

# *Hipparion* Datum Implies Miocene Palaeoecological Pattern

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## Research Article

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# Abstract

Here, we report well-preserved skulls and postcranial specimens of the subgenus *Hippotherium* from the Linxia Basin, Gansu, China. Based on morphological comparison, the species of subgenus *Hippotherium* in China, *Hipparion weihoense* and *Hipparion chiai*, should be ascribed to the same species, *H. weihoense*. The species *Hipparion prostylum* (later *Hipparion* aff. *brachypus*) from Maragheh, Iran should also be ascribed to *H. weihoense*. Phylogenetic analysis shows the subgenus *Hippotherium* derived from the North American genus *Cormohipparion*, and as a basal group of *Hipparion* in Eurasia, representing the *Hipparion* Datum. Analysis on locomotive ability indicates that *H. weihoense* likely lived in an open habitat, whereas other species of subgenus *Hippotherium* likely lived in closed habitats. This result indicates a palaeoecological pattern in the early Late Miocene in Eurasia: influenced by a series of geological events, aridification of mid-latitude Asia progressed, whereas Europe and North Africa remained relatively humid; as the genus originated from East Asia, *Hipparion* divided rapidly into different groups with differing functional morphology to occupy diverse niches.

## Introduction

The dispersal of *Hipparion* into the Old World, recognised as the *Hipparion* Datum, is one of the most significant palaeobiological events in the Late Miocene<sup>1-4</sup>. *Hipparion primigenium* in Europe is traditionally regarded as the earliest and most primitive *Hipparion* species in Eurasia<sup>4-6</sup>. Some authors proposed that it should be assigned to a valid genus *Hippotherium*<sup>6-8</sup>. Qiu et al.<sup>9</sup> indicated that all hipparion species in the Old World should be assigned within one genus, *Hipparion*, and that the taxon *Hippotherium* should be regarded as a subgenus. They reviewed the earliest *Hipparion* species found in China, *Hipparion weihoense* and *Hipparion chiai*, and ascribed them to the subgenus *Hippotherium*. They also ascribed the early species *Hipparion africanum* found in Bou Hanifia, Algeria and *Hipparion catalaunicum* from Hostalets, Spain to this subgenus. Consequently, the early evolution and distribution of the subgenus *Hippotherium* have great significance regarding the evolution of *Hipparion* and Late Miocene palaeoecology.

Research on *H. weihoense* and *H. chiai* in China remains insufficient. Liu et al.<sup>10</sup> erected these two species based on cranial and dentition material found in Lantian, Shaanxi. Liu<sup>8</sup> described another collection from Lantian. However, known specimens were limited to broken skulls, mandibles, isolated teeth, and metapodials. These two species are almost always found in the same locality. They have many morphological similarities, and *H. weihoense* specimens are much more abundant than *H. chiai*. Following the priority principle, the validity of *H. chiai* is suspect. Consequently, more and better-preserved specimens are required to evaluate the status of these two species.

Recently, we were able to study an excellent collection of specimens of the subgenus *Hippotherium* from the Linxia Basin, Gansu, China (S Fig.1), including a well-preserved skull found at the Shuanggongbei locality (S Fig.2); a broken skull accompanied by fore- and hindlimbs from the Niugou locality (S Figs. 3-5), and a number of specimens from other localities. These new findings provide more complete

information on cranial and postcranial morphology to compare with known specimens of the subgenus *Hippotherium* to better recognise *H. weihoense* and *H. chiai*. This material is also suitable to determine the locomotive ability of subgenus *Hippotherium* in China. Deng et al.<sup>11</sup> performed comprehensive locomotive analysis of the Tibetan *Hipparion zandaense*, which provides an ideal template for our research. Based on comparison with the known postcranial material of *H. primigenium* and *H. africanum*, we can seek clues regarding the environmental and ecological conditions of the early Late Miocene in Eurasia.

## Results

### Geological setting

The new specimens described were collected from three localities in Linxia Basin, Gansu, China: Houshan (LX 0008); Shuanggongbei (LX 0009); Niugou (LX 200204) (S Fig. 1).

