

Paleoecological comparison between late Miocene localities of China and Greece based on *Hipparion* faunas

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Deng T. 2006. — Paleoecological comparison between late Miocene localities of China and Greece based on *Hipparion* faunas. *Geodiversitas* 28 (3): 499-516.

ABSTRACT

Both China and Greece have abundant fossils of the late Miocene *Hipparion* fauna. The habitat of the *Hipparion* fauna in Greece was a sclerophyllous evergreen woodland. The Chinese late Miocene *Hipparion* fauna is represented respectively in the Guonigou fauna (MN 9), the Dashengou fauna (MN 10), and the Yangjiashan fauna (MN 11) from Linxia, Gansu, and the Baode fauna (MN 12) from Baode, Shanxi. According to the evidence from lithology, carbon isotopes, paleobotany, taxonomic framework, mammalian diversity and faunal similarity, the paleoenvironment of the *Hipparion* fauna in China was a subarid open steppe, which is different from that of Greece. The red clay bearing the *Hipparion* fauna in China is windblown in origin, i.e. eolian deposits. Stable carbon isotopes from tooth enamel and paleosols indicate that C₃ plants dominated the vegetation during the late Miocene in China. Pollens of xerophilous and sub-xerophilous grasses show a signal of steppe or dry grassland. Forest mammals, such as primates and chalicotheres, are absent or scarce, but grassland mammals, such as horses and rhinoceroses, are abundant in the Chinese *Hipparion* fauna. The species richness of China and Greece exhibits a similar trend with a clear increase from MN 9 to MN 12, but the two regions have low similarities at the species level. The entry of *Hipparion* led to a comparable radiation in China and Greece, but their dietary evolution is different. In conclusion, the ecosystems of the Chinese and Greek *Hipparion* faunas have an obvious dissimilarity in the late Miocene.

KEY WORDS
Hipparion fauna,
late Miocene,
paleoecology,
China,
Greece.

RÉSUMÉ

Comparaison paléocologique des faunes à Hipparion du Miocène supérieur de Grèce et de Chine.

La Chine et la Grèce ont toutes deux de nombreux fossiles du Miocène supérieur appartenant à la faune à *Hipparion*. En Grèce, l'habitat était un paysage boisé sclérophylle à feuilles persistantes. La faune à *Hipparion* chinoise du Miocène supérieur est représentée par les faunes de Guonigou (MN 9), de Dashengou (MN 10) et de Yangjiashan (MN 11) de Linxia, Gansu et la faune de Baode (MN 12) de Baode, Shanxi. D'après la lithologie, les isotopes du carbone, la paléobotanique, le cadre taxonomique, la diversité mammalienne et la similarité faunique, le paléoenvironnement de Chine était une steppe ouverte semi-aride différente de l'environnement grec. Les argiles rouges de la faune à *Hipparion* de Chine sont d'origine éolienne. Les isotopes stables du carbone de l'émail dentaire et les paléosols indiquent une dominance de plantes à C₃ au Miocène supérieur en Chine. Les pollens d'herbes xérophiles et sub-xérophiles donnent un signal de steppe ou de prairie sèche. Les animaux de forêts, tels que les primates et les chalicothères sont absents ou rares, tandis que les animaux de prairies, comme les équidés et les rhinocéros, sont abondants. La richesse en espèces augmente nettement de MN 9 à MN 12 à la fois en Chine et en Grèce, mais les deux régions se ressemblent peu au niveau spécifique. L'immigration d'*Hipparion* conduisit à une radiation similaire, mais l'évolution alimentaire fut différente en Chine et en Grèce. En conclusion, les écosystèmes des faunes à *Hipparion* chinoise et grecque différaient de façon évidente.

MOTS CLÉS

Faune à *Hipparion*,
Miocène supérieur,
paléocologie,
Chine,
Grèce.

INTRODUCTION

In China, many important late Miocene mammal localities are characterized by an abundance of species of mustelids, hyaenids, hipparionines, rhinocerotids, giraffids, and antelopes. The chalicotheres and mastodonts are rare, and tragulids absent in northern China, but these groups are abundant or present in late Miocene localities in Europe (Heissig 1999; Göhlich 1999; Gentry *et al.* 1999). Since the 19th century, the Eurasian late Miocene faunas from the stratified sites of Pikermi, east of Athens, Samos in the Eastern Aegean, Maragha in northwesternmost Iran, and Baode in northern China have been considered to represent the peak development of the "savanna fauna", which succeeded more forested,

warm-temperate biotopes, similar to the modern savannas of Africa (Bernor *et al.* 1996b; Solounias *et al.* 1999). The Pikermian mammal age had been created for the distinctive "savanna fauna" as typified by the Greek locality of Pikermi. Further work, however, in the abundantly fossiliferous basins of northern Spain led Crusafont (1965) to modify this usage in favor of two new "mammal stages", the Vallesian and Turolian, corresponding to the Bahean and Baodean in China (Li *et al.* 1984).

These faunas have also been widely termed "*Hipparion* faunas" because they contain, on the average, several species of the genus *Hipparion* (Bernor *et al.* 1996a). Kurtén (1952) provided a map of Eurasia, which included the most typical savanna-like localities. In this map, a vast region

of such faunas extends from the west (Greece) through south Russia, Turkey and Iran to the east in China, and the *Hipparion* faunas are clearly located in modern dry habitats. On the other hand, Bernor (1983) described many of these localities as unique, and subdivided the Old World evergreen woodland biome into provinces. Solounias *et al.* (1999) concluded that the habitat of these *Hipparion* faunas was not a savanna but a sclerophyllous evergreen woodland.

In fact, the fossiliferous deposits also show that the paleoenvironment of the Baode fauna in China is different from that in Europe. In Samos, Pikermi, and Maragha, the mammalian fossils are preserved in fluvial and lacustrine deposits. Conversely, the Baode *Hipparion* fauna of China is preserved in particular red clay deposits that have been considered to be the outcome of a monsoonal climate. Recently, abundant mammalian fossils have been discovered from the Linxia Basin. Although the *Hipparion* fauna in the Linxia Basin has a long chronological range, including the typical Vallesian and Turolian mammals, there is no obvious difference in ecology between taxa of the different ages. Like Baode, the *Hipparion* fauna from Linxia is collected from the red clay.

Three palaeozoogeographical provinces can be recognized in the late Miocene of Western Eurasia, among which the Greco-Iranian province (also known as the sub-Paratethyan province) is the closest to Eastern Asia. The classical and most fossiliferous localities, such as Pikermi, Samos, and Maragha, are located in the Greco-Iranian province. Therefore, it is important to compare similarities and differences in ecology between the late Miocene *Hipparion* faunas in China and Greece.

