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Authors: Hu, Ying, Chen, Yaoxing, Wang, Shuo, and Sun, Qingmin

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Pleistocene equid brain endocast from Shanxi Province, China

YING HU, YAOXING CHEN, SHUO WANG, and QINGMIN SUN



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Brain endocasts are rare in the fossil record because they are only preserved under exceptional conditions. An equid brain endocast from the early Pleistocene of Wanrong County, Shanxi Province, China, is reported in this paper. Measuring approximately $140 \times 95.2 \times 83$ mm, the new specimen represents a relatively advanced adult horse brain. Comparisons indicate that it is more derived than those of *Hyracotherium* and *Mesohippus* in having an expanded neocortex, and more than those of *Pliohippus* and *Hipparion* in having an enlarged network of branching sulci; in most characters involving these sulci, the Shanxi brain conforms to the extant species *Equus caballus*. The sulcus diagonalis of the *Equus* brain appears to have evolved conservatively during the early Pleistocene, whereas the sulcus suprasylvius seems to have evolved rapidly. The specimen demonstrates that the development of a high degree of complexity predates the enlargement of the brain in the horse, which increased in length, breadth, and especially height during the late Cenozoic.

Key words: Mammalia, *Equus*, equid brain, Pleistocene, Shanxi Province, China.

Ying Hu [hu.ing@263.net], College of Life Science, Tianjin Normal University, Tianjin 300387, P.R. China;

Yaoxing Chen [yxchen@cau.edu.cn], College of Veterinary Medicine at China Agricultural University, Beijing 100093, P.R. China;

Shuo Wang [uslarky@163.com], College of Life Science, Nankai University, Tianjin 300071, P.R. China; present address: Key Laboratory of Vertebrate Evolution and Human Origins of the Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China; University of the Chinese Academy of Sciences, Beijing 100049, China;

Qingmin Sun [qms1949@126.com], Yuncheng Normal Institute, Yuncheng 044000, Shanxi, P.R. China.

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Introduction

Knowledge of evolutionary change in the nervous system is indispensable for understanding vertebrate evolution as a whole. Yet, despite the abundance of well-preserved equid material in the fossil record, three-dimensionally preserved brains are rare, since soft brain tissue is preserved only under highly specific sedimentary conditions: most preserved brain endocasts are cemented by sand, and sometimes the organic ingredients of the brain are replaced by calcium compounds (Wang and Bao 1984). CT-scanning of the cranial cavity (Franzosa and Rowe 2005; Dong et al. 2006) offers a way to reconstruct cerebral morphology even when no brain fossil has been recovered as such, but usually fails to capture exact details of the brain sulci. Thus, although a natural brain endocast is unlikely to be preserved, it can provide more detailed

information about the function and evolution of the vertebrate nervous system than CT scans. The past few decades have seen reports of natural endocasts from a variety of animals, such as birds (Kurochkin et al. 2007), dinosaurs (Jerison 2004), and mammals (Edinger 1948; Radinsky 1976; Wang and Bao 1984; Kear 2003; Takai et al. 2003), including humans (Jerison 1975). Here, we add to this record by describing a nearly complete equid brain endocast from early Pleistocene sediments exposed in Shanxi Province, China, and discuss its evolutionary implications.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; CNHM, Carnegie Museum of Natural History, Pittsburgh, USA; LACM, Natural History Museum of Los Angeles County, Los Angeles, USA; TNU, Tianjin Normal University, Tianjin, China; USNM, United States National Museum, Washington, DC, USA.

