

New material of *Lophiparamys debequensis* from the Willwood Formation (early Eocene) of Wyoming, including the first postcrania of the genus

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Non-technical Summary.—We describe new material of a small early rodent, *Lophiparamys*. The material includes the first ankle bones of *Lophiparamys* and indicates that it spent more time climbing than other early rodents. The new material is also the first record of its species, *Lophiparamys debequensis*, from north-central Wyoming. It helps to clarify how *L. debequensis* differs from other species of *Lophiparamys*. A phylogenetic analysis of the relationships of *Lophiparamys* does not confidently show what other rodents it was related to, but it may have been related to living dormice.

Abstract.—We report new material of the rare early Eocene rodent *Lophiparamys debequensis* Wood, 1962 from the Willwood Formation of the southern Bighorn Basin, north-central Wyoming. The new material constitutes the first record of *L. debequensis* from the Bighorn Basin and documents aspects of the anatomy of *Lophiparamys* that were previously unknown, including a portion of the maxilla and a portion of the tarsus. The maxillary fragment demonstrates that *Lophiparamys* has a small P3 and a relatively large infraorbital canal. The tarsus of *Lophiparamys* is similar to that of other early rodents but differs in a few features that suggest an arboreal locomotor repertoire, including an asymmetric astragalar trochlea, long astragalar neck, transverse astragalar sustentacular facet, short calcaneal tuber, elongate calcaneal ectal facet, and circular calcaneal cuboid facet. The presence of arboreally adapted features in the tarsus of *Lophiparamys* is consistent with a hypothesized relationship between small-bodied Eocene microparamyine rodents and extant Gliridae. Phylogenetic analysis fails to consistently support this relationship or monophyly of Microparamyinae, but both remain plausible. Comparison of *L. debequensis* with other species of the genus emphasizes the distinctiveness of *L. debequensis* and suggests the presence of multiple lineages of *Lophiparamys*.

Introduction

Rodents constitute the most diverse extant clade of mammals and span an impressive range of habitat and locomotor preferences, including highly arboreal forms that may show gliding or prehensile adaptations, terrestrial cursors, obligate burrowers, semiaquatic forms, and numerous intermediates (Nowak, 1999). While the dense rodent fossil record serves as an important focus of systematic, functional, and biostratigraphic investigations (e.g., Luckett and Hartenberger, 1985), the rodent postcranial record is poorly documented compared with the dentognathic record. As a result, our understanding of rodent postcranial evolution is comparatively poor. This includes our understanding of initial stages of rodent locomotor diversification. While the locomotor adaptations of some of the earliest rodents are relatively well documented (e.g., Rose and Chinnery, 2004), there are numerous gaps, with the postcranial morphology of

many higher-level taxa remaining poorly documented or undocumented.

The earliest rodents are known from the late Paleocene and early Eocene of North America, Asia, and Europe (Jepsen, 1937; Wood, 1962; Rose, 1981; Ivy, 1990; Meng et al., 1994; Dawson and Beard, 1996; Lopatin and Averianov, 2004a, b; Smith et al., 2014). Paleocene records are limited and dominated by dentognathic remains, with the exception of undescribed associated partial skeletons from a limestone nodule from the Clarks Fork Basin, Wyoming, illustrated by Bloch and Boyer (2001) and cruropedal material referred to the stem rodent *Tribosphenomys minutus* Meng et al., 1994 by Meng and Wyss (2001) (see also Fostowicz-Freluk et al., 2018).

The early Eocene rodent record is much more substantial and includes considerable postcranial material. Rose and Chinnery (2004) reviewed North American early Eocene (Wasatchian) rodent postcrania, describing substantial new material primarily from the Willwood Formation in the Bighorn Basin, Wyoming. Aside from a single distal tibia referred by Rose and Chinnery (2004) to the sciuravid *Knightomys* Gazin, 1961, known Wasatchian rodent postcrania pertain to larger

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representatives of the family Paramyidae, primarily *Paramys* Leidy, 1871 but including *Franimys* Wood, 1962, *Notoparamys* Korth, 1984, and *Thisbemys* Wood in McGrew, 1959 (see also Rose and Von Koenigswald, 2007). The morphology of Wasatchian paramyids indicates generalized locomotor habits, combining features associated with arboreality and terrestriality in extant rodents. Outside North America, published postcrania of early Eocene rodents are limited to tarsals referable to the ctenodactyloid *Tamquammys* Shevyreva, 1971 from Nei Mongol, China (Fostowicz-Frelik et al., 2018). These indicate a generalized terrestrial habitus for the genus, lacking the arboreal adaptations present in paramyids (Fostowicz-Frelik et al., 2018). These records give some sense of the range of postcranial adaptations in early Eocene rodents, but the postcranial morphology of several groups of early Eocene rodents remains undocumented.

One of the latter groups of early rodents is Microparamyinae, comprising small-bodied early to late Eocene rodents known from North America and Europe (Wood, 1962; Escarguel, 1999; Dawson, 2001). Named by Wood (1962) as a subfamily of Paramyidae, Microparamyinae (or Microparamyini) has variously been considered a distinct assemblage of early rodents within Ischyromyidae, Paramyidae, or Reithroparamyidae (Michaux, 1968; Wilson, 1986; Korth, 1994; McKenna and Bell, 1997; Escarguel, 1999; Dawson, 2001, 2006) or subsumed within Reithroparamyidae (or Reithroparamyinae) (Black, 1971; Korth, 1984). Dawson (2001) marshalled evidence in favor of recognition of Microparamyinae as monophyletic with respect to other early rodents and provided a provisional diagnosis based on potentially derived characteristics of the dentition that distinguish microparamyines. Members of Microparamyinae play a potentially important role in rodent evolution. Dental morphology of European taxa that have been referred to Microparamyinae (*Hartenbergeromys* Escarguel, 1999, *Pantrogna* Hartenberger, 1971, *Sparnacomy* Hartenberger, 1971) has been considered indicative of a potential ancestry of extant dormice (Gliridae) (Hartenberger, 1971). However, the presence of an enlarged infraorbital canal in the European taxa conflicts with a postulated link to Gliridae (Hooker, 2010) and instead suggests a link to the endemic European Paleogene clade Theridomorpha (Vianey-Liaud and Marivaux, 2017, 2021; Vianey-Liaud et al., 2019). Recent studies have removed the European taxa from Microparamyinae altogether, assigning them to a basal position within the theridomorph radiation (Vianey-Liaud and Marivaux, 2017, 2021). However, Vianey-Liaud and Marivaux (2021) recovered *Microparamys sambucus* Emry and Korth, 1989 in a clade containing *Acritoparamys* Korth, 1984 and Gliridae, represented by *Eogliravus* Hartenberger, 1971, indicating that there remains a potentially close relationship between microparamyines and glirids.

With the removal of the European genera mentioned in the preceding, Microparamyinae comprises the North American genera *Churcheia* Storer, 2002, *Lophiparamys* Wood, 1962, *Microparamys* Wood in McGrew, 1959, and *Strathcona* Dawson, 2001, with *Mattimys* Korth, 1984 also potentially related (Wood, 1962; Dawson, 2001). Dawson (2001, p. 1112, 1114) identified six potential synapomorphies of Microparamyinae, including a strong anterolophid well separated from the protoconid, mesiodistally compressed trigonids (reflecting loss of

metalophid I), elongate postmetacristid, presence of an entolophid, rounded mesoconid, and a protocone positioned at a mesiodistal level between the paracone and metacone. However, Dawson's concept of Microparamyinae included *Pantrogna* and *Sparnacomy*. No diagnosis based on shared derived characters has been proposed for the more restricted grouping described in the preceding. This raises the possibility that Microparamyinae may not be a natural group.

Among microparamyines, *Lophiparamys*, the subject of the present contribution, is characterized by a distinctive profusion of accessory crests on the cheek teeth. *Lophiparamys* was named by Wood (1962) for *Paramys murinus* Matthew, 1918, erected on the basis of a pair of dentaries with the lower incisor and a complete cheek tooth series from the middle Wasatchian (Graybullian) of the Willwood Formation, Bighorn Basin, Wyoming. Wood (1962) also named a second, younger species, *Lophiparamys debequensis* Wood, 1962, for two isolated teeth from Lysitean (early late Wasatchian) levels in the DeBeque Formation of the Piceance Basin of northern Colorado. A third species, *Lophiparamys woodi* Guthrie, 1971, was subsequently named for isolated cheek teeth from the Lost Cabin Member of the Wind River Formation in the Wind River Basin of central Wyoming (Lostcabinian, latest late Wasatchian) (Guthrie, 1971). *Lophiparamys* is known from dentaries and isolated teeth together documenting the incisors and the upper and lower cheek dentition excluding P3 (Wood, 1962, 1965; Guthrie, 1967, 1971; Flanagan, 1986; Ivy, 1990; Strait et al., 2016). To date, nothing has been reported of the skull or postcranium.

We report here on new material of *Lophiparamys* from the Willwood Formation that meaningfully increases our knowledge of the genus, documenting the first postcranial material of a microparamyine. The material constitutes the first record of *L. debequensis* from the Bighorn Basin and provides insights into the ecology of Microparamyinae, with implications for the phylogenetic relationships of the group within Rodentia.

