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Two large squirrels (Rodentia, Mammalia) from the Junggar Basin of northwestern China demonstrate early radiation among squirrels and suggest forested paleoenvironment in the late Eocene of Central Asia

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Fossil evidence is indispensable for studying the derivation, divergence, and dispersal of squirrels as they responded to global Cenozoic climatic and paleoenvironmental change. Among these fossil records, the earliest known definitive fossil squirrels in Eurasia occur after the Eocene/Oligocene Boundary and are slightly younger than the oldest records in North America. Here, we report the discovery of two new extinct large squirrel species from the late Eocene of the Junggar Basin in northwestern China. The dental morphologies of these new taxa represent tree and flying morphotypes, and their estimated body masses are approximately 1.2 kg and 2.6 kg, respectively. In addition, these extinct lineages push the age of the first appearance of Sciuridae in northern Asia into the late Eocene. Together with *Douglassciurus* and *Oligospermophilus* from North America, these two new squirrels from the Junggar Basin are the earliest records of sciurids, and analysis of their teeth clearly demonstrates that the three principle morphotypes of sciurids (flying, ground, and tree squirrels) had diverged from one another by the late Eocene. That proposed late Eocene divergence among the major groupings of sciurids is consistent with some molecular clock analyses and helps to document that macroevolutionary timing and pattern. Comparison with modern squirrel analogs for body masses over 1 kg points to these early Chinese species as having occupied forested habitats, and that hypothesis is congruent with published palynological studies. Furthermore, these two new squirrel taxa from Jeminay provide new data to evaluate the examination of the long-term aridification of Central Asia.

KEYWORDS

body mass, forest paleohabitat, Junggar Basin, late Eocene, morphotype, Sciuridae

Introduction

Squirrels are a rodent group with small- to medium-sized bodies in the family Sciuridae, which is the fourth most diverse family of living mammals, consisting of 58 genera and ~285 extant species (Thorington and Hoffmann, 2005; Thorington et al., 2012). The fossil squirrels have been allocated to more than 35 extinct genera (McKenna and Bell, 1997; Fossilworks Group, 2022). Previous work has revealed that the geographic distribution and diversification of both fossil and living sciurids were affected significantly by global climate change during the Cenozoic (Mercer and Roth, 2003) and that the evolution of arboreality possibly aided the divergence of the arboreal group from their hypothetical terrestrial/fossorial ancestors (Steppan et al., 2004). Known fossil records point to the late Eocene as a critical period for the derivation, early divergence, and radiation of sciurids (Goodwin, 2008; Fabre et al., 2012). This temporal interval coincides with the global climatic shift from greenhouse to icehouse climates during the Eocene–Oligocene Transition (EOT) (Zachos et al., 2001; Liu et al., 2009; Hren et al., 2013; Hutchinson et al., 2021), and that climate change possibly initiated or enhanced the aridification of the Asian continental interior in combination with the uplift of the Tibetan Plateau and retreat of Paratethys (e.g., Dupont-Nivet et al., 2007; Abels et al., 2011; Miao et al., 2012; Miao et al., 2013; Bosboom et al., 2014; Fang et al., 2015; Sun and Windley, 2015; Li et al., 2018). As a consequence, the Eocene–Oligocene climatic shift led to the large-scale extinction of marine invertebrates and terrestrial floristic and faunal turnover (e.g., Collinson et al., 1981; Prothero and Emry, 1994; Prothero et al., 2003; Hooker et al., 2004; Retallack et al., 2004), such as the Grande Coupure in Europe and the Mongolian Remodelling in North Asia (Stehlin, 1910; Meng and McKenna, 1998).

Sciurids have been considered to have originated in North America on the eve of the EOT, with the representatives *Douglassciurus jeffersoni* known at about 36.6 Ma (Douglass, 1901; Emry and Korth, 1996; Emry and Korth, 2001) or *D. oaxacaensis* at about 40 Ma (Ferrusquia-Villafranca et al., 2018). From that hypothetical origin, squirrels are thought to have dispersed into Europe and South Asia soon after the EOT, as documented by fossils of *Oligopetes* (Vianey-Liaud, 1974; Heissig, 1979; Vianey-Liaud, 1985; De Bruijn and Ünay, 1989; Welcomme et al., 2001). Squirrels appear to have immigrated rather late to North Africa in the Miocene and to South America in the Pleistocene (De Bruijn, 1999). The Eurasian *Oligopetes* has been presumed to be a Grande Coupure immigrant (Dawson, 2003; Heissig, 2003). However, a large temporal gap exists between the EOT and the first appearance of Sciuridae in the Mongolian Remodelling of North Asia (Meng and McKenna, 1998). In recent years, the Paleogene records of sciurids in North Asia have continued to grow, and they have demonstrated that squirrels were rather diverse in the early Oligocene (Minjin, 2004; Wang and Qiu, 2004; Wang and Dashzeveg, 2005; Maridet et al., 2014). In addition, fossils have suggested that sciurids also might date back to the late Eocene (Wang, 2008). In fact, we can confirm Eocene occurrence in northern Asia through the recognition of two new fossil species of large arboreal squirrels from late Eocene sediments of the Junggar Basin in northwestern China. These fossils and the taxa they represent greatly aid in improving our understanding of the derivation, early divergence, and spatiotemporal distribution of sciurids, and they support the occurrence of forested paleohabitat in the late Eocene of Central Asia.

All of the extant and extinct squirrel species comprise a monophyletic Sciuridae, which is the sister group to Aplodontidae (Huchon and Douzery, 2001; DeBry, 2003; Montgelard et al., 2008; Blanga-Kanfi et al., 2009; Fabre et al., 2012). Traditionally, Sciuridae were split into the two subfamilies which are the Pteromyinae (the flying squirrels with their gliding membrane) and Sciurinae (the non-flying tree and ground squirrels) (e.g., Simpson, 1945; Hoffmann et al., 1993; Thorington et al., 2002). Based on dental and mandibular morphologies, De Bruijn, (1999) recognized three morphotypes among the squirrels that include “ground,” “tree,” and “flying” squirrels, and he elevated Pteromyinae and Sciurinae to the family level, raising the Sciuridae to superfamily rank. Qiu (2019) summarized the known 32 genera of sciurid fossils in China and divided them into four subfamilies. In that taxonomy (Qiu, 2019), flying squirrels are still treated as an independent subfamily, Pteromyinae. However, molecular phylogenetic studies refined the higher level systematic arrangement of the Sciuridae and its extant lineages of five subfamilies: Ratufinae, Sciurillinae, Sciurinae, Callosciurinae, and Xerinae (Mercer and Roth, 2003; Steppan et al., 2004). In this treatment, the “flying squirrels” are monophyletic (Thorington, 1984; Oshida et al., 1996) and are treated as a tribe within the subfamily Sciurinae (Mercer and Roth, 2003; Steppan et al., 2004; Thorington and Hoffmann, 2005; Fabre et al., 2012). In addition to the five living subfamilies, there are two extinct subfamilies. One is the subfamily Cedromurinae proposed by Korth and Emry (1991) for the two extinct genera *Cedromus* Wilson (1949) and *Oligospermophilus* Korth (1987) from the late Eocene to late Oligocene of North America. This clade was subsequently accepted by some paleontologists (McKenna and Bell, 1997; Wang and Dashzeveg, 2005; Goodwin, 2008). The other is the subfamily Aepyosciurinae erected by Wang and Qiu (2003) for a specialized sciurid group with unilaterally hypsodont and lophodont cheek teeth. At present, it includes only genus *Aepyosciurus* and is restricted in the late Neogene and Quaternary (early Pliocene to early Pleistocene) of the Tibetan Plateau and North China (Wang and Qiu, 2003; Qiu et al., 2005; Cai et al., 2013; Wang et al., 2013; Li et al., 2014). Based on their dental morphologies, the two new species in this text from Jeminay, northwestern China, should be placed in the subfamily Sciurinae.

