

亚洲早古近纪哺乳动物生物年代学 与生物地理学的新认识

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摘要:近期的研究极大地丰富了亚洲古新世和早始新世哺乳动物群信息,因此有必要对现存亚洲生物年代学和生物地理学框架做出调整。在定量和定性分析的基础上,将生物年代界线与主要的动物群更替事件对应起来,改进了古新世和早始新世亚洲陆相哺乳动物分期年代对比及生物地理学的认识。以往知之甚少的上湖期以原始啮形类和钝脚类为主,其后的浓山期则呈现出亚洲哺乳动物的地方性分异。随着新的基于啮形类以及真正的啮型类的出现,啮形类开始辐射。上湖期-浓山期的界线与北美 Torrejonian-Tiffanian 界线相当,并且动物群更替很可能是由全球变冷阶段的开始引发的。格沙头期哺乳动物进一步分化,亚洲土著类群急剧减少,以多瘤齿兽类、夜䟽类(nyctitheriids)、克莫土兽类(cimolestids)和食果猴为代表的北美迁入物种开始出现。而在北美,亚洲哺乳动物(包括北柱兽类和原恐角兽类)的第一次入侵发生于 Tiffanian-5a 期初期,第二次入侵发生于 Clarkforkian 初期,包含了啮齿类、裂齿类及冠齿兽类。因此格沙头期的开始可与北美 Tiffanian-5a 的开始相对比。伯姆巴期的开始以偶蹄类、奇蹄类和真灵长类的首次出现为标志,与古新世-始新世界线相当。这些类群在亚洲的出现与它们在北美和欧洲出现于始新世之初的情况类似。与格沙头期初期的动物群扩散不同,伯姆巴期的动物群扩散似乎持续了更长时间,并且也有可能直接发生在亚洲和欧洲之间。

关键词:亚洲,古新世,早始新世,上湖期,浓山期,格沙头期,伯姆巴期,生物年代学,生物地理学
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AN UPDATED MAMMALIAN BIOCHRONOLOGY AND BIOGEOGRAPHY FOR THE EARLY PALEOGENE OF ASIA

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Abstract Recent research has greatly increased the information available on Asian Paleocene and early Eocene mammal faunas, creating the need to update the existing Asian biochronological and biogeographical framework. Based on a quantitative and qualitative analysis, biochronological boundaries are refined to correspond to major faunal turnovers, and an improved age correlation and biogeography of the Paleocene and early Eocene Asian Land Mammal Ages (ALMAs) is proposed. The poorly known Shanghuan ALMA is characterised as an assemblage dominated by primitive gliriforms and pantodonts. The following Nongshanian ALMA shows an endemic diversification of Asian mammals. Gliriforms radiated,

with the appearance of new basal gliriforms and the first appearance of true Glires. The Shanghuan/Nongshanian boundary has been correlated to the Torrejonian/Tiffanian boundary in North America, and it is suggested here that the faunal turnover was possibly triggered by the start of a period of global cooling. The following Gashatan ALMA witnesses a further diversification and an abrupt reduction of the endemism of Asian mammals. Multituberculates, nyctitheriids, cimolestids and carpolestids appeared in the Gashatan faunas and represent North American immigrants. Conversely, a first wave of Asian mammals consisting of arctostylopids and prodinoceratids invaded North America at the start of Tiffanian-5a, and a second wave consisting of rodents, tillodonts and coryphodontids arrived in North America at the beginning of the Clarkforkian. The start of the Gashatan is therefore correlated with the start of North American Tiffanian-5a. The start of the Bumbanian ALMA is marked by the first appearance of artiodactyls, perissodactyls and true primates, similar to their appearance in North America and Europe at the start of the Eocene, and is correlated to the Paleocene-Eocene boundary. Contrasting with dispersal at the start of the Gashatan, dispersal during the Bumbanian seems to have been possible during a more extended period, and was also possible directly between Asia and Europe.

Key words Asia, Paleocene, early Eocene, Shanghuan, Nongshanian, Gashatan, Bumbanian, Biochronology, Biogeography

1 Introduction

Mammalian paleontology makes use of a biochronological system to designate intervals of time defined by specific events in the evolutionary history of mammals. In North America, detailed biochronological framework of North American Land Mammal Ages (NALMAs) has been established and correlated to the global timescale (see, e. g., Woodburne, 2004). Most European paleomammalogists use the MP reference level system, a biochronological system consisting of an ordered series of reference faunas to which other faunas are correlated, which is arguably better suited for the discontinuous European Paleogene terrestrial deposits (Sigé and Legendre, 1997). Study of the Asian Paleogene biochronology started only later (Romer, 1966), using an approach closely similar to the North American system. This was recently summarised by Wang et al. (2007a). However, the only detailed, formal definitions for the early Paleogene Asian Land Mammal Ages (ALMAs) were published by Ting (1998). New research efforts in the past decade have rapidly increased the information on Asian land mammal faunas. These advances have therefore created an important potential to update the Asian early Paleogene mammal biochronology. The previously small number of available absolute ages for these faunas has now been increased by a number of important new studies (Bowen et al., 2002, 2005; Ting et al., 2003; Clyde et al., 2008). These now also allow a better calibration of the age of the faunas and ALMAs, and an improved understanding of the evolution and migration of Asian early Paleogene mammals on a global scale.

2 Methods

In this update of the Asian Paleocene and early Eocene mammal biochronology, faunal data were compiled through a thorough review of the literature (Beard et al., 2010; Bowen et al., 2002; Huang, 2003, 2006; Huang and Zheng, 1997, 1999, 2003; Kondrashov and Lucas, 2004; Lopatin, 2006; Lopatin and Averianov, 2008; Lucas, 2004; Meng and McKenna, 1998; Meng et al., 1998, 2005, 2007a,b; Missiaen and Smith, 2008; Miyata, 2007; Ni et al., 2004, 2010; Russell and Zhai, 1987; Ting, 1998; Ting et al., 2003, 2004; Tong and Wang, 2006; Tong et al., 2003; Tsubamoto et al., 2004; Wang et al., 1998, 2007b, 2008a, b). This study compiled faunal data from 55 faunas in 30 stratigraphical sections. Forty-four of the faunas are generally placed in the Shanghuan to Bumbanian ALMAs which form the subject of this paper (Fig. 1), although the placement of specific faunas in particular ALMAs has var-

ied (Wang et al., 1998; Ting, 1998; Tsubamoto et al., 2004). In order to better characterise and define the end of the Bumbanian period, faunal data for 11 Arshantan or Irдинmanhan faunas were included. These faunas were selected because they were suggested to represent the oldest Arshantan/Irдинmanhan intervals (Lucas, 2004; Tsubamoto et al., 2004).



Fig. 1 Geographical distribution of Paleocene and early Eocene fossil mammal localities in Asia
Based on Miyata (2007), Russell and Zhai (1987), Ting (1998) and Wang et al. (1998)

As a starting point in this study, and as a test of previous biochronological hypotheses, the faunal data were quantitatively analysed by Appearance Event Ordination (AEO). AEO is a multivariate method to analyse locality-specific faunal lists together with available superpositional data, to infer global taxonomic ranges and to obtain a continuous temporal ordination of the analysed faunas (Alroy, 1994, 2000). Differing from previous AEO implementations, this work does not only analyse occurrences of species or genera, but also of families and orders. This approach allows inclusion of taxa that were left in open nomenclature, as well as some incorporation of the available phylogenetic information.

Subsequently, the faunal data and AEO results were studied together in detail to obtain an updated biochronology with special attention to the characterisation of the different ALMAs and to defining clear boundaries between them that correspond with major faunal turnovers. Finally, the biochronological data were integrated with available geochronological data for the Asian early Paleogene, to correlate the boundaries of the ALMAs on a global scale, and to place the mammal evolutionary and migration events in their wider context.

3 AEO results

Literature research initially yielded a data matrix of 55 faunas and 612 taxa, which was reduced to 202 informative, non-redundant species, genera, families, and orders. These data

Table 1 Results of Appearance Event Ordination of Early Paleogene Asian mammal faunas

