frontiers
in Ecology and Evolution

ORIGINAL RESEARCH
published: 13 November 2019
doi: 10.3389/fevo.2019.00429

The *Equus* Datum and the Early Radiation of *Equus* in China

Boyang Sun [1,2] ***and Tao Deng*** [1,2,3]*

[1] Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China, [2] CAS Center for Excellence in Life and Paleoenvironment, Beijing, China, [3] University of Chinese Academy of Sciences, Beijing, China

To approach a comprehensive understanding of the *Equus* Datum, we summarize the history of the study of Chinese fossil equids, from the "dragon bones" stage to scientific investigation, by Chinese, European and American people, and then review the stenonid species in China and discuss the phylogenetic relationships of early *Equus*. We conclude that there were at least two dispersal waves of *Equus* into the Old World from North America, and the second wave led to a radiation of the genus *Equus* in China. In China, the ages of the lower boundaries of the fossiliferous layers in classical Early Pleistocene faunal localities are all around 2.5 Ma (close to the age of the lower boundary of the Quaternary) according to magnetostratigraphic and biostratigraphic analyses. All of the geochronological results reveal China as an evolutionary center of *Equus* in Eurasia. In the late Neogene, the dominant equid lineage in China was Hipparionini. Even in the Pliocene, when hipparionines were not as widespread as before, there were still 5 genera and 7 species. In the Early Pleistocene, the hipparionines included only 2 genera and 2 species. In the meantime, global cooling caused Arctic ice sheets to form, lowering the sea level so that the Bering land bridge fell dry and allowed *Equus* to disperse into China. The rise of *Equus* was accompanied by the recession of hipparionines. The dispersal and radiation of *Equus* in China were not a coincidence, but a complicated process of adaptation and competition, and a comprehensive outcome of significant climatic, tectonic and biotic events.

Keywords: *Equus* Datum, stenonid, evolution, environment change, paleozoogeography

OPEN ACCESS

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****Correspondence:***
Tao Deng
dengtao@ivpp.ac.cn

Specialty section:
This article was submitted to Paleontology, a section of the journal Frontiers in Ecology and Evolution

Received: *30 January 2019*
Accepted: *23 October 2019*
Published: *13 November 2019*

Citation:
Sun B and Deng T (2019) The Equus Datum and the Early Radiation of Equus in China. Front. Ecol. Evol. 7:429. doi: 10.3389/fevo.2019.00429

INTRODUCTION

The *Equus* Datum, the first appearance of *Equus* in the Old World, was a remarkable biotic event in the Quaternary. It has often been used as a marker of the lower boundary of the Quaternary. This biotic event was contemporary with other important geologic and environmental events. *Equus* fossils are critical research material for studies on evolutionary, climatic, and environmental changes during the Quaternary in Eurasia (Deng and Xue, 1999a). Therefore, fossil *Equus* are essential for elucidating the Pleistocene paleobiology and paleoenvironment in Eurasia.

Chinese people were the first to obtain and utilize *Equus* fossils. Since historical times in China, vertebrate fossils, which were called "dragon bones," have been used as pharmaceutical material. The "dragon bones" include *Equus* skeleton fossils. Fossil teeth of *Equus* are also regarded as pharmaceutical material and called "dragon teeth." To review the history of paleontological research in Yushe Basin, Shanxi Province, Qiu and Tedford (2013) investigated historical records of "dragon bones" in the Shanxi area from ancient Chinese literature.

They consulted Li Shizhen's famous "Compendium of Materia Medica" and found that the first reliable record of "dragon bones" as pharmaceutical material was in a lost medical book written by Lei Xue, who lived in the Song Dynasty (420–479 A.D.) of the Southern Dynasties. According to Tao Hongjing (456–536 A.D.), who lived in the Liang Dynasty of the Southern Dynasties, the Shanxi area was listed as the only place of origin for "dragon bones." Finally, they concluded that the earliest reliable history of "dragon bones" can probably be traced to the fifth century, at least for Shanxi Province.

However, actual recognition of fossil *Equus* still depends on scientific observations and descriptions, which were initiated hundreds of years later by Western scholars. Matsumoto (1915) erected a new species, *E. leptostylus*, based on an isolated upper premolar from the Yinxu site, although this species was soon after considered invalid. However, the critical specimens for the *Equus* Datum date to the Early Pleistocene, which is when *Equus* invaded Eurasia. Later, they were called stenonid horses (see below). Vertebrate paleontologists from Europe and the United States began to study early *Equus* from China in the early twentieth century. Teilhard de Chardin and Piveteau (1930) reported the classic Pleistocene mammalian fauna, the Nihewan Fauna from Yangyuan, Hebei Province, and erected *Equus sanmeniensis*, which was the first named Chinese stenonid species. Zdansky (1935) first published a monograph of *Equus* in China based on the abundant specimens of the Lagrelius Collection housed in Uppsala, which were collected from Hebei, Henan, Shanxi, and Shandong by Andersson. Zdansky identified all stenonid specimens in this fossil series as *Equus* cf. *sanmeniensis*. Hopwood (1936) divided Eurasian *Equus* into caballines and zebrines. Early *Equus* species were considered zebrines, because they had a V-shaped linguaflexid like extant zebras. Colbert (1940) studied the *Equus* specimens collected from Yuanmou, Yunnan, by the Central Asiatic Expeditions research team of the American Museum of Natural History and erected *Equus yunnanensis*. He concluded that this new species was identical to the Pleistocene *Equus* from the upper Irrawaddy of Myanmar and was similar to the Pleistocene *Equus* of India in certain features. Eisenmann (1975) rediscovered *E. sanmeniensis* specimens in the Nihewan Fauna, which was divided into two different forms based on size by Teilhard de Chardin and Piveteau (1930). She erected a new species, *Equus teilhardi*, for the small form, and argued that in addition to its small size, its lack of an incisor cup distinguished it from other *Equus* species.

After 1949, as the economy was rebuilt and science progressed, Chinese scholars began to research early *Equus*. Chow and Liu (1959) described cheek tooth specimens of *Equus* collected from Pinglu, Shanxi Province, and erected a new species, *Equus huanghoensis*. Pei (1961) reported new specimens of *E. yunnanensis* collected from Yuanmou, Yunnan Province, and *Gigantopithecus* Cave in Liucheng, Guangxi Province. Liu (1973) reported a mandible specimen of *Equus* in Locality 1 of Zhoukoudian; he identified it as *E. sanmeniensis* and thus extended the last occurrence of this species to the Middle Pleistocene. Liu and You (1974) described much better specimens of *E. yunnanensis* than previously discovered, which included a skull and mandible. Forsten (1984) proposed a "stenonid pattern" to describe the V-shaped linguaflexid when she discussed the supraspecific classification of the Old World hipparionines. The term "stenonid" references *E. stenonis*, which was the first erected species among early *Equus*, and gradually came to be used as a generic term for early *Equus*, especially by the authors of certain extensive review publications (Alberdi et al., 1998; Deng and Xue, 1999a).

Deng and Xue (1999b,c), respectively, erected two new species, *Equus qingyangensis* and *Equus wangi*, based on the specimens collected from Bajiazui, Qingyang, Gansu. In the same year, they also published the most comprehensive review of early *Equus*, or stenonids: the monograph Chinese Fossil Horse of *Equus* and Their Environment (Deng and Xue, 1999a). Qiu et al. (2004) reported a new Pleistocene mammalian fauna, the Longdan Fauna, from Dongxiang, Gansu Province. They erected *Equus eisenmannae* based on the large equid form in this fauna. Dong and Fang (2005) reported some fragmented cranial specimens of *E. huanghoensis* found from Tangshan, Nanjing, Jiangsu Province, and supplied some important features of *E. huanghoensis*. Li et al. (2016) reported the most complete fossil record yet known of *E. huanghoensis*, which included a skull associated with a mandible from Yangshuizhan in Yangyuan, Hebei Province. Sun et al. (2017) rediscovered a skull and mandible in the Lagrelius Collection from Qixian, Shanxi Province, which was previously identified as *E.* cf. *sanmeniensis* by Zdansky (1935). They identified the skull and mandible, respectively, as *E. teilhardi* and *E. qingyangensis*.

In this article, we will review all the known stenonid species on the robust basis of our predecessors. We will reorganize all important information about these species, explore their early evolution, and further elucidate the *Equus* Datum.

MATERIALS AND METHODS

For phylogenetic analysis, we reorganized the data matrices from previous publications and summarized them in a new data matrix, which includes 16 taxa, and 53 characters. The phylogenetic analysis were performed using TNT 1.1 with a traditional search method (Goloboff et al., 2008), 1,000 replications and the trees-bisection-reconnection branch-swapping algorithm (TBR) applied in our analysis. All characters are equally weighted and additive. Gaps are treated as "missing" and multistate taxa interpreted as polymorphism. The resulting strict consensus tree is presented in **Figure 1**. Character list and data matrix are presented in the **Supplementary Information**.

Abbreviations: IGF, Instituto geologico di Firenze, Florence, Italy; IVPP V, vertebrate paleontology collection of Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; NHMUK PV M, cast at the Natural History Museum, London, UK; NIH, Nihewan collection of the Muséum national d'Histoire naturelle, Paris, France; NWUV, Institute of Cenozoic Geology and Environment, Northwest University, Xi'an, China; PMU M, Museum of Evolution of Uppsala University, Uppsala, Sweden; THP, Tianjin Natural History Museum, Tianjin, China.

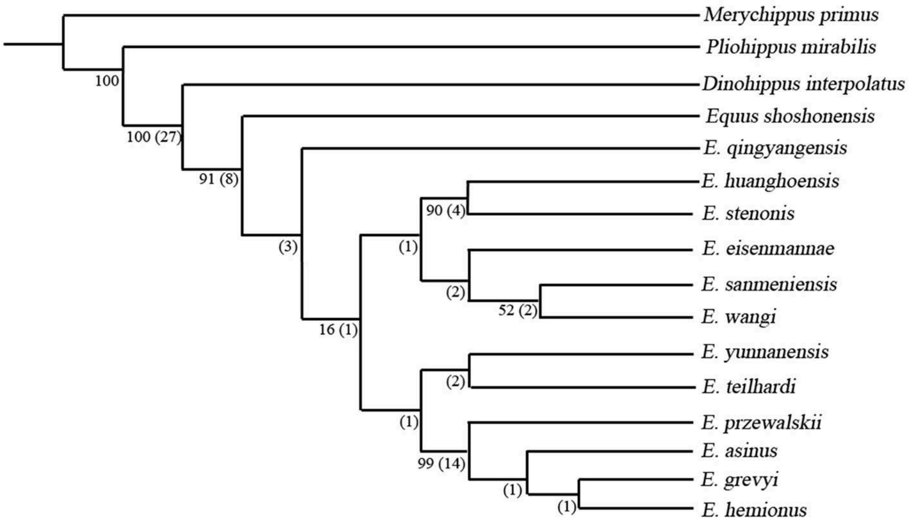

FIGURE 1 | Most parsimonious tree (MPT) obtained from phylogenetic analysis, Tree length = 148, consistency index = 0.635, retention index = 0.768. Numbers by the nodes denote the Bootstrap (outside brackets, not shown if value < 50) and Bremer values (in brackets, not shown if value < 1).

