

The first tetrapod from the mid-Miocene *Clarkia lagerstätte* (Idaho, USA)

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ABSTRACT

The *Clarkia lagerstätte* (Latah Formation) of Idaho is well known for its beautifully preserved plant fossils as well as a fauna of insects and fish. Here we present the first known tetrapod fossil from these deposits. This specimen, recovered from the lower anoxic zone of the beds, is preserved as a carbonaceous film of a partial skeleton associated with a partial lower incisor and some tooth fragments. The morphology of the teeth indicates that the first tetrapod reported from Clarkia is a rodent. Its skeletal morphology as well as its bunodont and brachydont dentition suggests that it is a member of the squirrel family (Sciuridae). It is a large specimen that cannot be assigned to a known genus. Instead, it appears to represent the first occurrence of a new taxon with particularly gracile postcranial morphology likely indicative of an arboreal ecology. This new specimen is a rare glimpse into the poorly known arboreal mammal fossil record of the Neogene. It supports a greater taxonomic and ecological diversity of Miocene Sciuridae than previously recognized and offers new lines of inquiry in the paleoecological research enabled by the unique preservation conditions of the Clarkia biota.

Subjects Paleontology, Taxonomy, Zoology

Keywords Sciuridae, Barstovian, Arboreality, *Clarkia lagerstätte*, Latah Formation, mid-Miocene

INTRODUCTION

The mid-Miocene is a critical interval for studies of the relationship between climate and paleoecological change. This is in large part due to the mid-Miocene climatic optimum (MMCO), a 2 °C warming event that peaked ca. 17 to 15 million years ago (Ma) and was the last sustained interval of climatic warming in the Cenozoic (*Zachos et al., 2001; Zachos, Dickens & Zeebe, 2008*). The magnitude of warming during the MMCO is consistent with predictions for climatic changes during the coming century (*IPCC, 2014*), and this has made the interval the subject of intensive paleontological and paleoecological study. The Inland Northwest of the United States (Idaho, eastern Oregon and Washington, and portions of surrounding states) is a natural laboratory for the study of the MMCO due not only to the detailed paleoclimatic (*Retallack, 2007, 2009; Takeuchi, Larson & Suzuki, 2007; Yang et al., 2011*) and paleoenvironmental (*Bestland et al., 2008;*

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[Harris et al., 2017](#); [Kohn & Fremd, 2007](#); [Sheldon, 2006](#)) records available in the region but also to the wealth of terrestrial fossil floras and faunas preserved there. These include the vertebrate faunas of the Mascall ([Downs, 1956](#); [Maguire, Samuels & Schmitz, 2018](#)), Sucker Creek ([Scharf, 1932](#)), and Virgin Valley formations ([Merriam, 1911](#)), which, along with other localities in the region, have served as the basis for several analyses of vertebrate macroecology ([Badgley & Finarelli, 2013](#); [Calede, Hopkins & Davis, 2011](#); [Harris, 2016](#); [Maguire, 2015](#); [Orcutt & Hopkins, 2013](#)).

While mammals have been the major focus of paleoecological research in the region, the Inland Northwest has also yielded an important insect fauna from the Latah Formation ([Carpenter, 1931](#)) and numerous fossil floras, notably from the Mascall ([Chaney, 1925, 1959](#); [Chaney & Axelrod, 1959](#); [Knowlton, 1902](#)), Sucker Creek ([Arnold, 1937](#); [Fields, 1996](#)), and Latah Formations ([Knowlton & Mann, 1925](#)). The abundance of contemporaneous fossils in the region from a wide variety of organisms could facilitate analyses of community structure through time across the MMCO. However, vertebrate, insect, and plant macrofossils rarely occur at the same sites, complicating such analyses. An exception to this rule is the Railroad Canyon section of Idaho, where data from phytoliths, stable isotopes from mammalian dental enamel, and vertebrate fossils have provided insight into ecosystem structure and community interactions before and during the MMCO ([Barnosky et al., 2007](#); [Harris, 2016](#); [Harris et al., 2017](#)). The *Clarkia lagerstätte* in the Idaho Panhandle ([Fig. 1](#)) represents another regional paleocommunity that could provide similar opportunities for integrative analyses of ecological change during the MMCO. This series of sites is best known for its rich flora ([Smiley & Rember, 1985a](#)). Leaves and needles are often preserved with original organic material intact, providing the unique opportunity to conduct biochemical analyses of Miocene plant tissue ([Huang et al., 1995](#); [Kim et al., 2004](#); [Lockheart, Van Bergen & Evershed, 2000](#); [Logan, Boon & Eglinton, 1993](#); [Logan, Smiley & Eglinton, 1995](#); [Soltis, Soltis & Smiley, 1992](#); [Yang & Huang, 2003](#)). Other terrestrial organisms recovered from the *lagerstätte* include fungus macrofossils ([Williams, 1985](#)), floral and fungal microfossils ([Gray, 1985](#)), insect fossils, and ichnofossils ([Lewis, 1985](#)). Although providing unparalleled opportunities for paleoecological analyses of a mid-Miocene forest ecosystem ([Batten, Gray & Harland, 1999](#); [Smiley & Rember, 1985b](#); [Smith & Elder, 1985](#)), the *Clarkia* fossil record has until now remained incomplete in one notable way. While salmonid, cyprinid, and centrarchid fish have been reported from the *lagerstätte* ([Smith & Miller, 1985](#)), no tetrapods have previously been reported from any of the *Clarkia* localities. Here we fill in this taxonomic gap by presenting the first known occurrence of a mammal, and indeed the first known tetrapod of any kind, from *Clarkia*.

GEOLOGICAL SETTING

The *Clarkia lagerstätte* consists of several outcrops of the Latah Formation near the town of Clarkia in the Idaho Panhandle ([Smiley & Rember, 1985a](#); [Fig. 1](#)). The portion of the Latah Formation that crops out at Clarkia was deposited on a lake bed formed when a Columbia River Basalt flow formed a natural dam of the proto-St. Maries

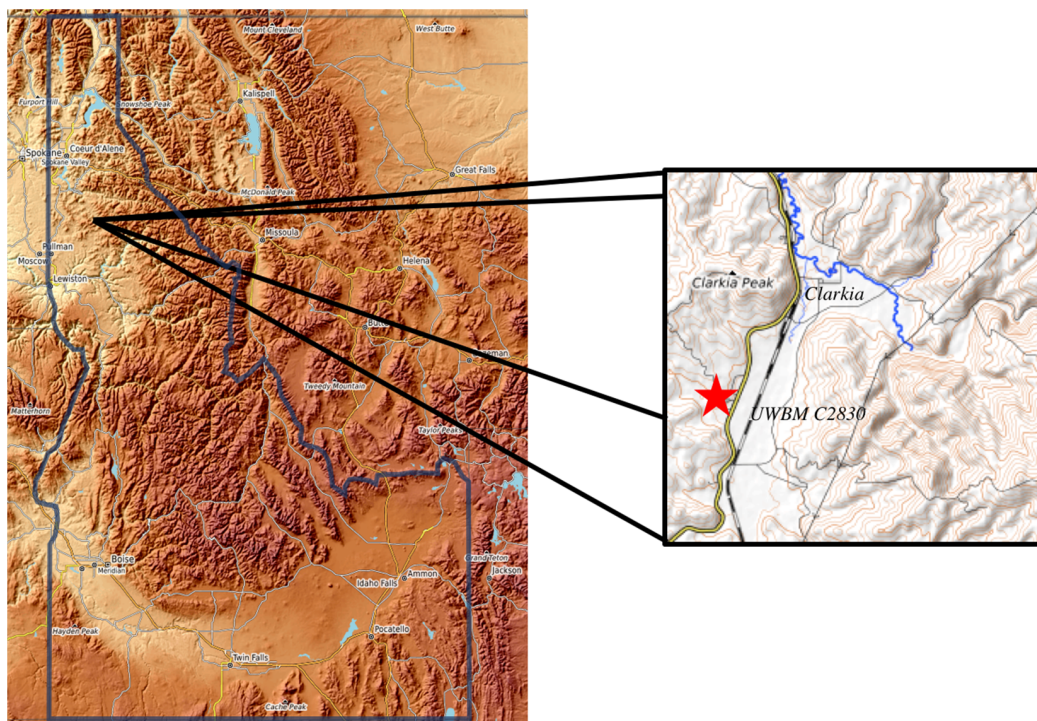


Figure 1 Location of UWBM C2830. UWBM C2830, the Clarkia type locality, is equivalent to UIMM P-33. The section from which the Clarkia rodent was recovered is at the north end of the Kienbaum family racetrack in Clearwater County, Idaho. [Full-size !\[\]\(ba1b80118482ccef74a5d718ca4d7242_img.jpg\) DOI: 10.7717/peerj.4880/fig-1](https://doi.org/10.7717/peerj.4880/fig-1)

River near the present town of St. Maries, Idaho (*Yang et al., 1995*). Sediments at Clarkia consist predominately of clay and silt (much of it derived from mica of the underlying Precambrian schist), with some sandy layers at the base of the section (*Smiley, Gray & Huggins, 1975*). Several ash layers are present throughout the section and can be attributed primarily to eruptions associated with the Yellowstone hotspot and to a lesser extent with the Cascade volcanoes (*Ladderud et al., 2015*). *Smiley, Gray & Huggins (1975)* divided the Clarkia *lagerstätte* into two zones: a lower unoxidized zone and an upper oxidized zone. While fossils are found throughout the section, the exquisitely detailed flora with preserved biomolecules for which Clarkia is known are found only in the lower zone.

