Character, Age and Ecology of the Hezheng Biota from Northwestern China

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Abstract   The Hezheng area of Gansu Province produces the most abundant mammal fossils in China as well as the whole Eurasia, and it also produces other Cenozoic fossils of different animals and plants. Therefore, all of them are named the Hezheng Biota. Mammals are very sensitive to environmental changes, and thus the evolution of mammalian faunas in the Hezheng area reflects the strong uplift of the Tibetan Plateau during the Late Cenozoic, which dramatically affects environmental changes. In the Hezheng area, micromammals are not very rich, but some of them still are important. It is relatively uncommon that three primates are found from the Middle Miocene and the Early Pleistocene deposits. Since the Middle Miocene, carnivores have become important components in the ecosystem of the Hezheng area, and dominated in the Early Pleistocene. The Middle Miocene is a time of high diversity for Proboscidea, characterized by shovel-tusked elephants. Perissodactyls in the Hezheng area are very abundant, especially Late Oligocene and Late Miocene rhinoceroses as well as the Late Miocene and Early Pleistocene horses. From the Middle Miocene, artiodactyls became important components of the mammalian faunas, especially bovids.

Key words: Hezheng, Gansu, Late Cenozoic, mammal, ecosystem, biochronology

1 Introduction

In recent years, field works in the Hezheng area resulted in an explosive growth of new knowledge of Chinese mammalian faunas of the Late Cenozoic. A continuous sedimentary sequence from the Oligocene to the Pleistocene is developed and exposed in the Linxia Basin, Gansu Province, which contains a large number of mammal fossils. The Hezheng area comprises almost the whole Hezheng County, the western half of Guanghe County, the southern half of Dongxiang County, Linxia City, the northern half of Linxia County, and the eastern border area of Jishishan County (Fig. 1). It is the most fossiliferous area of the Linxia Basin, covering about 1,300 km². Since the end of the 1980's, the area has become well known for its rich Late Cenozoic mammal fossils (Qiu et al., 1987, 1988b, 1990, 1991). However, only the Miocene mammals, especially fossils of the *Platybelodon* and *Hipparion* faunas, were known. Along with the recent field works and researches, the Late Oligocene *Dzungariotherium* fauna and the Early Pleistocene *Equus* fauna have been found in the Hezheng area. The Hezheng area produces the most abundant mammal fossils in China as well as the whole Eurasia.

Besides abundant mammal fossils, the Hezheng area also produces other Cenozoic fossils of different animals and plants; together they are here named as the Hezheng Biota. Reptile fossils of the Hezheng Biota are represented mainly by *Testudo* from the Late Miocene red clay deposits with a great number of specimens, which is an important member of the *Hipparion* fauna. The *Testudo* fossils in the Hezheng area generally are mass-burials of complete shells, and a large number of individuals of different ages and sizes are concentrated together. This high concentration seems to indicate sudden catastrophe that caused mass death and buried rapidly to form the spectacular fossiliferous beds. Some bird fossils also found from the Late Miocene red clays in the Hezheng area. For example, the earliest ostrich fossils in China have been described from the Upper Miocene in the Hezheng area (Hou et al., 2005). However, invertebrate fossils are very sparse in the Hezheng area, and only *Cypridea* was found from the Pliocene sandstone and conglomerate lens. The Late Cenozoic deposits in the Hezheng area do not produce large plant fossils, and they contain only rare pollen fossils (Ma et al., 1998).

Mammals are very sensitive to environmental changes. The strong uplift of the Tibetan Plateau during the Late Cenozoic might dramatically affect environments, which must be reflected in the evolution of mammalian faunas. The Hezheng area is located in the transitional zone between the Tibetan and Loess Plateaus. This area not only has mammalian assemblages to accurately determine their ages, but also has well-exposed deposits to reflect environmental changes. As a result, the Hezheng area provides a very good site for studying the uplift history of the Tibetan Plateau and its influence on environments. The
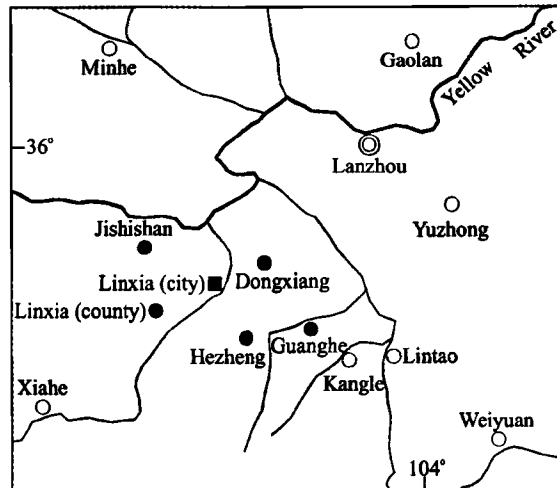
Fig. 1. A sketch map showing the location of the Hezheng area in northwestern China.

Hezheng area may be similar to or better than the classical Siwaliks on the southern border of the Tibetan Plateau. We focus to introduce the recent advances in the mammal researches of the Hezheng Biota.

2 Discovery and Research of the Hezheng Biota

In the Hezheng area, mammal fossils were used as the Chinese medicine, "dragon bones", in the past. Since the end of the 1950s, a large number of "dragon bones" have been found in the Hezheng area, but these fossils have not received much attention by scientific communities. During 1970–1984, for example, 918.6 tons of mammal fossils from the Hezheng area were used as medicine.