Materials and methods

Fossil sites

The new sciurid fossil specimens were discovered in Jeminay County in the northwestern part of the Xinjiang Uygur Autonomous Region of China. The new fossil sites are located in a gully west of the village of Xiaerhete, which is ~10 km south of the Irtysh River and 6 km northwest of the county seat of Jeminay County, close to the China–Kazakhstan border. The Jeminay area has produced middle Eocene fossil plants including *Taxodium* sp., *Ampelopsis* sp., *Populus* sp., and *Corylus* sp. and mammals including *Triplopus* sp., *Triplopus jeminaiensis*, *Lophialetes* sp., and Hyaenodontidae gen. et sp. indet. (Wang F. Y., 1984; Jin, 2000). Jin (2000) considered the Cenozoic sediments in Jeminay area and along the Irtysh River as an eastern extension of the neighboring deposits in the Zaysan Basin of Kazakhstan. The squirrel fossils derive from two extremely close sites (XJ20140619LQ03 and XJ20140626NI01, N47°28′, E86°47′, elevation 869 m) and from almost the same layer

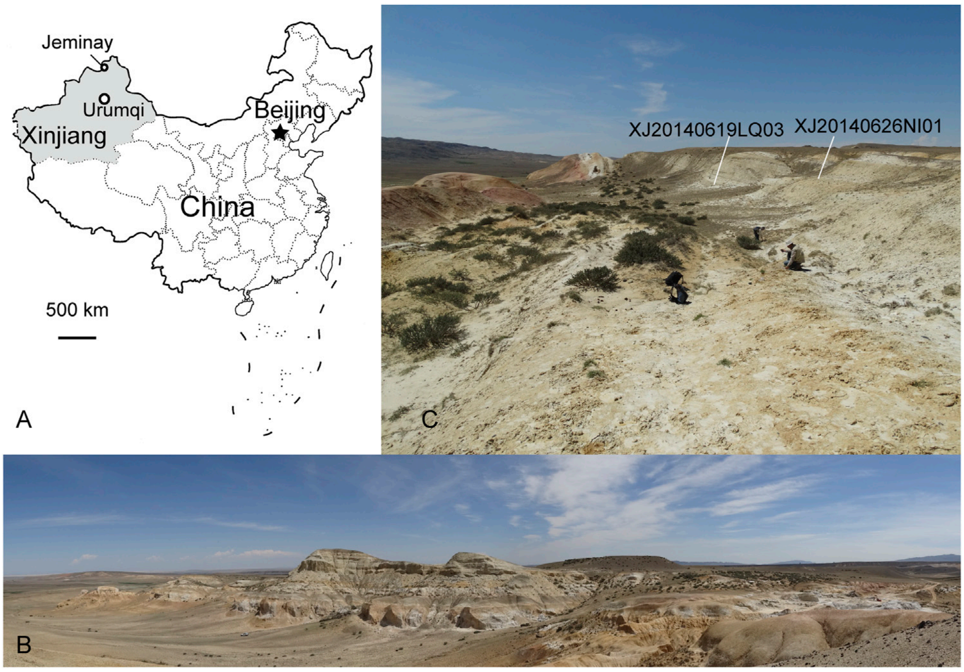

FIGURE 1
Late Eocene sciurid sites in Jeminay, northwestern Xinjiang, China. **(A)** Map showing the fossil sites located at Jeminay, Xijiang Uygur Autonomous Region, northwestern China; **(B)** panoramic view of the fossiliferous profile of the Keziletuogayi Formation that produced the additional material of fossil squirrels (photo taken by the first author QL on 20 June 2014); **(C)** a close-up view of the stratigraphy yielding the fossil squirrels.

(only a half-meter interval of two sites) consisting of ~5 m of yellowish fluvial sandstone, grayish white siltstone, and sandy mudstone of the Keziletuogayi Formation (Figure 1). A large anseriform fossil (cf. Romainvilliinae) was previously discovered and reported from this same layer (Stidham and Ni, 2014). Lithologically, the squirrel fossil layer can be correlated to the Keziletuogayi Formation yielding an A3 mammalian zone fauna from the nearby Keziletuogayi section. Paleomagnetic dating of that interval provides an age range of 34.0–35.0 Ma (Sun et al., 2014). The associated mammals from the Keziletuogayi section include Brontotheriidae, Amynodontinae, *Cadurcodon* cf. *C. ardynensis*, and *Ardynomys vinogradov*, and that fauna also confirms its late Eocene age.

Material

The fossil squirrel specimens include four enamel caps of one upper and three lower molars, collected by wet-sieving technique in 2014. The other rodent specimens are as yet unstudied. All specimens are housed at the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences, Beijing.

Comparative sample

For comparative purposes, we discuss all known late Eocene and early-late Oligocene sciurid genera (16 taxa). The following is a list of these genera.

Asian forms include *Sciurus* sp., *Oligosciurus*, *Kherem*, Marmotini gen. et sp. indet., and *Plesiosciurus* aff. *sinensis*. The specimens of *Sciurus* sp. reported by Bohlin (1946) include a right M3 (T. b. 202) and a right m2 (T. b. 593) from the late Oligocene Taben-buluk Basin of Gansu Province, China. *Oligosciurus* (Wang and Qiu, 2004) (type and only species: *O. dangheensis*) is based on the topotype jaw (IVPP V13556) from the lower Oligocene Paoniuquan Formation in the Danghe region of Gansu Province, China. The topotype belongs to an ontogenetically old individual with a heavily worn m1 and m2. *Kherem* (Minjin, 2004) comprises two members, *K. hsandgoliensis* (the type species) and *K. asiatica*, both of which were discovered in the Hsanda Gol Formation (early Oligocene) of the Valley of Lakes area, Mongolia (Minjin, 2004; Wang and Dashzeveg, 2005). *Kherem* was once assigned to the subfamily Cedromurinae recognized by Korth and Emry, (1991) (Wang and Dashzeveg, 2005). Recently, Maridet et al. (2014) treated *K. asiatica* as a synonym of *K. hsandgoliensis*, assigned *Kherem* to the subfamily Xerinae, and expanded the former temporal range from early Oligocene through early middle Miocene. We agree with Maridet et al. (2014) that *K. asiatica* is synonymous with *K. hsandgoliensis*. The material referred to as Marmotini gen. et sp. indet. described by Wang (2008) comprises a broken M1/2 (IVPP V 15003) from the Upper Eocene Houldjin Formation of Erenhot, Inner Mongolia, China. Its attribution to Sciuridae is doubtful. The specimens of *Plesiosciurus* aff. *sinensis* (Qiu and Lin, 1986) were discovered in Toglorhoi, Unkheltseg, Hotuliin Teeg, Ulann Tolgoi, and Loh (early Late Oligocene to early Middle Miocene) of the Valley of Lakes, Mongolia (Maridet et al., 2014, p. 274).