HISTORY

In the early 1920s, a great amount of mammalian fossils was recovered from Baode in Shanxi, China (Mateer & Lucas 1985). Prior to that, superb collections of large mammal fossils were collected from Pikermi, Samos, and Maragha. Pikermi and Samos are typical of the European late Miocene *Hipparion* faunas. Pikermi was the first important locality of

the *Hipparion* fauna to be discovered during the 19th century (Solounias 1981a, b). The Pikermi fauna comes from a roadside ravine just 21 km from Athens. At Pikermi, thousands of fossil vertebrates have been recovered from a number of imbricated bone lenses in the red clayey silt matrix. The *Hipparion* fauna of Samos is represented by a large, diverse sample pool from a number of fossiliferous horizons. Between 1850 and 1924, a succession of well organized paleontological expeditions recovered more than 30,000 specimens from these deposits (Solounias 1981b).

The Linxia fauna comes from many sites in the northeastern corner of the Tibetan Plateau. The fossils, which occur in red clay deposits, were collected during the 1950s by the local people in order to sell them to drugstores as “dragon bones”. Since the 1970s, the IVPP team has explored the Linxia Basin, collected abundant mammalian fossils of the Late Cenozoic and described them in several papers (Qiu *et al.* 1987, 1988, 1991, 2000; Qiu & Xie 1998; Deng 2001a, b, 2002; Wang & Qiu 2002; Liu *et al.* 2004). Deng *et al.* (2004b, c) discussed the Late Cenozoic biostratigraphy of the Linxia Basin and presented a detailed list of the mammalian fossils.

The Baode fauna is typical for the Chinese *Hipparion* fauna (Appendix 1). It is correlated to the latest Miocene, i.e. Turolian age of the European Neogene mammal chronology (Qiu *et al.* 1999). The Qaidam (Tsaidam) fauna, which was originally described by Bohlin (1937), has been considered to be the earliest *Hipparion* fauna in China, but it is proved a mixing of the material with middle and late Miocene elements (Deng & Wang 2004). The Bahe fauna discovered near Lantian, Shaanxi represents the Chinese Vallesian *Hipparion* fauna (Liu *et al.* 1978) correlated to the late Vallesian. A continuous sequence of the *Hipparion* fauna in the Linxia Basin includes the Guonigou fauna corresponding to MN 9, the Dashengou fauna to MN 10, and the Yangjiashan fauna to MN 11 (Appendix). The three horizons from Linxia are rich in fossils, and they are combined with the Baode fauna to reflect the paleoecology and related environmental changes of the late Miocene *Hipparion* fauna in China.

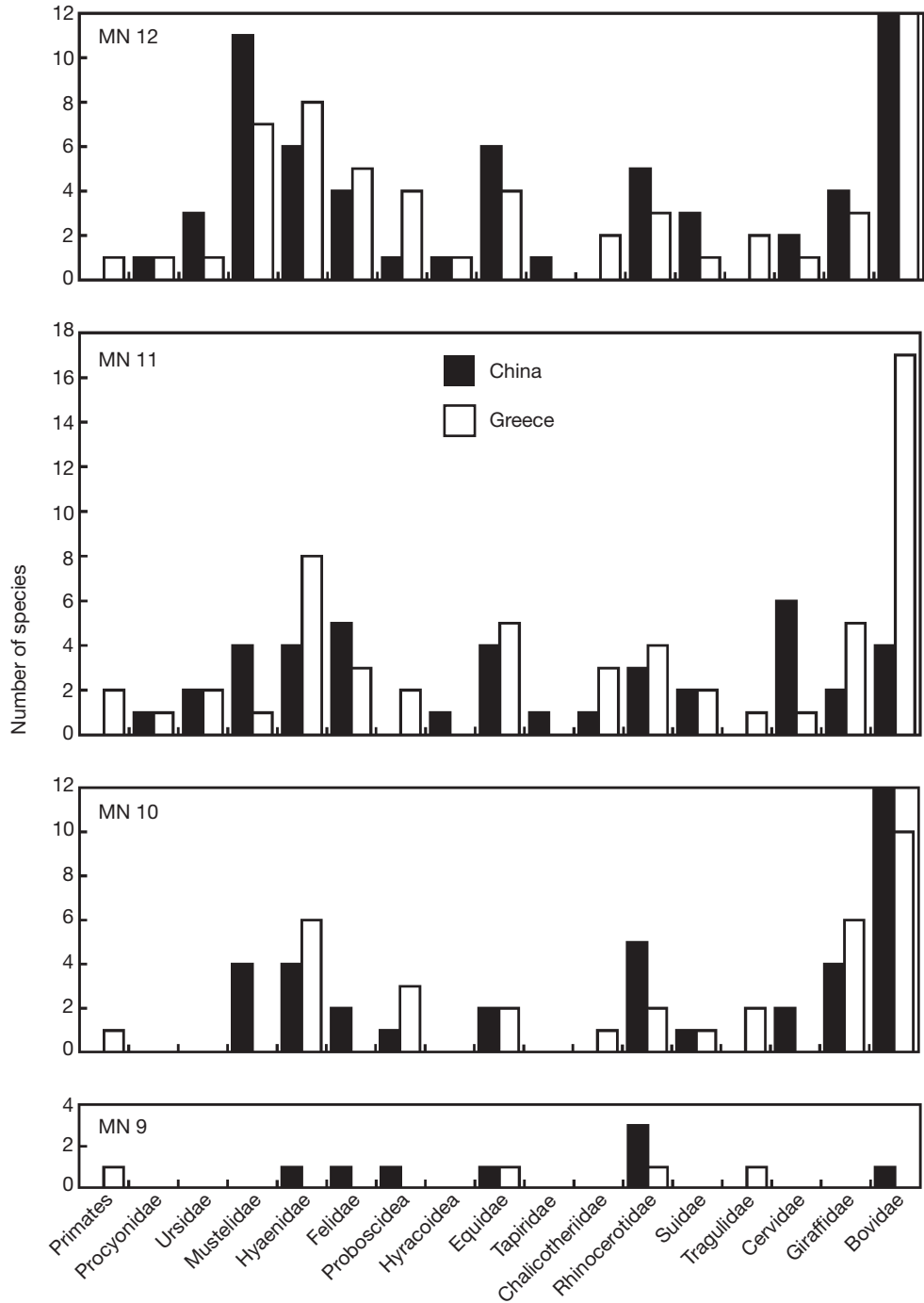


Fig. 1. — Taxonomic richness of the late Miocene *Hipparion* faunas from China and Greece at order or family level.

