protoconid to the posterolabial corner of the metaconid. The ectolophid is in the center of the tooth and oriented directly anteroposteriorly meeting the posterior wall of the metalophid II just labial to its center anteriorly and the center of the hypolophid posteriorly. A mesolophid extends lingually from the center of the ectolophid but ends well short of the lingual border of the tooth. The hypoconid and entoconid are transversely oriented ovals. The hypolophid extends labially from the entoconid and meets the ectolophid just anterior to its junction with the anterolingual corner of the hypoconid. The posterior cingulid is posteriorly bowed, extending from the posterolingal corner of the hypoconid and ending lingually by rising to join the apex of the entoconid.

The only referred lower molar, SDSM 154968 (Figure 30L), is similar in morphology to those of other species of the genus. The mesolophid is moderately long, transversely oriented, and extends for about half the distance from the ectolophid to the lingual margin of the tooth as in *Y. stewarti* and *Y. yarmeri* (Storer, 1978: figs. 8F-L; Wilson and Runkel, 1991: fig. 7; Emry and Korth, 1993: figs. 1.9-1.11) and not short and separate from the ectolophid and slightly oblique as in *Y. bumpi* (Wood, 1955: fig. 1A, C; Emry and Korth, 1993: figs. 1.15, 1.16). All other features are as described for other species.

Discussion—*Yoderimys massarae* is smaller than all other species of the genus except *Y. bumpi* (Table 31; Wood, 1955: 523; Storer, 1978: 39; Wilson and Runkel, 1991: table 9; Emry and Korth, 1993: table 1). It differs from all other species in the presence of a prominent anterior cingulid on p4 (=anterior arm of protoconid). The cheek teeth are less lophodont than in other species and the ectoloph on the upper molars is weakly developed, similar to that of other species of *Yoderimys* but the metacone is not modified (obliquely compressed) as in other species (Wood, 1955: fig. 8D; Storer, 1978: fig. 8 A, B; Emry and Korth, 1993: fig. 3).

Yoderimys massarae differs from *Zemidontomys* in having much less lophate and lower crowned cheek teeth with a complete ectoloph on the upper molars (Black, 1965; Emry and Korth, 1993). Species of *Litoyoderimys* have a similar degree of lophodonty to *Y. massarae* but lack the ectolophid on the upper molars (Wilson and Runkel, 1991; Emry and Korth, 1993). *Y. massarae* also differs from both of these genera with the presence of the anterior cingulid on p4.

All specimens of *Y. massarae* are from ant mounds below the UPW, echoing the occurrence of all other previously described species of the genus that are restricted to the Chadronian (Flynn, 2008a).

Genus *Litoyoderimys* Emry and Korth, 1993
Litoyoderimys grossus n. sp.
(Figures 30M-Q; Table 31)

Syntype Specimens—SDSM 154969, right p4 (Figure 30Q); 154970, right m1 or m2 (Figure 30P).

Referred Specimens—SDSM 154959, left M1 or M2; SDSM 154962, M3; SDSM 154966, right m1 or m2.

Diagnosis—Largest species of the genus; anterior cingulid better developed on lower molars than other species (more strongly attached to metalophid and variably doubled); p4 lacking anteroconid; mesolophid on lower molars longer and more distinct than in other species.

Localities—Recovered from ant mound 3 below the UPW; ant mound 14 on the UPW; ant mound 18 above the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Etymology—Latin, *grossus*, large.

Description—The referred M1 or M2, SDSM 154959, differs only in being larger than any reported for either of the known species (Table 31; Wood, 1974: table 15; Emry and Korth, 1993: 1056). It lacks the complete ectoloph of *Yoderimys* and labial connection of the mesoloph to the paracone in *Zemidontomys* (Figure 30M).

M3 has not been described for *Litoyoderimys*. The specimen from the ant mounds (SDSM 154962) is referred to this taxon based on similar size to the anterior molar (Table 31) and similarity to M3 of other yoderimyines (Figure 30N). It is nearly square in occlusal outline, being only slightly wider than long. It is heavily worn but it is evident that there was an anterior cingulum at least at the labial end. The wear facet for paracone is rectangular in occlusal outline and continuous lingually to the large crescentic wear facet for the protocone that extends posteriorly to the posterolingual corner of the tooth. There remains a small metacone, metaloph, and a slightly larger hypocone along the posterior margin of the tooth just labial to the protocone.

As with the upper molars, p4 does not markedly differ from that of other *Litoyoderimys* in the reduction of the trigonid and anteroconid relative to other yoderimyines (30Q). On lower premolars of *L. lustrorum* (p4) and *L. auogoleus* (dp4) there is a distinct anteroconid along the center of the anterior margin of the tooth enclosing a minute trigonid basin (Wood, 1974: fig. 35D; Emry and Korth, 1993: fig. 7.5). The referred p4 from the ant mounds is larger and there is no recognizable anteroconid. There is only a minute lophid at the anterolingual corner of the protoconid with a short, low anterior cingulid extending lingually from the base of its anterolingual corner.

The lower molars differ from those of other species of *Litoyoderimys* in being larger and having a slightly longer and more transversely oriented mesolophid. On the syntype, SDSM 154970 (Figure 30P) there is a double connection of the protolophid to the anterior cingulid. Short spurs extend anteriorly from the anterolabial corner of the metaconid and anterolingual corner of the protoconid that join the anterior cingulid.

Discussion—The Sioux County ant mound specimens referred to *Litoyoderimys* are similar to those previously described for other species of the genus (Wood, 1974; Emry and Korth, 1993). The ant mound specimens are referable to this genus based on: 1) having no ectoloph or modification of metacone on upper molars as in *Yoderimys*; 2) less lophate cheek teeth than *Zemidontomys*; and 3) a reduced trigonid on p4. Specimens of *L. grossus* are slightly larger than those previously described for species of *Litoyoderimys* (Table 31). The referred p4 completely lacks an anteroconid that is present on other species and one of the lower molars has a double connection of the metalophid to the anterior cingulid not known for any yoderimyine.

One of the specimens referred here to *Litoyoderimys grossus* is from an ant mound situated above the UPW (SDSM 154969) while the remainder are from ant mounds below the UPW. No other recognized species of yoderimyines have been reported from later than the Chadronian (Wood, 1980; Korth, 1994c; Flynn, 2008a).

Family Pipestoneomyidae Korth and Emry, 2013b
Pipestoneomys Donahoe, 1956
Pipestoneomys pattersoni Alf, 1962
(Figure 31; Table 32)

Referred Specimens—SDSM 154927, 154928, 154930, P4; SDSM 154929, left M2; SDSM 154926, 156973, right p4; SDSM 154925, left m1.

Localities—Recovered from ant mounds 3, 4, and 6 below the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Discussion—The cheek teeth of *Pipestoneomys* have been described in detail elsewhere (Donahoe, 1956; Black, 1965; Alf, 1962; Korth and Emry, 2013b). The Sioux County ant mound specimens are closer in size to those of *P. pattersoni* than the type species *P. bisulcatus* (Table 32; Korth and Emry, 2013b: tables 1, 2). The ant mound collection also more closely matches *P. pattersoni* in the relative proportions of p4 (narrower) and relative size of the upper molars (smaller).

P. bisculcatus is definitively known only from the Chadronian Pipestone Springs locality in Montana and *P. pattersoni* is limited to the Chadronian of Nebraska. All of the specimens reported here are from ant mounds below the UPW. West and Korth (1994)

reported a single p4 referable to *Pipestoneomys* from an ant mound on the Orella Member in Sioux County that may represent a different species.

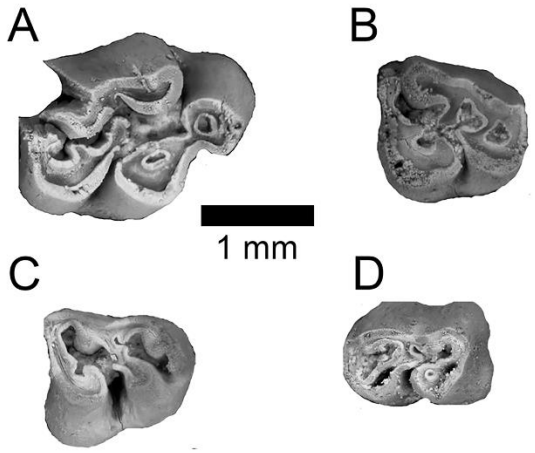

FIGURE 31. *Pipestoneomys pattersoni* from the ant mound collection from Sioux County, Nebraska. A, SDSM 154930, right P4 (broken). B, SDSM 154929, left M2. C, SDSM 154926, right p4. D, SDSM 154925, left m1. All figures to same scale.

Family Heliscomyidae Korth, Wahlert, and Emry, 1991
Genus *Heliscomys* Cope, 1873b
Heliscomys vetus Cope, 1873b
(Figures 32A-C; Table 33)

Referred Specimens—SDSM 137275, 151055, 151076, 151091, maxilla with P4-M3; SDSM 137265, 137270, 137271, 137278, 137288, 151071, 151073, 151079, 151081, 151098, maxilla with P4-M2; SDSM 151070, 151084, 151089, 155512, 155513, maxilla with P4-M1; SDSM 137233, 137256, 137279, 137284, 137285, 137287, 151049, 151054, 151080, 151092, 155524, dentary with i1, p4-m3; SDSM 137293, 151097, dentary with p4-m3; SDSM 137261, 137280, 151078, 151102, 152411, 155520, dentary with i1, p4-m2; SDSM 137272, 151065, 151074, dentary with p4-m2; SDSM 152409, dentary with i1, p4, m2; SDSM 137302, 151083, 152412, 152416, 155527, dentary fragment with i1, p4-m1; SDSM 151059, 151064, 151072, 155521, 155523, 155530, 155532, dentary fragment with p4-m1; SDSM 152404, 152407, 152410, 155526, dentary fragment with i1, p4; 152414, 155522, 155525, dentary fragment with p4.

Localities—Recovered from ant mounds 1, 3-7, 9, 12, and 16 below the UPW; ant mounds 13 and 14 on the UPW; ant mounds 8, 11, 18, and 19 above the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Discussion—The upper dentition of species of *Heliscomys* can be separated into subgenera (*Heliscomys* and *Syphyriomys*) based on the relative width of P4 to M1, the morphology of the lingual cingulum on M1 (continuous or not), and the presence of stylar cusps on the upper molars (Korth, 1995). The specimens from the Sioux County ant mounds referred here to *H. vetus* have an average ratio of length of P4 to M1 of 0.78 (range 0.68-0.88), a continuous lingual cingulum on M1 with a single, central stylar cusp, and continuous labial cingulum on M2 and M3 without any stylar cusps (Figure 32A); all matching the definition of the subgenus *Heliscomys*.

Korth et al. (2019a: table A11) also demonstrated that the length of p4 and its size relative to that of m1 was also significantly different between these subgenera. The specimens referred here to *H. vetus* have p4s that an average length of 0.46 mm (range = 0.40-0.53 mm) and an average p4 to m1 length ratio of 0.59 (range = 0.48-0.70), both much less than the specimens referred below to *H. hatcheri* (Table 33). The specimens of p4 referred here to *H. vetus* are mainly three-cusped (73 percent), whereas those referred below to *H. hatcheri* are four or five-cusped (75 percent). There also appears to be a slight difference in the width of the lower incisor. For those referred to *H. vetus* the width of i1 averages 0.36 mm (range 0.31-0.41; 26 specimens), whereas that of *H. hatcheri* averages 0.40 mm (range 0.32-0.48 mm; 13 specimens).

The measurements of the cheek teeth match that of *H. vetus* reported from other locations (Table 33; Wood, 1933: table 1; Wood, 1935: table II; Wood, 1937: 214; Galbreath, 1953: table 11). Specimens of *H. vetus* are known from nearly all ant mounds sampled in this study. Previously, *H. vetus* is reported from Orellan and Chadronian faunae (Flynn et al., 2008).

Heliscomys hatcheri Wood, 1939
(Figures 32D-E; Table 33)

Referred Specimens—SDSM 137249, 151101, maxilla with P4-M3; SDSM 137237, 137269, 137286, 137291, 137292, 137295, 151050, 151058, 152418, 155507, maxilla with P4-M2; SDSM 137316, 137319, 151062, 151063, 151090, 151099, 152420-15422, 155508-155511, 155518, partial maxilla with P4-M1; SDSM 152423, maxilla fragment with P4; SDSM 152417, maxilla fragment with M1; SDSM 151096, 137281, 137290, 137296, dentary with i1, p4-m3; SDSM 137245, 151057, 151094, dentary with p4-m3; SDSM 137294, 155529, dentary with i1, p4-m2; SDSM 151087, dentary with p4-m2; SDSM 151053, 151088, partial dentary with i1; p4-m1; SDSM 151056, 151093, 152415, partial dentary with p4-m1; SDSM 152408, 152413, 155528, 155531, 155533, dentary with i1, p4.

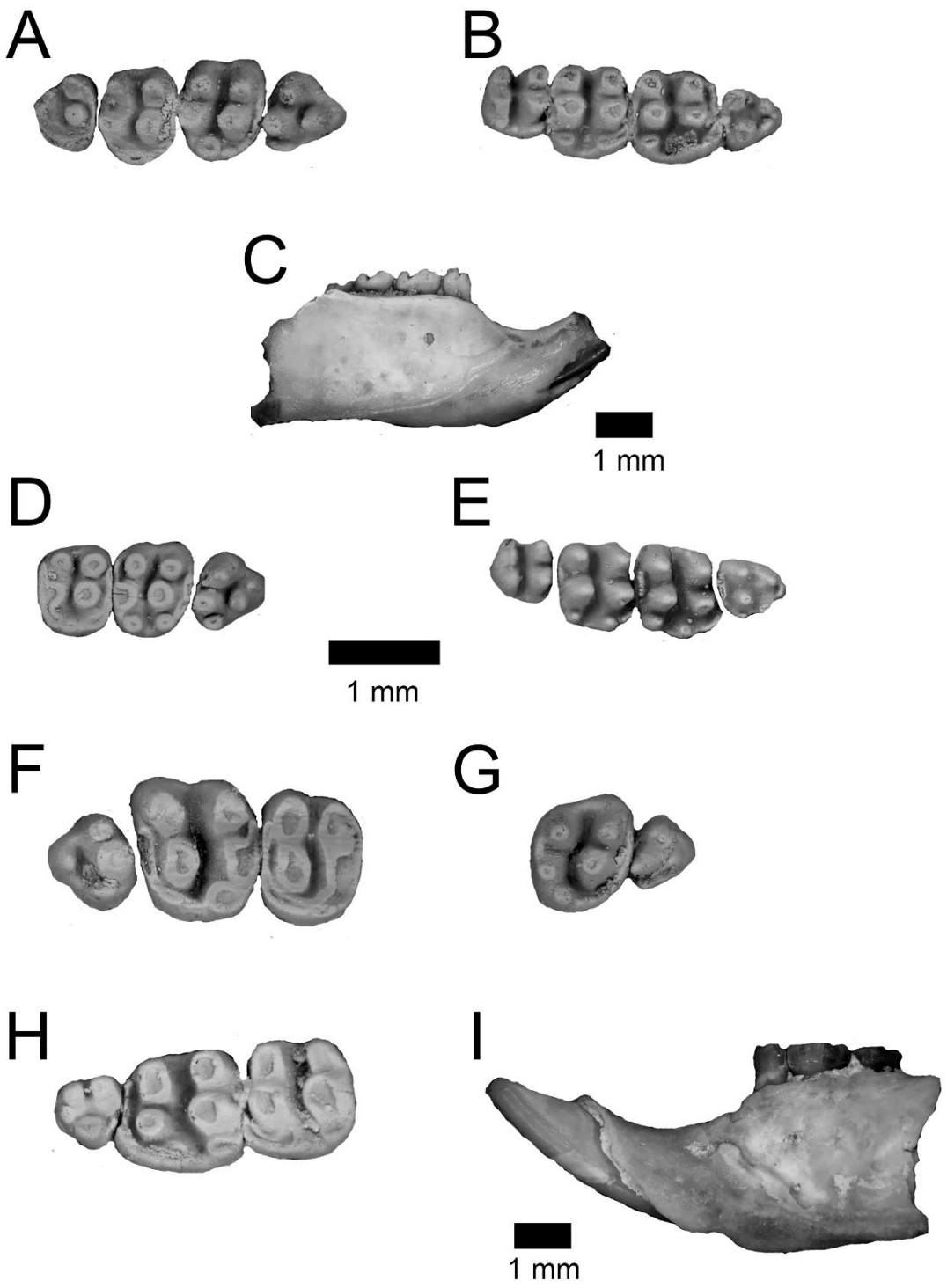

FIGURE 32. *Heliscomys* and *Megaheliscomys* from the ant mound collection from Sioux County, Nebraska. A-C, *H. vetus*. A, SDSM 151091, right P4-M3. B, C, SDSM 151054. B, right p4-m3. C, lateral view of dentary. D, E, *H. hatcheri*. D, SDSM 137269, right P4-M2. E, SDSM right 151057, p4-m3. F-I, *M. mcgrewi*. F, SDSM 152419, left P4-M2. G, SDSM 155516, right dP4-M1. H, I, SDSM 151077. H, left p4-m2. I, lateral view of dentary. All cheek teeth to same scale (center); dentaries (C, I) to different scale (above center, below right).

Localities—Recovered from ant mounds 1-4, 6, 7, 9, 15, and 16 below the UPW; ant mound 14 on the UPW; ant mounds 8, 11, and 17-19 above the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Discussion—The specimens referred here to *H. hatcheri* have all of the features of the premolars and upper molars that are diagnostic of the subgenus *Syphyriomys* (Korth, 1995; Korth et al., 2019a) and are distinguishable from the *H. vetus* specimens by: 1) P4 wider relative to M1 (P4W/M1W, average = 0.86, range = 0.74-0.94); 2) two distinct stylar cusps on M1 (Figure 32D); 3) p4 longer (average = 0.55 mm; range = 0.51-.059 mm); and 4) only 25 percent of the referred p4s are three-cusped (75 percent four or five-cusped). The size of these specimens also matches that of *H. hatcheri* from other localities (Table 33; Wood, 1939: table I). The specimens from the Sioux County ant mounds differ from the Chadronian *H. ostranderi* in having a proportionally larger P4/p4 (Korth et al., 1991: table 1) and stylar cusp on M2 (Figure 32D).

As with *H. vetus*, specimens of *H. hatcheri* have been collected from ant mounds situated below and above the UPW. Previously, this species was reported only from the Orellan and Whitneyan (Wood, 1937; Korth, 1994c; Korth et al., 2019a).

Heliscomys sp.

Referred Specimens—SDSM 137282, 137289, 151060, 152405, 152406, dentary with m1-m3; SDSM 151082, dentary with i1, m1-m2; SDSM 151068, 151100, 155539, 155542, partial dentary with m1-m2; SDSM 155534, 155537, 155540, 155543, dentary fragment with i1, m1; SDSM 152426, 155535, 155536, dentary fragment with m1; SDSM 155541, dentary fragment with m2; SDSM 155538, dentary fragment with m3.

Localities—Recovered from ant mounds 1, 4, 9, 15, and 16 below the UPW; ant mounds 13 and 14 on the UPW; ant mounds 10 and 19 above the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Discussion—Because lower dentitions of *Heliscomys* cannot be identified to species without the presence of p4 (Korth et al., 2019a), those lacking the premolar are listed here as uncertain. These specimens are not likely referable to a third species of *Heliscomys* but are clearly referable to the genus and are of similar size to those of both of the species identified from the Sioux County ant mounds.

Genus *Megaheliscomys* Korth, 2007b
Megaheliscomys mcgrewi (Korth, 1989b)
(Figures 32F-I; Table 34)

Referred Specimens—SDSM 155516, right maxilla with dP4-M1; SDSM 152419, 152424, maxilla with P4-M2; SDSM 151095, left maxilla with P4-M1; SDSM 151066, 155515, maxilla fragment with M1-M2; SDSM 155514, maxilla fragment with M1; SDSM 151077, left dentary with i1, p4-m2; SDSM 151061, left dentary with p4-m1; SDSM 152403, partial dentary with i1, m1-m2; SDSM 151051, left dentary with m1-m2.

Localities—Recovered from ant mounds 1, 3, 4, 6, and 7 below the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Description—The upper dentition of *M. mcgrewi* has been described elsewhere (Korth, 1989b, 2007b, 2019). The only upper cheek tooth not previously described is dP4 which is retained in SDSM 155516 (Figure 32G). It differs from the referred P4s in its smaller size, thinner enamel, and more splayed roots. In overall morphology it is similar to P4 but the central posterior cusp (protocone) is proportionally larger relative to the remaining cusps than in P4. The metacone, paracone, and hypocone are minute cuspules along the base of the enamel situated on the labial, anterior, and lingual sides of the protocone, respectively.

Only the anterior half of the dentary is preserved in any of the specimens referred here (Figure 32I). Morphologically, it does not differ markedly from that described for *Heliscomys* (Korth et al., 1991; Korth and Branciforte, 2007). The depth of the dentary below m1 can be measured on two specimens (SDSM 152403, 151077) and ranges from 2.75-3.30 mm. The diastema is shallow and long. The length of the diastema can be measured on SDSM 151077 (3.21 mm). Although no lower tooth rows are complete from p4-m3 in the collection, the measurement for p4-m2 in SDSM 151077 is only 2.83 mm. It appears that the diastema is very close to the same length as the tooth row and the depth of the dentary. The mental foramen is small and situated just below the dorsal margin of the diastema, just posterior to its center. The masseteric ridge runs anteriorly along the lateral side of the ventral margin of the dentary from below m2, then gently curves anterodorsally, ending posterior to the mental foramen.

The lower incisor is laterally flattened, gently rounded anteriorly, and is much longer than wide in cross-section. Enamel extends dorsally along approximately one-third of the lateral side and slightly less on the medial side. There is no ornamentation of the enamel.

The p4 is markedly smaller than m1 (Table 34), its length averaging 51 percent of that of m1. It is roughly triangular in occlusal outline. On one specimen (SDSM 151601) the p4 has three cusps, on the other, SDSM 151077 (Figure 32H) there is a minute fourth cusp. The talonid consists of two distinct cusps (entoconid, hypoconid) of equal size, aligned transversely. On

SDSM 151077, there is a minute hypoconulid along the posterior margin at the posterolingual corner of the hypoconid. A single large cusp (?metaconid) is along the anterior margin of the tooth, just lingual to its center. On both specimens there is a low ridge that runs posterolabially down the side of the metaconid. There is a minute protostylid low and posterior on SDSM 151077.

The m1 and m2 are similar to those of species of *Heliscomys* consisting of four cusps arranged in two transverse rows and an anterior cingulid that continues around the labial side of the tooth (Figure 32H). There are two distinct stylar cusps (protostylid, hypostylid), separated by a narrow break in the cingulum. The m1 is slightly longer than m2.

Discussion—Previously, the only lower dentition reported for this species was a single isolated m1 or m2 from the Orellan of Montana (Korth, 2019). The specimens referred here are done so based on the comparative size with those of upper molars and the fact that the proportion of the p4 relative to the molars is similar to that of the upper dentition. Although the size of the premolars relative to the first molars is the same as in other species, the measurements of the ant mound collection for the upper molars is slightly less than previously reported for this species but not significantly so (Table 34: Korth, 1989b: table 1; Korth, 2007b: table 1; Korth, 2019: table 9).

Previously, *M. mcgrewi* was reported only from the Orellan (Korth, 1989b, 2007b, 2019). All of the specimens referred here are from ant mounds situated below the UPW.

Family Florentiamyidae Wood, 1936
Genus *Ecclesimus* Korth, 1989b
Ecclesimus tenuiceps (Galbreath, 1948)
(Figures 33A-D; Table 34)

Referred Specimens—SDSM 151085, 155517, maxilla with P4-M2; SDSM 151086 right maxilla with P4-M1; SDSM 155519, left maxilla fragment with M1; SDSM 151067, right dentary fragment with dp4; SDSM 137276, left dentary with i1, p4-m2.

Localities—Recovered from ant mounds 3, 4, 6, and 7 below the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Description—The upper cheek teeth have been described previously (Galbreath, 1948; Korth, 1989b). The paracone on P4 is variable from large to absent. M1 and M2 are quadricuspate with a continuous anterior and lingual cingulum (Figure 33A).

The dentary is relatively deep for the size of the cheek teeth (depth below m1 = 2.66 mm). The diastema is shallow and relatively short, approximately half the length of the cheek tooth row, but cannot be measured with confidence owing to breakage (Figure 33D). The mental foramen is small and relatively high on the dentary but clearly below the dorsal margin of the diastema, lower than in *Heliscomys*. The masseteric fossa consists of a low ventral ridge that rises anterodorsally from a point ventral to m1 and ends posterior and slightly ventral to the mental foramen. There is a faint ridge marking the dorsal margin that arises from the anterior point of the ventral ridge and extends posteriorly to a point ventral to m2. The ridge is slightly bowed ventrally. The lower incisor is narrow in cross-section (L = 0.94 mm; W = 0.52 mm) with a flattened anterior enamel surface.

The p4 is markedly smaller than the molars and nearly square in occlusal outline being only slightly narrower anteriorly than posteriorly (Figure 33C). The trigonid consists of two equal size cusps (protostylid, metaconid) that are separated from one another by a central anteroposterior valley. Similarly, the talonid cusps (entoconid, hypoconid) are equal in size to one another as well as with the anterior cusps, and likewise, are separated from each other by a narrow anteroposterior valley. A central transverse valley separates the metalophid cusps from the hypolophid cusps. It is slightly narrower labially, the protostylid and hypoconid are slightly closer together than the lingual cusps.

The m1 and m2 are nearly identical in morphology and typical of geomyoids with two transverse lophids of two cusps each and two small labial stylids. The anterior cingulid wraps around the anterolabial corner of the tooth, ending in the protostylid.

The dp4 (SDSM 151067; Figure 33B) is referred here because of its similarity to the p4 and the splayed roots indicating that it is deciduous. There are seven identifiable cusps on the occlusal surface, and it is slightly longer than wide. An anterior cusp (anteroconid) is near the anterolingual edge of the tooth. The metalophid consists of two small cusps (metaconid, protostylid) along the lingual and labial sides of the tooth respectively, the metaconid being slightly larger and slightly more posterior. There is no distinct transverse valley. The cusps of the hypolophid are similar in size to one another and slightly larger than the trigonid cusps. The hypoconid is near the center of the tooth, just slightly labial to it. The entoconid is at the posterolingual corner of the tooth. A small, round hypostylid is at the posterolabial corner of the tooth. A minute hypoconulid is at the center of the posterior margin of the tooth.

Discussion—The lower dentition of *Ecclesimus tenuiceps* has not been previously described. The specimens referred here, SDSM 151067, 137276, are done so based on their equivalent size and crown height to the upper cheek teeth. These specimens can be distinguished from specimens referred to *Heliscomys* by their much more molariform dp4 and p4. The teeth of

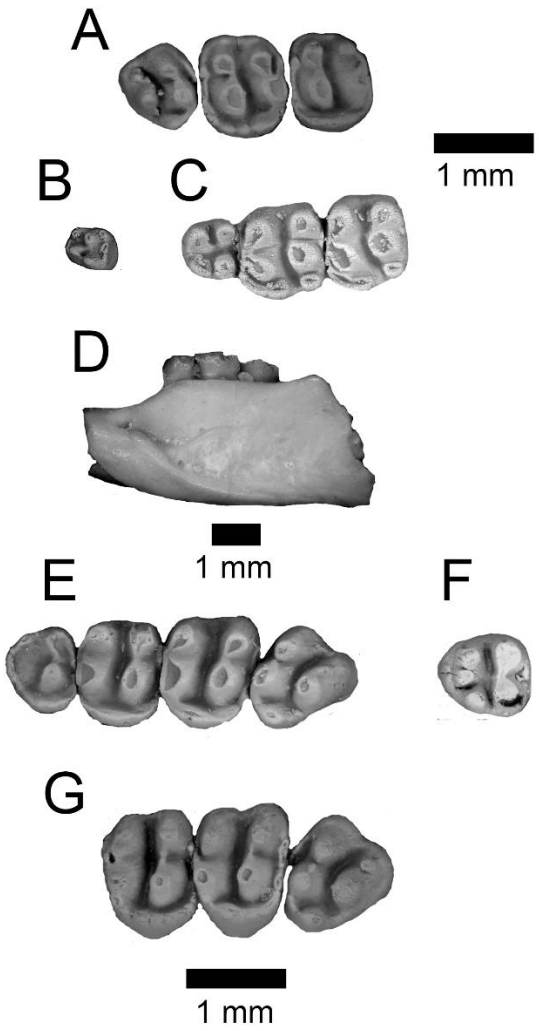

FIGURE 33. *Ecclesimus*, *Kirkomys*, and *Tenudomys* from the ant mound collection from Sioux County, Nebraska. A-D, *E. tenuiceps*. A, SDSM 151085, left P4-M2. B, SDSM 151067, left dp4. C, D, SDSM 137276. C, p4-m3 (occlusal view). D, lateral view of dentary. E-F, *Kirkomys miriamae*. E, SDSM 137301, right P4-M3. F, SDSM 151069, left p4. G, *T. bassilaris*, SDSM 151075, right P4-M2. All teeth to same scale (above and below), dentary to different scale (center).

this species are smaller and lower crowned than those of any species of *Megaheliscomys*, *Kirkomys*, and *Tenudomys* from the ant mound fauna.

Reeder (1960) described two new taxa of geomyoids from the Orellan of Nebraska and Colorado, *Apletotomeus crassus* and *Akmaiomys incohatus*. Both species have low-crowned cheek teeth and a generalized *Heliscomys*-like morphology of the molars. However, they were distinguished from *Heliscomys* by their relatively larger incisors and more molariform p4. Of these species, *A. incohatus* most closely matches the size of the cheek teeth referred here to *E. tenuiceps* (Reeder, 1960: table 2). However, the p4 of *A. incohatus* has a distinct cusp at the center of the anterior margin which is lacking in the referred specimen of *E. tenuiceps* from the ant mound collection.

Specimens of *E. tenuiceps* were recovered from only from ant mounds situated below the UPW. Previously, this species has been reported from the Orella Member, Brule Formation of Sioux County (Korth, 1989b). The holotype is from the Orellan Cedar Creek Member, White River Formation, northeastern Colorado (Galbreath, 1948, 1953).

Genus *Kirkomys* Wahlert, 1984
Kirkomys miriamae n. sp.
(Figures 33E, F; Table 35)

Type Specimen—SDSM 151069, left dentary fragment with p4 (Figure 33F).

Referred Specimens—SDSM 137277, left maxilla with P4-M2; SDSM 137301, right maxilla with P4-M3.

Diagnosis—Smallest species of the genus; P4/p4 more molariform than *K. parvus* (Troxell, 1923) or *K. nebraskensis* (Wood, 1937); protoconid on p4 near size of metaconid, similar to *K. martintau* (Korth, 2008); p4 longer than wide as in *K. parvus*; crown height of p4 similar to that of *K. martintau*, lower than other species.

Localities—Recovered from ant mounds 3 and 6 below the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Etymology—Named for Miriam S. Reading in gratitude for her moral and financial support of WWK for the past 30+ years.

Description—The p4 (SDSM 151069) is in a fragment of the dentary but there is no indication of the depth of the dentary or the morphology of the masseteric crest. The tooth is brachydont, only slightly longer than wide (Table 35), and nearly as wide anteriorly as posteriorly (Figure 33F). The metalophid consists of three cusps. The metaconid is at the anterolingual corner of the tooth. A protoconid of approximately equal size is labial to it and closely appressed to the metaconid, the cusps fusing at their bases. A protostylid is equal in size to the metaconid and is on the labial side of the trigonid separated from the protoconid by a distinct valley and situated slightly posterior to it. A deep transverse valley separates the metalophid from the hypolophid. The posterior half of the tooth consists of equal sized entoconid and hypoconid joined by a complete but narrow hypolophid. Near the center of the posterior margin of the tooth, posterior to the hypolophid, is a small but distinct hypoconulid.

P4 is four-cusped. The protocone is ovate in occlusal outline (anteroposteriorly compressed). There is no indication of a paracone or accessory cuspules (Figure 33E). The metaloph consists of three cusps, the

central (hypocone) is the largest and only slightly anteroposteriorly compressed. The metacone is continuous with the hypocone along the posterior margin of the tooth and only slightly smaller than the hypocone. A small posterior cingulum is posterior to the metacone on both specimens and ends labially posterior to the apex of the metacone. The hypostyle is only slightly smaller than the other cusps of the metaloph but is transversely compressed and blocks the transverse valley on the tooth lingually, causing it to bend anterolingually. The hypostyle is always separated from the protocone by this deep valley.

The M1 and M2 are wider than long and typically separated into two, two-cusped lophs. M1 is slightly larger than M2 (Table 35; Figure 33E). The protoloph consists of the paracone and protocone that are slightly anteroposteriorly compressed. A distinct valley separates the lingual side of the protocone from the lingual cingulum. The anterior cingulum originates along the anterior margin of the tooth even with the apex of the paracone, then proceeds lingually and wraps around the entire lingual border of the tooth, bending around the posterolingual corner and fusing with the apex of the hypocone. It continues slightly more labially before ending posterior to the metacone. There are no distinct stylar cusps along the lingual cingulum but there is a slight swelling along it lingual to the hypocone on SDSM 137277.

M3 is preserved only on SDSM137301 (Figure 33E). It is nearly circular in occlusal outline and smaller than M1 or M2. The protoloph and lingual cingulum are as in the anterior molars. The posterior half of the tooth is greatly reduced, and the only indication of a cusp is a low, round swelling along the posterior cingulum near its center (metaconule).

Discussion—The three specimens referred here are believed to represent a single species based on comparable morphology and size, larger than the specimens of heliscomyids and *Ecclesimus* in the ant mound collection and smaller than specimens of the only other geomyoid identified from this collection, *Tenudomys*. The *Kirkomys* specimens also differ from those of *Ecclesimus* in their more molariform p4 (see above), larger size, higher crowned cheek teeth, P4 longer than M1 (P4 shorter in *Ecclesimus*), p4 longer than wide (wider in *Ecclesimus*), and proportionally wider upper molars (Tables 34, 35).

Kirkomys miriamae is most similar to *Kirkomys martintau* in the morphology of the premolars (more molariform) and crown-height (lower than other species) but is markedly smaller (Table 35; Korth and Branciforte, 2007: table 11). All specimens of *K. miriamae* are from ant mounds situated below the UPW. This is the earliest reported occurrence of this genus. Elsewhere *Kirkomys* is known to range from the Whitneyan to Arikareean (Flynn et al., 2008).

Family ?Entoptychidae Miller and Gidley, 1918
Genus *Tenudomys* Rensberger, 1973
Tenudomys basilaris Korth, 1989b
(Figure 33G; Table 35)

Referred Specimens—SDSM 137273, left maxilla with P4-M3; SDSM 137274, 151075, maxilla with P4-M2; SDSM 152425, 155544, 155545, 155546, P4.

