Phylogenetic relationships of the Chinese fossil species of the genus *Equus* (Perissodactyla, Equidae)*

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Abstract The Chinese fossils of *Equus* began to appear from the beginning of the Quaternary at 2.5 Ma B.P., and the extant species of *Equus* still live in China under natural conditions at the present, which is unique in the world. 12 valid fossil species of *Equus* have been discovered in China, including the stenonid, caballoid and hemione representatives of *Equus*. The origin and evolution of the Chinese fossil species and other relevant species of *Equus* are discussed in detail. The proposed phylogenetic relationships and temporal distribution sequences including all the Chinese fossil species of *Equus* are established. Some mistakes in the earlier researches about the Chinese fossils of *Equus* are corrected.

Keywords: genus *Equus*, fossil species, phylogenetic relationship, Quaternary, China.

The genus *Equus* is one of the important Quaternary fossils. In China, located in the east of Eurasia, as in the whole continent, the temporal distribution of this genus lasts to the recent from the early Early Pleistocene and its species are very abundant. China is the native haunt of the unique extant wild horse (*E. przewalskii*) and two Asiatic asses (*E. hemionus* and *E. kiang*). Therefore, the research to the Chinese fossils of *Equus* is very important. The fossil records show that *Equus* originated from the North American *Pliohippus*, furthermore, the last common ancestor of *Equus* might have lived at 3.9 Ma B.P. according to the two-way comparisons of mtDNA sequence differences of the living species of this genus and the estimation of divergent time on the basis of the replacing rate 2% per Ma, which was identical with the appearing time of *E. simplicidens*, the earliest species of *Equus* in North America. The genus *Equus*, which originated in North America, dispersed into Eurasia through the Bering landbridge during the climatic cooling event at 2.5 Ma B.P.[1,2], and it evolved and radiated rapidly in the new ecosystems. 12 valid fossil species of *Equus* has been discovered in China[1)]. They can be divided into three types: stenonid, caballoid and hemione depending on their cheek tooth characters. According to the phylogenetic relationships, the hemione is closer to the stenonid. The living representatives of these three types are respectively stenonid zebras, hemione asses and half-asses, and caballoid wild and domestic horses. The proteinic and cellular evidence is identical with the morphologic types, which indicate that living zebras and asses belong to a different group from horses in the narrow sense. The proposed phylogenetic relationships of the Chinese fossil

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1) Deng, T., Chinese fossils of the genus *Equus* and their reflections on the climatic changes, *Ph. D. Thesis*, Xi'an: Northwest University, 1997, 1—150.

species of *Equus* are discussed as follows.

1 Chinese stenonid *Equus*

A typical character of stenonids is V-shaped linguaflexids on lower cheek teeth. All early North American *Equus* belong to stenonids. *E. simplicidens*, the first species of *Equus* has typical V-shaped linguaflexids. Therefore, the original region of stenonid horses should be in North America.

E. stenonis were distributed in Eurasia and North America during the Early Pleistocene. In China, it was discovered in Taigu (Shanxi Province)[3,4]. It is evidently related to the Pliocene *E. simplicidens* in North America, and the former can be inferred definitely to be one of the latter's descendants. *E. stenonis* has a long muzzle, and a rather deep nasal notch which extends to the level between P^3 and P^4 at deepest. It still has preorbital pits, though smaller than those of *E. simplicidens*, a deep groove along the nasal suture, and relatively primitive tooth structures such as short protocones and deep ectoflexids, which imply it is a rather primitive species though more advanced than *E. simplicidens*. It reached Europe about 2.0 Ma B.P., and one of its subspecies, *E. s. anguinus* was also discovered in the strata of about 2.0 Ma B.P. in North America[5]. In China, however, it might appear in the Xinyaozi fauna of about 2.5 Ma B.P., which shows that its original region might be in China and it was a radiated and evolved new species after the North American early horses dispersed into Eurasia. *E. stenonis* lived in Europe until 1.0 Ma B.P., and it might be the ancestor of the minor *E. stehlini* and large *E. bressanus*.