To date, the higher-level affinities of microparamyines among rodents have received only limited testing in a modern, rigorous phylogenetic context, and the affinities of *Lophiparamys* have never been rigorously tested. As noted, Vianey-Liaud and Marivaux (2021) included *Microparamys sambucus* in their phylogenetic analysis of theridomorph phylogeny, recovering *Microparamys* in a clade with *Acritoparamys* and the basal glirid *Eogliravus*. While Vianey-Liaud and Marivaux's (2021) analysis provides potential illumination of the affinities of microparamyines, its taxonomic sample is heavily skewed toward members of Theridomorpha, with limited, incomplete representation from other groups, constraining the potential positions in which *Microparamys* could be recovered. To remedy this and more fully explore the phylogenetic position of Microparamyinae within Rodentia, *Lophiparamys debequensis* and two species of *Microparamys*, *M. hunterae* Ivy, 1990 and *M. sambucus*, were added to the character–taxon matrix published by Marivaux et al. (2004). The latter matrix more comprehensively samples the diversity of early rodents than does Vianey-Liaud and Marivaux (2021) and includes early members of all major extant clades. The analysis is not intended to test microparamyine interrelationships, which will require, at a minimum, a revision of the speciose genus *Microparamys*, which is beyond the scope of this work.

Materials and methods

Dental terminology follows Vianey-Liaud and Marivaux et al. (2021), but character state descriptions from Marivaux et al. (2004), who use a slightly different terminology, have not been modified. Tarsal terminology follows Penkrot and Zack (2016) and Zack and Penkrot (2019)

Elements of USNM 527685 were imaged via computed tomography on a Nikon XTH 225 ST instrument at the Duke University Shared Materials Instrumentation Facility (SMIF). Material was scanned at a voxel size of 4.35 μ . Scanned specimens were modeled using Slicer 4.10.2, and models were subsequently manipulated in Mesh-Lab 2021.05.

Body masses of *L. debequensis* and *L. murinus* (Matthew, 1918) were estimated using the all-rodent equations of Freudenthal and Martín-Suárez (2013). For *L. debequensis*, tooth row lengths were calculated by first averaging the lengths of teeth representing the same locus and then summing the lengths of P4–M3 and p4–m3. For *L. murinus*, the length of the lower cheek tooth row was taken from Matthew (1918).

As noted, *Lophiparamys* and *Microparamys* were added to the character–taxon matrix published by Marivaux et al. (2004). To minimize assumptions of monophyly, particularly for the diverse, long-ranging *Microparamys*, both genera were represented by species rather than composite taxa. *Lophiparamys* was scored from *L. debequensis* on the basis of the material described in the following and Flanagan (1986). *Microparamys* was scored for two well-illustrated species, Wasatchian *M. hunterae* (Ivy, 1990; Strait et al., 2016) and Bridgerian *M. sambucus* (Emry and Korth, 1989). Inclusion of other microparamyine genera (*Strathcona* and *Mattimys*) was considered, but available descriptions and illustrations were not adequate to score most characters with confidence. The only additional change made to the matrix was scoring *Pantrogna* for character 1, describing the development of the infraorbital foramen, based on Vianey-Liaud et al. (2019). The matrix is available in TnT format as Supplementary Data Set 1, and the matrix and character list are available as Supplementary Data Set 2. The character list and matrix are also accessible on MorphoBank as project P4513 (<http://dx.doi.org/10.7934/P4513>).

Although the analysis by Marivaux et al. (2004) recovered a topology that is largely compatible with molecular estimates of rodent phylogeny (e.g., Huchon et al., 2002; Adkins et al., 2003; Montgelard et al., 2008; Asher et al., 2019), it differs in one respect, placing Gliridae closer to rats and mice and their relatives (Myomorpha) than to sciurids and apodontids (Sciuromorpha) (higher-level clades used sensu Asher et al., 2019). To test the potential impact of this discrepancy, the matrix was run both unconstrained and with a scaffold constraint enforcing monophyly of the three extant rodent suborders, Sciuromorpha, Myomorpha, and Ctenohystrica. Taxa constrained to membership in Sciuromorpha were *Bransatoglis* Hugueneay, 1967, *Glamys* Vianey-Liaud, 1989, *Palaeosciurus* Pomel, 1853, *Plesispermophilus* Filhol, 1883, *Prosciurus* Matthew, 1903, and *Protosciurus* Black, 1963. *Atavocricetodon* Freudenthal, 1996, *Eomys* Schlosser, 1884, *Nementchamys* Jaeger et al., 1985, *Pappocricetodon* Tong, 1992, *Primismithus* Tong, 1997, *Pseudocricetodon* Thaler, 1969, and *Sinosminthus*

Wang, 1985 were constrained to membership in Myomorpha, while *Branisamys* Hoffstetter and Lavocat, 1970, *Diatomys* Li, 1974, *Incamys* Hoffstetter and Lavocat, 1970, *Paraulacodus* Hinton, 1933, *Platypittamys* Wood, 1949, *Sallamys* Hoffstetter and Lavocat, 1970, and *Tataromys* Matthew and Granger, 1923 were constrained to membership in Ctenohystrica. Remaining ingroup taxa were not included in the constraint definition. While *Tataromys* is generally considered a stem ctenodactylid, Asher et al. (2019) recovered the genus outside crown Rodentia. Accordingly, the constraint was run with and without *Tataromys* included in the constraint definition.

Following Marivaux et al. (2004), the matrix was analyzed with all characters except 21 and 87 ordered. The matrix was analyzed in TnT version 1.5 (Goloboff and Catalano, 2016). The Sectorial Search algorithm under the New Technology search dialog was used, with the analysis continuing until shortest length trees had been recovered in 100 replicates beginning with a different starting tree. Retained trees were submitted to the Traditional Search algorithm for branch swapping to ensure that all shortest trees were identified. Decay indices were calculated by retaining successively less-parsimonious trees. Shortest trees were exported to WinClada version 1.00.08 (Nixon, 2002) to calculate tree statistics and examine character distributions.

Repositories and institutional abbreviations.—Specimens examined in this study are deposited in the following institutions: Pratt Museum of Amherst College (ACM), Cambridge, Massachusetts, USA; Carnegie Museum of Natural History (CM), Pittsburgh, Pennsylvania, USA; University of Arizona Laboratory of Paleontology (UALP), now in the collections of the New Mexico Museum of Natural History, Albuquerque, New Mexico, USA; National Museum of Natural History, Department of Paleobiology (USNM), Washington, D.C., USA.

Systematic paleontology

Mammalia Linnaeus, 1758

Eutheria Huxley, 1880

Rodentia Bowdich, 1821

Paramyidae Miller and Gidley, 1918

Microparamyinae Wood, 1962

Lophiparamys Wood, 1962

Type species.—*Paramys murinus* Matthew, 1918, designated by Wood (1962).

Other species.—*L. murinus* (Matthew, 1918), *L. debequensis* Wood, 1962, and *L. woodi* Guthrie, 1971.

Diagnosis (modified from Anderson, 2008).—Very small paramyids; cusps of upper molars difficult to distinguish among crests; slender mandible, anterior end of masseteric fossa inferior to m2; extensive crenulations of cheek teeth, numerous accessory ridges and crestlets; anterocingulid distinct from protoconid, the latter quite reduced in p4 as in *Franimys*; distinct postmetacristid; trigonid basin very reduced anteroposteriorly, filled in part with a mesially positioned

lingual metalophid I; postprotocristid (buccal part of metalophid II) curved in center.

Differential diagnosis.—Differs from *Churcheria* in presence of accessory cusps and crests on cheek teeth; mesostyles smaller on P4–M3; P4 less molarized, with a smaller metacone and poorly developed hypocone; short mesolophids on m1–3. Differs from *Mattimys* in denser, more elongate accessory cusps; weaker postmetacristids on p4–m3; p4 metaconid larger relative to paraconid; m1–3 trigonids mesiodistally compressed; m1–3 anterolophids less distinct lingually; short mesolophids on m1–3. Differs from *Microparamys* in presence of accessory cusps and crests on cheek teeth; P4 less molarized, with a smaller metacone and poorly developed hypocone; p4 metaconid larger relative to paraconid; p4 talonid smaller relative to trigonid; lower molars with lingual metalophid I projecting into the trigonid basin. Differs from *Strathcona* in presence of accessory cusps and crests on cheek teeth; M1–2 with uninflated conules; m1–3 anterolophids more lingually extensive; m1–2 talonids narrower, subequal to trigonid widths.

Remarks.—The diagnosis given by Anderson (2008) is largely retained, aside from adjustments in terminology to agree with the terminology used by Vianey-Liaud and Marivaux (2021). One characteristic, “entoconid distinctly separate from posterolophid” is removed from the generic diagnosis as this feature does not characterize *L. debequensis*. To aid in distinguishing *Lophiparamys* from other microparamyines, a differential diagnosis has been added.

Lophiparamys debequensis Wood, 1962
Figures 1–4; Tables 1, 2

1962 *Lophiparamys debequensis* Wood, p. 169, fig. 55d.

Holotype.—Isolated left m1 (CM 1217) from the DeBeque Formation, Piceance Creek Basin, Rio Blanco County, Colorado (Wood, 1962, fig. 56d).

Diagnosis.—Smallest species of *Lophiparamys*. Differs from both *L. murinus* and *L. woodi* in continuous posterolophid on lower teeth, without a cleft separating the entoconid from the hypoconulid; larger hypocones on M1–2, giving these teeth a more quadrate shape; lower, less dense crenulations on cheek teeth. Further differs from *L. murinus* in features unknown in *L. woodi*: more massive metaconid on p4; shorter p4 talonid; smaller metacone on P4; minute mesostyle on P4–M2.

