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Biostratigraphy and Diversity of Paleogene Perissodactyls from the Erlian Basin of Inner Mongolia, China

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ABSTRACT

Extant perissodactyls (horses, rhinos, and tapirs) comprise a small portion of living mammals, but fossil perissodactyls were more diverse and commonly dominated Paleogene faunas. Unfortunately, the taxonomy and distribution of some Chinese Paleogene perissodactyls remain controversial and unclear, hampering the correlation of Asian paleofaunas with paleofaunas from other continents. Here we clarify the temporal and spatial distribution of Paleogene perissodactyl species from the Erlian Basin based on published specimens, archives, and our recent fieldwork. The strata of the Erlian Basin range nearly continuously from the late Paleocene to the early Oligocene, and almost all Eocene Asian Land Mammal Ages (ALMA) are based on corresponding faunas from the Erlian Basin. We revise the most complete section of deposits at Erden Obo (= Urtyn Obo) that range in age from the late Paleocene to the early Oligocene in the Erlian Basin, and correlate it with other type formations/faunas in the basin based mainly on the perissodactyl biostratigraphy and lithostratigraphy. Furthermore, we discuss perissodactyl faunal components and their diversity from the early Eocene to the early Oligocene in the Erlian Basin, as well as the

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correlation between middle Eocene ALMAs and North American Land Mammal Ages based on perissodactyl fossils. The general decrease in perissodactyl diversity from the middle Eocene to the late Eocene can probably be attributed to a global climatic cooling trend and related environmental changes. The diversity of perissodactyls declined distinctly during the Eocene-Oligocene Transition, when global average temperatures dropped considerably.

INTRODUCTION

The Erlian Basin is located in central Inner Mongolia (Nei Mongol), near the China-Mongolia border (Jiang, 1983; Wang et al., 2012). Deposits of the Erlian Basin range nearly continuously from the late Paleocene to the Oligocene, and produce a large number of fossil mammals and other vertebrates. The lithostratigraphic units in the Erlian Basin include the Houldjin, Arshanto, Irdin Manha, Tukhum, Ulan Shireh, Shara Murun, Ulan Gochu, and Baron Sog formations, named by the Central Asiatic Expedition (CAE), as well as the Nomogen Formation and other lithological units that were proposed by later researchers (Jiang, 1983; Wang et al., 2012). The basin was first investigated by the Russian geologist V.A. Obruchev in 1892, and then during the 1920s, the CAE of the American Museum of Natural History extensively explored the area over five field seasons (fig. 1) (Andrews, 1932; Berkey and Morris, 1927). After the CAE suspended its work after 1930, the Sino-Soviet Paleontological Expedition (SSPE) conducted investigations in 1959–1960 the fossiliferous deposits of the Erlian Basin (Chow and Rozhdestvensky, 1960), followed by the Regional Geological Survey of the Nei Mongol Autonomous Region (1960s–1970s) (Jiang, 1983) and the Institute of Vertebrate Paleontology and Paleoanthropology, in collaboration with the American Museum of Natural History and Carnegie Museum of Natural History, from the 1980s to the present time (Meng et al., 2007; Wang et al., 2010; Jin, 2012; Wang et al., 2012). Derived from that extensive work, the Eocene Asian Land Mammal Ages (ALMA) were established based mainly on the mammalian faunas from the Erlian Basin (Romer, 1966; Tong et al., 1995; Wang et al., 2007; Vandenberghe et al., 2012).

The Eocene mammalian faunas of the Erlian Basin are dominated by diverse perissodactyls (Tong et al., 1995; Wang et al., 2007). Perissodactyls from the Erlian Basin consist of members of Tapiroidea, Rhinocerotoidea, Brontotheriidae, and Chalicotherioidea. Since the first report on perissodactyl paraceratheres from Houldjin (Osborn, 1923a), numerous studies, including many papers and some monographs, have contributed to our knowledge of perissodactyls based on the abundant, relatively complete material from the Erlian Basin. The brontotheres were reviewed by Granger and Gregory (1943) and Mihlbachler (2008) on the basis of numerous, complete skulls in the CAE collection. Wang (1982) described a skeleton of the brontothere *Rhinotitan mongoliensis* in detail based on material in the SSPE collection from Ula Usu. Radinsky (1965, 1967) studied the tapiroids and hyracodontids from the Paleogene of Asia based principally on the CAE collection. Xu (1966) analyzed many amynodont fossils collected by the SSPE from Inner Mongolia. Qiu and Wang (2007) reviewed the Asian Paraceratheriidae and studied a nearly complete skeleton of *Juxia* from Ula Usu. However, some perissodactyls from various localities in the Erlian Basin, particularly specimens in the CAE collection, were reported from horizons and formations that had been misinterpreted because of the complexity

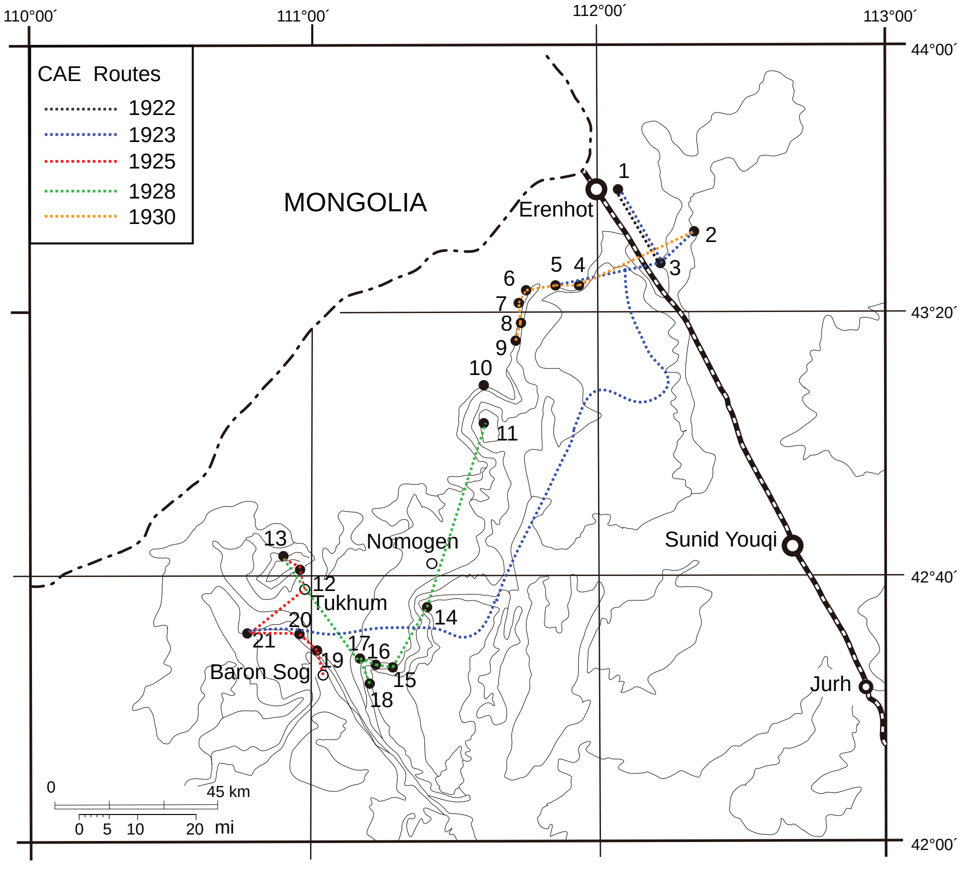


FIG. 1. Paleogene fossil localities in the Erlian Basin of Inner Mongolia, China, and the related routes of Central Asiatic Expeditions during 1920s (modified from Jiang, 1983; Mao and Wang, 2012; Wang et al., 2012). **1,** Houldjin; **2,** Arshanto; **3,** Irdin Manha; **4,** Daoteyin Obo (= Overnight Camp, 5 mi east of Camp Margetts); **5,** Duheminboerhe (= Camp Margettes); **6,** Nuhetingboerhe (= 6 mi west of Camp Margetts); **7,** Wulanboerhe; **8,** Huheboerhe (= 7 mi west and southwest [235°] of Camp Margetts); **9,** Chaganboerhe (= 10 mi southwest of Camp Margetts); **10,** Bayan Ulan; **11,** Nom Khong (= Holy Mesa); **12,** Wulantaolegai (= Viper Camp, 4 mi north of Tukhum Lamasery); **13,** Wulanhuxiu (= Chimney Buttes, 8 mi north of Tukhum Lamasery); **14,** Erden Obo (= Urtyn Obo); **15,** Ganggan Obo (= Ulan Shireh Obo); **16,** Heretu (= Spring Camp); **17,** Bayan Obo (= Twin Obos); **18,** Jhama Obo; **19,** Xilin Nor North (= 4 mi north of Baron Sog Lamasery); **20,** Ulan Gochu (= 8 mi north of Baron Sog Lamasery); **21,** Ula Usu. The black-and-white dashed line represents railway.

of correlating terrestrial stratigraphic sections. For instance, the names "Irdin Manha Formation" and "Houldjin Formation" applied by the CAE in the Huheboerhe area (Camp Margetts and neighboring areas) are mostly considered today to be Arshanto and Irdin Manha formations, respectively (Meng et al., 2007). On the other hand, most CAE specimens fortunately retain an association between their field numbers and related field notes, which indicate more specific, accurate layers in the local stratigraphic sections (Meng et al., 2007). Over the past decade, we have recovered many new perissodactyl fossil specimens in the Erlian Basin, and detailed studies of most of them are ongoing. Here, we clarify the distributions of the Paleogene perissodactyls at specific levels from the Erlian Basin based on published specimens, archives, and the preliminary results of our recent fieldwork (appendices 1, 2). In this paper, we focus on biostratigraphic and lithostratigraphic correlations rather than the morphology of perissodactyls from the Erlian Basin. Additionally, a revised correlation of the Eocene ALMAs with their corresponding NALMAs is proposed based mainly on perissodactyl fossils. It also worth noting that a decrease in perissodactyl diversity from the middle Eocene to the early Oligocene likely can be attributed to a cooling trend of global climatic change over that period of time.

MATERIAL AND METHODS

The perissodactyl fossils from the Erlian Basin are housed mainly at the Division of Paleontology, American Museum of Natural History (AMNH), and in the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP). A few CAE collections also are curated in the Field Museum (but sent by AMNH), and some CAE fossils that were sent to the Chinese Geological Survey Museum are missing. The Paleontological Institute of the Russian Academy of Sciences also houses some SSPE specimens from the Erlian Basin.

We checked field numbers of CAE specimens as recorded in Granger's CAE field notes that are stored in the AMNH Library. Those field numbers usually indicate specific and accurate horizons where the specimens were collected, contrasting with the lithological formations that sometimes have been misinterpreted or are otherwise misleading. Although some beds or formations recorded in the field notes were misinterpreted, we still use their original information, denoted with quotation marks. For example, the fossil-bearing layers from Wulanhuxiu originally were interpreted as "Shara Murun beds" in 1925, rather than the Ulan Shireh Formation. In some cases, some specimens' field numbers were not recorded in Granger's field notes, but rather on the labels associated with specimens, and a few specimens probably lack field numbers. On the other hand, the field numbers of a few specimens that were surface collected can be misleading, as exemplified by a single individual of *Schizotherium* recorded from different horizons with different field numbers (Radinsky, 1964a; Coombs, 1978).

RESULTS

Tapiroidea Gill, 1872

Lophialetidae Matthew and Granger, 1925c

Minchenoletes Wang et al., 2011

Wang et al. (2011) erected a new genus and species, *Minchenoletes erlianensis*, from the upper part of the Nomogen Formation at Nuhetingboerhe and Wulanboerhe (fig. 1). The specimens attributed to that taxon include maxillae, mandibles, and isolated teeth, and were unearthed from the NM-3 and 4 horizons of the Bumbanian ALMA.

Schlosseria Matthew and Granger, 1926

Only one species of *Schlosseria*, *S. magister*, has been named from the basin (Matthew and Granger, 1926). The holotype (AMNH FM 20241) was unearthed from the Arshanto Formation, about 7 mi north of the Telegraph Line (fig. 1). Radinsky (1965) assigned additional dental and postcranial material to *Schlosseria* cf. *S. magister* from Huheboerhe area. Those localities include Duheminboerhe, Daoteyin Obo, Huheboerhe, and Chaganboerhe. Our recent work confirms the presence of *Schlosseria magister* at Huheboerhe (Li and Wang, 2010), which ranges from As-1 to As-6 fossil-bearing horizons and was considered restricted to the Arshanto Formation. However, Radinsky (1965) also considered AMNH FM 81787 and 81788 as *Schlosseria* cf. *S. magister* from "?Houldjin gravels" (i.e., Irdin Manha Formation) at Chaganboerhe.

Radinsky (1965) reported a lower jaw with p2–m2 of ?*Schlosseria* (AMNH FM 26139) from "?Shara Murun beds" at Erden Obo (Urtyn Obo), and the fossil-bearing bed is probably equivalent to the "Basal White." Li and Wang (2010) described a partial skull of *S. magister* (IVPP V 16573) from the "Basal White" of Erden Obo. Our recent fieldwork also recovered some *Schlosseria* specimens from the basal layers at Wulanhuxiu, indicating the presence of Arshantan deposits in the section.

Lophialetes Matthew and Granger, 1925c

Only one species of *Lophialetes*, *L. expeditus*, is known from the Erlian Basin (fig. 2A) (Matthew and Granger, 1925c). The holotype (AMNH FM 19163) was found in the Irdin Manha Formation on the Irdin Manha escarpment. Radinsky (1965) also reported the species from both the "Irdin Manha" (i.e., Arshanto) and "Houldjin" (i.e., Irdin Manha) beds in the Huheboerhe area. However, he considered all these specimens as likely deriving from a single horizon. This proposal was supported by Li and Wang (2010) and Wang et al. (2010), who restricted *L. expeditus* to the IM-1 and IM-2 horizons of the Irdin Manha Formation.

Radinsky (1965) also reported *Lophialetes expeditus*? from the Ulan Shireh Formation at Wulantaolegai and Wulanhuxiu. These specimens are slightly smaller than Irdin Manha individuals of *L. expeditus*. He further assigned several larger specimens (AMNH FM 81687, 81690, and 81681) to *Lophialetes* sp. from the same bed at Wulanhuxiu (Radinsky, 1965). Those specimens are approximately 20% to 25% larger than specimens of *L. expeditus*? from the same bed, and ~12% larger than Irdin Manha fossils of *L. expeditus*.

Radinsky (1965) assigned several crushed skulls, jaws, and foot bones (AMNH FM 22091–22095) to *Lophialetes expeditus*? from the Tukhum Formation, which is overlain by the Shara Murun Formation at Ula Usu. He considered these specimens the same as Ulan Shireh *L. expeditus*? individuals. A lower jaw with p2–m2 (AMNH FM 26138) from "?Shara Murun beds" at Erden Obo was referred to *Lophialetes* sp., which corresponds in size to the larger Ulan Shireh *Lophialetes* fossils (Radinsky, 1965).

Zhongjianoletes Ye, 1983

Only one species of *Zhongjianoletes*, *Z. chowi*, known from a left mandible with a partial symphysis (IVPP V 6671), is known from the Ulan Shireh Formation at North Mesa (Ye, 1983). The species is very similar to *Lophialetes expeditus*, but is larger and lacks the p1 and probably incisors. Ye (1983) further considered that specimens referred to *Lophialetes* sp. by Radinsky (1965) from the same locality should belong to *Z. chowi*. Ye (1983) assigned some isolated M3s to *Zhongjianoletes* sp., which corresponds to the size of *Z. chowi* from the same horizon.