In the 1950s, the Geological Survey Team of Gansu found some fossils of the *Hipparion* fauna in the Neogene red deposits distributed widely in the Hezheng area, including *Hipparion*, *Chilotherium*, *Palaeotragus*, and *Gazella*. This team also found *Equus*, *Lynx*, *Ochotona*, and *Myospalax* from the Quaternary deposits in this area. In the 1980s, however, the scientific value of "dragon bones" from the Hezheng area was finally recognized by vertebrate paleontologists. Since 1987, Qiu and others have studied and published some mammal fossils found from the Hezheng area, including *Acerorhinus hezhengensis* (Qiu et al., 1987), *Dinocrocuta gigantea* (Qiu et al., 1988b), the *Dzungariotherium* fauna (Qiu et al., 1990), *Agriotherium inexpetans* (Qiu et al., 1991), the earliest hipparionine in China, *Hipparion dongxiangense*, and a large-sized elasmothere, *Parelasmotherium simplum* (Qiu and Xie, 1998). The original geological survey reported that the Cenozoic deposits started from the Pliocene, but the discovery of Qiu and others proved the presence of not only the rich Late Miocene *Hipparion* fauna, but also the typical Late Oligocene *Dzungariotherium* fauna. Guan (1988) and

Guan and Zhang (1993) studied the Middle Miocene mammalian fauna around Guanghe in the Hezheng area, and two fossiliferous layers can be seen in the Middle Miocene deposits, represented by *Platybelodon*, *Anchitherium*, *Hispanotherium* and *Kubanochoerus* in the upper layer and by small mammals in the lower one, respectively. In the 1990s, a research group of Lanzhou University developed a series of fruitful geological works in the Linxia Basin, and also found a lot of mammal fossils. However, these fossils had no exact locality information, making them a mixture between upper and lower horizons (Gu et al., 1995a, b). Since 2000, the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) has begun an extensive exploration in the Hezheng area, and found a large number of mammal fossils from the Late Oligocene and Early Pleistocene. As a result, a series of papers and monographs about the Cenozoic mammals in the Hezheng area have been published. The earliest mammalian fauna in the Hezheng area, the Late Oligocene *Dzungariotherium* fauna, contains 12 mammalian forms, which are dominated by rhinoceroses, including two forms of indricotheres (Qiu et al., 2004b, c; Deng, 2004a). Two Middle Miocene rhinocerotid species are found from the Hezheng area, including a small elasmothere *Hispanotherium matritense* (Deng, 2003) and a new acerathere *Alicornops laogouense* (Deng, 2004b), which demonstrate the dispersal of rhinoceroses between the west and east ends of Eurasia. Among the *Hipparion* fauna in the Hezheng area, a new ovibovine genus and species was described, which was an ancestor form of the extant North American muskox (Qiu et al., 2000); a lot of rhinoceroses were studied, such as a new species of *Parelasmotherium* (Deng, 2001a), the cranial ontogeny and skeleton structure of *Chilotherium* (Deng, 2001b, 2002a), the sexual dimorphism of *Iranotherium* (Deng, 2005a), and the validity of *Shansirhinus* (Deng, 2005b); a new porcupine species was described (Wang and Qiu, 2002); the Eurasian *Microstonyx* and *Promephitis* were revised according to the new material found from the Hezheng area (Liu et al., 2004; Wang and Qiu, 2004). Among the latest mammalian fauna in the Hezheng area, the Early Pleistocene *Equus* fauna, 32 mammalian species of six orders were described, including one new subfamily, two new genera, and 12 new species (Qiu et al., 2002, 2004a; Deng, 2002b; Wang and Qiu, 2003; Wang, 2005), such as the earliest woolly rhino, *Coelodonta nihowanensis*, and the largest horse in the world, *Equus eisenmannae*.

3 Systematic Paleontology

3.1 Micromammals (Rodentia and Lagomorpha)

Micromammals in the Hezheng area are not abundant, but some of them still are important forms. The known

species of Rodentia and Lagomorpha include the Late Oligocene *Tsaganomys altaicus*; the Middle Miocene *Alloptox* sp., *A. minor*, *Castor* sp., Ochotonidae gen. et sp. indet., *Megacricetodon sinensis*, *Heterosminthus orientalis*, and *Sayimys* cf. *obliquidens*; the Late Miocene *Prosiphneus* sp., *Pararhizomys hipparionum*, and *Hystrix gansuensis*; the Early Pleistocene *Aepyosciurus orientalis*, *Marmota parva*, *Castor anderssoni*, *Mimomys* cf. *gansunicus*, *Bahomys* sp., and *Sericolagus brachypus*; the Middle Pleistocene *Myospalax arvicolinus* and *Ochotona* cf. *thibetana*.

Based on *Aepyosciurus orientalis* found from the base of the Early Pleistocene loess deposits in the Hezheng area, Aepyosciurinae, a new subfamily of Sciuridae, was established (Wang and Qiu, 2003). Its unilaterally hypsodont and lophodont cheek teeth are unique among the sciurids so far known in the world. A certain degree of similarity can be observed between the cheek teeth of Aepyosciurinae and Anomalurinae living in tropical and subtropical forests in central and western Africa. *A. orientalis* might have lived in mountainous woodland or grassland and lived on harder leaves, barks, or even grass. This tends to show that the Hezheng area on the northeastern border area of the Tibetan Plateau had been lifted considerably in the Early Pleistocene, with drier climate, becoming a suitable habitat for *A. orientalis*. All these features of *A. orientalis* are similar to ground squirrels rather than to tree squirrels, so it seems to have lived on ground.

3.2 Primates

Primate fossils were rare in northwestern China, mainly represented by some isolated teeth. In the Hezheng area, not only teeth of *Pliopithecus* sp. were found from the Middle Miocene deposits, but also two monkey species, *Macaca* cf. *anderssoni* and *Paradolichopithecus gansuensis* (Plate I-1), were found from the Early Pleistocene loess deposits, which are relatively uncommon.

