Chapter 22

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Chapter 22

Rodents from the Chinese Neogene: Biogeographic Relationships with Europe and North America

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ABSTRACT

Cenozoic terrestrial deposits with a dense fossil record are widespread in China. At least 126 genera of rodents, belonging to 25 families and subfamilies, are known from the Neogene. Geographical distribution of the fossil rodents indicates that zoogeographic differentiation in China was already quite distinct and faunal provinces similar to the present day Palearctic Realm in North China and to the Oriental Realm in South China existed throughout Neogene time. An initial phase in development of the present Oriental region emerged by the early Miocene in southeastern Asia. Faunas in northern China were Holarctic in character and showed greater similarity in composition to Europe than to North America. Apparently, immigration and dispersal of rodents in the Holarctic Region repeatedly took place via the Bering Landbridge during the Neogene. Interchange of rodents between Asia and Europe tended to gradually increase during the Neogene, whereas it declined between Asia and North America after the late Miocene.

INTRODUCTION

The widespread Cenozoic terrestrial deposits and rich fossil record in China afford an opportunity to study the paleontology of this era. Research on the Chinese Neogene in zoogeography, biostratigraphy, biochronology, and systematic paleontology has advanced in the last 20 years due to efforts by paleontologists from China, Europe, and North America. The fossil record has been enriched greatly, and a large number of mammalian faunas are recognized in Neogene deposits. Chinese paleontologists have seriated the faunas and developed biochrons based on correlation with those of Europe. The Neogene biochronologic framework initiated by Chiu (Qiu) and others in 1979 has been refined significantly, with local Neogene biochrons continuously modified (Chiu et al., 1979; Li et al., 1984; Qiu, 1990; Qiu and Qiu, 1995; Tong et al., 1995; Qiu et al., 1999). To attain more precise biochronologic dating, a combination of biostratigraphic and paleomagnetic data is possible in some areas with long stratigraphic sections and rich mammal remains. A chronostratigraphic sequence with paleomagnetic data has been accomplished at Yushe and Lanzhou basin, mainly through cooperation with American and Swiss colleagues. Investigations of sequences with long composites of successive microfaunas and magnetostratigraphic control were initiated a couple of years ago in the Lantian area by a joint expedition from Finland and the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) and in Lingtai, Gansu, by Shaohua Zheng and others. A section with rich late Oligocene through middle Miocene remains in northern Junggar, Xinjiang, including magnetic stratigraphy analysis, is under study by Wenyu Wu and others. In addition, the two biotic

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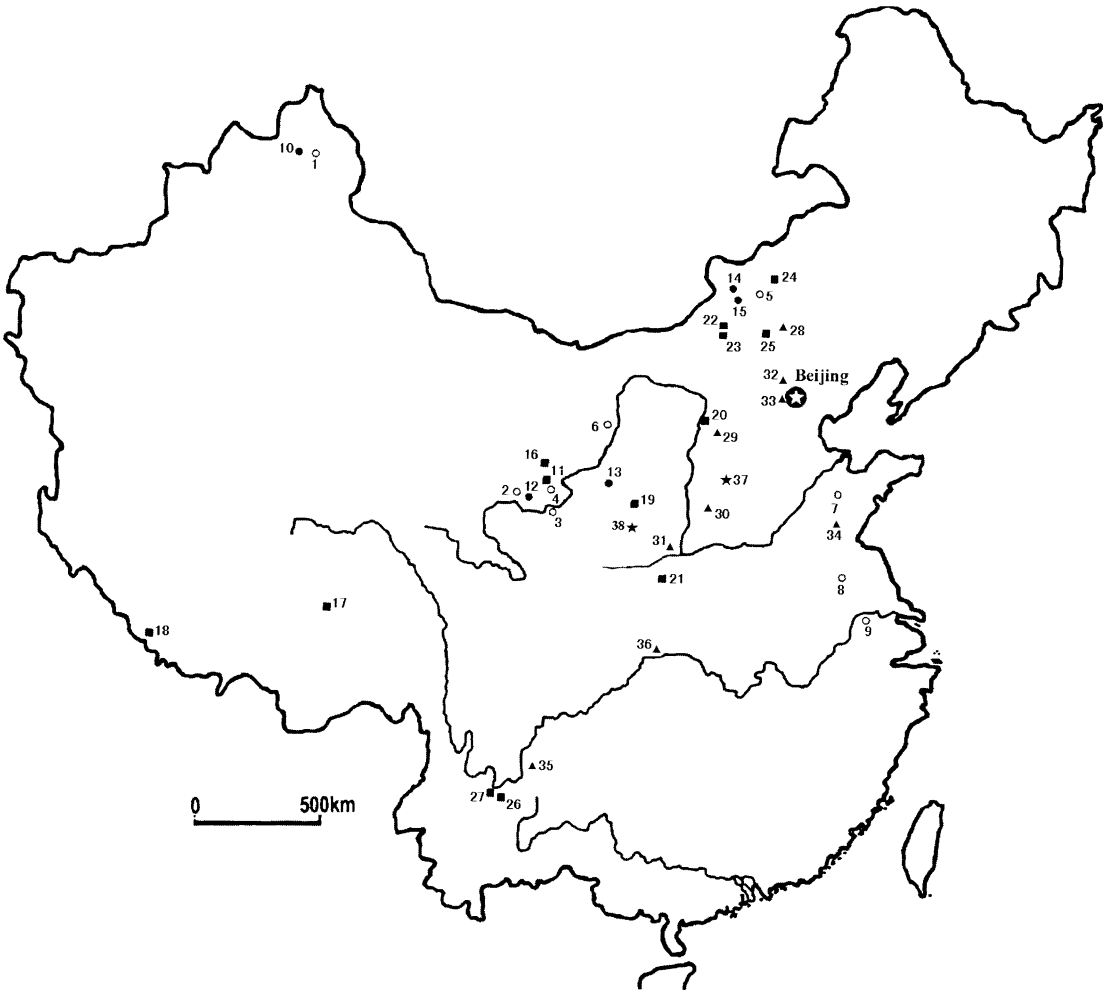

Fig. 22.1. Distribution of Neogene rodent localities in China. ^, Early Miocene (Xiejian + Shanwangian): 1, Suosuoquan; 2, Xiejia; 3, Gaolanshan; 4, Zhangjiaping; 5, Gashunyinadege; 6, Wuertu; 7, Shanwang; 8, Sihong (Songlinzhuang, Zhengji, Shuanggou); 9, Fangshan. ●, Middle Miocene (Tunggurian): 10, Halamagai; 11, Quantougou; 12, Lierpu (Qijia, Danshuilu); 13, Dingjiaergou; 14, Tunggur; 15, Tairum Nor. ■, Late Miocene (Baodean): 16, Songshan; 17, Bulong; 18, Jilong; 19, Qingyang; 20, Baode; 21, Lantian (Bahe); 22, Amuwusu; 23, Shala; 24, Baogedawula; 25, Ertemte (Harr Obo); 26, Shihuiba; 27, Yuanmou. ▲, Pliocene (Yushean): 28, Bilike; 29, Jingle; 30, Dingcun; 31, Youhe; 32, Daodi; 33, Zhoukoudian (Cap Travertine); 34, Yinan; 35, Zhaotong; 36, Wushan. ★, Late Miocene + Pliocene: 37, Yushe (Mahui; Gaozhuang; Mazegou; Haiyan; Jiayucun); 38, Lingtai (Wenwanggou).

provinces of northern and southern China have been recognized to persist throughout Neogene history (Qiu, 1996b; Tong et al., 1996).