Simplaletes Qi, 1980

Two species of *Simplaletes*, *S. sujiensis* and *S. ulanshirehensis*, are known from the Irdin Manha and Ulan Shireh, respectively (Qi, 1980). *Simplaletes sujiensis* was found in the Irdin Manha Formation, and *S. ulanshirehensis* was discovered in the Ulan Shireh Formation in 1959 by SSPE. Both of those species preserve only lower jaws with relatively heavily worn teeth, and lack the p1. Lucas et al. (1997) considered *Simplaletes* to be a junior synonym of *Schlosseria*.

Breviodon Radinsky, 1965

Two species of *Breviodon*, *B. acares* and *B.*? *minutus*, are known from the Wulanhuxiu and Irdin Manha, respectively (Radinsky, 1965). The holotype of *B. acares* is a mandible (AMNH FM 26113) characterized by the absence of p1–2 and it is about 30% smaller than Ulan Shireh material of *Lophialetes expeditus*?. Radinsky (1965) assigned a fragmentary skull (AMNH FM 81751) to *Breviodon* cf. *B. acares* from the "Irdin Manhan beds" at Huheboerhe. However, this specimen more likely was recovered from the Arshanto Formation instead of the "Irdin Manha Formation." A lower jaw with dp4–m2 (AMNH FM 81836) from the same locality may be conspecific with the fragmentary skull (Radinsky, 1965). Reshetov (1975) erected a new genus *Parabreviodon* based on AMNH FM 81751 as the generic type. A lower jaw (AMNH FM 26115, field no. 645) from Wulanhuxiu and a few isolated teeth (AMNH FM 81839) from the "Irdin Manha beds" (i.e., the Arshanto Formation) at Daoteyin Obo, respectively, were assigned to ?*Breviodon* based on inadequate material (Radinsky, 1965).

Radinsky (1965) reassigned the holotype of "*Lophialetes*" *minutus* (an isolated left upper molar, AMNH FM 20139) and some miscellaneous teeth (AMNH FM 81721A, 81721B, 81722) from the Irdin Manha Formation of the Irdin Manha escarpment to *Breviodon*? *minutus*. However, Reshetov (1979) considered *Breviodon acares* as a junior synonym of *B. minutus* based on the associated upper and lower cheek teeth. This notion was followed by Qi (1987), who also reported the species from the Arshanto Formation at Huheboerhe and Wulanboerhe.

Rhodopagus Radinsky, 1965

Two species of *Rhodopagus*, *R. pygmaeus* and *R.*? *minimus*, are known from North Mesa and Ula Usu, respectively (Radinsky, 1965). *Rhodopagus pygmaeus* is known mainly from the Ulan Shireh Formation, and Radinsky (1965) also assigned a couple of specimens (AMNH FM 81842, 81843) to ?*R. pygmaeus* from the type Irdin Manha bed. Radinsky (1965) transferred *Caenolophus*? *minimus* (AMNH FM 20310) from the Shara Murun Formation at Ula Usu to *Rhodopagus*? *minimus* based on its short trigonid and reduced cristid obliqua. Lucas and Schoch (1981) further considered that *Rhodopagus pygmaeus* is a junior synonym of *R. minimus*.

The phylogenetic position of *Rhodopagus* is controversial with its affinities to Lophialetidae, Helaletidae, or even Hyracodontidae (Lucas and Schoch, 1981). Our recent discovery of *Rhodopagus* from the "Basal White" of Erden Obo will probably clarify this phylogenetic mystery in the future.

Pataecops Radinsky, 1966

Only one species of *Pataecops*, *P. parvus*, is known from the upper part of the Nomogen Formation at Nuhetingboerhe and Wulanboerhe (Wang et al., 2011). Wang et al. (2011) pointed out that the holotype of the species from the Kholobolchi Formation of Mongolia is Bumbanian in age, as are specimens from the Erlian Basin. Although Radinsky (1965) assigned *Pataecops* to Lophialetidae, the phylogenetic position of *Pataecops parvus* is uncertain. If *P. parvus* belongs to rhinocerotoids rather than tapiroids (Lucas and Schoch, 1981; Dashzeveg and Hooker, 1997), it would extend the earliest record of rhinocerotoids into the earliest Eocene (Wang et al., 2011).

Deperetellidae Radinsky, 1965

Teleolophus Matthew and Granger, 1925c

Four species of *Teleolophus* have been reported from the Erlian Basin. *Teleolophus primarius* and *T.*? *rectus* are known from the Arshanto Formation in Huheboerhe area (Qi, 1987). The material of *Teleolophus primarius* is composed of several fragmentary mandibles, carpals, and phalanges from Wulanboerhe and Huheboerhe. *Teleolophus*? *rectus* is known from a left mandible with p4–m1 (IVPP V 5766) from Wulanboerhe (Qi, 1987).

Teleolophus medius, including the holotype, was reported from the Irdin Manha Formation at the Irdin Manha escarpment, and is known mainly from mandibles. Radinsky (1965) also assigned several upper dentitions (e.g., AMNH FM 26286) and a left fragmentary mandible with p3–m1 (AMNH FM 81796) to *T. medius*? from the Ulan Shireh Formation at Wulanhuxiu and Wulantaolegai. Ulan Shireh fossils of *T. medius*? are slightly smaller than Irdin Manha species, and have a slightly squarer M3. The material from Ulan Shireh provides a complete record of upper dental morphology of *Teleolophus medius*?. However, the paucity of lower teeth from Ulan Shireh hinders comparison with Irdin Manha specimens of *T. medius*, which are preserved primarily as lower dentitions. Recently, a large number of postcrania of *Teleolophus medius*? were reported from the Ulan Shireh Formation at Wulanhuxiu (Bai et al., 2018a).

Radinsky (1965) also referred several specimens to *Teleolophus* cf. *T. medius* from both the Arshanto and Irdin Manha formations in Huheboerhe area. Whether those CAE materials from the Arshanto Formation are conspecific with T. *primarius* and/or *T.*? *rectus* named by Qi (1987) needs further investigation. Radinsky (1965) referred a right mandible with p4–m3 (AMNH FM 81852, field no. 893) to *Teleolophus* sp. from the "?Houldjin gravels" at Huheboerhe. This specimen is similar to *T. medius*, but is about 20% larger.

Teleolophus magnum, known from a maxilla and a mandible (AMNH FM 26063), has been reported from the base of the "Middle Red" at Erden Obo (Radinsky, 1965). The morphology of *T. magnum* is somewhat intermediate between *T. medius* and *Deperetella cristata*. However, its stratigraphic horizon is even higher than that bearing *D. cristata* (Radinsky, 1965). Radinsky (1965) proposed three explanations for this discrepancy, and the possibility that the reported horizon bearing *T. mangus* is incorrect cannot be excluded.

Deperetella Matthew and Granger, 1925b

Only one species of *Deperetella*, *D. cristata*, is known from the Shara Murun Formation at Ula Usu. *Deperetella cristata* is represented by maxillae, mandibles, and many postcraninal elements (Radinsky, 1965). Radinsky (1965) referred a mandible with dp3–m1 (AMNH FM 26027) to *Deperetella* cf. *D. cristata* from "Shara Murun beds" at Twin Obos. This specimen is about 25% larger than Ula Usu fossils of *D. cristata*. Radinsky (1965) further referred a right mandible with a complete dentition except for p1 (AMNH FM 81807) to *Deperetella* sp. from the "?Houldjin gravels" at Huheboerhe. This specimen was assigned to *Deperetella* rather than to *Teleolophus* mainly based on the presence of complete hypolophids on p2–4.

Helaletidae Osborn, 1892

Heptodon Cope, 1882

Only one species of *Heptodon*, *H. minimus*, is known from the Arshanto Formation at Huheboerhe (Qi, 1987). This species is represented by several mandibles and an isolated m3, and it is characterized by the presence of p1 and relatively distinct cristid obliqua on the lower molars (Qi, 1987).

Desmatotherium Scott, 1883

Desmatotherium mongoliense was first reported by Osborn (1923b) from the Irdin Manha Formation on the Irdin Manha escarpment. The species has been referred to *Helaletes* and *Irdinolophus* (Radinsky, 1965; Dashzeveg and Hooker, 1997), but recent study confirms its affinity with *Desmatotherium* (Bai et al., 2017). The species has been reported from the Irdin Manha Formation on the Irdin Manha escarpment, Duheminboerhe, Huheboerhe, and Chaganboerhe (Bai et al., 2017).

Paracolodon Matthew and Granger, 1925a

Paracolodon (= *Desmatotherium*) *fissus* was first reported by Matthew and Granger (1925c) from the Irdin Manha Formation at Camp Margetts (fig. 2B). The species was assigned originally to *Desmatotherium*, and then referred to *Helaletes* or *Colodon* (Radinsky, 1965; Dashzeveg and Hooker, 1997). Based on a partial skull, Bai et al. (2017) recently assigned the species to *Paracolodon*, suggesting its ancestral relationship with *P. inceptus* from the Ergilin of Mongolia. *Paracolodon fissus* is present in the Irdin Manha Formation at Duheminboerhe and Daoteyin Obo.

Qi (1987) named a new species *Helaletes medius* based mainly on a fragmentary mandible with p4–m3 (IVPP V 5729) from the Arshanto Formation, Wulanboerhe. Bai et al. (2017) questioned the assignment of this species to *Helaletes*, and noted some similarities with *Schlosseria*.

Qi (1987) named a new species *Homogalax reliquius* based on two m3 specimens (IVPP V 5747, 5748) from Huheboerhe in the Arshanto Formation. The species was assigned initially to *Homogalax* on the basis of their robust hypoconulids (Qi, 1987). However, the lack of a "metastylid" and the presence of a relatively long trigonid suggest that the species is more similar to *Isectolophus* than to *Homogalax*. Furthermore, Lucas et al. (2003) considered *Homogalax reliquius* to be a junior synonym of *Isectolophus latidens*.

Rhinocerotoidea Gray, 1825

Hyrachyus Leidy, 1871

Two species of *Hyrachyus* have been reported from the Erlian Basin. *Hyrachyus neimongoliensis* (IVPP V 5721) was unearthed in the upper part of the Arshanto Formation at Huheboerhe (Qi, 1987). *Hyrachyus crista* is represented by several fragmentary maxillae with P4–M3 (IVPP V 5722), and was discovered in the Arshanto Formation at Bayan Ulan (Qi, 1987).

Qi (1987) assigned a left M3 (IVPP V 5728) to *Hyrachyus* sp. cf. *H. eximius* from the Arshanto Formation at Huheboerhe. He also noted some similarities in that species with the M3 of the helaletid *Paracolodon* (= *Colodon*) *inceptus*. Qi (1987) referred other miscellaneous teeth to *Hyrachyus* sp. from the Arshanto Formation at Daoteyin Obo and Huheboerhe (field no. 77028H_2, 77036-2, and 77039). However, whether or not all these specimens should be allocated to *Hyrachyus* is questionable. Radinsky (1965) assigned a left maxilla with P4–M3 (AMNH FM 81801) to cf. *Hyrachyus* from the Arshanto Formation at Huheboerhe.

Hyracodontidae Cope, 1879

Triplopus Cope, 1880

Two species of *Triplopus* have been reported from the Erlian Basin. *Triplopus*? *proficiens* was assigned initially to *Caenolophus* by Matthew and Granger (1925b). The holotype of the species (AMNH FM 20141), a mandible with p1–m3, was found in the Irdin Manha Formation at Irdin Manha. More complete material of *T.*? *proficien*s is known from the Ulan Shireh bed in Shara Murun region, and it is smaller with a straight distal border of m3 as compared with the Irdin Manha specimens (Radinsky, 1967). Radinsky (1967) further referred two mandibles (AMNH FM 26674, 26675) and a maxilla (AMNH FM 26673) from the “Irdin Manha beds” at Camp Margetts and Huheboerhe, respectively, to *T.*? *proficiens*. If the so-called “Irdin Manha beds” bearing *T.*? *proficiens* are indeed the Arshanto Formation, this species extends into the earlier Arshantan.

Triplopus? *progressus* is known from the Shara Murun Formation at Ula Usu (Radinsky, 1967), and was assigned initially to *Caenolophus* by Matthew and Granger (1925b). The species is known from a maxilla with M1–3 (AMNH FM 20298), m2–3 (AMNH FM 20309), and a M3 (AMNH FM 81872). Although *T.*? *progressus* is smaller than *T.*? *proficiens*, it is more advanced than the latter in having a reduced M3 metacone and parastyle (Radinsky, 1967).

Teilhardia Matthew and Granger, 1926

Only one species of *Teilhardia*, *T. pretiosa*, is known from the “lower red beds” at the base of the Shara Murun Formation at Ula Usu (Matthew and Granger, 1926). The species is known from a right mandible with p2–m3 (AMNH FM 20299), and the “lower red beds” were later called the Tukhum Formation (Berkey and Morris, 1927). However, whether *T. pretiosa* was found in the Tukhum Formation is controversial because some typical Sharamurunian taxa, such as *Rhodopagus*? *minimus*, *Deperetella cristata*, *Triplopus*? *progressus*, *Caenolophus promissus*, and *Pterodon hyaenoides*, were also recorded with the same field number used for *T. pretiosa* (field no. 191) (Wang et al., 2012). Radinsky (1967) suggested its affinity with amynodontids based on its relatively shorter premolars relative to the molars, proposing that it may be ancestral to *Caenolophus promissus* from the overlying Shara Murun Formation.

Ulania Qi, 1990a

Qi (1990a) reported *Ulania wilsoni* from the grayish-green sandstone of the lower part of the “Ulan Gochu Formation” at Erden Obo, and the horizon is probably equivalent to a part of the “Lower White” or the “Middle White” (Qi, 1990b; Wang et al., 2012). The species is known from what is thought to be parts of the same individual IVPP V 8922, including a maxilla, mandibles, carpals, and phalanges (Qi, 1990a). However, Qiu and Wang (2007) doubted the association of the specimens, and referred the maxilla to *Caenolophus*.

Ardynia Matthew and Granger, 1923b

Two species of *Ardynia* have been reported from the Erlian Basin: *A. praecox* and *A. kazachstanensis* (Radinsky, 1967). *Ardynia praecox* is known from AMNH FM 26039, which is composed of a skull, a mandible, and a few postcranial elements. The specimens are known from the “Ulan Gochu beds” at Erden Obo, and the field number (field no. 747) indicates their stratigraphic horizon as the “Middle Gray layer” (Bai et al., 2018b). *Ardynia kazachstanensis* is known from a mandible (AMNH FM 26183) from the “Baron Sog beds” at Nom Khong Obo, and the horizon is equivalent to the “Upper White” (Radinsky, 1967; Wang, 2003).

Proeggysodon Bai and Wang, 2012

Only one species of *Proeggysodon*, *P. qiui*, was unearthed from the upper part of the “Middle White” at Erden Obo (Bai and Wang, 2012). The species is known from a mandible with incisors, canine, and cheek teeth (IVPP V 18099), and the species is considered ancestral to the European Oligocene *Eggysodon*.

Paraceratheriidae Osborn, 1923

Pappaceras Wood, 1963

Three species of *Pappaceras*, *P. confluens*, *P. minuta*, and *P. meiomenus*, have been reported from the Erlian Basin (Wood, 1963; Lucas et al., 1981; Wang et al., 2016). Although Radinsky (1967) considered *Pappaceras* a junior synonym of *Forstercooperia*, the validity of *Pappaceras* has been supported by other authors (Qiu and Wang, 2007; Wang et al., 2016). The type of *P. confluens* (AMNH FM 26660) was recovered from the “Upper Gray clays” of the Arshanto Formation at Chaganboerhe. A referred mandible of *P. confluens* (AMNH FM 26666) was found in the Arshanto Formation at Huheboerhe. A left P2 of *P. confluens* (AMNH FM 26667) presumably derives from the Arshanto Formation in the Camp Margetts area.