Geological setting

The brain endocast reported here was recovered from the Sanmen Formation of Chenjiagou, Ronghe Town, Wanrong County (E 110°29'23"; N 35°18'39"), southwestern Shanxi Province, China (Fig. 1), which lies about 1.5 km south of Xizhuozi (Tang et al. 1983). A well-developed fluvial sedimentary sequence extending from the Pliocene to the Pleistocene is exposed in this area, and has yielded numerous fossils (Zhou and Zhou 1959, 1965; Tang et al. 1983; Huang and Ji 1984). The specimen was derived from a layer of cross-bedded fluvial sandstone (Supplementary Online Material, SOM at http://app.pan.pl/SOM/app59-Hu_etal_SOM.pdf; SOM 1; Tang et al. 1983), which has also yielded abundant fossils of *Equus sanmeniensis*, *E. przewalskii*, *E. cf. huanghoensis*, artiodactyls (Tang et al. 1983), carnivorans (Zhou and Zhou 1959, 1965; Tang et al. 1983; Huang and Ji 1984; Wang and Zhao 2006) and birds (Wang et al. 2006). Both *E. sanmeniensis* and *E. huanghoensis* appeared during the early Pleistocene (Deng and Xue 1999), with *E. sanmeniensis* becoming extinct at the start of the middle Pleistocene. The mammalian assemblage of Chenjiagou closely resembles the Linyi fauna, dated to the Nihewanian (early Pleistocene, or Calabrian–Gelasian, sensu Gradstein et al. [2012]) based on the occurrence of *Megantereon*, *Euctenoceros boulei*, and *Hipparion (Proboscideipparion) sinense* (SOM 2; Tong et al. 1995). Taken together, this suggests an early Pleistocene age (or Calabrian–Gelasian, about 0.8–2.6 Ma) for the fluvial sandstone of Chenjiagou (SOM 2; Zhou and Zhou 1959; Huang and Ji 1984; Tong et al. 1995; Wang and Zhao 2006; Gradstein et al. 2012).

Material and methods

Our observations and descriptions are based on a relatively complete natural brain endocast housed at Tianjin Normal University (TNU V44). For comparisons, we relied largely on descriptions of brain endocasts of *Hyracotherium*, *Miohippus*, *Meshippus*, *Neohipparion*, *Pliohippus*, and *Hipparion* (Tilney 1933; Edinger 1948; Radinsky 1976), as well as the brain of the extant horse *Equus caballus* (Edinger 1948, and a specimen housed at the China Agricultural University). We measured the new material following the protocols of Edinger (1948). The endocast was first measured with calipers, and then modeled in resin at a 1:1 scale. The volume of the brain was estimated by submerging the model and measuring the volume of water displaced. Relative brain size taking into account body size was assessed by calculating the encephalization quotient (EQ), following the methodology of Jerison (1970) (see SOM 3 for details).

Results

Description.—The brain endocast was cemented by sand and clay. The cerebral hemispheres are nearly complete, and

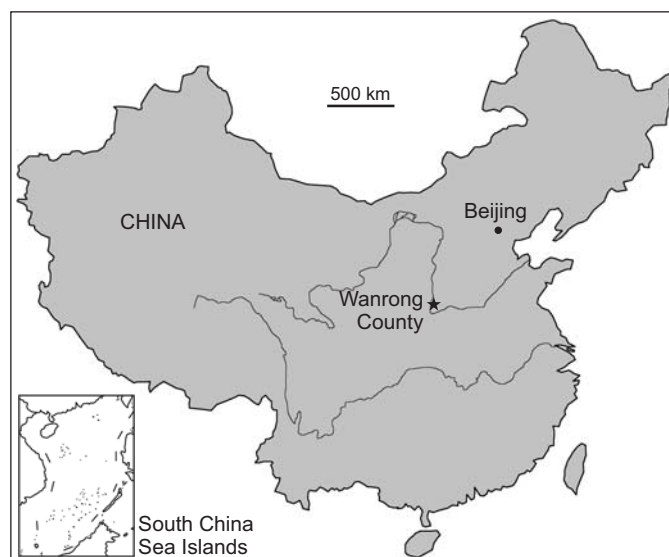


Fig. 1. Map showing the position of Wanrong County, Shanxi Province, China.

many details are visible on the dorsal, lateral and ventral surfaces in particular (Figs. 2, 3). The endocast is 140 mm long and 95.2 mm wide, and has a maximum height of 83 mm. Judging from its comparatively large volume of 465 ml, it represents a relatively advanced adult horse brain. The symmetrical cerebral hemispheres bear a complicated network of branched sulci, resembling the general pattern of neocortical fissures seen in modern horses.

