Contributions

from the Museum of Paleontology, University of Michigan

Vol. 32, no. 12, pp. 245–258 May 25, 2017

THREE NEW SCIURAVIDS (RODENTIA) FROM THE LATEST-EARLY TO MIDDLE EOCENE OF WYOMING: MOSAIC EVOLUTION AND THE ALPHA TAXONOMY OF *SCIURAVUS NITIDUS*

BY

DEBORAH K. ANDERSON[1]

Abstract — Sciuravids are a diverse group of early to middle Eocene rodents known from North America. The delineation among species of *Sciuravus* is challenging because of extensive intraspecific morphological variation. Previous studies have reviewed the type species of *Sciuravus*, *S. nitidus*, and have presented descriptions of several other species of the genus, but no comprehensive comparisons have been made to assess the validity of these species. In this study, a sample of sciuravids collected from two distinct biochronologic zones in the middle Eocene of the Green River Basin, Wyoming were compared to known species of *Sciuravus* from a variety of time intervals and geographic regions, making it possible to recognize the limits of intra- and interspecific variation. Several specimens fit into previously described species, but others did not. Discovery of specimens that exceeded the variation within known species categories led to the recognition of three new species of *Sciuravus*: *S. metalinguas*, *S. inclinatus*, and *S. nexus*. Description and analysis of the new species effectively clarifies the alpha taxonomy of *S. nitidus* and reveals a pattern of mosaic evolution—each species shares some crown pattern and/or zygomatic arch features with another species or two, some ancestral, some derived. In addition, I describe the upper dentition of *S. wilsoni*, a species that is significant to resolving questions about sciuravid origins and evolutionary relationships.

These sciuravid species evolved during the early to middle Eocene, a time period known to be associated with significant global climate change. The results reported here further support the growing evidence that changing climates directly influenced Eocene mammalian diversity and geographic distribution patterns.

INTRODUCTION

Sciuravids are a diverse group of rodents found in the early to middle Eocene (Wasatchian–Uintan) sediments of North America (Wilson, 1949). Their abundance peaked during the Bridgerian and Uintan (latest-early to middle Eocene), time periods marked by significant climatic shifts and major faunal turnovers (Walton and Porter, 2008; Woodburne et al., 2009a, b). Traditionally the term "sciuravids" has been used to refer collectively to three lineages: species of *Sciuravus*, species of *Knightomys* and *Prolapsus*, and species of *Pauromys* (Walton and Porter, 2008). Recent work has restricted the family name Sciuravidae to only one of these three lineages, species of *Sciuravus*, which are thought to be part of a stem group of Myomorpha, a diverse group of mouse-like rodents (Wood, 1955; Gazin, 1961; Dawson, 1966; Wang and Dawson, 1994; Porter, 2001). Although the origin of the Sciuravidae remains unclear (Dawson, 2015), its most likely sister taxon is *Microparamys*, an ischyromyid (Ivy, 1990; Rose, 2006) that also has a protrogomorphous skull structure, sciurognathous jaw, retains two upper premolars, and has brachydont cheek teeth (Wilson, 1938, 1949; Dawson, 1977; Walton and Porter, 2008). Sciuravids differ from

[1]St. Norbert College, 100 Grant Street, Street, De Pere, WI 54115 (deborah.anderson@snc.edu)

Microparamys and other ischyromyids in having the M1–2 hypocones and protocones subequal in size and separated from each other by a pronounced intervening valley; a metaloph complex; protoconule and metaconule fused to the inner cusp; and stronger protoloph, metaloph, and cingula (Wilson, 1938, 1949; Wood, 1959). Distinctive features of the lower teeth of the sciuravids include an entoconid separated from the posterolophid and compressed anteroposteriorly (Wilson, 1949), a well-developed hypolophid and protolophid, and a relatively small anterior cingulum.

Taxonomy of the *Sciuravus* lineage has been confusing and misleading because the type species, *Sciuravus nitidus*, has been used as a wastebasket taxon that collected specimens that could not be placed in one of the other *Sciuravus* species. As a consequence, the specimens currently ascribed to *S. nitidus* encompass a great deal of intraspecific variation (Wilson, 1938; Gunnell, 1998). It is possible that this practice of classifying 'unknowns' within *S. nitidus* has masked a more complex pattern of sciuravid evolution and biodiversity which may, in fact, be partially driven by known climatic changes during the early to middle Eocene (Woodburne et al., 2009a, b). This paper presents new evidence that documents biodiversity patterns in sciuravids and offers hypotheses on ancestral vs. derived character states within the *Sciuravus* lineage.

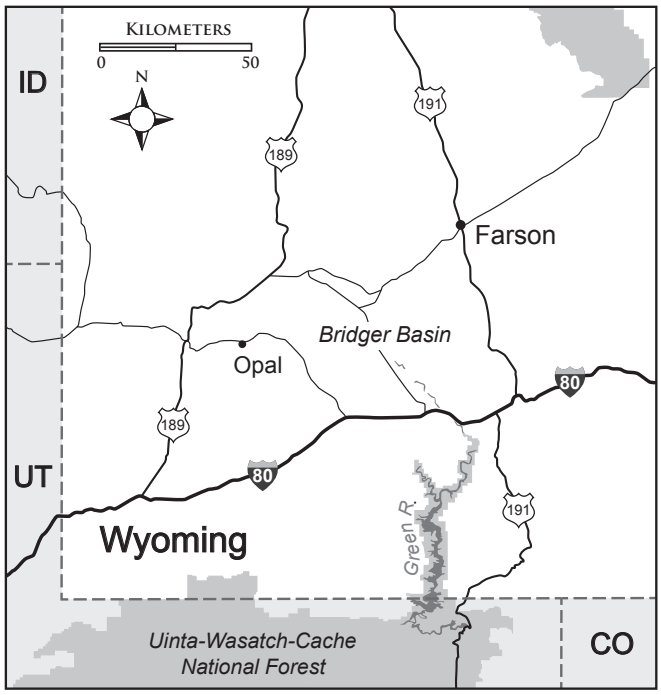


FIGURE 1 — Map of southwestern Wyoming showing the Greater Green River Basin. Specimens described in this study were collected from Bridger Basin, Opal, and Big Island-Blue Rim (west of Farson). Map designed by C. Abraczinskas and Google Maps 2017.

Materials and Methods

The sample of sciuravids used in this study includes 23 specimens collected from the southern Green River Basin of southwestern Wyoming (Fig. 1), which are cataloged at The University of Michigan Museum of Paleontology. The specimens are from two principal areas where Bridgerian biochron Br1b sediments can be found: Opal Bench in the vicinity of Opal, Wyoming along the northern portion of the Bridger Basin, and the Big Island-Blue Rim Badlands west of Farson, Wyoming (Gunnell, 1998). Additional specimens come from the Bridger Basin (Bridgerian biochron Br2) in the southeastern part of the Greater Green River Basin, Wyoming. Comparative samples used in this study include: the holotypic specimens of *S. nitidus* and *S. undans* housed at Yale Peabody Museum, the holotypic and referred material of *S. powayensis* housed at the Los Angeles County Museum, the holotypic specimen of *S. altidens* and referred material of *S. eucristadens* housed at Carnegie Museum of Natural History, and a collection of middle Bridgerian sciuravids housed at Denver Museum of Nature and Science.

Dental terminology used in this paper follows Wood and Wilson (1936), Wood (1962), Reig (1977), Flynn et al. (1986), and Marivaux et al. (2004). Teeth were measured to the nearest 0.01 mm using an optical micrometer fitted to a Bausch and Lomb dissection microscope. Measurements of lower molars were taken as described by Wood (1962). Upper molar length (AP) measurements were taken at the center of the crown. Width of M1–2 was measured along the protoloph (buccal margin of the paracone to lingual margin of protocone) and metaloph (buccal margin of metacone to lingual margin of hypocone; Fig. 2). The second breadth measurement was taken differently for P4 and M3, which may lack a hypocone. In this case, a measure was taken from the buccal margin of the metacone to the lingual margin of the protocone. Measurements are provided in Table 1.

