

# An Oasis in the Desert? History of Endemism and Climate in the Late Neogene of North China

by

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With 5 text figures

## Summary

In contrast to the global trend of mid-latitude drying in Late Neogene, North China appears to have experienced an increase in humidity during the latest Miocene, the Baodean land mammal age *sensu stricto*. This “favourable oasis” in time and space had a strong influence on the evolution of the herbivorous land mammals of the region. The locally improved conditions first caused an influx of immigrants from several directions and later the development of endemic taxa from both native and immigrant stock. Lack of published data hinders a study of the effect on the mammal fauna when the climate became dry, a process well underway by the Middle Pliocene, but ultimately the effects of the Baodean exception were erased and North China joined the Palaearctic faunal province. We hypothesise that the apparently high diversity and low endemism seen in the North Chinese land mammal faunas of the latest Miocene can be explained by a Koenigswaldian model, in which two separate faunal assemblages cyclically alternate and mingle in a transitional zone.

**Key words:** Baodean, fossil mammal, dispersal, Miocene, North China, palaeoclimate, red clay.

## Zusammenfassung

Entgegen dem globalen Trend einer Aridisierung des Klimas der mittleren Breiten im späten Neogen hat Nordchina im obersten Miozän (Baodean-Landsäugerstufe im engeren Sinne) offensichtlich eine Zunahme der Humidität erfahren. Diese zeitliche und räumliche „Oase“ beeinflusste die Evolution der herbivoren Landsäuger der Region in erheblichem Maße. Die lokal verbesserten Lebensumstände förderten zunächst eine verstärkte Einwanderung aus unterschiedlichen Richtungen und führten später zur Entwicklung endemischer Taxa aus autochthonen und zugewanderten Faunenelementen. Der Mangel an publizierten Daten erschwert die Untersuchung der Auswirkungen der Aridisierung des Klimas auf die Säugetierfauna, die sich seit dem mittleren Pliozän beobachten lässt. Der Einfluss der Baodean-Anomalie verschwindet unmittelbar und Nordchina wird zu einem Teil der paläarktischen Faunenprovinz. Wir erklären die hohe Diversität und den schwachen Endemismus der nordchinesischen Landsäugerfaunen des obersten Miozän durch ein Koenigswald'sches Modell, nach dem sich zwei getrennte Faunenassoziationen zyklisch ablösen und in einer Übergangszone vermischen.

