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## EDITED BY

K. Christopher Beard,  
University of Kansas, United States

## REVIEWED BY

Pauline Coster,  
National Geologic Nature Reserve of  
Luberon, France  
Wilma Wessels,  
Utrecht University, Netherlands

## \*CORRESPONDENCE

Qian Li  
liqian@ivpp.ac.cn

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# Rodent faunas, their paleogeographic pattern, and responses to climate changes from the early Eocene to the early Oligocene in Asia

Qian Li<sup>1,2\*</sup>, Qi Li<sup>1,3</sup>, Rancheng Xu<sup>1,4</sup> and Yuanqing Wang<sup>1,2,4</sup>

<sup>1</sup>Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China, <sup>2</sup>CAS Center for Excellence in Life and Paleoenvironment, Beijing, China, <sup>3</sup>Centre for Vertebrate Evolutionary Biology, Yunnan University, Kunming, China, <sup>4</sup>College of Earth and Planetary Sciences, University of Chinese Academy of Sciences, Beijing, China

Rodents are an important component in Paleogene terrestrial ecosystems. Their evolution and faunal turnover have likely been influenced and triggered by global climate change. Here, we compiled rodent faunas from the early Eocene to the early Oligocene in Asia to discuss rodent faunal turnover and its correlation with paleogeographic and paleoclimate changes. Successive rodent faunas from the early Eocene to the early Oligocene are recorded in East Asia, and rodent faunal turnover is obviously affected by paleoclimatic changes. During the Ulangochuan (after the middle Eocene climatic optimum), when temperatures declined slowly, the East Asian rodent fauna showed a clear decline in generic diversity and a transformation from ctenodactyloid-dominant to cricetid–dipodid-dominant faunas. During the Eocene–Oligocene transition (EOT) and global cooling, the East Asian rodent fauna exhibited a considerably high generic diversity of cricetids, dipodids, and ctenodactylids. The low temperatures during the Ulangochuan and Ergilian in East Asia served as a habituation ground for the cricetids and dipodids, which became preadapted for the EOT, successfully helping rodents become dominant faunas after EOT. The rodent faunas in South Asia formed a relatively unique group in much of the Eocene and early Oligocene; sometimes, they were closer to European or African than to Asian rodents. The greatly different paleoenvironment probably caused striking differences between the rodent faunas in South Asia and East Asia.

## KEYWORDS

Paleogene, climate change, rodent fauna, East Asia, South Asia

## Introduction

Today, rodents are the most diverse and abundant terrestrial mammals. Rodents constitute over half the species of living mammals, and their fossil forms are also extremely diverse. Rodents are found worldwide, except for Antarctica and some oceanic

islands, and they exhibit a number of different lifestyles and locomotor behaviors. While generalized rodent adaptation is terrestrial, various forms are more specialized for climbing, gliding, swimming, or digging. Because of their large populations and short gestation periods, rodents have more advantages than other mammals in fauna in terms of biostratigraphic comparison and the relationship between mammal evolution and climate change.

The rodent fossil record has expanded at a significant pace, and fossils are increasingly discovered in regions that have been previously less known for fossils. In Asia, the complex rodent evolutionary history began during the early Eocene, from which the oldest fossils have been found (Li et al., 1989; Meng and Li, 2010; Li and Meng, 2015). The Paleogene is a key period for the origin and evolution of rodents, and the paleoclimate had multiple changes during the Paleogene (Westerhold et al., 2020), such as the global cooling event during the Eocene–Oligocene transitional period (Meng and McKenna, 1998; Kraatz and Geisler, 2010; Zhang et al., 2012; Sun et al., 2014); thus, we focus on rodent fossil records in Asia from the early Eocene to the early Oligocene. Furthermore, by taking advantage of an updated Cenozoic timescale in Asia (Romer, 1966; Luterbacher et al., 2004; Vandenberghe et al., 2012; Wang et al., 2019; Speijer et al., 2020), we use all available rodent faunal data and analyze rodent composition and diversity at the genus level, noting the different rodent assemblages and faunal turnovers. We discuss the possible relationships between the rodent evolution and faunal turnover and paleoclimatic changes. In addition, because different rodent assemblages also appeared in different areas of Asia during the same period, we consider the possible relationships between faunal dispersal and paleogeographic transformation.

## Methods

### Biochronology

Following the principle of North American land mammal ages, Romer (1966) proposed some related Asian Paleogene land mammal ages on the basis of mammalian faunas from different stratigraphic levels, which have formed the foundation for further Asian Paleogene chronostratigraphic study (Wang et al., 2019). These land mammal ages have often been used in discussing intercontinental biostratigraphic correlation and mammalian dispersals. Now, the Bumbanian, Arshantan, Irdinmanhan, Sharamurunian, Ulangochuian, and Ergilian ages in the Eocene, and the Hsandagolian age in the Oligocene have been adopted as the Asian Paleogene land mammal ages in the geologic time scales (Luterbacher et al., 2004; Vandenberghe et al., 2012; Speijer et al., 2020).

For many years, the Ulangochuian land mammal age that is currently used in the Chinese Paleogene land mammal age

sequence was equivalent to both the Ulangochuian and Ergilian Asian land mammal ages (Tong et al., 1995; Vandenberghe et al., 2012). A recent investigation in the Erlian Basin, Nei Mongol, revealed that deposits between those with typical Ulangochuian and early Oligocene mammal faunas contain fossil mammals that are correlated to the Mongolian Ergilian fauna; thus, the Baiyinian land mammal age was proposed as the equivalent of the Ergilian in the Chinese Paleogene land mammal age sequence (Wang et al., 2019).

Here, these Asian Paleogene land mammal ages are used to indicate the evolution and turnover of rodent faunas in more detail. The ages of fossil localities are inferred based on the latest biostratigraphic, magnetostratigraphic, and radiometric dating.

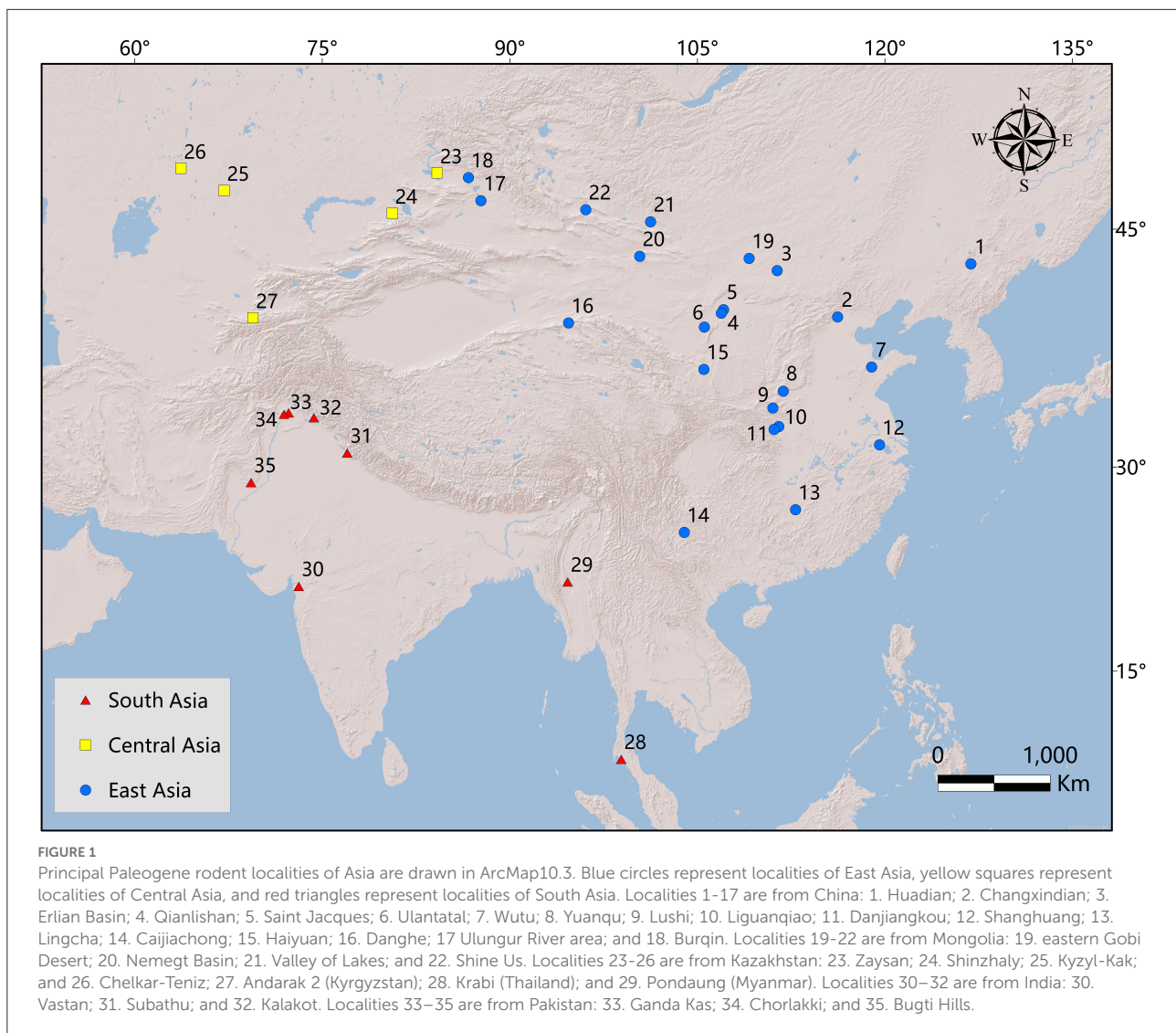
### Distribution of localities

Known rodent fossils are widely distributed in different areas of Asia, and the different mammalian fossil compositions may have been caused by paleogeographic patterns or may indicate different habitat conditions. The present study considers 35 localities that are biostratigraphically dated from the early Eocene to the early Oligocene (Appendix Tables 1–3) and assembled into three regions of Asia: East Asia (China and Mongolia), Central Asia (Kyrgyzstan and Kazakhstan), and South Asia (India, Pakistan, Thailand, and Myanmar) (Figure 1).