LFA	Mean	ELA	Fauna	Abb.	ALMA	LFA	Mean	ELA	Fauna	Abb.	ALMA
339	339.5	340	Ulan Shireh	UH	Arsh./Irdinm.	127	127.5	128	Bayan Ulan basal fauna	BU	Gash.
339	339.5	340	Hetaoyuan	HE	Arsh./Irdinm.	119	119.5	120	Naran Mbr Naran Bulak Fm	NA	Gash.
335	335.5	336	Lower Lushi	LO	Arsh./Irdinm.	23	115	207	Lower Lingcha Fauna	LL	Gash.
326	326.5	327	Upper Lushi	UP	Arsh./Irdinm.	110	110.5	111	Zhigden Mbr Naran Bulak Fm	ZH	Gash.
310	310.5	311	Khaychin Ula II-III-V	K2	Arsh./Irdinm.	95	107.5	120	Kaychin Ula 1	K1	Gash.
297	297.5	298	Irdin Manha at Irdin Manha	IM	Arsh./Irdinm.	100	100.5	101	Nomogen Fauna	NO	Gash.
273	273.5	274	Irdin Manha at Camp Margett	CM	Arsh./Irdinm.	95	95.5	96	Gashato Mbr 1 Fauna	G1	Gash.
262	262.5	263	Arshanto Fm	AS	Arsh./Irdinm.	82	82.5	83	Taizicun Fauna	TA	Gash.
242	242.5	243	Kholboldzi-Nur Fauna	KZ	Arsh./Irdinm.	73	73.5	74	Datang Mbr Nongshan Fm	DT	Nongsh.
236	236.5	237	Guanzhuang fauna	GU	Arsh./Irdinm.	73	73.5	74	Zhuguikeng Mbr Nongshan Fm	ZU	Nongsh.
220	220.5	221	Yuhuangding + Dacangfang	YD	Arsh./Irdinm.	67	67.5	68	Wangwu Mbr of Chijiang Fm	WW	Nongsh.
177	220	263	Niushan Mbr Fauna	NU	Bumb.	67	67.5	68	Upper mbr Doumu Fm	UD	Nongsh.
206	213.5	221	Akasaki fauna	AK	Bumb.	64	64.5	65	Lower mbr Doumu Fm	LD	Nongsh.
212	212.5	213	Yuhuangding Fm Fauna	YU	Bumb.	64	64.5	65	Upper part upper mbr of Wanghudun Fm	UW	Nongsh.
206	206.5	207	Upper Lingcha Fauna	UL	Bumb.	59	59.5	60	Lannikeng Mbr Chijiang Fm	LA	Nongsh.
187	200	213	Zhangshanji Fm Fauna	ZS	Bumb.	52	52.5	53	Tujinshan Fauna	TU	Nongsh.
199	199.5	200	Gomphos fauna of Erlan Basin	GF	Bumb.	52	52.5	53	Shuangtasi - Xuancheng Fauna	SX	Nongsh.
193	193.5	194	Shisanjianfang Fm Fauna	SH	Bumb.	52	52.5	53	Shuangtasi - Tongling Fauna	ST	Nongsh.
187	193.5	200	Gashato Mbr III	G3	Bumb.	35	35.5	36	Lower part upper mbr of Wanghudun Fm	MW	Nongsh.
187	193.5	200	Gashato Mbr II	G2	Bumb.	23	29.5	36	Shizikou Fm	SZ	Shangh.
187	193.5	200	Aguyt Mbr Naran Bulak Fm	AG	Bumb.	28	28.5	29	Lower mbr of Wanghudun Fm	LW	Shangh.
187	187.5	188	Bumban Mbr Naran Bulak Fm	BM	Bumb.	23	23.5	24	Upper part of Shanghu Fm	US	Shangh.
177	177.5	178	Ningjiashan Mbr of Xinyu Gr	NN	Bumb.	14	14.5	15	Zaoshi Fm	ZA	Shangh.
163	170.5	178	Tantou Fm	TT	Gash.	11	11.5	12	Lower part of Fangou Fm	LF	Shangh.
163	163.5	164	Wutu Fm Fauna	WU	Bumb.	11	11.5	12	Lower part of Shanghu Fm	LS	Shangh.
163	163.5	164	Dazhang Fm	DZ	Gash.						
150	150.5	151	Dabu Fm Fauna	DB	Ga sh.						
137	137.5	138	Subeng	SU	Gash.						
82	130	178	Pinghu Fauna	PI	Gash.						
127	127.5	128	Bayan Ulan upper fauna	PF	Gash.						

Abbreviations: LFA. latest first appearance; Mean. mean event number; ELA. earliest last appearance; Abb. abbrevia-
 ted faunal names; Shangh. Shanghuan; Nongsh. Nongshanian; Gash. Gashatan; Bumb. Bumbanian; Arsh./Irdinm. Arshan-
 tan/Irdinmanhan.

(Appendix) were analysed with the AEO module of the PAST 1.74 palaeontological statistics software (Hammer et al., 2001). The analysis demonstrated 7576 conjunctions of taxa, and 7565 first-before-last appearance event statements were implied by superpositional relationships. The analysis used maximum likelihood to optimise the sequence of the last appearance events, and 100 bootstrap replicates were made. The optimal sequence of the analysed faunas is shown in Table 1.

Most faunas studied here are broadly ranked in accordance with the generally accepted succession of Asian mammal faunas (Wang et al., 1998; Ting, 1998, 2003; Tsubamoto et al., 2004), and these results support the validity of the existing ALMAs. The ranking of some faunas differs from previous ideas, mainly for poorly known faunas (e. g. Dazhang Fm., Pinghu Fm.), as well as for the fauna from the Shuangtasi Fm, which was only tentatively assigned to the Gashatan ALMA (Ting, 1998). A detailed discussion of the placement of specific faunas in the different ALMAs, and on the definition of their boundaries and characteristics is given in the following sections and illustrated in Fig. 2.

4 Shanghuan ALMA

Characterisation Typical taxa: *Linnania* (Anagalidae).

Characteristic first appearances: Gliriformes; Pantodonta; Tillodontia; Mesonychia; Sarcodontidae.

Faunal evolution The Shanghuan is the first Cenozoic mammal age in Asia, and there are no Cretaceous Asian mammal faunas known that share taxa with the Shanghuan faunas (Kielan-Jaworowska et al., 2004). Because of this, all Shanghuan taxa represent first appearances and the definition of the Shanghuan is rather difficult. The Shanghuan faunas can be typically characterised as a mixture of very primitive taxa. Among these, the highest diversity is seen in the superorder Gliriformes, represented by the basal families Anagalidae, Astigalidae and Pseudictopidae (see Missiaen and Smith, 2008 for a definition of Gliriformes), and in the order Pantodonta, represented by the families Bemalambdidae, and Pantolambdodontidae. Additionally, primitive tillodonts, mesonychids, carnivorans and sarcodontids are already present in Asia from the Shanghuan.

Correlated lithostratigraphic units Lower and upper part of the Shanghu Formation (Nanxiong Basin, Guangdong Province); Shizikou Formation (Chijiang Basin, Jiangxi Province); Lower part of the Fangou Formation (Shimen Basin, Shaanxi Province); Zaoshi Formation (Chaling Basin, Hunan Province); Lower member of the Wanghudun Formation (Qianshan Basin, Anhui Province).

Discussion of correlations Many authors have divided the Shanghu Formation into a lower and an upper part, each with a distinct mammal fauna (Zhou et al., 1977; Wang et al., 1998; Ting, 1998). Others however did not make this distinction and suggested that the different levels from the Shanghu Formation yielded only a single fauna (Russell and Zhai, 1987; Bowen et al., 2002; Tsubamoto et al., 2004). Because both faunas do not have a single mammal species in common, they are treated as separate faunas here. The fauna from the upper part of the Shanghu Formation seems richer taxonomically, containing astigalids, tillodonts, carnivorans, and pantolambdodontid pantodonts, all of which are absent from the lower Shanghu fauna. Conversely, the lower Shanghu fauna contains three different genera of mesonychids, including the genus *Yantanglestes* which persists into the Nongshanian, while no mesonychids have been reported from the upper Shanghu fauna. Therefore, both stratigraphic and biochronological data suggest that the lower and upper Shanghu faunas represent distinct faunas. However, uncertainties about possible collecting or taphonomical biases do not allow to further interpret the age difference between both faunas.

		Faunal Characteristics		Interval	Faunal Characteristics		Correlated Lithostratigraphic Units	
ALMA	BUMBANIAN		Typical Taxa: <i>Rhombomylus</i> , <i>Gomphos</i> Characteristic FA: Primates, Perissodactyla, Artiodactyla, Condylarthra, Ctenodactyloidea Characteristic LA: Arctostylopidae, Eurymylidae, Mimotoniidae, Alagomyiidae, Prodinoceratidae	Heptodon	Typical Taxa: <i>Anatolostylops</i> Characteristic FA: Helaleitidae Characteristic LA: Arctostylopidae, Eurymylidae, Mimotoniidae, Prodinoceratidae	Ningjiasan Member of the Xinyu Group; Shisanjiantang Fm.; Middle mbr. of Yuhuangding Fm.; Akasaki Fm.; Zhangshanji Fm.; <i>Gomphos</i> beds of Nomogen Fm.; Niushan Fm.		
	Wasatchian			Homogal.	FA: Lophialeitidae, Eomoropidae, Ischyromyidae LA: Multituberculata, Asligalidae, Pseudictopidae, Alagomyidae	Wutu Fm.		
NALMA	Clarkf.		Typical Taxa: <i>Prionessus</i> , <i>Lambdopsalis</i> , <i>Pseudictops</i> , <i>Eomylus</i> , <i>Tribosphenomys</i> , <i>Pelaeostylops macrodon</i> , <i>Prodinoceras efremovi</i> Characteristic FA: Multituberculata, Rodentia, Dinocerata, Nyctitheriidae, Hyaenodontidae Characteristic LA: Pastoralodontidae, Phenacolophidae	Orientol.	Typical Taxa: <i>Orientolophus</i> Characteristic FA: Isectolophidae, <i>Gomphos</i> Characteristic LA: Cimolestidae	Upper part of Lingcha Fm.; Mbr. II and III of Gashato Fm.; Bumban and Aguyt Mbr of Naran-Bulak Fm.		
Age	Ypresian			Bothriost.	Typical Taxa: <i>Bothriostylops</i> Characteristic FA: Eurymylidae	Taizicun Fm.; Mbr I of Gashato Fm.; Nomogen Fm.; Lower part of Lingcha Fm.; Zhigden and Naran Mbr of Naran-Bulak Fm.; Dazhang Fm.; Tantou Fm.; Pinghu Fm.; Dabu Fm.		
GPTS	C24r		Typical Taxa: <i>Bothriostylops</i> , <i>Hsiuannania</i> , <i>Mimotona</i> , <i>Harpyodius</i> , <i>Altirambda</i> Characteristic FA: Gires, Arctostylopidae, Pastoralodontidae, Phenacolophidae	Asiostyl.	Characteristic FA: Mimotoniidae, Didymoconidae, Pastoralodontidae, Prodinoceratidae	Upper mbr. of Doumu Fm.; Wangwu Mbr. of Chijiang Fm.; Tujinshan Fm.; Shuangtasi Fm.; Datang Mbr of Nongshan Fm.		
	C25n			Upper mbr. of Wanghudun Fm.; Lower mbr. of Doumu Fm.; Lamlikeng Mbr. of Chijiang Fm.; Zhuguikeng Mbr of Nongshan Fm.				
Ma	C25r		Typical Taxa: <i>Limnania</i> Characteristic FA: Gliriformes, Pantodontia, Tillodontia, Mesonychia, Carnivora, Sarcodontidae			Lower and upper mbr. of Shanghu Fm.; Shizikou Fm.; Lower part of Fangou Fm.; Zaozhi Fm.; Lower mbr. of Wanghudun Fm.		
	C26n							
Epoch	C26r		Typical Taxa: <i>Bothriostylops</i> , <i>Hsiuannania</i> , <i>Mimotona</i> , <i>Harpyodius</i> , <i>Altirambda</i> Characteristic FA: Gires, Arctostylopidae, Pastoralodontidae, Phenacolophidae					
	60							
EARLY		LATE		MIDDLE		EARLY		
EOCENE		PALEOCENE						

