Chapter 16 Dynamic Small Mammal Assemblages of Yushe Basin

Lawrence J. Flynn and Wen-Yu Wu

Abstract Targeted prospecting and screening for microfossils has revealed rich small mammal assemblages at many stratigraphic levels from late Miocene through Pliocene to early Pleistocene formations of the Yushe Basin. The recovered rodents, lagomorphs, bats, and insectivorans include species of small body size not previously known from Yushe. These assemblages represent North China small mammal communities from about 6.5 to 2 Ma and may be used to characterize four land mammal stage/ages: Baodean, Gaozhuangian, Mazegouan, and Nihewanian. The fossil succession establishes diversity and stability in Pliocene small mammal faunas for Yushe Basin before significant turnover at the beginning of the Pleistocene. The Yushe Basin habitat was relatively moist, probably without strong annual temperature extremes, supporting high species diversity.

Keywords Yushe Basin • North China • Neogene • Rodentia • Lagomorpha • Chiroptera • Lipotyphla

16.1 Introduction

The influential monograph of Teilhard de Chardin (1942) on the fossil rodents of Yushe Basin focused light on the Pliocene small mammals of northeastern Asia for the first time. Through much of the 20th century, the Pliocene Epoch was perceived to have begun about 10 to 12 million years ago largely because terrestrial Hipparion faunas (Pontian stage equivalent) were thought to correlate to the early Pliocene (Berggren and van Couvering 1974); many Hipparion faunas are now known to be late Miocene in age. The title of the monograph by Teilhard New rodents of the Pliocene and lower Pleistocene of North China was appropriate. We now perceive the Pliocene as a relatively short period of time, about 5.3 to 2.6 Ma on the time scale of Gradstein et al. (2004). Strata of the Yushe Basin span much of Late Neogene time, from about 7 Ma in the oldest part of the Zhuozhanghe valley to the ~ 2.2 Ma fluvio-lacustrine sediments at the top, with overlying loess of younger ages. There are therefore, in addition to a long Pliocene sequence, late Miocene (Baodean Stage/Age and MN 13 zone equivalent) and Pleistocene assemblages in the basin. Teilhard de Chardin's (1942) monograph title is still descriptive because we find the Pliocene microfaunas, especially in the interval of about 4.8 to 3.0 Ma, to be highly fossiliferous, with two dozen small mammal species recorded as contemporaries in successive assemblages. Yushe Basin remains one of the best areas in China to study a relatively complete and fossiliferous sequence representing successive Pliocene faunas.

The richness of Yushe Basin assemblages indicates that Pliocene habitats there supported diverse mammal communities, which implies availability of moisture throughout the year and moderate annual temperature ranges. Yushe Basin is situated at the eastern edge of the Loess Plateau, but likely had equable climatic conditions throughout the year, not the extremes one expects for the continental interior. In addition to Rodentia, the orders Lagomorpha and Eulipotyphla (specifically the less inclusive Lipotyphla) show high Pliocene diversity in Yushe Basin. Pliocene Lagomorpha, for

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example, include up to four contemporary genera. Chiroptera (bats) are also recorded, but their diversity is greatly underrepresented compared to modern diversity. Taphonomic bias works against bat preservation, and insofar as each Yushe fossil specimen may represent a different species, likely there were many more bats in the community to be found. Other microfossils, especially fish, snakes, lizards, turtles, and some invertebrates were also recovered from 80 localities as surface finds or by organized screening (see Appendix).

In the following we summarize lipotyphlan, lagomorph and rodent biostratigraphy, noting occurrences of taxa and paleoenvironmental indicators for Yushe Basin. We then specify the succession of faunal associations to help to characterize North China land mammal stage/ages that are represented in Yushe Basin. This also provides an opportunity to review the timing of faunal turnover in the area. Finally, we attempt to analyze biogeographic patterns of taxon distributions to determine timing and direction of dispersal events.

16.2 Biostratigraphic Ranges 16.2.1 Hedgehogs, Moles, Shrews

The core group of the insectivorans is the monophyletic Lipotyphla. Few Yushe Basin fossils represent hedgehogs (Erinaceidae), but we find *Erinaceus* in the late Pliocene Mazegou Formation and in overlying Pleistocene deposits. This hedgehog is the extinct species *Erinaceus olgae*, known previously from Zhoukoudian 1 and 2. The material, although limited, may indicate size increase and survival of the species through the Pliocene-Pleistocene faunal turnover.