**Schlüsselwörter:** Baodean, fossile Säuger, Ausbreitung, Miozän, Nordchina, Paläoklima, Roter Ton.

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## Introduction

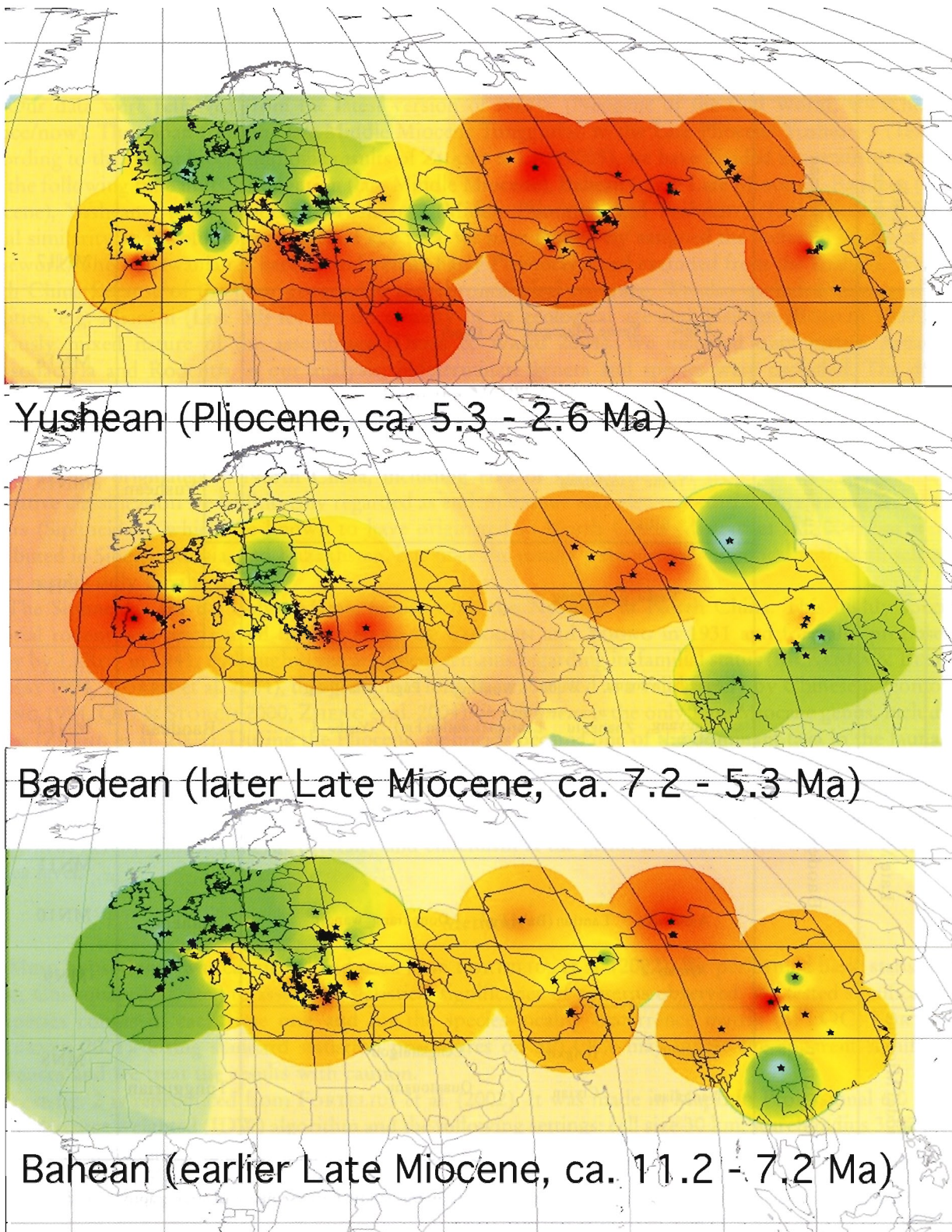
Understanding the evolution of communities importantly includes understanding the dispersal dynamics of their member species. This, in turn, requires some understanding of the dynamics of the physical and biotic factors that control the ecological success and dispersal of those species. In a series of contributions, WIGHART VON KOENIGSWALD (KOENIGSWALD & WERDELIN 1992, KOENIGSWALD & HEINRICH 1996, 1999, KOENIGSWALD 1999, 2003) has developed a model of land mammal dispersal in the context of the climatic cycles of the Pleistocene. In this model, the local alternation of “cold” and “warm” mammal communities in central Europe is seen as the expression of a dynamic where species permanently present in core areas in Siberia and the Mediterranean, respectively, extend and contract their ranges in tune with the glacial-interglacial cycles. In such a model, climate (and ultimately habitat) are primary determinants of dispersal and success. KOENIGSWALD (2003) concluded that, even during the climatic cycles of the Pleistocene Ice Age, humidity has been a more important control on land mammal dispersal than has temperature. FORTELIUS et al. (2003) also emphasised the role of ecological controls on dispersal and especially the establishment of successful populations in new areas. In the pre-Pleistocene Cenozoic, changes in humidity have clearly been the main environmental determinant of mammalian community evolution (e.g., BERNOR et al. 1996, AGUSTÍ et al. 1999).

The success of Koenigswald’s model of Pleistocene faunal evolution depends on the fact that Central Europe is a special case, where the effect of climatic fluctuations is emphasised by the dispersal dynamic between two separate and faunally distinct core areas. Such special cases are rare and precious in that they provide proof (in the original sense of testing) of general hypotheses. We believe that the latest Miocene land mammal faunas of North China provide another exceptional case: an area where in opposition to the global trend humidity appears to have increased (FORTELIUS et al. 2002), creating an island of exceptionally favourable circumstances on a continent otherwise moving towards increasingly harsh conditions (Text-fig. 1).

In the Loess Plateau area of North China, the well-developed fossil rich *Hipparion* red clay (ZDANSKY 1923, translation by JOKELA et al. 2005) has been intensely studied during nearly a century and provides a unique terrestrial record for the exploration of the past climate changes and for the study on the dynamic interactions between mammalian faunas and regional climatic changes. Grain size analysis, magnetic susceptibility, carbon and oxygen isotope, and other proxies have been used for the exploration of the global and or regional climatic changes during late Neogene (DING et al. 1998, 1999, AN et al. 2001, VANDENBERGHE et al. 2004).

We have hypothesized (FORTELIUS et al. 2002) that the increased summer rainfall resulting from the summer monsoon made possible the development in North China of the highly diverse and specialized mammal fauna collected from the red clay deposits (KURTÉN 1952). Indeed, deposition of the primarily wind-borne red clay itself was probably due to the same cause: enhanced entrapment of aeolian material in more humid and vegetated habitats (YANG & DING 2004) than in the preceding interval. We have subsequently discovered that these hypotheses echo ideas formulated by the Swedish explorers of Baode nearly a century ago: “According to Dr. Andersson, some areas in the steppe at certain times could, through a favourable combination of topographic and climatic conditions, support an especially lush vegetation, which naturally caused a concentration of animals into these areas. In the surroundings of Chi-Chia-Kou, we would thus see the remains of such an oasis.” (ZDANSKY 1923, translated in JOKELA et al. 2005: 7).