The fossil described herein was found at the Clarkia type locality (UWBM C2830, originally described as UIMM P-33) at the Kienbaum family racetrack during a North Idaho College trip to the locality in 2009. It was uncovered within Unit 2 of *Smiley & Rember (1985a)* in the lower part of the lower unoxidized zone (*Fig. 2*). The fossil was found immediately below an ash layer correlated with an ash from the Bully Creek Formation, dated to 15.65 ± 0.07 Ma. The basalt dam that created the lake is estimated to have been emplaced ~ 16.0 Ma, though the precise basalt flow responsible has not been identified and dated. (*Ladderud et al., 2015; Nash & Perkins, 2012*). These two dates indicate that the first known tetrapod from Clarkia likely dates to the Early Barstovian North American Land Mammal Age (NALMA). The boundary between the Barstovian and preceding Hemingfordian NALMA lies at 16 Ma (*Tedford et al., 2004*), making a

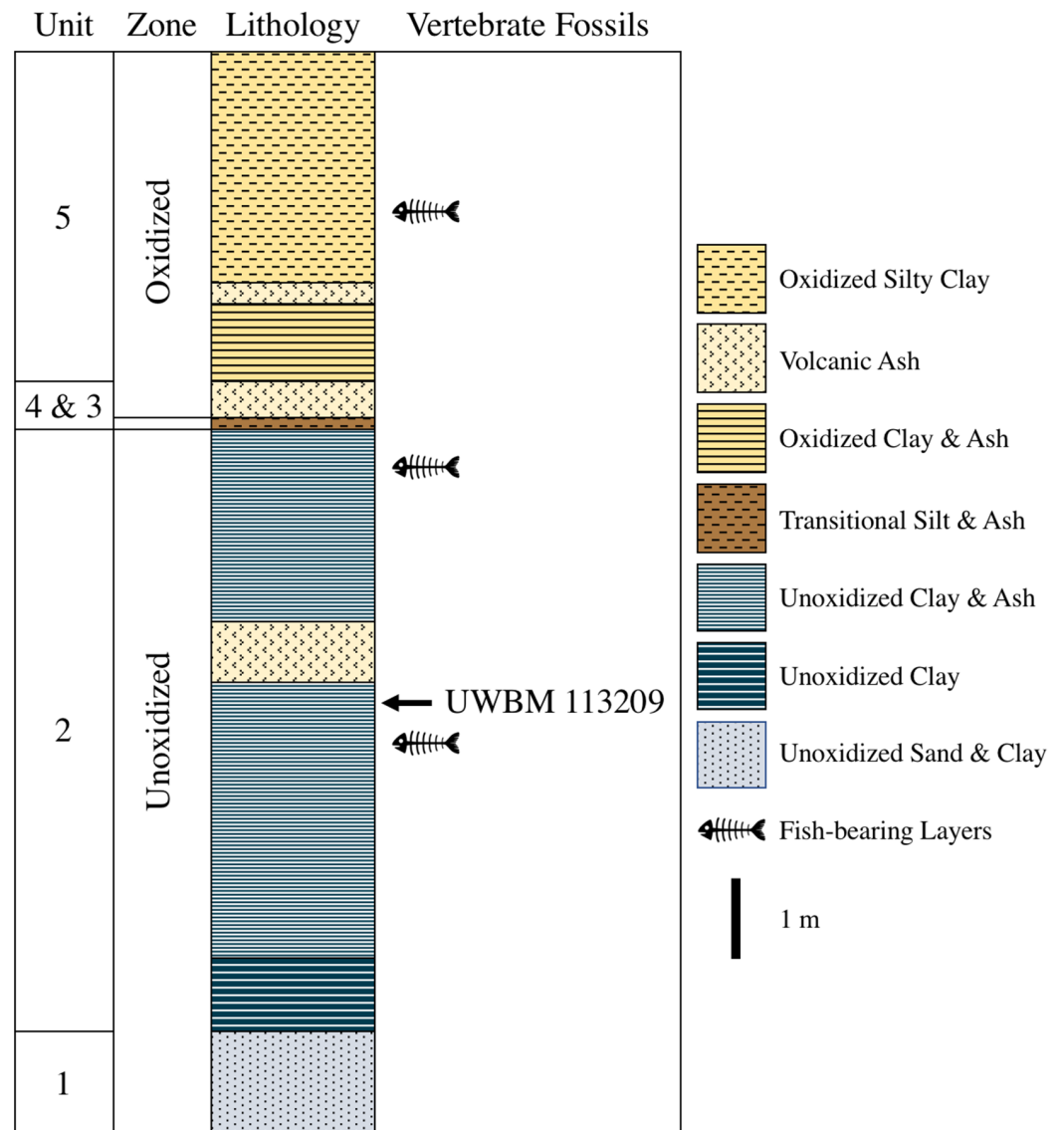


Figure 2 Stratigraphy of the Latah Formation exposed at UWBM C2830. Numbering, lithology, and color of units follows *Smiley, Gray & Huggins (1975)* and *Smiley & Rember (1985a)*. The total thickness of the section exposed at the Kienbaum racetrack is roughly 9 m.

Full-size DOI: 10.7717/peerj.4880/fig-2

Late Hemingfordian age possible as well. However, the specimen was recovered well above the base of the *Clarkia* sequence and as such, a Barstovian age is considerably more likely.

MATERIALS AND METHODS

The taxonomic frameworks for the rodents from the Inland Northwest discussed in this paper come from *Flynn & Jacobs (2008a, 2008b)*, *Flynn, Lindsay & Martin (2008)*, *Goodwin (2008)*, and *Hopkins (2008a)*. We collected the measurements given in this paper either from the literature or directly from specimens using Mitutoyo Digimatic CD-4 CX calipers. The specimen is deposited at the University of Washington Burke Museum of Natural History and Culture (UWBM) in Seattle, Washington (USA).

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA *Linnaeus, 1758*

Order RODENTIA *Bowdich, 1821*

Family Sciuridae *de Waldheim, 1817*

(Fig. 3)

Material—From the Latah Formation, Idaho: UWBM C2830: UWBM 113209 (partial skeleton preserved as a carbonaceous film including skull, partial dentary, partial left and right scapulae, humeri, radii, and ulnae; left(?) manus, and partial vertebral column associated with ribs and sternum; fragments of the cheek teeth and a partial lower incisor are preserved as three-dimensional elements).

Description—UWBM 113209 is preserved as a carbonaceous film of the skeleton. Only a partial lower incisor and fragments of the cheek teeth are preserved as three-dimensional elements. A mold of the upper incisor is also preserved. The chisel-shaped ever-growing lower incisor indicates that the first known tetrapod from the *Clarkia lagerstätte* is a rodent (*Luckett & Hartenberger, 1993; Landry, 1999*). The incisor is 3.3 mm thick dorsoventrally. Its anterior surface is smooth and convex. The diameter of the semi-circle formed by the incisor is 26.3 mm. The fragments of cheek teeth are scattered and no complete tooth is fully preserved. A few cuspules are preserved. They indicate that the specimen has a bunodont tooth shape associated with a brachydont crown height. We could not determine with certainty whether the fragments belong to the upper or lower cheek teeth. The skull is large (*Table 1*). No bone suture or process can be identified. The bones posterior to the upper diastema are too poorly preserved to be identified as specific elements. The dorsal surface of the cranium is somewhat convex. We estimate the upper diastema to be 20.2 mm long; the poor preservation of the cheek teeth prevents a more accurate measurement. The posterior portion of the skull and its articulation with the vertebral column are too poorly preserved to be described. Both the left and right forelimbs are partially preserved as carbonaceous films including the scapulae, humeri, radii, and ulnae. The posterior border of the scapula is convex. The nature of the preservation as a carbonaceous film prevents a detailed description of the morphology, processes, and articulation of the bones of the forelimb. Although the vertebrae are preserved as massive film without visible processes, several ribs can be individualized and the sternum is well preserved.