Fig. 2 Asian Paleocene and early Eocene mammal biochronology and correlations

Abbreviations; ALMA. Asian Land Mammal Age; NALMA. North American Land Mammal Age; GPTS. Geomagnetic Polarity Time Scale; Pu. Puercan; Clarkf. Clarkforkian; *Orientol.* *Orientolophus*; *Homogal.* *Homogalax*; *Bothriost.* *Bothriostylops*; *Asiostyl.* *Asiostylops*; FA. First appearance; LA. Last appearance Dashed lines indicate tentative subdivisions of ALMAs; crosshatching indicate absence of sufficient data for reliable correlation; correlation with North American biochronology and absolute ages based on Woodburne (2004) and Secord et al. (2006)

Subdivisions Ting (1998) divided the Shanghuan in the *Bemalambda* interval zone, containing the lower Shanghu, the lower Fangou and the lower Wanghudun fauna and the *Archaeolambda* interval zone, containing the other Shanghuan faunas. This subdivision is not supported by the results of the AEO here (see Table 1), especially for the lower Wanghudun fauna which may represent the youngest Shanghuan fauna. The presence of astigalids and tillodonts in the lower Wanghudun fauna suggest affinities with the upper Shanghu fauna rather than with the lower Shanghu fauna, and the presence of a pseudictopid is even shared with Nongshanian and younger faunas. Although the results of the AEO suggests that the lower Shanghu and lower Fangou faunas are the oldest Shanghuan faunas, this result is mainly based on the absence of taxa such as astigalids, tillodonts, carnivorans, and pantolambdodontid pantodonts, while only the presence of the mesonychid *Hukoutherium* positively unites both these faunas. I therefore agree with Ting (1998) that the faunas from the lower part of the Shanghu Formation and the lower part of the Fangou Formation probably represent the oldest known Shanghuan faunas, but refrain from subdividing the Shanghuan ALMA in two discrete biochrons.

Biogeography The early Paleocene Shanghuan faunas form an assemblage of primitive taxa. Some of these, such as gliriforms, tillodonts and sarcodontids are endemic to Asia during this period. Others, such as mesonychids and carnivorans are shared with North America, and pantodonts are even shared with North America and South America (McKenna and Bell 1997). However, the limited knowledge and primitive nature of these taxa do not allow any further biogeographical interpretation.

Age correlations The Shanghuan ALMA has been traditionally correlated to the early Paleocene Puercan and Torrejonian in North America (see Wang et al., 1998 for an overview), and this seems to be corroborated by recent studies (Clyde et al., 2008; Ting et al., 2011).

5 Nongshanian ALMA

Characterisation Typical taxa: *Bothriostylops* (Arctostylopidae); *Hsiuannania* (Anagalidae); *Mimotona* (Mimotonidae); *Harpyodus* and *Altlambda* (Pantodonta).

Characteristic first appearances: Glires; Arctostylopidae; Pastoralodontidae; Phenacolophidae.

Faunal evolution The Nongshanian is mainly characterised by a diversification and specialisation of taxa known from the preceding Shanghuan period. Especially the superorder Gliriformes shows a strong radiation. The basal gliriform families Anagalidae and Pseudictopidae were already present in the Shanghuan, but Pseudictopidae become more diversified in the Nongshanian. The specialised gliriform family Arctostylopidae appears and diversifies into six genera and nine species during the Nongshanian. Even more significantly, true Glires make their first appearance, represented by both Eurymylidae and Mimotonidae which are believed to be the primitive stem groups leading to rodents and lagomorphs respectively (Meng et al., 2003).

Correlated lithostratigraphic units Upper member of the Wanghudun Formation (Qianshan Basin, Anhui Province); Lower and Upper member of the Doumu Formation (Qianshan Basin, Anhui Province); Lannikeng and Wangwu Member of the Chijiang Formation (Chijiang Basin, Jiangxi Province); Tujinshan Formation (Jiashan Basin, Anhui Province); Shuangtasi Formation (Xuancheng and Tongling Basin, Anhui Province); Zhuguikeng and Datang Member of the Nongshan Formation (Nanxiong Basin, Guangdong Province).

Discussion of correlations The fossils from the upper member of the Wanghudun Formation have traditionally been placed in the Shanghuan ALMA (Ting, 1998; Tsubamoto et al., 2004). Other studies however made a distinction between the lower and the upper part of the upper member of the Wanghudun Formation (e.g. Qiu et al., 1977; Wang, 1995), and Wang

et al. (1998) placed the Shanghuan-Nongshanian boundary between the lower and upper part of the upper member of the Wanghudun Formation. The results of the AEO corroborates the distinction between both faunas made by Wang et al. (1998). This paper however suggests that the lower part of the upper member of the Wanghudun Formation may be Nongshanian in age, differing from previous studies (Wang et al., 1998; Ting, 1998; Tsubamoto et al., 2004). Because the pantodont *Bemalambda* sp., cf. *B. crassa* is present in the lower part of the upper member of the Wanghudun Formation, this extends the range of this otherwise typically Shanghuan genus into the Nongshanian. Conversely, the placement of this fauna in the Shanghuan would extend the otherwise typically Nongshanian genera *Mimotona* and *Harpyodus* into the Nongshanian. Therefore, because the appearance of *Harpyodus* and of the gliroid *Mimotona* is potentially more significant than the disappearance of *Bemalambda*, both the lower and upper fauna of the upper member of the Wanghudun Formation are here tentatively placed in the Nongshanian ALMA.

The faunas from the Tujinshan and Shuangtasi Formation in Anhui were only poorly known previously, and have been correlated to the Gashatan ALMA (Wang et al., 1998; Ting, 1998). On the other hand, the analysis of Ting et al. (2003) did not group the fauna from the Shuangtasi Formation with the typical Gashatan faunas, and a Nongshanian age for the Shuangtasi faunas was suggested but not discussed by Tsubamoto et al. (2004). A recent study of the Tujinshan fauna however added numerous taxa to this previously poorly known fauna and highlighted its similarities to the fauna from the Shuangtasi Formation (Huang, 2003). Based on the presence of the typically Nongshanian taxa *Hsiuannania*, *Bothriostylops*, *Mimotona* and *Harpyodus*, the faunas from the Tujinshan and Shuangtasi Formation are placed here in the Nongshanian and not the Gashatan ALMA, similar to the result of Tsubamoto et al. (2004).

The faunal data compiled here show the presence of *Sarcodon? zhaili* in the Tujinshan Formation fauna, of *Hyracolestes ermineus* in the fauna from the upper member of the Doumu Formation, and of *Palaeostylops iturus* in the fauna from the Shuangtasi Formation in the Xuancheng Basin. These Nongshanian occurrences are remarkable, as the taxa *Sarcodon*, *Hyracolestes* and *Palaeostylops* have been considered to be typically Gashatan taxa. It should however be noted that all three cases represent the only Nongshanian occurrences of these taxa. Moreover, the Nongshanian *Sarcodon? zhaili* differs taxonomically from the Gashatan sarcodontids *S. minor* and *S. pygmaeus* and was only tentatively assigned to the genus *Sarcodon* (Huang, 2003; Lopatin, 2006). The Nongshanian occurrences of *Sarcodon*, *Hyracolestes* and *Palaeostylops* may thus require further study, but based on current data these taxa are considered to be indicative but not diagnostic of a Gashatan age. However, based on the other taxa present in the Tujinshan, Upper Doumu and Shuangtasi faunas, these faunas are still clearly grouped with the other Nongshanian faunas, corroborating the distinct differences between Nongshanian and Gashatan faunas.

Subdivisions Ting (1998) subdivided the Nongshanian into an older *Asiostylops* interval zone, containing the Lannikeng, Lower Doumu, Zhuguikeng and Dazhang faunas, and a younger *Sinostylops* interval zone, containing the Upper Doumu, Datang and Wangwu faunas. The Taizicun fauna was tentatively considered as the youngest Nongshanian fauna, but was situated outside the *Sinostylops* interval zone. The younger age of the Taizicun fauna is confirmed by the results of the AEO, but this fauna is considered here as Gashatan in age (see next section).

However, most of the taxa that were suggested to be characteristic for either one of the interval zones, including *Asiostylops* and *Sinostylops*, are known from only a single occurrence, and therefore have limited value as biochronological markers. Similarly, the distinction of these two interval zones is not readily supported by the quantitative results (Table 1). Nevertheless, the faunas placed by Ting (1998) in the *Asiostylops* interval zone generally seem more primitive than those placed in the *Sinostylops* interval zone. Therefore, a subdivision of the Nongshanian

in two interval zones seems justified, albeit in modified form for which a tentative definition is provided here.

***Asiostylops* interval zone** Typical taxa: No taxa are currently known to be present in more than one fauna from this interval, and not in any other faunas.

Characteristic first appearances: Mimotonidae; Arctostylopidae; Pastoralodontidae; Phenacolophidae; Didymoconidae.

Correlated lithostratigraphic units: upper member of the Wanghudun Formation; Lower member of the Doumu Formation; Lannikeng Member of the Chijiang Formation; Zhuguikeng Member of the Nongshan Formation.

***Bothriostylops* interval zone** Typical taxa: *Bothriostylops* (Arctostylopidae).

Characteristic first appearances: Eurymylidae.

Correlated lithostratigraphic units: Upper member of the Doumu Formation; Wangwu Member of the Chijiang Formation; Tujinshan Formation; Shuangtasi Formation; Datang Member of the Nongshan Formation.

