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Early Pleistocene *Equus* (Equidae, Perissodactyla) from Andersson Loc. 32 in Qixian, Shanxi, China

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ABSTRACT

The *Equus* specimens of Andersson Loc. 32 in Qixian, Shanxi previously identified as *Equus* cf. *sanmeniensis* are rediscovered in this research. The skull has moderate size, deep nasal notch, clear preorbital fossa, undulated lateral outline, upper cheek tooth with simple fossette and incisor with incomplete cup, should be identified as *Equus teilhardi*. The mandible has cheek tooth with V-shaped linguaflexid, incisor with incomplete cup, moderate size, strong pli caballinid and deep ectoflexid on molar, should be identified as *Equus qingyangensis*. This skull is first record of a complete cranial material of *E. teilhardi*, reveals many important cranial features of *E. teilhardi*, supports anatomical comparison and phylogenetic discussion with other stenonid horses. The morphological differences between *E. teilhardi* and *E. qingyangensis* show their different niches, further explain the reason of their coexistence. Incomplete cup on incisor is an unstable feature. It has been found in several species of stenonid horses, likely a remaining feature derived from the most primitive *Equus*, *Equus simplicidens*. The small-sized stenonid horses with short limbs and incisors with incomplete cups likely have relation with *E. teilhardi*, such as *Equus yunnanensis* and *Equus stehlini*. *E. qingyangensis* has most primitive features in Eurasian stenonid horses.

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Stenonid horse; new record; relation; evolution

Introduction

Stenonid horse is the earliest *Equus* in Eurasia. The first occurrence of stenonid horse in Eurasia was regarded as the sign of the lower boundary of the Quaternary. The appearance, evolution and dispersal of the stenonid horses were contemporary with many important geological and environmental events, so they were regarded as important material for study on climate and environment changes in Quaternary (Deng & Xue 1999a). There are plenty of Early Pleistocene localities with stenonid horse fossils in China land, which attract researchers from all over the world. Since early twentieth century, European and American authors began to research on stenonid fossils from North China. Teilhard de Chardin and Piveteau (1930) described the Nihewan fauna and erected first species of stenonid horses in China, *Equus sanmeniensis*. Zdansky (1935) published first monograph of *Equus* in China. He described fossils of the Lagrelius Collection collected by Andersson and identified the specimens from Hebei, Henan, Shanxi, Shandong as *Equus* cf. *sanmeniensis*. Colbert (1940) described specimens from Yuanmou, Yunnan and erected a new species *Equus yunnanensis*. He indicated that this new species was identical to the specimens found in upper Irrawaddies of Burma, similar to the Pleistocene *Equus* of India.

After 1949, more and more new specimens of stenonid horses were reported by Chinese researchers. Chow and Liu (1959) erected a new species *Equus huanghoensis* based on cheek tooth specimens found in Pinglu, Shanxi. Pei (1961) described newly discovered specimens of *E. yunnanensis*. Liu (1973) reported the skull specimens of *E. sanmeniensis* found in Locality 1 of Zhoukoudian (Choukoutien) and extended the last occurrence of *E. sanmeniensis* even stenonid horse in North China to Middle Pleistocene. Liu and You (1974) reported more specimens of *E. yunnanensis* including skull and mandible and discussed on the relation between this species and other Asian *Equus*. Deng and Xue (1999b, 1999c) studied the specimens from Bajiazui locality, Qingyang, Gansu and erected two new species, *Equus qingyangensis* and *Equus wangi*. Qiu et al. (2004) reported the new specimens from Longdan, Dongxiang, Gansu and erected a new species *Equus eisenmannae*. Dong and Fang (2005) described the new specimens of *E. huanghoensis* found from Tangshan, Nanjing. Li et al. (2015) reported the first complete skull associated with mandible of *E. huanghoensis* from Yangshuizhan locality in Nihewan, Hebei.

However, the early research was relatively simple and lacked further comparison and discussion. Therefore, the early identify on stenonid fossils needs to be reviewed and modified. Teilhard de Chardin and Piveteau (1930) recognized that there were two types of *Equus* from Nihewan with significantly different body sizes but they still attributed them as the same species *E. sanmeniensis*. Eisenmann (1975) studied *Equus* specimens described by Teilhard de Chardin and Piveteau (1930) and identified the

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small type as a new species *Equus teilhardi*. She argued that this species should be distinguished from any other species of *Equus* in small body size and incisor lacking cup. Azzaroli (1982), Forsten (1986), Deng and Xue (1999a) followed this argument and regarded *E. teilhardi* as a valid species.

Zdansky (1935) identified plenty of *Equus* specimens as *E.* cf. *sanmeniensis*. Actually these specimens are different in body size and morphology. Forsten (1986) identified specimens of *E.* cf. *sanmeniensis* from Mianchi, Henan as *Equus* ?*huanghoensis* based on the features of upper cheek tooth. Liu (1973) and Deng and Xue (1999a) indicated that specimen from Qixian, Shanxi identified as *E.* cf. *sanmeniensis* by Zdansky (1935) is much smaller than other specimens of *E. sanmeniensis*. Based on our observation on this Qixian skull, exactly it should not be identified as *E. sanmeniensis*. Meanwhile, a mandible material from the same locality is also significantly different from *E. sanmeniensis*. Both of them should be rediscovered. Consequently, the purpose of present study is to clarify the taxonomic status of the stenonid horses from the Andersson Loc. 32 in Shanxi, Qixian, China and to further discuss on the relation between the new specimens and others stenonid horses in China and whole Eurasia.

Material and method

The material studied in this research includes a skull and mandible collected by Andersson in 1919, belong to his Locality 32, Qixian, Shanxi (Figures 1–3). The terminology of skull and mandible follows Sisson (1953), that of occlusal structures of teeth follows Qiu et al. (1987) and Deng and Xue (1999a). Measurements follow Eisenmann et al. (1988) and use * to mark estimated data. The following anatomical features will be mainly performed to compare the new specimens with other selected specimens of stenonid horses: body size, depth of nasal notch, length of snout, morphology and position of preorbital bar, basicranial proportion, cup on incisor and occlusal characters of upper and lower cheek teeth. The scatters of measurements analysis are modified from Qiu et al. (2004), by adding new data including those of *E. teilhardi* based on the Qixian skull, *E. huanghoensis* from Li et al. (2015) and *Equus asinus* measured from Muséum national d'histoire naturelle, Paris, France (Figures 4–7).

Abbreviation

PMU M: specimen number of vertebrate paleontology of Museum of Evolution of Uppsala University, Uppsala, Sweden.

NIH: specimen number of vertebrate paleontology of Muséum national d'histoire naturelle, Paris, France.

THP: specimen number of vertebrate paleontology of Tianjin Natural History Museum, Tianjin, China.

NWUV: specimens number of vertebrate paleontology of Institute of Cenozoic Geology and Environment, Northwest University, Xian, China.

NMNH: National Museum of Natural History, Washington DC, United States.

USNM: specimen number of vertebrate paleontology of NMNH.

Systematic paleontology

Class Mammalia Linnaeus 1758
Order Perissodactyla Owen 1848
Family Equidae Gray 1821
Genus *Equus* Linnaeus 1758
Equus teilhardi Eisenmann 1975
Figure 2

Equus cf. *sanmeniensis* (in part), Zdansky 1935

Holotype: NIH 001, a broken mandible with symphysis and left ramus, housed in Muséum national d'histoire naturelle, Paris, France.

Figure 1. Distribution of *E. teilhardi* and *E. qingyangensis* in China. Black star shows coexistence.

