Early Eocene Chalicothere *Litolophus* with Hoof-Like Unguals

Author(s) :Bin Bai, Yuanqing Wang, and Jin Meng
Source: Journal of Vertebrate Paleontology, 31(6):1387-1391. 2011.
Published By: The Society of Vertebrate Paleontology
URL: http://www.bioone.org/doi/full/10.1080/039.031.0615

Journal of Vertebrate Paleontology 31(6):1387–1391, November 2011

SHORT COMMUNICATION

EARLY EOCENE CHALICOTHERE *LITOLOPHUS* WITH HOOF-LIKE UNGUALS

BIN BAI,[1] YUANQING WANG,[*,1] and JIN MENG[2]; [1]Key Laboratory of Evolutionary Systematics of Vertebrates, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, P.O. Box 643, Beijing 100044, China, baibin@ivpp.ac.cn; wangyuanqing@ivpp.ac.cn; [2]Division of Paleontology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024, U.S.A., jmeng@amnh.org

The herbivorous Chalicotheriidae from Oligocene to Pleistocene are unique among perissodactyls in possessing claws rather than hooves (Coombs, 1983). The ungual phalanges of early chalicotheres, however, were almost unknown previously due to a sparse fossil record. Lucas and Schoch (1989) briefly mentioned that the Eocene chalicothere *Grangeria canina* possesses deep, narrow, and shallow fissured claws, but did not provide any more descriptions or illustrations. Recently, new specimens of the early Eocene chalicothere *Litolophus gobiensis*, including unguals and other parts of multiple skeletons, were unearthed from the Arshanto Formation in the Erlian Basin, Inner Mongolia, China (Meng et al., 2007; Bai et al., 2010; Wang et al., 2010). The *Litolophus* assemblage was caused by a catastrophic event, and *L. gobiensis*, represented by at least 24 individuals, was the most abundant larger mammal in the quarry (Bai et al., 2011). The species retains a tetradactyl hand with functional phalanges from digit II to digit V, which is a plesiomorphic character among perissodactyls. Phylogenetic analysis shows that *L. gobiensis* was a primitive member of the clade and basal to all other known chalicotheres apart from earliest Eocene forms (Bai et al., 2010). These new materials shed light on the ungual evolution of chalicotheres.

MATERIALS AND METHODS

Thirty isolated ungual phalanges are preserved in the assemblage, but most of them are immature and susceptible to breakage (IVPP V 16187.1–21). The material includes two mature unguals of digit III (V 16187.1–2), 12 mature and/or immature unguals of digit II (V 16187.3–14), five unguals of digit IV (V 16187.15–19), two immature unguals of manus digit V (V 16187.20–21), and nine unguals indeterminate to digit (V 16187.22–30). An immature right articulated pes of *L. gobiensis* preserves the ungual phalanges of digits II through IV (V 16200).

Institutional Abbreviation—IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing.

Anatomical Abbreviations—da, distal angle; **dp**, dorsal process; **lf**, lateral foramen; **mf**, medial foramen; **sn**, sagittal notch; **sp**, subungual process; **vf**, volar foramen; **ph2f**, phalanx 2 facet.

MORPHOLOGICAL DESCRIPTION

Ungual Phalanx of Digit III

An ungual phalanx of digit III (V 16187.1) referred to a mature pes is well preserved. The proximal facet for phalanx 2 is rectangular in outline, wider than high, concave dorsoventrally, and divided by a rather weak median ridge into two nearly equal portions (Fig. 1A).

The proximal border of the dorsal surface is slightly arched (Fig. 1B), and most of the dorsal surface is rough and porous. The distally placed sagittal notch is short and shallow, similar to a trough cutting the dorsodistal portion of the bone. A large dorsal foramen is located on either side of the sagittal notch, near the distal margin. The distal angles are prominent and pointed at the ends, whereas proximal angles are absent.