Localities—Recovered from ant mounds 1 and 3 below the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Description and Discussion —The only variation in P4 is the size of the paracone, ranging from completely absent to larger than on the holotype (Korth, 1989b: fig. 1E). The only difference in the upper molars of the referred maxilla versus the holotype is that there is a very short posterior cingulum that extends along the posterior margin of the tooth from the apex of the hypocone to the posterolingual base of the metacone on both M1 and M2 (not present in the holotype [Korth, 1989b: fig. 1E; Korth, 1993: fig. 2G]). The size and proportions of the upper molars (more transversely wide) and greater crown height distinguish these specimens from any of the other geomyoids in the ant mound collection.

All of the specimens referred here are from ant mounds situated below the UPW. The only other reported specimen of this species (holotype KUVP 19474) was recovered from the Orella Member (Orella D) of the Brule Formation in Sioux County (Korth, 1989b: fig. 1E; Korth, 1993: fig. 2G). There are no specimens of lower teeth of appropriate size with a geomyoid morphology in the ant mound collection that are likely assignable to this species.

Geomyoidea family uncertain
Genus *Diplolophus* Troxell, 1923
Diplolophus insolens Troxell, 1923
(Figure 34; Table 36)

Referred Specimens—SDSM 155504, left M2; SDSM 155505, 155506, m1; SDSM 152402, right m2; SDSM 155503, right m3.

Localities—Recovered from ant mounds 5 and 16 below the UPW; ant mound 19 above the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Discussion—Five specimens from the Sioux County ant mounds are clearly referable to *Diplolophus insolens*, the type and only species of the genus, which has been described elsewhere in detail (Troxell, 1923; Wood, 1937; Barbour and Stout, 1939). The uniqueness of the geomyoid-like dental morphology but muroid-like dental formula has made it difficult to assign to a family (Korth, 1994c; Flynn, 2008b). The most recent

suggestion is to refer it to the suborder Myodonta *incertae sedis* along with the similar genus *Nonomys* Emry and Dawson, 1972, in the subfamily Nonomyinae with no designated family (Walsh, 2010).

Previously, *D. insolens* was limited to the Orellan. However Flynn (2008b: fig. 24.3) figured it as occurring as early as the Duchesnean but this earliest occurrence from southern California was later identified as *Nonomys* by Walsh (2010), again limiting the occurrence of *Diplolophus* to the Orellan. However, in this collection specimens were recovered from ant mounds situated both below and above the UPW.

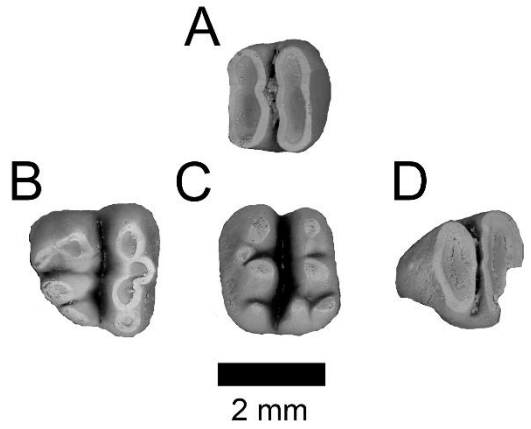

FIGURE 34. *Diplolophus insolens* from the ant mound collection from Sioux County, Nebraska. A, 155504, left M2. B, SDSM 155505, left m1. C, SDSM 152402, right m2. D, SDSM 155503, right m3. All figures to same scale.

Family Cricetidae Fischer de Waldheim, 1817
Genus *Eumys* Leidy, 1856
Eumys elegans Leidy, 1856
(Figures 35A-C; Tables 37, 38)

Referred Specimens—1747 specimens (see Appendix).

Localities—Recovered from all sampled ant mounds. Big Cottonwood Creek Member of the Chadron Formation.

Discussion—The cheek teeth of *Eumys elegans* have been described in detail elsewhere (e.g., Wood, 1937; Galbreath, 1953; Wahlert, 2004; Korth, 2018b), so no further description is offered here. This species has been separated from other species of the genus based on size, relative proportions of the molars, and morphology of the attachment of the metalophid to the anteroconid of m1. In dimensions of the molars the collection from Sioux County differs little from other samples of *E. elegans* (Tables 36, 37; Wood, 1937: 251; Galbreath, 1953: table 14; Korth, 2011, appendix; Korth 2018b: table 1). Wood (1937) named *E. brachyodus* from the Whitneyan and distinguished it from the similar sized *E. elegans* from the Orellan based on the proportions of the molars and connection of the metalophid to the anteroconid on m1. He noted that *E. brachyodus* was slightly larger with relatively wider molars and there was a double connection of the metalophid to the anteroconid on m1. However, it appears that the morphology of the connection of the anteroconid varied doubled in *E. brachyodus* much more frequently than in *E. elegans* (Korth et al., 2019a: fig. 15), evidenced in a different collection of *E. elegans* from the Orellan of Sioux County Nebraska (Korth, 2018b: fig. 6). The collection from the Sioux County ant mounds has distinctly narrower molars than *E. brachyodus* (Table 37; Korth, 2018b: table 5). Although the occurrence of the doubled connection of the anteroconid on m1 is more frequent than in other samples of *E. elegans*, it occurs in only nine percent of the m1s in the Sioux County collection, much less frequently than in samples of *E. brachyodus*, (19-38 percent: see Korth 2018b: fig. 6), more closely matching that of *E. elegans*.

E. elegans was recovered from all sampled ant mounds and was the most common non-lagomorph taxon recovered from all but two of the ant mounds (10 and 18). No differences in the size and morphology were noted between specimens of *E. elegans* recovered from ant mounds situated at different stratigraphic intervals (Tables 36, 37). This species is represented, by far, by the most specimens in the ant mound collections (greater than 1700 specimens) except for perhaps *Palaeolagus haydeni* (see below). Elsewhere *E. elegans* is limited to the Orellan (Wood, 1936; Korth, 2011).

Genus *Scottimus* Wood, 1937
Scottimus lophatus Wood, 1937
(Figures 35D-H; Tables 39, 40)

Referred Specimens—SDSM 152204, left maxilla with M1-M2; SDSM 152200, 152207, maxilla fragment with M2-M3; SDSM 152210, 152228, 154014, 154026, 154040, 154042, 155656, 155657, M1; SDSM 152216, 154048, M2; SDSM 154073, 155661, m1; SDSM 154052, 154057, 154059, m2; SDSM 154063, 154071, 155660, 155662, 155667, m3.

Localities—Recovered from ant mounds 1-4, 6, 7, 12, and 16 below the UPW; ant mound 13 on the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Discussion—*Scottimus* is distinct from the other late Eocene to Oligocene North American cricetids in the presence of anteroposterior connections of the molar cusps and lophs (-ids: Wood, 1936; Lindsay, 2008). There appear to be three species of *Scottimus* in the Sioux County ant mound collection. Specimens of *S. lophatus* can be distinguished from the other species present in: 1) being larger than other species (Tables 39, 40); 2) the posterior reentrant on the anterocone of M1

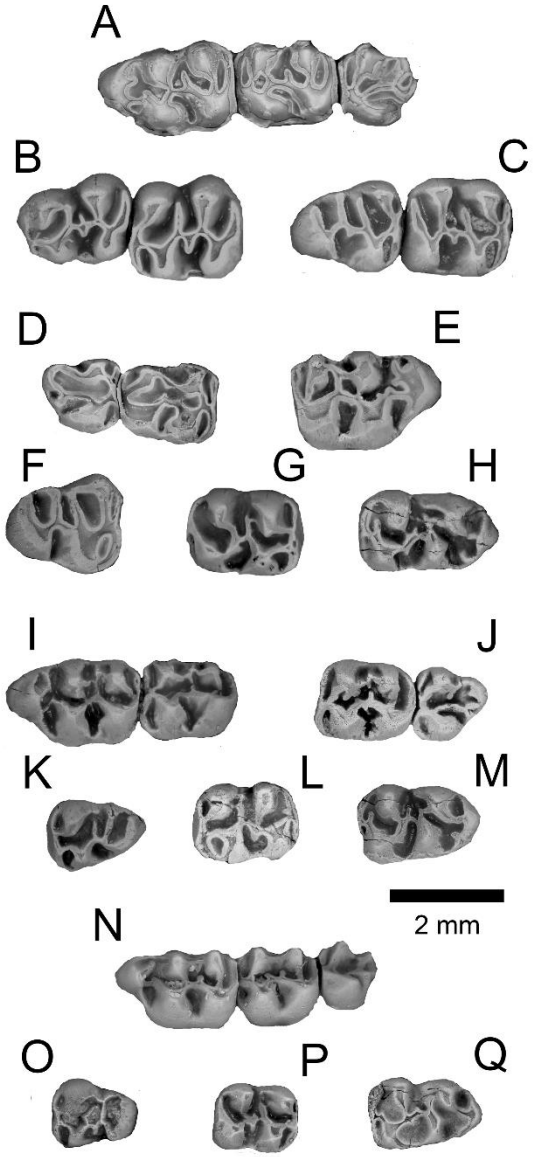

FIGURE 35. *Eumys* and *Scottimus* from the ant mound collection from Sioux County, Nebraska. A-C, *E. elegans*. A, SDSM 151995, left M1-M3. B, SDSM 151184, left m1-m2. C, SDSM right 151909, m2-m3. D-H, *S. lophatus*. D, SDSM 152207, right M2-M3. E, SDSM 152210, right M1. F, SDSM154063, right m3. G, SDSM 1154052, right m2. H, SDSM 155661, right m1. I-M, *S. exiguus*. I, SDSM 152209, left M1-M2. J, SDSM 152214, left M2-M3. K, SDSM 154056, left m3. L, SDSM 154064, left m2. M, SDSM 155666, right m1. N-Q. *S. ambiguus*. N, SDSM 152224, left M1-M3. O, SDSM 154058, left m3. P, SDSM 154060, right m2. Q, SDSM 155669, right m1. All figures to same scale.

is minute to absent; 3) the ectoloph on upper molars strongly angled (anterolingual to posterobuccal); 4) mesoloph on upper molars reduced or absent; and, 5) mesolophids lacking or greatly reduced on lower molars (Figures 35D-H).

Specimens of *S. lophatus* were recovered from ant mounds situated on or below the UPW. However, previously the record of this species was limited to the Whitneyan (Wood, 1936, 1980; Korth, 1994b; Lindsay, 2008).

Scottimus exiguus (Wood, 1937)
(Figures 35I-M; Tables 39, 40)

Referred Specimens—SDSM 137255, maxilla with M1-M3; SDSM 137258, 152205, 152209, 152212, 152233, 154012, maxilla with M1-M2; SDSM 152203; 152214, 152219, 153988, maxilla with M2-M3; SDSM 152213, 152220, 152223, 152231, 152232, 152234, 153989, 153990, 153995, 154001, 154011, 154013, 154016, 154018, 154025, 154030, 154034-154036, 154038, 154039, 154043, 154044, 154046, 154049-154051, 154087, 155654, 155358, 155658, M1; SDSM 152201, 152208, 153984, 153991, 153993, 153996, 154000, 154003, 154006-154008, 154010, 154015, 154019, 154020, 154023, 154024, 154027, 154028, 154033, 154037, 154041, 154047, 155655, 155659, 155672, M2; SDSM 153992, 153999, 154002, 154009, 154076, 154096, 155757, M3; SDSM 152178, 152182, partial dentary with m2-m3; SDSM 154054, 154068, 155666, m1; SDSM 154053, 154061, 154062, 154064, 154065, 154069, 154072, 154074, 154075, 155664, 155665, 155671, m2; SDSM 152199, 154056, 154066, 154070, 155668, m3.

Localities—Recovered from ant mounds 1-6, 9, 12, 15, and 16 below the UPW; ant mounds 13 and 14 on the UPW; ant mounds 8, 17, and 19 above the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Discussion—The dentition of *Scottimus exiguus* has been described elsewhere (Wood, 1936; Korth, 1981). Specimens referred here to *S. exiguus* are smaller than those of *S. lophatus* and larger than those of *S. ambiguus* in the ant mound collection (Tables 39, 40). Other than size, the specimens of *S. exiguus* differ from the other species of the genus in having: 1) a greater degree of lophodonty than in *S. ambiguus* and less than in *S. lophatus*; 2) the ectoloph diagonal with slight emargination on the posterior paracone on M1-M2 (not as great as *S. lophatus*, absent in *S. ambiguus*); and, 3) the posterior re-entrant on the anterocone of M1 smaller in size than in *S. ambiguus* and more narrowly open (often closed and opened buccally to posterobuccally; Figures 35I-M).

Unlike *S. lophatus*, *S. exiguus* is known from ant mounds situated below and above the UPW. Previously, this species was limited to the Orellan (Wood, 1936; Korth, 1981, 1994c; Lindsay, 2008).

Scottimus ambiguus Korth, 1981
(Figure 35N-Q; Tables 39, 40)

Referred Specimens—SDSM 152224, maxilla with left M1-M3; SDSM 152218, 152221, maxilla with M1-M2; SDSM 152230, partial maxilla with M2-M3; SDSM 152215, 152217, 152222, 152226, 152227, 153985-153987, 153997, 153998, 154004, 154005, 154021, 154022, 154029, 154032, 155652, 155653, M1; SDSM 152211, 153994, 154017, 154031, 154045, M2; SDSM 154055, 155669, m1; SDSM 154060, 154067, m2; SDSM 151160, 152186, 154058, m3.

Localities—Recovered from ant mounds 1, 3-7, 9, 12, 15, and 16 below the UPW; ant mound 13 on the UPW; ant mounds 8 and 19 above the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Discussion—Specimens of *Scottimus ambiguus* are easily distinguished from the other species of *Scottimus* from the ant mound collection by their smaller size (Table 39, 40). Morphologically, the *S. ambiguus* specimens differ from the other species in: 1) the posterior re-entrant on anterocone of M1 opens posteriorly to posterolabially (buccal to posterolabial or closed in others); 2) ectoloph on upper molars more weakly developed and oriented directly anteroposterior (angled in others); 3) lack of re-entrant valley on posterior wall of paracone on M1-M2; and, 4) the anteroposteriorly oriented lophids on the lower molars are also less well developed (Figures 35N-Q; Korth, 1981). This species is recovered from almost all of the ant mounds sampled in this study. Elsewhere, this species is known only from the Orellan of Colorado (Korth, 1981; Lindsay, 2008).

Genus *Willeumys* Wahlert, 2009
Willeumys viduus (Korth, 1981)
(Figures 36A-C; Table 41)

Referred Specimens—268 specimens (see appendix).

Localities—Recovered from all sampled ant mounds. Big Cottonwood Creek Member of the Chadron Formation.

Discussion—The morphology of the skull, dentary, and dentition of *W. viduus* has been described in detail elsewhere (Korth, 1981, 2018b; Korth and Tabrum, 2017; Korth et al., 2019a; Wahlert, 2009 [as *W. korthi*]). Other than *Eumys elegans*, *Willeumys viduus* is the best represented cricetid in the Sioux County ant mound collection (268 specimens). The record of *W. viduus* was originally limited to the Orellan of Nebraska (Korth, 1981) but was later identified from Whitneyan of Sioux County (Korth, 2018b) as well as the Whitneyan of Montana (Korth and Tabrum, 2017) and North Dakota (Korth et al., 2019a).

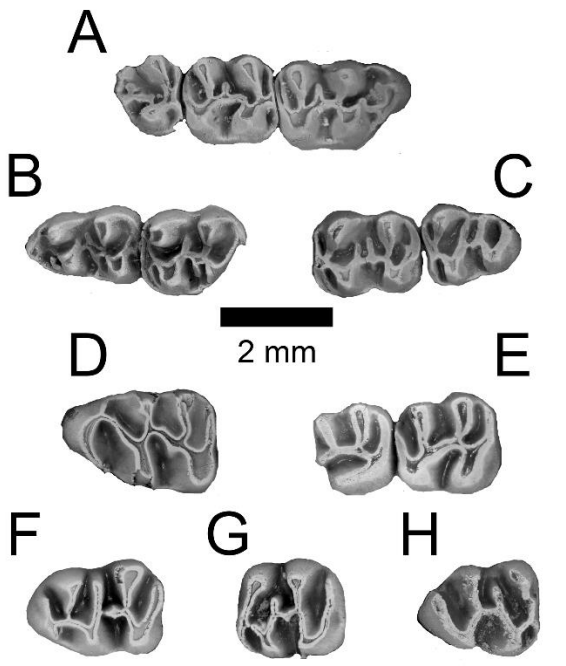

FIGURE 36. *Willeumys* and *Wilsoneumys* from the ant mound collection from Sioux County, Nebraska. A-C, *Willeumys viduus*. A, SDSM 152152, right M1-M3. B, SDSM 152179, left m1-m2 (partial). C, SDSM 152189, eft m2-m3. D-H, *Wilsoneumys planidens*. D, SDSM 153958, left M1. E, SDSM 152236, right M2-M3. F, SDSM 153974, left m1. G, SDSM 153975, left m2. H, SDSM 153976, right m3. All figures to same scale.

Genus *Wilsoneumys* Martin, 1980
Wilsoneumys planidens (Wilson, 1949)
(Figures 36D-H; Table 42)

Referred Specimens—SDSM 152235, 152238, maxilla with M1-M2; SDSM 152236, 152239, 152240, maxilla with M2-M3; SDSM 153958, 153965, 153967, 153969, 153970, 153973, M1; SDSM 153956, 153957, 153959-153961, 153964, 153966, 153968, 153971, 155673, 155674, M2; SDSM 152237, 153962, 153963, 153972, M3; SDSM 153974, m1; 153975, 153977, m2; 153976, 153978-153981, 153983, m3.

Localities—Recovered from ant mounds 1, 3-7, 9, 15, and 16 below the UPW; ant mound 13 on the UPW; ant mound 19 above the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Discussion—Detailed descriptions of the molars of *W. planidens* have been presented previously (Wilson, 1949; Galbreath, 1953; Setoguchi, 1978; Martin, 1980). The specimens referred here differ from those of all other cricetids from the Sioux County ant

mounds in having higher crowned and more lophate molars diagnostic of the genus (Martin, 1980). The Sioux County collection differs from the only other known species of the genus, *W. forcarius* Korth, 2019, in its slightly lower crowned cheek teeth and smaller size (Table 41; Wilson 1949: 49; Galbreath 1953: table 17; Setoguchi 1978: table 12; Korth, 2019: table 11).

Specimens of *W. planidens* were recovered from nearly all ant mounds sampled in this study but only one of those ant mounds was above the UPW (ant mound 19). This species was previously limited to the Orellan (Korth, 1994c: mistakenly listed as occurring in the Chadronian by Lindsay [2008: fig. 27.3]).

Order Lagomorpha Gidley, 1912
Family Leporidae Gray, 1821
Genus *Palaeolagus* Dice, 1929
Palaeolagus haydeni Leidy, 1856
(Figures 37, 38; Table 43)

Referred Specimens—SDSM 156803-156814, dP3 (37 specimens); SDSM 156815-156828, dP4 (71 specimens); SDSM 156981, maxilla with dP2-dP4; SDSM 156813, 156814, maxilla fragment with dP3-dP4; SDSM 156748-156781, 156967 (12 specimens), P3; SDSM 156783 (90+ specimens); SDSM 156784 (40+ specimens), upper molariform teeth; SDSM 156829-156835, 1156847, dp3 (24 specimens); SDSM 156836-156846, dp4 (31 specimens); SDSM 156567-156733, 156747, 156966, (23 isolated specimens), p3; SDSM 156782 (100+ specimens), SDSM 156785 (20+ specimens), lower molariform teeth; SDSM 156968, 7 isolated m3.

Localities— Recovered from all sampled ant mounds. Big Cottonwood Creek Member of the Chadron Formation.

Description and Discussion—All specimens of leporids from the Sioux County ant mounds are isolated cheek teeth, so only P2, P3, p3 and m3 could be separated with certainty. All other upper and lower molariform teeth (P4-M3; p4-m2) could not be separated from one another with confidence, so were grouped together in Table 43.

In terms of size, the ant mound specimens most closely match those of *P. haydeni* (Wood, 1940: 317-318; Korth and Dharmapuri, 2017: tables 2, 3); smaller than those of *P. temnodon* (Storer, 1981a: 5-9), *P. hemirhizis* (Korth and Hageman, 1988: table II), *P. subhypsodus* (Korth, 2007c: table 2), *P. intermedius* (Wood, 1940: 330), *P. hypsodus* and *P. philoi* (Dawson, 1958: tables 3, 4); and larger than in *P. burkei* (Wood, 1940: 327; Boyd et al., in press). The upper cheek teeth lack labial roots that are present or variably present in *P. temnodon*, *P. hemirhizis*, and *P. primus* (Wood, 1940; Korth and Hageman, 1988; Emry and Gawne, 1986). The crown height of the cheek teeth also appears most similar to that of *P. haydeni*, the internal reentrant on p3 remaining open until nearly the base of the crown (closes earlier to form an enamel lake in *P. primus* and *P. temnodon*; Figure 37M-P). The p3 lacks the accessory external reentrant and a posterolabially angled internal reentrant on the p3 of *P. hyposdus* (Dawson, 1958) and *P. subhypsodus* (Korth, 2007c).

The ant mound specimens differ from those of *Chadrolagus* in being higher crowned, having a proportionally longer p3, and the formation of fossettid on p3 does not occur until a very late stage of wear (wear stage 4 of Korth and Dharmapuri, 2017). None of the referred upper molariform teeth from the ant mound collection have the presence of a crescent plus the internal reentrant reduced to a small, isolated lake as in specimens of *Chadrolagus* (Figures 38G-J; Gawne, 1978). The ant mound specimens are clearly smaller and higher crowned than those of *Megalagus* (Matthew, 1903a; Wood, 1940; Dawson, 1958, 2008). Elsewhere, *P. haydeni* ranges from the latest Charonian to early Whitneyan (Dawson, 1958, 2008).

Order Carnivora Bowdich, 1821
Suborder Feliformia Kretzoi, 1945
Family Palaeogalidae Martin and Lim, 2001
Genus *Palaeogale* von Meyer, 1846
Palaeogale sp., cf. *P. minuta* Gervais, 1848
(Figure 39G, H)

Referred Specimen—SDSM 156848, right P4; SDSM 156560, 156849, 156850, m1.

Localities—Recovered from ant mounds 1 and 6 below the UPW; ant mound 8 above the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Measurements—P4: SDSM 156848, L = 4.57 mm, aW = 2.47 mm, pW = 2.13 mm. m1: SDSM 156560, L = 3.99 mm W = 1.48 mm; SDSM 156850, L = 3.98 mm, W = 1.51 mm.

Discussion—The specimens of m1 have the morphology of the genus *Palaeogale* with an open blade-like trigonid, lack of a metaconid and short talonid with a small distinct hypoconulid connected to the protoconid by a sharp shearing ridge (Baskin, 1998; Hayes, 2000; Martin and Lim, 2001; Famoso and Orcutt, in press). Similarly, the referred P4 agrees in morphology with that of *P. minuta* (Hayes, 2000: fig. 9E, F). In size, the specimens best match that of *P. minuta* (Hayes, 2000: table 8, fig. 10; Welsh, 2021: 112; Famoso and Orcutt, in press: table 2, fig. 4), the smallest species of the genus. *Palaeogale* has been reported as early as the Chadronian in North America (Tabrum et al., 1996; Baskin, 1998) but the only previous records of *P. minuta* are from the Arikareean of Florida (Hayes, 2000) and a report of *Palaeogale* sp. cf. *P. minuta* from the Hemingfordian of Nebraska (De Bonis, 1981).

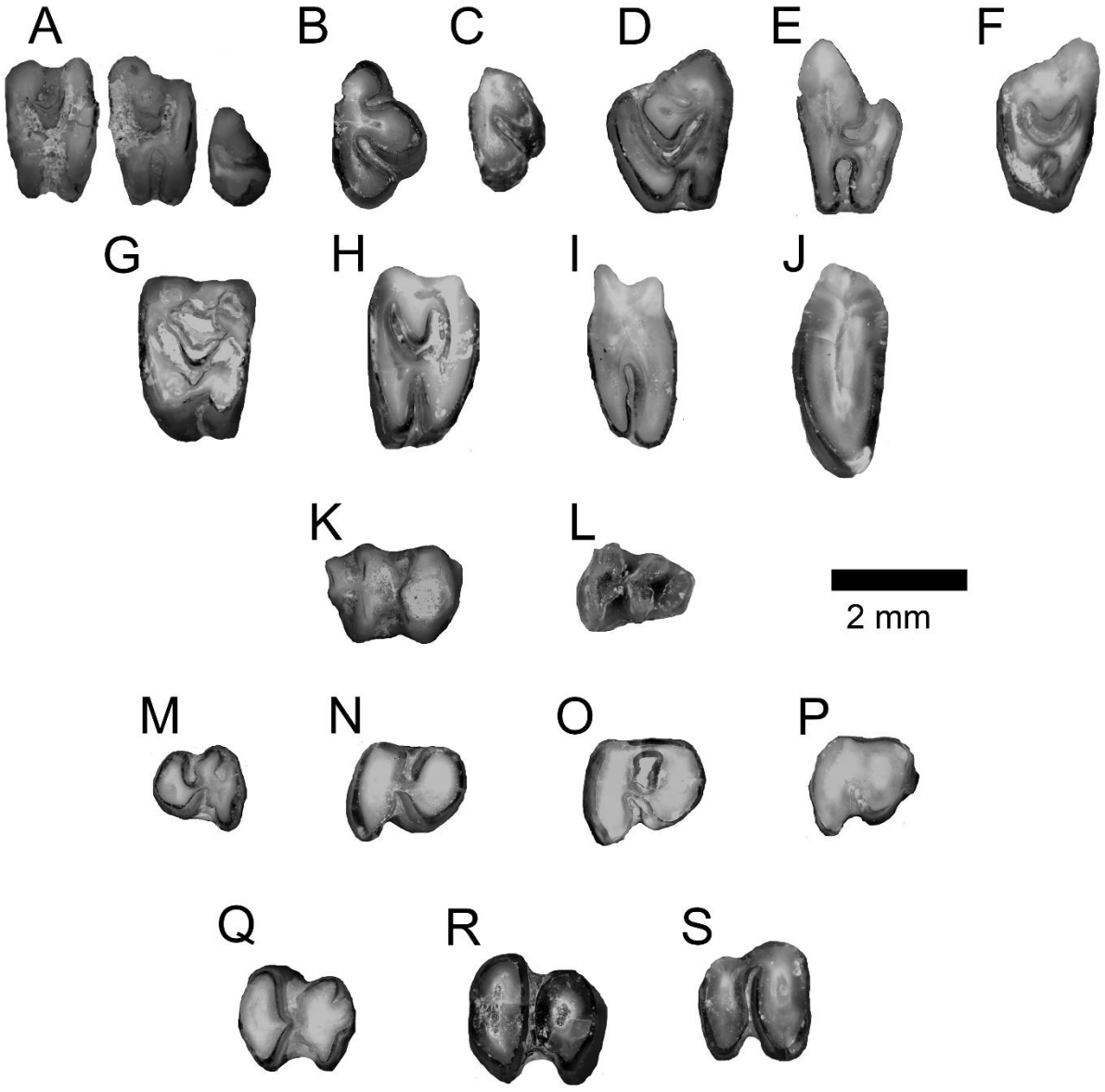

FIGURE 37. *Palaeolagus haydeni* from the ant mound collection from Sioux County, Nebraska. A, SDSM 156813, left dP2-dP4. B, SDSM 156786, right P3. C, SDSM 156786, right P3. D, SDSM 156759, left P3. E, SDSM 156760, right P3. F, SDSM 156778, left P3. G-J, SDSM 156783, upper molariform teeth. G, left. H, right. I, left. J, left. K, SDSM 156837, right dp4. L, SDSM 156830, right dp3. M, SDSM 156603, left p3. N, 156637, right p3. O, SDSM 156663, right p3. P, SDSM 156653, right p3. Q-S, SDSM 156382, lower molariform teeth. Q, left. R, left. S, right. All figures to same scale.

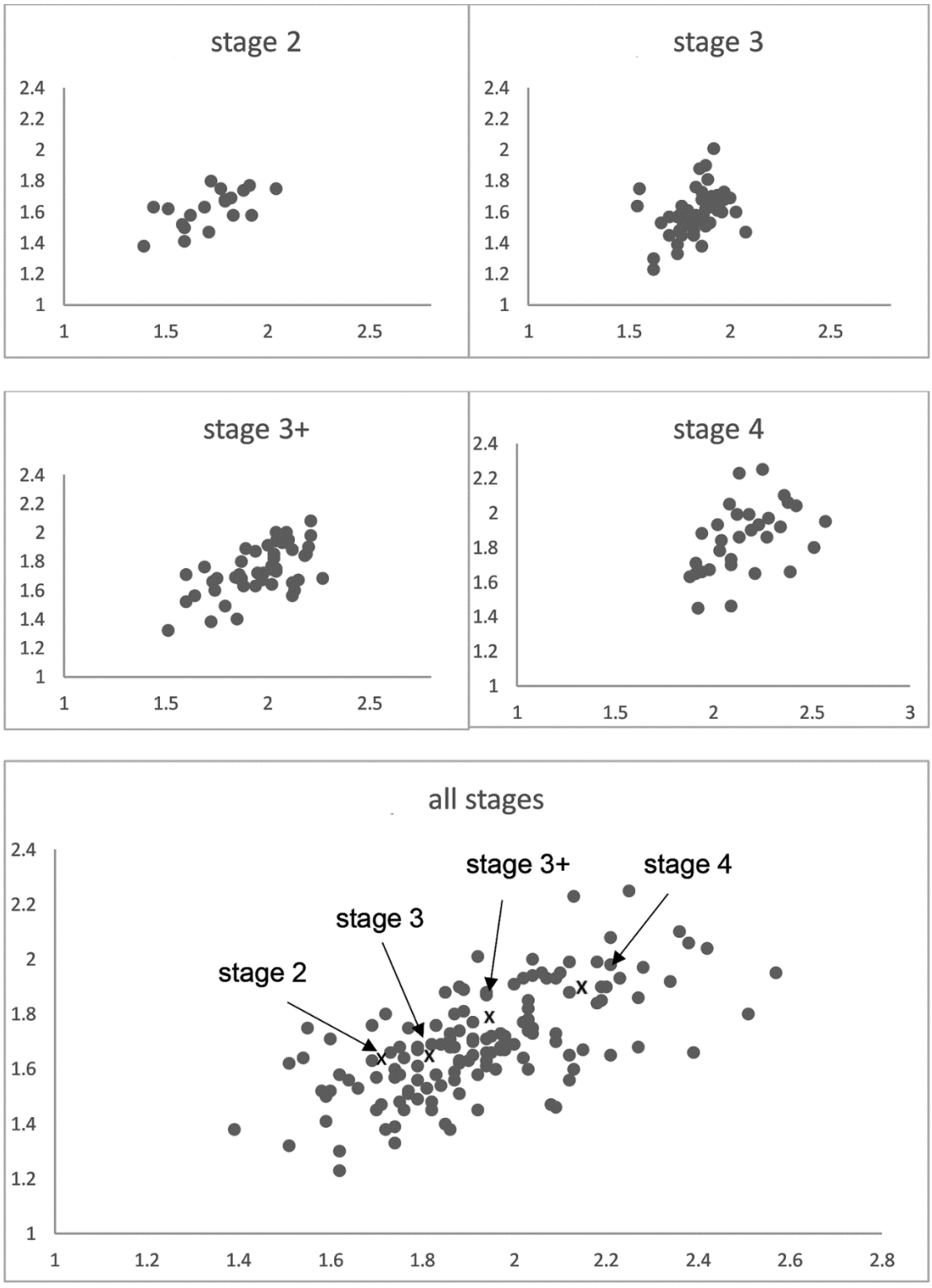

FIGURE 38. Scatter diagram of size of p3 (length vs. width) of *Palaeolagus haydeni* from the ant mound collection from Sioux County, Nebraska at different wear stages. Scales in mm. Wear stages after Korth and Dharmapuri (2017) and Boyd et al. (in press); stage 2 = little or no wear, stage 4 = heavily worn.

Suborder Caniformia Kretzoi, 1943

Discussion—Four caniform taxa are identified in this study, but additional isolated M2s and m3s not described in this study hint at either a broad range of morphological variation in some of these taxa (e.g., *Hesperocyon gregarius*) or the presence of additional taxa. The discussion below is restricted to those specimens that could be confidently referred to specific taxa or that represented unique morphologies. It should be noted that the true diversity of caniforms sampled in this study is likely higher but will require more detailed study or the collection of more compete material to decipher.

Superfamily Canoidea Simpson, 1931
Family Canidae Gray, 1821
Subfamily Hepserocyoninae Tedford, 1978
Genus *Hesperocyon* Scott, 1890
Hesperocyon gregarius (Cope, 1873a)
(Figures 39A-F; Table 44)

Referred Specimens— SDSM 156549, left dP3; SDSM 157007, right dP4; SDSM 156550, 156552-156553, M1 (all partial specimens); SDSM 155714, 156555, 156851, 156853, 156858, M2; SDSM 156855, M2 (partial specimen); SDSM 156472, 156866, 156867, dp4; SDSM 156561, 156861-156863, 156995-156999, 157001-157002, m2; SDSM 156562, 156564, 156566, 156864, 156865, 156868, m3.

Localities—Recovered from ant mounds 1-7, 9, and 15 below the UPW; ant mound 14 on the UPW; ant mounds 17 and 19 above the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Discussion—The specimens referred here differ little from those previously described for *Hesperocyon gregarius* in size and morphology (Table 44; Bryant, 1993: table 4; Wang, 1994: appendix II; Munthe, 1998). Due to the size of the cheek teeth of *H. gregarius* (larger than those of other species in the ant mound collection), the only complete cheek teeth are M2, m2, and m3. There are three specimens of dp4 and a single P4 (Figure 39A). Wang (1994: fig. 65) figured the range of *H. gregarius* extending from the late Duchesnean through the Whitneyan. Specimens of *H. gregarius* were recovered from ant mounds situated both below and above the UPW.

Subfamily Borophaginae Simpson, 1945
Otarocyon Wang et al., 1999
Otarocyon macdonaldi Wang et al., 1999
(Figure 40A)

Referred Specimens—SDSM 156558, right M2.

Locality—Recovered from ant mound 1 below the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Measurements—L = 2.45 mm, W = 3.89 mm (specimen is incomplete owing to breakage and measurements represent minimum values).