### Systematic Palaeontology

The specimens in the present research are described as following: Order Perissodactyla Owen, 1848; Family Equidae Gray, 1821; Genus *Hipparion* de Christol, 1832; Subgenus *Hippotherium* (Kaup, 1833); *Hipparion* (*Hippotherium*) *weihoense* Liu et al., 1978. Synonym including: *Hipparion chiai* Liu et al., 1978; *Hipparion prostylum* Bernor et al., 1985; *Hipparion chiai* Qiu et al., 1987; *Hipparion* cf. *chiai* Deng and Wang, 2004; *Hippotherium primigenium* Zouhri and Bensalmia, 2005; *Hippotherium weihoense* Liu, 2012; *Hippotherium chiai* Liu, 2012; *Hipparion* aff. *brachypus* Bernor et al., 2016; *Hipparion chiai* Li et al., 2017; *Hipparion chiai* Li et al., 2019. **Holotype.** A nearly complete skull, the posterior part of the orbit lost, IVPP V 3113.1. **Type locality.** Shuijiazui, Lantian, Shaanxi (63702.L4). **Referred specimen.** Specimens firstly described in the present research are collected from Linxia Basin, Gansu, China (S Fig. 1). IVPP specimens collected from Niugou Locality including: IVPP V 24396, skull of a very old individual; IVPP V 24397, right humerus; IVPP V 24398.1–2, left Mc IIIs; V24398.3–4, right McIIIs; IVPP V 24399.1–2, right femurs; IVPP V 24400.1–2, right tibias; IVPP V V24401.1–3, left Mt IIIs; IVPP V V24401.4–8, right Mt IIIs. HMV 1308, skull of a sub-adult individual; HMV 1429, skull of a juvenile individual; HMV 0476, skull of a sub-adult individule, Houshan Locality; HMV 1963, skull of an adult individual, Shuanggongbei Locality; HMV 1964, skull of an adult individual, Shuanggongbei Locality; HMV 0806, skull of an adult individual; **Revised diagnosis.** large hipparion horse. Moderately robust muzzle. Shallow nasal notch. Preorbital bar (POB) very long. Preorbital fossa (POF) strong, subtriangular-shaped with distinct anterior margin. Proportion of basal cranial relatively low. Cement on cheek tooth thick. Anterostyle/anterostylid short. Plications in pre- and postfossettes strong and complex at middle wear stage. Pli caballine usually single to double, sometimes complex. Protocone usually elongated at middle wear stage. Hypoconal groove deep at middle wear stage. Protostylid usually present. Metaconid rounded, and metastylid subtriangular with a pointed labial horn. Linguaflexid U-shaped. Pli caballinid usually present on premolar at middle wear stage. Limbs slender with high proportion of distal elements. **Distribution.**

Lantian and Fugu, Shaanxi; Qaidam, Qinghai; and Linxia Basin, Gansu, China; Maragheh, Iran. **Age.** Late Miocene, Bahean.

## Attribution and revision

The newly described specimens have a characteristic cranial and dentition diagnosis combination, including medium to large size, shallow nasal notch, long POB, developed POF with a posterior pocket, complex fossettes with long and strong folds, and elongated protocone with flat labial margin. All of these features are identical to the primitive hipparion species in China, *Hipparion (Hippotherium) weihoense*.

Liu et al.<sup>10</sup> reported a large *Hipparion* species discovered from Lantian, Shaanxi and erected the new species *Hipparion weihoense*. In the same text, they identified a smaller skull fragment and some teeth with similar features and stratigraphic position to *H. weihoense* as another new species *Hipparion chiai*. Qiu et al.<sup>9</sup> reviewed hipparion fossils from China and accepted the validity of both species. They ascribed these two species to subgenus *Hippotherium*, and regarded them as the most primitive hipparion horse in the Old World. Liu<sup>8</sup> described a series of specimens from Lantian, Shaanxi and identified parts of these specimens as *H. weihoense* and *H. chiai*. Based on the reported specimens from China, there is actually no clear boundary between the cranial features of these two species. Bernor et al.<sup>12</sup> identified the hipparion specimens from Maragheh, Iran as *Hipparion prostylum*. *H. prostylum* was first reported in France. Based on observation of the specimens of *H. prostylum* from the type locality (Luberon, France), now housed in the NMNH, Paris, we determined that the upper cheek teeth from Luberon have rounded protocone, single pli caballine, and simple and robust folds in fossettes. This combination of features, based on personal observation on specimens, is more similar to the subgenus *Cremohipparion*, such as *Hipparion forstenae* and *Hipparion gracile*. Later Bernor et al.<sup>13</sup> ascribed these Maragheh specimens as *Hipparion* aff. *brachypus*. *H. brachypus* is a huge-built form with deep nasal notch and very robust metapodials<sup>14</sup>, which are difficult to correspond to the Maragheh form. Morphologically, specimens from Maragheh, Iran are very similar to *H. weihoense* in China. Based on measurements of skulls (S Table. 1) the POF positions of these specimens are stably distributed; the difference is ontogenetic. The dimensions of the POF are more variable, but another hipparion species in Eurasia also has variable POFs: *Hipparion dermatorhinum*, found in Baode, Shanxi, China<sup>9</sup>. The measurements of Bernor et al.<sup>6</sup> show highly variable POF of *Hipparion primigenum*. Moreover, POF height is easily influenced by compressional deformation. In the sketches of the skulls of *H. weihoense* (S Fig. 6), most individuals have clearly or nearly subtriangular POFs; some POFs with significantly different shapes show clear evidence of deformation. The dentition was regarded as another important feature to distinguish these two species in previous research. Liu et al.<sup>10</sup> argued that *H. chiai* had a simpler fossette on the upper cheek tooth than that of *H. weihoense*. Based on recent ontogenetic sequence analysis, the fossette characters of hipparion largely depend on wear stage<sup>15,16</sup>. Liu et al.<sup>10</sup> also indicated that some large individuals of *H. chiai* had similar features on upper cheek teeth to those of *H. weihoense*. They did not

discuss the features of lower cheek teeth. In our sketches of reported upper and lower cheek specimens of both *H. weihoense* and *H. chiai*, there is no significant difference between these two taxa (S Fig. 7–8). Therefore, *H. weihoense*, *H. chiai*, and *H. prostylum* from Maragheh, Iran should be ascribed to the same species. Following the priority principle, all of these specimens belong to *H. weihoense*.