The longitudinal fissure is discernible, and the olfactory bulbs can be seen on the lower halves of the anterior faces of the cerebral hemispheres. The anterior portions of both olfactory bulbs are broken away, with the fractured surfaces measuring 24 mm (right) and around 20 mm (left) in diameter, respectively. The anterodorsal part of the right frontal lobe is missing. The sulci of the occipital lobe are shallow on both sides, making it difficult to distinguish particular features. The morphology of the right occipital region is particularly obscure, owing to some fragments of bony tissue that remain attached to the endocast. Most of the sulci of the frontal, temporal and apical lobes can be identified in left lateral view, while in the right hemisphere only the temporal and frontal lobes can be distinguished. In ventral view, only the optic tract, hypophysis and ventral surface of the cerebellum can be recognized, with the optic tract being distinctly larger than in the modern *Equus* specimen housed at the China Agricultural University.

Owing to the shallowness of the sulci, many characters relating to the pattern of fissuration are difficult to assess. The praesylvian and suprasylvian sulci are recognizable on both sides, although the suprasylvian sulcus is clearer on the left. The suprasylvian sulcus is located close to the longitudinal fissure and forms anterior, middle and posterior branches, with the middle branch being the deepest of the three. The left coronal sulcus is shallow, while the right one is not preserved. The left ectomarginal sulcus is deep and well