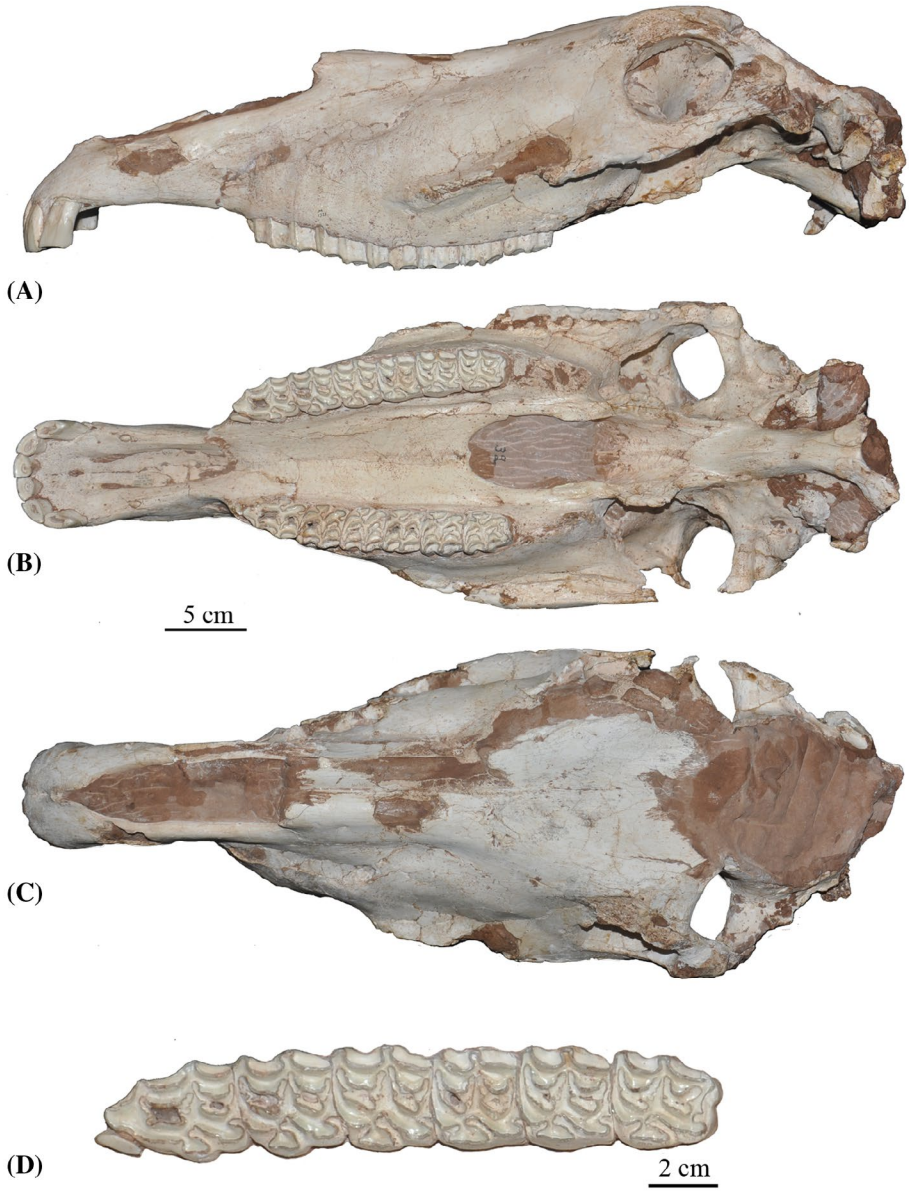

Figure 2. Skull of *E. teilhardi*, M 1321. A. left view; B. ventral view; C. dorsal view; D. occlusal view of left cheek tooth row.

Revised diagnosis: Middle size. The nasal notch extends above the mid-P2 to boundary of P2/P3. Snout is short. The preorbital fossa is shallow with an indistinct border. The lateral outline is undulated. A deep groove is along the nasal suture. Cups of incisors possibly incomplete even lacking. The upper cheek teeth have simple fossettes, short protocones and weak pli caballine. The lower cheek teeth have V-shaped linguaflexids and deep ectoflexids on molar that penetrate into the isthmuses even touch the linguaflexids on the lower molars. The limb bones are short and robust.

Distribution: Northwestern and northern China.

Age: Nihewanian, Early Pleistocene.

Description

The described material collected from Qixian is a relatively well-preserved skull with complete dentition, most of braincase and occipital part damaged, right zygomatic area broken. Skull is moderate-sized, dolichocephalic and has undulated outline as lateral view. Nasal has shallow middle groove. External frontal crest is strong. The supraorbital foramen is located laterally, and is big and below the frontal plane. Dorsal and posterior margins of orbit are rough, ventral and anterior margins are smooth and deep. Dorsal margin of premaxillary is rounded and thick; nasal notch is located dorsal of boundary of P2 and P3. Infraorbital foramen is located at the level of mesostyle of P2. Preorbital fossa is obvious, oval-shaped, anterodorsally oriented. Surface of lacrimal bone is smooth. Lacrimal sacci fossa is funnel-like and located anterointernal of orbit. Orbit is rather posterior on the skull and makes the whole facial part elongated. Temporal condyle is strong and adjacent to orbital bar. Postglenoidal process is transversely flat and erected, parallel with paramastoid process, but does not extend posteriorly. Ventral plane of basilar part is swollen, not constricted anteriorly. Basilar tubercles are rough and distributed on the two lateral sides of sphenoid. Corpus of sphenoid bone is a trigone with slight hollows on the two

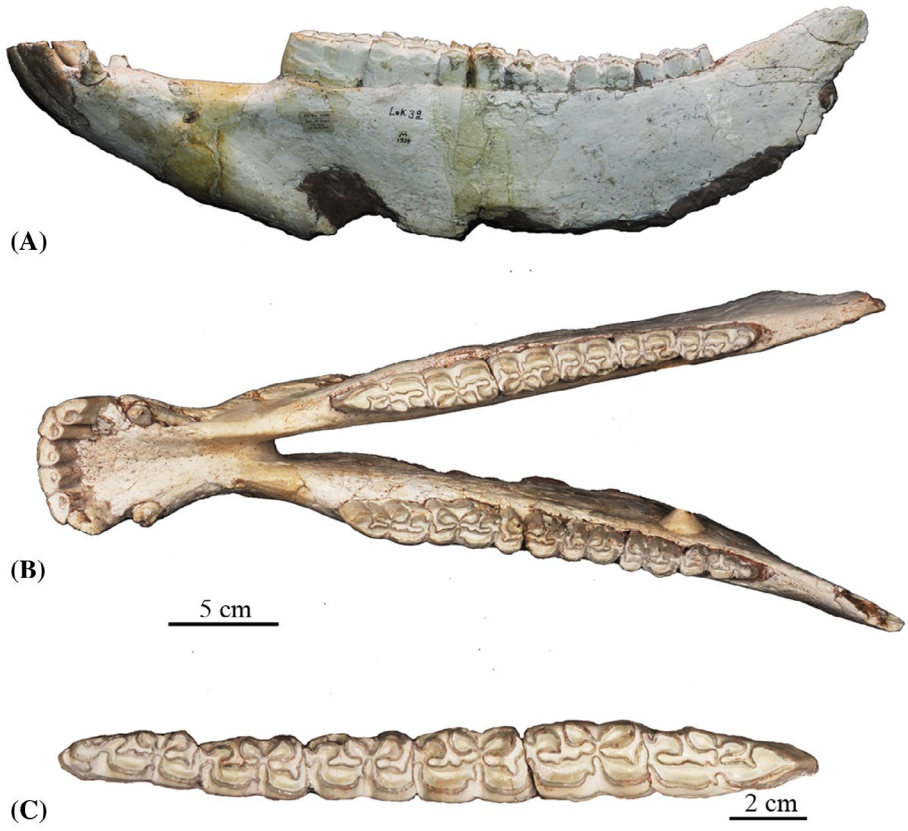

Figure 3. Mandible of *E. qingyangensis*, M 1324. A. left view; B. occlusal view; C. occlusal view of right cheek tooth row.

