A Late Pliocene Hipparion houfenense fauna from Yegou, Nihewan Basin and its biostratigraphic significance postprint

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Abstract

Currently, divergent views persist regarding the chronology of Late Cenozoic deposits in the Nihewan Basin, stemming from contradictions between biostratigraphic correlations based on mammalian fossils and magnetostratigraphic dating results. Biostratigraphic correlations indicate that the aeolian red clay exposed in the Sanggan River canyon, the fluviolacustrine red clay with sands and gravels, and the sandy clay of swamp facies on both sides of the lower reaches of the Huliu River belong to the Upper Pliocene, whereas magnetostratigraphic dating typically correlates them to the Lower Pleistocene. In October 2011, a collection of mammalian fossils was unearthed from a collapsed deposit block at Yegou in the Nihewan Basin, located approximately 300 m north of the Laowogou section, which is well known for Pliocene mammalian fossils from its lower part. The Yegou fossils are herein identified as 10 species within 9 genera: Nyctereutes tingi, N. sinensis, Pachycrocuta pyrenaica, Homotherium sp., Hipparion (Plesiohipparion) houfenense, Dicerorhinus sp., Muntiacus sp., Axis shansius, Gazella blacki, and Paracamelus sp. This fauna differs considerably from the classic Early Pleistocene Nihewan Fauna in composition and provides new evidence for the existence of the Upper Pliocene in the Nihewan Basin. Based on systematic description of the fauna, its composition and geological age are discussed, and the compositional characteristics of large mammals from Late Pliocene and Early Pleistocene mammalian faunas in the Nihewan Basin are summarized.

Full Text

Preamble

A Late Pliocene Hipparion houfenense Fauna from Yegou, Nihewan Basin and Its Biostratigraphic Significance

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Abstract

Chronological interpretations of Late Cenozoic deposits in the Nihewan Basin remain contentious, stemming from contradictions between biostratigraphic correlations based on mammalian fossils and magnetostratigraphic dating results. Biostratigraphic correlations indicate that the aeolian red clay exposed in the Sanggan River canyon, the fluvio-lacustrine red clay with sands and gravels, and the swamp-facies sandy clay on both sides of the lower Huliu River belong to the Upper Pliocene, whereas magnetostratigraphic dating typically correlates them to the Lower Pleistocene. In October 2011, a collection of mammalian fossils was unearthed from a collapsed deposit block at Yegou in the Nihewan Basin, located approximately 300 m north of the Laowogou section, which is well known for Pliocene mammalian fossils from its lower part. The Yegou fossils are herein identified as 10 species in 9 genera: *Nyctereutes tingi*, *N. sinensis*, *Pachycrocuta pyrenaica*, *Homotherium* sp., *Hipparion (Plesiohipparion) houfenense*, *Dicerorhinus* sp., *Muntiacus* sp., *Axis shansius*, *Gazella blacki*, and *Paracamelus* sp. This fauna differs considerably in composition from the classic Early Pleistocene Nihewan Fauna and provides new evidence for the existence of Upper Pliocene strata in the Nihewan Basin. Based on systematic description of the fauna, its composition and geological age are discussed, and the compositional features of large mammals from Late Pliocene and Early Pleistocene mammalian faunas in the Nihewan Basin are summarized.

Keywords: Nihewan Basin, Upper Pliocene, large mammals, *Hipparion (Plesiohipparion) houfenense*, biostratigraphy, magnetostratigraphy

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1 Introduction

In 2011, CHI Zhen-Qing of the Institute of Geology, Chinese Academy of Geological Sciences, invited ZHENG Shao-Hua of the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences to conduct a joint investigation in the Nihewan Basin. On October 4th of that year, the team discovered abundant large mammal fossils at Yegou, north of Daodi Village, which are herein identified as 10 species in 9 genera: *Nyctereutes tingi*, *N. sinensis*, *Pachycrocuta pyrenaica*, *Homotherium* sp., *Hipparion (Plesiohipparion) houfenense*, *Dicerorhinus* sp., *Muntiacus* sp., *Axis shansius*, *Gazella blacki*, and *Paracamelus* sp. The Yegou locality (N40°9 9.9 , E114°39 19.4) is located about 300 m north of the Laowogou section, the stratotype of the "Daodi Formation" (Du et al., 1988). The fossils were recovered from a large collapsed deposit block consisting of dark brownish-grey silty clay; however, the stratigraphic section is not exposed. Based on the fossils, lithology, and altitude, this horizon may be roughly correlated to Layer 9 of the Laowogou section, which has yielded *Hipparion* sp., *?Chilotherium* sp., *Axis shansius*, *Cervus* sp., *Antilospira* sp., etc. (as listed in Cai et al., 2004 and Cai et al., 2013). If taken as a unified fauna, they would represent a diverse *Hipparion houfenense* fauna.

On the one hand, the extensive presence of Pliocene strata on both sides of the Huliu River has been indicated by large mammal fossils from Luanshigedagou, Dannangou, and Huabaogou (Huang et al., 1974; Tang, 1980b; Wang, 1982) and small mammal fossils from Yuanzigou, Qijiazhuang, Jiangjungou, Laowogou, Hongyanangou, and Huabaogou (Zhang et al., 2003; Cai et al., 2004, 2013; Li et al., 2008). On the other hand, recent magnetostratigraphic dating results have placed the fossil-bearing layer of Luanshigedagou, Hongya Village between the "Gauss-Matuyama" boundary and the lower boundary of "Olduvai" (2.58-1.95 Ma); the upper fossil layer of Huabaogou, HBG-I, right above the upper boundary of "Olduvai" (<1.77 Ma); the lower fossil layer of Huabaogou, HBG-II, within "Olduvai" (1.95-1.77 Ma); and the fossil layers of DD-1~7 of Daodi or Laowogou between the "Gauss-Matuyama" boundary and the upper boundary of "Olduvai" (2.58-1.77 Ma) (Zhu et al., 2007; Deng et al., 2008; Deng, 2011; Ao et al., 2013). Consequently, an apparent contradiction exists between these results and biostratigraphic correlations based on mammalian fossils. The features of the Yegou *Hipparion houfenense* fauna, which comprises only large mammals, also indicate a Pliocene age. Its establishment accordingly provides additional evidence for the existence of Pliocene strata in the Nihewan Basin and for the necessity of cautious reinterpretation of these magnetostratigraphic dating results.

Abbreviations: F:AM, Frick Collection of American Museum of Natural History; IVPP V/V, catalogue number of vertebrates of Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences (IVPP, CAS); IVPP RV/RV, revised catalogue number of vertebrates of IVPP, CAS; JNTZ, catalogue number of Nanjing Museum; NNNM, catalogue number of Nihewan National Nature Reserve; NWUV, catalogue number of vertebrates of Northwest University; THP, catalogue number of Tianjin Natural History Museum; ZKD, Zhoukoudian; L, length; W, width; Tri, trigonid; Min, minimum; Max, maximum.

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2 Systematic Descriptions

Nyctereutes tingi **Tedford & Qiu, 1991 (Fig. 1 [Figure 1: see original paper])**

Material: Fragmentary right ramus with all teeth except i2 and m3 (IVPP V 18833.1, Fig. 1A); anterior portion of fragmentary left ramus with c–p2 (V 18833.2); right m1 (V 18833.3, Fig. 1B); right p4 (V 18833.4); fragment of right ramus with trigonid of m1 (V 18833.5).

Measurements: See Table 1 .

Description: The portion posterior to m2 is not preserved on IVPP V 18833.1, so the development of the subangular lobe is unclear. The horizontal ramus, especially the anterior portion, is relatively robust. The ventral profile of the horizontal ramus is almost straight, but the ramus gradually deepens posteriorly, measuring about 16.0 mm anterior to p3 and about 17.5 mm anterior to m1. The symphysis is oval-shaped in lingual view, with its posterior margin slightly exceeding the posterior end of p2 (Fig. 1A2). There are two mental foramina: the anterior one is larger and located below the diastema between p1 and p2, while the posterior one is smaller and positioned directly below p3 (Fig. 1A3).

The lower incisors are well preserved except for i2, set obliquely on the ramus with tips protruding dorsoanteriorly. The i1 is spatula-like with a truncated top and no lingual cusp. The i2 is missing, leaving an oblong alveolus larger than that of i1. The i3 is basically a triangular pyramid and distinctly larger than i1, which is characterized by a feeble distal cusp. The lower canine is conical and buccolingually compressed.

The p1 is unicuspid and single-rooted. The p2, p3, and p4 are basically similar in both size and morphology: they are buccolingually compressed to some extent and possess a developed principal cusp. No accessory cusps are developed on either p2 or p3, but there is a remarkable posterior accessory cusp on p4. The protoconid is the dominant cusp on m1, whereas the paraconid is slightly smaller and the metaconid the smallest. The talonid of m1 is simple, bearing only the hypoconid and entoconid, with the former higher than the latter. A transverse cristid between them divides the talonid into two parts, with the anterior part larger than the posterior part (see Fig. 1B1). No accessory cusps or tubercles could be discerned on the talonid of m1. The m2 is oval-shaped in occlusal view, with the anterior half broader than the posterior half. The metaconid is slightly taller than the protoconid but similar in size. The talonid of m2 bears a distinct hypoconid and a weak crest-like entoconid, with no accessory cuspids developed. A cingulid is slightly developed anterobuccally on the tooth.

IVPP V 18833.2 is a fragmentary left ramus preserving only the portion anterior to p3. Its teeth, such as c, p1, and p2, are generally similar to those of V 18833.1 in both size and shape. V 18833.3 is basically similar to the m1 of V 18833.1 in morphology but differs slightly in the development of a feeble tubercle on the posterior margin of the tooth (Fig. 1B1), which could be considered an embryonic hypoconulid. V 18833.4 is a right p4, similar to that of V 18833.1 in both shape and size. V 18833.5 bears a broken right m1; the preserved protoconid and metaconid are the same as those of V 18833.1 and V 18833.4 in morphology and no smaller than the latter two in size.

Comparisons and Discussion: Based on the morphology and size of the mandible and lower carnassial (m1) summarized in Tedford et al. (1995, 2009) and Daguenet and Sen (2019), the Yegou specimens are undoubtedly assigned to *Nyctereutes* of Canidae. The Yegou specimens are obviously larger than *Nyctereutes sinensis* from Yushe, Shanxi and Zhoukoudian, and extant *N. procyonoides* as well, but closer in size to *N. tingi* from Yushe (Table 1).

The ramus of V 18833.1 is relatively robust, with the anterior half especially deep, and therefore differs from *Nyctereutes sinensis*, which has an anteriorly shallow but posteriorly deep ramus such that the dorsal margin of the ramus slopes strongly downward anteriorly (see Tedford and Qiu, 1991: fig. 1B; Pei, 1934: fig. 5D [Figure 5: see original paper]). Consequently, the anterior portion of the ramus of *N. sinensis* is much slimmer: for example, the depth of V 350-2 from Loc. 1 of Zhoukoudian is only 13.8 mm anterior to p3, while that of V 12368.1-2 from Ningyang, Shandong is only 11.2-13.3 mm. In this feature, the Yegou specimen V 18833.1 is closer to the holotype of *N. tingi* (F:AM 97030) from Yushe, which has the same dimension of 15.1 mm.