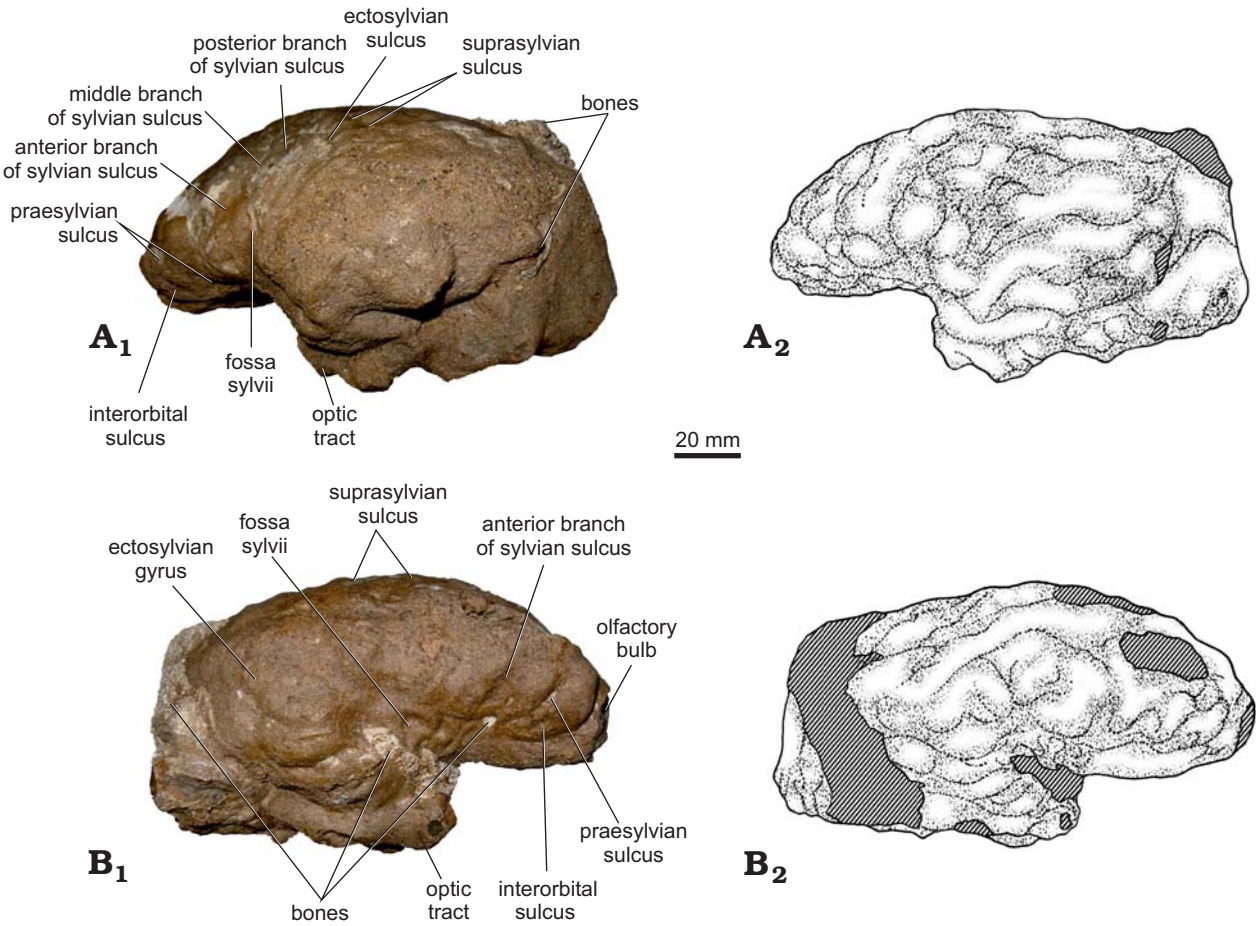


Fig. 2. Fossil equid brain endocast (TNU V44) from Shanxi Province, China (early Pleistocene) and associated bones in left lateral (A) and right lateral (B) views. Photographs (A₁, B₁) and sketches (A₂, B₂).

developed, extending forwards and curving towards the longitudinal fissure. By contrast, the right ectomarginal sulcus is poorly defined. The ectosylvian sulcus and the fossa sylvii can be clearly distinguished in left lateral view. Similarly, the interorbital sulcus and the frontal part of the praesylvian sulcus are well developed in the right hemisphere.

Comparisons.—The oldest evidence of equid brain morphology consists of a natural endocast of Eocene age, originally referred to *Hyracotherium* by Edinger (1948). Radinsky (1976) subsequently challenged this assignment, and

instead produced three artificial endocasts from a series of confidently identified *Hyracotherium* skulls. The latter have comparatively featureless surfaces, with only the sulcus suprasylvius, sulcus lateralis, and sulcus rhinalis being clearly distinguishable (Radinsky 1976). After *Hyracotherium*, the next reliable record comes from an endocast of *Mesohippus*, a 30-million-year-old taxon thought to be close to the ancestral line of modern horses (Edinger 1948). The frontal and occipital lobes of this taxon are significantly expanded and their lateral sulci visibly more elongated than in *Hyracotherium* (Radinsky 1976). Compared with both *Hyracotherium*

Table 1. Brain, body size estimates, and encephalization quotients (EQ) of fossil and modern horses.

Taxon	Material	Endocast volume (ml)	Body weight (kg)	EQ	Reference
<i>Hyracotherium</i>	AMNH55266-8	25	9	0.47	Radinsky 1976
<i>Mesohippus</i>	USNM22539	78	20	0.88	Jerison 1973
<i>Merychippus</i>	LA 368/3929	270	110	0.98	Jerison 1973
<i>Neohipparion</i>	CNHM P15871	160	150	0.47	Jerison 1973
<i>Pliohippus</i>	CNHM P15870	270	220	0.62	Jerison 1973
<i>Equus</i> sp.	TNU V44	465	300	0.83	this study
<i>Equus occidentalis</i>	LACM-17 C-3	870	640	0.98	Jerison 1973
modern horses				0.95	Radinsky 1976
modern zebras				1.09	Radinsky 1976