## Phylogenetic analysis

We used characters from Woodburne<sup>4</sup> as our basis, changed a repeated character for the skull, character 36, into a new one on tooth character, added 21 tooth characters from Liu<sup>8</sup>, and added two new characters on the postcranial and size. We partly followed the taxa in the matrix of Woodburne<sup>4</sup> and used *Parahippus leonensis*, *Merychippus primus*, and *Merychippus insignis* as outgroup taxa. Woodburne<sup>4</sup> erected five new species of the North American genus *Cormohipparion*. However, these species overlapped in character, geographic distribution, and age, and are better regarded as synonyms of the type species, *Cormohipparion occidentale*. We only accept the validity of three known species of this genus: *Cormohipparion goorisi*, *Cormohipparion quinni*, and *Cormohipparion occidentale*. We also added the Eurasian species *Hipparion (Hippotherium) weihoense*, *Hipparion (Hippotherium) africanum*, and *Hipparion (Hippotherium) catalaunicum*, and the subgenera *Cremohipparion*, *Baryhipparion*, *Sivalhippus*, *Plesiohipparion*, and *Proboscidipparion*. These 16 taxa and 62 characters constitute a new matrix. One MPT (most parsimonious tree) was obtained. We determined that all Eurasian hipparion subgenera form a monophyly, which fully supports the argument of Qiu et al.<sup>9</sup> on systematic palaeontology, classifying all Chinese hipparion horses as one genus. All other subgenera were derived from the subgenus *Hippotherium*. This interpretation also supports the phylogenetic relation between *Cormohipparion* and Old World hipparions proposed by MacFadden<sup>17</sup>. Consequently, subgenus *Hippotherium* should be regarded as the basal group of Eurasian hipparion horses representing the *Hipparion* Datum.

## Functional morphology

The well-preserved postcranial specimens from the Niugou locality indicate the locomotive ability of *H. weihoense*. A strong medial trochlear ridge (MTR) of the femur can fasten the medial patellar ligament, or parapatellar cartilage, and the patella when the knee joint is hyperextended<sup>18</sup>, forming a passive stay-apparatus to immobilise musculature in the knee extensors during long periods of standing. The femur MTR of *H. weihoense* is greatly enlarged relative to the lateral trochlear ridge, notably larger than in *Hipparion primigenium*, but similar to *Hipparion zandaense* from the Pliocene of the Zanda Basin. The ratio between the maximum depth of the MTR and the maximum length of the femur is 0.27 in *H. primigenium*<sup>6</sup>, whereas it is 0.32 in *H. weihoense* and 0.3 in *H. zandaense*<sup>11</sup>. Gracile limb bone is an indicator of cursorial ability, which is most clearly exhibited in the metapodials of ungulates<sup>19</sup>. The gracility of the metapodial shaft is represented by diminished breadth relative to length. In Fig. 2, above the zero line are the comparatively larger measurements, and below it are the smaller ones. The ratios between the maximum length and the minimum breadth indicate that *H. weihoense*, *H. zandaense*, and *C.*

*occidentale* have relatively slender metapodials (measurement 3 is smaller or slightly larger than measurement 1), but *H. primigenium* has very robust metapodials (measurement 3 is notably larger than measurement 1), and the subgenus *Proboscidipparion* (*Hipparion sinense* and *Hipparion pater*) and *H. houfenense* from the North China Plain also show increased robustness. Typically, metapodial robustness of horses has been considered a marker of evolutionary steps. Robust metapodials indicate primitive steps, whereas slender one indicates the opposite<sup>20, 21</sup>. Our results supplement this hypothesis with a trend of increased robustness with increased body size, and with metapodial robustness considerably influenced by environmental change. A high proportion of distal elements will lengthen the whole limb to keep its centre of mass situated proximally and to reduce its inertia, which allows for a long, rapid stride, as speed is the product of stride length and stride frequency<sup>22</sup>. Lengths of the distal elements of hindlimbs, Mt III, and the first hind phalange relative to proximal elements of *H. weihoense* and *C. occidentale* are significantly longer than those of *H. primigenium*, which indicates the stronger running ability of the former two. Both the advanced *H. houfenense* and *H. sinense* have these characteristics (Fig. 3). Consequently, *H. weihoense* was able to run fast and stand persistently, which is beneficial in open habitats. The running abilities of *H. primigenium* and *H. africanum* were weaker and more suited to slower movement in closed habitats<sup>6, 23</sup>, and their locomotive function stands in contrast to the inferred ecosystem and behaviour of *H. weihoense*.

## Discussion

In China, *H. weihoense* is mainly distributed in the Linxia Basin, Gansu [24]; the Qaidam Basin, Qinghai<sup>25</sup>; and Lantian<sup>8,10</sup> and Fugu<sup>16, 26, 27</sup>, Shaanxi. The former two are located respectively on the east and north margins of the Tibetan Plateau. Deng and Wang<sup>25</sup> indicated that *H. weihoense* (their *Hipparion* cf. *H. chiai* and *H. weihoense*) likely lived in an open habitat. Deng<sup>28</sup> performed cenogram analysis on all late Cenozoic mammalian faunae in Linxia Basin and indicated that the Bahean Guonigou and Dashengou faunae, in which *H. weihoense* firstly appeared and was dominant respectively, both suggested open conditions. Our analysis on the locomotive ability of *H. weihoense* in the present research firmly supports their conclusion. The open conditions of the Qaidam and Linxia basins imply that in early Late Miocene Tibetan Plateau likely had uplifted to a considerable elevation and blocked vapour from reaching the surrounding area of the plateau, thus forming an arid, open environment. However, An et al.<sup>29</sup> proposed enhanced aridity in the Asian interior in 9–8 Ma. An et al.<sup>30</sup> argued that north of the Tibetan Plateau had uplifted considerably in the early Late Miocene. They proposed the appearance of the north part and an important uplift/growth of the Tibetan Plateau in 10–7 Ma. These events occurred significantly later than the first occurrence of *Hipparion* in Eurasia. However, magnetostratigraphic investigation showed that onset of ‘Red Earth’ deposition predated 11.4 Ma<sup>31</sup>. Dettman et al.<sup>32</sup> indicated that in 12 Ma, there was a shift of carbonate  $\delta^{18}\text{O}$  values to  $-9\text{‰}$ , which implied a major reorganisation of atmospheric circulation patterns and a shift to more arid conditions at the NE margin of the Tibetan Plateau. Based on pollen data of Jiang and Ding<sup>33</sup>, the East Asian summer monsoon was generally strong between 20.1 and 14.2 Ma, decreased between 14.2 and 11.3 Ma, and has been weaker since 11.3 Ma. These results correlate