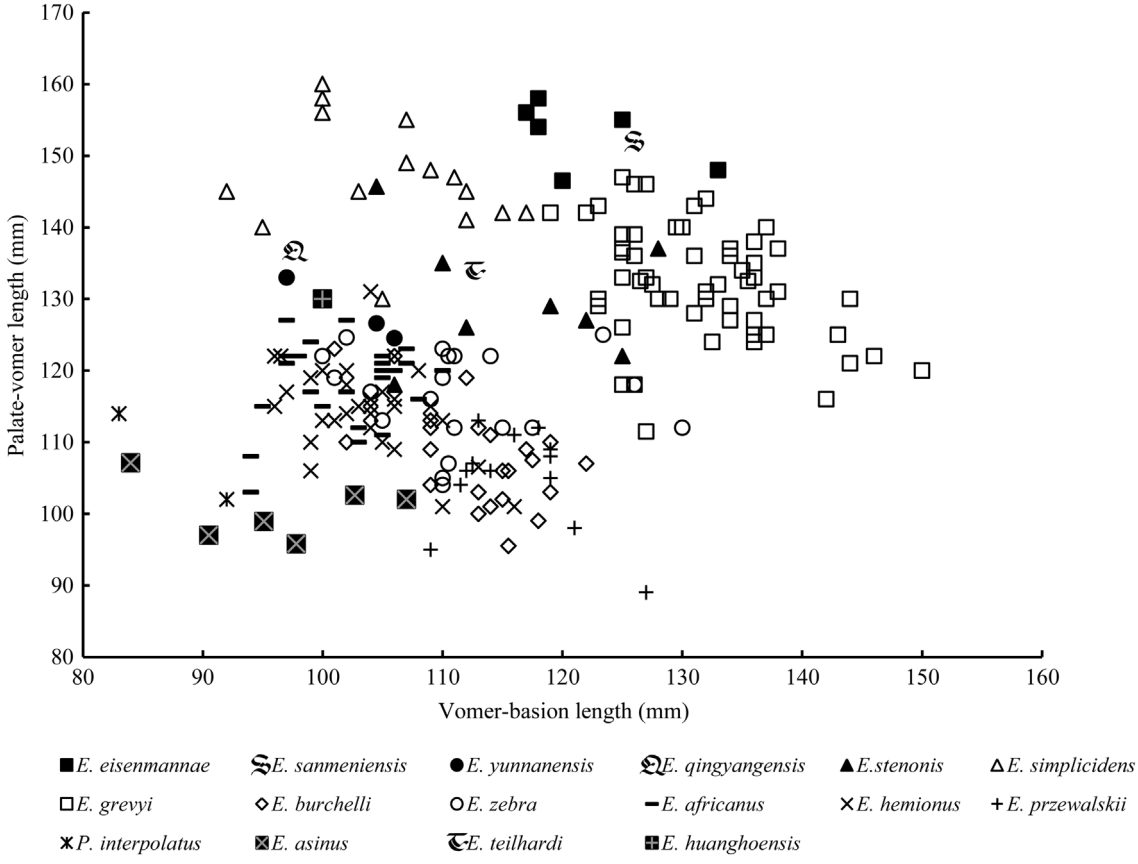

Figure 4. Comparison of basicranial proportion in several extinct and extant species of *Equus*.

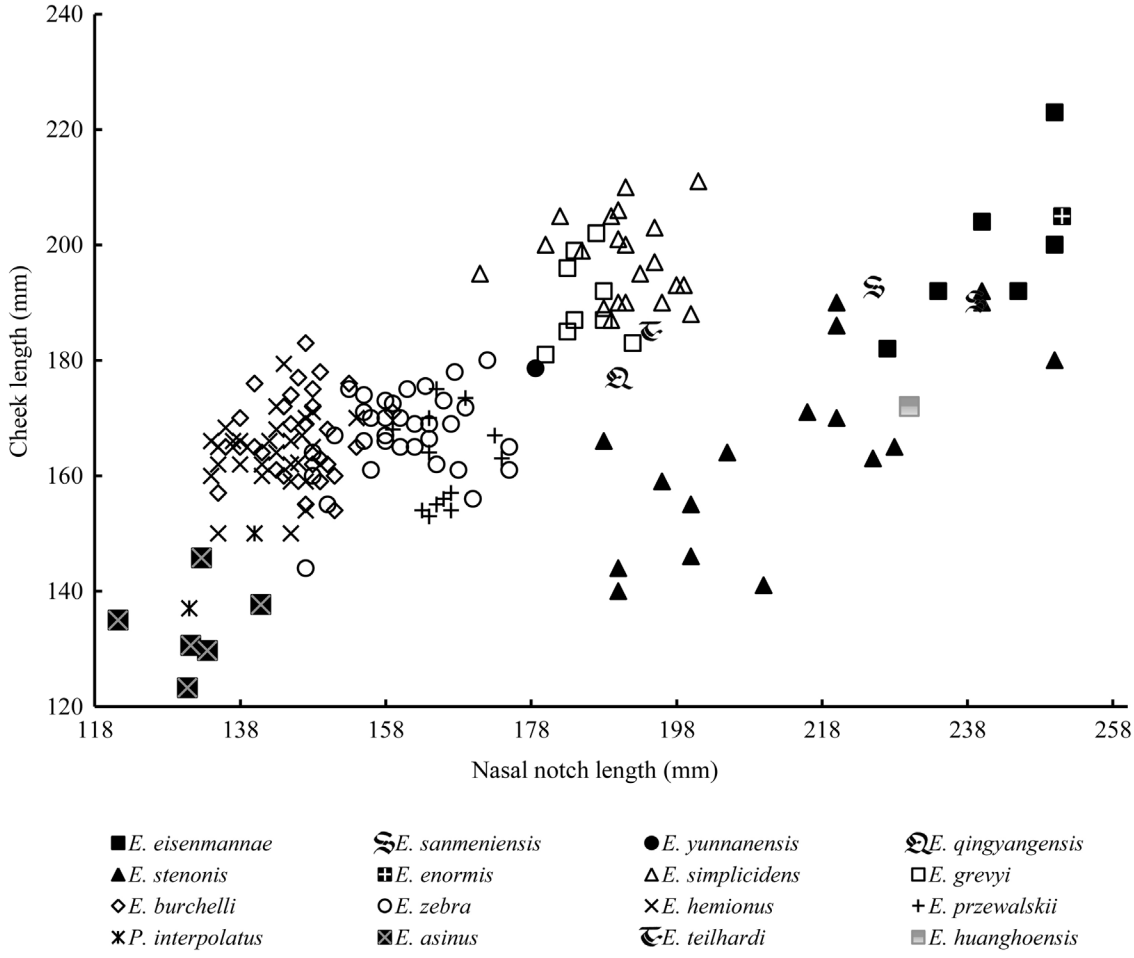

Figure 5. Comparison of lengths of palatine and basicranial in several extinct and extant species of *Equus*.

lateral sides; anterior margin near vomer is flat. The construction formed from posterior margin of basilar part to anterior end of sphenoid is arch-shaped. Hamulus of pterygoid is broken. Base of pterygoid processes distributed on the two lateral sides of sphenoid bone, forms towering wing-shaped crest anteriorly and is expanded dorsolaterally. Pterygoid appears near the most anterior margin of sphenoid bone. Alar canals distributed on the lateral sides of corpus of sphenoid bone; the posterior foramen of alar canal is clearly seen on the ventral plane. The distance between cheek teeth row is slightly decreased in anterior part. Surface of palatine plane is smooth, curved from lateral towards median, the part near P3 of the surface is flatter towards anterior and becomes a gradually curved plane towards posterior; the median suture is fused on anterior part and obvious on posterior part. Posterior margin of hard palate is at the level of boundary of M2 and M3. Anterior part of vomer is missed. Interalveolar tubercle is obvious, maxillary tubercle is swollen. Three foramens are present within maxillary recess: the bigger maxillary foramen; posterior palatine; and the smaller sphenopalatine foramen. Anterior foramen of palatine canal is open to posterior of protocone of M3; palatine groove gets shallow towards anterior and disappears near P2. Snout is short and moderately strong. Incisor foramen is big and oval, located in the posterior of the line linked with I3s.