SYSTEMATIC PALEONTOLOGY OF STENONIDS IN CHINA

We review all of the stenonids species in China in the order in which they were erected. All discussions are based on the classical descriptions and the most recent reports. The main localities of stenonids are shown in **Figure 2**.

Order Perissodactyla Owen, 1848
Family Equidae Gray, 1821
Genus *Equus* Linnaeus, 1758
Equus stenonis Cocchi, 1867

Holotype: IGF−560, adult skull with mandible, collected from the Lower Pleistocene of the upper Arno valley in Italy.

Diagnosis (following Deng and Xue, 1999a): large size, facial angle is very narrow, well-developed preorbital pit retained, deep groove along nasal suture, lateral outline of skull undulated, domed parietal, frontal also undulated laterally. DP1 present, diastema elongated, protocone short, hypocone extends lingually, plications complex. Linguaflexid sharply V-shaped, cup on lower incisor developed. Snout elongated, nasal notch very deep, its posterior margin is at the level of mesostyle or even the posterior margin of P3, and the anterior foramen of the palatine canal is open to the level of M3.

Age: Nihewanian, Early Pleistocene.

Distribution: Eurasia and North America.

Remarks: *Equus stenonis* was the first erected stenonid species (**Figure 3**). This species has been studied for a long time, and there is an abundance of specimens. Its fossil record is widespread in Eurasia, and there are many recognized subspecies, although some of them have been upgraded to species, such as *E. livenzovensis* (Alberdi et al., 1998). However, a definite record of *E. stenonis* in China was obtained late.

Azzaroli (1982) observed a skull collected from Taigu, Shanxi Province, that is housed in the Frick Collection in the AMNH. He identified this skull as *E. stenonis*. This is the earliest formal report of *E. stenonis* in China. Forsten (1986) studied the specimens collected from Taigu that are housed in the Licent Collection in the THP. She argued that the protocones of the Taigu specimens were longer than *E. stenonis* material from any locality in Europe, so the Frick specimen should not be considered this species. Azzaroli (1987) argued that the locality information of the Licent specimens was not clear and not comparable to the Frick specimen. Deng and Xue (1999a) observed the Frick specimen based on plate published by Azzaroli (1982) and recognized that many features indeed belonged to *E. stenonis*.

Azzaroli et al. (1988) proposed that *E. stenonis* dispersed into Europe about 2 Ma and survived until the end of the Early Pleistocene at 1 Ma. Deng and Xue (1999a) considered *E. stenonis* to be the probable ancestor of *E. stehlini* and *E. bressanus*, which are both common fossil equids found in Europe. Deng and Xue (1999a) described a molar of *E. stenonis* from Xinyaozi Fauna in Tianzhen, Shanxi and they noted that the age of the Xinyaozi Fauna was older than that of the Nihewan Fauna s. s. Azzaroli and Voorhies (1993) proposed that the North American subspecies *E. stenonis anguinus* occurred about 2 Ma. Therefore, the earliest record of *E. stenonis* known so far is in China, which was probably the center of origin of this species.

Equus sanmeniensis Teilhard de Chardin and Piveteau, 1930

Lectotype: NIH 002 (**Figure 4**), aged adult skull with mandible, collected from Nihewan, Yangyuan, Hebei Province, formally assigned by Eisenmann (1975).

Diagnosis (following Deng and Xue, 1999a): giant build, skull elongated, basal narrow and short so it shown an elongated snout with narrow frontal, DP1 stably present. Protocone elongated

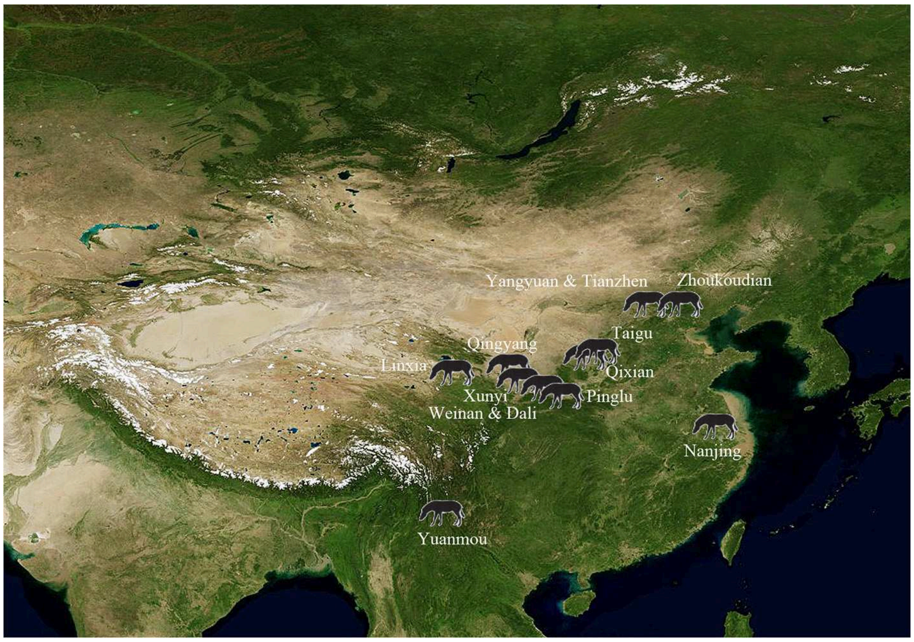

FIGURE 2 | Main localities of stenonids in China.

FIGURE 3 | Right lateral view of cast of holotype skull with mandible of *E. stenonis*, NHMUK PV M 29511.

FIGURE 4 | Right lateral view of lectotype skull of *E. sanmeniensis*, NIH 002, collected from Nihewan Basin.

and concave lingually, labial margins of para- and mesostyle often concave, pli caballine strong, but often diminished to absent by wear, M3 has isolated enamel ring and double-angled occlusal surface. Linguaflexid V-shaped, ectoflexid deep, penetrating into the isthmus, even touching the linguaflexid on lower molars, making lingual margin of linguaflexid and labial margin of ectoflexid flat. Plications complex, but often diminished to absent by wear.

Age: Nihewanian–Zhoukoudianian, Early to Middle Pleistocene.

Distribution: North and Northwest China, Siberia, probably Tajikistan.

Remarks: Teilhard de Chardin and Piveteau (1930) erected the first stenonid species in China, *E. sanmeniensis*. This species was distributed in northern China, Siberia, and Tajikistan from the Early to Middle Pleistocene (Deng and Xue, 1999a). This species evolved early, and was an outcome of the diversification of *Equus* that dispersed into Eurasia approximately 2.5 Ma (see below). *Equus sanmeniensis* has primitive features similar to the earliest *Equus* species in North America, *E. shoshonensis*, such as a transversely undulated lateral outline of skull, groove along the nasal suture, elongated facial part, and obvious preorbital pits. However, *E. sanmeniensis* differs from *E. stenonis* by having a less deep nasal notch and an elongated protocone. All of these features indicate that *E. sanmeniensis* and *E. stenonis* share derived features inherited from some common ancestor type, which most likely lived in North America, but they evolved along different trajectories. Therefore, we conclude that *E. sanmeniensis* and *E. stenonis* underwent parallel evolution, and they have a close but not an ancestor-descendant relationship. Early on, authors tended to identify more stenonid specimens as *E. sanmeniensis*. Teilhard de Chardin and Piveteau (1930) described all *Equus* species they found in the Nihewan Fauna as *E. sanmeniensis*, even though they noticed that there were two different types of specimens. Zdansky (1935) identified all of the stenonid specimens in his study as *E.* cf. *sanmeniensis*. Some of these have been revised (Eisenmann, 1975; Sun et al., 2017); however, we believe that lots of specimens of other stenonid species are still considered *E. sanmeniensis*.

Equus yunnanensis Colbert, 1940

Lectotype (assigned by Deng and Xue, 1999a): IVPP V 4250.1, female skull, about 7–8 years old, extrusion-deformed, well-preserved except for a little damage.

Paralectotype: IVPP V 4251, senile male mandible, coronoid process damaged. All of type specimens are collected from Madahaixigou, Youmou, Yunnan.

Diagnosis (following Deng and Xue, 1999a): Medium size, skull relatively large, frontal narrow, snout elongated. Lingual margin of I3 not enclosed, size of cheek teeth and length of protocone medium, enamel plications usually strong, linguaflexid V-shaped, metaconid and metastylid very rounded, ectoflexid shallow, rarely penetrates into the isthmus even on lower molars, pli caballinid not strong, posterior tip of m3 halberd-shaped. Distal limb robust.

Age: Nihewanian to Salawusuan, Early to Late Pleistocene.

Distribution: Yuanmou, Yunnan; Liucheng, Guangxi; Jianshi and Enshi, Hubei; Hanzhong, Shaanxi; Huili, Sichuan; Irawaddy, Myanmar.

Remarks: Colbert (1940) erected *E. yunnanensis* based only on isolated cheek teeth. Therefore, it was difficult for researchers to conduct enough work on morphology of this species. Fortunately, Liu and You (1974) discovered and reported well-preserved cranial and limb specimens from Yuanmou Basin. They observed much more morphological information than Colbert (1940) and further discussed the relationships of Asian *Equus*. They argued that *E. yunnanensis* should be considered a separate lineage distinct from other species in South Asia. They suggested that *Equus* sp. found in Huili, Sichuan Province, was likely derived from *E. yunnanensis*. Therefore, this lineage seemed to have dispersed to the north. Deng and Xue (1999a) thought that *E. yunnanensis* and *E. wangi* were closely related because they shared similar derived features, such as rounded double-knots and short ectoflexids. Pei (1961) noted that *E. yunnanensis* was an equid species similar to asses and horses based on its short ectoflexid. Deng and Xue (1999a) argued that short ectoflexids should not be thought to be particular to asses, because other equids, such as *E. wangi* and *E. przewalskii*, also have this feature. Based mainly on rounded double-knots and short ectoflexids, Deng and Xue (1999a) considered these species sister-groups. Gromova (1949) and Deng and Xue (1999a) both suggested that the different dental features, such as the morphology of enamel plications on the upper cheek teeth, were adaptations to different environments. As an increasing number of specimens have been discovered, the arguments regarding phylogenetic relationships were revised in recent years. We propose some new ideas about the relationship between *E. yunnanensis* and other stenonid species below.