European forms include *Palaeosciurus*, *Heteroxerus*, and *Oligopetes*. *Palaeosciurus* Pomel, 1853 comprises five European species: *P. feignouxi* (type species), *P. fissurae* (Dehm, 1950), *P. goti* (Vianey-Liaud, 1974), *P. sutteri* (Ziegler and Fahlbusch, 1986), and *P. ultimus* (Mein and Ginsburg, 2002), and a Chinese species *P. jiangi*

(Qiu, 2015). This genus ranges temporally from the earliest Oligocene to the early Miocene in Eurasia (de Bruijn, 1999; Qiu, 2015). *Palaeosciurus goti* from Mas de Got of France (MP22) was once regarded as the earliest sciurid in Europe (Vianey-Liaud, 1985). *Heteroxerus* Schaub (in Stehlin and Schaub, 1951, p. 200) (type species: *H. hürzeleri*) is a member of Xerini and ranges from the early Oligocene through the late Miocene in Europe (McKenna and Bell, 1997). Its holotype is a fragmentary lower dentition with m1-2 (Stehlin and Schaub, 1951, p. 201, figure 300). *Oligopetes* (Heissig, 1979) is the hitherto earliest known record of flying squirrels. It consists of three species, *O. radialis* (type species), *O. lophulus*, and *O. obtusus*, which all derive from the fissure fillings of Suevium (lower to middle Oligocene).

North American forms include *Protospermophilus*, *Cedromus*, *Miospermophilus*, *Miosciurus*, *Protosciurus*, *Oligospermophilus*, *Nototamias*, and *Douglassciurus*. *Protospermophilus* (Gazin, 1930) contains of a total of six species: *P. quatalensis* (type species), *P. wortmani*, *P. kelloggi*, *P. angusticeps*, *P. oregonensis*, and *P. malheurensis* (Cope, 1879; Gazin, 1930; Gazin, 1932; Matthew and Mook, 1933; Downs, 1956; Black, 1963). Temporally, they span from the early Arikareean to late Clarendonian NALMA (late Oligocene to late Miocene) (Goodwin, 2008). The genotype *P. quatalensis* is present in the Cuyama Basin (late Miocene) of California (USA). *Cedromus* (Wilson, 1949) consists of the type species *Cedromys wardi* and *C. wilsoni* (Korth and Emry, 1991). *Cedromus* ranges from the early Orellan to the late Whitneyan NALMA (early Oligocene to early Late Oligocene) (Goodwin, 2008). *Miospermophilus* (Black, 1963) comprises three species, namely, *M. bryanti* (type sepcies), *M. wyomingensis*, and the questionable *M. lavertyi* (Wilson, 1960; Black, 1963; Dalquest et al., 1996), and it spans from the early Arikareean to the late Clarendonian NALMA (late Oligocene to late Miocene) (Goodwin, 2008). *Miosciurus* (Black, 1963) contains one species, *M. ballovianus* (Cope, 1881). *Miosciurus ballovianus* is an early Arikareean NALMA (late Oligocene) sciurid from the United States, and thus far it has been found only in the "*Diceratherium* beds" (probably Turtle Cove Member, see Albright et al., 2008) of the John Day Formation of Oregon. *Protosciurus* (Black, 1963) includes *P. condoni* (type species), *P. mengi*, *P. rachelae*, and *P. tecuyensis* (Bryant, 1945). The genus ranges from early Orellan to early Hemingfordian NALMA (early Oligocene to late early Miocene), and it may have survived into the early Barstovian NALMA (early middle Miocene) (Goodwin, 2008). *Oligospermophilus* (Korth, 1987) (type and only species: *O. douglassi*), typical of the Orella Member of the Brule Formation (early Oligocene), Prairie Dog Creek of Nebraska (USA), was assigned originally to *Protosciurus* (Korth, 1981). *Nototamias* (Pratt and Morgan, 1989) is a chipmunk-sized sciurid with a *Tamias*-like upper dental pattern. Chronologically, it spans from the early Arikareean to the late Clarendonian NALMA (late Oligocene to late Miocene), similar to *Protospermophilus* (Goodwin, 2008). It comprises three species: *N. hulberti* (type species), *N. quadratus*, and *N. ateles* (Hall, 1930; Pratt and Morgan, 1989; Korth, 1992). *Douglassciurus* is a replacement name for *Douglassia* Emry and Korth (1996) (Emry and Korth, 2001). This genus consists of four species: *D. jeffersoni* (late Eocene), *D. sapphirus* (late Oligocene), *D. bjorki* (middle Oligocene), and *D. oaxacaensis* (late middle Eocene) (Douglass, 1901; Korth, 2009; Korth, 2014; Ferrusquia-Villafranca et al., 2018). The type species is *D. jeffersoni* from the Chadronian NALMA (late Eocene) Pipestone Springs Formation, Montana (USA), and it was originally referred to the genus *Sciurus* by Douglass (1901). Its generic and familial allocations were uncertain for a long time, attributed to *Prosciurus* (Matthew, 1903) of the Aplodontidae (Osborn and Matthew, 1909; Wood, 1937) or to *Cedromus* or *Protosciurus* of the Sciuridae (Wood, 1962; Black, 1963; Wood, 1980; Emry and Thorington, 1982).

Site and institutional abbreviations

IVPP, The Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing (China); MP, European Paleogene mammal faunal zones; XJ, prefix to Xinjiang of field localities of the IVPP; T.b., Taben-buluk area (Gansu Province, China) in Bohlin's (1946) pioneering work.

Measurements and nomenclature

Specimens were measured using an Olympus SZX7 microscope with a precision of +/− 0.01 mm. The length is defined as the anteroposterior chord. The width is defined along the chord perpendicular to the length. The dental terminology (Figure 2) is mostly adopted from Qiu (1996) and Qiu, (2019) except for our usage of "anterobuccal cingulid" to replace their "anterobuccal cingulum" on m1/2 and additions of "anterobuccal sinusid" and "protocone crest." The protocone crest is "a short crest extending anterobuccally from the protocone into the valley between the anterior cingulum and the protoloph" defined by Emry and Korth (1996), and it is equal to the "protostyl" used by Heissig (1979).

CT scanning and reconstruction

The specimens were CT-scanned using the 100 kv Micro–CT in the Key Laboratory of Vertebrate Evolution and Human Origins of the Chinese Academy of Sciences. The 3D virtual reconstruction was made with VGSTUDIO (Version 2.0, genuine authorized) software (Volume Graphics) installed in the computers of the laboratory following the standard procedure introduced by Ni et al. (2012).

Body mass estimation

Following Freudenthal and Martín-Suárez (2013), we first calculated the length of the lower tooth row using one of their regression equations ($\ln(\mathrm{LRsum}) = 0.51 \times \ln(\mathrm{L} \times \mathrm{W} \text{ of m1}) + 1.25$) applied to the Sciuridae (Freudenthal and Martín-Suárez (2013), p.7). Then, we substituted the tooth row length into their other equation ($\ln(\mathrm{mass}) = 3.023 \ln(\mathrm{row}) - 0.993$) to obtain a body mass estimate (Freudenthal and Martín-Suárez (2013), p.8).