It might seem reasonable to expect that an island of favourable conditions on an increasingly hostile continent will give rise to an increasingly endemic fauna. However, no previous study appears to have addressed North Chinese endemism in the Late Neogene quantitatively or tried to explore the processes involved. Here we undertake a preliminary analysis of the endemism of herbivorous small and large mammals of North China since the Late Miocene. For a rough indicator of climatic change we use mean hypsodonty of large mammals as a palaeoprecipitation proxy (FORTELIUS et al. 2002, ERONEN & ROOK 2004). The close relationship between rainfall and primary productivity makes this a useful general indicator of conditions favourable to herbivores: the higher the mean hypsodonty, the harsher we may expect the environment to have been.



Text-fig. 1. Colour-interpolated maps of Eurasian large mammal plant-eater mean hypsodonty by locality during the Bahean, Baodean, and Yushean, to show increased humidity in China in the latest Miocene, coincident with opposite changes in Western and Central Asia. Blue values indicate lack of increased crown height; greens, yellows and reds show the successive increase in crown height interpreted here as increasing aridity. From FORTELIUS et al. (2002), which see for a discussion of the corresponding precipitation values and a description of the data used.

	Epoch	Qiu and Qiu, 1995)	Representative localities	This paper	European MN	
Ma	Early Pleistocene	Nihewanian			MN17	
2.6	Pliocene	Yushean	Jingle Yushe_Mazegou Daodi	3	Yushean	MN16
			Yushe_gaozhuang Bilike	2		MN15
			Yushe_gaozhuang	1		MN14
5.3	Late Miocene	Baodean	Junggar_yaogou Wudu Wuxiang Fugu_Miaoliang Qingyang Zhangqiu Lantian (Lantian Fm) Yushe_I Baode Songshan Binxian Huade Hsinan	Baodean	MN13	
			Amuwusu Lantian (Bahe Fm) Dongxiang_wangji Qinan_2	Bahean	MN12 MN11 MN10 MN9	
11.2	Middle Miocene	Tunggurian	Tunggur Tongxin Lengshuigou Fangxian Cixian Quantougou	Tunggurian	MN8	

Text-fig. 2. Stratigraphic terminology and correlation of localities included in this study; Chinese mammal stratigraphy according to ZHANG & LIU (2005).

## Data and methods

### Data

Our data were retrieved from the latest version of NOW (Neogene of the Old World, [www.helsinki.fi/science/now](http://www.helsinki.fi/science/now)). They span from the late Middle Miocene Tunggurian to the Late Pliocene Yushean-3 (Text-fig. 2). According to the recent biochronologic results of ZHANG & LIU (2005), we have divided the studied time interval into the following time units: Tunggurian (late Middle Miocene), Bahean (early Late Miocene), Baodean (late Late Miocene), Yushean-1 (Early Pliocene), Yushean-2 (Middle Pliocene), and Yushean-3 (Late Pliocene). Based on faunal similarity and evolutionary stages of key taxa, we have tentatively assigned the included localities into this framework. The Nihewanian is here considered as Early Pleistocene and excluded from the analysis. We exclude South China because of the poor geographic and chronological coverage. We also excluded some problematic localities, e.g. Mianchi (Loc. 39) for the uncertainty of its geological age and Tsaidam (BOHLIN 1937) for the obviously mixed nature of the assemblage (DENG & WANG 2004). We included only orders Artiodactyla, Perissodactyla and Rodentia in our analysis; indeterminate genera and species were excluded. The data used are available from the authors on request or from the NOW Archives on the database website.

Despite considerable uncertainty regarding the systematics and distribution of Neogene mammals, we were able to classify the taxa into either endemic or non-endemic, with only a few left as uncertain. We define endemic taxa as having originated in North China, including taxa of known descent from earlier immigrants. In an alternative classification we additionally regarded as endemic some taxa also recorded from adjacent areas, e.g. the zokors (Siphneidae), which are known to have originated in North China (ZHENG et al. 2004) but were also distributed in Siberia, Russia, and Kazakhstan, but since the results were virtually identical with both schemes we report results only for the first.

The Siphneidae are the only endemic family from the Neogene of North China. This highly specialized fossorial rodent was first named by TEILHARD DE CHARDIN and YOUNG in 1931 and formally proposed as a family by LEROY in 1941. Although some argument remains regarding its familial status (MCKENNA & BELL 1997, LINDSAY 1994, NORRIS et al. 2004), this group has long been accepted as a valid family by Chinese paleontologists (ZHENG 1994, QIU & STORCH 2000, ZHENG et al. 2004). *Prosiphneus* is the only Late Miocene genus, including six species (ZHENG et al. 2004). During the Pliocene, siphneids became one of the dominant taxa in the faunas from North China, and showed strong diversification in their skull morphology. Although different generic names were suggested based on skull characters by our senior colleague Prof. ZHENG SHAOHUA in 1994, many fossil records with only teeth cannot be properly assigned to his generic scheme, and we thus conservatively use *Prosiphneus* herein. This lowers the diversity and endemism at the genus level somewhat but has no effect at the species level.