Equus huanghoensis Chow and Liu, 1959

Holotype: IVPP V 2385–2389, three upper premolars and two upper molars, collected from bank of Yellow River (Huanghe) in Sanmenxia, Pinglu, Shanxi Province.

Diagnosis (following Li et al., 2016): Large skull with elongated face and snout; outline of parietal part undulated as seen in lateral view. Nasal-frontal-parietal part with hollow in middle part and upturned anterior end, middle groove of nasal bone narrow. Nasal notch deepens to reach level of boundary of P3/P4. Orbit posterior of cheek teeth row, anterior foramen of palatine canal opens posteriorly; interalveolar margin long. Occipital plane pentagonal, and supramagnum protuber strong. Protocone shortened, mesostyle robust, pli caballine very weak, and plication simple. Mandible elongated. Condyle of mandible elongated transversely with rounded anterior margin and cupped internally posterior margin. Cups of lower i3 enclosed, pli caballinid weak to absent, enamel plication of post-flexid strong, and linguaflexid V-shaped. **Locality and age:** Nihewanian, Early Pleistocene. **Distribution:** Nihewan, Hebei; Linyi, Shanxi; Sanmenxia, Pinglu, Shanxi; Xunyi, Shaanxi; Nanjing, Jiangsu.

Remarks: Chow and Liu (1959) erected *Equus huanghoensis* based on five isolated upper cheek teeth collected from Sanmenxia, Pinglu, Shanxi Province. Forsten (1986) reviewed numerous classical specimens of Chinese fossil *Equus*. She identified a skull from the Lagrelius Collection in the Museum of Evolution, Uppsala University, as? *Equus huanghoensis* based on the very short protocone of this specimen. Deng and Xue (1999a) described *E. huanghoensis* specimens from Xunyi, Shaanxi Province, and stated that *E. huanghoensis* is primitive because of its very short protocone, and further identified this species as a stenonid. Dong and Fang (2005) reported some fragmented cranial material of *E. huanghoensis* from Tangshan, Nanjing, Jiangsu Province. Li et al. (2016) reported the most complete material ever known of *E. huanghoensis* from Nihewan, Yangyuan, Hebei Province, which included a complete skull with a broken mandible, and described all of the critical features of this species (**Figure 5**). *Equus huanghoensis* is a very large stenonid species with deep nasal notch, lower cranial proportion, elongated snout and facial part, and V-shaped linguaflexid. All of these features supported Deng and Xue's argument that *E. huanghoensis* is a stenonid species. Based on the measurements of Nihewan material, *E. huanghoensis* is one of the *Equus* species with the largest absolute and relative palatal lengths, and is similar to *E. eisenmannae*, which was the largest *Equus* species in China (Qiu et al., 2004; **Figure 6**). Deng and Xue (1999a) suggested that the age of *E. huanghoensis* was in the Early Nihewanian (2.5–1.8 Ma). Ao et al. (2013b) suggested that the age of the *E. huanghoensis* specimens from Nihewan was around 1.7 Ma. This is the youngest record of *E. huanghoensis* ever known in China. In addition, the Nihewan material is smaller compared with the holotype from Sanmenxia. Li et al. (2016) indicated that the P4 and M2 lengths of the holotype are around 1.16 times larger than those of the Nihewan specimen. The ratio between the length of the basilar and cheek tooth row is generally stable in *Equus* (**Figure 7**). Based on this ratio, the holotype teeth should belong to a very large individual whose basilar length was 647.28 mm, in contrast with that of *E. eisenmannae* (625 mm, Qiu et al., 2004).

Equus teilhardi Eisenmann, 1975

Holotype: NIH 001, a broken mandible with symphysis and left ramus.

Diagnosis (following Sun et al., 2017): Middle size. The nasal notch extends above the mid-P2 to the boundary of P2/P3. Snout short, preorbital fossa shallow with indistinct border, lateral outline is undulated, deep groove along nasal suture. Cups of incisors possibly incomplete or even lacking. The upper cheek teeth have simple fossettes, short protocones and weak plis caballines. The lower cheek teeth have V-shaped linguaflexids and deep ectoflexids on molar that penetrate into the isthmuses, even touching the linguaflexids on the lower molars. The limb bones are short and robust. **Distribution:** Northwestern and northern China. **Age:** Nihewanian, Early Pleistocene.

FIGURE 5 | Left lateral view of skull of *E. huanghoensis*, NWUV 1403.1, collected from Yangshuizhan Locality, Nihewan Basin. Scale bar = 5 cm.

Remarks: When Teilhard de Chardin and Piveteau (1930) erected *E. sanmeniensis*, they recognized two forms of Nihewan specimens with different body sizes. However, they did not resolve this issue and still identified all specimens as *E. sanmeniensis*. In Zdansky's study on Chinese fossil *Equus*, he described many specimens with different features and from different localities as *Equus* cf. *sanmeniensis*. Later, when Eisenmann studied Nihewan equids housed in Paris, she erected *E. teilhardi* based on a broken mandible. Eisenmann (1975) only listed two features in the diagnosis: small size and lack of lower incisor cup. Forsten (1986) studied the equid materials of the Nihewan fauna collected by Licent and identified two fragmented cranial specimens (THP 00150, 00151) as *E. teilhardi*. She proposed many important features for cranial and dental morphology. Deng and Xue (1999a) described a left ramus fragment (NWUV 1243) from Bajiazui, Qingyang, Gansu Province. They focused on the absence of a cup on the lower incisor of *E. teilhardi* and argued that this species should be regarded as a lineage distinct from other Eurasian stenonids. Sun et al. (2017) reviewed the equid specimens in the Lagrelius Collection described by Zdansky (1935) and recognized a skull from Qixian, Shanxi Province, as *E. teilhardi* (**Figure 8**). The features of this skull are basically identical to those described by Forsten. Based on measurements of Qixian material, Sun et al. (2017) noted that *E. teilhardi* had relatively shorter distal limbs

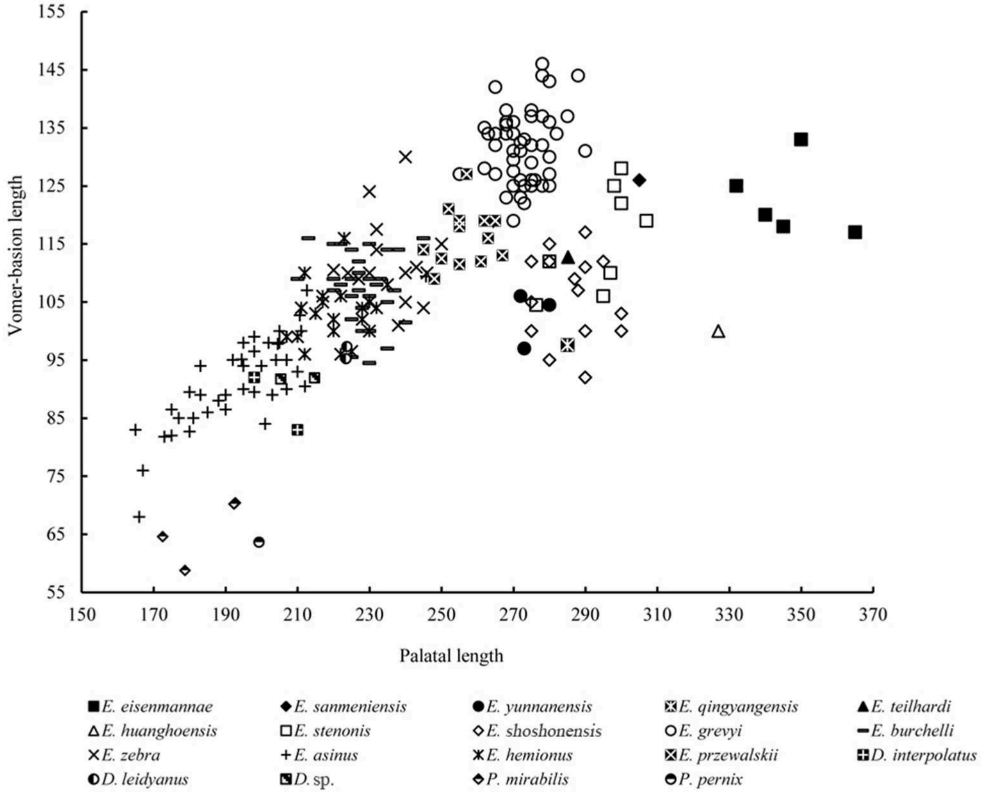

FIGURE 6 | Comparison of lengths of palatine and basicranial in several extinct and extant species of Equidae. Abbreviations of genera: *E*, *Equus*; *D*, *Dinohippus*; *P*, *Pliohippus* (same in below).

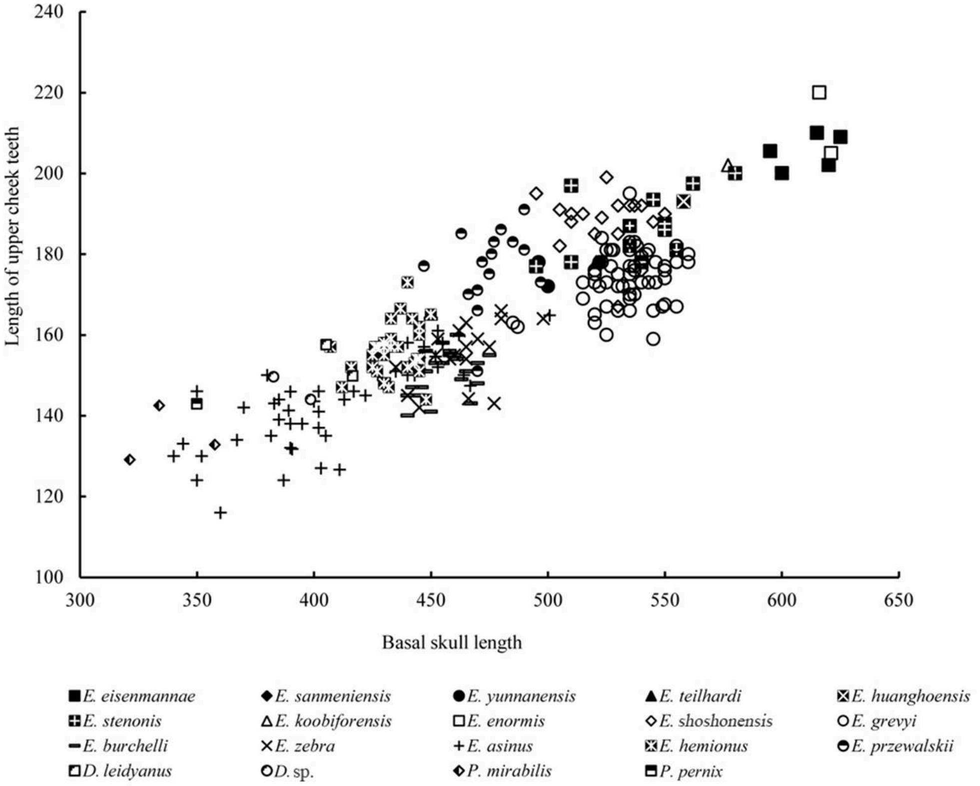

FIGURE 7 | Comparison of cheek tooth row length and basilar length in several extinct and extant species of Equidae.