with the first occurrence of *Hipparion* in Eurasia (Vienna Basin Pannonian C: 11.3 Ma<sup>4</sup>; 11.4–11 Ma<sup>34</sup>; Guonigou fauna: 11.5 Ma<sup>35</sup>). The considerable uplift of the Tibetan Plateau likely occurred earlier than that reported in previous research, or aridification caused by uplift of the Tibetan Plateau influenced the surrounding area earlier. The earliest appearance of *H. weihoense* in the Linxia Basin was occurred in Guonigou fauna<sup>24</sup>. We infer that the open, arid habitat to which *H. weihoense* was adapted in the area surrounding the Tibetan Plateau appeared around 11 Ma. Dettman et al.<sup>32</sup> also confirmed that the period of greatest aridity at the NE margin of the Tibetan Plateau was from 9.6 to 8.2 Ma, which is well consistent with other climate records. This was the age in which *H. weihoense* thrived in related areas<sup>24, 36</sup>. Liu et al.<sup>10</sup> argued that this component of the *Hipparion* fauna in Lantian, Shaanxi is an indication of a grassland environment. Deng and Wang<sup>25</sup> agreed with their argument. Xue et al.<sup>27</sup> argued that the Lamagou fauna in Fugu, Shaanxi, in which *Chilotherium* and *Acerorhinus* were dominant and *H. weihoense* (their *Hipparion chiai*) was present, lived in an open habitat. This interpretation implies that influence of Tibetan Plateau aridification reached as far as Shaanxi. *H. weihoense* was highly adapted to open habitat and rapidly dispersed into these areas. We have confirmed that *H. weihoense* was also distributed in Maragheh, Iran in the early Late Miocene. Gavillot et al.<sup>37</sup> indicated that Zagros had significant tectonic activity around 12–8 Ma, which led to the uplift of Persian Plateau. Mouthereau et al.<sup>38</sup> indicated that deformation throughout the Arabia/Eurasia collision zone and uplift of the Persian Plateau occurred after 15–12 Ma. Ballato et al.<sup>39</sup> studied stable oxygen isotopes of Miocene lacustrine and palustrine sediments (~17.5–7.6 Ma) from northern Iran and interpreted that the results primarily reflected precipitation changes, showing an increase in aridity. The Maragheh area, at the northern margin of the Persian Plateau, was likely influenced by lack of vapour from the south cause by this movement and thus became more arid. Zhang et al.<sup>40</sup> argued that Tibetan Plateau uplift and Paratethys retreat occurred at the same time. Retreat of the Paratethys would further reduce vapour delivery to Asia. Thus, habitats of *H. weihoense* in other localities were likely similar to the Linxia Basin (Fig. 4). *Iranotherium morgani* was also discovered in the Linxia Basin, China and Maragheh, Iran with *H. weihoense*. Deng<sup>41</sup> argued that the giant body size and hypsodont cheek teeth with wrinkled enamel and rich cement imply that *I. morgani* was a grazer. The Maragheh fauna is a bit younger than the Dashengou fauna in Linxia Basin; therefore, *I. morgani* likely originated in northwestern China and then dispersed westward to central Asia, which had an open habitat similar to that they had adapted to in China. Phylogenetic analysis shows that *H. weihoense* likely originated from East Asia. Based on the distribution of *H. weihoense* in China, it likely dispersed into Iran through the Qaidam Basin, along the northern margin of the Tibetan Plateau. Therefore, there was significant exchange of taxa between China and Iran in the early Late Miocene.

In comparison, *Hipparion africanum* and *Hipparion primigenium* both have robust metapodials, and *H. primigenium* also has a high proportion of proximal elements of limbs, all of which indicate a closed habitat. Böhme et al.<sup>42</sup> estimated precipitation for Southwest and Central Europe in Miocene and proposed a dry period during 13–11 Ma, end of which is the time *Hipparion* arrived in Eurasia. Later environment in Europe had generally been humidifying. Fortelius et al. [43] also indicated that the habitat

in Europe and North Africa, the respective habitats of *H. primigenium* and *H. africanum*, was relatively closed during 11-8 Ma. In the same period, in the habitat of *H. weihoense*, western China–Central Asia, especially the eastern margin of Tibetan Plateau, high–crowned ungulates were dominant, which indicates an open habitat. Böhme et al.<sup>42</sup> proposed a term “washhouse climate” for analogy of a climate under high precipitation during 10.3-9.8 Ma. This age is consistent with that of Höwenegg (10.3 Ma<sup>4</sup>) and slightly younger Eppelsheim in Germany, where specimens of *H. primigenium* were abundant.