Biogeography The appearance of arctostylopids and of the enigmatic genus *Ernanodon* during the Nongshanian was previously interpreted as evidence of mammal exchange between Asia and South America (Patterson and Pascual, 1972; Ting, 1979; Gingerich, 1985). More recent study has however shown that arctostylopids are not related to South American notoungulates (Missiaen et al., 2006), and also the affinities of *Ernanodon* to South American xenarthrans are now no longer supported (Kondrashov and Agadjanian, 2005; Rose, 2006). Therefore, the Nongshanian seems to represent an assemblage of endemic Asian groups, and there is no real evidence for mammal dispersal between Asia and any other continent at the start or during the Nongshanian. Some of the newly appearing Nongshanian groups, such as basal gliroids, true glires and pastoralodontid pantodonts, represent a further diversification of taxa already present in Asia during the Shanghuan. Other newly appearing taxa, such as phenacolophids and didymoconids represent Asian endemic groups, even though their phylogenetic origin is still unknown (McKenna and Bell, 1997; Rose, 2006).

Age correlations The start of the Nongshanian was correlated to the late Torrejonian (Wang et al., 1998, 2007a) or the start of the Tiffanian (Ting, 1998) in North America, and this latter correlation has recently been confirmed by absolute dating (Clyde et al., 2008).

Although both boundaries seem to be synchronous, they are not directly linked. As described here, the Shanghuan-Nongshanian boundary represents a diversification and specialisation of typically endemic Asian mammals. Similarly, the Torrejonian-Tiffanian boundary can be characterised as an endemic turnover of taxa already present in North America (Krause and Maas, 1990), and recent detailed work on this transition even suggests the existence of a distinct overlap zone, and a more gradual transition between the Torrejonian and Tiffanian (Higgins, 2003). It has been suggested that faunal turnover in this period in North America resulted from the start of a global climatic cooling, but both the precise timing and the effects of this are still unclear (Krause and Maas, 1990; Zachos et al., 2001; Higgins, 2003; Secord, 2008). Because the Shanghuan-Nongshanian boundary represents a similar endemic turnover in the same period, it is suggested here that climatic cooling may have triggered or influenced the faunal turnover at the Shanghuan-Nongshanian boundary in Asia.

6 Gashatan ALMA

Characterisation Typical taxa: *Prionessus* and *Lambdopsalis* (Multituberculata); *Pseudictops* (Pseudictopidae); *Eomylus* (Eurymylidae); *Tribosphenomys* (Rodentia); *Palaeostylops macrodon* (Arctostylopidae); *Sarcodon pygmaeus* (Sarcodontidae); *Prodinoceras efremovi* (Dinocerata); *Dissacus serratus* (Mesonychidae).

Characteristic first appearances: Taeniolabididae and Neoplagiaulacidae (Multituberculata); Rodentia; Dinocerata; Nyctitheriidae; Hyaenodontidae.

Characteristic last appearances: Pastoralodontidae; Phenacolophidae.

Faunal evolution The beginning of the Gashatan is marked by a further diversification of Asian endemic taxa, as well as by the arrival of North American immigrants. The orders Rodentia and Dinocerata and an important number of families make their first appearance in the Gashatan. For Rodentia (Meng et al., 1994, 2003; Asher et al., 2005) and Dinocerata (Schoch and Lucas, 1985; Beard, 1998) it has been argued that these groups evolved in Asia during the Paleocene, and also limnocyonine hyaenodontids appear earlier in Asia than anywhere else in Laurasia (Meng et al., 1998; Bowen et al., 2002). On the other hand, for taeniolabidid and neoplagiaulacid multituberculates, nyctitheriids, cimolestids, and carpolestids, more primitive forms are known from older faunas in North America but not in Asia, and these taxa are most probably North American immigrants. The start of the Gashatan thus also seems to coincide with a sudden and significant mammal exchange between North America and Asia, and a sharp decrease of the endemism of the Asian faunas.

Correlated lithostratigraphic units Taizicun Formation (Turpan Basin, Xinjiang Uygur Autonomous Region); Member I of the Gashato Formation (Ulan Nur Basin, Nei Mongol Autonomous Region); Nomogen Formation (Erlian Basin, Nei Mongol Autonomous Region); Lower part of the Lingcha Formation (Hengyang Basin, Hunan Province); Zhigden and Naran Member of the Naran-Bulak Formation (Nemegt and Bugin-Tsav Basin, Mongolia); Dazhang and Tantou Formation (Tantou Basin, Henan Province); Pinghu Formation (Chijiang Basin, Jiangxi Province); Dabu Formation (Turpan Basin, Xinjiang Uygur Autonomous Region).

Discussion of correlations The Taizicun Formation has been variously correlated to the Nongshanian (Ting 1998; Tsubamoto et al., 2004) or to the Gashatan (Wang et al., 1998; Bowen et al., 2002; Ting et al., 2003), and is placed exactly in between the typical Nongshanian and Gashatan faunas by the results of the AEO (Table 1). The Taizicun fauna shares the presence of the pantodont *Archaeolambda speciosa* with the very poorly known Nongshanian Zhuguikeng fauna. However, none of the typical Nongshanian taxa *Bothriostylops*, *Hsiuannania*, *Mimotona*, *Harpyodus* and *Altisambda* are present in the Taizicun fauna. This fauna does include four different species of *Prodinoceras*, a genus that is mostly known from Gashatan faunas, as well as from the Bumbanian Ningjiashan fauna. The Taizicun Formation fauna is therefore correlated here to the Gashatan rather than to the Nongshanian ALMA, confirming most previous ideas (Wang et al., 1998; Ting et al., 2003).

Similarly, the faunas from the Pinghu and Dabu Formation and from the Dazhang and Tantou Formation have been variously placed in the Gashatan ALMA and in either the Bumbanian or Nongshanian ALMAs respectively (Russell and Zhai, 1987; Wang et al., 1998; Ting, 1998; Ting et al., 2003; Tsubamoto et al., 2004). The Pinghu and Dabu faunas do not contain Bumbanian markers but did yield specimens attributed to *Prodinoceras*, and therefore this study corroborates their previously noted Gashatan affinities (Russell and Zhai, 1987; Wang et al., 1998). The Dazhang fauna contains an unidentified pseudictopid as well as *Yuesthonyx tingae*, a tillodont similar to a form described from the Bumbanian Wutu fauna (Tong and Wang, 2006). The Dazhang fauna thus does not contain a single typical Nongshanian taxon, and based on the results of the AEO and the absence of modern taxa the Dazhang fauna is placed here in the Gashatan ALMA. The Tantou Formation overlying the Dazhang Formation is only known to contain a *Prodinoceras*-like unit and is here tentatively placed in the Gashatan ALMA, similar to correlations in some previous studies (Russell and Zhai, 1987; Wang et al., 1998). Because of the poor knowledge of these four faunas, their correlation to the Gashatan here is to be considered somewhat tentative and subject to change if more information becomes available.

Absolute age studies suggest a late Paleocene age for the lower part of the Lingcha Forma-

tion, and the Lower Lingcha fauna has been accepted as a Gashatan fauna by several authors (Bowen et al., 2002; Ting et al., 2003; Tsubamoto et al., 2004). However, this fauna only consists of an unidentified species of *Archaeolambda*, a genus that has been reported in faunas ranging from the early Paleocene Shanghuan to the middle Eocene Arshantan, and therefore does not have any stratigraphic value. The Lower Lingcha fauna is considered here to be Gashatan in age, based on the results of the isotope analysis (Bowen et al., 2002) and AEO, but does not represent a well known, typically Gashatan fauna.

Subdivisions The Gashatan faunas form a relatively homogenous assemblage. It has been argued that the fauna from the Dabu Formation is younger than that from the Taizicun Formation (Wang et al., 1998), a suggestion confirmed here by AEO. However, both quantitative and qualitative methods fail to show a discrete faunal turnover during the Gashatan, and no subdivisions are proposed here.

Traditionally Gashatan faunas have been studied from the Gashato and Naran Bulak Formation in Mongolia and from the Nomogen Formation in Nei Mongol (Inner Mongolia). However as defined here, the Gashatan groups faunas from nine different basins, including faunas from northwest and southeast China. Although these latter faunas are less well known, they are clearly grouped with the typical Gashatan faunas and share genera and species with them. This therefore also indicates the absence of strong provincialism of mammal faunas during the Gashatan.

Biogeography The presence of the families Neoplagiulacidae, Taeniolabididae, Nyctitheriidae, Cimolestidae and Carpolestidae in Gashatan faunas indicates the appearance of North American immigrants in Asian faunas. Conversely, alagomyid rodents, arctostylopids, prodinoceratids, tillodonts and coryphodontids are thought to have originated in Asia and to have subsequently dispersed into North America during the Gashatan (Schoch and Lucas, 1985; Meng et al., 1994; Beard, 1998; Secord et al., 2006). The Gashatan is thus characterised by an important and significant exchange of mammals between Asia and North America in both directions (Fig. 3A). This pattern is significantly different from the one-way, strictly Asia-into-North America dispersal scenario that has been proposed in the East of Eden hypothesis (Beard, 1998, 2002).

The Paleocene Asian immigrants in North America seem to arrive in two distinct waves. The first one consists of arctostylopids and prodinoceratids and marks the start of Tiffanian-5a. The second one consists of alagomyids, coryphodontids and tillodonts and marks the start of the Clarkforkian, approximately 1.3 Ma later (Secord et al., 2006). The quality of the dense North American fossil record suggests that it is unlikely that rodents and tillodonts arrived significantly earlier than Clarkforkian-1 (Gingerich, 2006). Moreover, the presence of a limnocyonine hyaenodontid in the Gashatan Bayan Ulan fauna, and their invasion of North America only later at the Paleocene-Eocene boundary (PEB) corroborate that opportunities for mammal exchange between Asia and North America were limited during the Gashatan.

Because these mammal migrations took place across the high-latitude Bering land bridge, it seems significant that the start of the mammal exchanges roughly coincides with the start of a global warming trend (Zachos et al., 2001). In this respect, it may also be noteworthy that the assemblage of taxa invading Asia is especially close to middle to late Tiffanian faunas described from western Canada (Fox, 1990). Taxa from these more northern regions were possibly better adapted to disperse across higher latitudes.