In addition, the m1 talonid of V 18833.1 and V 18833.3 is relatively simple in construction, bearing no tubercles except the hypoconid and entoconid, and consequently differs from *Nyctereutes sinensis*, whose m1 talonid tends to be more complicated. For example, the entoconid of *N. sinensis* from Loc. 1 of Zhoukoudian normally splits into 2-3 cuspids (Pei, 1934), and an extra cuspid—the hypoconulid—is even developed on the m1 of *N. sinensis* from Renzidong, Fanchang, Anhui (Liu and Qiu, 2009). It should be noted that a transverse cristid developed between the hypoconid and entoconid, with subsequent division of the talonid into two unequal parts, are the primary morphological features distinguishing *N. tingi* from *N. sinensis* (Tedford and Qiu, 1991). According to such morphological criteria, the Yegou specimens could be referred to *N. tingi* without doubt, which further confirms the assertion of the existence of *N. tingi* in the Nihewan Basin proposed by Farjand et al. (2021).

The m2 of V 18833.1 is quite simple in morphology: a cingulid is only slightly developed on its anterobuccal margin, and the entoconid is crest-like on the talonid with no accessory cuspids except the entoconid and hypoconid. The Yegou specimens are exactly in accordance with *Nyctereutes tingi* in m2 morphology as well.

Based on the morphology and size of both the rami and teeth described above, the Yegou specimens are apparently closer to *Nyctereutes tingi* as a whole, although they are fragmentary and lack certain key diagnostic parts such as the subangular lobe and angular process of the mandible.

Nyctereutes tingi was originally established based on material from the Mazegou and Gaozhuang formations in the Yushe Basin (Tedford and Qiu, 1991). It is a fairly primitive species at an evolutionary stage roughly correlatable to *N. donnezani* of the Ruscinian of Europe. The species was also reported at Lingtai, Gansu (Huang et al., 1993) and Danangou of the Nihewan Basin (Farjand et al., 2021). Known records indicate that *N. tingi* is distributed only in Pliocene strata. For that reason, the discovery of *N. tingi* at Yegou proves that Pliocene strata do exist in the Nihewan Basin.

Fossil *Nyctereutes* has a continuous stratigraphic distribution in Chinese strata from the Early Pliocene onward and shows an evolutionary trend of gradual body size reduction (Pei, 1934; Teilhard de Chardin and Pei, 1941). Dental measurements of *N. tingi* from the Yushe Basin clearly reveal such a trend: teeth from the Gaozhuang Formation are generally larger than those from the Mazegou Formation (based on WANG Xiao-Ming' s unpublished data). In dental size, the material from Yegou is much closer to that from the Mazegou Formation (Late Pliocene) but smaller than that from the Gaozhuang Formation (Early Pliocene).

Nyctereutes sinensis **(Schlosser, 1903) (Fig. 2 [Figure 2: see original paper])**

Material: Fragmentary cranium lacking the rostrum (IVPP V 18834.1, Fig. 2); fragmentary right ramus with m2 (V 18834.2); fragmentary right ramus with only alveoli of p1–3 preserved (V 18834.3).

Measurements: See Table 2 .

Description: V 18834.1 is an incomplete cranium. The nasals, premaxillae, and maxillae are broken off, and both zygomatic arches and the right tympanic bulla are also missing. It is distinctly larger than the extant species *Nyctereutes procyonoides*. In lateral view, the dorsal profile of the frontal and parietal first runs posterodorsally, reaching its highest point approximately above the postglenoid process, then runs horizontally posteriorly (Fig. 2D, E).

In dorsal view, the frontal area is fairly broad, with maximal breadth between the postorbital processes of 53.5 mm, comparable to the greatest neurocranium breadth. The central portion of both frontals bulges strongly, forming a deep depression along the frontal suture between the frontals. The vulpine groove is also developed on the surface adjacent to the frontal postorbital process, indicating that the frontal sinus is developed but does not expand into the tip of the postorbital process. The postorbital process is rather robust. The posterodorsal rim of the orbit is not straight but curved and concave. The strong, ridge-like parasagittal crest also makes a concave curve, extending from the postorbital process posteromedially and joining its counterpart slightly posterior to the frontoparietal suture, which makes the postorbital process very pointed (Fig. 2A). The sagittal crest is also massive, projecting about 3.0 mm from the parietal surface. The sagittal crest, especially its anterior portion, is broad, with a central longitudinal groove running throughout along the midline. The postorbital constriction is not strong, with a width of 37.1 mm, which is broader than the distance between the orbits (less than 33.2 mm) and about the same as the braincase width. The surface of the parietal is relatively smooth, not as rough as that of the extant species. In ventral view, the tympanic bulla is strongly inflated, especially at the middle and posterior portions. The anterolateral side is less dilated, and the anterior margin aligns with the postglenoid process without exceeding it (Fig. 2B).

V 18834.2 is a fragmentary ramus with only the m2 still in position. The dorsal profile of the horizontal ramus slopes significantly downward anteriorly. As a result, the anterior portion of the ramus is shallower, with a depth of only 14.4 mm anterior to p3. The m2 (about 5.9 mm in width) is similar to that of V 18833.1 of *Nyctereutes tingi* in morphology but evidently narrower. A cingulid is developed anterobuccally and is more distinct than in V 18833.1. The metaconid is quite small but discernible.

V 18834.3 preserves only the portion anterior to p4, including the alveoli of p1–3. The anterior portion of the ramus is shallower, with a depth of about 13.2 mm anterior to p3.

Comparisons and Discussion: Although the cranium of V 18834.1 is incomplete, the preserved portion can be compared with species of *Nyctereutes*. It is distinctly larger than extant *N. procyonoides* but roughly comparable in size to *N. sinensis* from Yushe, Shanxi (Table 2).

Regarding cranial morphology, V 18834.1 appears to combine characteristics of both *Nyctereutes sinensis* and *N. tingi*. On the one hand, V 18834.1 is quite similar to specimen JNTZ 7571 of *N. sinensis* from Tuozidong, Nanjing in the following aspects: (1) almost equal size; (2) robust, pointed, and protruding postorbital process; (3) curved and ridge-like parasagittal crest; (4) high and broad sagittal crest with a central longitudinal groove running throughout; and (5) anterior margin of the tympanic bulla not exceeding the postglenoid process (Liu et al., 2007:26, fig. 2.4). Moreover, cranium V 18834.1 also resembles that of *N. sinensis* (=Liu, 2019: *Nyctereutes* cf. *N. tingi*) from the Nihewan Basin described by Liu (2019), such as NNNM 13-18 (see Liu, 2019: fig. 23 [Figure 23: see original paper]), in all features listed above except for the fifth one. Nevertheless, it is worth noting that neither central bulging of the frontal nor depression along the frontal suture could be discerned in JNTZ 7571 and NNNM 13-18.

On the other hand, V 18834.1 is also similar to specimens of *Nyctereutes tingi* from Yushe, Shanxi in the following characteristics: (1) the dorsal profile of the parietal is relatively flat rather than convex in lateral view; (2) the neurocranium is laterally inflated so poorly that its maximal width is almost equal to that across the postorbital processes; and (3) the postorbital constriction is so weak that its width is evidently greater than the distance between the orbits.

As a whole, nevertheless, the Yegou specimens seem closer to *Nyctereutes sinensis*, while retaining some primitive features similar to *N. tingi*. It should be noted that cranium V 18834.1 is incomplete, and the analysis mentioned above is largely based on reconstruction (see the white plaster part in Fig. 2). Whether the reconstruction is correct has a direct bearing on the conclusion of similarity between V 18834.1 and *N. tingi*. In other words, its similarity to *N. tingi* cannot be assured at the moment. Under such circumstances, it seems more reasonable to assign the Yegou specimens described herein to *N. sinensis*. If that is the case, there would be co-occurrence of both *Nyctereutes* species at Yegou, Nihewan Basin—a situation similar to that in the Yushe Basin (Tedford and Qiu, 1991).

The morphological differences between V 18834.2-3 and V 18833.1 are as follows: (1) the ramus of the former is relatively slim, with the anterior portion especially shallow and the dorsal profile sloping significantly; (2) the m2 is relatively narrow, but the cingulid and entoconid are much better developed on the tooth. In these morphological characters, nevertheless, V 18834.2-3 exactly show the diagnostic features for *N. sinensis*.

In terms of chronological distribution, *Nyctereutes sinensis* has extensive Late Pliocene and Early Pleistocene records, such as those from the Yushe Basin of Shanxi (Tedford and Qiu, 1991), the Nihewan Basin of Hebei (Teilhard de Chardin and Piveteau, 1930; Liu, 2019), Wushan of Chongqing (Huang and Zhong, 1991), Ningyang of Shandong (Zhang, 2001), Fanchang of Anhui (Liu and Qiu, 2009), Mianchi of Henan (Zdansky, 1924), Tuozidong, Nanjing of Jiangsu (Liu et al., 2007), and so on. In addition, some *Nyctereutes* fossils from Middle Pleistocene horizons, such as Loc. 13 and Loc. 1 of Zhoukoudian, were also assigned to *N.* "sinensis" (Pei, 1934; Teilhard de Chardin and Pei, 1941), but the systematic identification of these *Nyctereutes* fossils remains doubtful and disputed. In terms of morphology, they are actually closer to the extant species rather than earlier fossil species (Soria and Aguirre, 1976; Tedford and Qiu, 1991).

The differences between the Yegou specimen V 18834.1 and the Zhoukoudian specimens of *N.* "sinensis" lie in the following features: the frontal postorbital process of the former is more protruding; the postorbital constriction is not strong; and the surface of the parietal is relatively smooth. All these features are basically consistent with *Nyctereutes* fossils from Nihewan and Tuozidong, Nanjing (Teilhard de Chardin and Piveteau, 1930; Liu et al., 2007; Liu, 2019). The morphology of V 18834.1 actually provides further support for the judgment and analysis of Soria and Aguirre (1976), Tedford and Qiu (1991), and others.

If the reconstruction of V 18834.1 is reliable, it would be slightly more primitive than other known crania assigned to *Nyctereutes sinensis* (such as those from Nihewan and Tuozidong), with a flat parietal and less dilated neurocranium. In this respect, the specimens described herein seem to be no later in age than those from the Mazegou Formation of the Yushe Basin.

Pachycrocuta pyrenaica **(Depéret, 1890) (Fig. 3 [Figure 3: see original paper])**

Material: Fragmentary ramus with p3–m1 (IVPP V 18835, Fig. 3).

Measurements: See Table 3 .

Description: V 18835 is a left broken ramus lacking the portion anterior to p3 and most of the ascending ramus. The horizontal ramus is relatively slim, with a depth of 37.7 mm anterior to p3 and 43.4 mm posterior to m1. In occlusal view, p3, p4, and m1 are almost rectangular in shape. The principal cusp of p3 leans posteriorly and is massive but buccolingually compressed. The posterior accessory cusp is low. No discernible anterior accessory cusp is developed, but a swollen enamel ridge formed anterolingually around the base of the crown probably represents a rudimentary cuspid. Feeble cingulids are discernible at the anterior and posterior margins of the tooth.