### Taxonomy

Known rodent fossils were classified into different rodent families, and the taxonomic system of the family that was adopted in our analysis is as follows: Alagomyidae, Orogomyidae (Dashzeveg, 1990b), Aplodontidae (Wood, 1980), Anomaluroidea (Marivaux et al., 2005), Archetypomyidae (Meng et al., 2007), Castoridae, Sciuridae (McKenna and Bell, 1997), Ctenodactylidae (Wang, 1997a, 2001b), Cricetidae (Wang et al., 2020), Cylindrodontidae (Wood, 1980; Wang, 2019), Diatomyidae (Mein and Ginsburg, 1997), Dipodidae (Qiu and Wang, 2019), Eomyidae (Fejfar et al., 1998), Ischromyidae (Anderson, 2008), Tsaganomyidae (Wang, 2001a), and Zelomyidae (Dawson et al., 2003a).

Regarding ctenodactylids, recent phylogenetic analysis indicated that some families or subfamilies, such as Cocomyinae, Advenimurinae (Dashzeveg, 1990a), Tamquammyidae (Averianov, 1996; Tong, 1997), Yuomyidae (Dawson et al., 1984; Tong, 1997), and Chapattimyidae (Averianov, 1996), are probably paraphyletic (Li and Meng, 2015). Because of the poor preservation of some early ctenodactylid rodents and the complicated history of taxonomic studies on the group, it is extremely difficult to conduct a thorough phylogenetic analysis of ctenodactylids. Some researchers have suggested the use of Ctenodactyloidea without reference to a specific family for the



Eocene genera [Dashzeveg and Meng, 1998](#); [Li and Meng, 2015](#)). Here, we also followed this opinion; most Eocene genera of ctenodactylids included Ctenodactylidae as a monophyletic is a generally accepted view; here, late Eocene *Karakoromys* and Oligocene ctenodactylids were included in Ctenodactylidae ([Wang, 1997a, 2001b](#)).

Indeterminate taxon identifications and taxonomic modifications, such as “cf.” or “?”, or some cases of “sp.”, were included in our analyses as a record.

## Diversity and sampling biases

The simplest method to count the number of taxa to measure biodiversity may produce biases that distort the diversity pattern due to the different preservation and sampling intensities of various fossils. The rarefaction method is widely

used in paleontology for removing biases ([Gotelli and Colwell, 2001](#); [Shen et al., 2004](#); [Huang, 2012](#)); here, paleobiological biodiversity curves were corrected using rarefaction by PAST software ([Hammer et al., 2001](#)).

## Results

### Bumbanian rodent assemblage

Early Eocene Bumbanian rodent fossil assemblages are present in China, Mongolia, and India. In China, the Bumbanian rodent fossil localities are present in multiple regions, including Hunan, Hubei, Nei Mongol, Shandong, and Henan ([Li, 1963](#); [Dawson et al., 1984](#); [Li et al., 1989, 2018](#); [Hu, 1995](#); [Tong, 1997](#); [Guo et al., 2000](#); [Wible et al., 2005](#); [Tong and Wang, 2006](#); [Meng and Li, 2010](#); [Li and Meng, 2015](#)). In addition, abundant rodent

fossils are found in the Bumban Member of the Naran-Bulak Formation of the Tsagan Khushu locality in the Nemegt Basin of Mongolia (Shevyreva, 1989; Dashzeveg, 1990a,b), and an ischyromyid rodent, *Meldimys*, is recorded in the lower Eocene Vastan lignite mine of western India (Rana et al., 2008); this occurrence is the oldest record of a rodent from India.

The Bumbanian rodent assemblages from China and Mongolia are similar in the dominance of original ctenodactylids, and original rodents such as *Alagomys* are also present (Figure 2) (Appendix Table 1). Ctenodactylid rodents in Bumbanian, as the oldest known rodents with modern features in Asia, already have a high diversity and are represented by different ctenodactylid genera known primarily from China and Mongolia.

Except for ctenodactylids, other basal rodent families are present in China and Mongolia. *Alagomys* is from the Erlian Basin of Nei Mongol of China and the Nemegt Basin of Mongolia. However, the validity of the familial association of *Alagomys* is still unknown. Meng and Wyss (2001) excluded *Alagomys* from the Rodentia, but others pointed out that *Alagomys* is close to true rodents and is generally considered the most primitive rodent (Dawson, 2015). Based on the similarities of *Alagomys* and the original ctenodactylids and cylindrodontids, we also adopted *Alagomys* in Rodentia and Alagomyidae (Dashzeveg, 1990b). *Archetypomys* is a primitive rodent and occupies an intermediate phylogenetic position between alagomyids and rodents of modern features. Primitive ischyromyids, such as *Actioparamys* and *Taishanomys*, are also present in the Bumbanian rodent assemblage from China. *Orogomys* from the Nemegt Basin of Mongolia was classified as Orogomyidae (Dashzeveg, 1990b).

## Arshantan rodent assemblage

The Arshantan rodent assemblages are known in East, Central, and South Asia. In East Asia, Arshantan rodents appeared in the Erlian Basin of Nei Mongol and in the Junggar Basin of Xinjiang, China (Meng et al., 2001; Li and Meng, 2010, 2015; Li et al., 2018; Li, 2019). The ~2,900 Arshantan rodent specimens collected from the Erlian Basin represent at least 323 individuals, as counted by the minimum number of individuals (MNI), and rodents from the Erlian Basin have an absolute advantage in both number and species diversity. In Central Asia, abundant rodents are known at the Andarak 2 locality in Kyrgyzstan (Averianov, 1996) and the Zaysan Depression in eastern Kazakhstan (Shevyreva, 1984, 1996). The South Asian Arshantan rodents were described in the lower middle part of the Subathu Formation of the type area in Himachal Pradesh, northwestern sub-Himalaya, India (Gupta and Kumar, 2015).

In the Arshantan rodents, whether in East Asia, Central Asia, or South Asia, ctenodactylids are a dominant element (Figure 3). In China, ctenodactylids contain the primitive

ctenodactylid *Tamquammys*, *Chenomys*, *Simplicimys*, and *Advenimus*. Among them, *Tamquammys*, *Advenimus*, and *Chenomys* were present in the Bumbanian and in the Arshantan assemblage.