E. sanmeniensis was distributed across northern China and was also discovered in Siberia and Tajikistan dating from the Early and Middle Pleistocene. Its advent was very early and it was an outcome of the radiation and evolution after *Equus* dispersed into Eurasia about 2.5 Ma B.P. It has some primitive characters similar to *E. simplicidens*, such as shallow preorbital pits, deep groove along the nasal suture, transversally undulated forehead, and strong deflection of the braincase. But its nasal notch is not deep and its protocones are narrow and long, which indicate that *E. sanmeniensis* and *E. stenonis* had in evolved different directions, although both of them are early primitive horses in Eurasia and derive many primitive characters from *E. simplicidens*. As a result, they are two pedigrees of parallel evolution, and they have a common ancestor and a close but not ancestor-descendant relationship.

Until now, *E. wangi* has been discovered only from the early Early Pleistecene strata in Qingyang (Gansu Province). It derives other primitive characters from *E. simplicidens*. According to a broken skull, it is estimated to have preorbital pits and a deep groove along the nasal suture. Differing from *E. stenonis* and *E. sanmeniensis* whose metastylids have sharp post-angles, *E. wangi* has rather circular double-knots. Depending on double-knots, the latter seem to be more primitive than the former two species. However, it has very short ectoflexids that never penetrate into the isthmuses, which is an evolved characteristic. As to ectoflexids, *E. wangi* seem to be more evolved than *E. stenonis* and *E. sanmeniensis*. Therefore, *E. wangi* is of a different pedigree from *E. stenonis* and *E. sanmeniensis* and has a more distant relationship with them based on comprehensive comparisons.

E. yunnanensis was distributed in southern China and Irawaddy, Burma during the Pleistocene. It has a close relationship with *E. wangi* because of its very circular double-knots and short ectoflexids that never penetrate the isthmuses. It was considered to be an equid similar to both the ass and the

horse because of its short ectoflexids[6]. However, short ectoflexids are not one of characteristics of asses only. For example, *E. wangi* has short ectoflexids and so does *E. przewalskii*. Only living zebras seldom have this characteristic, therefore, it can not be thought to be peculiar for asses. *E. yunnanensis* and *E. wangi* might speciate in different ecological environments after their common North American ancestor dispersed into Asia, which can be implied from their enamel plications. There are thick enamel and strong plications on the cheek teeth of *E. wangi* but thin enamel and fine plications on those of *E. yunnanensis*, moreover, the latter has very robust limb bones. Gromova considers that fine enamel plications and robust limb bones are adaptive to moist grasslands and the reverse is also true[7], which coincides with the distribution of *E. yunnanensis* in south and *E. wangi* in north.

E. qingyangensis was distributed in northern and northwestern China during the Early Pleistocene. Its cheek tooth structures are very similar to *E. sanmeniensis*. But its limb bones are very slender, which is an evolved characteristic and different from *E. sanmeniensis* evidently. Its limb bones are the slenderest among the early horses in Eurasia. It seems that no any species has a close relationship with *E. qingyangensis*. Because its period began from the Quaternary lower limit at 2.5 Ma B.P. and its skull has some primitive characters similar to *E. simplicidens*, it might have come directly into Eurasia as an early species of the North American *Equus*.

E. teilhardi was also distributed in northern and northwestern China during the Early Pleistocene. Its obvious character is a lack of cups on lower incisors, which is the first record in Eurasia. This feature has been found in some species of the genus *Equus* from California, South America and Africa. Its lower cheek tooth structures are similar to *E. stenonis* from St. Vallier in Europe. Its cheek tooth sizes and proportions are similar to *E. yunnanensis* and the smaller *E. stenonis* from Seneze in Europe[8]. Its position is relatively isolated among the genus *Equus* in Eurasia. The lack of cups on lower incisors exist in the geographical population of the living *E. burchelli* in Africa[9,10]. This lack in I_3 and incomplete cups on I_{1-2} were reported in *E. fraternus* from Florida. The incomplete cups on I_3 were discovered in *E. yunnanensis*. Perhaps, there are closer relationships between these species.

