

A primitive species of *Chilotherium* (Perissodactyla, Rhinocerotidae) from the Late Miocene of the Linxia Basin (Gansu, China)

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A skull with its articulated mandible attributed to *Chilotherium primigenius* sp. nov. from the Late Miocene of the Linxia Basin (Gansu, China), is described. This early Late Miocene species is the earliest and most primitive in the genus *Chilotherium*. Compared with the other Late Miocene species of *Chilotherium*, a tentative lineage of *C. primigenius*→*C. wimani*→other species of *Chilotherium* is proposed. A Late Miocene Asian radiation is suggested for this genus, starting from Linxia *C. primigenius*. The origin and dispersal history of the genus *Chilotherium* are discussed and correlated with major faunal exchanges. The sequence of the Late Miocene *Hipparion* fauna in the Linxia Basin, which yields the remains described herein, is also discussed.

KEY WORDS: *Chilotherium*, Late Miocene, Linxia Basin, new species.

Introduction

Late Cenozoic terrestrial deposits from the Linxia Basin (Gansu, China) have yielded many mammalian fossils. In these faunas, rhinocerotids are very abundant and species-rich. The rhinocerotids have essentially been collected and studied since the 1980s (Qiu *et al.*, 1987, 1990; Qiu & Xie, 1998; Guan, 1988; Guan & Zhang, 1993). Recently, we have collected many new rhinocerotid material (Deng, 2001b, c, 2002a, b, 2003; Qiu *et al.*, 2002). Qiu *et al.* (1987) attributed a skull with its articulated mandible from the Linxia Basin to *Acerorhinus hezhengensis* and considered that it differed from the species of the genus *Chilotherium*. They established a new tribe Chilotheriini, including the genera *Acerorhinus* and *Chilotherium*. Their material was recovered from unnamed Late Miocene deposits at Dashengou (Hezheng, Linxia Basin). Deng (2001a) described much more material of *Chilotherium wimani* from Fugu (Shaanxi, China) than Ringström (1924), and considered that *C. wimani* was the most primitive species of *Chilotherium*. The species of *Chilotherium* form a group considered to be closely related to the genus *Acerorhinus* (Qiu *et al.*, 1987).

We have collected thousands of mammalian fossils in the Linxia Basin, including carnivores, rodents, perissodactyls, proboscideans, artiodactyls, and primates (Deng, 2001b, c, 2002a, b, 2003; Qiu *et al.*, 2000, 2001; Wang and Qiu, 2002; 2003). An almost complete skull with its articulated broken mandible from a small and primitive species of *Chilotherium* has been discovered at Zhongmajia in Hezheng. Its morphology is different from all the known spe-

cies of *Chilotherium*, leading to the description of a new species.

Systematic palaeontology

Family Rhinocerotidae Owen, 1845
Subfamily Aceratheriinae Dollo, 1885
Tribe Chilotheriini Qiu *et al.*, 1987
Genus *Chilotherium* Ringström, 1924

Chilotherium primigenius sp. nov.
(Figures 1-2, Tables 1-3)

Holotype — HMV 0102, an adult skull with its articulated mandible. This mandible lacks the posterior part of the horizontal ramus, the lower part of ascending ramus and the left anterior corner of symphysis.

Etymology — The specific name, *primigenius*, is a Latin word, and means the first. This new species is considered the most primitive species of *Chilotherium*.

Type locality — Zhongmajia (35° 24' 47.0" N, 103° 24' 30.6" E; altitude: 2218 m), 6 km southeast to the Hezheng County seat in Gansu Province, China. The specimen is collected from the gray green sandstone and conglomerate in the bottom of the Liushu Formation. The bed bearing this fossil is of the early Late Miocene, corresponding to early and middle MN 9.

Diagnosis — Ventral surface of mandibular symphysis flat (different from concave surfaces of other known *Chilotherium* species); parietal crests very slightly separated, forming a sagittal crest different from the broadly separated parietal crests of *C. anderssoni*, *C. habereri*, *C. samium*, *C. schlosseri* and *C. kowalevskii*, and also different from the slightly separated parietal crests lacking a sagittal crest of *C. xizangensis*, *C. wimani*, *C. persiae* and *C. kiliasi*.