FIGURE 8 | Left lateral view of skull of *E. teilhardi*, PMU M 1321, collected from Qixian, Shanxi, housed in Museum of Evolution, Uppsala University. Scale bar = 5 cm.

than most Eurasian stenonids. Additionally, based on the I3 character of Qixian material and observation of other early *Equus* specimens, such as *E. shoshonensis* in the Hagerman Collection, Sun et al. (2017) argued that the lack of a lower incisor cup of *E. teilhardi* was due to variation. Some European stenonid horses, such as *E. stehlini*, also have incomplete lower incisor cups (Azzaroli, 1965, 1982). Based on skull and post-cranial morphology, Sun et al. (2017) hypothesized that *E. teilhardi* and *E. yunnanensis* were probably closely related.

Equus qingyangensis Deng and Xue, 1999b

Holotype: NWUV 1128, the middle and back of a skull with all cheek teeth, about 12 years. **Diagnosis:** Medium size. Nasal notch extends above back of P2, preorbital pit is shallow with indistinct border, deep groove along the nasal suture. The upper teeth have long protocones and weak plis caballines. The lower teeth have typical V-shaped linguaflexids and deep ectoflexids that penetrate into the isthmuses or even touch the linguaflexids on the lower molars. The limb bones are slender. The metacarpal middle shaft index is smaller than 13.5 and the metatarsal smaller than 12.0. It was the early species of *Equus* with the most slender limb bones in Eurasia. **Distribution:** Northwestern and northern China. **Age:** Nihewanian, Early Pleistocene.

Remarks: Deng and Xue (1999b) erected a new stenonid species, *E. qingyangensis*. According to their description, although *E. qingyangensis* is morphologically similar to *E. sanmeniensis*, except for the large body size of the latter, *E. qingyangensis* has some impressive features that have never been found in known stenonid horses in China. For example, its skull has about a 12 mm distance between the temporal condyle and the posterior margin of the orbital bar (Deng and Xue, 1999a). This is a primitive feature because of its presence in the hipparionine genus *Proboscidipparion* (Qiu et al., 1987), and in some primitive equid species, based on our observation, such as *Pliohippus*. In contrast, these two constructs are adjacent in most extinct and extant *Equus* species. The Mc III of *E. qingyangensis* is more slender than those of all known stenonid horses, with a middle shaft index of 13.3 (Deng and Xue, 1999a). Eisenmann and Deng (2005) collected measurements of *E. qingyangensis*, other Eurasian stenonids, and North American early *Equus*, and conducted a series of statistical analyses. They concluded that *E. qingyangensis* are similar to *E. shoshonensis* but different from *E. stenonis* based on cranial and post-cranial proportions. Our plot also shows that *E. qingyangensis* has very low ratio of cranial part (**Figure 9**), which has been regarded as a primitive feature (Qiu et al., 2004). Sun et al. (2017) found a similar phenomenon. Based on observation of the Hagerman Collection, they indicated that *E. shoshonensis* also have about a 10–12 mm distance between the temporal condyle and the posterior margin of the orbital bar, which is identical to that of *E. qingyangensis*. Eisenmann and Deng (2005) argued that *E. shoshonensis* and *E. qingyangensis* probably have a direct ancestor-descendant relationship and represent a lineage that is distinct from the Eurasian species *E. stenonis*. Sun et al. (2017) also hypothesized that *E. qingyangensis* may be a direct descendant of *E. shoshonensis* and the earliest and most primitive stenonid species in Eurasia.

Equus wangi Deng and Xue, 1999c

Holotype: NWUV 1170, complete upper and lower cheek tooth rows that belong to an individual, and the upper tooth rows go with the remains of the maxillae, about 5 years.

Diagnosis: Teeth are very large. DP1 present. Protocones long, narrow and middle-grooved. Mesostyles flat or lightly middle-grooved. Enamel plications strong, especially on the premolars. Hypoconal grooves on premolars with flat bottoms. The m3 has a double-angled back margin and an enamel lake within its hypocone. The double–knots are very circular so that their metastylids do not have posterior angles. Linguaflexids wide and sharply V-shaped. Ectoflexids shallow so that they never penetrate into isthmuses even on molars, and post-flexids correspondingly long. Plis caballinid much developed. Enamel plications of post-flexids strong. Entoconids on premolars with sharp beak-shaped ends. Hypoconulid on m3 like a short dagger with a wide and round end.

Distribution: Qingyang, Gansu.

Age: Nihewanian, Early Pleistocene.

Remarks: Deng and Xue (1999c) erected a new species, *E. wangi*, based on cheek tooth rows and a cranial fragment from Bajiazui, Qingyang, Gansu Province. They estimated that this species has a deep mid-nasal groove and preorbital pit based on the broken skull. The cheek tooth size of *E. wangi* is very large, similar to *E. sanmeniensis*, *E. huanghoensis*, and *E. eisenmannae*. However, *E. wangi* has obvious morphological differences from *E. sanmeniensis* and *E. huanghoensis*. *Equus wangi* has features in common with *E. yunnanensis*, such as circular metastylids and shallow ectoflexids (Deng and Xue, 1999a). Qiu et al. (2004) noted that *E. eisenmannae* has many characters in common with *E. wangi*, including large cheek teeth, short plis caballine, simple mesostyles, strong enamel plications, rounded double-knots, shallow ectoflexids, and elongated post-flexids. Another unusual feature of *E. wangi* is its beak-shaped entoconid. According to Qiu et al. (2004) and Wang and Deng (2011), *E. eisenmannae* also has similar lower premolar structures. Therefore, *E. wangi* is probably more closely related to *E. eisenmannae* than other stenonid species. In addition, *E. wangi* is similar to *E. shoshonensis* from Hagerman, Idaho, USA based on its very circular double-knot, beak-shaped premolar, and sharp V-shaped linguaflexid (Deng and Xue, 1999a). *Equus shoshonensis* was the earliest *Equus* species, whereas *E. yunnanensis* and *E. eisenmannae* occurred during the beginning of the Quaternary in China. Consequently, *E. wangi* should be a very primitive lineage. Deng and Xue suggested that first occurrence of *E. wangi* was between 2.5 and 2.4 Ma.

Equus eisenmannae Qiu et al., 2004

Holotype: IVPP V13552, a complete adult and male skull (**Figure 10**) with its mandible, about 12 years old.

Diagnosis: (1) giant size with a basal skull length of 613.8 mm on average; (2) longer face than in any known horses; (3) shallow preorbital fossa; (4) high vomer index (111.2–133.9); (5) long distance between orbit and third molar; (6) rounded double-knots of lower cheek teeth; (7) shallow labial valleys on lower molars. Character states 2–6 are primitive within horses; character states 1 and 7 are considered derived.

Distribution: Longdan, Dongxiang County, Gansu Province.

Age: Nihewanian, Early Pleistocene.

Remarks: *Equus eisenmannae* was the most recently erected stenonid species in China. This species is very interesting. Based on measurement and comparison, Qiu et al. (2004) noted that *E. eisenmannae* was one of the largest *Equus* species (**Figure 7**). Furthermore, facial and snout lengths, and absolute and relative palatal lengths, were all larger than those of any other known *Equus* species (**Figures 6**, **11**, **12**). However, based on the method proposed by Eisenmann and Karchoud (1982), Qiu et al. (2004), and Sun et al. (2017) compared the Mc III and cranial basilar lengths among all Chinese stenonid horses and determined that *E. eisenmannae* has the largest relative robustness of Mc III. *Equus eisenmannae* also has the most abundant cranial material record among Chinese stenonids, including several complete skulls from different fossiliferous levels. Qiu et al. (2004) noticed that individuals from different levels have morphologic differences; for example, individuals from the upper level have larger cranial proportions, deeper ectoflexids in the lower molars, and sharper post-erolingual angles of the metastylid. Wang and Deng (2011) performed univariate and multivariate analyses on all specimens from different levels in the locality where *E. eisenmannae* was recovered. They concluded that the differences between *E. eisenmannae* samples across the two stratigraphic intervals were not significant enough to warrant recognizing two species. They also discussed some critical trends in equid evolution based on their comparison between *E. eisenmannae* and modern horses (Forsten, 1988; Azzaroli, 1992; Eisenmann, 1996; Prado and Alberdi, 1996; Eisenmann and Baylac, 2000). Qiu et al. (2004) summarized the important features of *E. eisenmannae* and indicated that its beak-shaped entoconids on the lower premolars and rounded double-knots were similar to those of *E. wangi*, and its oval entoconids on the lower molars and shallow labial valley not reaching the isthmus were similar to those of *E. yunnanensis* and *E. wangi*. They also argued that *E. eisenmannae* is a transitional form between North American plesippines and Eurasian allohippines (i.e., stenonids).