Paradolichopithecus gansuensis is evidently larger than all known species of *Macaca*, and it is slightly larger than *Procynocephalus* (Qiu et al., 2004a). *P. gansuensis* differs from *P. arvernensis*, *P. geticus*, and *P. sushkini* in the following features: there is a facial depression on the maxillary and a deep labial fossa on the mandible in *P. gansuensis*, which are not so obvious in the other species of the genus; the anterior root of the zygomatic arch is located more anteriorly in *P. gansuensis* (at the middle of M3) than in the other species of the genus (in the posterior half of M3); M2 is larger than M3 in *P. gansuensis*, whereas it is smaller than M3 in the other species of the genus; the para- and metacone and meta- and entoconid of the molars are more lophodont in *P. gansuensis*. The presence of a facial

depression and a mandibular fossa in *P. gansuensis* is highly perplexing and interesting. A mandibular fossa can be occasionally seen in some specimens of *Macaca florentina*. However, this character is considered highly diagnostic of the African *Papio*.

3.3 Carnivora

Among the Late Oligocene mammalian fauna in the Hezheng area, there is only one creodont species, *Megalopterodon* sp. Since the Middle Miocene, carnivores have become important components in the ecosystem of the Hezheng area, being 22% in large mammals during the Middle Miocene, increseaing to 39% during the Late Miocene, and reaching the highest 57% during the Early Pleistocene. The carnivores in the Hezheng area include the Middle Miocene *Hemicyon teilhardi*, *Amphicyon tairumensis*, *Percrocuta tungurensis*, and *Pseudaelurus guangheensis*; the Late Miocene *Simocyon primigenius*, *Agriotheriun inexpetans*, *Indarctos zdanskyii*, *Parataxidea sinensis*, *Pleisiogulo* sp., *Promephitis parvus*, *P. hootoni*, *Melodon majori*, *Sinictis* sp., *Ictitherium* sp., *Hyaenictitherium hyaenoides*, *H. wongii*, *Adcrocuta eximia*, *Dinocrocuta gigantea* (Plate I-4), *Machairodus* sp., *M. palanderi* (Plate I-3), *Felis* sp., *Metailurus* sp., and *M. minor*; the Early Pleistocene *Vulpes chikushanensis*, *Canis teilhardi*, *C. longdanensis*, *C. brevicephalus*, *Sinicuon* cf. *dubius*, *Eirictis robusta*, *Meles teilhardi*, *Chasmaporthetes progressus*, *Pachycrocuta licenti*, *Crocuta honanensis*, *Homotherium crenatidens*, *Megantereon nihowanensis*, *Sivapanthera linxiaensis* (Plate I-2), *Panthera palaeosinensis*, *Felis teilhardi*, and *Lynx shansius*.

Agriotherium inexpetans from the Hezheng area is the most primitive species of this genus with small size, and it is the first discovery of *Agriotherium* together with typical *Hipparion* fauna elements in China (Qiu et al., 1991). The discovery is in favor of the viewpoint that *Agriotherium* and *Indarctos* have probably rather different origins. *Agriotherium* might derive from a group of animals similar to *Dinocyon teilhardi*. On the other hand, *Indarctos* might well originate from some group of the hemicyonines other than *Dinocyon*. After the close relationships between ursavines and ailuropodines were recognized (Qiu and Qi, 1989), it becomes more and more evident that there were two major lineages in the evolution of the Late Neogene ursine animals. One was the *Ursavus* group and its derivatives: ailuropodines and the true ursines. The other is the lineage of hemicyonines, which comprises two subbranches: hemicyonines *s.s.* with their derivative *Indarctos* on the one hand, and *Dinocyon* and *Agriotherium* on the other.

Promephitis is a widespread Late Tertiary Eurasian skunk in Mephitidae, but many of the currently recognized

nine species were established on isolated dental material. A new collection of *Promephitis* from the Hezheng area yielded the largest and best-preserved sample of this genus, including two contemporaneous species, each represented by more than a dozen skulls. Such a wealth of new information prompts us to re-evaluate Chinese *Promephitis* taxonomy and zoogeography in the Late Miocene. Recent discoveries of *Promephitis* from the Hezheng area make the Chinese record of *Promephitis* unrivaled in terms of quality, quantity, and species diversity. *Promephitis parvus* from the Hezheng area represents the smallest known species of the genus and is also the most primitive in cranial and dental morphologies (Wang and Qiu, 2004). *P. hootoni* is the most common Chinese species, and the Turkish occurrence of *P. hootoni* must be the result of westward expansion of its range.

Eirictis was a new genus established on the basis of the material from the Hezheng area, and it is a large-sized mustelid (Qiu et al., 2004a). In *Eirictis*, the mandible and the lower teeth are almost indistinguishable from those of the European *Pannonictis*. The only possible distinction lies in the m1 morphology. In *Pannonictis* the talonid is about as high as the trigonid, whereas in m1 of *Eirictis* the trigonid is higher than talonid. However, P4 of the two forms are quite different. In *Pannonictis* it is meline in pattern, i.e., the protocone is triangular in crown view followed by a shelf-like hypocone. In *Eirictis* the protocone is musteline in pattern, i.e., cone-shaped, without hypocone. Similar combination of musteline P4 with meline m1 can only be found in *Eyra*, a living mustelid of South America. Although similar to *Eirictis* in carnassials, *Eyra* differs widely from the latter in skull structure. In *Eyra* no unified sagittal crest is present, on the contrary, there are only lyrate-form parietal ridges.