North American species *C. occidentale* also had very slender Mt III and a high proportion of distal elements of hind limbs (Fig. 3-4). The habitat type in the end of the Middle Miocene and the early Late Miocene was likely open, based on the diversity and population of grazers in North America<sup>44, 45</sup>. According to Mihlbachler et al.<sup>46</sup>, hypsodont Equinae species first occurred in 16 Ma, and later became dominant in 12 Ma. The result of representative SEM photomicrographs of tooth microwear by Hayek et al.<sup>47</sup> showed that *C. occidentale* were most likely grazers. Based on phylogenetic analysis, the origin of the subgenus *Hippotherium* was likely in East Asia (not traditionally considered Europe), derived from the grazing *C. occidentale*. This dispersal route and evolutionary change is also consistent with the parsimony principle of evolution. Based on North American palaeoecology, a dominantly open habitat existed in North America significantly earlier than in Eurasia. This habitat led to the emergence of grazing *Cormohipparion* species, which would later give rise to the Eurasian *Hipparion* to preadapt for open environments. *Hipparion* occurred in Eurasia, and rapidly adapted to the widespread open habitat and developed high diversity. This is another typical example of environmental preadaptation of late Cenozoic megaherbivores. Deng et al.<sup>48</sup> argued that mammalian fossils found in Pliocene strata in the Tibetan Plateau suggest that some megaherbivores first evolved in Tibet before the beginning of the famous Ice Age in Pleistocene. The cold winters high in Tibet served as a habituation ground for megaherbivores, which became preadapted for the Ice Age, and successfully expanded to the Eurasian mammoth steppe. The following constitute the ecological pattern of the early Late Miocene: the Tibetan Plateau and Persian Plateau uplifted, and the Neotethys Ocean retreated, which aggravated aridification of mid–latitude Asia and promoted considerable expansion of grassland. In the meantime, Europe and North Africa still had relatively closed habitats. *Hipparion* was derived from the North American *Cormohipparion* and dispersed into Eurasia. They were highly adapted to open environments, widespread over Eurasia in the general environment of aridness. They also responded sensitively to environmental change, showed excellent adaptation ability for humidifying habitat in Europe and arid one in Asia. The taxon divided rapidly into different groups with different functional morphology to occupy diverse niches in the Old World.

## Conclusion

(a) Morphologic comparison indicates *Hipparion weihoense*, *Hipparion chiai* and *Hipparion prostylum* in Iran should be the same species, *Hipparion weihoense*. This also confirmed the distribution area of *H. weihoense* is Western China-Central Asia.

(b) The phylogenetic analysis shows *Hipparion weihoense*, *Hipparion primigenium* and *Hipparion africanum* constitute a monophyly derived from North American genus *Cormohipparion* and represented the *Hipparion* datum in early late Miocene in Eurasia.

(c) The first complete record of postcranial of *H. weihoense* revealed the functional morphology and paleoecology of this species. The locomotive comparison among *H. weihoense*, *H. primigenium* and *H. africanum* implies the ecologic pattern in early late Miocene: *Hipparion* could highly adapt the environment change and live in diverse niches.

## Methods

### Terminology and measurements.

The terminology of maxilla and mandible structures follows Sisson<sup>49</sup> and Budras et al.<sup>50</sup>, detailed description on cranial and postcranial material is presented in the Supplementary Information (SI). All measurements follow Eisenmann et al.<sup>51</sup>, and were taken using calipers to the nearest 0.1 mm (S Tables 1–5).

### Phylogenetic analyses.

We created a new data matrix, which includes 16 taxa, and 62 characters (S Table 6). The phylogenetic analysis was performed using TNT 1.1 with a traditional research method<sup>52</sup>; 1,000 replications and the trees–bisection–reconnection branch–swapping algorithm (TBR) were applied in our analyses. All characters are equally weighted and non–additive. Gaps are treated as “missing”, and multistate taxa are interpreted as polymorphism. The analyses yielded one parsimonious tree, which is presented in Fig. 1. Other results (character list and the data matrix) are presented in the SI.

### Functional morphology.

We use the method of ratio diagrams of metapodials and proportions of limb bones described by Deng et al.<sup>11</sup> to perform a morphological analysis on our new postcranial material (Figs. 2–3) with the data in S Tables 3–5.

## Declarations

### Institution abbreviations.

HMV, Hezheng Paleozoological Museum, Hezheng, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; AMNH, American Museum of Natural History, New York, USA; MNHN, Muséum national d’Histoire naturelle, Paris, France.

## Authors' contributions.

T. D. conducted fieldwork and acquired data; T. D. and B. S. designed research; W. H. and S. C. performed laboratory preparation; B. S. and Y. L. performed observation and measurement; B. S. analysed the data; B. S. wrote the paper, and T. D. and Y. L. revised content. All authors approved the final version of the paper and agreed to be accountable for all aspects of the work.

## Competing interests.

The authors declare no competing interests.