### Methods

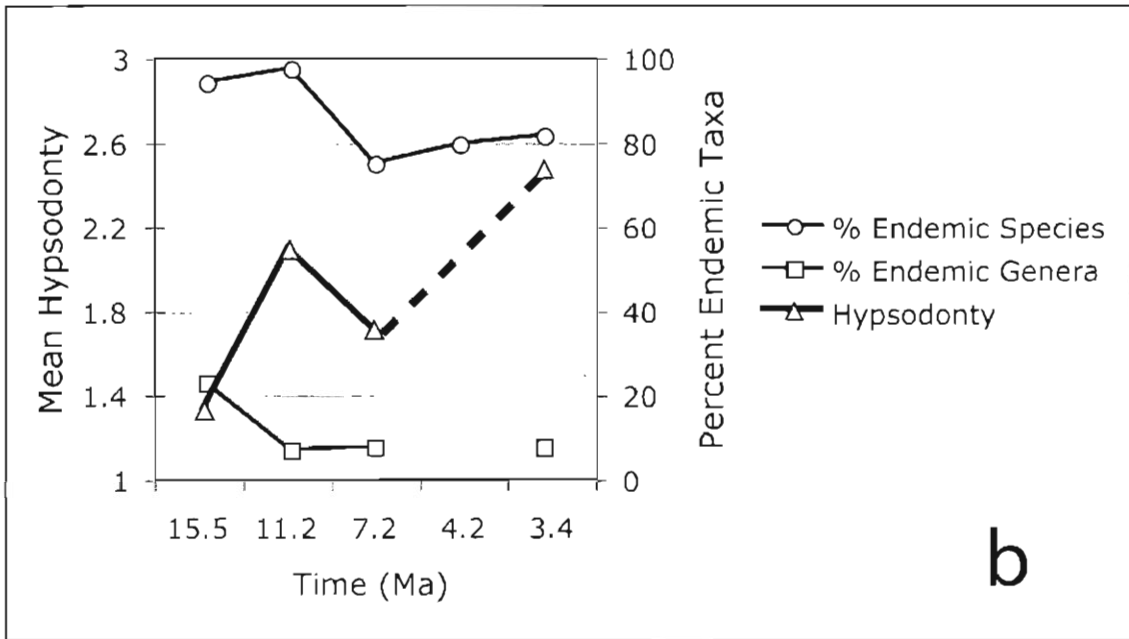
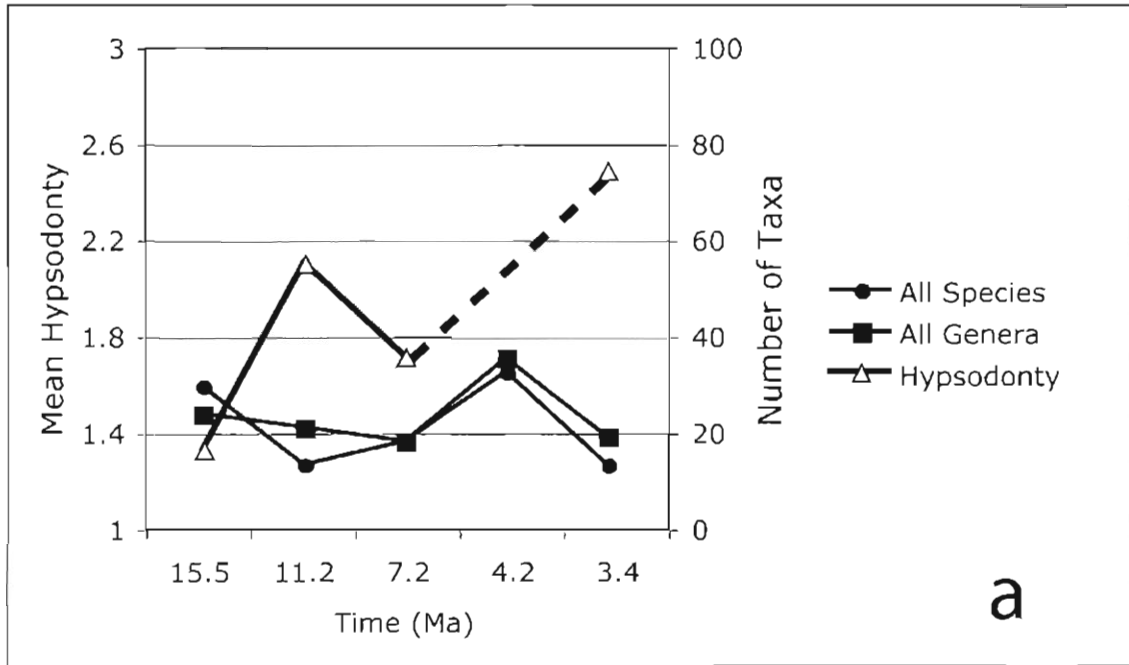
Mean hypsodonty was calculated and used as in FORTELIUS et al. (2002). We performed basic statistical tests (t-test, Chi-square-test, etc.) to assess the statistical significance of patterns observed. We tested significance both for species counts in each time unit and for the species-locality occurrence matrix (SPLOC; FORTELIUS & HOKKANEN 2001). Using standard statistical procedures on SPLOCs may inflate the apparent significance of differences and we treat the results with caution.