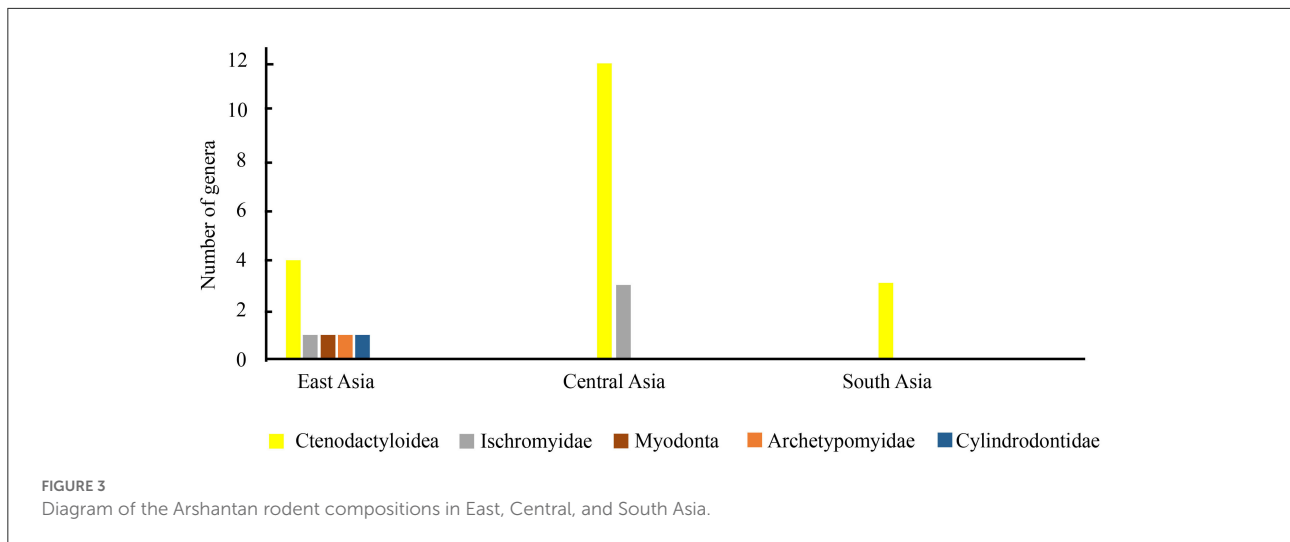
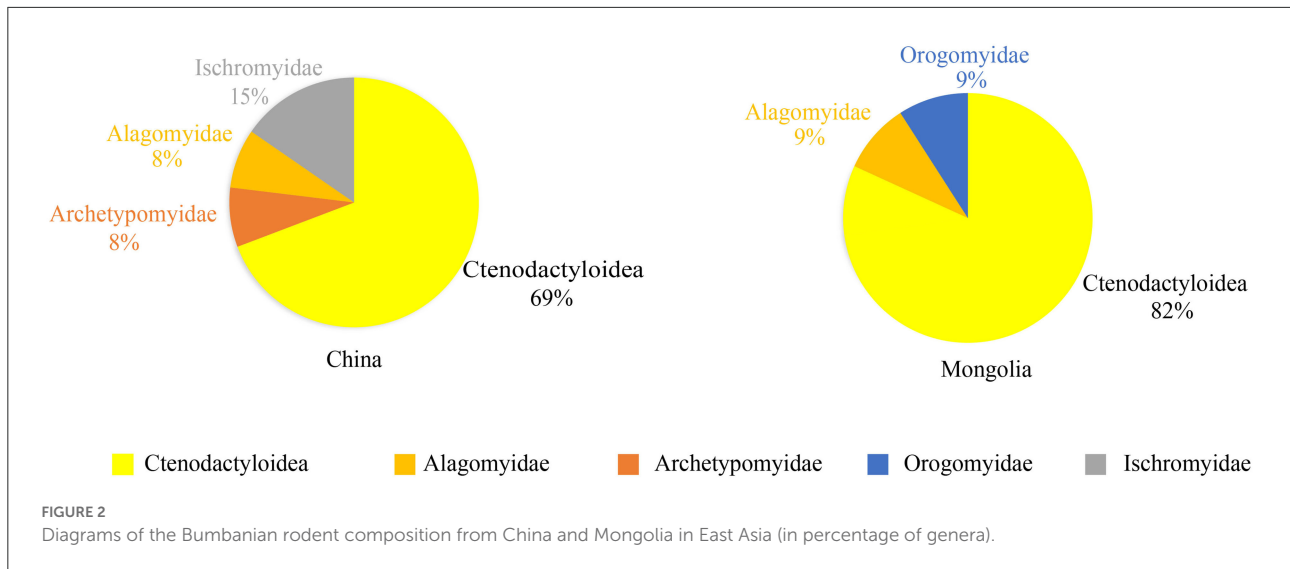
In Central Asia, ctenodactylid rodents have high generic richness and are clearly different from East and South Asian ctenodactylids in genera (Appendix Tables 1–3). Only *Advenimus* is present in East and Central Asia, which may suggest that some faunal exchanges occurred between East and Central Asia during the Arshantan. Only ctenodactylids *Subathumys*, *Birbalomys*, and *Chapattimys* are present in South Asia. Except for various ctenodactylids, in East Asia, the primitive myodont *Erlanomys* (Li and Meng, 2010), the basal cylindrodontid *Gobiocylindrodon* (Li et al., 2019), the primitive rodent *Archetypomys*, and some ischyromyid fossils (Li, 2016) from the Arshantan rodent assemblage are present (Figure 3). In Central Asia, the ischyromyids *Mneiomys*, *Paramys*, and *Abrosomys* were found in the Zaysan depression in Kazakhstan (Shevyreva, 1984, 1996).

The ctenodactylids in Central Asia were classified as Chapattimyidae or Tamquammyidae by Averianov (1996) and Shevyreva (1984, 1989), and South Asian ctenodactylids were included in Chapattimyidae (Gupta and Kumar, 2015). The phylogenetic analysis of these families indicated that they are not monophyletic (Li and Meng, 2015). Resolving phylogenetic problems is difficult and beyond the scope of this study. However, the P4/p4 morphology, either molariform or nonmolariform, has been frequently emphasized as an important characteristic in ctenodactylid rodents. The ctenodactylids classified as yuomyids and chapattimyids are distinguished from other ctenodactylids by their molariform P4/p4 morphology. Recently, the characteristics of the molariform P4/p4 morphology have also been further clarified by Li and Meng (2015). According to the P4/p4 morphology, in the Arshantan, most East Asian ctenodactylids present nonmolariform premolars, and the ctenodactylids with molariform premolars are more commonly found in Central and South Asia. Gupta and Kumar (2015) described *Subathumys* from the Subathu Formation of India and pointed out that chapattimyids originated in the sub-Himalayan region during the Ypresian. According to the aforementioned description, ctenodactylids with molariform premolars quite possibly originated from South Asia; they moderately diversified in Arshantan and spread rather quickly into Central Asia.

In summary, the Arshantan rodent assemblages in East, Central, and South Asia are distinct, and they rarely have the same genera.

## Irdinmanhan rodent assemblage

The middle Eocene Irdinmanhan rodent assemblage is found in China in East Asia, eastern Kazakhstan in Central