The skull of *Dinocrocuta gigantea* is exceptionally robust, and shows a series of characters different from any known hyaenid forms. The most remarkable among them are: the general short and high proportion, the sharp bending of the skull roof, the thick and much widened nasal bones, and the exceptionally long meatus acusticus. The body weight of *D. gigantea* is estimated to be over 210 kg, three times larger than the largest extant *Crocuta crocuta* in Africa and 60–70 kg heavier than the modern African lion. *D. gigantea* is so large that it is an uncommon carnivore in any period. The huge size of *D. gigantea* may not to be used to catch herbivores larger than it. The weight is one of important conditions in fights, but fights are the last step to kill the adversary in the hunting. Too heavy individuals directly affect their abilities of running and turning abruptly. *D. gigantea* depends on its body weight to rob preys of other animals, which may be the primary reason to cause it to enlarge.

3.4 Proboscidea

The earliest proboscidean fossils in the Hezheng area were found from Dalanggou, Guanghe, and they were a lot of huge and curved tusks of *Gomphotherium* sp. of the late Early Miocene. The Middle Miocene was a highly diversified time of Proboscidea in the Hezheng area, characterized by *Platybelodon grangeri* (Plate II-8). As a result, the Middle Miocene mammalian fauna is named as the *Platybelodon* fauna, also including proboscidean *Gomphotherium* and *Zygolophodon*. In the Late Miocene, the diversity and number of Proboscidea reduced obviously, and only *Tetralophodon* sp. and *T. exoletus* existed. Proboscidean fossils have not been found from the Pliocene and Pleistocene deposits in the Hezheng area.

Platybelodon grangeri is a shovel-tusked gomphothere, and it is found only in northwestern China, firstly from Tunggur, Inner Mongolia. Its skull is relatively long and narrow, with a pair of reduced round upper tusks. The horizontal ramus of the mandible is relatively straight, and the symphysis is narrow at posterior end and rapidly expanded anteriorly, with two big shovel-like lower incisors. The high crowned molars have abundant cement. The nasal opening is slightly behind the anterior border of the orbit, and the infraorbital foramen is big, facing anteriorly with a tube almost horizontally positioned. The wear facet on its lower incisors is faced antero-ventrally. It can be deduced that *P. grangeri* had a rather long, forward extended trunk, which was opposite and covered the forward protruding tusks and symphysis. *P. grangeri* uses its long trunk and specialized long symphysis and tusks to gather food.

3.5 Perissodactyla

Perissodactyls in the Hezheng area are very abundant. Rhinoceroses were over 70% in diversity during the Late Oligocene, and horses and rhinoceroses are dominant in number during the Late Miocene. The mammalian faunas of the Late Miocene and Early Pleistocene are named as the *Hipparion* and *Equus* faunas, respectively. The earliest equid fossils in the Hezheng area appeared in the Middle Miocene, and they were some broken smaller teeth of *Anchitherium* sp. from Wangshijie. Some larger individuals of *Anchitherium gobiensis* were found from the later locality Laogou. In the beginning of the Late Miocene, *Hipparion* dispersed to Eurasia from North America, and *Hipparion dongxiangense* from Wangji, Dongxiang was the known earliest species of the genus in China (Qiu and Xie, 1998). Chalicotheres and tapirs also were found from the Hezheng area. Perissodactyls in the Hezheng area include the Late Oligocene *Schizotherium ordosium*, Hyracodontidae gen. et sp. indet., *Ardynia* sp., *A. altidentata*, *Allacerops* sp., *Dzungariotherium orgosense*,

Paraceratherium yagouense (Plate II-1), *Ronzotherium* sp., and *Aprotodon lanzhouensis*; the Middle Miocene *Anchitherium gobiensis*, *Alicornops laogouense* (Plate II-5), *Hispanotherium matritense*, and *Chalicotherium* sp.; the Late Miocene *Sinohippus zitteli*, *Hipparion* sp., *H. dongxiangense*, *H. chiai*, *H. weihoense*, *H. coelophyes*, *H. dermatorhinum*, *Ancylotherium* sp., *Acerorhinus hezhengensis*, *Chilotherium wimani*, *Iranotherium morgani* (Plate II-3), *Parelasmotherium simplym*, *P. linxiaense*, *Dicerorhinus ringstromi* (Plate II-6), and *Tapirus teilhardi*; the Early Pliocene *Hipparion* sp. and *Shansirhinus ringstromi* (Plate II-2); the Early Pleistocene *Hipparion sinense*, *Equus eisenmannae* (Plate II-7), *Coelodonta nihowanensis* (Plate II-4), and *Hesperotherium* sp.

Hipparion dongxiangense is a very small three-toed horse, with a length of a single upper tooth less than 20 mm and a width less than 17 mm. *H. dongxiangense* is readily distinguishable from all other hipparionine species so far known from China and adjacent areas. It is even smaller than the smallest species in China, *Hipparion parvum*. The upper cheek teeth of the small sized species are generally quadrate in crown form, but the lengths of the teeth of *H. dongxiangense* are greater than the widths. *H. matthewi* and *H. periafricanum* are also small in size, but their upper cheek teeth are always quadrate in crown form, with rather rounded protocone. The structure in the hypoconal part of the teeth of *H. dongxiangense* is rather unique for a Chinese hipparionine species. Similar structure is often observed in North American hipparionines of the Middle Miocene, for example, in *Cormohipparion goorisi* (MacFadden, 1984). This may allude to the early geological age of *H. dongxiangense* in comparison with the other Baodean species.

Equus eisenmannae is a giant true horse, and its holotype has the basal skull length of 625 mm, longer than that of the largest known horse, *E. enormis* from Vallecito Creek, California, basal skull length of which varies 616–621 mm (Downs and Miller, 1994). The giant size of *E. eisenmannae* implies that it inhabited a cold environment with a vegetation of tough grasses. Among the all known horses, *E. eisenmannae* has the longest face (Qiu et al., 2004a). The expanded preorbital region is to accommodate a larger dental battery for mastication of an increased supply of foodstuffs, particularly for the grazing clades that fed on low-digestibility grasses. Moreover, a long face can keep its eyes out for danger while grazing. *E. eisenmannae* inhabits in a very rigorous environment, and its long face may help to keep it away from the attack of predators. *E. eisenmannae* is transitional between plesippine in North America and allohippine horses in the Old World.

