

## Paleogene mammalian fauna exchanges and the paleogeographic pattern in Asia

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**Abstract** Mammals are the most important elements in Cenozoic terrestrial ecosystem. The composition and the character of a mammalian fauna are controlled by evolution time and evolutionary rate. Here we took 50 Asian Paleogene mammalian faunas as representatives and applied Bayesian Tip-dating method to infer the relationships and divergence times among these faunas. Based on the results of Bayesian Tip-dating analyses, we discussed the correlation between the paleogeographic changes and the mammalian fauna turn-overs. Compared with the traditional fauna correlation and sorting, Bayesian Tip-dating analyses revealed more detailed similarities reflected via the divergence times among the 50 faunas. We discovered that the early Eocene mammalian fauna, which firstly appeared in India subcontinent, is similar to the faunas of the same age in other parts of Asia. It is likely that a passage for the mammalian dispersal was formed before early Eocene. Bayesian inferring suggests that the first appearance of the dispersal passage is during 64.8–61.3 Ma. This time window is close to the time estimation for the initial time of India-Asia collision. During 57.1–47.2 Ma, India subcontinent probably had a habitat different from the main part of Asia, as it was reflected from the composition of the mammalian faunas. It is probably correlated with the uplifted Gangdese Mountain and shallow seas and lowlands on both sides of the collision region. The very remote divergence time (64.8 Ma) estimated by Bayesian inferring reflects the mammalian fauna turnover during the Eocene-Oligocene transition, obviously affected by the global cooling. Till the end of Oligocene, the Arabic Peninsula and Asian mainland remained separated and the mammalian faunas did not show clear connection.

**Keywords** Paleogene, Mammalian fauna, Tibetan Plateau, India subcontinent

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### 1. Introduction

Extant mammals include 5488 species (IUCN data). Even though mammals are not as diverse as birds, given their diverse ecological adaptive pattern and huge population size,

mammals occupy the exceptional position in the Cenozoic terrestrial ecosystem, and are extremely important for maintaining the ecosystem balance. The species diversity and morphology diversity of mammals are controlled by two main factors: (1) The diversity of resources and niches provided by the habitats (Hutchinson, 1959; MacArthur, 1972; Rabosky, 2009), and (2) the evolutionary rate and evolution

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time (Fischer, 1960; Wiens et al., 2011). The diversity of extant mammals from certain area can reflect the quality of the habitat, and existing history of this habitat (Oliveira et al., 2016). The morphological diversification and the process of speciation of Cenozoic mammals are correlated with the habitat changes and large-scale climate and environment fluctuation. Although the diversity of the mammalian fossils is not the actual diversity of the mammalian fauna, to some extent, it can reflect the habitat conditions, particularly the large-scale habitat character. For example, we used certain forest indicator species to reconstruct the paleoenvironment, and deduced that large area of tropical jungles was still present during the early Oligocene in Yunnan, China (Li and Ni, 2016; Ni et al., 2016a). We classified fossil mammals from the late Miocene Yuanmou *Lufengpithecus* locality into different habitat types, and used the combination of these types to deduce that *Lufengpithecus* lived in forest-dominant environment with patches of shrubs and open windows (Ni and Qiu, 2002). Different mammalian fossil compositions can reflect not only the habitat conditions, but also the evolutionary levels of the faunas. From the different evolutionary levels, it is possible to deduce the evolution time of these faunas. On the world wide scale, paleontologists have sequenced the compositions of the mammalian fossils and set up the frameworks of the Cenozoic Mammalian Ages, which are comparable across large areas. The relatively accurate and complete mammalian age system includes the Asian Land Mammal Age (ALMA), European Land Mammal Age, and North American Land Mammal Age (Aguilar et al., 1997; Gunnell et al., 2009; Qiu et al., 2013; Ting et al., 2011; Vandenbergh et al., 2012; Woodburne, 2004).

Paleogene is a key period for the origin and evolution of the crown groups of mammals. We joined an international collaboration and developed the largest total-evidence data matrix for mammals. The phylogenetic analyses based on this data matrix revealed that the crown groups of the placental mammals originated within a period as short as 200 ka after the Cretaceous-Paleogene (K-Pg) transition. This explosive origin event was conjunct the rapid global warming event (O'Leary et al., 2013; MacLeod et al., 2018). During the 10 million years after the K-Pg boundary, mammals on Europe, Asia, North America and other continents experienced "experimental" radiations. It appeared condylarthrans, pantodonts, plesiadapiforms, glires etc. Stepping on the short transitional period of Paleocene-Eocene Thermal Maximum, the ancestors of the modern mammals at the order level suddenly appeared, and quickly dispersed among Asia, Europe and North America continents. Similar and continuous habitats must have been present across these continents enabling the quick migrations of the still small body-sized ancestral forms of primates, perissodactyls, artiodactyls, rodents and other mammals (Beard, 2008; Beard and Dawson, 2009; Ni et al., 2013, 2005, 2016b; Rose, 2006).