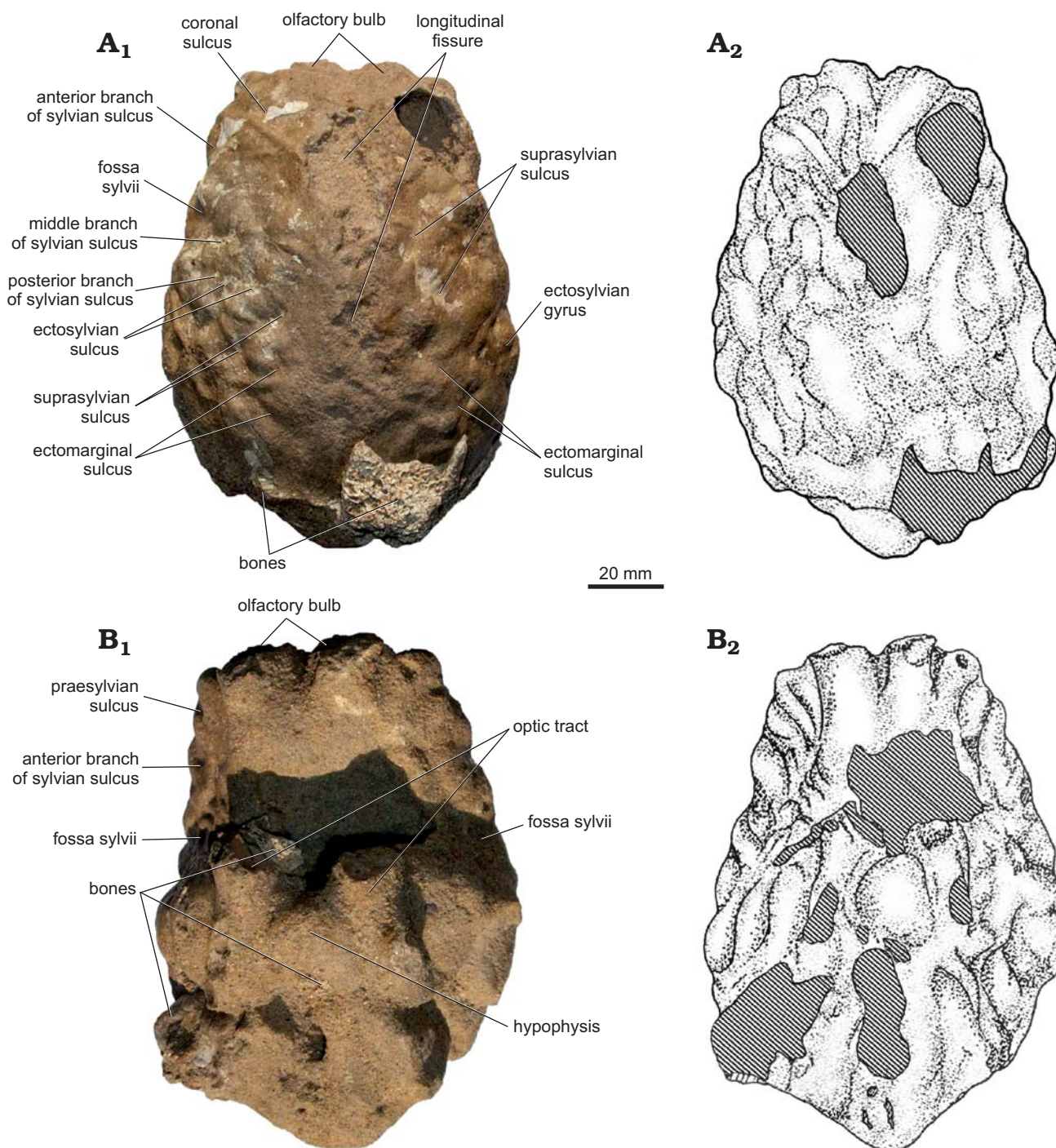


Fig. 3. Fossil equid brain endocast (TNU V44) from Shanxi Province, China (early Pleistocene) and associated bones in dorsal (A) and ventral (B) views. Photographs (A₁, B₁) and sketches (A₂, B₂).

and *Mesohippus*, TNU V44 clearly has a more expanded neocortex.

Two endocasts of *Pliohippus* (AMNH 10844 and CNHM P15870) and a further one belonging to *Hipparion* (AMNH 10732a) are only slightly smaller than TNU V44 (Edinger 1948). However, the maximum length to width ratio of the *Hipparion* endocast is about 1.3, in contrast to 1.47 in TNU V44, reflecting the more slender shape of the brain of *Hipparion*. In addition, while the sulcus diagonalis is similar

in TNU V44 and *Pliohippus*, the sulcus suprasylvius of the former is longer and more sinuous, thus indicating that the sulcus diagonalis was relatively conservative in the transition from *Pliohippus* to more derived equids, whereas the sulcus suprasylvius was more progressive. Furthermore, in accordance with its large optic tract, TNU V44 has a much broader and higher occipital lobe, indicating more advanced visual abilities. Finally, although the anterior portions of the olfactory bulbs are missing, they are located much closer

to the cerebrum and do not project as far rostrally as in *Pliohippus*.