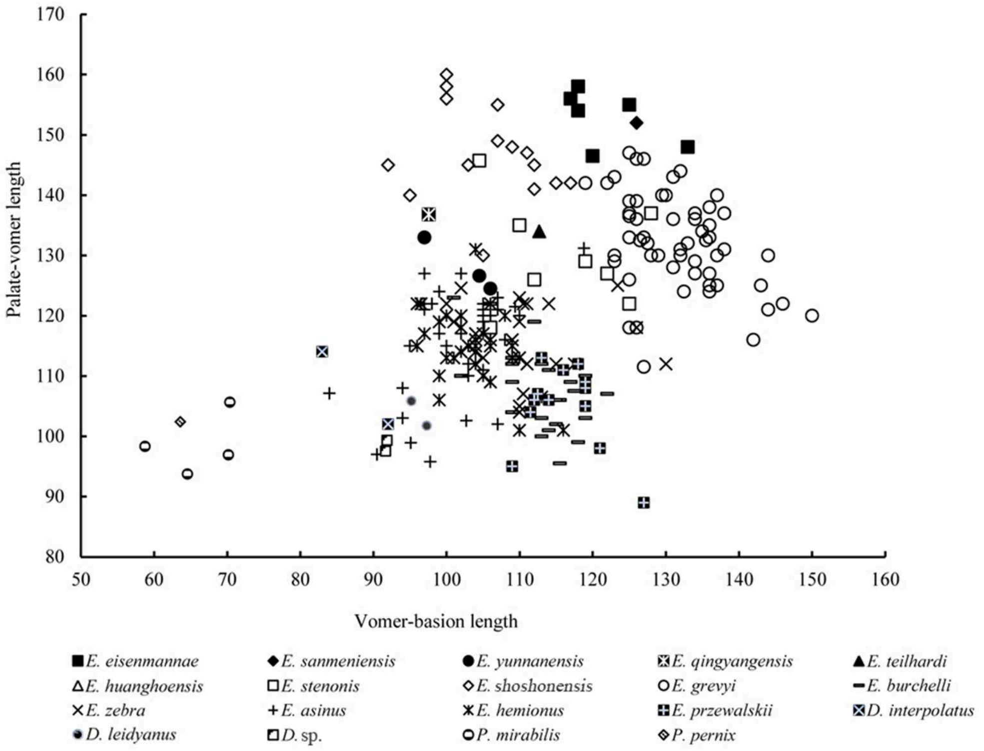

FIGURE 9 | Comparison of basicranial proportion in several extinct and extant species of Equidea.

FIGURE 10 | Right lateral view of holotype skull of *E. eisenmannae*, IVPP V 13552, collected from Longdan Locality, Linxia Basin. Scale bar = 5 cm.

SUMMARY OF CHINESE STENONID PHYLOGENETIC RELATIONSHIPS

Deng and Xue (1999d) reviewed all of the fossil equids in China and summarized their relationships in a phylogenetic tree. They proposed that *E. teilhardi* and *E. huanghoensis* are two independent lineages alone and traced these two species directly back to *E. shoshonensis*. They could not recognize diagnostic properties of these two species because of lack of complete material. Deng and Xue (1999a) considered the other stenonid species they reviewed to be a clade, within which *E. qingyangensis* was a separate lineage that they suggested directly dispersed into Eurasia as a New World origin. *Equus wangi* and *E. yunnanensis* are sister groups, as were *E. stenonis* and *E. sanmeniensis*. The establishment of these groups was also based on the morphological similarities we discussed above. As new lineages are discovered and more complete material of known species reported, it is necessary to perform a new review of the stenonid horses in China.

Some authors have suggested that *Equus* originated within genus *Dinohippus*, a large monodactyl form constrained to the New World (Bennett, 1980; Dalquest, 1988; MacFadden, 2005, 2006; Pagnac, 2006). In the current research, we try to figure out the origin of *Equus* in different method and then obtain different conclusions. In our plots, stenonids are more similar to *Pliohippus* in cranial proportion rather than to *Dinohippus*, caballoids, hemiones, asinines, and zebrines (**Figures 6**, **9**, **11**, **12**). On the other hand, we perform a phylogenetic analysis. The analysis yield one parsimonious tree, shows a new phylogenetic relation between primitive monodactyl equids, stenonids, and some extant species (**Figures 1**, **13**). In this phylogenetic tree, a monophyletic clade consists of species of *Equus* forms sister groups with species of *Dinohippus*. Moreover, the clade consists of *Equus* and *Dinohippus* forms sister groups with species of *Pliohippus*.

Eisenmann and Deng (2005) agreed with Deng and Xue's argument regarding the phylogenetic position of *E. qingyangensis*. Consequently, there were likely at least two dispersal waves of *Equus* into the Old World, with one wave represented by *E. qingyangensis*. Eisenmann and Deng (2005) argued that *E. shoshonensis* may be the direct ancestor of *E. qingyangensis*. In our result of new phylogenetic analysis, *E. qingyangensis* is attributed in a clade distinguished from all other species. This probably represents an independent dispersal event,

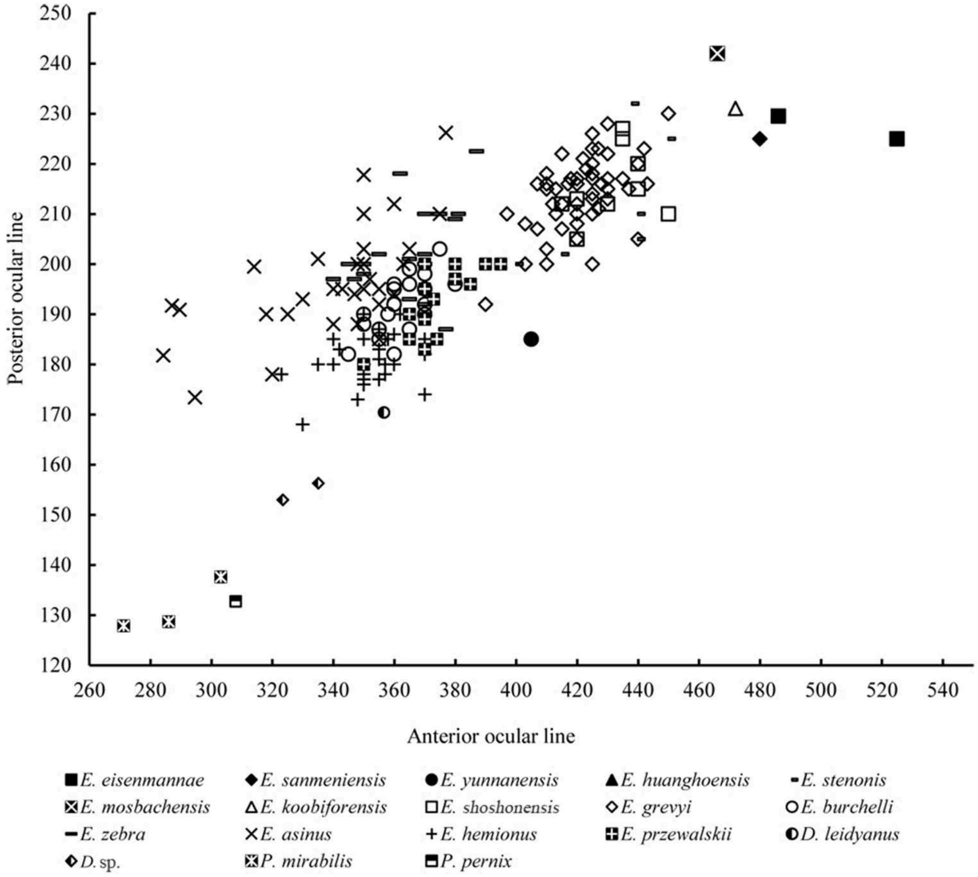

FIGURE 11 | Comparison of anterior and posterior ocular lengths in several extinct and extant species of Equidae.

and accords with the arguments of Deng and Xue (1999a) and Eisenmann and Deng (2005).

In the new phylogenetic tree, large-sized stenonid species form a clade. Large body size is a primitive character. Body size decrease was an important trend in equid evolution (Eisenmann and Baylac, 2000; Wang and Deng, 2011). The earliest *Equus* species in Europe, *E. livenzovensis*, is also very large, and is thought to have lived 2.5 Ma in Italy, Spain, and Russia. According to geochronological data, the first occurrences of *E. huanghoensis* and *E. eisenmannae* were close to the lower boundary of the Quaternary (see below). Although these huge species of Chinese stenonid have primitive body size and early geohistorical distribution, their features are derived. This probably suggested that the differentiation of early *Equus* was significantly earlier than 2.58 Ma. Qiu et al. (2004) considered *E. eisenmannae* to be the ancestor of *E. sanmeniensis* and *E. stenonis*. Based on morphology of cranial and dental features, *E. eisenmannae* is more closely related to *E. sanmeniensis* than *E. stenonis*. They share some morphological similarities, such as extremely large body size (basilar length of type skull of *E. sanmeniensis* is 585 mm, this length of *E. eisenmannae* is 613 mm), shallow nasal notch, elongated protocone, and strong enamel plications on upper cheek teeth. In addition, based on morphological features, *E. wangi*, *E. sanmeniensis* and *E. eisenmannae* probably have the closest relationship, fits the result of our phylogenetic analysis. *Equus wangi* and *E. sanmeniensis* formed a lineage as sister groups, which form a group with *E. eisenmannae*. *Equus huanghoensis* and *E. stenonis* shared features such as a transversely undulated forehead, very deep nasal notch, short protocone, and very weak enamel plications on upper cheek teeth. These similarities also fit the result of our phylogenetic analysis, in which *Equus huanghoensis* and *E. stenonis* form sister groups.

Previously, due to poor material, it was difficult to recognize the phylogenetic position of *E. teilhardi* (Eisenmann, 1975; Forsten, 1986). Recently, a report on a nearly complete skull of *E. teilhardi* provided a perfect opportunity to discuss this species (Sun et al., 2017). Most stenonid species have large body size, elongated facial part and limbs. In contrast, *E. teilhardi* has medium body size, a short snout and robust metapodials (Sun et al., 2017). *E. yunnanensis* has similar cranial and post-cranial features as *E. teilhardi*, such as body size, cranial proportions and limb shape. In the result of our phylogenetic analysis, *E. teilhardi* forms sister groups with *E. yunnanensis*. This result fits the similarities above in morphology feature. Due to the introduction of extant species (caballoid,