The global cooling event during the Eocene-Oligocene transitional period is coincident with the fundamental mammalian fauna turnovers. The mammalian fauna change is termed as Grand Coupure in Europe and Mongolian Remodelling in Asia (Kraatz and Geisler, 2010; Meng and McKenna, 1998; Sun et al., 2015). In the southern part of Asia, there is not enough data to examine the fauna turnover, but our research on the fossil primates revealed that paleoenvironmental changes across the Eocene-Oligocene transition changed the evolutionary trajectory of primates. We called this phenomena the "evolutionary filter" effect of the dramatic paleoenvironment change (Ni et al., 2016a).

In the Paleogene of Asia, not only the paleoclimate changes, but also the paleogeographic transformation caused by India-Asia collision and the subsequent disappearance of Tethys, retraction of Paratethys, and the uplift of the Tibetan Plateau, all affected the evolution and transition of mammals. However, there is few researches on how the Paleogene mammalian fauna turnovers could reflect the paleogeographic transformations. Here we summarized and checked about 3000 Asian Paleogene mammalian fossil records, and selected, combined and calibrated 50 mammalian faunas, which included relatively complete and representative records, to carry out fauna analyses. We used Bayesian inferring and Tip-dating methods to reconstruct the relationships among different mammalian faunas, and to estimate the divergence time between these faunas. Then we discussed the possible relationships between the mammalian fauna evolution and turnovers and the paleogeographic transformations.

Bayesian Tip-dating method is widely used in the inference of phylogenetic relationships. It usually takes species as the Operational Taxonomic Units (OTUs), and molecular sequence data or morphological codings as the characters. The differences of the molecular sequences or morphological codings of two given OTUs can be proximately regarded as the evolutionary distance between these two OTUs, and the evolutionary distance is the product of evolutionary rate and divergence time. The evolutionary rate and divergence time are statistically indistinguishable without other assumption and information. Bayesian Tip-dating method relies on the assumption of molecular clock: Either assuming that the evolutionary rate is constant across the different branches of the phylogenetic tree (strict molecular clock model, Zuckerkandl and Pauling, 1965), or assuming that the evolutionary rate is proximately stable across the different branches of the phylogenetic tree (relaxed molecular clock model, Drummond et al., 2006; Huelsenbeck et al., 2000; Kishino et al., 2001; Lepage et al., 2007; Thorne et al., 2002). The latter model is widely used in modern dating analyses. Bayesian Tip-dating method also needs to use the ages of the fossil tips. The time differences between the fossil tips and the extant species provide information for Bayesian Tip-

dating method to infer the dates of the internal nodes of the phylogenetic tree, therefore the evolutionary rate and divergence time can be co-estimated. The so-called Bayesian Tip-dating method, as its name indicates, uses Bayesian inferring algorithm—Markov chain Monte Carlo (MCMC, Hastings, 1970; Metropolis et al., 1953) to estimate the posterior distribution of the parameters. The fossil ages with their uncertainties, topology of the phylogenetic tree, distribution of the time across the tree, variation of evolutionary rates, and the parameters of the relaxed clock model are all integrated into the prior distribution.

Bayesian Tip-dating method can combine the fossil ages and morphological data, and estimate the topology of the phylogenetic tree, divergence time, and evolutionary rate in the same analysis. The prior and posterior distributions reflect the accuracy of these parameters. The traditional phylogenetic analysis methods based on parsimony criterion can reconstruct the topology of the phylogenetic tree, but cannot estimate the divergence time and the evolutionary rate at the same time. Parsimony-based methods summarize the most parsimonious trees only, thus do not reflect the uncertainty of the estimation of the tree topology. The divergence time and evolutionary rate have to be calculated separately. Information of the original data were largely lost during the calculation. Bayesian Tip-dating method covers these shortages of the parsimony analysis. It has been widely used in the total-evidence (molecular and morphological data) based phylogenetic analyses (Gavryushkina et al., 2017; Lee, 2016; O'Reilly et al., 2015; Ronquist et al., 2012a; Ronquist et al., 2016; Zhang et al., 2016), and the morphological data based analyses (Bapst et al., 2016; King et al., 2016; Lee et al., 2014; Matzke and Wright, 2016).

In this research, we took the Asian Paleogene mammalian fauna as the OTUs, and the composition of the mammalian genus, family and order as the characters. Similar to the phylogenetic analysis for the species, the difference between two mammalian faunas can also be regarded as the evolutionary distance, which is correlated with the fauna exchanges, evolutionary rate and the divergence time between the two faunas. Because every mammalian composition has a relatively accurate age estimate, we can use Bayesian Tip-dating methods, under the hypothesis as in a phylogenetic analysis, to reconstruct the relationship of transformation among different faunas and estimate the divergence time among the faunas.