INSTITUTIONAL ABBREVIATIONS

CM — Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A.
DMNH — Denver Museum of Nature and Science, Denver, Colorado, U.S.A.
UM — University of Michigan Museum of Paleontology, Ann Arbor, Michigan, U.S.A.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Order RODENTIA Bowditch, 1821
Family SCIURAVIDAE Marsh, 1871
SCIURAVUS Marsh, 1871

Sciuravus metalinguas, new species
Figs. 3A, B, 4D, E; Table 1

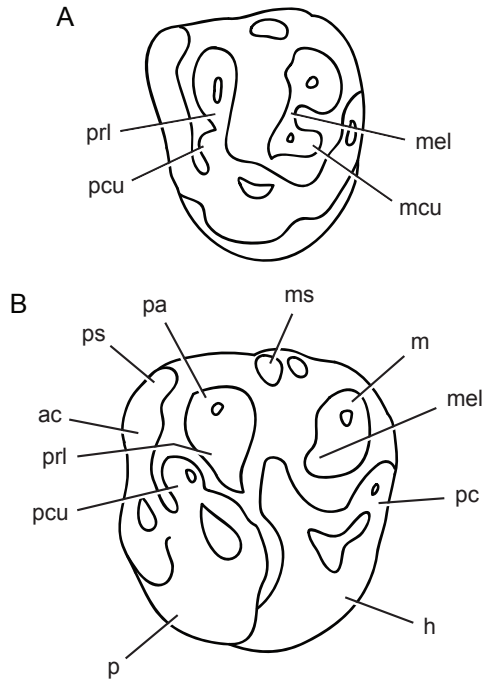


FIGURE 2 — Diagram of cheek teeth of *Sciuravus* showing occlusal morphology and related nomenclature of the left upper premolar four (**A**) and left upper molar one (**B**). Nomenclature was modified after Wood and Wilson (1936). Anterior is towards the left; buccal is towards the top. Abbreviations: *ac*, anterior cingulum; *h*, hypocone; *m*, metacone; *mcu*, metaconule; *mel*, metaloph; *ms*, mesostyle; *p*, protocone; *pa*, paracone; *pc*, posterior cingulum; *pcu*, protoconule; *prl*, protoloph; *ps*, parastyle.

Holotype.— UM 95757, right maxillary fragment preserving P4–M1 and a partial zygomatic arch.

Type locality.— The holotype is from The University of Michigan Locality BB-58, Uinta County, Green River Basin, Wyoming.

Formation, age, and distribution.— Bridger Formation, middle Eocene, middle Bridgerian, Bridgerian biochron Br2.

Etymology.— The species epithet comes from the Greek word *meta*, which means "behind," and the Latin word *lingua*, which means "tongue." Combined, these terms refer to the presence of a transversely elongated lingual spur behind the M1 metacone, which is on the lingual side of the molar.

Diagnosis.— *S. metalinguas* differs from all other species of *Sciuravus* in having the following unique characters: a metacone with a short lingually directed spur, mesostyle connected to the paracone, and protoloph spur completely separated from the paracone on M1. It differs from *Sciuravus nitidus* in having P4 with a distinct hypocone set apart from the protocone and a well-developed cingulum wrapping around the buccal aspect of the metacone, P4 metaconule distinctly smaller than metacone, posterior edge of zygomatic root anterior to P4, and M1 hypocone and protocone separated by a deep valley. *S. metalinguas* differs from *S. wilsoni* in being larger, having posterior aspect of zygomatic arch forming a 90 degree angle, P4 paracone and metacone closer together, and a less prominent lingual cusp on the anterior cingulum of M1. It differs from *S. popi* in having a relatively larger P4 hypocone and the posterior cingulum wrapping around the metacone buccally, the connection between M1 hypocone loph and metacone is at buccal end of loph instead of from the side as in *S. popi*. It differs from *S. powayensis* in being larger, having posterior aspect of zygomatic arch forming a 90 degree angle, a distinct P4 hypocone, and lacking an enamel connection between posterior aspect of hypocone and posterolingual aspect of metacone on M1.

Referred material.— DMNH 24656, right maxillary fragment preserving P4–M1 and a partial zygomatic arch. The specimen comes from Denver Museum of Nature and Science Locality 885 *Smilodectes*, located in the Black's Fork Member of the Bridger Formation in Sweetwater County, Wyoming. DMNH 24656 preserves all of the diagnostic features of *S. metalinguas* described above, as well as the other characters that further distinguish it from other Bridgerian species of *Sciuravus*. The main distinction between these two specimens is that the P4 and M1 of DMNH 24656 are slightly more worn, which makes the P4 hypocone appear less rounded.

Description.— Both specimens of *Sciuravus metalinguas* (Figs. 3A, 4D, E) preserve an alveolus for P3. The posterior edge of the anterior zygomatic root extends out laterally, forming nearly a 90 degree angle with the upper tooth row. The posterior edge lies anterior to P4. The zygoma is ridged ventrally. This ridge ends anterolateral to the P3 alveolus in a slightly rounded knob.

TABLE 1 — Measurements (in mm) for the upper teeth of three new species of *Sciuravus* from the middle Eocene. Abbreviations: *AP*, anteroposterior length; *TR*, transverse width; *WML*, transverse width at metaloph; *WPL*, transverse width at protoloph.

		S. metalinguas UM 95757	*S. inclinatus* UM 100804	*S. nexus* UM 100746
P3	AP	–	1.35	1.09
	TR	–	1.39	1.22
P4	AP	1.74	1.9	1.83
	WPL	2.37	2.16	2.01
	WML	2.35	2.35	2.11
M1	AP	2.07	2.21	2.09
	WPL	2.42	2.27	2.29
	WML	2.37	2.19	2.22
M2	AP	–	2.24	–
	WPL	–	2.35	–
	WML	–	2.14	–
M3	AP	–	2.14	–
	WPL	–	2.29	–
	WML	–	2.30	–

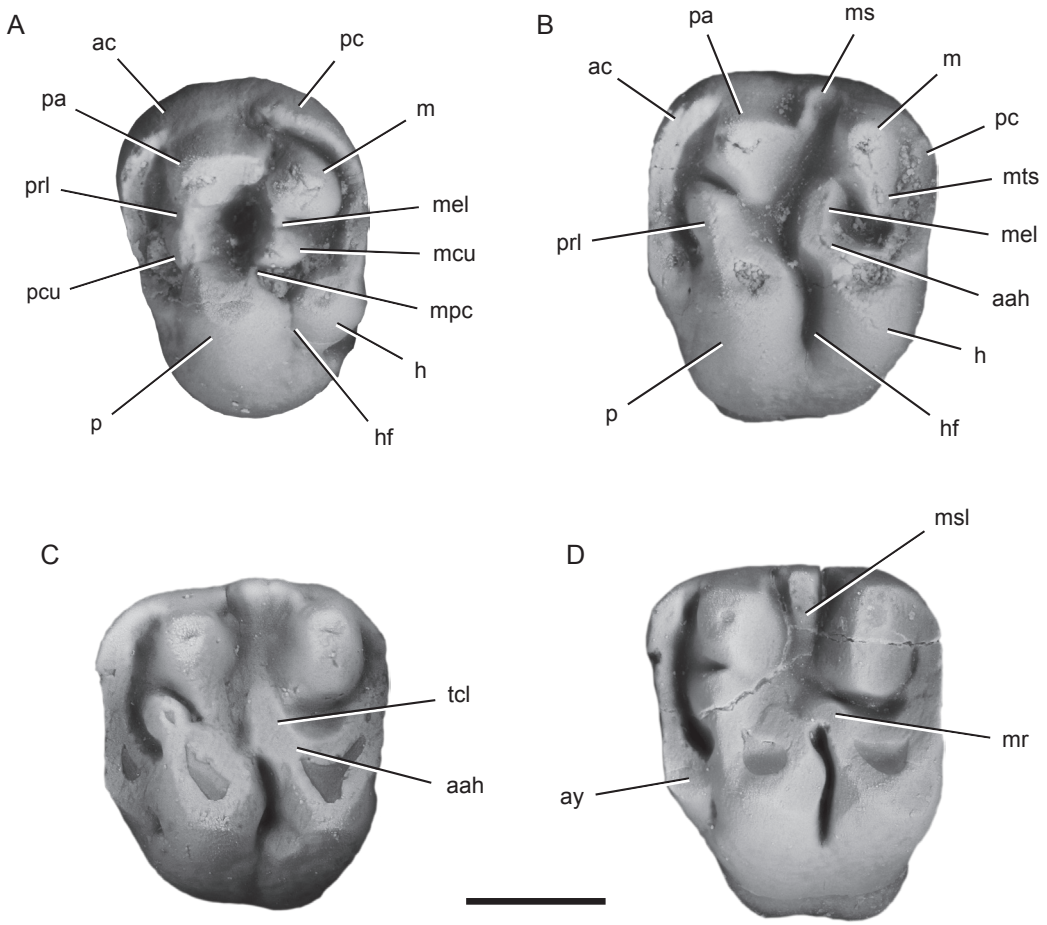
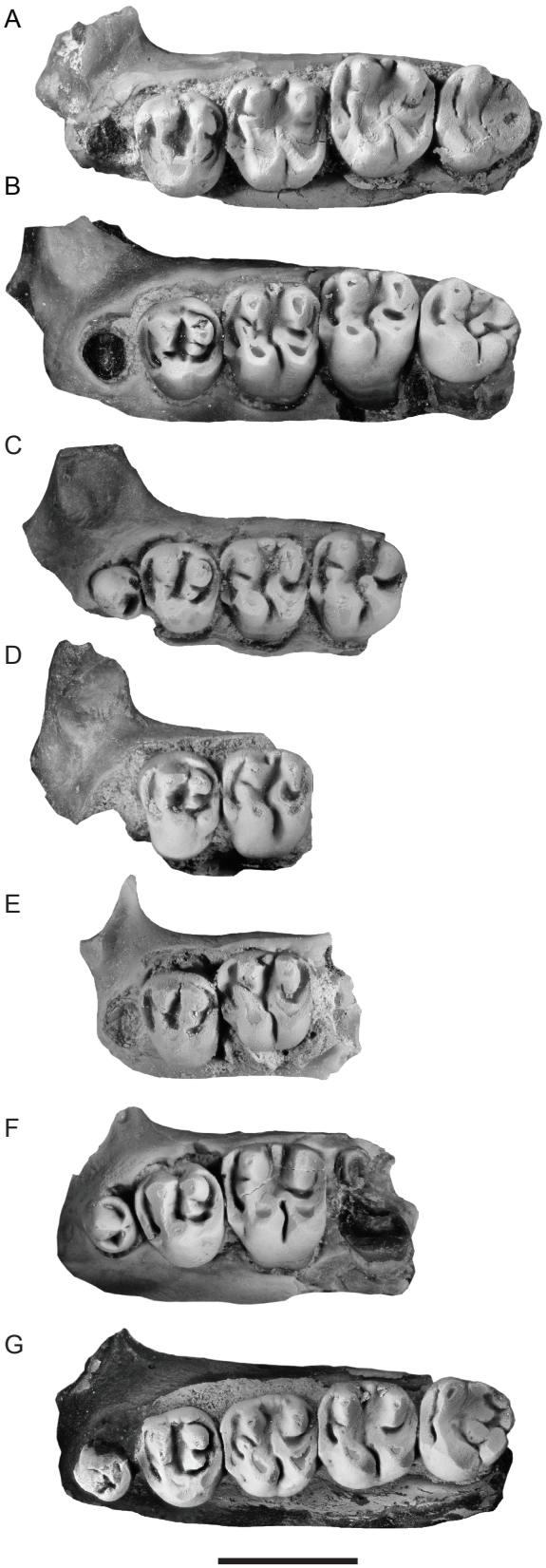