Progress in research on the Chinese Neogene partly should be ascribed to the great advances in intensive collection and study of small mammals, particularly rodents in the last 20 years. Knowledge of fossil rodents prior to the 1980s was based on a handful of specimens at a few localities. To date, more than 40 assemblages of rodents have been recovered from Neogene deposits of different ages. Figure 22.1 shows the distribution of major localities of Neogene rodents in China. Available collections prove that fossil rodents in this country are as abundant and diverse as in Europe and North America. Fig-

ure 22.2, a correlation chart, serves as a framework for evaluating faunas. Subdivision of the Chinese Neogene mammalian ages and intercontinental correlation of rodent assemblages in the correlation chart are mainly based on Li et al. (1984); Qiu and Qiu (1995); Tong et al. (1995); and Qiu et al. (1999). In this paper, we review the fossil record of Chinese Neogene rodents and are pleased to dedicate this effort to Dr. Richard H. Tedford for his contributions to the development of Chinese Neogene paleontology and his works that inspire great respect.

MAJOR CHINESE NEOGENE RODENT FAUNAS

Neogene rodent localities are centered largely in northern and northwestern China, scattered in southwestern areas and the area between the Yangtze River and the Huai River, but so far not known in southeastern and northeastern parts of China. A set of local rodent faunas in central Inner Mongolia and the middle part of the Yellow River valley characterize very well the history of Chinese Neogene rodents in North China. The best representative and highly significant Neogene local faunas are the Suosuoquan fauna, Xiejia fauna, Sihong fauna, Tunggur fauna, Amuwusu fauna, Shihuiba fauna of Lufeng, Yushe faunas, Ertemte fauna, Wenwanggou faunas of Lingtai, Bilike fauna, Daodi fauna, and Wushan fauna.

The Suosuoquan fauna has been variously considered late Oligocene (Tong et al., 1995) and early Miocene (Qiu and Qiu, 1995; Qiu et al., 1999). It is here referred to the earliest Neogene fauna of China because the nine rodents associated with other mammals are derived species of the genera present in latest Oligocene faunas, such as at Taben-buluk.

The Xiejia fauna well represents the early Miocene in northwestern China, and contains survivors of endemic Oligocene forms, but with definitely advanced species characters (Li and Qiu, 1980). The species of *Parasminthus* in this fauna shows more derived morphology than that of Suosuoquan.

The Sihong (Xiacaowan or Hsiatsaowan) fauna, consisting of 17 species of rodents from the Songlinzhuang, Zhengji, and Shuanggou sites, represents the very few early Miocene assemblages of eastern China (Li et al., 1983). It is composed of quite a number of rodents and other mammals either particular to the present Palearctic region or distributed over the Oriental region and tropical/subtropical areas today. The fauna is closely related to the early Miocene Li Mae Long fauna of Thailand.

The Third Central Asiatic Expedition organized by the American Museum of Natural History initially investigated the Tunggur fauna. The site was re-collected by Chinese paleontologists in 1986, who recovered 21 rodent taxa to be added to the so-called *Platybelodon* fauna. This is the most diverse and abundant middle Miocene fauna known in China and all of Asia (Stirton, 1934, 1935; Wood, 1936; Li, 1963; Qiu, 1996a).

The Amuwusu fauna (19 taxa) contains either Tunggurian relict forms or very primitive Baodean elements (Qiu and Wang, 1999), and is considered an earliest late Miocene fauna in China.

The Shihuiba fauna from the Lufeng hominoid locality, including 19 species of rodents, is the best represented late Miocene fauna in South China. It exhibits a quite different composition from that of the contemporary faunas of North China and is obviously Oriental in character (Qiu et al., 1985).

The Ertemte fauna was first discovered in 1919 and studied by Schlosser in 1924. Recollection in 1980 added a rodent fauna with up to 32 forms and made it the richest fauna among the numerous late Miocene rodent assemblages in North China (Schlosser, 1924; Fahlbusch et al., 1983). It reflects a typical temperate steppe or forest–grassland environment, like that of the present day Palearctic province.

The Yushe faunas (containing Mahui, Gaozhuang, Mazegou, and Haiyan assemblages) and Wenwanggou fauna, spanning from about 6–7 Ma to 2 Ma, have long composites of successive rodents and magnetostratigraphic control (Flynn, 1993, 1997; Flynn et al., 1995, 1997; Zheng and Zhang, 2000). They have the potential to provide a key reference for the late Neogene faunas of North China.

The Bilike fauna, containing 30 rodents, shows strong similarities with the Ertemte

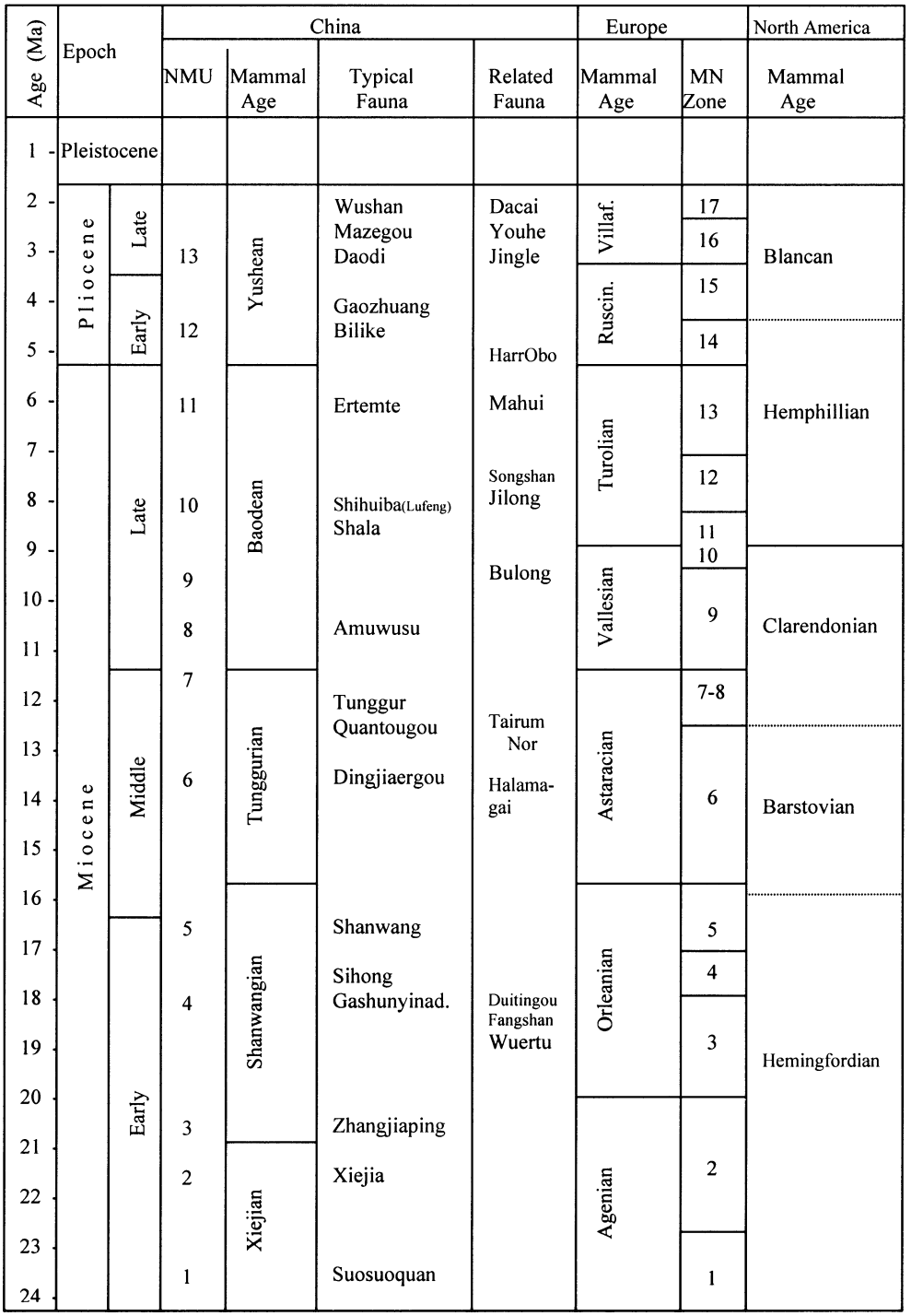

Fig. 22.2. Correlation of Chinese Neogene biochrons with those of Europe and North America.