There are several moles (Talpidae) preserved in Late Neogene deposits of Yushe Basin. Yushe Basin records the oldest dated *Scaptochirus*, identified by its distinctive humerus and lower molar. A new species of *Yanshuella* is represented by mandibular material in the late Miocene of Yushe Basin; a younger (~ 3 Ma) humerus is also referred and to this species. The South China mole *Yunoscaptor* sp. occurs as dental material from early Pliocene localities of Yushe Basin, and a number of humeri represent the genus in the late Miocene. Also found in the early Pliocene is the water mole *Desmana*, an indicator of streams and ponds, therefore reinforcing a reconstruction of moist habitat in this part of Shanxi Province.

Shrew diversity suggests moist, equable climatic conditions. The Pliocene of Yushe Basin includes a neomyine shrew (*Soriculus praecursus*) and the larger beremendiines *Beremendia pohaiensis* and *Lunanosorex lii*, which occur elsewhere in North China. *Sorex* appears in the early Pleistocene of Yushe Basin, and *Crocidura* is found in younger loess. The presence of two other shrews is also indicated among the scant remains of the group in late Miocene deposits.

16.2.2 Pikas, Rabbits, Hares

The fossil pika *Ochotona lagreli*, widespread throughout North China, is well represented in the late Miocene and early Pliocene of Yushe Basin. More than one species of pika is represented, including small body size *Ochotona*, perhaps *O. nihewanica*, but the fragmentary nature of the fossils prevents diagnostic recognition at the species level. *Ochotonoides complicidens*, well known in the Pleistocene of North China, is found in loess deposits of Yushe Basin. We describe (Chap. 4) a good sample of a new, older species *Ochotonoides teilhardi* from the late Pliocene of Yushe. It first appears at about 3.3 Ma, and continues into the earliest Pleistocene.

The large rabbit Alilepus annectens is recorded in the late Miocene of Yushe Basin, mostly within the Mahui Formation, but ranging into the base of the overlying Gaozhuang Formation. A smaller species of the genus (A. parvus) is named herein based on a late Miocene skull from the Mahui Formation. A new long-jaw rabbit, Hypolagus mazegouensis, is found in the late Pliocene of Yushe Basin; it is preceded by a much smaller Hypolagus in the early Pliocene. We see two species of the leporid genus Trischizolagus in the early Pliocene of Yushe Basin; one is Trischizolagus mirificus, otherwise known from the early Pliocene of Inner Mongolia. Another new rabbit species from the late Pliocene or, possibly, early Pleistocene deposits of Yushe Basin is assigned to Sericolagus. Further leporid diversity is suggested by Yushe specimens, including a latest Miocene fossil that presents Nekrolagus-like morphology. The early Pleistocene loess adds the extant hare Lepus to the fossil record.

16.2.3 Rodents

The field campaigns of the Sino-American teams of 1987– 1991 specifically targeted small rodents. We knew that the Yushe Basin sequence should include multiple fossiliferous horizons, and we were successful in identifying superposed microfaunas, many of which could be related directly to paleomagnetic sections, and therefore assigned interpolated dates. We applied the techniques of wet-screening to process bulk samples of sediments from Yushe Basin localities, and found the small body size microfauna to be richly represented, especially small rodents, many not previously known in Yushe Basin. The biostratigraphic ranges of all small mammals are shown in Fig. 16.1a, b.

As is generally the case in the Neogene of Asia, squirrels were diverse in Shanxi Province. The flying squirrels *Pliopetaurista* and *Hylopetes* and the chipmunk *Eutamias* characterized late Miocene and early Pliocene faunas. There is also a record of the rock squirrel *Sinotamias* in the early Pliocene and the tree squirrel *Sciurus* in the late Pliocene. *Hylopetes* persisted into the late Pliocene. Remains of the large *Marmota*, an immigrant from North America and collected as surface finds, occur in the early Pleistocene Haiyan Formation.

Yushe beavers, which are large rodents, have been known for nearly a century. Teilhard de Chardin (1942) thought there were perhaps four lineages in Yushe Basin, but one (Eucastor) was later to be determined an artefact of misidentification (Chap. 6). Two beaver lineages are encountered in the Miocene and Pliocene: Sinocastor and Dipoides. In our interpretation, Sinocastor is a subgenus of Castor, and is quite distinct from the castoroidine group represented by Dipoides. While Castor appears to have originated in the Palaearctic biogeographic region, with the oldest records occurring in Europe, Dipoides may be an immigrant to Eurasia from North America. Different species of Dipoides (and perhaps also Sinocastor) characterize Miocene and Pliocene assemblages. Such beavers are absent from the early Pleistocene of Yushe Basin; instead, the large castoroidine Trogontherium is encountered in the Haiyan Formation.