Systematic Paleontology

Order Rodentia Bowdich, (1821).

Family Sciuridae (Fischer de Waldheim, 1817)
Subfamily Sciurinae (Fischer de Waldheim, 1817)
Genus *Junggarisciurus* gen. nov.
Junggarisciurus *jeminaiensis* sp. nov.
Figures 3A1–5, B1–5, C1–5

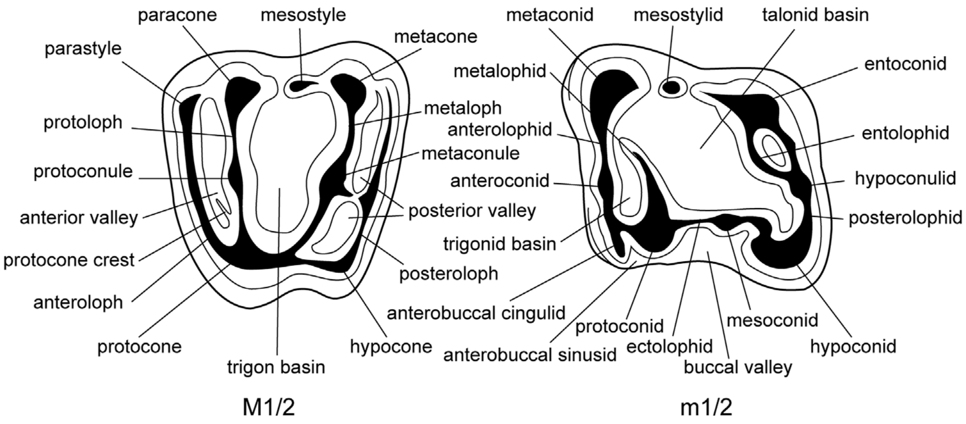

FIGURE 2
Dental nomenclature of the Sciuridae molars (cited from Qiu, 1996; Qiu, 2019).

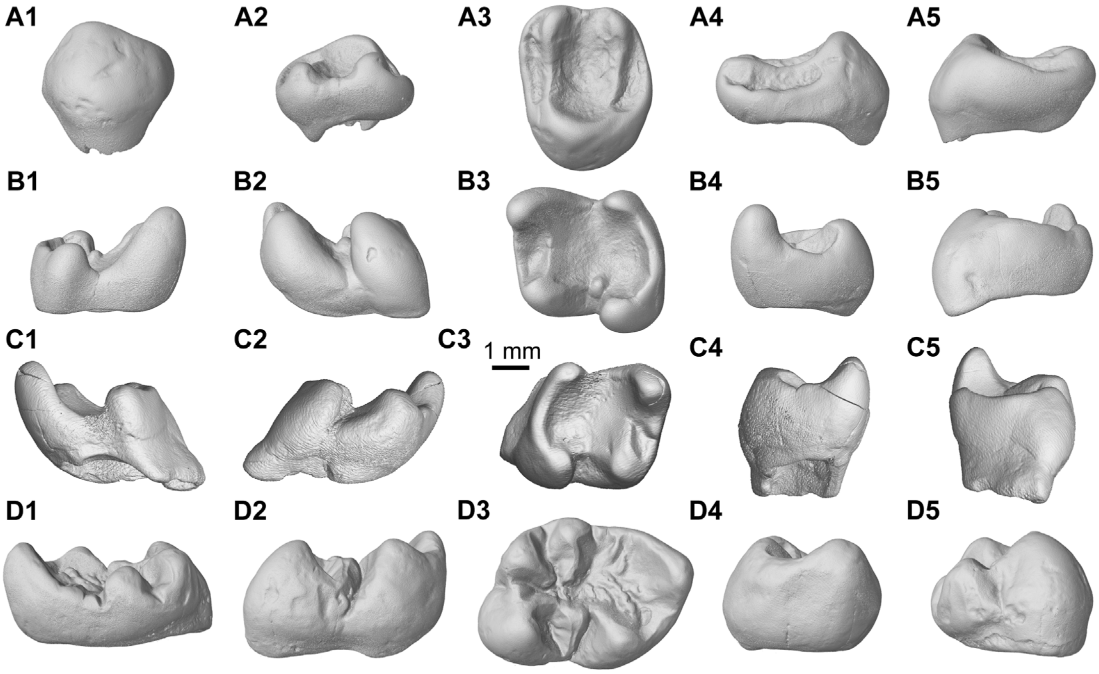

FIGURE 3
3D virtual reconstruction of the molars of *Junggarisciurus jeminaiensis* gen. et. sp. nov. and *Eopetes irtyshensis* gen. et. sp. nov. **(A1–A5)** IVPP V23185, holotype of *J. jeminaiensis*, left M1/2; **(B1–B5)** IVPP V23186, left m1/2; **(C1–C5)** IVPP V23280, paratype, right m1/2; **(D1–D5)** IVPP V31378, holotype of *E. irtyshensis*, right m1/2.1, lingual view; 2, buccal view; 3, occlusal view; 4, anterior view; 5, posterior view. All in the same scale (bar equals 1 mm).

Etymology. "Junggar," Mongolian, referring to the Junggar Basin, the provenance of this new taxon; "sciurus" is from Greek *skiourus* (squirrel); "Jeminay," Mongolian, is the nearby county seat of the fossil sites.

Holotype. IVPP V23185, an isolated left M1/2 (Figures 3A1–5), collected from IVPP field site XJ20140619LQ03.

Paratype. IVPP V23280, a right m1/2 (Figures 3C1–5), collected from IVPP field site XJ20140619LQ03.

Referred specimen. IVPP V23186, a left m1/2 (Figures 3B1–5), collected from IVPP field site XJ20140626NI01.

Type Locality and Age. Jeminay, northwestern Xinjiang Uygur Autonomous Region, China, the Keziletuogayi Formation, late Eocene, 34.0–35.0 Ma.

Generic diagnosis

A large-sized sciurid. Molars are brachydont with incipient rugose floor in the trigon and talonid basins. M1/2 outline is quadrate; protocone is anteroposteriorly expanded; hypocone is absent; protoconule, metaconule, and mesotyle are indistinct; anterocone is reduced; protoloph and metaloph are complete and nearly parallel; metaloph is constricted at its junction with protocone; and protocone crest and ectoloph are absent. The m1/2 outline is more rectangular, metaconid is sharp, entoconid is well-delimited, mesoconid is developed or indistinct, hypoconulid and mesostylid are absent, trigonid basin is wide and enclosed by complete metalophid, talonid basin is incompletely enclosed with two notches near the center of the buccal and lingual sides, anterobuccal cingulid and entolophid are absent, anterobuccal sinusid at the junction of the protolophid is absent, ectolophid is weak and discontinuous, posterolophid is continuous and connected to entoconid. Slightly larger than *Protosciurus condoni* and remarkably larger than other known late Eocene–Oligocene sciurids. Furthermore, *Junggarisciurus jeminaiensis* differs from *Kherem* of Xerinae and *Palaeosciurus*, *Oligopetes*, *Protospermophilus*, *Miospermophilus*, *Protosciurus*, *Nototamias*, *Douglassciurus*, *Plesiosciurus* aff. *sinensis*, and Marmotini gen. et sp. of Sciurinae in its protoloph parallel to the metaloph on M1/2. Furthermore, it differs from *Kherem* and *Heteroxerus* of Xerinae and *Oligopetes*, *Miospermophilus*, and *Miosciurus* of Sciurinae in the absence of an anterobuccal sinusid on m1/2. It differs from *Sciurus* sp. (Sciurinae) in its less quadrate outline and well-developed metalophid, trigonid basin, and entoconid on m1/2. Compared to the taxa of Cedromurinae, it differs from *Cedromus* in its less developed or absent anteroconid, entolophid, and ectolophid on m1/2. It differs from *Oligospermophilus* by having more rounded corners, an absence of a hypocone and mesostyle on M1/2, and a less developed anteroconid, an entoconid merged into the posterolophid, and the absence of a mesostylid on m1/2. It differs from *Oligosciurus* in the presence of a mesostylid and mesoconid, a wide trigonid, a narrow buccal valley, and absence of an entolophid.