FIGURE 3 — Terminology of diagnostic and common dental surface features of the three new species of *Sciuravus*. Surface features are mainly based on Wood and Wilson (1936), Wood (1962), Reig (1977), Flynn et al. (1986) and Marivaux et al. (2004). **A**, **B**, *S. metalinguas* right P4 and M1 (holotype; UM 95757); **C**, *S. inclinatus* left M1 (holotype; UM 100804); **D**, *S. nexus* left M1 (holotype; UM 100746). Anterior is towards the left, buccal is towards the top in all images; specimens in A and B are reversed. Scale bar = 1 mm. Abbreviations: *aah*, anterior arm of hypocone; *ac*, anterior cingulum; *ay*, anterostyle; *h*, hypocone; *hf*, hypoflexus; *m*, metacone; *mcu*, metaconule; *mel*, metaloph; *mpc*, metacone-protocone conection; *mr*, mure; *ms*, mesostyle; *msl*, mesoloph; *mts*, metalingual spur; *p*, protocone; *pa*, paracone; *pc*, posterior cingulum; *pcu*, protoconule; *prl*, protoloph; *tcl*, third central loph.

The most distinctive upper tooth of *S. metalinguas* is P4 (Fig. 3A, 4D). On this tooth the paracone and metacone are bulbous and closely spaced, and there is no mesostyle. An anterior cingulum is present, ending at the anterobuccal aspect of the paracone. A protoconule is present, but it is not well defined because it blends with the protoloph, which joins the anterior aspect of the protocone lingually. The metaconule is distinct and smaller than the metacone. A short, narrow metaloph is directed essentially transversely. A diminutive metacone-protocone connection joins the metaconule to the protocone. An extension of the posterior cingulum circumscribes the metacone buccally, leaving space for a narrow valley between the two. The hypocone is well defined in the less worn specimen (Fig. 3A, 4D) and separated from the protocone by a hypoflexus that extends part way along the lingual aspect of the tooth.

The anterior and posterior cingula of the first upper molar (Fig. 3B, 4D) are well developed and somewhat rounded where they join the buccal cusps. A minute mesostyle is present, and the protocone and hypocone are subequal. The loph from the protocone extends anterobuccally and ends anterior to the paracone, leaving the anterior and central valleys confluent. In early stages of wear, the protocone and hypocone remain separated by the hypoflexus opening buccally, indicating the absence of a mure (Fig. 4E). An enamel extension connects the paracone to the mesostyle. The most distinctive feature of M1 is a transversely elongated metalingual spur surrounded by a well-defined crescent shaped furrow. A forwardly bending metaloph outlines the anterior aspect of this furrow. The metaloph extends from the anterior arm of the hypocone to the central valley, turns sharply and extends buccally to meet up with the metacone anterolingually.



An interesting problem is suggested by the metalingual spur. Is this crest composed of (1) a segment of posteriorly shifted metaloph joining a metaconule to the metacone; (2) a mesolophule running toward the mesocone from an indistinct metaconule; or (3) a neomorphic metalophule? Presence of a forwardly bending metaloph is a primitive feature (Wood, 1959) found in earlier-occurring sciuravids, such as *S. nitidus* and *S. wilsoni* (Fig. 4A, C). *S. metalinguas* has a centrally located, forwardly bending metaloph. We can rule out the first option because it is unlikely that a distal part of this metaloph detached, migrated posteriorly, and changed orientation. Mesolophules are advanced crests found between the protoloph and metaloph (Flynn, 1986; Marivaux et al., 2004, 2015). We can eliminate the second option because the lingual extension found in *S. metalinguas* is posterior to the metaloph. Metalophules are posterolabially directed crests that extend from the metacone and sometimes meet up with the posterior cingulum (Oliver and Peláez-Campomanes, 2014). Metalophules are considered to be an advanced feature of cricetids, which are an advanced group of myomorphs (Wang and Dawson, 1994; Marivaux et al., 2004; Rose, 2006). Given that the metalingual spur is a slightly more specialized condition than present in other early-appearing sciuravids, it likely represents an intermediate condition, a neomorph metalophule. Until more is known of the sciuravids and their phylogenetic relationships, this conclusion remains speculative.

Comparisons.— The holotype of *S. metalinguas* (Fig. 4D) includes an anterior zygomatic root, P3 alveolus, and only slightly worn P4–M1. The angle between the zygomatic arch and maxillary teeth is most similar to that of *S. nitidus* (Fig. 4A), which is distinct from *S. metalinguas* in having its posterior edge in line with the P4 protoloph instead of being anterior to P4. In contrast, the zygomatic root of *S. powayensis* (Fig. 4B) and *S. wilsoni* (Fig. 4C) extends anterolateral to P4, creating an obtuse angle. Presence of a ventral ridge on the zygoma is a common feature among species of *Sciuravus*.

The P4 of *S. metalinguas* is most similar in overall morphology to that of two other species known from the Bridger Basin, *S. powayensis* and *S. popi*. In all three species, the premolars are small relative to the molars and have crowded

FIGURE 4 — Maxillae shown in occlusal view to highlight differences in the zygomatic arch morphology in several species of *Sciuravus*. The posterior edge of the anterior zygomatic root ranges from nearly a 90 degree angle in UM 95757 and DMNH 24656, to an obtuse angle in UM 100714 and UM 110570. Positioning of the posterior edge of the anterior zygomatic root varies from on a line with P3 in UM 110570 and 100714, to on a line with the P4 anterior cingulum in UM 100746. **A**, *S. nitidus* right P4–M3 (DMNH 33955); **B**, *S. powayensis* left P4–M3 (UM 100714); **C**, *S. wilsoni* right P3–M2 (UM 110570); **D**, *S. metalinguas* right P4–M1 (holotype; UM 95757); **E**, *S. metalinguas* right P4–M1 (DMNH 24656); **F**, *S. nexus*, left P3–M1 (holotype; UM 100746); **G**, *S. inclinatus*, left P3–M3 (holotype; UM 100804). Anterior is towards the left in all images; maxillae are aligned at P4. Photographs A, C, D and E are reversed. Scale bar = 3 mm.