The p4 is slightly larger than p3. The principal cusp is robust and tall but leans posteriorly. It has anterior and posterior accessory cusps of equal size. The three cusps align almost in a straight line oblique to the long axis of the tooth, with the anterior accessory cusp positioned lingually and the posterior one buccally. The anterior cingulid is less developed than the posterior one.

The anterior portion of m1 (where the paraconid is located) is slightly broader than the posterior portion (the talonid). The paraconid is slightly longer than the protoconid but they are almost equal in height. The metaconid is developed at the posterolingual corner of the protoconid, with only half the height of the latter. The two cusps are separated by a shallow groove. The talonid is robust and broad, with the trigonid comprising only 78% of the total length of the tooth. The hypoconid and entoconid are distinct: the hypoconid appears almost as a ridge parallel to the long axis of the tooth, while the entoconid is low and conical on the lingual side. A curved ridge connects the hypoconid and entoconid at the posterior margin of the talonid; several cuspids or tubercles developed on it could be regarded as a rudimentary hypoconulid. A weak cingulid is developed on both the anterior and posterior margins of the tooth.

Comparisons and Discussion: In terms of dental size and morphology, the Yegou specimen described above (especially the m1) is conspicuously closest to *Pachycrocuta* in Hyaenidae. It can be distinguished from *P. brevirostris* and *P. licenti* by its smaller size, relatively narrow premolars, and an m1 with a more developed metaconid and talonid. The Yegou specimen virtually approximates *P. pyrenaica* and *P. perrieri* in both size and morphology.

In dental length, the Yegou specimen is nearly the same as *Pachycrocuta pyrenaica* and *P. perrieri*, completely falling within the variation range of these two species (Table 3). However, in dental width, the Yegou specimen is closer to *P. pyrenaica* from Yushe, Shanxi, and distinctly narrower than *P. perrieri* (distinctly less than its mean, see Table 3). Morphologically, *P. pyrenaica* differs from *P. perrieri* in its much narrower premolars (mainly P2/p2, P3/p3) (Howell and Petter, 1980; Qiu, 1987).

It seems not convincing enough to identify a species solely on the basis of tooth size. The lower carnassial of V 18835 would provide extra robust evidence for that. *Pachycrocuta pyrenaica* is relatively primitive in shape: the shearing blades of the carnassials (P4 and m1) are relatively short, shown as a lower value in the proportion of the trigonid to the total length of the tooth on m1 (i.e., Tri/m1 in Table 3) (Howell and Petter, 1980). The trigonid of the Yegou specimen is relatively short (about 78% of total length) and comparable to *P. pyrenaica* from other localities but shorter than *P. perrieri* (completely outside the variation range of the latter, see Table 3). Moreover, the metaconid of m1 is usually reduced or absent in *P. perrieri* (Howell and Petter, 1980; Qiu, 1987). For example, the metaconid on m1 of JNTZ 6401 from Tuozidong, Nanjing is vestigial in the shape of an enamel tubercle on the posterolateral side of the protoconid near its base (Liu et al., 2007). The metaconid on m1 of the Yegou specimen is small but completely separated from the protoconid by a distinct shallow notch and functions as an independent cusp (see Fig. 3B, C), which is quite different from the vestigial metaconid on m1 of *P. perrieri.*

Pachycrocuta pyrenaica was first discovered at Serrat d' en Vacquer, France. Depéret (1890) originally named it *Hyaena arvernensis* var. *pyrenaica.* However, "Hyaena arverensis" should be a junior synonym of "Hyaena perrieri" (Howell and Petter, 1980; Qiu, 1987). In fact, as early as 1954, Viret already clarified the situation but emphasized that the specimens from Serrat d' en Vacquer, France, didn' t belong to *perrieri* at all but represented another independent species "Hyaena donnezani" (Viret, 1954). Howell and Petter (1980) attributed the authorship of the species name to Charles Depéret based on the principle of priority. They also pointed out that the species didn' t belong to the extant genus *Hyaena* Brisson, 1762, but to the fossil genus *Pachycrocuta* Kretzoi, 1938. The name of the species was consequently revised as *P. pyrenaica* (Depéret, 1890).

Regarding size and morphology, certain similarities do exist between *Pachycrocuta pyrenaica* and *P. perrieri*, sometimes making them difficult to distinguish. As a result, *P. pyrenaica* was even questioned as a probable synonym of *P. per-*

rieri (Werdelin and Solounias, 1991; Turner et al., 2008). The Yegou specimen V 18835 bears the typical morphology of *P. pyrenaica* (based on the standard of Howell and Petter, 1980), which provides powerful support for the validity of the species. If only dental length is considered, it would be somewhat difficult to differentiate the Yegou specimen from small-sized *P. perrieri*. For example, taking the Yegou specimen V 18835 as *P. pyrenaica* and the Tuozidong specimen JNTZ 6401 from Nanjing as *P. perrieri*, the lengths of p3, p4, and m1 would be 21.2, 22.5, 25.0 mm and 20.8, 23.0, 25.8 mm respectively, while the corresponding widths would be 13.2, 12.6, 12.0 mm and 14.5, 14.4, 13.6 mm respectively. It is easy to notice that the p4 and m1 of V 18835 are slightly shorter than those of JNTZ 6401, but conversely, its p3 is longer than that of the latter. Nevertheless, the teeth of V 18835 are distinctly narrower than those of JNTZ 6401 (data for the latter from Liu et al., 2007). In addition, JNTZ 6401 can be distinguished from V 18835 in m1 by the following characteristics: relatively long trigonid (21.6 mm, 83.7% of total length); short talonid; and reduced metaconid as a dependent tubercle. The present authors have no intention of discussing in depth the validity of *P. pyrenaica*, which is beyond the scope of this paper, but the Yegou specimen V 18835 would provide a good example to support the conclusion of Viret (1954) and Howell and Petter (1980).

In terms of morphology, *Pachycrocuta pyrenaica* is undoubtedly more primitive than *P. perrieri*, which is probably derived from the former (Schütt, 1972; Howell and Petter, 1980; Qiu, 1987). Their geochronological distribution also supports this hypothesis: *P. pyrenaica* occurs only in pre-Villafranchian strata in Europe, such as Serrat d' en Vacquer of France (Depéret, 1890), Layna (Crusafont and Sondaar, 1971) and La Calera II (Adrover et al., 1976) of Spain, and Odessa Catacomb of Ukraine (Howell and Petter, 1980), while *P. perrieri* occurs slightly later in Villafranchian and younger strata, such as Etouaires (Croizet and Jobert, 1828) and Saint-Vailler (Viret, 1954) of France, Villaroya and Puebla de Valverde of Spain (Croizet and Jobert, 1828), Vald' Arno of Italy (Weithofer, 1889), Hajnáčka of Slovakia (Fejfar, 1964), and so on. Fossil records of *P. pyrenaica* are relatively scarce in China, known only from Yushe, Shanxi (Qiu, 1987) and Zanda, Xizang (Tseng et al., 2016, = *P. perrieri*). In contrast, records of *P. perrieri* are more extensive, known from Yushe, Shanxi and the Nihewan Basin of Hebei (Qiu, 1987), Ningyang, Shandong (Zhang, 2001), Tuozidong, Nanjing of Jiangsu (Liu et al., 2007), Wushan of Chongqing (Huang and Zhong, 1991, = *P. licenti*; Zhang, 2001), and Shanyangzhai, Qinhuangdao of Hebei (Liu, unpublished). The geochronological distribution of the two *Pachycrocuta* species in China is similar to that in Europe. Except in the Yushe Basin, *P. perrieri* is only distributed in the Early Pleistocene (equivalent to middle and late Villafranchian). Although *P. perrieri* and *P. pyrenaica* co-occurred in the Yushe Basin, the former is only known from the upper part of the Mazegou Formation, with an age equivalent to early Villafranchian, while *P. pyrenaica* is known from the lower part of the Mazegou Formation, the Gaozhuang Formation, and even the Mahui Formation of the Upper Miocene, with an age equivalent to or even older than the Ruscinian (Qiu, 1987; Deng and Hou, 2011). The discovery of *P. pyrenaica* at Yegou in the Nihewan Basin not only expands the distribution of this species but also provides reliable evidence for determining the age of the Yegou fauna.

***Homotherium* sp. (Fig. 4 [Figure 4: see original paper])**

Material: Anterior half of left ramus with i2, c, and p4 (IVPP V 18836.1, Fig. 4); fragmentary right ramus with i3 (V 18836.2).

Measurements: See Table 4 .

Description: V 18836.1 is the anterior half of a left ramus with the portion posterior to p4 missing. The symphysis is well preserved, though the portion beneath the canine is slightly broken. In rostral view, the symphysis is nearly rectangular with height greater than width. Multiple nutrient foramina can be discerned on the surface. In lingual view, the symphysis has a nearly vertical rough surface, with the upper part slightly wider than the lower. The posterior margin terminates approximately at the posterior edge of the canine (Fig. 4C). In buccal view, the mesial portion of the symphysis, especially the upper third, distinctly protrudes anteriorly so much that the incisor row is conspicuously anterior to the canine (Fig. 4A). The ventral margin of the symphysis is at about the same level as that of the horizontal ramus due to the missing mandibular flange, but the dorsal margin of the symphysis is apparently higher than that of the horizontal ramus, so the implant positions for the incisor and canine are higher than those for the cheek teeth (Fig. 4A, C). The robust, ridge-like mental crest is developed beneath the canine, but most of the ventral portion is missing, and the mandibular flange is missing as well. However, judging from the surrounding structures, the mandibular flange might have been very well developed.

The p1 and p2 are not developed at all, so there is a diastema of 38.1 mm between the canine and p3. The dorsal margin of the ramus within the diastema slopes upward anteriorly from the anterior end of p3. Approximately beneath the midpoint of the diastema, a mental foramen 10.7 mm in diameter is developed right above the ventral margin of the ramus. There is another mental foramen 6.6 mm in diameter posterodorsal to the anterior mental foramen, with a distance of 14.0 mm between them. Beneath the smaller mental foramen, there is an anteroventrally running ridge, indicating the existence of a mandibular flange (although not preserved). In occlusal view, the dorsal edge of the diastema forms a sharp crest that is lingually concave (Fig. 4B).

In occlusal view, the incisors and canine are densely aligned and form a unitary anteriorly convex arc (Fig. 4B). The i1 and i3 have already fallen off, leaving only oval alveoli. Judging from the shape of the alveoli, i1 to i3 gradually increase in size. The i2 is conical and slightly bends posteriorly. Two distinct crests are developed on the anteromedial and posterodistal sides respectively; both crests are serrated, but the posterodistal one is sharp. Although p3 has shed off, the gourd-shaped alveolus (length/width: 12.9 mm/7.4 mm) clearly indicates that the tooth had two detached roots. The p4 is large and buccolingually compressed. In occlusal view, it appears approximately rectangular. The principal cusp is robust, tall, and leans posteriorly. Two thin, sharp lateral crests run forward and backward respectively from the principal cusp; the anterior lateral crest is serrated. The two blunt-tipped accessory cusps are nearly equal in size and height. There is a second cuspid posterior to the posterior accessory cusp. A weak cingulid is developed only on the posterolingual margin of the tooth.