GEOLOGY AND CHRONOLOGY

Late Miocene deposits in northern China consist primarily of red clay and lack materials for isotopic dating. At present, magnetostratigraphy is widely used for dating Chinese Neogene deposit sequences. Detailed paleomagnetic analyses have been performed in Baode and Linxia, which provide reliable chronological data that agree to the mammalian fossil evidences.

The base of the Baode Formation rests unconformably on Carboniferous sandstones and shales. The lower part of the Baode Formation is a 15 m thick conglomerate, and the upper part is 30 m thick red clay. Overlying the Baode Formation is the Pliocene red clay of the Jingle Formation. The *Hipparion* fauna in the Baode Formation is characteristically represented in the localities of Daijiagou (Tai-Chia-Kou, Zdansky's Lok. 30) and Jijiagou (Chi-Chia-Kou, Zdansky's Lok. 43, 108-111, and 113), and includes abundant material of *Chilotherium*, *Hipparion*, *Samotherium*, *Gazella* and others. We collected and measured paleomagnetic samples at 20 cm intervals from the Jijiagou section. Comparisons of our measurements to the Geomagnetic Polarity Time Scale (Cande & Kent 1995) indicate that the fossiliferous beds of the Baode Formation are correlated to C3Ar, with an age of about 6.5-7.0 Ma, corresponding to MN 12 (Yue *et al.* 2004; Deng *et al.* 2004a).

The Linxia Basin is located on the triple-junction of the northeastern Tibetan Plateau, West Qinling Mountain and the Loess Plateau, and is delineated by high angle deep thrusts. The basin is filled with 700-2000 m thick Tertiary deposits that are dominated by lacustrine mudstones and red clays, by fluvial conglomerates or sandstones, and 30-200 m of Quaternary loess (Li *et al.* 1995). The late Miocene *Hipparion* fauna of the Linxia Basin has been collected from the red clay of the Liushu Formation that is underlain by the sandstones and fine conglomerates of the middle Miocene Hujialiang Formation, and overlain by the red clay of the early Pliocene Hewangjia Formation.

The thickness of the Liushu Formation is variable in different sections, which was caused by later differential erosions. In the center of the Linxia Basin,

the thickness of the red clay deposits of the Liushu Formation is about 90 m generally. Based on their position in the sections, the various localities with *Hipparion* fauna can be divided into three distinct horizons of lower, middle, and upper, which yielded the Guonigou, Dashengou, and Yangjiashan faunas, respectively (Deng *et al.* 2004b). According to the paleomagnetic records for the bulk faunas from each horizon, the Guonigou fauna is correlated to the Chron C5r.1r, with an age of 11.1 Ma, corresponding to MN 9; the Dashengou fauna is correlated to the Chron C4Ar.2r, with an age of 9.5 Ma, corresponding to MN 10; and the Yangjiashan fauna is correlated to the Chron C4r.1n, with an age of 8.3 Ma, corresponding to MN 11 (Deng 2006). Comparably, the age of the Maragha fauna is 9-7.6 Ma (MN 10 to mid-MN 12), the age of the Samos fauna is 7.2-7.0 Ma (late MN 12), and the inferred age of the Pikermi fauna is 8.3-8.2 Ma (MN 11) according to Bernor *et al.* (1996b). The magnetostratigraphic results of Kostopoulos *et al.* (2003) also indicated that the Samos fauna should be correlated to MN 11 and MN 12.

LITHOLOGY

The *Hipparion* faunas of both Baode and Linxia are included in red clay deposits. Sedimentological and geochemical studies proved that this Neogene red clay is windblown in origin as is the overlying Pleistocene loess (Ding *et al.* 1998a; Guo *et al.* 2001). One of the most striking features of the red clay sequence is the existence of many horizontal carbonate nodule horizons. The thickness of these horizons ranges from 10 cm to >100 cm, with most of the nodules being < 10 cm in diameter. The cement matrix within most of the nodule horizons is a reddish, weathered soil material.

The climate during the red clay deposition is interpreted as being continuously warm with relatively small-amplitude oscillations (Evans *et al.* 1991; Sun *et al.* 1998; Ding *et al.* 1998a, b; Guo *et al.* 2001). Studies of the depositional rate and the magnetic susceptibility variation of the eolian red clay sequence indicate indirectly the evolutionary history of the East Asian winter and summer

monsoon (light red clay and red clay alternations) in the late Miocene (An *et al.* 2000). During the late Miocene, the summer monsoon was relatively weak. Magnetic susceptibility measurements and lithologic features suggest that the late Miocene red clay in China represents a considerably dry climate (Ding *et al.* 1999; Qiang *et al.* 2004). Particle analyses imply a relatively remote provenance of the red clay materials and a relatively stable wind system transporting them (Ding *et al.* 1999). On the basis of carbonate nodule distribution, it was estimated that the average annual rainfall was 400 mm during late Miocene (Zhang *et al.* 1997), which is much less than the 1000 mm estimated for Greece (Solounias *et al.* 1999). The red clay also contains numerous late Miocene xerophilous snail fossils (dry and cold forms) (Pei *et al.* 2004). The continuous sedimentary sequence in the Linxia Basin shows that the forest-dwelling *Platybelodon* fauna of the middle Miocene is located in fluvial and lacustrine sandstones and conglomerates, but the *Hipparion* fauna of the late Miocene, from an open habitat, is located in eolian red clay deposits.

ISOTOPIC RECORD

Quade *et al.* (1994) studied the carbon and oxygen composition of pedogenic carbonates associated with paleosols to estimate the proportion of C₃ and C₄ plants from the Miocene and Pliocene sites in Greece and Turkey. Evidence from paleosols in well known fossil-bearing formations in the lower Axios Valley (Nea Messimbria Fm. at Vathilikos, Vallesian) in Macedonia, Samos (Mytilini Fm. at Mytilini, Turolian), Pikermi, Pasalar in NW Turkey, and Rhodes, show that Mio-Pliocene biomasses were dominated by C₃ plants, as the entire region is today. Solounias *et al.* (1999) indicated that these sites contained soil carbonate in association with paleosols, which suggests that the mean annual precipitation has remained about at 1000 mm for the last 11 Ma. They implied that during the late Miocene, the Greek region was dominated by forest and woodland. The moisture regime could have been either winter- or summer-dominated, or both. Quade *et al.* (1994) considered that the

classic fossil-bearing localities of the lower Axios Valley, Samos and Pikermi in Greece were not savannas, as previously thought, but rather woodlands or forests. The dental microwear data of ungulate fossils also comfort the existence of wooded landscapes in northern Greece during the late Turolian (Merceron *et al.* 2005a). On the other hand, some authors have different opinions about the late Miocene paleoenvironment of Greece and Western Eurasia. Merceron *et al.* (2005b) indicated the presence of open landscapes with an important grassy herbaceous layer during the late Vallesian, and an environment of bushy and/or wooded areas with a grassy herbaceous layer during the early Turolian in northern Greece. Koufos (2006) considered that in the Southeastern Mediterranean the environment was open and dry during the whole Vallesian.