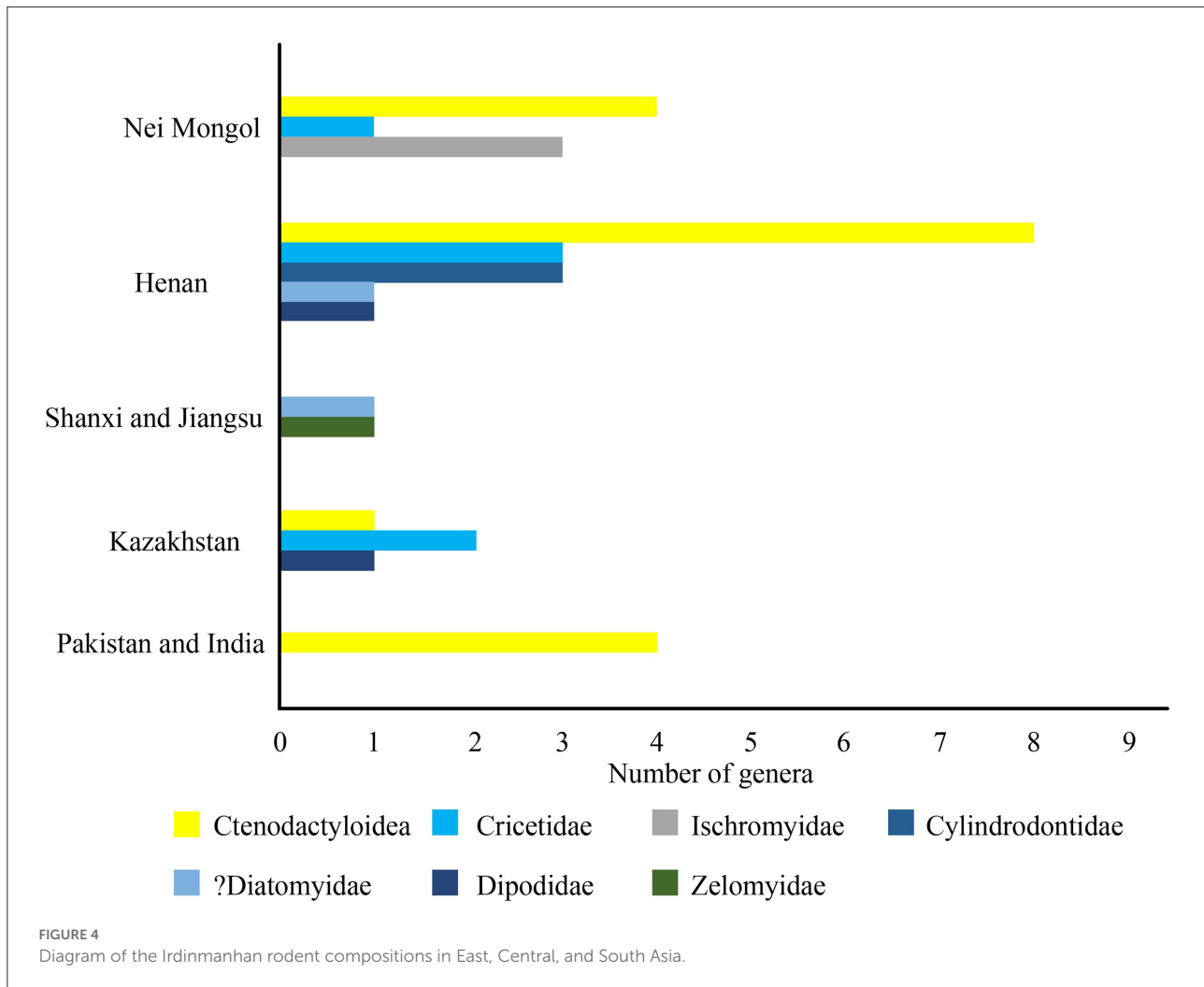


Asia, and Pakistan and India in South Asia. In China, the Irдинmanhan rodent fossil localities are known in Nei Mongol, Henan, Jiangsu, and Shanxi (Li, 1963, 2012; Tong, 1997; Dawson et al., 2003a, 2010; Li and Meng, 2013, 2015; Li et al., 2016, 2018; Fostowicz-Frelik et al., 2021). Irдинmanhan rodents are found in the Kolpak Formation of the Shinzhalı River in eastern Kazakhstan (Emry et al., 1998b). In South Asia, Irдинmanhan rodents have been recorded in the upper part of the Subathu Formation in India (Sahni and Khare, 1973; Sahni and Srivastava, 1976; Kumar et al., 1997a,b; Gupta and Kumar, 2015), the Kuldana Formation of the Ganda Kas area, and the Mami Khel Formation of the Chorlakkı area in Pakistan (Hussain et al., 1978; Hartenberger, 1982; Dawson et al., 1984; Thewissen et al., 2001).

In East Asia, the Irдинmanhan rodent assemblage has more derived members than the Bumbanian and Arshantan

rodent assemblages, such as cricetids, dipodids, zelomyids, and ? diantomyids (Appendix Table 1). The rodent faunas in some localities of the Erlıan Basin in Nei Mongol and the Shipıgou locality in Henan have been studied in detail based on the MNI (Tong, 1997; Li, 2016). The generic rodent number in Henan is the highest in China. Ctenodactyloids are major components in Henan and Nei Mongol, and cricetids, ischyromyids, and cylindrodontids are moderately diversified in the Irдинmanhan rodent assemblage (Figure 4). The few fossils of Zelomyidae and ? Diatomyidae appeared in the fissure D in the Shanghuang fissure in Liyang, Jıgansu, and Huoshıpu of the Yuanqu Basin, Shanxi (Dawson et al., 2003a, 2010).

The Irдинmanhan rodents in Kazakhstan are similar to those in China, and they also contain ctenodactyloids, dipodids, and cricetids. Ctenodactyloid *Saykanomys* and cricetid *Pappocricetodon* are present in China and Kazakhstan. In



South Asia, the Irindinmanhan rodent assemblage is distinctly different from the rodent assemblage in East and Central Asia and is characterized by only ctenodactyloids that were classified as *Chapattimyidae* (Gupta and Kumar, 2015). The Irindinmanhan rodents in India and Pakistan are very similar; the dominant elements in these areas are *Birbalomys* and *Chapattimys*, which first appeared in the Arshantan rodent assemblage in India (Gupta and Kumar, 2015), extended to the Irindinmanhan assemblage and showed high species diversity.

## Sharamuronian rodent assemblage

The middle Eocene Sharamuronian rodent fossil localities are in Nei Mongol, Shanxi, Jilin, Jiangsu, and Henan in China (Dawson, 1968; Wang and Dawson, 1994; Tong, 1997; Wang et al., 1998; Meng et al., 1999; Dawson et al., 2003a; Li et al., 2016;

Li, 2018, 2019). The Sharamuronian of the Asian Paleogene land mammal age proposed by Romer (1966) was derived from the Paleogene mammal fauna found in the Ula Usu locality of the Erlian Basin, Inner Mongolia. Studies on Sharamuronian rodent fossils in the classic locality are very limited (Li, 1975). Recently, abundant rodent fossils were found in the Ula Usu locality, and a detailed study of these fossils has been carried out.

In known localities, many rodent fossils of the Shanghe-Zhaili fauna in the Yuanqu Basin of Shanxi and the Erlian Basin of Nei Mongol are present, showing a variety of genera and species. The Sharamuronian rodent assemblages in the Yuanqu and Erlian Basins show similarities in family composition; they all contain ctenodactyloids, cricetids, dipodids, and ischryomyids, and many genera are present in both localities (Table 1). However, zelomyids and cylirodontids are present in the Yuanqu and Erlian basins, respectively. The ctenodactyloids in the Yuanqu Basin show higher generic richness than those in the Erlian Basin, and *Gobiomys* is the

dominant ctenodactyloid genus in the Erlian Basin. Detailed analysis of the rodent fauna of the Sharamuronian in the Yuanqu and Erlian basins has been carried out based on the MNI. The results showed that cricetids and dipodids are dominant in the Yuanqu Basin, but in the Erlian Basin, ctenodactyloids and dipodids are dominant and secondary, respectively (Tong, 1997).

In other localities, such as Huadian in Jilin, Shanghuang fissure fillings in Jiangsu, and Lushi in Henan, only zelomyids of the Sharamuronian rodent fauna have been discovered in these areas (Dawson et al., 2003a).

In addition to China, a few Sharamuronian rodent materials have been found in South Asia. The Pondaung Formation of central Myanmar has yielded one of the most diversified Eocene land mammal faunas in South Asia. Geochronological evidence has definitely established a late middle Eocene age for the mammal-bearing strata of the Pondaung Formation, and both fission track analyses of zircon grains and paleomagnetic studies of strata from the Pondaung area suggest an age of approximately 40 Ma (Tsubamoto et al., 2002; Khin et al., 2014; Jaeger et al., 2019). Therefore, the age of the Pondaung fauna corresponds to the Sharamuronian, based on biostratigraphy, nannoplankton assemblage, and magnetostratigraphic and radiometric dating. Some rodent specimens from the Pondaung Formation have been reported and included in the rodent superfamily Anomaluroidea, which is currently limited to tropical and subtropical forests of western and central Africa (Tsubamoto et al., 2000; Dawson et al., 2003b; Marivaux et al., 2005). The rodent *Pondaungimys* from the Pondaung Formation is similar to *Nementchamys*, an anomaluroid from the late middle Eocene strata of Algeria. The close relationship between *Pondaungimys* and *Nementchamys* emphasizes the widespread South Asian–North African distribution of anomaluroid rodents, thus suggesting communication between South Asia and Africa during the Sharamuronian (Marivaux et al., 2005).

## Ulangochuian rodent assemblage

Of the reported Ulangochuian rodents in East Asia, localities restricted to the redefined Ulangochuian land mammal age mainly include Nei Mongol and Yunnan in China (Wang, 1985, 2001a; Wang and Meng, 1986; Li, 2018, 2019, 2021).

In Nei Mongol, Ulangochuian rodents were reported in the Lower White to Middle White beds of the Erden Obo section in the Erlian basin, Nei Mongol (Li, 2018, 2019, 2021). The classic Houldjin site in the Erlian Basin is another important locality. A recent investigation showed that the reported Houldjin fauna was represented by a mixed assemblage due to reworking (Wang, 2008; Wang et al., 2009); thus, here, we do not include these fossils. The rodent in the lower part of the

Chijiachong Formation of Qujing, Yunnan, was considered as the Ulangochuian rodent (Wang, 1985, 2001a; Wang and Meng, 1986; Maridet and Ni, 2013).

The Ulangochuian rodent assemblage in Yunnan and Nei Mongol contains ctenodactyloid, cricetid, and dipodid rodents, and the cylindrodontid rodents are present only in Nei Mongol (Figure 5). In both localities, ctenodactyloids are moderately diversified and show different generic compositions, but *Gobiomys* in Nei Mongol and *Youngomys* in Yunnan are a sister group in the phylogenetic analysis (Wang, 2001c). However, some genera appear in both localities during the Ulangochuian, such as cricetid *Eocricetodon*, dipodid *Allosminthus*, *Sinosminthus*, and *Heosminthus*.

## Ergilian rodent assemblage

Late Eocene Ergilian rodent faunas are found in China and Mongolia in East Asia, Kazakhstan in Central Asia, and Thailand in South Asia.

Based on the biostratigraphic correlation, the age of the Upper Red beds of the Erden Obo section in the Erlian Basin, Nei Mongol, China, is the Ergilian land mammal age (Li, 2018). Ulantatal in Nei Mongol is another important site. Recently, Wasiljeff et al. (2020) derived a chronostratigraphic framework for the Ulantatal sequence, using paleomagnetic reversal stratigraphy and biostratigraphic correlation, and the time spanned by the strata was 35 to 27 Ma (from the latest Eocene to late Oligocene). The rodents in the lower part of the Kekeamu section in Ulantatal were representative of the latest Eocene (Wasiljeff and Zhang, 2022). In Mongolia, the Ergilian rodents were reported in the Ergilin Dzo Formation in the eastern Gobi Desert of Mongolia (Dashzeveg, 1993). The Zaysan Basin, eastern Kazakhstan, has a sedimentary section that includes strata spanning the Eocene–Oligocene boundary. The upper part of the Aksyr svita contains mammals, including abundant rodents that typically occur in the Ergilin Dzo fauna of Mongolia (Emry et al., 1998a).