Description — Skull: The skull face is high. The premaxillary bone is retracted into a vertical flake with a sharp anterior end. The upper incisors are absent. Both ends of premaxillary bones are in close proximity. In ventral view, the premaxillary bone is thin and sharp, and its end is at the same level with the nasal tip. The nasal notch is narrow and deep, and its bottom is located at the level of M1/P4 boundary. A large infraorbital foramen on the maxillary face is located near the bottom of the nasal notch. The distance between the bottom of the nasal notch and the orbit is very short, 55.5 mm. The wide and prominent anterior margin of the orbit is located at the level of the middle of M2, and connects downward with the anterior margin of zygomatic arch. A frontward face is in front of the large and round orbit. The postorbital process is well developed on the frontal bone, but absent on the the zygomatic bone. The supraorbital and lacrimal tubercles are relatively marked. There is a notch between the postorbital process and supraorbital tubercle, and there is another one between the supraorbital and the lacrimal tubercles. The zygomatic arch is projecting highly to form a strong facial crest with a right angle, and its anterior end is located at the level of P4/M1 boundary. This arch is constricted inward at the level of the postorbital process, while its posterior part is expanded outward as a semicircle. The widest part of the zygomatic arch is located at the level of the postorbital process. On the posterior end of the zygomatic arch, its posterior upper corner is rounded, and its posterior margin is straight and inclined forward. In ventral view, the zygomatic arch is very thin. The occipital elevation is high. The occipital surface and lateral margins incline forward obviously. The lower part of the occipital surface is broken. The foramen magnum is onion-shaped, with a sharp upper end. The occipital crest has a wide and shallow central groove, and its two lateral corners are rounded. The lateral margins of the occipital crest are straight and parallel each other. The nuchal ligament depression is wide and shallow. The exterior lateral crest is strong, and a deep vertical depression is present between this crest and the lateral margin of the occipital crest. The median crest on the nuchal ligament depression connects with the upper end of the foramen magnum. The cranial top is smooth and flat, and it is the widest at the level of the supraorbital tubercle. The nasals are narrow and long, and extend flatly and straight. The nasal top is convex, and its base has a marked constriction. The nasal tip is appreciably truncated and slightly rough. The nasal lateral margins are drooping markedly posteriorly and curved inward. The nasal ventral surface also is convex, so the middle part of the nasal transversal section is lentoid. The connection between the nasal and

frontal bones is slightly erect. The braincase is very narrow, with steep exterior walls. The parietal crest is slightly projecting sideward to form a brim. The two parietal crests meet posteriorly to form a sagittal crest with the smallest width of 18 mm, from where they diverge to reach the lateral ends of the occipital crest. The posttympanic process is thin, with a smooth anterior and a rough posterior surface. This process expands slightly sideward, and declines forward to fuse with the postglenoid process on the upper part of the latter. As a result, a pseudoauditory meatus exists between them. The postglenoid process is thin longitudinally, with a triangular transverse section. The interior surface of the postglenoid process is smooth, and the exterior surface has a vertical groove posteriorly. The end of the postglenoid process curves forward. The temporal condyle is flat and straight, and its interior margin spaces out the postglenoid process by a deep groove. The articular surface behind the temporal condyle is narrow, with a continuous wide crest on its exterior and posterior margins to form a transverse flute parallel to the temporal condyle. The pterygoid bones are high, with a deep valley between them. The maxillary tubercle is well developed, with a sharp posterior end. The palatal surface is smooth and narrowly arched. The posterior margin of the palate is V-shaped, and its bottom is located at the level of the protocone of M3. Mandible: There is a long distance between the ascending ramus and m3. The upper part of anterior margin of the ascending ramus is thin and rounded. The coronoid process is well developed, and strongly curved backward. The condyloid process is very wide transversely and narrow longitudinally, especially narrower interiorly. Near the interior end of the condyloid process, there is a marked constriction. On the posterior part of the condyloid process, there is a narrow and deep transverse groove with a sharp bottom and a well-developed transverse crest. In top view, the mandibular symphysis expands strongly sideward to form a shovel. The alveolar margin is a crest with a straight posterior part, and its anterior part expands outward to be close to i2. There is a wide U-shaped valley between the two alveolar margins. The posterior margin of the mandibular symphysis is located at the level of p3/p4 boundary. In front view, the alveolar margin between the second lower incisors is thin and uplifted. The ventral surface of the mandibular symphysis is broad and flat, on which there are some large nutrient foramina distributed densely and irregularly, four on the right side. Upper teeth: The premolars have been worn deeply to reach the root. The labial walls of the upper cheek teeth are flat. DP1 has a single root. The molars also have been worn to be close to the root. As a result, M3 becomes a quadrangle. On the molars, the protocone is constricted; the entrance of median depression is wide, with some pillars; the lingual margins of protocone and hypocone are straight. There is a well-developed enamel board on the posterior wall of M3. Lower teeth: The first lower incisors are absent, and the second lower incisors are very strong tusks with a worn, backward oriented lingual surface.