fauna and represents, on the whole, a sort of modernized Ertemte fauna (Qiu and Storch, 2000).

The Daodi fauna is a younger Neogene assemblage with 13 well-represented rodents and one of the best records of a late Pliocene small mammal community in North China (Cai, 1987).

The Wushan fauna from cave deposits of Central China consists of 30 rodents. It was considered Pleistocene in age by Zheng in 1993. The assemblage represents the youngest Neogene fauna, that is, late Pliocene rather than Pleistocene in age, if the age interpretation of 2 Ma for the locality is correct (Huang and Fang, 1991).

MAJOR GROUPS OF CHINESE NEOGENE RODENTS

One hundred and twenty-six genera of rodents within 25 groups (families and subfamilies) and representing Protrogomorpha, Sciuromorpha, Myomorpha, and Hystricomorpha are known in the Chinese Neogene. Figure 22.3 lists major groups of Neogene rodents with their temporal and geographical distribution, and relationships to Europe and North America.

CTENODACTYLIDAE: Ctenodactylidae flourished in central and northeastern Asia during the Oligocene, but declined greatly in the early Miocene and made their last occurrence in the early middle Miocene of Dingjiaergou. Six genera, *Tataromys*, *Yindirtemys*, *Prodistylomys*, *Distylomys*, *Prosayimys*, and *Sayimys*, grouped in three subfamilies, Tataromyinae, Distylomyinae, and Ctenodactylinae, have been reported mainly in the Mongolia–Xinjiang areas and northern edge of Qinghai–Tibet Plateau. All the genera except *Sayimys* can be found in Oligocene deposits (Wang, 1977) at low abundance except for the common *Yindirtemys*. Survivors migrated southwestward through Asia to the Mediterranean area and North Africa after the early Miocene, and were affected by change of environment caused by uplift of the Himalayas. See Wang's (1997) significant revision of the family.

TACHYORYCTOIDIDAE: Two genera of this family, *Aralomys* and *Tachyoryctoides*, have been recognized in the same regions where ctenodactylids occur. *Aralomys* is known from Kazakhstan and is represented by quite a number of specimens from Suosuoquan, which were previously reported as *Tachyoryctoides obrutschewi* and *T. pachygnathus* (Qiu et al., 1999). Li and Qiu (1980) described *Tachyoryctoides kokonorensis* from Xiejia (early Miocene) and indeterminate species of this genus were reported at Halamagai, Zhangjiaping, Dingjiaergou, Wuertu, and Gashunyinadege (Qiu et al., 1999; Qiu and Wang, 1999). It is clear that the two genera are survivors from Oligocene faunas, and endemic to central and northeastern Asia. They coexisted with and disappeared simultaneously with ctenodactylids in the Miocene.

TSAGANOMYIDAE: *Tsaganomys* is the only Neogene genus of Tsaganomyidae, and it first appeared in the early Oligocene in the Mongolian plateau. *Tsaganomys* cf. *altaicus* collected from Gaolanshan (previously Lanzhou) represents the last record of the family (Qiu et al., 1999).

DIATOMYIDAE: *Diatomys shantungensis*, collected from Shanwang and Sihong, is the only Chinese species of this family. *Diatomys* was first considered indeterminate to family and questionably referred to Geomyoidea (Li, 1974). Some students transferred it to the family Pedetidae (McKenna and Bell, 1997). We follow P. Mein and L. Ginsburg (1997) in their definition of a new family for this genus plus probably *Fallomus*. *Diatomys* is also known from Thailand, Pakistan, and Japan (Kato and Otsuka, 1995), and appears to be a kind of wet/warm-adapted animal distributed in a tropical or subtropical area.

APLODONTIDAE: Aplodontid rodents are quite well known in Holarctic Oligocene deposits in Europe and North America, but are represented in China by scarce materials of four genera. These are *Promeniscomys*, *Haplomys*, *Prosciurus*, and *Ansomys*, of which only *Ansomys* survived into the Miocene (Rensberger and Li, 1986; Qiu, 1987; Wang, 1987). *Ansomys* may have evolved from a *Prosciurus*-like ancestor, and made its first appearance in the early Miocene. *Ansomys orientalis* was described from Sihong and *A. shanwangensis* from Shanwang (Qiu, 1987; Qiu and Sun, 1988), and questionable *An-*