While the brain endocast of *Hipparion* resembles TNU V44 in terms of its complexity, some obvious differences also exist, including a straight middle part of the sulcus suprasylvius and a sulcus lateralis running parallel to the longitudinal fissure (Edinger 1948). By contrast, both of these sulci are sinuous in TNU V44. Neither an artificial endocast nor a detailed description of the olfactory bulbs of *Hipparion* was available to us, thus preventing their comparison with those of TNU V44.

In *Equus*, the sulcus suprasylvius extends anterodorsally in the anterior part of the cerebrum, before curving and running caudally further posteriorly. By contrast, the left lateral sulcus continues anteriorly across the cruciate and ansate sulci, forming a long, anteroposteriorly oriented, undulating, multi-branched line (Edinger 1948). In general, the morphology of TNU V44 closely resembles that of the brain of an extant horse, with the exception of a somewhat shallower frontal lobe and a sulcus suprasylvius located much closer to the longitudinal fissure (Sisson 1956; Georg 2005), although the latter may well be reflective of the high degree of intraspecific variation found in extant *Equus* (Edinger 1948). Detailed morphological variation aside, the gross volume of TNU V44 appears slightly smaller than is typical for *Equus caballus*. According to Edinger (1948) and our own measurements, the brain capacity of *Equus caballus* is around 580–750 ml, compared to 465 ml in TNU V44. It is thus possible that TNU V44 may represent an early type of *Equus* brain.

Taking body size into account (SOM 3; Table 1), the brain volume of *Equus occidentalis* is 3.2 times, and its body size 2.9 times, that of *Pliohippus*, indicating that both features evolved in synchrony. The EQ of TNU V44 is 0.83, meaning that its brain was about 83% the size one would expect in an average living mammal of similar body weight. This value is smaller than that of Pleistocene *Equus occidentalis* and modern horses, but distinctly larger than that of Paleogene and Neogene equids, thus providing additional evidence that TNU V44 likely represents an early Pleistocene *Equus* brain.

Discussion

While the brains of TNU V44 and *Equus caballus* are significantly larger than those of *Neohipparion* and *Pliohippus*, *Pliohippus* displays a pattern of sulci comparable in complexity to that of *Equus*, and more complex than that seen in *Neohipparion*. Taking into account their stratigraphic context (Fig. 4), this may indicate that the complex sulci characteristic of *Equus* appeared before the early Pleistocene, and that the subsequent evolution of the brain during the Pleistocene was primarily a matter of enlargement. However, the latter was likely not proportional: while, despite its overall smaller size, the brain of *Neohipparion* is about as high as that of *Pliohippus*, the brains of TNU V44 and *Equus caballus*