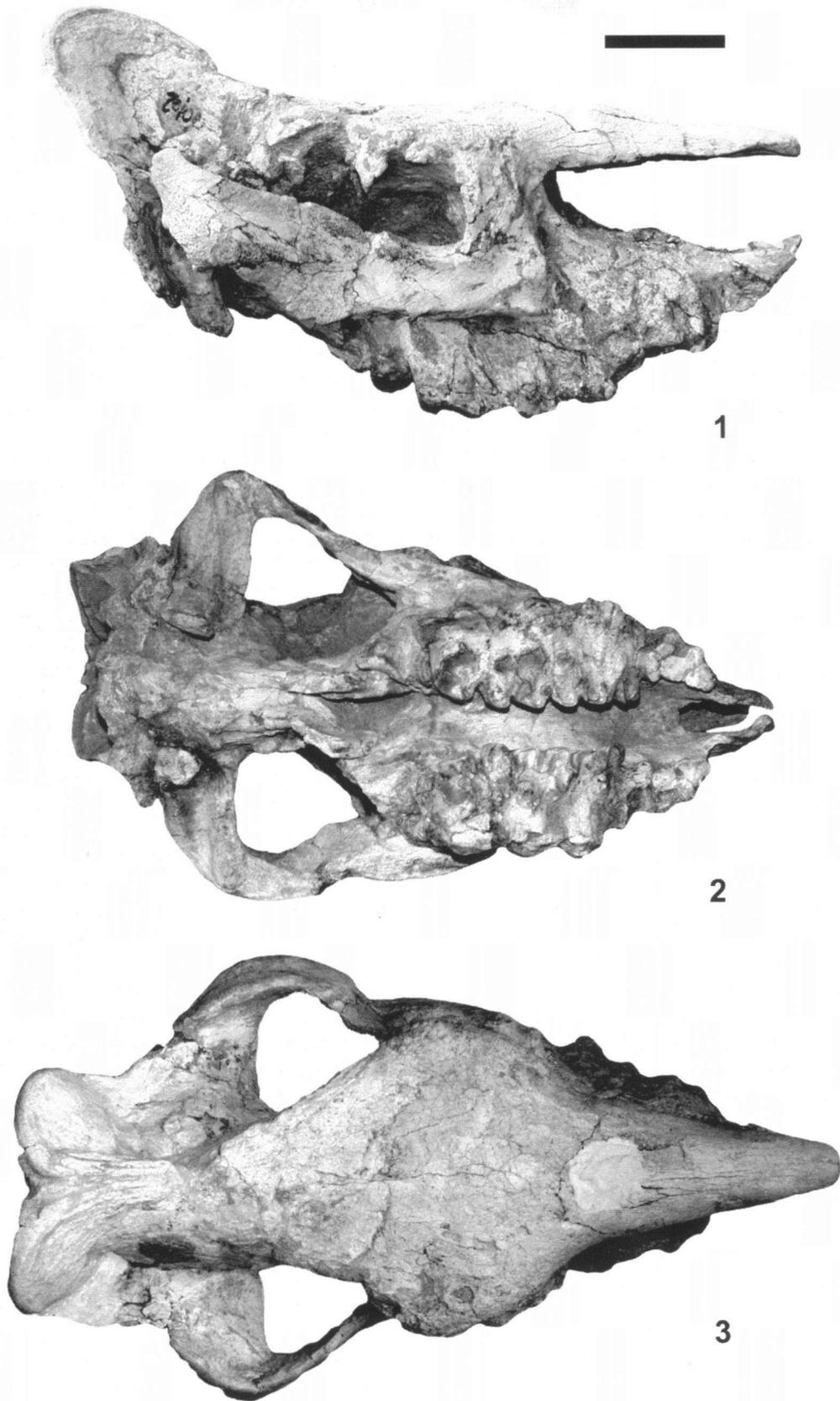


Figure 1. *Chilotherium primigenius* sp. nov. Holotype (HMV 0102), Liushu Formation, Late Miocene, Zhongmajia, Hezheng County, Gansu Province, China. 1, lateral view of skull. 2, ventral view of skull. 3, dorsal view of skull. Scale bar = 6 cm.