Description—The labial portion of the crown is missing, with the breakage occurring just labial to the apices of the paracone and metacone. The triangular paracone is larger and taller than the circular metacone. A broadly rounded ridge extends from the posterolabial margin of the paracone, ending before reaching the metacone. The anterolabial corner of the paracone is damaged, so the presence or absence of a parastyle and any connection to the paracone cannot be assessed. A faint ridge may be present on the lingual surface of the paracone extending anterolingually to a small paraconule. The paraconule is a small swelling along the anterior margin of the crown about halfway between the paracone and the protocone. It is transversely elongated and anteroposteriorly narrow, with a faint crista extending along the anterior margin of the crown, either to a parastyle or the anterolabial corner of the crown, and a second crista extending posterolingually to connect with the anterolabial corner of the protocone. The protocone is situated near the anterior margin of the crown, only slightly posterior to the paracone. A very faint ridge extends posterolabially from the posterior margin of the protocone until it reaches the posterior margin of the crown, where it continues labially along the posterior margin, ending before reaching the metacone. At the location where that crista turns labially, a second faint crista extends lingually a short distance, ending before reaching the edge of the lingual cingulum. The location where those three cristas connect along the posterior margin may represent a very rudimentary metaconule but if present, it is much smaller than the paraconule. The lingual cingulum arises along the anterior margin of the crown level with the anterior end of the paraconule, extends broadly around the protocone, and ends along the posterior margin at a point level with where it arises on the anterior margin. The morphology of the labial cingulum differs from many early canid taxa in that it is not curved strongly posterolingual to the protocone (Wang, 1994; Wang et al., 1999; Tedford et al., 2009); rather, it is directed more lingually, with the lingual apex situated approximately midway between the paracone and metacone and only slightly posterior to the protocone.

In anterior view (Figure 40A) there is a deep valley between the protocone, and the labial wall formed by the paracone and metacone. Additionally, the apex of the lingual cingulum extends at least as high, or higher, than the protocone. There is a large, transversely elongate lingual root situated below the lingual cingulum and

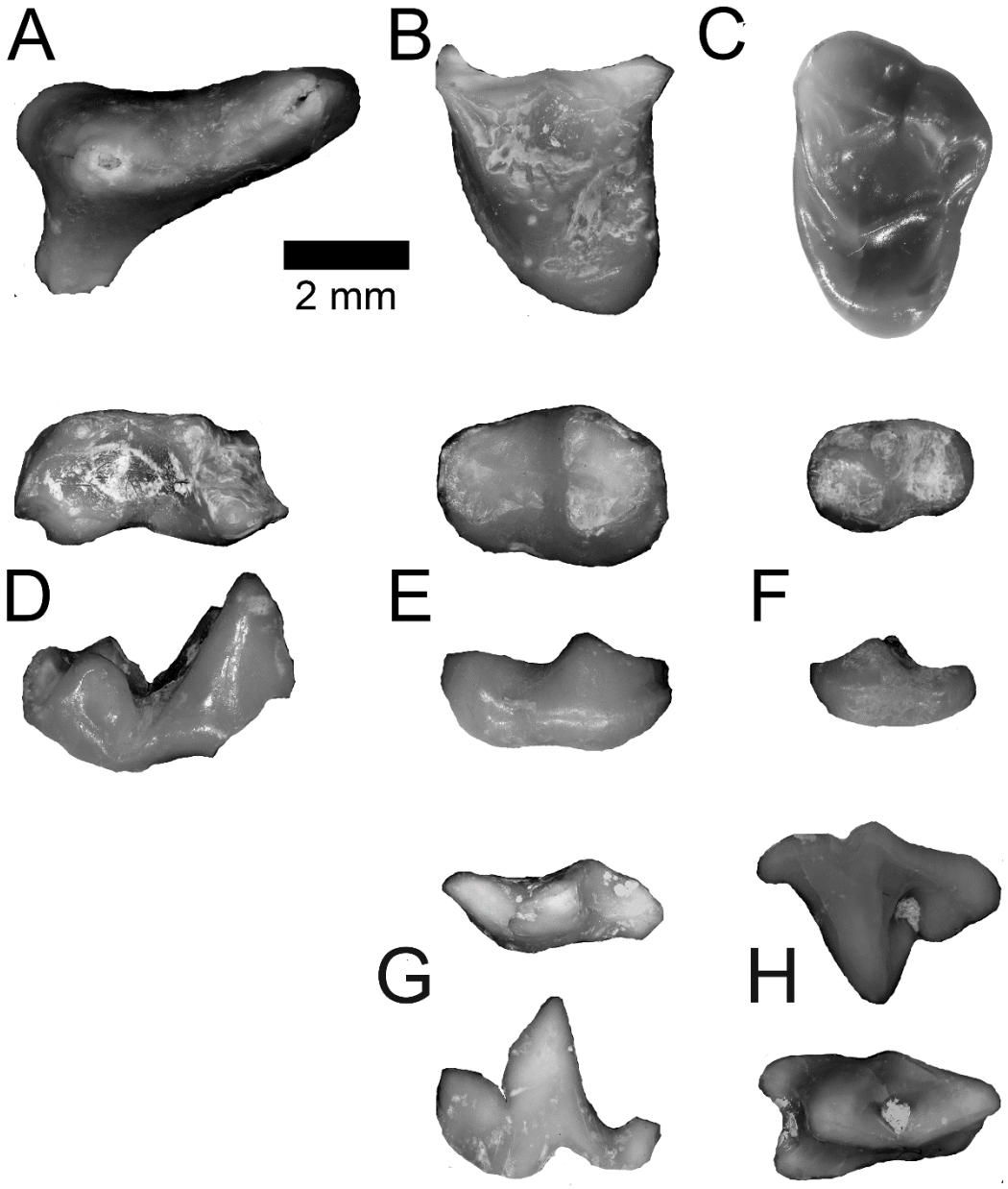

FIGURE 39. *Hesperocyon* and *Palaeogale* from the ant mound collection from Sioux County, Nebraska. A-F, *Hesperocyon gregarius*. A, SDSM 156549, left dP3. B, SDSM 156552, left M1 (partial). C, SDSM 156858, left M2; D, SDSM 156472, right dp4 (partial). E, SDSM 156561, right m2. F, SDSM 156562, left m3. G-H, *Palaeogale* cf. *P. minuta*. G, SDSM 156560, left m1. H, SDSM 156848, right P4. D-G, occlusal view above, labial view below; H, labial view above, occlusal view below. All figures to same scale.

protocone. The dorsal surface of the labial margin indicates there were two labial roots, though their relative sizes are uncertain.

Discussion—*Otarocyon macdonaldi* is the oldest definitive borophagine canid yet identified and is previously reported from the Orellan of South Dakota and Montana (Wang et al., 1999). The M2 of *O. macdonaldi* has not been described in detail, but it was illustrated in the holotype by Wang et al. (1999: fig. 16). The morphology of the referred specimen described above agrees with that illustrated for the holotype, and the size of this specimen when complete would be slightly smaller than that reported for *O. macdonaldi* (L = 2.8-3.4 mm, W = 4.7-5.0 mm: Wang et al., 1999:

appendix III), which is one of the smallest species of borophagine canids. Given that the M2 of *O. macdonaldi* is currently only known from two specimens, this slight difference is not considered problematic for referring SDSM 156558 to this taxon. Wang et al. (1999) noted that *Otarocyon* differs from other basal borophagines in having a high lingual cingulum on M2. This specimen was recovered from an ant mound well below the UPW, which could make it the earliest record of a borophagine canid. However, the specimen is a bright white color, differing from the typical tan to deep brown color of most specimens in this study, which could indicate a long period of residence on the surface prior to recovery. Thus, the possibility cannot be excluded that this specimen was originally preserved in an Orellan fauna and was transported downslope to within the foraging range of this ant mound.

Superfamily Ursoidea Fischer von Waldheim, 1817
Ursoidea indet.
(Figure 40B)

Referred Specimens—SDSM 157006, left m2 or m3.

Locality—Recovered from ant mound 2 below the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Measurements—L = 2.66 mm, W = 2.29 mm.

Description—The occlusal shape of the referred lower molar is oval; longer than wide and very low crowned (Figure 40B). The trigonid consists of a metaconid and protoconid, the former situated slightly more anterior than the latter. The trigonid is closed anteriorly by a low ridge that is continuous from the metaconid to the protoconid and bows slightly anteriorly. A low, broad cingulid wraps around the anterolabial corner of the tooth at the base of the protoconid and continues along the base of the labial side to the posterior margin of the hypoconid. The talonid basin is filled with low, wide crenulations. A distinct entoconid is anteroposteriorly compressed at the posterolingual corner of the tooth. The lingual ridge along the lingual side of the tooth has three smaller swellings (?cusps) and is continuous with the posterolingual corner of the metaconid. There is also an additional small cuspule directly posterior to the metaconid.

Discussion—The crenulation on the enamel of this lower molar is consistent with the type and only known species of *Nothocyon*, *N. giesmarianus* (Cope, 1878), and distinct from other canids and arctoids (Wang and Tedford, 1992; Munthe, 1998). The overall size of the ant mound specimen is smaller than m3 of *N. giesmarianus* (similar in size to the m3 of *Subparictis gilpini*: Wang et al., in press) but is more molariform in morphology, more closely resembling the m2 of *N. giesmarianus* (Wang and Tedford, 1992: table 1, fig. 2B; Wang et al., in press: fig. 17). However, the length to width ratio of SDSM 157006 (1.16) resembles that of known subparictid m3s (mean = 1.17; range = 1.21-1.13: Wang et al., in press) and is less than that for known subparictid m2s (mean = 1.37; range = 1.46-1.25: Wang et al., in press). The m3s of most basal arcoids are poorly sampled or completely unknown (Wang et al., in press) and it is possible this could be an m3 from a poorly known taxon, an m3 from an undescribed basal arctoid that retained a more molariform m3, or a very small m2 from an undescribed basal arctoid.

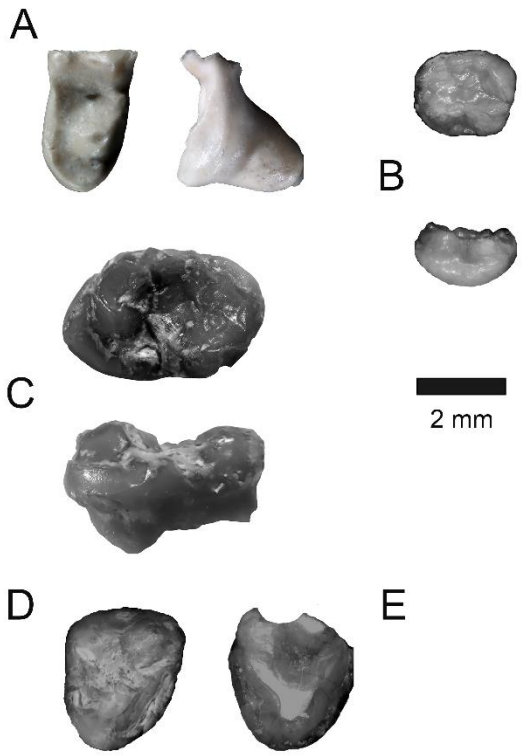

FIGURE 40. *Otarocyon macdonali*, Ursoidea indet., *Subparictis dakotensis*, and *Stibarus* sp., cf. *S. obtusilobus* from the ant mound collection from Sioux County, Nebraska. A, *O. macdonali*, SDSM 156558 (occlusal view left, anterior view right). B. Ursoidea indet., SDSM 157006, left m2 or m3 (occlusal view above, labial view below). C, *S.dakotensis*, SDSM 157000, left m2 (occlusal view above, labial view below). D-E, *Stibarus* sp., cf. *S. obtusilobus*. D, SDSM 157003, right M2. E, SDSM 157004, right M2.

Family Subparictidae Baskin and Tedford, 1996
Genus *Subparictis* Clark and Guensburg, 1972
Subparictis dakotensis (Clark, 1936)
(Figure 40C)

Referred Specimen—SDSM 157000, left m2.

Locality—Recovered from ant mound 3 m below the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Measurements—L = 5.12 mm, aW = 3.73 mm, pW = 3.24 mm.

Description—The single m2 is missing enamel around the anterolingual and lingual margins. There are also several areas where the enamel surface is pitted. The trigonid is reduced in size relative to the talonid both anteroposteriorly and labiolingually but sits higher than the talonid in labial view. The protoconid is shifted lingually and is slightly smaller than the metaconid. A ridge extends from the anterolingual margin of the protoconid towards the anterolingual corner of the crown, then curves posteriorly, following the lingual margin of the tooth until it connects to the anterior margin of the metaconid. There is no evidence of a paraconid along this ridge. A second, lower ridge extends from the posterolingual margin of the protoconid to the posterolabial margin of the metaconid, completely enclosing the small trigonid. A cristid extends posteriorly from the posterolingual margin of the metaconid along the lingual margin of the tooth, curving labially to follow the posterior margin of the talonid, then extending anterolabially to end at the moderately-developed hypoconid. A slight cristid obliqua extends from the anterolingual margin of the hypoconid towards the posterior margin of the trigonid, ending posterolingual to the protoconid. There is a swelling along the posterolingual corner of the talonid that is equal to the hypoconid in height that may represent the entoconid. There may be some smaller cusps along the cristid between the entoconid and metaconid, but the damage to the enamel makes this impossible to confirm. The floor of the talonid is also marked by a series of discontinuous, rounded ridges. A broad anterolingual cingulid is present beginning anterior to the hypoconid, extends around the labial and anterior margins of the protoconid, and ends near the anterolingual margin of the tooth. Two wear facets are present on this cingulid, the first along the labial margin between the hypoconid and protoconid, and the second (larger) facet is at the anterolabial corner of the crown.

Discussion—This species was originally referred to *Parictis* Scott, 1893, and included in the family Ursidae. It was later included as a subgenus *Parictis* (*Subparictis*) by Clark and Guensburg (1972). Later, *Subparictis* was raised to the rank of genus including *S. dakotensis* (Wang and Tedford, 1992), retaining only the type species *P. primaevus* in *Parictis*. Baskin and Tedford (1996) erected the family Subparictidae that included only species of *Parictis* and *Subparictis*. However, Hunt (1998) argued against the use of both *Subparictis* and Subparictidae, including all species in *Parictis* and referring the genus to the subfamily Amphicynodontinae of the Ursidae. Wang et al. (in press) conducted a thorough review of North American basal arctoids in which they supported the separation of *Parictis* and *Subparictis* as proposed by Baskin and Tedford (1996) based on the referral of new specimens to both taxa. Their phylogenetic analysis recovered a monophyletic Subparictidae composed of *Parictis*, *Subparictis*, *Nothocyon*, and a new basal arctoid taxon from the Whitneyan of North Dakota.

The referred m2 is similar in size to other specimens of *S. dakotensis* (Wang et al., in press: table 2) and closely resembles the m2 of AMNH 12244 from Custer County, South Dakota (Wang et al., in press: fig. 13). *S. dakotensis* and *Subparictis montanus* differ from *Subparictis parvus* and *Subparictis gilpini* in that the protoconid on m2 is shifted lingually. *S. montanus* is smaller than *S. dakotensis* (Wang et al., in press: table 2) and has a pronounced protostylid situated posterolabial to the protoconid on m2. These differences support the referral of SDSM 157000 to *S. dakotensis*. Previously, *S. dakotensis* was reported from the Chadronian of South Dakota, Nebraska, Colorado, and Wyoming (Baskin and Tedford, 1996: 489) and the Whitneyan of South Dakota (Wang et al., in press). The specimen here referred to this taxon was recovered from an ant mound situated below the UPW.

Order Artiodactyla Owen, 1848
Family Leptochoeridae Marsh, 1894
Genus *Stibarus* Cope 1873a
Stibarus sp., cf. *S. obtusilobus* Cope 1873a
(Figure 40D, E)

Referred Specimens—SDSM 157003, 157004, right M3.

Localities—Recovered from ant mounds 3 and 9 below the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Measurements— SDSM 157003, L = 3.16 mm, W = 4.02 mm; SDSM 157004; L = 3.17, W = N/A.

Description—The referred M3s are triangular in occlusal outline, wider than long and narrower lingually than labially (Figures 40D, E). The three major cusps (paracone, metacone, protocone) are of nearly equal size, the metacone being slightly smaller. There is no evidence of a hypocone. A distinct centrocrista connects the apices of the paracone and metacone, resulting in a labially closed central valley, and is continuous with a paracrista that extends anteriorly from the paracone to the anterior margin of the tooth. There is a distinct paraconule that is continuous with the protocone along a preprotocrista. The postprotocrista extends posterolabially from the protocone but ends labially before joining the metacone. The anterior and posterior cingulae extend along the base of the crown from the protocone ending respectively at the anterolingual base of the paracone and posterolingual base of the metacone.

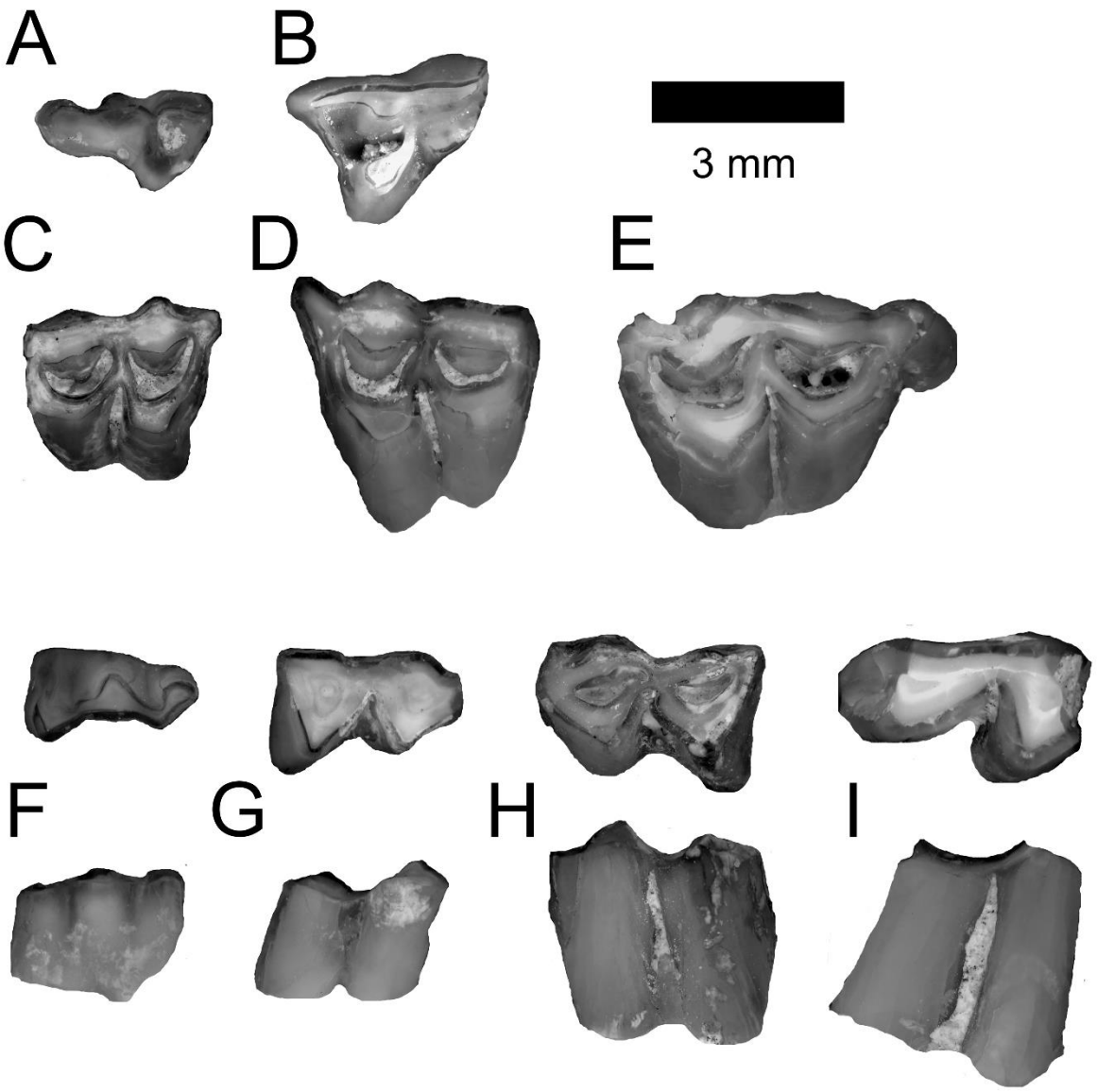

FIGURE 41. *Hypisodus minimus* from the ant mound collection from Sioux County, Nebraska. A, SDSM 156957, left P3. B, SDSM 156742, left P4. C, SDSM 156873, right M1. D, SDSM 156870, left M2. E, SDSM 156911, left M3. F, SDSM 156945, right p4. G, SSM 156736, right m1. H, SDSM 156739, left m2. I, SDSM 156740, right m3. F-I, occlusal view above, labial view below. All figures to same scale.

Discussion—*Stibarus* is the smallest leptochoerid taxon (Edwards, 1976) and includes four species: *Stibarus obtusilobus*, *Stibarus quadricuspis*, *Stibarus montanus*, and *Stibarus yoderensis*. Only the lower dentition of *S. montanus* has been described, preventing comparison with these specimens, but the size of the lower dentition of that taxon indicates that it represents a larger species than the specimens reported here (MacDonald, 1955: 455). The closure of the central valley between the paracone and metacone noted in the referred specimens is also seen in *S. yoderensis* (MacDonald, 1955: fig. 6) but in that taxon the metaconule is larger than the paraconule on the M3 whereas the metaconule is absent on these specimens. The M3 of *S. quadricuspis* has a blunted lingual apex and the cingulum is complete around the lingual margin of the crown (MacDonald, 1955: pl. 46, fig. 4), features that are absent in these specimens. *S. obtusilobus* is the smallest species of the genus and these specimens fall within the reported size range (L = 2.7-3.3 mm, W = 3.8-4.2 mm: MacDonald, 1955: 451). These specimens also resemble the M3 of *S. obtusilobus* in the more pointed

lingual margin, in that the cingulum does not extend around the lingual margin, and in the metaconule being rudimentary or absent (MacDonald, 1955: fig. 5), though the lingual margin is roughened but not formed into a cingulum in SDSM 157004 (Figure 40D). Overall, these two M3s most closely resemble the size and morphology of *S. obtusilobus*, but differ in the labial closure of the central valley.

This taxon is previously reported from the Orella and Whitney Members of the Brule Formation in Nebraska, as well as the Chadronian and Orellan of Colorado and the Orellan of South Dakota and Wyoming (Edwards, 1976). Both specimens referred here are from ant mounds below the UPW.

Family Hypisodontidae Osborn, 1910
Genus *Hypisodus* Cope, 1873b
Hypisodus minimus Cope, 1873b
(Figure 41; Table 45)

Referred Specimens—SDSM 156883, 156957, 156958, 156960, 156964 P3; SDSM 156737, 156742, 156907, 156963, P4; SDSM 156873, 156875-156877, 156881, M1; SDSM 156741, 156870-156872, 156874, 156878-156880, M2; SDSM 156738, 156911, M3; SDSM 156885, 156945, 156959, p4; 156736, 156884 (in part), 156886, m1; SDSM 156739, 156884 (in part), m2; SDSM 156740, 156882, m3.

Localities—Recovered from ant mounds 1, 3, 4, 6, 7, 9, 15, and 16 below the UPW; ant mound 13 on the UPW; ant mounds 8, 10, 11, 17, and 18 above the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Discussion—The small size, greater crown height, and the flat labial walls of the upper molars and lingual walls of lower molars match the diagnosis of *Hypisodus* (Scott, 1940; Webb, 1998; Meehan and Martin, 2004). In the last review of the genus only two species were recognized, the type species *H. minimus* and a new, slightly larger species *H. retallacki* (Meehan and Martin, 2004). The specimens from the ant mound collection best match the size of the type species *H. minimus* (Table 45; Meehan and Martin, 2004: table 1, fig. 3). The specimens reported here are from ant mounds situated both below and above the UPW. Elsewhere, *H. minimus* ranges from the late Duchesnaean to the early Arikareean (Webb, 1998).

Family Leptomerycidae Zittel, 1893
Genus *Leptomeryx* Leidy, 1853
Leptomeryx sp., cf. *L. exilis* Cook, 1934
(Figure 42; Table 46)

Referred Specimens—SDSM 156948, 156949, 156954, dP3; SDSM 156894, 156904, 156906, 156952, dP4; SDSM 156896, 156898, 156903, 156910, P2; SDSM 156887, 156889, 156891, 156897, 156901, 156902, 156951, 156982, P3; SDSM 156900, 156905, P4; SDSM 156888, 156890, 156892, 156895, 156899, 156909, M1 or M2; SDSM 156908, M3 (partial); SDSM 156918, 156923, 156929, 156930, 156932, 156941 (part), 156953, 156956, 156965, dp3; SDSM 156921, 156938, 156939, 156941, 156962, dp4; SDSM 156914 (in part), 156915, 156916, 156920, 156934, 156937, 156940, 156961, p2; SDSM 156914 (in part), 156922, 156926, 156927, 156942, 156943, p3; SDSM 156912, 156913, 156917, 156919, 156924, 156928, 156931, 156933, 156936, 156944, p4; SDSM 156925, 156935, m1 or m2.

Localities—Recovered from ant mounds 1-7, 9, 12, 15, and 16 below the UPW; ant mounds 13 and 14 on the UPW; ant mounds 8, 10, 11, 18, and 19 above the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Discussion—Only two genera of leptomerycids have been reported from the Chadronian and Orellan: *Leptomeryx* Leidy, 1853, and *Hendryomeryx* Black, 1978 (see Webb, 1998). The cheek teeth from the Sioux County ant mounds are higher crowned and have more fully developed crests than in *Hendryomeryx* (Wilson, 1974; Black, 1978; Storer, 1981b; Heaton and Emry, 1996; Webb, 1998). The specimens are small for *Leptomeryx*, comparable in size to those of the smallest species *L. exilis* (Table 45) but have smooth enamel on the cheek teeth and lack thr well-developed protostyle on upper molars of *L. exilis* (Cook, 1934; Korth and Diamond, 2002). All Chadronian species of *Leptomeryx* and the Orellan type species *L. evansi* are larger than the ant mounds specimens and can have moderate to heavily crenulated enamel on the molars (Heaton and Emry, 1996). The ant mound specimens also lack the accessory ridge running posteriorly from the apex of the protoconid in the on the lower molars (*Palaeomeryx* fold) of *L. evansi* and *L. speciosus* (Heaton and Emry, 1996: fig. 10; Korth and Diamond, 2002: fig. 1).

The morphology of m3 distinguishs the species of *Leptomeryx* (Heaton and Emry, 1996: fig. 9). However, there are no m3s referable to *Leptomeryx* in the ant mound collection likely due to their larger size. In addition, proportions of the referred upper molars in the ant mound collection (longer than wide) differ from that of other species of *Leptomeryx* where the upper molars are generally equal in length and width or wider than long (Table 45; Scott, 1940: 553; Korth and Diamond, 2002: tables 1, 4). There are only two complete upper molars (M1 or M2) in the ant mound collection (SDSM 156895, 156899). Elsewhere *L. exilis* has been reported from the Orellan and Whitneyan (Korth and Diamond, 2002).

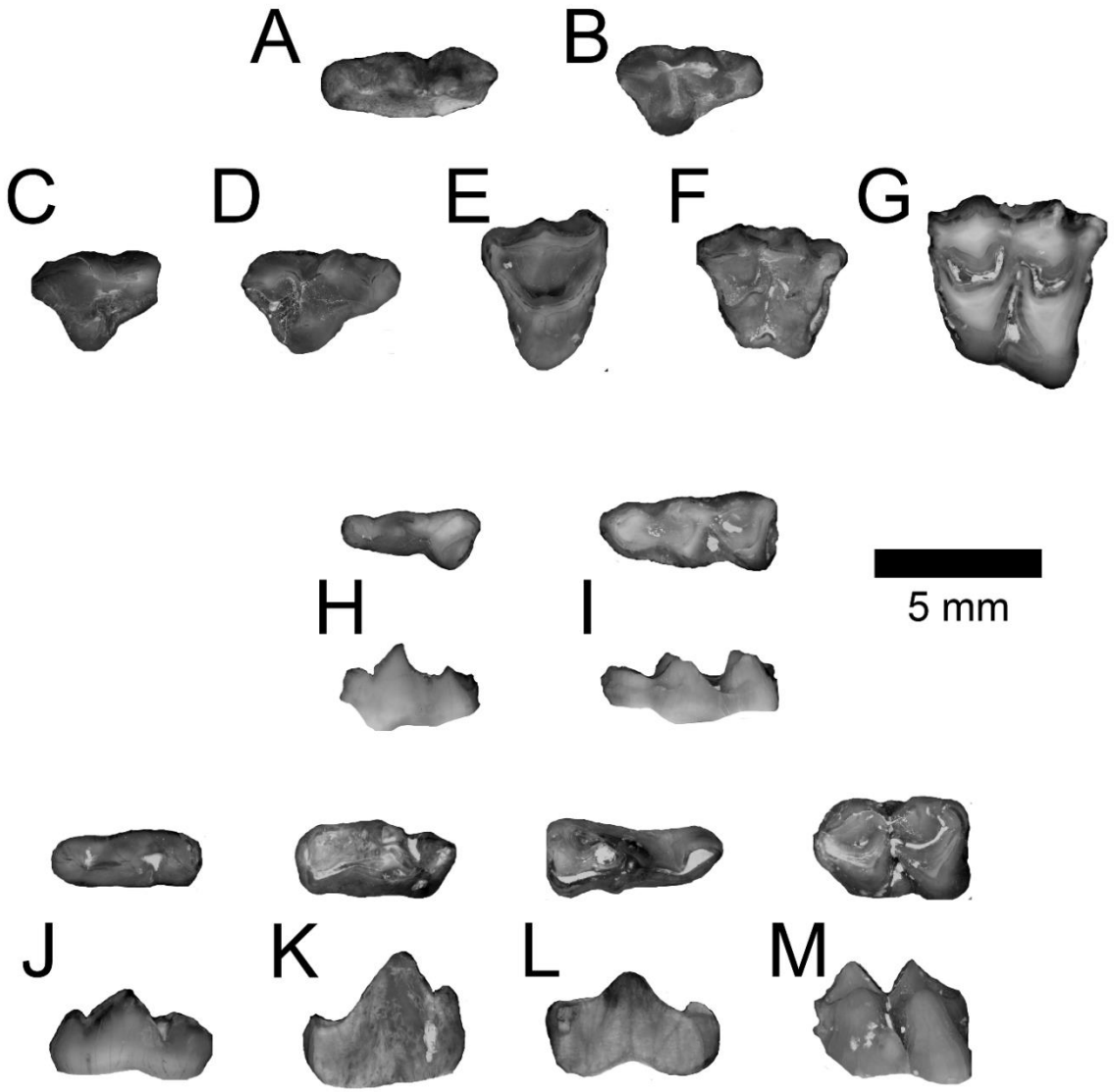

FIGURE 42. *Leptomeryx* cf. *L. exilis* from the ant mound collection from Sioux County, Nebraska. A, SDSM 156948, left dP3. B, SDSM 156906, left dP4. C, SDSM 156896, left P2. D, SDSM 156887, right P3. E, SDSM 156905, left P4. F, SDSM 156895, right M1 or M2. G, SDSM 156908, right M3. H, SDSM 156932, right dp3. I, SDSM 156941, left dp4. J, SDSM 156934, left p2. K, SDSM 156926, right p3. L, SDSM 156936, right p4. M, SDSM 15935, left m1 or m2. All figures to same scale.

?*Leptomeryx* sp. indet.
(Figure 43)

Referred Specimens—SDSM 156946, left dP3; SDSM 156947 (partial), dP4; SDSM 156893, 156950 (partial), P3; SDSM 156955, dp3 (partial).

Localities—Recovered from ant mounds 1 and 3 below the UPW; ant mound 13 on the UPW; ant mounds 10 and 19 above the UPW. Big Cottonwood Creek Member of the Chadron Formation.

Measurements—dP3: SDSM 156946, L = 5.67 mm, W = 2.32 mm; dP4: SDSM 156947, W = 3.02 mm. P3: SDSM 156893, L = 6.28 mm, W = 4.77 mm; SDSM 156950, L = 6.61 mm. dp3: SDSM 156955, W = 2.73 mm.

Discussion—A few isolated deciduous premolars and P3s of an uncertain artiodactyl are present in the ant mound collection. In crown height they are similar to those of *Leptomeryx*; however, the size of the complete P3 (SDSM 156893: Figure 43C) is larger than those of *L.* cf. *exilis* but smaller than *L. evansi* (Scott, 1940: 553). It is possible that they may belong to *L. elissae*, a species previously reported from the Orellan of Sioux County, Nebraska because of their comparable size (Korth and Diamond, 2002: table 3). However, the latter species is only known from lower dentitions and no deciduous teeth so direct comparisons are impossible.

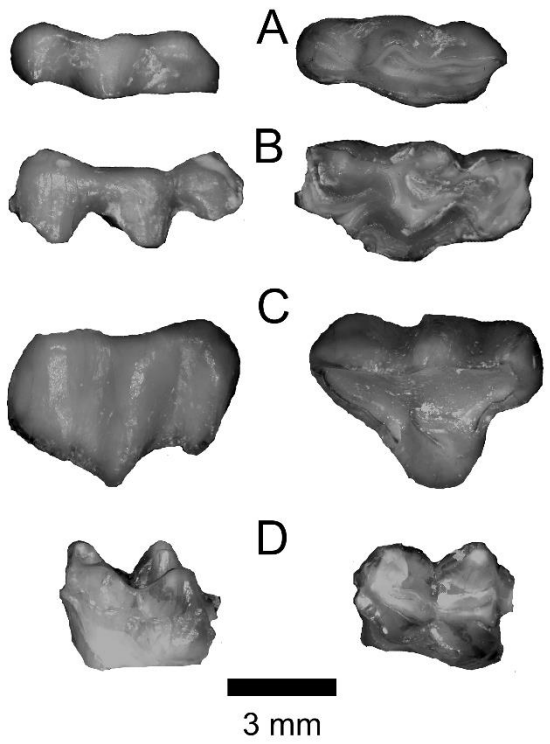

FIGURE 43. ?*Leptomeryx* sp. from the ant mound collection from Sioux County, Nebraska. A, SDSM 156946, left dP3. B, SDSM 156947, right dP4 (partial); C, SDSM 156893, right P3. C, SDSM 156955, left dp3 (partial). Labial view on left, occlusal view on right. All figures to same scale.

DISCUSSION

Not including the lagomorph specimens, 5,938 identifiable mammalian teeth and jaws were recovered from the 19 ant mounds sampled in this study. Those specimens represent 81 distinct taxa, 65 of which are identified at least tentatively to the species level (Table 47). This collection is the largest and most diverse micromammal collection described from the White River Group of Nebraska, though as discussed below, this collection time averages at least two temporally distinct faunae (Chadronian and Orellan). Given that all of the specimens included in this study were recovered from *Pogonomyrmex occidentalis* ant mounds, a review of the collection habits of these ants and the impacts and limitations they impart on this study is warranted before making interpretations from these data.