The $\delta^{13}\text{C}$ values of soil carbonate from the latest Miocene (Baodean or Turolian) red clay at Lingtai in Gansu, China fall between -9.6 and -7.8‰, indicating a C₃-dominated ecosystem (Ding & Yang 2000). Analyses of the red clay of the late Miocene Liushu Formation in the Linxia Basin resulted in its $\delta^{13}\text{C}$ values between -8.8 and -6.1‰, with an average of -7.5‰. Apparently, the results from the red clay bearing the *Hipparion* fauna in China are identical to those in Greece, and imply that a savanna dominated by C₄ plants did not exist in the late Miocene.

Carbon isotopic evidence from fossil teeth from Samos supports the paleosol reconstruction (Quade *et al.* 1994). Analyses of the Samos fossil teeth yielded a range of $\delta^{13}\text{C}$ values between -13.0 and -9.6‰, with an average value of -11.4‰. This implies a dietary intake in the range of -26 to -22.6‰, with an average of -24.4‰. This is consistent with a diet composed largely or entirely of C₃ plants for the Samos herbivores. Solounias *et al.* (1999) found that most species, even the hipparionines (*Hipparion dietrichi*, *H. giganteum*, *H. proboscideum*), produced a C₃ signal. This is a remarkable discovery substantiating the hypothesis proposed by the paleosols, that the Samos paleoenvironment consisted of forests and woodlands. Hipparionines must have either browsed or grazed on C₃ grasses within the woodlands. Solounias *et al.* (1999) indicated that in the Aegean region, C₃ biomasses have dominated

TABLE 1. — $\delta^{13}\text{C}$ value of herbivore tooth enamel of the *Hipparion* fauna from the Linxia Basin.

Taxa	N	Minimum (‰)	Maximum (‰)	Average (‰)
<i>Hipparion dongxiangense</i>	7	-10.5	-8.7	-9.4
<i>Hipparion weihoense</i>	4	-11.5	-9.5	-10.2
<i>Hipparion chiai</i>	6	-11.6	-9.1	-10.5
<i>Hipparion dermatorhinus</i>	10	-10.6	-9.2	-9.9
<i>Hipparion coelophyes</i>	8	-10.2	-9.2	-9.6
<i>Chilotherium wimani</i>	19	-12.0	-8.9	-10.5
<i>Parelasmotherium linxiaense</i>	5	-10.1	-9.8	-9.9
<i>Cervavitus novorossiae</i>	4	-10.9	-9.9	-10.4
<i>Samotherium</i> sp.	3	-10.0	-9.6	-9.8
<i>Gazella</i> sp.	2	-9.7	-9.1	-9.4

the ecology of the depositional basins over the past 11 Ma.

Stable carbon isotope compositions of tooth enamel were determined for 10 herbivores of the *Hipparion* fauna from the Linxia Basin, including five species of *Hipparion* (*H. dongxiangense*, *H. weihoense*, *H. chiai*, *H. dermatorhinus*, *H. coelophyes*) as well as *Chilotherium wimani*, *Parelasmotherium linxiaense*, *Cervavitus novorossiae*, *Samotherium* sp., and *Gazella* sp. (Wang & Deng 2005). Their $\delta^{13}\text{C}$ values are between -12 and -8.7‰, with an average of -10.1‰, indicating a typical C_3 diet. The results indicate that there are no significant differences between the diets of various herbivores (Table 1). All carbon isotopic data from analyses of the enamel samples from the upper Miocene in the Linxia Basin are not indicative of C_4 plant ingestion, and even the extremely hypsodont *Hipparion* does not produce a C_4 signal. The tooth enamel of *Samotherium major* from Samos produced the most ^{13}C -enriched values, indicating that *S. major* had a C_4 component in its diet (Solounias *et al.* 1999). Conversely, *Samotherium* sp. from Linxia displayed a typical C_3 diet. In conclusion, the Chinese late Miocene *Hipparion* fauna did not live in a savanna habitat.

PALEOBOTANY

Numerous Miocene floras from the Mediterranean region have been sampled and studied. The general conclusion is that these floras represent subtropical forests and woodlands. The existence of widespread savannas and grasslands has not been reported

from such flora (Dorofeyev 1966; Bernor *et al.* 1988, 1990). Paleobotanists who have analyzed floras from Greece, presumably closer in age to Pikerimi, interpret them to represent woodland. There is no palynological or paleobotanical evidence for widespread savannas in the Pikerimian Biome, whose mammals most likely inhabited sclerophyllous evergreen woodlands with a humid and warm climate (Solounias *et al.* 1999; Steenbrink *et al.* 2000). Such woodlands were not an uninterrupted continuum of trees. Many regions were geographically highly heterogeneous and were often separated by low and high mountains, lakes, and rivers (Akgün *et al.* 2000; Ioakim *et al.* 2005).

The late Miocene red clay in China has not produced large plant fossils but rare pollen fossils. During the Bahean (Vallesian) age in northwestern China, conifers were absolutely dominant and primarily composed of *Pinus* and *Picea*; grasses were mainly composed of *Artemisia* and *Chenopodiaceae*; and temperate or warm temperate broadleaves were rare (1.52-20.12%) and mainly included *Betula*, *Salix*, *Quercus*, and *Ulmus* (Ma *et al.* 2004). A pollen analysis of the red clay of the Liushu Formation showed that grasses increased significantly and became dominant, especially xerophilous and sub-xerophilous grasses, along with some broadleaves of temperate and warm temperate zones. The pollen include mainly *Chenopodium*, *Artemisia*, and Gramineae, accompanied by Compositae, Ranunculaceae, Cruciferae, Umbelliferae, Polygonaceae, *Betula*, *Quercus*, *Salix*, *Fraxinus*, Cupressaceae, Taxodiaceae, and *Juniperus*, suggesting that the vegetation of the Liushu Formation belonged to an arid steppe (Ma *et al.* 1998).