Comparisons and Discussion: Although the material is quite limited, a series of important anatomical features have been revealed: the mental crest and mandibular flange are developed at the symphysis; the incisor row is anteriorly convex; the canine, incisors, and molars have lateral crests with serration; and the implant position of the incisors and canine is higher than that of the cheek teeth. By these convincing features, the Yegou specimens described above should undoubtedly be assigned to the saber-tooth group, namely Machairodontinae. Based on the size and morphology of the mandibular flange and mental crest, they should definitely be excluded from *Megantereon*. Consequently, only *Machairodus* and *Homotherium* are applicable for further discussion about their assignment.

It is generally accepted that *Machairodus* and *Homotherium* are phylogenetically close to each other, with the latter probably derived from the former (de Beaumont, 1975, 1978; Kurtén and Anderson, 1980; Sharapov, 1989; Sotnikova, 1992; Liu, 2003). It is not troublesome to distinguish the two genera when specimens are plentiful and complete; however, it is rather difficult when material is scarce and fragmentary. Teilhard de Chardin and Leroy (1945) once assigned three mandibles from Yushe (RV 45016–45018 in Table 4, Teilhard de Chardin and Leroy, 1945: fig. 6 [Figure 6: see original paper]) to *Machairodus palanderi* (= *Epimachairodus palanderi*). Judging from current knowledge, there seem to be at least two differences between these Yushe mandibles and other mandibles identified as *Machairodus*: (1) the Yushe specimens are smaller, especially RV 45016 and RV 45017 (see measurements in rows 1, 3, 4, 9, 10 of Table 4), and even smaller than *M. kurteni*; (2) the premolars of both the large individual (RV 45018) and the slender individuals (RV 45016 and RV 45017) are smaller than in species of *Machairodus*, especially p3. In *Machairodus*, p3 is generally large; even in *M. palanderi*, which has a relatively reduced p3, its length can still reach 15.1 mm (Zdansky, 1924). The p3 usually has bifurcated two roots (Sharapov, 1989; Sotnikova, 1992: fig. 4), and 2–3 cusps are developed on p3 (Sotnikova, 1992; Anton et al., 2004; Qiu et al., 2008). Among the Yushe mandibles, the p3s of RV 45016 and RV 45018 are single-rooted; the p3 of RV 45017 is likely two-rooted but fused together at least at the upper part; the p3s of RV 45016 and RV 45018 have fallen off, leaving only the alveolus; the p3 of RV 45017 is preserved but has only one cusp. It can thus be concluded that compared with Miocene species of *Machairodus*, the p3 of the Yushe specimen has been greatly reduced, making its assignment to *Machairodus* unconvincing.

Sotnikova (1992) pointed out differences between *Machairodus* and *Homotherium* in the implantation and arrangement of their incisors and canine when studying specimens of *M. kurteni* from Kazakhstan. In *Homotherium*, the incisors and canine are densely aligned with no gap between the central incisor and canine; the incisors are upright with tips pointing dorsally. In *Machairodus*, there is a small gap between the canine and incisors, and the incisors are implanted obliquely with tips pointing anterodorsally. Judging from these differences, the Yushe specimens are apparently consistent with *Homotherium* but distinct from *Machairodus* (see Teilhard de Chardin and Leroy, 1945: fig. 6).

Nonetheless, the Yushe specimens are not completely identical to *Homotherium*. RV 45018 is relatively robust, with a mandible comparable to that of *Homotherium crenatidens* from Renzidong, Anhui and Seneze, France, while RV 45016 and RV 45017 are distinctly more slender. Moreover, their p3 is relatively developed and markedly larger than in later *Homotherium* species (see Table 4). How to identify the Yushe specimens is obviously beyond the scope of this paper, but at least two conclusions can be drawn from the above comparisons: (1) they should be assigned to *Homotherium* rather than *Machairodus*; (2) they probably represent a relatively primitive form in the *Homotherium* clade, consistent with the age of the stratum from which they came.

Although the assignment of the Yushe specimens to *Homotherium* is not confirmed at the moment, the Yegou specimen shows some unambiguous morphological features of *Homotherium*. The incisors and canine are densely aligned with no gap between them. The incisors are upright and point dorsally. The incisors and canine are so aligned that they form an anteriorly convex arc with the mesial ones more anteriorly implanted. Serrations are present on all preserved teeth. The last two features are more developed than in species of *Machairodus*. Moreover, the size and robustness of the mandible are completely consistent with that of *H. crenatidens* from Renzidong, Anhui (see Table 4). The only difference is its larger premolars.

Presently, the taxonomic significance of premolar size (mainly P3 and p3) among *Homotherium* species remains disputed. As a highly specialized felid, the anterior premolars of *Homotherium* probably lost their physiological function. Under such circumstances, the size and morphology of these non-functional premolars would change significantly. For that reason, it is highly risky to distinguish species based on these changes (e.g., Ficcarelli, 1979).

However, judging from the general evolutionary trend of *Homotherium*, the gradual degeneration of premolars is an indisputable fact. Their morphology (e.g., cusp and root) and size virtually reflect the evolutionary stage of the species. *Homotherium* might consequently be divided into several different evolutionary stages or different species (e.g., Sharapov, 1989). To that end, the authors observed and measured some specimens (see Table 4) and found that the evolutionary stages of *Homotherium* could indeed be established roughly. For species of the middle Villafranchian and later (e.g., Renzidong, Anhui and Seneze, France), the length of p3 generally does not exceed 10.0 mm. The p3 of *H. cuii* from Middle Pleistocene Jinniushan is completely lost (Zhang et al., 1993). For species of and before the early Villafranchian (e.g., Yushe, Shanxi), the length of p3 is generally no less than 10.0 mm. The length of the p3 alveolus of the Yegou specimen is 12.9 mm, comparable to RV 45016 from Yushe and much larger than in species of the middle Villafranchian and later. Based on measurements in Table 4, the Yegou specimen is situated somewhere between *Machairodus kurteni* from Kazakhstan and *H. crenatidens* from Renzidong, Anhui, and most likely represents a transitional form between them (relatively speaking, the Yushe specimens are not good enough to represent such a transitional form: the teeth of RV 45018 are somewhat distorted while the mandibles of RV 45016 and RV 45017 are so slender that they probably represent a different phylogenetic clade). It could be inferred that the Yegou specimens probably represent an early form of *Homotherium* or the earliest representative of *H. crenatidens* (because the morphology and size of mandible V 18836.1 are highly consistent with specimens from Renzidong, Anhui). Unfortunately, V 18836.1 is the only identifiable specimen collected at Yegou. It is impossible to comprehensively evaluate and analyze p3 variation, and the possibility that the large p3 of V 18836.1 represents individual variation cannot be ruled out at the moment. Although the premolars of *Homotherium* generally tend to be reduced, some individuals with extreme variation did occur repeatedly. For example, *H. crenatidens* from Val d' Arno, Italy has reduced premolars, but there is still one p3 with a length of 12.0 mm (Ficcarelli, 1979), comparable to the Yegou specimen. If based only on such an isolated p3, it would be less credible to presume that the Yegou specimen represents an early primitive form of *Homotherium*. Nonetheless, if associated animals such as *Nyctereutes tingi* and *Pachycrocuta pyrenaica* are taken into account, the present authors would be more confident of such a presumption and consequently identify the Yegou specimens herein as *Homotherium* sp. for the moment. Further identification and inference still await more and better material to be clarified.

Hipparion (Plesiohipparion) houfenense **Teilhard de Chardin & Young, 1931 (Figs. 5-6)**

Material: Fragmentary right maxilla with P3-M2 (IVPP V 18837.1, Fig. 5C) and left and right mandibular corpora with p2-m3 (V 18837.2, V 18837.3, Fig. 5A) of the same individual; fragmentary right maxilla with M1-3 (V 18837.4); 1 left and 1 right P2 (V 18837.5-6); fragmentary right mandibular corpus with p2-m3 (V 18837.7, Fig. 5B); distal portions of two right humeri (V 18837.8, Fig. 6D; V 18837.9); proximal portion and distal portion of the same left Mc III (V 18837.10, Fig. 6A; V 18837.11); proximal portion of left Mc IV (V 18837.12); right talus (V 18837.13, Fig. 6E); right calcaneus (V 18837.14, Fig. 6G); proximal portion of right Mt III (V 18837.15, Fig. 6B); proximal portion of right Mt II (V 18837.16, Fig. 6C); and ungual phalanx of central digit (V 18837.17, Fig. 6F).

Measurements: See Tables 5-12.

Description: IVPP V 18837.1 is a fragmentary maxilla with P3-M2. The facial crest terminates above the anterior margin of M1. The preorbital fossa is located above P3, and the foramen fossa is above P4. In occlusal view, the center of the posterior margin of the hard palate is approximately level with the posterior portion of M2 (Fig. 5C1). On V 18837.4, the major palatine foramen is visible and level with the posterior portion of M2, whereas the minor palatine foramina are not discernible.

On V 18837.1, the size of the upper cheek teeth gradually decreases from P3 to M2 (Fig. 5C1). The parastyle is only broadened on P3-M1, where it is bifid and made up of two ribs and one median cleft. The anterior rib and median cleft are not developed on M2. The size of the median cleft gradually decreases from P3 to M1. The mesostyle is only slightly elongated on P3-M1 but not on M2. The labial wall of the paracone and metacone is labially concave, and their lingual walls are lingually convex. The angle between the anterior lingual and posterior lingual walls tends to become smaller from P3 to M2, but all are less than 90°. The anterolabial corner of the postfossette extends more labially than the posterolabial corner of the prefossette on the cheek teeth. The hypoconal groove is shallow, and the hypoconal constriction is distinct. The counting of enamel plications in the form "anterior wall of the prefossette.posterior wall of prefossette-anterior wall of postfossette.posterior wall of postfossette/pli caballin" is as follows: P3 = 6.10-7.2/4, P4 = 6.8-6.2/3, M1 = 6.7-6.1/1, M2 = ?-3.1/1. The protocone length index (= protocone length/tooth length\$$\times 100) isasfollows: P3 = 23.8, P4 = 29.2, M1 = 35.0, M2 = 27.3. Theprotoconewidth/lengthindex (= width/length \times$\$100) is as follows: P3 = 70.8, P4 = 64.4, M1 = 61.3, M2 = 70.0.

The size of V 18837.4 is small. The major palatine foramen lies between M2 and M3. The parastyle is elongated on M1 but not bifid; it is not elongated on either M2 or M3. Its extent of labial protruding gradually decreases from M1 to M3. The hypoconal groove is shallow, and the hypoconal constriction is distinct. The counting of enamel plications is as follows: M1 = 6.8-3.1/3, M2 = 6.9-3.2/2, M3 = 5.8-4.2/2. The protocone length index: M1 = 34.1, M2 = 31.8, M3 = 19.7. The protocone width/length index: M1 = 69.7, M2 = 68.6, M3 = 57.6.