Occurrence.—Previously reported material comes from the early late Wasatchian (Wa6) of the DeBeque Formation of the Piceance Basin of northern Colorado (Wood, 1962), the Lysite Member of the Wind River Formation in the Wind River Basin of central Wyoming (Wood, 1965; Guthrie, 1967), and the Regina Member of the San Jose Formation in the San Juan Basin of northwestern New Mexico (Flanagan, 1986).

Newly referred material is from United States Geological Survey locality D-1830, Willwood Formation, Bighorn Basin, Big Horn County, Wyoming (see Bown et al., 1994 for details). D-1830 is at the 501-meter level in the Willwood section in the

southern Bighorn Basin (Bown et al., 1994), which Chew (2005) places within the Wa6 biochron of the Wasatchian North American Land Mammal Age, consistent with other material referred to *L. debequensis*.

Description.—Flanagan (1986) has provided an extensive description of the dental morphology of *Lophiparamys debequensis*, which will not be repeated here. Instead, the present description will describe the maxilla and tarsals of *L. debequensis* and note where the dentition of USNM 527685 differs from the descriptions and illustrations provided by Flanagan (1986).

Maxilla.—USNM 527685 includes a maxillary fragment with P4, the first cranial material known for the genus (Fig. 1). Directly anterior to P4, the fragment preserves a portion of a relatively large P3 alveolus (Fig. 1.1). The preserved portion of the P3 alveolus is 0.69 mm in maximum width, and the diameter of the complete alveolus would have been at least slightly greater. Dorsal to the tooth row, the ventromedial margin of the infraorbital canal is preserved (Fig. 1.2). The canal is relatively low on the rostrum, and the preserved portion indicates a minimum transverse diameter of 1.38 mm, similar in diameter to the 1.47 mm width of P4. The foramen is comparatively large, relatively larger than in *Franimys*, *Notoparamys*, *Paramys*, *Pseudotomus* Cope, 1872, *Quadratimus* Korth, 1984, or *Reithroparamys* Matthew, 1920 as documented by Wood (1962) and Korth (1994).

Upper dentition.—On P4 (Fig. 2.1–2.3), the buccal metalophule is more continuous between the metaconule and metacone than in the San Juan Basin material, where it is broken up into a series of isolated cusps. The loph described by Flanagan (1986, p. 201) as “an arm of the paracone ... directed lingually into the [trigon] basin” is present in USNM 527685, but it is not connected to the paracone. Instead, it extends mesiobuccally from the metaconule, forming a partial buccal mesoloph. Lingually, there is less of a furrow between the protocone and hypocone in USNM 527685.

M1 and M2 of USNM 527685 (Fig. 2.4–2.11) are very similar to the San Juan Basin material, differing primarily in having a more conical hypocone with a lower endoloph connecting the hypocone to the protocone. This is the opposite condition from P4, with the Wyoming material having a less distinct P4 hypocone and more distinct hypocones on M1–2. On both M3s of USNM 527685 (Fig. 2.12–2.14), the lingual protoloph overlaps the buccal protoloph mesially, failing to form a complete protoloph between the protocone and paracone. This contrasts with the specimen illustrated by Flanagan (1986), although it is implied that not all specimens in the San Juan Basin sample have a complete protoloph. Otherwise, the morphology of M3 in USNM 527685 is nearly identical to the New Mexican material.

Lower dentition.—On the lower dentition, p4 of USNM 527685 (Fig. 3.1–3.3) differs notably from UALP 15766, the tooth illustrated by Flanagan (1986, fig. 2e) as p4 of *L. debequensis*. The San Juan specimen has a distinctly shorter, broader trigonid. In USNM 527685, the trigonid is much taller than the talonid, similar in length, and only slightly narrower. In the San Juan specimen, the trigonid is lower (but still taller than the talonid), much shorter mesiodistally than the talonid, and substantially narrower. The trigonid of USNM 527685 further differs

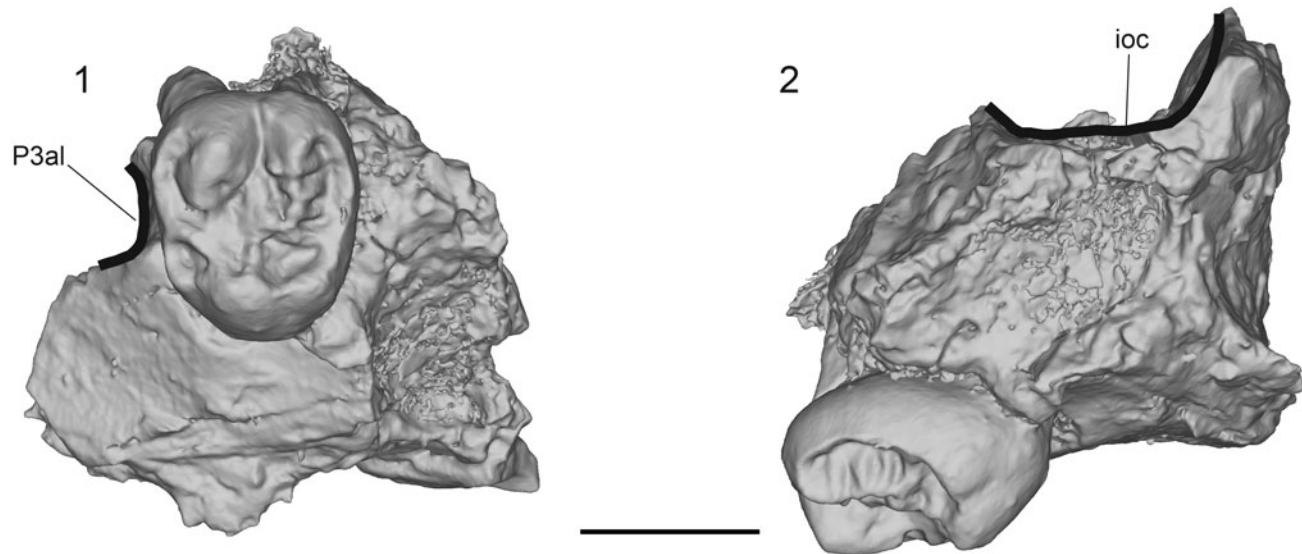


Figure 1. Left maxillary fragment of USNM 527685, *Lophiparamys debequensis*: (1) ventral and slightly lateral view; (2) posteroventral view. ioc = infraorbital canal; P3al = alveolus for P3. Scale bar = 1 mm.

in having a more massive metaconid and in lacking metalophid II. The talonid has a much smaller, shorter basin, lacks an incipient entolophid, and has a lingually concave posterolophid, contrasting with a convex lophid in the San Juan Basin specimen. While some of the differences in lophid development may represent individual variation, the proportions of the trigonid and talonid are very distinct. The proportions of UALP 15766 (Flanagan, 1986, fig. 2e) recall the morphology of dp4 in many placentals, and the form of the tooth closely resembles dp4 of *Paramys adamus* Dawson and Beard, 1996 illustrated by Dawson and Beard (1996). Accordingly, UALP 15766 is re-identified as dp4 of *Lophiparamys debequensis*, making the p4 of USNM 527685 the first definitive p4 of *L. debequensis*.

The morphology of m1 and m2 of USNM 527685 (Fig. 3.4–3.11) is similar to the San Juan Basin material, but the two left lower molars of the Wyoming specimen have stronger, more lingually extensive mesolophids than in either illustrated San Juan Basin tooth. None of the Wyoming m1s or m2s has an entolophid as well developed as in the two New Mexican teeth illustrated by Flanagan (1986). In both of these specimens, the lophid is nearly complete except for a notch near mid-width, while the entolophid is restricted to the lingual half of the talonid basin in the Wyoming teeth. The m3s of USNM 527685 (Fig. 3.12–3.14) also closely match the morphology of the San Juan Basin specimens but differ from the specimen illustrated by Flanagan (1986) in having a weak but continuous lophid closing the buccal margin of the talonid. In the San Juan specimen, the ectolophid and mesial arm of the hypoconid both fail to contact the mesoconid.

Astragalus.—On the astragalus of USNM 527685 (Fig. 4.1–4.6), the tibial facet on the astragal body is strongly convex and distinctly grooved, dividing the facet into a broad lateral and narrow medial portion. In addition to being wider, the lateral side of the tibial facet is also distinctly longer than the medial side. The lateral side of the tibial facet is gently convex while the medial side is flat. The facet ends abruptly medially and laterally as sharp rims where it meets the medial tibial

facet and fibular facet, respectively. The tibial facet extends to the proximal margin of the astragal body, where it is continuous with the weakly defined groove for m. flexor digitorum lateralis. There is no astragal foramen.

On the lateral surface of the astragal body, the fibular facet is oriented directly laterally. The facet is relatively shallow, forming a thin strip proximally and deepening distally. The presence of a dorsally oriented lateral process at the distolateral corner of the astragal body creates a shallow concavity at the distal end of the fibular facet. The fossa between the fibular and ectal facets is weakly defined and positioned on the proximal half of the lateral surface of the astragal body.

The astragal body medial to the fibular facet is nearly vertical, with only a slight dorsal orientation. A wedge-shaped medial tibial facet occupies much of this surface. Ventral to this facet, the poorly defined proximomedial plantar tuberosity forms a ventromedially directed swelling at the proximal end of the astragal body. At the distomedial corner of the astragal body, there is a narrow, proximodorsally oriented shelf, potentially a weak cotylar fossa.

On the ventral surface of the astragal body, the ectal facet is relatively broad, particularly at its proximal margin. The facet is oriented ventrally with a small lateral component, but a strip along the medial margin is oriented medially. The long axis of the ectal facet runs proximally and somewhat medially to distally and somewhat laterally, resulting in a lateral overhang of the distal margin and producing the lateral process noted in the preceding.

