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

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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.
THE FIRST TETRAPOD FROM THE MID-MIOCENE CLARKIA LAGERSTÄTTE (IDAHO, USA).

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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.
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, 2008). The magnitude of warming during the MMCO is consistent with predictions for climatic changes during the coming century (IPCC 2013), 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, Retallack 2009, Takeuchi et al. 2007, Yang et al. 2011) and paleoenvironmental (Bestland et al. 2008, Harris et al. 2017, Kohn and Fremd 2007, Sheldon 2003) 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 et al. 2018), Sucker Creek (Scharf 1935), 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 (e.g., Badgley and Finarelli 2013, Calede et al. 2011, Harris 2016, Maguire 2015, Orcutt and 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 and Cockerell 1931) and numerous fossil floras, notably from the Mascall (Chaney 1925, 1959, Chaney and Axelrod 1959, Knowlton 1902), Sucker Creek (Arnold 1937, Fields 1996), and Latah Formations (Knowlton and 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 et al. 2000, Logan et al. 1993, 1995, Soltis et al 1992, Yang
and 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 et al. 1999, Smiley and Rember 1985b,
Smith and 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 and 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 and 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 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 et al. 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 et al. (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 and 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 and 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 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.

MATERIAL AND METHODS

The taxonomic frameworks for the rodents from the Inland Northwest discussed in this paper come from Flynn and Jacobs (2008a), Flynn and Jacobs (2008b), Flynn et al. (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 reposited 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 and 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 et al. 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 et al. 2008) do reach such 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 et al. 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 et al. 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 and Jacobs 2008a, Hopkins 2008a): *Liodontia* and *Tardontia*. Both are known from the Inland Northwest (Calede et al. 2011, Shotwell 1958,) and overlap in size with UWBM 113209 (Calede et al. 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 and 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 and Hopkins 2012a, Calede et al. 2011), most genera are much larger than UWBM 113209 (Calede et al. 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 (Caled and 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 (Caled and Hopkins 2012b, Fagan 1960, Galbreath 1984, Korth 2000).

Among the genera of the family Castoridae known from the early Barstovian of North
America (Flynn and 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 et al. 2018). However, similarly
to *Mesogaulus*, it is much too robust to compare well with UWBM 113209 (Prieto et al. 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 (e.g., Korth 2002, Matthew and 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 et al. 2018, Orcutt and 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*, *P. oregonensis* (originally described as *Arctomyoides 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 Arikareean 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 and Samuels 2015).

*Protosciurus* is present in the northwest of the United States during the Arikareean and Hemingfordian (Black 1963, Goodwin 2008, Korth and 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 and 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. *P. montanus* also differs from UWBM 113209 in its deep and robust dentary (Goodwin
This dentary houses a very large incisor (depth 7.3 mm, Downs 1956), much larger than that of UWBM 113209. The lower incisor of *P. 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 alike *Arctomyoides* (Goodwin 2008). However, alike *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 *P. oregonensis* (10.0 mm; Downs 1956) is shorter than that of UWBM 113209 (Table 1). The lower incisor of *P. oregonensis* is also slightly deeper (3.7 mm; Downs 1956) than that of UWBM 113209. Finally, UWBM 113209 differs from *P. 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 *P. 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 and Emry 1991). Nonetheless, prior to the work of Hayes (2005), *Cedromus* was only known from the Orellan and Whitneyan (Korth and 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 *P. mengi* and *P. rachelae* (Hopkins 2007, Korth and Samuels 2015). Additionally, the lower incisor of UWBM 113209 is much thicker than the incisors of *P. mengi* and the skull roof of UWBM 113209 does not display the characteristic supraorbital shelf of *P. rachelae* (Korth and Samuels 2015). A third species of *Protosciurus*, *P. condoni* is much larger than the Clarkia rodent (Black 1963, Hopkins 2007). *P. condoni* also differs from the Clarkia rodent in its shortened lower diastema (Black 1963). *P. 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 and Evans 2005, Emry and Thorington 1982, Korth and Samuels 2015, Rose and Chinnery 2004, Thorington et al. 1997, 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 et al. 2005, Korth and 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 et al. 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 et al. 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 et al. 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 sciurin (skull length 48.2 mm; Samuels, pers. comm. 2018) but its lower incisor is proportionately not as thick (3.9 mm diameter; Samuels, pers. comm. 2018). 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 Sciurus olsonii (Emry et al. 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 Arikareean-aged Protosciurus (Goodwin 2008, Hopkins 2007, Korth and 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, Best 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. 2016). 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 and Elder 1985); UWBM 113209 was recovered from the lowest of these layers. Smith and 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 paleoecommunity 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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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.

Figure 2 – Stratigraphy of the Latah Formation exposed at UWBM C2830: Numbering, lithology, and color of units follows Smiley et al. (1975) and Smiley and Rember (1985). The total thickness of the section exposed at the Kienbaum racetrack is roughly 9 m.

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.

Table 1 – Summary of the measurements of UWBM 113209. Linear measurements in mm. Mass in g. * denotes estimate.
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.
Figure 2

Stratigraphy of the Latah Formation exposed at UWBM C2830.

Numbering, lithology, and color of units follows Smiley et al. (1975) and Smiley and Rember (1985). The total thickness of the section exposed at the Kienbaum racetrack is roughly 9 m.

| Unit | Zone          | Lithology                      | Vertebrate Fossils |
|------|---------------|--------------------------------|--------------------|
| 5    | Oxidized      | Oxidized Silty Clay            | Fish-bearing Layers|
| 4 & 3| Oxidized Clay & Ash | Volcanic Ash                  |                    |
|      | Unoxidized    | Oxidized Clay & Ash            |                    |
| 2    | Unoxidized    | Transitional Silt & Ash        |                    |
|      |               | Unoxidized Clay & Ash          |                    |
| 1    | Unoxidized    | Unoxidized Clay                |                    |
|      |               | Unoxidized Sand & Clay         |                    |

1 m
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.
Table 1 (on next page)

Summary of the measurements of UWBM 113209.

Linear measurements in mm. Mass in g. * denotes estimate.
| 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   |