Zokors (Myospalacinae) also range to large size for rodents. They were diverse and well represented in Yushe Basin, and formed the basis for the analyses of Teilhard de Chardin (1942) and Zheng (1994, 1997; Zheng et al. 2004; Liu et al. 2013, 2014). Fossil zokors (Chap. 9) have considerable stratigraphic importance and their distribution through time corresponds very roughly to the tripartite division of the Yushe sequence into three zones postulated by Licent and Trassaert (1935) and adopted by Teilhard de Chardin (1942). The late Miocene Zone I is characterized by the relatively primitive *Prosiphneus murinus*, which occurs in the Mahui Formation and basal part of the Gaozhuang Formation. The Pliocene Nanzhuanggou

Member of the Gaozhuang Formation (Zone II) yields *Pliosiphneus* and the earliest mesosiphneine *Chardina*. *Pliosiphneus lyratus* ranges through the uppermost Gaozhuang Formation into the base of the Mazegou Formation (also Zone II). Otherwise, the Mazegou Formation is characterized by the more advanced *Mesosiphneus*. The early Pleistocene Haiyan Formation, and arguably the overlying Yushe red loam, designated Zone III by Licent and Trassaert (1935), yield the derived *Yangia* and *Eospalax*. The large *Y*. *tingi* and *E. fontanieri*, respectively concave and convex occiput species, show changes in dentition (clinomegodonty: lengthened molars and inclined reentrant folds) that likely correspond to early Pleistocene changing food sources requiring more processing, either tougher or less nutritious vegetation.

Like beavers and zokors, the large-body-size bamboo rats and porcupines occur as surface finds. They are represented by extinct species of the living genera *Rhizomys* and *Hystrix*, respectively. Bamboo rats are committed fossorial species, and indicate significant rainfall. A field study of extant *Rhizomys sinensis* documents 1100 mm of rain per year in its habitat (He 1984).

Dipodoids, a group of rodents expected to be found in Yushe Basin, heretofore have been completely unknown. The very small birch mouse *Sicista* suggests vegetation cover, and modern species are capable of hibernation with seasonal temperature change. Extinct lophocricetines are also present. Known only in the Yushe Basin from the late Miocene Mahui Formation, these small rodents may be under-represented in the fossil record, or Yushe Basin may be near the southern limit of the range of both *Sicista* and *Lophocricetus*. A few specimens of a larger dipodoid, a fossil species of the modern jerboa genus *Dipus*, occur sporadically in early Pliocene to early Pleistocene deposits. Among other rodents, a tiny dormouse found by screening is documented in the Pliocene of Yushe Basin, despite bias against retrieval of such small fossils.

Several groups of small muroids present in the microfauna are recovered by screening. Hamsters are an example and show moderate diversity. A hallmark of the Mahui and Gaozhuang formations is the conservative Neocricetodon grangeri, which is closely related to Late Neogene hamster species distributed throughout Eurasia. Upper levels of the Gaozhuang Formation and the Mazegou Formation (Zone II) produced species of Allocricetus and Cricetinus. Two of these are new, which is not unexpected given the limited fossil record of early Pliocene deposits elsewhere in northern Asia. Cricetulus appears in the Mazegou Formation and with Phodopus characterizes Yushe Zone III. Unlike hamsters, Yushe Basin gerbils show little diversity. Until the late Pleistocene appearance of modern gerbils, only Pseudomeriones is encountered (Zone I). The Yushe Basin record is important because it suggests that the genus shows chronoclinal increase in crown height, with late Miocene specimens



Fig. 16.1 Biostratigraphic ranges observed for small mammals of Yushe Basin. Plotted on the left side of Fig. 16.1a, b is the observed stratigraphy with composite thickness and magnetostratigraphy (after Opdyke et al. 2013), which yields estimated ages (Ma). Small mammal localities of Yushe Basin (YS numbers) are plotted by stratigraphic position. Species occurrences in Yuncu Subbasin are indicated by filled dots, vertical lines connecting single species. Tancun Subbasin species occurrences (open dots) supplement the biostratigraphic ranges (localities found in systematic accounts). These are plotted by Tancun subbasin magnetostratigraphy (see Tedford et al. 2013) and by stratigraphic reference to the C3An-C3r chron boundary and the Mahui Formation-Gaozhuang Formation contact



Fig. 16.1 (continued)

attributed to *P. latidens* and the type species *P. abbreviatus* restricted to the latest Miocene and Pliocene.