Comparison—Although most of the detailed morphology of the skeleton of UWBM 113209 cannot be described and the teeth are fragmented, the size of the specimen as well as elements of its dentition allow the taxonomic identity of UWBM 113209 to be constrained. Based on skull length, we estimate the body mass of the animal at around 492 g (using the regression formula provided by *Bertrand, Schillaci & Silcox, 2015*). Only a few rodent families present in North America during the late Hemingfordian and Barstovian reach such a large body size including the Aplodontiidae (including Mylagaulidae), Castoridae, and Sciuridae. Although some rodents of the clade Geomorpha (*Geomyidae, Heteromyidae*, and their fossil relatives; *Flynn, Lindsay & Martin, 2008*) do reach such

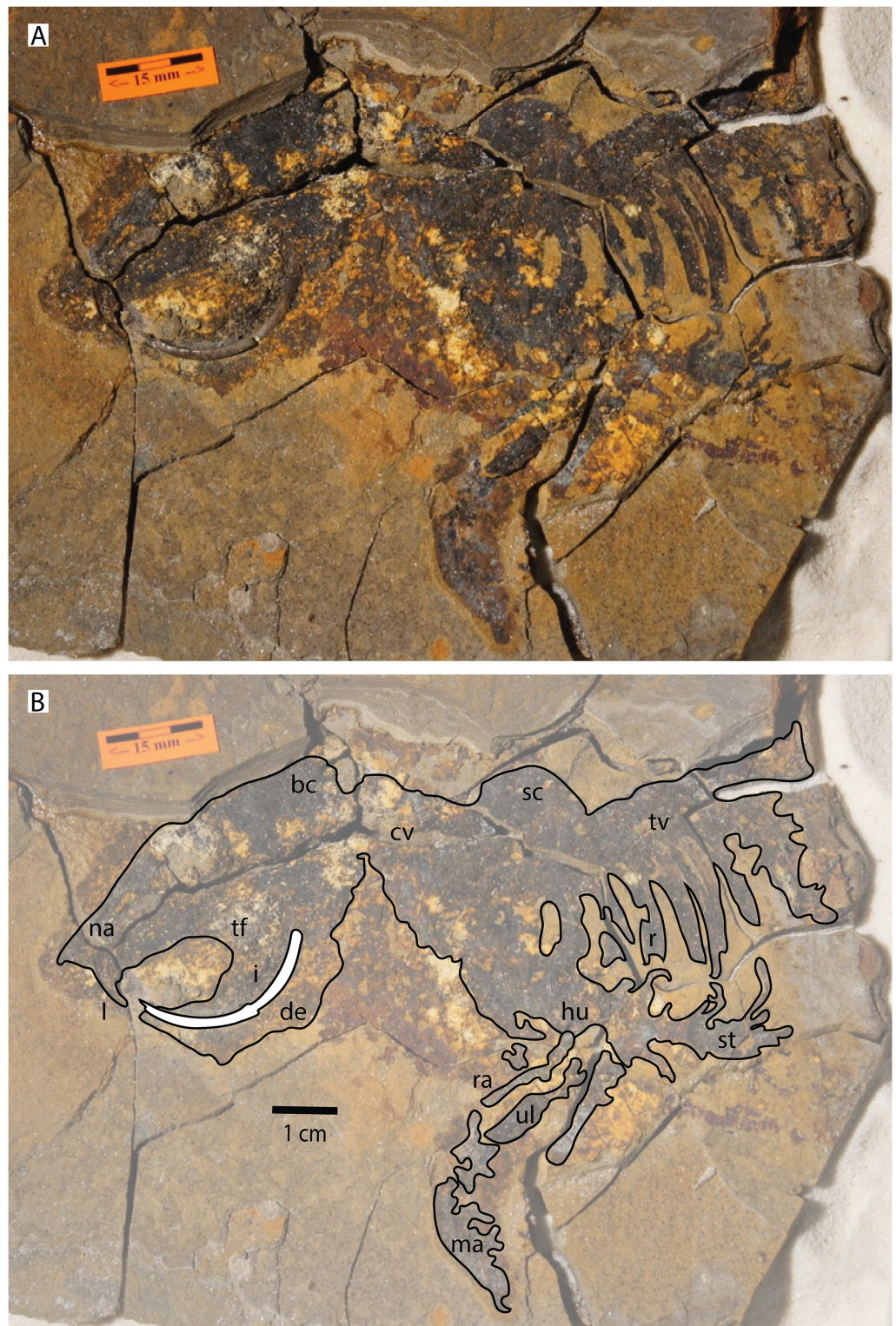


Figure 3 Photograph and line drawing of UWBM 113209. (A) Photo of UWBM 113209, (B) line drawing showing approximate outline of the skeleton. Abbreviations: bc, back of the cranium; cv, cervical vertebrae; de, dentary; hu, humerus; I, upper incisor; i, lower incisor; ma, manus; na, nasals; ra, radius; sc, scapula; st, sternum; tf, tooth fragments; tv, thoracic vertebrae; ul, ulna. Photo by Bill Richards and illustration by Winifred Kehl. [Full-size !\[\]\(1679558f37f6db0dd8360a2a7e913e90_img.jpg\) DOI: 10.7717/peerj.4880/fig-3](https://doi.org/10.7717/peerj.4880/fig-3)

Table 1 Summary of the measurements of UWBM 113209.

Measurement	Value
Dorsoventral thickness of lower incisor	3.3
Diameter of semi-circle formed by incisor	26.3
Skull length	56.5
Upper diastema	20.2*
Lower tooth row length	13.4*
Body mass	492

Notes:

Linear measurements in millimeter. Mass in gram.

* Denotes estimate.

large sizes today, none of the taxa present during the Barstovian in the Inland Northwest, or even North America as a whole, did (Barnosky *et al.*, 2007; Calede, Hopkins & Davis, 2011; Munthe, 1977). The largest geomorph from the Barstovian, *Geomys (Nerterogeomys)* cf. *G. (N.) paenebursarius* (Tedford, 1981) is estimated to have been two-thirds the size of the modern *Geomys bursarius* (Strain, 1966), an animal that weighs as much as 473 g (Connior, 2011), putting the maximum size of *Geomys (Nerterogeomys)* cf. *G. (N.) paenebursarius* at around 312 g. *Geomys (Nerterogeomys)* cf. *G. (N.) paenebursarius* further differs from UWBM 113209 by the shape of its lower incisor. *Geomys (Nerterogeomys)* has a flattened lower incisor (Dalquest, 1978; Flynn, Lindsay & Martin, 2008) whereas the *Clarkia* rodent has a convex incisor.

We used the body mass of UWBM 113209 calculated using skull length to estimate the length of the lower tooth row (LTRL; using the regression formula of Hopkins, 2008b, Table 2 for non-muroid rodents under 500 g). Although this estimate may not be very accurate because it is derived from an estimate of the body mass of UWBM 113209, which is itself determined from a measurement of the skull length based on a carbonaceous impression, the absence of a preserved tooth row prevents a direct measurement on the specimen. The lower tooth row length estimate (Table 1) allows comparisons of the body mass of UWBM 113209 with the database of Hopkins (2007) who surveyed the body mass of North American Aplodontiidae, Castoridae, and Sciuridae from the late Eocene through the end of the Miocene.

Only two aplodontiid genera (excluding mylagaulids) are known from the Barstovian (Flynn & Jacobs, 2008a; Hopkins, 2008a): *Liodontia* and *Tardontia*. Both are known from the Inland Northwest (Calede, Hopkins & Davis, 2011; Shotwell, 1958) and overlap in size with UWBM 113209 (Calede, Hopkins & Davis, 2011; Hopkins, 2007). However, they differ greatly in morphology. The diastemata of *Liodontia* and *Tardontia* are much shorter than that of UWBM 113209 (Gazin, 1932; Morea, 1981; Shotwell, 1958). The dentaries of both *Liodontia* and *Tardontia* are also overall much more robust than that of UWBM 113209 (Gazin, 1932; Shotwell, 1958). Additionally, both *Liodontia* and *Tardontia* display typical derived aplodontiid hypsodont dentitions (Flynn & Jacobs, 2008a; Gazin, 1932; Hopkins, 2008a; Shotwell, 1958) that are quite unlike the bunodont–brachydont dentition of UWBM 113209.