The type of *P. minuta* (AMNH FM 26672) was found in the “Upper Gray clays” of the Arshanto Formation at Chaganboerhe (Lucas et al., 1981). The species also is known from the Arshanto Formation at Huheboerhe and Daoteyin Obo (Lucas et al., 1981; Wang et al., 2018). A nearly complete mandible of *P. minuta* (AMNH FM 26056) also was reported from the Shara Murun Formation (?), 6 mi east of Spring Camp at East Mesa.

The type of *P. meiomenus* is known from a nearly complete skull (IVPP V 20254), which was found in the upper part of the Arshanto Formation at Huheboerhe (fig. 2C) (Wang et al., 2016). Wang et al. (2018) further separated the original specimens of *F. minuta* into different groups (i.e., *P. minuta*, *P. meiomenus*, and *P*. sp.) mainly based on the presence or absence of p1.

Forstercooperia Wood, 1938

Two species of *Forstercooperia*, *F. totadentata* and *F. ulanshirehensis*, have been reported from the Erlian Basin (Wood, 1938; Wang et al., 2018). *Forstercooperia totadentata* (AMNH

FM 20116) was discovered in the Irdin Manha Formation at Irdin Manha. Recently, Wang et al. (2018) reported a new species *F. ulanshirehensis* from the Ulan Shireh Formation at Wulanhuxiu and Wulantaolegai, as well as from the Irdin Manha Formation at Irdin Manha. *Forstercooperia ulanshirehensis* is known from a nearly complete skull, mandibles, and some fragmentary maxillae. Wang et al. (2018) further considered "*Forstercooperia*" *huhebulakensis*, erected by Qi (1987), to be a junior synonym of *Pappaceras confluens*.

Juxia Chow and Chiu, 1964

Two species of *Juxia*, *J. sharamurenensis* and *J. shoui*, have been reported from the Erlian Basin (Chow and Chiu, 1964; Qi and Zhou, 1989; Qiu and Wang, 2007). *Juxia sharamurenensis*, known from a nearly complete skeleton (IVPP V 2891), was discovered in the Shara Murun Formation at Ula Usu (fig. 2D). Additional specimens housed at the American Museum of Natural History were referred to *J. sharamurenensis* (Radinsky, 1967), but they have not been studied in detail. Those specimens include: skeletal material (AMNH FM 20286–20288) from the Shara Murun Formation at Ula Usu, a mandible (AMNH FM 26753) from the base of "Lower Gray" at Erden Obo, and a mandible (AMNH FM 26750) from the "Shara Murun Formation" at Twin Obos.

Juxia shoui, known from a fragmentary skull with C–M2 (IVPP V 8757) and a lunar (IVPP V 3268), was recorded from the "Ulan Gochu Formation" at Erden Obo (Qi and Zhou, 1989). The lunar was discovered in the "Lower White" where the skull (V 8757) presumably was also found.

Urtinotherium Chow and Qiu, 1963

Two species of *Urtinotherium*, *U. intermedium* and *U. parvum*, have been reported from the Erlian Basin (Chow and Qiu, 1963; Qiu and Wang, 2007). The type of *U. intermedium* (IVPP V 2769) was recovered from the "Middle Gray" at Erden Obo. Qiu and Wang (2007) referred a radius (AMNH FM 26062) to *U. intermedium* from the same horizon and locality. Qiu and Wang (2007) also referred a mandible (AMNH FM 26032) from the "Ulan Gochu Formation" at Jhama Obo to the species, and the specimen was initially assigned to "*Indricotherium*" *parvum* by Radinsky (1967). *Urtinotherium intermedium* is also known from an atlas (AMNH FM 26390) and a right Mc III (AMNH FM 26389) from the "Houldjin Formation" at Huheboerhe and Camp Margetts, respectively. Qiu and Wang (2007) further considered "*Dzungariotherium erdenensis*" (IVPP V 8803) from the "Ulan Gochu Formation" at Erden Obo (Qi, 1989) to be a synonym of *U. intermedium*. However, its specific horizon remains unclear.

Urtinotherium parvum is known from a maxilla with P1–M3 (EMM 0146) from the "Lower White" at Erden Obo, and a few postcranial specimens (AMNH FM 26190) from the "Baron Sog beds" at Jhama Obo.

Paraceratherium Forster-Cooper, 1911

Only one species of *Paraceratherium*, *P. grangeri*, has been reported from the Erlian Basin (Qiu and Wang, 2007). The following specimens were assigned to the species: AMNH FM 26166 and 26179 from the "Baluchitheres bed" (= "Upper White") at Erden Obo and AMNH FM 26387 from the "Houdljin gravels" at Daoteyin Obo (Qiu and Wang, 2007).

Aralotherium Borissiak, 1939

Qiu and Wang (2007) assigned some dental and postcranial material (e.g., EMM 0016) to *Aralotherium* sp. from the type Houdljin Formation near Erlian Hot.

Amynodontidae Scott and Osborn, 1883

Rostriamynodon Wall and Manning, 1986

Only one species of *Rostriamynodon*, *R. grangeri* (fig. 2E), is known from the "Irdin Manha Formation," 2 mi east of Camp Margetts (Wall and Manning, 1986). The species is known from a complete skull and mandible (AMNH FM 107635), and likely was unearthed from the Irdin Manha Formation, rather than the Arshanto Formation (Bai et al., 2017). *Rostriamynodon grangeri* was considered to be a primitive member of the amynodontids (Wall and Manning, 1986).

Caenolophus Matthew and Granger, 1925b

Two species of *Caenolophus*, *C. promissus* and *C. obliquus*, have been named from the Shara Murun Formation at Ula Usu (Matthew and Granger, 1925b; Radinsky, 1967). *Caenolophus promissus* is known from a maxilla with P3–M3 (AMNH FM 20297) and a mandible with m1–2 (AMNH FM 20304) (Matthew and Granger, 1925b). *Caenolophus obliquus* is known from a maxilla with DP3–DP4, P3–M2 (AMNH FM 20296) (Matthew and Granger, 1925b). *Caenolophus* was originally assigned to the Hyracodontidae (Matthew and Granger, 1925b), but Radinsky (1967) suggested its affinity with the amynodontids.

Sharamynodon Osborn, 1936

Osborn (1936) briefly described a nearly complete skeleton of "*Amynodon*" *monogoliensis* (AMNH FM 20278) from the Shara Murun Formation at Ula Usu (fig. 2F). Kretzoi (1942) considered the species as a new genus, *Sharamynodon*. Xu (1966) reported additional material of the species from the same horizon and locality. Wall (1981) also referred a partial skeleton (AMNH FM 21601) to the species from the Shara Murun Formation (gray beds), 4 mi north of Baron Sog Lamasery.

Sianodon Xu, 1965

Only one species of *Sianodon*, *S. ulausuensis*, has been reported from the Shara Murun Formation at Ula Usu (Xu, 1966). The species is known from a nearly complete skull (IVPP V 3215). *Sianodon ulausuensis* is more primitive than *S. bahoensis* in having a relatively longer facial part and three upper incisors. Xu (1966) also assigned a maxilla with M2–3 (IVPP V 3221) to *Sianodon* sp. from the same horizon and locality.

Lushiamynodon Chow and Xu, 1965

Only one species of *Lushiamynodon*, *L. sharamurenensis*, has been reported from the Shara Murun Formation at Ula Usu (Xu, 1966). The species is known from an incomplete juvenile cranium with DP1–M1 (IVPP V 2892), a juvenile mandible (IVPP V 2892.1), a posterior part of the cranium (IVPP V 2892.2), and some postcraninal material (Xu, 1966). A mandible with m2–3 (IVPP V 3217) of *L. sharamurenensis* also has been reported from the "same horizon" at "Ulan Shireh Obo," which was situated about 30 km northeast of Ula Usu. The so-called "Ulan Shireh Obo" (= Ulan Shireh) is located in the North Mesa, north of Tukhum Sumu, with the deposits of Ulan Shireh Formation roughly equivalent to the Irdin Manha Formation (Chow and Rozhdestvensky, 1960; Wang et al., 2012).

Gigantamynodon Gromova, 1954

Only one species of *Gigantamynodon*, *G. promisus*, has been reported from the Shara Murun Formation at Ula Usu (Xu, 1966). The species is known from a mandible with p2–m3 (IVPP V 3218) and many postcranial specimens (IVPP V 3218.1-28). However, Wall (1989) considered *Gigantamynodon* a nomen dubium (Lucas and Emry, 1996; Lucas et al., 1996).

Cadurcodon Kretzoi, 1942

Two species of *Cadurcodon*, *C. matthewi* and *C. houldjinensis*, have been reported from the Erlian Basin (Wall, 1981; Wang et al., 2009). The type species of *Cadurcodon matthewi* (AMNH FM 26029) was found in the "Ulan Gochu beds" at Jhama Obo (Wall, 1981). *Cadurcodon matthewi* is considered to be more primitive than *C. ardynensis* (Wall, 1981). *Cadurcodon houldjinensis*, known mainly from isolated teeth (e.g., EMM 0126), was discovered from the Houldjin Formation at Houldjin and near the Erenhot Railway Station (Wang et al., 2009). Wang et al. (2009) considered that three specimens of "*Cadurcotherium*" sp. (AMNH FM 19183, field no. 36) from the Houldjin Formation, 5 mi south of Iren Dabasu (Matthew and Granger, 1923a) should be assigned to *C. houldjinensis* (m2) or *C. ardynensis* (P4 and M1/2).

Xu (1966) referred a maxilla with P2–3 (IVPP V 3222), a right m1 (IVPP V 3222.1), and a canine (IVPP V 3222.2) to *Cadurcodon* sp. from the Urtyn Obo Formation at Urtyn Obo (= Erden Obo). However, their specific stratigraphic horizons are uncertain.

Amynodontopsis Stock, 1933

Two species of *Amynodontopsis*, *A. parvidens* and *A. tholos*, were named by Wall (1981) from the Erlian Basin. The type of *A. parvidens*, known from a skull and mandible (AMNH FM 26043), was collected from the top of the "Lower White" at Erden Obo. Wall (1981) recognized two different sizes of the species: the small-size group includes AMNH FM 26045, 26046, and 26050; and the large-size group includes AMNH FM 26041, 26042, 26043, and 26051. He attributed the size differences to sexual dimorphism, because all the specimens were collected from the base of the "Middle Red" at Erden Obo, with the exception of AMNH FM 26046 that was recorded from the "Middle Red" bed and AMNH FM 26043 from top of the "Lower White" at Erden Obo. Wall (1981) also referred AMNH FM 26044 from the base of "Middle Red" at Erden Obo to *A. parvidens*. The species also is known from the following horizons and localities: AMNH 21599 from the base of upper red bed (Ulan Gochu Formation) 4 mi north of Baron Sog Lamasery; AMNH FM 26053 from the "Ulan Gochu beds" at Nom Khong Obo; AMNH 26178 possibly from the "Baron Sog bed" south of Jhama Obo; and AMNH FM 26038 from the "Ulan Gochu Formation" at Jhama Obo (Wall, 1981).

The holotype of *Amynodontopsis tholos*, comprising a skull and a lower jaw (AMNH FM 26035), was collected from the top of gray beds (= "Ulan Gochu") at Ulan Shireh Obo (= Ganggan Obo on East Mesa) (Wall, 1981). The distribution of the species also includes the "Ulan Gochu beds," south of Jhama Obo (AMNH FM 26031), and the "Lower White or Gray (pink)" at Nom Khong Obo (AMNH FM 26054, 26055, and 26057). Wall (1981) assigned a mandible (AMNH FM 26053, field no. 786) to *A. tholos*. However, it contradicts the fact that the specimen is also listed as *A. parvidens*, as discussed above. The specific stratigraphic horizon where AMNH FM 26053 was collected is uncertain, and is probably below the "Upper Red" bed.

Zaisanamynodon Belyaeva, 1971

Lucas et al. (1996) referred some CAE specimens to *Z. borisovi* from the Erlian Basin. The species is known from the "Middle White" (AMNH FM 26052, 26049) at Erden Obo, the Baron Sog Formation at Baron Sog Mesa (AMNH FM 21602), the "Ulan Gochu beds" at Ulan Shireh Obo (= Ganggan Obo) (AMNH FM 26034), and the "Houldjin gravels" at Camp Margetts. Lucas et al. (1996) further referred a symphysis with i2 and c (AMNH FM 26170) to *Z. borisovi* from the "Baron Sog Formation" at Erden Obo.

Rhinocerotidae Gray, 1821

Aprotodon Forster-Cooper, 1915

Only one species of *Aprotodon*, *A. lanzhouensis*, has been reported from the Houldjin Formation near the Erenhot Railway Station (Wang et al., 2009). The specimens consist of i2 (EMM 0082) and some cheek teeth (e.g., EMM 0079), and are characterized by extremely long and curved lower tusks (Wang et al., 2009).

Symphysorrhachis Beliajeva, 1954

Wang et al. (2009) referred a mandible with m2–3 (EMM 0123) and M1/2 (EMM 0078) to *Symphysorrhachis* sp. from the Houldjin Formation near the Erenhot Railway Station. Wang et al. (2009) further assigned an M3 (AMNH FM 19184) from Houldjin, originally referred to *Caenopus* or *Praeaceratherium* sp. by Matthew and Granger (1923a), to *Symphysorrhachis* sp.

Brontotherioidea Marsh, 1873

Brontotheriidae Marsh, 1873

Microtitan Granger and Gregory, 1943

Two species of *Microtitan*, *M. mongoliensis* and *M.*? *elongatus*, have been reported from the Ulan Shireh Formation at North Mesa and the Arshanto Formation at Daoteyin Obo, respectively (Granger and Gregory, 1943; Qi, 1987). *Microtitan mongoliensis* is known from a mandible with p2–m3 (AMNH FM 22099) and a maxilla with C–M3 (AMNH FM 21611). *Microtitan mongoliensis* initially was assigned to "*Metarhinus*?" by Osborn (1925) based a fragmentary mandible with p4–m1 (AMNH FM 20167), lacking diagnostic characters except for its small size. AMNH FM 20167 was discovered in the Irdin Manha Formation on the Irdin Manha escarpment (Osborn, 1925). Later, Granger and Gregory (1943) erected a new genus *Microtitan* for "*Metarhi-*

nus?" *mongoliensis* and selected AMNH FM 22099 as a neotype. Mihlbachler (2008) further pointed out that AMNH FM 20167 actually was made up of multiple individuals.

Microtitan? *elongatus* was erected by Qi (1987) based on P3–M3 (IVPP V 5767) from the Arshanto Formation at Daoteyin Obo. However, Mihlbachler (2008) considered the species a nomen dubium. Qi (1987) further referred a M2 (IVPP V 5768) to *Microtitan* sp. from the Arshanto Formation at Huheboerhe. It is noteworthy that, based on our fieldwork over the past decade, no brontotheres have been found in the Arshanto Formation in the Huheboerhe area. Consequently, the horizon bearing *Microtitan*? *elongatus* and *Desmatotitan* sp. (as discussed below) recorded as the Arshanto Formations is questionable.

Desmatotitan Granger and Gregory, 1943

Only one species of *Desmatotitan*, *D. tukhumensis*, has been reported from the Ulan Shireh Formation at Wulantaolegai (Granger and Gregory, 1943). The species is known only from the type AMNH FM 21606, which is composed of a mandible with i1–c and p2–m3. *Desmatotitan tukhumensis* is probably allied either with *Metatelmatherium* or *Microtitan mongoliensis* (Granger and Gregory, 1943; Mihlbachler, 2008).

Qi (1987) referred a single m3 (IVPP V 5769) to *Desmatotitan* sp. from the upper part of Arshanto Formation at Huheboerhe.