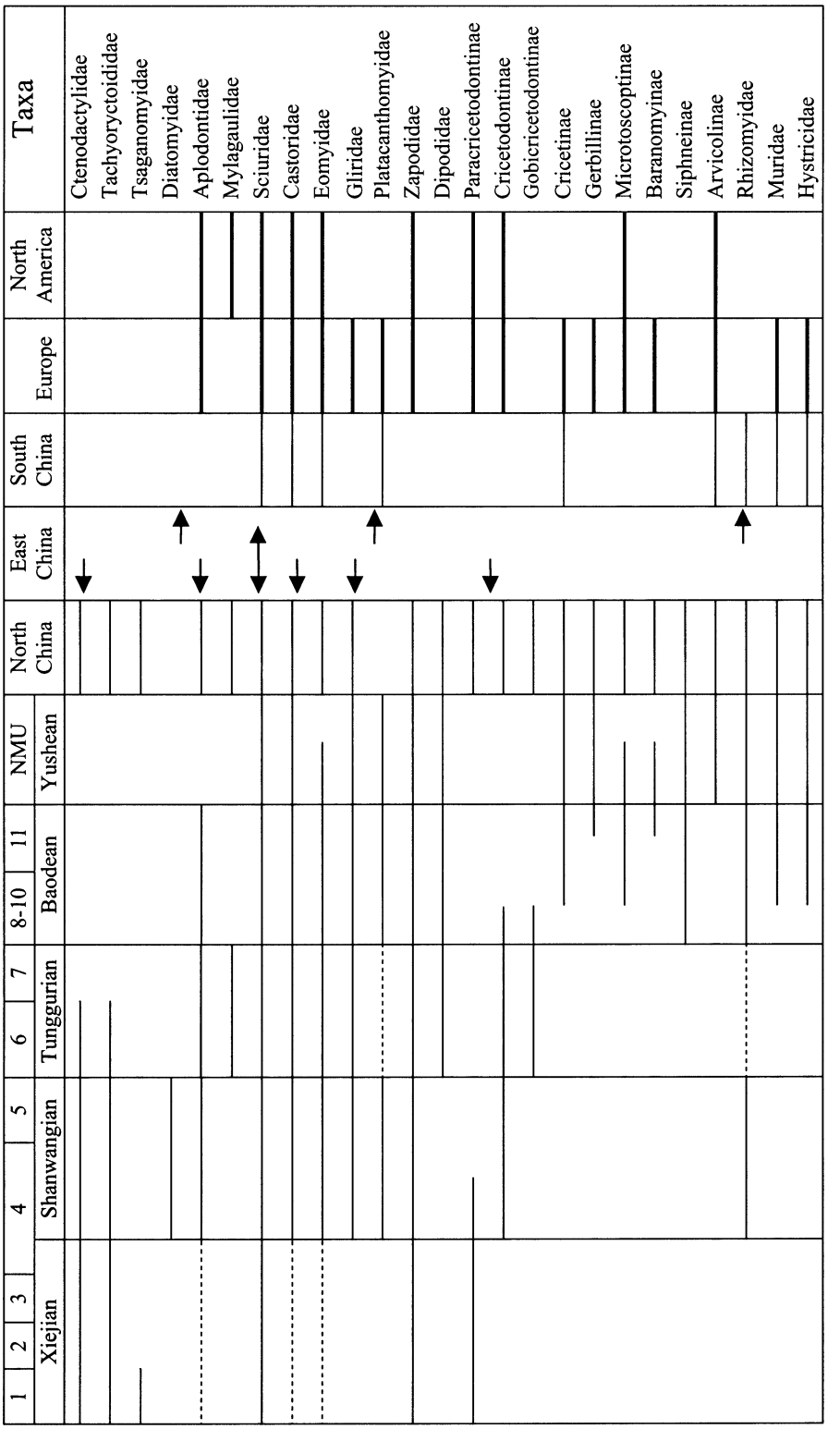

Fig. 22.3. Biogeographic relationships of major groups of Neogene rodents found in China.

somys was reported from Gashunyinadege, Tunggur, Amuwusu, and Shala of Inner Mongolia (Qiu and Wang, 1999). In addition, the aplodontine *Pseudaplodon* is known from the Mio/Pliocene of Ertemte and Harr Obo, Inner Mongolia, and represents the last record of this family in Asia (Fahlbusch et al., 1983). An upper and a lower premolar from Amuwusu, similar to those of *Meniscomys* of North America, may represent a meniscomyine rodent in the Old World.

MYLAGAULIDAE: Mylagaulids are quite diverse in North America, and also known from Zaisan Basin, Kazakhstan. *Sinomylagaulus halamagaiensis* described by Wu (1988) from Halamagai Formation, Junggar Basin, represents the only record of this family in China.

SCIURIDAE: We recognize 23 genera of sciurid rodents, with Sihong, Ertemte, Shihuiba (Lufeng), and Wushan being relatively diverse and common squirrel faunas (Qiu et al., 1985; Qiu and Lin, 1986; Qiu, 1991; Zheng, 1993). An undiagnosed new species of *Palaeosciurus* from Suosuoquan represents the oldest record of the family (Qiu et al., 1999). *Palaeosciurus*, *Eutamias*, *Sciurus*, *Tamiasciurus*, *Atlantoxerus*, *Heteroxerus*, *Sciurotamias*, *Miopetaurista*, *Pliopetaurista*, *Petinomys*, *Albanensia*, *Pteromys*, and *Hylopetes* show affinities either to Europe or to North America, whereas *Sinotamias*, *Prospermophilus*, *Tamiops*, *Callosciurus*, *Dremomys*, *Parapetaurista*, *Shuanggouia*, *Plesiosciurus*, *Meinia*, and *Belomys* are restricted in geographical distribution to Asia. Generally, sciurids were not so diverse as they were in Europe and North America during Neogene time, and flying squirrels are not as common as they are in European sciurid faunas. Sciurids found in China demonstrate apparently ecologic provinciality throughout the Neogene, with dominance of ground squirrels in the north, and of tree and flying squirrels in the south.

CASTORIDAE: Eight genera of beavers, *Youngofiber*, *Anchitheriomys*, *Steneofiber*, ?*Hystricops*, *Castor*, *Dipoides*, *Trogontherium*, and *Eucastor*, have been recovered from Sihong, Tunggur, Halamagai, Amuwusu, Yushe, Ertemte, Bilike, and Wushan (Li, 1963; Chow and Li, 1978; Zheng, 1993; Xu, 1994; Qiu, 1996a; Flynn et al., 1997; Wu et al., 1998). All the taxa, except *Youngofiber*, can be found in the European and North American Neogene. *Youngofiber* was a massive form also known from Mizunami, Japan (Tomida and Setoguchi, 1994) as well as Sihong. The occurrence together with *Diatomys* in both places suggests existence of a connection between the Chinese mainland and the Japanese islands during the early Miocene. An indeterminate genus from Shihuiba and ''*Castor*'' from Zhaotong, Yunnan, represent the southernmost records of beavers in China, even in the Old World. Associated with the beavers at Shihuiba are some small mammals confined to the present tropical or subtropical areas, such as tree shrew, mole shrew, spiny dormouse, and bamboo rats (Qiu et al., 1985). Xu (1994) presented a thorough review of castorid rodents found in North and East China.

EOMYIDAE: Eomyids are another cosmopolitan group of fossil rodents, but they are poorly diversified with limited material in China. Two genera, *Keramidomys* and *Leptodontomys*, have been determined from early Miocene (Gashunyinadege) through early Pliocene (Harr Obo) localities, and these usually occur together in the Miocene deposits of North China (Zheng and Li, 1982; Fahlbusch et al., 1983; Qiu, 1996a; Qiu and Wang, 1999). *Keramidomys* failed to persist into the Pliocene. An undetermined genus of this family from Shihuiba is a bunodont eomyid, which shares dental similarities with *Eomys* or *Pentabuneomys* of Europe, or with *Adjidaumo* of North America (Qiu, 1994).

GLIRIDAE: Since the finding of *Myomimus* at Ertemte, dormouse material has been found at several localities, one after another. Nevertheless, only three genera, *Microdyromys*, *Miodyromys*, and *Myomimus*, are recognized, and specimens of the first two taxa are rather rare (Wu, 1985, 1986; Qiu, 1996a; Flynn et al., 1997; Wu et al., 1998; Qiu and Wang, 1999). All three genera are commonly known in Europe, but do not occur in South China. Neither *Microdyromys* nor *Miodyromys* survived into the Pliocene.

PLATACANTHOMYIDAE: *Platacanthomys* and *Typhlomys*, confined to the present Oriental region, are known from Shihuiba (Qiu, 1989) and Yuanmou recently. Zheng (1993) described three species of *Typhlomys* from

Wushan. An isolated tooth from Sihong, assigned to *Neocometes*, represents the third genus of platacanthomyid rodents found in China. The latter is also known from Thailand. Remains of these animals are not found in North China.

ZAPODIDAE: The nine genera representing this family in North China are *Litodonomys*, *Parasminthus*, *Heterosminthus*, *Eozapus*, *Protozapus*, *Sinozapus*, *Plesiozapus*, *Sicista*, and *Lophocricetus*. *Litodonomys* and *Parasminthus* are known only from early Miocene localities, such as Suosuoquan and Xiejia, whereas *Heterosminthus* is mainly middle Miocene, Quantougou, Dingjiaergou, and Tunggur, for example (Li and Qiu, 1980; Qiu, 1996a; Qiu et al., 1999). Remains of the other forms derive mainly from the late Miocene and Pliocene deposits. *Eozapus*, *Sicista*, and *Lophocricetus* are common members of the Ertemte and Harr Obo faunas (Qiu, 1985; Fahlbusch, 1992). Specimens of *Protozapus* reported from Wenwanggou and *Plesiozapus* from Amuwusu are inadequate and need further identification. Only *Eozapus* and *Sicista* persist to the present day.