Text-fig. 2 is reproduced from FORTELIUS et al. (2002). It was made in MapInfo Professional 6.0 using the inverse distance weighted (IDW) algorithm and the following settings: cell size 30 km, search radius 3000 km, grid border 1100 km, number of inflections 9, values rounded to 1 decimal. The inflection values were manually set to the range 0.7–3 for all maps, and a mask was manually superimposed to fade out areas more than 1000 km from the nearest data point (opacity 50%).

### Results

**Whole dataset.** The history of richness and endemism for the whole dataset is shown in Text-fig. 3, with mean hypsodonty as a rough inverse proxy for rainfall and productivity level. As one might expect, there appears to be a negative correlation between hypsodonty and richness (Text-fig. 3a), with all taxonomic levels peaking at

# All Mammals



Text-fig. 3. Taxonomic richness, endemism, and hypsodonty of North Chinese mammals during five time units of late Neogene time (entire dataset). Time units are indicated by the age of their base, in millions of years: 15.5 = Tungurian, 11.2 = Bahean, 7.2 = Baodean, 4.2 = Yushean-2, 3.4 = Yushean-3.

the hypsodonty minimum of the Baodean (base at 7.2 Ma). A significant detail is that the Bahean (11.2 Ma) shows higher hypsodonty and lower richness than either the preceding Tungurian (15.5 Ma) or the subsequent Baodean. The Baodean/Bahean difference in hypsodonty is questionably significant for species numbers but highly significant for species occurrences ( $df = 318$ ,  $t = 3.344$ ,  $P < 0.0009$ ). Owing to poor sampling no hypsodonty value can be calculated for the Early and Middle Pliocene (Yushean-1 and Yushean-2; 4.2 Ma) but by the Late Pliocene (Yushean-3; 3.4 Ma) hypsodonty is already higher than at any time in the Miocene, and richness is at a minimum at all taxonomic levels.

The richness of endemic taxa follows the trends seen for all taxa, except that the number of endemic genera is low throughout and shows relatively little variation. Richness is notoriously sensitive to sampling, and we cannot exclude the possibility that the pattern is driven by sampling. As is usual in palaeontology, there is a positive correlation ( $r = 0.793$ ) between the number of taxa and the number of localities for each time unit; however with such a small number of time units the correlation is only marginally significant (Bartlett Chi-square statistic = 3.476,  $df = 1$ ,  $P = 0.062$ ).

The ratio of species to genera also shows a peak when richness is highest, going from 1.3 in the Bahean to 2.2 in the Baodean.

Except for the Tungurian-Bahean interval, the history of endemism is roughly in phase with mean hypsodonty (Text-fig. 3b) and thus in antiphase with richness. Especially noteworthy is the fact that endemism is lowered during the hypsodonty minimum and richness maximum of the Baodean (7.2 Ma). The Baodean/Bahean difference is again questionably significant for species numbers per time unit but highly significant for species occurrences ( $N = 322$ , Chi-square = 32.031,  $P < 0.0001$ ). The trend is similar at the genus and species levels, but the endemism is much higher at the species level, over 80% except at the Baodean minimum. It is definitely possible that the high species-level endemism is partly artificial, reflecting taxonomic practise rather than palaeobiology, but it seems unlikely that this hypothetical bias would distort the relative degree of endemism between time units.

**Small versus large mammals.** There is a major sampling problem that affects our analysis: The Pliocene large mammal record of North China is much poorer than the Miocene one, partly owing to the lack of published information from the rich and extensively studied Yushe record. In contrast, the small mammal record is richer for the Pliocene than for the Miocene, and especially rich for the Early Pliocene. The dataset is much too small to allow meaningful correction of these biases by statistical means, especially when broken down into subsets, but showing the differences is helpful for interpreting the overall pattern.