The sustentacular facet is oriented ventrally. Proximally, a narrow strip of the sustentacular facet extends onto the proximomedial plantar tuberosity, facing distally. The main portion of the facet is weakly but uniformly concave and somewhat expanded transversely, particular toward the distolateral margin, giving the facet a triangular rather than circular appearance and occupying the full width of the neck. The sustentacular facet is isolated medially and distally from the navicular and medial tarsal facets by a shallow depression.

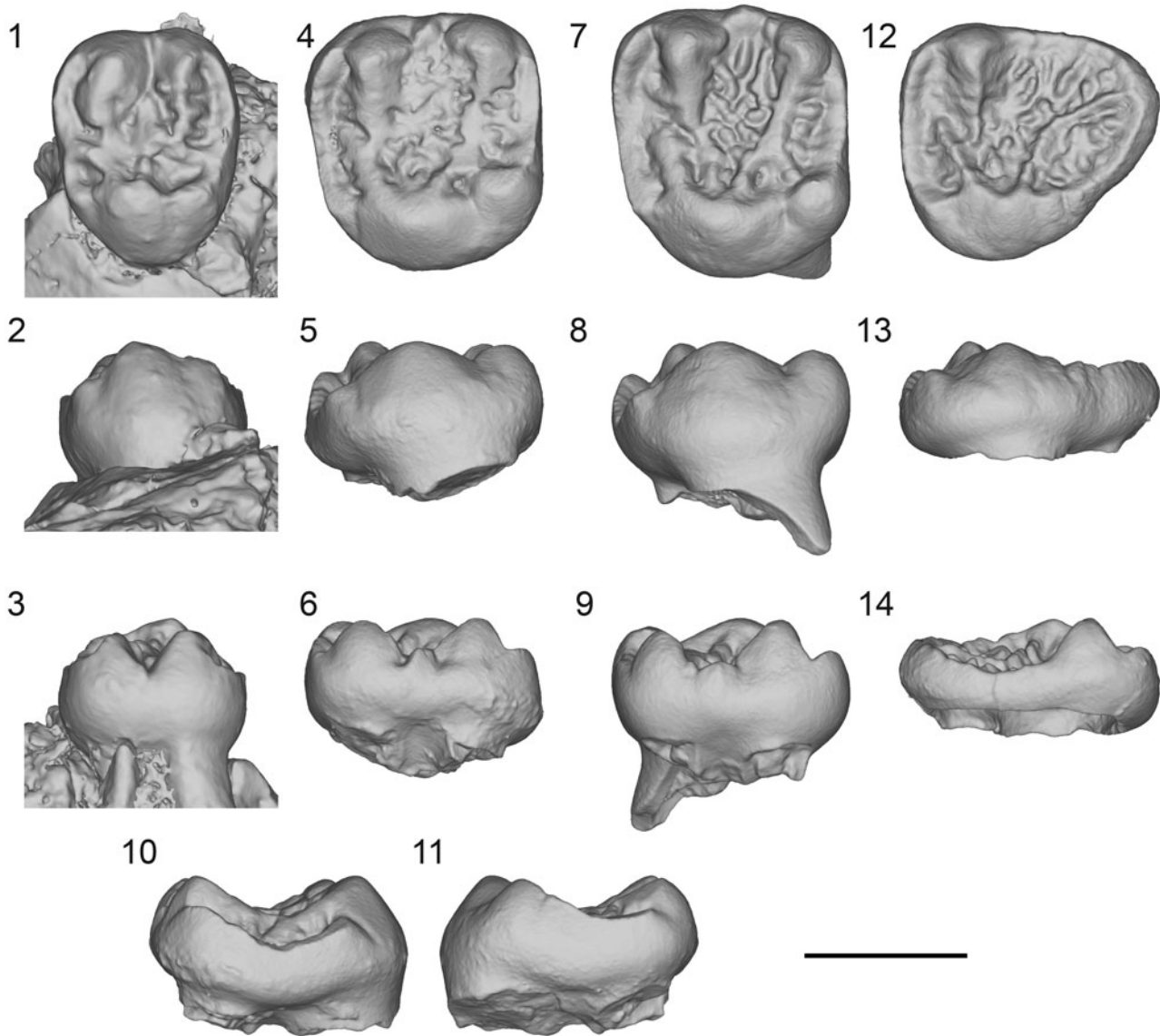


Figure 2. Upper cheek teeth of *Lophiparamys debequensis*: (1, 4, 7, 12) occlusal view; (2, 5, 8, 13) lingual view; (3, 6, 9, 14) buccal view; (10) mesial view; (11) distal view. (1–3) USNM 527685a, left P4. (4–6) USNM 527685b, left M1. (7–11) USNM 527685c, right M2 (reversed). (12–14) USNM 527685e, right M3 (reversed). Scale bar = 1 mm.

The astragalar neck is distinct and moderately elongated, such that the astragalus distal to the body is only slightly shorter than the body itself. The neck projects distomedially, and only the lateral half of the astragalar head overlaps the body transversely. On the astragalar head, the navicular facet is uniformly convex and wider than long. The long axis of the facet is slightly oblique dorsolaterally. At its lateral margin, the navicular facet overhangs the astragalar neck. The facet for the medial tarsal is continuous with the navicular facet and extends proximally along the astragalar neck. The facet ends abruptly at its proximal margin, with the astragalar neck abruptly narrowing at this level.

Calcaneus.—On the calcaneus of USNM 527685 (Fig. 4.7–4.12), the calcaneal tuber is short, approximately half the length of the body. As is typical of early rodents, the dorsal margin of the tuber is concave, with the proximal margin overhanging the remainder of the tuber. The endplate of the

tuber is oval in proximal view and concave, with a raised U-shaped rim that opens dorsally. The medial rim is more proximally projecting than the lateral margin. The rim continues onto the ventral surface of the tuber as a smooth, ventrally and slightly proximally oriented surface that tapers onto the medial and lateral surfaces of the tuber. More dorsally on the lateral surface, there is a raised, U-shaped facet, continuous with and slightly distal to the endplate.

More distally, the ectal facet is smoothly convex, curving from a medial orientation proximally to a distal orientation distally. The medially and distally facing portions are approximately equal in length. While the primary orientation of the ectal facet is distomedial, there is a modest dorsal inclination. In medial view, the facet can be seen to narrow slightly near its midpoint. Lateral to the ectal facet, a fibular facet is lacking, as is typical of rodents.

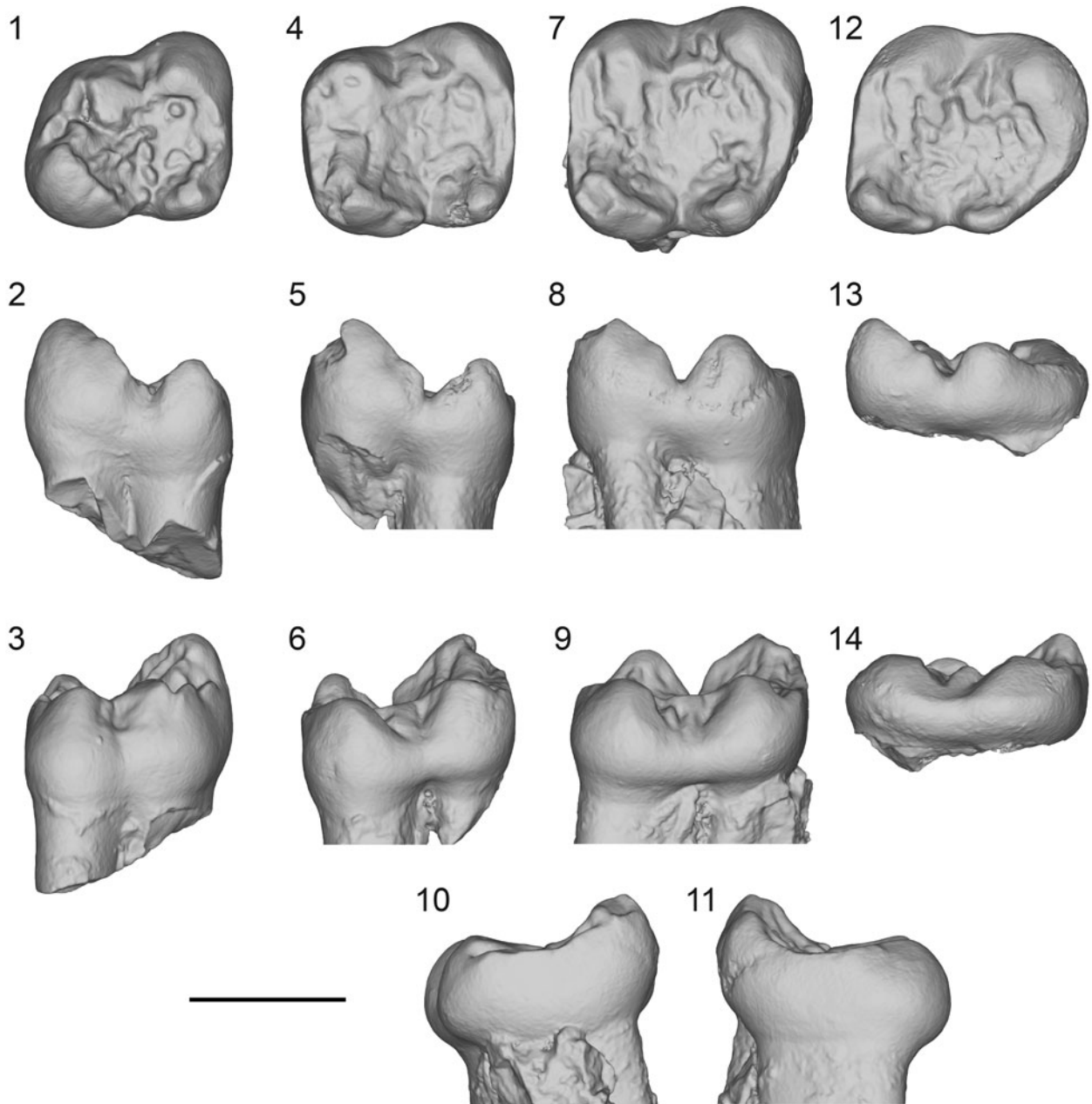


Figure 3. Lower cheek teeth of *Lophiparamys debequensis*: (1, 4, 7, 12) occlusal view; (2, 5, 8, 13) lingual view; (3, 6, 9, 14) buccal view; (10) mesial view; (11) distal view. (1–3) USNM 527685f, right p4. (4–6) USNM 527685h, right m1. (7–11), USNM 527685j, right m2. (12–14) USNM 527685k, left m3 (reversed). Scale bar = 1 mm.