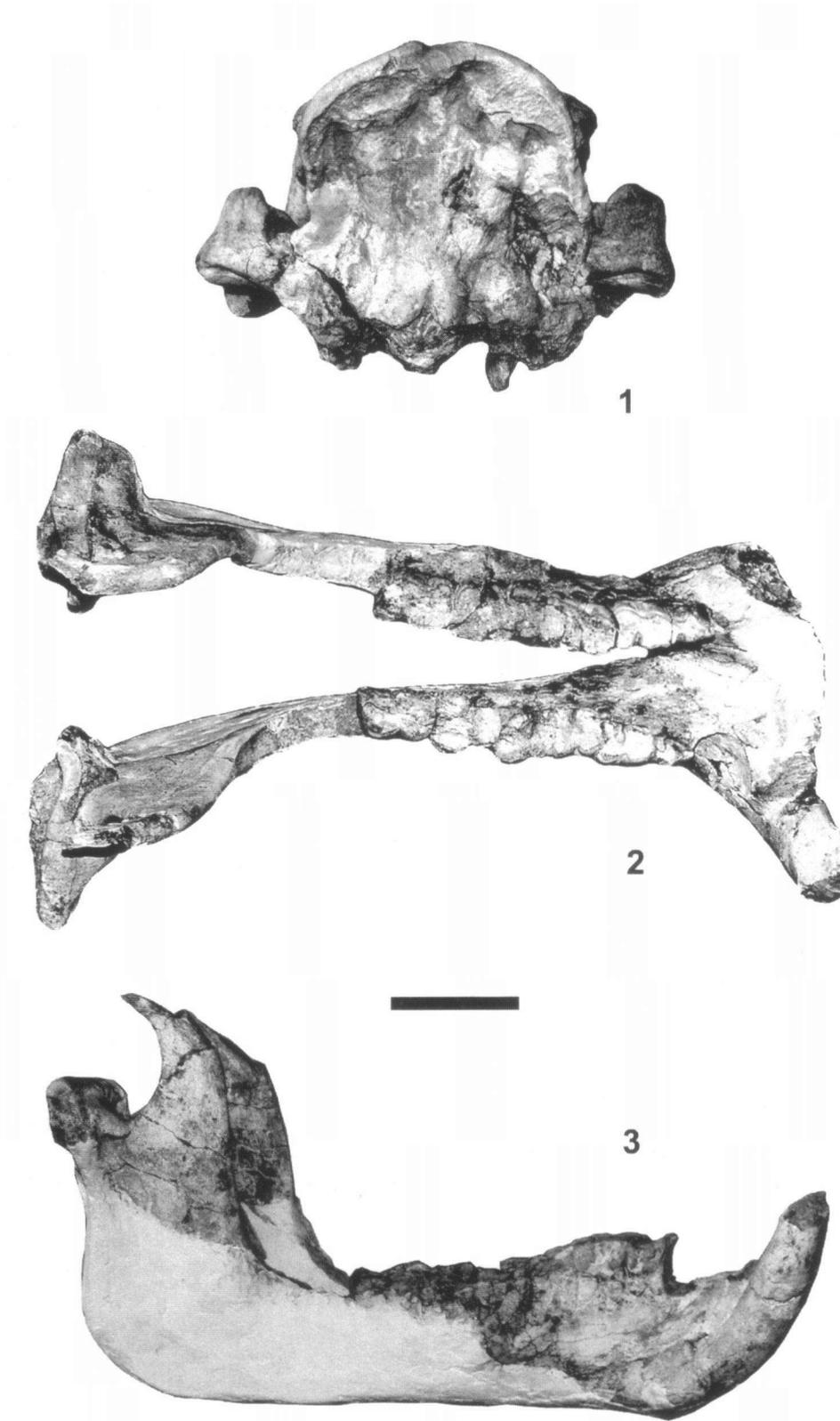


Figure 2. *Chilotherium primigenius* sp. nov. Holotype (HMV 0102), Liushu Formation, Late Miocene, Zhongmajia, Hezheng County, Gansu Province, China. 2-1, occipital view of skull. 2-2, dorsal view of mandible. 2-3, lateral view of the right side of the mandible. Scale bar = 6 cm.

The two tusks extend outward and upward markedly, and their medial flanges also are almost erect. The transverse section of the crown of i2 is a round triangle with an interior sharp angle, but that of the root is an oval. The base of crown of i2 is 37 mm wide and 26 mm thick.

The distance between the tusks is relatively large, about 80 mm. The lower cheek teeth also are worn deeply. The anterior end of talonid of p2 is sharp and projecting forward. The talonids of p2 and p3 are much better developed than the trigonids. On the lower cheek teeth, the lingual cingulum is absent, and the V-shaped labial groove is wide and shallow.

Discussion — Since Ringström (1924) established the genus *Chilotherium*, twelve species have been described, and 19 other species have been referred to this genus (Table 4). Ringström (1924) referred two species from Siwalik into the genus *Chilotherium*, i.e. *C. blanfordi* (Lydekker, 1884) and *C. fatehjangense* (Pilgrim, 1910). Foster-Cooper (1934) changed *Aprotodon smith-woodwardi*, a new genus and species established by him in 1915, to *Chilotherium smith-woodwardi*. Heissig (1975) attributed *C. blanfordi* and *C. fatehjangense* to the genus *Aprotodon*. Qiu & Xie (1997) reassigned *C. smith-woodwardi* to its original name *A. smith-woodwardi*. There are essential differences between *Aprotodon* and *Chilotherium*: *Aprotodon* has a proportionally larger and wider symphysis than *Chilotherium*; the horizontal ramus of *Aprotodon* is curved not only in side view (lower border curved) but also in dorsal view (both extremities deflect outward), which is seldom seen in rhinocerotids; *Aprotodon* has semi-molariform premolars, while *Chilotherium* fully molariform (Qiu & Xie, 1997). Matthew (1929) revised *Rhinoceros sivalensis* var. *intermedius* described by Lydekker (1884) from Siwalik into *C. intermedium*, and Heissig (1975) placed *C. intermedium* in the new subgenus *Subchilotherium*. Heissig (1989) raised the subgenus *Subchilotherium* to the genus rank, so the species became *S. intermedium*. The mandibular symphysis of *Subchilotherium* is narrow, and different from the widely expanded one of *Chilotherium*. As a result, there is not any real species of *Chilotherium* in the Siwalik faunas. Ringström (1924) referred four species of *Aceratherium* from Samos (Greece) into *Chilotherium*, including *C. samium* (Weber, 1905), *C. schlosseri* (Weber, 1905), *C. wegneri* (Andree, 1921), and *C. angustifrons* (Andree, 1921). At the same time, he referred *Teleoceras poticus* and *Aceratherium kowalevskii* from Odessa (Ukraine) into *Chilotherium* as *C. ponticum* (Niezabitowski, 1913) and *C. kowalevskii* (Pavlov, 1913). Heissig (1975) merged *C. wegneri* and *C. ponticum* into *C. schlosseri*, and attributed *C. angustifrons* to *C. kowalevskii*. Therefore, only *C. samium*, *C. schlosseri* and *C. kowalevskii* are considered to be valid species of *Chilotherium* from Samos and Odessa. Geraads & Koufos (1990) described a new species, *Aceratherium kiliasi* from Pentalophos (Greece). Because its mandibular symphysis is broadly expanded, Heissig (1999) attributed *A. kiliasi* to *Chilotherium kiliasi*. Zbyszewsky (1952) described a new species, *Chilotherium quintanelensis* from Portugal, but this species later turned