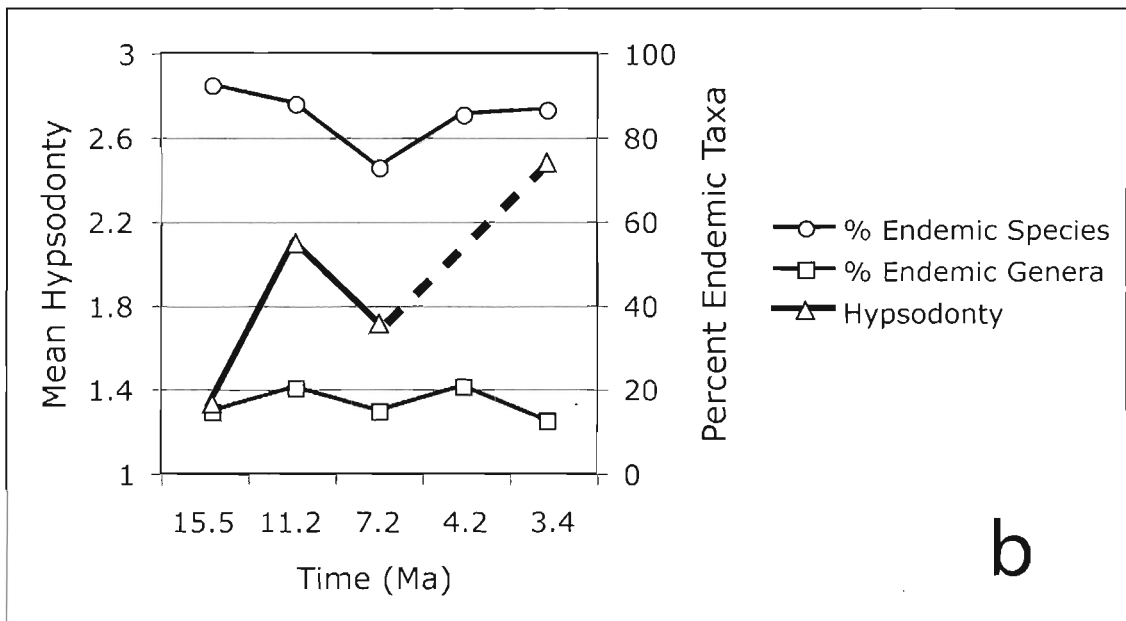
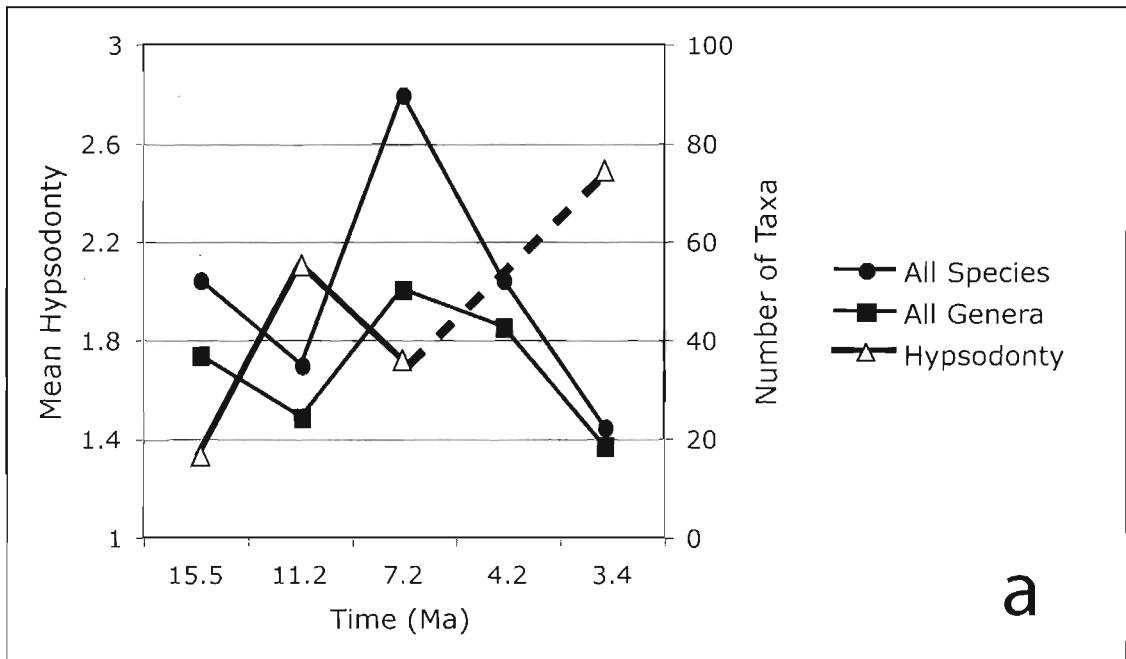
Text-fig. 4 shows the results for rodents. The richness pattern (Text-fig. 4a) is very different from that seen for the whole data and probably reflects primarily sampling. Despite this, the pattern of endemism (Text-fig. 4b) is similar to what is seen for the whole data, with the lowest value seen in the Baodean. Possible differences are that species endemism is even higher in the Tungurian-Bahean interval, and that there is less increase of endemism in the Pliocene than seen for the whole dataset.

The corresponding patterns for perissodactyls and artiodactyls are shown in Text-fig. 5. The richness pattern for the Miocene is essentially as for the whole dataset, while there are almost no data for the Pliocene. The pattern of endemism is again similar to the whole dataset and to the rodent pattern, with a minimum at the Baodean. Rather than the questionable differences between datasets we emphasise the similar pattern of endemism despite the markedly different history of apparent richness.