The presence of North American immigrants in Gashatan faunas has been documented particularly well in the Subeng site; five immigrant families are present at Subeng, and neoplagiulacids, cimolestids and carpolestids are even exclusively known from Subeng during the Gashatan (Missiaen and Smith, 2008). The Subeng mammal fauna thus represents a unique link between Asia and North America, and it is probable that this was at least partly influenced by environmental factors. It has been suggested that the Subeng site had a more closed, humid

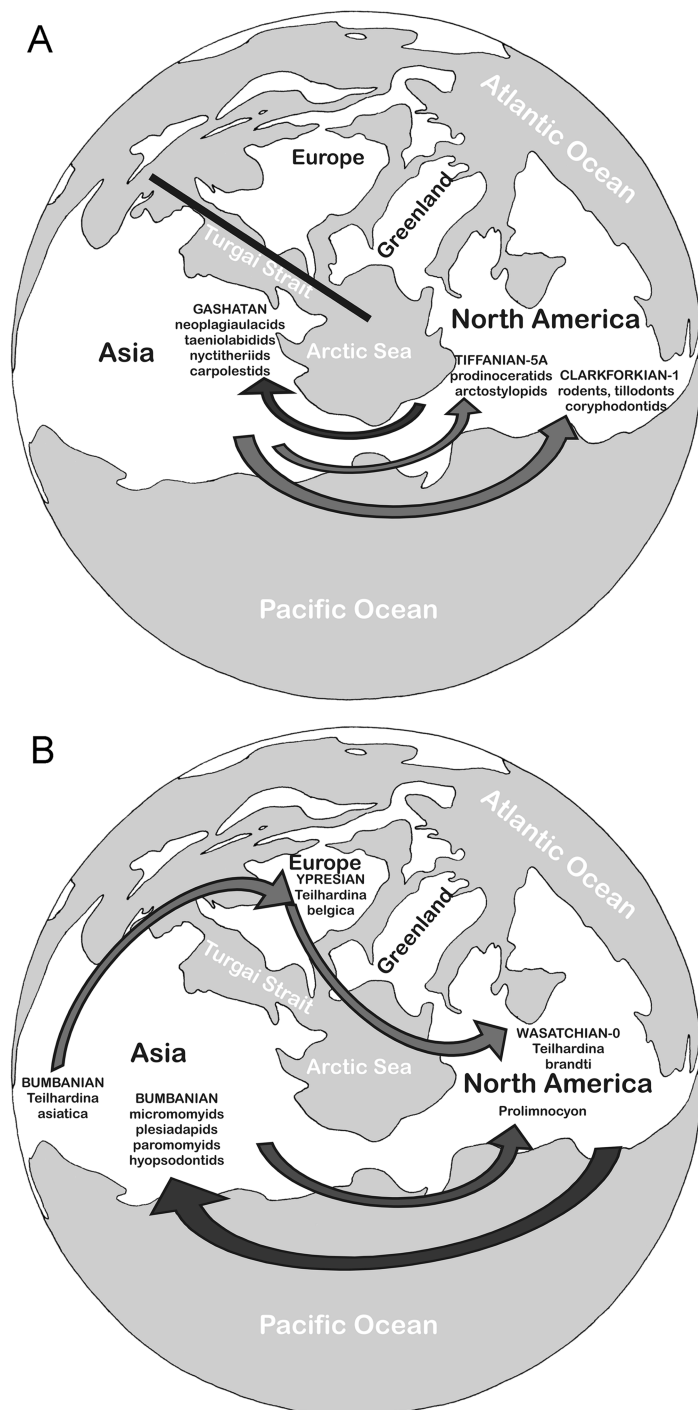


Fig. 3 Asian mammal biogeography during the Gashatan and Bumbanian
Biogeographical map of the Northern Hemisphere in polar projection during the Gashatan (A) and Bumbanian (B). Bumbanian migration of primates is based on Smith et al. (2006) and Gingerich et al. (2008). Direct migration between Asia and Europe has also been suggested for hyopsodontid condylarths and perissodactyls (Hooker and Dashzeveg, 2003; Kondrashov, 2004). Map modified from Hooker and Dashzeveg (2003)

local environment whereas the other Gashatan faunas from Nei Mongol and Mongolia had a more open, semi-arid environment. The local environment at Subeng was probably more suitable for the North American forest adapted immigrants, resulting in higher number of shared taxa. The isolation and endemism of Asian mammal faunas was therefore probably influenced by ecological factors, with the Subeng site serving as a stepping stone or refugium for the North American immigrants (Van Itterbeeck et al., 2007; Missiaen and Smith, 2008).

Age correlations The marked faunal exchange of Asian and North American mammals during the Gashatan allows a better mammal biochronological correlation than for the preceding ALMAs. The arrival of prodinoceratids and advanced arctostylopids at the start of Tiffanian-5a, and of alagomyids, tillodonts and coryphodontids at the beginning of Clarkforkian-1 (Secord et al., 2006), suggests that the Gashatan is at least as old as Tiffanian-5a. This is also confirmed by absolute age studies, which have placed the Lower Lingcha fauna within chron 24r and the *Lambdopsalis* fauna from the Nomogen Formation at Nuhetingboerhe within chron 25r (Bowen et al., 2002; Sun et al., 2009), correlating these Gashatan faunas to the Late Paleocene North American upper Tiffanian to upper Clarkforkian period (Secord et al., 2006). The Nongshanian-Gashatan boundary is therefore correlated here with the Tiffanian-4b-Tiffanian-5a boundary, corroborating some of the previous studies (Wang et al., 1998, 2007a), although both biochronological and magnetostratigraphical studies have suggested that this boundary may prove to be still slightly older (Bowen et al., 2005; Missiaen and Smith, 2008).

7 Bumbanian ALMA

Characterisation Typical taxa: *Rhombomylus* (Eurymylidae); *Gomphos* (Mimotonidae).

Characteristic first appearances: Primates; Perissodactyla; Artiodactyla; Condylarthra Ctenodactyloidea.

Characteristic last appearances: Arctostylopidae; Eurymylidae; Mimotonidae; Alagomyidae; Prodinoceratidae.

Faunal evolution The Gashatan-Bumbanian boundary coincides with a major turnover in the Asian mammal faunas. In the Bumbanian, the modern mammal orders Artiodactyla, Perissodactyla and true Primates (sensu Gingerich, 1989, excluding plesiadapiforms) appear, and at least for Perissodactyla a considerable diversity is observed already during the Bumbanian. Also at the beginning of the Bumbanian, more derived rodent families appear, and despite their success in the preceding period, almost all basal gliriforms and gliroids disappear by the end of the Bumbanian, possibly because of the competition with these more evolved rodents.

Additionally, the archaic families Micromomyidae, Plesiadapidae, Paromomyidae and Hyopsodontidae have their first appearance in Asia in the Bumbanian. These taxa are however already known in the North American Paleocene (McKenna and Bell, 1997), and their appearance thus unambiguously demonstrates the immigration of North American mammals into Asia at the Gashatan-Bumbanian boundary.

The results of the AEO suggest that the Wutu fauna is older than any other Bumbanian fauna. This result is similar to that of previous quantitative analyses (Bowen et al., 2002; Tsubamoto et al., 2004), but is distinctly different from all other interpretations of the age of the Wutu fauna (Wang et al., 1998; Ting, 1998; Tong and Wang, 2006). It is suggested here that this problematic result the Wutu fauna may be an artefact of the AEO method, caused by the very complete study of the exceptionally rich Wutu site (Tong and Wang, 2006), demonstrating the presence of otherwise Paleocene lineages that may not have been present or recovered in other Bumbanian sites.

Correlated lithostratigraphic units Upper part of the Lingcha Formation (Hengyang

Basin, Hunan Province); Member II and III of the Gashato Formation (Ulan Nur Basin, Mongolia); Bumban and Aguyt Member of the Naran-Bulak Formation (Nemegt Basin, Mongolia); Wutu Formation (Wutu Basin, Shandong Province); Ningjiashan Member of the Xinyu Group (Yuanshui Basin, Jiangxi Province); Shisanjianfang Formation (Turpan Basin, Xinjiang Uygur Autonomous Region); middle member of the Yuhuangding Formation (Xichuan Basin, Henan Province); Akasaki Formation (Kumamoto Prefecture, Japan); Zhangshanji Formation (Laian District, Anhui Province); *Gomphos* beds of Nomogen Formation (Erlian Basin, Nei Mongol Autonomous Region); Niushan Formation (Niushan Basin, Shandong Province).

Discussion of correlations All of the typical Bumbanian faunas, except the Wutu fauna (see above), are clearly grouped together in results of the AEO. These results also confirm the difference between the Bumbanian fauna from the middle member of the Yuhuangding Formation and the Arshantan fauna from the uppermost part of the Yuhuangding Formation and the base of the overlying Dacangfang Formation (Lucas, 2004), suggesting that the Bumbanian-Arshantan boundary is present in the Yuhuangding Formation.

Subdivisions Although there have been few detailed biochronological studies of the important Bumbanian ALMA, it is generally accepted that the Upper Lingcha and the Bumban member fauna are probably the oldest Bumbanian faunas (Ting, 1998; Tong and Wang, 2006), and this is compatible with the absolute dating of the Lingcha Formation (Bowen et al., 2002).

Ting (1998) subdivided the Bumbanian ALMA in three biochrons, based on the appearance of specific perissodactyl genera. This subdivision of the Bumbanian seems to be consistent with a more general pattern of faunal turnover, which is most readily, but not exclusively, demonstrated by the diversification of perissodactyls. Because the poorly known faunas from Member III of the Gashato Formation and from the Aguyt Member of the Naran-Bulak Formation only yielded a single taxon, the mimotonid *Gomphos*, they are identical to that from Member II of the Gashato Formation and there is no biochronological reason to separate them. These three faunas are therefore placed in the *Orientolophus* interval zone, together with the Bumban fauna and the Upper Lingcha fauna. This does however leave only the Wutu fauna within the *Homogalax* interval, which therefore is difficult to truly characterise. An updated definition of these intervals is tentatively proposed here.