Acrotitan Ye, 1983

Ye (1983) erected a new genus and species *Acrotitan ulanshirehensis* from the Ulan Shireh Formation at Wulanhuxiu. The species is known from a fragmentary mandible with p3–4 (IVPP V 6686), and is characterized by two pairs of lower incisors (Mihlbachler, 2008).

Epimanteoceras Granger and Gregory, 1943

Only one species of *Epimanteoceras*, *E. formosus*, has been reported from the Ulan Shireh Formation at Wulantaolegai (Granger and Gregory, 1943; Mihlbachler, 2008). The type of *E. formosus* is known from a complete skull with complete dentition (AMNH FM 21613). Granger and Gregory (1943) erected a new genus and species *Dolichorhinoides angustidens* based on a partial skull with P1–M3 (AMNH FM 21607) from the Ulan Shireh Formation at Wulanhuxiu. However, Mihlbachler (2008) considered the species a junior synonym of *E. formosus*.

Hyotitan Granger and Gregory, 1943

Only one species of *Hyotitan*, *H. thomsoni*, was discovered in the Erlian Basin. The type of *H. thomsoni*, known from a mandible (AMNH FM 26401), was collected from the "Houldjin gravels" at Camp Margetts. However, Mihlbachler (2008) proposed that *H. thomsoni* could be a synonym of *Qufutitian zhoui*.

Metatelmatherium Granger and Gregory, 1938

Two species of *Metatelmatherium*, *M. ultimum* and *M. parvum*, have been reported from the Erlian Basin. Granger and Gregory (1943) erected a new species *Metatelmatherium crista-*

tum based on a skull and mandible (AMNH FM 26411) from the "Irdin Manha Formation" at Camp Margetts. Mihlbachler (2008) considered *M. cristatum* a junior synonym of the Uintan *M. ultimum* from North America, but Mader (1989, 1998) regarded them as two different species. Furthermore, Bai et al. (2017) pointed out that the horizon bearing AMNH FM 26411 is actually in the Irdin Manha rather than the Arshanto Formation. *Metatelmatherium parvum*, known from a fragmentary mandible with p3–4 (AMNH FM 20168), was found in the Irdin Manha Formation at Irdin Manha (Granger and Gregory, 1943). However, Mihlbachler (2008) considered the species a nomen dubium because it lacks diagnostic characters.

Protitan Granger and Gregory, 1943

The genus *Protitan* was erected by Granger and Gregory (1943) and originally included six species: *P. grangeri*, *P. robustus*, *P. minor*, *P. bellus*, *P. obliquidens*, and *P.*? *cingulatus*. Granger and Gregory (1943) further considered *Dolichorhinus olseni* and "*Manteoceras*?" *irdinensis* named by Osborn (1925) as junior synonyms of *P. grangeri*. However, Mihlbachler (2008) synonymized *P. robustus*, *P. bellus*, and *P. obliquidens* with *P. grangeri*, and considered *P.*? *cingulatus* a nomen dubium. Thus, according to the revision by Mihlbachler (2008), only two species of *Protitan*, *P. grangeri* and *P. minor*, are valid species.

The type of *Protitan grangeri*, known from a complete skull and mandible (AMNH FM 20103), is from the Irdin Manha Formation at Irdin Manha (fig. 2G). The species is also known from the following horizons and localities: Irdin Manha Formation at Irdin Manha (AMNH FM 19179, 20104 [holotype of *P.* "*robustus*], 20108, 20109 [holotype of "*Dolichorhinus olseni*"], 20111 [holotype of "*Manteoceras*? *irdinensis*"], 20112–20114, 20119, 20120, 20123, 20125 [holotype of *P*. "*obliquidens*"], and 20126); "Houldjin gravels" at Camp Margetts (AMNH FM 26421); and "lower red bed" at Spring Camp of East Mesa, Shara Murun region (AMNH FM 26104 [holotype of *P. bellus*]).

The type of *Protitan minor*, a skull (AMNH FM 26416), probably is from the top of "Irdin Manha" at 0.5 mi west of Camp Margetts. Mihlbachler (2008) also referred a partial skull (AMNH FM 26417) to *P. minor* from "?Irdin Manha beds," 1 mi west of Camp Margetts. However, Bai et al. (2017) have pointed out that the horizon bearing AMNH FM 26416 is indeed within the Irdin Manha Formation.

Four mandibles (AMNH FM 26410, 26415, 26418, and 26408) initially assigned to *P. minor* or *P. grangeri* were considered to represent a new species (Camp Margetts "taxa A") by Mihlbachler (2008). These specimens derive from the "Houldjin gravels" or ""Irdin Manha beds" in the Camp Margetts area.

The type of "*Protitan*?" *cingulatus*, composed of a mandible with p1–m3 (AMNH FM 26412), was unearthed from the "Houldjin gravels" at Chaganboerhe. Mihlbachler (2008) also referred AMNH FM 26403 from the "Houldjin gravels" at Camp Margetts and AMNH FM 20110 from the Irdin Manha Formation at Irdin Manha to the species.

Qi et al. (1992) referred a single m3 and some postcrania (IVPP V 10104) to *Protitan* sp. from the so-called "Tukhum Formation" at Erden Obo. However, the horizon is equivalent to the "Low Red" bed.

Gnathotitan Granger and Gregory, 1943

Only one species of *Gnathotita*n, *G. berkeyi*, has been reported from the Erlian Basin (Granger and Gregory, 1943; Mihlbachler, 2008). *Gnathotita*n *berkeyi* was assigned initially to *Telmatherium* by Osborn (1925), and later Granger and Gregory (1943) erected the genus *Gnathotita*n for the species. The species is characterized by its disproportionately large and deep mandible (Mihlbachler, 2008). The type of *G. berkeyi* is known from a mandible with c–m3 (AMNH FM 20106) from the Irdin Manha Formation at Irdin Manha. Mihlbachler (2008) also referred the following specimens to *G. berkeyi* from the Irdin Manha Formation at Irdin Manha: AMNH FM 20107, 20115, 20121, and 141231 (formerly part of AMNH FM 20106). As noted by Mihlbachler (2008), two specimens (AMNH FM 20124, 20127) originally referred to *G. berkeyi* by Osborn (1925) were sent to the Chinese Geological Survey in October 1928 and are unfortunately lost. Both specimens were from the Irdin Manha Formation at Irdin Manha.

Rhinotitan Granger and Gregory, 1943

Two species of *Rhinotitan*, *R. kaiseni* and *R. andrewsi*, have been recognized from the Shara Murun Formation at Ula Usu (Granger and Gregory, 1943; Wang, 1982; Mihlbachler, 2008). Osborn (1923b, 1925) named three new brontothere species from Ula Usu: *Protitanotherium mongoliensis*, *Protitanotherium andrewsi*, and *Dolichorhinus kaiseni*, but Granger and Gregory (1943) later erected a new genus *Rhinotitan* for these three species. Wang (1982) further considered *R. andrewsi* as a junior synonym of *R. mongoliensis* (Takai, 1939). However, Mihlbachler (2008) treated *R. mongoliensis* as a nomen dubium.

The type of *R. kaiseni*, known from a skull and mandible (AMNH FM 20252), was unearthed from the Shara Murun Formation at Ula Usu. AMNH FM 20257 and FMNH P 14048 (formerly AMNH FM 20260) were referred to *R. kaiseni* from the same horizon and locality. The type of *R. andrewsi*, known from a skull (AMNH FM 20271), is from the Shara Murun Formation at Ula Usu. AMNH FM 20254, 20261, 20263, IVPP V 3254-1, 3254-2, PIN 2198-3, 2198-5, and 7130-3 have been assigned to *R. andrewsi* from the same horizon and locality as the holotype. Mihlbachler (2008) further referred many specimens to *Rhinotitan* sp. from the Shara Murun Formation at Ula Usu, 4 mi north of Baron Sog Lamasery.

Pachytitan Granger and Gregory, 1943

Only one species of *Pachytitan*, *P. ajax* (AMNH FM 21612), is known from the Shara Murun Formation (gray beds), 4 mi north of Baron Sog Lamasery in the Shara Murun region (Granger and Gregory, 1943; Mihlbachler, 2008). AMNH FM 21612 is a fragmentary skull with left I3, C, and P2–M3. *Pachytitan ajax* is very close to *Rhinotitan*, but is more advanced than the latter in having more molarized premolars that resemble those of *Embolotherium* or *Parabrontops* from the Erlian Basin (Granger and Gregory, 1943; Mihlbachler, 2008). Cranially, *Pachytitan* most resemble *Rhinotitan andrewsi* and *Diplacodon elatus* (Mihlbachler, 2008).

Titanodectes Granger and Gregory, 1943

Granger and Gregory (1943) erected a new genus, *Titanodectes*, comprising *T. minor* and *T. ingens*, from the Erlian Basin. However, Mihlbachler (2008) considered both of them synonymous with *Embolotherium grangeri*. Considering that the horizons and localities bearing *Titanodectes* and *Embolotherium* are different, and that none of the reliable lower dentition of *E. grangeri* has been reported, we still regard *Titanodectes* as a valid genus. The type of *T. minor*, known from an incomplete mandible with front teeth and p2–m1 (AMNH FM 26132), is from the "Shara Murun Formation" at Spring Camp in the East Mesa. Granger and Gregory (1943) further referred AMNH FM 26021 from the "Lower White" of Erden Obo, AMNH FM 26012 from the "Ulan Gochu beds" at Twin Obos, and AMNH FM 21600 from the Shara Murun Formation (gray beds), 4 mi north of Baron Sog Lamasery to the species. However, Mihlbachler (2008) referred AMNH FM 26021 to *Parabrontops* cf. *P. gobiensis*. The type of *Titanodectes ingens*, known from a mandible (AMNH FM 26005), is from the "Ulan Gochu beds" at Jhama Obo. *Titanodectes* is considered to be in certain respects intermediate between *Rhinotitan* and *Embolotherium* (Granger and Gregory, 1943; Mihlbachler, 2008).

Embolotherium Osborn, 1929

Osborn (1929) erected a new genus, *Embolotherium*, which includes *E. andrewsi*, *E. grangeri*, and *E. loucksii*, from the Shara Murun region and Erden Obo. *Embolotherium* is characterized by its large, upward extended nasal horns (Osborn, 1929). Granger and Gregory (1943) further named a new species *E. ultimum* from the Baron Sog Mesa. However, Mihlbachler (2008) considered *E. ultimum* and *E. loucksii* as a junior synonyms of *E. andrewsi* and E. *grangeri*, respectively. Thus, only two species of *Embolotherium* are recognized as valid.

The type of *Embolotherium grangeri*, known from a complete skull (AMNH FM 26002), is from the base of "Middle Red" at Erden Obo (Osborn, 1929). Mihlbachler (2008) referred following specimens to *E. andrewsi* from the Erlian Basin: AMNH FM 26004 from the base of "Middle Red" layer at Erden Obo; AMNH FM 26040 from the base of "Ulan Gochu beds" at Twin Obos; AMNH FM 21610 (holotype of *E. louksii*) from the base of Ulan Gochu Formation, 4 mi north of Baron Sog Lamasery; and AMNH FM 26018 from the surface of a plain, 2 mi south of Baron Sog Lamasery.

The type of *Embolotherium andrewsi*, known from a nearly complete skull (AMNH FM 26001), is from the "Middle White" layer at Erden Obo (fig. 2H) (Osborn, 1929). Mihlbachler (2008) referred the following specimens to *E. andrewsi* from the Erlian Basin: those largely from the "Middle White" layer at Erden Obo (AMNH FM 26003, 26000 (presented to the Chinese Geological Survey Museum), 26011, 26006–26008, and IVPP V 11959); those from the "Ulan Gochu Formation" at Jhama Obo (AMNH FM 26009 and 26010); those from East Mesa (PIN 2200-1 and 2200-2); and those from the Baron Sog Formation at Baron Sog Mesa (AMNH FM 21604 [holotype of *E. ultimum*] and AMNH FM 22114). AMNH FM 20352 actually is from the Ardyn Obo Beds at Ardyn Obo (field no. 245), instead of the "Ulan Gochu Formation" at Erden Obo as mentioned by Mihlbachler (2008).

Parabrontops Granger and Gregory, 1943

Only one species of *Parabrontops*, *P. gobiensis*, has been reported from the Erlian Basin (Osborn, 1925; Granger and Gregory, 1943). The species *P. gobiensis* was initially assigned to

Brontops by Osborn (1925). The type of the species, known from a distorted skull (AMNH FM 20354), is from the Ardyn Obo beds at Ardyn Obo (field no. 253) (Osborn, 1925; Granger and Gregory, 1943), rather than the Urtyn Obo Formation at Urtyn Obo as mentioned by Mihlbachler (2008). In detail, the locality 253 is situated "near trail, 1 mi northwest of Obo point." AMNH FM 26020, known from a partial skull, was unequivocally referred to *P. gobiensis* (Granger and Gregory, 1943; Mihlbachler, 2008) and is from the "Middle White" layer at Erden Obo. Mihlbachler (2008) referred the following specimens to *Parabrontops* cf. *P. gobiensi*s: AMNH FM 26019 ("Middle White" layer, Erden Obo); AMNH FM 26021 ("Lower Gray" layer, Erden Obo); and AMNH FM 26131 ("Shara Murun beds," Spring Camp). However, Granger and Gregory (1943) assigned AMNH FM 26021 to *Titanodectes minor* as discussed above.

Metatitan Granger and Gregory, 1943

Granger and Gregory (1943) named three species within a new genus *Metatitan*: *M. primus*, *M. progressus*, and *M. relictus*. However, Mihlbachler (2008) erected a new genus, *Nasamplus*, for *M. progressus*, and thus only two species are included in *Metatitan*.

The type of *Metatitan primus*, known from a partial skull and mandible (AMNH FM 26101), was discovered at Big Red Draw, 1 mi southwest of Chimney Butte Camp at North Mesa. The horizon bearing AMNH FM 26101 is probably equivalent to the Ulan Shireh Formation at Wulanhuxiu. Mihlbachler (2008) further referred a mandible (AMNH FM 26102) to the species from the middle of the upper red beds at the northwest promontory, 1 mi northwest of Chimney Butte Camp.

The type of *Metatitan relictus*, known from a skull and mandible (AMNH FM 26391), is from the "Houldjin gravels," 1 mi west of Camp Margetts. *Metatitan* is considered to be derived from *Rhinotitan* and to bridge the morphological gap between *Embolotherium* and most other horned brontotheres with the paired frontonasal horns (Granger and Gregory, 1943). The following specimens from the "Houldjin gravels" in the Camp Margetts area are referred to *M. relictus* (Granger and Gregory, 1943; Mihlbachler, 2008): AMNH FM 26395–26399; AMNH FM 26402; 26404–26407; 26420; 26427; and 26429. Mihlbachler (2008) further proposed that AMNH FM 26400, originally assigned to *Metatitan relictus* (Granger and Gregory, 1943), probably represents a new species (Camp Margetts "taxa B"). AMNH FM 26400 is from the "Houldjin gravels," 1 mi west of Camp Margetts.

Wang et al. (2009) referred a maxilla with P1–3 (IVPP V 15714) and several isolated lower teeth to *Metatitan* sp. from the Houldjin Formation at Houldjin and near Erenhot Railway Station.

Nasamplus Mihlbachler, 2008

The genus *Nasamplus* was erected by Mihlbachler (2008) for "*Metatitan*" *progressus* (Granger and Gregory, 1943). The type species, known from a fragmentary skull (AMNH FM 26014), is from the "Ulan Gochu beds" at Jhama Obo.