V 18837.5 and V 18837.6 are the left and right P2, respectively. The anterostyle is not inflated. The size of the hypoconal groove is comparable to that of the hypoconal constriction. The left P2 is slightly smaller. The mesostyle extends more labially. The protocone is relatively short and small, with its lingual margin concave lingually. The protocone of the right P2 is long and robust, with its lingual margin straight but anterolabially oblique. The counting of enamel plication of the two teeth is 4.2-3.1/1 and 3.4-4.2/2, respectively. The protocone length index: 21.5 and 25.1. The protocone width/length index: 61.6 and 72.9.

Mandible and Mandibular Cheek Teeth (Fig. 5A-B): The larger left and right mandibular corpora should belong to the same individual. Only the right horizontal ramus is relatively complete (V 18837.3, Fig. 5A). The depth beneath p2 on the lingual side is 72.0 mm. The depth between p4 and m1 is 88.5 mm. The depth beneath m3 is 98.0 mm.

The p2 is slightly longer than p3. The paraconid is robust. The anterior lobe of the double-knot (the metaconid) is rounded and about half the size of the posterior lobe (the metastylid). The double-knots of p3 and p4 are triangular and equal in size. The double-knots of m1-3 are also triangular, but the metaconids gradually become larger than the metastylid from m1 to m3. The isthmus is short on p2-4 but distinct; it is not developed on m1-3. The lingual flexid is U-shaped, shallowest on p2 and gradually becoming deeper afterward. The ectoflexid is also shallow on p2 but gradually becomes deeper afterward. The pli caballinid and pli antecaballinid are distinct on p3-m3 of the smaller specimen V 18837.7 (Fig. 5B), whereas only the pli antecaballinid is distinct on the larger specimen V 18837.3 (Fig. 5A). No pli caballinid or pli antecaballinid are developed on p2 of either specimen. The protostylid is developed on both specimens, but the pli hypostylid and ectostylid are not developed. On V 18837.7, m3 is slightly longer than m2, similar to the holotype RV 31031 from Jingle. The m3 of V 18837.3 is distinctly larger than m2 and similar to THP10733 from Yushe.

Humerus (V 18337.8, Fig. 6D): The lateral supracondylar crest extends posteriorly and distally to the posterior margin of the lateral ligament fossa, weakens medially, and terminates behind the articular surface of the lateral epicondyle. The distal breadth of the articular surface of the medial condyle (33.0 mm) is about twice that (16.0 mm) of the lateral condyle. The trochlear depth on the medial condyle side (37.0 mm) is about 1.3 times that (28.0 mm) on the lateral condyle side. The sagittal crest between the medial and lateral condyles is rounded anteriorly but sharp posteriorly and extends posterolaterally.

Mc III (V 18837.10, Fig. 6A): The proximal articular surface consists of the smaller lateral articular facet with the unciform (os carpale IV) and the larger medial articular facet with the magnum (os carpale III). The two facets meet at an obtuse angle, with a depth-to-width ratio of about 4:6. The articular facet with the magnum is flat but slightly tilts medially. There is a distinct protruding point at the posteromedial corner. The posterior margin of the facet is straight and parallel to the volar surface. The articular facet with the unciform is rectangular, concave at the anterior portion and flat at the posterior portion, tapering posteriorly. The ridge where the two facets intersect is sharp anteriorly and blunt posteriorly. There is another articular facet with Mc IV lateral to the articular facet with the unciform, divided into a wider anterior part and narrower posterior part that are connected. The diaphysis is wide and dorsovolarly compressed, with a longitudinal groove tapering distally on the volar surface. The depression above the distal articular surface on the dorsal side is not well defined. The attachment tuberosity for the collateral ligaments is situated anteriorly, and in lateral view, the contact surface for the lateral phalanges above it bends anteriorly. The sagittal crest of the distal articular surface is widened and rounded at the dorsal end but sharp and extends proximally at the volar end. A ridge extends proximally from the volar end of the sagittal crest and separates the distal portion of the diaphysis into two approximately equal depressions on the volar side. The distal articular surface is divided by the sagittal crest into a wider lateral part and narrower medial part, with the depth of the lateral part greater than that of the medial part.

Mc II: The proximal half is preserved. The volar side of the diaphysis is concave, with the depth of the diaphysis greater than that of the contact surface with Mc III. The proximal articular surface is flat, perpendicular to the diaphysis, and slightly higher than the proximal articular surface of Mc III when in anatomical position. There are two separated articular facets with Mc III on the medial side and one with Mc I on the lateral side.

Talus (V 18837.13, Fig. 6E): The talus is asymmetrical. The lateral condyle is distinctly wider than the medial condyle, but its depth is distinctly less. The slope of the medial wall of the lateral condyle is gentle. The dorsoplantar distance between its distal end and the distal articular facet is 10.0 mm. The medial wall of the medial condyle is nearly vertical and extends posteriorly about half the depth of the body; the distal portion of the medial wall does not bend medially. The depth at the median groove of the trochlea is about 70% of that of the lateral condyle. There are four articular facets with the calcaneus. The medial facet is a long strip shape with its long axis proximodistally oriented; its medial margin is convex, while the lateral margin is concave. It is 31.0 mm long and 13.5 mm wide. The lateroproximal facet is a transverse, anteriorly convex curved surface oriented mediodistally. The proximolateral margin intersects with the lateral wall of the lateral condyle. The tongue-shaped facet or lateral facet is small, with a pointed proximal margin and rounded distal margin; the proximodistal dimension is 9.0 mm, and the mediolateral dimension is 5.0 mm. The lateroproximal facet and lateral facet are not connected. The laterodistal facet is rectangular, wider anteriorly and narrower posteriorly, with an anteroposterior dimension of 10.0 mm and proximodistal dimension of 7.0 mm. The distal facet is triangular. A concave rough surface medially stretches into the facet from the middle part of its lateral margin and terminates behind the distal end of the medial condyle. The width of the distal facet is 45.5 mm, and the depth is 34.0 mm. The posterior pointed protrusion exists but is weak. The medial proximal protuberance is distinct and posterior to the proximal end of the medial condyle of the trochlea, extending posteriorly about 6.0 mm. The distal protuberance is relatively strong and protrudes medially. The two protuberances are connected by a shallow ridge.

Calcaneus (V 18837.14, Fig. 6G): The calcaneal tuberosity is damaged. The medial articular facet is a long strip shape and slightly concave, with its posteromedial margin leaning medially. Its length is 35.2 mm, and width is 16.3 mm. This facet corresponds to the medial articular facet of the talus. The proximolateral articular facet is nearly circular, divided into two perpendicular parts by a transverse ridge, with width 22.3 mm and depth 21.0 mm. The tongue-shaped or lateral articular facet is rectangular and connected with the proximolateral articular facet, with width 8.4 mm and length 16.2 mm. The distolateral articular facet is trapezoid, with the distolateral margin pointed, dorsodistal dimension 20.0 mm, and plantarodistal dimension 7.2 mm. The distal articular facet is laterally wider and medially narrower, with the plantaromedial third suddenly shrinking. In lateral view, the angle between the lateral margin of the distal articular facet and the dorsodistal margin beneath the tongue-shaped facet is acute.

Mt III (V 18837.15, Fig. 6B): Only the proximal portion is preserved. The depth is slightly less than the breadth at the middle of the diaphysis. The plantar side is distinctly concave. The vascular impression is distinct on the lateral side of the proximal Mt III, intersecting with the dorsal margin of the diaphysis about 3 cm beneath the proximal articular facet at an angle of about 45°, then running distally along the lateral margin of Mt IV. There is a concave non-articular rough surface extending anteromedially into the center of the proximal articular facet from the plantarolateral corner. The proximal articular surface consists of the medial articular facet with the small cuneiform (os tarsalia I+II), the middle articular facet with the big cuneiform (os tarsale III), and the lateral articular facet with the cuboid (os tarsale IV). The articular facet with the small cuneiform is the smallest, semi-circular, and intersects with the facet with the big cuneiform at an angle larger than 90°. The articular facet with the big cuneiform is the largest and horseshoe-shaped, with both wings and the plantar and dorsal ends prominent. The facet intersects with the articular facet with the cuboid at an angle of about 120°. The latter is relatively large, flat, and rectangular. There are two isolated articular facets on the medial and lateral sides of the proximal articular surface, articulating with Mt II and Mt IV respectively.

Ungual phalanx of central digit (V 18837.17, Fig. 6F): The angle between the sole and the dorsal line is about 45°. The rough area for insertion of the flexor digitorum profundus is distinct and large on the posterior surface, where there is a protuberance in the center. The articular facet is semi-circular, with the anterior margin slightly convex and the posterior margin straight. It is made up of two concave surfaces: the lateral and medial.

Comparisons and Discussion: *Hipparion houfenense* or its conformis species have been known from Jingle, Shanxi (Teilhard de Chardin and Young, 1931), Pucheng, Shaanxi (Jen, 1965, = *Hipparion* cf. *huofenense*), Huoxian, Shanxi (Tong et al., 1975, = *Hipparion* cf. *huofenense*), Yushe, Shanxi (Qiu et al., 1980), Weinan, Shaanxi (Xue, 1981), Yuxian, Hebei (Tang and Ji, 1983, = *Hipparion* cf. *huofenense*), Lingtai, Gansu (Zhang et al., 1999: p2–m3 length, 145.5 mm). Among these, the material from Huoxian has been excluded from *H. houfenense* (Qiu et al., 1980); the material from Weinan has been assigned to *H. (Proboscidipparion) pater* (Qiu et al., 1987); and the material from Pucheng has been assigned to *H. (Plesiohipparion) huangheense* (Qiu et al., 1987). The smaller mandible from Yegou (V 18837.7) is close to specimens from Jingle, whereas the larger mandibles (V 18837.2–3) are close to Yushe specimens. The main difference between these forms is that m3 of the former lacks an extra posterior lobe. The size of the Yegou upper cheek teeth is comparable to Yushe specimens, but the protocone length index is greater, meaning the protocone of the former is more rounded than that of the latter. The Mc III, Mt III, and ungual phalanx from Yegou are all smaller than Yushe specimens, and the humerus and talus are also smaller than specimens from Jingle and Yushe. Due to the limited sample size, the smaller dimensions probably do not indicate primitiveness but rather individual variation. For example, specimens with a greater protocone length index may represent aged individuals, whereas the smaller limb bones may represent young individuals.

Dicerorhinus sp. (Fig. 7 [Figure 7: see original paper])

Material: Proximal portion of left Mc II (IVPP V 18838.1, Fig. 7D); distal portion of left Mc III (V 18838.2, Fig. 7A); distal portions of 2 left Mt IIs (V 18838.3, Fig. 7B; V 18838.4); distal portions of 2 left Mt IVs (V 18828.5; V 18838.6, Fig. 7C); right patella (V 18838.7, Fig. 7E); distal portion of left radius (V 18838.8, Fig. 7G); left calcaneus (V 18838.9, Fig. 7F); proximal portion of left calcaneus (V 18838.10).