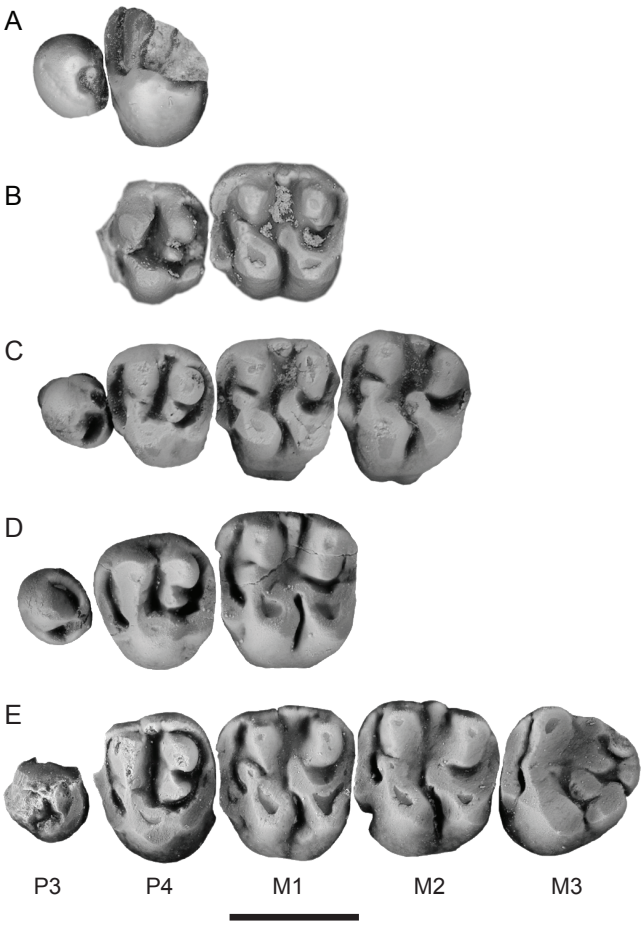


FIGURE 5 — An occlusal view of *Sciuravus sp*. specimens with P3–P4 illustrates some of the morphological differences between *S. inclinatus* and four other species of *Sciuravus*. In the *S. inclinatus* holotype (UM 100804), the P3 is roughly molariform, similar to that of *S. wilsoni* (UM 110570), but distinct from the conical P3 of the *S. nexus* holotype (UM 100746) and *S. nitidus* (DMNH 30139). In UM 100804, the P4 paracone and metacone are set further apart than those of UM 100739. In the *S. inclinatus* holotype (UM 100804), the P4 hypocone is less well defined and the metaconule is relatively larger compared to that of *S. popi* (UM 100739) and *S. wilsoni* (UM 110570). **A**, *S. nitidus* right P3–partial P4 (DMNH 30139); **B**, *S. popi* left P4–M1 (UM 100739); **C**, *S. wilsoni* right P3–M2 (UM 110570); **D**, *S. nexus* left P3–M1 (holotype; UM 100746); **E**, *S. inclinatus* left P3–M3 (holotype; UM 100804). Anterior is towards the left in all images; teeth are aligned at P4/M1. Photographs A and C are reversed. All teeth were coated with ammonium chloride. Scale bar = 2 mm.

buccal cusps, a transversely directed metaloph, and a well-defined metaconule. *Sciuravus metalinguas* differs from these species in having a P4 with a well-defined protoconule and posteriorly extended paracone at the buccal aspect, leaving a very narrow space between paracone and metacone. In other species of *Sciuravus*, the central valley of P4 is more open and often includes a mesostyle. Development of the hypocone as a distinct cusp, a feature shared with *S. popi*, sets *S. metalinguas* apart from *S. powayensis*. Presence of a buccal cingulum that is isolated from the metacone is a feature shared only with *S. powayensis*. In other species of *Sciuravus*, such as *S. wilsoni* and *S. nitidus*, the posterior cingulum wraps partly around the metacone, connecting with it buccally.

Sciuravus metalinguas resembles most species of *Sciuravus* in having well-developed cingula, subequal lingual cusps, a deep central valley, and a mesostyle on M1. The anterior and posterior cingula extend to meet up with buccal cusps, a feature also found in *S. popi*. Isolation of the protoloph is a feature shared with other species of *Sciuravus*, but is most pronounced in *S. wilsoni* and *S. metalinguas*, where it even persists in molars with moderate wear (Fig. 4C, E). A short loph (potentially a mesolophule) extends from the oblique anterior arm of the hypocone buccodistally toward the metacone. A similar feature is found in *S. wilsoni* and *S. popi*. However, *S. metalinguas* is distinct in having a longer, more well-defined buccal aspect of the loph, which clearly isolates the unique and short metalingual spur. Only the beginnings of such an extension (albeit angled) can be found in some specimens of *S. wilsoni* (Fig. 4C), whereas it is clearly developed and consistently present in *S. metalinguas*. In *S. popi* (Fig. 5B), a short buccodistally directed spur joins the hypocone and metacone, and a shortened loph extends from the oblique anterior arm of the hypocone into the central valley.

Sciuravus inclinatus, new species
Figs. 3C, 4G, 5E; Table 1

Holotype.— UM 100804, left maxillary fragment with P3–M3, partial zygomatic arch.

Type locality.— The holotype is from The University of Michigan Locality BB-38, Bridger Formation, Sweetwater County, Green River Basin, Wyoming.

Formation, age, and distribution.— Early middle Eocene, early Bridgerian, Bridgerian biochron Br1b.

Etymology.— The species epithet is derived from the Latin word *inclinare*, which means "to lean," in reference to the presence of a downward sloping oblique anterior arm of the hypocone on M1–3.

Diagnosis.— *S. inclinatus* differs from all other species of *Sciuravus* in having an inclined, well-defined anterior arm of the hypocone extending anterobuccally (= third central loph) into the central basin of M1–3, double mesostyles on P4–M1, and an anteroposteriorly compressed protocone and hypocone on M1–M2. *S. inclinatus* differs from *S. nitidus* in being larger and having the posterior edge of zygomatic root less angular and more rounded, a transversely oriented protoloph on P4, the posterior cingulum wrapping around buccal aspect of metacone on P4, the paracone and metacone of M1 widely spaced, a weak connection between metacone and third central loph on M1, protoconules submerged in the short rounded protolophs of M1–2, and isolation of M3 hypocone. *S. inclinatus* differs from *S. wilsoni* in being larger, having a triangular P4 with no hypocone and metaconule similar in size to metacone, and having a weak connection between metacone

and third central loph on M1. *S. inclinatus* differs from *S. popi* in being larger and having a more widely spaced paracone and metacone on P4, a triangular P4 with transversely oriented protoloph and no hypocone, a P4 metaconule nearly same size as metacone, a P4 posterior cingulum wrapping around buccal aspect of metacone, M1–M2 hypoflexus extending only halfway down the lingual face of the molar, a weak connection between third central loph and metacone in M1, and isolation of M3 hypocone. *S. inclinatus* differs from *S. powayensis* in being larger with less bulbous cusps and having P4 metaconule nearly as large as metacone, P4 close in size to M1, less prominent mesostyles on M1–3, lack of enamel connection between posterobuccal aspect of hypocone and posterolingual aspect of metacone on M1–2, M1 protocone and metacone widely spaced, M3 more molariform and less rounded in outline. *S. inclinatus* differs from *S. eucristadens* in having the posterior aspect of the zygomatic arch positioned anterior to P4, a triangular P4 with no hypocone, P4 similar in size to M1, a valley between P4 posterior cingulum and metacone, and M1–2 with short rounded cuspate protocone lophs.

Description.— *Sciuravus inclinatus* is slightly larger than *S. nitidus* and similar in size to *S. eucristadens* (Table 1). The holotypic specimen, UM 100804 (Fig. 4G), preserves a left P3–M3 and part of the zygomatic arch, the posterior edge of which is on a line with the P4 anterior cingulum.

The lingual half of the upper third premolar is preserved (Fig. 4G, 5E). There is evidence of a tiny protocone and a low posterolingual cingulum. The beginnings of two elevations in the protoloph and metaloph position likely represent the base of one small posterolingual cusp and one larger anterolingual cusp.

The fourth upper premolar is nearly the same size as M1 and triangular in outline. There is no indication of a hypocone. The paracone and metacone are well separated by a deep central valley. Between the two cusps, there are two mesostyles. Adjacent to the posterior mesostyle is another small cusp, the terminal cusp of the posterior cingulum, which is positioned anterobuccal to the metacone. The metacone is a large, bulbous cusp connected to the metaconule via a ridge. The metaloph is essentially transversely oriented, meeting up with the center of the protocone. There is no protoconule. An incipient shallow protoloph is present in place of this cuspule. The anterior cingulum wraps around the buccal aspect of the paracone.

The most distinctive upper tooth is M1, in which the paracone and metacone are well separated by a double mesostyle (Fig. 3C, 4G). The paracone is connected to the protocone via a protoloph. Distinct from this ridge, there is a short anterobuccally directed protoloph that bears a distinct protoconule. Protocone and hypocone are well separated by a hypoflexus that extends halfway down the lingual face of the tooth. The anterior arm of the hypocone plus the 'mesolophule' (= third central loph) extends anterobuccally into the central basin, a feature unique to *S. inclinatus*. In other species of *Sciuravus*, the third central loph has a uniform height and width as it extends towards either the central basin and/or metacone. The third central loph of *S. inclinatus* changes in height, sloping down into the central basin, and the width varies from narrow to wide to tapered. Lingually, the M1 hypocone has a mesial outgrowth and is anteroposteriorly compressed, which is distinct from the crescent shape hypocone of *S. nitidus*. The basin between the third central loph and metacone wall is shallow, but there is no connection between the two.

