Functional innovation and adaptive evolution of the *Proboscidipparion* horse during the late Cenozoic in East Asia

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Equidae is a classic paradigm for elucidating biological macroevolution. The trends of increasing body size, higher tooth crowns, and reduced toe numbers signify an adaptive shift from a diet of tree and shrub leaves in close forest to a diet of coarse grass in open grassland. As one of the most successful clades within the Equidae, the hipparionine horses exhibited remarkable species diversity during the late Cenozoic, with a widespread coexistence of multiple equid species, indicating significant ecological niche differentiation.[1] However, in East Asia, equid fossils have long been predominantly utilized as tools for stratigraphic correlation and paleoenvironmental reconstruction, with relatively limited research on their paleoecology and interspecific competition mechanisms.

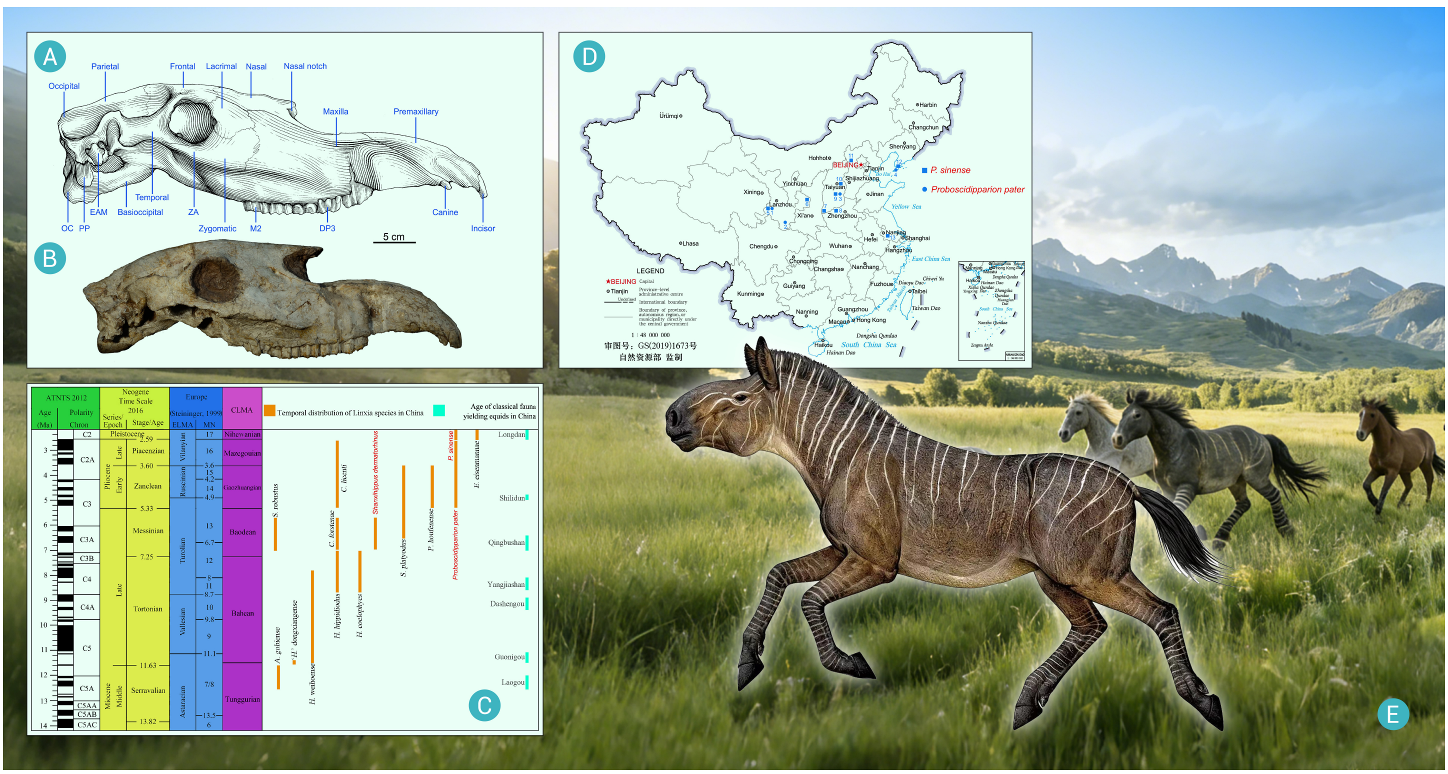

Figure 1. Fossils, distribution, and reconstruction of *Proboscidipparion* (A) Skull of *P. sinense*, HMV 1872 from the Early Pleistocene in Dongxiang, Gansu. (B) Skull of *P. pater*, THP 14312 from the Early Pliocene in Yushe, Shanxi. (C) Chronological order of equid fossils in the Linxia Basin. (D) Sites of *Proboscidipparion* in China. (E) Ecological reconstruction of *Proboscidipparion*. OC: Occipital condyle; PP: Paroccipital process; EAM: External auditory meatus; ZA: Zygomatic arch; M2: Second upper molar; DP3: Third upper deciduous premolar. 1, 5. Linxia, Gansu; 2. Xihe, Gansu; 3, 9. Yushe, Shanxi; 4, 12. Dalian, Liaoning; 6. Heshui, Gansu; 7. Ruicheng, Shanxi; 8. Mianchi, Henan; 10. Shouyang, Shanxi; 11. Yangyuan, Hebei; 13. Nanjing, Jiangsu.

ECOLOGICAL RECONSTRUCTION: FROM THE TAPIR-LIKE MISCONCEPTION TO THE GRASSLAND PIONEER

Since its discovery in East Asia in 1927, *Proboscidipparion*, the long-nosed three-toed horse (Figures 1 A & B) has been speculated in early studies to have lived in a near-water environment and fed on leaves due to its skull morphology resembling that of tapirs. This hypothesis contradicts its widespread distribution in sites such as Nihewan in Hebei, Mianchi in Henan, Yushe and Shouyang in Shanxi, Dongxiang and Heshui in Gansu during the Early Pleistocene grassland expansion (Figure 1D). Recent stable isotope studies have conclusively proven that it is an herbivore with an ecological niche in open grassland environment.[2] This raises a core scientific question: if not used for browsing leaves, what is the morphological functional significance of the unique "long nose" structure of the *Proboscidipparion* horse? And what is the relationship between its origin and dispersal process and the uplift of the Tibetan Plateau and global climate change during the late Cenozoic?