Paraceratherium yagouense is a small indricothere, its length of muzzle anterior to DP1 not surpassing DP1–DP4

(Qiu et al., 2004b). It has no upper incisors, canines, and P1. The cheek teeth are highly crowned, with thin layers of cement. They have large antecrochet, anterior protocone and hypocone constriction grooves, high and ridge-formed anterior and posterior cingula, lacking lingual cingulum, often with pillar-formed tubercles in the middle of anterior cingulum, medisinus, postfossette and posterior to antecrochet. Although small compared with majority of the other indricotheres, *P. yagouense* is much larger than any other rhinocerotids. The following characters of the skull show its *Paraceratherium* affinity: the wide distance between the postglenoid and mastoid processes, the strongly reduced muzzle, the wide and thin nasal bones, the presence of metaloph in DP1, the high crowned cheek teeth, and the presence of vertical groove on the flattened inner surface in upper molars.

Alicornops laogouense is a middle-sized acerathere, and its skull is the largest of the genus (Deng, 2004b). The nasals are narrow, and the skull is very high, with a lozenge-shaped roof. The frontal bone is narrowing posteriorly, and the surface between the parietal crests is narrow. The *Platybelodon* fauna bearing *A. laogouense* in the Hezheng area corresponds to MN 6. With the discovery of *A. laogouense*, it appears that the genus *Alicornops* dispersed from western Europe through eastern Europe, western Asia and southern Asia, to the Far East. In China, *A. laogouense* lived together with *Hispanotherium matritense*, which inhabited a warm environment (Deng and Downs, 2002). A large number of fossils of Amebelodontidae, which favored habitats near water, were found with *A. laogouense* in the Hezheng area. This shows that lakes and rivers were abundant in the environment in which this rhinocerotid species lived.

Acerorhinus hezhengensis is a large-sized acerathere (Qiu et al., 1987). It is relatively frequent in the Late Miocene *Hipparion* fauna of the Hezheng area, but much less abundant than *Chilotherium wimani*. Its sagittal crest is absent, and the area bordered by the rather straight parietal crests is wide and flat. The nasal notch is deeply incised, and the orbit is situated comparatively low. The symphysis is not widened, but ascends anteriorly. The median valleys on the upper premolars are blocked only when heavily worn. The upper molars have strong protocone constrictions and antecrochets, and their labial walls are undulating, with prominent paracone ribs and parastyle folds. The most marked difference from *Shansirhinus* and *Chilotherium* is that the symphysis of *Acerorhinus* is not specially widened, with a distance between i2 equal to or less than the distance between p2. On the other hand, the three genera differ from all the other members of Aceratheriinae, so they are placed in the tribe Chilotheriini.

Iranotherium morgani is the only known rhinoceros with

a rugosity for larger masseteric and temporalis musculature on each zygomatic arch of the male individual, which suggests that this species was sexually dimorphic (Deng, 2005a). *I. morgani* has a large size with a huge nasal horn, and its skull is particularly elongate and dorsally concave. The nasal horn of the male is much larger than that of the female, and a strong and rough hemispherical hypertrophy is present on the posterior part of the zygomatic arch of the male. The sexually dimorphic characters of the male and female skulls of *I. morgani* show that the male skull is more massive, with stronger zygomatic arches. Premolars are significantly shortened. The cheek teeth of *I. morgani* are hypsodont and have wrinkled enamel, indicating that it was a grazer in open grassland. *I. morgani* is likely to have first appeared in northwestern China, later dispersing westward to central Asia.

Coelodonta nihowanensis was first found from Nihewan, Hebei Provnice, but its material included only a milk tooth row. It was clearly considered a primitive species of woolly rhino, and implied that the woolly rhino actually originated in Asia. A complete adult skull with mandible and a partial juvenile skull of *C. nihowanensis* were found from the earliest loess deposits in the Hezheng area. *C. nihowanensis* has more primitive characters than *C. antiquitatis*, such as smaller size, weaker frontal horn, larger posterior hole of nasal septum, and triangular M3. *C. nihowanensis* from the Hezheng area is by far the earliest remains of the woolly rhino in the world, and the origination of the woolly rhino, which was distributed widely in north Eurasia during the Late Pleistocene, is affirmed from northern China at the beginning of the Quaternary. It has also been hypothesized that *Coelodonta* underwent an adaptive radiation during the Pliocene and thereafter, which resulted in the multitude of species described in the literature.

3.6 Artiodactyla

In the Late Oligocene, artiodactyls were relatively rare, but from the Middle Miocene, they became important components of mammalian faunas in the Hezheng area. Artiodactyls found from the Hezheng area include the Late Oligocene *Paraentelodon macrognathus*; the Middle Miocene *Listriodon mongoliensis*, *Kubanochoerus gigas* (Plate I-6), *Dorcatherium* sp., *Moschus* sp., *Palaeotragus tungurensis*, and *Turcocerus* sp.; the Late Miocene *Chleuastochoerus stehlini*, *Microstonyx major* (Plate I-7), *Dicrocerus* sp., *Metacervulus* sp., *Cervavitus novorossiae*, *Samotherium* sp., *Honanotherium schlosseri*, *Palaeotragus microdon*, *Gazella* sp., *Hezhengia bohlini* (Plate I-8), *Miotragocerus* sp., *Sinotragus* sp., *Protoryx* sp., and *Shaanxispira* sp.; the Early Pleistocene *Sus* sp., *Nipponicervus longdanensis*, *Gazella* cf. *blacki*, *Leptobos*

brevicornis (Plate I-5), and *Hemibos gracilis*.