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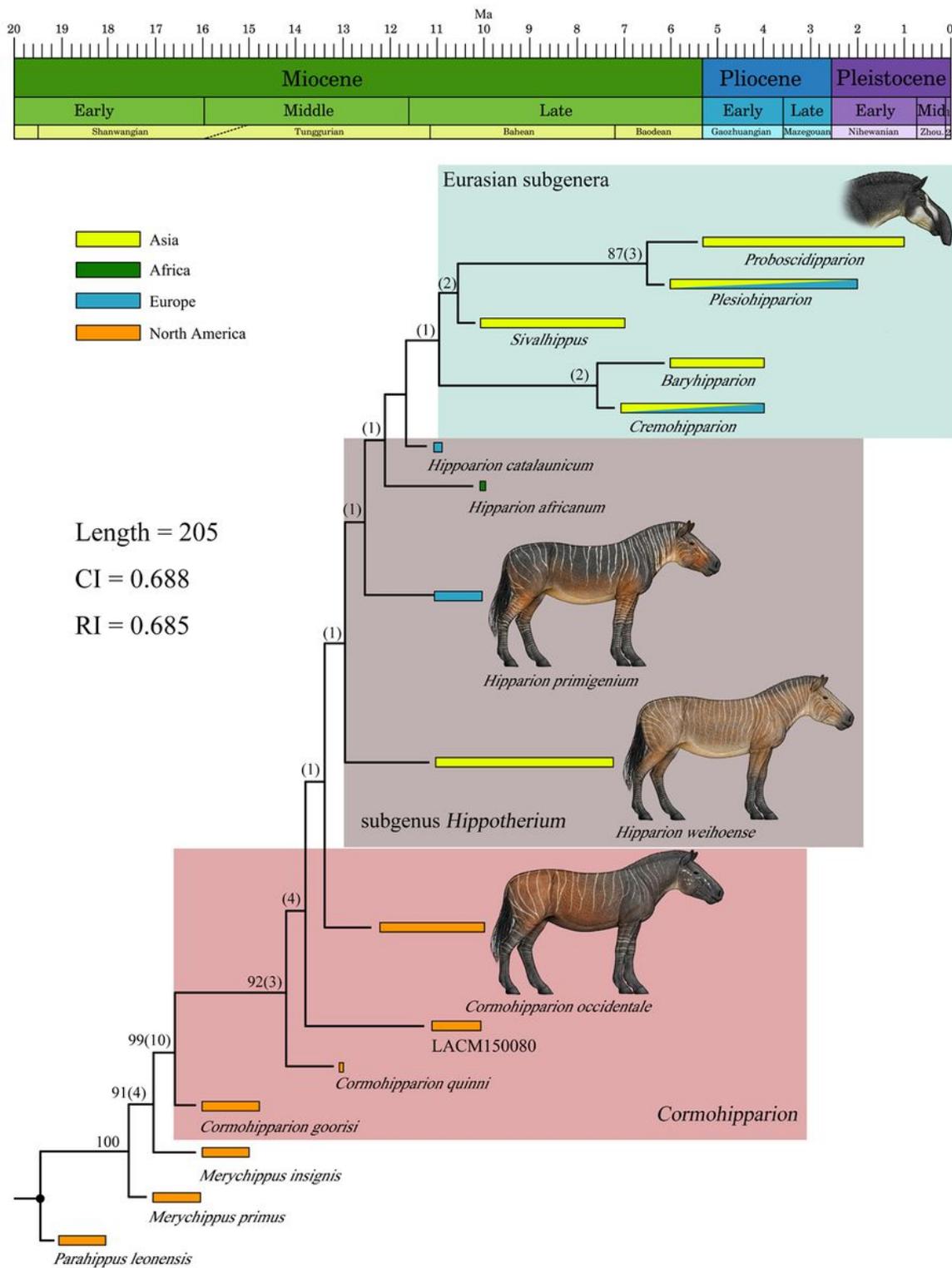
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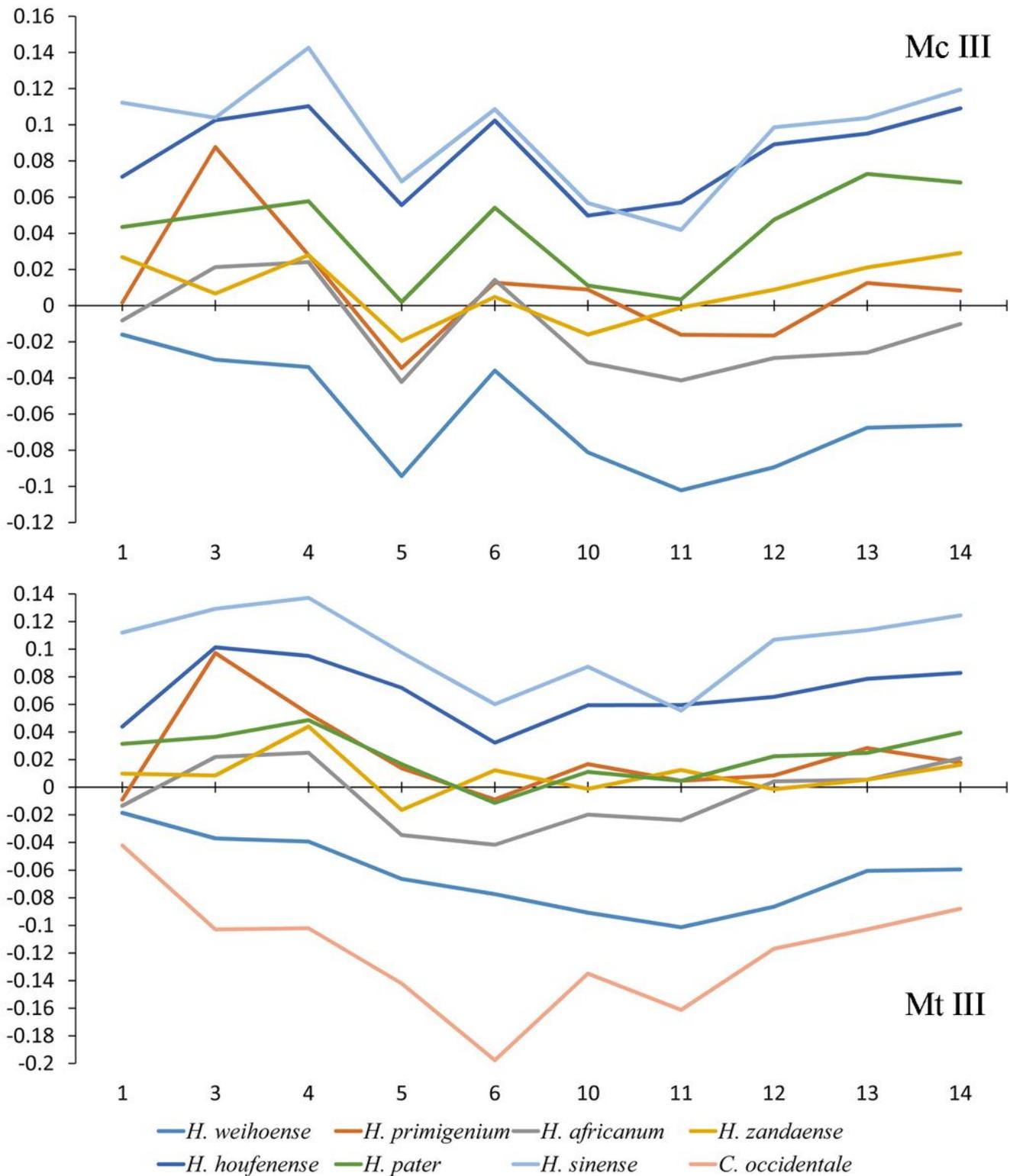
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## Figures