Derived muroids of Yushe Basin include two groups of Avicolinae. Representing the Tribe Arvicolini, an indeterminate species of Mimomys is encountered high in the Gaozhuang Formation at 4.3 Ma. Two species occur in the Mazegou Formation, Mimomys cf. M. youhenicus and M. gansunicus. The early Pleistocene Haiyan Formation produces the derived Villanyia fanchangensis and Borsodia chinensis. Microtus occurs in overlying loess. These records are important for the stratigraphy of Yushe Basin and of North China in general. The other arvicoline group, Prometheomyini, occurs in Yushe Basin mainly as two successive species, Germanomys yusheica in the Gaozhuang Formation and Germanomys progressiva in the Mazegou Formation, both new species. There is evidence of Stachomys also in Yushe Basin. Yushe Arvicolinae are absent from the Miocene Zone I. Zone II is characterized by Mimomys cf. M. youhenicus and appearance of M. gansunicus and by Germanomys. Zone III is distinguished by Villanvia and Borsodia and Mimomys gansunicus.

Muridae are the dominant family of rodents in the late Neogene of North China in both abundance and diversity. The murid cohort is largely stable, with congeneric species replacing earlier species. Some species are long-ranging, both Karnimatoides hipparionus and Chardinomys yusheensis spanning the Miocene-Pliocene boundary and at least 1.5 million years. Yushe Basin Zone I includes Karnimatoides, Apodemus orientalis, Huaxiamys primitivus, and Tedfordomys jinensis. Zone II is typified by Karnimatoides hipparionus, Apodemus qiui and A. zhangwagouensis, Huaxiamys downsi, Micromys tedfordi, and Chardinomys yusheensis, replaced by C. nihowanicus. Zone III and overlying loess continue with C. nihowanicus and advanced species of Apodemus and Micromys.

16.3 Faunal Units

The foregoing very briefly outlines the small mammal biostratigraphy observed in Yushe Basin, based largely through amassing samples from stratigraphically discrete screening localities. Details are given in previous chapters. These biostratigraphic observations form the basis for the conceptually distinct process of recognizing successive faunas based on small mammals, and using these to typify biochrons (see Tedford 1995), steps which lead ultimately to recognizing the stage/ages of Qiu et al. (2013). The latter authors greatly advanced the conceptual basis for Chinese Land Mammal Stage/Ages of the Neogene. Yushe Basin biostratigraphy contributes substantially to four of these, and the small mammal components are revised here.

In Yushe Basin, the late Miocene Baodean Land Mammal Stage/Age fauna is represented in the Mahui Formation, and we observe that Baodean assemblages continue into the lower part of the Gaozhuang Formation. Both the upper limit of this stage/age and the Miocene/Pliocene boundary occur near the top of the Taoyang Member of the Gaozhuang Formation. Baodean age small mammals observed in Yushe Basin are listed in Table 16.1. Characteristic Baodean elements of Yushe Basin are the talpid Yanshuella primaeva, the lagomorphs Ochotona lagreli and Alilepus (A. annectens and A. parvus), and the rodents Pliopetaurista rugosa, Tamias cf. T. ertemtensis, Dipoides anatolicus, Prosiphneus murinus, Neocricetodon grangeri, Pseudomeriones latidens, Karnimatoides hipparionus, Apodemus orientalis. Huaxiamys primitivus, Tedfordomys jinensis, Chardinomys vusheensis, and Brachyrhizomys shajius.

 Table 16.1
 Yushe Basin small mammals of the Baodean mammal stage/age

Lipotyphla
cf. Paenelimnoecus sp.
cf. Sulimskia sp.
Yanshuella primaeva
Lagomorpha
Ochotona lagreli
Alilepus annectens
Alilepus parvus
Rodentia
Pliopetaurista rugosa
Hylopetes yuncuensis
Tamias cf. T. ertemtensis
Lophocricetus sp.
Dipoides anatolicus
Sinocastor zdanskyi
Prosiphneus murinus
Neocricetodon grangeri
Pseudomeriones latidens – P. abbreviatus
Karnimatoides hipparionus
Apodemus orientalis
Huaxiamys primitivus
Micromys sp.
Tedfordomys jinensis
Chardinomys yusheensis
Brachyrhizomys shajius

Pliocene faunas of Yushe Basin embrace two successive stage/ages (Qiu et al. 2013). Characteristic mammalian players in each are similar; a number of genera are shared, but with species substitutions. The similarity of the successive assemblages suggests an enduring Yushe Basin Pliocene chronofauna. Webb (1984) applied the concept of the "chronofauna" to Miocene large mammal assemblages of North America. A chronofauna represents a community that persists without change in structure for a time interval usually greater than one m.y. Its characteristic assemblage remains largely constant, although species substitutions through time may be observed. This is the case for the Pliocene small mammal faunas of Yushe Basin, which show different species in the early and late Pliocene, but mostly the same or closely related genera.