Upper cheek teeth are complete. Upper incisors are heavily worn, left I3 has incomplete cups. Upper canines are very small. The average length of cheek teeth is about 176 mm; left DP1 is present and heavily worn, right DP1 is broken.

P2: anterostyle is short and subtrangular. Postflex is wide; Pli caballine is weak. Parastyle is small; mesostyle is robust, flat to slight curved labially, oblique anteriorly. Protocone is short and subtriangular. Connection between protoloph and protocone is short and wide. Hypocone is wide and rounded, weakly constricted, hypoconal groove is not deep. Enamel is rather thick, but thin on margins of prefossette and postfossette; enamel plication is simple, only strong on posterior wall of prefossette and anterior wall of postfossette. The angles of pre- and postfossette are robust.

P3: protocone is flat lingually, wide and rounded labially, constricted lingually, shaped triangularly. Postflex is deep, whose basal part is wide. Pli caballine is single and very weak. Parastyle is robust, rounded labially, slight curve posteriorly. Labial wall is curved, wide, and deep. Mesostyle is robust and has a tip extended posteriorly. Hypocone is rounded and blunt, not obviously constricted. Hypoconal groove is V-shaped. Enamel plications are weak.

P4: similar to P3, but smaller; protoloph and metaloph are more oblique, and have more than 30° crossing with the major axis. Parastyle is flat labially; mesostyle is sharp and long labially, hypocone is next to posterior side of tooth.

M1: protocone is short, wide and rounded labially, nearly triangular lingually; lingual margin is flat, small anteriorly, large

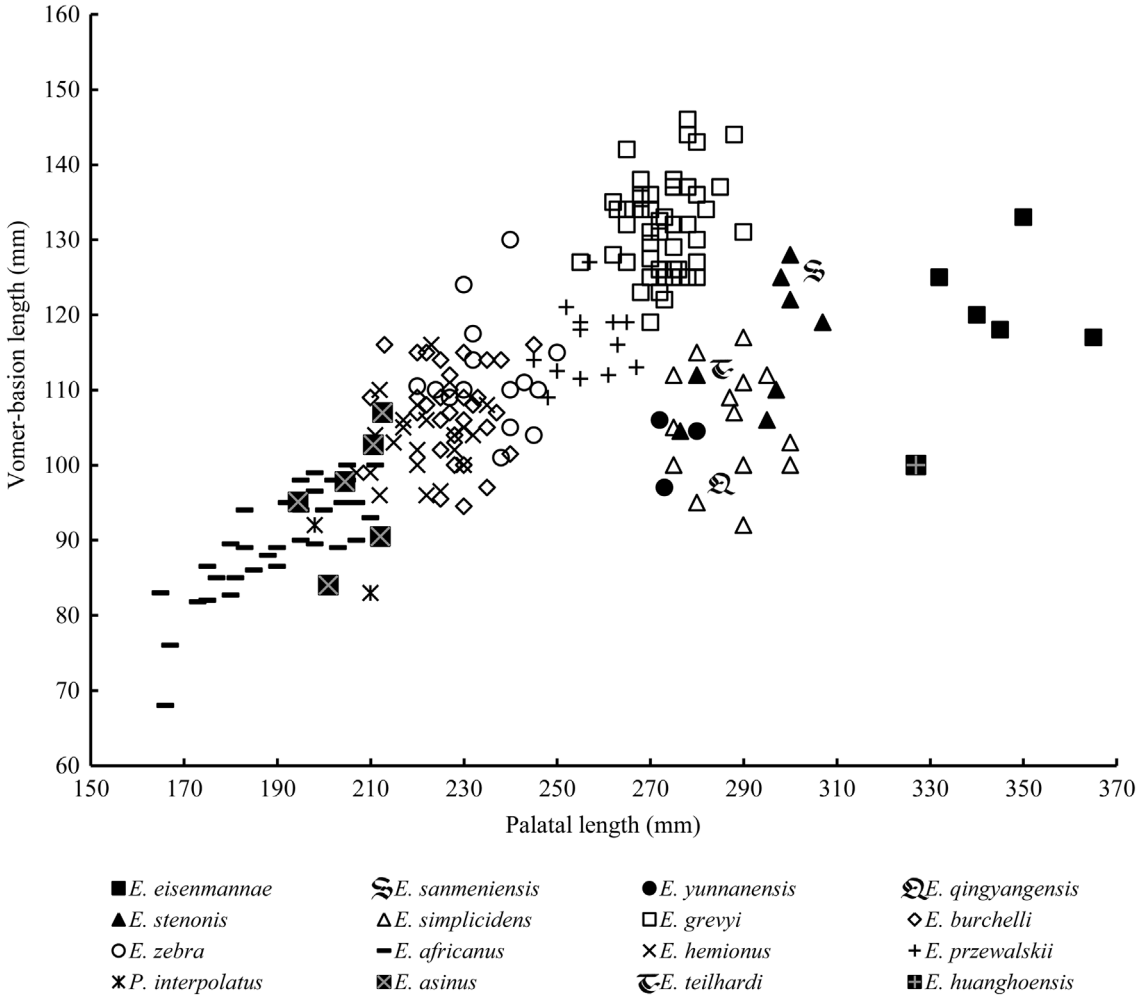

Figure 6. Comparison of lengths of nasal notch and cheek in several extinct and extant species of *Equus*.

posteriorly, pointed at ends. Protoloph and metaloph are oblique. Preflex is shallow and narrow; postflex is wide and deep. Parastyle is rounded in top, not oblique. Mesostyle is narrow and blunt. Hypocone is not constricted; hypoconal groove is V-shaped.

M2: similar to M1, slightly large; protocone is slightly longer; Pli caballine is weaker; postflex is narrow and deep.

M3: protocone is elongated posteriorly, slightly curved lingually, pointed at ends. Postflex is deep, wide basally. Pli caballine is single and small. Parastyle extends labially; mesostyle is small. Labial wall is curved, wide and shallow. Hypocone is strongly constricted.

Comparison

Deng and Xue (1999a) ascribed Eurasian *Equus* into three morphological groups, stenonid, caballoid and hemiones. The elongated facial part, deep nasal notch, obvious preorbital fossa, low basicranial proportion and V-shaped linguaflexid show that the Qixian material should be identified as stenonid horse. And the moderate body size, incomplete cups on incisor, simple fossettes on upper cheek teeth and deep ectoflexid on molar are identical to *Equus teilhardi* (Figure 2, Table 1).