Factors Impacting Ant Mound Collections—There are a myriad of factors that impact the final composition of paleontological collections. These factors can occur predepositionally (e.g., taxon specific habitat preferences), syndepositionally (e.g., size sorting effects based on depositional setting), postdepositionally (e.g., differential erosion rates of adjacent fossiliferous beds), during collection (e.g., collector biases; sampling method biases), or after collection (e.g., culling of 'suboptimal' fossils prior to accessioning; Clark and Kietzke, 1967). It is impossible to recover a collection of fossils that was not influenced in some way by at least one these factors; however, understanding the factors that impacted a collection helps to avoid erroneous interpretations or inappropriate comparisons of the resulting data.

Discussions regarding collection biases in paleontology typically focus on differential sampling of the original set of preserved fossils by humans (e.g., Whitaker and Kimmig, 2020). When working with ant mound collections paleontologists must keep in mind that the ants themselves are the primary collectors of the fossils under study and they significantly impact the resulting collection of fossils before they ever enter into the care of paleontologists.

The most important question to ask regarding ant mound collected fossils is where they came from, especially if those fossils will be used for biostratigraphic assessment. This seems a simple question at first but it becomes more complicated the deeper you delve into it as the answer depends a lot on where the ant mounds are located. At the simplest level, are the fossils present on the exterior surface of the mound removed from the subsurface during the excavation of tunnels and chambers by the ants, or are they gathered from the surface and brought back to the mound? An experiment with captive *Pogonomyrmex occidentalis* ants appeared to show that the fossils situated on the exterior surface of these ant mounds come from both subsurface excavations and surface gathering (Matthias and Carpenter, 2004). However, that study provided the ants with only a limited surface area to forage from (60 cm by 60 cm), which is a poor representation of the natural environment. Excavation and examination of sediment from a natural *P. occidentalis* ant mound revealed that the subsurface sediment did not contain the same grain sizes as the sediment found on the exterior of the ant mound suggesting the majority of the mound is constructed from grains gathered on the surface (Todd and

Schoville, 2001). Given these results, it is likely that most fossils recovered from ant mounds are collected loose on the surface surrounding the mound but a small contribution from the subsurface cannot be discounted. Mature colonies of *P. occidentalis* have a documented subsurface depth of just under three meters (Lavigne, 1969) and that value was used as the maximum subsurface stratigraphic sampling range for each of the mounds sampled in this study (Figure 44).

Surface foraging by *P. occidentalis* for both food and resistant objects to place on their mounds is conducted over a wide area. In areas of moderate to high topographic relief, such as in this study, understanding the foraging range of these ants is necessary to estimate the stratigraphic range of rocks sampled by each mound. Clemens (1964) briefly reported on an experiment where glass beads were scattered around an ant mound to evaluate how far away the ants were foraging. After one year he returned to the ant mound and was able to estimate the ants had foraged beads from at least 50 feet (15.2 meters) away from the mound. An extensive study of the foraging habits of *P. occidentalis* was conducted by Schoville et al. (2009) in an area just a few miles to the west of the current study site (Figure 2: AS). One of the experiments conducted in that study involved the placement of rings of different colored beads at set distances from four ant mounds (a fifth mound was originally included but was destroyed after four weeks), allowing the foraging distance of each ant mound to be easily visually assessed for distances up to 48 meters away. At the conclusion of the study (13 weeks) they noted that the vast majority of the beads foraged (~95 percent) came from within 20 meters of the mound, with only two of the mounds foraging beads from between 20 and 48 meters away (Schoville et al., 2009). For the purposes of this study, we calculated two stratigraphic ranges of surface sampling for each ant mound: the stratigraphic range sampled within 20 meters of the mound and stratigraphic range sampled out to 48 meters from the mound (Figure 44). It should be noted that sampling could extend beyond 48 meters, especially from well-established colonies, but available studies only tested out to 48 meters. It is noted that the stratigraphic ranges sampled by each mound are more extensive above than below the level of the mound because most mounds are situated on relatively flat areas adjacent to vertically extensive outcrops (Figures 3 and 44).

Most prior studies focused on surface foraging by *P. occidentalis* were concerned with how far the ants travel away from their mounds to retrieve objects. However, an equally important question to consider in paleontological studies is what other processes could be transporting and depositing fossils into the foraging range of an ant mound. Immediately to the west of the ant mounds sampled in this study are extensive outcrops of the Brule Formation (tens of meters vertical relief: USGS, 1980). Within the study area drainage off these outcrops via seasonal streams runs from west to east, and all of the ant mounds sampled in this study sit either within or immediately adjacent to these drainages (Figure 3). During periods of local moderate to high rainfall loose fossils could be transported downslope and deposited into the areas adjacent to these ant mounds. Similarly, small pieces of rock that may contain *in situ* microfossils can be transported within foraging distance of the ant mounds by these streams, deposited, and eventually erode enough to release the fossils. In the study area armoured mudballs (*sensu* Tanner, 1996; Mather et al., 2008) up to 10 cm in diameter are present within these drainages that could have brought loose microvertebrate fossils or pieces of rock downslope to within foraging range of the sampled ant mounds.

Given the predominance of specimens referred to Orellan taxa from these ant mounds (see below), it is clear that a substantial proportion of the material included in this study were subjected to downslope transport that brought the specimens into the foraging ranges of these ant mounds. Downslope transport of Orellan taxa has long been hypothesized as a factor impacting ant mound collections and loose surface collections from paleontological localities within the Chadron Formation below the UPW in this region of Sioux County, Nebraska. The first evidence came from the presence of the typically Orellan (= Middle Oligocene in Hough and Alf, 1956) *Eumys elegans* in the faunal list from the "interesting ant hill fauna" presented by Hough and Alf (1956). Re-examination of those and other fossils collected by Raymond Alf from ant mounds in this region of Sioux County, Nebraska led Guthrie and Allen (1974) to conclude that most of the teeth recovered from those ant mounds were originally from the overlying Brule Formation and not part of the Chadronian fauna. Similarly, the original rodent faunal list from the nearby Chadronia Pocket locality (Wood, 1969) sampled via collection of loose specimens on the surface of the outcrop was later shown to contain downslope transported Orellan taxa (e.g., *E. elegans* and *Palaeolagus haydeni*) that were not documented when *in situ* rocks from that locality were screen washed for microvertebrate fossils (Ostrander, 1985). In that case, the source of the Orellan taxa was suggested to be reworking from the adjacent Quaternary terraces around the locality (Wood, 1980; Ostrander, 1985) based on a study from South Dakota that showed Quaternary and Oligocene fossils are concentrated in Quaternary terraces and were often reworked and incorporated into adjacent ant mounds (Wilson, 1971: *contra* Johnson, 1966). Similar terraces are present in the study area and may be a second source of some of the recovered Orellan fossils. As discussed below, this downslope transport of

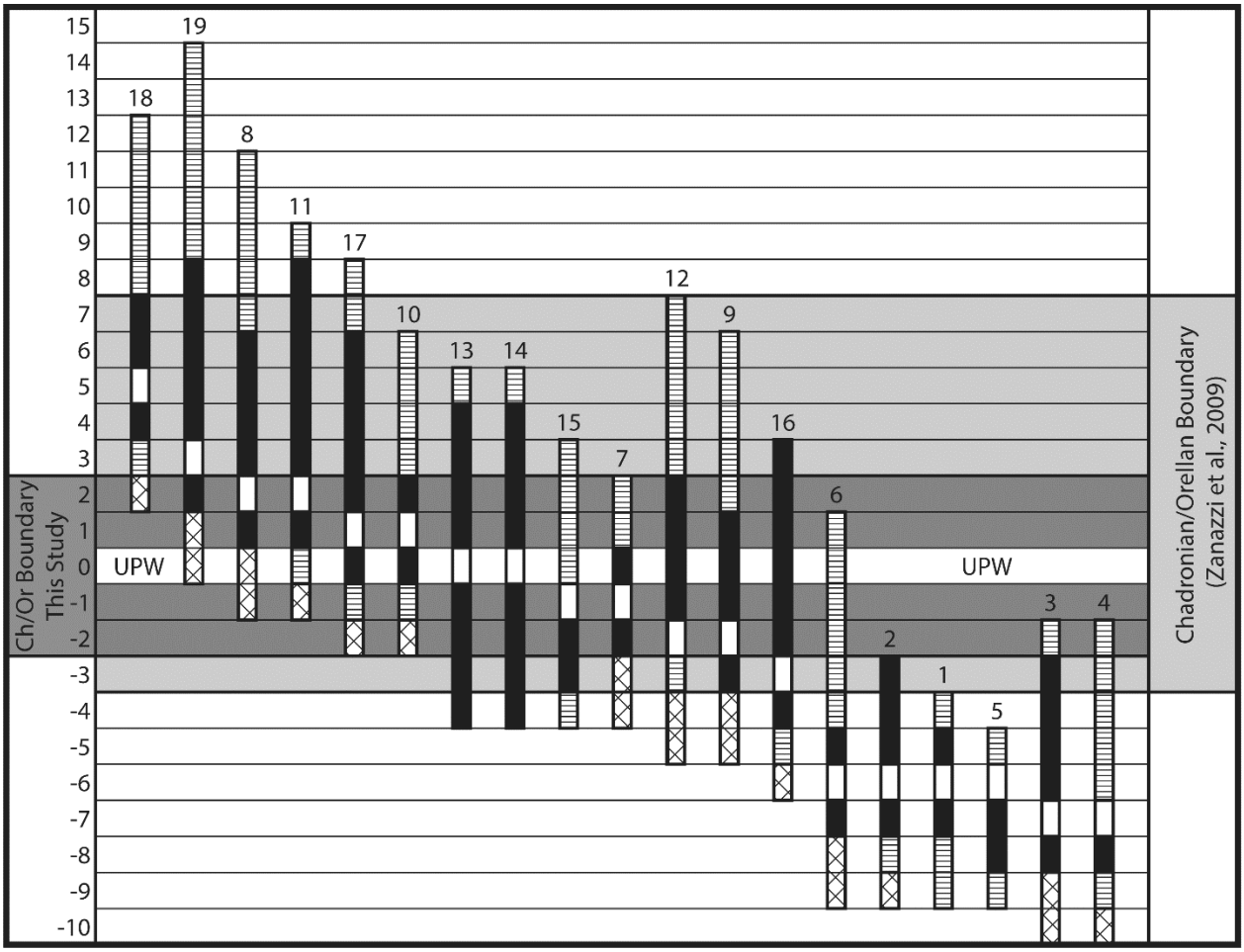

FIGURE 44. Stratigraphic sampling ranges for the 18 ant mounds sampled in this study (ant mounds 13 and 14 combined). In each column, white boxes indicate the position of the mound, black boxes indicate the surface stratigraphy sampled within a 20-meter radius of the mound, striped boxes indicate the surface stratigraphy sampled within a 48-meter radius, and cross-hatched boxes indicated the subsurface stratigraphy sampled up to three meters below the ant mound. Abbreviations: Ch, Chadronian; Or, Orellan; UPW, upper purplish-white layer. Scale on left in meters.

microvertebrate fossils has important implications for interpreting the results of this study.

In addition to addressing the question of where the ants recover the fossils is the equally important question of how they recover the fossils. Ants do not gather an unbiased sample of fossils from the surrounding rocks, rather, they impart their own sampling biases on the resulting collection that must be taken into consideration. The first sampling bias these ants apply is related to size. The small size of the ants necessarily places an upper limit on the size of the fossils that can be gathered and deposited on the ant mound. This clearly rules out all of the larger taxa present in the White River Group and the upper size limit of isolated teeth in this collection corresponds with the size of isolated teeth from the small-bodied artiodactyl *Leptomeryx* and the early canid *Hesperocyon* (Tables 44 and 47) and the length of complete toothrows from the cricetid rodents *Eumys elegans* and *Willeumys viduus* (Tables 37 and 41). Some research has been done on the size preferences of objects gathered by species of *Pogonomyrmex* ants. Smith and Tschinkel (2005) found a significant preference for medium (~12.5 mm long) versus large (~25 mm long) pieces of toothpicks in *Pogonomyrmex badius* (Florida harvester ant), though smaller sizes were not tested. Schoville et al. (2009) tested the preference of *P. occidentalis* ants for three different sizes of glass beads: small (~1.5-2.5 mm diameter; 11 mg weight), medium (2.5 mm diameter; 25 mg weight), and large (4.0 mm diameter; 75 mg weight). Their results showed that the ants preferentially recovered the medium sized beads (66 percent of foraged beads) over the small (22 percent of foraged beads) and large beads (11 percent of foraged beads).

The medium and small beads were also collected from farther away (up to 48 meters) than the large beads (up to 14 meters). That observed preference for medium sized glass beads is congruent with prior studies of natural *P. occidentalis* ant mounds that found that the individual gravel clasts on the mound averaged 25 mg in weight, 3.76 mm in width, and 2.76 mm in length (Nagel, 1969). Those results also suggest a preference for elongated rather than spherical objects, a fact also anecdotally reported by Clark (1966) who noted ant mounds situated on black shales had preferentially collected elongated selenite crystals over rounded carbonate nodules. Such a preference may explain the large number of lagomorph teeth recovered from these ant mounds, and the fact that some of the smallest taxa sampled in this study are represented by elongated partial to complete jaws with teeth rather than isolated teeth (e.g., *Heliscomys hatcheri*). However, shape preferences in species of *Pogonomyrmex* has not been rigorously tested in the same way that overall size has been, so the degree of bias towards one shape over another remains uncertain.

While there is a clear size bias practiced by the ants, studies show it is a selection preference but not an exclusive preference, as they do collect objects smaller and larger than their preferred size or weight range, just at a lower rate (Schoville et al., 2009). Their sampling preferences can also be impacted by the size or weight of material available to forage. On ant mounds situated adjacent to a trail composed of gravel with an average maximum size of 6.7 mm, the average size of gravel returned to the mound was 4.7 mm (Todd and Schoville, 2001), higher than the average maximum size of 3.76 mm reported by Nagel (1969). Additionally, native gravel recorded from a rebuilt *Pogonomyrmex salinus* mound averaged 17.1 mg (~25 percent of total collection) while the average weight of the experimental aquarium gravel introduced to the environment to study their mound building behavior was 22.4 mg. Thus, it is clear that these ants do not sample randomly from the available range of mound building material, though the average size or weight of recovered objects in influenced by the set of available objects for sampling. Similar to how shape preference has not been rigorously tested in these ants, it is not certain to whether the size or the weight (or both) of the foraged objects is the more important factor influencing the selection preferences of these ants.

Another potential bias that has been tested is the color of the foraged objects on the ant mounds. Smith and Tschinkel (2005: 872) found no significant preference by *P. badius* ants when they were offered equal numbers of red, yellow, green, and blue pieces of toothpicks. While multiple colors of glass beads were used in the study by Schoville et al. (2009), they were used to denote distances from the ant mound and no test for color preference was performed in that study. Reynolds (1991: fig. 1) also used five different colors of aquarium gravel to evaluate foraging distance in *P. salinus* (turquoise, purple, blue, green, and white, from closest to farthest from mound). However, they also recorded the number of objects of each color placed on the mound and tested for significant differences between the different colors and for a correlation with the distance of each color from the mound. That study found no correlation between distance from the mound and the amount of each color of gravel foraged but did find significant differences between all of the colors except purple and white, which were equally abundant (Reynolds, 1991: table 1). The color closest to the mound, turquoise, was the least abundant, while blue gravel, which was the middle band amongst the other colors, was most abundant (aside from native gravel). These results suggest that there may be some color related bias in *P. salinus*, despite none being documented in *P. badius*. This differential result could indicate variable bias against color in different species of *Pogonomyrmex*, especially since *P. badius* typically forages charcoal fragments to place on their mounds while other species forage coarse sand and gravel from the local environment. Thus, at this time the possibility cannot be ruled out that *P. occidentalis* exhibits a bias for particular colors of foraged objects. This could have an impact on this study in that fossils exposed on the surface for greater lengths of time tend to have their colors altered (typically becoming lighter colored) and a preference for or against lighter colors by the ants could impact the potential for downslope transported specimens to be placed on the mound.

The observations summarized above impact the interpretation of the results of the current study in several ways. First, the vast majority of specimens in this study were likely foraged from the surface by the ants, but a small contribution from subsurface excavations cannot be ruled out. Thus, taxa only recorded from one or two specimens on an ant mound could have been sampled from the subsurface, while more abundant taxa were likely surface collected. Second, it is clear that there is the potential for significant downslope transport of micromammal specimens into the foraging range of all of the sampled ant mounds, obscuring the local first appearances of these taxa. Third, the data reported by Schoville et al. (2009) indicate most of the fossils collected from each ant mound was foraged within 20 meters of the mound, with specimens sparsely collected out to at least 48 meters from the mound. This fact has little impact on Orellan and younger taxa, where downslope transport can move specimens into close proximity to the ant mound. Conversely, local last appearances of Chadronian taxa within the sampled stratigraphic section should serve as reliable upper bounds for the true

distribution of those taxa, providing insight into the position of the Chadronian-Orellan boundary. Finally, the reported faunal list is certainly impacted by size and or weight related selection biases exhibited by the ants and may be impacted by biases for or against certain shapes and colors. Taken together, these facts indicate the collection of fossils described in this study should not be treated as an accurate reflection of the fauna or the thanatocoenosis (*sensu* Clemens, 1964) of any specific stratum from the study area.

Biostratigraphic Assessment—Biostratigraphic assessment is typically carried out by identifying local first appearance datums (FADs) of previously identified index taxa within a stratigraphically controlled collection. FADs are preferred over last appearance datums (LADs) because it is difficult to determine if the absence of a taxon from a collection is a real absence in the sampled fauna or the result of insufficient sampling or collection biases. Alternatively, the identification of a taxon that elsewhere first appears or is restricted to a specific biozone provides strong support for assigning a fauna to that biozone, especially when multiple such taxa are present. This was the first method used in this study to assess the stratigraphic position of the Chadronian-Orellan boundary in relation to UPW in the study area. The lowest set of ant mounds (ant mounds 1-6: Table 48) are situated well below the previously suggested level of the Chadronian-Orellan boundary to the north at Toadstool Geological Park and Campground (2 meters [±5 meters] above the UPW: Zanazzi et al., 2009) and should preserve a late Chadronian fauna lacking in taxa that elsewhere first appear in the Orellan. It was possible to work our way up the faunal lists of the ant mounds at each successive stratigraphic interval and identify first occurrences Orellan index taxa are, along with disappearances of Chadronian taxa.

Of the 81 taxa identified from the full ant mound collection (not counting *Palaeolagus haydeni*), 65 were identified to the species level, making them the most useful for biostratigraphic analysis. Ten of those taxa are new species without previously documented biostratigraphic distribution, making them uninformative in the first round of biostratigraphic assessment. An additional 10 taxa have biostratigraphic ranges that cross the Chadronian-Orellan boundary, making them uninformative for this study. Of the remaining 45 taxa, 35 elsewhere first appear in Orellan or younger biozones (Table 47) and are most useful for attempting to determine the stratigraphic position of the Chadronian-Orellan boundary.

In practice, this strategy did not work (Table 47). In fact, an opposite pattern was recorded in the stratigraphic collection than was expected. All the 27 taxa with Orellan or younger FADs that were recovered from the upper set of ant mounds were also present in the lower set of ant mounds (Tables 47, 48; Figure 45). An additional six taxa with Orellan or younger FADs are present in the middle set of ant mounds, with all but one (*Eutypomys* sp., cf. *E. hibernodus*: 1 specimen) also present in the lower set of ant mounds. Two final taxa with Orellan or younger FADs are restricted to the lower set of ant mounds (Table 47). Not only is there no clear lower extent of the distribution of these Orellan and younger taxa but they also make up the majority of the specimens identified in this study (69.9 percent) and the four most abundant taxa with Orellan, or younger FADs were recovered from every ant mound (*E. elegans*, *H. fugax*, *A. relictus*, *W. viduus*: Table 47).

Given these data, two quick alternative interpretations could be made that appear erroneous. The first is that the Chadronian-Orellan boundary in the study area is situated lower than seven meters below the UPW. The second is that the Chadronian-Orellan boundary does occur within the stratigraphic range sampled in this study and the Orellan taxa in the lower set of ant mounds represent biostratigraphic range extensions for these taxa. The preferred hypothesis focuses on the possibility of downslope transport of microvertebrate fossils to within the foraging range of these ant mounds as detailed above. Given the close proximity of these ant mounds to vertically extensive exposures of the Brule Formation, the placement of these ant mounds within or adjacent to seasonal streams, and the contrast between the typical highly fossiliferous Brule Formation and the previously reported low productivity of the 'Chadron C' portion of the Big Cottonwood Creek Member below the UPW (Ostrander, 1985), it is likely that microvertebrate fossils originally derived from Orellan (and possibly younger) faunae were transported downslope through the combined actions of erosion and ant foraging, overprinting an Orellan faunal signal on all of the sampled ant mounds. As a result, using the local FADs of typical Orellan or younger taxa to identify the stratigraphic position of the Chadronian-Orellan boundary is not possible in this study.

Given this downslope contamination of Orellan specimens, an alternative approach of tracking the local LADs of taxa elsewhere restricted to Chadronian faunae was used to estimate the position of the Chadronian-Orellan boundary. This approach was used in part because a plausible natural mechanism could not be identified that would result in the upslope transport of microvertebrate specimens other than the ants bringing up from beneath while tunneling. Thus, the recorded local LADs of Chadronian taxa recorded in this study should provide reasonable minimum estimates of their stratigraphic distributions.

Eleven taxa identified in this study (ten species and one identified only to genus: Table 49) are elsewhere only known from Chadronian faunae. These taxa are represented by 73 specimens, or just 1.2 percent of the

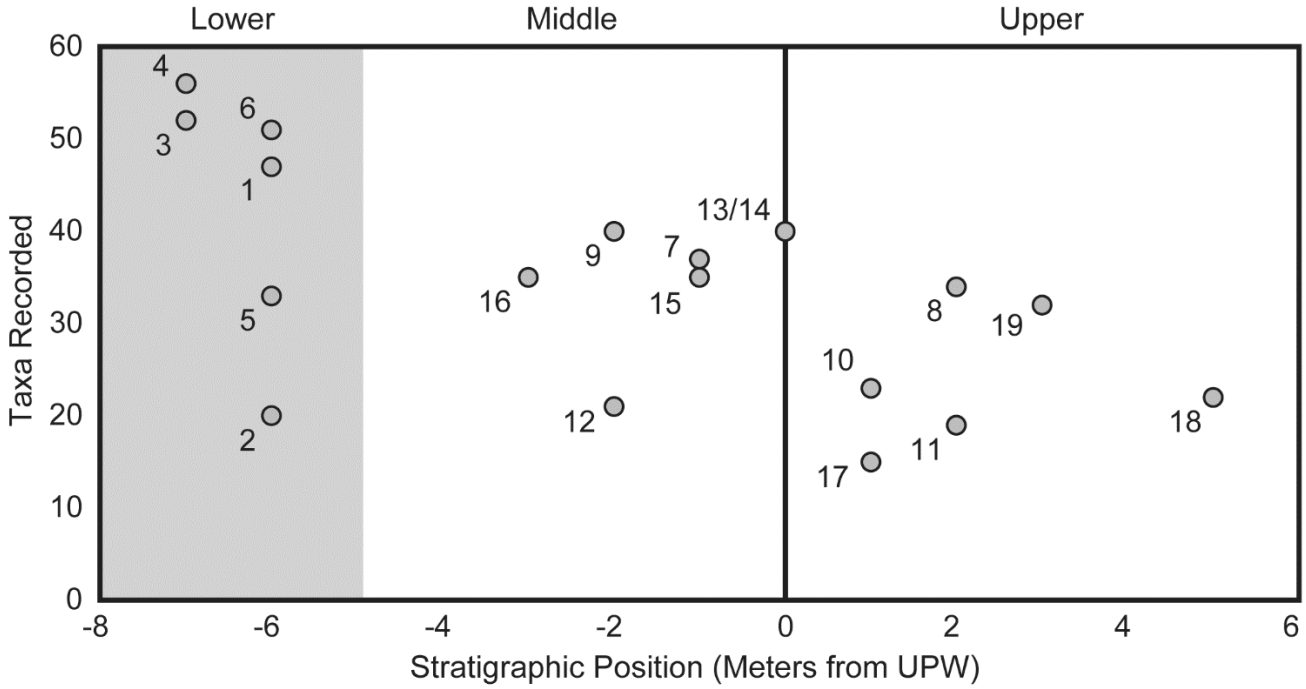

FIGURE 45. Graph of the number of taxa sampled at each ant mound versus the stratigraphic position of each ant mound relative to the position of the upper purplish-white layer (UPW). The lower, middle, and upper divisions correspond to the ant mound groupings defined in Table 48.

specimens identified in this study. The stratigraphic distribution and number of referred specimens recovered at each interval was recorded for these taxa based on the stratigraphic placement of each ant mound (Table 49). Nine of the 11 taxa are recorded from the lower set of ant mounds (seven to six meters below the UPW), represented by 52 specimens. The other two taxa (*M. paradoxus* [n=2] and *Apternodus* sp., cf. *A. major* [n=1]) along with six other taxa are recorded from the middle set of ant mounds (three to zero meters below the UPW), represented by 18 specimens. Three of those taxa are sampled from the upper set of ant mounds (one to five meters above the UPW), represented by just three specimens. Taken together, the distribution and relative abundance of these taxa provides strong support for the lower set of ant mounds being positioned on rocks that preserve a late Chadronian fauna. Sampling from the middle set of ant mounds shows a marked decrease in both the number of Chadronian taxa and specimens, with only three taxa persisting above the UPW.

Of the three taxa only occurring in ant mounds situated above the UPW, two are species of the insectivore *Micropternodus* (Table 49). One of them, *Micropternodus montrosensis*, is only known from Chadronian faunae reported from the Pine Ridge Escarpment (Ostrander, 1983, 1985). The other species, *Micropternodus borealis*, is reported from Chadronian faunae across the Great Plains region (Montana, Nebraska, North Dakota, and Wyoming: Russell, 1960; Ostrander, 1985; Tabrum et al., 1996; Tabrum et al., 2001; Kihm and Schumaker, 2004). *Micropternodus* does persist across the Chadronian-Orellan boundary (e.g., Stirton and Rensberger, 1964) but these two species are previously only recorded from Chadronian faunae. The only other taxon sampled above the UPW is the eomyid rodent *Aulolithomys vexilliames*, which is elsewhere only recorded from the Chadronian portion of the section at the Flagstaff Rim locality in Wyoming (Korth and Emry, 1997; Emry and Korth, 2012) and the genus is not reported from younger faunae. It is possible that these taxa could represent range extensions into the Orellan but given the absence of these taxa from ant mounds above this level that conclusion is not supported at this time.

Biostratigraphic Distribution of New Species—Ten new species were identified in this study (Table 50). While those taxa obviously do not have previously recorded biostratigraphic ranges, some inferences can be made by comparing the reported stratigraphic distributions of these new taxa (Table 50) to those of taxa elsewhere restricted to the Chadronian (Table 49). Two taxa (*Paradjidaumo patriciae* and *Ischyromys brevidens*) were recorded at all sampled ant mounds, demonstrating they were present in the overlying Orellan fauna. Whether they were also present in the Chadronian fauna or if their presence on the lower ant

mounds is solely the result of downslope transport is uncertain. Three other taxa (*Costepeiromys attasorus*, *Cedromus modicus*, and *Litoyoderimys grossus*) were less abundant but were sampled from all three stratigraphic groups of ant mounds and all three are recorded from at least one of the two highest stratigraphic intervals sampled in this study (Table 50). These taxa are considered present in the overlying Orellan fauna, though whether they were also present in the underlying Chadronian fauna is uncertain. If this inference is correct, this would be the youngest occurrence of the genus *Litoyoderimys*, which is elsewhere restricted to Chadronian and older faunae (Wood, 1974; Wilson, 1977; Emry and Korth, 1993).

The cylindrodontid rodent *Siouxlindrodon sullivani* is moderately abundant in this collection (n=40) and is recorded from all six mounds within the lower set of ant mounds but is absent from all of the other ant mounds (Table 50). These factors strongly support the recognition of this taxon as having a Chadronian LAD, making it the most abundant taxon sampled in this study with a Chadronian LAD. Ostrander (1985: p. 228) noted the presence of an indeterminate genus and species of cylindrodontid rodent at the Raben Ranch local fauna. This material was not examined, so it is uncertain if those specimens are also referrable to this taxon.

The eomyid rodent *Yoderimys massarae* is less abundant (n=8) but is also limited to the lower set of ant mounds, recorded at the four best-sampled ant mounds in that interval (Table 48). Elsewhere, all other described species of *Yoderimys* are restricted to Chadronian faunae (e.g., Wood, 1955; Kihm, 1987; Wilson and Runkel, 1991; Pearson and Hoganson, 1995; Storer, 1996) and Ostrander (1985) noted the presence of *Yoderimys bumpi* or *Yoderimys* sp. at four of the six Chadronian sites he reviewed from Sioux County, Nebraska. Based on those data, *Y. massarae* is recognized as having a Chadronian LAD.

Six specimens were referred to the insectivore *Oligoryctes tenutalonidus* in this study, half from the lower set of ant mounds and half from the middle set. The highest local occurrence of *O. tenutalonidus* is from an ant mound situated on the UPW (Table 50), consistent with the last appearances of many of the Chadronian taxa sampled in this study (Table 49). *Oligoryctes cameronensis*, elsewhere restricted to Chadronian faunae (e.g., Hough, 1956; Van Houten, 1964; Tabrum et al., 1996, 2001; Kihm and Schumaker, 2004), was reported from four of the six Chadronian faunae in Sioux County, Nebraska discussed by Ostrander (1985), and was recorded up to one meter below the UPW in this study (Table 49). The only other described species, *Oligoryctes altitalonidus*, was not sampled in this study but elsewhere in the Great Plains region persists across the Chadronian-Orellan boundary (e.g., Emry, 1992; Tabrum et al., 2001). *O. tenutalonidus* is tentatively identified here as having a Chadronian LAD, though additional sampling above the Chadronian-Orellan boundary may contradict that interpretation.

The remaining two newly recognized species, *Kirkomys miriamae* and *Protansomys gulottai*, are each only known from three specimens. The former is the earliest report of the genus, which elsewhere first appears in Whitneyan faunae (e.g., Korth, 2014). Despite being restricted to the lower set of ant mounds (Table 50), additional sampling is needed before a Chadronian LAD can be confidently inferred for this taxon. *Protansomys gulottai* is a new genus and species with no other referred species. Its highest occurrence in the local section is from an ant mound situated two meters above the UPW (Table 50). Given the low sample size and high stratigraphic placement, no a biostratigraphic distribution of this taxon can be proposed at this time.

Position of the Chadronian-Orellan Boundary—Overall, there is a clear pattern of decreasing abundance and diversity of Chadronian taxa through the sampled stratigraphic section (Table 51). The observed stepwise pattern of local LADs is likely at least partially the result of incomplete sampling of the youngest portions of these lineages given that it is unlikely that the youngest possible occurrence of every taxon would be recovered without intensive sampling. However, while the stepwise pattern of stratigraphic disappearances of these taxa is likely at least in part a sampling artifact, the overall trend of decreasing abundance of Chadronian taxa is interpreted as a real signal in the stratigraphically controlled data.

The identification in this study of three new taxa that are restricted to the Chadronian biozone increases the number of Chadronian taxa sampled in this study to 14 (13 out of a total of 65 taxa identified to the species level). These taxa are represented by 126 specimens, or 2.1 percent of the total number of non-leporid specimens identified in this study. Chadronian taxa are much more abundant from the lower set of ant mounds (seven to six meters below the UPW), both in terms of the number of taxa present and the number of specimens referred to those taxa (Table 51). However, some caution is warranted when interpreting those numbers because 45 percent of the total specimens identified in this study were from the lower set of ant mounds, as opposed to 37 percent from the middle set and 18 percent from the upper set. This can be corrected for differential sampling by comparing the rate of sampling for Chadronian taxa at different stratigraphic intervals in this study rather than the raw number of specimens identified (Table 51). These values show that the increased diversity and abundance of Chadronian taxa from the lower set of ant mounds is not solely a factor of increased sampling from

that stratigraphic interval. The lowest stratigraphic intervals produced one specimen referrable to a Chadronian taxon for every 24 to 28 identifiable specimens collected. This rate decreased to one out of every 92 to 128 identifiable specimens collected for the middle set of ant mounds and fell to a low of one out of every 158 to 206 specimens from ant mounds situated one to two meters above the UPW that produced Chadronian taxa (Table 51).

The decreasing rate of recovery of Chadronian taxa in relation to higher stratigraphic position could be influenced by several factors, including: 1) downslope transport and accumulation of specimens of Chadronian taxa, artificially increasing the number of specimens recovered from the lower set of mounds and decreasing the number recovered from the middle and upper sets (if present at those elevations); 2) the presence of a transitional Chadronian-Orellan fauna with a decreasing abundance of Chadronian taxa leading up to the Chadronian-Orellan boundary; and 3) the sampled stratigraphic interval contains the Chadronian-Orellan boundary, placing an upper limit on the recovery of Chadronian taxa. It is likely that the first factor somewhat impacts the sampling rate of Chadronian taxa given the clear evidence of downslope transport of Orellan taxa throughout the sampled stratigraphic interval. The second factor may be impacting this collection but that hypothesis is difficult to test solely based on specimens collected from ant mounds; instead, detailed sampling of *in situ* specimens obtained via screen washing rocks from different stratigraphic intervals would provide the best test of that hypothesis. The final hypothesized factor, the presence of the Chadronian-Orellan boundary within the middle to upper portion of the sampled stratigraphic interval best explains the observed data and is likely the most important factor contributing to the observed distribution of Chadronian taxa in this study.

The interpretation of these data accepted here is that the Chadronian-Orellan boundary is situated near the level of the UPW. Refinement of that estimation requires study of the stratigraphic sampling ranges of individual ant mounds in this study (Figure 44: methods discussed above). As discussed above, surface gathering activities are more likely to result in the recovery of microvertebrate fossils by the ants than subsurface excavations. No Chadronian taxa are sampled from ant mounds 19 and 18, which are situated at three meters and five meters above the UPW, respectively. Ant mound 18 samples down to three meters above the UPW via surface gathering and could potentially sample down to two meters above the UPW via subsurface excavations. Chadronian taxa are absent from this ant mound but only 71 identifiable specimens were found, which is less than the average sampling rate of Chadronian taxa from the middle to upper portion of the sampled stratigraphic range (Table 51). The stratigraphic sampling interval of ant mound 19 completely overlaps that of ant mound 18 (Figure 44) and 492 identifiable specimens were recovered from this mound (Table 48), which should be sufficient to record the presence of at least one Chadronian taxon even at the lowest reported sampling rate (206 specimens: Table 51). The fact that Chadronian taxa are absent from the combined collection from these two ant mounds (n=563: Table 48) provides support for the hypothesis that the Chadronian-Orellan boundary is situated below the surface gathering range of these ant mounds (two meters above the UPW: Figure 44).