Specific diagnosis

Same as that of the generic diagnosis.

Measurements (in mm)

M1/2 (IVPP V23185): length × width = 3.63 × 4.75; m1/2 (IVPP V23186): 4.30 × 3.95; m1/2 (IVPP V23280): 4.15 × 3.90.

Description

The holotype M1/2 (Figures 3A1–5) has a quadrate outline that is wider than long. There are three marginal cusps and four lophs, which form a wide and deep middle and two narrow and shallow marginal depressions with an incipient rugose surface. The lingual main cusp is far higher than the buccal. Tooth anterior and buccal walls are less curved, while the posterior and lingual are rather rounded. The protocone is conspicuously large and anteroposteriorly expanded. The hypocone is absent. The paracone and metacone are small and nearly the same size. The anterocone is reduced and inconspicuous, merging with the anteroloph. Both the protoconule and metaconule are absent. No distinct parastyle, protoconule, or metaconule is present. The mesostyle is extremely small and inconspicuous. Both the protoloph and metaloph are complete, nearly parallel to each other, and extend slightly anterolingually toward the protocone. The protoloph is strong, and the metaloph is constricted distinctly at its junction with the protocone. The anteroloph and posteroloph are lower than the protoloph and metaloph. A protocone crest similar to that of *Douglassciurus jeffersoni* (see Emry and Korth, 1996) and an ectoloph resembling *Oligopetes* (Heissig, 1979) are not present. The trigon basin is deep and wide. The anterior valley is slightly narrower than the posterior. No roots are preserved.

The m1/2s (Figures 3B1–5, C1–5) have a nearly rectangular outline and are slightly anterobuccal-posterolingually compressed. There are four marginal cusps and three transverse lophs, surrounding a small, shallow anterior trigonid basin and a large, deep posterior talonid basin with a less rugose floor compared to *Oligopetes* and *Palaeosciurus*. The two anterior cusps project more than the two posterior cusps. The anterolingual metaconid is the highest and positioned slightly more anteriorly than the protoconid. The lingual entoconid is situated opposite of the buccal hypoconid, and it is well-delimited at lingoposterior corner of the tooth. The mesoconid is well developed on the referred specimen (IVPP V23186) but indistinct on the paratype (IVPP V23280). The anteroconid can be observed on the IVPP V23280 but merges with the anterolophid of the IVPP V23186. The hypoconulid and mesostylid are both absent. The metalophid is complete and encloses the trigonid basin. The ectolophid is weak and discontinuous. The posterolophid is strong and continuous, and it connects the hypoconid and entoconid. No entolophid (or hypolophid) is present. The buccal and lingual valleys are present as deep notches of external margin of the talonid basin. The anterobuccal cingulid is absent. There is no trace of an anterobuccal sinusid between anterolophid and protoconid. No roots are preserved.

Remarks

The Jeminay sample generally resembles that of living Sciurini, particularly *Sciurus,* by having a quadrate outline, a complete protoloph and metaloph, an absent metaconule on M1/2, a developed metalophid enclosing the trigonid basin, and a conspicuous entoconid on m1/2. It seems reasonable to refer the m1/2 to the tree squirrels (Qiu, 2019). However, it differs from *Sciurus* in its larger tooth size and having a transverse metalophid parallel to the anterolophid, a larger trigonid basin in contrast to that of *Sciurus*, and a V-shaped notch between the metaconid and entoconid on m1/2. For further comparative purposes, we discuss all known late Eocene and early-late Oligocene sciurid genera (16 taxa, above). The Jeminay sample differs from these taxa in both its dental size and morphology (see Generic diagnosis).

Genus *Eopetes* gen. nov.

Eopetes irtyshensis sp. nov.

Figures 3D1–5.

Etymology. “Eo-,” Greek, means dawn; “petes” is derived from the Sanskrit “patara” meaning flying; “Irtysh,” Mongolian, refers the Irtysh River near the holotype locality.

Holotype. IVPP V31378, an isolated right m1/2 (Figures 3D1–5), collected from IVPP field site XJ20140619LQ03.

Type Locality and Age. Jeminay, northwestern Xinjiang Uygur Autonomous Region, China, the Keziletuogayi Formation, late Eocene, 34.0–35.0 Ma.

Generic diagnosis

A large-sized sciurid. Lower molar brachydont with rugose floor and extra ridges in the talonid basin. Entoconid, hypoconulid, mesoconid, and ectomesolophid well-developed. Entoconid relatively isolated. No anterobuccal cingulid or sinusid. Protolophid low and extending posterolingually. Metastylid and mesostylid well developed. Trigonid basin posteriorly open. Compared to taxa of flying squirrels, it differs from *Oligopetes* by the presence of well-developed entoconid and hypoconulid and the absence of anterobuccal cingulid and anterobuccal sinusid and having a crowded talonid basin. It differs from *Parapetaurista*, *Miopetaurista*, *Hylopetodon*, *Yunopterus*, *Hylopetes*, *Pteromys*, *Petaurista*, and *Aeretes* in the absence of an anterobuccal cingulid and sinusid, a limited talonid basin, and a robust hypoconulid. It differs from *Belomys*, *Trogopterus*, and the *Pliopetaurista* in lophs being conspicuously weaker than the cusps.

Species diagnosis

Same as that of the generic diagnosis.

Measurements (mm)

The holotype m1/2 (IVPP V31378), length × width = 5.8 × 4.6.

Description and comparison

The tooth is brachydont with heavily built cusps and extra ridges. It has a rhomboid occlusal outline with projecting anterolingual metaconid and posterobuccal hypoconid corners. The metaconid is the highest of the main cusps, and it is situated further anteriorly than the protoconid. Posterior to the lingual part of the metaconid, the metastylid is present and has a short transverse ridge. No anterobuccal cingulid is present. The anteroconid is situated between the metaconid and the protoconid, is much lower than them, and is connected to them through thin ridges. The protoconid is subtriangular in outline, and it is separated from the posterior mesoconid. The trigonid is open posteriorly. The protolophid is low and wavy, derives from the anterolingual part of the protoconid, and extends posterolingually into the talonid basin, failing to reach the entoconid. The mesoconid is prominent, subtriangular in shape, and as high as the entoconid. The ectomesolophid is derived from the mesoconid, tapers buccally, slopes ventrally, and interrupts the buccal valley (=hypoflexid) by an anterior narrow groove and a posterior enclosed fossa surrounded by the ectolophid, hypoconid, mesoconid, and ectomesolophid. The mesostylid is present on the lingual margin, and it is situated between the metastylid and entoconid. The entoconid is nearly isolated and opposite the mesoconid. The entolophid is short and bulging and is buccally contracted. The ectolophid is short and longitudinally links the mesoconid and the hypoconid. The hypoconid has a long anterobuccal crest and a short posterior arm with an extra cuspid. A notch exists between the posterior side of the hypoconid and hypoconulid. The hypoconulid is triangular in shape, lower than the hypoconid, higher than the entoconid, and as large as the entoconid. The hypoconulid is separated from the entoconid. The anterior part of the talonid basin has a wrinkled surface, but the posterior part is occupied by the heavily built entoconid and hypoconulid. The space demarcated by the entoconid, hypoconulid, and ectolophid is quite limited.