## Discussion

Despite the many biases and uncertainties that affect our results, a relatively clear overall picture is beginning to emerge. The North Chinese faunas of the (later) Neogene have been moderately endemic at the genus level throughout and, probably, very endemic at the species level, although the latter impression may change when more taxonomic species-level revision is undertaken. The development in the latest Miocene of a “favourable oasis” in North China, during a time when Western and Central Eurasia was already experiencing significant drying (KUTZBACH et al. 1993, FORTELIUS et al. 2002), clearly resulted in an influx of species from the surrounding areas. These immigrants were of several kinds and came from different directions. Perhaps the most interesting

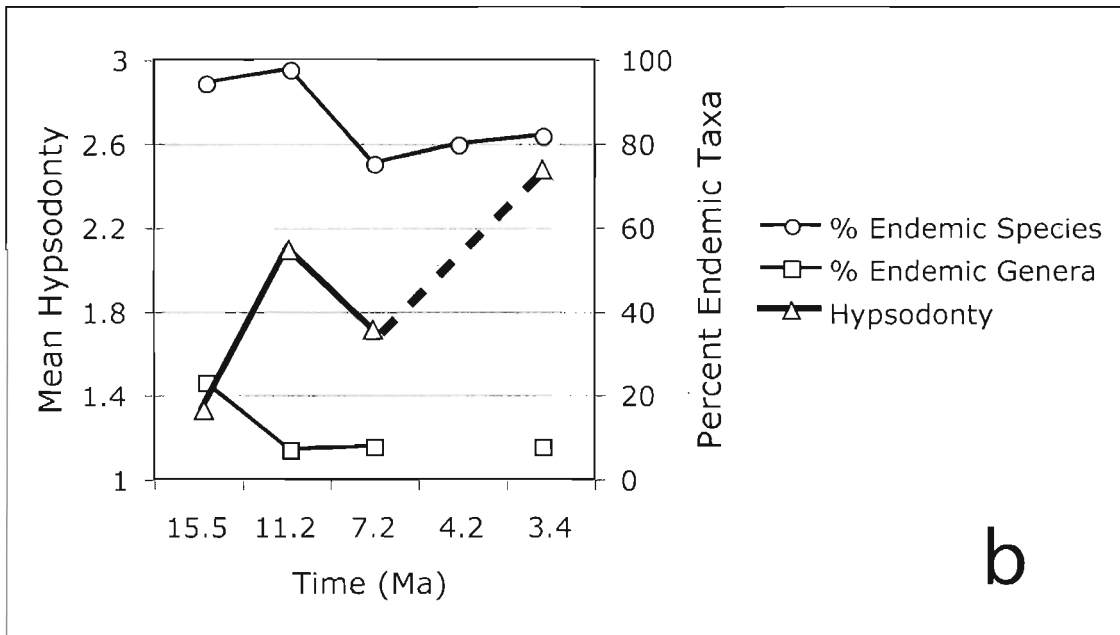
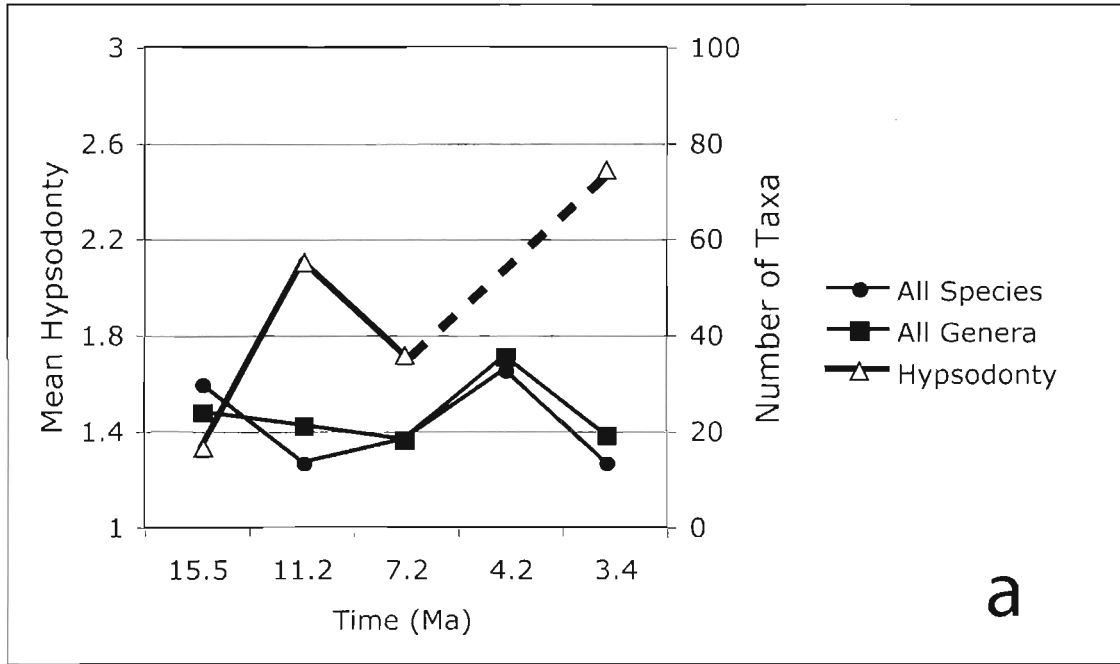
# Rodents