## 2. Material and methods

The rough data used in this research is from the Paleobiology Database (<https://paleobiodb.org>). We checked 3264 Asian Cenozoic mammalian fossil records, selected and calibrated the mammalian fossil compositions from 784 different fossil

sites and layers. The sites and layers that have the same age and are geographically close to each other were combined into the faunas. Based on their representativity and completeness, 50 faunas (Table 1) of these combined sites and layers were selected as fauna OTUs. Each fauna OUT records the presence (scored as 1) and absence (scored as 0) of all the Paleogene mammalian fossils from Asia at the genus, family and order levels. Absence of some fossil records in a fauna may not indicate that the species of the fossil were actually absent in the fauna. It may simply be because of the incompleteness of the fossil records. We assumed that the absence of mammals caused by the incompleteness of fossil record is a random error. This type of random errors follow the same distribution in different faunas. To determine the root of the relationship tree of the faunas, we defined a dummy fauna that evolved independently and had no element changes with the Asian faunas during the whole Cenozoic period. Such a dummy fauna could have existed in the real world, for example, some mammalian faunas from South America or Australia may have totally different history compared with Asia mammalian faunas. In our previous research, we suggested that the crown placental mammals rapidly originated during a short period of 200 ka in the beginning of Paleocene (O'Leary et al., 2013). The majority of the Paleogene mammalian faunas from Asia are placental mammals. We therefore assumed that the root of the relationship tree of the Asian Paleogene mammalian faunas fell in the period of 65.8–66 Ma.

Bayesian Tip-dating analyses were performed in MrBayes 3.2 (Ronquist et al., 2012b). We used the Lewis Mk model (Lewis, 2001) to describe the transition between the states of presence and absence (1 and 0) of the mammalian fauna elements. We used the Gamma model (Yang, 1994) to describe the rate variation of the transitions in the genus, family and order subgroups. The changes of the evolutionary rate along a phylogenetic tree are described with the independent Gamma rate model (Lepage et al., 2007): The means of the evolutionary rates are identical on different clades and the deviations are positively correlated with the branch lengths. Mammalian fauna OUTs were regarded as the tips of the relationship tree. Based on the oldest and the youngest ages of a mammalian fauna, uniform distribution was assigned to this branch of mammalian fauna. The age of the root follows a uniform distribution with a range of 65.8–66 Ma. We used the independently evolved outgroup (the dummy fauna) to constrain the topology of the relationship tree, to define the root, and to keep the inner group monophyletic. In MrBayes 3.2, we ran two independent MCMC calculations (runs). Each had 8 chains (1 cold chain, 7 hot chains), and ran for 10 million iterations. Every 1000 iterations, the runs recorded the states of parameters that MCMC examined. Every run generated 100 thousand samples. The first 30% samples were dropped (burn-in), and the rests of the samples from the

**Table 1** Asian Paleogene mammalian faunas used for Bayesian Tip-dating analyses

Asian land mammal age	Mammalian fauna	Region/country	Age (Ma)	Genus number	Family number	Order number
Tabenbulakian	Anatolia V	Turkey	23.03–28.1	11	8	4
	Bugti-Chitarwata Upper	Pakistan	23.03–28.1	38	15	5
	Hsanda Gol Upper	Mongolia	23.03–28.1	31	15	6
	Tabenbuluk-Yindirte	Gansu	23.03–28.1	15	10	6
	Tieersihabahe	Xinjiang	23.03–28.1	12	11	4
	Xianshuihe Upper	Gansu	23.03–28.1	14	8	4
Hsandagolian-Tabenbulakian	Harrat Al Ujayfa	Saudi Arabia	23.03–33.9	7	4	4
Hsandagolian	Anatolia IV	Turkey	28.1–33.9	26	10	2
	Bugti-Chitarwata Lower	Pakistan	28.1–33.9	30	17	4
	Hsanda Gol Lower	Mongolia	28.1–33.9	60	25	8
	Keziletuogayi	Xinjiang	28.1–33.9	14	11	4
	Qingshuiying-Ulantatal-Kekeamu-Wulanbulage	Ningxia-Inner Mongolia	28.1–33.9	59	25	8
	Tabenbuluk-Dingdangou	Gansu	28.1–33.9	10	9	4
	Taqah-Thaytiniti	Oman	28.1–33.9	20	13	6
Xianshuihe Lower-Xiagu	Gansu	28.1–33.9	17	13	5	
Ulangochuian-Ergilian	Caijiachong-Xiaotun-Shinao	Yunnan-Guizhou	33.9–38	13	7	3
	Ergilin	Mongolia	33.9–38	37	22	10
	Gongkang-Yongning	Guangxi	33.9–38	12	9	4
	Krabi	Thailand	33.9–38	22	11	6
	Ulan Gocho-Houldjin-Erden Obo	Inner Mongolia	33.9–38	40	22	8
Sharamurunian	Heti Zhaili-Chugouyu	Henan	38–41	20	16	6
	Nadu-Dongjun	Guangxi	38–41	25	15	5
	Pondaung	Myanmar	38–41	35	19	6
	Shara Murum	Inner Mongolia	38–41	43	20	10
Irdinmanhan-Sharamurunian	Lumeiyi	Yunnan	38–47.8	20	11	4
	Subathu Upper	Pakistan-India	38–47.8	20	11	4
	Ulan Shireh	Mongolia	38–47.8	27	14	8
Irdinmanhan	Chorlakki-Ganda Kas	Pakistan	41–47.8	38	16	5
	Heti Rencun-Lushi-Hetaoyuan-Minggang	Henan	41–47.8	89	40	13
	Shanghuang	Jiangsu	41–47.8	18	14	6
	Sindkhatuti	India	41–47.8	7	3	3
	Irdin Manha	Inner Mongolia	41 – 47.8	36	16	9
Arshantan	Arshanto	Inner Mongolia	47.8–55	21	10	6
	Chorlakki-Ganda Kas Lower	Pakistan	47.8–55	5	4	3
	Subathu Lower	Pakistan-India	47.8–55	6	3	2
Bumbanian-Arshantan	Yuhuangding	Henan	47.8–56	13	7	4
	Cambay Shale	India	53–56	25	16	7
Bumbanian	Bumban	Mongolia	55–56	35	16	8
	Ghazij	Pakistan	55–56	14	6	3
	Lingcha-Songzi	Hunan-Hubei	55–56	18	11	6
	Nomogen Upper	Inner-Mongolia	55–56	11	7	6
	Wutu	Shandong	55–56	41	32	13
Gashatan	Nomogen Lower	Inner Mongolia	56–57	26	15	8
	Gashato	Inner Mongolia	56–59.2	11	7	3
	Tujinshan-Shuangtasi	Anhui	56–59.2	10	5	3
	Naran Bulak	Mongolia	56–59.2	23	16	11
Nongshanian	Chijiang-Nongshan	Jiangxi-Guangdong	59.2–61.6	17	10	4
	Doumu-Qianshan-Xuancheng	Anhui	59.2–61.6	13	9	5
Shanghuan	Shanghu	Guangdong	61.6–66	15	8	5
	Wanghudun-Qianshan	Anhui	61.6–66	25	9	5