The highest stratigraphic recovery of Chadronian taxa in this study was at ant mounds 8, 11, and 17 (one specimen each), which are situated between one and two meters above the UPW. A fourth ant mound (10) is also situated within this interval (+1 meter: Table 48) but produced no Chadronian taxa. These four ant mounds produced a combined total of 521 identifiable specimens, so it is not surprising that one of these mounds failed to sample Chadronian taxa given the average sampling rate through much of the sampled stratigraphic interval. The lowest stratigraphic interval subjected to surface gathering by these four mounds ranged from one meter above the UPW to one meter below the UPW and possible sampling via subsurface excavations ranged from one to two meters below the UPW (Figure 44). Given the lack of plausible mechanisms noted in this study for upslope displacement of microvertebrate fossils, the recovery of three Chadronian taxa from this interval either indicates the Chadronian-Orellan boundary is within or above this interval, or these three taxa (*M. montrosensis*; *M. borealis*; and *A. vexilliames*) persisted for a short time after the Chadronian-Orellan boundary.

Six ant mounds are situated either on or up to two meters below the UPW (7, 9, and 12-15: Table 48). Those ant mounds recorded a higher sampling rate for Chadronian taxa than those situated higher (Table 51). Eight Chadronian taxa are recorded from this interval, including the three recorded at the higher stratigraphic interval (Table 51). The lowest surface gathering interval for these six mounds ranges from two to four meters below the UPW, and the potential subsurface excavation interval ranges from four to five meters below the UPW (Figure 44). The increased abundance and diversity of Chadronian taxa recorded from these mounds indicates the Chadronian-Orellan boundary is positioned above the lowest intervals sampled by these mounds.

Given these data, it is proposed here that the Chadronian-Orellan boundary within the study area is situated at the UPW with a margin of error that accounts for the uncertainty of the stratigraphic intervals sampled by these ant mounds of ±2 meters. This proposed

placement is within the lower range of the estimate provided by Zanazzi et al. (2009) of 2 meters above the UPW ±5 meters based in part on artiodactyl biostratigraphy. Thus, these two hypotheses are potentially in agreement with each other, though it is certainly possible that local differences in sedimentation rate could result in variation in the position of the Chadronian-Orellan boundary between the two study areas even over this relatively short distance. These hypotheses are also in agreement with the recognition very early on in this area that the UPW served as an approximate boundary between the Chadronian and Orellan faunae in this region (e.g., Schultz and Stout, 1938, 1955).

Sampling—This study was based on 5,938 identifiable teeth or jaws from small-bodied mammalian taxa, not counting those specimens referred to the leporid *Palaeolagus haydeni* which were not cataloged individually. Sampling of these non-leporid specimens at individual ant mounds ranged from a low of 70 specimens (ant mound 18) to a high of 611 specimens (ant mound 6). One question often raised in microvertebrate fossil studies concerns the minimum sample size required to adequately sample a fauna (e.g., Jamniczky et al., 2003, 2008). Of course, the answer to that question will vary depending on sampling strategy, taxa of interest, diversity of the sampled fauna, and other factors. However, the large sample size available in this study and the range of variation in sample sizes between individual ant mounds allows some questions regarding sampling strategies for ant mound collections to be investigated.

The entire set of specimens of this study were examined at one time, so there is no data on the effects of successive sampling on the number or relative abundance of taxa recorded either from a single ant mound or from the entire collection. An additional complicating factor when comparing results from different ant mounds is that the mounds situated lower in stratigraphy sampled a larger total set of taxa as a result of the downslope transport of specimens from the Orellan fauna, while those higher in stratigraphy had a smaller total number of taxa to sample because they were not sampling Chadronian taxa. This stratigraphic limitation to taxon sampling can be seen by simply graphing the number of taxa recovered from ant mounds situated at each stratigraphic interval (Figure 45). However, a few broad generalizations related to sample size can be reported based on these data. Regardless of individual sample sizes, every ant mound produced a unique list of sampled taxa that is not replicated by or redundant with any other single ant mound, and nine of the eighteen ant mound samples recorded unique taxon occurrences (1, 2, 3, 4, 5, 6, 10, 13-14 [faunal lists combined], and 15). We can also look at the contributions of each ant mound in compiling the distribution of taxa within each of the three stratigraphic intervals reviewed in Table 47. Of the 18 ant mound collections in this study, only ant mound 12, which has the lowest sample size within the middle group (n=103: Table 48), does not contribute a unique record of the presence of a taxon recorded in Table 47. However, ant mound 12 does provide the local highest stratigraphic occurrence of the Chadronian taxon *Aulolithomys* sp., cf. *A. bounites* recorded in this collection (Table 49), so every ant mound does provide unique information relevant to this study.

There are two instances where ant mounds situated at the same stratigraphic interval produced similar numbers of identifiable specimens, providing clear points of comparison that largely avoid any biases caused by stratigraphic differences in taxon abundance. At the lowest stratigraphic interval sampled in this study (seven meters below the UPW), ant mounds 4 and 3 produced the second and third highest number of identifiable specimens (596 and 571, respectively: Table 48). Their stratigraphic position means that they sampled both from the adjacent late Chadronian fauna and from the downslope transported Orellan fauna, providing them the opportunity to sample the largest number of taxa of any ant mounds in this study. Despite their similar sample sizes, ant mound 3 recorded the presence of seven more taxa than ant mound 4 (Table 48). However, the less diverse ant mound 4 recorded the presence of nine taxa that were not recorded from ant mound 3, and a total of 15 taxa recorded at ant mound 3 were not recorded from ant mound 4. As a result, of the 66 taxa recorded at this stratigraphic interval, only 42 (64 percent) were recorded from both ant mounds. While these two ant mounds together produced a total of 1167 specimens, the four ant mounds situated one meter higher in stratigraphy (-6 meters from UPW: Table 48) produced 1469 specimens, roughly 25 percent of the total specimens included in this study. Despite that intensive sampling, six taxa that are recorded in the middle or upper groups of ant mounds (Table 48) were not recorded from any of the four ant mounds situated six meters below the UPW but were recorded from at least one of the ant mounds situated seven meters below the UPW (*Blacktops* sp.; *Cylindrodon nebraskensis*; *Litoyoderimys grossus*; *Oligoryctes* sp., cf. *O. cameronensis*; *Oligoryctes tenutalonidus*; *Stibarus* sp., cf. *S. obtusilobus*).

The two ant mounds situated one meter below the UPW produced 376 and 368 identifiable specimens, respectively (7 and 15: Table 48). They also recorded the presence of a similar number of taxa, 37 at ant mound 7 and 34 at ant mound 15, resulting in similar taxon sampling rate (TSR) values of 10.2 and 10.8, respectively (Table 48). Despite these similarities, only 60 percent (27 out of 45) of the taxa recorded from this stratigraphic interval are recorded at both ant mounds,

similar to the percent of overlapping taxa noted in the two mounds situated seven meters below the UPW discussed above. These data indicate that increased sampling would be needed to sample the full fauna present at a given stratigraphic interval from a single mound.

It is logical to expect that sampling relatively rare taxa is difficult to accomplish without intensive sampling, but these data also show that consistent sampling of the most common taxa from a study site can also be difficult. Of the 20 most abundant non-leporid taxa recorded in this study (Table 47), all but one (*Siouxlindrodon sullivani*: n = 40) are inferred present in the Orellan fauna. This means that the remaining 19 taxa should be available for sampling at all of the ant mounds in this study given the documented downslope transport of Orellan taxa. This is the case for the six most abundant taxa recovered in this study, which are known from a total of 4,345 specimens, or 73 percent of the total collection, and the least abundant of those species (*Willeumys viduus*) is known from 268 specimens (Table 47). The remaining thirteen taxa are known from between 40 and 133 specimens, indicating that it requires between 133 and 268 total specimens (between 2.2 percent and 4.5 percent of the total collection) for a species to be sampled at all of the ant mounds.

Consistent sampling of the most abundant taxa is undoubtedly impacted not just by the total sample size, but also by the sample sizes for individual ant mounds. If the four ant mounds with less than 100 specimens are eliminated (2, 11, 17, and 18), then 10 of those 19 taxa (all among the 14 most abundant taxa) are sampled at the remaining 14 ant mounds. Increasing the cutoff to 200 specimens per ant mound eliminates two more ant mounds (10 and 12) and results in 15 out of 19 of those taxa being sampled from the remaining 12 ant mounds. In fact, only one taxon in the top 15 most abundant species (*Scottimus exiguus*: n = 97) is not recorded at all remaining ant mounds when a limit of 200 specimens per ant mound is imposed. Recovery of all 19 of these taxa from every ant mound requires a minimum of 400 specimens sampled per ant mound, which only seven of the ant mound collections included in this study achieve (Table 48). These data provide additional support for the recognition of *S. sullivani* as a Chadronian taxon, given that it is known from 40 specimens that were recovered from all six ant mounds in the lower group regardless of individual sample sizes (Table 48), and it is completely absent from the remaining 12 ant mound collections in the middle and upper groups.

One final metric that can be examined is the rate at which taxa are sampled at each ant mound, here termed the Taxon Sampling Rate (TSR: Table 48), which is obtained by dividing the number of identifiable specimens recovered from an ant mound by the number of taxa recorded at that ant mound. Overall, TSR values increase as the number of specimens recovered from an ant mound increases (Figure 46A). This trend fits with expectations that as the number of taxa recorded at an ant mound increases and there are fewer additional taxa left to sample, it will become progressively more difficult to retrieve any remaining taxa. However, a closer examination reveals some stratigraphic patterns that can be used to inform future sampling decisions in the study area and elsewhere. All six ant mounds that produced less than 150 specimens have similarly low TSR values (3.3-5.7: Table 48) suggesting the early rate of taxon sampling is relatively constant in all three stratigraphic groupings, averaging 20 taxa identified from the first 93 specimens collected. If these numbers of taxa are subtracted from specimens from the remaining 12 ant mound collections, a corrected taxon sampling rate from the resulting values (cTSR: Table 48), and a stratigraphic trend is revealed (Figure 46B). With increased sampling at ant mounds in the upper group cTSR values quickly increase, suggesting the overall fauna is relatively well-sampled despite the fact that fewer total taxa are recorded from those ant mounds (Figure 46C). A similar trend is seen in the middle group of ant mounds, though the increase in cTSR is less dramatic (Figure 46B) and the total number of taxa sampled at those ant mounds is higher (Figure 46C). A different trend is noted from ant mounds in the lower group, where cTSR values only slightly increase with increased sampling (Figure 46B) and the number of taxa recorded at each ant mound continues to steadily increase (Figure 46C).

The data outlined above can be used to make a few inferences about the faunae sampled in this study and the adequacy of our sampling methods. First, it is clear that the number of taxa available for the ant mounds to sample decreases up section through the sampled stratigraphic interval (Figures 45 and 46). The recovery of more taxa from the lower stratigraphic intervals is not solely the result of increased sampling at that level as shown by the different rates of increase in cTSR for ant mounds in the three stratigraphic groupings (Table 48). Increasing taxonomic sampling beyond 35 taxa per ant mound is more difficult for the upper group of ant mounds while the middle group of ant mounds faces similar difficulty around the forty taxa per ant mound level. Alternatively, ant mounds in the lower group showed only a slight increase in cTSR even after sampling more than 50 taxa (Table 48, Figure 46). It is hypothesized that this pattern is related to the position of the Chadronian-Orellan boundary near the UPW (the boundary between the upper and middle group of ant mounds), limiting the number of taxa that could be sampled by the upper group of ant mounds.

Comparison of cTSR values reveals that any additional sampling focused on recovering additional taxa thus far unrecorded from the collection would best

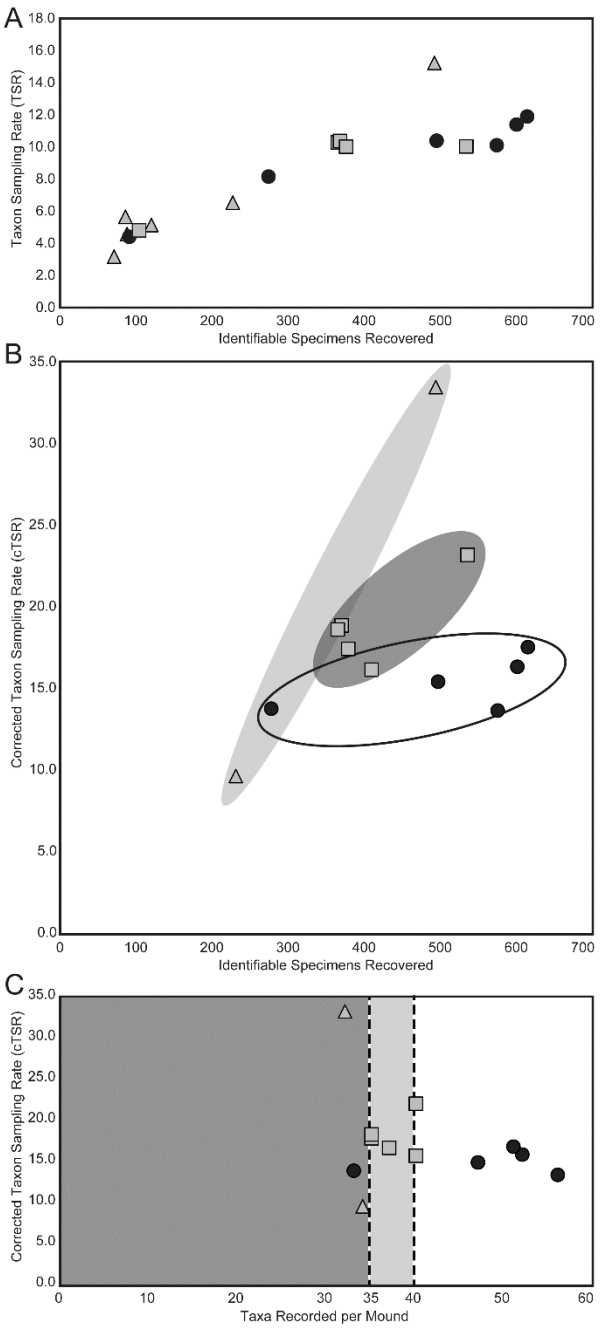

FIGURE 46. Graphs of taxon sampling rates for the 18 ant mounds sampled in this study (and mounds 13 and 14 combined). A, graph of taxon sampling rate (TSR) versus the number of identifiable specimens recovered at each mound. B, graph of corrected taxon sampling rate (cTSR) versus the number of identifiable specimens recovered at each mound. C, graph of corrected taxon sampling rate (cTSR) versus the number of taxa recorded at each mound. All data provided in Table 48. Grey triangles denote upper group ant mounds, grey squares denote middle group ant mounds, and black circles denote lower group ant mounds. The Y axes in A and B are to scale. In B, ellipses highlight general trends in the different groups, but are not mathematically calculated. In C, the dark grey region highlights the area with 35 or less taxa per ant mound and the light grey region highlights the area with between 35 and 40 taxa recorded per ant mound.

be focused on ant mounds within the lower group (Table 48), all of which have relatively low cTSR values and a steady rate of continued taxa sampling (Figure 46). However, if the goal of additional sampling is to continue documenting the highest stratigraphic occurrences of Chadronian taxa to better document the position of the Chadronian-Orellan boundary, additional sampling should be focused on ant mounds within the upper and middle groups of ant mounds. These two objectives would require different amounts of collecting effort to implement, as ant mounds within the lower group sample an additional taxon (new to that mound, not necessarily to the study as a whole) for every 14 to 17 additional specimens recovered (Table 48), while the rate of sampling specimens referrable to Chadronian taxa from the middle and upper ant mounds is one new specimen for every 92 to 206 specimens recovered (Table 51). As a result, a few hundred new specimens from lower ant mounds would likely provide new information on taxa that were either rare or previously unreported in this study, while several thousand specimens would likely be required to better assess the stratigraphic position of the Chadronian-Orellan boundary in the study area.

In terms of broader sampling strategies to implement when conducting ant mound studies, these data provide some useful insights. There are clear advantages to sampling multiple ant mounds within a given stratigraphic interval as opposed to focusing sampling efforts on a single mound. As outlined above, every ant mound in this study recorded a unique combination of taxa and even heavily sampled ant mounds at the same stratigraphic interval only shared around two-thirds of taxa in common. It may be that sampling ant mounds at different horizonal locations within the same stratigraphic interval allows for different depositional environments or habitats to be sampled, expanding the list of taxa recorded from a given stratigraphic interval. Regardless, increasing the number of sampled ant mounds in a study of this nature has clear advantages over repetitive, targeted collecting from only a few ant mounds. In terms of sample sizes per ant mound, the best results (in terms of consistent sampling of more abundant taxa) were obtained in this study when at least 400 identifiable specimens were recovered from a given ant mound. Of course, in many instances the number of identifiable specimens recovered from an ant mound is beyond the control of the researchers and depends on the number of specimens available to the ants and their rate of collection. However, as mentioned above, even a relatively small sample from a unique ant mound typically provides important data relevant to this type of study. Therefore, ant mounds should not be excluded from a study just because they produced a small number of specimens.

Rather, it is suggested here that TSR and cTSR values could be used as a guide for when additional sampling at an ant mound would produce diminishing returns on worker effort and focus would be better spent locating and sampling new ant mounds at the same stratigraphic interval, if present.

CONCLUSIONS

Microvertebrate collections derived from ant mounds are subject to additional taphonomic factors that are either not encountered or whose affects are amplified relative to other collection methods (e.g., screen washing; surface collecting). These additional factors include the large surface area these ants recover fossils from, the possibility of subsurface excavation of fossils, and the downslope transport of fossils derived from younger faunae into the foraging range of the ant mound. As demonstrated above, these factors can be accounted for when interpreting the data derived from the study of an ant mound collection, facilitating use of these collections for conducting some biostratigraphic studies. Unless evidence is presented to the contrary, ant mound collections should be assumed to be subject to downslope transport of younger fossils and the taxon lists compiled from such collections should not be considered representative of a single fauna and possible revisions to first appearances of taxa should be treated cautiously.

Even in instances when downslope contamination can be ruled out, the ants themselves are not unbiased and their selection preferences for or against fossils of different sizes, dimensions, and possibly colors may skew our interpretation of the relative abundance of taxa within a fauna. These biases may also result in some taxa that are present being excluded from a faunal list based solely on specimens derived from ant mounds. As such, when comparing faunal lists from different sites that were generated using different collection methods (e.g., surface collecting, ant mound sampling, screen washing) one must consider the different post-depositional taphonomic biases that could differentially impact those collections before making conclusions regarding faunal or paleoenvironmental differences. Additionally, as reported by prior researchers, the use of ant mound collections for quantitative studies of diversity, relative abundance, or paleoecological inferences is problematic and should be avoided (Clark and Kietzke, 1967; Lofgren, 1995).

All that being said, these cautionary statements regarding the use of microvertebrate collections derived from ant mounds should not be viewed as a reason to avoid the recovery or study of those collections. As was documented over one hundred years ago (e.g., Hatcher, 1896), ant mounds artificially concentrate microvertebrate specimens into easily identified locations that require a relatively small amount of time in the field to collect and return to the lab for further study. There is likely no greater return on field time spent in terms of raw numbers of specimens collected than sampling ant mounds. These collections can be critical for recovering microvertebrate specimens from rocks where they are rare components of the fauna, such as mammalian fossils from many Late Cretaceous deposits in the Western Interior of North America. Even in typically highly fossiliferous units like the White River Group, ant mound collections can provide numbers of difficult to sample small-bodied taxa that would require a substantial investment of time to obtain via other sampling strategies. So long as the factors that can impact these collections are acknowledged and properly accounted for, ant mound sampling should continue to be one of the primary field techniques used to recover microvertebrate fossils.

The use of ant mound sampling in this study resulted in the recovery of over 6,000 identifiable micromammal specimens. That collection contains at least ten new species, a number that may increase with additional sampling given that several other specimens were noted as different from currently described taxa but were lacking in sufficient numbers of specimens to support the naming of a new species. The large sample size also allowed tooth positions that were previously unknown for several taxa to be identified and described for the first time (e.g., *Adjidaumo intermedius*; *Eutypomys hibernodus*, *Ecclesimus tenuiceps*, *Micropternodus montrosensis*) and in some cases the number of specimens here referred to some taxa exceeded the total number of specimens previously referred to that taxon (e.g., *A. intermedius*). These results speak to the benefits of ant mound collections. However, failure to recognize the biases outlined above could have led to many erroneous interpretations of these data. If this collection had been considered to represent a distinct local fauna (*sensu* Wilson, 1959) then numerous biostratigraphic range extensions would have resulted, likely of Chadronian taxa into the Orellan NALMA given the dominance of Orellan taxa in the collection. That incorrect inference could then have led to infer a much lower stratigraphic position for the Chadronian-Orellan boundary within the study area based on the FADs of typically Orellan taxa that would be incompatible with prior interpretations (e.g., Zanazzi et al., 2009). Instead, careful consideration of the sources of fossils recovered on the ant mounds allowed for a different approach to be taken when interpreting these data. The focus on the highest stratigraphic occurrences of Chadronian taxa in this study, rather than the lowest stratigraphic occurrences of Orellan taxa, resulted in a hypothesized position of the Chadronian-Orellan boundary within the study area that fits both

with these data and with previously proposed placements of that boundary.

There are several potential avenues for additional work on this collection. As previously mentioned, the non-mammalian fossils recovered from these ant mounds were distributed to other workers with expertise in those taxonomic groups and future reports on those specimens should follow this study and provide a broader look into the Chadronian through Orellan faunae preserved in this region of Sioux County, Nebraska. A more direct follow-up to this study is also in progress, with mammalian specimens recovered from an additional set of ant mounds situated stratigraphically higher on rocks of the overlying Brule Formation currently being sorted and identified. Those specimens should help clarify which of the taxa identified in this study were derived from the overlying Orellan fauna. That new set of ant mounds may also sample the overlying Whitneyan fauna, which could allow the placement of the Orellan-Whitneyan boundary to be investigated in the study area in a manner similar to that employed in this study for the Chadronian-Orellan boundary. One final project also underway is a re-evaluation of the original set of fossils that formed the basis of the "interesting anthill fauna" reported by Hough and Alf (1956). That study was one of the first to provide a faunal list based on specimens recovered from ant mounds in the White River Group, but questions remain as to the geographic and stratigraphic position of that sample. It is our hope that all of these projects together will help clarify the faunae and history of paleontological collection of the Chadron and Brule Formations in Sioux County, Nebraska.

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TABLES

TABLE 1. Dental measurements of *Herpetotherium fugax* from the Sioux County Ant Mounds. Abbreviations: CV, coefficient of variation; L, anteroposterior length; M/m, molar; Max, maximum; Min, minimum; N, number of specimens; p, premolar; SD, standard deviation; W, transverse width. All measurements in mm.

	M1L	M1W	M2L	M2W	M3L	M3W	M4L	M4W
N	56	58	103	101	69	82	8	8
Mean	1.89	1.68	1.88	1.93	1.83	2.12	1.12	2.04
Min	1.62	1.44	1.59	1.61	1.35	1.80	0.90	1.86
Max	2.24	2.13	2.25	2.27	2.19	2.55	1.33	2.26
SD	0.14	0.12	0.13	0.12	0.15	0.15	0.14	0.12
CV	7.52	7.27	7.08	6.31	8.16	6.93	12.22	5.67

	p3L	p3W	m1L	m1W	m2L	m2W	m3L	m3W	m4L	m4W	m1-m4L
N	12	12	74	75	95	102	72	78	50	50	1
Mean	1.40	0.64	1.80	0.99	1.93	1.12	1.91	1.09	1.74	0.93	7.24
Min	1.21	0.54	1.53	0.82	1.47	0.88	1.52	0.91	1.41	0.70	
Max	1.57	0.70	2.15	1.22	2.33	1.33	2.30	1.34	2.04	1.13	
SD	0.10	0.05	0.12	0.08	0.15	0.09	0.15	0.09	0.15	0.09	
CV	7.39	7.97	6.91	8.17	7.84	8.15	7.74	8.00	8.70	9.22	

TABLE 2. Dental measurements of *Copedelphys stevensoni* from the Sioux County Ant Mounds. Abbreviations: CV, coefficient of variation; L, anteroposterior length; M/m, molar; Max, maximum; Min, minimum; N, number of specimens; SD, standard deviation; W, transverse width. All measurements in mm.

SDSM#	M2L	M2W	M3L	M3W
150622	1.22	1.31	1.13	1.38
150623	1.31	1.47	1.11	1.59
150624	1.17	1.32	1.13	1.46
150625	-	-	1.25	1.51
Mean	1.23	1.37	1.16	1.49

	m1L	m1W	m2L	m2W	m3L	m3W	m4L	m4W
N	4	4	7	7	9	9	8	8
Mean	1.11	0.63	1.29	0.73	1.20	0.69	1.17	0.66
Min	1.04	0.56	1.18	0.63	1.11	0.64	0.93	0.57
Max	1.19	0.69	1.42	0.80	1.33	0.78	1.35	0.73
SD	0.07	0.05	0.08	0.06	0.07	0.05	0.16	0.06
CV	5.93	8.71	6.56	8.28	5.92	7.46	14.06	9.32

TABLE 3. Dental measurements of *Nanodelphys hunti* from the Sioux County Ant Mounds. Abbreviations: CV, coefficient of variation; L, anteroposterior length; M/m, molar; Max, maximum; Min, minimum; N, number of specimens; SD, standard deviation; W, transverse width. All measurements in mm.

	M1L	M1W	M2L	M2W	M3L	M3W	M4L	M4W	M1-M4L
N	6	5	21	19	19	19	6	7	1
Mean	1.33	1.18	1.33	1.55	1.27	1.65	0.69	1.72	4.67
Min	1.21	1.09	1.13	1.38	1.04	1.38	0.61	1.48	
Max	1.50	1.31	1.56	1.68	1.42	1.88	0.77	1.83	
SD	0.11	0.09	0.11	0.09	0.10	0.12	0.06	0.13	
CV	8.17	7.63	8.16	6.11	8.29	7.24	8.93	7.39	

	m1L	m1W	m2L	m2W	m3L	m3W	m4L	m4W
N	24	24	21	21	17	17	11	11
Mean	1.19	0.62	1.32	0.71	1.29	0.70	1.22	0.66
Min	1.04	0.49	1.20	0.63	1.19	0.61	1.07	0.50
Max	1.38	0.72	1.48	0.80	1.43	0.76	1.33	0.78
SD	0.10	0.06	0.08	0.04	0.07	0.05	0.09	0.09
CV	8.00	9.57	5.93	5.33	5.15	6.46	7.15	13.97

TABLE 4. Dental measurements of *Leptictis dakotensis* and *Blacktops* sp. from the Sioux County Ant Mounds. Abbreviations: CV, coefficient of variation; d, deciduous tooth; L, anteroposterior length; M/m, molar; Max, maximum; Min, minimum; N, number of specimens; SD, standard deviation; W, transverse width; +, estimated length, actual length slightly greater. All measurements in mm.

L. dakotensis

	P4L	P4W	P5L	P5W	M1L	M1W	M2L	M2W	M3L	M3W
N	2	2	2	2	1	1	4	2	4	4
M	2.87	2.69	3.06	3.64	3.23	4.96	2.71	4.55	1.94	3.33
Min	2.84	2.53	2.99	3.58			2.37	4.43	1.78	3.10
Max	2.90	2.84	3.12	3.70			2.88	4.67	2.05	3.45

	p5L	p5W	m1L	m1W	m2L	m2W	m3L	m3W
N	6	8	15	17	8	8	10	14
M	4.13	2.39	3.46	2.64	3.09	2.33	3.20	2.17
Min	3.88	2.19	3.30	2.29	2.98	2.16	2.88	1.84
Max	4.38	2.58	3.73	2.98	3.18	2.49	3.48	2.58
SD	0.24	0.16	0.11	0.23	0.09	0.12	0.22	0.19
CV	5.79	6.88	3.26	8.51	2.77	5.03	6.97	8.74

Blacktops sp.

SDSM #	dP5L	dP5W	P5L	P5W	M1L	M1W	M2L	M2W	M3L	M3W
150734	-	-	3.1+	4.5+	-	-	-	-	-	-
156452	-	-	-	-	-	-	-	-	2.46	3.94
156493	-	-	3.4	3.89	-	-	-	-	-	-
156494	3.66	*	-	-	-	-	-	-	-	-

	dp5L	dp5W	p5L	p5W	m1 or m2L	m1 or m2W	m3L	m3W
150768	-	-	-	-	3.64	3.40	-	-
156470	-	-	-	-	3.70	3.29	-	-
156471	-	-	-	-	-	-	4.24	2.71
156473	-	-	-	-	-	-	4.73	2.53
156495	4.63	2.05	-	-	-	-	-	-
156977	-	-	4.82	2.66	-	-	-	-

TABLE 5. Dental measurements of *Sinclairella dakotensis* and *Apatemys* sp. from the Sioux County Ant Mounds. Abbreviations: L, anteroposterior length; M/m, molar; P, premolar; W, transverse width. All measurements in mm.

Sinclairella dakotensis						
SDSM#	P3L	P3W	M2L	M2W	M3L	M3W
156361	-	-	3.24	3.97	-	-
156362	2.18	1.45	-	-	-	-
156547	-	-	-	-	2.88	3.69
	m1L	m1W	m2L	m2W	m3L	m3W
156357	-	-	3.21	2.22	-	-
156358	-	-	-	-	4.82	2.46
156360	-	-	3.45	2.3	-	-
156548	-	-	-	-	5.32	2.60
156969	-	-	3.81	2.42	-	-
156970	3.87	2.19	-	-	-	-
Apatemys sp.						
	m1L	m1W	m2L	m2W	m3L	m3W
156359	2.95	1.71	-	-	-	-
156971	-	-	2.37	1.65	-	-
156972	-	-	2.39	1.70	-	-

TABLE 6. Dental measurements of *Centetodon* from the Sioux County Ant Mounds. Abbreviations: CV, coefficient of variation; L, anteroposterior length; M/m, molar; Max, maximum; Min, minimum; N, number of specimens; P/p, premolar; SD, standard deviation; W, transverse width; †, indicates M1/M2 or m1/m2. All measurements in mm.

Centetodon marginalis										
	P3L	P3W	P4L	P4W	M1L	M1aW	M1pW	M2L	M2aW	M2pW
N	1	1	8	9	8	9	7	2	2	4
Mean	1.23	0.97	1.84	1.88	1.75	2.16	2.52	1.37	2.41	2.33
Min			1.59	1.63	1.63	1.89	2.27	1.35	2.20	2.13
Max			2.04	1.99	2.04	2.34	2.78	1.38	2.62	2.53
SD			0.16	0.12	0.14	0.13	0.17			0.21
CV			8.87	6.20	8.00	6.21	6.78			9.00

	p3L	p3W	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W
N	3	3	19	19	18	18	12	14	23	21
Mean	1.15	0.55	1.62	0.85	1.79	1.12	1.67	1.12	1.51	0.95
Min	1.03	0.50	1.39	0.71	1.49	0.96	1.58	0.98	1.19	0.78
Max	1.28	0.61	1.88	0.97	2.00	1.32	1.89	1.28	1.73	1.09
SD			0.14	0.08	0.14	0.10	0.09	0.11	0.15	0.09
CV			8.91	8.88	7.61	9.15	5.28	9.76	9.87	9.72

Centetodon wolffi						
SDSM#	p4L	p4W	m1L†	m1W†	m3L	m3W
150669	-	-	2.48	1.53	-	-
150676	-	-	2.50	1.42	-	-
150678	-	-	-	-	1.94	1.39
150692	-	-	2.77	2.08	-	-
150700	-	-	-	-	2.39	1.79
150702	-	-	2.03	1.50	-	-
150706	2.06	1.01	-	-	-	-
150709	-	-	2.21	1.80	-	-
156486	2.07	0.99	-	-	-	-
Mean	2.06	1.00	2.40	1.67	2.17	1.59

TABLE 7. Dental measurements of *Proterix minimus* and *Micropternodus* from the Sioux County Ant Mounds. Abbreviations: ht, labial height of protoconid; L, anteroposterior length; M/m, molar; P/p, premolar; W, maximum transverse width; †, indicates M1/M2 or m1/m2; +, estimated length, actual length slightly greater. Measurements in mm.

Proterix minimus		
SDSM #	M1L	M1W
150911	1.67	2.08
150912	1.78	2.31

SDSM #	m1L	m1W	m2L	m2W
150913	1.73	1.06	1.58	1.01
150914	1.97	1.12	-	-
150915	-	-	1.48	0.92

Micropternodus borealis						
SDSM #	P4L	P4W	M1L	M1W	M2L	M2W
150917	1.71+	2.12+	-	-	-	-
156511	2.03	2.29	-	-	-	-

SDSM #	m1L	m1W	m1ht	m2L	m2W	m2ht	m3L	m3W
150920	-	-	-	2.41	2.11	-	-	-
150921	2.31	2.13	-	-	-	-	-	-
150922	-	-	-	-	-	-	-	1.63
150923	2.17	1.71	2.75	-	-	2.75	-	-
156512	-	-	-	2.37	2.22	-	-	-
157008	2.24	1.90	2.85	-	-	-	-	-

Micropternodus cf. *montrosensis*		
SDSM #	P4L	P4W
150918	1.64+	3.37

	m1L†	m1W†	m1ht†	m3L	m3W
150919	-	-	-	2.19	2.90
150960	2.73	2.88	3.21	-	-

TABLE 8. Dental measurements of *Domnina gradata* from the Sioux County Ant Mounds. Abbreviations: a, lower antemolar; CV, coefficient of variation; D, dorsoventral depth (i1 only); L, anteroposterior length; M/m, molar; Max, maximum measurement; Min, minimum measurement; N, number of specimens; P, premolar; SD, standard deviation; W, transverse width. All measurements in mm.

	P4L	P4W	M1L	M1W	M2L	M2W
N	8	7	12	12	12	12
Mean	1.91	1.61	1.95	2.17	1.72	1.96
Min	1.81	1.43	1.85	1.98	1.57	1.71
Max	2.04	1.78	2.04	2.33	1.89	2.13
SD	0.09	0.11	0.05	0.11	0.10	0.13
CV	4.88	6.82	2.79	4.89	5.94	6.46

	a4L	a4W	m1L	m1W	m2L	m2W	m3L	m3W	m1-m3L	i1W	i1D
N	3	3	42	46	39	44	22	26	5	3	2
Mean	0.82	0.90	2.10	1.28	1.80	1.16	1.46	0.89	5.16	0.86	1.03
Min	0.75	0.84	1.88	1.11	1.52	0.93	1.26	0.77	4.72	0.78	1.02
Max	0.90	0.93	2.39	1.44	2.10	1.36	1.63	1.00	5.50	0.91	1.03
SD	0.08	0.05	0.11	0.09	0.11	0.09	0.08	0.07	0.30	0.07	0.01
CV	9.21	5.50	5.24	6.77	5.99	8.15	5.35	7.81	5.88	7.95	0.69

TABLE 9. Dental measurements of *Noritrimylus compressus* from the Sioux County Ant Mounds. Abbreviations: CV, coefficient of variation; L, anteroposterior length; M/m, molar; Max, maximum; Min, minimum; N, number of specimens; SD, standard deviation; W, transverse width. All measurements in mm.