Paraentelodon macrognathus was established as a new species by Qiu et al. (1990) according to the material from the Hezheng area. Its premolars, canines and probably also the incisors are very much enlarged relative to the molars. The mere gigantism of *P. macrognathus* excluded the necessity to compare it with the small-sized *Entelodon* and *Archaeotherium* commonly occurred in the Oligocene of Europe and North America. Among the specialized American entelodonts of the Late Oligocene and Early Miocene, only *Dinohyus* attained approximately the size of *P. macrognathus*. Still, it is easy to distinguish them. *Dinohyus* differs from *P. macrognathus* by less degree of enlargement of the incisors, canines and premolars relative to the molars, by less reduced M3 and the entoconid of m3. American forms of the Late Oligocene and Early Miocene were derived from the American *Archaeotherium* and represented an independent lineage different from the Eurasian one.

Previously, *Kubanochoerus gigas* was represented only by teeth and limb bones from Tongxin, Ningxia (Qiu et al., 1988a). Recently, a number of complete skulls and mandibles of *K. gigas* is found from the Hezheng area. The most peculiar feature of *Kubanochoerus* may be the presence of a large, single frontal "horn", which projects upward and anteriorly. Its base is located just anterior to the paired protuberances over the orbits. It is interesting to note that the "horn" consists apparently of two parts: a pedicle, about 50 mm long, and the "horn" itself, about 70 mm in length. The top of the pedicle is hemispherical in form and the top surface is rather rough. The "horn" sits on the top of the pedicle, with its base well adapted to the pedicle top. Apparently the "horn" has an ossification center of its own. Similar kind of "horn" is usually found only in giraffids.

Several large suid cranial remains attributed to *Microstonyx major* were found from the Hezheng area. The new material confirms the presence of *Microstonyx* in the Late Miocene of the area. The Chinese form belongs to a small-sized eastern population with reduced premolar row and clear sexual bimodality. Statistical comparison shows that *M. major* was a polymorphic species and reinforces recognition of *Hippopotamodon* as a separate genus, defined by relatively stout premolars resulting from a different underlying pattern of allometric growth. The presence of *Microstonyx* in northern China and the distinct suid assemblage that lived there suggest biogeographic connections between northern China and western Eurasia in contrast to isolation from southern China and the Indian subcontinent. The environment of the Chinese latest Miocene suids (both *Microstonyx* and the small, endemic *Chleuastochoerus*) appears to have been more humid than that of contemporaneous populations in western Eurasia.

Hezhengia bohlini is a medium-sized ovibovine and one of the most characteristic forms of the *Hipparion* fauna in the Hezheng area (Qiu et al., 2000). Its horncores are robust and short, and stretch horizontally. The horncore bases are strongly converging posteriorly, leaving a narrow sagittal slit between them. The parietal bones almost are perpendicular to the frontals. The occipital surface has a protruded lambdoid crest, and the condyles have lateral accessory articular surfaces. Among the abundant Late Miocene ungulate fossils in the Hezheng area, many skulls are referable to *H. bohlini*, the second largest group in number next only to *Chilotherium wimani*. The earliest and most primitive ovibovine is probably *Mesembriacerus* from the European Vallesian of Macedonia, Greece (Bouvrain and de Bonis, 1984), and it is smaller in size and far more primitive than *Hezhengia*. In the Turolian ovibovines, *Plesiaddax* is more or less close to *Hezhengia*.

4 Biochronology of the Hezheng Biota

All mammal fossils of the *Dzungariotherium* fauna from the Hezheng area show clearly that they belong to the Late Oligocene (Deng et al., 2004a, b; Qiu et al., 2004b, c). Fang et al. (2003) gave an age of ~21 Ma for this fauna according to a paleomagnetic dating, but it was based on an incorrect correlation to the Early Miocene. Because this fauna can be correlated correctly to the Tabenbulukian of the Chinese mammal ages, its paleomagnetic polarity zonation (Fang et al., 2003, Fig. 3) may be explained within C7n.2n, with an age of 25 Ma.

Fossils of the *Platybelodon* fauna of the Hezheng area are the typical Middle Miocene forms, and this fauna corresponds to MN 6 of the European mammal zones (Deng et al., 2004a, b). On the other hand, the age of this fauna has not been well coordinated between the paleomagnetic dating and the mammalian correlation. The paleomagnetic zones of the sandstones and conglomerates bearing the *Platybelodon* fauna are mainly reversed, so they seem to correspond to C5r with an age of ~12 Ma that is situated in MN 7/8. On the other hand, sandstones and conglomerates have rapid or varied sedimentary rates, so their paleomagnetic ages are difficult to determine.

Fossils of the *Hipparion* fauna of the Hezheng area can be distinctly divided into four horizons, represented by the localities Guonigou, Dashengou, Yangjiashan, and Shilidun, respectively. The first three horizons belong to the Late Miocene, and the last one belongs to the Early Pliocene. According to paleomagnetic measurements, the Guonigou fauna is within C5r.1r, with an age of 11.1 Ma, corresponding to MN 9; the Dashengou fauna is within C4Ar.2r, with an age of 9.5 Ma, corresponding to MN 10; the Yangjiashan fauna is within C4r.1n, with an age of 8.3

Ma, corresponding to MN 11; and the Silidun fauna is within C3n.4n, with an age of 5.0 Ma, corresponding to MN 14.