On the medial side of the calcaneus, there is a small proximodistal overlap between ectal and sustentacular facets, but the latter is largely distal to the former. Both the sustentaculum and the sustentacular facet are relatively large and circular. The sustentacular facet is oriented dorsally and slightly distally. The articular surface of the facet does not extend onto the proximal margin of the sustentaculum. There is no distal extension of the sustentacular facet, nor is there a distal sustentacular facet at the distal margin of the calcaneus.

The body of the calcaneus distal to the sustentaculum is neither elongated nor compressed. On the lateral side of the body, the peroneal tubercle is positioned between sustentaculum and cuboid facet. The tubercle is elongated and projects substantially

from the calcaneal body, tapering somewhat laterally. The lateral margin of the peroneal tubercle is expanded dorsoventrally, bearing an oblique groove in lateral view. There is a well-defined dorsal sulcus between this endplate of the tubercle and the calcaneal body.

On the ventral side of the body, the plantar tubercle is positioned medial to the long axis of bone. The tubercle is well defined but does not project ventral to the remainder of the bone. The tubercle reaches the distal margin of the calcaneus but does not overhang the cuboid facet. The latter facet is nearly transverse in its orientation with a slight (less than 10°) medial inclination. The width and depth of diamond-shaped facet are subequal. The facet is essentially flat, with no meaningful concavity.

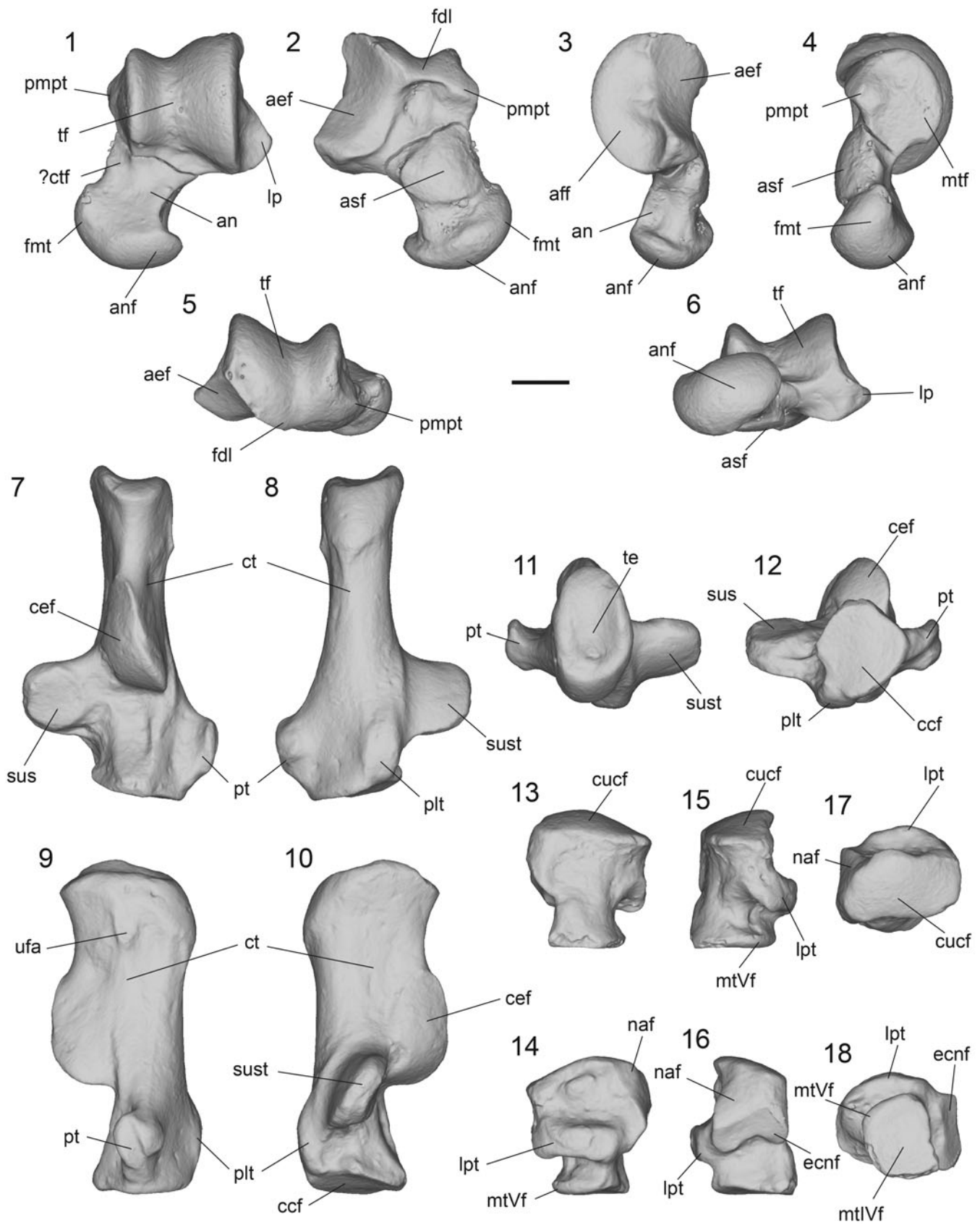


Figure 4. Left tarsals of *Lophiparamys debequensis*: (1, 7, 13) dorsal view; (2, 8, 14) ventral view; (3, 9, 15) lateral view; (4, 10, 16) medial view; (5, 11, 17) proximal view; (6, 12, 18) distal view. (1–6) USNM 527685r, astragalus (reversed from right side). (7–12) USNM 527685p, calcaneus. (13–18) USNM 527685s, cuboid (reversed from right side). aef = astragalus ectal facet; aff = astragalus fibular facet; an = astragalus neck; anf = astragalus navicular facet; asf = astragalus sustentacular facet; ccf = calcaneal cuboid facet; cef = calcaneal ectal facet; ct = calcaneal tuber; ?ctf = possible cotylar fossa; cucf = cuboid calcaneal facet; ecnf = cuboid ectocuneiform facet; fdl = groove for flexor digitorum lateralis; fmt = medial tarsal facet; lp = lateral process; lpt = long plantar tubercle; mtf = medial tibial facet; mtIVf = facet for metatarsal IV; mtVf = facet for metatarsal V; naf = cuboid navicular facet; plt = plantar tubercle; pmpt = proximomedial plantar tuberosity; pt = peroneal tubercle; sus = calcaneal sustentacular facet; sust = sustentaculum; te = endplate of calcaneal tuber; tf = tibial facet; ufa = U-shaped facet on calcaneal tuber. Scale bar = 1 mm.

Cuboid.—The cuboid of USNM 527685 (Fig. 4.13–4.18) is distinctly broader proximally than distally. At the proximal end, the calcaneal facet is approximately twice as wide as deep. The facet is slightly wider medially than laterally and is oriented proximally and slightly dorsally, with no lateral inclination. The calcaneal facet is weakly convex, matching the concavity of the calcaneal cuboid facet. Medially, there is no astragalus facet, and the calcaneal facet has an extensive contact with the navicular facet.

The navicular facet itself is approximately triangular and occupies the entire depth of the medial surface proximally, tapering ventrodistally and approaching mid-length of the bone. The facet is oriented medially and somewhat ventrally and is somewhat convex.

At its distal margin, the navicular facet is sharply offset from a distomedially oriented ectocuneiform facet. The latter facet is flat and “C” shaped in medial view, with a concave distal margin. There is no distal ectocuneiform facet. The cuboid is constricted toward the lateral side distal to ectocuneiform facet.

On the ventral surface of the cuboid, the long plantar tubercle projects directly ventrally and extends slightly distal to the level of the ectocuneiform facet. The tubercle is relatively weak and does not project substantially ventral to the remainder of bone. Its orientation is horizontal, lacking a proximolateral curve toward the calcaneal facet.

The dorsal and lateral margins of the distal end of the cuboid are slightly damaged, but it appears to have been deeper than wide, dominated by the facet for metatarsal IV. This facet is oriented distally and is slightly concave. At the ventrolateral corner of the facet for metatarsal IV is a narrow facet for metatarsal MT V, oriented laterally as well as distally.