Measurements: See Table 13 .

Description: IVPP V 18838.8 is the distal portion of a radius (Fig. 7G). The diaphysis is robust and anteroposteriorly compressed. The medial margin is flat and thick, while the lateral margin is compressed and thin. The anterior surface is slightly convex, and the posterior surface is slightly concave. The distal outline is triangular. There is a tuberosity with a rough surface on the lateral side that contributes to the maximal distal breadth. The anterior portion of the distal articular facet is concave, whereas the posterior portion is convex. The distal articular facet is divided into a larger medial part and smaller lateral part by a low ridge. The lateral part articulates with the ulnar carpal, and the medial part articulates with the radial carpal. The medial articular facet with the radial carpal is semi-circular and intersects with the articular facet with the ulnar carpal at approximately a right angle.

Only the proximal half of Mc II is preserved (V 18838.1, Fig. 7D). The proximal outline is triangular. On the medial side, there is a triangular rough surface beneath the proximal articular surface. Posterior to this surface is a long bar-like protuberance, and there is another protuberance medial to the surface. The articular facet with the trapezium (os carpale I) is the largest and semi-circular, concave in the middle and separated from the long strip-like, anteroposteriorly oriented articular facet with the trapezoid (os carpale II) by a sharp ridge. The articular facet with Mc III is oval with its major axis anteroposteriorly oriented, separated from the facet with the trapezoid by a proximally convex low ridge.

Only the distal half of Mc III is preserved (V 18838.2, Fig. 7A). The diaphysis is broad and dorsovolarly compressed, with the lateral side rougher than the medial side. The proximal margin of the distal articular facet on the dorsal side is proximally convex. The sagittal crest is not seen on the dorsal side but is strong on the volar side, where it extends proximally and connects to a large tuberosity.

The patella is complete (V 18838.7, Fig. 7E). It is a large sesamoid bone that is robust and rectangular in outline. The dorsal surface of the bone, for tendon insertion, is convex and rough. The articular surface with the patellar surface of the femur is also rectangular, with a broad, rounded ridge dividing it into lateral and medial parts.

Calcaneus: V 18838.9 is an incomplete calcaneus with only the tuberosity broken off (Fig. 7F). V 18838.10 preserves only the tuberosity and part of the body. Its body is stout. The tuberosity is robust, with a rough posterior surface. Curved ridges can be seen on the mediodistal margin of the tuberosity. The lateral side of the body proximal to the cochlear process is slightly convex, but the medial side is slightly concave; both sides are smooth. The articular surface with the talus is divided into two parts by the calcaneal groove. The lateral facet is circular and convex, and the medial facet is tadpole-shaped and concave. The calcaneal groove is deep, extending first distally then distolaterally beneath the lateral facet, where it becomes shallow and merges with the distal margin of the lateral facet. The distal articular facet with the cuboid (os tarsalia IV+V) is semi-circular, concave, and intersects with the medial facet with the talus at an angle slightly larger than 90°.

There are two Mt IIs, one larger than the other. Only the distal portion is preserved (V 18838.3, Fig. 7B). The depth of the diaphysis is larger than the breadth. The medial margin is relatively flat and thicker than the lateral margin. The medial surface is rough. The maximal breadth of the distal articular facet is at the midpoint of the depth. The sagittal crest is only prominent on the plantar side. The articular surface is higher than the diaphysis surface on the dorsal side of the larger specimen and at the same level on the smaller specimen. The sagittal crest is robust and distinctly exceeds the articular surface proximally on the plantar side of the larger specimen but only slightly on the smaller specimen. The difference in size and morphology probably reflects not only variation but also interspecific distinction.

There are two Mt IVs as well, one larger and one smaller. Only the distal portion is preserved (V 18838.6, Fig. 7C). The morphology is basically the same as that of Mt II.

Comparisons and Discussion: Three rhinocerotid species are known from Early Pleistocene deposits of the Nihewan Basin: the distinctly small-sized *Dicerorhinus mercki* (= *Stephanorhinus kirchbergensis*), medium-sized *Coelodonta nihowanensis*, and large-sized *Elasmotherium peii* (Teilhard de Chardin and Piveteau, 1930; Deng and Zheng, 2005: *Elasmotherium caucasicum*; Tong et al., 2014). Among these, only limb bones of the latter two species have been unearthed (Teilhard de Chardin and Piveteau, 1930; Deng and Zheng, 2005). In terms of measurements (Table 13), the sizes of Mc III, calcaneus, and Mt II described here are distinctly smaller than corresponding elements of Early Pleistocene *Elasmotherium peii* from the same basin. The radius is similar in size, but Mc II-III and Mt II, IV are distinctly larger than in Early Pleistocene *Coelodonta nihowanensis* from the same basin. Although *Dicerorhinus mercki* is also known from the Nihewan Basin, there are only limb bones from Yegou, which lack decisive diagnostic morphological characters. Consequently, the new material is temporarily identified as *Dicerorhinus* sp.

A Mc II close to the Yegou specimen is known from the red clay layer of Renjiagou, Lingtai, Gansu (Zhang et al., 1999: Rhinocerotidae gen. et sp. indet.), with proximal length/width of 55.0 mm/41.0 mm and minimal breadth/depth of the diaphysis of 39.5 mm/23.3 mm. The magnetostratigraphic age of this horizon is 3.5-3.4 Ma (Sun et al., 1998; Zhang et al., 1999). The size of the Yegou specimen is also very close to that of *Dicerorhinus megarhinus* (Christol, 1835) from Hajnáčka, southern Slovakia (Fejfar, 1964). Based on the coexisting *Mimomys hajnackensis* Fejfar, 1961, its geological age should be Early Villanyian, >3 Ma (Repenning et al., 1990).

Gazella blacki **Teilhard de Chardin & Young, 1931 (Fig. 8 [Figure 8: see original paper])**

Material: Left horn core with pedicle and partial frontal bone but without tip (IVPP V 18839.1, Fig. 8B); left horn core without pedicle but with tip slightly damaged (V 18839.2); 1 left and 1 right fragmentary mandibular corpora with p2-m3 (V 18839.3; V 18839.4, Fig. 8A); fragmentary right mandibular corpus with p2 alveoli and p3-m3 (V 18839.5); fragmentary right mandibular corpus with p3-p4 (V 18839.6); fragmentary right mandibular corpus with m3 (V 18839.7).

Measurements: See Table 14 .

Description: V 18839.1 (Fig. 8B) is a fragmentary horn core with the dorsal half missing and a small portion of frontal bone preserved at the pedicle. The supraorbital foramen can be seen anterior to the pedicle of the core. The postcornual fossa is deep and oval on the lateral side of the pedicle. The horn core slightly bends caudally, with coarse, parallel longitudinal ridges (or grooves). Judging from the suture preserved on the medial side, the minimal distance between the pedicles is about 2.4 cm. The horn core extends caudolaterally.

The other specimen does not have frontal bone preserved, and the tip is slightly damaged (V 18839.2). Its curvature is similar to that of V 18839.1. Although the rostral surface is damaged, the longitudinal ridges (or grooves) do not appear as coarse as those of V 18839.1.

All mandibular specimens are incomplete. The length of p2-p4 is 38% of that of the lower cheek teeth row but greater than that of m2-m3. The p2 is single-lobed with a pointed protoconid and two roots. Both p3 and p4 have anterior, middle, and posterior valleys; the middle and posterior valleys can both reach the labial side. The metaconid and paraconid are not completely fused on p4. The protoconid is pointed. The morphology of lower molars is similar to that of other gazelles, but the goat fold is present anterolaterally in young individuals.

Comparisons and Discussion: The material described in this paper is slightly larger than *Gazella blacki* from Xiaohongao, Hefeng and Renjiagou, Lingtai, and distinctly smaller than *G. sinensis* from the Nihewan Basin (Table 14). The average ratios of p2-p4 length to p2-m3 length in percentage for these three forms are 38.2% (Xiaohongao), 36.2% (Renjiagou), and 35.3% (Nihewan) respectively. The material here is therefore closer to *G. blacki* than to *G. sinensis*.

When studying gazelle fossils from North China, especially Yushe, Chen (1997a,b) pointed out that *Gazella blacki* is a valid species and a typical form for the Late Pliocene of North China. The magnetostratigraphic age provided by Chen (1994) is ca. 3 Ma. *Gazella* cf. *G. blacki* also occurs in many Early Pleistocene faunas, such as Wenxi, Houma (Tang, 1980a), Xihoudu, Ruicheng (Chia and Wang, 1978), Xicun, Tunliu, Shanxi (Zong et al., 1982), and Longdan, Dongxiang, Gansu (Qiu et al., 2004). In this regard, *G. blacki* is probably a long-lasting species spanning from the Late Pliocene to Early Pleistocene.

Axis shansius **Teilhard de Chardin & Trassaert, 1937 (Fig. 9 [Figure 9: see original paper])**

Material: Antler fragment (IVPP V 18841.1, Fig. 9A); fragmentary right maxilla with P2-M3 (V 18841.2, Fig. 9B); right P3 (V 18841.3); distal portion of right radius (V 18841.4, Fig. 9C); distal portion of left tibia (V 18841.5, Fig. 9D); 1 left and 1 right tali (V 18841.6, Fig. 9E; V 18841.7); proximal portions of 2 Mt III-IVs (V 18841.8, Fig. 9F; V 18841.9).

Measurements: See Table 15 .

Description: The antler (V 18841.1, Fig. 9A) is fragmentary, preserving only the portion where the main beam and brow tine bifurcate. The lateral side of the main beam is damaged. The medial surface is concave, with longitudinal grooves and ridges visible. The lateral surface is flat, with grooves and ridges less clear. Judging from the longitudinal orientation of the main beam, the angle between it and the brow tine is probably greater than 90°.

Enamel rugosity is distinct on the surface of the upper cheek teeth (V 18841.2, Fig. 9B). Spurs are developed on the buccal side of the crescent crests formed by the protocone and metaconule. The cingulum is developed on the lingual and medial sides. The lingual side of P2 and P3 is double-lobed, with the protocone and metaconule developed. P4 is single-lobed. The parastyle and mesostyle are more developed than the metastyle on M1-3. The extent of buccal protruding of the parastyle is greater than that of the metastyle. The length of P2-4 is 88% of that of M1-3.

Only the distal portion of the radius (V 18841.4, Fig. 9C) is preserved, with the lateral side damaged. The medial articular facet is convex, and the lateral articular facet is posteriorly positioned and concave.

Only the distal portion of the tibia (V 18841.5, Fig. 9D) is preserved. The articular portion is complete. Articulation with the talus is carried out by two facets: two anteroposteriorly oriented parallel concave grooves, with the lateral one wider than the medial but the latter deeper. Articulation with the lateral malleolus (vestigial distal end of the fibula) is carried out by two small facets on the lateral side: the anterior one larger and the posterior one smaller, separated by a notch.

There are two tali: left (18841.6, Fig. 9E) and right (18841.7). The right one is smaller, but their morphologies are identical.