The East and Central Asian Ergilian assemblage consists of ctenodactyloids, cricetids, dipodids, and cylindrodontids, and cricetids and dipodids are dominant. The rodent genera from Kazakhstan are all present in China and Mongolia in East Asia (Figure 6). In East Asia, the composition and dominant taxa of the Ergilian rodent assemblage are also similar to those of the Ulangochuian rodent faunas (Appendix Table 1). Ctenodactyloid *Gobiomys*, dipodid *Allosminthus*, *Heosminthus*, and *Sinosminthus* are present in the Ulangochuian and in the Ergilian assemblages.

In South Asia, *Baluchimys krabiense* has been found in the late Eocene strata in the Krabi Basin, Thailand. The striking affinities between *B. krabiense* and the late Eocene African *P. algeriensis* suggest faunal exchanges between South Asia and Africa during the Eocene (Marivaux et al., 2000).

TABLE 1 Sharamurunian rodent assemblages in China.

		Nei Mongol	Shanxi	Jilin	Jiangsu	Henan
Ctenodactyloidea	<i>Gobiomys</i>	✓				
	<i>Yuomys</i>	✓	✓			
	<i>Xueshimys</i>		✓			
	<i>Zodiomys</i>		✓			
	<i>Anadianomys</i>		✓			
	<i>Protataromys</i>		✓			
Dipodidae	<i>Primisminthus</i>	✓	✓			
	<i>Allosminthus</i>	✓	✓			
	cf. <i>Sinosminthus</i>		✓			
Cylindrodontidae	<i>Gobiocylindrodon</i>	✓				
	<i>Proardynomys</i>	✓				
Cricetidae	<i>Pappocricetodon</i>	✓	✓			
	<i>Raricricetodon</i>		✓			
Ischyromyidae	<i>Eosischyromys</i>	✓				
	<i>Hulgana</i>	✓	✓			
Zelomyidae	<i>Andersomys</i>		✓			
	<i>Zelomys</i>			✓		
	<i>Haozi</i>					✓
	<i>Suomys</i>				✓	

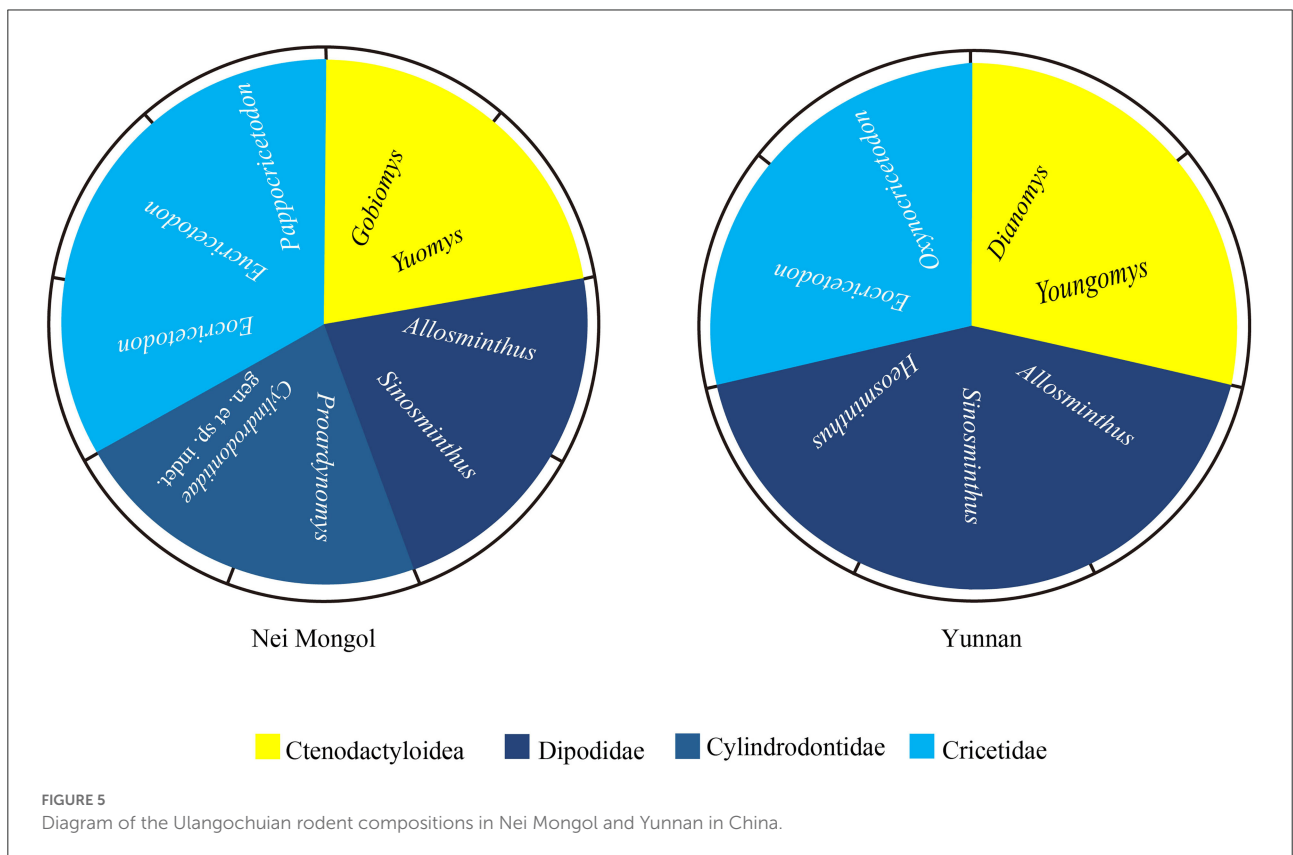
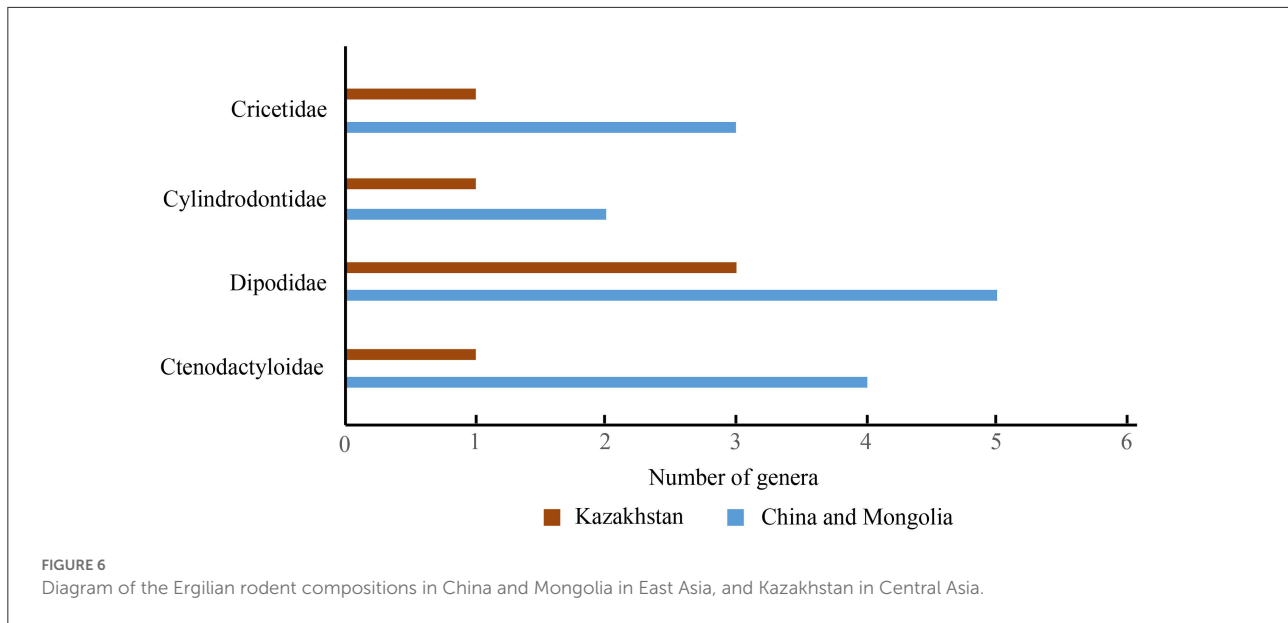


FIGURE 5 Diagram of the Ulangochuian rodent compositions in Nei Mongol and Yunnan in China.