This m1/2 has a complicated occlusal structure, with a rugose talonid surface, extra ridges, and a prominent entoconid. It seems reasonable to refer the m1/2 to the grouping of flying squirrels (Qiu, 2019). The m1/2 has a heavily built entoconid, hypoconulid, and meseoconid, and it lacks an anterobuccal cingulid or sinusid. That morphology resembles that of some genera of flying squirrels, such as the extant *Belomys* and *Trogopterus* and the fossil *Pliopetaurista*, but the morphology differs from other flying squirrels in the absence of an anterobuccal cingulid and sinusid, a limited talonid basin, and a robust hypoconulid (Qiu, 2019). Furthermore, the morphology of this m1/2 is so unique as to distinguish it from other Oligocene flying squirrels such as *Oligopetes* or the living representatives through its lophs being conspicuously weaker than the cusps. Although this taxon is represented currently by only one lower tooth, it is worth erecting a new genus and species for it given its large size and unique morphology.

Results

Derivation and early divergence of sciurids

The family Sciuridae is generally thought to have derived from the Ischyromyidae (including Paramyinae) in North America (Matthew, 1910; Wilson, 1949; Wood, 1962; Black, 1963; Emry and Thorington, 1984; Korth, 1984; Emry and Korth, 1996). Korth and Emry (1991) proposed that the Sciuridae possibly shares with the Aplodontidae a common ancestor that arose from a *Reithroparamys*-like ischyromyid with the Aplodontidae. Their view was accepted by many researchers (Korth, 1994; Emry and Korth, 1996; Mercer and Roth, 2003; Goodwin, 2008) but is still questioned by a few (de Bruijn, 1999; Heissig, 2003). *Junggarisciurus jeminaiensis* from the Junggar Basin is easily distinguished from *Reithroparamys* or other ischyromyids, and it displays conspicuous dental features, such as the lack of a hypocone, protoconule, and metaconule on M1/2, the absence of an anterobuccal sinusid at the junction of the anteroconid and protoconid, an inconspicuous ectolophid, the absence of an entoconid crest, and a joining of the entoconid and posterolophid on m1/2 (Wood, 1962). It seems that there is no close affiliation between the sciurid *J. jeminaiensis* and the ischyromyid *Reithroparamys*. *Junggarisciurus jeminaiensis* shares some characters with the ischyromyid *Hulgana ertnia*, which was erected based on the material collected from the Upper Eocene “Ulan Gochu” beds at Jhama Obo, East Mesa, Inner Mongolia (China) (Dawson, 1968). The shared characteristics include large size, deep talonid basin relative to the main cusps, outline of the lower molar rhomboid, indistinct conules, and absent hypocone, style (id)s, and hypolophid. However, *Hulgana ertnia*’s P4-M2 have an anterolingual protrusion of the protocone with crests converging on the protocone and a concavity at the lingual-posterior of the protocone, and its lower molars have incompletely enclosed the trigonid and lack a mesoconid. Furthermore, on the buccal side the mandible of *H. ertnia*, the apex of the masseteric ridges is situated far posteriorly (posterior to m2), but that of the Sciuridae is placed anteriorly (m1 or posterior p4) (Qiu, 2019). Unfortunately, the specimen of *Junggarisciurus jeminaiensis* has no jaw, so the situation of the apex of the masseteric ridges of this species is unknown. *Eopetes irtyshensis* has a special dental morphology on m1/2 with crenulations and stylids, the presence of a robust entoconid, hypoconulid, and mesoconid, and the absence of an anterobuccal sinusid, resembling that of some flying squirrels, particularly the extant *Belomys* and *Trogopterus* and extinct

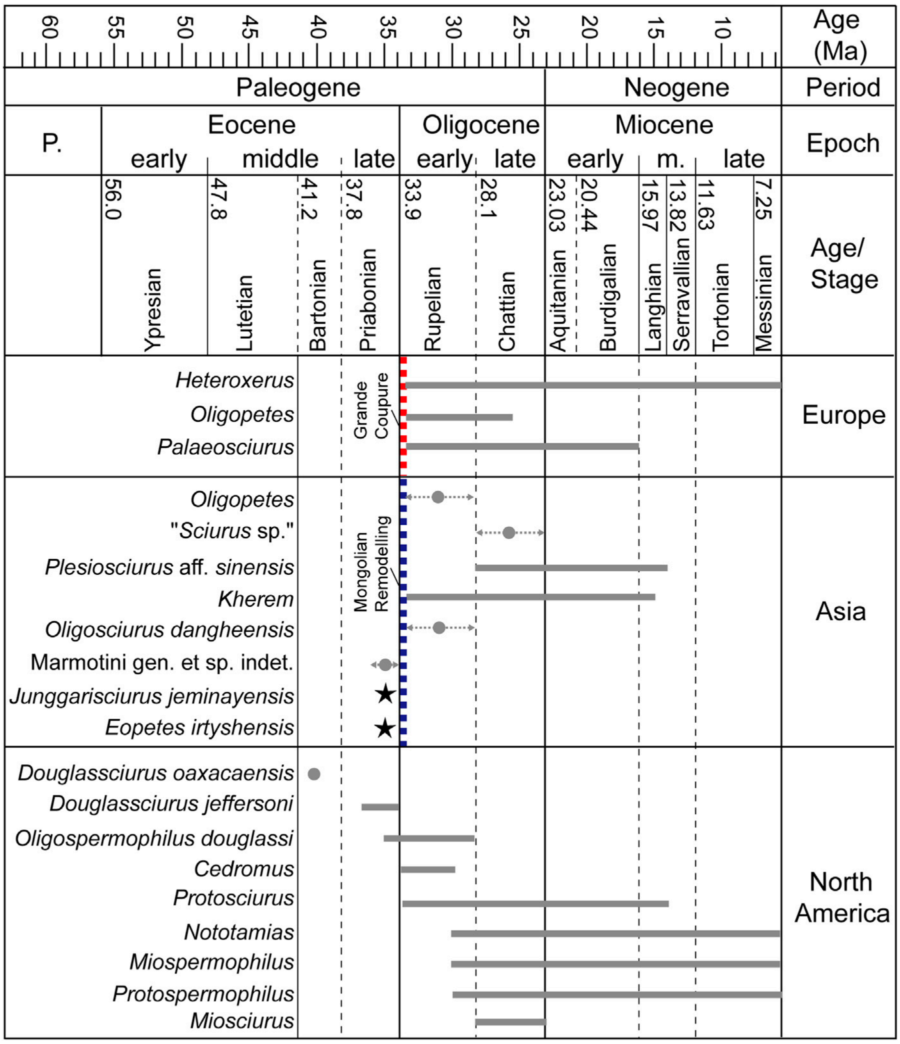

FIGURE 4
Chronologic ranges of Eocene to Oligocene sciurids from North America, Asia, and Europe. The fossil records of sciurids span the Eocene/Oligocene boundary in both North America and Asia but appear later in the early Oligocene of Europe. *Douglassciurus oaxacaensis* is the earliest member of sciurids in late middle Eocene*, Junggarisciurus jeminaiensis*, *Eopetes irtyshensis*, *Douglassciurus jeffersoni,* and *Oligospermophilus douglassi* form the second earliest confident records of sciurids in the late Eocene. Red dashed line, Grande Coupure; blue dashed line, Mongolian Remodelling; gray dot with dashed arrowed line, estimated date; asterisks, *J. jeminaiensis* and *E. irtyshensis* from Jeminay, northwestern Xinjiang, China. Abbreviations: *P*., Paleogene; m., middle Miocene.