DIPODIDAE: Neogene dipodid rodents found include *Protalactaga*, *Paralactaga*, *Sminthoides*, *Brachyscirtetes*, and *Dipus*. The earliest Neogene record of this family is an indeterminate species of *Protalactaga* represented by an upper molar from Wuertu fauna (Qiu et al., 1999); that it possibly is a derived species of *Parasminthus* cannot be excluded. *Protalactaga* occurs usually in the middle Miocene of North China, such as in the Quantougou, Tunggur, and Dingjiaergou faunas. These rather primitive jumping mice failed to survive into the late Miocene. The other genera are known from the late Miocene and Pliocene (the indeterminate species of *Paralactaga* from Dingjiaergou in a previous faunal list may be *Protalactaga major*). *Sminthoides* is quite common in late Neogene deposits, whereas *Brachyscirtetes* and *Dipus* are relatively scarce. The questionable *Dipus* from Amuwusu probably represents the first record of the three-toed jerboa. Both zapodids and dipodid rodents are found only in North China.

PARACRICETODONTINAE: *Eucricetodon youngi* from Xiejia is the only representative of this group found in the Neogene of China (Li and Qiu, 1980). The indeterminate species previously reported as *Eumyarion* sp. based on a lower molar from Tunggur has been transferred to *Gobicricetodon* (Qiu, 1996a).

CRICETODONTINAE: Five genera in this group, *Megacricetodon*, *Democricetodon*, *Primus*, *Spanocricetodon*, and *Paracricetulus*, have been recovered from the early and middle Miocene. *Megacricetodon* and *Democricetodon* had a large geographic distribution and made their first appearance in early Miocene (Sihong, Wuertu, Gashunyinadege) as in Europe. They seem to have thrived in North China in the middle Miocene. Wessels (1996) argued that *Megacricetodon* did not occur in Pakistan and that all material from the Indian subcontinent previously assigned to *Megacricetodon* should be allocated as the myocricetodontine *Sindemys*. The tiny cricetodontine *Primus* is known from the early Miocene of Pakistan, and similar species occur in the equivalent age Sihong fauna. *Spanocricetodon* from the Shanwangian of eastern China (Fangshan) is also known from Pakistan and Thailand. Young (1927) described *Paracricetulus schaubi* from Hsien Shui Ho (Quantougou) based on a fragmentary upper jaw with a damaged M1. Additional material has been collected from the type locality, and further study will deepen understanding of this genus. *Cricetodon* itself, which is known from the Miocene of Europe and western Asia, seems not to appear in eastern Asia. Records of ''*Cricetodon*'' from Suosuoquan, Dingjiaergou, and a similar genus from Sihong are misidentified (vide infra).

GOBICRICETODONTINAE: Gobicricetodontine rodents are relatively large-size cricetids with mesodont and bunolophodont cheek teeth, and include two genera, *Plesiodipus* and *Gobicricetodon*. *Plesiodipus* is known from several middle and early late Miocene localities of North China (Lierpu in Xining Basin, Quantougou, Tunggur, and Amuwusu). It was thought to include ancestry of siphneines, which flourished later in northeastern Asia (Qiu et al., 1981). Qiu (1996a) described two species of *Gobicricetodon* from Tunggur. Previously reported *Cricetodon* sp. from Suosuoquan, Halamagai, Dingjiaergou,

and Amuwusu should be referred to this genus.

CRICETINAE: Cricetines rapidly replaced the archaic cricetids and diversified since the late Miocene. Including Wushan in the late Pliocene, 11 genera of this group, *Sinocricetus*, *Nannocricetus*, *Kowalskia*, *Neocricetodon*, *Bahomys*, *Cricetulus*, *Cricetinus*, *Allocricetus*, *Phodopus*, *Chuanocricetus*, and *Amblycricetus*, have been recognized in the late Neogene. *Sinocricetus* and *Nannocricetus* from Shala in North China and *Kowalskia* from Shihuiba in South China represent the first appearance of this subfamily (Baodean age). They are quite common in the late Miocene and early Pliocene faunas (Ertemte, Yushe, Bilike, Wenwanggou, etc.). *Neocricetodon* is known only from the late Miocene of Yushe (Schaub, 1934; Flynn et al., 1997). *Bahomys*, a form of cricetid with rather complex occlusal structure, was first described from the Pleistocene of Lantian (Chow and Li, 1965), and recently reported from the Pliocene of Wenwanggou (Zheng and Zhang, 2000). The six other genera occur in the Yushean Pliocene (Yushe Basin, Wenwnggou, and Wushan). Differential diagnosis of these taxa is not so clear, and definition and reallocation of late Neogene cricetines remains undone. In addition, three damaged teeth from Shala have been referred to *Microtocricetus*, but this taxon awaits more material for confirmation.

GERBILLINAE: *Pseudomeriones* is the single published representative of this group, and occurs frequently in the late Miocene and Pliocene of North China (Qingyang, Yushe, Ertemte, Wenwanggou, Bilike, and Ningxian). Two species of the genus, at different stages of evolution, have been recognized (Teilhard, 1926; Zhang, 1999).

MICROTOSCOPTINAE: Microtoscoptine rodents have a Holarctic distribution. *Microtoscoptes*, first named by Schaub in 1934, represents this subfamily in China. Fahlbusch (1987) described the additional material from Ertemte and Harr Obo in detail. More recently remains of this animal have been reported from Shala that may represent the earliest record of the genus (Qiu and Wang, 1999).

BARANOMYINAE: Two taxa can be referred to Baranomyinae. These include *Microtodon atavus* and *Anatolomys teilhardi* from Ertemte, Harr Obo, and Bilike of central Inner Mongolia. They are very common in the Ertemte and Harr Obo faunas, but rare in Bilike. Baranomyine rodents seem to be replaced by the arvicolines that arise abruptly during the early Pliocene in this region, and persist into the Pleistocene only in eastern Europe.

SIPHNEINAE: Siphneines are a group of rodents derived probably from a *Pleisodipus*-like ancestor and endemic to central and northeastern Asia. They made their first occurrence in the very early late Miocene (Amuwusu) and had a rapid Pliocene radiation in the great land mass. They are commonly known in the late Neogene faunas of North China (see table 22.1) and are potentially very useful in biochronological correlations. On the basis of the presence or absence of molar roots, Teilhard and Young (1931) assigned these animals to two genera—the rooted *Prosiphneus* and rootless *Siphneus* (= *Myospalax*). Zheng (1994, 1997), however, based on patterns of their occipital shield and corresponding skull features, grouped them into three subfamilies, the convex-skulled Prosiphneinae, the flat-skulled Myospalacinae, and the concave-skulled Mesosiphneinae, comprising together 10 genera. Zheng's proposal may be reasonable, but incomplete knowledge of skulls and great molar similarity in various species make it difficult to allocate the isolated teeth that usually occur in deposits. In addition, evolutionary relationships of the diverse extant *Myospalax* species with various siphneines remain to be solved. According to Zheng's definition, the Neogene siphneine genera are *Myotalpavus*, *Prosiphneus*, *Chardina*, *Mesosiphneus*, *Pliosiphneus*, *Episiphneus*, and *Youngia*. The first two appeared in the late Miocene, whereas the others are Pliocene.