**Figure 1**

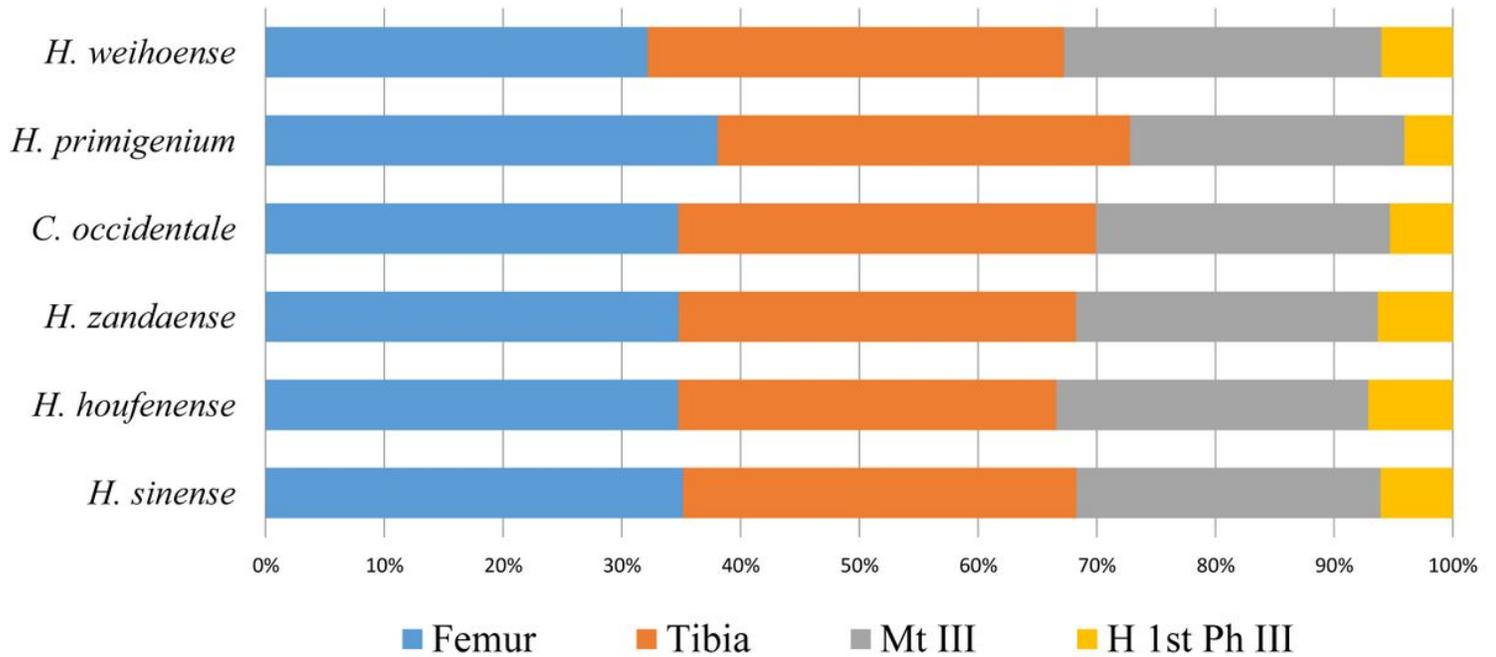
Correlation of geographical distributions and phylogenetic relationship of *Cormohipparion* and Eurasian *Hipparion* lineage based on the strict consensus tree from most-parsimonious trees. Numbers by the nodes respectively denote the Bremer values inside brackets and bootstrap values outside brackets.