two runs were compared. The most important indicators were the average standard deviation of split frequencies (ASDSF) and the effective sample size (ESS). It usually requires that  $ASDSF < 0.01$  and  $ESS > 100$ .

### 3. Results

The results of Bayesian Tip-dating runs show that the ASDSF reached 0.0085, and the ESS of all the parameters were all greater than 100. The MCMC trajectories of the parameter estimations in the two runs tended to be stabilized and consistent. Therefore, we combined the two MCMC samples from the two runs to estimate the posterior distribution of all the parameters, including the relationships and the divergence time of all the mammalian faunas.

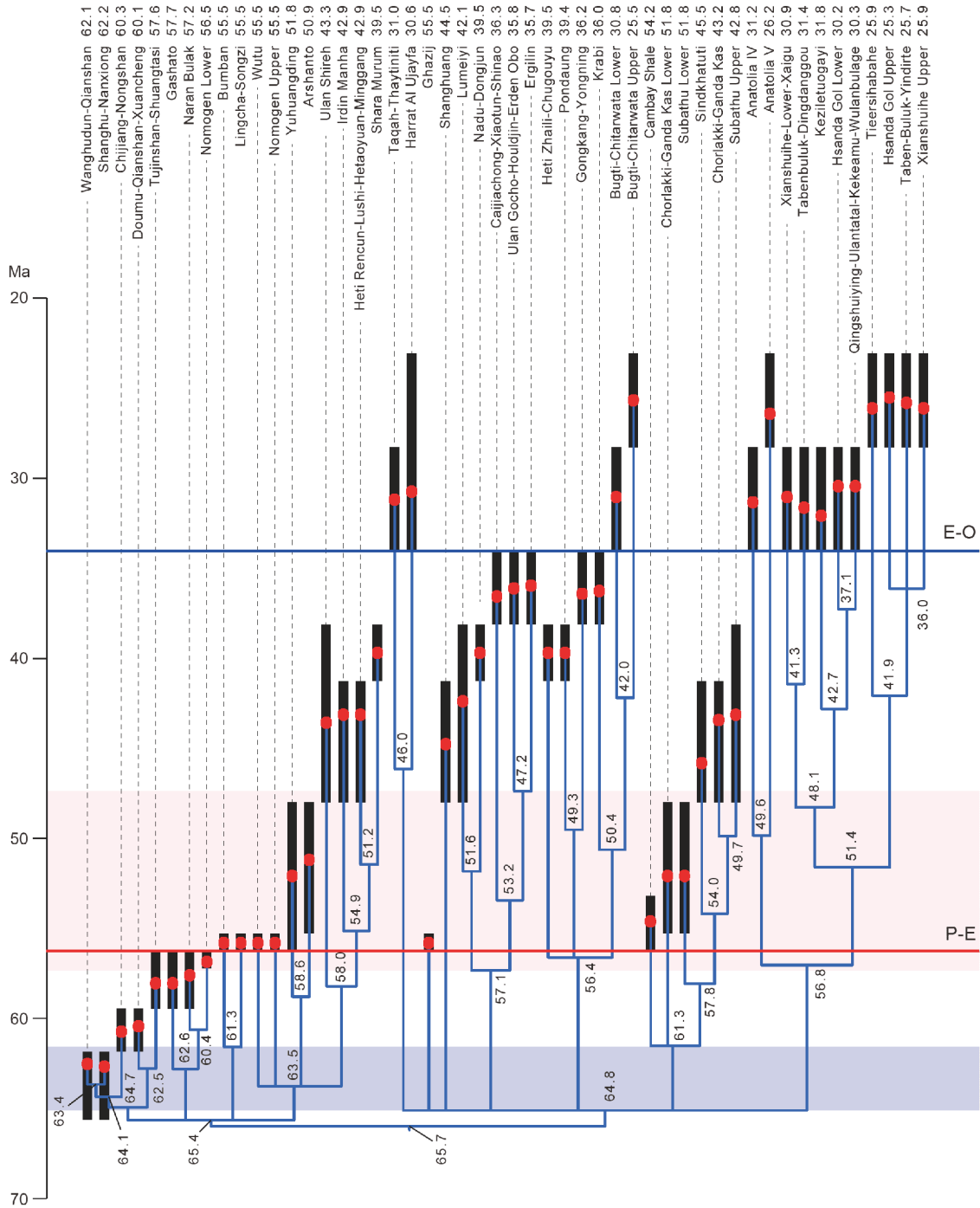
Early and middle Paleocene mammalian fossils were discovered only from Guangdong, Jiangxi, Hunan and Anhui provinces in southern China. Bayesian analyses indicated that the Shanghu, Wanghudun, Chijiang and Doumu faunas, which belong to the Shanghuan and Nongshanian of AL-MAs, have close relationships. The divergence time of these faunas is 64.7–63.4 Ma (Figure 1). The compositions of these faunas are similar, all including the widely distributed early and middle Paleocene mammals, such as bema-lambdids, pastoralodontids, anagalids, miacids, hyopso-dontids, pseudictopids, zhelestids, mimotonids, tillodonts, etc. Bemalambdids and pastoralodontids belong to Pantodonta. They usually had robust body-build. Bemalambdids was regarded as the most primitive pantodonts. In Paleocene and early Eocene, pantodonts were distributed in Asia, Europe and North America. Tillodonts had close relationship with pantodonts at higher systematic ranks, but had smaller body size. They were distributed in the Holarctic region. Zhelestids were regarded as the close relatives of the most primitive ungulates. They also have a broad distribution area. Similar forms were discovered in Europe, Asia and North America. Mimotonids belong to glires. Anagalids and pseudictopids had close phylogenetic relationships with glires. The three groups were discovered from Asia only, but they were common animals and had broad distribution area.