Although a diverse fauna of mylagaulids is known from the Inland Northwest ([Barnosky et al., 2007](#); [Calede & Hopkins, 2012a](#); [Calede, Hopkins & Davis, 2011](#)), most genera are much larger than UWBM 113209 ([Calede, Hopkins & Davis, 2011](#)). Only the genus *Mesogaulus* is similar in size to UWBM 113209 ([Dorr, 1956](#); [Hopkins, 2007](#)). Despite similar sizes, the morphologies of the two rodents are quite different. Thus, the diastema of *Mesogaulus* is much shorter ([Dorr, 1956](#)), its skull and dentary are more robust than those of UWBM 113209 ([Galbreath, 1984](#)), and its lower incisor is larger ([Wilson, 1960](#)). The teeth of mesogauline mylagaulids (including *Mesogaulus*) are also very much unlike those of UWBM 113209. They are typically very large, high-crowned, and display a complex occlusal surface composed of enamel lakes ([Calede & Hopkins, 2012a](#); [Shotwell, 1958](#)). The postcranial skeleton of UWBM 113209 provides additional evidence that the *Clarkia* rodent is not a mylagaulid, given its gracile forelimbs unlike those found in mylagaulids ([Calede & Hopkins, 2012b](#); [Fagan, 1960](#); [Galbreath, 1984](#); [Korth, 2000](#)).

Among the genera of the family Castoridae known from the early Barstovian of North America ([Flynn & Jacobs, 2008b](#)), *Anchitheriomys* is much larger than UWBM 113209 and only *Euroxenomys* overlaps in size with UWBM 113209 ([Hopkins, 2007](#)). This genus is known from other Barstovian-aged deposits of the northwest ([Maguire, Samuels & Schmitz, 2018](#)). However, similarly to *Mesogaulus*, it is much too robust to compare well with UWBM 113209 ([Prieto, Casanovas-Vilar & Gross, 2014](#)). Although several species of *Monosaulax*, another castorid genus, are known from the early Barstovian, including from the Northwest ([Shotwell, 1968](#)), they are much larger than UWBM 113209 ([Hopkins, 2007](#)). Some species of *Monosaulax* from the late Barstovian are smaller than UWBM 113209 ([Hopkins, 2007](#)). Nonetheless, similarly to *Euroxenomys*, the morphology of the dentary and skull of *Monosaulax* is much more robust than UWBM 113209; the diastema of *Monosaulax* is also shorter than that of UWBM 113209 ([Korth, 2002](#); [Matthew & Cook, 1909](#); [Shotwell, 1968](#); [Stirton, 1935](#)). The bunodont–brachydont tooth morphology of UWBM 113209 is quite unlike the lophodont dentition characteristic of Castoridae, providing one more line of evidence that the *Clarkia* rodent is not a beaver.

The low crowned and bunodont teeth of UWBM 113209 combined with its large size and gracile build support the interpretation that the first known tetrapod remains from the *Clarkia lagerstätte* belong to the family Sciuridae. The early Barstovian-aged sciurid fauna of the Inland Northwest is very species-rich ([Biedron, 2016](#); [Goodwin, 2008](#); [Maguire, Samuels & Schmitz, 2018](#); [Orcutt & Hopkins, 2013](#)). Nonetheless, only a few taxa from this or neighboring regions are similar in size to UWBM 113209. *Palaeoarctomys montanus* ([Douglass, 1903](#)) from the Barstovian of Montana is slightly larger (LTRL = 15.1 mm) than UWBM 113209 ([Hopkins, 2007](#)). Another taxon from Montana, *Arctomyoides arctomyoides* ([Douglass, 1903](#)), is also slightly larger than UWBM 113209 (LTRL = 15.4 mm, [Bryant, 1945](#)). Within the genus *Protospermophilus*, *Protospermophilus oregonensis* (originally described as *A. oregonensis*, [Downs, 1956](#)) is slightly smaller than the *Clarkia* rodent (LTRL = 12.2 mm, [Hopkins, 2007](#); LTRL = 11.9 mm, [Downs, 1956](#)). A set of sciurid specimens from the Arikarean of Nebraska named “*P. vondrai*” in an unpublished dissertation ([Martin, 1973](#)) is also only slightly smaller than the *Clarkia*

rodent (LTRL = 12.94 mm, [Hopkins, 2007](#)). Although referred to *Protospermophilus* by [Martin \(1973\)](#), this set of specimens was later assigned to *Cedromus* by [Hayes \(2005\)](#). Only one other Miocene-aged sciurid genus overlaps in size with the Clarkia rodent: *Protosciurus* ([Hopkins, 2007](#); [Korth & Samuels, 2015](#)). *Protosciurus* is present in the northwest of the United States during the Arikareean and Hemingfordian ([Black, 1963](#); [Goodwin, 2008](#); [Korth & Samuels, 2015](#)); it is also reported in the early Barstovian of Texas ([Goodwin, 2008](#)). *Spermophilus*-grade ground squirrels (i.e., sciurid species formerly referred to the genus *Spermophilus* prior to reassessment of ground squirrel phylogeny by [Helgen et al., 2009](#)) are common during the Barstovian ([Orcutt & Hopkins, 2013](#)), but they are all smaller than UWBM 113209 ([Hopkins, 2007](#)).

Although *Palaeoarctomys montanus* is similar in tooth row length to the Clarkia rodent, its skull, measuring 100 mm ([Douglass, 1903](#)), is much longer than that of the Clarkia rodent. Additionally, its diastema (16.8 mm, [Black, 1963](#)) is shorter, if only slightly, than that of UWBM 113209. *Palaeoarctomys montanus* also differs from UWBM 113209 in its deep and robust dentary ([Goodwin, 2008](#)). This dentary houses a very large incisor (depth 7.3 mm, [Downs, 1956](#)), much larger than that of UWBM 113209. The lower incisor of *Palaeoarctomys montanus* bears striations on its anterior surface ([Goodwin, 2008](#)) whereas the lower incisor of the Clarkia rodent is smooth. Taken together, these features suggest that *Palaeoarctomys* is an unlikely candidate for the taxonomic affinities of the Clarkia sciurid.

Arctomyoides arctomyoides is larger than UWBM 113209 but its diastema is much shorter than that of UWBM 113209 (13.0 mm; [Black, 1963](#)). The depth of the lower incisor of *A. arctomyoides* (3.8 mm; [Black, 1963](#)) is greater than that of UWBM 113209. UWBM 113209 displays a long and shallow diastemal depression ([Fig. 2](#)), a characteristic of *Arctomyoides* ([Bryant, 1945](#); [Goodwin, 2008](#)) and lacks a medial groove on the lower incisor like *Arctomyoides* ([Goodwin, 2008](#)). However, like *Palaeoarctomys montanus*, the lower incisor of *A. arctomyoides* is finely striated whereas that of UWBM 113209 is smooth. The poor preservation of UWBM 113209 prevents a rigorous comparison with the diagnostic characters of *Arctomyoides* summarized by [Goodwin \(2008\)](#), especially with regard to the cheek teeth, but the smooth incisor of the Clarkia sciurid suggests that it is not a member of the genus *Arctomyoides*.

The morphology of the dentary of UWBM 113209 is broadly similar to that of the dentary of *Protospermophilus oregonensis* ([Downs, 1956](#)) but the length of the diastema of *Protospermophilus oregonensis* (10.0 mm; [Downs, 1956](#)) is shorter than that of UWBM 113209 ([Table 1](#)). The lower incisor of *Protospermophilus oregonensis* is also slightly deeper (3.7 mm; [Downs, 1956](#)) than that of UWBM 113209. Finally, UWBM 113209 differs from *Protospermophilus oregonensis* in its lack of striations on the anterior surface of the lower incisor. It thus appears unlikely that the Clarkia rodent represents a specimen of *Protospermophilus oregonensis*. The poor preservation of UWBM 113209 bars a comparison with the diagnostic characters of *Protospermophilus* summarized by [Bryant \(1945\)](#) and [Goodwin \(2008\)](#). As such, we cannot exclude the possibility that the Clarkia rodent represents a new large species within the genus *Protospermophilus*.

The cranial morphology of the *Cedromus* material from the Arikareean of Nebraska is poorly known ([Martin, 1973](#)); so is the skull and dentition of UWBM 113209. As a consequence, it is difficult to assess the similarities between the two similarly-sized squirrels or determine whether or not UWBM 113209 possesses diagnostic characters of the Cedromurinae ([Korth & Emry, 1991](#)). Nonetheless, prior to the work of [Hayes \(2005\)](#), *Cedromus* was only known from the Orellan and Whitneyan ([Korth & Emry, 1991](#)) and the assignment of the Arikareean-aged Nebraska material to *Cedromus* is the youngest occurrence of a genus, and subfamily, no less than about 12 million years older than the *Clarkia* rodent ([Tedford et al., 2004](#)). The *Clarkia* rodent therefore likely represents a different taxon than the Arikareean-aged *Cedromus*.