The small mammals observed in Yushe Basin for the Gaozhuangian and Mazegouan stage/ages are listed together in Table 16.2 for comparison. In addition to species shared with the younger Mazegouan assemblage, characterizing early Pliocene Gaozhuangian components are Yunoscaptor sp., Soriculus praecursus, Ochotona lagreli, Trischizolagus spp., Pliosiphneus antiquus, Chardina truncatus, Neocricetodon grangeri, Allocricetus primitivus, Germanomys yusheica, Mimomys sp., Karnimatoides hipparionus, Apodemus qiui, Huaxiamys downsi. Chardinomys vusheensis.

Characteristic late Pliocene Mazegouan species include Erinaceus olgae, Beremendia pohaiensis, Lunanosorex lii, Ochotonoides teilhardi, Hypolagus mazegouensis, Sericolagus yushecus, Mesosiphneus praetingi (followed by M. intermedius), Allocricetus cf. A. ehiki, Cricetulus sp., Germanomys progressiva, cf. Stachomys sp., Mimomys cf. M. youhenicus, Mimomys gansunicus, Apodemus zhangwagouensis, Chardinomys nihowanicus.

The early Pleistocene Haiyan Formation contains assemblages that represent the early Nihewanian Stage/Age (Table 16.3). This assemblage differs considerably from the preceding faunas, and its diversity is much less, corresponding to change in climate and, presumably, different nutritional resources. Distinctive species are *Sorex* sp., *Marmota* sp., *Trogontherium cuvieri*, *Hystrix refossa*, *Yangia trassaerti*, *Yangia tingi*, *Cricetulus barabensis*, *Phodopus* sp, *Mimomys gansunicus*, *Villanyia fanchangensis*, *Borsodia chinensis*, *Chardinomys nihowanicus*.

The later Pleistocene of Yushe Basin is represented by loess deposits. The limited lateral extent of the loess, which is partly removed by erosion, and the restricted paleohabitat of loess deposits explain why we have relatively few species of that age. Recovered fossils reveal continued elements
 Table 16.2
 Yushe Basin Pliocene small mammals of the Gaozhuangian and Mazegouan stage/ages

Gaozhuangian land mammal stage/age	Mazegouan land mammal stage/age			
Lipotyphla				
Yunoscaptor sp.	Erinaceus olgae			
Scaptochirus sp.	Scaptochirus sp.			
Desmana sp.	Beremendia pohaiensis			
Soriculus praecursus	Lunanosorex lii			
Lagomorpha				
Ochotona lagreli	Ochotona sp.			
Hypolagus sp.	Ochotonoides teilhardi			
Trischizolagus mirificus	Hypolagus mazegouensis			
cf. Trischizolagus dumitrescue	Sericolagus yushecus			
Rodentia				
Pliopetaurista rugosa	Pliopetaurista rugosa			
Hylopetes yuncuensis	Hylopetes yuncuensis			
Tamias cf. T. ertemtensis	Sciurus sp.			
Dipus fraudator	Dipus fraudator			
Dipoides majori	Dipoides majori			
Sinocastor anderssoni	Sinocastor anderssoni			
Brachyrhizomys shansius	Brachyrhizomys shansius			
Hystrix gansuensis	Hystrix gansuensis			
Myomimus sp.	(no Gliridae recorded)			
Pliosiphneus antiquus	Pliosiphneus lyratus (early only)			
Pliosiphneus lyratus	Mesosiphneus praetingi			
Chardina truncatus	M. intermedius/M. praetingi			
Neocricetodon grangeri	Allocricetus cf. A. ehiki			
Allocricetus primitivus	Cricetulus sp.			
Cricetinus mesolophidos	Cricetinus mesolophidos			
Germanomys yusheica	Germanomys progressiva			
Mimomys sp.	cf. Stachomys sp.			
Karnimatoides hipparionus	Mimomys cf. M. youhenicus			
Apodemus qiui	Mimomys gansunicus			
Huaxiamys downsi	Apodemus zhangwagouensis			
Micromys chalceus/M. tedfordi	Micromys tedfordi			
Chardinomys yushensis	Chardinomys nihowanicus			

(Erinaceus, Ochotonoides complicidens, Apodemus) and new appearances: the white-tooth shrew Crocidura, modern Lepus, Yangia epitingi, Eospalax fontanieri, Microtus cf. M. complicidens, and the modern gerbil Meriones.