During the early Baodean (early Turolian) age, grasses in Linxia, northwestern China were dominant and principally composed of *Artemisia* (19.32-55.76%), Chenopodiaceae (8.69-28.26%), *Ephedra* (1.53-44.44%), and Compositae (2.85-26.08%); conifers (0.51-32.9%) and temperate or warm temperate broadleaves (0-12.25%) decreased dramatically and only included rare *Picea*, *Pinus*, *Salix*, and *Corylus*. The pollen data indicate an arid or sub-arid steppe in the Linxia Basin (Ma *et al.* 2004). Wu (2001) indicated that the latest Miocene (Baodean or Turolian) flora in northwestern China was dominated by grasses, such as *Artemisia*, Chenopodiaceae, Compositae, Liliaceae, and Gramineae, and rare trees and shrubs included Pinaceae, Betulaceae, Salicaceae, Ulmaceae, and Tamaricaceae, which represent a steppe environment. On the other hand, the pollens from the Baode Formation in Baode, northeastern China are dominantly angiosperms with a few gymnosperms being present. Broadleaves are mainly *Ulmus*, and secondarily *Betula*, *Quercus*, *Carpinus*, *Corylus*, and *Liquidambar*. Conifers are dominated by *Picea*. Grasses include Chenopodiaceae, Compositae, and especially *Artemisia*. The pollen data indicate that the Baode region was in an environment mixed with forest, shrub and grassland in a comparatively cool and wet climate during the late Baodean (late Turolian) (Zheng *et al.* 1999).

To sum it up, the climate in northern China gradually became more arid during the late Miocene, resulting in sparse vegetation and rare forest plants. Based on geological records, aridity in regions north of the Tibetan Plateau developed along with the uplift of this plateau, and caused changes in the vegetation and ecosystems of these regions. As a result, the vegetation degenerated from a broad-leaf woodland into a steppe environment, and this was characterized by a pollen record of dominant Chenopodiaceae and *Artemisia* as a signal of steppe or dry grassland during that time (Li 1985).

TAXONOMIC FRAMEWORK

The Greco-Iranian province or the sub-Paratethyan province extends from the former Yugoslavia to

Iran and possibly Afghanistan (Bonis *et al.* 1979, 1992b). In this province, the differences between the two groups of localities, Vallesian and Turolian, are summarized by the following characteristics: same low percentage of localities with deinotheres, less with suids and giraffids, presence of some tragulids, and replacement of large primates (hominoids) by small primates (cercopithecoids). There is no significant difference in the percentages of localities with perissodactyls. Rhinocerotids, tapirids, chalicotherids or equids are similarly represented in Vallesian and Turolian sites (Bonis *et al.* 1999).

Primates are present in the Greek *Hipparion* fauna, but are absent in the Chinese fauna. Hyaenids, proboscideans, chalicotheres, giraffids, and bovids are more abundant in the Greek *Hipparion* fauna than in the Chinese fauna. On the other hand, mustelids, equids, rhinocerotids, and cervids are generally more abundant in the Chinese *Hipparion* fauna than in the Greek fauna (see statistical comparisons in Figure 1). Therefore, faunal components indicated that the Greek *Hipparion* fauna lived in a more forested environment while the Chinese fauna dwelled in a more open habitat.

Studies of recent mammalian faunas have led to the conclusion that the composition of a fauna depends on the ecology and environment. Actually, it is relatively simple to differentiate a forest fauna from an open environment fauna by the application of several methods (Andrews *et al.* 1979; Legendre 1986; Bonis *et al.* 1992a; Andrews 1995). If the taxonomy is examined at the species or even the genus level, it will reflect geographical or stratigraphical variations more than ecological differences, because two similar environments could have different specific or generic taxa (Bonis *et al.* 1999). Andrews *et al.* (1979) have also observed that taxonomic comparisons by order produced statistically significant differences between faunas. Insofar as there are very few micromammals from the late Miocene fossiliferous sites of Greece and China, due to a taphonomic bias, we only took into account the large mammals.

Some large mammals could be by themselves precise indicators of paleoenvironment. In several localities in Greece, such as Pikermi, Chomateres, and Dytiko, chalicotherines are generally associ-

ated with several suids, tragulids, and a number of cervids (Bonis *et al.* 1999). On the other hand, the schizotherines are never associated with tragulids or tapirids but with many bovids or giraffids. It seems likely that schizotherines lived in different habitats than did chalicotherines. A schizotherine has never been found in association with a hominoid. For example, *Ancylotherium* is present in Pentalophos, which is a Greek Vallesian locality without hominoids (Bonis *et al.* 1999). Only one schizotherine species (*Ancylotherium* sp.) is found in the Linxia Basin, with scarce suids and cervids, and notably, no tragulids in its accompanying mammals, but a tapirid species (*Tapirus* cf. *telleri*). Like Pikerimi, *Ancylotherium* has been associated with several bovids and giraffids in the Linxia Basin, including the four bovids, *Gazella* sp., *Miotragocerus* sp., *Protoryx* sp., and *Sinotragus* sp., and the two giraffids, *Honanotherium schlosseri* and *Palaeotragus microdon* during the late Miocene (Bahean and Baodean). Until now, no primate has been discovered in the *Hipparion* fauna of northern China. In Greece, equids and proboscideans occur in every locality. Similarly, equids and proboscideans occur in every locality of Linxia and Baode. Equids were very abundant and relatively diversified during the late Miocene in China, and eight species of *Hipparion* (*H. chiai*, *H. coelophyes*, *H. dermatorhinum*, *H. dongxiangense*, *H. forstenae*, *H. hippidiodus*, *H. placodus*, *H. weihoense*) and *Sinohippus zitteli*, a brachyodont anchitheres, were discovered from Baode and Linxia. Proboscideans were poorly diversified in Baode and Linxia with two species of *Tetralophodon* (*T. exoletus* and *Tetralophodon* sp.). On the other hand, four genera and six species of proboscideans were discovered from the upper Miocene in Greece. *Pliohyrax orientalis* and *Pliohyrax* sp. appeared in Baode and Linxia, respectively. As in the Greek localities, Hyracoidea is uncommon in the Chinese localities.

In the late Miocene *Hipparion* fauna of northern China, the turnover from the Bahean (Vallesian) to the Baodean (Turolian) was completely different from that of Greece. On a continuous section in the Linxia Basin, taxonomic composition of faunas between the Bahean and Baodean ages shows no marked changes. Unlike Greece, China had no deinotheres, but the proboscidean *Tetralophodon*

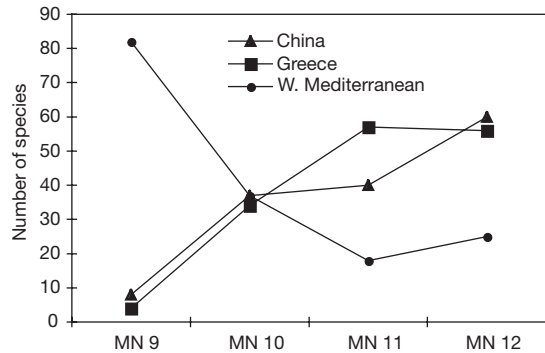


Fig. 2. — Diversity (species richness) for the *Hipparion* faunas from China, Greece, and Western Mediterranean.

maintained a low presence during the Bahean and Baodean ages, which was somewhat similar to that of Greece. Greece had less suids during the Turolian age. On the contrary, suids were more abundant in northern China, increasing to three genera and species (*Chleuastochoerus stehlini*, *Microstonyx major*, and *Postpotamochoerus hyotherioides*) during the Baodean while only one species (*Chleuastochoerus stehlini*) during the Bahean. There are no tragulids or primates during the Bahean and Baodean in northern China. Tapirids and chalicotheriids make an initial appearance during the Baodean. Numbers of rhinocerotids and equids show no marked variation between the Bahean and Baodean ages.