There are four known species of *Protosciurus* ([Goodwin, 2008](#)). The *Clarkia* rodent is somewhat larger than *Protosciurus mengi* and *Protosciurus rachelae* ([Hopkins, 2007](#); [Korth & Samuels, 2015](#)). Additionally, the lower incisor of UWBM 113209 is much thicker than the incisors of *Protosciurus mengi* and the skull roof of UWBM 113209 does not display the characteristic supraorbital shelf of *Protosciurus rachelae* ([Korth & Samuels, 2015](#)). A third species of *Protosciurus*, *Protosciurus condoni* is much larger than the *Clarkia* rodent ([Black, 1963](#); [Hopkins, 2007](#)). *Protosciurus condoni* also differs from the *Clarkia* rodent in its shortened lower diastema ([Black, 1963](#)). *Protosciurus tecuyensis* is the same size as the *Clarkia* rodent ([Hopkins, 2007](#)). The species is known from a single partial lower jaw ([Black, 1963](#); [Bryant, 1945](#)) and, because of the poor morphology of this type and that of the *Clarkia* specimen, no rigorous comparison between the two squirrels can be undertaken. Despite the morphological differences between the *Clarkia* rodent and known species of *Protosciurus*, similarities in size and general cranial morphology leave the possibility that UWBM 113209 represents a new species within *Protosciurus*.

The forelimbs of UWBM 113209 are gracile and elongated relative to those of members of the tribe Marmotini including the marmot *Marmota*, the ground squirrel *Spermophilus*, and the prairie dog *Cynomys*; they resemble more closely those of tree squirrels (Tribes Sciurini and Callosciurini; [Bezuidenhout & Evans, 2005](#); [Emry & Thorington, 1982](#); [Korth & Samuels, 2015](#); [Rose & Chinnery, 2004](#); [Thorington, Darrow & Betts, 1997](#); [Thorington et al., 2005](#)). Indeed, when accounting for size difference, the forelimb of UWBM 113209 is gracile and more similar to that of the small Clarendonian-aged tree squirrel *Sciurus olsonii* from Nevada, the Arikareean-aged *Protosciurus mengi*, or the modern *Callosciurus prevostii* from southeast Asia than the more robust ground squirrels of the genus *Spermophilus* ([Emry, Korth & Bell, 2005](#); [Korth & Samuels, 2015](#); [Thorington et al., 2005](#)). Thus, although the manus of UWBM 113209 is poorly preserved, the visible digits are thin and similar in proportion (although bigger in absolute size) to those of tree squirrels like *S. olsonii*.

DISCUSSION

The first known tetrapod specimen from the *Clarkia lagerstätte*, UWBM 113209, represents a new occurrence of a rodent from the family Sciuridae. Its discovery not only expands the faunal list of this internationally important locality but increases our understanding of the scope of squirrel diversity during the mid-Miocene. In the absence

of more complete material, and particularly more complete cheek teeth whose morphology can be studied, the *Clarkia* sciurid cannot currently be assigned to a lower taxonomic level than family. Even so, its large size, proportionately large diastema, shallow dentary, skull shape, and smooth convex lower incisor suggest that UWBM 113209 does not belong to a known sciurid species but might instead represent a new taxon. Only three large-bodied squirrels have been described from the Barstovian: *Arctomyoides*, *Palaeoarctomyoides*, and *Protospermophilus*, all of which have been interpreted as basal terrestrial squirrels (Goodwin, 2008). While the poor preservation of the postcrania of UWBM 113209 precludes a detailed morphometric analysis, its morphology suggests that the *Clarkia* squirrel is ecologically distinct from previously described mid-Miocene taxa. There is a strong relationship between postcranial morphology and locomotion in extant small mammals including rodents, and the gracile forelimb of UWBM 113209 is a trait correlated with arboreal and scansorial lifestyles (Chen & Wilson, 2015; Samuels & van Valkenburgh, 2008). The interpretation of the specimen as a tree-dweller is further supported by the paleoenvironment of the *Clarkia* lagerstätte, which preserves a densely forested landscape (Smiley & Rember, 1985b). Together, these two lines of evidence suggest that UWBM 113209 is neither a basal terrestrial squirrel nor a ground squirrel (Tribe Marmotini), but possibly a tree squirrel.

If, as its morphology suggests, UWBM 113209 is interpreted as a tree squirrel, it provides insight into a portion of sciurid ecological diversity seldom captured in the fossil record (Emry, Korth & Bell, 2005), as most localities of comparable age preserve grassland rather than forest ecosystems (Strömberg, 2011). It also illuminates the evolution of tree squirrels during the Miocene. The youngest confirmed occurrence of *Protosciurus* dates back to the Hemingfordian (Goodwin, 2008) and the oldest occurrence of *Sciurus* is Clarendonian in age (Emry, Korth & Bell, 2005) leaving a hole in the fossil record of tree squirrels during the Barstovian. Recent work in the Mascall Formation of Oregon has uncovered a yet-to-be-described member of the tribe Sciurini that provides evidence for tree squirrels during the Barstovian (Maguire, Samuels & Schmitz, 2018). The *Clarkia* rodent adds to this growing fossil record. The two animals differ in morphology; the *Clarkia* rodent is much larger (Table 1) than the Mascall sciurid (skull length 48.2 mm; Samuels, 2018, personal communication) but its lower incisor is proportionately not as thick (3.9 mm diameter; J. X. Samuels, 2018, personal communication). Taken together, these two animals suggest the presence of a diverse tree squirrel fauna in the northwestern United States during the early Barstovian that will illuminate the transition from Hemingfordian-aged to Clarendonian-aged tree squirrels.

The *Clarkia* squirrel is considerably larger than coeval squirrels and the Clarendonian-aged *S. olsonii* (Emry, Korth & Bell, 2005); estimates based on lower tooth row length and skull length indicate a body mass of 77.2–85.7 g for *S. olsonii* and of 492 g for UWBM 113209. However, the size of UWBM 113209 is comparable to that of certain species of Arikarean-aged *Protosciurus* (Goodwin, 2008; Hopkins, 2007; Korth & Samuels, 2015). Its estimated mass is also well within the range of modern Sciurini, which range from 81.2 g in *Microsciurus* to 1225 g in *Rheithrosciurus* (Hayssen, 2008). The *Clarkia* squirrel is most similar in estimated mass to the modern *S. alleni*, *S. aureogaster*,

S. carolinensis, and *S. variegatoides*. However, these comparisons do not shed further light on the locomotor ecology of UWBM 113209, as the locomotor ecologies of these species range from largely terrestrial in *S. alleni* to largely arboreal in *S. variegatoides* (Best, 1995a, 1995b).

Recent stratigraphic work at the *lagerstätte* has focused mainly on tephrostratigraphy due to its proximity to several active volcanic centers (Geraghty, 2017; Ladderud et al., 2015). Because it cannot be definitively identified below the family level, UWBM 113209 is not biostratigraphically informative, but its presence does indicate that conditions favorable to the preservation of small mammals did exist there. Miocene rodents and other small mammals are frequently used to distinguish NALMA subdivisions, including the early Barstovian (Tedford et al., 2004). While UWBM 113209 is the only tetrapod recovered from Clarkia to date, future discoveries could allow existing tephrostratigraphic work to be supplemented with biostratigraphic data, further solidifying the age of the *lagerstätte*. Fish, the only vertebrates previously found at Clarkia, have only been reported from the type locality, and even there, they appear only in certain layers (Smith & Elder, 1985); UWBM 113209 was recovered from the lowest of these layers. Smith & Elder (1985) suggest that, even though some evidence indicates relatively low sedimentation rates in the fish-bearing units, cold temperatures (<10–15 °C) and anoxic conditions favor the preservation of articulated vertebrate specimens in these layers. If this is the case, these layers are the ones that should be targeted in the search for new tetrapod fossils at Clarkia.

CONCLUSIONS

The specimen described here, UWBM 113209, is a sciurid, and, in all probability, a tree squirrel, making it the first tetrapod of any kind reported from the Clarkia *lagerstätte*. The squirrel represents a significant addition to an already exceptionally preserved mid-Miocene ecosystem. It augments our understanding of a uniquely well-preserved paleo community and the presence of leaves preserved in direct association with the specimen may provide further insight into the nature of species interactions within the Clarkia community. On a broader scale, UWBM 113209 indicates a greater taxonomic and ecological diversity of mid-Miocene Sciuridae than had previously been recognized and provides a unique window onto the paleobiology of infrequently preserved tree squirrels.

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The authors declare that they have no competing interests.

Author Contributions

- Jonathan J. M. Calede conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, approved the final draft.
- John D. Orcutt conceived and designed the experiments, performed the experiments, prepared figures and/or tables, authored or reviewed drafts of the paper, approved the final draft.
- Winifred A. Kehl contributed reagents/materials/analysis tools, prepared figures and/or tables, authored or reviewed drafts of the paper, approved the final draft.
- Bill D. Richards contributed reagents/materials/analysis tools, prepared figures and/or tables, authored or reviewed drafts of the paper, approved the final draft.

Data Availability

The following information was supplied regarding data availability:

The specimen described here is deposited in the University of Washington Burke Museum (UWBM), Seattle, Washington, USA.