The dorsal part of the distal end is covered by irregular foramina or grooves, except where the surface is interrupted by the sagittal notch (Fig. 1C). The plantar part of the distal end, which is roughly lenticular, convex, and almost smooth, would have served to insert the deep digital flexor tendon, and its two extremities are pointed and separated from the distal angles by a notch. The plantar part of the distal end extends onto the plantar surface of the bone and makes up the distal portion of the plantar surface.

Along the proximal border of the plantar surface there is a rather narrow strip of smooth area that would have articulated with the distal sesamoid (Fig. 1D). Below the articular area for the distal sesamoid is a concave strip bearing some small foramina. The distal part of the plantar surface is occupied by a convex, smooth surface, continuous with the plantar portion of the distal end without a prominent boundary.

In side view, the ungual is proximodistally short, and a foramen is present at the distoplantar corner (Fig. 1E–F). The lateral foramen is more prominent and larger than the medial one. On the lateral and medial sides just below the proximal surface, a narrow smooth depression marks the attachment site of the collateral ligament.

The ungual phalanx of digit III of the immature right articulated pes (V 16200) is similar to the mature unguals of digit III, but it differs from the mature ones in that the sagittal notch and distal angles are less well developed, and in that the plantar part of distal end is less convex (Fig. 2A–F). Furthermore, the proximal border of the dorsal surface is more arched in the immature individual than in the mature one, and the dorsal surface is slightly less transversely extended in the immature individual. A supposed ungual phalanx of digit III of a mature manus (V 16187.2) is broken on its lateral distal angle; however, it differs from that of pes in that the former has a less developed distal angle, less transversely extended contours both on the proximal and dorsal surfaces, and a nearly straight proximal border on the dorsal surface.

Ungual Phalanx of Side Digit

Except for a right articulated immature pes (V 16200), which preserves side unguals of digits II and IV (Fig. 2), most of the available side unguals are isolated and cannot be directly assigned to definite positions. However, their positions can be deduced based on the immature articulated pes. The immature ungual of digit II of the pes (V 16200) is similar to that of digit III in having side foramina, a well-developed sagittal notch, and a dorsoventrally concave proximal facet, and in that the bone does not taper distally (Fig. 2G–L). However, the ungual of digit II differs from that of digit III in that (1) the proximal surface of the former is less transversely broad and is divided by a moderately distinct median ridge into a larger medial portion and a smaller

*Corresponding author.