**Figure 2**

Ratio diagrams of metapodials of *H. weihoense* and other equids. Measurement numbers: 1, maximal length; 3, minimal breadth; 4, depth of the shaft; 5, proximal articular breadth; 6, proximal articular depth; 10, distal maximal supra-articular breadth; 11, distal maximal articular breadth; 12, distal maximal depth of the keel; 13, distal minimal depth of the lateral condyle; 14, distal maximal depth of the medial

condyle. The y axis is the logarithm (base 10) of ratios between the measurements of each species and the reference species (Asiatic wild ass *Equus hemionus onager*, zero line).



**Figure 3**

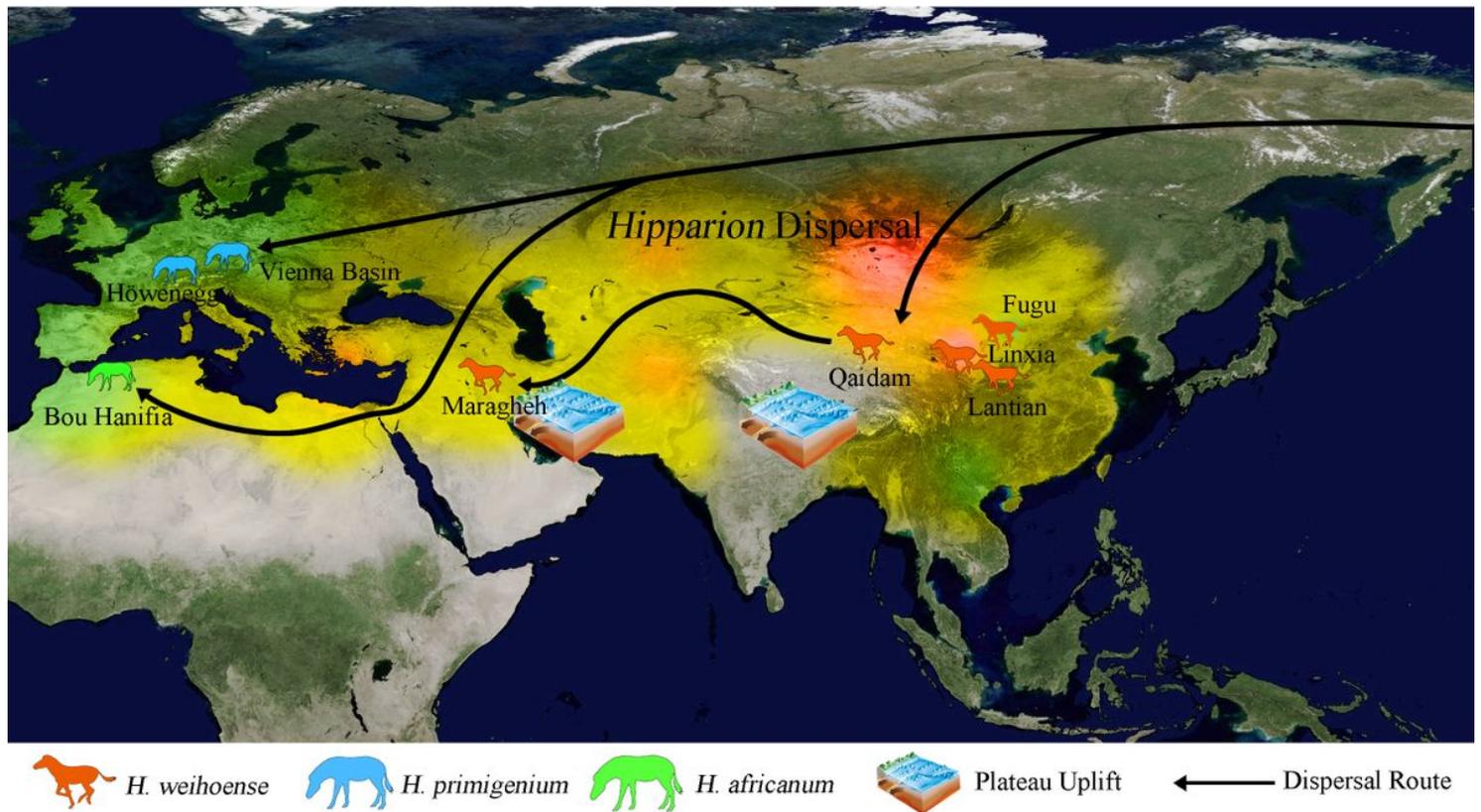
Proportions of hind limb bones in *H. weihoense* and other equids.



**Figure 4**

Artist's reconstruction of *Hipparion weihoense* in Dashengou fauna in Linxia Basin, Gansu, China, one individual is standing and another one is feeding on grass. In the background, three hyenas

*Hippocenturus wongii* are hunting the horses *Hipparion weihoense*. Based on Deng et al.24.



**Figure 5**

Hipparion Datum revealed by distribution and dispersal of subgenus Hippotherium in Eurasia. Dispersal route is referred to Garcés et al.3. Greens, yellows and reds distributed in Mid-latitude Asia, Europe and North Africa after Fortelius et al.43, show the successive increase in crown height interpreted here as increasing open degree. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

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