16.4 Turnover, Biogeography, and Dispersal

We have proposed that the Yushe Pliocene faunas show stability in general, with continuity of associations at the genus level, and substitution of congeners at the species

Fable 16.3	Yushe Basin	small	mammals	of the	Nihewanian	mammal
stage/age						

Lipotyphla
Sorex sp.
Lagomorpha
Ochotona cf. O. nihewanica
Ochotonoides teilhardi
Leporidae, indet.
Rodentia
Marmota sp.
Trogontherium cuvieri
Hystrix refossa
Dipus fraudator
Yangia trassaerti
Yangia tingi
Cricetulus barabensis
Phodopus sp.
Mimomys gansunicus
Villanyia fanchangensis
Borsodia chinensis
Micromys cf. M. tedfordi
Micromys cf. M. minutus
Chardinomys nihowanicus

level (Flynn et al. 1991). This pattern is supported by the present analysis (Fig. 16.1a, b) and is consistent with the recognition of a Yushe Pliocene chronofauna, which includes assemblages representing two mammalian stage/ages: Gaozhuangian and Mazegouan. Faunal turnover events cluster at the beginning and, especially, the end of the chronofauna.

The Yushe Basin Pliocene faunal stability is rooted in the late Baodean land mammal stage/age assemblages. The limits of the Baodean biochron are not yet fully constrained, but magnetostratigraphy shows that Baode deposits of the Lantian area date back to 7.2 Ma (Zhu et al. 2008); the younger limit of the Baodean stage/age may be best approximated in Yushe Basin. We find that Baodean assemblages persist low in the Gaozhuang Formation and that the Baodean/Gaozhuangian age boundary is quite near the Miocene/Pliocene boundary, which occurs near the top of the Taoyang Member of the Gaozhuang Formation. Faunal correlation to the key reference locality, Ertemte, agrees that the age of Ertemte is late Baodean, and suggests an age for it between 6.0 and 5.5 Ma.

Magnetostratigraphy in Yushe Basin (Opdyke et al. 2013) dates the disconformity between the Gaozhuang and Mazegou formations, which is chosen as the division between corresponding land mammal stage/ages. The hiatus is perhaps a half million years long around 4 Ma. The Mazegou Formation is truncated above by a slight angular unconformity at about 2.9 Ma. In Yushe Basin the overlying Haiyan Formation is constrained by its reversed magnetozone,

which is considered chron C2r.2r, ca. 2.6–2.2 Ma (Opdyke et al. 2013). The Mazegou-Haiyan hiatus could be over a half million years in duration, and the faunal turnover at this time is profound. Possibly this stage/age boundary could be better temporally constrained in Nihewan Basin.

The geographic extent of the faunas that represent these biochrons is widespread (Tedford et al. 1991), spanning from North China to Kazakhstan, Kyrgyzstan, Tajikistan, and probably Afghanistan, and northward through Mongolia, into Siberia (see faunal lists of Erbajeva and Alexeeva 2013). Regarding historical biogeography, it appears that many of the small mammal species evolved within the Palaearctic biogeographic province, so that replacement of Baodean and Gaozhuangian taxa would have been by species derived largely from neighboring subprovinces. However, some mixing between North China and South China is evident and some long-distance dispersers may be identified.

Although Yushe Lipotyphla include widely distributed genera, the talpids and soricids are generally endemic to East Asia. The large shrew *Beremendia* and the water mole *Desmana* are known across Eurasia, and a possible late Miocene blarinine (*Sulimskia*) suggests immigration of that tribe from North America. Other insectivores are more local: the talpids *Scaptochirus*, *Yanshuella* and *Yunoscaptor*, and the shrews *Lunanosorex* and *Soriculus* are mainly endemic; some like *Soriculus* and *Yunoscaptor* suggest early Pliocene mixing of elements from South China. Pleistocene *Sorex* and *Crocidura* are, of course, widespread.

Fossil ochotonids were as diverse as they are today and, like today, may have had limited areas of distribution of species. *Ochotonoides teilhardi* appears to have originated in the biogeographic subprovince of North China. Earliest leporines of Yushe are *Alilepus* and (later) *Hypolagus*, both derived from immigrant stock from North America. Pliocene *Trischizolagus* is widespread across Eurasia, in contrast to *Sericolagus*, which appears to be endemic to northeast Asia. Pleistocene *Lepus* is an immigrant from North America, but *Ochotonoides complicidens* evolved endemically.

Like Lipotyphla and Lagomorpha, squirrels include both local widespread and elements. Tamias. Sciurus. Pliopetaurista, and Hylopetes are Eurasian (the first two Holarctic) and Sinotamias is Chinese; Marmota is a later immigrant from North America. Among dipodoids, Lophocricetus and Dipus are Asian, but the birch mouse Sicista is widespread across the Palaearctic, as is the glirid Myomimus. Beavers are distinctive in reflecting long-distance dispersal: Dipoides has its ancestry in North America, Trogontherium is pan-Eurasian in distribution, and the Castor group (locally Sinocastor) is Holarctic. Hystrix is also widespread in the late Miocene, but Brachyrhizomys, appearing by 6 Ma and thriving to about 3 Ma is one of the few rodents that likely expanded its range northward from South China.