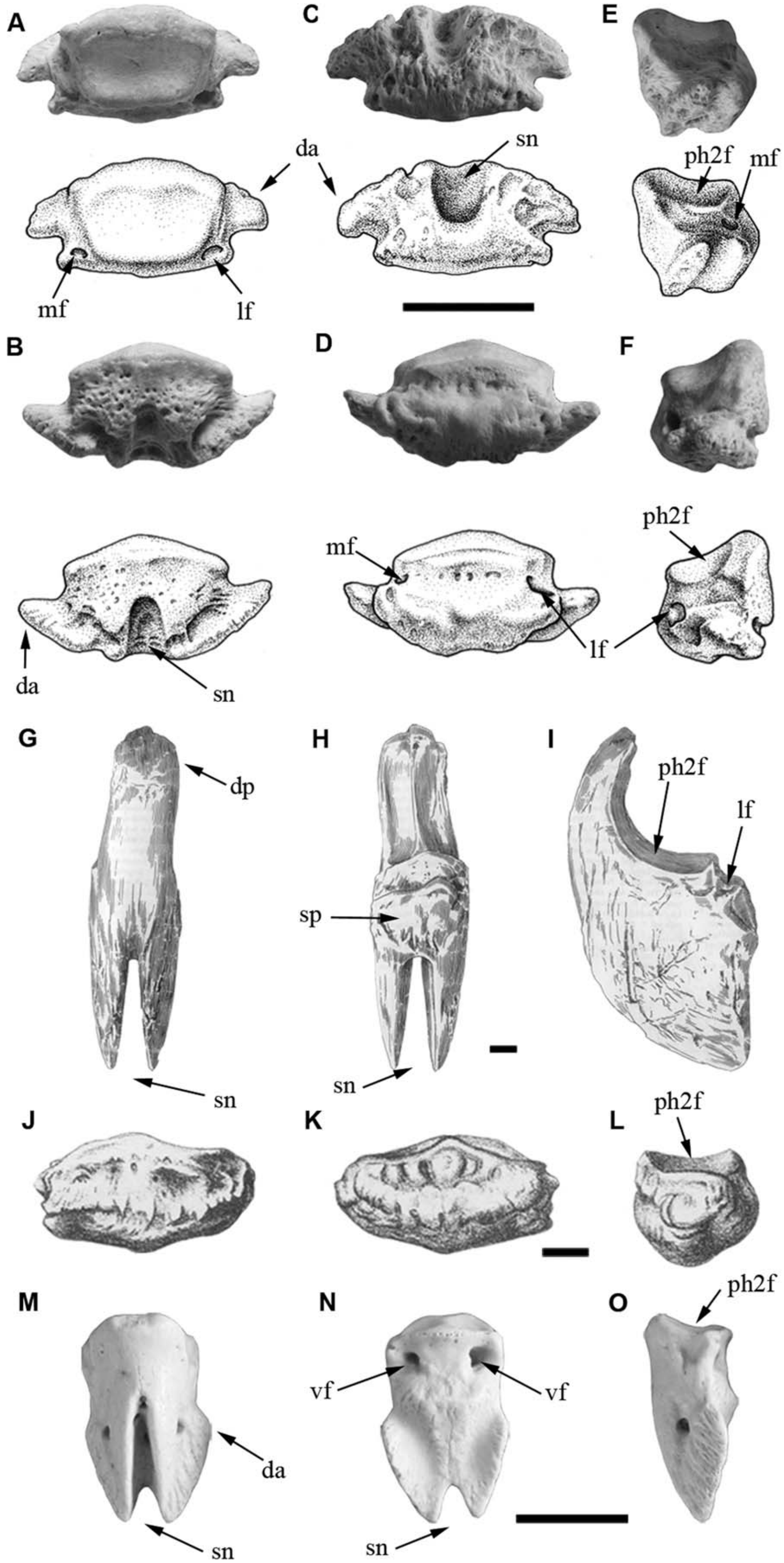

FIGURE 1. Comparison of ungual phalanges between *Litolophus gobiensis* and compared perissodactyls. **A**–**F**, ungual phalanx of pes digit III of *L. gobiensis* (IVPP V 16187.1) in **A**, proximal, **B**, dorsal, **C**, distal, **D**, plantar, **E**, medial, and **F**, lateral views. Ungual phalanx of digit II of Chalicotheriinae *Anisodon grande* (**G**–**I**, after Zapfe, 1979:fig. 99), Brontotheriidae *Brontops robustus* (**J**–**L**, after Osborn, 1929:pl. 217), and of digit III of Tapiroidea *Lophialetes* (**M**–**O**). **G**, **J**, **M**, dorsal view; **H**, **K**, **N**, volar/plantar view; **I**, **L**, **O**, side view. Scale bars equal 10 mm.