SDSM #	M1L	M1W	M2L	M2W
150865	1.65	1.92	-	-
150866	1.57	1.86	1.11	1.85

	m1L	m1W	m2L	m2W	m3L	m3W	m1-m3L
N	15	16	20	20	5	7	3
Mean	1.90	1.19	1.46	1.03	1.19	0.77	4.22
Min	1.71	1.09	1.37	0.92	1.09	0.61	4.18
Max	2.08	1.33	1.56	1.13	1.37	0.90	4.28
SD	0.10	0.07	0.06	0.05	0.11	0.09	0.06
CV	5.06	5.99	4.32	5.21	9.49	12.20	1.31

TABLE 10. Ratios of mean lengths of lower molars in species of *Noritrimylus* and *Pseudotrimylus.* Abbreviations: L, anteroposterior length; m, molar.

	m3L/m1L	m2L/m1L	m3L/m2L	Reference
Sioux Co. collection	0.60	0.76	0.79	This study
N. compressus	0.64	0.79	0.81	Galbreath, 1953; Repenning, 1967
N. metaxy	0.79	0.87	0.90	Korth, 2020a
N. dakotensis	-	0.94	-	Macdonald, 1970
P. blacki	0.72	0.86	0.84	Martin and Lim, 2004
P. roperi	0.70	0.82	0.85	Wilson, 1960

TABLE 11. Dental measurements of *Oligoscalops galbreathi* and *Oligoryctes tenutalonidus* from the Sioux County Ant Mounds. Abbreviations: L, anteroposterior length; M/m, molar; P/p, premolar; W, transverse width. All measurements in mm.

Oligoscalops galbreathi

SDSM #	P4L	P4W	M2	M2W	M3L	M3W
150896	1.77	1.72	-	-	-	-
150897	-	-	-	-	1.17	1.83
150898	-	-	1.58	2.07	-	-
150900	-	-	1.93	2.32	-	-
150901	1.97	2.01	-	-	-	-
Mean	1.87	1.87	1.76	2.20	1.17	1.83

SDSM #	m1L	m1W	m2L	m2W	m3L	m3W
150902	-	-	-	-	1.37	0.86
150903	2.05	1.19	-	-	-	-
150904	-	-	2.17	1.54	-	-
150905	1.90	1.28	-	-	-	-
150907	-	1.25	-	-	-	-
150908	-	-	2.01		1.54	1.03
150909	-	-	2.07	1.75	1.69	1.46
150910	2.03	1.53	-	-	-	-
156446	1.99	1.58	-	-	-	-
Mean	1.99	1.37	2.08	1.65	1.53	1.12

Oligoryctes tenutalonidus

SDSM #	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W	m1-m3L
150890	-	-	0.80	0.72	0.83	0.67	0.89	0.60	2.57
150891	-	-	0.78	0.59	0.80	-	-	-	-
150892	-	-	0.79	0.58	0.80	0.61	-	-	-
150606	-	-	-	-	0.70	0.65	1.00	0.56	-
150648	-	-	-	-	-	-	1.04	0.54	-
156356	0.71	0.55	0.87	0.72	0.79	0.67	-	-	-
Mean	0.71	0.55	0.81	0.65	0.78	0.65	0.98	0.57	2.57

TABLE 12. Dental measurements of upper cheek teeth of *Ischyromys brevidens* from the Sioux County Ant Mounds. Abbreviations: CV, coefficient of variation; d, deciduous tooth; L, anteroposterior length; M, molar; Max, maximum; Min, minimum; N, number of specimens; P, premolar; SD, standard deviation; W, transverse width; †, indicates M1/M2. All measurements in mm.

All levels								
	dP4L	dP4W	P4L	P4W	M1L†	M1W†	M3L	M3W
N	80	82	10	10	113	101	51	48
Mean	3.53	3.10	3.09	3.66	3.44	3.38	3.45	3.15
Min	3.06	2.63	2.83	3.24	2.69	2.75	2.86	2.65
Max	3.92	3.67	3.33	4.07	4.13	3.99	4.04	3.58
SD	0.21	0.22	0.17	0.29	0.31	0.28	0.29	0.18
CV	5.93	7.25	5.65	7.82	8.99	8.41	8.31	5.79
Below UPW deep (1-6)								
N	37	39	1	3	60	56	30	29
Mean	3.51	3.10	3.27	3.52	3.51	3.45	3.48	3.17
Min	3.06	2.63		3.24	2.69	2.75	2.86	2.66
Max	3.92	3.67		3.88	4.13	4.07	3.96	3.58
SD	0.20	0.24		0.33	0.31	0.28	0.28	0.19
CV	5.78	7.74		9.35	8.89	8.24	8.07	6.15
Below UPW shallow (7, 9, 12-16)								
N	18	19	4	4	25	21	15	14
Mean	3.57	3.17	3.00	3.64	3.35	3.34	3.40	3.10
Min	3.10	2.87	2.83	3.26	2.97	2.77	2.91	2.65
Max	3.88	3.51	3.33	4.07	3.89	3.99	4.04	3.40
SD	0.22	0.20	0.23	0.35	0.29	0.30	0.29	0.17
CV	6.22	6.21	7.79	9.63	8.52	8.86	8.48	5.51
Above UPW								
N	24	23	2	1	30	26	6	5
Mean	3.51	3.06	3.09	3.73	3.37	3.30	3.45	3.19
Min	3.13	2.73	3.08		2.84	2.85	3.06	3.09
Max	3.85	3.53	3.09		3.99	3.88	3.88	3.41
SD	0.22	0.22	0.01		0.28	0.29	0.35	0.13
CV	6.17	7.22	0.23		8.47	8.93	10.00	4.10

TABLE 13. Dental measurements of lower cheek teeth of *Ischyromys brevidens* from the Sioux County Ant Mounds. Abbreviations: CV, coefficient of variation; d, deciduous tooth; L, anteroposterior length; m, molar; Max, maximum; Min, minimum; N, number of specimens; p, premolar; pW, posterior transverse width; SD, standard deviation; W, transverse width; †, indicates m1/m2. All measurements in mm.

All levels								
	dp4L	dp4W	p4L	p4W	m1L†	m1W†	m3L	m3W
N	132	134	25	26	83	82	52	53
Mean	3.49	2.54	3.59	3.10	3.48	3.25	3.59	3.28
Min	2.96	2.04	3.15	2.40	3.00	2.67	3.06	2.85
Max	4.57	3.43	4.20	3.74	3.90	3.84	4.18	3.88
SD	0.25	0.22	0.30	0.30	0.21	0.28	0.26	0.26
CV	7.18	8.69	8.44	9.58	6.02	8.51	7.36	8.03
Below UPW deep (1-6)								
N	57	60	13	14	48	48	38	40
Mean	3.56	2.59	3.58	3.05	3.49	3.29	3.59	3.30
Min	3.07	2.04	3.20	2.40	3.00	2.67	3.17	2.85
Max	4.57	3.43	4.20	3.74	3.83	3.84	4.18	3.88
SD	0.28	0.25	0.29	0.31	0.20	0.29	0.25	0.24
CV	7.95	9.80	8.10	10.27	5.60	8.71	6.90	7.37
Below UPW shallow (7, 9, 12-16)								
N	49	49	11	11	20	19	6	5
Mean	3.45	2.53	3.61	3.15	3.46	3.22	3.66	3.36
Min	3.06	2.10	3.22	2.66	3.08	2.80	3.06	2.92
Max	3.85	3.02	4.18	3.48	3.90	3.67	4.16	3.71
SD	0.21	0.19	0.32	0.29	0.23	0.29	0.43	0.40
CV	6.03	7.58	8.95	9.27	6.59	8.93	11.63	11.83
Above UPW								
N	18	17	1	1	15	15	8	8
Mean	3.42	2.47	3.64	3.11	3.49	3.15	3.56	3.15
Min	3.06	2.23			3.18	2.87	3.23	2.85
Max	3.79	2.84			3.89	3.58	3.97	3.74
SD	0.22	0.19			0.24	0.20	0.23	0.27
CV	6.57	7.72			6.90	6.49	6.41	8.51

TABLE 14. Dental measurements of cheek teeth of *Siouxlindrodon sullivani* from the Sioux County Ant Mounds. Abbreviations: CV, coefficient of variation; L, anteroposterior length; M/m, molar; Max, maximum; Min, minimum; N, number of specimens; P/p, premolar; SD, standard deviation; W, transverse width; †, indicates M1/M2 or m1/m2. All measurements in mm.

	P4L	P4W	M1L†	M1W†	M3L	M3W
N	4	4	10	10	2	2
Mean	1.66	2.37	1.83	2.53	1.76	2.08
Min	1.54	2.21	1.60	2.20	1.75	2.00
Max	1.83	2.59	2.02	2.98	1.76	2.16
SD	0.13	0.18	0.14	0.23		
CV	7.65	7.70	7.54	8.91		

	p4L	p4W	m1L†	m1W†	m3L	m3W
N	3	3	16	16	3	3
Mean	1.62	1.73	1.91	2.02	1.95	1.88
Min	1.50	1.68	1.78	1.85	1.73	1.76
Max	1.68	1.78	2.03	2.33	2.14	2.08
SD			0.07	0.13		
CV			3.76	6.20		

TABLE 15. Dental measurements of upper cheek teeth of *Altasciurus relictus* from the Sioux County Ant Mounds. Abbreviations: CV, coefficient of variation; d, deciduous tooth; L, anteroposterior length; M, molar; Max, maximum; Min, minimum; N, number of specimens; P, premolar; SD, standard deviation; W, transverse width. All measurements in mm.

All levels										
	dP4L	dP4W	P4L	P4W	M1L	M1W	M2L	M2W	M3L	M3W
N	1	1	41	44	128	125	6	6	29	29
Mean	1.76	1.83	1.80	2.08	1.67	2.13	1.63	2.11	1.78	1.91
Min			1.63	1.83	1.39	1.85	1.53	2.00	1.62	1.74
Max			2.02	2.47	1.94	2.54	1.83	2.34	1.94	2.11
SD			0.12	0.15	0.12	0.17	0.11	0.12	0.09	0.10
CV			6.93	7.01	7.19	8.13	6.89	5.77	5.21	5.29
Below UPW deep (1-6)										
N			17	18	48	45			8	8
Mean			1.82	2.14	1.69	2.14			1.79	1.92
Min			1.63	1.91	1.46	1.87			1.66	1.78
Max			2.02	2.47	1.94	2.54			1.87	2.09
SD			0.13	0.16	0.12	0.19			0.07	0.10
CV			7.32	7.65	7.22	8.86			4.06	5.36
Below UPW shallow (7, 9, 12-16)										
N	1	1	12	14	53	55	4	4	13	13
Mean	1.76	1.83	1.80	2.04	1.67	2.13	1.66	2.16	1.78	1.90
Min			1.65	1.86	1.43	1.85	1.53	2.04	1.62	1.74
Max			2.00	2.23	1.90	2.53	1.83	2.34	1.92	2.11
SD			0.12	0.11	0.12	0.18	0.13	0.13	0.10	0.11
CV			6.87	5.46	7.24	8.63	7.75	5.96	5.62	5.96
Above UPW										
N			6	6	23	21			4	4
Mean			1.75	2.08	1.67	2.14			1.72	1.87
Min			1.65	1.93	1.39	1.86			1.62	1.77
Max			1.99	2.28	1.90	2.47			1.80	1.99
SD			0.12	0.12	0.11	0.12			0.09	0.09
CV			6.92	5.54	6.78	5.71			5.07	4.86

TABLE 16. Dental measurements of lower cheek teeth of *Altasciurus relictus* from the Sioux County Ant Mounds. Abbreviations: CV, coefficient of variation; AW, metalophid width; d, deciduous tooth; L, anteroposterior length; m, molar; Max, maximum; Min, minimum; N, number of specimens; p, premolar; PW, hypolophid width; SD, standard deviation; W, transverse width. All measurements in mm.

All levels													
	dp4L	dp4W	p4L	p4W	m1L	m1AW	m1PW	m2L	m2AW	m2PW	m3L	m3AW	m3PW
N	3	3	30	29	76	61	72	70	56	69	45	43	36
Mean	1.75	1.41	1.73	1.62	1.66	1.48	1.60	1.74	1.63	1.70	1.98	1.66	1.56
Min	1.70	1.36	1.61	1.46	1.46	1.25	1.37	1.47	1.39	1.43	1.72	1.35	1.27
Max	1.78	1.44	1.95	1.88	2.00	1.95	1.84	1.92	1.90	1.98	2.24	1.90	1.88
SD	0.04	0.04	0.08	0.10	0.11	0.13	0.11	0.10	0.12	0.11	0.13	0.12	0.13
CV	2.49	3.09	4.77	5.93	6.74	8.71	6.88	5.59	7.21	6.75	6.71	7.39	8.42
Below UPW deep (1-6)													
N	1	1	11	11	33	26	32	31	23	31	15	13	13
Mean	1.70	1.43	1.74	1.65	1.64	1.47	1.59	1.73	1.58	1.68	1.94	1.63	1.52
Min			1.62	1.50	1.46	1.26	1.37	1.47	1.39	1.43	1.72	1.35	1.27
Max			1.88	1.77	1.86	1.64	1.84	1.92	1.76	1.95	2.19	1.90	1.88
SD			0.09	0.09	0.12	0.11	0.12	0.10	0.10	0.11	0.13	0.16	0.16
CV			4.96	5.40	7.36	7.49	7.66	5.96	6.36	6.55	6.94	9.92	10.60
Below UPW shallow (7, 9, 12-16)													
N			11	11	28	23	28	25	19	23	21	22	17
Mean			1.72	1.59	1.66	1.47	1.62	1.76	1.68	1.73	1.96	1.65	1.58
Min			1.61	1.46	1.47	1.31	1.44	1.64	1.46	1.48	1.74	1.49	1.45
Max			1.85	1.71	1.87	1.65	1.82	1.89	1.90	1.98	2.15	1.84	1.76
SD			0.07	0.08	0.08	0.10	0.09	0.08	0.11	0.11	0.12	0.10	0.09
CV			3.94	5.26	4.67	6.82	5.72	4.54	6.72	6.54	6.10	5.95	5.97
Above UPW													
N	1	1	2	2	11	8	10	10	10	11	6	5	5
Mean	1.77	1.36	1.67	1.60	1.69	1.45	1.59	1.77	1.67	1.75	2.03	1.67	1.58
Min			1.66	1.60	1.50	1.25	1.39	1.65	1.52	1.57	1.94	1.57	1.34
Max			1.68	1.60	1.81	1.60	1.76	1.82	1.86	1.86	2.19	1.83	1.78
SD					0.09	0.12	0.13	0.06	0.10	0.09	0.10	0.10	0.17
CV					5.15	8.41	8.29	3.10	5.92	5.05	4.81	5.69	10.85

TABLE 17. Dental measurements of cheek teeth of *Altasciurus clausulus* and *A. albiclivus* from the Sioux County Ant Mounds. Abbreviations: AW, metalophid width; CV, coefficient of variation; L, anteroposterior length; M/m, molar; P/p, premolar; PW, hypolophid width; Min, minimum; Max, maximum; N, number of specimens; SD, standard deviation; W, transverse width. All measurements in mm.

Altasciurus clausulus

	P4L	P4W	M1L	M1W	M2L	M2W	M3L	M3W
N	7	7	12	12	2	2	5	4
Mean	1.55	1.79	1.40	1.80	1.49	1.99	1.52	1.59
Min	1.43	1.68	1.29	1.69	1.47	1.96	1.44	1.50
Max	1.61	1.97	1.49	1.86	1.50	2.01	1.59	1.70
SD	0.07	0.10	0.06	0.06	0.02	0.04	0.07	0.09
CV	4.21	5.52	4.47	3.06	1.43	1.78	4.56	5.88

	p4L	p4W	m1L	m1AW	m1PW	m2L	m2AW	m2PW	m3L	m3AW
N	2	2	4	4	3	3	3	4	3	2
Mean	1.45	1.24	1.54	1.49	1.39	1.20	1.32	1.52	1.45	1.60
Min	1.42	1.18	1.45	1.30	1.36	1.14	1.28	1.45	1.32	1.60
Max	1.48	1.29	1.58	1.67	1.40	1.24	1.37	1.56	1.52	1.60
SD			0.06	0.16	0.02	0.06	0.05	0.05	0.11	
CV			4.00	10.61	1.67	4.58	3.59	3.28	7.61	

Altasciurus albiclivus

	P4L	P4W	M1L	M1W	M2L	M2W	M3L	M3W
N	3	3	8	8	-	-	9	7
Mean	2.18	2.63	1.98	2.59	-	-	2.03	2.22
Min	2.12	2.34	1.89	2.56	-	-	1.92	2.08
Max	2.25	2.83	2.12	2.66	-	-	2.23	2.33
SD			0.08	0.03			0.11	0.08
CV			4.12	1.35			5.42	3.61

	p4L	p4W	m1L	m1AW	m1PW	m2L	m2AW	m2PW	m3L	m3AW	m3PW
N	5	5	6	6	6	7	7	7	4	4	4
Mean	2.03	1.87	1.98	1.69	1.85	2.04	1.87	1.97	2.34	2.10	1.96
Min	1.91	1.56	1.91	1.65	1.74	1.94	1.80	1.89	2.24	2.03	1.83
Max	2.14	2.07	2.11	1.73	1.98	2.22	1.95	2.03	2.53	2.16	2.11
SD	0.09	0.20	0.08	0.03	0.10	0.09	0.06	0.05	0.13	0.05	0.12
CV	4.66	10.46	4.13	1.85	5.20	4.50	3.08	2.41	5.75	2.54	6.15

TABLE 18. Dental measurements of cheek teeth of *Campestrallomys siouxensis* from the Sioux County Ant Mounds. Abbreviations: d, deciduous tooth; L, anteroposterior length; M/m, molar; P, premolar; W, transverse width; †, indicates M1/M2 or m1/m2; *, indicates measurement could not be made due to breakage. All measurements in mm.

SDSM#	dP4L	dP4W	P4L	P4W	M1L†	M1W†	M3L	M3W
155371	-	-	-	-	2.23	2.71	-	-
155372	-	-	-	-	2.40	2.91	-	-
155385	-	-	*	2.59	-	-	-	-
155465	2.00	2.16	-	-	-	-	-	-
155466	-	-	-	-	2.14	2.48		
155467	-	-	-	-	-	-	2.66	2.70
155468	-	-	-	-	-	-	2.35	2.40
155469	*	2.19	-	-	-	-	-	-
155470	-	-	-	-	2.48	2.94	-	-
155471	-	-	2.19	2.46	-	-	-	-
155472			2.17	2.48	-	-	-	-
155473	-	-	-	-	-	-	2.50	2.43
155474	-	-	-	-	2.22	2.64	-	-
155475	-	-	-	-	-	-	2.80	2.85
Mean	2.00	2.18	2.18	2.51	2.29	2.74	2.58	2.60

SDSM#	m1L†	M1W†	m3L	m3W
155478	-	-	2.70	*
155481	-	-	2.22	1.96
155482	2.34	2.33	-	-
155483	-	-	2.24	1.86
155740	2.36	2.09	-	-
Mean	2.35	2.21	2.39	1.91

TABLE 19. Dental measurements of upper cheek teeth of aplodontids from the Sioux County Ant Mounds. Abbreviations: L, anteroposterior length; M/m, molar; P/p, premolar; W, transverse width; †, indicates M1/M2 or m1/m2. All measurements in mm.

SDSM #	P4L	P4W	M1L	M1W	M3L	M3W
Pelycomys spp.						
155699†	-	-	2.50	3.05	-	-
155749	2.57	3.02	-	-	-	-
152479†	-	-	2.43	2.89	-	-
Haplomys galbreathi						
155686	-	-	1.65	2.01	-	-
155687	1.71	1.95	-	-	-	-
Costepeiromys attasorus						
155712	-	-	-	-	2.45	2.39
155713	-	-	-	-	2.19	2.29
Protansomys gulottai						
155688†	-	-	1.23	1.76	-	-

TABLE 20. Dental measurements of lower cheek teeth of aplodontids from the Sioux County Ant Mounds (part 1). Abbreviations: L, anteroposterior length; m, molar; p, premolar; W, transverse width; †, indicates m1/m2; *, indicates measurement could not be made due to breakage. All measurements in mm.

SDSM #	p4L	p4W	m1L†	m1W†	m2L	m2W	m3L	m3W
Pelycomys spp.								
152475	-	-	*	2.80	-	-	-	-
152499	-	-	-	-	-	-	3.45	2.76
155700	-	-	*	2.86	-	-	-	-
155748	2.85	2.60	-	-	-	-	-	-
Oropyctis cf. *pediasius*								
152477	-	-	-	-	-	-	2.88	2.64
155460	2.44	2.50	-	-	-	-	-	-
155696	2.48	2.59	-	-	-	-	-	-
155967	-	-	2.55	2.63	-	-	-	-
155968	-	-	-	-	2.50	2.54	-	-
156492	2.54	2.43	-	-	-	-	-	-
Haplomys galbreathi								
152481	-	-	1.55	1.58	1.64	1.73	-	-
155677	-	-	-	-	1.62	1.74	-	-
155678	-	-	1.68	1.57	-	-	-	-
155679	-	-	1.55	1.51	-	-	-	-
155680	-	-	1.57	1.47	-	-	-	-
155681	-	-	-	-	-	-	1.90	1.54
155682	-	-	1.65	1.60	-	-	-	-
155683	-	-	-	-	-	-	1.74	1.47
155684	-	-	-	-	-	-	1.72	1.62
155685	-	-	1.68	1.65	-	-	-	-
Mean	-	-	1.61	1.56	1.63	1.74	1.79	1.54

TABLE 21. Dental measurements of lower cheek teeth of additional aplodontids (part 2) and *Epeiromys* sp. from the Sioux County Ant Mounds. Abbreviations: L, anteroposterior length; m, molar; W, transverse width; †, indicates m1/m2. All measurements in mm.

SDSM #	m1L	m1W	m2L	m2W	m3L	m3W
Ansomys cf. *cyanotephrus*						
155690	-	-	1.90	1.97	-	-
155691	-	-	-	-	1.98	1.63
152448	-	-	-	-	1.74	1.37
152482	-	-	-	-	1.75	1.7
Protansomys gulottai						
152447	1.34	1.24	1.31	1.20	-	-
155689†	1.51	1.37	-	-	-	-
Epeiromys sp.						
155701	-	-	-	-	2.60	2.42
155702	-	-	-	-	3.05	2.64
Costepeiromys attasorus						
155705	-	-	2.16	2.05	-	-
155706	-	-	-	-	2.18	2.14
155707	-	-	-	-	1.88	1.69
155708	-	-	-	-	2.40	2.01
155709	-	-	-	-	2.35	2.2
155710	-	-	-	-	2.30	1.97
155711	1.92	1.78	-	-	-	-
155763	1.72	1.70	-	-	-	-
Mean	1.82	1.74	2.16	2.05	2.22	2.00

TABLE 22. Dental measurements of cheek teeth of *Protosciurus mengi* from the Sioux County Ant Mounds. Abbreviations: L, anteroposterior length; M/m, molar; P/p, premolar; W, transverse width; †, indicates M1/M2 or m1/m2; *, indicates measurement could not be made due to breakage. All measurements in mm.

SDSM #	P4L	P4W	M1L†	M1W†	M3L	M3W
152486	-	-	2.80	3.38	-	-
152488	-	-	-	-	2.95	3.25
152492	-	-	-	-	3.11	*
152494			2.74	3.20	-	-
152496	2.59	3.00	-	-	-	-
155367	-	-	2.66	3.2	-	-
155484	-	-	-	-	2.63	*
155485	*	3.08	-	-		
155486	-	-	-	-	2.84	2.70
155487	-	-	-	-	3.01	3.20
155488	2.36	3.08	-	-	-	-
155489	-	-	2.43	3.06	-	-
155490	-	-	2.67	3.23	-	-
155491	-	-	2.63	3.08	-	-
155744	2.53	*	-	-	-	-
Mean	2.49	3.05	2.66	3.19	2.91	3.05

SDSM #	p4L	p4W	m1L†	m1W†	m3L	m3W
152498	-	-	*	2.77	-	-
152492	-	-	-	-	3.06	*
152509	-	-	-	-	3.04	2.83
152502	-	-	-	-	2.92	2.58
155480	-	-	-	-	2.95	2.45
155492	-	-	2.78	3.02	-	-
155495	2.63	2.38	-	-	-	-
155501					3.10	2.61
Mean	2.63	2.38	2.78	2.90	3.01	2.62

TABLE 23. Dental measurements of cheek teeth of *Douglassciurus bjorki* from the Sioux County Ant Mounds. Abbreviations: L, anteroposterior length; M/m, molar; P/p, premolar; W, transverse width; †, indicates M1/M2 or m1/m2; *, indicates measurement could not be made due to breakage. All measurements in mm.

SDSM#	dP4L	dP4W	P4L	P4W	M1L†	M1W†	M3L	M3W
152483	-	-	-	-	-	-	2.82	*
152484	-	-	-	-	2.23	2.69	-	-
152487	-	-	-	-	-	-	2.82	2.77
152489	-	-	2.28	2.69	-	-	-	-
152493	-	-	-	-	-	-	2.74	*
152490	-	-	-	-	2.12	*		
152495	-	-	-	-	-	-	2.78	2.98
152491	2.18	2.27	-	-	-	-	-	-
152478	-	-	-	-	2.31	2.85	-	-
Mean	2.18	2.27	2.28	2.69	2.22	2.77	2.79	2.88

SDSM#	p4L	p4W	m1L†	m1W†	m3L	m3W
152501	-	-	-	-	3.28	2.61
152504	-	-	2.79	2.58	-	-
152505	-	-	2.60	*	-	-
152506	-	-	2.52	2.31	-	-
152507	-	-	-	-	3.18	2.58
152510	-	-	2.64	2.47	-	-
152511	-	-	-	-	2.96	2.62
152512	-	-	2.57	2.51	-	-
155461	-	-	2.62	2.46	-	-
155462	-	-	2.6	2.6	-	-
155494	2.61	2.33	-	-	-	-
155498	-	-	-	-	3.06	2.68
155499	-	-	-	-	2.92	2.49
155500	-	-	-	-	3.09	2.53
155723	-	-	-	-	3.38	2.54
155742	2.57	2.34	-	-	-	-
155743	-	-	2.59	2.88	-	-
155754	-	-	-	-	*	2.63
Mean	2.59	2.34	2.62	2.54	3.12	2.59

TABLE 24. Dental measurements of cheek teeth of *Cedromus modicus* and *Oligospermophilus douglassi* from the Sioux County Ant Mounds. Abbreviations: CV, coefficient of variation; d, deciduous tooth; L, anteroposterior length; M/m, molar; Max, maximum; Min, minimum; N, number of specimens; P/p, premolar; SD, standard deviation; W, transverse width; †, indicates M1/M2 or m1/m2. All measurements in mm.

Cedromus modicus								
	dP4L	dP4W	P4L	P4W	M1L†	M1W†	M3L	M3W
N	5	5	5	5	21	20	9	7
Mean	2.20	2.22	2.49	2.89	2.56	3.07	2.76	2.80
Min	2.02	2.01	2.29	2.65	2.33	2.82	2.53	2.59
Max	2.29	2.36	2.69	3.03	2.78	3.29	3.00	3.03
SD	0.11	0.15	0.15	0.15	0.14	0.14	0.15	0.14
CV	4.80	6.56	5.86	5.25	5.30	4.48	5.50	5.13

	dp4L	dp4W	p4L	p4W	m1L†	m1W†	m3L	m3W
N	1	2	9	9	3	3	5	5
Mean	2.53	2.18	2.31	2.22	2.46	2.61	3.05	2.46
Min		2.05	2.20	1.98	2.33	2.42	2.96	2.30
Max		2.30	2.57	2.68	2.56	2.77	3.12	2.65
SD			0.13	0.21	0.12	0.18	0.07	0.15
CV			5.62	9.65	4.84	6.76	2.14	6.29

Oligospermophilus douglassi								
	dP4L	dP4W	P4L	P4W	M1L†	M1W†	M3L	M3W
N	1	1	1	2	18	17	5	5
Mean	1.60	2.13	2.03	2.18	1.86	2.29	2.07	2.17
Min				2.01	1.66	1.98	1.95	2.06
Max				2.34	2.10	2.48	2.19	2.30
SD					0.11	0.13	0.10	0.10
CV					6.00	5.56	4.99	4.45

			p4L	p4W	m1L†	m1W†	m3L	m3W
N			13	12	26	26	4	4
Mean			1.91	1.95	1.92	2.03	2.27	2.05
Min			1.69	1.69	1.72	1.77	2.15	1.85
Max			2.05	2.10	2.15	2.35	2.51	2.13
SD			0.13	0.12	0.11	0.15	0.17	0.13
CV			6.90	5.99	5.80	7.14	7.30	6.46

TABLE 25. Dental measurements of cheek teeth of *Adjidaumo minimus* from the Sioux County Ant Mounds. Abbreviations: L, anteroposterior length; M/m, molar; P/p, premolar; W, transverse width; †, indicates M1/M2 or m1/m2. All measurements in mm.

SDSM #	P4L	P4W	M1L	M1W	M2L	M2W	M3L	M3W	P4-M3L
137299	0.73	0.85	0.87	1.02	0.79	0.99	-	-	-
151052	0.82	0.85	0.86	0.95	-	-	-	-	-
151128	0.84	0.87	0.93	1.03	0.75	1.00	0.56	0.89	3.48
151145	0.88	0.88	0.91	1.02	0.79	0.96	-	-	-
151129	0.87	0.89	-	-	-	-	-	-	-
Mean	0.83	0.87	0.89	1.01	0.78	0.98	0.56	0.89	3.48

SDSM #	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W	p4-m3L
137238	0.71	0.78	0.93	0.92	-	-	-	-	-
137317	-	-	0.92	0.90	0.91	0.92	-	-	-
151151	0.73	0.72	0.85	0.82	0.84	0.89	-	-	-
152358	-	-	-	-	0.86	0.91	0.85	0.82	-
152361	0.80	0.68	0.88	0.92	0.81	0.92	-	-	3.94
152376	0.74	0.72	0.98	0.87	-	-	-	-	-
152377†	-	-	0.84	0.79	-	-	-	-	-
154909†	-	-	0.84	0.82	-	-	-	-	-
154916	0.80	0.76	-	-	-	-	-	-	-
Mean	0.76	0.73	0.89	0.86	0.86	0.91	0.85	0.82	3.94

TABLE 26. Dental measurements of cheek teeth of *Adjidaumo intermedius* from the Sioux County Ant Mounds. Abbreviations: CV, coefficient of variation; d, deciduous tooth; L, anteroposterior length; M/m, molar; Max, maximum; Min, minimum; N, number of specimens; P/p, premolar; SD, standard deviation; W, transverse width. All measurements in mm.

	dP4L	dP4W	P4L	P4W	M1L	M1W	M2L	M2W	M3L	M3W	P4-M3L
N	1	1	49	49	46	44	10	10	3	3	1
Mean	0.89	0.91	1.00	1.09	1.07	1.25	0.99	1.22	0.73	0.98	3.96
Min			0.85	0.96	0.95	1.11	0.94	1.15	0.72	0.94	
Max			1.19	1.28	1.22	1.41	1.06	1.31	0.74	1.02	
SD			0.08	0.09	0.06	0.07	0.04	0.05	0.01	0.04	
CV			8.17	8.13	5.93	5.47	4.26	4.43	1.59	4.11	

	dp4L	dp4W	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W	p4-m3L
N	3	2	17	18	47	46	28	27	17	17	4
Mean	0.81	0.69	0.94	0.93	1.06	1.04	1.05	1.08	1.04	1.01	4.55
Min	0.77	0.65	0.79	0.84	0.93	0.90	0.91	0.93	0.94	0.89	4.38
Max	0.83	0.72	1.00	1.12	1.22	1.19	1.20	1.23	1.18	1.12	4.83
SD			0.05	0.07	0.07	0.06	0.08	0.08	0.07	0.06	0.20
CV			5.23	7.03	6.77	5.83	7.42	7.38	7.18	6.14	4.31

TABLE 27. Dental measurements of cheek teeth of *Paradjidaumo patriciae* from the Sioux County Ant Mounds. Abbreviations: CV, coefficient of variation; d, deciduous tooth; L, anteroposterior length; M/m, molar; Max, maximum; Min, minimum; N, number of specimens; P/p, premolar; SD, standard deviation; W, transverse width. All measurements in mm.

	dP4L	dP4W	P4L	P4W	M1L	M1W	M2L	M2W	M3L	M3W	P4-M3L
N	2	2	186	184	257	251	22	24	17	16	3
Mean	1.21	1.22	1.42	1.51	1.35	1.57	1.22	1.49	0.97	1.29	5.05
Min	1.19	1.21	1.21	1.24	1.15	1.34	1.10	1.27	0.85	1.13	4.82
Max	1.22	1.23	1.68	1.75	1.58	1.88	1.55	1.69	1.17	1.44	5.22
SD	0.02	0.01	0.09	0.10	0.09	0.11	0.09	0.11	0.10	0.10	0.21
CV	1.76	1.16	6.35	6.55	6.37	7.01	7.60	7.48	10.33	7.38	4.07

	dp4L	dp4W	p4L	p4W	m1L	m1W	m1h	m2L	m2W	m2h	m3L	m3W	p4-m3
N	6	6	112	112	212	210	199	37	37	35	19	19	2
Mean	1.40	1.05	1.51	1.32	1.38	1.42	0.42	1.28	1.39	0.39	1.37	1.23	5.43
Min	1.28	0.98	1.23	1.12	1.18	1.24	0.28	1.11	1.27	0.29	1.20	1.04	5.31
Max	1.54	1.10	1.80	1.55	1.71	1.67	0.69	1.41	1.59	0.53	1.52	1.39	5.55
SD	0.10	0.04	0.10	0.09	0.10	0.09	0.07	0.07	0.08	0.06	0.09	0.09	0.17
CV	7.22	4.26	6.38	7.09	7.20	6.07	17.62	5.47	5.97	15.53	6.55	6.92	3.13

TABLE 28. Dental measurements of cheek teeth of *Paradjidaumo* sp., cf. *P. validus* from the Sioux County Ant Mounds. Abbreviations: L, anteroposterior length; M/m, molar; P/p, premolar; W, transverse width; *, indicates measurement could not be made due to breakage; †, indicates M1/M2 or m1/m2. All measurements in mm.