REFERENCES

- Arnold CA. 1937.** Observations on the fossil flora of Eastern and Southeastern Oregon. *Part I. Contributions from the Museum of Paleontology, University of Michigan* 5:79–102.
- Badgley C, Finarelli JA. 2013.** Diversity dynamics of mammals in relation to tectonic and climatic history: comparison of three Neogene records from North America. *Paleobiology* 39(3):373–399 DOI 10.1666/12024.
- Barnosky AD, Bibi F, Hopkins SSB, Nichols R. 2007.** Biostratigraphy and magnetostratigraphy of the mid-Miocene Railroad Canyon sequence, Montana and Idaho, and age of the mid-tertiary unconformity west of the continental divide. *Journal of Vertebrate Paleontology* 27(1):204–224 DOI 10.1671/0272-4634(2007)27[204:bamotm]2.0.co;2.
- Batten DJ, Gray J, Harland R. 1999.** Palaeoenvironmental significance of a monospecific assemblage of dinoflagellate cysts from the Miocene Clarkia Beds, Idaho, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology* 153(1):161–177 DOI 10.1016/S0031-0182(99)00103-0.
- Bertrand OC, Schillaci MA, Silcox MT. 2015.** Cranial dimensions as estimators of body mass and locomotor habits in extant and fossil rodents. *Journal of Vertebrate Paleontology* 36(1):e1014905 DOI 10.1080/02724634.2015.1014905.
- Bestland EA, Forbes MS, Krull ES, Retallack GJ, Fremid T. 2008.** Stratigraphy, paleopedology, and geochemistry of the middle Miocene Mascall Formation (type area, central Oregon, USA). *Paleobiology* 28(2):41–61.
- Best TL. 1995a.** *Sciurus alleni*. *Mammalian Species* 501:1–4 DOI 10.2307/0.501.1.

- Best TL. 1995b.** *Sciurus variegatoides*. *Mammalian Species* **500**:1–6 DOI [10.2307/3504282](https://doi.org/10.2307/3504282).
- Bezuidenhout AJ, Evans HE. 2005.** *Anatomy of the Woodchuck (Marmota monax)*. Vol. 13. Lawrence: American Society of Mammalogists.
- Biedron EM. 2016.** The Sciuridae (Rodentia: Mammalia) of Cave Basin (Oregon), a new middle Miocene microfossil locality. MS thesis, University of Oregon.
- Black CC. 1963.** A review of the North American Tertiary Sciuridae. *Bulletin of the Museum of Comparative Zoology* **130**:109–248.
- Bowdich TE. 1821.** *An Analysis of the Natural Classifications of Mammalia: For the Use of Students and Travelers*. Paris: J. Smith.
- Bryant MD. 1945.** Phylogeny of Nearctic Sciuridae. *American Midland Naturalist* **33**(2):257–390 DOI [10.2307/2421337](https://doi.org/10.2307/2421337).
- Calede J, Hopkins SSB. 2012a.** Intraspecific versus interspecific variation in Miocene Great Basin mylagaulids: implications for systematics and evolutionary history. *Zoological Journal of the Linnean Society* **164**(2):427–450 DOI [10.1111/j.1096-3642.2011.00765.x](https://doi.org/10.1111/j.1096-3642.2011.00765.x).
- Calede J, Hopkins SSB. 2012b.** New material of *Alphagaulus pristinus* (Mammalia: Rodentia: Mylagaulidae) from the Deep River Formation (Montana, USA): implications for ecology, ontogeny, and phylogeny. *Journal of Vertebrate Paleontology* **32**(1):151–165 DOI [10.1080/02724634.2012.634356](https://doi.org/10.1080/02724634.2012.634356).
- Calede J, Hopkins SSB, Davis EB. 2011.** Turnover in burrowing rodents: the roles of competition and habitat change. *Palaeogeography, Palaeoclimatology, Palaeoecology* **311**(3–4):242–255 DOI [10.1016/j.palaeo.2011.09.002](https://doi.org/10.1016/j.palaeo.2011.09.002).
- Carpenter FM. 1931.** Insects from the Miocene (Latah) of Washington. *Annals of the Entomological Society of America* **24**(2):307–309 DOI [10.1093/aesa/24.2.307](https://doi.org/10.1093/aesa/24.2.307).
- Chaney RW. 1925.** The Mascall flora: its distribution and climatic relation. *Carnegie Institute of Washington Publication* **349**:23–48.
- Chaney RW. 1959.** Miocene floras of the Columbia Plateau, Part I: composition and interpretation. *Carnegie Institute of Washington Contributions to Paleontology* **617**:1–134.
- Chaney RW, Axelrod DI. 1959.** Miocene floras of the Columbia Plateau, Part II: systematic considerations. *Carnegie Institute of Washington Contributions to Paleontology* **617**:135–237.
- Chen M, Wilson GP. 2015.** A multivariate approach to infer locomotor modes in Mesozoic mammals. *Paleobiology* **41**(2):280–312 DOI [10.1017/pab.2014.14](https://doi.org/10.1017/pab.2014.14).
- Connior MB. 2011.** *Geomys bursarius* (Rodentia: Geomyidae). *Mammalian Species* **43**:104–117 DOI [10.1644/879.1](https://doi.org/10.1644/879.1).
- Dalquest WW. 1978.** Early Blancan mammals of the beck ranch local fauna of Texas. *Journal of Mammalogy* **59**(2):269–298 DOI [10.2307/1379912](https://doi.org/10.2307/1379912).
- De Waldheim FG. 1817.** Adversaria zoologica. *Mémoires de la Société Impériale des Naturalistes de Moscou* **5**:357.
- Dorr JA Jr. 1956.** Anceney local mammal fauna, latest miocene, Madison valley formation, Montana. *Journal of Paleontology* **30**:62–74.
- Douglass E. 1903.** New vertebrates from the Montana Tertiary. *Annals of the Carnegie Museum* **2**:145–199.
- Downs T. 1956.** The Mascall fauna from the Miocene of Oregon. *University of California Publications in Geological Sciences* **31**:199–354.
- Emry RJ, Thorington RW Jr. 1982.** Descriptive and comparative osteology of the oldest fossil squirrel, *Protosciurus* (Rodentia: Sciuridae). *Smithsonian Contributions to Paleobiology* **47**:1–35 DOI [10.5479/si.00810266.47.1](https://doi.org/10.5479/si.00810266.47.1).

- Emry RJ, Korth WW, Bell MA. 2005.** A tree squirrel (Rodentia, Sciuridae, Sciurini) from the late Miocene (Clarendonian) of Nevada. *Journal of Vertebrate Paleontology* **25**(1):228–235
DOI [10.1671/0272-4634\(2005\)025\[0228:atsrss\]2.0.co;2](https://doi.org/10.1671/0272-4634(2005)025[0228:atsrss]2.0.co;2).
- Fagan SR. 1960.** Osteology of *Mylagaulus laevis*, a fossorial rodent from the Upper Miocene of Colorado. *University of Kansas Paleontological Contributions* **9**:1–32.
- Fields PF. 1996.** The Succor Creek flora of the Middle Miocene Sucker Formation, southwestern Idaho and eastern Oregon; systematics and paleoecology. PhD dissertation, Michigan State University.
- Flynn LJ, Jacobs LL. 2008a.** Aplodontoidea. In: Janis CM, Gunnell GF, Uhen MD, eds. *Evolution of Tertiary Mammals of North America Volume 2: Small Mammals, Xenarthrans, and Marine Mammals*. Cambridge: Cambridge University Press, 377–390.
- Flynn LJ, Jacobs LL. 2008b.** Castoroidea. In: Janis CM, Gunnell GF, Uhen MD, eds. *Evolution of Tertiary Mammals of North America Volume 2: Small Mammals, Xenarthrans, and Marine Mammals*. Cambridge: Cambridge University Press, 391–405.
- Flynn LJ, Lindsay EH, Martin RA. 2008.** Geomorpha. In: Janis CM, Gunnell GF, Uhen MD, eds. *Evolution of Tertiary Mammals of North America Volume 2: Small Mammals, Xenarthrans, and Marine Mammals*. Cambridge: Cambridge University Press, 428–455.
- Galbreath EC. 1984.** On *Mesogaulus paniensis* (Rodentia) from Hemingfordian (middle Miocene) deposits in northeastern Colorado. *Special Publication of the Carnegie Museum of Natural History* **9**:85–89.
- Gazin CL. 1932.** A Miocene mammalian fauna from south-eastern Oregon. *Carnegie Institution of Washington Publications* **418**:37–86.
- Geraghty CS. 2017.** Tephrochronology of the mid-Miocene Clarkia Lake sedimentary deposits. MS thesis, Washington State University.
- Goodwin TH. 2008.** Sciuridae. *Evolution of Tertiary Mammals of North America Volume 2: Small Mammals, Xenarthrans, and Marine Mammals*. Cambridge: Cambridge University Press, 355–376.
- Gray J. 1985.** Interpretation of co-occurring megafossils and pollen: a comparative study with Clarkia as an example. In: Smiley CJ, ed. *Late Cenozoic History of the Pacific Northwest*. San Francisco: Pacific Division, AAAS, 185–244.
- Harris EB. 2016.** Effects of the mid-Miocene climatic optimum on ecosystem structure and plant-animal interactions: a phytolith and stable isotope perspective. PhD dissertation, University of Washington.
- Harris EB, Stromberg CAE, Sheldon ND, Smith SY, Vilhena DA. 2017.** Vegetation response during the lead-up to the middle Miocene warming event in the Northern Rocky Mountains, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology* **485**:401–415
DOI [10.1016/j.palaeo.2017.06.029](https://doi.org/10.1016/j.palaeo.2017.06.029).
- Hayes FG. 2005.** Paleomagnetism and biostratigraphy of the Pine Ridge Arikaree Group (late Oligocene-early Miocene), Nebraska. PhD dissertation, University of Nebraska.
- Hayssen V. 2008.** Patterns of body and tail length and body mass in Sciuridae. *Journal of Mammalogy* **89**(4):852–873 DOI [10.1644/07-mamm-a-217.1](https://doi.org/10.1644/07-mamm-a-217.1).
- Helgen KM, Cole FR, Helgen LE, Wilson DE. 2009.** Generic revision in the Holarctic ground squirrel genus *Spermophilus*. *Journal of Mammalogy* **90**(2):270–305
DOI [10.1644/07-mamm-a-309.1](https://doi.org/10.1644/07-mamm-a-309.1).
- Hopkins SSB. 2007.** Causes of lineage decline in the Aplodontidae: testing for the influence of physical and biological change. *Palaeogeography, Palaeoclimatology, Palaeoecology* **246**(2–4):331–353 DOI [10.1016/j.palaeo.2006.10.006](https://doi.org/10.1016/j.palaeo.2006.10.006).