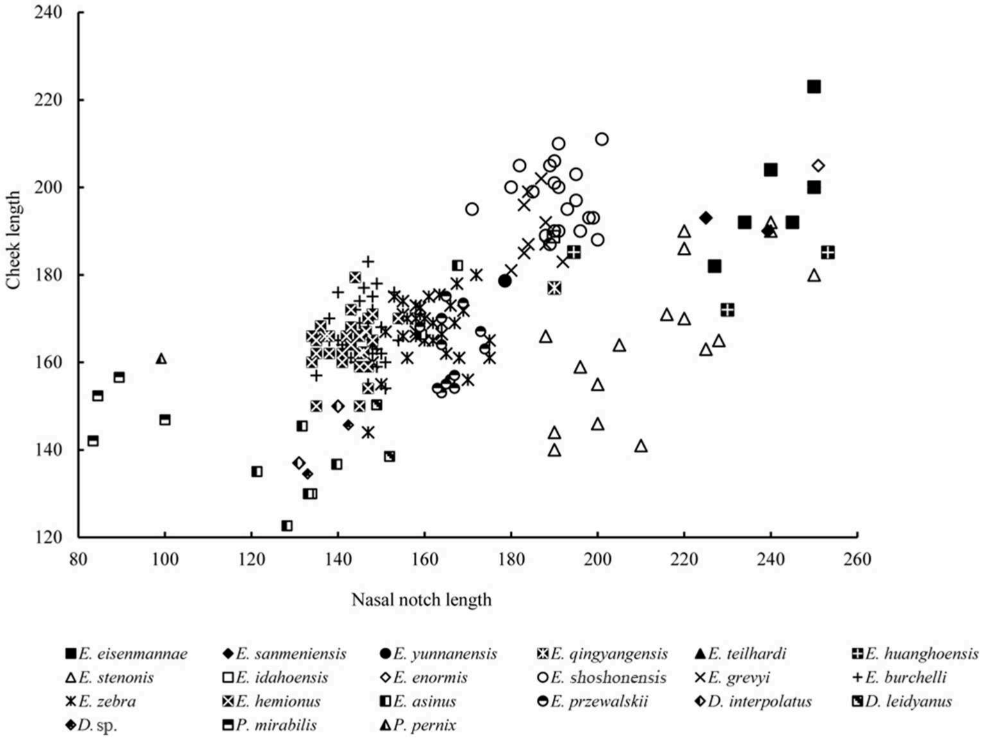

FIGURE 12 | Comparison of lengths of nasal notch and cheek in several extinct and extant species of Equidae.

hemione, asinine, and zebrine), we achieve a completely new pattern of early evolution of *Equus*. The clade consisting of *E. teilhardi* and *E. yunnanensis* forms sister groups with all extant species, distinct from the clade that consists of all other stenonid species. Based on this result, probably the "stenonids" are not a phylogenetic unit any more, but just a morphologic concept. *E. teilhardi* and *E. yunnanensis* are not typical stenonid species, they both have relatively short facial part and robust limbs, which are more similar to most extant species. Probably these two species are closer to extant forms rather than other stenonid species.

THE *EQUUS* DATUM IN CHINA AND THE LOWER BOUNDARY OF THE QUATERNARY

Deng and Xue (1997) demonstrated once again the significance of the *Equus* Datum. They argued that the first appearance of *Equus* can be considered an easily recognized sign of the lower boundary of the Quaternary in Eurasia. Indeed, the first appearance of *Equus* was roughly contemporary with many important geological events around 2.5 Ma, such as the Matsuyama/Gauss boundary as determined by magnetostratigraphy, the beginning of loess accumulation in China, the appearance of the ice cap in the Arctic (Backman, 1979) and the first strengthening of neotectonism (Zhu et al., 1994). In recent decades, we put substantial effort into describing the classical localities of the Early Pleistocene in China to correlate the Quaternary mammalian paleontology in China relative to that throughout Eurasia.

Nihewan Basin

In 1924, Barbour observed the strata of Nihewan, Yangyuan, Hebei Province (**Figure 2**) and established a stratigraphic unit, the Nihewan Beds. Afterwards, Barbour, Licent, Teilhard de Chardin, and Piveteau further studied the Nihewan Beds and their mammalian fossils. In 1948, IGC (International Geology Congress) regarded the Villafranchian as the lower boundary of the terrestrial Pleistocene in Europe, which suggested that the Nihewan Beds represented the lower boundary of the Pleistocene in China. The suggestion was formally approved and used by Chinese geologists in 1954.

Along with research progress, a lot of different viewpoints about the Nihewan Beds have emerged, the main three of which are: (1) the Nihewan Beds are assigned to the Lower Pleistocene; (2) the Nihewan Beds consist of the Lower Pleistocene and Middle Pleistocene; and (3) the Nihewan Beds may include Lower–Middle Pleistocene and Upper Pleistocene, and even Pliocene (Wei and Xie, 1989).

Tang and Ji (1983) established the Dongyaozitou Formation and its accompanying Dongyaozitou Fauna on the basis of the Dongyaozitou section in Yuxian, Hebei Province. Based on the components of this fauna, Deng and Xue (1999a) assigned it to the Pliocene.

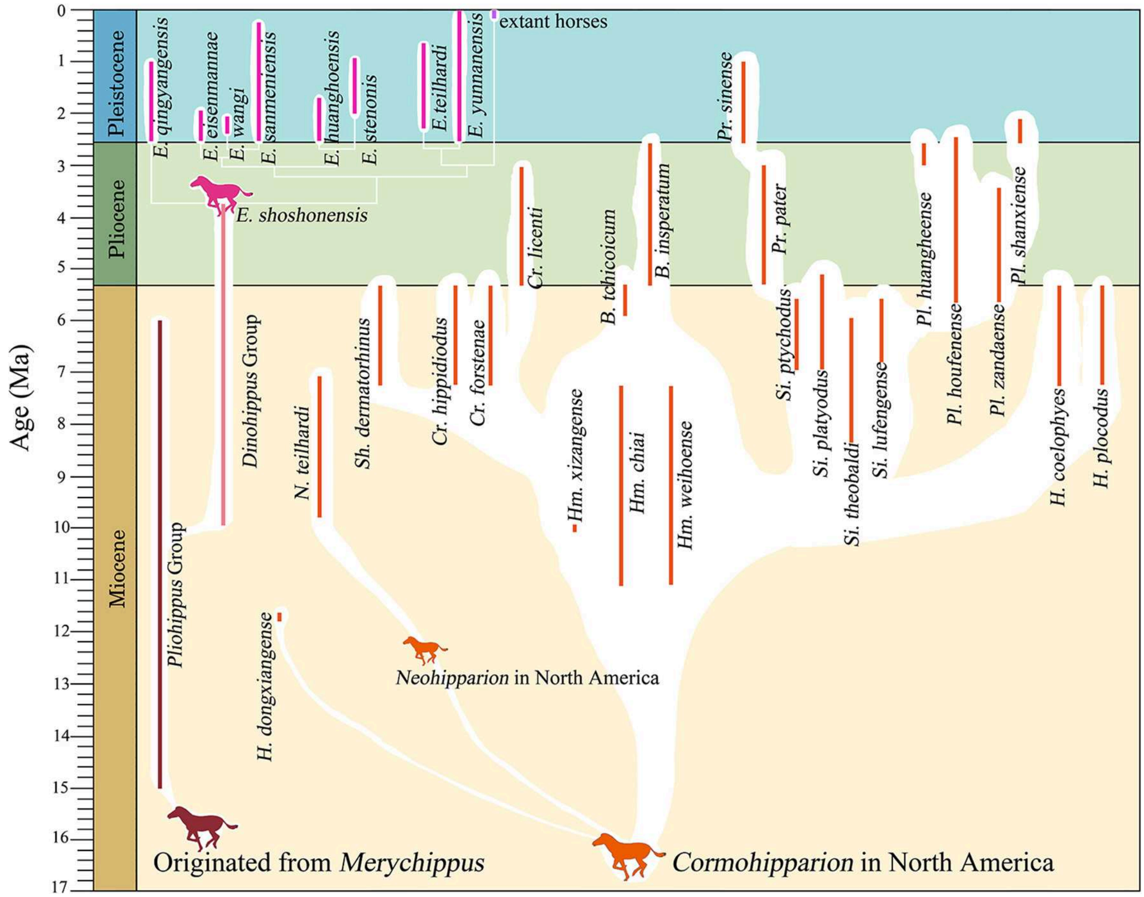

FIGURE 13 | Proposed phylogenetic interrelationships of species of hipparionine and genus *Equus* in China, based on Qiu et al. (1987), Li and Li (1990), Deng and Xue (1999a), MacFadden (2005), Sun (2013), Wolf et al. (2013), Deng et al. (2016), Bernor et al. (2018), and Sun et al. (2018). Abbreviations of genera: H, *Hipparion* (a polyphyletic group including all the species with undefined attribution); N, *Neohipparion*; Sh, *Shanxihippus*; Cr, *Cremohipparion*; Hm, *Hippotherium*; B, *Baryhipparion*; Pr, *Proboscidipparion*; Si, *Sivalhippus*; Pl, *Pliohipparion*; E, *Equus*.

Li (1984) discovered typical Nihewan Fauna in the Danangou section above the Dongyaozitou Formation in Yuxian. Most of the fossils are the main members of the Nihewan Fauna. Based on the primitive features of the micromammals, this section was shown to represent the earliest horizon of the Pleistocene (i.e., the Nihewan Formation) (Zheng, 1981). Because the Nihewan Fauna is located between the two formations in Danangou, Yuxian, the first appearance of *Equus* corresponds to their boundary.

Wu et al. (1995) studied the age of the Nihewan Beds, especially the lower boundary of the Quaternary, by amino acid dating. The dating samples are bones collected from a grayish-white gravel bed in the lower part of the Dongyaozitou Formation in Yuxian, which is 2.78 Ma old. Wu et al. thought that the lower boundary of the Quaternary in this region should be the lower boundary of the Nihewan Formation but above the Dongyaozitou Formation in the Danangou section, and that it was about 2.5 Ma old.

Cai et al. (2004) chose the Danangou section as the type section of Nihewan Formation. They divided this section into four informal lithological members. They noted that *Equus* was accompanied by hipparionines in member 2. They suggested that the base of member 2 corresponded to the lower boundary of the Quaternary (about 2.58 Ma) based on the micromammalian fossil assemblage. Recently, an increasing number of studies on magnetostratigraphy suggested that the oldest sediments of the Nihewan beds date back to about 2.5 Ma, which is roughly corresponds to the Plio-Pleistocene boundary (Zhu et al., 2007; Deng et al., 2008; Gibbard and Head, 2010; Liu et al., 2012, 2018; Ao et al., 2013a).

Yuanmou Basin

The Yuanmou Basin in Yunnan Province has been the type region of the Early Pleistocene strata in South China (**Figure 2**), and it has been researched for as long as the Nihewan region. In the 1920s—1930s, Walter Granger collected mammalian fossils from the Yuanmou Basin. In the 1940s, Colbert (1940) studied these fossils and named a fossil horse among them *E. yunnanensis*. He thought that these fossils corresponded to the fauna of the Upper Irrawaddy in Myanmar and the Early

Pleistocene Nihewan Beds in North China based on the horse's small size and some primitive features of its teeth.