The late Paleocene Gashatan ALMA mammalian fossils were distributed in a very large area. They were discovered in Anhui, Henan, Inner Mongolia, Xinjiang provinces of China, and many localities in Mongolia. The late Paleocene Tujinshan-Shuangtasi mammalian fauna is geographically close to the Doumu fauna of Qianshan in Anhui Province, and the former probably was a successor of the latter. The divergence time of the two faunas is around 62.5 Ma. The pantolambdodontids in the Tujinshan-Shuangtasi fauna, which are the late Paleocene and early Eocene pantodonts, together with the anagalids and mimotonids, show continuity with the Doumu fauna. The three late Paleocene mammalian

faunas included in the analyses, the Nomogen Lower from the Inner Mongolia of China, the Naran Bulak and Gashato from Mongolia, have a divergence time about 62.6 Ma, not differing much from the early and middle Paleocene Shanghu and Wanghudun mammalian faunas. The Gashatan representative mammalian faunas of Inner Mongolia and Mongolia from northern Asia have some new elements, including hapalodectids, eurymylids, alagomyids, nyctitheriids, carpolestids, lambdopsalids, and neoplagiaulacids. The diversity of the faunas was increased, but also keep some taxa close to the early and middle Paleocene taxa, such as pastoralodontids, hyopsodontids, pseudictopids, and arctostyloids, showing the evolutionary continuity from the early and middle mammalian faunas. Eurymylids are stem glires. They have very high diversity. Alagomyids were usually accepted as the most primitive rodents (Meng et al., 2007). They were also discovered in North America. Hapalodectids, nyctitheriids and carpolestids had similar taxa in North America and Europe. Lambdopsalids and neoplagiaulacids are two groups of multituberculates. They had far phylogenetic relationships with the Cretaceous multituberculates from Asia, instead, they had close relationship with the taeniolabidoids and neoplagiaulacids from North America. As far west as the Lianmuqin, Dabu and South Gobi late Paleocene localities in Xinjiang, the faunas of these localities show similarities with the late Paleocene localities from Inner Mongolia and Mongolia, even though these localities in Xinjiang do not have enough fossils to be included in our analyses.