ARVICOLINAE: High-crowned rodents evidently increased in abundance in northeastern Asia since the late Miocene. Like the microtoscoptines, baranomyines, and siphneines in the late Miocene, arvicolines show a Pliocene radiation. *Aratomys*, *Mimomys*, *Germanomys*, *Hyperacrius*, *Villanyia*, *Microtus*, *Clethrionomys*, and *Eothenomys* are the genera of this group found in the Pliocene of China. The oldest certain arvicoline

TABLE 22.1
Faunal List for the Major Reference Faunas

SUOSUOQUAN FAUNA (9 taxa)
Prodistylomys xinjiangensis
Aralomys sp.
Palaeosciurus sp. nov.
Atlantoxerus sp. nov.
Parasminthus cf. *P. asiaecentralis*
Litodonomys spp. 1, 2
cf. *Litodonomys* sp.
Gobicricetodon sp. nov.

XIEJIA FAUNA (7 taxa)
Yindirtemys suni
Tachyoryctoides kokonorensis
Atlantoxerus sp.
Parasminthus xiningensis
P. huangshuiensis
P. lajeensis
Eucricetodon youngi

SIHONG FAUNA (17 taxa)
Sayimys sp.
Diatomys cf. *D. shantungensis*
Ansomys orientalis
Eutamias sihongensis
Plesiosciurus sinensis
Sciurinae gen et sp. indet.
Parapetaurista tenurugosa
Shuanggouia lui
Youngofiber sinensis
Microdyromys orientalis
Neocometes sp.
cf. *Gobicricetodon* sp.
Megacricetodon sp.
Democricetodon sp.
Primus sp.
Cricetidae gen. et sp. indet.
Rhizomyidae gen. et sp. indet.

TUNGGUR FAUNA (24 taxa)
Ansomys? sp.
Eutamias aff. *E. ertemtensis*
Sinotamias primitivus
Atlantoxerus orientalis
Anchitheriomys tungurensis
Steneofiber tungurensis
Hystricops? sp.
Leptodontomys lii
Leptodontomys aff. *L. gansus*
Keramidomys fahlbuschi
Microdyromys wuae
Microdyromys sp.
Heterosminthus orientalis
Protalactaga grabaui
P. major
Gobicricetodon flynni
G. robustus
Gobicricetodon sp.
Plesiodipus leei

TUNGGUR FAUNA (*contd.*)
P. progressus
Megacricetodon sinensis
M. pusillus
Democricetodon lindsayi
D. tongi

AMUWUSU FAUNA (19 taxa)
Ansomys? sp. nov.
Meniscomyinae indet.
Eutamias sp.
Tamiasciurus sp.
Sciurus sp.
cf. *Miopetaurista* sp.
Steneofiber sp.
Castor sp.
Keramidomys cf. *K. fahlbuschi*
Microdyromys cf. *M. wuae*
Heterosminthus orientalis
Protalactaga cf. *P. grabaui*
P. cf. *P. major*
cf. *Dipus* sp.
Gobicricetodon sp.
Plesiodipus sp.
Democricetodon sp.
Cricetidae indet.
Prosiphneus sp. nov.

SHIHUIBA FAUNA (19 taxa)
Tamiops sp.
Sciurotamias sp.
Callosciurus sp.
Dremomys sp.
cf. *Albanensia* sp.
Hylopetes sp.
Castoridae gen. et sp. indet.
Leptodontomys sp.
Eomyidae gen. et sp. indet.
Platacanthomys dianensis
Typhlomys primitivus
T. hipparionum
Kowalskia hanae
Brachyrhizomys nagrii
B. cf. *B. pilgrimi*
B. tetracharax
Progonomys yunnanensis
Yunomys wui
Hystrix sp.

YUSHE FAUNA
MAHUI ASSEMBLAGE (15 taxa)
Eutamias ertemtensis
Tamiasciurus sp.
? *Petinomys* sp.
Pliopetaurista rugosa
Dipoides anatolicus
Castor anderssoni
Sicista sp.
Lophocricetus sp.

YUSHE FAUNA (*contd.*)
MAHUI ASSEMBLAGE (*contd.*)
Neocricetodon grangeri
Pseudomeriones abbreviatus
Prosiphneus murinus
Apodemus orientalis
Karnimata hipparionum
Huaxiamys primitivus
Hystrix sp.

GAOZHUANG ASSEMBLAGE (26 taxa)
Eutamias cf. *E. ertemtensis*
Tamiasciurus sp.
Pliopetaurista rugosa
Dipoides majori
Castor anderssoni
Myomimus sp.
Sminthoides fraudator
Neocricetodon grangeri
Cricetinus n. sp.
Allocricetus n. sp.
Pseudomeriones abbreviatus
Prosiphneus murinus
Chardina truncatus
Mesosiphneus praetingi
Germanomys sp.
Mimomys sp.
Rhizomys shansius
Apodemus qiui
Karnimata hipparionum
Micromys chalceus
M. tedfordi
Huaxiamys primitivus
H. downsi
Charidinomys yusheensis
Charidinomys sp.
Hystrix sp.

MAZEGOU ASSEMBLAGE (19 taxa)
Tamiasciurus sp.
Sciurus sp.
Pliopetaurista rugosa
Dipoides majori
Castor anderssoni
Eucastor youngi
Sminthoides fraudator
Cricetinus n. sp.
cf. *Allocricetus bursae*
cf. *A. ehiki*
Cricetulus sp.
Mesosiphneus praetingi
Germanomys sp.
Mimomys irtyshensis
Rhizomys shansius
Apodemus zhangwagouensis
Micromys tedfordi
Charidinomys louisi
Hystrix sp.

TABLE 22.1
(Continued)

HAIYAN FAUNA (13 taxa)
Marmota robusta
Trogontherium cuvieri
Sminthoides sp.
Phodopus sp.
Cricetulus barabensis
Youngia tingi
cf. *Micromys minutus*
cf. *M. praeminutus*
Chardinomys nihowanicus
Borsodia chinensis
Mimomys orientalis
M. (*Cromeromys*) *gansunicus*
Hystrix sp.

ERTEMTE FAUNA (32 taxa)
Pseudaplodon asiaticus
Eutamias ertemtensis
Sciurus sp.
Sinotamias gravis
Prospermophilus orientalis
Pliopetaurista rugosa
Petinomys auctor
Castor anderssoni
Dipoides majori
Leptodontomys gansus
Myomimus sinensis
Eozapus similis
Sicista sp.
Lophocricetus grabaui
L. pusillus
Paralactaga anderssoni
Brachyscirtetes wimani
Sminthoides fraudator
Sinocricetus zdanskyi
Nannocricetus mongolicus
Kowalskia neimengensis
K. similis
Pseudomeriones abbreviatus
Microtoscoptes praetermissus
Microtodon atavus
Anatolomys teilhardi
Prosiphneus eriksoni
Apodemus orientalis
Orientalomys cf. *O. similis*
Karnimata hipparionum
Occitanomys pusillus
Micromys chalceus

WENWANGGOU FAUNAS
(46 taxa, ca. 7 to 2 Ma)
Eutamias sp.
Sinotamias sp.
Atlantoxerus sp. 1
Atlantoxerus sp. 2
Gliridae gen. et sp. indet.
Protozapus sp.
Paralactaga sp.
Sminthoides sp.
Nannocricetus mongolicus