The late Miocene *Hipparion* fauna of China also contrasts with that of the adjacent Afghanistan. In the middle Turolian Molayan locality of Afghanistan, for example, the correlation between dental microwear, morphology, and isotopic data clearly indicates an open, arid, and hilly environment, where evergreen sclerophyllous shrubs and C_3 grasses made up the majority of the vegetation (Merceron *et al.* 2004).

MAMMALIAN DIVERSITY

Fortelius *et al.* (1996) separated western Eurasia into two major blocks, “West” and “East”, which are also called the Western and Eastern Mediterranean. During the late Miocene, the species richness of

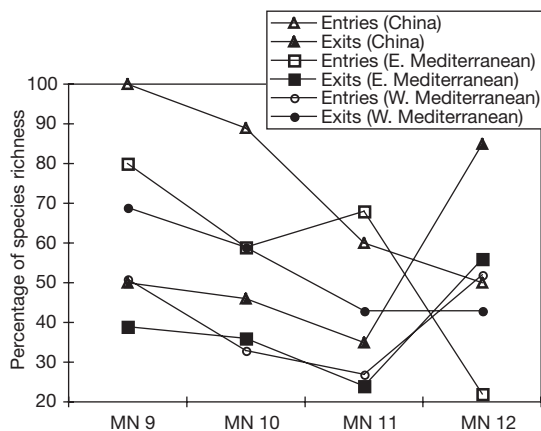


FIG. 3. — First and last appearances of taxa in China, Eastern Mediterranean, and Western Mediterranean as a percentage of species richness.

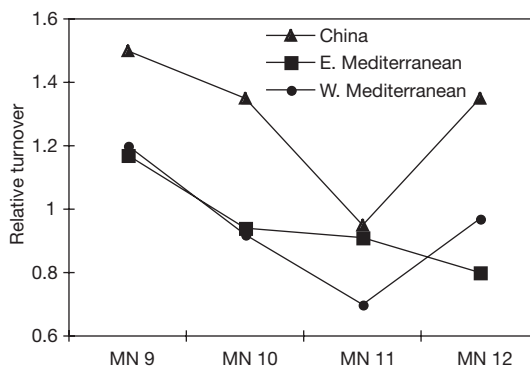


FIG. 4. — Relative turnover (summed first and last appearances divided by species richness) in China, Eastern Mediterranean, and Western Mediterranean.

Greece and China exhibited a similar trend, i.e. species richness obviously increased from MN 9 to MN 12 (Fig. 2). Both regions were different from the Western Mediterranean, where species richness dramatically decreased from MN 9 to MN 11 under the mid-Vallesian crisis (Moyà-Solà & Agustí 1990; Fortelius *et al.* 1996). In Greece and China, species richness was relatively low in MN 9, and rapidly increased in MN 10. Species richness was high throughout the Turolian, but species number in China was less than those in Greece during MN 11. In China, a cooling event at the beginning of the late Miocene caused a decrease in mammalian diversity (Deng & Downs 2002). On the other hand, Fortelius *et al.* (1996) considered that the low species richness of the Vallesian in the Balkans, the Black Sea and Anatolia corresponds to the insufficient record of Vallesian mammals. Indeed, the recent study for the Sinap Formation shows that mammals were very abundant in Anatolia during early Vallesian, and large mammals in MN 9 include at least one species of Primates, eight species of Carnivora, one species of Tubulidentata, two species of Proboscidea, seven species of Perissodactyla, and 13 species of Artiodactyla (Fortelius *et al.* 2003). Both Greece and China exhibited a striking increase in species richness from MN 9 to MN 12, because the Eastern Mediterranean encountered a steady immigration

of East Asian elements and a local evolutionary radiation of open country large herbivores and carnivores.

The diagrams of percent entries and exits in China are similar to the Eastern Mediterranean but are different from the Western Mediterranean (Fig. 3). In China, there were more entries than exits from MN 9 to MN 11 and there were less entries than exits during MN 12. China also exhibited a sharp entry peak during MN 9, indicating that local speciation was the dominant source of new taxa at that time. China showed a decline in entries from MN 10 to MN 12. China's general decline of exits from MN 9 to MN 12 is conceivably related to the progressive expansion of seasonal and open country habitats. Fortelius *et al.* (1996) considered that the Eastern Mediterranean had the similar trend to China, but the discovery of abundant Vallesian mammal fossils from the Sinap Formation in Anatolia somewhat changed this viewpoint (Fortelius *et al.* 2003). In China, the diagram for relative turnover (summed entries and exits divided by species richness) is similar to the Western Mediterranean but is different from the Eastern Mediterranean (Fig. 4). The relative turnover rate in China shows a decline from MN 9 to MN 11, followed by an increase from MN 11 to MN 12.

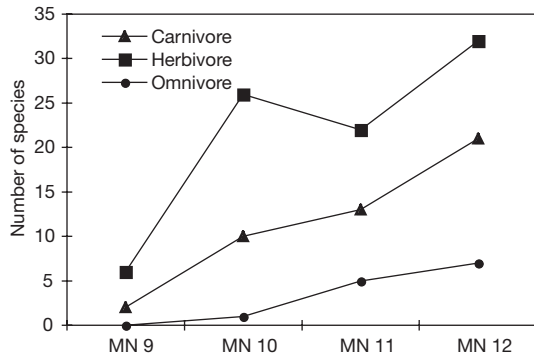


FIG. 5. — Diversity (species richness) of dietary categories in China.

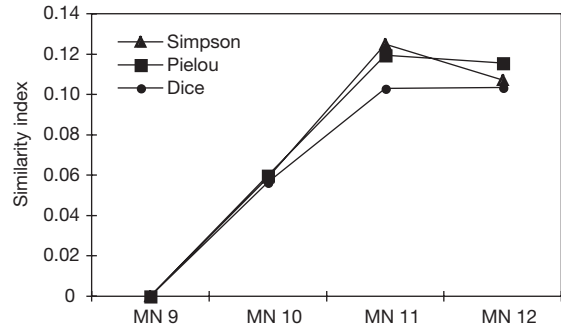


FIG. 6. — Mean similarity indices between Greece and China for each MN unit.