Pliopetaurista (Qiu, 2019). *Eopetes irtyshensis* differs from *Reithroparamys* or other ischyromids in having a robust hypoconulid, a weaker metalophid, and an entolophid extending toward the mesoconid. It seems that the Sciuridae were not derived directly from any known ischyromids. In fact, there is still a large time gap between the records of latest ischyromids (early middle Eocene) and the earliest sciurids (late Eocene) (Tong and Li, 2019).

Mercer and Roth (2003) used the age of *Douglassicurus* (36 Ma) as the calibration of their molecular-clock tree of sciurids, which yielded an estimated divergence date of 50 Ma for the node joining *Aplodontia* and Sciuridae. It seems that we should explore for the origins of sciurids in the middle or even early Eocene (the interval of 50–36 Ma) of North America or Asia. Recent discovery of *Douglassciurus oaxacaensis* from late middle Eocene (about 40 Ma) Oaxaca, Mexico, seems to prove this judgment. Mercer and Roth (2003) also estimated that the divergence of the five major clades of squirrels had arisen penecontemporaneously with the EOT. These late Eocene squirrels from Jeminay lived in northwestern China at about 35–34 Ma in the late Eocene. The discovery of *Junggarisciurus jeminaiensis* and *Eopetes irtyshensis* provides a minimum age of calibration for the Sciurinae crown group fairly close to the molecular clock estimated late Eocene 36 Ma split. Based on the fossil-calibrated molecular-clock phylogeny of modern squirrel genera by Mercer and Roth (2003); Roth and Mercer (2008) further investigated the macroevolutionary processes among the linages since the origin of the Sciuridae. Roth and Mercer (2008) described the diversification of squirrels as taking place in three phases: initial (36–30 Ma); intervening (30–7 Ma); and recent (~7 Ma to present) phases. Their results show that the initial phase of squirrel evolution was a rapid burst of diversification (Roth and Mercer, 2008). The two new taxa from Jeminay indicate that there were at least two genera of Sciurinae that occurred in late Eocene Asia.

TABLE 1 Measurements (in mm) of M1/2s and m1/2s of late Eocene-Oligocene sciurids. a.-p., anteroposterior length; tr., maximum transverse width. Measurements of taxa 2–10 and 12–21 derive from the references listed in this table, and those of taxon 11 are estimated from the illustration by Stehlin and Schaub (1951, p. 201). All sources are in the References.

		M1/2		m1/2	
	Taxa (references)	Range of a.-p.	Range of tr.	Range of a.-p.	Range of tr.
1	*Junggarisciurus jeminaiensis* (this text)	3.63	4.75	4.15–4.30	3.90–3.95
2	*Eopetes irtyshensis* (this text)	-	-	5.8	4.6
3	*Oligosciurus dangheensis* (Wang and Qiu, 2004)	-	-	1.60–1.80	1.80–2.0
4	*Kherem hsandgoliensis* (Minjin, 2004)	-	-	1.85–2.10	1.96–2.10
5	*Kherem hsandgoliensis* (Wang and Dashzeveg, 2005)	2.20–2.30	3.10	2.10–2.50	2.30–2.70
6	*Kherem hsandgoliensis* (Maridet et al., 2014)	1.99–2.11	2.51–2.60	2.53–2.59	2.58–2.65
7	*Sciurus* sp. (Bohlin, 1946)	-	-	1.70	1.80
8	Marmotini gen. et sp. indet. (Wang, 2008)	2.10	2.10	-	-
9	*Plesiosciurus* aff. *sinensis* (Maridet et al., 2014)	1.42	1.70–1.82	1.58–1.66	1.50–1.63
10	*Palaeosciurus goti* (Vianey–Liaud, 1974)	1.50–1.83	1.81–2.07	1.65–1.99	1.61–2.01
11	*Oligopetes radialis* (Heissig, 1979)	1.70–2.0	2.05–2.20	1.75–1.90	1.70–1.90
12	*Heteroxerus hürzeleri* (Stehlin and Schaub, 1951)	-	-	1.64–1.87	1.84–1.95
13	*Douglassciurus jeffersoni* (Emry and Korth, 1996)	2.63–3.01	3.45–3.90	2.52–3.10	2.82–3.33
14	*Douglassciurus sapphirus* (Korth, 2009)	1.77–1.90	2.23–2.28	1.84–1.92	1.94–2.25
15	*Douglassciurus bjorki* (Korth, 2014)	2.22–2.75	2.76–3.29	2.12–?	2.24–?
16	*Douglassciurus oaxacaensis* (Ferrusquia-Villafranca et al., 2018)	-	-	1.65–1.91	1.63–1.69
17	*Oligospermophilus douglassi* (Korth, 1987)	1.92–2.19	2.32–2.64	-	-
18	*Cedromus wardi* (Korth and Emry, 1991)	-	-	2.47–2.71	2.70–2.79
19	*Cedromus wilsoni* (Korth and Emry, 1991)	2.17–2.30	2.83–3.0	2.15–2.32	2.37–2.75
20	*Protosciurus condoni* (Black, 1963)	3.40–3.60	3.80–4.0	3.30–3.60	3.40–3.80
21	*Protosciurus mengi* (Black, 1963)	-	-	2.50–2.80	2.70–3.10
22	*Protospermophilus quatalensis* (Gazin, 1930)	2.20–2.30	2.60–2.70	2.0–2.40	2.30–2.70
23	*Miospermophilus bryanti* (Black, 1963)	1.50–1.75	2.0–2.20	1.60–1.80	1.80–2.0
24	*Miosciurus ballovianus* (Black, 1963)	1.50	1.70	1.50–1.60	1.50–1.70
25	*Nototamias hulberti* (Pratt and Morgan, 1989)	1.0–1.30	1.20–1.56	0.98–1.28	1.24–1.61