Early Eocene fossil localities are present in large area in Asia. In China, the early Eocene localities are known in Guangdong, Hunan, Hubei, Henan, Shandong, Xinjiang and Inner Mongolia. They are also known in Mongolia, Kyrgyzstan, Japan, India and Pakistan. The early Eocene Bumbanian faunas, which have enough fossil records to be included in the Bayesian analyses, include Lingcha-Songzi, Wutu, Yuhuangding, Nomogen Upper, and Bumban. The age of these faunas lasts for about 1 Ma from the very beginning of the Eocene. Although geographically these faunas were far away from each other, the compositions of them are quite similar to each other. The results of Bayesian Tip-dating analyses suggested that the divergence times among these faunas are short, within a range of 63.5–61.3 Ma. In these faunas, it first appeared many crown group mammals, including primates, rodents, perissodactyls, artiodactyls, erinaceomorphs, and soricomorphs. At the same time, these faunas also share some successors from the Paleocene faunas, such as hyopsodontids and arctostyloids. The late early Eocene Arshantan faunas have more derived elements when compared with the Bumbanian faunas, such as the lagomorphs, eomorpid and lophialetid perissodactyls, and chyromyid and zelomyid rodents. The divergence time between the Arshanto fauna and the early Eocene Yuhuangding





**Figure 1** Divergence times of Asian Paleogene mammalian faunas. Black bars indicate the age of the mammalian faunas; red dots and the numbers following the fauna names are the mammalian ages estimated by Bayesian inferring; blue lines indicate the cluster relationships among faunas; numbers at the internal nodes are the divergence times estimated by Bayesian inferring; red and blue transverse lines indicate the Paleocene-Eocene boundary and Eocene-Oligocene boundary respectively. Paled purple shadow indicates the time period when the dispersal passage was formed between India subcontinent and Asia mainland for the first time. Paled reddish shadow indicates the theoretical time period when special habitat probably was formed south to the Gangdese Mountain.

fauna is 58.6 Ma. The divergence time between the two faunas and the Wutu plus Nomogen Upper faunas is shorter than that between the two faunas and the other two Bumbanian Lingcha-Songzi plus Bumban faunas.

Some northeastern Asian middle Eocene Irдинmanhan and

Sharamurunian faunas, such as the Yuanqu-Mianchi-Lushi-Minggan from Shanxi and Henan provinces, the Irдин Manha and Shara Murum faunas from Inner Mongolia, and the Ulan Shireh fauna from Mongolia, were clustered together, not only showing the similarities between them, but also sug-

gesting the continuity in chronology. The divergence time among these 4 faunas is between 58.0–51.2 Ma. Similarly, the continuities between the 4 faunas and the Paleocene and early Eocene faunas from eastern Asia are clear, as it was reflected in the continuous diversification in rodents, perissodactyls and lagomorphs. Cricetids, gobiomyids, yuomyids, leporids, strenulagids, amynodontids, brontotheriids and deperetellids appeared in the 4 faunas, and for the first time, stem anthropoid eosimiids started to evolve. The Ir-dinmanhan Shanghuang fissure filling fauna in Jiangsu Province does not show any difference from other Ir-dinmanhan faunas at the family and order level, and also has eosimiids. However, the composition of this fauna is much more peculiar than other faunas. It has more diverse artiodactyls but fewer perissodactyls. There is only one perissodactyl, the smallest brontotheriid *Nanotitanops shanghuangensis* was discovered in the fauna. The earliest-known entelodontid and diatomyid were from this fauna. Bayesian analyses suggest that Shanghuang fauna is far away from all the other middle Eocene faunas from Asia.

There is no Paleocene mammalian fossil record from India subcontinent. The earliest-known mammalian fossils from India subcontinent belong to the Chorlakk-Ganda Kas Lower and Ghazij faunas from Pakistan, the Cambay Shale and Subathu Lower faunas from India. The ages of these fauna were estimated as early Eocene. Although the Ghazij fauna has eomoropids, brontotheriids and omomyids, which are typical elements of Arshantan and Ir-dinmanhan faunas, it has some endemic mammals such as perissobunids and quettacyonids, which are not known from other faunas of similar age. Bayesian analyses suggest that the Ghazij fauna is far from other early Eocene faunas from India-Pakistan. The divergence times among Chorlakk-Ganda Kas Lower, Cambay Shale and Subathu Lower faunas are between 61.3–57.8 Ma. The divergence times among Sindkhatuti, Chorlakk-Ganda Kas Upper, and Subathu Upper are between 54.0–49.8 Ma. These six faunas form a large clade, suggesting the continuity in chronology. The mammalian faunas from India subcontinent usually have some peculiar elements, such as the basal cetaceans, which were only known from there; the chapattimyid rodents, which otherwise were only known from the Wutu fauna; and the diacodexeid artiodactyls, which were only known from the Andarak Alai Beds of Kyrgyzstan outside of India subcontinent.