The previously reported skull and mandibular specimens of *E. teilhardi* include holotype, a broken mandible with symphysis and left ramus (NIH 001, Eisenmann 1975), two skull fragments (THP 00150, 00151, Forsten 1986) and a left ramus fragment (NWUV 1243, Deng & Xue 1999a). Eisenmann (1975) only assigned two features for diagnosis for this species: small body size and lack of cup on the lower incisor. Forsten (1986) recognized two skull fragments of *E. teilhardi* from Nihewan housed in Tianjin Natural History Museum and proposed more features for diagnosing this species, including nasal notch extending to the mid-P2, upper cheek teeth row at late wear stage having a length of 178–180 mm, DP1 present, protocone having a heel, pli caballin lacking on tooth at late wear stage, mesostyle concave or flat labially and simple on molars. These features are very similar as the Qixian material. Forsten (1986) listed that plication count of *E. teilhardi* is 0–8, average is 4.3. This is also identical to the Qixian material (Figure 2; Tables 1 and 3).

The Qixian material is well preserved and has complete snout and basilar part. So anatomical comparison can be performed with other Eurasian stenonid horses. Beside the significant difference in body size, *Equus sanmeniensis* is morphologically similar as *E. teilhardi*. The specimens of *E. teilhardi* found in Nihewan and Qixian were regarded as smaller individuals of *E. sanmeniensis* (Teilhard de Chardin & Piveteau 1930; Zdansky 1935). *E. sanmeniensis* also has typically stenonid features shared with *E. teilhardi*, such as elongated skull, obvious preorbital fossa, middle

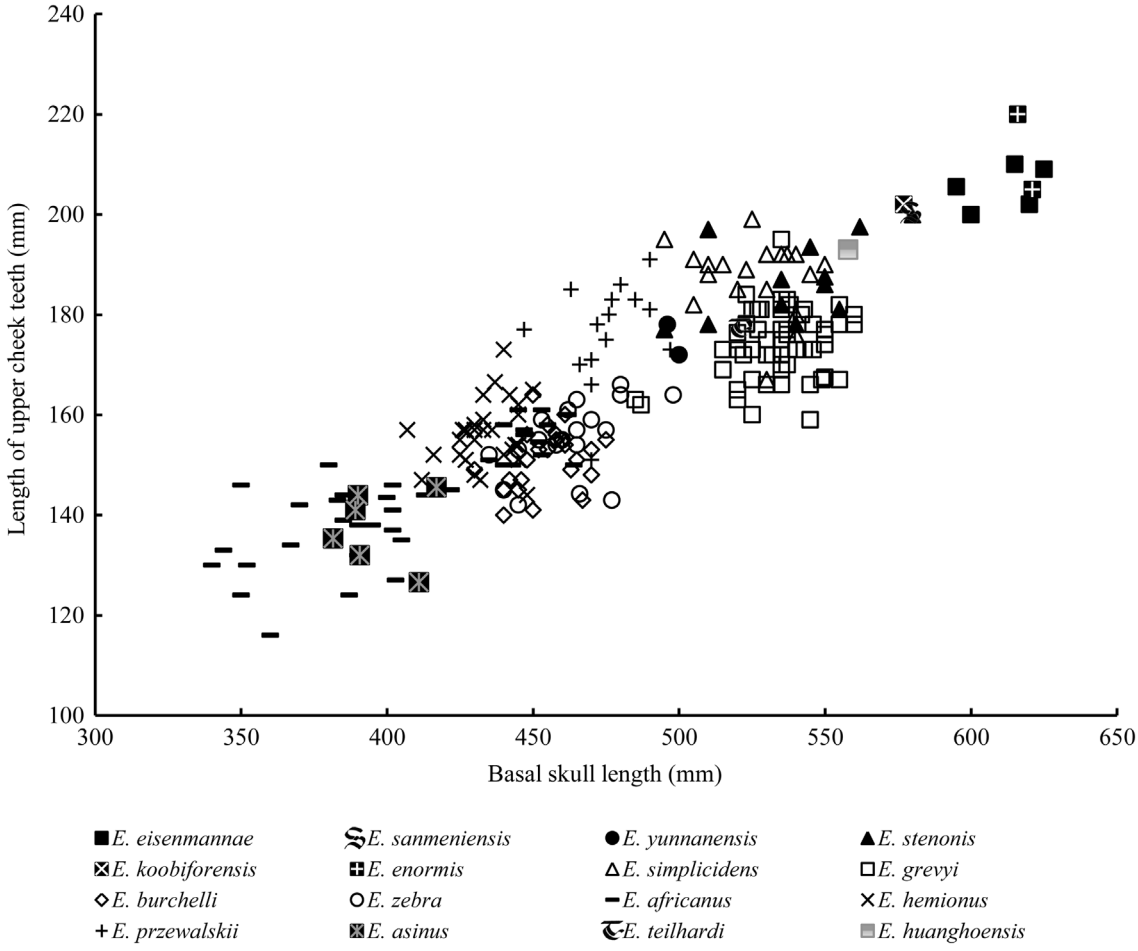

Figure 7. Comparison of lengths of cheek tooth row and basilar in several extinct and extant species of *Equus*.

groove on nasal bone, deep nasal notch, low basicranial proportion and so on. Therefore the position of nasal notch and ratio between palate-vomer length and vomer-basilar length on the Qixian material are same as those of holotype of *E. sanmeniensis* (Figure 4). However, *E. sanmeniensis* has higher ratio between lengths of cheek and nasal notch (Figure 5), more elongated protocone and stronger pli caballine, more complicated fossettes on upper cheek teeth (Liu 1973; Forsten 1986; Deng & Xue 1999a). Moreover no incomplete cup on incisor was reported on *E. sanmeniensis* in the previous studies. The morphology of postcranial material is another important feature for horse. Eisenmann and Karchoud (1982) proposed method of comparing the lengths of Mc III and cranial basilar length. The cranial basilar length of the Qixian material is 520.6 mm, the largest record of length on Mc III of *E. teilhardi* is 220 mm (Teilhard de Chardin & Piveteau 1930). Based on available data now, the highest ratio we can get is 0.42. Qiu et al. (2004) listed the ratios of known early *Equus* species in the following: *Equus enormis* is 0.44, *Equus simplicidens* is 0.45, *E. sanmeniensis* is 0.49, *Equus livenzovensis* is 0.48, *Equus koobiforensis* is 0.34, that of *Equus stenonis* is 0.45, *Equus mosbachensis* is 0.49, *Equus eisenmannae* is 0.39. So the relative length of Mc III of *E. teilhardi* is much shorter than that of *E. sanmeniensis*.

Equus eisenmannae, *Equus stenonis* and *Equus huanghoensis* are very large to giant stenonid horses in China. These three species also share many similarities, such as elongated snout, rather deep nasal notch even reaching the boundary of P3 and P4 (Azzaroli 1965, 1982; Forsten 1986; Deng & Xue 1999a; Qiu et al. 2004; Li et al. 2015). These features are significantly different from those of *E. teilhardi*. *E. eisenmannae* has elongated protocone and rounded metaconid and metastylid whereas *E. teilhardi* has short protocone and angular pointed lingually on metastylid (Qiu et al. 2004). *E. stenonis* has subsquare orbit, *E. huanghoensis* has round one (Li et al. 2015), whereas *E. teilhardi* has oval orbit similar as that of *E. eisenmannae*. *E. teilhardi*, *E. stenonis* and *E. huanghoensis* have undulated skull outline as lateral view whereas *E. eisenmannae* has flatten frontal part. *E. eisenmannae* and *E. huanghoensis* have the largest absolute and relative palatal lengths in *Equus*, they also have lower basicranial proportion than most of other Eurasian stenonid horses (Figures 4 and 6). However, *E. teilhardi* share some similarities with these three species on upper cheek tooth such as simple fossettes and weak pli caballin.