Squirrels have been divided typically into three morphotypes (ground, tree, and flying) based on their dental and jaw morphologies (e.g., De Bruijn, 1999; Qiu, 2019). *Junggarisciurus jeminaiensis* belongs to the tree squirrel morphotype because it possesses a less rugose surface of the trigon and talonid basins, a complete metaloph, a nearly parallel protoloph and metaloph of M1/2, and a well-delimited entoconid of m1/2. The morphology of *Eopetes irtyshensis* is consistent with that of a typical flying squirrel because it exhibits a complicated dental pattern with a distinct rugose floor of the talonid basin, extra ridges and stylids, and a prominent entoconid. Of the known records, North America is possibly the birthplace of squirrels. *Douglassciurus oaxacaensis* from late middle Eocene (about 40 Ma) in Oaxaca, southeastern Mexico, is possibly the earliest squirrel (Ferrusquia-Villafranca et al., 2018). Due to the lack of upper molars, the morphotype of *D. oaxacaensis* is uncertain. Four late Eocene species, *Douglassciurus jeffersoni* and *Oligospermophilus douglassi* from North America and *Junggarisciurus jeminaiensis* and *Eopetes irtyshensis* from Central Asia, are the second earliest records of the Sciuridae (Figure 4). These fossil records demonstrate that by the late Eocene, the sciurids had diverged into the three principle morphotypes, represented by the earliest flying squirrel *Eopetes irtyshensis* from northwestern China (this text), the earliest ground squirrel *Oligospermophilus douglassi* from North America (Korth, 1987), and the earliest tree squirrels *Douglassciurus jeffersoni* from North America (Emry and Korth, 1996) and *Junggarisciurus jeminaiensis* from Jeminay, northwestern China (this text).

After the Eocene/Oligocene boundary, members of Sciuridae rapidly spread into Europe and flourished across the Holarctic region during the Oligocene. That radiation is demonstrated by the occurrence of eight genera in the early Oligocene, represented by *Heteroxerus* (ground) and *Palaeosciurus* (tree) in Europe, *Oligopetes* (flying) in Europe and South Asia, *Kherem* (ground) and *Oligosciurus* (tree) in North Asia, and *Oligospermophilus* (ground), *Cedromus* (ground) and *Protosciurus* (tree) in North America (Figure 4). With the oldest sciurid records from Asia and North America predating the first occurrences in Europe, it would seem that sciurids are a component of the European Grand Coupure. Without a phylogenetic context, it is not presently possible to determine if the first sciurids in Europe came from Asia or North America. However, a hypothesis of an Asian origin for those dispersers would seem more likely given the preponderance of mammalian lineages known to have dispersed from Asia to Europe at the start of the Oligocene (coincident with climatic changes and the loss of seaway barriers). In parallel, the published bird (Anatidae: cf. Romainvilliinae) from the same bed as these new sciurid taxa represents an Asian record (late Eocene) predating the group's first appearance in Europe (Oligocene) as another indicator of potential central-Asia-to-Europe dispersal (Stidham and Ni, 2014).

Body mass estimation and paleohabitat

The large size of these fossils is a striking feature of the two new fossil sciurid taxa from Jeminay, northwestern China. The smaller *Junggarisciurus jeminaensis* is slightly larger than *Protosciurus condoni* and remarkably larger than the 22 other Eocene-to-Oligocene compared taxa in Table 1. To understand the rodents' paleoecological roles, we estimated their body mass from these isolated cheek teeth using published methods (e.g., Legendre, 1989; Hopkins, 2008; Goodwin and Bullock, 2012; Freudenthal and Martín-Suárez, 2013). Following the regression equations of Freudenthal and Martín-Suárez (2013, p.7 and p. 8, see Body mass estimation in Materials and methods in this text), we calculated that the average body masses of *Junggarisciurus jeminaensis* and *Eopetes irtyshensis* were ~1.2 kg and 2.6 kg, respectively. Among living squirrels, the majority of taxa have average body weights less than 1.0 kg. Only a few are over 1.0 kg, including a tree squirrel *Rheithrosciurus macrotis*, several flying squirrels *Ratufa*, *Petaurista*, *Petinomys crinitus*, and *Aeromys tephromelas*, and most species of ground squirrels *Cynomys* and *Marmota* (Thorington and Heaney, 1981; Ernest, 2003; Hayssen, 2008; Jones et al., 2009; Thorington et al., 2012; Freudenthal and Martín-Suárez, 2013). *Marmota* has an extreme body mass ranging up to 8.0 kg, but *Cynomys* is normally less than 2 kg. Both of them are well adapted to their fossorial steppe environments. The other large living tree and flying squirrels (body mass concentrated in the range of 1–2 kg) all dwell in forests, ranging across tropical rainforest, subtropical deciduous, mixed deciduous and moist evergreen, coniferous and broadleaf, montane and riparian forests. Forests supply large tree or flying squirrels with diverse foods, including seeds, fruits, nuts, bark, insects, and even bird eggs (Thorington et al., 2012). Emry and Thorington (1984) considered that the large tree squirrels should have relatively few competitors, other than birds, for the rich source of nutrients in the forest.

Compared to the monsoon-dominated climatic pattern after the Oligocene–Miocene Transition (OMT), the Paleogene climate of China is considered to have displayed a typical zonal pattern (Wang F. Y., 1984; Sun and Wang, 2005; Guo et al., 2008). During the Eocene and Oligocene, the Junggar Basin is hypothesized to have been situated in a warm-temperate zone (Wang P. X., 1984) or in a subtropical humid vegetation zone of northern China (Sun and Wang, 2005) and to have had a humid environment, contrasting with the arid or semi-arid belt of Guo et al. (2008). In the late Eocene Irtysh River area, fossil pollen assemblages are dominated by coniferous plants like *Pinuspollenites*, *Piceaepollenites*, *Abiespollenites*, and *Podocarpidites*, and broadleaved taxa such as *Betulaepollenites*, *Quercoidites*, *Ulmipollenites*, and *Juglanspollenites*, pointing to a mixed coniferous and broadleaved forest paleoenvironment (Sun et al., 2014). The occurrence of the large tree squirrel *Junggarisciurus jeminaensis* and the flying squirrel *Eopetes irtyshensis* helps to support this palynological hypothesis of the existence of a forested paleoenvironment in the late Eocene Irtysh River area rather than arid conditions.

Conclusion and perspectives

Based on the large dimensions and unusual morphology of these isolated molar fossils, we erect two new fossil genera and species of squirrels from the late Eocene of the Jeminay area of the Junggar Basin in northwestern China. *Junggarisciurus jeminaensis* displays molars with a "tree squirrel" morphotype, and *Eopetes irtyshensis* has a lower molar with a "flying squirrel" morphotype. These fossils and taxa are first two confirmed representatives of sciurids in the late Eocene of North Asia and they extend the first appearance of squirrels into the Eocene of Asia.

The impressive size of these two new species from the Junggar Basin leads to estimated body masses of *Junggarisciurus jeminaensis* and *Eopetes irtyshensis* being ~1.2 kg and 2.6 kg, respectively. All of the extant species of tree or flying morphotype squirrels over 1 kg inhabit forested habitats, and it would seem likely to regard *J. jeminaensis* and *E. irtyshensis* as having lived in late Eocene forests of Central Asia, consistent with the palynologic analysis by Sun et al. (2014). That interpretation of a forested habitat in the late Eocene of Central Asia will feed into future work investigating the process and pattern of aridification of Central Asia.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in the article/Supplementary Material.

Author contributions

XN and QL led and CQ and HG participated in the fieldwork in the Jeminay area for correlating the stratigraphy and collecting fossils. QL digitized the fossil specimens. QL, XN, and TS wrote the manuscript draft. All authors discussed and revised the manuscript.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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