The middle Eocene Sharamurunian and the late Eocene mammalian faunas were clustered into two large groups: One includes Heti Zhaili-Chugouyu fauna in Henan, Gongkang-Yongle fauna in Guangxi, Pondaung fauna in Myanmar, and Krabi fauna in Thailand, with a divergence time of 56.4–49.3 Ma; the other includes Lumeyi fauna in Shilin of Yuannan, Caijiacong-Xiaotun-Shinao fauna in Qujing, Shilin, and Panxian of Guizhou, Nadu-Dongjun fauna of Guangxi, Ulan Gocho-Houldjin-Erden Obo fauna of Inner Mongolia fauna,

and the Ergilin fauna of Mongolia, with a divergence time of 57.1–47.2 Ma. The two large groups suggest that India subcontinent, the south, southwest and north parts of China do not have zoogeographic difference. Common elements increased in south and north faunas. For example, the anthracotheriids, which were first known in Henan and Yunnan of China, dispersed to India subcontinent and Mongolia during the late middle Eocene Sharamurunian and late Eocene. The lophiomerycids, which were first known from the Sharamurunian of Pondaung in Myanmar, dispersed to northern China and Mongolia during late Eocene.

Oligocene sediments are mainly exposed in northern Asia. The Oligocene mammalian faunas selected for analyses were clustered in a large group. The divergence time of this group is between 51.4–36.0 Ma. Different from the Eocene forest dwellers, the Oligocene mammals from northern Asia lived mainly in open environments, including diverse small-body sized glires, such as dipodids, zapodids, ctenodactylids, cylindrodontids, leporids, and large-body sized mammals such as *Paraceratherium* and entelodonts. The Oligocene mammalian faunas barely have phylogenetic continuity with the Eocene mammalian faunas in northern Asia. The direct ancestors of these Oligocene mammals and the Eocene mammals from northern Asia probably were divergent since early Paleocene. Their divergence time is 64.8 Ma. The early and late Oligocene mammalian faunas from Anatolia in Turkey form a separate group. They were divergent from other Oligocene faunas from Asia as early as 56.8 Ma. The two Oligocene faunas from Anatolia seem to have continuity in composition. They have some common elements with other Asian Oligocene faunas at genus and family level, such as *Eucrietodon*, *Palaeohypsodontus*, glirids and lophiomerycids. On the other hand, the two faunas from Anatolia share the *Bransatoglis* glirids, which are not known from other Asian Oligocene faunas.

The Oligocene layers from the Bugti Hill in Pakistan have yielded very diverse mammalian fossils. Although they are similar to other Asian mammalian faunas at the order and family levels, the Bugti Hill faunas have more forest-type species, particularly diverse primates. In southeastern Asia, only the Lijiawa locality in Yunnan Province has yielded similar diverse Oligocene primate fossils. However, the Lijiawa fauna has not been fully described, so it was not included in our analyses. The Bugti Hill faunas show continuity with the late Eocene faunas from southern Asia. The two Bugti Hill faunas and the late Eocene Krebi fauna from Thailand have a divergence time of 50.4 Ma, later than the divergence time between the Anatolia faunas and the Oligocene faunas from northern Asia.

The two Oligocene mammalian faunas from the Arabic Peninsula, Taqah-Thaytiniti and Harrat Al Ujayfa, which were included in our analyses, formed a clade far away from other groups. The two faunas have some taxa, such as arsi-

notheriids, proboscideans, phiomysids, hyracoideans, and propithecids, which were not known in all the other Asian Paleogene mammalian faunas. Bayesian analyses suggest that the two fauna from Arabic Peninsula were divergent from other Asian faunas at 64.8 Ma.

#### 4. Discussion

For the first time we sorted and clustered the Asian Paleogene mammalian faunas by applying Bayesian Tip-dating methodology. The analyses were based on the Mk model (Lewis, 2001). In the application, we assumed that the dispersal between mammalian faunas was random, and any common element shared by two faunas was the result of random dispersal. We assumed that the dispersal event was an instant event, and the geographic distance does not affect the dispersal when there is no geographic barrier between two faunas. Under a time scale of millions of years, our assumption for analysis is reasonable. The fossil records support our assumption, for example, primates, perissodactyls, artiodactyls and many other mammals “simultaneously” dispersed across a broad area of Europe, Asia and North America during the Paleocene-Eocene Thermal Maximum (Beard, 2008; Beard and Dawson, 2009; Ni et al., 2005, 2013, 2016b; Rose, 2006). With the geological chronological scale, the impact of geographic distances is little.

The absence of certain mammals in a fauna is reasonable to be the result of lack of fossil record. The cording method used here is impossible to distinguish the true absence of the animal and the incompleteness of the fossils. Bayesian analyses do not distinguish the two types of absence either. We combined the local faunas that are geologically close to each other to increase the completeness of the cording. The method improved the data quality for certain degrees, however, the incompleteness of fossil records is the “inherent problem” of paleontology. We can only improve the fossil records via continuous accumulation to approach the real situation.

On time dimension, the result of Bayesian analyses shows that the 50 faunas in our analyses were sorted in a similar pattern as the results of traditional mammalian fauna sorting and sequencing. During the Paleocene-Eocene transition and Eocene-Oligocene transition, the results of Bayesian analyses show that the late Paleocene, early Eocene, late Eocene and early Oligocene mammalian faunas were all clustered in their own groups, similar to the believes based on traditional methodology. Our new results presented a tree-like topology, and depicted the similarities among different faunas in a more detailed way. The divergence times between different faunas predicted by Bayesian Tip-dating reflect the similarities. The further two faunas were separated on this tree

topology, the longer the two faunas were divergent.