Chalicotherioidea Gill, 1872

Litolophus Radinsky, 1964b

Only one species of *Litolophus*, *L. gobiensis*, is known from the basin (Colbert, 1934; Radinsky, 1964b; Bai et al., 2010). Colbert (1934) erected a new species "*Grangeria*" *gobiensis*, and later Radinsky (1964b) proposed the new genus *Litolophus* for the species. The type of *L. gobiensis*, known from a crushed skull and mandible (AMNH FM 26645), is from the base of the Arshanto Formation at Nuhetingboerhe. Other referred specimens were collected from the same horizon and locality. Recently, many cranial and postcranial specimens have been collected from the "chalicothere pit" (Bai et al., 2011a; Bai et al., 2011b) at the same horizon and locality as CAE *Litolophus* collections.

Schizotherium Gervais, 1876

Coombs (1978) referred AMNH FM 26061 and AMNH FM 103336 to *Schizotherium* cf. *S. avitum* from Erden Obo. The right maxilla with P2–M3 (AMNH FM 26061), in association with left maxilla with P3–4 and M2–3, is composed of two parts: an anterior part with P2–3 recorded from the "Ulan Gochu beds" (probably the "Upper Red"), and a posterior part with P4–M3 found from the "Middle White" (Coombs, 1978). This discrepancy may be the result of drift of weathered-out material down the steep slopes (Radinsky, 1964a; Coombs, 1978). A left mandible with p4–m2 (AMNH FM 103336) was found in the "Baron Sog bed" (= "Upper White") at Erden Obo (Coombs, 1978). In addition, Colbert (1934) assigned a Mc III (AMNH FM 26188) to *Schizotherium* sp., and noted that the specimen was presumably from the "Baron Sog beds" at Nom Khong Shireh. Actually, AMNH FM 26188 is recorded as coming from "?Baron Sog beds" at Erden Obo (Wang, 2003).

DISCUSSION

Based on the data about the temporal and spatial distribution of Paleogene perissodactyls from the Erlian Basin (figs. 2–4), we address some long-standing problems about the biostratigraphic correlation of the Paleogene sediments in the Erlian Basin, and discuss perissodactyl diversity through the early Eocene to the early Oligocene in the following section.

"Houldjin Formation" in the Huheboerhe area

Granger and Berkey (1922) named the Houldjin beds on the Houldjin escarpment, which are dominated by yellow, pebbly gravels about 4.6 m (fig. 5A) (Berkey and Morris, 1927). The Houldjin fauna at the type locality includes a variety of perissodactyl taxa such as the brontotheriid *Metatitan* sp., paraceratheriid *Aralotherium* sp., amynodontids *Cadurcodon ardyensis* and *C. houldjinensis*, rhinocerotids *Aprotodon lanzhouensis* and *Symphysorrhachis*? sp. (Matthew and Granger, 1923a; Qiu and Wang, 2007; Wang et al., 2009). The age of the Houldjin fauna remains controversial and varies in age estimates from the late Eocene to the late Oligocene (Qiu and Wang, 2007; Wang et al., 2009). This discrepancy is attributed to the fragmentary material known from the formation and probably a mixture of taxa from different horizons (Wang et al., 2012).

Meng et al. (2007) pointed out that the so-called "Houldjin Formation" and "Irdin Manha Formation" by CAE in the Huheboerhe area are mostly Irdin Manha and Arshanto formations, respectively (Wang et al., 2010). Though Wang et al. (2012) noticed the "yellow gravels" present in Huheboerhe area, it is uncertain whether they belong to the Houldjin Formation. However, some perissodactyls from the "Houldjin gravels" in the Huheboerhe area obviously are more advanced than those from type Irdin Manha Formation, including the deperetellid *Deperetella* sp., amynodontid *Zaisanamynodon borisovi*, paraceratheriids *Urtinotherium intermedium* and *Paraceratherium grangeri*, and possibly the brontothere *Metatitan*. It is notable that except for *Deperetella* sp. and *Metatitan*, the other species are recorded either by an isolated tooth or postcrania, hampering the comparisons with Houldjin fauna from the type locality. Qiu and Wang (2007, p169) also mentioned a maxilla with P3–M2 of *Allacerops turgaica* from the "Houldjin gravels" at Daoteyin Obo. These advanced perissodactyls are indicative of a late Eocene Ergilian and/or early Oligocene Hsandagolian age. Whether those taxa recovered from the "yellow gravels" warrant further investigation, strata younger than the Irdin Manha Formation likely are present in the Huheboerhe area (Qiu and Wang, 2007). As noted by Meng et al. (2007: 18), the "Houldjin gravels may be represented only by a thin layer of loose sand and conglomerates forming the Gobi surface" in the Huheboerhe area.

Ulan Shireh Formation at the North Mesa

In 1925, the CAE investigated Wulantaolegai (4 mi north of Tukhum Lamasery) and Wulanhuxiu (8 mi north of Tukhum Lamasery) at North Mesa for the first time (fig. 1), and all collections were recorded from the "Shara Murun beds" (Granger, 1925). Granger (1925: 66) further noted that all fossils were from layers below an "apple red stratum." During the second investigation of the North Mesa, Granger (1928: 6) divided the sediments at "Chimney Butte" (Wulanhuxiu) into 14 layers from the top to the bottom (fig. 6), with layers 3–5 grouped into an upper "red member" and layers 6–14 grouped into a lower "white member" (fig. 5B). Almost all specimens were collected from the "Buckshot's Quarry" at Chimney Butte, which is equivalent to layer 9 of Granger's (1928) sketch and roughly layer 4 of Li et al. (2016a). The exception is that of the creodont *Sarkastodon mongoliensis* (AMNH FM 26302, field no. 641) from the relatively lower layer 12 (Granger, 1938). A few specimens, such as AMNH FM 26115 of *Breviodon* sp. and AMNH FR 6697 of fossil turtle *Anosteira mongoliensis* (Gilmore, 1931), not otherwise recorded from the "Buckshot's Quarry" in the Chimney Butte section were labeled with the field number 645. In addition, a few specimens of the brontothere *Metatitan primus* (AMNH FM 26101, 26102) and turtles were collected from Big Red Draw and Northwest Promontory, which are located 1 mi southwest and northwest of the Chimney Butte Camp, respectively. AMNH FM 26102 is from the middle of upper red beds (Granger, 1928). Thus, almost all the previous CAE collections from North Mesa probably were unearthed from the lower "white member" and below the "red member," with an exception of *Metatitan primus* (Wang et al., 2012). Similarly, Chow and Rozhdestvensky (1960) noted that most of the fossils from North Mesa (= Ulan Shireh) collected by SSPE were from the lower part of the formation.

Berkey et al. (1929) named the Ulan Shireh Formation for the deposits at North Mesa, which are dominated by red clays, though gray clays, sands, and gravels also are present (fig. 5B). The Ulan Shireh Formation is considered equivalent to the Tukhum Formation (Berkey et al., 1929), and the mammalian fauna from the Ulan Shireh Formation is considered to be

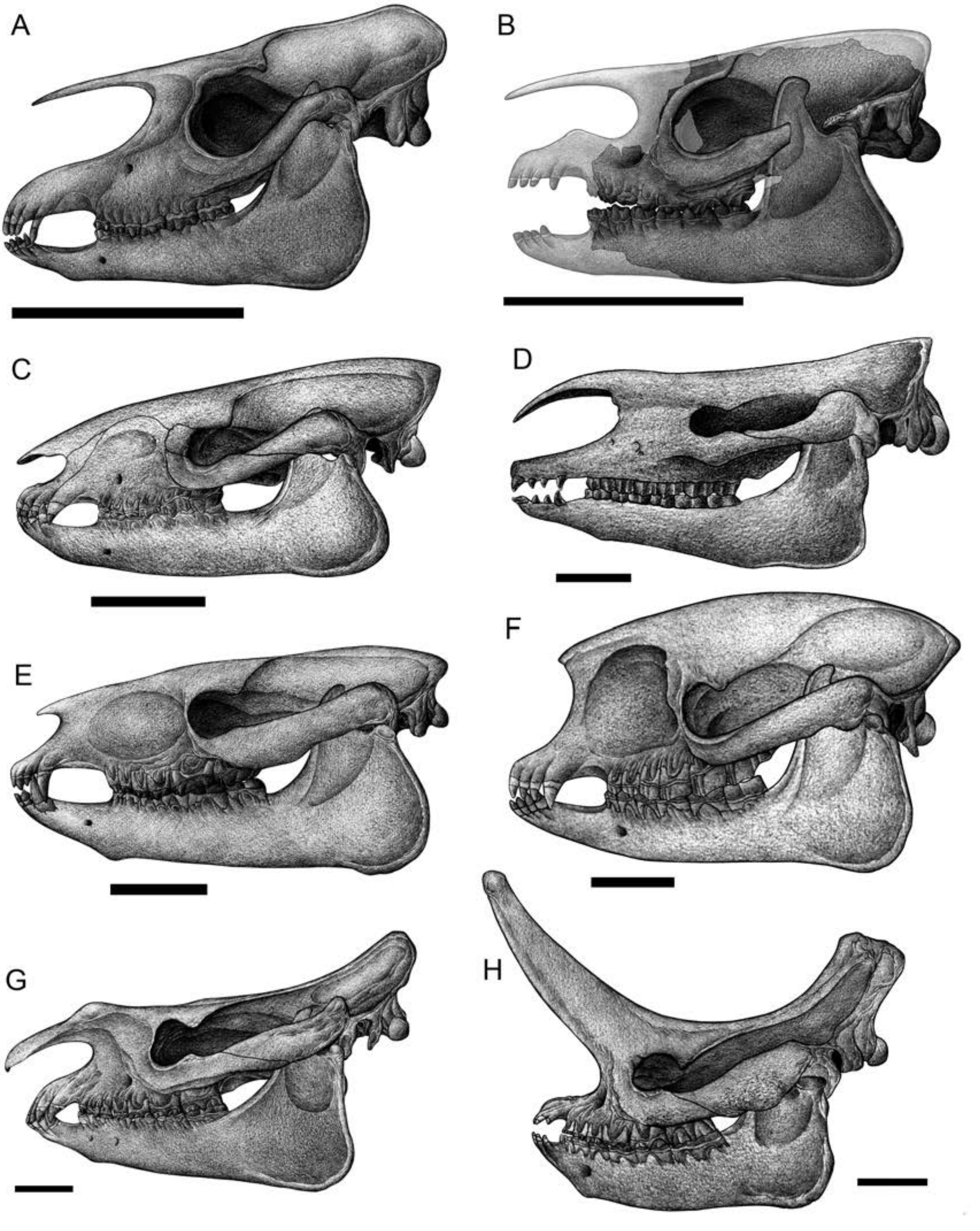


FIG. 2. Cranial and mandibular reconstructions of typical Eocene perissodactyls from the Erlian Basin of Inner Mongolia, China. tapiroid **A,** *Lophialetes expeditus*; **B,** *Paracolodon fissus*; paraceratheriid **C,** *Pappaceras meiomenus*; **D,** *Juxia sharamurenensis*; amynodontid **E,** *Rostriamynodon grangeri*; **F,** *Sharamynodon mongoliensis*; brontotheriid **G,** *Protitan grangeri*; **H,** *Embolotherium andrewsi*. Scale bar equals 10 cm.

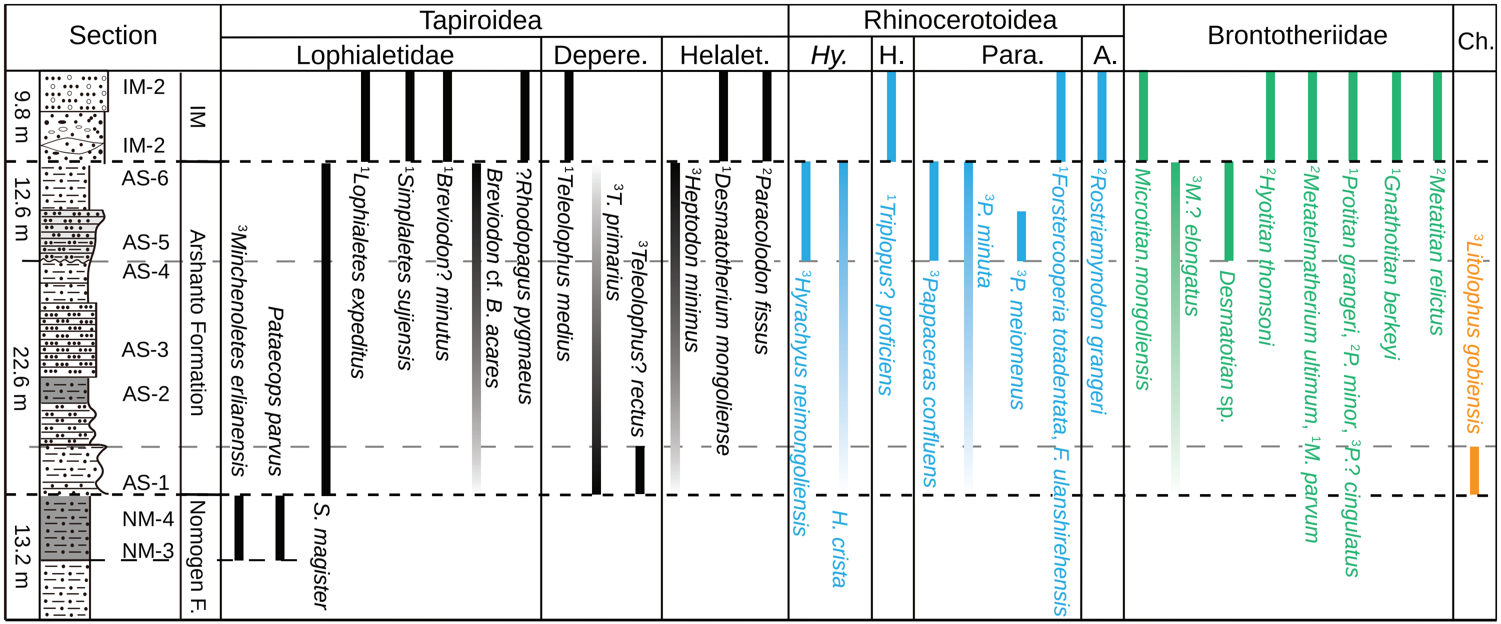


FIG. 3. Stratigraphic distributions of perissodactyl fossils and taxa in the Nomogen, Arshanto, and Irdin Manha formations on the Irdin Manha escarpment and in the Huheboerhe area. The profile of section and fossil-bearing horizons are modified from Meng et al. (2007) and Wang et al. (2010). The superscripts in front of taxa indicate the localities of holotypes: numbers 1, 2, and 3 refer to Irdin Manha escarpment, Camp Margetts and nearby localities, and Huheboerhe escarpment, respectively. Abbreviations: **A.,** Amynodontidae; **Ch.,** Chalicotherioidea; **Depere.,** Deperetellidae; **H.,** Hyracodontidae; **Helalet.,** Helaletidae; ***Hy.*,** *Hyrachyus*; **IM,** Irdin Manha Formation; and **Para.,** Paraceratheriidae.