SDSM #	P4L	P4W	M1L†	M1W†
154949	-	-	1.74	1.84
154958	-	-	1.67	1.8
150992	1.73	1.84	-	-
154624	1.73	1.78	-	-
154686	1.74	1.76	-	-
154706			1.7	1.95
Mean	1.73	1.79	1.70	1.86

SDSM #	p4L	p4W	m1L†	m1W†	m1h†	m3L	m3W
154323	-	-	1.85	1.65	0.64	-	-
154348	-	-	1.76	1.69	0.53	-	-
154437	1.95	1.63	-	-	-	-	-
154481	-	-	1.81	1.83	0.6	-	-
154534	-	-	-	-	-	1.69	1.53
154747	-	-	1.85	1.69	*	-	-
154850	-	-	1.78	1.73	0.5	-	-
Mean	1.95	1.63	1.81	1.72	0.57	-	-

TABLE 29. Dental measurements of cheek teeth of *Centimanomys major* from the Sioux County Ant Mounds. Abbreviations: L, anteroposterior length; M/m, molar; P/p, premolar; W, transverse width; *, indicates measurement could not be made due to breakage; †, indicates M1/M2 or m1/m2. All measurements in mm.

SDSM #	dP4L	dP4W	P4L	P4W	M1L†	M1W†	M2L	M2W	M3L	M3W
154918	-	-	-	-	2.86	3.27	-	-	-	-
154921	2.75	2.43	-	-	-	-	-	-	-	-

SDSM #	dp4L	dp4W	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W
152428	-	-	-	-	-	-	-	-	2.62	2.57
152429	-	-	-	-	2.72	2.64	-	-	-	-
154917	-	-	-	-	-	-	2.79	2.93	-	-
154919	-	-	-	-	-	-	2.69	2.97	-	-
154920	-	-	-	-	2.88	*	-	-	-	-
154922	-	-	-	-	-	-	-	-	3.32	2.79
154923	-	-	-	-	2.85	2.78	-	-	-	-
154924	-	-	-	-	-	-	2.91	*	-	-
155774	2.51	2.09	-	-	-	-	-	-	-	-
Mean	2.51	2.09	-	-	2.82	2.71	2.80	2.95	2.97	2.68

TABLE 30. Dental measurements of cheek teeth of *Aulolithomys* sp. cf., *A. bounites* from the Sioux County Ant Mounds. Abbreviations: L, anteroposterior length; M/m, molar; P/p, premolar; W, transverse width; †, indicates M1/M2 or m1/m2. All measurements in mm.

SDSM #	P4L	P4W	M1L†	M1W†	M3L	M3W
152427	-	-	1.52	1.77	-	-
154947	-	-	1.68	1.89	-	-
154948	1.65	1.64	-	-	-	-
154952	-	-	1.8	1.72	-	-
154954	-	-	1.69	1.81	-	-
154955	-	-	1.54	1.87	-	-
154956	-	-	1.63	1.76	-	-
Mean	1.65	1.64	1.66	1.81		

SDSM #	p4L	p4W	m1L†	m1W†	m3L	m3W
154931	-	-	1.72	1.7	-	-
154932	-	-	1.75	1.76	-	-
154933	-	-	-	-	1.52	1.54
154934	-	-	1.78	1.85	-	-
154935	-	-	1.62	1.6	-	-
154936	-	-	1.69	1.61	-	-
154937	-	-	1.59	1.69	-	-
154938	1.63	1.38	-	-	-	-
154940	1.72	1.62	-	-	-	-
154941	1.64	1.49	-	-	-	-
154942	-	-	-	-	1.78	1.72
154943	-	-	1.75	1.73	-	-
154944	1.64	1.5	-	-	-	-
154945	-	-	1.66	1.82	-	-
154951	-	-	1.78	1.84	-	-
155694	-	-	1.68	1.63	-	-
Mean	1.66	1.50	1.70	1.72	1.65	1.63

TABLE 31. Dental measurements of cheek teeth of *Yoderimys massarae* and *Litoyoderimys grossus* from the Sioux County Ant Mounds. Abbreviations: L, anteroposterior length; M/m, molar; P/p, premolar; W, transverse width; *, indicates measurement could not be made due to breakage; †, indicates M1/M2 or m1/m2. All measurements in mm.

Yoderimys massarae						
SDSM #	P4L	P4W	M1L†	M1W†	M3L	M3W
152430	-	-	1.6	1.8	-	-
154960	-	-	1.67	1.68	-	-
154961	-	-	1.77	1.96	-	-
154963	-	-	1.69	*	-	-
154964	-	-	1.73	1.81	-	-
154965	-	-	1.65	1.77	-	-
Mean	-	-	1.69	1.80	-	-

SDSM #	p4L	p4W	m1L†	m1W†	m3L	m3W
154967	1.85	1.56	-	-	-	-
154968	-	-	1.78	1.57	-	-

Litoyoderimys grossus						
SDSM #	P4L	P4W	M1L†	M1W†	M3L	M3W
154959	-	-	1.95	2.24	-	-
154962	-	-	-	-	1.72	1.85

SDSM #	p4L	p4W	m1L†	m1W†
154966	-	-	2.01	1.86
154969	1.97	1.89	-	-
154970	-	-	1.98	1.98

TABLE 32. Dental measurements of cheek teeth of *Pipestoneomys pattersoni* from the Sioux County Ant Mounds. Abbreviations: L, anteroposterior length; M/m, molar; P/p, premolar; W, transverse width; *, indicates measurement could not be made due to breakage. All measurements in mm.

SDSM #	P4L	P4W	M1L	M1W	M2L	M2W
154927	*	2.05	-	-	-	-
154928	*	2.04	-	-	-	-
154929	-	-	-	-	1.38	1.34
154930	2.53	1.92	-	-	-	-

SDSM #	p4L	p4W	m1L	m1W	m2L	m2W
154925	-	-	1.63	1.35	-	-
154926	1.88	1.53	-	-	-	-
156973	1.94	1.59	-	-	-	-

TABLE 33. Dental measurements of cheek teeth of *Heliscomys* from the Sioux County Ant Mounds. Abbreviations: CV, coefficient of variation; L, anteroposterior length; M/m, molar; Max, maximum; Min, minimum; N, number of specimens; P/p, premolar; SD, standard deviation; W, transverse width. All measurements in mm.

Heliscomys vetus									
	P4L	P4W	M1L	M1W	M2L	M2W	M3L	M3W	P4-M3L
N	17	17	17	17	12	11	4	4	4
Mean	0.68	0.73	0.76	0.94	0.67	0.87	0.52	0.67	2.77
Min	0.56	0.64	0.65	0.85	0.57	0.79	0.49	0.62	2.58
Max	0.79	0.85	0.84	1.11	0.78	1.00	0.55	0.71	3.03
SD	0.07	0.06	0.05	0.07	0.06	0.06	0.03	0.05	0.22
CV	10.69	8.84	6.96	6.95	8.51	6.76	5.14	6.69	8.08

	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W	p4-m3L
N	43	42	35	34	24	24	13	13	13
Mean	0.46	0.49	0.78	0.79	0.71	0.79	0.58	0.62	2.83
Min	0.36	0.39	0.69	0.70	0.61	0.70	0.52	0.56	2.56
Max	0.53	0.58	0.85	0.88	0.82	0.86	0.64	0.69	3.00
SD	0.04	0.04	0.04	0.05	0.05	0.04	0.04	0.04	0.11
CV	8.35	9.02	5.13	6.16	6.58	5.53	6.58	6.63	3.73

Heliscomys hatcheri									
	P4L	P4W	M1L	M1W	M2L	M2W	M3L	M3W	P4-M3L
N	26	25	26	25	11	10	2	2	2
Mean	0.73	0.80	0.75	0.92	0.68	0.87	0.58	0.73	2.99
Min	0.58	0.68	0.68	0.81	0.63	0.84	0.56	0.71	2.98
Max	0.80	0.90	0.83	1.01	0.72	0.95	0.59	0.75	2.99
SD	0.06	0.05	0.04	0.06	0.03	0.03	0.02	0.03	0.01
CV	7.69	6.69	4.93	6.15	3.83	3.71	3.69	3.87	0.24

	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W	p4-m3L
N	21	21	16	16	11	11	7	7	7
Mean	0.55	0.53	0.78	0.81	0.71	0.82	0.58	0.61	2.90
Min	0.51	0.45	0.69	0.71	0.68	0.74	0.52	0.54	2.74
Max	0.59	0.58	0.87	0.92	0.76	0.89	0.61	0.68	3.12
SD	0.02	0.03	0.05	0.06	0.03	0.05	0.03	0.06	0.12
CV	4.15	6.45	6.77	7.18	4.22	6.19	5.59	9.18	4.12

TABLE 34. Dental measurements of cheek teeth of and *Megaheliscomys*, and *Ecclesimus* from the Sioux County Ant Mounds. Abbreviations: L, anteroposterior length; M/m, molar; P/p, premolar; W, transverse width. All measurements in mm.

Megaheliscomys mcgrewi								
SDSM #	dP4L	dP4W	P4L	P4W	M1L	M1W	M2L	M2W
151066	-	-	-	-	1.02	1.3	0.96	1.36
151095	-	-	0.79	0.84	1.03	1.29	-	-
152419	-	-	0.78	0.8	1.05	1.27	0.94	1.2
152424	-	-	0.84	0.87	1.05	1.38	0.87	1.28
155514	-	-	-	-	1.09	1.23	-	-
155515	-	-	-	-	1.08	1.2	0.93	1.13
155516	0.52	0.65	-	-	0.97	1.14	-	-
Mean			0.80	0.84	1.04	1.26	0.93	1.24

SDSM #	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W
151061	0.59	0.68	1.17	1.17	-	-	-	-
151051	-	-	1.06	1.00	0.94	1.06	-	-
151077	0.57	0.61	1.10	1.09	0.94	1.07	-	-
152403	-	-	1.04	0.96	0.86	0.98	-	-
Mean	0.58	0.65	1.09	1.06	0.91	1.04		

Ecclesimus tenuiceps								
SDSM #	P4L	P4W	M1L	M1W	M2L	M2W	M3L	M3W
151086	0.88	1.09	0.93	1.07	-	-	-	-
151085	0.77	0.98	0.88	1.10	0.86	1.04	-	-
155517	0.78	0.89	0.87	1.00	0.89	1.00	-	-
155519	-	-	0.89	1.00	-	-	-	-
mean	0.81	0.99	0.89	1.04	0.88	1.02		

SDSM #	dp4L	dp4W	p4L	p4W	m1L	m1W	m2L	m2W
151067	0.54	0.43	-	-	-	-	-	-
137276	-	-	0.56	0.68	0.95	1.02	0.93	1.08

TABLE 35. Dental measurements of cheek teeth of *Tenudomys* and *Kirkomys* from the Sioux County Ant Mounds. Abbreviations: L, anteroposterior length; M/m, molar; P/p, premolar; W, transverse width; *, indicates measurement could not be made due to breakage. All measurements in mm.

Kirkomys miriamae									
SDSM #	P4L	P4W	M1L	M1W	M2L	M2W	M3L	M3W	P4-M3L
137277	1.17	1.18	1.10	1.22	1.01	1.26	-	-	-
137301	1.07	1.21	0.97	1.21	0.88	1.13	0.79	0.95	4.00

SDSM #	p4L	p4W
151069	1.04	0.91

Tenudomys basilaris								
SDSM #	P4L	P4W	M1L	M1W	M2L	M2W	M3L	M3W
137273	1.26	1.43	1.13	1.48	1.01	*	-	-
137274	*	1.20	1.03	1.38	-	-	-	-
151075	1.23	1.28	1.02	1.37	0.97	1.41	-	-
152425	1.08	1.34	-	-	-	-	-	-
155544	1.29	1.28	-	-	-	-	-	-
155545	1.20	1.33	-	-	-	-	-	-
155546	1.24	1.40	-	-	-	-	-	-

TABLE 36. Dental measurements of cheek teeth of and *Diplolophus insolens* from the Sioux County Ant Mounds. Abbreviations: L, anteroposterior length; M/m, molar; W, transverse width. All measurements in mm.

SDSM #	M1L	M1W	M2L	M2W	M3L	M3W
155504	-	-	1.72	2.28	-	-

SDSM #	m1L	m1W	m2L	m2W	m3L	m3W
152402	-	-	2.3	2.61	-	-
155503	-	-	-	-	2.34	2.61
155505	2.43	2.35	-	-	-	-
155506	2.35	2.27	-	-	-	-
Mean	2.42	2.35	2.1	2.64	1.92	2.47

TABLE 37. Dental measurements of upper molars of *Eumys elegans* from the Sioux County Ant Mounds. Abbreviations: CV, coefficient of variation; L, anteroposterior length; M, molar; Max, maximum; Min, minimum; N, number of specimens; SD, standard deviation; W, transverse width. All measurements in mm.

All levels										
	M1L	M1W	M2L	M2W	M3L	M3W	M1-M3L	M1 W/L	M2 W/L	M3 W/L
N	382	461	338	337	133	132	3	375	330	125
Mean	2.89	1.90	1.99	1.85	1.58	1.71	6.14	0.66	0.93	1.08
Min	2.35	1.54	1.68	1.56	1.24	1.49	5.98	0.56	0.77	0.83
Max	3.35	2.27	2.39	2.20	1.99	2.04	6.33	0.78	1.08	1.28
SD	0.17	0.13	0.12	0.11	0.14	0.12	0.18	0.03	0.05	0.07
CV	5.96	6.69	6.07	6.02	8.68	6.90	2.90	5.30	5.66	6.75
Below UPW deep (1-6)										
N	164	215	145	143	47	47	1	161	142	46
Mean	2.89	1.89	2.00	1.86	1.58	1.70	5.98	0.66	0.93	1.08
Min	2.51	1.61	1.75	1.61	1.38	1.49		0.56	0.77	0.83
Max	3.29	2.27	2.31	2.12	1.84	1.94		0.78	1.08	1.22
SD	0.16	0.13	0.11	0.10	0.12	0.11		0.04	0.05	0.07
CV	5.45	6.72	5.65	5.32	7.42	6.35		5.51	5.46	6.83
Below UPW shallow (7, 9, 12-16)										
N	129	144	87	86	55	54	2	127	85	54
Mean	2.92	1.91	1.99	1.84	1.56	1.70	6.22	0.65	0.93	1.10
Min	2.60	1.61	1.77	1.58	1.34	1.53	6.10	0.59	0.82	0.96
Max	3.27	2.14	2.23	2.06	1.78	1.99	6.33	0.74	1.05	1.25
SD	0.16	0.11	0.10	0.10	0.10	0.10	0.16	0.03	0.05	0.07
CV	5.40	5.56	5.23	5.34	6.52	5.59	2.62	4.84	5.54	6.08
Above UPW										
N	75	87	63	66	20	20		74	63	20
Mean	2.86	1.89	1.98	1.84	1.64	1.70		0.66	0.93	1.04
Min	2.49	1.60	1.78	1.64	1.44	1.49		0.58	0.80	0.91
Max	3.26	2.24	2.22	2.06	1.99	2.04		0.73	1.05	1.20
SD	0.18	0.13	0.10	0.10	0.13	0.12		0.03	0.06	0.07
CV	6.36	7.14	4.87	5.48	8.17	7.28		4.94	5.99	6.82

TABLE 38. Dental measurements of lower molars of *Eumys elegans* from the Sioux County Ant Mounds. Abbreviations: CV, coefficient of variation; L, anteroposterior length; m, molar; Max, maximum; Min, minimum; N, number of specimens; SD, standard deviation; W, transverse width. All measurements in mm.

All levels									
	m1L	m1W	m2L	m2W	m3L	m3W	m1W/L	m2 W/L	m3 W/L
N	347	353	310	320	178	173	339	306	166
Mean	2.37	1.73	2.17	1.92	2.20	1.85	0.73	0.88	0.84
Min	1.89	1.30	1.89	1.42	1.89	1.45	0.60	0.73	0.65
Max	2.97	2.20	2.65	2.38	2.64	2.24	0.89	1.03	0.97
SD	0.16	0.12	0.12	0.13	0.14	0.12	0.05	0.04	0.05
CV	6.82	7.00	5.56	6.87	6.21	6.69	6.69	5.01	5.95
Below UPW deep (1-6)									
N	160	165	149	156	85	84	159	147	81
Mean	2.35	1.74	2.17	1.92	2.20	1.85	0.74	0.89	0.84
Min	1.89	1.30	1.94	1.42	1.89	1.45	0.60	0.73	0.65
Max	2.84	2.20	2.52	2.33	2.49	2.11	0.89	1.03	0.96
SD	0.17	0.13	0.12	0.14	0.14	0.13	0.05	0.05	0.06
CV	7.15	7.60	5.53	7.04	6.13	7.07	7.26	5.10	6.66
Below UPW shallow (7, 9, 12-16)									
N	125	128	107	108	65	63	121	105	59
Mean	2.37	1.72	2.16	1.92	2.21	1.86	0.73	0.88	0.84
Min	2.04	1.41	1.89	1.57	1.96	1.58	0.61	0.78	0.71
Max	2.68	1.99	2.43	2.25	2.64	2.24	0.86	1.01	0.97
SD	0.15	0.11	0.11	0.12	0.15	0.13	0.04	0.04	0.05
CV	6.25	6.43	5.20	6.45	6.72	6.89	6.12	4.93	5.49
Above UPW									
N	62	60	54	56	28	26	59	54	26
Mean	2.40	1.74	2.18	1.91	2.15	1.83	0.73	0.88	0.85
Min	2.01	1.49	1.90	1.65	2.00	1.64	0.62	0.78	0.77
Max	2.97	2.00	2.65	2.38	2.36	1.98	0.83	0.98	0.92
SD	0.17	0.11	0.14	0.14	0.10	0.08	0.04	0.04	0.04
CV	6.91	6.43	6.33	7.30	4.66	4.53	5.74	4.93	4.70

TABLE 39. Dental measurements of upper molars of *Scottimus* from the Sioux County Ant Mounds. Abbreviations: CV, coefficient of variation; L, anteroposterior length; M, molar; Max, maximum; Min, minimum; N, number of specimens; SD, standard deviation; W, transverse width. All measurements in mm.

Scottimus lophatus							
	M1L	M1W	M2L	M2W	M3L	M3W	M1-M3L
N	9	9	5	4	2	1	
Mean	2.88	1.88	2.21	1.73	1.72	1.71	
Min	2.68	1.78	1.95	1.63	1.70	1.71	
Max	3.12	2.02	2.35	1.81	1.73	1.71	
SD	0.12	0.09	0.16	0.08	0.02		
CV	4.09	4.62	7.03	4.38	1.24		
Scottimus exiguus							
N	32	35	37	35	12	12	1
Mean	2.51	1.61	1.76	1.49	1.37	1.40	5.44
Min	2.40	1.44	1.56	1.30	1.23	1.26	
Max	2.68	1.78	2.04	1.77	1.55	1.55	
SD	0.09	0.09	0.14	0.11	0.11	0.10	
CV	3.41	5.66	8.11	7.60	7.71	6.79	
Scottimus ambiguus							
N	19	21	9	7	2	2	1
Mean	2.24	1.45	1.49	1.37	1.10	1.16	4.92
Min	2.11	1.31	1.37	1.31	1.04	1.14	
Max	2.37	1.55	1.58	1.47	1.15	1.18	
SD	0.08	0.06	0.06	0.05	0.08	0.03	
CV	3.44	4.21	4.15	3.99	7.10	2.44	

TABLE 40. Dental measurements of lower molars of *Scottimus* from the Sioux County Ant Mounds. Abbreviations: CV, coefficient of variation; L, anteroposterior length; m, molar; Max, maximum; Min, minimum; N, number of specimens; SD, standard deviation; W, transverse width. All measurements in mm.

Scottimus lophatus						
	m1L	m1W	m2L	m2W	m3L	m3W
N	1	2	3	3	5	5
Mean	2.64	1.54	2.21	1.67	2.19	1.61
Min		1.52	2.16	1.65	2.10	1.52
Max		1.55	2.28	1.71	2.30	1.87
SD			0.06	0.03	0.07	0.15
CV			2.83	1.92	3.30	9.07
Scottimus exiguus						
N	3	3	14	14	6	6
Mean	2.34	1.44	1.92	1.52	1.82	1.39
Min	2.31	1.36	1.76	1.36	1.71	1.24
Max	2.38	1.52	2.25	1.75	1.94	1.50
SD	0.04	0.08	0.14	0.11	0.10	0.10
CV	1.54	5.56	7.57	7.37	5.53	7.27
Scottimus ambiguus						
N	2	2	2	2	3	3
Mean	2.07	1.43	1.66	1.29	1.53	1.23
Min	1.98	1.36	1.64	1.27	1.46	1.19
Max	2.15	1.49	1.67	1.31	1.63	1.28
SD					0.09	0.05
CV					5.81	3.85

TABLE 41. Dental measurements of molars of *Willeumys viduus* from the Sioux County Ant Mounds. Abbreviations: CV, coefficient of variation; L, anteroposterior length; M/m, molar; Max, maximum; Min, minimum; N, number of specimens; SD, standard deviation; W, transverse width. All measurements in mm.

	M1L	M1W	M2L	M2W	M3L	M3W	M1-M3L
N	77	88	52	52	17	17	7
Mean	2.34	1.45	1.63	1.47	1.24	1.34	5.56
Min	1.94	1.20	1.35	1.25	1.02	1.19	5.06
Max	2.76	1.71	1.81	1.68	1.48	1.59	6.20
SD	0.14	0.10	0.08	0.10	0.10	0.10	0.43
CV	6.01	6.83	5.03	6.56	7.94	7.72	7.77

	m1L	m1W	m2L	m2W	m3L	m3W
N	56	60	65	66	18	16
Mean	2.04	1.30	1.78	1.41	1.76	1.41
Min	1.54	0.98	1.54	1.14	1.53	1.19
Max	2.29	1.61	2.12	1.77	2.02	1.67
SD	0.14	0.12	0.12	0.13	0.15	0.14
CV	7.04	9.35	7.01	9.00	8.32	9.83

TABLE 42. Dental measurements of molars of *Wilsoneumys planidens* from the Sioux County Ant Mounds. Abbreviations: CV, coefficient of variation; L, anteroposterior length; M/m, molar; Max, maximum; Min, minimum; N, number of specimens; SD, standard deviation; W, transverse width. All measurements in mm.

	M1L	M1W	M2L	M2W	M3L	M3W
N	4	8	16	16	7	7
Mean	2.83	1.82	1.99	1.89	1.68	1.82
Min	2.78	1.68	1.83	1.65	1.43	1.56
Max	2.88	2.00	2.23	2.13	1.89	1.99
SD	0.04	0.09	0.11	0.14	0.16	0.14
CV	1.47	5.00	5.39	7.33	9.56	7.87

	m1L	m1W	m2L	m2W	m3L	m3W
N	1	1	2	2	6	6
Mean	2.51	1.76	2.09	1.93	2.24	1.92
Min			2.01	1.83	1.89	1.76
Max			2.17	2.03	2.53	2.20
SD					0.22	0.18
CV					9.63	9.42

TABLE 43. Measurements of cheek teeth of *Palaeolagus haydeni* from the Sioux County Ant Mounds. Abbreviations: aW, anterior transverse width; d, deciduous tooth; L, anteroposterior length; Lm, lower molariform (p4, m1, or m2); Max, maximum; Min, minimum; N, number of specimens; pW, posterior transverse width; SD, standard deviation; UM, upper molariform (P4, M1, or M2); W, transverse width. All measurements in mm.

	dP3L	dP3W	dP4L	dP4W	P2L	P2W	P3L	P3W	UML	UMW
N	36	35	71	62	92	92	124	124	113	113
Mean	1.47	2.20	1.60	2.11	1.10	1.74	1.62	2.47	1.56	2.59
Min	1.17	1.62	1.26	1.20	0.64	1.15	1.30	1.83	1.22	1.90
Max	1.70	2.80	2.01	2.78	1.59	2.42	1.95	3.31	2.10	3.52
SD	0.14	0.32	0.18	0.32	0.22	0.28	0.18	0.32	0.18	0.32

	dp3L	dp3aW	dp3pW	dp4L	dp4aW	dp4pW	p3L	p3W	LmL	Lmaw	LmpW
N	21	23	20	25	25	31	154	159	61	61	61
Mean	2.29	1.39	1.66	2.17	1.55	1.59	1.93	1.70	2.07	2.03	1.73
Min	1.85	1.12	1.33	1.76	1.30	1.26	1.39	1.23	1.70	1.50	1.30
Max	2.93	1.74	2.23	2.48	1.94	1.93	2.57	2.25	2.48	2.39	2.13
SD	0.30	0.17	0.24	0.17	0.18	0.18	0.21	0.18	0.17	0.19	0.17

TABLE 44. Dental measurements of *Hesperocyon gregarius* from the Sioux County Ant Mounds. Abbreviations: aW, anterior transverse width; CV, coefficient of variation; d, deciduous tooth; L, anteroposterior length; M/m, molar; Max, maximum; Min, minimum; N, number of specimens; P/p, premolar; pW, posterior transverse width; SD, standard deviation; W, transverse width. All measurements in mm.

	dP3L	dP3aW	dP4L	dP4W	P4pW	M2L	M2aW	M2pW
N	1	1	1	1	1	4	4	5
Mean	6.21	6.69	3.85	3.99	4.00	3.61	5.64	4.82
Min						3.43	4.82	4.20
Max						3.82	6.13	5.45
SD						0.16	0.59	0.53
CV						4.53	10.51	10.91

	dp4L	dp4W	m2L	m2W	m3L	m3W
N	2	3	9	11	6	6
Mean	4.60	2.23	4.70	3.02	2.59	1.84
Min	4.38	2.09	4.04	2.58	2.31	1.67
Max	4.81	2.30	5.15	3.39	2.98	2.02
SD	0.30	0.12	0.41	0.28	0.22	0.13
CV	6.62	5.32	8.72	9.33	8.69	7.33

TABLE 45. Dental measurements of lower molars of *Hypisodus minimus* from the Sioux County Ant Mounds. Abbreviations: L, anteroposterior length; M, mean; Min, minimum; Max, maximum; N, number of specimens; W, transverse width. All measurements in mm.

	P3L	P3W	P4L	P4W	M1L	M1W	M2L	M2W	M3L	M3W
N	4	4	4	3	5	4	8	5	1	1
Mean	2.68	1.86	3.07	2.58	3.28	3.08	3.91	3.41	5.73	3.98
Min	2.37	1.63	2.65	2.38	2.95	2.96	3.39	3.17		
Max	2.99	2.08	3.50	2.70	3.61	3.30	4.36	3.77		

	p4L	p4W	m1L	m1W	m2L	m2w	m3L	m3W
N	2	3	3	2	2	3	2	2
Mean	2.78	1.49	3.15	2.12	3.57	2.26	4.48	2.20
Min	2.59	1.44	3.00	1.90	3.26	2.08	4.32	1.98
Max	2.96	1.52	3.26	2.34	3.88	2.56	4.63	2.41

TABLE 46. Dental measurements of lower teeth of *Leptomeryx* sp., cf. *L. exilis* from the Sioux County Ant Mounds. Abbreviations: CV, coefficient of variation; d, deciduous tooth; L, anteroposterior length; M/m, molar; Max, maximum; Min, minimum; N, number of specimens; P/p, premolar; SD, standard deviation; W, transverse width; †, indicates M1/M2 or m1/m2. All measurements in mm.

	dP3L	dP3W	dP4L	dP4W	P2L	P2W	P3L	P3W	P4L	P4W	M1L†	M1W†	M3L	M3W
N	2	3	2	4	6	6	8	6	2	2	6	2	1	1
Mean	5.56	2.04	4.86	3.71	4.52	2.82	5.36	3.17	3.85	4.57	5.08	4.06	5.55	6.06
Min	5.46	1.98	4.61	2.89	3.90	2.63	4.69	2.90	3.80	4.56	4.67	4.00		
Max	5.65	2.08	5.11	4.04	5.14	3.02	5.93	3.48	3.89	4.57	5.73	4.12		
SD	0.13	0.06	0.35	0.55	0.49	0.15	0.50	0.24			0.41			
CV	2.42	2.70	7.27	14.77	10.77	5.38	9.25	7.69			8.03			

	dp3L	dp3W	dp4L	dp4W	p2L	p2W	p3L	p3W	p4L	p4W	m1L†	m1W†
N	5	9	1	8	8	8	6	7	8	11	2	2
Mean	4.16	1.88	5.60	2.48	4.51	1.76	5.04	2.14	5.82	2.54	5.31	3.62
Min	3.73	1.55	5.60	2.33	3.98	1.48	4.42	1.98	5.47	2.06	4.92	3.27
Max	5.00	2.18		2.61	4.95	1.93	5.61	2.43	6.24	2.95	5.70	3.96
SD	0.53	0.18		0.10	0.33	0.18	0.48	0.17	0.28	0.25		
CV	12.72	9.54		3.88	7.38	10.08	9.54	7.77	4.75	9.66		

TABLE 47. Stratigraphic occurrence of mammals from the Sioux County Ant Mounds (based on placement of the ant mounds) compared with previously recorded biostratigraphic occurrence ranges. Abbreviations: A, stratigraphic range spanning from one to five meters above the upper purplish white layer (UPW); Ar, Arikareean; B1, stratigraphic range spanning from the UPW to five meters below the UPW; B2, stratigraphic range spanning from five meters below the UPW and lower; Du, Duchesnean; Ch, Chadronian; Hf, Hemingfordian; n. sp., new species (no prior documented range); Or, Orellan; Wh, Whitneyan; ?, species not determined (based on range of genus); —, uncertain species (no range available).

Specimens	Taxon	B2	B1	A	Biostrat.
>2000	*Palaeolagus haydeni*	X	X	X	Ch-Wh
1747	*Eumys elegans*	X	X	X	Or
749	*Paradjidaumo patriciae*	X	X	X	n. sp.
585	*Ischyromys brevidens*	X	X	X	n. sp.
557	*Herpetotherium fugax*	X	X	X	Or-Ar
439	*Altasciurus relictus*	X	X	X	Or-Wh
268	*Willeumys viduus*	X	X	X	Or-Wh
133	*Adjidaumo intermedius*	X	X	X	Or
108	*Domnina gradata*	X	X	X	Or
97	*Scottimus exiguus*	X	X	X	Or
84	*Nanodelphys hunti*	X	X	X	Or-Wh
81	*Centetodon marginalis*	X	X	X	Or
76	*Leptictis dakotensis*	X	X	X	Or-Wh
66	*Leptomeryx* sp., cf. *L. exilis*	X	X	X	Or-Wh
72	*Oligospermophilus douglassi*	X	X	X	Ch-Wh
61	*Cedromus modicus*	X	X	X	n. sp.
61	*Heliscomys vetus*	X	X	X	Ch-Or
48	*Heliscomys hatcheri*	X	X	X	Or
41	*Altasciurus albiclivus*	X	X	X	Or
35	*Wilsoneumys planidens*	X	X	X	Or
34	*Scottimus ambiguus*	X	X	X	Or
33	*Altasciurus clausulus*	X	X	X	Wh
33	*Hypisodus minimus*	X	X	X	Du-Ar
31	*Hesperocyon gregarius*	X	X	X	Du-Wh
28	*Noritrimylus compressus*	X	X	X	Or
27	*Douglassciurus bjorki*	X	X	X	Wh
25	*Copedelphys stevensoni*	X	X	X	Or-Wh
22	*Protosciurus mengi*	X	X	X	Or
19	*Campestrallomys siouxensis*	X	X	X	Ar
14	*Adjidaumo minimus*	X	X	X	Ch-Wh
22	*Oligoscalops galbreathi*	X	X	X	Ch-Or
13	*Paradjidaumo* sp., cf. *P. validus*	X	X	X	Or
12	*Haplomys galbreathi*	X	X	X	Or
12	*Micropternodus borealis*	X	X	X	Ch
11	*Blacktops* sp.	X	X	X	Or
11	*Centetodon wolffi*	X	X	X	Or-Wh

10	*Costepeiromys attasorus*	X	X	X	n. sp.
5	*Litoyoderimys grossus*	X	X	X	n. sp.
5	*Proterix minimus*	X	X	X	Wh
5	*Diplolophus insolens*	X	X	X	Ch
5	?*Leptomeryx* sp.	X	X	X	—
5	*Aulolithomys vexilliames*	X	X	X	Ch
3	*Hesperopetes* sp.	X	X	X	Ch-Wh
3	*Micropternodus* cf. *M. montrosensis*	X	X	X	Ch
4	*Palaeogale* cf. *minuta*	X		X	Ar
3	*Protansomys gulottai*	X		X	n. sp.
2	*Oropyctis* sp.	X		X	—
2	*Ankylodon* sp., cf. *A. progressus*		X	X	?Ch-?Or
23	*Scottimus lophatus*	X	X		Wh
23	*Aulolithomys* sp., cf. *A. bounites*	X	X		Ch
11	*Megaheliscomys mcgrewi*	X	X		Or
9	*Sinclairella* sp., cf. *S. dakotensis*	X	X		Ch-Wh
7	*Pelycomys* sp.	X	X		?Ch-?Or
6	*Oligoryctes tenutalonidus*	X	X		n. sp.
6	*Ecclesimus tenuiceps*	X	X		Or
6	*Oropyctis* sp., cf. *O. pediasius*	X	X		Wh
4	*Ansomys* sp., cf. *A. cyanotephrus*	X	X		Wh
4	*Cylindrodon nebraskensis*	X	X		Ch
3	Omomyidae Indeterminate	X	X		—
2	*Oligoryctes* sp., cf. *O. cameronensis*	X	X		Ch
2	*Stibarus* sp., cf. *S. obtusilobus*	X	X		Ch-Or
2	*Metanoiamys paradoxus*		X		Ch
1	*Eutypomys* sp., cf. *E. hibernodus*		X		Or
1	Chiroptera Indeterminate		X		?Ch
1	*Apternodus* sp., cf. *A. major*		X		Ch
40	*Siouxlindrodon sullivani*	X			n. sp.
11	*Centimanomys major*	X			Ch
8	*Yoderimys massarae*	X			n. sp.
7	*Tenudomys basilaris*	X			Or
7	*Pipestoneomys pattersoni*	X			Ch
6	*Proscalops* sp.	X			?Ch-Hf
3	*Kirkomys miriamae*	X			n. sp.
3	*Apatemys* sp.	X			—
3	*Amphechinus* sp.	X			?Ar
2	Cylindrodontidae Indeterminate (small)	X			—
2	*Epeiromys* sp.	X			?Or-?Wh
2	*Herpetotherium valens*	X			Ch-Or
1	*Pseudallomys* sp.	X			?Or
1	Ursoidea indet.	X			—
1	*Campestrallomys* sp.	X			—
1	Cylindrodontidae Indeterminate (large)	X			—

1	*Subparictis dakotensis*	X	Ch-Wh
1	*Otarocyon macdonaldi*	X	Or
1	*Altasciurus* sp.	X	—

TABLE 48. Sampling and diversity data for the ant mounds sampled in this study. Ant mounds 13 and 14 were combined because they were in the same location and ant mound 13 replaced ant mound 14 after a flood. Reported specimens are the number of identifiable specimens from each ant mound, not the total number of specimens collected. Abbreviations: cTSR, corrected taxon sampling rate; Elev., elevation of the ant mound relative to the closest exposure of the UPW; TSR, taxon sampling rate (specimens/taxa).