Pei (1961) suggested that the Early Pleistocene strata, which had yielded *E. yunnanensis*, should correspond to the Pinjor and Tatrot Beds of the Upper Siwalik in the Indo-Pakistani subcontinent, and its geological age should correspond to the Villafranchian in Europe. After discovering human fossils in 1965, a lot of researchers began to study this region and proposed some different viewpoints.

The fossiliferous beds in the Yuanmou Basin are included in the Yuanmou Formation, which is subdivided into four members. Li (1981) thought the fossils that were collected from the Yuanmou Basin could be divided into two groups: one group at Members 1–2, which contains Late Pliocene forest mammals, and another group at Members 3–4, which contains some surviving Neogene mammals. The latter's extinction rate was rather high, but there are also some Quaternary mammals that were widespread in North and South China, such as *E. yunnanensis*. Members 3–4 do not contain forms of the *Ailuropoda-Stegodon* Fauna; therefore, it should be assigned to the Early Pleistocene.

Qian and Zhou (1991) separated the fossils from Members 1–2 of the Yuanmou Formation from the previously confused "Yuanmou Fauna" and named them the Shagou Fauna. Chow (1961) first thought that this fauna corresponded to that of the Dhok Pathan Beds of the Middle Siwalik in India, which have yielded a similar fauna and date to the Late Pliocene. The Shagou Fauna does not contain *Equus*. The Xiaohe Fauna is under the Shagou Fauna. Qian et al. thought that the Xiaohe Fauna corresponded to the Middle Siwalik Fauna in South Asia, the Baode Fauna in North China, and the Lufeng Fauna in Yunnan, so it should undoubtedly be assigned to the Pliocene. Qian et al. had a different viewpoint from Chow (1961), but Zhang et al. (1978) and some other authors thought that the Xiaohe Fauna is actually included in the Shagou Formation and this formation belongs to the Pliocene.

The Yuanmou Fauna is located above the Shagou Fauna and collected from Members 3–4 of the Yuanmou Formation. The Yuanmou Fauna contains rich mammalian fossils, including *Homo erectus yuanmouensis*, which is famous in Chinese paleoanthropology research, in its upper part, mammalian survivors of the Neogene, of which the extinction rate was 93%, and Early Pleistocene mammals. Deng and Xue (1999a) indicated that firstly Yuanmou Fauna contains Early Pleistocene mammal such as *E. yunnanensis*, *Canis yuanmouensis*, *Hyaena licenti*, *Stegodon elephantoides*, *Axis shansius*, *Axis* cf. *rugosus*, *Rusa yunnanensis*, etc.; there are also some survivors of the Neogene mammals; and the members which commonly occur in the *Ailuropoda-Stegodon* fauna in the Pleistocene in south China such as *Ailuropoda*, *Tapirus*, *Ursus*, *Pongo,* and *Macaca*. They concluded that Yuanmou Fauna has been shown to be the earliest Early Pleistocene fauna.

Because *Equus* is absent from the Shagou Fauna, *E. yunnanensis* is the first appearance of *Equus* in the Yuanmou Fauna and its earliest appearance was in Member 3 of the Yuanmou Formation. Paleomagnetic dating revealed that the Matsuyama/Gauss boundary, which is located on the bottom of Member 3 (Qian and Zhou, 1991), dates to about 2.58 Ma. Moreover, according to the fission track dating performed by Qian and Zhou (1991), the age of the upper section of Shagou Formation was 2.59 Ma. *Equus yunnanensis* happens to appear at this boundary, which thus corresponds well with the lower boundary of the Quaternary.

According to a highly resolved magnetostratigraphic analysis performed by Zhu et al. (2008), the sediments of the Yuanmou Basin, which were divided into 17 polarity units, should be grouped into three distinct directional intervals. The base of Group I, which represented the lower boundary of the Quaternary, dates to 2.58 Ma.

Linxia Basin

The Linxia Basin is located in the east of Gansu Province (**Figure 2**). Since the end of the 1980s, the Linxia Basin has been famous for its wealth of fossil mammals. In May of 1999, while identifying the "dragon bones" obtained by a local "dragon bone" dealer, Zhanxiang Qiu noticed some canid fossils from loess deposits. Based on the dealer's information, Qiu found a very fossiliferous locality in Longdan Village, Dongxiang Autonomous County. After about 1 year, Qiu and his colleagues collected more than 100 specimens, mainly skulls and mandibles. Consequently, the Longdan Fauna became one of the most important Early Pleistocene mammalian faunas in China.

The Longdan Fauna described by Qiu et al. (2004) includes 31 species of 29 genera. The presence of *Equus* and the absence of Middle Pleistocene species indicates that the age of the Longdan Fauna is Early Pleistocene. Additionally, Wang (2005), Qiu et al. (2009), and Deng (2012), respectively, reported specimens of *Castor anderssoni*, *Ursus yinanensis*, and *Proboscidipparion sinense* from Longdan. Qiu et al. noted that the Longdan Fauna and the Nihewan Fauna shared only eight species. They determined that the Simpson similarity index (i.e., the number of common taxa divided by the number of total taxa of the fauna with fewer taxa) was only 25.8%. The number of genera commonly shared by the two faunas is 17, and the similarity index at the generic level is thus 58.6%.

Qiu et al. (2004) suggested that differences in composition between the Longdan and Nihewan Faunas may reflect differences in geologic ages and paleoenvironments. The Longdan Fauna was slightly older than the Nihewan Fauna based on the observation that the Longdan Fauna contains some primitive forms and the Nihewan Fauna includes a large number of advanced forms. For example, the extremely large horse *E. eisenmannae* represented a very primitive lineage that was similar to the earliest horse in Europe, *E. livenzovensis*.

Although no agreement has been reached regarding the geologic age of the Nihewan Fauna, many paleontologists consider it to be around 1.8 Ma (Liu and Liu, 2000; Qiu, 2000). Previous paleomagnetic data indicated that the Longdan is 2.55–2.16 Ma old (Qiu et al., 2004). The results of paleoenvironmental and chronological analysis performed by Zan et al. (2016) demonstrated that the age of the Longdan Fauna was 2.5–2.2 Ma.

Other Sections

The loess in southeastern Shanxi Province is, from bottom to top, divided into Old Red Loam, New Red Loam, Lishi Loess, Malan Loess, and Holocene Loess. The Old Red Loam is distributed in the eastern Yushe Basin. Cao et al. (1995) discovered a lot of mammalian fossils in the basal conglomerate bed of the Old Red Loam. Most of these fossils are teeth of *Equus* sp., and they are intact and not abraded, which means that they are probably not reworked and most likely represent the true horizon at which *Equus* appears. Under the Old Red Loam, the Yushe Group contains hipparionines but not *Equus*. According to paleomagnetic studies (Shi, 1994; Shi et al., 1994), the Old Red Loam was deposited 2.5–1.5 Ma; therefore, its lower boundary was 2.5 Ma. The *Equus* fossils were collected from the basal conglomerate bed of this boundary.

In the Youhe District in Weinan, Shaanxi Province (**Figure 2**), the strata that contained the Early Pleistocene Nihewan Fauna are yellowish-brown coarse deposits, and they are informally called "Yellow Sanmen"; the strata that contained the Pliocene Youhe Fauna are green or grayish-green mudstones or marls, and are called "Green Sanmen." In the Youhe section, *Equus first* appears in the Yellow Sanmen, under which the Green Sanmen is only observed from Borehole W7 in Yancun, Weinan, which indicates that the Matsuyama Chron is recorded in the Yellow Sanmen, which dates to approximately 3.0–2.58 Ma. Zhu et al. (1995) conducted a paleomagnetic study on the Songjiabeigou section in Youhe, Weinan, and they also found that the Matsuyama/Gauss boundary is located between the Sanmen Formation (i.e., the Yellow Sanmen) and the Youhe Formation (i.e., the Green Sanmen). Consequently, the sections in the Youhe District demonstrate that the first appearance of *Equus* was at the Matsuyama/Gauss boundary at 2.58 Ma. Tang et al. (1983) described the Linyi Fauna, which included *E. huanghoensis* reported by Chow and Chow (1965). Based on the composition, Tang et al. (1983) stated that the age of the Linyi Fauna corresponded to the middle to late Villafranchian, which is the same as the Sanmen Formation. Therefore, the first occurrence of *E. huanghoensis* should be about 2.58 Ma at the lower boundary of the Quaternary.

In 1961, Xue and Wang collected plenty of mammalian fossils from Bajiazui, Qingyang, Gansu Province (Deng and Xue, 1999a; **Figure 2**). These fossils were obtained from sandstone at the base of the section, the age of which was identified as Early Pleistocene (Wang et al., 1966; Wang and Xue, 1982). Deng and Xue (1999a,b,c) studied the *Equus* specimens of this mammalian fauna and erected two new species, *E. qingyangensis* and *E. wangi*, and identified a known species, *E. teilhardi*. Deng and Xue (1999a) indicated that *E. qingyangensis* occurred around 2.5 Ma based on the position of fossils and loess between fluvial-lacustrine deposits. As we discussed above, *E. qingyangensis* was very primitive, especially on its very low cranial proportions, which are similar to those of the earliest *Equus* in the world, *E. shoshonensis* (**Figure 12**).

SCENARIO OF *EQUUS* DATUM AND EARLY EVOLUTION

Based on the information detailed above, we can describe the pattern of the early evolution of stenonids in China. There is no doubt that stenonids first arrived in China at the lower boundary of the Quaternary. It also can be confirmed that at least five stenonid species simultaneously appeared in China about 2.5 Ma (**Figure 14**). This is not strange. Equids are all highly cursorial and able to migrate very long distances in a relatively short time. When stenonids arrived in Eurasia and dispersed, the time difference of their dispersal was negligible on a geochronological scale. But why could stenonids radiate and produce high diversity as soon as they appeared in Eurasia, even only in China? Was that a coincidence?