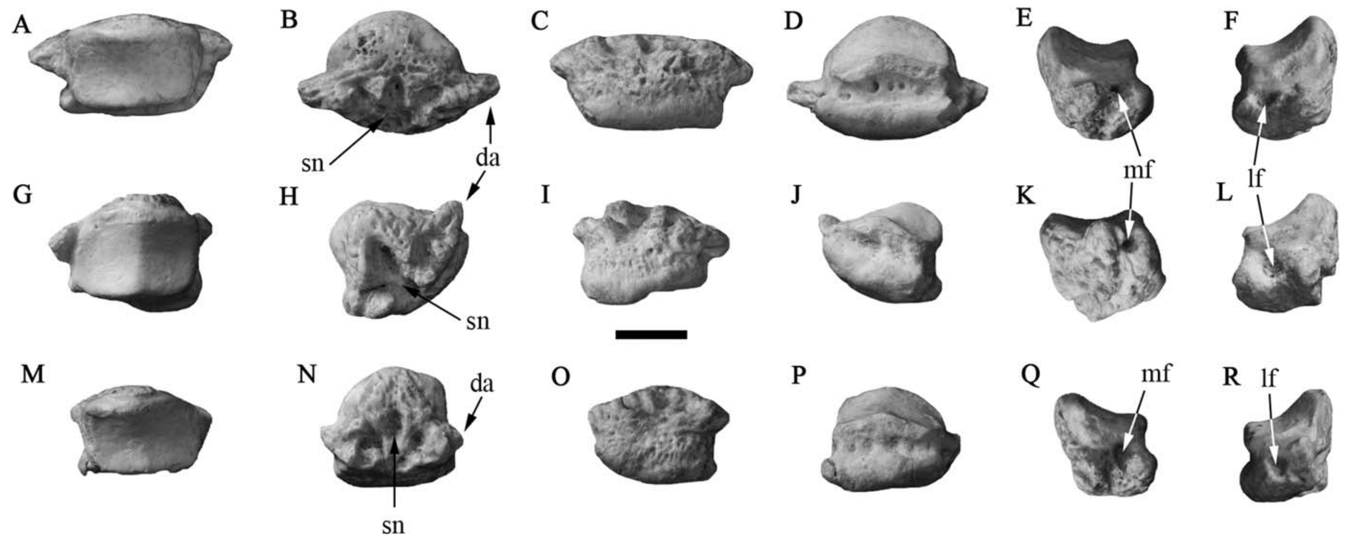

FIGURE 2. Ungual phalanges from digits II to IV of *Litolophus gobiensis* from an immature articulated right pes (IVPP V 16200). Ungual phalanx of digit III (**A**–**F**), digit II (**G**–**L**), and digit IV (**M**–**R**). **A**, **G**, **M**, proximal view; **B**, **H**, **N**, dorsal view; **C**, **I**, **O**, distal view; **D**, **J**, **P**, plantar view; **E**, **K**, **Q**, medial view; **F**, **L**, **R**, lateral view. Scale bar equals 5 mm.

lateral portion; the median ridge is somewhat laterally inclined (Fig. 2G); (2) the distal and proximal surfaces of the former converge on the medial side, giving the dorsal surface a roughly triangular shape (Fig. 2H); (3) the dorsal surface of the former slopes gradually downward in the medial direction, so that the lateral side of the sagittal notch is higher than the medial one (Fig. 2H, I); and (4) on the ungual of digit II, the medial distal angle is better developed than the lateral one (Fig. 2H). Several mature unguals of digit II are almost identical to the immature ones in their proportions and qualitative characters, despite their larger size. However, the differences between the unguals of digit II of the manus and those of pes are not obvious.

The immature ungual of pes digit IV is similar to that of digit II in having asymmetric characters (Fig. 2M–R). However, the proximal surface of ungual of digit IV is divided by a median ridge into a smaller medial portion and a larger lateral portion (Fig. 2M). The dorsal surface of the ungual of digit IV is more rectangular than triangular and is less distinctly slanted than that of digit II (Fig. 2N). The sagittal notch of the ungual of digit IV is weak and pit-like, and the distal angles are rather weak, consisting only of slight prominences (Fig. 2N–O). Both the medial and lateral foramina of the ungual of digit IV are equally well developed (Fig. 2Q, R). A mature ungual of digit IV of the pes (V 16187.15) differs from the immature one in that the sagittal notch and dorsal foramina are better developed, and that a lateral foramen is sometimes hardly discernable. Four presumed unguals of digit IV of manus (V 16187.16–19) are different from those of the pes in having more symmetric and transversely extensive proximal and dorsal surfaces, and shallower sagittal notches.