The presence of true horse and the absence of the typical Middle Pleistocene forms immediately date the *Equus* fauna of the Hezheng area in the Early Pleistocene, which is slightly older than that of the Nihewan fauna. The paleomagnetic data show a longer duration of time. The Matsuyama/Gauss boundary is determined 0.5 m below the lower fossiliferous bed of the *Equus* fauna in the Hezheng area, whereas the lower boundary of the Reunion subchron is defined just above the upper fossiliferous bed. This would mean that the time span during which the fossils were embedded lasted about 0.39 my, thus, from 2.55 Ma to 2.16 Ma (Qiu et al., 2004a).

5 Ecology of the Hezheng Biota

Ecological features of mammalian faunas show that dramatic environmental changes occurred in the Hezheng area during the Late Cenozoic: mainly warm and humid forests mixed with some open lands in the Late Oligocene; denser forests and more water bodies in the Middle Miocene; hot and subarid steppes with marked seasonal variations in the Late Miocene; and cold and dry climate with a strong elevation increase in the Early Pleistocene. The particular geological position of the Hezheng area implies that its evolution of mammalian faunas is closely related to the uplift of the Tibetan Plateau during the Late Cenozoic.

Rhinoceroses dominated the Late Oligocene *Dzungariotherium* fauna in the Hezheng area, and predators were relatively primitive, including only rare creodonts represented by *Megalopterodon*. In the Siwalik area on the southern border of the Tibetan Plateau, there was also the distribution of indricotheres in the Late Oligocene. In the global range, a great regression took place at 30 Ma, with nearly simultaneous disappearance of the Turgai Strait (Haq et al., 1987). The first uplift of the "Tibetan Plateau" might occur in a large area at the latest Early Oligocene (Qiu et al., 1997). On the other hand, the discoveries of indricotheres on the south and north sides of the Tibetan Plateau indicate that the plateau had no enough height to prevent dispersals of huge mammals, so indricotheres, aprotodons and chalicotheres were free to migrate between the south and north sides of the "Tibetan Plateau" (Qiu et al., 1997).

Along with the coming of the Miocene, most of the Oligocene mammals were extinct, and no component of the *Dzungariotherium* fauna survived in the Middle Miocene *Platybelodon* fauna. The framework of the *Platybelodon* fauna also changed obviously. Newly appeared

proboscideans occupied an important position in the fauna, carnivores became significant faunal components, and artiodactyls exceeded perissodactyls in diversity and became the most diverse group in the fauna. In the same period, *Platybelodon* was found from many localities on the north side of the Tibetan Plateau, while this proboscidean form has no trace in the Indian subcontinent on the south, which suggested that the Tibetan Plateau was high enough to baffle interchanges of large mammals. Within a larger extension, the dispersal event of *Anchitherium* between North America and Eurasia was recorded in the *Platybelodon* fauna of the Hezheng area. This event occurred in a cold stage between the Late Oligocene and the Middle Miocene at about 23 Ma when the sea level dropped so that the Bering Strait connected and became a land bridge (Woodburne and Swisher, 1995). *Anchitherium* found in the Hezheng area was later than the earliest record of this genus in Eurasia. In fact, *Anchitherium* found in the whole Asia was later than in Europe, and the earliest record of this genus in Asia was from the late Early Miocene Sihong fauna in Jiangsu Province, with an age of about 18 Ma (Deng, 2004a). But it is inconsistent with the disperasl route of *Anchitherium*, and has to wait for finding more fossils to solve. Originally, *Anchitherium* was recorgnized to live in China until the early Late Miocene Amuwusu fauna (Qiu, 1988). But a new field survey shows that *Anchitherium* is still collected from the Middle Miocene deposits below the *Hipparion* bed. The extinction of *Anchitherium* was obviously due to the replacement of forests by expanded steppes.

The mammalian fauna in the Hezheng area dramatically changed again at the coming of the Late Miocene, and no species of the *Platybelodon* fauna survived the *Hipparion* fauna. The earliest *Hipparion* migrated into Asia from North America through the Bering land bridge at 11.2 Ma, then rapidly dispersed to Europe and northern Africa, which following high adapting radiation was an important event in Eurasia (Woodburne and Swisher, 1995; Bernor et al., 1996). *Hipparion* entered into Siwaliks of the Indian subcontinent also relatively early, almost at the same time with the other regions in Eurasia. At that time, the Tibetan Plateau became a more sufficient barrier for animal disperasals, so *Hipparion* should enter into the subcontinent from the west (Woodburne et al., 1996). The earliest European hipparionine was *Hipparion primigenium* found from the Vienna Basin, while the Chinese one was *H. dongxiangense* found from the Hezheng area (Qiu and Xie, 1998). Among the *Hipparion* fauna in the Hezheng area, Siphneidae, Rhizomyidae, and Hystricidae appeared; Mustelidae, Hyenidae, and Felidae began to radiate greatly; Equidae was well diversitified, Rhinocerotidae was markedly dominant in number, and

Chalicotheridae and Tapiridae tended to decline; Bovidae and Giraffidae were well developed. Components of the *Hipparion* fauna at high level taxon have been similar to the modern mammalian fauna (Tong et al., 1995). Along with the earth went into a new climatic phase, the global environment had a dramatic change at the Miocene terminal. This change was also reflected in the mammalian fauna of the Hezheng area. After the largest diversity in the Late Miocene, species of *Hipparion* began to reduce so that the diversity and number of the Early Pliocene *Hipparion* fauna in the Hezheng area sharply decreased. The European and North American fossil records markedly underwent a significant extinction event near the Miocene terminal (Hulbert, 1995). On the other hand, the ecosystem of the *Hipparion* fauna in the Hezheng area had some remarkable differences from the European one. For example, the Greek Late Miocene *Hipparion* fauna from Pikermi lived in a sclerophyllous evergreen woodland, similar to the modern environmemt mixed with forest and grassland in the monsoon region of northern India (Solounias et al., 1999), but different from the Late Miocene steppe in the Hezheng area.