out to be a *Hispanotherium matritense* (Villalta & Crusafont, 1955). Similarly, another species, *Chilotherium ibericum*, described by Antunes (1972) from Portugal, was also later attributed to *Hispanotherium matritense* (Heissig, 1975). Borissiak (1915) described a new species *Aceratherium zernowi* from Odessa, and Kretzoi (1942) created a new genus *Acerorhinus* for this species. Heissig (1975) reduced the genus *Acerorhinus* to the rank of subgenus of the genus *Chilotherium*, so that *Acerorhinus zernowi* became *C. (Acerorhinus) zernowi*. Heissig also referred one species of *Aceratherium* and two species of *Diceratherium* from China into this subgenus of *Chilotherium*, including *C. (A.) hipparionum* (Koken, 1885), *C. (A.) palaeosinense* (Ringström, 1924), and *C. (A.) tsaidamense* (Böhlén, 1937). Qiu *et al.* (1987) considered that the subgenus *Acerorhinus* should be ranked a genus, so above-mentioned four species of the subgenus *Acerorhinus* became *Acerorhinus zernowi*, *A. hipparionus*, *A. palaeosinensis*, and *A. tsaidamensis*. In fact, the genus *Acerorhinus* has a strongly constricted nasal base and a relatively narrow mandibular symphysis, which are very different from the genus *Chilotherium*. Ringström (1924) revised *Rhinoceros persiae* from Maragha (Iran) described by Pohlig (1885) into *Chilotherium persiae*. This species has the typical characters of *Chilotherium*, especially a widely expanded mandibular symphysis. On the other hand, the M3 of this species is quadrangular, with a rudimental posterior depression, which is different from other species of *Chilotherium*. Most species of *Chilotherium* have been recorded from Neogene deposits of China. Ringström (1924) described three new species of *Chilotherium* and one revised species described by Schlosser (1903) from the *Hipparion* fauna in northern China, but Heissig (1975) merged *C. planifrons* into *C. anderssoni*, and synonymized *C. wimani* with *C. habereri*. However, *C. wimani* has a narrow surface between the parietal crests, a concave cranial profile, and well-developed parastyle folds on the upper cheek teeth, which characters can obviously be distinguished from *C. habereri*, so *C. wimani* is a valid separate species (Deng, 2001a, c, 2002a). Tung *et al.* (1975) showed that the surface between the parietal crests of *C. fenhoense* is wider than that of *C. anderssoni*. However, the width between the parietal crests of *Chilotherium* is variable (Deng, 2001a, c), and the larger width of *C. fenhoense* falls within the range of variation of *C. anderssoni*. From Late Miocene deposits of Tibet, Ji *et al.* (1980) described a new species of *Chilotherium*, *C. xizangensis*, and Zheng (1980) added another species, *C. tanggulaense*. The widely expanded mandibular symphysis of *C. xizangensis* underlines its attribution to *Chilotherium*. The dental characters of *C. tanggulaense* show that it should be referred into *Subchilotherium*. Heissig (1975) revised *Rhinoceros pygmaeus* described by Ringström (1927) only based upon limb bones from Guide, Qinghai (previously Kansu) into *Chilotherium (Subchilotherium) pygmaeum*. Because *Subchilotherium* has been raised as a genus, *C. pygmaeum* is now referred to as *S. pygmaeum*. Schlosser (1903) described a new species, *Rhinoceros brancoi* based upon a specimen of the cheek teeth with complicated enamel plications from northern China. Kretzoi (1942)

created a new genus for this species, *i.e.* *Shansirhinus*, but Heissig (1975) renamed it as *Chilotherium brancoi*. More discoveries from China prove that the genus *Shansirhinus* is valid. *Chilotherium yunnanensis* from Yunnan described by Tang *et al.* (1974), *C. cornutum* from Shanxi (Qiu & Yan, 1982), and *C. tianzhuensis* from Gansu (Zheng, 1982) should be referred into *Shansirhinus* as well.

In conclusion, nine species of *Chilotherium* are valid: *C. samium*, *C. schlosseri*, *C. kowalevskii*, and *C. kiliasi* from Europe, *C. anderssoni*, *C. habereri*, *C. wimani*, and *C. xizangensis* from China, and *C. persiae* from Iran. All nine species have a strongly concave ventral surface of the mandibular symphysis, while *C. primigenius* has a relatively flat ventral surface. *Chilotherium anderssoni*, *C. habereri*, *C. samium*, *C. schlosseri*, and *C. kowalevskii* have broadly separated parietal crests (Schlosser, 1903; Weber, 1905; Pavlow, 1913; Ringström, 1924). On the other hand, *C. primigenius* has very poorly separated parietal crests that form a sagittal crest backwards. *Chilotherium xizangensis*, *C. wimani*, *C. persiae*, and *C. kiliasi* have the slightly separated parietal crests (Ji *et al.*, 1980; Ringström, 1924; Deng, 2001a, c; Geraads & Koufos, 1990), but they do not form a sagittal crest. The surface between the parietal crests of *C. wimani* is very narrow, and this species has a tendency to form a sagittal crest. The M3 of *C. persiae* is unique by its quadrangular occlusal surface in all known species of *Chilotherium*, so the triangular M3 of *C. primigenius* can be easily distinguished from *C. persiae*. Consequently, *C. primigenius* is a new species different from other species of *Chilotherium*. The relatively small size (Table 1-3) is characteristic of skull, mandible and teeth of *C. primigenius*. It is much smaller than *C. wimani*, but a little larger than *C. xizangensis* (Ji *et al.*, 1980).