Two presumed unguals of manual digit V are relatively poorly preserved (V 16187.20–21). The bone is mainly similar to the other side unguals in having a distinct sagittal notch and side foramina. However, the proximal surface of the ungual of digit V is higher than wide, whereas those of the other unguals are wider than high; the dorsal surface of the ungual of digit V has an approximately square outline.

COMPARISON AND DISCUSSION

Comparisons between the ungual phalanges of *Litolophus* and those of various other perissodactyls, including derived chalicotheres, brontotheres, tapiroids, rhinocerotoids, and equoids, show that the unguals of *Litolophus* are different from those of derived chalicotheres, but display a combination of hoof-like features present in other perissodactyl groups.

The ungual phalanges of *Litolophus* differ from those of derived chalicotheres in being proportionally transversely broad and longitudinally short (Fig. 3) and in lacking deep fissures, prominent dorsal processes and subungual processes (Fig. 1G–I; Table 1) (Coombs, 1978, 1983; Zapfe, 1979; Anquetin et al., 2007). In addition, the ungual phalanx of *Litolophus* has well-developed distal angles and a shallow proximal articular surface for the phalanx 2, whereas the claw of derived chalicotheres lacks distal angles and has a conspicuous curved

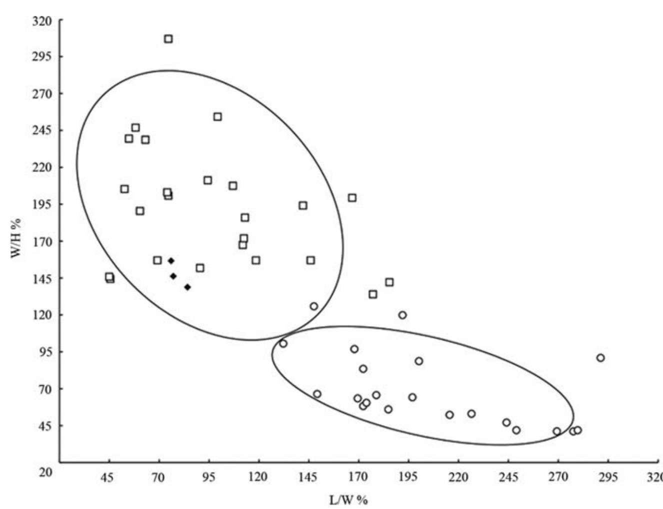

FIGURE 3. Scatter diagram of length/width (L/W) ratio vs. width/height (W/H) ratio for ungual phalanges of derived chalicotheres (open circles) and various other perissodactyls (open squares). Three median ungual phalanges of *Litolophus gobiensis* are shown (filled rhombuses). *Litolophus* falls into the 95% confidence ellipse containing data points of non-chalicothere hooves. See Supplementary Data 1 for original data.

TABLE 1. Comparisons of ungual characters between *Litolophus* and some other perissodactyls.

	Litolophus	*Anisodon*	*Brontops*	*Lophialetes*
Sagittal notch	Prominent	Deeply fissured	Absent	Prominent
Distal angle	Present	Absent	Absent	Present
Distal end	Blunt	—	Blunt	Thin
Position of ventral foramina	Lateral	Lateral	Lateral	Ventral
Dorsal process	Absent	Present	Absent	Absent
Subungual process	Absent	Present	Absent	Absent

proximal articular surface that indicates extensive dorsoventral flexibility of the claw. The foramina, presumably homologous to volar foramina of hooves in most other perissodactyls for transmitting digital arteries (Sisson et al., 1975), are laterally placed in the ungual phalanges of *Litolophus*, probably in association with the proximodistal shortening of the bones. The similar placement of the foramina in derived chalicotheres is instead associated with transverse compression of the bone.