Text-fig. 4. Taxonomic richness, endemism, and hypsodonty of North Chinese rodents during five time units of late Neogene time. Time units are indicated by the age of their base, in millions of years: 15.5 = Tungurian, 11.2 = Bahean, 7.2 = Baodean, 4.2 = Yushean-2, 3.4 = Yushean-3.



# Ungulates



Text-fig. 5. Taxonomic richness, endemism, and hypsodonty of North Chinese artiodactyls and perissodactyls during five time units of late Neogene time. Time units are indicated by the age of their base, in millions of years: 15.5 = Tungurian, 11.2 = Bahean, 7.2 = Baodean, 4.2 = Yushean-2, 3.4 = Yushean-3.

group consists of archaic forest forms, such as anchitherine horses (which reappear here after having been apparently extinct in Eurasia for at least two million years; cf. ZDANSKY [1935]) and the small suine pig *Chleuastochoerus*. Their geographic origin is unknown but it seems likely that they came from South China or Southwest Asia, where the sampling of Late Miocene mammals is relatively poor. Another important group of immigrants is the deer, especially the genus *Cervavitus*, a northern or western immigrant, which becomes very common in the Baodean.

Poor sampling in the Early Pliocene makes it difficult to determine when the humid phase in North China ended. In the red clay deposits of Baode the Mio-Pliocene boundary is well marked lithologically and there is plenty of Pliocene sediment exposed, but hardly any mammalian fossils have been recovered from the Pliocene part. However the Middle Pliocene small mammals from Bilike (Inner Mongolia) show high diversity and abundance of Cricetidae and Dipodidae and the presence of, for instance, *Prosiphneus*, *Ochotona*, and *Atlantoxerus*, suggesting a temperate environment of steppe or grassland (QIU & STORCH 2000). The diversity and crown height increase of siphneids in the Pliocene also demonstrate a strong tendency of aridification (ZHENG 1997), especially in the Late Pliocene. In any case it seems that by the Middle Pliocene the favourable episode was over and North China had become more arid and similar to the rest of mid-latitude Eurasia. Our data are woefully inadequate, especially for large mammals, but as far as they go they indicate that endemism remained high during the Pliocene. Finally the endemic fauna with roots in the Baodean went extinct, new immigrants arrived, and North China joined the Palaearctic faunal province.

In order to fully explain the somewhat counterintuitive main result of this study, namely that the “oasis” created by the Baodean exception gave rise not to a more endemic fauna but instead to lowered regional endemism, one would need to resolve the internal history of the Baodean, both spatially and temporally. This we cannot yet achieve, but ongoing fieldwork by our team in the Late Miocene of the Chinese Loess Plateau suggests the following hypothetical scenario to be tested when more data become available.

It appears increasingly clear that the regional model proposed by KURTÉN (1952) to explain the original observation of SCHLOSSER (1899) has solid support both in ecomorphology and in taxonomy. According to this model, a dry-adapted, northeastern “dorcadoïdes” assemblage mingles with a more humid-adapted, southeastern “gaudryi” assemblage near the western margin of the Loess Plateau, much as in the model of KOENIGSWALD (1999, 2003) the glacial and interglacial assemblages mingled in the Pleistocene of Europe. It is furthermore evident that the sedimentary record of the Baodean red clay deposits show evidence of wet-dry cyclicity (cf. VANDENBERGHE et al. 2004). We therefore hypothesise that the apparently lowered endemism of the Baodean faunas reflects at least in part the lack of temporal resolution, which causes an artificial fusion of two essentially separate land mammal assemblages in the latest Miocene of Northern China. This hypothesis could also explain the apparent maxima of taxon richness and species per genus counts observed in the classic Baodean faunas.

### Acknowledgements

We thank the Editors for the opportunity to pay homage to our mentor, colleague and friend Xiao Kongnihua, usually known outside China as Wighart v. Koenigswald. We also thank our field team members Anu Kaakinen, Ben Passey, Liu Liping, Jussi Eronen, Majid Mirzaie Ataabadi and Aleksis Karne for many discussions of the questions addressed in this paper. Special thanks to Liu Liping for help with the data compilation and Jussi Eronen for help with producing Text-fig. 2. The manuscript benefited significantly from constructive reviews by Ray Bernor and Lars Werdelin. This study was supported by grants from the Academy of Finland and the National Science Foundation of China.

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