Equidae originated in North America 56 Ma and was restricted to this continent from the Eocene to the Oligocene (MacFadden, 2005; Bai et al., 2018). Since the Early Miocene, there have been several migrations of Equidae to the Old World (MacFadden, 2005). This is probably related to the Mi-1 glaciation (Zachos et al., 2001). Based on diversity, geographic distribution, and population, Anchitheriinae was not a prosperous lineage in Eurasia. For example, only two genera with four species of Anchitheriinae have been found in China (Hou et al., 2007). In the beginning of the Late Miocene, a much more successful clade, Hipparionini, appeared in Eurasia. The earliest species was *Hipparion dongxiangense*, which was found in Guonigou, Dongxiang, Gansu Province; the first occurrence of *H. dongxiangense* was 11.5 Ma (Fang et al., 2016). Throughout the Late Miocene, hipparionine originated and diversified into a successful taxon in China, with 8 genera and 17 species. In the Pliocene, four genera with three species of hipparionine survived, and one new genus and three new species originated (Qiu et al., 1987; Li and Li, 1990; Sun, 2013; Deng et al., 2016; Bernor et al., 2018; Sun et al., 2018; **Figure 13**). Although the diversity decreased significantly, Hipparionini was still the main member of the mammalian fauna in the Pliocene. In the Pliocene, the first appearance of *Equus* was in North America (3.5 Ma, Winans, 1989). According to O'Regan et al. (2010), the Bering Strait was likely exposed about 3.3 Ma, which allowed the North American *Equus* species to invade Eurasia (**Figure 15**). However, they likely did not migrate until later because hipparionine species were still the dominant equids in Eurasia, at least in East Asia (**Figure 13**).

Stable carbon isotopic analysis performed by Hou et al. (2006) indicated that the habitats in western China were steppes dominated by C3 grasses during the Late Miocene and Early Pliocene instead of savannas dominated by C4 plants. They suggested that C4 plants dispersed into northern China in the Pliocene along with the strengthening of the East Asian summer monsoon. Simultaneously, the diversity of the *Hipparion* fauna in East Asia gradually declined. They also suggested that Miocene equids in North America faced a similar crisis because of C4 plant dispersal 7–5 Ma. The dispersal of C4 plants has been explained to be correlated with a decrease in atmospheric CO_2 (Cerling et al., 1993, 1997; Wang et al., 1994). Janis et al. (2000) suggested that the observed decline in species

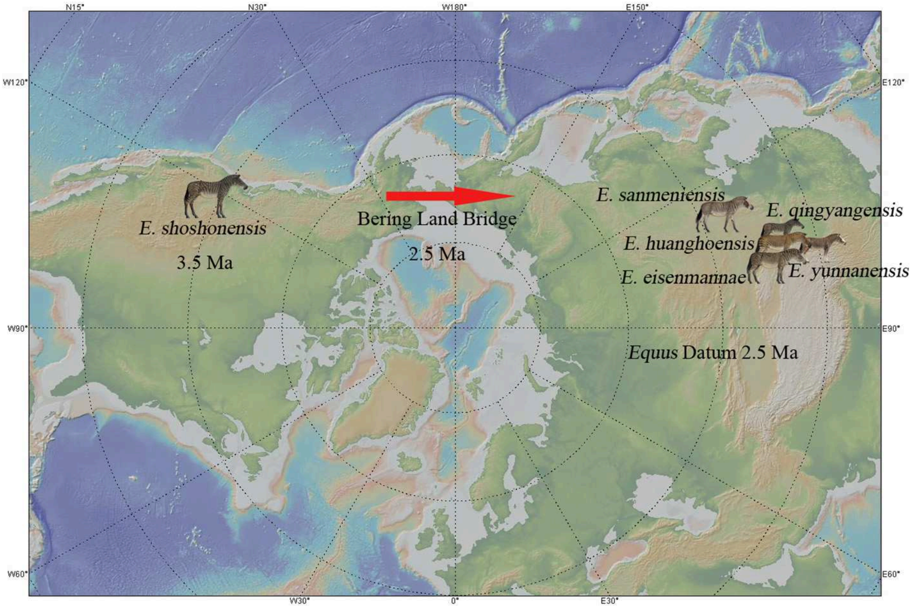

FIGURE 14 | Origin of *Equus* in North America and the *Equus* Datum in China.

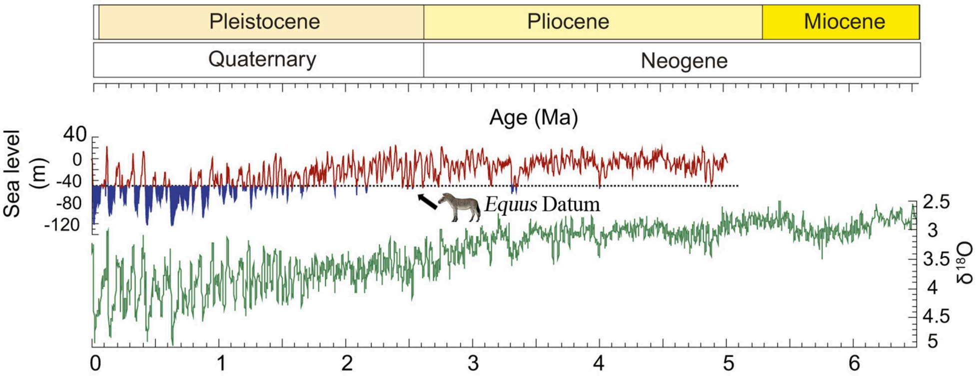

FIGURE 15 | *Equus* Datum, global sea-level and global benthic $\delta^{18}O$ compilation. Blue shading of the sea-level curve indicates times when global sea-level dropped below 50 m and the Bering Strait was likely exposed (modified after O'Regan et al., 2010).

richness of North American horses may represent a gradual decline in primary productivity, which would be consistent with a decrease in atmospheric CO_2. In summary, we propose that, after the Early Pliocene, hipparionine species declined as a result of decreased primary productivity of vegetation in their habitats.

The massive recession of *Hipparion* was initiated in the Early Pleistocene, by which only two genera and two species survived (Qiu et al., 1987; Deng, 2012; Bernor et al., 2015). This recession was mostly the result of accumulation and aggravation of the constant decline of primary productivity of the vegetation and partly influenced by climate change. The beginning of the Pleistocene was when *Equus* first immigrated into Eurasia. As described in our discussion above, at least five stenonid species (*E. qingyangensis*, *E. eisenmannae*, *E. sanmeniensis*, *E. huanghoensis*, and *E. yunnanensis*) simultaneously appeared in China at the very beginning of the Pleistocene. Compared with hipparionine, stenonids had obvious advantages. First, monodactyl feet adapted to vertical standing made *Equus* the perfect steppe runner. In addition, the V-scars of *Equus* are developed on the first phalanx of both fore and hind digit III, and are much wider and flatter than those of hipparionines (Deng et al., 2012). Additionally, all stenonid species have very elongated face. Qiu et al. (2004) indicated that the elongated jaw could accommodate a larger cheek tooth row, which would be a powerful adaptation for chewing coarse food, like dry grass. In contrast, hipparionines in the Early Pleistocene, such as *Proboscidipparion sinense*, had relatively small cheek teeth. Moreover, the global climate became colder in the Early Pleistocene, and the animals with larger body sizes were better adapted to the cold environment according to Bergmann's rule (Qiu et al., 2004). The famous Early Pleistocene fauna, the Nihewan Fauna, consisted of large animals, such as, *Coelodonta nihowanensis*, *Elasmotherium* sp., *Paracamelus gigas*, and *Bison palaeosinensis* (Cai et al., 2013). The stenonid horses, especially *E. eisenmannae*, are very large. Only very large hipparionine species, including *Proboscidipparion sinense* and *Plesiohipparion shanxiense*, survived in the beginning of the Pleistocene in China (Qiu et al., 1987; Deng, 2012; Bernor et al., 2015); consequently, plenty of open habitats and ecological niches were available for the new incoming lineages. As *Equus* arrived in Eurasia, its adaptations to this new situation helped it radiate and disperse rapidly. Deng et al. (1999, 2002) performed carbon isotopic analysis on mammalian fossils in the Quaternary in China and revealed an environment dominated by C3 plants in northern China in the Early Pleistocene that was led by strengthening of the East Asian winter monsoon along with Quaternary glaciation. Therefore, the primary productivity of vegetation likely increased significantly, and stenonid horses, which had been widespread in northern China, faced an opportunity for further evolution.

Equus shoshonensis has often been regarded as ancestral to all stenonids and even all *Equus* species (Deng and Xue, 1999a). Skinner and Hibbard (1972) argued that there were marked similarities between the skulls and dentitions of the extinct North American *E. shoshonensis* (his *E. simplicidens*) and the living Grévy's zebra, *E. grevyi*. Based on our observation and comparison of *E. shoshonensis* fossils and specimens of extant *E. grevyi* housed in several museums, these two species are similar in absolute size, and in cranial and distal limb proportions. However, our phylogenetic analysis places *E. grevyi* in the smallest clade formed by extant horses (**Figures 1**, **13**). The similarities discussed above, which are referred to functional morphology, should relate to similar habitat. *E. grevyi* lives in a semi-desert environment in northern East Africa with negative mean annual climatic water balance (Schulz and Kaiser, 2013). *Equus shoshonensis* probably lived in a similar environment to that of modern *E. grevyi*. Therefore, *Equus* was probably adapted to arid environments from the very beginning. When the Bering land bridge opened at the beginning of the Pleistocene (**Figures 14**, **15**), *Equus* immigrated into Eurasia from North America, where it first stopped in East Asia. Since 2.5 Ma, a stronger winter monsoon system and higher continental desiccation occurred in China, most probably due to strong uplift of the Tibetan Plateau (An et al., 2001). *Equus* was well-adapted to this climate and rapidly radiated into a considerably dominant member of the Early Pleistocene mammalian fauna, the *Equus* Fauna.

DATA AVAILABILITY STATEMENT

All datasets for this study are included in the article/**Supplementary Material**.

AUTHOR CONTRIBUTIONS

BS and TD designed the conceptual model and contributed equally to the writing of the manuscript.

FUNDING

This work was supported by the Chinese Academy of Sciences (grant nos. XDB26030302, XDA20070203, QYZDY–SSW–DQC022, and GJHZ1885), the Special Research Program of Basic Science and Technology of the Ministry of Science and Technology (grant no. 2015FY310100), and the National Natural Science Foundation of China (41430102).

ACKNOWLEDGMENTS

The editor Dr. Leonardo Santos Avilla, reviewers Dr. David Marjanović and Dr. Xiaoke Qiang greatly improve our manuscript. Mr. Yu Chen (IVPP) provided art work in our manuscript. Dr. Shiqi Wang (IVPP) and Mr. Hanwen Zhang (University of Bristol) provided pictures of skull specimens. Dr. Wenhui Liu (National Museum of China) provided very important literatures for references. Drs. Haibing Wang and Shunxing Jiang (IVPP) provided helpful support on phylogenetic work. Dr. Guillaume Billet (Muséum national d'Histoire naturelle) provided access to observations on type specimens of the Nihewan fauna. Mses. Judy Galkin and Eleanor Hoeger (American Museum of Natural History) respectively provided accesses to observations on specimens of fossil horses and extant zebras. We appreciate all of their contributions.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2019.00429/full#supplementary-material

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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