WENWANGGOU FAUNAS (*contd.*)
Bahomys sp.
Kowalskia sp.1
Kowalskia sp. 2
Allocricetus bursae
A. ehiki
Cricetinus mesolophidus
? *Cricetulus* sp.
Pseudomeriones abbreviatus
P. complicidens
Prosiphneus sp.
Chardina sinensis
C. truncatus
Mesosiphenus praetingi
M. intermedius
Yangia n. sp.
Y. omegodon
Y. trassaerti
Pliosiphneus n. sp. 1
Pliosiphneus n. sp. 2
Eospalax n. sp.
Allosiphneus teihardi
Microtus (*Allophaiomys*) *terrae-rubrae*
Mimomys (*Borsodia*) n. sp.
M. (*Cromeromys*) *gansunicus*
Apodemus n. sp.
Karnimata hipparionum
? *Occitanomys* n. sp.
Micromys tedfordi
M. cf. *M. chalceus*
Micromys n. sp.
Micromys sp.
Huaxiamys downsi
H. primitivus
Huaxiamys n. sp.
Chardinomys yusheensis
C. louisi
Allorattus engesseri

BILIKE FAUNA (30 taxa)
Eutamias ertemtensis
Tamiasciurus sp.
Prospermophilus orientalis
Atlantoxerus sp.
Castor cf. *C. anderssoni*
Myomimus sinensis
Sicista wangi
Sicista sp.
Sinozapus volkeri
Lophocricetus grabaui
L. pusillus
Paralactaga suni
Brachyscirtetes cf. *B. robustus*
Sminthoides fraudator
Sinocricetus progressus
Nannocricetus mongolicus
Kowalskia zhengi
Kowalskia cf. *K. similis*
Pseudomeriones abbreviatus

BILIKE FAUNA (*contd.*)
Microtodon cf. *M. atavus*
Anatolomys cf. *A. teilhardi*
Prosiphneus cf. *P. eriksoni*
Aratomys bilikeensis
Apodemus lii
Apodemus sp.
Orientalomys sinensis
Micromys kozaniensis
Chardinomys bilikeensis
Huaxiamys sp.
Allorattus engesseri

DAODI FAUNA (14 taxa)
Eucastor sp.
Paralactaga sp.
Sminthoides sp.
cf. *Nannocricetus* sp.
Cricetidae gen. et sp. indet.
Prosiphneus sp.
Mimomys orientalis
Germanomys sp.
Apodemus cf. *A. atavus*
Karnimata sp.
Chardinomys nihewanicus
Micromys aff. *M. tedfordi*
Huaxiamys cf. *H. downsi*
Saidomys sp.

WUSHAN FAUNA (30 taxa)
Sciurotamias teilhardi
Tamiops swinhoei
Petinomys sp.
Belomys parapearsoni
Pteromys spp.
Typhlomys intermedius
T. macrurus
Chuanocricetus lii
Amblycricetus sichuanensis
Cricetinae gen. et sp. indet.
Mimomys peii
Clethrionomys sebaldi
Eothenomys melanogaster
Rhizomys brachyrhizomyoides
Mus sp.
Apodemus chevrieri
A. cf. *A. peninsulae*
A. dominans
Hapalomys eurycidens
H. angustidens
H. gracilis
Chiropodomys primitivus
Vernaya wushanica
Vernaya sp.
Leopoldamys edwardsioides
Niviventer preconfucianus
Wushanomys brachyodus
W. hypsodontus
Hystrix subcristata
H. magna

is *Aratomys* from the early Yushean, which dominates the Bilike fauna (Qiu and Storch, 2000). Zheng and Li (1986, 1990) reviewed the *Mimomys* of China. Since then, more material has been recovered from Yushe, Wenwanggou, and Daodi. *Germanomys* is reported from Yushe, Daodi, and Jingle. The later arvicolines include the poorly known *Hyperacrius*, *Villanyia*, and *Microtus* from Dachai, and *Clethrionomys* and *Eothenomys* from Wushan (Zheng and Li, 1990; Zheng, 1993).

RHIZOMYIDAE: Fossil rhizomyids in eastern Asia are not so diverse as in the Siwaliks of Pakistan and India. An indeterminate rhizomyid from Sihong (also Shanwang) represents the earliest record of the family in China. Only subfamily Rhizomyinae is certainly recognized in the Neogene deposits. They are primitive species of *Rhizomys* (*Brachyrhizomys*) from Lufeng and Yuanmou, and more advanced *Rhizomys* (*Brachyrhizomys*) *shansius* from Yushe. Flynn (1993) added a species of *Rhizomys* to the Miocene fauna of Yushe. Flynn and Qi (1982) and Qi (1986) described three species of *Brachyrhizomys* from Lufeng, which occur together at about 8 Ma in Pakistan. A species reported previously as *Brachyrhizomys hehoensis* from Bulong, Tibet, is considered congeneric with *Pararhizomys* (Jacobs et al., 1985). *Pararhizomys* from Fugu, Shanxi, is poorly known and, if truly a rhizomyid, represents the northernmost distribution of this family in China. *Rhizomys* occurs also in the late Pliocene fauna of Wushan (Zheng, 1993).

MURIDAE: Murid rodents appeared in China much later than in the Indian subcontinent. *Progonomys* and *Yunomys* associated with hominoids and *Brachyrhizomys* from Shihuiba, Lufeng, are considered the oldest murids so far known in China (Qiu and Storch, 1990), but an undescribed *Progonomys* from Lantian, Shaanxi, may represent a murid appearing earlier than those of Lufeng (Zhaoqun Zhang, personal commun.). The murid group has really flourished since the latest Miocene. At least 19 genera of this group have been recognized, with the Lufeng, Ertemte, Harr Obo, Bilike, Yushe, Wenwanggou, Daodi, and Wushan faunas being the most productive. *Apodemus*, *Orientalomys*, *Karnimata*, *Occitanomys*, and *Micromys* occur in Ertemte and Harr Obo. In addition to these elements, *Chardinomys* and *Huaxiamys* are often found in the Pliocene, as at Yushe, Bilike, Wenwanggou, and Daodi (Jacobs and Li, 1982; Wu and Flynn, 1992; Cai and Qiu, 1993; Flynn et al., 1997; Qiu and Storch, 2000; Zheng and Zhang, 2000). *Huaxiamys*, *Chardinomys*, and *Allorattus* were apparently restricted in geographical distribution to the Pliocene of North China. Storch (1987) reported *Rhagapodemus* from Harr Obo. *Saidomys* is known from the late Pliocene of Afghanistan and occurs in the equivalent age fauna of Daodi. Further, Zheng (1993) determined *Mus*, *Hapalomys*, *Chiropodomys*, *Vernaya*, *Leopoldamys*, *Niviventer*, and *Wushanomys* from Wushan, which represent the earliest occurrence of these genera.

HYSTRICIDAE: Porcupines are quite common in the Pleistocene faunas of South China. Neogene hystricids are represented by a single genus, *Hystrix*, with limited specimens. An indeterminate species from Shihuiba is the oldest record of the genus so far known (Qiu et al., 1985). Porcupines extended northward to Yushe in distribution during the Pliocene (Flynn et al., 1997). Zheng (1993) reported *H. subcristata* and *H. magna* from Wushan, which herald the common porcupines of the Pleistocene.