Characters checked on skull, mandible and teeth of *C. primigenius* allow us to investigate the relationships of this new species using cladistic analyses (Fig. 3).

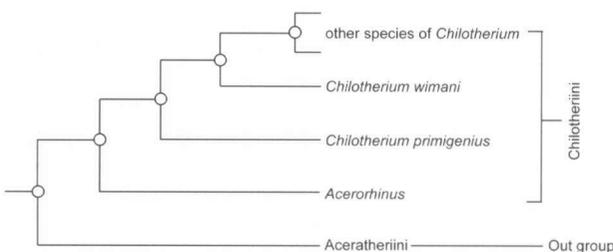


Figure 3. Phylogenetic relationships of *Chilotherium primigenius* sp. nov.

Node 1, Outgroup. Node 2, genus *Acerorhinus*. Node 3, fused posttympanic process with the postglenoid one, low parietal crest, narrow zygomatic arch without a projection of posterodorsal angle, gradually narrowing cranial dorsal surface before the orbit, strong broadening of the mandibular symphysis, well-developed structures on the cheek teeth, comparatively small P2, upturned medial flanges of i2, flat labial wall of upper cheek teeth. Node 4, thick posttympanic process, obviously separated parietal crests, wide nasal notch, long distance between the bases of i2 and p2,

concave ventral surface of the mandibular symphysis. Node 5, broadly separated parietal crests, weak lingual cingulum, low occipital surface, robust paroccipital process, slender postglenoid process, well-developed postorbital process, weak supraorbital tubercle, thin upper orbital margin, narrow nasal bone, low and rounded braincase, high crown of the cheek teeth, strong constriction of the protocone, and comparatively large P2. Other species of *Chilotherium* include *C. anderssoni*, *C. habereri*, *C. samium*, *C. schlosseri*, *C. kowalevskii*, *C. xizangensis*, *C. persiae*, and *C. kiliasi*.

The cladogram shows that *C. primigenius* shares many synapomorphies (Fig. 3, node 3) with the other species of *Chilotherium*, but not with the primitive chilotheres *Acerorhinus* and other rhinocerotids as a whole: fused posttympanic process with the postglenoid process, low parietal crest, narrow zygomatic arch without a projection of posterodorsal angle, gradually narrowing cranial dorsal surface before the orbit, strong broadening of the mandibular symphysis, well-developed secondary structures on the cheek teeth, comparatively small P2, and upturned medial flanges of i2 are apomorphies and mean that *C. primigenius* is truly a member of the genus *Chilotherium*. Meanwhile, some apomorphic characters of the other species of *Chilotherium* are lacking: thick posttympanic process, obviously separated parietal crests, wide nasal notch, long distance between the bases of i2 and p2, concave ventral surface of the mandibular symphysis, which also characterize the “*C. wimani*”-other *Chilotherium* species clade” (containing *C. anderssoni*, *C. habereri*, *C. samium*, *C. schlosseri*, *C. kowalevskii*, *C. xizangensis*, *C. persiae*, and *C. kiliasi*)” (Fig. 3, node 4), are absent in this species. Consequently, *C. primigenius* is the sister group of other species of *Chilotherium*. The second dichotomy within the genus *Chilotherium* (Fig. 3, node 5) sets *C. wimani* as the sister group of the remaining species of *Chilotherium*. These latter species are defined by markedly separated parietal crests, weak lingual cingulum, low occipital surface, robust paroccipital process, slender postglenoid process, well-developed postorbital process, weak supraorbital tubercle, thin upper orbital margin, narrow nasal bone, low and rounded braincase, high crown of the cheek teeth, strong constriction of the protocone, and comparatively large P2. *Chilotherium primigenius* and *C. wimani* are distinct from other species of *Chilotherium*. Only cranial and dental characters have been discussed so far, because postcranial remains attributed to *C. primigenius* are entirely unknown. It is impossible to define the characteristics of the skull at the basal node of the genus *Chilotherium*.

Chilotherium primigenius is the most primitive species of *Chilotherium* described so far. This species shares many exclusive characters with the other species of *Chilotherium*. For its known characters, *C. primigenius* constitutes the ancestral morphotype of the genus *Chilotherium*. Moreover, it implies that the genus itself is older. The locality with *C. primigenius* corresponds to the early Late Miocene (early and middle MN 9). But a Middle Miocene origin is probable. For example, some doubtful remains of *Chilotherium* sp. were reported from Halamagai (Xinjiang, China) by Chow (1957) and from Jiulongkou (Hebei, China) by