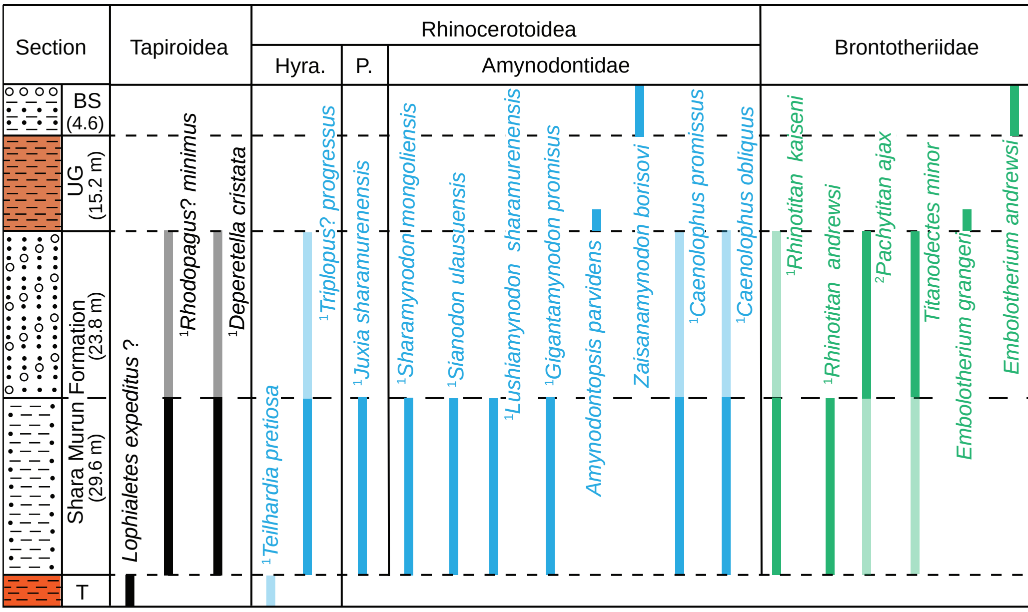


FIG. 4. Stratigraphic distributions of perissodactyl fossils and taxa in the Tukhum, Shara Murun, Ulan Gochu, and Baron Sog formations at Baron Sog Mesa. The profile of the section is based on the sketch at Xilin Nor North (= 4 mi north of Baron Sog Mesa) (Granger, 1925, see also Wang et al., 2012, fig. 2A). The superscripts in front of taxon names indicate the localities of the holotypes: numbers 1, and 2 refer to Ula Usu and 4 mi north of Baron Sog Mesa, respectively. Abbreviations: **BS**, Baron Sog Formation; **Hyra.**, Hyracodontidae; **P.**, Paraceratheriidae; **T**, Tukhum Formation; and **UG**, Ulan Gochu Formation.

homogenous and roughly correlated to the Irdinmanhan (Radinsky, 1964a; Ye, 1983; Wang et al., 2012). However, recent investigation suggests that the upper part of the section probably belongs to the Sharamurunian (Li et al., 2016a), and the basal part may extend down into the Arshantan (Mao and Wang, 2012; Bai et al., 2018a).

Assuming that most previous collections from Wulanhuxiu and Wulantaolegai are from a relatively lower horizon (roughly equivalent to the "white member"), the lower part of the Ulan Shireh Formation can be correlated with the Irdin Manha Formation based on their shared species (fig. 3; appendix 1) including lophialetids *Lophialetes expeditus*, *Zhongjianoletes chowi*, and *Rhodopagus pygmaeus*, the deperetellid *Teleolophus medius*, the hyracodontid *Triplopus proficiens*, the paraceratheriid *Fostercooperia ulanshirhensis*, and the brontotheriid *Microtitan mongoliensis*. They also share the lophialetid genera *Simplaletes* and *Breviodon*. The brontothere *Metatitan primus* has been reported from the Big Red Draw and North Promontory in North Mesa, and similarly, many specimens *Metatitan relictus* have been found in the Irdin Manha Formation near Camp Margetts. However, the Irdin Manha Formation also bears the paraceratheriid *Forstercooperia totadentata*, helaletids, and some brontotheres that have not been reported yet or are different from those of the Ulan Shireh Formation. *Teleolophus medius*? also has been reported from the middle horizon of upper part of the Ulan Shireh Formation ("red member") at Wulanhuxiu (Bai et al., 2018a).

Comments on the Shara Murun and Ulan Gochu Formations

The Shara Murun Formation at Baron Sog Mesa was mentioned first by Berkey and Granger (1923) without description. Berkey and Morris (1927) formally named the Shara Murun Formation as consisting of two members: an upper member dominated by white and light-gray sandstone with gravels; and a lower member dominated by sandy clay with varied colors (Berkey and Morris, 1927; Wang et al., 2012) (fig. 4, 7A; see also Wang et al., 2012: fig. 2A). Later, the "Shara Murun Formation" also was applied to some strata at East Mesa, Erden Obo, and Nom Khong Obo (Osborn, 1929; Qi, 1990b). However, these correlations remain controversial (Wang et al., 2012). For the sake of clarity, we listed perissodactyls from the Shara Murun Formation exclusively at Baron Sog Mesa (fig. 4).

Though the mammalian fauna from the Shara Murun Formation is considered to be homogeneous, species may be recovered from different members and represent different evolutionary stages. This hypothesis is supported by the fact that the brontotheres *Titanodectes minor* and *Pachytitan ajax* are considered more advanced than *Rhinotitan*, resembling *Embolotherium* to some extent (Granger and Gregory, 1943; Mihlbachler, 2008), and their co-occurrence in a single horizon seems improbable. *Rhinotitan*, *Juxia sharamurenensis*, and various amynodontids collected by SSPE were found in the lower part of the Shara Murun Formation near the Well of Ula Usu (Chow and Rozhdestvensky, 1960). On the other hand, both *Titanodectes minor* and *Pachytitan ajax* were recorded from the "gray beds" of the Shara Murun Formation, 4 mi north of Baron Sog Mesa, and that horizon is more likely to be in the upper, gray and white, member rather than a lower, red and brown, member (Berkey et al., 1929: fig. 4; Wang et al., 2012: fig. 2A). Thus, it is reasonable to infer that the mammalian faunas from the lower and upper parts of the Shara Murun Formation are probably heterogeneous, and they should be treated with caution.

The Ulan Gochu Formation was named by Berkey et al. (1929) as a wedge-shaped mass of red clay along the Baron Sog Mesa (fig. 7B). The Ulan Gochu Formation overlies the Shara Murun Formation, and is overlain by the Baron Sog Formation. The "Ulan Gochu Formation" later was expanded to include a much wider extension of the strata at Erden Obo and Nom Khong Obo (Osborn, 1929), and its boundaries with the underlying "Shara Murun Formation" are uncertain in these areas. The previous mammalian fauna from the "Ulan Gochu Formation" is mainly from East Mesa (Twin Obos and Jhama Obo) and/or Erden Obo (Li and Ting, 1983; Russell and Zhai, 1987; Tsubamoto et al., 2004). For the sake of clarity, we consider the perissodactyls of Ulan Gochu Formation exclusively from Baron Sog Mesa where the formation was named. Only *Embolotherium grangeri* and *Amynodontopsis parvidens* have been reported from typical Ulan Gochu Formation outcrops (Osborn, 1929; Granger and Gregory, 1943; Mihlbachler, 2008). Interestingly, *Titanodectes minor* from the upper part of the Shara Murun Formation even was considered to be a synonym of *Embolotherium grangeri* (Mihlbachler, 2008), indicating that the perissodactyls from the upper part of the Shara Murun Formation are more similar to those from the overlying Ulan Gochu Formation than to those from the lower part of the Shara Murun Formation.

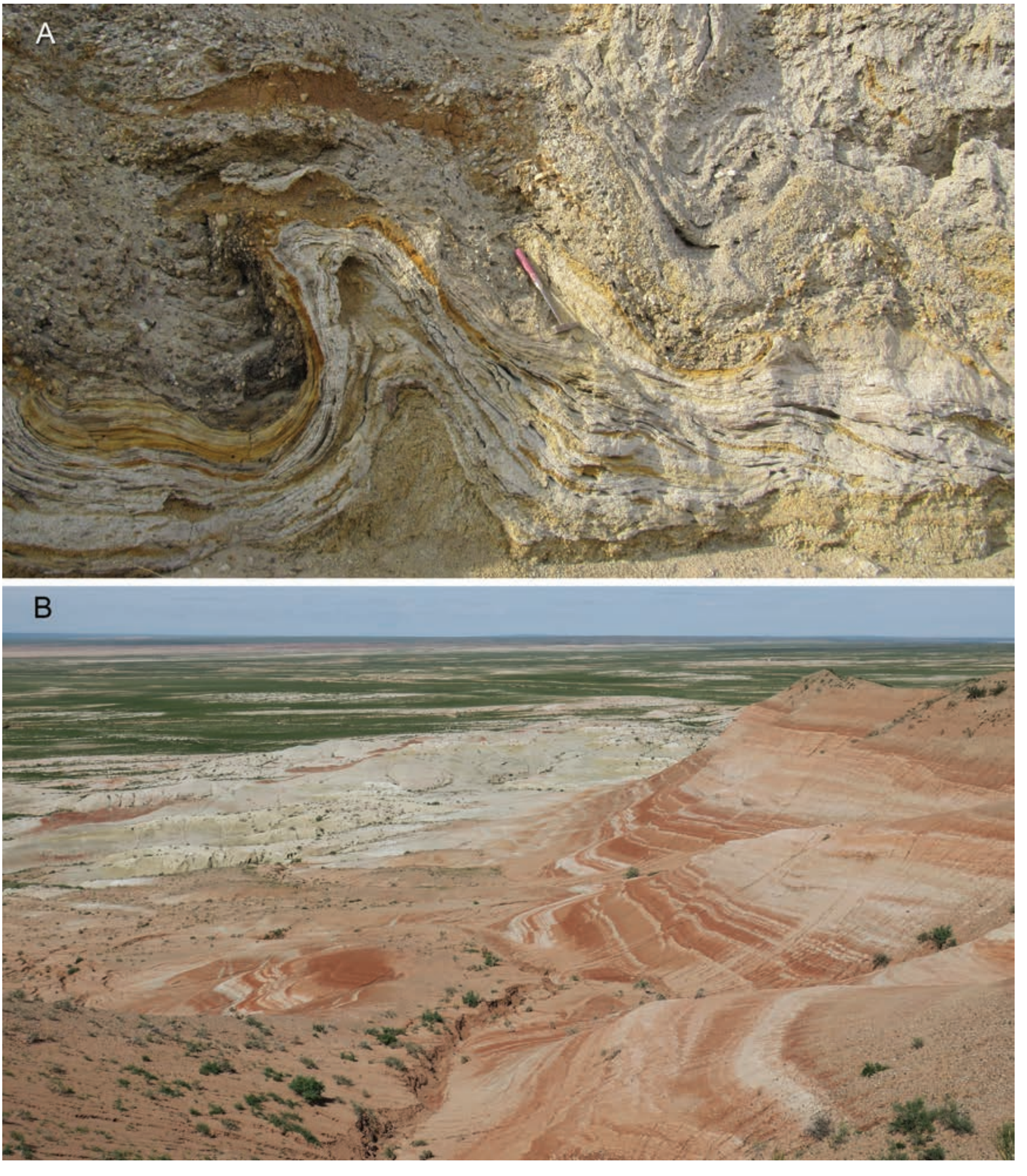


FIG. 5. Paleogene outcrops on the Houldjin escarpment and Wulanhuxiu (= Chimney Butte, 8 mi north of the Tukhum Lamasery): **A**, the yellow and gray, pebbly gravels of the Houldjin Formation on the Houldjin escarpment near the Erenhot Railway Station; **B**, the outcrops at Wulanhuxiu, showing a steep, upper "red member" and a gradual, lower "white member."

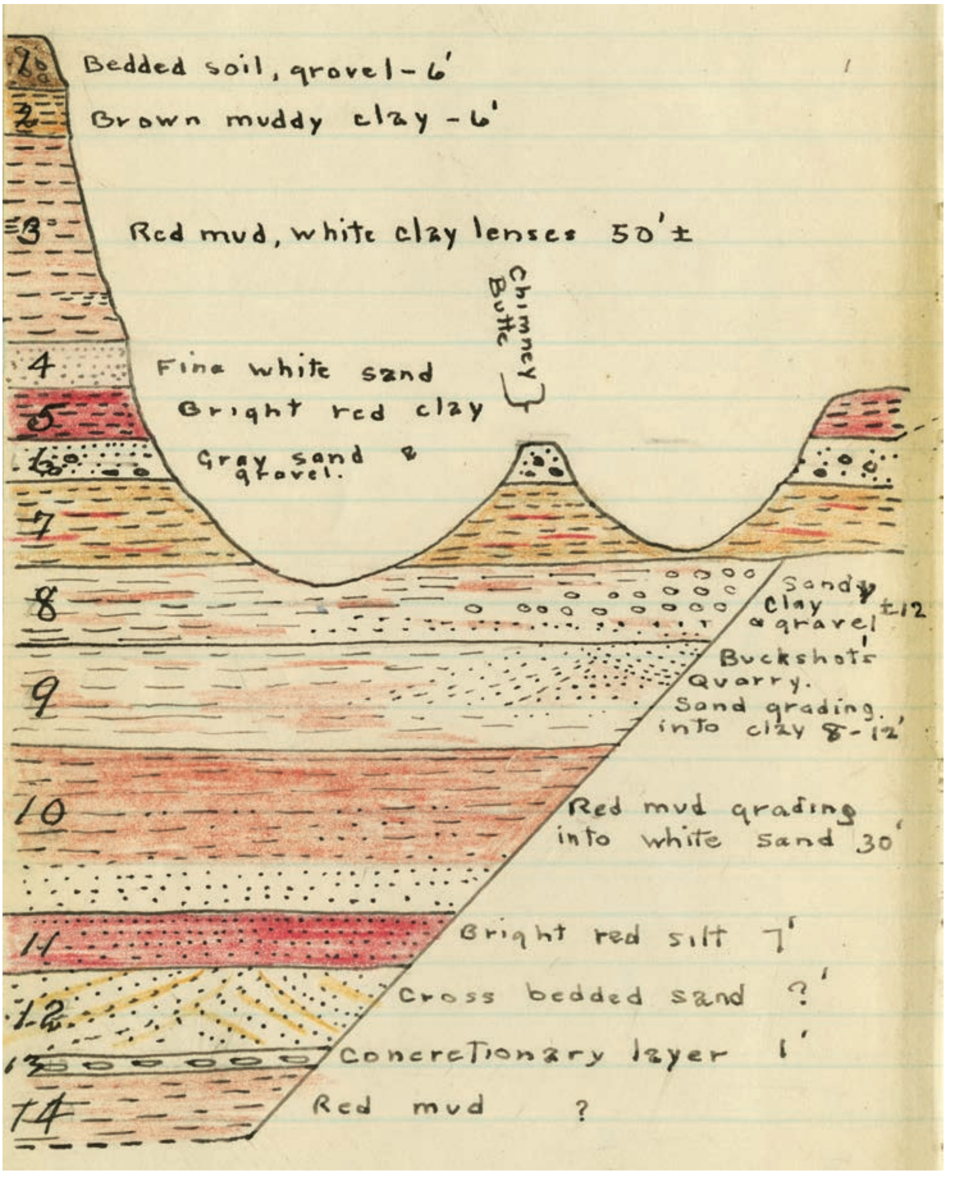


FIG. 6. Sketch profile from Wulanhuxiu (= Chimney Butte, 8 mi north of Tukhum Lamasery) at North Mesa (Granger, 1928: 6). The layers 3–5 are grouped into an upper "red member", and the layers 6–14 are grouped into a lower "white member."

FIG. 7. Paleogene outcrops in the Shara Murun region: **A**, the outcrops at Ula Usu, where the Shara Murun Formation was named, showing an upper member dominated by white sandstones and a lower member dominated by sandy clays with varied colors; **B**, the outcrops at Xilin Nor North (= 4 mi north of Baron Sog Lamasery), showing the red clays of the Ulan Gochu Formation overlying the grayish white sandstones of the upper part of the Shara Murun Formation.