Litolophus and hoofed perissodactyls retain the above listed primitive features and thus resemble one another, whereas derived chalicotheres have modified their unguals from this basal condition. Ungual phalanges of *Litolophus* are characterized by a combination of hoof-like features that distinguish them from typical hooves of other perissodactyls: proximodistally shortened, a blunt distal end, a short and shallow sagittal notch, and prominent distal angles. In addition, the volar foramina of normal-hoofed perissodactyls are ventrally positioned and lead into semilunar canals within the bones, transmitting digital arteries (Sisson et al., 1975).

Proximodistal shortening of the ungual phalanges are also present in some hoofed perissodactyls, such as the brontotheres *Rhinotitan* and *Brontops* and the amynodontid *Lushiamynodon* (Osborn, 1929; Xu, 1966; Wang, 1982) (Fig. 1J–L). In these forms, the unguals are blunt anteriorly and the volar foramina are laterally positioned (Table 1). On the other hand, the sagittal notches and distal angles are poorly developed or absent in these forms. For those that have a typical hoof, including most tapiroids (e.g., *Lophialetes* and *Schlosseria*) (Fig. 1M–O), some equoids (e.g., *Hyracotherium*), and some rhinocerotoids (e.g., *Hyrachyus* and *Juxia*) and brontotheres (e.g., *Palaeosyops*) (Osborn, 1929; Radinsky, 1965; Qiu and Wang, 2007), the development of sagittal notches and distal angles is generally similar to that of *Litolophus*. However, exceptions occur. For example, the hooves of *Subhyracodon* and *Equus* lack the sagittal notches (Scott, 1941), showing a mosaic distribution of the characters.

Figure 3 plots the length/width (L/W) ratio against the width/height (W/H) ratio for the unguals of derived chalicotheres and some other perissodactyls (Supplementary Data 1; available online at www.vertpaleo.org/jvp/JVPcontents.html). The unguals of derived chalicotheres (open circles) are concentrated in the lower right of the diagram, whereas those of non-chalicothere perissodactyls (open squares) are concentrated in the upper left. In Figure 3 the claws of derived chalicotheres have L/W ratios larger than 120% because of their laterally compressed morphology, whereas those of other perissodactyls usually have values of less than 120%. The claws of derived chalicotheres have W/H ratios smaller than 120%, and in most cases smaller than 95%. By contrast, the W/H ratios of other perissodactyls are almost all larger than 120%, and most of them are even larger than 145%. *Litolophus gobiensis* unguals clearly fall into a 95% confidence ellipse drawn with respect to the data points representing non-chalicothere hooves.

Because *Litolophus* is basal to all other known chalicotheres apart from earliest Eocene forms (Bai et al., 2010), the ungual morphology of *Litolophus* demonstrates that the transformation from hooves to claws in chalicotheres took place after the divergence of the early Eocene *Litolophus*. The claws of derived chalicotheres is an adaptation probably associated with bipedal browsing (Coombs, 1983), a behavior that was not present in *Litolophus*.

ACKNOWLEDGMENTS

We thank Chuankui Li, Zhanxiang Qu, Tao Deng, Xijun Ni, Xun Jin, Qian Li, Ping Li, Haowen Tong, Shuhua Xie, Wei Zhou, Shijie Li, C. Beard, M. Coombs, and L. Holbrook for support and discussion; Wei Gao and Yong Xu for the photography and drawings, respectively; and C. Sullivan for the improvement of the English in the manuscript. The review comments of M. Coombs, P. O. Antoine, and editors greatly improved the final manuscript. This work was supported by the National Natural Science Foundation of China (40532010, 41002009, and J 0930007), the Major Basic Research Projects of MST of China (2006CB806400), the Key Laboratory of Evolutionary Systematics of Vertebrates, CAS (2010LESV006), and NSF grant (BCS-0820603).