Chen and Wu (1976). The described material from Halamagai is only a right M1. This molar has a sharply demarcated parastyle fold, and its protocone is not constricted. As a result, this molar should belong to *Acerorhinus* instead of *Chilotherium* (Deng, 2000; Deng & Downs, 2002). Tong *et al.* (1990) also reported that there are some questionable fossils of *Chilotherium*, but they did not describe these fossils. The referred material from Jiulongkou comprises the anterior part of a young skull, the left maxillary bone of another young skull, and a P2, but they have no diagnosis of *Chilotherium*. At the moment, Zhongmajia in the Linxia Basin is the locality with the oldest undoubted remains of the genus *Chilotherium*. Because the most primitive species of *Chilotherium*, *C. primigenius* and *C. wimani*, originated in China, an East Asian origin for this genus is suggested. Heissig (1989) considered that *Chilotherium* emerged in the early Middle Miocene of South Asia with *Subchilotherium* from the lower Siwalik series. The first appearance of *C. wimani* was necessarily later than that of *C. primigenius*, and must precede that of the other species of *Chilotherium*. In Zhongmajia locality of the Linxia Basin, the bed bearing *C. wimani* remains is located above the bed containing *C. primigenius*. The earliest records of the genus *Chilotherium* outside the Linxia Basin are in western China: *C. habereri* is present in Bahe (Lantian, Shaanxi) (Liu *et al.*, 1978) at location attributed to late MN 9-10 (Qiu *et al.*, 1999).

In Europe, the first appearance of *Chilotherium* is in Pentalophos (Greece): *C. kiliasi* (Geraards & Koufos, 1990) is present at the location attributed to MN 11-12 (Heissig, 1999). Hence the dispersal of the genus *Chilotherium* towards Europe can be considered to begin with the arrival of *C. kiliasi*. This event is situated between the murid event at 9.6 Ma and *Gazella* event at 6.9 Ma (Made, 1999). During the MN 10-13 Zones, at least four species of *Chilotherium* were present in South and East Europe.

The stratigraphical position of the Linxia *Hipparion* fauna containing abundant fossils of *Chilotherium* has always been a problem. Fang *et al.* (1997) arranged the chronological position of the Linxia *Hipparion* faunas and determined their paleomagnetic ages. But there was an obvious error in this sequence, *i.e.* the first appearance of *Hipparion* in the Linxia Basin at 15.4-12.5 Ma (Middle Miocene). According to our recent field observations and correlations, the Late Miocene *Hipparion* faunas in the Linxia Basin can be divided into four levels. The bed containing the specimen of *C. primigenius* corresponds to the first *Hipparion* level, *i.e.* the early Late Miocene.

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Measures	<i>C. primigenius</i>	<i>C. wimani</i>	<i>C. xizangensis</i>
3 Distance between nasal tip and occipital crest	390	502.8 (483-528)	-
4 Distance between nasal tip and bottom of nasal notch	133.5	148.5 (132-162)	-
5 Minimal width of braincase	72	84.9 (74-91.5)	-
6 Distance between occipital crest and postorbital process	203	257.9 (246.5-267)	-
7 Distance between occipital crest and supraorbital tubercle	225.5	264.9 (214.5-289.5)	-
8 Distance between occipital crest and lacrimal tubercle	233.5	320.3 (299.5-332)	-
9 Distance between nasal notch and orbit	55.5	68.1 (60-81)	54
14 Distance between nasal tip and orbit	186	210.8 (198.5-223)	-
15 Width of occipital crest	114	151.5 (140.2-168.4)	-
16 Width between mastoid processes	~145	195.5 (184-219)	-
17 Minimal width between parietal crests	18	44.9 (29-67)	-
18 Width between postorbital processes	147	140.3 (133.3-148)	~124
19 Width between supraorbital tubercles	158	157.7 (147-164.3)	~120
20 Width between lacrimal tubercles	152	160.4 (143-184.8)	-
21 Maximal width between zygomatic arches	228	262.7 (248-280)	-
22 Width of nasal base	83	88.1 (75-98)	60
23 Height of occipital surface	113	134 (120-158)	-
25 Cranial height in front of P2	117	141.2 (121-158)	-
26 Cranial height in front of M1	138	168 (139-192)	137
27 Cranial height in front of M3	165	172 (155.5-189)	132
28 Palatal width in front of P2	42	44.3 (37.5-55.5)	-
29 Palatal width in front of M1	25	43.7 (27-57)	-
30 Palatal width in front of M3	28	56.9 (45-72)	-

Table 1. Measurements (mm) of the skull of *Chilotherium primigenius* sp. nov. and comparisons with other species of *Chilotherium*. Ten specimens of *C. wimani* were measured. Numbers in front of measuring method in Table 1 correspond with those of Guérin (1980, table 1, p. 47).

Measures	<i>C. primigenius</i>	<i>C. wimani</i>	<i>C. xizangensis</i>
1 Length	~340	471.6 (455-485)	-
9 Distance between ramuses in front of m1	29	62 (54-69)	33
10 Distance between ramuses in front of m3	30	77.3 (65-88.3)	39
11 Length of symphysis	96.5	117.5 (110-126)	108
14 Transverse diameter of condyle	76	90.5 (89-92)	-

Table 2. Measurements (mm) of the mandible of *Chilotherium primigenius* sp. nov. and comparisons with other species of *Chilotherium*. Five specimens of *C. wimani* were measured. Numbers under measurements correspond with those of Guérin (1980, table 3, p. 52).