E. huanghoensis was discovered from the Early Pleistocene strata only in Pinglu and Linyi (Shanxi Province) and Xunyi (Shaanxi Province). Without enough materials to work with, its relationships have not been thoroughly thrashed out. According to the limited specimens, its protocones are very short, which is a primitive characteristic and identical with *E. simplicidens*. It is also similar to *E. stenonis* from Olivola and Seneze in Europe mainly because of their short-wide protocones and narrow-deep postprotoconal valleys. Its lingual margins of protocones are obviously middle-grooved, on the other hand, those of *E. simplicidens* are lingually protruding or flat at most, which indicate it is more evolved than *E. simplicidens*. It might derive from *E. simplicidens* rather directly, however, its definite relationships need more investigation to be determined.

Generally, the stenonid are thought to be primitive because its appearance was earlier than the caballoid and the hemione. At times the horse niche in a fossil fauna in China was shared by two, even three, species of equids, such as at Nihowan of Yangyuan (Hebei Province), Linyi (Shanxi Province), Lintai (Gansu Province) and so on, although the exact contemporaneity of the species is not always certain. However, the contemporaneity of *Equus* and a species of *Hipparion* (usually *H.*

sinense) is well-documented from almost all the Early Pleistocene beds in China, such as those at Nihewan, Bajiazui of Qingyang (Gansu Province), Haiyan of Yushe (Shanxi Province) and so on. When two stenonid horses lived together, their sizes were different, such as the small *E. teilhardi* and the large *E. sanmeniensis* in Nihewan as well as the middle-sized *E. qingyangensis* and the large *E. wangi* in Bajiazui. Sympartric speciation has been evoked before to explain sympatry of fossil horses, but there is little evidence for speciation in sympatry of large animals such as horses. Although ungulates may favor isolation from other conspecific groups, isolation in sympatry is probably seldom complete or extensive enough over time to be effective for speciation[11,12]. In the Late Miocene mammalian fauna, several species of horses——in North America representing different equid genera, in Eurasia representing the single genus *Hipparion*——shared the horse niche. In the Late Pliocene and Quaternary, as a faint echo of the ecological diversity of the Late Miocene horse environment, two, seldom three, equids might occur together[8]. Different species occupied different ecological niches and grazed different grass undisturbedly each other. Most probably, however, the speciation process happened through normal geographic isolation and by the secondary coming together of forms formerly separated by geographic barriers. This was completely possible during the opening of the Bering landbridge at 2.5 Ma B.P.

2 Chinese caballoid *Equus*

The caballoid might have appeared firstly in North American then dispersed into Eurasia. Its earliest record was *E. scotti* from the Irvingtonian Red Cloud Formation in Nebraska[13]. The earliest caballoid fossils in Eurasia were discovered from the strata of 0.7 Ma B.P. in Sebiria[14]. In Europe, the undoubtable caballoid horse was *E. mosbachensis* from a locality of 0.6 Ma B.P., Graues Mosbach[15].

E. beijingensis was discovered to have lived only in the late Middle Pleistocene or early Late Pleistocene in the locality 21 of Zhoukoudian, the earliest caballoid in China. Liu thought that its ancestor might be *E. sanmeniensis*[16], but the opinion is not tenable, as the age of *E. beijingensis* is about 0.2 Ma B.P. On the other hand, the caballoid *E. mosbachensis* appeared in Europe as early as 0.6 Ma B.P. Therefore, the Chinese caballoid was an immigrant according to the present evidence. After the caballoid appearance in Europe, it mostly displaced the original stenonids. There were many localities in which the stenonid and the caballoid lived together, such as Budapest-Varberg (Hungary), Kolkotova Balka (Moldavia), the Norfolk Forest Bed (England), and Süssenborn (Germany)[8]. In China, however, they have not been discovered to have lived in the same areas. The ancestor of *E. beijingensis* might have immigrated from North America or Europe. We believe that its ancestor was *E. mosbachensis* because of their many similarities.