- Hopkins SSB. 2008a.** Phylogeny and evolutionary history of the Aplodontoidea (Mammalia: Rodentia). *Zoological Journal of the Linnean Society* **153**(4):769–838 DOI [10.1111/j.1096-3642.2008.00399.x](https://doi.org/10.1111/j.1096-3642.2008.00399.x).
- Hopkins SSB. 2008b.** Reassessing the mass of exceptionally large rodents using toothrow length and area as proxies for body mass. *Journal of Mammalogy* **89**(1):232–243 DOI [10.1644/06-mamm-a-306.1](https://doi.org/10.1644/06-mamm-a-306.1).
- Huang Y, Lockheart MJ, Collister JW, Eglinton G. 1995.** Molecular and isotopic biogeochemistry of the Miocene Clarkia Formation: hydrocarbons and alcohols. *Organic Geochemistry* **23**(9):785–801 DOI [10.1016/0146-6380\(95\)80001-8](https://doi.org/10.1016/0146-6380(95)80001-8).
- Intergovernmental Panel on Climate Change (IPCC). 2014.** Climate change 2014: synthesis report. In: Pachauri RK, Meyer LA, eds. *Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Geneva: IPCC, 151 pp.
- Kim S, Soltis DE, Soltis PS, Suh Y. 2004.** DNA sequences from Miocene fossils: an ndhF sequence of *Magnolia latahensis* (Magnoliaceae) and an rbcL sequence of *Persea pseudocarolinensis* (Lauraceae). *American Journal of Botany* **91**(4):615–620 DOI [10.3732/ajb.91.4.615](https://doi.org/10.3732/ajb.91.4.615).
- Knowlton FH, Mann A. 1925.** Flora of the Latah Formation of Spokane, Washington and Coeur d'Alene, Idaho. *USGS Professional Paper* **140**:17–55.
- Knowlton FH. 1902.** Fossil flora of the John Day Basin, Oregon. *U.S. Geological Survey Bulletin* **204**:1–153.
- Kohn M, Fremd T. 2007.** Tectonic controls on isotope compositions and species diversification, John Day Basin, central Oregon. *Paleobiology* **27**(2):48–61.
- Korth WW. 2000.** Review of Miocene (Hemingfordian to Clarendonian) mylagaulid rodents (Mammalia) from Nebraska. *Annals of the Carnegie Museum* **69**:227–280.
- Korth WW. 2002.** Topotypic cranial material of the beaver *Monosaulax pansus* Cope (Rodentia, Castoridae). *Paludicola* **4**:1–5.
- Korth WW, Emry RJ. 1991.** The skull of *Cedromus* and a review of the Cedromurinae (Rodentia, Sciuridae). *Journal of Paleontology* **65**(6):984–994 DOI [10.1017/s0022336000033291](https://doi.org/10.1017/s0022336000033291).
- Korth WW, Samuels JX. 2015.** New rodent material from the John Day Formation (Arikareean, middle Oligocene to early Miocene) of Oregon. *Annals of the Carnegie Museum* **83**(1):19–84 DOI [10.2992/007.083.0102](https://doi.org/10.2992/007.083.0102).
- Ladderud JA, Wolff JA, Rember WC, Brueseke ME. 2015.** Volcanic ash layers in the Miocene Lake Clarkia beds: geochemistry, regional correlation, and age of the Clarkia flora. *Northwest Science* **89**(4):309–323 DOI [10.3955/046.089.0402](https://doi.org/10.3955/046.089.0402).
- Landry SO Jr. 1999.** A proposal for a new classification and nomenclature for the Glires (Lagomorpha and Rodentia). *Zoosystematics & Evolution* **75**(2):283–316 DOI [10.1002/mmnz.19990750209](https://doi.org/10.1002/mmnz.19990750209).
- Lewis SE. 1985.** Miocene insects from the Clarkia deposits of northern Idaho. In: Smiley CJ, ed. *Late Cenozoic History of the Pacific Northwest*. San Francisco: Pacific Division, AAAS, 245–264.
- Linnaeus C. 1758.** *Systema Naturae*. Stockholm: L. Salvii.
- Lockheart MJ, Van Bergen PF, Evershed RP. 2000.** Chemotaxonomic classification of fossil leaves from the Miocene Clarkia lake deposit, Idaho, USA based on n-alkyl lipid distributions and principal component analyses. *Organic Geochemistry* **31**(11):1223–1246 DOI [10.1016/S0146-6380\(00\)00107-8](https://doi.org/10.1016/S0146-6380(00)00107-8).
- Logan GA, Boon JJ, Eglinton G. 1993.** Structural biopolymer preservation in Miocene leaf fossils from the Clarkia Site, Northern Idaho. *Proceedings of the National Academy of Sciences of the United States of America* **90**(6):2246–2250.