Materials.—The type and material referred by Wood (1962, 1965), Guthrie (1967), and Flanagan (1986); USNM 527685,

left maxillary fragment with P4, left M1, right M2, two right M3s, right p4, right and left m1s, right and left m2s, right and left m3s, several incisor fragments, left and right calcanei, and a right astragalus and cuboid. At least two individuals are represented judging from the presence of two right M3s. Material referred by Guthrie (1971) is specifically excluded following Korth (1984).

USNM 527685 is from a paucispecific concentration of teeth, jaws, and bones collected from two dinner-plate sized, thin concentrations approximately one meter apart at locality USGS D-1830, which also includes a larger rodent and the microsypid plesiadapiforms *Microsypops* Leidy, 1872 and *Nipptomomys* McKenna, 1960. Although the dental and tarsal material was not found in articulation, we are confident that the tarsals are correctly reassociated with the teeth of *L. debequensis*. The tarsals are clearly referable to Rodentia, and the size of the tarsals indicates derivation from a very small rodent. *Lophiparamys debequensis* is the only small rodent in the assemblage. The appropriateness of the tarsals for reassociation with *L. debequensis* is confirmed by addition of dental and tarsal measurement from USNM 527685 to the regression of tarsal length on dental area first presented by Coillot et al. (2013). These demonstrate that the tarsals are of appropriate size to pertain to the same taxon as the *Lophiparamys* teeth in USNM 527685 (Fig. 5). Among the other taxa in the assemblage, both the larger rodent and *Microsypops* are also represented postcranially, indicating that it is reasonable to expect the presence of *Lophiparamys* postcrania given the relative abundance of dental material of the genus.

Remarks.—The new dental material permits a revision of the diagnosis of *L. debequensis*. Wood (1962) provided a relatively extensive diagnosis of the species. However, several features listed pertained to the upper dentition and could not be compared with *L. murinus*, the only other species known at that time, making them essentially generic diagnostic features. Of the remaining features, three—small size, “crenulations in the talonid basin forming distinct ridges,” and “entoconid continuous with posterolophid”—remain valid. The “distinct ridges” referred to by Wood (1962) contrast with the “very complex crenulations of the enamel” included in the diagnosis

Table 1. Dental measurements of *Lophiparamys debequensis* material from the Bighorn Basin. L = maximum length; TaW = maximum talonid width; TrW = maximum trigonid width; W = maximum width of upper teeth. All measurements in millimeters.

Specimen	Locus	Side	L	W	TrW	TaW
USNM 527685a	P4	Left	1.16	1.47	—	—
USNM 527685b	M1	Left	1.47	1.59	—	—
USNM 527685c	M2	Right	1.47	1.68	—	—
USNM 527685d	M3	Right	1.64	1.52	—	—
USNM 527685e	M3	Right	1.60	1.47	—	—
USNM 527685f	p4	Right	1.34	—	1.11	1.22
USNM 527685g	m1	Left	1.33	—	1.08	1.22
USNM 527685h	m1	Right	1.37	—	1.22	1.31
USNM 527685i	m2	Left	1.48	—	1.37	1.46
USNM 527685j	m2	Right	1.52	—	1.41	1.47
USNM 527685k	m3	Left	1.65	—	1.42	1.37
USNM 527685l	m3	Right	1.69	—	1.52	1.50

Table 2. Tarsal measurements of *Lophiparamys debequensis* material from the Bighorn Basin. H = maximum dorsoventral height; L = maximum proximodistal length; W = maximum mediolateral width. All measurements in millimeters.

Specimen	Element	Side	L	W	H
USNM 527685r	astragalus	Right	5.82	3.40	2.63
USNM 527685p	calcaneus	Left	—	3.78	2.87
USNM 527685q	calcaneus	Right	4.12	3.44	2.13
USNM 527685s	cuboid	Right	2.41	2.18	1.87

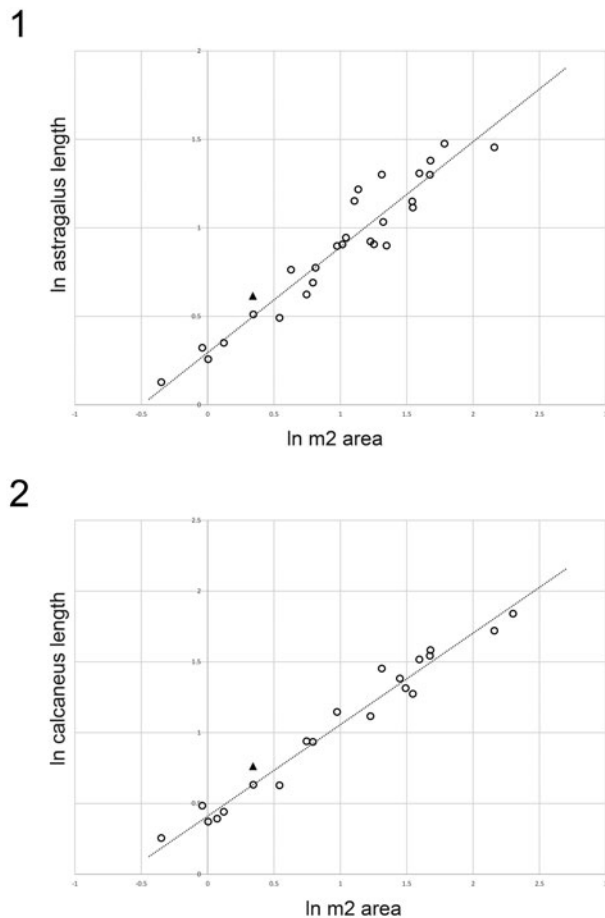


Figure 5. Natural logarithm transformed astragalular and calcaneal lengths of *Lophiparamys debequensis*, USNM 527685, and a variety of other early Cenozoic mammals plotted against m2 area: (1) astragalus, slope is 0.6075 and intercept is 0.2711; (2) calcaneus, slope is 0.6465 and intercept is 0.4033. Modified from Zack and Penkrot (2019) using data from Coillot et al. (2013) and Zack and Penkrot (2019). Filled triangles indicate *Lophiparamys*; open circles indicate other mammalian taxa.

of *L. murinus* and correspond to the less-dense crenulations cited in the revised diagnosis. An additional feature, “metalophid straight,” does not appear to consistently differentiate *L. debequensis* from *L. murinus* (e.g., Flanagan, 1986, fig. 2f).

Since Wood’s (1962) published diagnosis, additional material of both *L. debequensis* and *L. murinus* has been described, collectively improving sample sizes of both species and increasing the number of loci that can be directly compared (Wood, 1965; Flanagan, 1986; Ivy, 1990; Strait et al., 2016). A third species of *Lophiparamys*, *L. woodi*, has also been described (Guthrie, 1971). The only new diagnosis of *L. debequensis* published in that time was by Flanagan (1986). However, the features cited in that diagnosis are typical of *Lophiparamys* as a whole and do not distinguish *L. debequensis* from *L. murinus* and *L. woodi*. Accordingly, a new diagnosis of the species is provided in the preceding.

Results

Body mass estimation.—Using the all-rodent regression equations from Freudenthal and Martín-Suárez (2013), a body

mass estimate of 34.4 grams was obtained for *Lophiparamys debequensis* on the basis of the upper tooththrow and 19.9 grams on the basis of the lower tooththrow. While the upper and lower mass estimates differ substantially, both are within the range of variation of the extant hazel dormouse, *Muscardinus avellanarius* (Linnaeus, 1758), which Freudenthal and Martín-Suárez (2013) reported as ranging between 9 and 43 grams. Body mass of *L. murinus* was estimated at 46.3 grams on the basis of the lower tooththrow, more than double the estimate from the lower dentition of *L. murinus*, overlapping the lower range of variation of the extant European edible dormouse, *Glis glis* (Linnaeus, 1766), which Freudenthal and Martín-Suárez (2013) reported as ranging between 40 and 250 grams.

Phylogenetic analysis.—Analysis of the unconstrained character–taxon matrix produced 216 trees (length = 1,312 steps; consistency index [CI] = 0.15; retention index [RI] = 0.64), the majority rules consensus of which is shown in Figure 6.1. In the majority of trees, Microparamyinae is paraphyletic, with the two species of *Microparamys* forming the sister taxon of a clade comprising Gliridae, Sciuravidae, and Myomorpha. *Lophiparamys* forms the sister taxon to this clade. Among the remaining trees, some reverse the positions of *Microparamys* and *Lophiparamys*, with the latter closer to Gliridae, Sciuravidae, and Myomorpha. The remainder recover a monophyletic Microparamyinae as the sister taxon of Gliridae, Sciuravidae, and Myomorpha. The consensus topology is otherwise very similar to that recovered by Marivaux et al. (2004). Full strict and majority rules consensus trees for both this analysis and the constrained analysis are available as Supplementary Data Set 3.

When monophyly of the three primary extant rodent subclades (Sciuromorpha, Myomorpha, Ctenohipstrica) was enforced, 993 most parsimonious trees were recovered (length = 1,318 steps; CI = 0.15; RI = 0.64). The same trees were recovered regardless of whether *Tataromys* was included in the constraint definition. The majority rules consensus for the constrained analysis is shown in Fig. 6.2. Almost all trees produced by the constrained analysis recover *Lophiparamys* as the sister taxon of Gliridae. *Microparamys* is recovered in an unresolved tritomy with this grouping and a clade that includes Sciuridae, Aplodontidae, Theridomorpha, and members of Paramyidae and Reithroparamyidae. Some trees resolve *Microparamys* as the sister taxon of *Lophiparamys* plus Gliridae. A very small number of trees (~1%) recover a monophyletic Microparamyinae. In these trees, Sciuravidae rather than Microparamyinae forms the sister taxon of Gliridae. In most trees, sciuravids are resolved basal to Myomorpha.