The second upper molar is very similar to M1. Notable differences include positioning of the protoloph, which is in line with and close to the lingual aspect of the protocone. There is a single mesostyle between the buccal cusps. An incipient connection has developed between the mesolophule and metacone.

The third upper molar has a rounded lingual aspect, a well-developed protoloph, large protocone, and distinct anterior cingulum. As in M1–2, the metacone is relatively small. A protoloph connects the paracone and protocone, and the protoconule is submerged. The hypocone is well developed and isolated from the protocone and posterolophid. An inclined third central loph extends essentially anteroposteriorly and is located lingual to the metaconule.

Comparisons.— The P3 of *S. inclinatus* (Fig. 5E) is unique among members of *Sciuravus* because of its distinct protocone, low posterior cingulum and two lingual cusps. Although P3 is rarely preserved, only one other species of *Sciuravus* has a P3 with two cusps, *S. wilsoni* (Fig. 5C), but these cusps are on the buccal aspect of the premolar. In contrast, in most other species of *Sciuravus* with a known P3 (such as *S. nitidus*), this tooth consists of a single conical cusp and a posterolingual cingulum (Fig. 5A).

Premolar four and the anterior zygomatic root of *Sciuravus inclinatus* (Fig. 4G) are most similar to those of *S. nitidus* (Fig. 4A). In both species, the P4 lacks a distinct hypocone and has a relatively large metaconule. In contrast, the P4 of two early Bridgerian species of *Sciuravus*, *S. popi* and *S. wilsoni*, includes a well-developed hypocone and small metaconule (Fig. 5B, C). The relative size of P4 is also distinct in other species of *Sciuravus*. In *S. inclinatus*, P4 is similar in size to M1, a trait shared with *S. nitidus*, and *S. wilsoni*. In *S. popi*, *S. powayensis*, and *S. eucristadens* the premolar is small compared to M1. In addition, the closely spaced paracone and metacone and absence of a mesostyle make the P4 of *S. popi*, *S. powayensis*, and *S. eucristadens* distinct from *S. inclinatus*.

The posterior edge of the zygomatic arch is on a line just anterior to P4 in *S. inclinatus*, as it is in *S. nitidus*. Although the zygomatic arch is fragmented, an inferior extension of bone suggests that *S. inclinatus* has a ventral ridge similar to that of *S. nitidus* and other species of *Sciuravus*. It is unclear whether or not a terminal knob was present, a feature well developed in *S. powayensis*. Distinct from *S. inclinatus*, the anterior root of the zygomatic arch of *S. wilsoni* and *S. powayensis* extends anterolaterally, creating a wider space between this and the maxillary teeth, and the posterior edge is on a line with P3.

The upper molars of *S. inclinatus* (Fig. 3C, 4G) are quite similar to those of *S. nitidus*. On M1–2, the protocone and hypocone are subequal in size and are well separated by a deep hypoflexus that extends halfway down the lingual face

of the tooth. This condition is distinct from that of *S. popi*, in which the hypoflexus of M1–2 extends nearly to the limit of the enamel. Other features of M1–2 that *S. inclinatus* shares with *S. nitidus* include well-developed anterior and posterior cingula, relatively shallow and open basins between the buccal cusps, and similar protocone spur morphology. On M1 the protoconule is somewhat anterior to the paracone, whereas on M2 it extends more directly to the paracone. Thus, it is primarily the third central transverse crest extending to the central basin that makes the M1–2 of *S. inclinatus* distinct from those of *S. nitidus*. In contrast, the M1 of *S. popi*, *S. wilsoni*, and *S. powayensis* are distinct from *S. inclinatus* in having the paracone and metacone closer together and variation in the protoloph morphology. A double cuspule and closer association between the protoconule and protocone characterizes *S. popi*. The M1 protoconule of *S. wilsoni* and *S. powayensis* (Fig. 4B, C) differs from that of *S. inclinatus* in being more transversely directed and more widely separated from the protocone along the anteroposterior axis until very worn. There are other differences in morphology between *S. inclinatus* and coeval species of *Sciuravus* that are common to both M1 and M2. On the lingual side of the molar, the hypocone of M1–2 is transversely compressed in *S. popi* and *S. powayensis*. In *S. eucristadens*, the lingual aspect of the protocone and hypocone of M1–2 is more rounded and less crescentic than those of *S. inclinatus*. In M1–2 of *S. wilsoni*, the lingual aspect is relatively narrow compared to those of *S. inclinatus*.

The third upper molar of *S. inclinatus* resembles that of *S. nitidus* and other species of *Sciuravus* in having a well-developed anterior cingulum, strong protoloph with no break, relatively large protocone, a metaconule, and evidence of a hypocone. The degree of hypocone development most closely matches that of *S. powayensis* (Fig. 4B), in which this cusp is isolated along the lingual and posterior aspect. The M3 of *S. inclinatus* is distinct from *S. powayensis* in its long anterior cingulum, well-developed metaconule, and lingually shifted metacone, like that of *S. popi* (Rasmussen et al., 1999). Posteriorly, the M3 of *S. powayensis*, *S. nitidus*, and *S. eucristadens* (Burke, 1937; Dawson, 1968) is rather triangular in outline.

Sciuravus nexus, new species
Figs. 3D, 4F, 5D; Table 1

Holotype.— UM 100746, left maxillary fragment with P3–M1 and a partial zygomatic arch.

Type locality.— The holotype is from The University of Michigan Locality BB-32, Sweetwater County, Green River Basin, Wyoming.

Formation, age, and distribution.— Bridger Formation, early middle Eocene, early Bridgerian, Bridgerian biochron Br1b.

Etymology.— The species epithet is derived from the Latin word *nexus*, past participle of *nectere*, which means to bind. This species is named for the unique connection between the protocone and hypocone.

Diagnosis.— *S. nexus* differs from all other species of *Sciuravus* in having an M1 with a well-developed median mure connecting the posterobuccal aspect of the protocone to the anterior arm of the hypocone, absence of mesolophule, metaloph equal in width to metacone, and a minute mesostyle with mesoloph. *S. nexus* differs from *S. nitidus* in having P4 with a distinct hypocone, metaconule significantly smaller than metacone and straight protoloph, and lack of a connection between hypocone and metacone on M1. *S. nexus* differs from *S. wilsoni* in its larger size, P3 with a single cusp, angle of posterior aspect of zygomatic root, which is more acute and posteriorly located, and its M1 with mesostyle-mesoloph and protocone blending with protoloph. It differs from *S. popi* in its larger size, a relatively large P4 compared to M1, P4 protoloph essentially straight, and absence of a cuspate mesostyle on M1. *S. nexus* differs from *S. powayensis* in having the posterior edge of the anterior zygomatic root on a line with P4, a molariform P4 lacking extension of posterior cingulum along buccal face of metacone, absence of a mesoloph-metacone connection on M1 and posterior arm of hypocone-metacone connection on M1–2, and absence of a isolated protoconule on M1. *S. nexus* differs from *S. eucristadens* in the quadrate outline of P4, the presence an anterostyle, and a well-defined hypoflexus on M1.

Description.— The holotype of *Sciuravus nexus* (Fig. 4F) includes a well-preserved and only slightly worn left P3–M1 and partial zygomatic root. The anterior zygomatic root extends out with its posterior edge in line with the anterior cingulum of P4. The P3 most closely resembles that of *S. eucristadens* in having an anterobuccal peak and low posterolingual cingulum. The cingulum circumscribes a lingual depression that is wider than the valley defined by a posterobuccal cingulum on the other side of P3.

Premolar four (Fig. 4F, 5D) has a hypocone separated by a faint shallow groove on the lingual face, but this cusp would have become less defined with wear. The metacone is relatively large and bulbous; it is equal in size to the paracone and set nearby. The buccal metaloph is directed essentially transversely. The metaconule is much smaller than the metacone, well developed, and connected to the posterobuccal aspect of the protocone via a short, narrow lingual metaloph. The protoloph runs transversely with no breaks and incorporates a protoconule as large as the metaconule. There is no mesostyle. Instead, there is a small cup-like depression buccal to the paracone and metacone. Anterior and posterior cingula are well developed. The posterior cingulum wraps partially around the buccal aspect of the metacone.

The most distinctive tooth of *S. nexus* is M1 (Fig. 3D, 4F), which bears a crest extending between the anterior arm of the hypocone joins the posterobuccal aspect of the protocone. There is no mesolophule between the median mure and the metacone, leaving a wide valley lingual to the metacone. The hypocone and protocone are well separated along the lingual aspect of the tooth (i.e., there is a narrow and deep hypoflexus). The protoloph is rounded and only slightly separated from the paracone. The paracone and metacone are well separated, with a minute mesostyle and a short mesoloph

filling the space between them. The anterior cingulum is well developed and reaches the buccal aspect of the paracone. Lingually, the anterior cingulum bears a small anterostyle. In the buccal part of the anterior cingulum, a small enamel swelling that indicates the presence of a minute parastyle. The posterior cingulum is straight and ends at the posterobuccal aspect of the metacone.