## Hsandagolian rodent assemblage

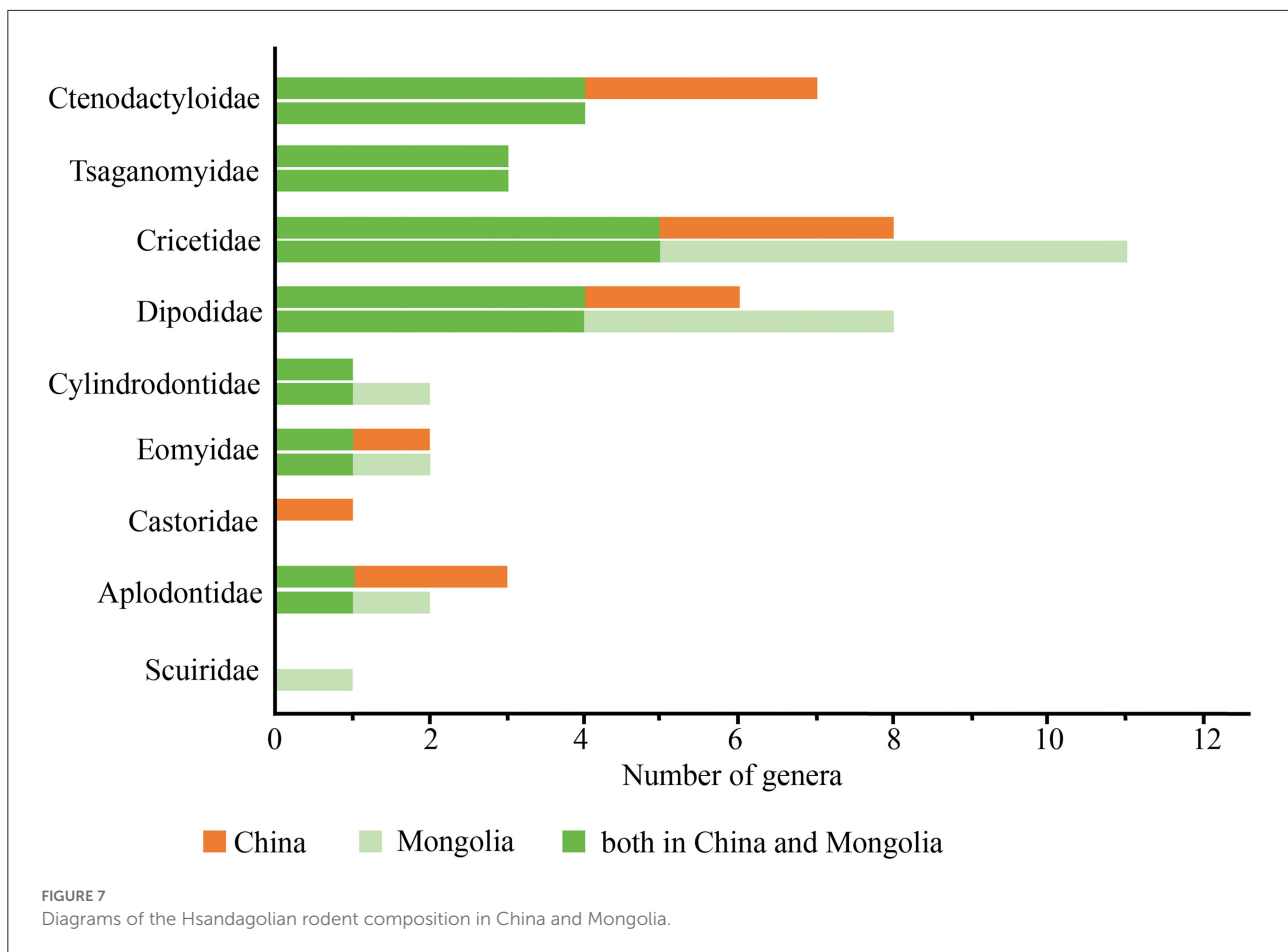
The Hsandagolian age corresponds to the Rupelian Stage and the lower part of the Chattian Stage (Speijer et al., 2020); thus, Hsandagolian includes the early Oligocene and part of the late Oligocene. Hsandagolian mammalian fossils are distributed in China, Mongolia, and Pakistan in Asia. In China, the Hsandagolian rodent mammals are found in the Ulantatal area, the “Upper White” beds of the Erlian Basin, Saint Jacques area and Qianlishan district in Nei Mongol (Wang, 1987; Wang and Emry, 1991; Wang and Qiu, 2003; Gomes Rodrigues et al., 2014; Li, 2018, 2021), the Burqin Basin in the northern area of Xinjiang (Wu et al., 2004; Ye et al., 2005), the Qingshuiying Formation in Haiyuan in Ningxia (Wang et al., 1994), the lower part of the Paoniuan Formation in the Danghe Basin of Gansu (Wang and Qiu, 2004), and the upper part of the Caijiachong Formation in Qujing in Yunnan (Maridet and Ni, 2013; Li et al., 2017). The Oligocene deposits of the Ulantatal area in Nei Mongol contain rich rodent fossils, and a review of the rodent list was provided (Gomes Rodrigues et al., 2014). Based on earlier research in the area, the Ulantatal sequence was considered to be constrained to the Oligocene (Wang, 1997b; Gomes Rodrigues et al., 2014). Recently, Wasiljeff et al. (2020) redefined the stratigraphy and suggested that the Ulantatal Formation spans from the latest Eocene to the late Oligocene. Here, the Hsandagolian rodent assemblage in the Ulantatal area has been revised based on the latest work. The abundant Hsandagolian rodent fossils are mainly distributed in northern China, but few materials have been reported in South China.

Cenozoic sediments of the Valley of Lakes are rich in fossils that provide unique evidence of mammal evolution in Mongolia. The strata are intercalated with basalt flows, and  $^{40}\text{Ar}/^{39}\text{Ar}$

data of the basalts frame the time of sediment deposition and mammal evolution and enable a composite age chronology for the Valley of Lakes area. Based on the radiometric ages of basalt and magnetostratigraphic data, the ages of Mongolian biozones A-C range from 33 to 25.6 Ma and correspond to the Hsandagolian (Daxner-Höck et al., 2010; Kraatz and Geisler, 2010). A total of 70 fossil beds in the Taatsiin Gol and Taatsiin Tsagaan Nuur areas in the Valley of Lakes yielded more than 19,000 mammal fossils, and rodent species composed 50% of the 175 mammal species in the study area (Daxner-Höck et al., 2017). Recently, a rich and diverse fossil assemblage in the Shine Us locality in southwestern Mongolia was described (Daxner-Höck et al., 2019).

The compositions of the Hsandagolian rodent assemblage in China and Mongolia are similar, and they include diverse small- to middle-sized rodents, such as dipodids, cricetids, ctenodactylids, cylindrodontids, eomyids, and large body-sized rodent tsaganomyids (Figure 7). Many genera in the Hsandagolian rodent assemblage are present in both Mongolia and China. In addition, in the Hsandagolian assemblage, castorids are found in China, and scuirids are present in Mongolia. In the Hsandagolian rodent assemblage in East Asia, cricetids, dipodids, and ctenodactylids are dominant, and some rodents are the earliest records of their family in China or Mongolia, such as Tsaganomyidae, Castoridae, and Aplodontidae.

The Asian record of the Dipodidae and Cricetidae dates back to the middle Eocene, where those families diversified and played a dominant role in Oligocene rodent communities. Recently, some dipodids and cricetids have been reported in European Oligocene strata (de Bruijn et al., 2019; Wessels et al., 2020), and these materials are the nearest fossil relatives to



those in Asian. As a result, dipodids and cricetids immigrated from Asia to Europe in the early Oligocene, and rodent faunal exchange over a large area was possible during the period, such as Dipodidae and cricetid Pappocricetodontinae.

A few rodent materials in Kazakhstan have been reported by Shevyreva (1971), and they are described as *Karakoromys* and *Prosciurus*. In the southwestern Sulaiman geological province (Balochistan, Pakistan), terrestrial detrital facies from the Bugti Hills region have yielded rich tertiary vertebrate faunas. The age of the lower Chitarwata Formation in the Bugti Hills is still controversial (Métais et al., 2017), but the rodents and the perissodactyls from the lower Chitarwata Formation clearly suggest an early Oligocene age (Marivaux et al., 1999; Welcomme et al., 2001; Marivaux and Welcomme, 2003; Métais et al., 2009; Antoine et al., 2013), which is correlative with the MP21-22 bio-horizons in Europe. The Bugti rodent fauna did not consist only of buluchimyines that were initially interpreted as a subfamily of the ctenodactyloid Chappatimyidae (sciurognathous) by Flynn et al. (1986) and yielded dipodids, anomaluroids, sciuroids, diatomyids, and typical early Oligocene cricetids (Appendix Table 3). Recently, a phylogenetic analysis showed no support for

the monophyly of a baluchimyine clade, so “baluchimyines” were reinterpreted as Hystricognathi *incertae sedis*, and the phylogenetic results supported that “baluchimyines” and tsaganomyids were representatives of an initial phase of the diversification of hystricognathous rodents in Asia (Marivaux et al., 2002). The Pakistan Hsandagolian rodent fauna is significantly different from that in China and Mongolia; only Cricetidae and Dipodidae at the family level are common elements in East and South Asian rodent faunas, but the genera of these two families are different.