When Microparamyinae is recovered as monophyletic, unambiguous synapomorphies describe aspects of p4 morphology: presence of a weak hypoconulid (character 26, state 1) and absence of metalophid II (character 30, state 0).

Discussion

Comparative tarsal morphology.—The morphology of the proximal tarsus of *Lophiparamys* is broadly similar to other early Eocene rodents (Wood, 1962; Rose and Chinnery, 2004;

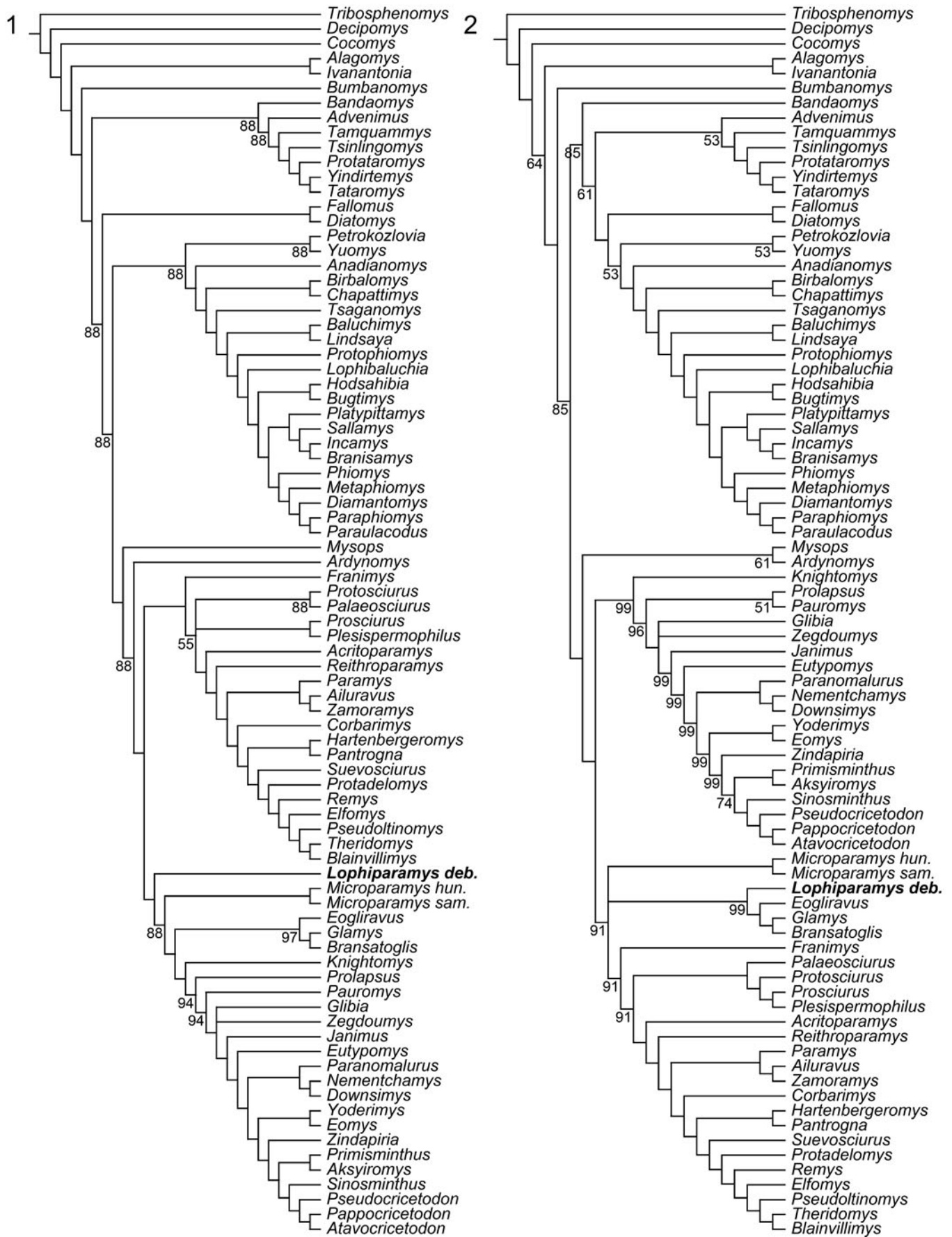


Figure 6. Phylogenetic relationships of *Lophiparamys*. (1) Majority rule consensus of 216 most parsimonious trees (L: 1,312, CI: 0.15, RI: 0.64) recovered by analysis of the unconstrained Marivaux et al. (2004) matrix. (2) Majority rule consensus of 993 most parsimonious trees (L: 1,318, CI: 0.15, RI: 0.64) recovered by analysis of the Marivaux et al. (2004) matrix with Sciuromorpha, Myomorpha, and Ctenostryica constrained to monophyly. Numbers at nodes correspond to percentage of trees recovering the node in question where less than 100. For readability, outgroups are not shown. The full trees, including outgroups, are shown in the Supplementary Data Set 3.

Rose and Von Koenigswald, 2007; Fostowicz-Frelik et al., 2018). Important shared features of the astragalus include a deeply but asymmetrically grooved tibial facet extending to the proximal margin of the astragal body, absence of an astragal foramen, limited extension of the astragal body medial to the tibial facet, prominent lateral process, isolated sustentacular facet, distinct neck, and a transverse navicular facet that is smoothly continuous with a facet for the medial tarsal that terminates abruptly on the medial surface of the astragal neck. On the calcaneus, broadly shared features include a short tuber with a distinctive dorsal deflection of its proximal margin, absence of a fibular facet, sustentacular facet lacking a distal extension and having minimal proximodistal overlap with the ectal facet, prominent peroneal tubercle positioned between the cuboid and sustentacular facets, and a nearly horizontal cuboid facet. Cuboid morphology is poorly documented in early rodents, but a proximally oriented calcaneal facet with limited mediolateral inclination, lack of an astragal facet, and a substantial constriction between the proximal and distal halves of the cuboid are all shared with the cuboid of cf. *Paramys copei* Loomis, 1907 described and illustrated by Rose and Chinnery (2004), although *Franimys* has a small astragal facet (Wood, 1962).

Despite these similarities, subtle features distinguish the *Lophiparamys* tarsus from contemporary rodents, including *Franimys*, *Notoparamys*, *Paramys*, and *Tamquammys*. On the astragalus, the medial ridge of the tibial facet is shorter relative to the lateral ridge than in other early Eocene rodents. The sustentacular facet has a distinctive distolateral extension, which is shared with *Notoparamys* but not with species of *Paramys* or *Tamquammys*. The astragal neck of *Lophiparamys* is relatively longer than in other early rodents, particularly *Notoparamys*. The astragal head of *Lophiparamys* is less dorsoventrally compressed than in other early North American rodents and is comparable to *Tamquammys*.

On the calcaneus, *Lophiparamys* has a shorter tuber than other early Eocene rodents. The ectal facet is more elongated, extending further proximally. The sustentacular facet is relatively smaller than in other early rodents. The peroneal tubercle is slightly more distal than in other North American taxa, a feature shared with *Tamquammys*. *Lophiparamys* also differs from the early glirid *Eoglyiravus hammeli* Thaler, 1966 (see Vianey-Liaud et al., 2022 for specific attribution) in this feature, but tarsal comparisons cannot otherwise be made due to the articulated nature of the skeleton of *E. hammeli* (Storch and Seiffert, 2007). The cuboid facet is broader and more nearly circular than in other early Eocene rodents. Comparisons of the cuboid itself are limited, but the constriction between the proximal and distal portions of the cuboid is more substantial than in *Paramys* or *Franimys*.

Tarsal function.—With the exceptions of the size of the calcaneal sustentacular facet and the position of the peroneal

tubercle, the features that distinguish the tarsus of *Lophiparamys* from other early Eocene rodents are associated with arboreal locomotion on extant rodents. At the crurotarsal joint, an asymmetric astragal tibial facet is typical of arboreal rodents (Ginot et al., 2016) and facilitates inversion of the pes during plantarflexion. A relatively short calcaneal tuber is characteristic of a diversity of arboreal mammals, including many rodents and primates (e.g., Rose and Chinnery, 2004).

At the subastragal joint, asymmetry in the length of the astragal and calcaneal ectal facets and the transverse expansion of the astragal sustentacular facet would permit greater mobility between the astragalus and calcaneus. Elongation of the calcaneal ectal facet would facilitate hind foot reversal during plantarflexion, an important adaptation in many arboreal mammals, including some extant rodents (e.g., *Sciurus* Linnaeus, 1758) (Jenkins and McLearn, 1984; Meldrum et al., 1997). Expansion of the astragal sustentacular facet would also increase mobility by facilitating inversion and eversion at the subastragal joint (Hooker, 2001).

At the transverse tarsal joint, the rounded shapes of both the astragal head and calcaneal cuboid facet are indicative of multiaxial mobility at the transverse tarsal joint (Szalay and Drawhorn, 1980; Candela and Picasso, 2008) and consistent with habitual use of inverted and everted postures.

Taken as a whole, the morphology of the tarsus of *Lophiparamys debequensis* indicates greater multiaxial mobility than in other early rodents and suggests that *L. debequensis* was more scansorial or arboreal than its contemporaries.