The zokors (Myospalacinae), endemic to eastern Asia (China including Tibet, Mongolia, parts of Siberia and Kazakhstan) are a relatively young group derived from middle Miocene muroids. They diversified through the later Neogene, with species distributions of limited geographical extent in keeping with their restricted mobility, being fossorial specialists. They did not penetrate greatly into South China, but did invade Tibet (Li and Wang 2015).

Late Neogene hamsters of Yushe Basin show diversity at the generic level, with Pliocene lineages of *Neocricetodon*, *Allocricetus* and *Cricetinus*, and the addition of *Cricetulus* in the late Pliocene. Similar diversity is noted across Eurasia and makes species distinctions problematic. North China *Neocricetodon*, very close to species of *Kowalskia*, may be the senior synonym of the latter. Regardless of generic content, the hamsters are widely distributed, which indicates lack of dispersal barriers for them. Hamsters (*Kowalskia hanae* Qiu, 1995) spread to South China during the late Miocene (Ni and Qiu 2002). Like hamsters, the gerbil lineage *Pseudomeriones* occurs widely across Asia.

Arvicoline genera are also distributed throughout the Palaearctic. These rodents evolve rapidly, and quite possibly there is endemism at the species level in China. Our analysis of *Germanomys* raises the possibility that the Yushe lineage is distinct from that of Europe, which may call for a separate genus name. Chinese *Mimomys* species, too, may be distinct and until species level systematics are worked out across Eurasia, provincial names will prevail. Nonetheless, similar assemblages of *Mimomys, Villanyia*, and *Borsodia* are found from Europe to China.

Two late Miocene murines of Yushe Basin, Karnimatoides and Tedfordomys, are similar to older lineages of South Asia, specifically the Siwaliks of Pakistan. They are close to Karnimata and Progonomys, respectively. The biogeographic significance of this resemblance is still unclear, but Flynn and Wessels (2013) hypothesize that faunal connection of Yushe Basin and the Siwaliks was indirect - the two murine lineages dispersed westward from South Asia, spread around the Mediterranean region, and migrated eastward to China at temperate latitude. This scenario calls for wide dispersal but not a direct south-to-north connection. End-Miocene and Pliocene murines are a mix of endemic groups and widespread genera. Chardinomys, hallmark of Yushe Basin microfaunas, is endemic to China, as is Huaxiamys and Allorattus. If Niviventer is correctly identified in Yushe Basin, it would be an element shared with Southeast Asia. In contrast, the genera Apodemus and Micromys, like many other late Neogene rodents, show a great Palaearctic distribution.

The biogeographic signal presents Yushe Basin as part of a wide subprovince covering much of northern Asia to the Ural Mountains, throughout which the Baodean, Gaozhuangian, Mazegouan and Nihewanian stage/ages may be recognized (see Tedford et al. 1991). This subprovince is part of the Palaearctic biogeographic region. Throughout the later Neogene, new species appear to derive mainly from this or neighboring subprovinces within the Palaearctic region.

Notable biogeographic exceptions are late Miocene introductions of taxa: Leporidae, the beaver *Dipoides*, and a possible blarinine shrew disperse from North America. Also a bamboo rat (*Brachyrhizomys*), some insectivorans, and perhaps *Niviventer* expand to Yushe Basin from South China. Other murines appear in North China, not directly from the south, but via dispersion from the west. *Castor* (*Sinocastor*) and possibly *Hystrix* spread eastward into North China from Europe. Through the Pliocene, hamsters, arvicolines, mice, and some insectivorans show wide connections across the Palaearctic. Pleistocene assemblages introduce exotic elements, such as *Marmota* and *Lepus* ultimately from North America, and *Trogontherium* from Europe.

16.5 Closing

The Yushe Basin field campaigns of 1987–1991 succeeded in recovering diverse small mammals from all stratigraphic units of the Yuncu and Tancun subbasins. Chapter 1 of this volume outlines the techniques we used to retrieve small mammal teeth by wet screening fossiliferous sediment. Meticulous care in collecting resulted in samples from productive localities that reasonably well reflect communities of the last six million years in Shanxi Province. Research last century (e.g., Teilhard de Chardin 1942) was based on surface finds of fossils, which built good collections of beavers, zokors, and lagomorphs, and limited representation of other small mammal groups. This is the foundation for our opportunity to investigate 20 groups of small mammals.