## Discussion

### South Asian rodent faunas

Using the updated Paleogene timescale in Asia (Wang et al., 2019; Speijer et al., 2020), we compiled a list of Asian rodent genera from the early Eocene to the early Oligocene (Appendix Tables 1–3). In general, the most complete rodent record from the early Eocene to the early Oligocene in Asia is recorded in East Asia, followed by South Asia, and there

are fewer Central Asian rodent records. Central Asia and East Asia share many common elements at the levels of rodent families and genera, but the rodent faunas in South Asia show unique characteristics.

In the Bumbanian ischyromyid *Meldimys* from India, which is close to the European ischorymids, the chapattimyids of Ctenodactyloidea are the only rodent group during the Arshantan and Irдинmanhan (Thewissen et al., 2001; Gupta and Kumar, 2015). In recent years, studies have suggested that some mammals from the Indian subcontinent and Asia mainland, such as perissodactyls and primates, have close phylogenetic connections at the genus level (Rose et al., 2009; Missiaen and Gingerich, 2012, 2014). These facts indicate that there was no impassable geographic barrier for the early Eocene mammals on the two patches of land. Ni et al. (2020) also pointed out that before the Sharamurunion of the Eocene, the mammalian faunas on the Indian subcontinent formed a relatively isolated group and were different from those on the Asian mainland. A recent study suggested the probable presence of strong seasonal rainfall similar to the modern South Asian monsoon in early Eocene India (Spicer et al., 2016; Ding et al., 2017). Obviously, the paleoenvironment in South Asia was different from the environment in East and Central Asia during the early Eocene. Therefore, before the Sharamurunion of the Eocene, the rodent faunas in South Asia formed a relatively isolated group and included some endemic species probably because the difference was caused by different paleoenvironments.

In the Sharamurunion assemblage, the anomaluroid *Pondaungimys* was found in Myanmar (Dawson et al., 2003b; Marivaux et al., 2005), and Hystricognathi *Baluchimys* was reported in the Ergilian in Thailand (Marivaux et al., 2000). They had close phylogenetic relationships with rodents from Africa and suggest the occurrence of faunal exchanges between South Asia and Africa during the Sharamurunion and Ergilian. Recent research has shown that since the Sharamurunion of the Eocene, the mammalian faunas in South and East Asia have started to mix together (Ni et al., 2020), but rodent faunas have not exhibited this situation. Rodent fossils from South Asia are present only in limited locations, and only a few specimens are present, so more complete and numerous specimens are needed to assess the rodent relationship between South and East Asia.

The Hsandagolian rodents from East Asia are mainly concentrated in the northern areas of East Asia (northern China and southern Mongolia). The Hsandagolian rodent faunas in South Asia are significantly different from those in China and Mongolia. Ni et al. (2016) suggested that the Indian subcontinent and Yunnan maintained large areas of tropical jungle habitats in the early Oligocene (Ni et al., 2016). Pound and Salzmann (2017) used an extensive palynological dataset and presented global vegetation and terrestrial temperature reconstructions for the Eocene–Oligocene transition (EOT). As a result, at the boundary of the Eocene and Oligocene, the reconstructed terrestrial temperatures showed a decline

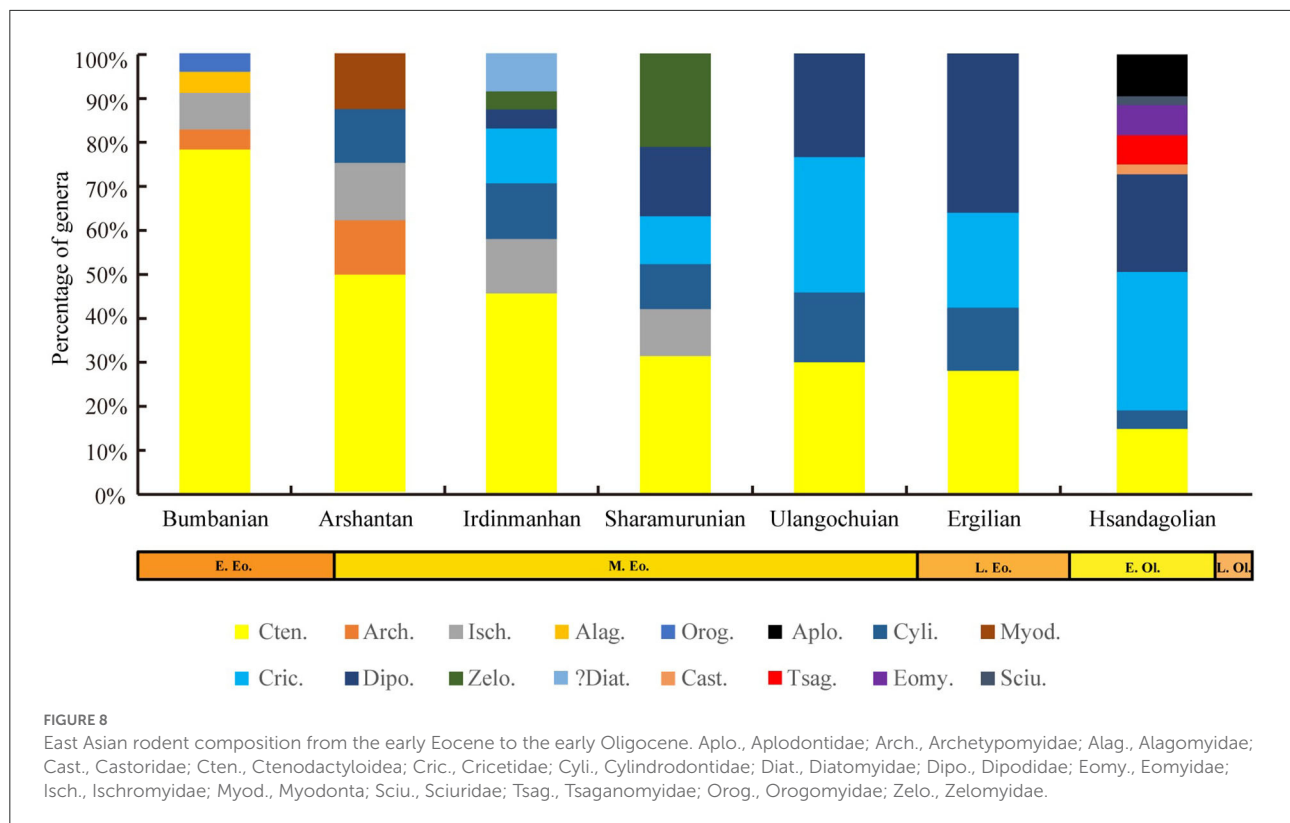
in the mean annual temperature ranges in the area that included northern China and southern Mongolia; by contrast, no change in temperature was reconstructed for India and tropical Asia. In addition, recent paleoclimate research has suggested that the Central Asian (Mongolia and northern China) steppe desert has existed since at least the Eocene (Barbolini et al., 2020). Obviously, during the early Oligocene, the paleoenvironment was different between South Asia and northern China and southern Mongolia, and the striking difference in the paleoenvironment probably caused the difference in rodent faunas.

## East Asian rodent succession from the early Eocene to the early Oligocene and responses to paleoclimatic changes

In general, from the early Eocene to the early Oligocene, rodent faunas in East Asia have obvious succession, and generic rodent diversity fluctuated in relation to paleoclimatic changes. At the beginning of the early Eocene, ctenodactyloid rodents were the dominant elements and moderately diverged as early as the earliest Eocene during the Paleocene–Eocene thermal maximum (PETM) (Figures 8, 9, Table 2). An abrupt increase in diversity during the Irдинmanhan and Sharamurunion is likely related to the rising temperatures of the middle Eocene climatic optimum. Cricetids and dipodids were first found in the Irдинmanhan and Sharamurunion and had some diversity.

A conspicuous event occurred between the Sharamurunion and the Ulangochuian; the generic diversity of rodents was reduced (Figure 9), and the ctenodactyloid-dominant rodent faunas were gradually replaced by the cricetid-dipodid-dominant faunas (Figure 8). Based on the MNI, the rodent assemblages of the Erden Obo section in Nei Mongol also showed a transformation from ctenodactyloid-dominant to cricetid-dipodid-dominant faunas in the Eocene Ulangochuian (Li, 2018). Similarly, perissodactyls and the entire mammalian fauna from China showed a similar abrupt decrease after the Sharamurunion in terms of the number of both species and genera (Wang et al., 2007; Bai et al., 2020). Bai et al. (2020) named the event the “Ulan Gochu Decline”, and the event was comparable to the contemporaneous post-Uintan decline of the North American land fauna (Berggren and Prothero, 1992) and probably related to the sustained cooling following the middle Eocene climatic optimum (MECO).