E. przewalskii showed up in northern China and Mongolia from the early Late Pleistocene. Because of its long face, large teeth, thick enamel and weak plications, small molars, complete cups on lower incisors, slender metapodials and phalanges, Gromva considered that it was impossible to have derived from any Europe horses, and that it was one of the Asian aborigines. Furthermore, she notes that the above-mentioned characters were similar to those of *E. sanmeniesis*, so feels that *E. przewalskii* might be a descendant of *E. sanmeniensis* or its close relatives[7]. In the discussion about *E. beijingensis*, we think it is obviously not tenable that the stenonid *E. sanmeniesis* was the ancestor of the caballoid *E. beijingensis* and *E. przewalskii* depending on the temporal sequence. The ectoflexids of

E. przewalskii and *E. beijingensis* are more similar, as a result , the direct ancestor of the former is the latter whose ancestor is the European *E. mosbachensis*. Conclusively, *E. przewalskii* can be found its origin from the European horses. In fact, its distribution was not limited to Asia, and its fossils have been discovered in Lunel-Viel, France[17].

E. dalianensis was distributed in North China during the Late Pleistocene. Because of its skull characters similar to *E. przewalskii*, it evidently had a common origin with *E. przewalskii*. They lived together in the Gulongshan fauna from Fuxian (Liaoning Province) and the Yanjiagang fauna from Harbin (Heilongjiang Province)[18], therefore, there was no ancestor-descendant relationship between them and both of them were descendants of *E. beijingensis* under parallel evolution.

3 Chinese hemione *Equus*

The distribution of the extant hemione is limited only in Asia. However, it is distributed in North America during the geological period, of which the earliest record was *E. calobatus* from Rock Creek of 0.7 Ma B.P. in Texas[15]. The fossils like the small hemione were discovered from the strata of 1.4 Ma B.P. in Turkana, East Africa, but there were metapodials and no skulls[19], so it cannot be determined whether they were the earliest hemione. It remains inconclusive whether the original hemione region was in the New World or the Old World. In Eurasia, the closest ancestor of the Late Pleistocene hemione might be *E. hydruntinus* with its small size, primitive cheek teeth and slender limb bones characteristically. The age of *E. hydruntinus* from Lunel-Viel in southern France was about 0.3 Ma B.P., and its skull was closer to the hemione than any other species of *Equus*. The metacarpals of *E. hemionus* from the Gulongshan fauna in Fuxian are similar to those of *E. hydruntinus*[18]. The latter ancestor might be *E. altidens* whose age was 0.7 Ma B.P. from Süssenborn, Germany.

E. hemionu began to be widely distributed in southern Eurasia from the Late Pleistocene. It was the earliest hemione in China. Forsten thought that the fossils of the genus *Equus* from the localities 21, 22, 23 of Zhoukoudian might be the earliest hemione in China[8], and they were contemporary with *E. beijingensis*, the earliest caballoid in China. However, there was no evidence of limb bones so that this viewpoint was tentative. The definite *E. hemionus* appeared first in the Dingcun fauna. Because the skull of *E. hydruntinus* was very similar to that of *E. hemionus* and the former limb bones were slightly more robust than the latter, which was a primitive character, *E. hydruntinus* should be the direct ancestor of *E. hemionus*.

E. kiang began to be distributed in East Asia and Alaska from the Late Pleistocene. Because its many characters are similar to *E. hemionus*, some people consider that it is a subspecies of *E. hemionus*. In any case, they should have a common ancestor, *E. hydruntinus*. According to the ecological characteristics, their distribution regions do not overlap, and their fossils have not been discovered together. *E. kiang* lived in very cold environments with high humidity, on the contrary, *E. hemionus* lived in dry zones. Therefore, they may be two species brought by radiation and evolution to different ecological regions.