Equus wangi is a large-sized stenonid horse, lengths of its upper and lower cheek teeth rows are respectively 195 and 196 mm. The folds on the fossettes of its upper cheek teeth are very complicated. The metaconid and metastylid are rounded. The ectoflexids are shallow on premolar and molar. The hypoconulid on m3 likes a short dagger with a wide and round end. The large size and these very specialized dentition features are significantly different from *E. teilhardi*.

Equus yunnanensis and *Equus qingyangensis* are small to moderate stenonid horses. Qiu et al. (2004) estimated that the basilar

Table 1. Measurements of skull of *E. teilhardi* from Qixian (mm).

Item	
1. Muzzle length	136.1
2. Palatal length	149.1
3. Vomerine length	134
4. Post-vomerine length	112.7
5. Post-palatl length	236.2
6. Basilar length	520.6
7. Premolar length	96.1
8. Molar length	77.6
9. Upper cheek teeth length	176.8
10. Choanal length	94
11. Minimal breadth of the choanae	39
12. Maximal breadth of the choanae	47.5
13. Palatal breadth	72.1
14. Minimal muzzle breadth	44.2
15. Muzzle breadth	62.7
16. Length of fossa temporalis	87.6
17. Length between basion and the foramen ethmoidalis	160.9
18. Frontal breadth	*188.7
23. Anterior ocular line	435.8
28. Antero-posterior perpendicular to the former	64.5
29. Orbital diameter perpendicular of the former	51
30. Length of the naso-incisival notch	194.5
31. Cheek length	185.2
32. Distance between the orbit and the Preorbital fossa	80
33. Length of the preorbital fossa	58.9
34. Distance between the back of the Preorbital fossa and the foramen infra-orbital	75
35. Height of the preorbital fossa	24.3
36. Distance between the preorbital fossa and the facial crest	81.9
37. Height of back of the foramen infra orbitale above the alveolar border	70
38. Height of back of the Preorbital fossa above the alveolar border	77.5

length of *E. qingyangensis* is 512 mm. This size is similar as *E. teilhardi*. Deng and Xue (1999a) indicated that *E. qingyangensis* is a very primitive species showed with very low basicranial proportion (Figures 4 and 6) and present distance between temporal condyle and posterior margin of orbital bar. Eisenmann and Deng (2005) proposed close relation between *E. qingyangensis* and the most primitive species of *Equus*, *E. simplicidens* (their *Equus shoshoensis*) based on the basicranial proportion. *E. teilhardi* has a higher basicranial proportion than *E. qingyangensis* (Figures 4 and 6) and its temporal condyle is adjacent to posterior margin of orbital bar like most *Equus*. The basilar length of *E. yunnanensis* is 496 mm (Liu & You 1974), significantly smaller than *E. teilhardi*. *E. yunnanensis* also has complicated and fine folds in fossettes on upper cheek teeth, elongate protocone, very rounded metastylid and shallow ectoflexids both on premolar and molar which are different from *E. teilhardi* (Liu & You 1974; Eisenmann 1975). *E. yunnanensis* has I3 with incomplete cup (Deng & Xue 1999a). The Qixian material also has this feature but only on left I3.

Forsten (1986) indicated *E. teilhardi* has similar cheek teeth as *Equus senezensis* on dimension. *E. senezensis* is a moderate stenonid horse found in Europe. Its cranial basilar length is 497 mm (Alberdi et al. 1998), almost same as *E. yunnanensis*, smaller than *E. teilhardi*. It has shallow ectoflexid close to or reaching the open of isthmus on premolar and molar, metastylid with similar length and width and a rectangular posterolabial part instead of a pointed tip (Eisenmann 1980). These features are different from *E. teilhardi*. *Equus stehlini* is a small European stenonid horse. Its basilar length is only 480 mm (Alberdi et al. 1998), smaller than any of the Chinese stenonid horses (Deng & Xue 1999a; Qiu et al. 2004; Li et al. 2015). However, its short protocone, deep ectoflexid on molar, incomplete cup on lower incisor and short limb (Azzaroli 1982; Alberdi et al. 1998) are similar as *E. teilhardi*. *E. sivalensis* is another small stenonid horse in Euraisa. Azzaroli (1982) estimated its skull size is similar as *E. stehlini* and indicated that the length of P3-M3 of type of *E. sivalensis* is only 123 mm. *E. sivalensis* has short protocone similar as *E. teilhardi* (Colbert 1940). However, its short distance between anterior margin of orbit and posterior margin of M3 and complicated fossettes on upper cheek teeth are different from *E. teilhardi* (Colbert 1940; Azzaroli 1982). *Equus livenzovensis* and *Equus namadicus* are both large stenonid horses in Eurasia. *E. livenzovensis* has huge body size, shallow nasal notch and elongated limbs (Azzaroli 1982; Alberdi et al. 1998; Qiu et al. 2004). *E. namadicus* has flat frontal surface, this is a rare feature found in stenonid horses (Azzaroli 1982). It also has elongated protocone (Colbert 1940; Azzaroli 1982). These two large-sized species are significantly different from *E. teilhardi*.

Equus qingyangensis Deng et Xue, 1999b
Fig. 3

Equus cf. *sanmeniensis* (in part), Zdansky 1935

Holotype: NWUV 1128, the middle and back of a skull with all cheek teeth, about 12 years, housed in Institute of Cenozoic Geology and Environment, Northwest University, Xian, China.

Diagnosis: Middle size. The nasal notch extends above the back of P2. The praeoribial pit is shallow with an indistinct border. A deep groove is along the nasal suture. The upper teeth have long protocones and weak pli caballine. The lower teeth have typical V-shaped linguaflexids and deep ectoflexids on molar that penetrate into the isthmuses even touch the linguaflxids on the lower molars. The limb bones are slender. The metacarpal middle shaft index is smaller than 13.5 mm and the metatarsal smaller than 12.0 mm. It was the early species of *Equus* with the most slender limb bones in Eurasia.

Distribution: Northwestern and northern China.

Age: Nihewanian, Early Pleistocene.

Description

The mandible is complete in symphysis and horizontal ramus, vertical ramus completely missed, ventral margin of horizontal ramus and cement on some molars are broken. The mandible is elongated and thin. The symphysis is narrowest in the part anterior to mental foramen, near the mental foramen and far from canine. Mental foramen is deep, positioned dorsally and posteriorly between the premolar and canine. The posterior part of horizontal ramus is curved laterally and swollen externally.