Extant mammals exhibit two types of "long noses" or elongated trunks. One is a flexible, tubular extension formed by the nasal and upper buccal muscles, used at least partially for grasping food, known as the proboscis. Living tapirs and elephants possess similar elongated trunks, but the tapir's trunk extends only slightly forward beyond its feeding teeth (incisors). Unlike elephants, the tapir's trunk has nasal cartilage anterior to the nasal bones, with undegenerated upper and lower jaws and a complete dental row of incisors, canines, and premolars. Beyond feeding, the tapir's trunk also functions for directional olfaction and may have diving-related adaptations. The other type, seen in species like moose (*Alces alces*), saiga antelope (*Saiga tatarica*), dik-diks (*Madoqua guentheri* and *M. kirki*), and elephant seal (*Mirounga*), lacks grasping capability. This structure, termed the "prorhiscis", features a trunk nearly equal in length to the nostrils, with the nostrils opening at the trunk's tip. It lacks buccal composition and feeding functions.

The early ecological hypothesis of "feeding on leaves near water" of *Proboscidipparion* based on morphological similarity to tapirs has been thoroughly revised by the latest research data. Stable isotope analysis reveals that the carbon isotope values of *Proboscidipparion sinense* (Figure 1A) and *P. pater* (Figure 1B) not only fall within the typical range of C_3 herbivores, but are also higher than those of any other contemporary fauna, strongly suggesting an open-grassland habitat. This conclusion perfectly aligns with its morphological features, such as its extremely hypsodont teeth, complex enamel plications, and slender limbs adapted for running. Therefore, *Proboscidipparion* is a successful adaptor in the late Cenozoic grassland ecosystem of East Asia, rather than a resident of forest or marsh edges.

This case suggests that relying solely on morphological analogy (such as a resemblance to tapir skulls) may be misleading in paleoecological reconstruction, and it is necessary to combine multiple lines of evidence such as geochemistry (e.g. stable isotopes) for comprehensive interpretation. Furthermore, it provides a clear research subject and starting point for exploring how various equid species coexisting in the same area (such as *Proboscidipparion* and other hipparionine horses or early true horses) mitigate interspecific competition through dietary differentiation (feeding on different plant species or parts) or micro-habitat selection.