LITERATURE CITED

Anquetin, J., P. O. Antoine, and P. Tassy. 2007. Middle Miocene Chalicotheriinae (Mammalia, Perissodactyla) from France, with a discussion on chalicotheriine phylogeny. Zoological Journal of the Linnean Society 151:577–608.

Bai, B., Y. Q. Wang, and J. Meng. 2010. New craniodental materials of *Litolophus gobiensis* (Perissodactyla, "Eomoropidae") from Inner Mongolia, China, and phylogenetic analyses of Eocene chalicotheres. American Museum Novitates 3688:1–27.

Bai, B., Y. Q. Wang, J. Meng, X. Jin, Q. Li, and P. Li. 2011. Taphonomic analyses of an early Eocene *Litolophus* (Perissodactyla, Chalicotherioidea) assemblage from the Erlian Basin, Inner Mongolia, China. PALAIOS 26:187–196.

Coombs, M. C. 1978. Reevaluation of early Miocene North American *Moropus* (Perissodactyla, Chalicotheriidae, Schizotheriinae). Bulletin of Carnegie Museum of Natural History 4:1–62.

Coombs, M. C. 1983. Large mammalian clawed herbivores: a comparative study. Transactions of the American Philosophical Society 73(7):1–96.

Lucas, S. G., and R. M. Schoch. 1989. Taxonomy and biochronology of *Eomoropus* and *Grangeria*, Eocene chalicotheres from the western United States and China; pp. 422–437 in D. R. Prothero and R. M. Schoch (eds.), The Evolution of Perissodactyls. Clarendon/Oxford University Press, New York/Oxford.

Meng, J., Y. Q. Wang, X. J. Ni, K. C. Beard, C. Sun, Q. Li, X. Jin, and B. Bai. 2007. New stratigraphic data from the Erlian Basin: implications for the division, correlation, and definition of Paleogene lithological units in Nei Mongol (Inner Mongolia). American Museum Novitates 3570:1–31.

Osborn, H. F. 1929. Titanotheres of ancient Wyoming, Dakota, and Nebraska. United States Geological Survey Monographs 55:1–894.

Qiu, Z. X., and B. Y. Wang. 2007. Paracerathere fossils of China. Palaeontologia Sinica, new series C 29:1–396. [Chinese 1–248; English 249–386]

Radinsky, L. B. 1965. Early Tertiary Tapiroidea of Asia. Bulletin of American Museum of Natural History 129:181–264.

Scott, W. B. 1941. The mammalian fauna of the White River Oligocene. Part 5. Perissodactyla. Transactions of the American Philosophical Society 28:747–980.

Sisson, S., J. D. Grossman, and R. Getty. 1975. The Anatomy of Domestic Animals. 5th edition. W. B. Saunders Company, Philadelphia, Pennsylvania, 2480 pp.

Wang, B. 1982. [Osteology and phylogenetic relationships of *Rhinotitan mongoliensis*]. Academia Sinica Institute of Vertebrate Paleontology and Paleoanthropology Memoirs 16:1–75. [Chinese]
Wang, Y.-Q., J. Meng, K. C. Beard, Q. Li, X.-J. Ni, D. L. Gebo, B. Bai, X. Jin, and P. Li. 2010. Early Paleogene stratigraphic sequences, mammalian evolution and its response to environmental changes in Erlian Basin, Nei Mongol, China. Science China: Earth Sciences 53:1918–1926.
Xu, Y. X. 1966. Amynodonts of Inner Mongolia. Vertebrata PalAsiatica 10:123–162. [Chinese 123–155; English 155–162, 190]
Zapfe, H. 1979. [*Chalicotherium grande* (BLAINV.) aus der miozänen Spaltenfüllung von Neudorf an der March (Devinska Nova Ves, Tschechoslwakei)]. Neue Denkschriften des Naturhistorischen Museums in Wien 2:1–282. [German]

Submitted December 29, 2010; revisions received June 11, 2011;
accepted August 2, 2011.
Handling editor: Jessica Theodor.