The dietary evolution of the Chinese *Hipparion* faunas is different from that of the Eastern and Western Mediterranean (Fig. 5). Carnivores exclude omnivorous ursids and procyonids; herbivores include proboscideans, hyraxes, perissodactyls, and artiodactyls except suids; and omnivores include ursids, procyonids, and suids. From MN 9 to MN 12, species numbers of carnivores, herbivores, and omnivores followed an increasing trend, which was caused by a continual increase in diversity. Only herbivores showed a slight drop during MN 11. In the Chinese *Hipparion* faunas, omnivores were the scarcest, carnivores were moderately abundant, and herbivores had the highest abundance. Evident from the above-mentioned trend, the habitat of the late Miocene faunas became increasingly more open, providing a year-round supply of low-fiber (plant) food.

Janis (1982) suggested that the entry of *Hipparion* into the Old World would in itself have initiated the diversification of other ungulate groups by competition leading to niche partitioning, perhaps through direct impact on the vegetation and feeding successions. Actually, this is the reason why the mammal diversity began to increase by a large scale during MN 10 in China, Greece, and other places. On the other hand, the entry of *Hipparion* never led to a comparable radiation in the Western Mediterranean, nor was there any diversification

of the contemporaneous bovid fauna (Fortelius *et al.* 1996).

FAUNAL SIMILARITY

Fortelius *et al.* (1996) applied three indices for investigating faunal similarity and/or difference in western Eurasia. We also apply the three indices to compare the *Hipparion* faunas between China and Greece. The Dice index (Sokal & Sneath 1963) is calculated as $2A/(2A + B + C)$. A = present in both faunas; B = present in fauna 1, absent in fauna 2; C = absent in fauna 1, present in fauna 2. The Simpson index (Simpson 1943) is calculated as $A/(A + E)$, where E is the smaller of B or C. The Pielou index (Cody 1993) is calculated as $A(B + C)/2BC$.

Here we compare the Chinese late Miocene *Hipparion* fauna with the Greek fauna. In China, the mammalian faunas corresponding to MN 9 are very few, and the Guonigou fauna is representative. The Chinese mammalian faunas of MN 10 are represented by the Dashengou fauna from the Linxia Basin, with the added components of the Qaidam fauna from Delingha, Qinghai (Bohlin 1937; Deng & Wang 2004), the Bahe fauna from Lantian, Shaanxi (Liu *et al.* 1978; Zhang *et al.* 2002), and the Lamagou fauna from Fugu, Shaanxi (Xue *et al.* 1995; Deng 2000). The Chinese mammalian faunas

of MN 11 are represented by the Yangjiashan fauna from the Linxia Basin, with the added components of the Miaoliang fauna from Fugu, Shaanxi (Xue *et al.* 1995). The Chinese mammalian faunas of MN 12 are represented in the Baode fauna. Late Miocene micromammalian fossils being scarce in China, the comparison of the late Miocene *Hipparion* faunas between China and Greece is limited to only large mammals.

In Greece, the late Miocene (MN 9 to MN 13) is very well known from several localities, but the MN 9 faunas are also scarce. In our comparison, the Greek mammalian list from MN 9 to MN 12 is based mainly on the summaries of Bonis & Koufos (1999) and Bernor *et al.* (1996b), excluding the micromammalian fossils.

Dice similarity indices were calculated between the two regions (Fig. 6). The results indicate that China and Greece had few similarities at the species level during the entire late Miocene. However, it is obvious that the similarity of the *Hipparion* faunas between the two regions increased gradually. There were no common species between China and Greece during MN 9, but there were two common species (*Hyaenotherium wongii* and *Dinocrocuta gigantea*) during MN 10, with a similarity index of 0.0563. There were five common species (*Simocyon primigenius*, *Hyaenotherium hyaenoides*, *H. wongii*, *Adcrocuta eximia*, and *Microstonyx major*) during MN 11, with a similarity index of 0.1031, and there were six common species (*Simocyon primigenius*, *Hyaenotherium hyaenoides*, *H. wongii*, *Adcrocuta eximia*, *Metailurus major*, and *Microstonyx major*) during MN 12, with a similarity index of 0.1034. These results imply that the faunal exchange or dispersal was gradually strengthened between China and Greece. On the other hand, the common species between the two regions were mainly carnivores, especially hyaenids, and ungulates included only the omnivore suid *Microstonyx major*. Bonis *et al.* (1999) indicated that many carnivores are ubiquitous animals. For example, tigers currently reside from southern Asia to the polar circle and until recently, lions inhabited Europe as well as South Africa. Also, jaguars are known from sea level up to the higher Andes Plateau. Therefore, the gradually increased

similarity between the *Hipparion* faunas in China and Greece cannot imply that the two regions have increasingly similar environments. In contrast, great differences between ungulate taxa indicate that the two regions have obvious distinctions in environments. As shown in Figure 6, the Dice, Simpson, and Pielou indices reveal the same or more dramatic trends. The lowest indices are seen at MN 9 at the initial stage of the hipparionine dispersal. The earliest species of *Hipparion* dispersed into Asia from North America across the Bering landbridge at 11.2 Ma, and rapidly reached Europe and North Africa. The succeeded high adaptive radiation was a very important event in Eurasia (Woodburne & Swisher 1995; Bernor *et al.* 1996a). The result of the adaptive radiation reflects that the faunas between the eastern and western parts of Eurasia had no obvious similarity at the species level because of environmental differences. Beginning in MN 10, and culminating in MN 11-12, the East Asian fauna extended into Europe, and immigrants and their descendant species replaced more archaic forms, so that faunal similarity reached a maximum in MN 12 (Fortelius *et al.* 1996).

Acknowledgements

I wish to thank the organizers of the fifth International Symposium on Eastern Mediterranean Geology (ISEMG) for inviting me to participate in this symposium. I thank Prof. Z. X. Qiu, Prof. B. Y. Wang, and Dr. X. J. Ni from the Institute of Vertebrate Paleontology and Paleoanthropology in Beijing, Dr. X. W. Wang from the Los Angeles County Museum, and Dr. Y. Wang from the Florida State University (FSU) in Tallahassee for their beneficial discussions. I am grateful to Dr. V. Eisenmann from the Muséum national d'Histoire naturelle in Paris (MNHN) for her French translation, and to Dr. D. Biasatti from FSU for her English improvement. Dr. S. Sen (MNHN) and two anonymous are thanked for their helpful suggestions and constructive comments. This work was supported by National Natural Science Foundation of China (40232023).