FUNCTIONAL INNOVATION: AN ADAPTIVE INTERPRETATION OF THE PROHISCIS STRUCTURE

Anatomical evidence confirms that *Proboscidipparion* possesses a soft trunk similar to that of tapirs, but its feeding behavior has shifted to directly grazing on surface herbaceous plants with its incisors and muzzle. So, what is the function of this remarkable structure? By comparing the functional morphology of the prorhiscis structure of the saiga antelope, a mammal living in open grasslands today, with that of the *Proboscidipparion* horse, we can propose the following adaptive hypothesis:

Firstly, in the cold and dry grassland environment during winter, a prorhiscis can increase the path length of air before entering the lungs, serving to preheat and humidify the cold air, protect the lungs, and reduce heat loss. In summer, the rich mucosal surface area within the nasal cavity aids in efficient heat dissipation through water evaporation. Secondly, the open grassland is prone to wind and sandstorm, and the extended nasal passage can more effectively filter dust and particulate matter from the air, protecting the respiratory tract. More importantly, as a mammal that needs to run quickly for safety or migration, *Proboscidipparion* experiences a surge in oxygen consumption and heat production during high-speed movement. A larger nasal cavity volume allows for more oxygen to be inhaled with a single breath, and at the same time, the process of breathing can also more effectively expel the body heat generated during running, thereby supporting its ability to "run faster and longer".

Therefore, the "long nose" or prorhiscis of *Proboscidipparion* is not a relic of a feeding tool, but an active adaptive innovation evolved in response to specific ecological environments (cold, dry, dusty open grassland) and physiological needs (oxygen supply and heat dissipation during high-speed running). This reflects the precise coupling of form and function in evolution.

ORIGIN, PRE-ADAPTATION AND DISPERSAL: CORROBORATION OF THE "OUT OF TIBET" THEORY

To address the origin and dispersal of *Proboscidipparion*, it is necessary to integrate fossil records from key sites. In the Yushe Basin of Shanxi Province, *P. pater* from the Pliocene and *P. sinense* from the Early Pleistocene are present, but there is a lack of records of their more ancient direct ancestor, *Shanxihippus dermatorhinus*.[3] In the Linxia Basin of Gansu Province, located on the northeastern edge of the Tibetan Plateau, *S. dermatorhinus* was discovered in the top of the Late Miocene Liushu Formation, and *P. pater* directly appeared in the bottom of the overlying Early Pliocene Hewangjia Formation,[4] with the two perfectly aligned in the chronological order (Figure 1C).

This stratigraphic sequence strongly suggests that the *Proboscidipparion* horse originated from the Linxia Basin region on the northeastern edge of the Tibetan Plateau. More importantly, the Linxia Basin experienced a cold climate due to its high altitude background during the Pliocene, which was different from North China (such as the Yushe Basin) that was located at lower altitudes and experienced drastic climate fluctuations during the Pliocene warm period and Early Pleistocene glacial period. This implies that *Proboscidipparion* had already adapted to the relatively cold and arid environment in its origin, exhibiting "pre-adaptation" characteristics to the upcoming Quaternary glacial climate.

Therefore, the dispersal history of *Proboscidipparion* from the northeastern edge of the Tibetan Plateau to regions such as North China perfectly aligns with the "Out of Tibet" theoretical model:[5] during the uplift of the Tibetan Plateau, some animal groups evolved adaptive traits in the high-altitude cold environment; subsequently, as global climate became colder and drier, these groups that had previously adapted to the cold climate were able to smoothly spread to surrounding low- and mid-altitude areas and achieve success. *Proboscidipparion* is a vivid example of this macroevolutionary process in the late Cenozoic East Asian equids.

SUMMARY AND OUTLOOKS

Based on a comprehensive analysis of existing materials, we have reached the following conclusions: (1) The *Proboscidipparion* horse is a typical herbivore of open grassland, and the early ecological hypothesis of "resembling tapirs and feeding on foliage near water" has been refuted by stable isotope evidence. (2) The characteristic prorhiscis structure of *Proboscidipparion* is a result of convergent evolution with the saiga, with its core function being to regulate breathing (preheat/humidify/filter air) and enhance physiological performance in movement (improve oxygen supply and heat dissipation efficiency), representing an active adaptive evolution in response to the specific environment of grassland (Figure 1E). (3) *Proboscidipparion* originated in the Linxia Basin on the northeastern edge of the Tibetan Plateau, and its dispersal history is a result of "pre-adaptation" to the climate during the Quaternary glacial period, providing strong paleontological evidence for the important Cenozoic biogeographic theory of "Out of Tibet".

This study not only clarifies the biological truth of an important fossil taxon, but also demonstrates how to deeply interpret the adaptive strategies and evolutionary history of ancient taxa through the cross-integration of multidisciplinary evidence (morphology, stable isotope geochemistry, paleoecology, ethology, and biostratigraphy), and contributes a specific case to understanding the relationship between the Tibetan Plateau uplift and mammalian evolution during the late Cenozoic in East Asia. Future research can further utilize CT scanning for three-dimensional nasal reconstruction and aerodynamic simulation to deepen the understanding of the niche differentiation mechanism of the *Proboscidipparion* horse.

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AUTHOR CONTRIBUTIONS

All authors contributed to the manuscript and approved the final version.

DECLARATION OF INTERESTS

The authors declare no competing interests.