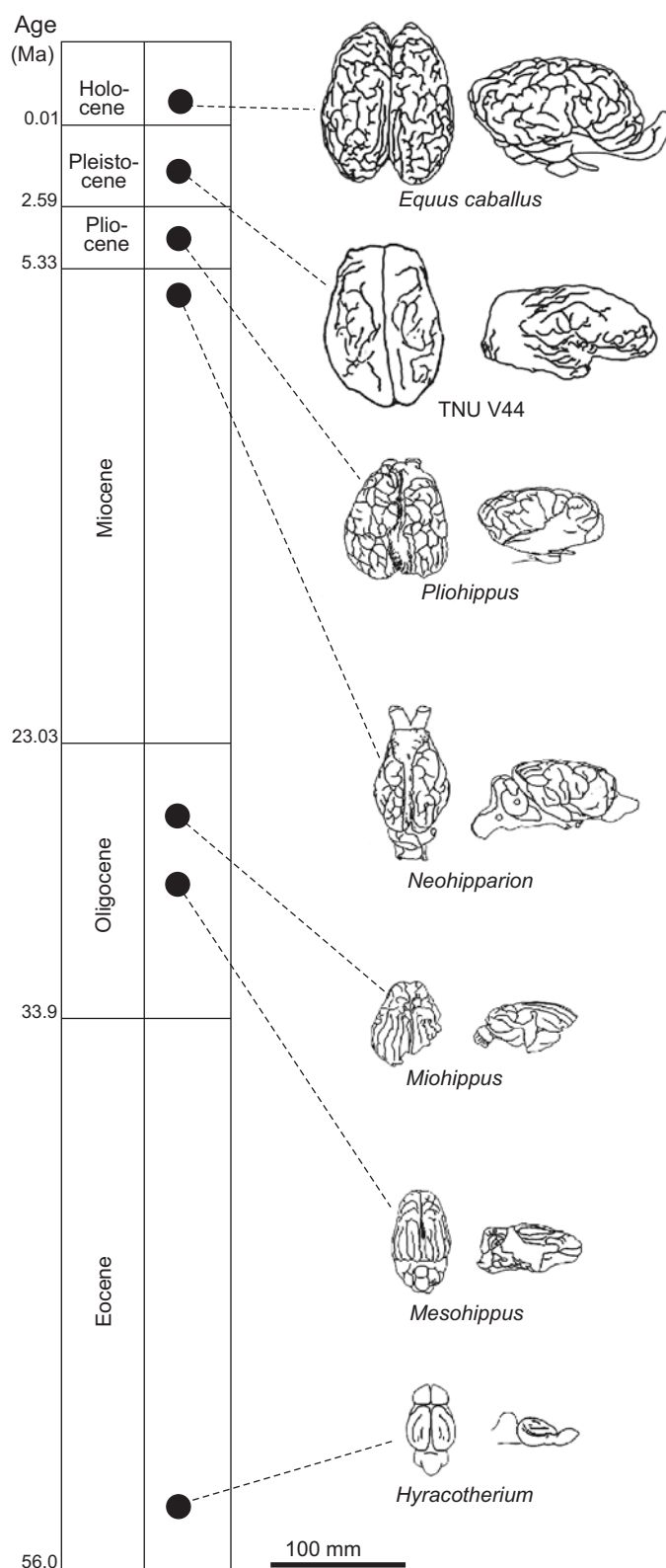


Fig. 4. Evolutionary trends in equid brain morphology. Drawings of the brains of *Pliohippus*, *Neohipparion*, *Miohippus*, and *Mesohippus* are based on Edinger (1948); the drawing of the brain of *Hyracotherium* is based on Radinsky (1976); the brain of the extant horse *Equus caballus* is based on the specimen housed at the China Agricultural University. All specimens are shown to the same scale. Numerical ages are taken from Gradstein et al. (2012).

are both significantly higher. This implies that, during the Pleistocene, the height of the cerebrum increased to a larger degree than its length and width, and is in agreement with the previous suggestion that, during the late stages of equid evolution, enlargement of the brain no longer occurred through increases in length alone, but rather through simultaneous increases in length, width and height (Edinger 1948).

From the comparisons above, it is possible to identify two major morphological stages of brain evolution in the horse (Fig. 4, Table 1): the first stage, occurring from the Eocene through to the Pliocene, involved the evolution of increasingly complex patterns of sulci; by contrast, the second stage, occurring during the Pleistocene, mainly involved brain enlargement, as shown by *Equus* (but not the Pleistocene representatives of *Hipparion*). In connecting the two stages, the early Pleistocene marks a critical point in equid evolution, with the second stage possibly triggered by the migration of *Equus* out of its original habitat.

The genus *Equus* first appeared about 3.5 Ma ago in North America, before rapidly spreading into Eurasia via the land bridge connecting the two continents around 2.5 Ma (Deng and Xue 1999). Adaptation to this new environment, made even more variable by strong winter monsoons causing periodic fluctuations in the climate and vegetation patterns of East Asia (Liu and Ding 1992), possibly resulted in the evolution of improved visual (as reflected in the enlargement of the brain and optic tract) and auditory (as reflected in the higher cerebrum and temporal lobe) abilities, as well as an increase in body size (Xue et al. 2006). In turn, the enlargement of the brain likely had important consequences in terms of gregariousness, territorial establishment and defense, reproduction and rearing of the young, feeding, and social organization (Butler and Hodos 2005).

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