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*Submitted on 23 December 2005;
accepted on 14 June 2006.*

APPENDIX

Components of the late Miocene *Hipparion* faunas in China. Notes: 1, Qaidam; 2, Bahe; 3, Lamagou; 4, Miaoliang; 5, undescribed new species.

Order	Family	Species	Linxia			Baode (MN 12)			
			Guonigou (MN 9)	Dashengou (MN 10)	Yangjiashan (MN 11)				
Rodentia	Hystricidae	<i>Hystrix gansuensis</i>			+				
	Rhizomyidae	<i>Pararhizomys hipparionum</i>		+	+				
	Cricetidae	<i>Prosiphneus</i> sp.		+					
Carnivora	Castoridae	<i>Sinocastor zdanskyi</i>				+			
	Procyonidae	<i>Simocyon primigenius</i>			+	+			
	Ursidae	<i>Agriotherium inexpectans</i>				+			
		<i>Indarctos lagrelii</i>				sp.	+		
		<i>Indarctos sinensis</i>					+		
		<i>Indarctos zdanskyi</i>					+		
		Mustelidae	<i>Eomellivora wimani</i>					+	
			<i>Lutra aonychoides</i>					+	
			? <i>Melodon incertum</i>					+	
			<i>Melodon majori</i>		+			+	
			<i>Mustela palaeosinensis</i>					+	
			<i>Parataxidea crassa</i>					+	
			<i>Parataxidea sinensis</i>					+	
			<i>Plesiogulo brachygnathus</i>					sp.	+
			<i>Promephitis hootoni</i>		+		+		
			<i>Promephitis maeotica</i>						cf.
		<i>Promephitis parvus</i>		+		+			
		<i>Proputorius minimus</i>						+	
		<i>Sinictis dolicocephalus</i>					sp.	+	
	Hyaenidae	<i>Adcrocuta eximia</i>				+	+		
<i>Dinocrocuta gigantea</i>		+	+						
<i>Hyaenotherium hyaenoides</i>			+		+	+			
<i>Hyaenotherium wongii</i>			+		+	+			
<i>Ictitherium gaudryi</i>					sp.	sp.	+		
<i>Ictitherium sinense</i>							+		
? <i>Lycyaena dubia</i>							+		
Felidae	<i>Felis</i> sp.				+	+			
	<i>Machairodus palanderi</i>		sp.		+	+			
	<i>Machairodus tingii</i>					sp.	+		
	<i>Metailurus major</i>					sp.	+		
	<i>Metailurus minor</i>					+	+		
Proboscidea	Gomphotheriidae	<i>Tetralophodon exoletus</i>	sp.	+		+			
Hyracoidea	Procaviidae	<i>Pliohyrax orientalis</i>				sp.	+		
Perissodactyla	Equidae	<i>Hipparion chiai</i>		+					
		<i>Hipparion coelophyes</i>				+	+		
		<i>Hipparion dermatorhinum</i>				+	+		
		<i>Hipparion dongxiangense</i>	+						
		<i>Hipparion forstenae</i>						+	
		<i>Hipparion hippidioides</i>						+	
		<i>Hipparion placodus</i>						+	
		<i>Hipparion platyodus</i>						+(4)	
		<i>Hipparion weihoense</i>			+				
		<i>Sinohippus zitteli</i>					+	+	
		Tapiridae	<i>Tapirus telleri</i>					cf.	
			<i>Tapirus teilhardi</i>						+
		Chalicotheriidae	<i>Ancylotherium</i> sp.				+		
		Rhinocerotidae	<i>Acerorhinus fuguensis</i>				+(3)		
			<i>Acerorhinus hezhengensis</i>				+	+	
<i>Acerorhinus palaeosinensis</i>							+		
<i>Acerorhinus tsaidamensis</i>					+(1)				

Order	Family	Species	Linxia			Baode (MN 12)
			Guonigou (MN 9)	Dashengou (MN 10)	Yangjiashan (MN 11)	
		<i>Chilotherium anderssoni</i>				+
		<i>Chilotherium habereri</i>				+
		<i>Chilotherium</i> sp. ⁽⁵⁾	+			
		<i>Chilotherium wimani</i>		+	+	
		<i>Dicerorhinus ringstromi</i>			+	+
		<i>Iranotherium morgani</i>		+		
		<i>Parelasmotherium linxiaense</i>	+			
		<i>Parelasmotherium simplum</i>	+			
		<i>Sinootherium lagrelii</i>				+
Artiodactyla	Suidae	<i>Chleuastochoerus stehlini</i>		+	+	+
		<i>Microstonyx major</i>			+	+
		<i>Postpotamochoerus hyotherioides</i>				+
	Cervidae	<i>Cervavitus demissus</i>			+(4)	
		<i>Cervavitus novorossiae</i>			+	+
		<i>Dicrocerus</i> sp.		+		
		<i>Eostyloceros blanfordi</i>		sp.(1)	+(4)	
		<i>Metacervulus</i> sp.			+	
		<i>Muntiacus lacustris</i>			cf.(4)	
		<i>Procapreolus latifrons</i>			+(4)	+
	Giraffidae	<i>Honanotherium schlosseri</i>		+	+	+
		<i>Palaeotragus coelophrys</i>				cf.
		<i>Palaeotragus decipiens</i>		cf.(2)		
		<i>Palaeotragus microdon</i>		+(2)	+	+
		<i>Samotherium</i> sp.		+		+
	Bovidae	<i>Dorcadoryx triquetricornis</i>		+(2)		
		<i>Gazella altidens</i>		sp.	sp.	+
		<i>Gazella dorcadooides</i>				+
		<i>Gazella gaudryi</i>		+(2)		
		<i>Gazella paotehensis</i>				+
		<i>Hezhengia bohlini</i>		+		
		<i>Lantiantragus longirostralis</i>		+(2)		
		<i>Miotragocerus</i> sp.		+	+	
		<i>Palaeoryx sinensis</i>				+
		<i>Paraprotoryx minor</i>				+
		<i>Plesiaddax depereti</i>				+
		<i>Protoryx</i> sp.		+(2)	+	
		<i>Qurliqnorina cheni</i>		+(1)		
		<i>Shaanxiplina baheensis</i>	sp.	+(2)		
		<i>Shaanxiplina chowi</i>		+(2)		
		<i>Sinotragus wimani</i>			sp.	+
		<i>Tossunnoria pseudibex</i>		+(1)		
		<i>Tragocerus spectabilis</i>				+
		? <i>Tragoreas anderssoni</i>				+
		? <i>Tragoreas lagrelii</i>				+
		? <i>Tragoreas palaeosinensis</i>				+
		<i>Tsaidamotherium hedinii</i>		+(1)		
		<i>Urmiatherium intermedium</i>				+