The newly studied *Gomphos* beds from the upper part of the Nomogen Formation are biostratigraphically interesting but difficult to correlate. *Gomphos elkema* has only been found associated with other mammals in one other fauna, the Bumban Mbr. fauna, and is therefore suggestive for an early Bumbanian age (Meng et al., 2004). The primate *Baataromomys* was also described from the *Gomphos* beds (Ni et al., 2007), but because this taxon is not known from any other Asian faunas and the opinions on its evolutionary position are not unanimous (Ni et al., 2007 vs Beard, 2008 or Gingerich et al., 2008), *Baataromomys* currently does not allow a precise biochronological interpretation. Finally, the *Gomphos* beds of the Nomogen Formation have however also yielded a new species of *Anatolostylops* (Wang et al., 2008b), previously only known from the late Bumbanian Shisanjianfang fauna, and fossils tentatively identified as *Uintatherium*, *Pataecops* and a new genus of Lophialetidae (Bai, 2006; Wang et al., 2007b). The fauna from the *Gomphos* beds is definitely Bumbanian and Early Eocene in age, but is difficult to place in one of the three Bumbanian intervals used here. Differing from previously expressed opinions (Meng et al., 2004, 2007b), this study tentatively places it in the *Heptodon* interval based on the results of AEO, with the caveat that its interpretation is subject to change when more taxa from this interesting new fauna get published.

***Orientolophus* interval** Typical taxa: *Orientolophus*.

Characteristic first appearances: Isectolophidae; *Gomphos* (Mimotonidae).

Characteristic last appearances: Cimolestidae.

Correlated lithostratigraphic units: Upper part of the Lingcha Formation; Member II and III

of the Gashato Formation; Bumban and Aguyt Member of the Naran-Bulak Formation.

***Homogalax* interval** First appearances: Lophialetidae; Eomoropidae; Ischyromyidae.

Last appearances: Multituberculata; Astigalidae; Pseudictopidae; Alagomyidae.

Correlated lithostratigraphic units: Wutu Formation.

***Heptodon* interval** Typical taxa: *Anatolestylops* (Arctostylopidae).

Characteristic first appearances: Helaletidae.

Characteristic last appearances: Arctostylopidae; Eurymylidae; Mimotonidae; Prodinoceratidae.

Correlated lithostratigraphic units: Ningjiashan Member of the Xinyu Group; Shisanjianfang Formation; middle member of the Yuhuangding Formation; Akasaki Formation; Zhangshanji Formation; *Gomphos* beds of Nomogen Formation; Niushan Formation.

Biogeography The start of the Bumbanian is characterised by the first appearance of a number of archaic and modern mammal groups. During the Bumbanian, phenacodontid and hyopsodontid condylarths, and micromomyid, paromomyid and plesiadapid plesiadapiforms make their first Asian appearance (Tong and Wang, 2006). However, all these groups were already present much earlier in the North American Paleocene, and therefore probably represent North American immigrants. On the other hand, limnocyonine hyaenodontids were present during the Gashatan, and disperse into North America at the start of Wasatchian. These exchanges indicate that the Bumbanian is a period of intense two-way migration between Asia and North America, possibly as a response to the globally warm climate during this period (Zachos et al., 2001) which facilitated dispersal across the Bering land bridge (Fig. 3B).

The geographical origin of the newly appearing modern mammal groups is still unclear, although a number of papers have suggested an Asian origin (Beard, 1998; Hooker and Dashzeveg, 2003; Ni et al., 2004). In contrast with the dispersal at the start of the Gashatan, Bumbanian mammal dispersal seems not to have been restricted to exchanges between Asia and North America. The recently discovered early Eocene Vastan fauna from India suggests the exchange of lagomorphs between East Asia and India during the early Eocene (Rose et al., 2008). However, the bats, rodents and tillodonts from Vastan seem unrelated to early Eocene Asian forms but are remarkably close to European taxa (Smith et al., 2007; Rana et al., 2008; Rose et al., 2009). Direct migration of Asian mammals to Europe has been suggested for primates, perissodactyls and hyopsodontid condylarths (Hooker and Dashzeveg, 2003; Kondrashov, 2004; Smith et al., 2006; Gingerich et al., 2008; but see Ni et al., 2007; Beard, 2008). Because dispersal between Asia and Europe could take place at lower latitudes across the Turgai Strait, the opening of this migration route is probably less dependent on climate changes. Hooker and Dashzeveg (2003) tried to correlate the dispersal of perissodactyls and condylarths with sea level falls in the Turgai area, but the timing of these sea level falls, and the factors influencing dispersal across the Turgai Strait are still poorly understood.

Age correlations This updated Asian mammal biochronology confirms that the start of the Bumbanian is characterised by the first appearance of the modern mammal orders Artiodactyla, Perissodactyla and Primates, similar to their appearance at the base of the Eocene in North America and Europe. This traditional biochronological correlation of the Gashatan-Bumbanian boundary with the Paleocene-Eocene boundary (Ting, 1998; Wang et al., 1998; 2007a) has moreover been corroborated by all recent absolute age studies (Bowen et al., 2002, 2005; Ting et al., 2003; Sun et al., 2009).

The correlation of the *Orientolophus*, *Homogalax* and *Heptodon* intervals to the North American Sandcouleean, Graybullian and (Lysitean + Lostcabinian) intervals (Ting, 1998) is only weakly supported by biochronological data. Given the few and sometimes inconsistent absolute ages for Bumbanian and Arshantan faunas (Bowen et al., 2002, 2005; Sun et al., 2009), no age correlations are suggested for the boundaries between these intervals and for the end of

the Bumbanian ALMA.

8 Conclusions

The Shanghuan faunas are a poorly known assemblage of primitive taxa, dominated by primitive gliriforms and pantodonts, and especially the pantodont *Bemalambda* is typical of this period. The primitive and endemic nature of these faunas complicates a biochronological correlation, but chronostratigraphical data correlate the Shanghuan to the early Paleocene Puercan and Torrejonian biozones in North America (Clyde et al., 2008; Ting et al., 2011).

The start of the following Nongshanian is characterised by an endemic diversification of the Shanghuan mammal groups. Especially gliriforms radiate, with the appearance of the basal gliriform family Arctostylopidae, and the first appearance of true Glires, represented by Eurymylidae and Mimotonidae. Because both the start of the Nongshanian and the Tiffanian represent synchronous turnovers of endemic taxa, they are suggested to be independent faunal turnovers triggered by the start of a period of global cooling (Zachos et al., 2001).

The start of the Gashatan witnesses an abrupt reduction of the Asian endemism and a further diversification of the Asian faunas. Some of the groups that make their first appearance, such as prodinoceratids, hyaenodontids and rodents, supposedly evolved from Asian ancestors. However, the Gashatan mammal faunas are also significantly enriched by North American immigrants such as multituberculates, nyctitheriids, cimolestids and carpolestids. Conversely, a wave of Asian immigrants consisting of arctostylopids and prodinoceratids invades North America at the start of Tiffanian-5a, and a second wave consisting of rodents, tillodonts and coryphodonts arrives at the start of the Clarkforkian (Secord et al., 2006). The start of the Gashatan is therefore correlated to the start of North American Tiffanian-5a.

The start of the Bumbanian is characterised by the appearance of the first artiodactyls, perissodactyls and primates, similar to their appearance in North America and Europe at the start of the Eocene (Gingerich, 1989, 2006), and is correlated to the Paleocene-Eocene boundary based on mammal biochronology and on chronostratigraphy (Bowen et al., 2002; Sun et al., 2009). The Bumbanian represents a period of extensive Laurasian mammal exchange and, contrasting with dispersal at the start of the Gashatan, during the Bumbanian dispersal was probably also possible directly between Asia and Europe.

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Appendix Data matrix used in the Appearance Event Analysis

The matrix was created by first compiling the presence of all species, genera, families and orders in all analysed faunas. Subsequently, all taxa only present in a single fauna (singleton taxa) were removed because they are not biochronologically informative. Finally, wherever one taxon and the hierarchically higher taxon (e. g. species and genus) have the same distribution, the hierarchically higher taxon was removed to avoid redundancy. The resulting matrix includes all strictly biochronologically informative taxa, but is not a complete list of all taxa present in all analysed faunas.

	DZULLZPWLS	ULUMLTDTSS	ULABNZTKKS	DNCGPBSGGG	WZHYNNAGK	AIULU	TUSSFAIWAZ	DDWWWITZUXT	LLGMAHA21H	BOMFFU321	USEDUNUKUZ	SMHOP
Order Multituberculata	0000000000	0000000000	0000111000	0100011001	1000000000	00000						
Mesodmops	0000000000	0000000000	0000000000	0000001000	1000000000	00000						
Prionessus lucifer	0000000000	0000000000	0000110000	0100011001	0000000000	00000						
Lambdopsalis bulla	0000000000	0000000000	0000000000	0100011000	0000000000	00000						
Sphenopsalis nobilis	0000000000	0000000000	0000000000	0100000001	0000000000	00000						
Obtusodon hanhuaensis	0000000000	0101000000	0000000000	0000000000	0000000000	00000						
Family Astigalidae	0010000000	0000100000	0000000000	0000001000	1000000000	00000						
Astigale	0010000000	0000100000	0000000000	0000000000	0000000000	00000						
Family Arctostylopidae	1000000110	1000000111	0001110001	0101111001	1000000000	00000						
Palaeostylops	0000000000	0000000010	0000110000	0100111001	0000000000	00000						
Palaeostylops macrodon	0000000000	0000000000	0000110000	0100010001	0000000000	00000						
Palaeostylops iturus	0000000000	0000000010	0000110000	0100111001	0000000000	00000						
Bothriostylops	1000000100	0000000111	0000000000	0000000000	0000000000	00000						
Bothriostylops progressus	0000000000	0000000111	0000000000	0000000000	0000000000	00000						
Wanostylops	0000000000	0000000110	0000000000	0000000000	0000000000	00000						
Anatolestylops	0000000000	0000000000	0000000001	0001000000	0000000000	00000						
Family Anagalidae	1011110010	1101100110	0000000000	0000000001	0000000000	00000						
Hsiuannania	0000000010	1100000110	0000000000	0000000000	0000000000	00000						
Hsiuannania maguensis	0000000000	0000000110	0000000000	0000000000	0000000000	00000						
Linnania	0011100000	0000000000	0000000000	0000000000	0000000000	00000						
Family Pseudictopidae	1000000010	0101101000	0000110000	0100111001	1000000000	00000						
Pseudictops	0000000000	0000000000	0000110000	0100111001	0000000000	00000						
Pseudictops lophiodon	0000000000	0000000000	0000110000	0100111001	0000000000	00000						
Anictops tabiepedis	0000000000	0001100000	0000000000	0000000000	0000000000	00000						
Paranictops	0000000000	0001100000	0000000000	0000000000	0000000000	00000						
Order Mixodontia	0000000000	1000000100	1001111011	0100111001	0100100000	00000						