As it has been noted, under the assumption that the geographic distance does not influence the dispersal, and within a similar time scope, the difference between two faunas can be interpreted as the results of their adaption to different habitats or the separation by zoogeographic barriers. Since the beginning of Eocene, the India subcontinent and the mainland of Asia shared many common elements at the levels of order and family. This fact indicates that there was no impassable geographic barrier for the early Eocene mammals on the two patches of lands. Researches in recent years have suggested that some mammals from India subcontinent and Asia had close phylogenetic connections at the genus level. For example, the isctolophid and lophialetid perissodactyls of the Ghazij fauna were closely related to other Asian perissodactyls (Missiaen and Gingerich, 2012, 2014). The presence of *Eotitanops* and *Palaeosyops* from India subcontinent suggests that the fauna exchanges with North America were present, and the exchanges must go through eastern Asia (Missiaen et al., 2011). The early Eocene strepsirrhines from India and Pakistan were primitive primates. They had close phylogenetic relationships with the strepsirrhine from eastern Asia and Europe (Rose et al., 2009). We therefore deduce that the difference of the compositions of the Asian Paleogene mammalian faunas was caused by habitat variation.

There is no Paleocene mammalian faunas discovered from India subcontinent. The early Eocene mammalian faunas from India subcontinent are similar with those on Asian mainland. After the long isolation since the breakup of Gondwana, passage for mammal dispersal must have formed before early Eocene. The results of Bayesian Tip-dating analyses suggest that the divergence time between the mammalian faunas from India subcontinent and Asia mainland is between 64.8–61.3 Ma, which is the theoretical time scope when the passage was formed. This time estimation is close to the suggested initial time (65–59 Ma) of India-Asia collision (Ding et al., 2005; Ding et al., 2017a; Hu et al., 2016; Hu et al., 2017; Wu et al., 2014; Yao et al., 2015).

Before the Sharamuranian (56–41 Ma) of Eocene, the mammalian faunas on India subcontinent formed a relatively isolated group, and included a few endemic species, probably being the result of possessing habitats different from the Asian mainland. A recent research in paleobotany have suggested that South Asian Monsoon was not formed during the Paleogene, and there is no evidence for the Proto-Tibetan Plateau higher than 4000 m (Spicer et al., 2017). However, the probable presence of strong seasonal rainfall similar to the modern South Asian Monsoon (Ding et al., 2017b), the probable presence of the Andean-type Gangdese Mountain higher than 5000 m (Ding et al., 2014), and the probable presence of remaining shallow sea and lowland on both wings (Thailand-Myanmar, Pakistan) of the collision region



(Ding et al., 2016, 2017a; Wu et al., 2014), must have produced a paleoenvironment south to the Gangdese, which was very different from the environment on the mainland of Asia. The difference probably caused the overall differences of mammalian fauna compositions on India subcontinent and the Asia mainland.

Since the Sharamuruni (41–39 Ma) of Eocene, the mammalian faunas on India subcontinent and southern and northern Asia started to mix together on the Bayesian tree, suggesting that the previous differences of habitats must have disappeared. There is no Paleogene mammalian fossil record on the table of Tibetan Plateau, so we are not able to examine the impact of Tibetan Plateau on the direct cross-plateau dispersals of mammals between the south and north areas to the plateau. However, via a route from Yunnan and Guangxi, the mammals can disperse even the Tibetan Plateau is high enough as a zoogeographic barrier. The Bayesian analyses reveal that the divergence times of the Sharamuruni faunas were within a range of 57.1–47.2 Ma. This time scope is not the estimation for the disappearance of habitat difference, but the minimum estimation of the existence of barrier of habitat difference (Figure 1).

Oligocene mammalian mammals from Asia included in the analyses showed the obvious impact of the global cooling event across the Eocene-Oligocene boundary. The remote theoretical divergence times (64.8 Ma) between the Eocene and Oligocene faunas reflected the Eocene-Oligocene turnover-event of mammalian faunas (Kraatz and Geisler, 2010; Meng and McKenna, 1998; Sun et al., 2015). The striking differences between the mammalian faunas from India subcontinent and northern Asia must be the results of great difference in habitats. Our previous researches suggested that India subcontinent and Yunnan remained large areas of tropical jungle habitats in Oligocene (at least in early Oligocene, Li and Ni, 2016; Ni et al., 2016a). The two Oligocene mammalian faunas from the Arabic peninsula are geographically close to the faunas from Anatolia, and the latitudes of these faunas are similar. However, the compositions of these faunas are very different. The Bayesian analyses suggest that the divergence time between the Oligocene mammalian faunas from Arabic Peninsula and the faunas from the rest areas of Asia was in Paleocene (64.8 Ma). This result suggests that a zoogeographic barrier almost impassable between the Arabic Peninsula and the mainland of Asia was present until the end of the Oligocene.

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