Correlation of the Erden Obo section

Osborn (1929) first reported the Erden Obo (= Urtyn Obo) section based on Granger's (1928) sketch, and divided the section into eight units from the bottom to the top: "Basal Red," "Basal White," "Lower Red," "Lower White" (19.8 m), "Middle Red" (21.3 m), "Middle White or Gray" (9.1 m), "Upper Red" (29.0 m), and "Upper White" (7.6 m) (figs. 8, 9). Osborn (1929) correlated the "Basal Red" to the "?Arshanto Formation," the "Basal White" to the "Shara Murun Formation," the upper part of the "Lower White" to the "Upper Red" collectively to the "Ulan Gochu Formation," and the "Upper White" to the "Baron Sog Formation." The "Lower Red" and the lower part of the "Lower White" were considered either the "Shara Murun" and/or "Ulan Gochu" formations. Different correlations of the Erden Obo section in the Erlian Basin have been proposed since Osborn (1929), and were reviewed in detail by Wang et al. (2012). Among them, Jiang (1983) measured and divided the section of Erden Obo into 23 layers, and proposed several new lithological units for the sediments. However, Qi (1990b) applied conventional formational names to the deposits based on the same division of layers of Jiang (1983). Wang et al. (2012) suggested that the "Basal Red" should be Nomogen Formation and the "Upper White" should be the Upper Naogangdai Formation, and the correlation of other layers at Erden Obo remains unclear. Various perissodactyl fossils have been reported from different units at Erden Obo with the exception of the "Basal Red," and they can contribute to a refinement of the biostratigraphic correlation with other type localities in the Erlian Basin.

The "Basal Red" layer is equivalent to layers 1–4 of Jiang's section, and is dominated by light brownish-red sandy mudstones (Jiang, 1983; Qi, 1990b). The "Basal White" layer is equivalent to layers 5–6 of Jiang's section, and is dominated by grayish white, light-green coarse sandstones and grayish white siltstones and fine sandstones (Jiang, 1983; Qi, 1990b). Recently, on the basis of rodent fossils, Li et al. (2018) correlated upper part of the "Basal Red" to the Nomogen Formation of Bumbanian age, and they further correlated the lower part and middle part of "Basal White" to the upper part of the Arshanto Formation and lower part of the Irdin Manha Formation, respectively. Similarly, Mao and Wang (2012) mentioned the presence of the Arshantan coryphodontid *Eudinoceras mongoliensis* from the base of "Basal White." Among the perissodactyls, both *Schlosseria magister* and *Lophialetes expeditus*? have been reported from the "Basal White" (fig. 10) (Radinsky, 1965; Li and Wang, 2010), supporting the correlation of the bed with both the Arshanto and Irdin Manha formations as suggested by Li et al. (2017). However, whether the two species are from different horizons is unknown. In recent fieldwork, we collected a partial skull of a relatively primitive deperetellid, which is similar to those from the Arshanto Formation, from the lower part of "Basal White," in addition to specimens of cranial material of the Irdinmanhan *Teleolophus medius* from the middle part of "Basal White."

The "Lower Red" layer is usually considered to be equivalent to layer 7 of Jiang's section, which is dominated by light brick-red sandy clays (Jiang, 1983; Qi, 1990b). However, we consider the "Lower Red" layer also to include the overlying layer 8 of Jiang's section, which is dominated by mudstones with variable colors (see discussion below) (Jiang, 1983; Qi, 1990b). Qi et al. (1992) referred a single m3 and some postcrania to *Protitan* sp. from so-called "Tukhum Formation" (layer 7 of Jiang's section), which is equivalent to a part of the "Lower

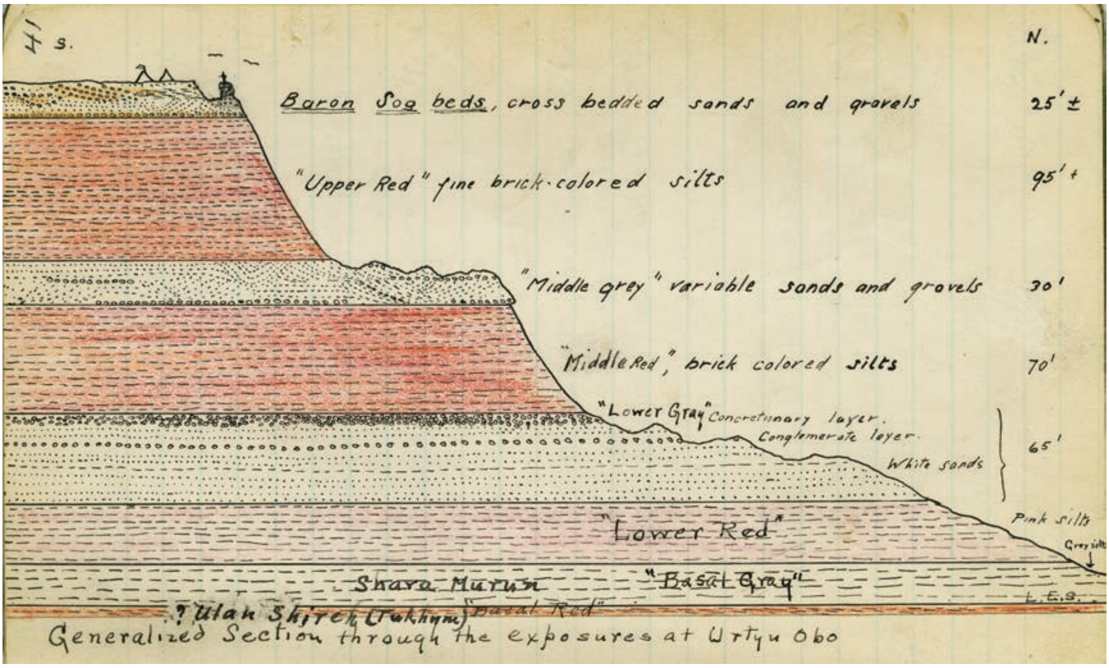


FIG. 8. Sketch profile from Erden Obo (= Urtyn Obo) (Granger, 1928: 41).

Red" bed (Wang et al., 2012) (fig. 10). However, Qi et al. (1992) noted that the m3 also is similar to that of *Rhinotitan*. Our recent fieldwork uncovered *Caenolophus promissus* and *Teilhardia pretiosa* from the "Lower Red" layer. The type specimen of *C. promissus* is known from the Shara Murun Formation, but that of *T. pretiosa* is recorded from the underlying Tukhum Formation at Ula Usu (Matthew and Granger, 1925b; 1926) (fig. 4). However, the horizon bearing *Teilhardia pretiosa* is controversial (Wang et al., 2012). In addition to perissodactyl fossils, the "Lower Red" bed also bears the lagomorph *Gobiolagus aliwusuensis* (Fostowicz-Frelik et al., 2012), and the rodents *Gobiomys exiguus*, *Gobiomys neimongolensis*, and *Yuomys magnus* (Li, 2017). *Gobiolagus* and the type specimens of *Gobiomys neimongolensis* are considered to be Sharamurnian in age (Meng et al., 2005; Fostowicz-Frelik et al., 2012; Li, 2017). As a result, the "Lower Red" bed is most likely correlative to the lower member of the Shara Murun Formation (Qiu and Wang, 2007).

According to Granger's (1928) sketch, the "Lower Gray" is composed mainly of "white sands" with a "conglomerate layer" in the upper part and a "concretionary layer" at the top (figs. 8, 9A) (Wang et al., 2012: fig. 2B). The base of the "Lower White" first was considered to be equivalent to layer 10 of Jiang's section and correlated to the upper part of the Shara Murun Formation (Wang, 2001). Wang (2007a) later considered the "Lower White" to be equivalent to layers 8–9 and 10–13 of Jiang's section, and grouped the "Lower White" into the "Ulan Gochu Formation," spanning from the "Lower White" to "Upper Red" (Qiu and Wang, 2007; Wang et al., 2012). Although Wang (2007a) noted that layers 8–9 of Jiang's section are same as layers 10–13 in lithology (grayish white sandstone), the layer 9 is mainly dominated by the

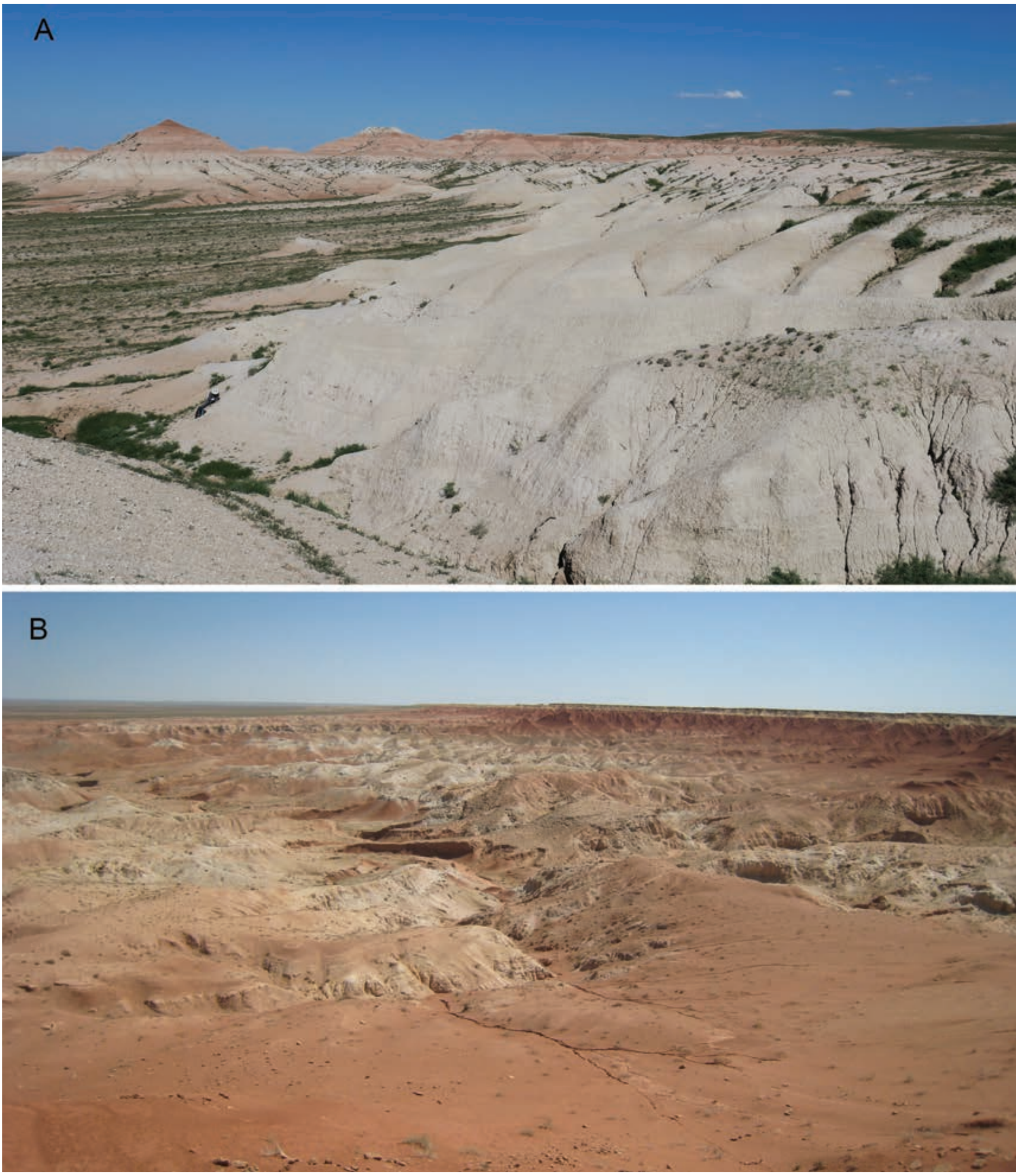


FIG. 9. Paleogene outcrops at Erden Obo: **A**, the outcrops of the "Lower Red," "Lower White," and "Middle Red." The lower-right part of the photo is mainly the "Lower White," which overlies the "Lower Red" and is overlain by the "Middle Red" as shown by the hill, far left; **B**, the outcrops of the "Middle Red," "Middle White," "Upper Red," and "Upper White." The lower-right part of the photo is mainly the basal part of the "Upper Red," which overlies the "Middle White" and is overlain by the "Upper White (or yellow)." The top of the "Upper White" forms the Gobi surface.

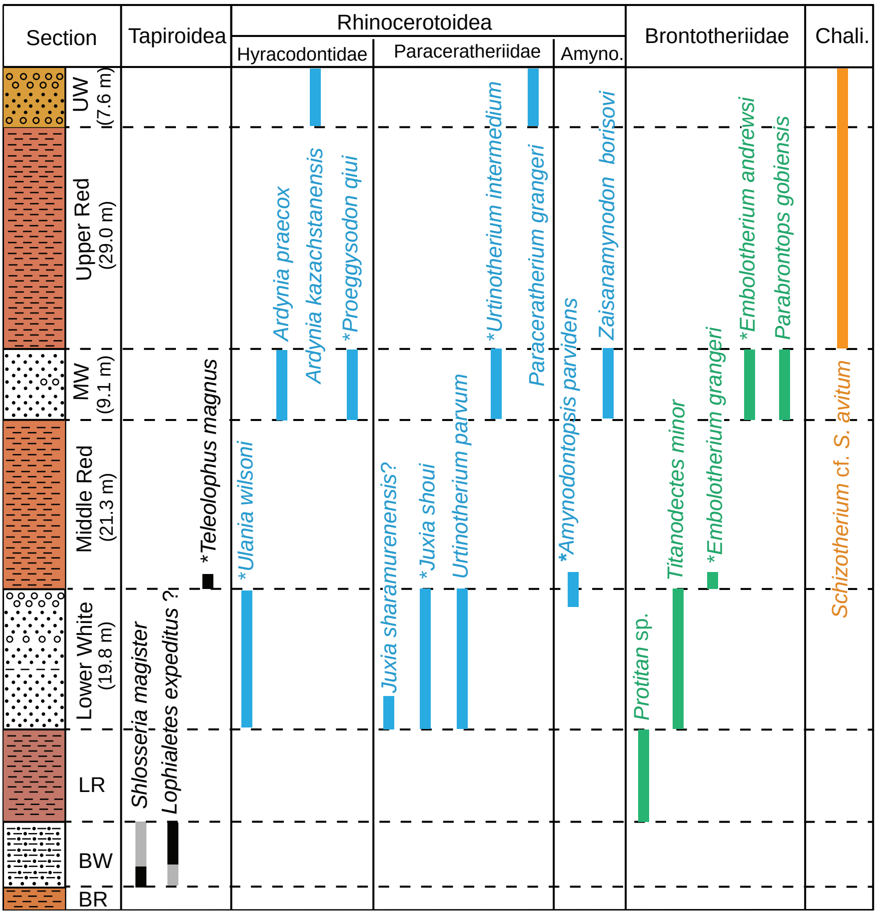


FIG. 10. Stratigraphic distributions of perissodactyl fossils and taxa from Erden Obo. The profile of section is based on the sketch by Granger (1928) and modified from Li (2017). The asterisks in front of taxa indicate where the holotype occurred in the section. Abbreviations: **Amyno.**, Amynodontidae; **BR**, Basal Red; **BW**, Basal White; **Chali.**, Chalicotherioidea; **LR**, Lower Red; **MW**, Middle White; and **UW**, Upper White.

grayish green mudstones with two lens of feldspathic quartz coarse sandstones (fig. 9A) (Jiang, 1983). Based on our recent fieldwork, we regard the "Lower White" as likely equivalent to layers 9–10 of Jiang's section (Jiang, 1983; Qi, 1990b).