The cup is enclosed on i1 and i2, but not enclosed on i3. Lower canine is strong, labial wall is erected; lingual wall is oblique.

p2: paraconid is large, subtriangular, extends lingually, connected with protoconid labially. Metaconid is small and oval. Metastylid is large, leaf-shaped with a short stem, extends more lingually than metaconid. Linguaflexid opens towards anterolabial side and wide V-shaped. Entoconid is big and irregular. Hypoconulid is pointed. Protoconid is narrow and with slightly swollen lingual and labial walls. Hypoconid is elongated and

robust with lingual and labial walls. Pli caballinid is strong. Ectoflexid is shallow, far from isthmus. Horns of preflexid are asymmetric; the anterior one is long and extends anterolabialy; the posterior one is short. Postflexid is elongated and with a swollen bottom.

p3: parastylid is small and simple; extends lingually; lingual margin is on the same level of metaconid. Metaconid is big and oval. Metastylid is subtriangular and constricted in root. Linguaflexid is wide, V-shaped. Isthmus is slightly oblique. Entoconid is rounded and large; hypoconulid is small. Labial wall of protoconid is swollen, and hypoconid is elongated, with a flat labial wall. Pli caballinid is a big bulge. Anterior horn of preflexid is long and extends anterolabially; and posterior one extends posteriorly. Bottom of postflexid is undulated. Ectoflexid does not reach the open of isthmus.

p4: similar to p3, but slightly smaller. Metastylid is slightly shorter; pli caballinid is stronger; ectoflexid is close to the open of isthmus.

m1 is similar to m2; the main differences from p3 to p4 are: paraconid extends more lingually; metaconid is subtriangular and metastylid is oval, stem of metastylid becomes shorter; of entoconid is smaller and more rounded; Ectoflexid is longer, deeper into isthmus, and near the bottom isthmus. Pli caballinid is more slender but still clear.

m3, metaconid and metastylid are smaller and more rounded; bottoms of lingua- and ectoflexid are wide and rounded, face and cling to each other in isthmus. Entoconid is sharply elongated anterolingually. Hypoconulid extends strongly posteriorly, at which, end is rounded and base is constricted; labial walls of protoconid and metaconid are straight. Pli caballinid is just clear. Bottoms of pre- and post-flexid are swollen.

Comparison

The V-shaped linguaflexid shows typical stenonid feature. The moderate size of the mandible, large dimension of the lower cheek teeth, incomplete cup on i3 support attribution of this specimen to *Equus qingyangensis* described by Deng and Xue (1999b, 1999a) (Figure 3; Table 2).

Deng and Xue (1999a) indicated that dimension of lower cheek teeth of *E. qingyangensis* is smaller than that of *E. sanmeniensis*, moreover the pli caballinid of *E. sanmeniensis* is very weak to absent whereas that of *E. qingyangensis* is usually clear to strong. The latter is identical to the Qixian material. On Qixian material, pli caballinid is strong even on molars. *E. eisenmannae* and *E. wangi* are both very large-sized stenonid horses, their lower cheek teeth have very rounded metaconid and metastylid, shallow ectoflexids on premolar and molar and beak-shaped entoconid which are different from those of *E. qingyangensis* (Deng & Xue 1999a, 1999b; Qiu et al. 2004). *E. huanghoensis* is another very large stenonid horse, its metaconid is elongated, pli caballinid is almost absent (Li et al. 2015). *E. teilhardi* and *E. yunnanensis* are medium-sized stenonid horses similar as *E. qingyangensis*. But *E. teilhardi* possibly often has lower incisors lacking cups (Eisenmann 1975; Deng & Xue 1999a) and *E. yunnanensis* has rounded metaconid and metastylid, shallow ectoflexids on premolar and molar(Liu & You 1974; Deng & Xue 1999a). *E. qingyangensis* has relatively larger lower cheek teeth (Table 4). Its mandible size is similar as *E. teilhardi* and *E. yunnanensis*, but the dimension of its lower cheek teeth is significantly larger than those of the latters. *E. senezensis* found in Seneze, France is similar as *E. qingyangensis* in size of upper cheek teeth. The length of lower cheek tooth row of *E. senezensis* is 185 mm. But its ectoflexids on premolar and molar are both shallow, close to or reach the open of isthmus. Metastylid has similar length and width, with a rectangular posterolabial part instead of a pointed tip (Eisenmann 1980). These are different from *E. qingyangensis*. *E. qingyangensis* has incomplete cup on i3, this is a special feature only found on some primitive species such as *E. simplicidens*

Table 3. Upper cheek tooth measurements of *E. teilhardi* from Qixian (mm).

Items	Teeth	Left	Right	Teeth	Left	Right
L	P2	38.8	39.3	M1	23.9	24.4
W		*28	27		27.5	27.1
PL		8.2	8.3		11.3	11.2
PI		21.1	21.1		47.3	45.9
L	P3	30.6	29.8	M2	25	25.7
W		29.3	27.9		27.4	26.4
PL		10.4	9.8		10.9	11.3
PI		40	32.9		43.6	44
L	P4	28.2	27.6	M3	26.1	27.4
W		30.4	29.4		24.9	23.6
PL		10.6	9		10.9	10.8
PI		37.6	32.6		41.8	39.4

Notes: L, length; W, width; PL, protocone length; PI, protocone index.

Table 2. Measurements of mandible of *E. qingyangensis* from Qixian and Qingyang (mm).

Items	M 1324	NWUV 1134	NWUV 1135	NWUV 1133.2	NWUV 1136
2. Muzzle length	125	126.8		101	
3. Premolar length	100.7	98.8	105.2	111.2	106.8
4. Molar length	88.2	88.5			
5. Lower cheek teeth length	189.2	186			
6. Distance between back of alveole of m3 and posterior edge of ascending ramus			135		
7. Muzzle breadth	52.8	62.2		37	
8. Height of the mandible at the condyle			180		
9. Height of the ascending ramus			163		
11. Height of the jaw between p4 and m1		92	64.8	67	77
12. Height of the jaw in front of p2	69.3	72.2	45.2	45.6	55.3
13. Length of the symphysis	85	99.5		59.5	
14. Minimal breadth of the symphysis	41.2	36.5	29.2	34	

Note: Measurements of *E. qingyangensis* of Qingyang from Deng and Xue (1999a).
*estimated data.

Table 4. Lower cheek tooth measurements of *E. qingyangensis* from Qixian and Qingyang (mm).

		M 1324		Qingyang		
Teeth	Items	Left	Right	Av.	Min.	Max.
p2	L	37.9	39	34.9	31	39.1
	W		15.4	15.1	14.2	16.5
	FL	15.1	15.7	14.9	12.5	17.2
	FI	39.8	40.3	42.8	36.4	46.7
p3	L	32.2	31.7	30.1	29	32.4
	W	19.1	18.4	16.2	13.3	18.7
	FL	15.5	15.7	15.1	14	17.1
	FI	48.1	49.5	50.2	46.4	52.8
p4	L	29.8	29.5	28.9	28	30.4
	W		18	16.2	14.1	17.9
	FL	14.5	14.2	12.8	9.3	16
	FI	48.7	48.1	44.3	33.2	52.6
m1	L	27.8	28.6	26.8	26	28.1
	W			14.2	12.5	15.8
	FL	8.8	9	9.3	6.9	12.2
	FI	31.7	31.5	34.5	26.3	43.4
m2	L	27	26.8	27.1	26.2	27.9
	W			13.7	12.5	15.3
	FL	9.2	10.2	8.9	8	10.4
	FI	34.1	32.4	33	30.1	37.7
m3	L	32.7	32.3	33.9	31.6	36.2
	W		12.4	12.2	11.1	13.2
	FL	9.3	9.6	9	7.9	10
	FI	28.4	29.7	26.3	25	27.6

Notes: L, length; W, width; FL, postflexid length; FI, postflexid index. Measurements of *E. qingyangensis* of Qingyang from Deng and Xue (1999a).

and *E. eisenmannae*, and highly specialized species such as *E. teilhardi*.