Teeth	M1	M2	M3	p2	p3	p4	m1	m2	m3
<i>C. primigenius</i>									
L	29	33.5	36.5	19.5	26	28.5	26.5	32	37.5
W	51	51	45	13	21	24	26	29	25
<i>C. wimani</i>									
L	38.4	48.7	48.7	23.9	29.3	35.7	39.6	46.4	46.9
W	59.5	61	56.8	17.4	20	25.8	27.7	28.4	25.9
<i>C. xizangensis</i>									
L	41.2	41	35.6	25.2	29	32	36.4	39.2	40
W	50.8	48.5	41.8	18.2	24.3	22.1	23.4	20.9	18.9

Table 3. Measurements (mm) of the cheek teeth of *Chilotherium primigenius* sp. nov. and comparisons with other species of *Chilotherium*. L = Length; W = Width; the data of *C. wimani* are mean values (N = 5).

Known species of <i>Chilotherium</i>	Revised species	Distribution
<i>C. blanfordi</i> (Lydekker, 1884)	<i>Aprotodon blanfordi</i> (Lydekker, 1884)	Siwalik
<i>C. fatehjangense</i> (Pilgrim, 1910)	<i>Aprotodon fatehjangense</i> (Pilgrim, 1910)	Siwalik
<i>C. smith-woodwardi</i> (Foster-Cooper, 1915)	<i>Aprotodon smith-woodwardi</i> Foster-Cooper, 1915	Siwalik
<i>C. ibericum</i> Antunes, 1972	<i>Hispanotherium matritense</i> (Prado, 1863)	Portugal
<i>C. quintanelensis</i> Zbyszewski, 1952	<i>Hispanotherium matritense</i> (Prado, 1863)	Portugal
<i>C. zernowi</i> (Borissiak, 1915)	<i>Acerorhinus zernowi</i> (Borissiak, 1915)	Odessa
<i>C. palaeosinense</i> (Ringström, 1924)	<i>Acerorhinus palaeosinensis</i> (Ringström, 1924)	China
<i>C. hipparionum</i> (Koken, 1885)	<i>Acerorhinus hipparionum</i> (Koken, 1885)	China
<i>C. tsaidamense</i> (Bohlin, 1937)	<i>Acerorhinus tsaidamensis</i> (Bohlin, 1937)	China
<i>C. intermedium</i> (Lydekker, 1884)	<i>Subchilotherium intermedium</i> (Lydekker, 1884)	Siwalik
<i>C. tanggulaense</i> Zheng, 1980	<i>Subchilotherium intermedium</i> (Lydekker, 1884)	China
<i>C. pygmaeum</i> (Ringström, 1927)	<i>Subchilotherium pygmaeum</i> (Ringström, 1927)	China
<i>C. brancoi</i> (Schlosser, 1903)	<i>Shansirhinus brancoi</i> (Schlosser, 1903)	China
<i>C. yunnanensis</i> Tang <i>et al.</i> , 1974	<i>Shansirhinus brancoi</i> (Schlosser, 1903)	China
<i>C. tianzhuensis</i> Zheng, 1982	<i>Shansirhinus ringstromi</i> Kretzoi, 1942	China
<i>C. cornutum</i> Qiu & Yan, 1982	<i>Shansirhinus ringstromi</i> Kretzoi, 1942	China
<i>C. samium</i> (Weber, 1905)	<i>C. samium</i> (Weber, 1905)	Samos
<i>C. schlosseri</i> (Weber, 1905)	<i>C. schlosseri</i> (Weber, 1905)	Samos
<i>C. ponticum</i> (Niezabitowski, 1912)	<i>C. schlosseri</i> (Weber, 1905)	Odessa
<i>C. wegneri</i> (Andree, 1921)	<i>C. schlosseri</i> (Weber, 1905)	Samos
<i>C. kowalevskii</i> (Pavlow, 1913)	<i>C. kowalevskii</i> (Pavlow, 1913)	Odessa
<i>C. angustifrons</i> (Andree, 1921)	<i>C. kowalevskii</i> (Pavlow, 1913)	Samos
<i>C. kiliasi</i> (Geraads & Koufos, 1990)	<i>C. kiliasi</i> (Geraads & Koufos, 1990)	Pentalophos
<i>C. anderssoni</i> Ringström, 1924	<i>C. anderssoni</i> Ringström, 1924	China
<i>C. planifrons</i> Ringström, 1924	<i>C. anderssoni</i> Ringström, 1924	China
<i>C. fenhoensis</i> Tung <i>et al.</i> , 1975	<i>C. anderssoni</i> Ringström, 1924	China
<i>C. habereri</i> (Schlosser, 1903)	<i>C. habereri</i> (Schlosser, 1903)	China
<i>C. gracile</i> Ringström, 1924	<i>C. habereri</i> (Schlosser, 1903)	China
<i>C. wimani</i> Ringström, 1924	<i>C. wimani</i> Ringström, 1924	China
<i>C. xizangensis</i> Ji <i>et al.</i> , 1980	<i>C. xizangensis</i> Ji <i>et al.</i> , 1980	China
<i>C. persiae</i> (Pohlig, 1885)	<i>C. persiae</i> (Pohlig, 1885)	Maragha

Table 4. Revision of the genus *Chilotherium*