Comparisons.— Premolar four (Fig. 4F, 5D) of *S. nexus* has a quadrate outline, a feature shared with *S. wilsoni* and *S. popi*. The quadrate shape is created by the presence of a hypocone that is more distinct in *S. nexus* than that of *S. nitidus* and *S. eucristadens*, but less isolated than that of *S. wilsoni* and *S. popi*. Presence of a closely spaced paracone and metacone and absence of a mesostyle makes *S. nexus* similar to *S. eucristadens* and *S. popi*. In contrast, the buccal cusps of *S. wilsoni* and *S. nitidus* are positioned further apart, and *S. nitidus* has a mesostyle. *Sciuravus nexus* resembles *S. wilsoni* in having a P4 with prominent anterior and posterior cingulum that are well separated from the protoloph and metaloph, respectively. A straight, complete protoloph sets *S. nexus* apart from other coeval species of *Sciuravus*, which have an anteriorly directed bend or discontinuity in the protoloph at the site of the protoconule.

In general appearance and outline, the M1 (Fig. 3D, 5D) of *S. nexus* closely resembles that of *S. nitidus*. Four cusps, well-developed cingula, and a distinct mesostyle form the basic pattern of the molar. The protocone and hypocone are subequal, the lingual aspect of the protocone is rounded and that of the hypocone is anteroposteriorly compressed. Paracone and metacone are well separated and subequal in size. A characteristic that makes *S. nexus* distinct from *S. nitidus* is the nature of the hypoflexus, which completely separates the protocone and hypocone at the crown surface and extends halfway down the lingual face of the molar. This feature is shared with *S. wilsoni* and *S. powayensis*. In *S. popi*, the lingual cusps are also separated from one another on the crown surface by a well-marked hypoflexus. The difference is that the hypoflexus extends nearly to the root of the tooth along the lingual aspect. Presence of a short mesoloph is also found in M1–2 of *S. powayensis*, but that of *S. nexus* is longer, reaching further into the central basin. The most distinctive feature of *S. nexus* is the presence of a median mure that joins the mesial extremity of the anterior arm of the hypocone and the posterobuccal aspect of the protocone. Dawson (1968) noted a similar feature in some unnamed sciuravids from Powder Wash, but these specimens also had a connection between the hypocone and metacone, which *S. nexus* does not.

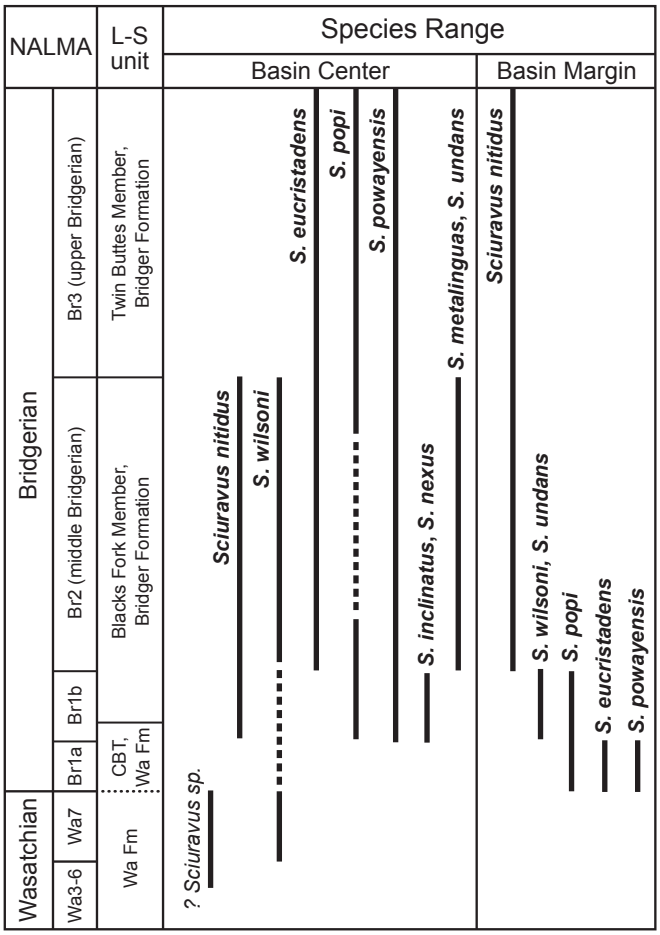


FIGURE 6 — The stratigraphic distribution of Bridgerian *Sciuravus* species. *S. wilsoni* is the oldest definitive species of *Sciuravus*. "*Sciuravus* sp." is a slightly older specimen tentatively assigned to the genus, but its affinities remain unclear. See text for further discussion of *Sciuravus sp.* origins. The three new species, *S. inclinatus, S. nexus,* and *S. metalinguas*, originated in the early–middle Bridgerian. Relative size of lithostratigraphic (L-S) units is approximate. Abbreviations: *CBT*, Cathedral Bluffs Tongue; *NALMA*, North American Land Mammal Age; *Wa Fm*, Wasatchian Formation.

SCIURAVID DIVERSITY AND EVOLUTIONARY RELATIONSHIPS

Discovery of three new species of *Sciuravus* (*S. metalinguas*, *S. inclinatus*, *S. nexus*) adds to the diversity of Bridgerian sciuravids from North America. The new taxa first appear in the early-middle Bridgerian (biochronological zones Br1b–Br2; Gunnell et al., 2009; Fig. 6), when *Sciuravus* diversity peaked with a total of nine distinct species. Several of these species persisted in the upper Bridgerian, but diversity then declined to one species of *Sciuravus* in the lower Uintan (*S. altidens*; Peterson, 1919). Peak *Sciuravus* species diversity is coincident with the Early Eocene Climatic Optimum (Woodburne et al., 2009b), whereas the decline in sciuravid diversity occurred during a time period marked by climatic deterioration.

It remains unclear when and where the first members of the genus *Sciuravus* originated. *Sciuravus* sp. has been reported from as early as Wasatchian biochron Wa3 (Walton and Porter, 2008), but these records have never been substantiated. The oldest definitively identified species of *Sciuravus* is *S. wilsoni*

(Gazin, 1961) from Wasatchian biochron Wa7 of the Green River Formation, a basin center environment (Fig. 6). The advanced position of the posterior edge of the anterior root of the zygoma and advanced molar crown features found in this species and other late early Eocene specimens from North America suggest that members of the Genus *Sciuravus* may have originated elsewhere. Perhaps *Sciuravus* originated and diversified in Asia before immigrating to North America in the late Wasatchian (Wa7) or early Bridgerian (Br1a). An Asian origin for the sciuravids is consistent with the proposed close phylogenetic relationships between "sciuravids" and other early Eocene myomorphs known from Asia (Wang and Dawson, 1994; Porter, 2001). Similarly, several other early Eocene North American taxa are presumed to have originated in Asia (e.g., *Lambdotherium* and *Eotitanops*; Gunnell, pers. comm.; Beard, 1998; but see Mihlbachler, 2008 for a differing opinion).

However, the fossil record does not support an Asian origin for the sciuravids (*Sciuravus*, *Knightomys*, *Prolapsus*, and *Pauromys*). There are no definitive 'sciuravid-like' rodents in the fossil record of Asia during the Eocene (Dawson, 2015). Although one group of middle-to-late Eocene Asian rodents, the Zelomyidae (Dawson et al., 2003), shares the ancestral protrogomorphous/sciuragnathous zygomasseteric structure and advanced quadrate molar morphology with sciuravids, other significant differences in molar morphology preclude a close relationship (e.g., development of selenodonty in advanced forms of some zelomyids; Dawson et al., 2003).

The results presented in this study are consistent with a North American origin and diversification of *Sciuravus*, most likely from an ischyromyid ancestor. Species of *Sciuravus* (*S. wilsoni*, *S. nitidus*) are known to appear approximately 3–5 million years after the first ischyromyids (*Acritoparamys*, *Paramys*, *Microparamys*; Anderson, 2008), which dominated the early Eocene record of North America. When *Sciuravus* first appeared, the skull and dental morphology included a mix of ancestral and derived features. Primitive features shared with the ischyromyids include: the zygomasseteric structure, pauciserial incisor enamel (Wang and Dawson, 1994), and brachydont cheek teeth. On the other hand, derived features such as a well-developed hypocone as large and distinct from the protocone, a P4 hypocone, and well-developed oblique protoloph and metaloph, make *Sciuravus* unique compared to ischyromyids.