Ant Mound	Group	Elev.	Specimens	Taxa	TSR	cTSR
18	Upper	+5	70	21	3.3	—
19	Upper	+3	490	32	15.3	33.1
8	Upper	+2	227	34	6.7	9.6
11	Upper	+2	88	19	4.6	—
10	Upper	+1	120	23	5.2	—
17	Upper	+1	86	15	5.7	—
13/14	Middle	0	534	40	13.4	22.1
7	Middle	-1	376	37	10.2	16.6
15	Middle	-1	368	34	10.8	19.6
9	Middle	-2	407	40	10.2	15.7
12	Middle	-2	103	20	5.2	—
16	Middle	-3	365	35	10.4	18.1
6	Lower	-6	611	51	12.0	16.7
1	Lower	-6	493	48	10.3	14.3
5	Lower	-6	274	33	8.3	13.9
2	Lower	-6	91	20	4.6	—
4	Lower	-7	596	50	11.9	16.8
3	Lower	-7	571	57	10.0	12.9

TABLE 49. Stratigraphic distribution of taxa within the Sioux County ant mound sample elsewhere restricted to Chadronian faunae. Stratigraphic positions based on placement of ant mounds relative to the upper purplish-white layer (UPW = 0). No ant mounds were sampled at the -5-, -4-, or 4-meter intervals. No Chadronian restricted taxa were recovered from the +3 m and +5 m levels. Numbers reported are the numbers of specimens referred to that taxon from each stratigraphic interval. See Table 48 for stratigraphic placements of individual ant mounds. Abbreviations: Sp., total number of specimens.

Sp.	Taxon	-7	-6	-5	-4	-3	-2	-1	0	1	2	3	4	5
12	*Micropternodus borealis*	2	2				2	2	3		1			
5	*Aulolithomys vexilliames*		2					2			1			
3	*Micropternodus* cf. *montrosensis*		1						1	1				
2	*Metanoiamys paradoxus*					1		1						
4	*Cylindrodon nebraskensis*	3						1						
23	*Aulolithomys* cf. *bounites*	11	9			2	1							
2	*Oligoryctes* cf. *cameronensis*	1					1							
1	*Apternodus* cf. *major*					1								
11	*Centimanomys major*	8	3											
7	*Pipestoneomys pattersoni*	3	4											
3	*Apatemys* sp.	2	1											

TABLE 50. Stratigraphic distribution of new species recognized in this study within the Sioux County ant mound collection. Stratigraphic positions are based on placement of ant mounds relative to the upper purplish-white layer (UPW: = 0). No ant mounds were sampled at the -5-, -4-, or 4-meter intervals. Numbers reported are the numbers of specimens referred to that taxon from each stratigraphic interval. See Table 48 for stratigraphic placements of individual ant mounds. Abbreviations: Sp., total number of specimens.

Sp.	Taxon	-7	-6	-5	-4	-3	-2	-1	0	1	2	3	4	5
749	*Paradjidaumo patriciae*	74	141			65	61	123	82	58	54	54		12
585	*Ischyromys brevidens*	120	191			23	36	53	46	29	18	51		10
61	*Cedromus modicus*	20	15			3	5	2	2	3	4	6		1
5	*Litoyoderimys grossus*	1					1		2					1
10	*Costepeiromys attasorus*	2	4				1			1		2		
3	*Protansomys gulottai*		2								1			
6	*Oligoryctes tenutalonidus*	3						2	1					
40	*Siouxlindrodon sullivani*	12	28											
8	*Yoderimys massarae*	4	4											
3	*Kirkomys miriamae*	2	1											

TABLE 51. Distribution of Chadronian taxa identified in this study relative to the UPW. Stratigraphic positions are based on placement of ant mounds relative to the upper purplish-white layer (UPW: = 0). No ant mounds were sampled at the -5-, -4-, or 4-meter intervals. Numbers reported are the numbers of specimens referred to that taxon from each stratigraphic interval. Inferred Chadronian taxa counts the ghost lineages for taxa sampled at higher stratigraphic intervals. Sampling rate is the total number of identifiable specimens from that stratigraphic interval divided by the number of specimens from that interval that are referred to Chadronian taxa. See Table 48 for stratigraphic placements of individual ant mounds. Abbreviations: Sp., total number of specimens.

Sp.	Taxon	-7	-6	-5	-4	-3	-2	-1	0	1	2	3	4	5
12	*Micropternodus borealis*	2	2				2	2	3		1			
5	*Aulolithomys vexillames*		2					2			1			
3	*Micropternodus* cf. *montrosensis*		1						1	1				
6	*Oligoryctes tenutalonidus*	3						2	1					
2	*Metanoiamys paradoxus*					1		1						
4	*Cylindrodon nebraskensis*	3						1						
23	*Aulolithomys* cf. *bounites*	11	9			2	1							
2	*Oligoryctes* cf. *cameronensis*	1					1							
1	*Apternodus* cf. *major*					1								
40	*Siouxlindrodon sullivani*	12	28											
11	*Centimanomys major*	8	3											
8	*Yoderimys massarae*	4	4											
7	*Pipestoneomys pattersoni*	3	4											
3	*Apatemys* sp.	2	1											
	Chadronian Taxa Present	10	9	—	—	3	3	5	3	1	2	0	—	0
	Inferred Chadronian Taxa	14	14	—	—	9	8	6	4	3	2	0	—	0
	Specimens	49	54	—	—	4	4	8	5	1	2	0	—	0
	Sampling Rate	24	28	—	—	92	128	93	107	206	158	0	—	0

APPENDIX:
LISTS OF REFERRED SPECIMENS OF SELECTED SPECIES FROM SIOUX COUNTY ANT MOUNDS.

Herpetotherium fugax

Upper Dentition:, SDSM 145002, 145024, 150487,**partial maxilla with P3-M1**; SDSM 145001, 150535, 150626, 156396, **partial maxilla with M1-M2**; SDSM 144990, 144991, 144933, 144994, 144999, 150440, 150464, 150511, 150529, 150531, 150536, 156419, **partial maxilla with M2-M3**; SDSM 144992, 150439, **maxilla with M2-M4**; SDSM 144998, 145000, 150555, **partial maxilla with M3-M4**; SDSM 145005, 145009, 145011, 145012, 145014, 145018, 145019, 145021, 145025, 145028-145030, 145032, 145034, 145042, 145044, 145065-145067, 145069, 145075, 145077, 145080, 145081, 145086, 145095, 145096, 150443, 150446, 150455, 150467, 150469, 150475, 150479, 150478, 150483, 150495, 150498, 150503, 150505, 150508, 150510, 150513, 150154, 150520, 150525, 150528, 150538, 150538, 150543, 150546, 150549, 156366-15368, 156372, 156379, 156380, 156382, 156392, 156397, 156420, **M1**; SDSM 145003, 145004, 145006, 145007, 145013, 145015-145017, 145023, 145026, 145027, 145031, 145035, 145037, 145041, 145043, 145045, 145046, 145048, 145051, 145053, 145055, 145058, 145060, 145062, 145093, 145068, 145070-145073, 145076, 145079, 145083-145085, 145087, 145089, 145092, 145094, 145097-145102, 150437, 150444, 150445, 150452-150454, 150456-150460, 150462, 150470, 150472-150474, 150476, 150477, 150482, 150485, 150488, 150490, 150494, 150496, 150497, 150499-150502, 150506, 150512, 150515, 150518, 150521, 150524, 150526, 150530, 150532, 150540, 150542, 150544, 150547, 150548, 150553, 150945, 156369, 156370, 156373, 156374, 156378, 156381, 156383, 156385-156387, 156390, 156395, 156399, 156418, **M2**; SDSM 145008, 145010, 145020, 145022, 145036, 145038-145040, 145049, 145050, 145052, 145054, 145056, 145059, 145061, 146064, 145078, 145082, 145088, 145090, 145091, 145093, 150211, 150435, 150436, 150436, 150438, 150441, 150442, 150447-150451, 150461, 150463, 150465, 150466, 150468, 150471, 150478, 150481, 150484, 150489,150491-150493, 150504, 150507, 150509, 150516, 150517, 150519, 150522, 150523, 150527, 150533, 150534, 150537, 150541, 150545, 150550-150552, 150637, 156375-156377, 156384, 156388, 156389, 156391, 156393, 156398, 156400, 156401, 156421, **M3**; SDSM 150486, 150944, **M4**.

Lower Dentition: SDSM 145104, 150353, 150378, 150410, 150420, 150424, 150630, 150937, **partial dentary with p3-m1**; SDSM 150421, **partial dentary with p3-m2**; SDSM 150384, **dentary with m1-m3**; SDSM 150192, 150198, 150357, 150371, 150386, 150399, 150643, 150938, **dentary with m1-m2**; SDSM 150402, 150429, **dentary with m1-m4**; SDSM 145103, 150190, 150194, 150197, 150199, 150201, 150203, 150278, 150313, 150374, 150380, 150383, 150385, 150400, 150401, 150415, 150419, 150629, 156416, **partial dentary with m2-m3**; SDSM 150191, 150193, 150196, 150202, 150204, 150205, 150207, 150312, 150356, 150376, 150382, 150387, 150388, 150396, 150403, 150408, 150422, 150423, **partial dentary with m3-m4**; SDSM 150208, 150218, 150229-105234, 150241, 150243, 150244, 150252, 150254, 150257, 150261, 150263, 150264, 150266, 150272, 150273, 150276, 150286, 150292, 150293, 150295, 150305, 150309, 150315, 150321, 150328, 150329, 150332, 150334, 150335, 150341, 150345, 150348, 150351, 150355, 150359, 150363, 150364, 150368, 150369, 150375, 150377, 150379, 150392, 150404, 150414, 150430, 150627, 150634, 150943, 156409, 156411, 156415, 156417, **m1**; SDSM 150189, 150209, 150210, 150214-150217, 150219-150221, 150225, 150236-150238, 150242, 150245-150247, 150249, 150251, 150253, 150256, 150258, 150262, 150267, 150268, 150271, 150274, 150277, 150279, 150281, 150282, 150287, 150289, 150294, 150296, 150300, 150301, 150304, 150306, 150308, 150310, 150318, 150323, 150325, 150326, 150331, 150333, 150337-150340, 150342, 150347, 150349, 150354, 150366, 150370, 150372, 150373, 150395, 150397, 150398, 150406, 150407, 150409, 150411, 150412, 150416, 150431, 150434, 150632, 150638, 156407, 156410, 156414, **m2**; SDSM 150212, 150222-150224, 150226, 150240, 150248, 150250, 150265, 150270, 150283, 150288, 150290, 150297-150299, 150302, 150307, 150311, 150314, 150316, 150317, 150319, 150322, 150327, 150330, 150336, 150343, 150352, 150358, 150360, 150367, 150381, 150393, 150405, 150413, 150417, 150418, 150425, 150427, 150432, 150942, 156403-156406, 156408, **m3**; SDSM 150206, 150213, 150227, 150228, 150235, 150255, 150259, 150260, 150269, 150275, 150280, 150284, 150285, 150303, 150320, 150324, 150346, 150350, 150361, 150362, 150365, 150389-150391, 150394, 150426, 150428, 150433, 150936, 150939-150941, 156402, 156412, 156413, **m4**.

Ischyromys brevidens

Upper dentition: SDSM 155781, 155790, 155792, 155798, 155801, 155805, 155806, 155808-155810, 155814, 155815, 155817-155820, 155823, 155825, 155838, 155840, 155842, 155849, 155850, 155858, 155861, 155864, 155869, 155870, 155872, 155895, 155903, 155906, 155914, 155917, 155924, 155925, 155928, 155932, 155933, 155949, 155952, 155954, 155957, 155962, 155964, 155965, 155969-155971, 155978-155982, 155986, 155989-155993, 155995, 155996, 155998, 156000, 156003, 156006, 156007, 156009, 156011, 156012, 156015, 156016, 156019, 156023, 156025, 156332, 156337, 156345-156347, 156535, 156990, **dP4**; SDSM 155821, 155867, 155868,

155873, 155880, 155881, 155887, 155901, 155941, 156005, 156024, 156336, 156491, **P4**; SDSM 137267, 155777, 155779, 155780, 155783, 155787-155789, 155793, 155797, 155802, 155811, 155813, 155816, 155824, 155826, 155827, 155830, 155831, 155836, 155839, 155843-155847, 155852, 155853, 155855, 155857, 155859, 155860, 155862, 155874, 155877, 155878, 155883, 155885, 155886, 155888-155890, 155894, 155896-155898, 155900, 155904, 155905, 155907-155912, 155916, 155918, 155920-155923, 155926, 155927, 155930, 155934-155940, 155942-155946, 155950, 155951, 155956, 155958, 155959, 155961, 155963, 155966-155968, 155972, 155974, 155975, 155977, 155983, 155985, 155987, 155999, 156001, 156002, 156004, 156010, 156014, 156017, 156020, 156333, 156334, 156338-156342, 156344, 156490, 156532, 156533, **M1 or M2**; SDSM 15778, 155782, 155784-155786, 155791, 155799, 155803, 155807, 155865, 155866, 155833, 155834, 155812, 155822, 155828, 155829, 155832, 155835, 155837, 155841, 155848, 155851, 155854, 155856, 155863, 155871, 155875, 155876, 155879, 155882, 155884, 155891-155893, 155899, 155902, 155912, 155915, 155919, 155931, 155947, 155953, 155955, 155960, 155973, 155976, 155984, 155988, 155994, 155997, 156008, 156013, 156018, 156021, 156022, 156335, 156343, 156534, **M3**;

Lower dentition: SDSM 156026, 156027, 156031,156033, 156035, 156039, 156041-156043, 156046, 156048, 156051-156053, 156055, 156056, 156061-156064, 156066, 156069-156072, 156077, 156080, 156082, 156093, 156099, 156102, 156103, 156108, 156111, 156118, 156123, 156124, 156126, 156132-156135, 156137, 156139, 156141, 156143-156145, 156147, 156148, 156151-156153, 156155, 156156, 156161, 156165, 156166, 156171-156173, 156175, 156179, 156180, 156182, 156186, 156190-156194, 156198, 156208, 156210-156212, 156214-156217, 156220, 156221, 156224, 156225, 156227-156231, 156233-156235, 156237-156239, 156241, 156244, 156247, 156252, 156256,156259-156261, 156264, 156269, 156270, 156272, 156275, 156278, 156281, 156282, 156284, 156290, 156292, 156294, 156296, 156300-156204, 156306, 156311, 156314, 156316, 156320-156322, 156324, 156325, 156537, 156983-156988, **dp4**; SDSM 156037, 156054, 156065, 156079, 156083, 156097, 156109, 156127,156140, 156149, 156157, 156188, 156196, 156202, 156242, 156243, 156245, 156249, 156251, 156258, 156265, 156268, 156293, 156298, 156315, 156326, 156327, **p4**; SDSM 156029, 156030, 156040, 156044, 156045, 156047, 156049, 156057-156060, 156067, 156068, 156073, 156075, 156078, 156081, 156086-156088, 156090-156092, 156094,156095, 156098, 156100, 156106, 156110, 156112-156115, 156119, 156121, 156122, 156125, 156130, 156131, 156136, 156146, 156150, 156158, 156159, 156162, 156164, 156167, 156169, 156177, 156178, 156181, 156184, 156187, 156189, 156197, 156199-156201, 156203, 156205, 156209, 156213, 156218, 156219, 156222, 156232, 156240, 156246, 156250, 156253, 156255, 156266, 156267, 156271, 156274,156276, 156277, 156280, 156286, 156287, 156295, 156297, 156299, 156308, 156312, 156313, 156317, 156318, 156323, 156328, 156536, **m1 or m2**; SDSM 156028, 156032, 156034, 156036, 156038, 156050, 156074, 156076, 156084, 156089, 159096, 156101, 156104, 156105, 156107, 156116, 156117, 156120, 156128, 156429, 156138, 156142, 156154, 156160, 156163, 156168,156170, 156174, 156176, 156183, 156185, 156195, 156204,156206, 156207, 156223, 156226, 156236, 156248, 156254, 156257, 156262, 156263, 156273, 156279, 156283, 156285, 156288, 156289, 156291, 156305, 156307, 156309, 156310, 156319, 156332, **m3**.

Altasciurus relictus

Upper dentition: SDSM 137235, 137252, 137303, 152260, 152261, 152280, **maxilla fragment with P4-M1**; SDSM 137254, **maxilla with M1-M3**; SDSM 152282, 152284, **maxilla fragment with M1-M2**; SDSM 137251, 152522, 154989, **maxilla fragment with M2-M3**; SDSM 155051, **dP4**; SDSM 152253, 152269, 152271, 152273, 152274, 154982, 154990, 154997, 155001, 155002, 155007, 155008, 155010, 155024, 155037, 155059, 155064, 155070-155074, 155087, 155099, 155103, 155105, 155112, 155118, 155130, 155132, 155133, 155135, 155141, 155145, 155147, 155149, 155715, 155716, 155719, **P4**; SDSM 152254-152258, 152262, 152265, 152266, 152268, 152270, 152272, 152276, 152278, 152279, 152281, 152283, 152521, 152523-152525, 154972, 154976-154979, 154981, 154983, 154985-154987, 154991, 154992, 154996, 154998, 155004-155006, 155009, 155011-155015, 155017-155021, 155025-155027, 155030, 155034, 155036, 155038-055042, 155044, 155045, 155047, 155049, 155050, 155052-155054, 155056, 155058, 155061-155063, 155066, 155067, 155069, 155076, 155079, 155081, 155082, 155085, 155086, 155088-155092, 155094-155096, 155100-155102, 155104, 155107, 155108, 155110, 155114-155117, 155120, 155121, 155123, 155124, 155126-155129, 155131, 155134, 155136-155140, 155144, 155146, 155148, 155151-155155, 155157-155159, 155776, 156496, **M1 or M2**; SDSM 154980, 154984, 154988, 154993-154995, 154999, 155000, 155016, 155024, 155028, 155032, 155046, 155048, 155055, 155068, 155075, 155093, 155133, 155122, 155125, 155156, 155161, 155717, **M3**.

Lower dentition: SDSM 137248, **dentary fragment with p4-m1**; SDSM 152437, 155721, **dentary fragment with m1-m2**; SDSM 137247, 155194, 155349, **dentary fragment with m2-m3**; SDSM 155290, 155337, **dp4**; SDSM 152434, 152442, 152445, 152457, 155166, 155170, 155175,155176, 155181, 155185, 155186, 155208, 155222, 155235, 155242, 155249, 155286, 155297, 155299, 155306, 155326, 155328, 155334, 155338, 155345, 155390,

155720, 155725, 155727, 155733, **p4**; SDSM 152438, 152440, 152444, 152449, 152462-152466, 155163, 155167, 155171, 155172, 155177, 155183, 155184, 155189, 155191-155193, 155198-155203, 155207, 155210, 155211, 155213, 155217, 155218, 155220, 155224, 155227, 155228, 155232, 155239, 155245, 155247, 155255, 155260, 155261, 155268, 155269, 155273, 155274, 155278, 155279, 155281, 155282, 155285, 155288, 155289, 155291, 155295, 155303, 155307, 155308, 155323-155325, 155331, 155341, 155342, 155347, 155356, 155358, 155359, 155365, **m1**; SDSM 151962, 152431, 152432, 152435, 152439, 152441, 152450, 152451, 152455, 155164, 155165, 155168, 155178-155180, 155182, 155188, 155190, 155196, 155197, 155206, 155226, 155231, 155236, 155238, 155240, 155241, 155243, 155244, 155246, 155248, 155250, 155252, 155253, 155259, 155262, 155264, 155267, 155270, 155276, 155280, 155283, 155287, 155292, 155294, 155296, 155298, 155302, 155305, 155309, 155310, 155314, 155315, 155319, 155329, 155335, 155336, 155344, 155350, 155354, 155355, 155362, 155363, 155730, 155731, **m2**; SDSM 152433, 152443, 152452-152454, 152456, 152460, 155169, 155173, 155209, 155212, 155214, 155221, 155223, 155225, 155229, 155230, 155234, 155237, 155254, 155256, 155257, 155265, 155271, 155272, 155275, 155293, 155300, 155301, 155304, 155311, 155313, 155316-155318, 155321, 155332, 155343, 155353, 155364, **m3**.

Adjidaumo intermedius

Upper dentition: SDSM 151107, **maxilla with P4-M3**; SDSM 151140, 152392, 152396, **maxilla with P4-M2**; SDSM 137244, 137318, 151112, 151115, 151116, 151119-151123, 151130, 151133, 151137, 151146, 151152, 152380, 152382, 152383, 152387-152389, 152393-152395, 152398, 154888, **maxilla with P4-M1**; SDSM 152381, 152397, **maxilla with M1-M3**; SDSM 151103, 151127, 152385, 152391, **maxilla with M1-M2**;
SDSM **maxilla with M2-M3**; SDSM 137242, 151106, 151108, 151124, 151141, 151157, 152384, 152390, 154872, 154873, 154875, 154876, 154878, 154879, 154882-154884, 154886, 154887, 154889, **P4**; SDSM 152386, 152399, 154632, 154651, 154874, 154877, 154880, 154881, 154885, 154890, **M1 or M2**.

Lower Dentition: SDSM 152362, **dentary with p4, m2-m3**; SDSM 137257, **dentary with p4-m2**; SDSM 151104, 151111, 151135, 151154, 151156, 152379, 154891, 154907, **partial dentary with p4-m1**; SDSM 137298, **dentary with dp4-m3**; SDSM 137313, 152359, **dentary with dp4-m1**; SDSM 137234, 151105, 151109, 151110, 151132, 151134, 151144, 151148, **dentary with m1-m3**; SDSM 151114, 151117, 151118, 151126, 151131, 151147, 152357, 152360, 152363-152366, 152374, **partial dentary with m1-m2**; SDSM 151125, 152378, 154899, **partial dentary with m2-m3**; SDSM 152367, 152369, 152372, 154897, 154904, 154910, 154911, 154913, **p4**; SDSM 151113, 151153, 152368, 152373, 154892-154895, 154901–154903, 154905, 154906, 154908, 154912, 154914, 154915, **m1 or m2**; SDSM 151155, **m2**; SDSM 151158, 154896, 154898, 154900, **m3**.

Paradjidaumo patriciae

Upper dentition: SDSM 137230, 137232, 137264, **maxilla with P4-M3**; SDSM 137239, 137304, 137307, 150963, 150964, 150966, 150970, 150973-150976, 150980, 150983, 151000, 151002, 151003, 151008, 151011, 151012, 151020, 151025, 151027, 151030-151033, 151036, 151040-151042, 151045, 151150, 152316, 152319, 152322, 152324, 152325, 152330,152349, 152350, 152355, 152356, 154589, 154764, **maxilla with P4-M1**; SDSM 150989, 151043, **maxilla with dP4-M1**; SDSM 137259, 151029, 151136, **maxilla with P4-M2**; SDSM 150998, 151037, **maxilla with M1-M3**; SDSM 137243, 137250, 151005, 151016, 151017, 151149, 152320, 154806, **maxilla with M1-M2**; SDSM 137314, 152326, 152347, **maxilla with M2-M3**; SDSM 137308, 137315, 150981, 150986, 150988, 150990, 150993, 150996, 151138, 151142, 151143, 152321, 152323, 152327, 152328, 152332, 152333, 152335, 152337, 152338, 152342, 152344, 152345, 152348, 152356, 154553, 154556-154558, 154561, 154567, 154569, 154574, 154576-154579, 154581, 154584, 154587, 154588, 154592, 154595, 154598, 154599, 154602, 154608, 154617, 154618, 154622, 154623, 154625, 154633, 154637, 154640, 154646, 154650, 154656, 154659, 154660, 154662, 154663, 154671, 154672, 154676, 154677, 154679, 154682, 154685, 154687, 154688, 154693, 154694, 154698, 154700, 154709, 154710, 154715, 154717, 154719, 154720, 154722-154726, 154732-154735, 154737, 154739-154744, 154749, 154751, 154758, 154759, 154762, 154763, 154766, 154769, 154771, 154772, 154774, 154776, 154779, 154783-154786, 154790, 154796-154800, 154804, 154805, 154816, 154820, 154823, 154824, 154828, 154832, 154838, 154841, 154842, 154846, 157012, **P4**; SDSM 150994, 151024, 152313-152316, 152331, 152334, 152336, 152339-152341, 152343, 152346, 152352, 1252353, 152400, 154551, 154552, 154554, 154555, 154560, 154562-154566, 154568, 154570-154573, 154575, 154580, 154582, 154583, 154585, 154586, 154590, 154591, 154593, 154594, 154596, 154597, 154600, 154601, 154603-154607, 1545609-154616, 154619-154621, 154626-154631, 154635, 154636, 154638, 154639, 154641-154645, 154652-154655, 154657, 154658, 154661, 154664-154670, 154673-154675, 154678, 154680, 154681, 154683, 154684, 154689, 154691, 154692, 154695-154697, 154701-154705, 154707, 154708, 154744-154714, 154716, 154718, 154721, 154727-154731, 154736, 154738, 154745, 154746, 154748, 154750, 154752-154757, 154760, 154765, 154767, 154768, 154770,

154773, 154775, 154777, 154778, 154780-154782, 154787, 154789, 154791-154793, 154795, 154801-154803, 154807-154815, 154817-154819, 154821, 154822, 154825-154827, 154829-154831, 154833-154837, 154839, 154840, 154843-154845, 154847,154848, 154871, 155764, 155765, **M1 or M2**; SDSM 151010, 154871, **M2**; SDSM 151013, 154559, 154761, 154794, **M3**.

Lower dentition: SDSM 150984, 151028, **dentary with p4-m3**; SDSM 137260, 150999, 151023, 151026, **dentary with p4-m2**; SDSM 137268, 137310, 150967, 150978, 151018, 151035, 151038, 152292, **dentary with p4-m1**; SDSM 150979, **dentary with dp4-m2**; SDSM 137305, **dentary with dp4-m1**; SDSM 137228, 137229, 137246, 151006, **dentary with m1-m3**; SDSM 137241, 150977, 151001, 151007, 151021, 151022, 151034, 151039, 151047, 151048, 152289, 152291, 156452, **dentary with m1-m2**; SDSM 137240, 152298, 152317, 152329, 157013, **dentary with m2-m3**; SDSM 137253, 150971, 150985, 150987, 150995, 151139, 152285-152287, 152295, 152296, 152305, 152310-152312, 152371, 152375, 154318, 154322, 154331, 154332, 154337, 154338, 154341, 154342, 154344, 154347, 154353, 154356, 154358, 154361, 154362, 154368, 154372, 154379, 154386, 154387, 154394, 154396-154401, 154403, 154413, 154414, 154417, 154419, 154420, 154426, 154429, 154433, 154435, 154436, 154439-154442, 154445, 154446, 154457, 154459, 154463, 154465, 154467, 154474, 154475, 154478, 154487, 154489, 154490, 154494, 154499, 154500, 154503, 154504, 154512-154514, 154519, 154525, 154526, 154531, 154565-154537, 154541, 154543, 154546, 154548, 155766, 155773, 156451, 156994, **p4**; SDSM 154502, 154849, 154852, 155769, 155772, **dp4**; SDSM 150969, 151004, 151009, 151046, 152297, 152299, 152301, 152303, 152306, 152351, 152354, 152370, 154319-154321, 154324, 154327-154330, 154333-154336, 154339, 154340, 154343, 154345, 154346, 154349-154352, 154355, 154357, 154359, 154360, 154363-154367, 154369-154371, 154373-154378, 154380, 154381, 154383-154385, 154388-154393, 154395, 154402, 154404-154412, 154415, 154416, 154421-154425, 154427-154429, 154432, 154434, 154438, 154443, 154444, 154447, 154449, 154451-154456, 154458, 154460-154462, 154464, 154467, 154469, 154470, 154472, 154473, 154476, 154477, 154479, 154480, 154482-154486, 154488, 154491-154493, 154495154498, 154501, 154505, 154506, 154508-154511, 154515, 154517, 154518, 154520-154524, 154532, 154533, 154538-154540, 154542, 154544, 154545, 154549, 154500, 154851, 154853-154870, 155770, 155701, 155775, **m1 or m2**; SDSM 150991, 151044, 152290, 152300, 152304, 152309, 154431, 154471, 154507, **m2**; SDSM 152294, 152302, 152307, 152308, 154326, 154354, 154382, 154468, 154547, 155767, 155768, **m3**.

Eumys elegans

Upper dentition: SDSM 151995, 152030, 152059, 152127, 153910, **maxilla with M1-M3**; SDSM 137262, 137263, 137266, 151968, 151972, 151979, 151981, 152013, 152014, 152016, 152021, 152022, 152026, 152029, 152031, 153504, 153791, 153791, **partial maxilla with M1-M2**; SDSM 137300, 137306, 151959, 151963, 151964, 151967, 151969, 151970, 151973, 151974, 151976, 151980, 151982-151984, 151987, 151991, 151997, 151999, 152011, 152028, 152055, 152060, 152062, 152063, 152065, 152074, 152078, 152106, 152115, 152160, 153799, 153922, 153929, 153458, 153495, 153799, 153799, 154136, 154139, **partial maxilla with M2-M3**; SDSM 137307, 151961, 151965, 151971, 151992, 152001, 152002, 152004-152007, 152010, 152015, 152018, 152020, 152024, 152025, 152032, 152034, 152035, 152038-152040, 152043-152047, 152049, 152052-152054, 152056, 152057, 152064, 152066, 152070, 152072, 152075-152077, 152079-152084, 152087, 152090, 152092, 152093, 152095, 152096, 152098-152100, 152102, 152104, 152108-152111, 152114, 152118-152124, 152128-152132, 152162, 152229, 152528, 153230-153234, 153238, 153243, 153245, 153248-153250, 153252, 153256, 153257, 153262-153266, 153275-153279, 153282, 153284, 153286-153289, 153292-153296, 153301, 153303, 153308, 153310, 153311, 153313, 153317-153322, 153324, 153328, 153329, 153331, 153334-153336, 153338, 153339, 153343, 153345-153347, 153349, 153353, 153355, 153356, 153359, 153360, 153362, 153364, 153368-153373, 153376, 153378, 153379, 153381-153384, 153386-153390, 153393, 153394, 153396, 153397, 153401-153418, 153422-153426, 153428-153431, 153435, 153438, 153440, 153442-153445, 153447, 153449, 153451, 153453, 153454, 153456, 153458-153460, 153462-153464, 153466, 153470, 153473-153475, 153482, 153483, 153486, 153487, 153489-153492, 153497, 153498, 153501, 153502, 153504, 153507, 153508, 153510, 153512, 153514, 153518, 153521, 153522, 153524, 153525, 153527, 153529, 153531-153534, 153538, 153540-153542, 153547, 153548, 153550, 153551, 153553, 153556, 153558, 153560, 153563, 153564, 153568, 153570-153572, 153574-153578, 153590, 153581, 153585-153587, 153589, 153592-153595, 153598, 153600, 153602-153647, 153619, 153621, 153622, 153625, 153634-153637, 153639, 153647, 153648, 153650, 153653, 153655-153657, 153659-153662, 153664-153666, 153669, 153670, 153673, 153789-153795, 153797, 153798, 153800, 153801, 153803, 153805, 153807-153809, 153812-153814, 153820, 153823, 153824, 153826-153828, 153834-153839, 153841, 153843, 153845-153848, 153854, 153857, 153859, 153862, 153866, 153867, 153869, 153873-153878, 153880, 153882, 153883, 153885, 153888-153892, 153897, 153898, 153900, 153901, 153903-153909, 153912, 153914, 153915, 153918, 153919, 153921, 153925-153928, 153931-153934, 153938-153940, 153943-153948, 153951, 143952,

153955, 154083, 154145, 154305, 154306, 154309, 154312, 155602-155610, 155612, 155613, 156353, 156519, 156531, 156992, **M1**; SDSM 15160,151975, 151985, 151986, 151990, 151993, 151996, 191998, 152008, 152012, 152017, 152019, 152023, 152033, 152036, 152037, 152041, 152042, 152048, 152050, 152051, 152058, 152068, 152069, 152071, 152085, 152086, 152097, 152101, 152103, 152105, 152107, 152112, 152113, 152116, 152117, 152126, 152134, 152135, 152164, 152166,152526, 153228, 153229, 153236, 153237, 153239-153242, 153244, 153247, 153251, 153253, 153255, 153258-153261, 153267-153269, 153271, 153273, 153274, 153280, 153285, 153290, 153291, 153297-153300, 153302, 153304-153307, 153309, 153312, 153315, 153316, 153323, 153325-153327, 153330, 153332, 153337, 153340-153342, 153344, 153348, 153350-153352, 153354, 153363, 153377, 153380, 153385, 153391, 153395, 153399, 153419-153421, 153432-153434, 153436, 153437, 153439, 153446, 153448, 153450, 153455, 153457, 153461, 153465, 153467, 153469, 153471, 153472, 153476-153480, 153484, 153488, 153493, 153494, 153496, 153499, 153500,153503, 153505, 153506, 153509, 153511, 153513, 153515-153517, 153523, 153528, 153530, 153535, 153537, 153539, 153543-153546, 153555, 153559, 153565-153567, 153569, 153579, 153583, 153584, 153588, 153590, 153591, 153597, 153620, 153623, 153624, 153627-153629, 153631-153633, 153638, 153640-153643, 153646, 153649, 153652, 153651, 153654, 153658, 153663, 153667, 153668, 153674, 153675, 153802, 153804, 153806, 153810, 153811, 153815-153819, 153822, 153825, 153829-153833, 153840, 153850-153853, 153855, 153858, 153860, 153863-153865, 153868, 153870-153872, 153884, 153886, 153887, 153893, 153895, 153896, 153899, 153902, 153913, 153920, 153924, 153930, 153935-153937, 153942, 153953, 153954, 154101, 154109, 154110, 154128, 154130, 154138, 154141, 154161, 154162, 154167, 154168, 154304, 154307, 154310, 154311, 154313-154316, 155593, 155600, 155610, 155611, 155617-155619, 155623, 155646, 155647, 156517, 156518, 156520-156525, 156530, **M2**; SDSM 151966, 151988, 151989, 151994, 152000, 1512003, 152009, 152027, 152067, 152073, 152088, 152089, 152091, 152094, 152125, 152133, 152170, 153227, 153253, 153246, 153254, 153270, 153272, 153281, 153283, 153314, 153333, 153357, 153358, 153361, 153365-153367, 153374, 153375, 153392, 153398, 153400, 153427, 153441, 153452, 153468, 153481, 153519, 153520, 153526, 153536, 153549, 153554, 153557, 153561, 153562, 153573, 153582, 153596, 153599, 153601, 153618, 153626, 153630, 153644, 153645, 153796, 153821, 153842, 153844, 153856, 153861, 153879, 153881, 153894, 153911, 153916, 153917, 153941, 153949, 154091, 154108, 154131, 154146, 154303, 154308, 155595, 155597, 155599, 155614-155616, 155620-155622, 155695, **M3**.

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