There are two metatarsals (V 18841.8-9, Fig. 9F), both preserving only the proximal half. The groove on the dorsal side is narrow and extends distally to a very low position. On the medial side of the proximal end of the groove, there is a distinct vascular impression. The plantar groove is wider. The proximal plantar foramen is located at the proximal end of the plantar groove, proximodorsally penetrating the proximal metatarsal and opening at the center of the articular surface with the tarsals.

Comparisons and Discussion: In terms of limb bone size (Table 15), the Yegou material is very close to *Cervus* sp. from Jingle (Teilhard de Chardin and Young, 1931). In terms of antler morphology and size, the Yegou specimen (V 18841.1) is comparable to Early Pleistocene *Axis shansius* from Zone III of Yushe, Shanxi, but the antler is slightly longer. It is closer to the antler of Late Pliocene *A. shansius* from Guide, Qinghai (Zheng et al., 1985). The dimensions of the upper cheek teeth are also generally consistent with the holotype of *A. shansius.*

Muntiacus sp. (Fig. 10A [Figure 10: see original paper])

Material: Fragmentary right maxilla with M2-3 (IVPP V 18840, Fig. 10A).

Measurements: M1: length, 10.8 mm; anterior width, 12.3 mm; posterior width, 11.3 mm. M2: length, 10.8 mm; anterior width, 12.0 mm; posterior width, 10.3 mm.

Description: This is a small-sized muntjac. The molars are low-crowned. The morphologies of M2 and M3 are similar. There is strong rugosity on the enamel surface. The protocone is more developed than the hypocone, and the paracone is more developed than the metacone. The parastyle and mesostyle are more developed than the metastyle. The paracone rib is stronger than the metacone rib. Both teeth are 4-rooted. The only difference is that M2 is slightly larger than M3.

Comparisons and Discussion: The morphology and size of the teeth are consistent with *Muntiacus.* Due to the lack of antlers, it is difficult to identify it to species level.

Paracamelus sp. (Fig. 10B-E)

Material: Right M2 (IVPP V 18842.1, Fig. 10C); right M3 (V 18842.2, Fig. 10B); distal portion of left humerus (V 18842.3, Fig. 10E); manual 4th proximal phalanx (V 18842.4, Fig. 10D).

Measurements: See Tables 16-18.

Description: The molars (IVPP V 18842.1-2, Fig. 10B, C) are large and anteriorly wider. The sloping of the lingual wall of the molars is gentle, so the flaring of the crown is not distinct. The protocone and metaconule are nearly equal in size, but the protocone extends more lingually. The parastyle is more developed than the mesostyle. The metastyle is extremely weak or not developed. The paracone rib is more robust than the metacone rib. The shrinking of the posterior lobe of M3 is more distinct than that of M2. The metastyle is relatively distinct on M3.

Only the distal portion of the humerus is preserved (V 18842.3, Fig. 10E). The lateral ligament pit is deep. The distal maximal breadth is located where the lateral epicondylar crest contacts the margin of the ligament pit. The medial ligament pit is shallow, with a robust, short ridge posteroproximal to it. The trochlea of the humerus is broader than the capitulum, and the groove between them is shallow. The anteroproximal margin of the trochlea is more proximally positioned on the medial side. The posteroproximal margin of the trochlea extends proximally into the olecranon fossa. The posterodistal margin of the medial epicondyle meets the posterodistal margin of the diaphysis at an angle slightly less than 90°.

The distal articular surface of the proximal manual phalanx of the 4th digit (V 18842.4, Fig. 10D) is damaged, but the length of the bone is measurable. The proximal lateral ligament tuberosity is more prominent than the medial one, but the shape and size of the muscle insertion area on both sides are similar. The proximal articular surface is elliptical, with a depression at the center of the posterior portion dividing it into two parts: the lateral part narrower and higher than the medial part. The distal end is slim and narrow, with weak ligament tuberosities on both sides.

Comparisons and Discussion: Material of *Paracamelus gigas* from Quaternary strata in the Nihewan Basin is limited to one calcaneus and the distal portion of one radius (Teilhard de Chardin and Piveteau, 1930). That of *Paracamelus* sp. from Late Pliocene strata is also limited to one talus (Tang, 1980b). Yegou is therefore the first locality in the Nihewan Basin to yield dental remains.

Maxilla with complete dentition, humerus, talus, and metatarsal are known from the Upper Pliocene at Renjiagou, Lingtai, Gansu, assigned to *Paracamelus* sp. (Zhang et al., 1999). The size (M2 and M3 length, 42.0 mm) and morphology (including shrinking posterior lobe, developed parastyle and mesostyle, weak metastyle) are the same as the Yegou specimen, but the humerus is neither described nor figured, so it cannot be compared with the Yegou specimen.

The phalanx (V 18842.4) from Yegou is distinctly larger than that of *Paracamelus gigas* from Loc. 1, Zhoukoudian (Young, 1932) and Mianchi, Henan (Zdansky, 1926), and even larger than that of extant camels.

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3 Composition and Age of the Late Pliocene Hipparion houfenense Fauna in the Nihewan Basin

Localities or horizons yielding fossils of large mammals including *Hipparion* are relatively rare in the Nihewan Basin. In addition to Yegou and Laowogou (Cai et al., 2004), there are the following localities: (1) the red clay layer of Luanshigedagou, Hongya Village, yielding *Hipparion* sp. and *Chilotherium* sp. (Huang et al., 1974: Layer 3); (2) the red clay layer of the "Yuxian Formation" of the upper portion of the Huabaogou section (Layer 3), Xiyaozitou Village, yielding *Postschizotherium* sp., *Viverra* sp., *Hipparion houfenense*, *Gazella blacki*, *Gazella* spp., and *Antispiroides hopeiensis* (Wang, 1982; Li et al., 2008); (3) the red clay layer of the "Huliuhe Formation" of the lower portion of the Huabaogou section (Layer 1), Xiyaozitou Village, yielding *Canis* sp., *Canis multicuspus*, *Nyctereutes sinensis*, *Hipparion* cf. *H. hippidiodus*, *Hipparion* sp., *Palaeotragus* spp., *Gazella blacki*, and *Gazella* sp. (Wang, 1982; Li et al., 2008); and (4) the red clay layer of the Danangou section, Dongyaozitou Village, yielding *Lynx variabilis*, *Nyctereutes* cf. *sinensis*, *Hipparion* cf. *H. houfenense*, *Paracamelus* sp., *Antilospira yuxianensis*, and *Palaeotragus progressus* (Layer 1 of Tang, 1980b and Tang and Ji, 1983; Layer 1-2 of Zheng and Cai, 1991 and Cai et al., 2004, 2013; Li et al., 2008).

If the horizon of the Yegou *Hipparion houfenense* fauna can be correlated to Layer 9 of the Laowogou section (Cai et al., 2004), Layer 1 or 3 of the Huabaogou section (Wang, 1982), and Layer 1 (Tang, 1980b; Tang and Ji, 1983) or Layer 1-2 (Zheng and Cai, 1991; Cai et al., 2004, 2013) of the east cliff section of Danangou, then the large mammals of the Late Pliocene mammalian fauna of the Nihewan Basin should tentatively include at least the following 27 forms:

Canis sp. [-]
Canis multicuspus Wang, 1982 [-] (nomen nudum)
Nyctereutes tingi Tedford & Qiu, 1991
Nyctereutes cf. *N. sinensis* (Schlosser, 1903) [-]
Nyctereutes sinensis (Schlosser, 1903)
Pachycrocuta pyrenaica (Depéret, 1890)
Homotherium sp.
Lynx variabilis Tang, 1980 [+]
Viverra sp. [-]
Hipparion houfenense (Teilhard de Chardin & Young, 1931)
Hipparion cf. *H. houfenense* (Teilhard de Chardin & Young, 1931) [-]
Hipparion cf. *H. hippidiodus* Sefve, 1927 [-]
Hipparion sp. [-]

Dicerorhinus sp.
Chilotherium sp. [-]
Postschizotherium sp. [-]
Muntiacus sp.
Axis shansius Teilhard de Chardin & Trassaert, 1937
Cervus sp. [-]
Gazella spp. [-]
Gazella blacki Teilhard de Chardin & Young, 1931
Antilospira sp. [-]
Antilospira yuxianensis Tang, 1980 [+]
Antispiroides hopeiensis Wang, 1982 [-] (nomen nudum)
Palaeotragus spp. [-]
Palaeotragus progressus Tang & Ji, 1983 [+]
Paracamelus sp.

Although most of these fossils have not been systematically studied (species with [-]) or have only been briefly described (species with [+]) and need further taxonomic revision, their Pliocene age (compared with the classic Early Pleistocene Nihewan fauna) is affirmative. These taxonomic names are tentatively retained here for discussion in the sense of the fossil entities they represent, including unidentified species and nomina nuda. Among them, *Viverra*, *Nyctereutes*, *Dicerorhinus*, *Muntiacus*, *Gazella*, and *Axis* are extant genera with no extant species. Such a dominant proportion of extinct species is not possessed by any other Early Pleistocene faunas.

The key features of the Late Pliocene *Hipparion houfenense* fauna of the Nihewan Basin, represented by the 10 large mammals described here, are as follows: (1) coexistence of *Gazella blacki* and *Hipparion (Plesiohipparion) houfenense*; (2) coexistence of *Nyctereutes tingi* and *N. sinensis*; (3) appearance of *Pachycrocuta pyrenaica*; and (4) coexistence of *Axis shansius* and *Paracamelus*.

According to the first feature, the age of the fauna is directly comparable to those of the red clay of Layer 1, 3 of the Huabaogou section near Xiyaozitou Village in Yuxian Basin (Wang, 1982), the Jingle red clay of the Renjiagou section, Lingtai, Gansu (Zhang et al., 1999), the red clay of Xiaohongao, Hefeng, Jingle, Shanxi (Teilhard de Chardin and Young, 1931; Chen, 1994), and the Mazegou Formation of Yushe, Shanxi (Flynn et al., 1991; Deng and Hou, 2011).

According to the second feature, *Nyctereutes tingi* has only Pliocene stratigraphic records in the Yushe Basin (Tedford and Qiu, 1991) and Leijiahe, Lingtai, Gansu (Huang et al., 1993) so far, while the coexistence of *N. tingi* and *N. sinensis* occurs only in the Yushe Basin and the Nihewan Basin. According to the third feature, *Pachycrocuta pyrenaica* is known only from pre-Villafranchian strata in France, Spain, and Ukraine (Depéret, 1890; Crusafont and Sondaar, 1971; Adrover et al., 1976; Howell and Petter, 1980), whereas in China it is known only from the lower Mazegou Formation, the Gaozhuang Formation of Pliocene, and even the upper Mahui Formation of Upper Miocene in the Yushe Basin (Qiu, 1987; Deng et al., 2010; Deng and Hou, 2011). According to the fourth feature, in addition to Late Pliocene records of *Axis shansius* in Guide, Qinghai (Zheng et al., 1985) and Laowogou, Daodi Village, the Nihewan Basin (Cai et al., 2004), the holotype of this species comes from Zone III of Yushe, Shanxi (belongs to the Lower Pleistocene). *Paracamelus* also has both Pliocene records, such as Danangou, the Nihewan Basin (Tang, 1980b) and Renjiagou, Lingtai (Zhang et al., 1999), and Pleistocene records (Teilhard de Chardin and Piveateu, 1930; Teilhard de Chardin and Trassaert, 1937; Young, 1932). Taken as a whole, the age of the Yegou *Hipparion houfenense* fauna should be the Late Pliocene before 2.6 Ma.