	DZULLZPWLS ULUMLTDTSS ULABNZTKKS DNCGPBSGGG WZHYYNNACK AIULU TUSSEFAIWAZ DDWWWIZUXT LLGMAHA21H BOMFFU321 USEDUNUKUZ SMHOP
Family Eurymylidae	0000000000 1000000100 0001111011 0100111001 0100100000 00000
<i>Eomylus</i>	0000000000 0000000000 0000110010 0100011001 0000000000 00000
<i>Eomylus zhigdenensis</i>	0000000000 0000000000 0000110010 0000000001 0000000000 00000
<i>Eomylus bayanulanensis</i>	0000000000 0000000000 0000000000 0000011000 0000000000 00000
<i>Paleomylus</i>	0000000000 0000000000 0000000000 0000110000 0000000000 00000
<i>Eurymylus laticeps</i>	0000000000 0000000000 0000100000 0000000001 0000000000 00000
<i>Sinomylus</i>	0000000000 0000000100 0000110000 0000000000 0000000000 00000
<i>Rhombomylus turpanensis</i>	0000000000 0000000000 0001000001 0000000000 0100100000 00000
Order Rodentia	0000000000 0000000000 1001010100 0011011000 1010100110 11101
Family Alagomyidae	0000000000 0000000000 0001010000 0000011000 1000000000 00000
<i>Tribosphenomys minutus</i>	0000000000 0000000000 0000010000 0000011000 0000000000 00000
<i>Alagomys</i>	0000000000 0000000000 0001000000 0000000000 1000000000 00000
Family Ischyromyidae	0000000000 0000000000 0000000000 0010000000 1000000000 11000
Superfamily Ctenodactyloidea	0000000000 0000000000 1001000100 0011000000 1010100000 10101
<i>Adenimys</i>	0000000000 0000000000 0000000000 0010000000 0000100000 10100
<i>Adenimys burkei</i>	0000000000 0000000000 0000000000 0010000000 0000000000 10000
<i>Saykanomys</i>	0000000000 0000000000 0000000100 0000000000 0010000000 00000
<i>Tamquammys</i>	0000000000 0000000000 0000000000 0000000000 0010000000 10000
<i>Tsinlingomys youngi</i>	0000000000 0000000000 0000000000 0000000000 0010000000 00001
Family Mimotonidae	0000000000 1101000100 0011000000 0001000110 0000000000 00000
<i>Gomphos</i>	0000000000 0000000000 0011000000 0001000110 0000000000 00000
<i>Gomphos elkema</i>	0000000000 0000000000 0001000000 0001000110 0000000000 00000
<i>Mimotona</i>	0000000000 1101000100 0000000000 0000000000 0000000000 00000
Order Lagomorpha	0000000000 0000000000 0001000100 0001000000 0010000001 00101
Family Leporidae	0000000000 0000000000 0000000000 0000000000 0010000000 00101
<i>Lushilagus lohoensis</i>	0000000000 0000000000 0000000000 0000000000 0010000000 00001
<i>Shamolagus</i>	0000000000 0000000000 0000000000 0000000000 0010000000 00100
Order Leptictida	0000000000 0001000000 0000000000 0000010000 1000000000 00000
Family Leptictidae	0000000000 0000000000 0000000000 0000010000 1000000000 00000
Order Lipotyphla	0000000000 0000000000 1001010100 0000011001 1010000000 10000
Family Nyctitheriidae	0000000000 0000000000 0001010000 0000011001 1000000000 00000
<i>Bumanius</i>	0000000000 0000000000 0001000000 0000001000 0000000000 00000
<i>Praolestes nanus</i>	0000000000 0000000000 0000010000 0000000001 0000000000 00000
Family Micropternodontidae	0000000000 0000000000 1000000000 0000000000 0000000000 10000
Family Apternodontidae	0000000000 0000000000 0000000100 0000000000 0010000000 00000
Order Creodonta	0000000000 0000000000 0000100100 0001010000 1010000010 01101
Family Hyaenodontidae	0000000000 0000000000 0000100100 0000010000 1010000010 01101
<i>Neoparapterodon rechetovi</i>	0000000000 0000000000 0000000100 0000000000 0000000000 01000
<i>Propterodon</i>	0000000000 0000000000 0000000000 0000000000 0010000000 00101
Family Oxyanidae	0000000000 0000000000 0000100000 0000000000 1010000000 01100
<i>Sarkastodon</i>	0000000000 0000000000 0000000000 0000000000 0010000000 01100
<i>Sarkastodon mongoliensis</i>	0000000000 0000000000 0000000000 0000000000 0000000000 01100
Order Carnivora	0010000000 0001000000 0000000000 0000010000 1010010000 01101
Family Viverravidae	0000000000 0000000000 0000000000 0000010000 1000000000 00000
Family Miacidae	0010000000 0001000000 0000000000 0000000000 1010010000 01101
<i>Miacis</i>	0000000000 0000000000 0000000000 0000000000 0010010000 01001
<i>Miacis lushiensis</i>	0000000000 0000000000 0000000000 0000000000 0010000000 00001

	DZULLZPWLS ULUMLTDTSS ULABNZTKKS DNCGPBSGGG WZHYYNNACK AIULU
	TUSSFAIWAZ DDWWWIZUXT LLGMAHA21H BOMFFUU321 USEDUNUKUZ SMHOP
<i>Pappictidops</i>	0010000000 0001000000 0000000000 0000000000 0000000000 00000
Family Didymoconidae	0000000010 0011000000 1000010100 0000000000 0010000000 11100
<i>Archaeoryctes</i>	0000000010 0010000000 0000010000 0000000000 0000000000 10000
<i>Ardynictis</i>	0000000000 0000000000 0000000100 0000000000 0010000000 00000
<i>Kennatherium shirens</i>	0000000000 0000000000 0000000100 0000000000 0000000000 00100
Family Sarcodontidae	0011100000 1000000100 0001010100 0100011001 0000000000 00000
<i>Carnilestes</i>	0011000000 0000000000 0000000000 0000000000 0000000000 00000
<i>Hyracolestes ermineus</i>	0000000000 1000000000 0000010000 0000011001 0000000000 00000
<i>Sarcodon</i>	0000000000 0000000100 0000010000 0100010001 0000000000 00000
<i>Sarcodon pygmaeus</i>	0000000000 0000000000 0000010000 0100000001 0000000000 00000
Order Didelphodonta	0000000000 0000000000 1001010100 0000001000 0000000000 00000
Family Palaeoryctidae	0000000000 0000000000 0000010100 0000000000 0000000000 00000
Family Cimolestidae	0000000000 0000000000 1001000000 0000001000 0000000000 00000
<i>Tsaganius ambiguus</i>	0000000000 0000000000 0001000000 0000001000 0000000000 00000
Family Esthonychidae	1010010000 0000101000 0000000000 0000000000 1011000110 00011
<i>Chungchienia</i>	0000000000 0000000000 0000000000 0000000000 0010000000 00010
<i>Kuanchuanius</i>	0000000000 0000000000 0000000000 0000000000 0001000010 00000
<i>Yuesthonyx</i>	0000000000 0000001000 0000000000 0000000000 1000000000 00000
Order Pantodonta	1111110111 1001100111 1100111111 1110010000 1001110111 11111
Family Harpyodidae	0010000010 0001000110 0000000000 0000000000 0000000000 00000
<i>Harpyodus</i>	0000000010 0001000110 0000000000 0000000000 0000000000 00000
<i>Harpyodus progressus</i>	0000000000 0000000110 0000000000 0000000000 0000000000 00000
<i>Bemalambda</i>	0011110001 0001100000 0000000000 0000000000 0000000000 00000
<i>Bemalambda nanhsiungensis</i>	0001010000 0000000000 0000000000 0000000000 0000000000 00000
Family Pastoralodontidae	1000000000 1010000000 0000000000 0100010000 0000000000 00000
<i>Pastoralodon lacustris</i>	0000000000 0000000000 0000000000 0100010000 0000000000 00000
<i>Altilambda</i>	1000000000 1010000000 0000000000 0000000000 0000000000 00000
<i>Altilambda pactus</i>	1000000000 0010000000 0000000000 0000000000 0000000000 00000
Family Pantolambdodontidae	1110000111 1000000111 0101111010 0000000000 1000000001 10100
<i>Archaeolambda</i>	0110000101 1000000111 0101101010 0000000000 0000000001 00000
<i>Archaeolambda speciosa</i>	0100000000 0000000000 0000001000 0000000000 0000000000 00000
<i>Archaeolambda tabiensis</i>	0000000100 1000000000 0000000000 0000000000 0000000000 00000
<i>Nanlingilambda</i>	1000000010 0000000000 0000000000 0000000000 0000000000 00000
<i>Pantolambdodonton</i>	0000000000 0000000000 0000000000 0000000000 0000000001 10100
<i>Pantolambdodonton fortis</i>	0000000000 0000000000 0000000000 0000000000 0000000000 10100
Family Coryphodontidae	0000000000 0000000000 1000100101 1000000000 1001110111 11111
<i>Asiocoryphodon</i>	0000000000 0000000000 1000000000 0000000000 0001100100 00000
<i>Asiocoryphodon conicus</i>	0000000000 0000000000 0000000000 0000000000 0001100000 00000
<i>Coryphodon</i>	0000000000 0000000000 0000100001 0000000000 0000010010 00000
<i>Eudinoceras</i>	0000000000 0000000000 0000000000 0000000000 0000000011 01111
<i>Eudinoceras mongoliensis</i>	0000000000 0000000000 0000000000 0000000000 0000000000 01100
<i>Heterocoryphodon</i>	0000000000 0000000000 0000000000 0000000000 1001100000 00000
<i>Heterocoryphodon flerowi</i>	0000000000 0000000000 0000000000 0000000000 0001100000 00000
<i>Wutucoryphodon</i>	0000000000 0000000000 0000000000 1000000000 1000000000 00000
Family Pantolestidae	0000000000 0000000000 0001010000 0000000000 0000000001 01000
Order Pholidota	1000000000 0000000000 0000010000 0000000000 1000000000 00000
<i>Ernanodon</i>	1000000000 0000000000 0000010000 0000000000 0000000000 00000