- Logan GA, Smiley CJ, Eglinton G. 1995.** Preservation of fossil leaf waxes in association with their source tissues, Clarkia, northern Idaho, USA. *Geochimica et Cosmochimica Acta* **59(4)**:751–763 DOI [10.1016/0016-7037\(94\)00362-P](https://doi.org/10.1016/0016-7037(94)00362-P).
- Luckett WP, Hartenberger JL. 1993.** Monophyly or polyphyly of the Order Rodentia: possible conflict between morphological and molecular interpretations. *Journal of Mammalian Evolution* **1(2)**:127–147 DOI [10.1007/bf01041591](https://doi.org/10.1007/bf01041591).
- Maguire KC. 2015.** Dietary niche stability of equids across the mid-Miocene Climatic Optimum in Oregon, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology* **426**:297–307 DOI [10.1016/j.palaeo.2015.03.012](https://doi.org/10.1016/j.palaeo.2015.03.012).
- Maguire KC, Samuels JX, Schmitz MD. 2018.** The fauna and chronostratigraphy of the middle Miocene Mascall type area, John Day Basin, Oregon, USA. *Paleobiology* **35**:1–51.
- Martin LD. 1973.** The mammalian fauna of the lower Miocene Gering Formation of western Nebraska and the early evolution of the North American Cricetidae. PhD dissertation, University of Kansas.
- Matthew WD, Cook HJ. 1909.** A Pliocene fauna from western Nebraska. *Bulletin of the American Museum of Natural History* **26**:361–414.
- Merriam JC. 1911.** *Tertiary Mammal Beds of Virgin Valley and Thousand Creek in Northwestern Nevada*. Vol. 6. Berkeley: University of California Publications: Geology, 199–304.
- Morea MF. 1981.** *The Massacre Lake local fauna (Mammalia, Hemingfordian) from northwestern Washoe County, Nevada*. PhD dissertation, University of California, Riverside.
- Munthe J. 1977.** A new species of *Gregorymys* (Rodentia, Geomyidae) from the Miocene of Colorado. *Paleobiology* **26**:1–12.
- Nash BP, Perkins ME. 2012.** Neogene fallout tuffs from the Yellowstone hotspot in the Columbia Plateau region, Oregon, Washington, and Idaho, USA. *PLOS ONE* **7(10)**:e44205 DOI [10.1371/journal.pone.0044205](https://doi.org/10.1371/journal.pone.0044205).
- Orcutt JD, Hopkins SSB. 2013.** Oligo-Miocene climate change and mammal body-size evolution in the northwest United States: a test of Bergmann's rule. *Paleobiology* **39(4)**:648–661 DOI [10.1666/13006](https://doi.org/10.1666/13006).
- Prieto J, Casanovas-Vilar I, Gross M. 2014.** *Euroxenomys minutus minutus* (Rodentia, Castoridae) from Gratkorn (Austria, Styria). *Palaeobiodiversity & Palaeoenvironments* **94(1)**:163–170 DOI [10.1007/s12549-013-0148-2](https://doi.org/10.1007/s12549-013-0148-2).
- Retallack GJ. 2007.** Cenozoic paleoclimate on land in North America. *Journal of Geology* **115(3)**:271–294 DOI [10.1086/512753](https://doi.org/10.1086/512753).
- Retallack GJ. 2009.** Cenozoic cooling and grassland expansion in Oregon and Washington. *Paleobiology* **28**:89–113 DOI [10.1086/512753](https://doi.org/10.1086/512753).
- Rose KD, Chinnery BJ. 2004.** The postcranial skeleton of early Eocene rodents. *Bulletin of Carnegie Museum of Natural History* **36**:211–244 DOI [10.2992/0145-9058\(2004\)36\[211:tpscoe\]2.0.co;2](https://doi.org/10.2992/0145-9058(2004)36[211:tpscoe]2.0.co;2).
- Samuels JX, Van Valkenburgh B. 2008.** Skeletal indicators of locomotor adaptations in living and extinct rodents. *Journal of Morphology* **269(11)**:1387–1411 DOI [10.1002/jmor.10662](https://doi.org/10.1002/jmor.10662).
- Scharf DW. 1932.** *A Miocene Mammalian Fauna from Sucker Creek, Southeastern Oregon*. Master's thesis, California Institute of Technology. Available at <http://resolver.caltech.edu/CaltechTHESIS:01082010-114352859>.
- Sheldon ND. 2006.** Using paleosols of the Picture Gorge Basalt to reconstruct the middle Miocene climatic optimum. *Paleobiology* **26(2)**:27–36.
- Shotwell JA. 1958.** Evolution and biogeography of the aplodontid and mylagaulid rodents. *Evolution* **12(4)**:451–484 DOI [10.2307/2405958](https://doi.org/10.2307/2405958).

- Shotwell JA. 1968.** Miocene mammals of southeast Oregon. *Bulletin of the University of Oregon Museum of Natural History* **14**:1–67.
- Smiley CJ, Gray J, Huggins LM. 1975.** Preservation of Miocene fossils in unoxidized lake deposits, Clarkia, Idaho. *Journal of Paleontology* **49**:833–844.
- Smiley CJ, Rember WJ. 1985a.** Physical setting of the Miocene Clarkia fossil beds, northern Idaho. In: Smiley CJ, ed. *Late Cenozoic History of the Pacific Northwest*. San Francisco: Pacific Division, AAAS, 11–31.
- Smiley CJ, Rember WJ. 1985b.** Composition of the Miocene Clarkia flora. In: Smiley CJ, ed. *Late Cenozoic History of the Pacific Northwest*. San Francisco: Pacific Division, AAAS, 95–112.
- Smith GR, Elder RL. 1985.** Environmental interpretation of burial and preservation of Clarkia fishes. In: Smiley CJ, ed. *Late Cenozoic History of the Pacific Northwest*. San Francisco: Pacific Division, AAAS, 85–93.
- Smith GR, Miller RR. 1985.** Taxonomy of fishes from Miocene Clarkia lake beds, Idaho. In: Smiley CJ, ed. *Late Cenozoic History of the Pacific Northwest*. San Francisco: Pacific Division, AAAS, 75–83.
- Soltis PS, Soltis DE, Smiley CJ. 1992.** An rbcL sequence from a Miocene Taxodium (bald cypress). *Proceedings of the National Academy of Sciences of the United States of America* **89**(1):449–451 DOI [10.1073/pnas.89.1.449](https://doi.org/10.1073/pnas.89.1.449).
- Stirton RA. 1935.** A review of Tertiary beavers. *University of California Publications in Geological Sciences* **29**:391–458.
- Strain WS. 1966.** Blancan mammalian fauna and Pleistocene formations, Hudspeth County, Texas. *Bulletin of the Texas Memorial Museum* **10**:1–55.
- Strömberg CAE. 2011.** Evolution of grasses and grassland ecosystems. *Annual Review of Earth Planetary Science* **39**(1):517–544 DOI [10.1146/annurev-earth-040809-152402](https://doi.org/10.1146/annurev-earth-040809-152402).
- Takeuchi A, Larson PB, Suzuki K. 2007.** Influence of paleorelief on the Mid-Miocene climate variation in southeastern Washington, northeastern Oregon, and western Idaho, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology* **254**(3–4):462–476 DOI [10.1016/j.palaeo.2007.06.023](https://doi.org/10.1016/j.palaeo.2007.06.023).
- Tedford RH. 1981.** Mammalian biochronology of the late Cenozoic basins of New Mexico. *Geological Society of America Bulletin* **92**(12):1008–1022 DOI [10.1130/0016-7606\(1981\)92<1008:mbotlc>2.0.co;2](https://doi.org/10.1130/0016-7606(1981)92<1008:mbotlc>2.0.co;2).
- Tedford RH, Albright LB III, Barnosky AD, Ferrusquia-Villafranca I, Hunt RM Jr, Storer JE, Swisher CC III, Voorhies MR, Webb SD, Whistler DP. 2004.** Mammalian biochronology of the Arikareean through Hemphillian interval (late Oligocene through early Pliocene Epochs). In: Woodburne MO, ed. *Late Cretaceous and Cenozoic Mammals of North America*. New York: Columbia University Press, 169–231.
- Thornington RW, Schennum CE, Pappas LA, Pitassy D. 2005.** The difficulties of identifying flying squirrels (Sciuridae: Pteromyini) in the fossil record. *Journal of Vertebrate Paleontology* **25**(4):950–961 DOI [10.1671/0272-4634\(2005\)025\[0950:tdoifs\]2.0.co;2](https://doi.org/10.1671/0272-4634(2005)025[0950:tdoifs]2.0.co;2).
- Thornington RW, Darrow K, Betts ADK. 1997.** Comparative myology of the forelimb of squirrels (Sciuridae). *Journal of Morphology* **234**(2):155–182 DOI [10.1002/\(sici\)1097-4687\(199711\)234:2<155::aid-jmor4>3.3.co;2-c](https://doi.org/10.1002/(sici)1097-4687(199711)234:2<155::aid-jmor4>3.3.co;2-c).
- Williams JL. 1985.** Thecamoebian scales from a Miocene lacustrine deposit in northern Idaho. In: Smiley CJ, ed. *Late Cenozoic History of the Pacific Northwest*. San Francisco: Pacific Division, AAAS, 69–71.
- Wilson RW. 1960.** Early Miocene rodents and insectivores from northeastern Colorado. *University of Kansas Paleontological Contributions* **7**:1–92.

- Yang H, Huang Y. 2003.** Preservation of lipid hydrogen isotope ratios in Miocene lacustrine sediments and plant fossils at Clarkia, northern Idaho, USA. *Organic Geochemistry* **34**(3):413–423 DOI [10.1016/S0146-6380\(02\)00212-7](https://doi.org/10.1016/S0146-6380(02)00212-7).
- Yang H, Smiley CJ, Sprenke KF, Rember WC, Knowles CR. 1995.** Subsurface evidence for rapid formation of the Clarkia Miocene lake in northern Idaho. *Northwest Science* **69**:52–59.
- Yang J, Spicer RA, Spicer TEV, Li C-S. 2011.** ‘CLAMP Online’: a new web-based palaeoclimate tool and its application to the terrestrial Paleogene and Neogene of North America. *Palaeobiodiversity and Palaeoenvironments* **91**(3):163–183 DOI [10.1007/s12549-011-0056-2](https://doi.org/10.1007/s12549-011-0056-2).
- Zachos J, Pagani M, Sloan L, Thomas E, Billups K. 2001.** Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* **292**(5517):686–693 DOI [10.1126/science.1059412](https://doi.org/10.1126/science.1059412).
- Zachos JC, Dickens GR, Zeebe RE. 2008.** An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature* **451**(7176):279–283 DOI [10.1038/nature06588](https://doi.org/10.1038/nature06588).