Comparing the new species to the type specimen of *S. nitidus* and other species of *Sciuravus* known from similar stratigraphic levels helps to clarify the alpha taxonomy of *Sciuravus,* a first step to sorting out evolutionary relationships. Key features that are useful for distinguishing the new species from characteristic *S. nitidus* and the earliest known species, *S. wilsoni*, include variations in the morphology of the posterior edge of the anterior aspect of the zygomatic root, P4 morphology, and the nature of the hypocone loph and protoconule/protoloph in the upper molars. Among these features, morphology of the zygomatic root is likely to have significance for understanding the evolutionary relationships between sciuravids and other rodents.

Positioning of the anterior root of the zygoma has shifted over time from above M1 in the alagomyids to above P4 in the ischyromyids (Dawson and Beard, 1996). Among the sciuravids in which the zygomatic arch is preserved, the posterior edge of the anterior root of the zygoma is either on a line with the P4 anterior cingulum (found in *S. nitidus*) or anterior to P4 (condition of *S. wilsoni*). The shift in position of the zygoma relative to the tooth row is associated with changes in the arrangement of the masseter muscle, which may increase biting efficiency. Previous studies investigating the role of the zygomatic arch in feeding show that it is highly stressed during gnawing and chewing (Cox et al., 2012). Differences in the morphology of the zygoma may reflect adaptations to changes in the food type consumed. However, allometric constraints and dental development are also likely to have played a role in differentiation of the zygomatic arch among species of *Sciuravus* (Firmat et al., 2014).

The three new species share with *S. nitidus* and *S. wilsoni* the presence of a hypocone on P4, a feature considered to be an advanced trait in rodents (Marivaux et al., 2004). However, the usefulness of this characteristic for establishing evolutionary relationships is limited by the fact that the hypocone has evolved many times among Cenozoic mammals (Hunter and Jernval, 1995). There are variations in the degree of P4 hypocone development that could be used for establishing evolutionary relationships among taxa. For example, a strongly developed hypocone is considered to represent a more advanced character state than a weakly developed, shelf-like hypocone (Marivaux et al., 2004). Unfortunately, this polarity is somewhat inconsistent with the known biostratigraphic record of *Sciuravus*. One of the oldest, definitive species of *Sciuravus*, *S. wilsoni*, has a distinct P4 hypocone that is set apart from the protocone, whereas two later appearing species, *S. nitidus* and *S. inclinatus* do not have this trait (the hypocone appears to have developed as a swelling of the protoloph). The P4 hypocone is most well defined as a nearly isolated cusp in *S. popi*, stratigraphically the second oldest species of *Sciuravus*. One likely explanation for the appearance of this trait in the two oldest species of *Sciuravus* is that older specimens of *S. nitidus* and *S. inclinatus* (or other older species that lack a distinct P4 hypocone) have yet to be discovered.

Higher-level phylogenetic relationships of taxa traditionally shown to be members of the Sciuravidae (i.e., the three lineages previously described), were recently investigated by Porter (2001). Results of his analyses confirm that *Sciuravus*, *Knightomys*, and *Prolapsus* are basal members of the suborder Myomorpha, which includes the more advanced Myodonta (= Cricetidae and Dipodidae; Walton and Porter, 2008). A clade composed of the traditional sciuravids was shown to be paraphyletic, whereas the Genus *Sciuravus* was shown to be monophyletic and basal to *Knightomys*. Results of Porter's (2001) analyses revealed a lack of biogeographic signal at the family level (likely due to the wide geographic distribution of taxa) and were deemed inconclusive at the species level. Unfortunately, only three species of *Sciuravus* were considered by Porter (2001) to be complete enough to include in the analyses (*S. nitidus*, *S. powayensis*, *S. eucristadens*). Other

recent phylogenetic studies that include the "Sciuravidae" do not include *Sciuravus* as part of the analysis, instead using *Knightomys*, *Prolapsus*, and *Pauromys* (Marivaux et al., 2004, 2011, 2015). Outcomes of the current study include a review of distinguishing characters based on additional specimens for most species of *Sciuravus.* This makes it possible to include *Sciuravus sp.* in future phylogenetic analyses and will contribute to resolving the phylogeny of the *Sciuravus* lineage.

Among the currently known species of *Sciuravus*, *S. nitidus* exhibits the least derived sciuravid pattern for the zygomatic arch and relatively uncomplicated molar crown features. Thus, *S. nitidus* potentially represents the ancestral condition for this lineage. In other species, such as *S. wilsoni, S. metalinguas*, and *S. powayensis*, the zygomatic arch position is anterior to P4, the hypocone of P4 is well developed, and there is a well-developed hypocone arm on M1–2, all of which are derived conditions (Dawson and Beard, 1996; Marivaux, 2004). When all of the dental characters are codified, each species of *Sciuravus* discussed in this paper exhibits a mosaic of derived and ancestral characters. It is currently not clear if any of these species could be considered to represent a 'model' ancestral or derived morphology. These observations are based on a preliminary review of available character states for species discussed in this paper and need to be validated in subsequent analysis.

Another facet of sciuravid evolution revealed by this study is the significant overlap in species found in the basin margin with those of the basin center. This highlights the possibility that several species of *Sciuravus* potentially originated in one environment and migrated to another, later in time (Fig. 6). For at least three species (*S. popi*, *S. eucristadens*, *S. powayensis*), all of which have the longest fossil records, the migration appears to have been from a basin margin to a basin center environment. This potential period of speciation, at the Wasatchian/Bridgerian boundary, is consistent with other findings, which revealed an increase in the diversity of perissodactyls, artiodactyls, and other rodents during the same time period (Gunnell and Bartels, 1994), coincident with significant climatic change.

CONCLUSIONS

To summarize, The description of three new species of Green River Basin sciuravids adds to our knowledge of the Sciuravidae lineage in several ways. First, development of a P4 hypocone appears early in the fossil record of this group, first appearing in *S. wilsoni*, one of the oldest species known currently. Second, most of the differences between species are found in P4 morphology (differences in relative cuspule size and position, P4 hypocone development, nature of the anterior cingulum-metacone relationship) and the type of (or lack of) connection between the metacone and hypocone. Third, this study expands our knowledge of known species by documenting the upper dentition of *S. wilsoni* for the first time. Fourth, several species common to the basin margin and basin center first appear in the basin margin (*S. powayensis*, *S. eucristadens*, *S. popi*), highlighting the potential influence diverse ecological environments may have had on speciation.

The question of a North American vs. Asian origin for the sciuravids remains unresolved. Newly described species from the Bridger Formation are consistent with a North American diversification of *Sciuravus*. However, the discovery of advanced maxillary features in new specimens of *S. wilsoni* leaves open the possibility that some sciuravids evolved and diversified elsewhere and later migrated to North America. Even though the new species do not help to resolve questions about the origin of members of the genus *Sciuravus*, they do confirm that the early-middle Bridgerian was a time of high sciuravid species diversity. It appears that several species of *Sciuravus* evolved simultaneously, with subtle, but distinct differences in crest and cusp morphology, making it possible for them to successfully fill new niches during the Early Eocene Climatic Optimum.

The goal of this paper was to describe three new species of *Sciuravus,* which were discovered among the Bridger Basin material, and compare each one to contemporaneous species of *Sciuravus*. The results presented here can be used to conduct a more comprehensive phylogenetic analysis of the Sciuravidae lineage and to facilitate inclusion of *Sciuravus* species in future taxonomic investigations to help resolve details of early Eocene rodent relationships that are not presently apparent.

ACKNOWLEDGEMENTS

The author would like to thank P. D. Gingerich (UM), R. K. Stucky (DMNH), C. Norris and D. Brinkman (YPM), K. C. Beard (formerly from the CM), S. A. McLeod (LACM), for access to specimens. I am grateful to G. F. Gunnell who contributed immensely to the preparation of the manuscript. I thank the reviewers, G. F. Gunnell and L. Mariavaux, whose comments greatly improved the manuscript. I thank K. Flesch who conceived the specific epithet "*metalinguas*." I thank C. Abraczinskas for creating the map in Figure 1, and I thank B. Pirman who helped with figure editing.

LITERATURE CITED

ANDERSON, D. K. 2008. Ischyromyidae. In C. M. Janis, G. F. Gunnell, and M. D. Uhen (eds.), Evolution of Tertiary Mammals of North America: Vol. II, Cambridge University Press, New York, pp. 311–325.

BEARD, K. C. 1998. East of Eden: Asia as an important center of taxonomic origination in mammalian evolution. In C. K. Beard and M. Dawson (eds.), Dawn of the Age of Mammals in Asia, Bulletin of Carnegie Museum of Natural History, 34, pp. 5–39.

BOWDITCH, T. E. 1821. An Analysis of the Natural Classifications of Mammalia for the Use of Students and Travelers. J. Smith, Paris, 115 pp.

BURKE, J. J. 1937. A new *Sciuravus* from Utah. Annals of the Carnegie Museum, 27: 1–9.

COX, P. G., E. J. RAYFIELD, M. J. FAGAN, A. HERREL, T. C. PATAKY, and N. JEFFERY. 2012. Functional evolution of the feeding system in rodents. PLoS ONE, 7(4): e36299.