	DZULLZPWLS ULUMLTDTSS ULABNZTKKS DNCGPBSGGG WZHYYNNAGK AIULU TUSSEFAIWAZ DDWWWIZUXT LLGMAHA21H BOMFFUU321 USEDUNUKUZ SMHOP
Family Carpolestidae	0000000000 0000000000 0000000000 0000001000 1000000000 00000
Order Primates	0000000000 0000000000 1001000000 0011000000 0000000000 00001
Family Omomyidae	0000000000 0000000000 1000000000 0011000000 0000000000 00000
Family Hyopsodontidae	0000000000 0000000000 0001000001 0000000000 1000000010 00000
<i>Hyopsodus</i>	0000000000 0000000000 0001000001 0000000000 0000000000 00000
Order Dinocerata	0000001000 0000010000 0000111110 1011011001 1001010010 10010
Family Prodinoceratidae	0000001000 0000010000 0000111010 1000011001 1000010000 00000
<i>Prodinoceras</i>	0000001000 0000000000 0000111010 1000011001 0000010000 00000
<i>Prodinoceras plantigradum</i>	0000000000 0000000000 0000110000 0000001000 0000000000 00000
<i>Prodinoceras xinjiangensis</i>	0000000000 0000000000 0000000000 1000010000 0000000000 00000
Family Uintatheriidae	0000000000 0000000000 0000000000 0011000000 0001000010 10010
<i>Gobiatherium</i>	0000000000 0000000000 0000000000 0010000000 0001000000 10000
<i>Gobiatherium mirificum</i>	0000000000 0000000000 0000000000 0010000000 0000000000 10000
<i>Uintatherium</i>	0000000000 0000000000 0000000000 0001000000 0000000000 00010
Order Mesonychia	1101110110 0000100110 1001111100 0111011001 1010000001 11111
Family Hapalodectidae	0000000000 0000000000 1001010100 0000001000 1000000001 11000
<i>Hapalodectes serus</i>	0000000000 0000000000 0000000000 0000000000 0000000000 11000
Family Mesonychidae	1101110110 0000100110 1001101100 0111011001 1000000000 11111
<i>Dissacus</i>	0000010000 0000000010 1001100000 0101011001 1000000000 00000
<i>Dissacus serratus</i>	0000000000 0000000000 0000000000 0100011000 0000000000 00000
<i>Hukoutherium</i>	0001100000 0000000000 0000000000 0000000000 0000000000 00000
<i>Mesonyx</i>	0000000000 0000000000 0000000000 0000000000 0000000000 11000
<i>Mongolonyx dolichognathus</i>	0000000000 0000000000 0000000000 0010000000 0000000000 10000
<i>Pachyaena</i>	0000000000 0000000000 0000100000 0000010000 0000000000 01000
<i>Yantanglestes</i>	1001000000 0000100000 0000000000 0000000000 0000000000 00000
Family Triisodontidae	0000000000 0000000000 0000000000 0010000000 0010000000 01001
<i>Andrewsarchus mongoliensis</i>	0000000000 0000000000 0000000000 0010000000 0000000000 01001
Order Artiodactyla	0000000000 0000000000 0001000100 0000000000 1000000000 01111
Family Dichobunidae	0000000000 0000000000 0001000000 0000000000 0000000000 00001
<i>Gobiohyus</i>	0000000000 0000000000 0000000100 0000000000 0000000000 01111
<i>Gobiohyus orientalis</i>	0000000000 0000000000 0000000000 0000000000 0000000000 01101
<i>Gobiohyus robustus</i>	0000000000 0000000000 0000000000 0000000000 0000000000 01001
Order Perissodactyla	0000000000 0000000000 1001000101 0011000000 1011111111 11111
Family Palaeotheriidae	0000000000 0000000000 0000000000 0000000000 0000000011 00000
Family Isectolophidae	0000000000 0000000000 1001000000 0000000000 1000000101 10000
<i>Orientolophus</i>	0000000000 0000000000 1001000000 0000000000 0000000000 00000
<i>Homogalax</i>	0000000000 0000000000 0000000000 0000000000 1000000000 10000
Family Helaletidae	0000000000 0000000000 0000000001 0010000000 0000111010 10001
<i>Heptodon</i>	0000000000 0000000000 0000000001 0000000000 0000011000 10000
<i>Helaletes</i>	0000000000 0000000000 0000000000 0010000000 0000000010 10000
<i>Helaletes fissus</i>	0000000000 0000000000 0000000000 0010000000 0000000000 10000
<i>Hyrachyus</i>	0000000000 0000000000 0000000000 0000000000 0000000010 10000
Family Deperetellidae	0000000000 0000000000 0000000100 0010000000 0010000011 11101
<i>Deperetella</i>	0000000000 0000000000 0000000100 0000000000 0010000000 00001
<i>Irdinolophus</i>	0000000000 0000000000 0000000000 0000000000 0000000011 01000
<i>Teleolophus</i>	0000000000 0000000000 0000000100 0000000000 0010000010 11100
<i>Teleolophus medius</i>	0000000000 0000000000 0000000100 0000000000 0000000000 01100

	DZULLZPWLS ULUMLTDTSS ULABNZTKKS DNCGPBSGGG WZHYYNNAGK AIULU
	TUSSFAIWAZ DDWWWIZUXT LLGMAHA21H BOMFFUU321 USEDUNUKUZ SMHOP
Family Lophialetidae	0000000000 0000000000 0000000100 0011000000 1011000011 11111
<i>Breviodon</i>	0000000000 0000000000 0000000100 0010000000 0010000011 11111
<i>Breviodon minutus</i>	0000000000 0000000000 0000000100 0000000000 0010000010 11101
<i>Lophialetes</i>	0000000000 0000000000 0000000100 0010000000 0010000011 11110
<i>Lophialetes expeditus</i>	0000000000 0000000000 0000000100 0010000000 0010000000 11100
<i>Schlosseria</i>	0000000000 0000000000 0000000000 0000000000 0011000011 11100
<i>Schlosseria magister</i>	0000000000 0000000000 0000000000 0000000000 0001000001 10000
Family Hyracodontidae	0000000000 0000000000 0000000100 0011000000 0011000011 11101
<i>Forstercooperia</i>	0000000000 0000000000 0000000000 0010000000 0000000000 11101
<i>Forstercooperia grandis</i>	0000000000 0000000000 0000000000 0010000000 0000000000 10000
<i>Forstercooperia totadentata</i>	0000000000 0000000000 0000000100 0000000000 0000000000 01000
<i>Pataecops parvus</i>	0000000000 0000000000 0000000000 0001000000 0000000001 00000
<i>Prohyracodon</i>	0000000000 0000000000 0000000000 0000000000 0010000000 00001
<i>Rhodopagus</i>	0000000000 0000000000 0000000000 0000000000 0010000011 01101
<i>Rhodopagus minimus</i>	0000000000 0000000000 0000000000 0000000000 0010000000 00001
<i>Rhodopagus pygmaeus</i>	0000000000 0000000000 0000000000 0000000000 0000000000 01100
<i>Triplopus proficiens</i>	0000000000 0000000000 0000000100 0000000000 0000000000 01100
Family Aymynodontidae	0000000000 0000000000 0000000100 0010000000 0010000001 10101
<i>Lushiamynodon</i>	0000000000 0000000000 0000000000 0000000000 0000000000 00101
<i>Sianodon</i>	0000000000 0000000000 0000000000 0000000000 0010000000 00001
<i>Teilhardia</i>	0000000000 0000000000 0000000000 0000000000 0000000001 10000
Family Eomoropidae	0000000000 0000000000 0000000000 0010000000 1001000010 01001
<i>Eomoropus</i>	0000000000 0000000000 0000000000 0000000000 0001000000 00001
<i>Litolophus gobiensis</i>	0000000000 0000000000 0000000000 0010000000 0000000000 01000
Family Brontotheriidae	0000000000 0000000000 0000000100 0010000000 0010000011 11101
<i>Desmatotitan</i>	0000000000 0000000000 0000000000 0000000000 0000000000 10100
<i>Epimanteoceras</i>	0000000000 0000000000 0000000000 0000000000 0000000000 01100
<i>Metatelmatherium</i>	0000000000 0000000000 0000000000 0010000000 0000000000 11000
<i>Metatelmatherium cristatum</i>	0000000000 0000000000 0000000000 0010000000 0000000000 10000
<i>Microtitan</i>	0000000000 0000000000 0000000100 0000000000 0000000000 11100
<i>Microtitan mongoliensis</i>	0000000000 0000000000 0000000100 0000000000 0000000000 01100
<i>Protitan</i>	0000000000 0000000000 0000000100 0010000000 0000000000 11101
<i>Protitan grangeri</i>	0000000000 0000000000 0000000000 0000000000 0000000000 01001
<i>Protitan minor</i>	0000000000 0000000000 0000000000 0010000000 0000000000 10000
Family Phenacolophidae	1100000010 0000000000 0000001000 0000000001 0000000000 00000