Since the beginning of the Quaternary, the climate had become cold and dry, and the diversity had reduced in the Hezheng area. The Early Pleistocene *Equus* fauna of the Hezheng area had a unique composition: firstly, the number of small mammals is unexpectedly low, with five species of Rodentia and one of Logmorpha, and without Insectivora and small species of Mustelidae; secondly, the number of Carnivora species is high and specimens of Carnivora are particularly numerous, which outnumber even the total number of herbivores; thirdly, artiodactyls, especially deer, are usually abundant in the Early Pleistocene faunas in Eurasia, but poorly represented in both numbers of species and of specimens; fourthly, elephants, racoon-dogs, and camels, which are common elements in the Early Pleistocene faunas in Eurasia, are totally absent. The low number of species of small mammals in the Hezheng area can be accounted for by the collecting bias. However, the biased collection cannot account for the unbalanced distribution of large animals. It is possible that unbalanced relationships of carnivores versus herbivores and artiodactyls versus perissodactyls reflect the true picture of the fossil community. Taken as a whole, the Hezheng area should have been an area of predominantly steppe, mixed shrub and bush areas, occasionally with small patches of forest and woodland. Loess might have just started to deposit, covering only small tops of the low mountains in this area. In the Early Pleistocene, the Tibetan Plateau was already uplifted considerably. The strong uplift of the Tibetan Plateau must have caused great environmental changes in the Hezheng area. A stronger winter monsoon

system and a higher continental desiccation had occurred during this time span. The deteriorated climatic conditions in this area, such as lower temperature and less precipitation, are also reflected in the loess deposits, which are thick, but without marked paleosols.

Acknowledgements

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Explanation of Plates

Specimens described herein are preserved at the Hezheng Paleozoological Museum (HMV) and Institute of Vertebrate Paleontology and Paleoanthropology (V).

Plate I

1. *Paradolichopithecus gansuensis*, HMV 1142, maxilla, crown view.
2. *Sivapanthera linxiaensis*, HMV 1221, skull, lateral view.
3. *Machairodus palanderi*, HMV 0173, skull, lateral view.
4. *Dinocrocuta gigantea*, HMV 1281, skull, lateral view.
5. *Leptobos brevicornis*, HMV 1244, skull, lateral view.
6. *Kubanochoerus gigas*, HMV 1254, skull, lateral view.
7. *Microstonyx major*, HMV 0976, skull, crown view.
8. *Hezhengia bohlini*, HMV 1412, skull, lateral view.

Scale bars: 2 cm for fig. 1, and 5 cm for others.

Plate II

1. *Paraceratherium yagouense*, V 13820, skull, lateral view.
2. *Shansirhinus ringstromi*, V 13764, skull, lateral view.
3. *Iranotherium morgani*, HMV 1098, skull, lateral view.
4. *Coelodonta nihowanensis*, HMV 0980, skull, lateral view.
5. *Alicornops laogouense*, HMV 0982, skull, lateral view.
6. *Dicerorhinus ringstromi*, HMV 1115, skull, lateral view.
7. *Equus eisenmannae*, HMV 1105, skull, lateral view.
8. *Platybelodon grangeri*, HMV 0940, skull and mandible, lateral view.

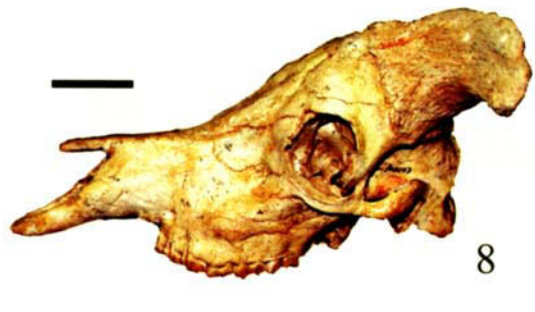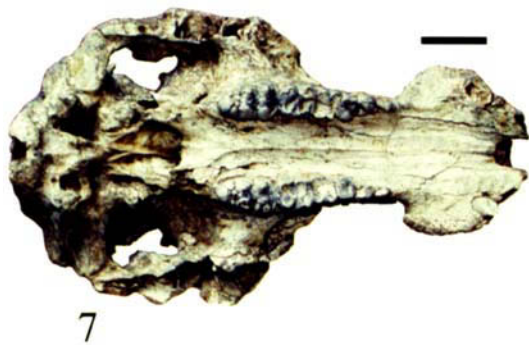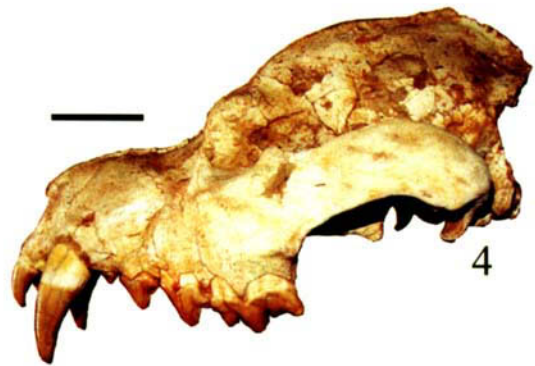Scale bars: 20 cm for fig. 8, and 10 cm for others.

Plate I
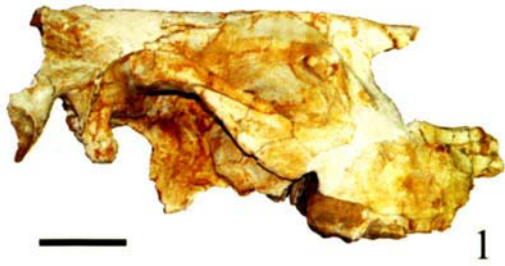
Plate II