Systematic implications.—The results of the phylogenetic analysis fail to clearly resolve the affinities of either *Lophiparamys* or Microparamyinae. The unconstrained results place *Lophiparamys* and *Microparamys* basal to Gliridae plus Myomorpha and do not consistently recover a monophyletic Microparamyinae. The constrained results link *Lophiparamys* to Gliridae in the majority of trees but only rarely recover microparamyine monophyly. Neither of these results is well supported.

Taken as a whole, it remains plausible that *Lophiparamys*, *Microparamys*, and potentially other taxa historically linked with Microparamyinae (e.g., *Strathcona*) represent a monophyletic assemblage within Rodentia. While both analyses fail to unambiguously support microparamyine monophyly, the clade is recovered by some most parsimonious trees in both analyses, particularly the unconstrained analysis. In the same vein, a link between Microparamyinae and Gliridae is supported only by the constrained analysis, with stronger support for a special relationship between *Lophiparamys* and Gliridae than between *Microparamys* and Gliridae. Although a microparamyine–glirid clade receives equivocal support, it cannot be meaningfully rejected.

One shortcoming of the analysis performed here is the lack of non-dental character data beyond a few basic characters

associated with zygomatic and mandibular structure, including a complete absence of postcranial characters. As described in the preceding, the tarsus of *Lophiparamys* displays features shared with extant Gliridae that could provide additional character support to link microparamyines and dormice. The astragalar features, at a minimum, are also present in the Eocene glirid *Glamys* (Collinson and Hooker, 2000, fig. 8). Unfortunately, postcranial morphology is generally poorly known in early rodents, including the majority of the taxa included in the matrix of Marivaux et al. (2004). Effectively bringing postcranial anatomy to bear on early rodent affinities will require substantial effort to identify and document early rodent postcranial remains.

A few further comments can be made on the systematics of *Lophiparamys* and microparamyines. First, the apparently greater affinity of *Lophiparamys* than *Microparamys* for Gliridae in the constrained analysis is driven in part by the presence of additional crests shared by *Lophiparamys* and glirids. *Lophiparamys* and glirids share the presence of an upper molar endoloph (66–0) and a well-developed posterior arm of the lower molar metaconid (100–2), while *Lophiparamys* and *Eogiliravus* share the presence of an anterior arm of the lower molar hypococonid (90–1). The fact that *Lophiparamys* has a general profusion of supernumerary crests, many of which are not present in glirids, raises the possibility that these apparent synapomorphies may also prove to be spurious. In the absence of additional evidence, it would be premature to regard *Lophiparamys* as more closely related to Gliridae than is *Microparamys*.

A second issue warranting further comment is the phylogenetic implications of the size of the infraorbital foramen in *Lophiparamys*. In early glirids for which this region is documented, the infraorbital foramen is relatively small (Vianey-Liaud, 1985, 1994). In *Eogiliravus*, the oldest unambiguous glirid, the foramen has also been described as small (Storch and Seiffert, 2007). By contrast, the maxillary fragment of USNM 527685 demonstrates that *Lophiparamys* has a relatively large infraorbital foramen. The preserved margin of the infraorbital canal indicates that the infraorbital foramen was comparable to *Sparnacomyys*, *Hartenbergeromyys*, and *Pantrogna* (Hooker, 2010; Vianey-Liaud et al., 2019) and larger than most paramyids (Wood, 1962; Wahlert, 1974; Korth, 1994). As noted by Hooker (2010), a foramen of this gauge is not consistent with a derivation of glirids from *Sparnacomyys* and related taxa, contra Hartenberger (1971), and this argument can now be extended to *Lophiparamys*, implying homoplasy in this feature if *Lophiparamys* is closely related to glirids.

Another factor complicating any potential relationship between Microparamyinae and Gliridae is the near absence of European microparamyines. The early fossil record of dormice is restricted to Europe (e.g., Vianey-Liaud, 1994; Storch and Seiffert, 2007), and glirids are unknown outside of Europe until the Miocene (Maridet et al., 2011), making a European origin likely (Lu et al., 2021). If microparamyines are ancestral to glirids, a European microparamyine record should be expected. Unfortunately, most taxa previously considered to represent European microparamyines (e.g., Hartenberger, 1971; Escarguel, 1999) now appear to be basal theridomorphs (Vianey-Liaud and Marivaux, 2017, 2021). The sole potential exception is *Microparamys nanus* Teilhard de Chardin, 1927, from the

earliest Eocene Belgian Dormaal fauna (Teilhard de Chardin, 1927; Wood, 1962), but Escarguel (1999) indicated that material referred to *M. nanus* likely represents *Pantrogna* and *Sparnacomyys* as well, and Vianey-Liaud and Marivaux (2021) indicated that at least some Dormaal rodents show indications of theridomorph affinities. The apparent absence of a European record of microparamyines constitutes an additional argument against a relationship to glirids.

Evolution of Lophiparamys.—The three species of *Lophiparamys* have largely nonoverlapping stratigraphic ranges. The type species, *L. murinus*, includes the temporally earliest records of the genus, with specimens recorded from the earlier part of the Wasatchian (Wa2–4) in the Willwood Formation of the Greater Bighorn Basin of northern Wyoming, the main body of the Wasatch Formation in the Washakie Basin of southern Wyoming, and possibly from the Golden Valley Formation of North Dakota (Wood, 1962; Jepsen, 1963; Ivy, 1990; Strait et al., 2016). As indicated in the preceding, records of *L. debequensis* are restricted to the early late Wasatchian (Wa6) of Colorado, New Mexico, and Wyoming. The youngest species, *L. woodi*, is known only from the latest Wasatchian (Wa7) of the Lost Cabin Member of the Wind River Formation in the Wind River Basin (Guthrie, 1971).

To date, there have been only two potential instances of overlap in the stratigraphic ranges of species of *Lophiparamys*, both involving potential records in Wa7 of species other than *L. woodi*. White (1952) recorded *Paramys murinus* from the Lost Cabin Member of the Wind River Formation. This record is almost certainly in error as it describes a specimen with “entirely smooth enamel,” inconsistent with the crenulate enamel of *Lophiparamys*. Guthrie (1971) subsequently referred the specimen to the sciuravid *Knightomys*. In the same paper, Guthrie (1971) recorded both *L. debequensis* and *L. woodi* from the Lost Cabin Member, the former primarily on the basis of two isolated teeth, a p4 and an m3. Korth (1984) questioned this referral, noting that these teeth, as illustrated by Guthrie (1971, fig. 14) indicate an animal larger rather than smaller than *L. woodi* and do not appear to be consistent with the measurements provided for the same specimens. In addition, Korth (1984) was unable to locate either tooth in the CM collections.

The apparent lack of stratigraphic overlap between species of *Lophiparamys* could be consistent with the three species forming a lineage beginning with *L. murinus* and continuing through *L. debequensis* to *L. woodi*. The fact that *L. debequensis* is smaller than either the older *L. murinus* or younger *L. woodi* might argue against this possibility, but complex patterns of size change are apparent in other early Eocene lineages (e.g., Gingerich, 1991, 1994; Silcox et al., 2008). There are a number of morphological distinctions between *Lophiparamys debequensis* and *L. murinus* that cannot be evaluated in *L. woodi* due to limited material and poor illustration of the latter taxon. In particular, this includes contrasts in premolar morphology, with *L. murinus* having a more molarized P4 with a larger metacone and associated larger p4 talonid than *L. debequensis*. While these features emphasize the distinction of *L. debequensis* from *L. murinus*, they do not address the relationship of either species to *L. woodi*. However, there are

several variable features that can be compared across all three species, and all appear to contrast *L. debequensis* with its older and younger relatives.

An unbroken posterolophid is present on almost all lower cheek teeth of *L. debequensis* from the Bighorn, San Juan, and Wind River basins (Wood, 1962, 1965; Flanagan, 1986; this study), suggesting that this is a characteristic feature of the species. The one possible exception, the m3 of ACM 11245, has not been illustrated, making it difficult to evaluate Wood's (1965) claim that the entoconid on this tooth is "quite isolated." By contrast, both *L. murinus* and *L. woodi* consistently have a notch in the posterolophid isolating the entoconid from the remainder of the lophid (Wood, 1962; Guthrie, 1971; Strait et al., 2016). This is also present in Guthrie's (1971) purported Lostcabinian *L. debequensis* m3, casting further doubt on the identification of this specimen. In addition to the continuous posterolophid, specimens of *L. debequensis* differ from both *L. murinus* and *L. woodi* in having lower, less-dense enamel ridges. This is most apparent on the lower cheek teeth. In *L. debequensis*, enamel ridges are relatively low and few in number, while in *L. murinus* and *L. woodi* they are denser and, at least in *L. murinus*, appear taller. On the upper cheek teeth, the buccal protoloph and buccal metalophule of *L. debequensis* may be somewhat simpler and more linear than in the other species, in which they are broken up by extra longitudinal spurs. Finally, M1 and M2 of *L. debequensis* are more quadrate than M1–2 of *L. murinus* and *L. woodi* due to a relatively larger hypocone.

Taken together, the size and morphology of the dentition of *Lophiparamys* does not support their placement in a single lineage. Deriving *Lophiparamys woodi* from the older *L. debequensis* would require reversals in several features that distinguish *L. debequensis* from *L. murinus* in addition to a reversal in the direction of size change. This indicates that multiple lineages of *Lophiparamys* were present for at least part of the Wasatchian and suggests that much remains to be documented about the evolution of this rare, poorly known rodent.

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Declaration of competing interests

The authors declare no competing interests.

Data availability statement

All Supplementary Data are available on Morphobank: <http://dx.doi.org/10.7934/P4513>.

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