The Mazegou Formation of the Yushe Basin, Shanxi is the horizon yielding the richest fossils of Late Pliocene large mammals, with 65 forms currently preliminarily identified (Flynn et al., 1991; Deng and Hou, 2011; Wang et al., 2017), containing nearly all species of large mammals from Late Pliocene localities in North China. It is therefore a helpful standard for comparison when determining if a fauna is Late Pliocene in age. For example, the sand layer of Guide and the Leijiahe Formation of Lingtai can be correlated to the Mazegou Formation by sharing *Anancus sinensis*; the Leijiahe Formation can also be correlated to the Mazegou Formation by sharing *Hipparion pater*. Accordingly, based on the combinations of *Nyctereutes tingi*-*N. sinensis* and *Homotherium* sp.-*Dicerorhinus* sp.-*Paracamelus* sp., the Yegou horizon can also be correlated to the Mazegou Formation.

Nyctereutes tingi, *Pachycrocuta pyrenaica*, *Homotherium* sp., *Hipparion (Plesiohipparion) houfenense*, and *Gazella blacki* of the Late Pliocene Yegou *Hipparion houfenense* fauna of the Nihewan Basin are more primitive than *N. sinensis*, *Pachycrocuta brevirostris/licenti*, *Homotherium crenatidens*, *Hipparion (Proboscidipparion) sinense*, and *Gazella sinensis* of the Early Pleistocene fauna from the Xiashagou-Nihewan Village area, respectively. Consequently, the age of the former fauna should be older.

In the Nihewan Basin, localities or horizons yielding common faunal elements with the Yegou *Hipparion houfenense* fauna include: (1) Layer 9 of Laowogou, sharing *Hipparion* and *Axis shansius* (Cai et al., 2004); (2) Layer 1 of the east cliff section, Danangou, Dongyaozitou Village, sharing *Hipparion* cf. *H. houfenense* (Tang, 1980b; Tang and Ji, 1983); (3) Layer 1 of Huabaogou, Xiyaozitou Village, sharing *Nyctereutes sinensis* and *Gazella blacki* (Wang, 1982); and (4) Layer 3 of Huabaogou, Xiyaozitou Village, sharing *Hipparion houfenense* and *Gazella blacki* (Wang, 1982). Based on biostratigraphic correlations (Li et al., 2008; Cai et al., 2013), Layer 3 of the Huabaogou section can be correlated to Layer 9 of Laowogou; Layer 1 of Huabaogou can be correlated to Layer 2 of Laowogou; and Layer 1 of the east cliff section of Danangou can be correlated to Layer 16–19 of Laowogou. Accordingly, the horizon of the Yegou *Hipparion houfenense* fauna can be generally correlated to the above horizons, especially Layer 9 of Laowogou.

Presently, magnetostratigraphic dating results of horizons of the *Hipparion houfenense* fauna characterized by *Hipparion (Plesiohipparion) houfenense* and

Gazella blacki are not completely consistent. The red clay of Xiaohongao, Jingle has been dated to 3 Ma (Chen, 1994). The red clay of Renjiagou, Lingtai has been dated to 3.5-3.4 Ma (Sun et al., 1998; Zhang et al., 1999). The Mazegou Formation has been dated to 3.6-2.6 Ma (Flynn and Qiu, 2013). The fossil layer of the east cliff section, Danangou, Dongyaozitou Village has also been dated to 3.04-2.58 Ma (Liu et al., 2021). It can be inferred from these results that the age of the Yegou horizon should fall within the range of 3.6-2.6 Ma. Only the red clay of Layer 1, 3 of the Huabaogou section is unexpectedly younger, with magnetostratigraphic ages ranging 1.95-1.77 Ma (Zhu et al., 2007; Deng et al., 2008; Deng, 2011). The most likely reason for this is that depositional hiatus in the Huabaogou section may have been ignored by these investigators. This, once again, proves the importance of mutual compatibility between biostratigraphy and magnetostratigraphy. For magnetostratigraphic dating results to be robust, it is necessary to carefully verify if the correlation of polarity chrons to GPTS is compatible with biostratigraphy based on fossils, especially when contradictions arise. If contradictions arise, the results are subject to cautious reinterpretation, as is the case for the results mentioned above.

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4 Features of Late Pliocene and Early Pleistocene Mammalian Faunas (Large) in the Nihewan Basin

In recent years, many Late Pliocene horizons yielding *Hipparion houfenense* have been discovered in North China, such as Layer 1 (Tang, 1980b; Tang and Ji, 1983) or Layer 1-2 (Zheng and Cai, 1991; Cai et al., 2004, 2013) of the Danangou section, Dongyaozitou Village and Layer 1, 3 of the Huabaogou section, Xiyaozitou Village in the Nihewan Basin (Wang, 1982), Renjiagou, Lingtai (Zhang et al., 1999) and the Leijiahe Formation (Huang et al., 1993) in Lingtai, Gansu, the Mazegou Formation of Yushe (Flynn et al., 1991; Deng and Hou, 2011) and Xiaohongao, Jingle (Zhou, 1988; Chen, 1994) in Shanxi, the sand layer of Guide in Qinghai (Zheng et al., 1985), and so on. The discovery of these Late Pliocene horizons with fossils of large mammals provides a better understanding of the general features of the *Hipparion houfenense* fauna in China. It should be noted that *Lynx variabilis*, *Hipparion* cf. *H. houfenense*, *Paracamelus* sp., *Antilospira yuxianensis*, etc. in the "Pliocene-Early Pleistocene transitional mammalian fauna" derived from Layer 1 of the east cliff section of Danangou in the Nihewan Basin (Tang, 1980b; Tang and Ji, 1983) should be Late Pliocene in age (Zheng and Cai, 1991; Cai et al., 2004, 2013). Based on fossils of large mammals derived from the above horizons, the Late Pliocene mammalian fauna (large) in the Nihewan Basin is characterized by: (1) few Early Pliocene forms, such as *Nyctereutes tingi* Tedford & Qiu, 1991, *Pachycrocuta pyrenacia* (Depéret, 1890), *Hipparion* cf. *H. hippidiodus* Sefve, 1927, and *Palaeotragus* sp.; (2) several species unique to the Late Pliocene, such as *Canis multicuspus* Wang, 1982 (nomen nudum), *Lynx variabilis* Tang, 1980, *Hipparion (Plesiohipparion) houfenense* (Teilhard de Chardin & Young, 1931), *Antilospira yuxianensis* Tang, 1980, *Antispiroides hopeiensis* Wang, 1982 (nomen nudum), and *Palaeotragus progressus* Tang & Ji, 1983; (3) some Late Pliocene-Early Pleistocene transitional forms, such as *Homotherium* sp. (Yegou), *Nyctereutes sinensis* (Schlosser, 1903), *Gazella blacki* Teilhard et Chardin & Young, 1931, and *Paracamelus* sp. (Yegou, Danangou); and (4) no extant species.

In addition to the classic Early Pleistocene Nihewan mammalian fauna (large) with multiple revisions and supplements (Teilhard de Chardin and Piveteau, 1930; Qiu, 1987, 2000), numerous Early Pleistocene horizons yielding fossils of large mammals have been discovered in the Nihewan Basin in recent years, such as the Xiaochangliang site (You et al., 1980; Tang et al., 1981, 1995; Chen et al., 1999; Zhang et al., 2008), the Majuangou site (Wei et al., 2003; Cai and Li, 2004; Cai et al., 2008), the west section of Danangou (Tang et al., 1981; Li, 1984), Layer 3, 5 of the east cliff section of Danangou (Tang, 1980b; Tang and Ji, 1983), and so on. Based on fossils of large mammals derived from these horizons, the Early Pleistocene mammalian fauna (large) in the Nihewan Basin is characterized by: (1) few Late Pliocene-Early Pleistocene transitional forms, such as *Zygolophodon* sp. (Danangou), *Nyctereutes sinensis* (Schlosser, 1903), *Crocuta honanensis* (Zdansky, 1924), *Hipparion* sp. (Xiaochangliang, Majuangou, Danangou), *Elasmotherium* sp. (Nihewan Village), and *Postschizotherium chardini* von Koenigswald, 1932; (2) many species unique to the Early Pleistocene, including *Mammuthus trogontherii* Pohlig, 1885, *Canis chiliensis* Zdansky, 1924, *Canis c. var. palmidens* Teilhard de Chardin & Piveteau, 1930, *Eucyon minor* (Teilhard de Chardin & Piveteau, 1930), *Erictis pachygnatha* (Teilhard de Chardin & Piveteau, 1930), *Meles chiai* Teilhard de Chardin, 1940, *Lutra licenti* Teilhard de Chardin & Piveteau, 1930, *Casmaporthetes progressus* (Qiu, 1987), *Pachycrocuta licenti* (Pei, 1934), *Homotherium crenatidens* Fabrini, 1890, *Megantreon nihowanensis* (Teilhard de Chardin & Piveteau, 1930), *Sivapentahera* cf. *S. pleistocaenicus* (Zdansky, 1925), *Lynx shansius* Teilhard de Chardin, 1945, *Hipparion (Proboscidipparion) sinense* (Sefve, 1927), *Equus sanmeniensis* Teilhard de Chardin & Piveteau, 1930, *Coelodonta nihowanensis* Kahlke, 1969, *Muntiacus bohlini* (Teilhard de Chardin, 1940), *Eucladoceros boulei* Teilhard de Chard & Piveteau, 1930, *Nipponicervus elegans* (Teilhard de Chardin & Piveteau, 1930), *Elaphurus bifurcates* Teilhard de Chardin & Piveteau, 1930, *Spirocerus wongi* Teilhard de Chardin & Piveteau, 1930, *Gazella sinensis* Teilhard de Chardin & Piveteau, 1930, and *Bison palaeosinensis* Teilhard de Chardin & Piveteau, 1930; and (3) a considerable number of Middle to Late Pleistocene and extant species, such as *Canis* sp. (Majuangou), *Vulpes* sp. (Danangou), *Martes* sp. (Xiaochangliang), *Ursus thibetanus* G. Cuvier, 1823, *Viverra* sp. (Xiaochangliang), *Felis* sp. (Nihewan Village), *Sus* cf. *S. lydekkeri* Zdansky, 1928, *Axis* sp. (Danangou), *Cervus* sp. (Nihewan Village, Xiaochangliang), *Gazella* sp. (Xiaochangliang), *Gazella* cf. *G. subgutturosa* (Güldenstädt, 1780), *Ovis* sp. (Nihewan Village), *Ovis shantungensis* Matsumoto, 1926, *Bison* sp. (Xiaochangliang), and so on.

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Note: Figure translations are in progress. See original paper for figures.

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