The Asian mammalian faunal turnover during the EOT was known as the “Mongolian remodeling”, with the perissodactyl-dominant fauna replaced by the rodent/lagomorph-dominant fauna, and it was a turnover that was attributed to the dramatic drop in temperature at the end of the Eocene (Meng and McKenna, 1998). Perissodactyls in China showed a



decrease in terms of generic number during the EOT, but the decline was not as obvious as in the “Ulan Gochu Decline” (Bai et al., 2020). However, during the EOT, the generic diversity of rodents obviously increased (Figure 9), cricetid–dipodids were still dominant elements in rodent faunas (Figure 8), and the generic diversity of cricetids and dipodids also obviously increased compared with that in the Ulangochuian and Ergilian.

In summary, the Eocene rodent faunas in East Asia showed two different changes in diversity, which may be related to global climatic declines. The first change occurred after the MECO when temperatures declined slowly and manifested as a clearly decreased diversity of rodents and a transformation from ctenodactyloid-dominant to cricetid–dipodid-dominant faunas. The second change occurred at the EOT and may have been a response to the sudden global drop in temperature; the change was manifested as a high generic diversity of cricetids, dipodids, and ctenodactylids and the appearance of rodent families such as Tsaganomyidae, Castoridae, and Eomyidae.

Based on the aforementioned discussion, after the dramatic drop in temperature, rodents became the dominant element in the Oligocene mammal fauna, but not overnight. The low temperatures during the Ulangochuian and Ergilian in East Asia served as a habituation ground for the cricetids and dipodids, which became preadapted for the EOT, successfully helping the rodent become the dominant fauna after the EOT.

## Conclusion

Successive Asian rodent faunas from the early Eocene to the early Oligocene are recorded in East Asia, and the rodent records in Central and South Asia are incomplete. Central Asia and East Asia share many common elements at the rodent family and genus levels. The rodent faunal turnover in East Asia was obviously affected by paleoclimatic changes. During the Irдинmanhan and Sharamurunion, East Asian rodent faunas showed an increase in the diversity of genera and families, which may be related to the rising temperatures of the mid-Eocene climatic optimum. In the Ulangochuian (after the MECO), when temperatures declined slowly, the rodent fauna showed a clear decline in the diversity at the genus level and a transformation from ctenodactyloid-dominant to cricetid–dipodid-dominant faunas. During the Eocene–Oligocene transition (EOT) and global cooling, the East Asian rodent fauna is shown by the considerably high generic diversity of cricetids, dipodids, and ctenodactylids. The low temperatures during the Ulangochuian and the Ergilian in East Asia served as a habituation ground for the cricetids and dipodids, which became preadapted for the EOT, successfully helping the rodent as the dominant fauna after the EOT.

Before the Sharamurunion of the Eocene and the early Oligocene, the South Asian rodent faunas showed unique characteristics, and the striking differences between the rodent

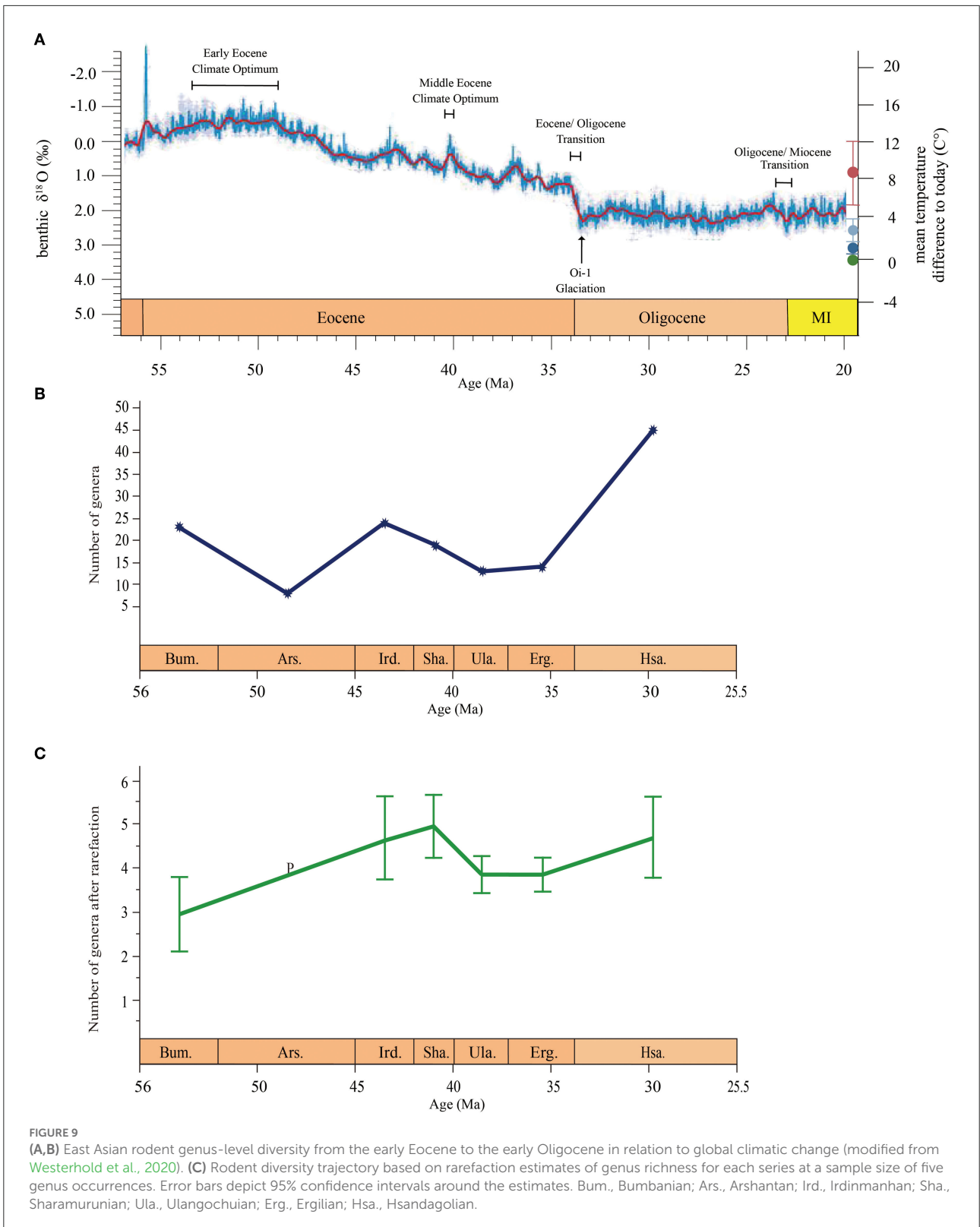


TABLE 2 Generic numbers of different rodent groups from early Eocene to early Oligocene in East Asia.

	Bumbanian	Arshantan	Irdinmanhan	Sharamuronian	Ulangochuian	Ergilian	Hsandagolian
Cten.	18	4	11	6	4	4	7
Arch.	1	1					
Isch.	2	1	3	2			
Alag.	1						
Orog.	1						
Cyli.		1	3	2	2	2	2
Myod.		1					
Cric.			3	2	4	3	14
Dipo.			1	3	3	5	10
Zelo.			1	4			
?Diat.		2	2				
Cast.							1
Tsag.							3
Eomy.							3
Scui.							1
Aplo.							4
Sum	23	10	24	19	13	14	45
N. Loc.	6	2	5	6	2	3	10

Aplo, Aplodontidae; Arch, Archetypomyidae; Alag, Alagomyidae; Cast, Castoridae; Cten, Ctenodactyloidea; Cric, Cricetidae; Cyli, Cylindrodontidae; Diat, Diatomyidae; Dipo, Dipodidae; Eomy, Eomyidae; Isch, Ischromyidae; Myod, Myodonta; Scui, Sciuridae; Tsag, Tsaganomyidae; Orog, Orogomyidae; Zelo, Zelomyidae; N. Loc., the number of localities.

faunas in South Asia and those in East Asia were probably the result of different paleoenvironmental habitats. In the Sharamuronian and Ergilian, rodents in South Asia have close phylogenetic relationships with rodents from Africa and suggest the occurrence of faunal exchanges between South Asia and Africa.

## Data availability statement

The original contributions presented in the study are included in the article/[Supplementary material](#), further inquiries can be directed to the corresponding author.

## Author contributions

QiaL designed the study and wrote the manuscript. QiL and RX analyzed the data. YW helped revise the manuscript and gave some useful suggestions. All authors contributed to the manuscript and approved the submitted version.

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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.

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## Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2022.955779/full#supplementary-material>

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