Preliminary faunal analysis for Yushe Basin (Flynn et al. 1991) saw overall stability in the small mammal assemblages. It was apparent that the Pliocene faunas became enriched in species diversity, and that the Pleistocene ushered in considerable changes that greatly altered the mammalian community. Presently we see the Miocene-Pleistocene faunal change as less than that at the Pliocene-Pleistocene boundary. The assemblages from 6 to 3 Ma remained largely similar at the level of the genus, differences lying in species substitutions, and in addition of new elements inserted into the fauna (some from Europe or North America). The Yushe Basin presented favorable habitat to maintain an evolving community through most of the Pliocene. The fauna was mainly a variant of the North China biogeographic sub-province, but with a mix of a few South China elements.

We find diverse moles (Talpidae) and shrews (Soricidae), including good material of some taxa, a diversity that correlates with moist, mild conditions. One Pliocene genus, *Desmana*, is aquatic. Hedgehogs (*Erinaceus*) are in evidence since late in the Pliocene. Two families of bats are present, but Chiroptera are terribly under-represented. Ochotonid and leporid Lagomorpha are well represented by jaw and some cranial material. Two or three pikas (Ochotonidae) co-occur in the Pliocene of Yushe Basin, and at least three leporid genera co-occur in that epoch. Pleistocene loess yields *Ochotonoides, Ochotona*, and *Lepus*.

Squirrels are diverse, if under-represented, and there is good fossil material of the flying squirrel *Pliopetaurista*. This genus plus *Hylopetes* and the tree squirrel *Sciurus* imply some tree cover. So, too, the birchmouse *Sicista*, and possibly *Lophocricetus* indicate woodlands, but the jerboa *Dipus* indicates open terrain. The dormouse *Myomimus* is not arboreal but suggests thick vegetation, as does the chipmunk *Tamias* and the large body-size porcupine, *Hystrix*.

Bamboo rats prefer moist conditions and adequate vegetation to support fossorial life. A smaller species appears in the late Miocene and the larger *Brachyrhizomys shansius* typifies the Pliocene of Yushe. Two lineages of beavers coexist through the late Miocene and Pliocene. Both appear to be aquatic lineages. The larger body-size genus *Trogontherium* is the sole beaver of the Pleistocene. In contrast to these indicators of moist to aquatic conditions, the diverse zokors indicate nearby open terrain. They diversify endemically and species appear to have restricted distributions.

The extinct gerbil lineage *Pseudomeriones* accents the late Miocene fauna of Yuncu and Tancun subbasins. Fossils are clearly lower-crowned than *Pseudomeriones abbreviatus* and all but one worn specimen are older than 6 Ma. *P. abbreviatus* has been described from the Pliocene of Zhangcun subbasin. The *Pseudomeriones* lineage shows increasing hypsodonty, the earlier late Miocene fossils of Yushe Basin representing *P. latidens*. Latest Miocene *Pseudomeriones*, as at Ertemte, is the higher crowned *P. abbreviatus*. Being extinct, we do not know the environmental indications for *Pseudomeriones*, but modern gerbils indicate open conditions. The diverse hamsters (Cricetinae) also suggest open conditions, and occur in all Yushe formations.

Arvicolinae appear in the Pliocene, first the *Germanomys* lineage at 4.7 Ma, and then early *Mimomys* at 4.3 Ma. *Germanomys* disappears in the late Pliocene, but Arvicolini dominate Pleistocene microfaunas. Although we do not know the habitat preferences of *Germanomys*, and generally we reconstruct mild, moist conditions in the Pliocene of Yushe, we think of *Mimomys* and allied arvicolines as indicators of lower mean annual temperature. This is likely the climate by Pleistocene time, when we see considerable faunal turnover.

The Murinae are successful and dominant in the Pliocene of Yushe. Early genera would be consistent with warm conditions, if their close relatives are taxa of South Asian distribution, as is thought to be the case. Other terminal Miocene and Pliocene murine genera of Yushe Basin show wide Palaearctic distribution at more temperate latitudes. The hamsters, mice, and arvicolines also suggest wide dispersal with limited geographic barriers, and partly open habitat perhaps under cooling climatic conditions. Later species of these and other groups appear to be closely related to living species in the region.

Concerning small mammals in general, an ecological scenario emerges indicating well-watered, mild habitat with patchy woodlands and open terrain for the Miocene and Pliocene of Yushe Basin. In addition to several taxa that are likely aquatic or arboreal, some species suggest open, seasonally dry habitat. Yushe Basin provided an enclave of favorable habitat, likely without the extremes of more continental interior settings, and stability since the late Miocene supported a Pliocene Yushe chronofauna for the small mammals. Yushe Basin assemblages of eastern Shanxi Province may be seen as documenting the history of a late Neogene woodland fauna, contrasting with drier contemporary faunas of the interior, in affirmation of the late Miocene variation in faunal assemblages reconstructed by Kurtén (1952).

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