Discussion

The stenonid specimens found from Locality 32 in Qixian, Shanxi including *E. teilhardi* and *E. qingyangensis*. This is the second record of coexistence of these two species after report on Bajiazui locality, Qingyang, Gansu by Deng and Xue (1999a) (Figure 1). Although *E. teilhardi* and *E. qingyangensis* have similar body size, some of their morphological differences show significantly different niches. *E. qingyangensis* has very elongated and slender metapodials. Deng and Xue (1999a) indicated that *E. qingyangensis* has the most slender limbs in Eurasian early *Equus*. Based on estimation on basilar length by Qiu et al. (2004) and measurements of Mc III of Deng and Xue (1999a), the ration between lengths of basilar and Mc III is about 0.47–0.5, longer than most of stenonid horses we have discussed above. By comparison, the metapodial of *E. telhardi* is very short and robust as *E. sanmeniensis* (Teilhard de Chardin & Piveteau 1930). *E. qingyangensis* has a larger dimension of cheek teeth than *E. teilhardi*, based on very similar sizes between their skull and mandible. Bernor and Scott (2003) and Deng et al. (2012) argued that the horse with very slender limbs will have high ability on running. Qiu et al. (2004) indicated the larger cheek tooth row will be more powerful on grazing. Consequently, compared with *E. teilhardi*, *E. qingyangensis* should live in a relatively open environment and more tended to grazing.

Some authors considered that cup lacking on lower incisor showed the unknown relation of *E. teilhardi* with other species, its taxonomic status should be isolated in Pleistocene in Eurasia (Eisenmann 1975; Forsten 1986; Deng & Xue 1999a). Azzaroli (1965, 1982) reported incomplete cup on lower incisor in *E. stehlini*. The similar feature also can be found on *E. simplicidens*. A skull associated with a mandible of *E. simplicidens*, USNM 12573, housed in NMNH has incomplete cup both on i2 and i3. *E. simplicidens* was most primitive *Equus* and regarded as ancestor of all fossil and extant *Equus* (Deng & Xue 1999a; Qiu et al. 2004). The incomplete cup on incisor found on Eurasian *Equus* was likely a remaining feature derived from *E. simplicidens* or even more primitive lineage. It was also found on primitive *Equus* species in Eurasia such as *E. qingyangensis*, *E. yunnanensis* and *E. eisenmannae*. The skull of USNM 12573 has incomplete cups on I3 whereas another skull specimen of *E. simplicidens* USNM 13791 has complete cups on upper incisors. The Qixian skull of *E. teilhardi* has incomplete cup only on left I3. This variation shows that the cup incompleteness should be unstable in the same species even the same individual. It can be present on some species just more frequently than others. This feature will be occasionally present on some individuals but can be stable within a geographic population like *Equus burchelli* mentioned by Eisenmann (1975). But coexistence of *E. teilhardi* and other species such as *E. sanmeniensis* and *E. qingyangensis* has eliminated the possibility that *E. teilhardi* has isolated geographic population in Eurasia (Deng & Xue 1999a). So we believe that the cup lacking on holotype of *E. teilhardi* is an extremely specialized sample caused by variation.

Deng and Xue (1999a) inferred that *E. teilhardi* and *E. yunnanensis* should have relatively close relation based on incomplete cup on incisor. Although some primitive species such as *E. qingyangensis* and *E. eisenmannae* have i3s with incomplete cups, records of incomplete cup on upper incisor are only present in *E. teilhardi* and *E. yunnanensis* in Eurasian stenonid horses. Moreover, their relative palatine lengths and basicranial proportions are similar (Figures 4 and 6). Liu and You (1974) argued that *E. yunnanensis* was long-snout type stenonid horse. Actually, stenonid horses can be divided into two different groups based on ratio between lengths of nasal notch and facial part. *E. teilhardi* and *E. yunnanensis* both belong to the group with a relatively short nasal notch length (Figure 5). These two species also have short and robust metapodials (Teilhard de Chardin & Piveteau 1930; Liu & You 1974; Deng & Xue 1999a). Consequently, *E. teilhardi* and *E. yunnanensis* should have close relation. However, *E. yunnanensis* has more complicated and fine folds in fossettes on upper cheek teeth and more elongated protocone (Liu & You 1974; Deng & Xue 1999a). *E. yunnanensis* has very rounded metaconid and metastylid, very shallow ectoflexids on premolar and molar whereas *E. teilhardi* has a sharp tip on metastylid pointed lingually and its ectoflexid penetrates into isthmus on molars. The rounded metaconid and metastylid is a primitive feature but the shallow ectoflexid on molar is an advanced one (Deng & Xue 1999a). *E. stehlini* has small body size, short snout and short metapodial (Alberdi et al. 1998). Azzaroli (1982) reported a mandible specimen of *E. stehlini* has i2 and i3 lacking cups while i1s are lost, two other specimens with incomplete cups on i3. These similarities of *E. stehlini*, *E. teilhardi* and *E. yunnanensis* show the potential relation of them.

Eisenmann and Deng (2005) indicated that the skulls and limb bones of *E. qingyangensis* from Qingyang, Gansu are astonishing similar to those of *E. simplicidens* from Hagerman,

Idaho and different from the usual Villafranchian *E. stenonis*. The most important similarity of *E. qingyangensis* to *E. simplicidens* is the low basicranial proportion. This proportion of *E. qingyangensis* is almost lower than any other stenonid horses in Eurasia. Another important feature is the distance between temporal condyle and posterior margin of orbital bar. In most *Equus*, temporal condyle and posterior margin of orbital bar are adjacent, only *E. simplicidens* and *E. qingyangensis* have about 10–12 mm distance between these two constructs. This feature is also present on hipparion horse so it is a primitive one (Qiu et al. 1987; Deng & Xue 1999a). These two species also have shallow nasal notch and lower incisors with incomplete cup. Compared with *E. simplicidens*, *E. qingyangensis* has some advanced features such as weaker preorbital fossa, slender limb and pointed tip on metastylid. Deng and Xue (1999a) argued that *E. qingyangensis* should be occurred at the base of Quaternary so it is one of the oldest *Equus* in Eurasia. Wang and Deng (2011) compared *E. eisenmannae* with modern horses and discussed on some trends which they thought played an important role in equid evolution (Forsten 1988; Azzaroli 1992; Eisenmann 1996; Prado & Alberdi 1996; Eisenmann & Baylac 2000). Body size decreases, skull elongates, lengths of interalveolar and cheek tooth row decrease, and nasal notch deepens even above P3 or P4. These are also reflected from our data (Figures 4–7). *E. qingyangensis* is a species very close to but a little more advanced than *E. simplicidens*. The former should be a direct descendant of the latter and should be regarded as one of the earliest and most primitive stenonid horses in Eurasia. By comparison, *E. teilhardi* is a bit more advanced than *E. qingyangensis* on skull features. However, they have been found coexisted in two localities, and *E. teilhardi* has shorter and more robust metapodials which is primitive feature (Deng & Xue 1999a). So *E. teilhardi* should not be the descendant type of *E. qingyangensis*. Origins of some Chinese stenonid horses have been figured out. Qiu et al. (2004) indicated that *E. sanmeniensis* and *E. stenonis* should be descendants of *E. eisenmanae*. However, discovery of origin of *E. teilhardi* needs more material and further research.

Conclusion

The PMU M 1321 from Qixian, Shanxi Province is the first record of a complete skull for *Equus teilhardi*. This skull comfirms arguments on this species of previous authors and provides more important features for diagnosing this species, including the moderately deepened nasal notch, strong preorbital fossa, I3 with incomplete cup, short snout and low basicranial proportion.

The PMU M 1324 from Qixian, Shanxi Province is a mandible of *Equus qingyangensis*. Its features resemble those of the specimens of this species in Qingyang, Gansu Province well. It is the second record of coexist of *E. qingyangensis* and *E. teilhardi*. The new skull material of *E. teilhardi* shows its significant differences from *E. qingyangensis*, which clearly confirm the different ecological niches of these two species. Incomplete cup on incisor is a common feature found in stenonid horses, especially the primitive species, such as *E. simplicidens*. And this is also an unstable feature. *E. teilhardi* likely had close relation to stenonid species which is small-sized and with incomplete cup on incisor.

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