DAWSON, M. R. 1966. Additional late Eocene rodents (Mammalia) from the Uinta Basin, Utah. Annals of the Carnegie Museum, 38: 97–144.

———. 1968. Middle Eocene rodents (Mammalia) from northeastern Utah. Annals of the Carnegie Museum, 39: 327–370.

———. 1977. Late Eocene rodent radiations: North America, Europe and Asia. Géobios (Mémoire Spécial), 1: 195–209.

———. 2015. Emerging perspectives on some Paleocene sciurognaths rodents in Laurasia: the fossil record and its interpretation. In P. G. Cox and L. Hautier (eds.), Evolution of the Rodents, Advances in Phylogeny, Functional Morphology and Development, Cambridge University Press, United Kingdom, pp. 70–86.

DAWSON, M. R. and K. C. BEARD. 1996. New late Paleocene rodents (Mammalia) from the Eureka Sound Group of Ellesmere Island, Canada. Canadian Journal of Earth Sciences, 38: 1107–1116.

DAWSON, M. R., X. S. HUANG, C. K. LI, and B. Y. WANG. 2003. Zelomyidae, a new family of Rodentia (Mammalia) from the Eocene of Asia. Vertebrata PalAsiatica, 41: 249–270.

FIRMAT, C., I. LOZANO-FERNANDEZ, J. AGUSTI, G. H. BOLSTAD, G. CUENCA-BESCOS, T. F. HANSEN, and C. PELABON. 2014. Walk the line: 600000 years of molar evolution constrained by allometry in the fossil rodent *Mimomys savini*. Philosophical Transactions of the Royal Society B, 369: 20140057.

FLYNN, L., L. L. JACOBS, and I. U. CHEEMA. 1986. Baluchimyinae, a new ctenodactyloid rodent subfamily from the Miocene of Baluchistan. American Museum Novitates, 2841: 1–58.

GAZIN, C. L. 1961. New sciuravid rodents from the Lower Eocene Knight Formation of western Wyoming. Proceedings of the Biological Society of Washington, 74: 193–194.

GUNNELL, G. F. 1998. Mammalian fauna from the lower Bridger Formation (Bridger A, early Middle Eocene) of the southern Green River Basin, Wyoming. Contributions from the Museum of Paleontology, University of Michigan, 30: 83–130.

GUNNELL, G. F. and W. BARTELS. 1994. Early Bridgerian (middle Eocene) vertebrate paleontology and paleoecology of the southern Green River Basin Wyoming. Contributions to Geology, University of Wyoming, 30: 57−70.

GUNNELL, G. F., P. C. MURPHEY, R. K. STUCKY, K. E. B. TOWNSEND, P. ROBINSON, J.-P. ZONNEVELD, and W. BARTELS. 2009. Biostratigraphy and biochronology of the latest Wasatchian, Bridgerian, and Uintan North American Land Mammal "Ages". In Papers on Geology, Vertebrate Paleontology, and Biostratigraphy in Honor of Michael O. Woodburne, Museum of Northern Arizona Bulletin 65, Flagstaff, Arizona, pp. 279–330.

HUNTER, J. P. and J. JERNVAL. 1995. The hypocone as a key innovation in mammalian evolution. Proceedings of the National Academy of Sciences of the United States of America, 92: 10718–10722.

IVY, L. D. 1990. Systematics of late Paleocene and early Eocene Rodentia (Mammalia) from the Clark's Fork Basin, Wyoming. Contributions from the Museum of Paleontology, University of Michigan, 28: 21–71.

LINNAEUS, C. 1758. Systema Naturae, Tenth Edition (*Systema Naturae Per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, Cum Characteribus, Differentiis, Synonymis, Locis. Tomus I. Editio Decima, Reformata*). Laurentii Salvii, Holmiae (Stockholm), 824 pp.

MARIVAUX, L., ESSID, E. M., MARZOUGUI, W., HAYET, K. A., MERZERAUD, G., TABUCE, R. and M. VIANEY-LIAUD. 2015. The early evolutionary history of anomaluroid rodents in Africa: new dental remains of a zegdoumyid (Zegdoumyidae, Anomaluroidea) from the Eocene of Tunisia. Zoologica Scripta, 44: 117–134.

MARIVAUX, L., ADACI, M., BENSALAH, M., GOMES RODRIGUES, H., HAUTIER, L., MAHBOUBI, M., MEBROUCK, F., TABUCE, R., and M. VIANEY-LIAUD. 2011. Zegdoumyidae (Rodentia, Mammalia) from the early to middle Eocene of Algeria (Gour Lazib, Western Sahara): new dental evidence. Journal of Systematic Palaeontology, 9: 563–588.

MARIVAUX, L., M. VIANEY-LIAUD, and J.-J. JAEGER. 2004. High-level phylogeny of early Tertiary rodents: dental evidence. Zoological Journal of the Linnean Society, 142: 105–134.

MARSH, O. C. 1871. Notice of some new fossil mammals and birds from the Tertiary formations of the West. American Journal of Science, 2: 120–127.

MIHLBACHLER, M. C. 2008. Species taxonomy, phylogeny, and biogeography of the Brontotheriidae (Mammalia; Perissodactyla). Bulletin of the American Museum of Natural History, 311: 1–475.

OLIVER, A. and P. PELÁEZ-CAMPOMANES. 2014. Early Miocene evolution of the rodent *Megacricetodon* in Europe and its palaeobiogeographical implications. Acta Palaeontologica Polonica, 61: 211–219.

PETERSON, O. A. 1919. Material discovered in the Uinta Basin. Annals of the Carnegie Museum, 12: 63–66.

PORTER, R. M. 2001. A cladistic analysis of the Sciuravidae (Mammalia; Rodentia) and implications for rodent phylogeny. Senior Thesis, Amherst College, Amherst, 93 pp.

RASMUSSEN, D. T., G. C. CONROY, A. R. FRISCIA, K. E. TOWNSEND, and M. D. KINKEL. 1999. Mammals of the middle Eocene Uinta Formation. In D. D. Gillette

(ed.), Vertebrate Paleontology in Utah, Utah Geological Survey Miscellaneous Publications, 99-1: 401–420.

REIG, O. A. 1977. A proposed unified nomenclature for the enamelled components of the molar teeth of the Cricetidae (Rodentia). Journal of Zoology, London, 181: 227–241.

ROSE, K. 2006. The Beginning of the Age of Mammals. John Hopkins University Press, Baltimore, MD, 428 pp.

WALTON, A. H. and R. M. PORTER. 2008. Sciuravidae. In C. M. Janis, G. F. Gunnell, and M. D. Uhen, (eds.), Evolution of Tertiary Mammals of North America: Vol. II, Cambridge University Press, New York, pp. 336–354.

WANG, B.-Y. and M. R. DAWSON. 1994. A primitive cricetid (Mammalia; Rodentia) from the middle Eocene of Jiangsu Province, China. Annals of the Carnegie Museum, 63: 239–256.

WILSON, R. W. 1938. Review of some rodent genera from the Bridger Eocene. Part II. American Journal of Science, 35: 207–222.

———. 1949. Early Tertiary rodents of North America. Carnegie Institute, Washington Publication, 584: 67–164.

WOOD, A. E. 1955. A revised classification of the rodents. Journal of Mammalogy, 36: 165–187.

———. 1959. Rodentia. In P. O. McGrew (ed.), The Geology and Paleontology of the Elk Mountain and Tabernacle Butte Area, Wyoming. Bulletin of American Museum of Natural History, 117, pp. 157–169.

———. 1962. The early Tertiary rodents of the family Paramyidae. Transactions of the American Philosophical Society, 52: 1–261.

WOOD, A. E. and R. W. WILSON. 1936. A suggested nomenclature for the cusps of the cheek teeth of rodents. Journal of Paleontology, 10: 388–391.

WOODBURNE, M. O., G. F. GUNNELL, and R. K. STUCKY. 2009a. Climate directly influences Eocene mammal faunal dynamics in North America. Proceedings of the National Academy of Sciences, 106: 13399–13403.

———, ———, and ———. 2009b. Land mammal faunas of North America: Rise and fall during the Early Eocene Climatic Optimum. Denver Museum of Nature and Science Annals 1: 1–80.

Museum of Paleontology, The University of Michigan
1109 Geddes Avenue, Ann Arbor, Michigan 48109-1079
Daniel C. Fisher, Director

Contributions from the Museum of Paleontology, University of Michigan is a medium for publication of reports based chiefly on museum collections and field research sponsored by the museum. When the number of issued pages is sufficient to make a volume, a title page plus table of contents will be sent to libraries on the Museum's mailing list (and to individuals on request). Separate issues may be obtained from the Publications Secretary (paleopubs@umich.edu). Jeffrey A. Wilson, Editor.

Publications of the Museum of Paleontology are accessible online at: http://deepblue.lib.umich.edu/handle/2027.42/41251

ISSN 0097-3556