On the basis of the evidence now available, the phylogenetic relationships and temporal distributions of the Chinese fossil species of the genus *Equus* are shown in figure 1.

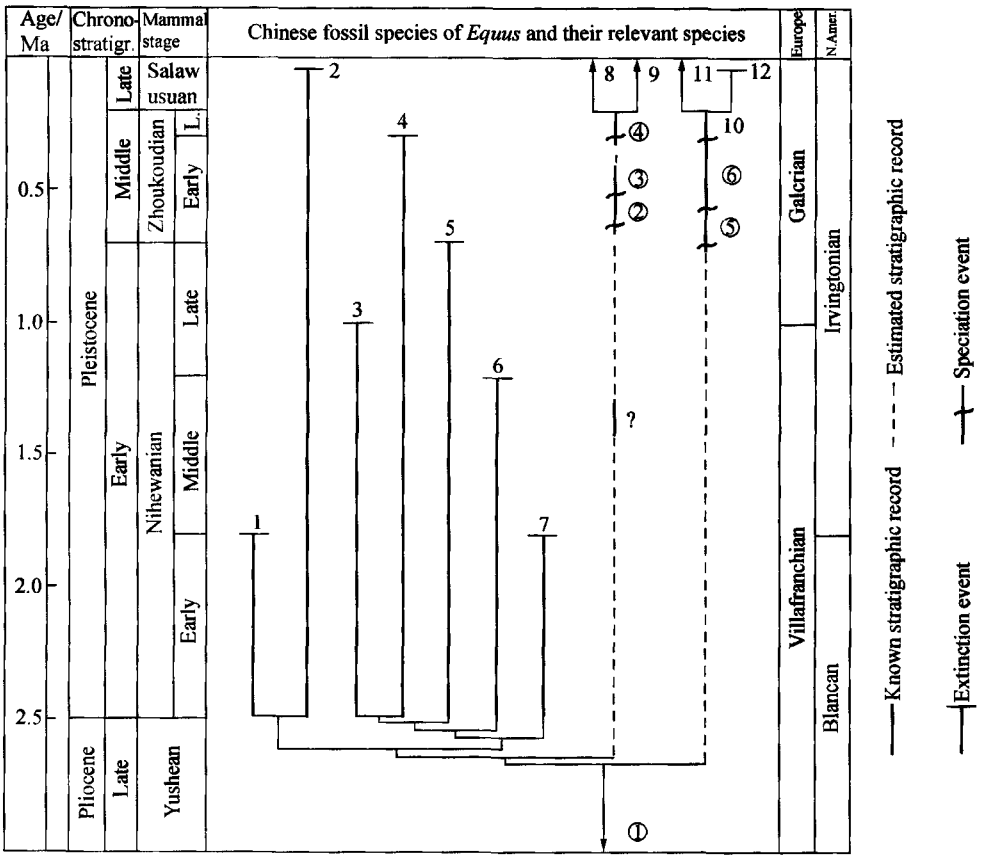

Fig. 1. Phylogenetic relationships and temporal distributions of the Chinese fossil species of the genus *Equus*. 1, *E. wangi*; 2, *E. yunnanensis*; 3. *E. stenonis*; 4, *E. sanmeniensis*; 5, *E. teilhardi*; 6, *E. qingyangensis*; 7, *E. huanghoensis*; 8, *E. hemionus*; 9, *E. kiang*; 10, *E. beijingensis*; 11, *E. przewalskii*; 12, *E. dalianensis*. ① *E. simplicidens*, ② *E. calobatus*; ③ *E. altidens*; ④ *E. hydruntinus*; ⑤ *E. scotti*; ⑥ *E. mosbachensis*.

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