ZOOGEOGRAPHIC REGIONS OF CHINESE NEOGENE RODENTS

Distributions of extant land vertebrates demonstrate clearly two different zoogeographic provinces in China. A line roughly from the Qin Ling Mt. to the Huaihe River separates the northern Palearctic Realm from the southern Oriental Realm. Distribution and changes of the fossil rodents indicate that similar regions existed during the Neogene. The numerous localities, especially in North China, record high faunal diversity and long-term stabilities of faunas through Neogene time.

In the northern region, the history of rodents is characterized by extinction of archaic elements and the establishment of the Muridae and other semiarid or arid-adapted muroids, Dipodidae, Zapodidae, and Cricetidae, as major elements in the faunas. Early Mio-

cene faunas are dominated by groups that originated in the Oligocene or earlier, Ctenodactylidae, Tachyoryctoididae, Tsaganomyidae, Sciuridae, Paracricedontinae, and Zapodidae. New elements of the fauna are Cricetodontinae, Gliridae, and Eomyidae. By the middle Miocene in this region rodents enter a new stage: archaic groups, except for Zapodidae, decline greatly or become extinct, and living groups dominate Neogene faunas since then. Cricetodontinae and Gobicricetodontinae replace Paracricetodontinae, advanced members of Zapodidae flourish, and Dipodidae first appear. By the late Miocene most archaic groups disappear. An initial diversification of Cricetinae ends the dominance of Cricetodontinae and Gobicricetodontinae of the middle Miocene. The northern area in this period was where the high-crowned cricetids (Microtoscoptinae, Baranomyinae, and Siphneinae) were highly diversified and radiated with the first appearance of Gerbillinae and Muridae. As in the middle Miocene, those groups established in the early and middle Miocene, such as Eomyidae, Gliridae, Dipodidae, and advanced genera of Zapodidae, continue as important elements in late Miocene faunas. The Pliocene faunas continued the diversity of the late Miocene with the appearance of arvicolines. Eomyidae, Microtoscoptinae, Baranomyinae, and Aplodontidae disappeared early in the Pliocene. Among the 12 groups surviving to the present day, Castoridae, Zapodidae, Dipodidae, Gliridae, Cricetinae, Gerbillinae, and Siphneinae are particular to, or mainly distributed over the Holarctic, Palearctic, or Nearctic regions and live today in the Chinese Palearctic region. Family Aplodontidae occurs in the western coastal areas of North America, families Rhizomyidae and Hystricidae (occurring only as far north as Shanxi during the Pliocene) are confined to the present tropical or subtropical areas of South China, and families Sciuridae and Muridae are widespread across the Old World. Apparently, the rodent faunas in the North are distinctly Holarctic in character and reflect a relatively arid temperate steppe or forest–grassland environment.

The southern Chinese record in general is not well documented, but the Shihuiba fauna of Lufeng well represents the late Miocene of the area. The fauna includes an extinct family (Eomyidae), two eurytopic families (Sciuridae and Muridae, although most of the Sciuridae live in tropical–subtropical zones), two Holarctic or Palearctic groups (Castoridae and Cricetinae), and three families (Platacanthomyidae, Rhizomyidae, and Hystricidae) confined to the present Oriental region or tropical–subtropical regions. Associated with the rodents are some small mammals endemic to the Oriental region (Tupaiidae, Echinosoricinae) or mainly distributed in tropic or subtropical areas (Pteropidae and Hipposideridae). Thus, the late Miocene Shihuiba fauna is quite different in composition from those faunas in the North, and reflects a tropical or subtropical mosaic forest environment. Geographical distribution and characters of faunas seem to suggest distinct zoogeographic differentiation of animals between South and North China during the late Miocene. Palearctic and Oriental regions similar to those of the present day are fairly clear in China at that time.

Inadequate collection in South China makes it difficult to reconstruct the evolutionary history of the Chinese Oriental Realm. However, composition of the early Miocene Sihong and Shanwang faunas in the East likely indicates that a predecessor of the Oriental Province developed before the late Miocene, as the later Shihuiba fauna confirms. The Sihong fauna contains nine groups of rodents, of which five become extinct or disappear in China (fig. 22.3). Among the four persistent groups, Castoridae and Gliridae are Holarctic or Palearctic, whereas Platacanthomyidae and Rhizomyidae are restricted to the Oriental Region. Apparently, the Sihong fauna shows both Holarctic and Oriental components. In addition to Diatomyidae, Rhizomyidae are known from Shanwang (Li Fenglin, personal commun.). Diatomyidae, Platacanthomyidae, Cricetodontinae, and Rhizomyidae are also recorded in Thailand (Mein and Ginsburg, 1997). Among nonrodent taxa, primates and Echinosoricinae, which generally live in tropical to subtropical forests, are present in both Sihong and Thailand. This implies that an initial zoogeographic province similar to the present Oriental region developed during the early Miocene in southeastern Asia from

southeastern China (northward up to Shandong peninsula) to Indo-China.

BIOGEOGRAPHIC RELATIONSHIPS WITH EUROPE AND NORTH AMERICA

Of the 25 groups of Chinese Neogene rodents shown in figure 22.3, 8 have close relationships neither to Europe nor to North America. They are mainly endemic to northeastern Asia. Of the others, 16 show affinity with Europe and 10 with North America. Among the 126 recognized genera, 44 (35% of the total) are congeneric with European representatives and only 12 (nearly 10%) are shared with North American faunas. Apparently, the Chinese Neogene rodent faunas display stronger affinities with those of Europe than with North America.

Rodent taxa shared among the Eurasian and North American continents seem to indicate that interchange in the Holarctic region had taken place via the Bering Landbridge during the Neogene. However, high endemism of early Miocene faunas implies that migration happened mainly after the early middle Miocene. The groups that were active in this event are Aplodontidae, Sciuridae, Castoridae, and Eomyidae. Families and subfamilies showing affinities with North America are also found in Europe, except for Mylagaulidae (fig. 22.3). The greater similarities of the Chinese Neogene rodent faunas to those of Europe than North America might have resulted from the filtering action of the Bering Landbridge. It is clear that those elements distributed in tropical to subtropical areas, like Platacanthomyidae and Rhizomyidae in the Oriental region and Erethizontidae in southern North America, were unable to withstand the rigors of the bridge. North American groups such as the Florentiamyidae or even the successful Geomyidae and Heteromyidae, and the later Sigmodontinae obviously were filtered out by the Bering Landbridge.

The number of genera shared with Europe or North America varied at different times. Those shared with European faunas are 8 in the early Miocene, 8 in the middle Miocene, 24 in the late Miocene, and 25 in the Pliocene; with North America these figures are 3, 5, 7, and 4, respectively. This may reveal that the interchange of rodents between Asia and Europe increased after the middle Miocene. In contrast, dispersal of rodents between Asia and North America reached its peak during the late Miocene, and then declined. Low levels continued into the Pleistocene and possibly reflected frequent interruption of land connection between the two continents and shifts of global climate.

In spite of the close relationships to Europe, the Chinese Neogene rodent faunas differ significantly. Even since the middle Miocene, European faunas contain few elements restricted presently to eastern Asia: few high-crowned cricetids (temperate forest–grass lands) and no dipodids adapted to arid steppe. Some European families, such as Trilophomyinae, Calomyscinae, Spalacinae, and Anomalomyinae never reached China. This probably indicates that the interchange of rodents in the Neogene between Asia and Europe took place mainly among Palearctic groups. Differentiation of faunal composition might possibly result from different environmental preferences for these rodents, and different ecotypes or biotic subprovinces within the pre-Palearctic region as exist today. Europe must have been more forested and damper than the Palearctic Chinese regions during the Neogene.

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