The perissodactyl fossils from the "Lower White" include five genera and six species (fig. 10). *Juxia sharamurenensis* (AMNH FM 26753, field no. 734) is recorded from the base of the "Lower White" (Radinsky, 1967), and *Amynodontopsis parvidens* is known from the top of "Lower White," and by abundant material from the base of overlying "Middle Red" bed. *Urtinotherium parvum* is known from the "Lower White" with IVPP field number 199102, which is the same horizon as IVPP field number 199104 bearing abundant small mammals according to B.Y. Wang's field notes. The horizon bearing *Ulania wilsoni* was reported as the base of "Ulan Gochu Formation" with a grayish green sandstone (Qi, 1990a), most likely is the "Lower White" (Qi, 1990b). The horizon producing the type of *Juxia shoui* was reported as the "Ulan Gochu Formation" (Qi and Zhou, 1989). However, Qiu and Wang (2007) suggested that layer may be the "Lower White" based on a lunar found in that layer, which presumably belong to *J. shoui*. *Titanodectes minor* (AMNH FM 26061, field no. 769) also was reported from the base of the "Lower White" and probably unearthed from the base according to Osborn's sketch (Osborn, 1929: fig. 2). Thus, the "Lower White" has produced *Amynodontopsis parvidens*, *Urtinotherium parvum*, *Juxia shoui*, *J. sharamurenensis*?, *Ulania*, and *Titanodectes minor*. It is necessary to note that whether the mandible with p2, p4–m3 (AMNH FM 26753) should be assigned to *Juxia sharamurenensis* remains controversial, because *J. shoui*, which is preserved only as a partial skull with a similar size, is also present in the same layer (Qi and Zhou, 1989). Considering that *Urtinotherium parvum* and *Juxia shoui* are more derived than *J. sharamurenensis* from the lower member of the Shara Murun Formation, and *Titanodectes minor* also is known from the upper member of the Shara Murun Formation, we believe that the "Lower White" can be correlated with the upper member of the Shara Murun, as suggested by Wang (2001).

In addition to perissodactyl fossils, various small mammalian fossils have been reported from the "Lower White," including the rodents *Gobiomys exiguus*, *G. asiaticus* (Wang, 2001), *Pappocricetodon antiquus*, *P*. sp., and *P*.? sp. (Wang, 2007b), the lagomorph *Desmatolagus vetustus* (Wang, 2007a), the primate *Eosimias* sp. (Wang, 2008b), the insectivores *Anatolechinos neimongolensis* and Erinaceidae gen. et sp. indet., and an indeterminate chiropteran (Microchiroptera) (Wang, 2008a). All the small mammalian fossils were collected from a single pocket (IVPP Loc. 1991004), dominated by grayish-white sandstone with conglomerates. The horizon is considered to be equivalent to layer 10 of Jiang's section (Jiang, 1983; Wang, 2001), belonging to the "Lower White."

The "Middle Red" layer has been considered equivalent to layers 14–15 of Jiang's (1983) section (Qiu and Wang, 2007; Wang et al., 2012). However, the "Middle Red" layer is more likely equivalent to layers 11–15 of Jiang's section, which is dominated by light brick-red silty mudstones and deep brownish red mudstones with grayish-white fine sandstone and siltstone at the base (fig. 9A) (Jiang, 1983; Qi, 1990b). The perissodactyl fossils from the "Middle Red" are relatively rare, and all were discovered from the base of the unit. These taxa include *Teleolophus magnum*, *Amynodontopsis parvidens*, and *Embolotherium grangeri* (Osborn, 1929; Radinsky, 1965; Wall, 1981; Mihlbachler, 2008) (fig. 10). The latter two species also are known from the base of the Ulan Gochu Formation at Baron Sog Mesa, and considering *Embolotherium loucksii* as a junior synonym of *E. grangeri* (Mihlbachler, 2008) (fig. 4). Thus, the "Middle Red" is likely correlative to the Ulan Gochu Formation at Baron Sog Mesa (Qi, 1990b; Qiu and Wang, 2007). The rodents *Gobiomys exiguus* and *G. neimongolensis* have been reported from "Middle Red" (Li, 2017). However, only the cylindrodont *Ardynomys olsoni* has been reported from the Ulan Gochu Formation, 4 mi north of Baron Sog Mesa (Wang and Meng, 2009). It is noteworthy that the perissodactyls from the "Lower White" are more similar to those from the overlying "Middle Red" in sharing *Amynodontopsis parvidens* and similar brontothere taxa than to those from underlying "Lower Red."

The "Middle White" layer is equivalent to layers 16–17 of Jiang's section (Qiu and Wang, 2007; Wang et al., 2012), which is dominated by grayish white sandstones with gravels (fig. 9B) (Jiang, 1983; Qi, 1990b). The "Middle White" has a relatively diverse set of perissodactyl fossils (fig. 10), including *Ardynia praecox* (Radinsky, 1967; Bai et al., 2018b), *Proeggysodon qiui* (Bai and Wang, 2012), *Urtinotherium intermedium* (Chow and Qiu, 1963; Qiu and Wang, 2007), *Zaisanamynodon borisovi* (Lucas et al., 1996), *Embolotherium andrewsi*, and *Parabrontops gobiensis* (Osborn, 1925; Osborn, 1929; Granger and Gregory, 1943; Mihlbachler, 2008). *Zaisanamynodon borisovi* and *E. andrewsi* (= *E. ultimum*) also are known from the Barson Sog Formation at Baron Sog Mesa (Granger and Gregory, 1943; Lucas et al., 1996; Mihlbachler, 2008) (fig. 4). In addition, the artiodactyl *Lophiomeryx anagare* was recorded from both the "Middle White" bed (AMNH FM 26259, field no. 752) and the Baron Sog Formation at Baron Sog Mesa (AMNH FM 22113, field no. 593) (Wang, 2003). Thus, the "Middle White" can be correlated with the Baron Sog Formation, partly in agreement with Qi (1990b)'s proposal. Recently, Li (2017) reported the presence of the rodent *Gobiomys neimogolensis* in the "Middle White."

The "Upper Red" layer is equivalent to layers 18–20 of Jiang's (1983) section, which is dominated by variegated mudstones, brick-red sandy clays with calcareous nodules, and deep brownish red, bright red mudstones (fig. 9B) (Jiang, 1983; Qi, 1990b). Jiang (1983) named the Lower Naogangdai Formation for both the "Middle White" and "Upper Red" layers. Only the chalicothere *Schizotherium* cf. *S. avitum* is known from "Upper Red" (Coombs, 1978) (fig. 10). In contrast, rodent fossils are relatively much more diverse, including cricetids (*Eucricetodon wangae*, *E.* sp., and *Pappocricetodon siziwangqiensis*), dipodids (*Heosminthus nomogenesis*, *Sinosminthus* sp., *Allosminthus* cf. *A. majusculus*, *Allosminthus ernos*, and *A.* cf. *A. diconjugatus*), and ctenodactyloids (*Gobiomys exiguus*, and *G. neimongolensis*) mainly from the lower and middle parts of the "Upper Red" beds (Li et al., 2016a, 2016b, 2016c; 2017). Li et al. (2016b, 2016c) suggested that the "Upper Red" is the late Eocene and correlative with the Ergilian.

The "Upper White" layer is equivalent to layers 21–23 of Jiang's section, which is dominated by grayish white, yellow coarse sandstones, liver-colored mudstone, and loose yellow sandy gravels (fig. 9B) (Jiang, 1983; Qi, 1990b). Jiang (1983) named the Upper Naogangdai Formation for the "Upper White" layer. Considering that the "Upper White" bed at Erden Obo can be correlated to that at Nom Khong (Wang, 2003), the perissodactyl fossils from the "Upper White" of both localities include *Ardynia kazachstanensis*, *Paraceratherium grangeri*, *Zaisanamynodon borisovi*, and *Schizotherium* cf. *S. avitum* (Coombs, 1978; Lucas et al., 1996; Wang, 2003) (fig. 10). In addition, tsaganomyid rodents *Tsaganomys altaicus* and *Cyclomylus intermedius* have been reported from the bed (Wang, 2003). The "Upper White" is considered to be late early Oligocene in age and different from the "Baron Sog Formation" (Wang, 2003), which is correlative to the underlying "Middle White." The late early Oligocene age for the "Upper White" is further supported by the occurrence of *Ardynia kazachstanensis*, the type specimen of which was unearthed from the late early Oligocene deposits of Chelkar Teniz, Kazakhstan (Russell and Zhai, 1987; Qiu et al., 2004; Bai et al., 2018b). Although *Zaisanamynodon borisovi* is indicative of the late Eocene Ergilian, material of the species from the "Upper White" is represented only by a symphysis with i2 and canine (AMNH FM 26170) (Lucas et al., 1996), which is too incomplete to allow a confident taxonomic assignment.

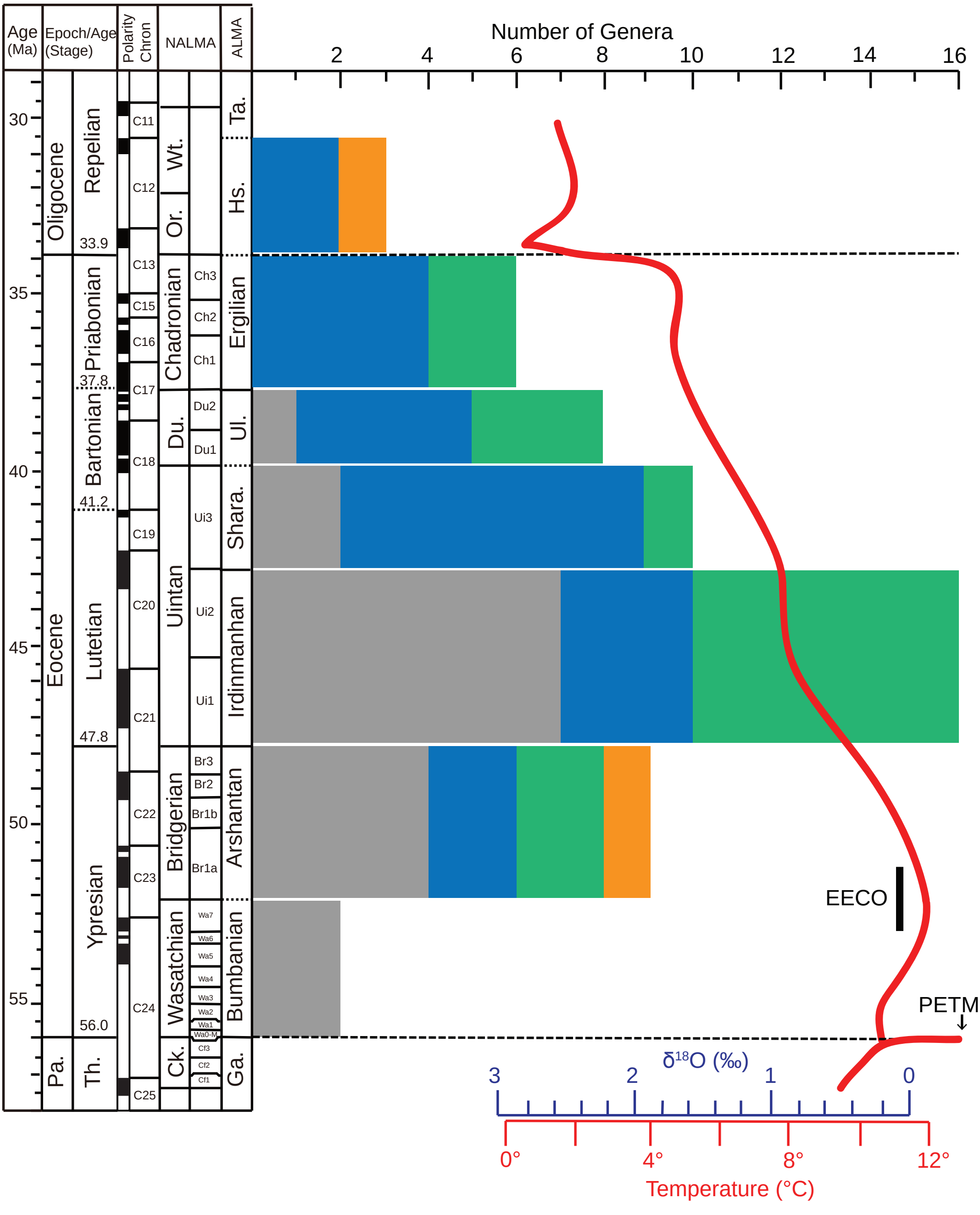
Diversity of Perissodactyls during Paleogene ALMAs

In the Gashantan, only some fragmentary teeth have been assigned to Perissodactyla without further determination (Meng et al., 1998). However, Meng et al. (1998) noted their similarities with the brontothere *Lambdotherium*. However, Tong et al. (2004) considered these materials to be similar to the condylarth *Olbitherium*.

In the early Eocene Bumbanian (Bowen et al., 2005; Ting et al., 2011), the lophialetid *Minchenoletes erlianensis* and presumably the hyracodontid *Pataecops parvus* are known (Wang et al., 2011) (fig. 11). However, *Pataecops* initially was included in the Lophialetidae (Radinsky, 1965).

Perissodactyls from the middle Eocene Arshantan are dominated by members of Tapiroidea (figs. 3, 11), including lophialetids (*Schlosseria magister* and *Breviodon* cf. *B. acares*), deperetellids (*Teleolophus primaries* and *T.*? *rectus*), and the helaletid *Heptodon minimus*. The basal rhinocerotoid *Hyrachyus* and paraceratheriid *Pappaceras* also appeared in the Arshantan, but chalicotheres are represented only by *Litolophus gobiensis* from the base of the Arshanto Formation (Colbert, 1934; Bai et al., 2010; 2011a). Brontotheres are scarce with only some fragmentary material of *Microtitan* and *Desmatotitan* known (Qi, 1987). However, there is question as to whether those brontotheres were recovered in the Arshanto Formation. Based on our recent fieldwork, some new taxa of ceratomorphs have been found in the Arshanto Formation, indicating that the current diversity of perissodactyls in the Arshantan is probably underestimated. The Arshantan is usually correlated to the Bridgerian NALMA (Tong et al., 1995; Wang et al., 2007; Sun et al., 2009). Furthermore, the fauna from the upper part of Arshanto Formation exhibits some transitional features. *Schlosseria magister* and the coryphodontid *Eudinoceras* represent handover taxa from earlier strata, but the appearances of *Pappaceras* and *Simplicimys bellus* are indicative of a close relationship with that of the overlying Irdin Manha Formation (Li and Wang, 2010; Mao and Wang, 2012; Li and Meng, 2015; Wang et al., 2016).

The correlation of the Ulan Shireh Formation is still debatable, although we propose correlating it with the Irdin Manhan Formation. The perissodactyls from the Irdinmanhan are restricted to those from type Irdin Manha escarpment and Huheboerhe area. In the Irdinmanhan, perissodactyls reached their highest diversity and were dominated by brontotheres (figs. 3, 11), including six genera and seven species: *Microtitan mongoliensis*, *Hyotitan thomsoni*, *Metatelmatherium ultimum*, *M. parvum*, *Protitan grangeri*, *P. minor*, *P.*? *cingulatus*, *Gnathotitan berkeyi*, and *Metatitan relictus*. It is interesting to note that a large number of specimens of *Protitan grangeri* are known from Irdin Manha escarpment, and the contemporaneous *Metatitan relictus* is common at Duheminboerhe. Tapiroids from the Irdinmanhan become more diverse than those from the Arshantan, and they include seven genera and species: lophialetids (*Lophialetes expeditus*, *Simplaletes sujiensis*, *Breviodon minutus*, and ?*Rhodopagus pygmaeus*), the deperetellid *Teleolophus medius*, and helaletids (*Desmatotherium mongoliense* and *Paracolodon fissus*). Paraceratheriids are represented by *Forstercooperia totadentata* and *F. ulanshirhensis*. The hyracodontid *Triplopus* and amynodontid *Rostriamynodon* emerged during the Irdinmanhan. Bai et al. (2017) correlated the Irdinmanhan roughly with Ui1 and Ui2 subages of the Uintan NALMA based solely on perissodactyl fossils. Similarly, based on the small mam-


Age (Ma)
Epoch/Age (Stage)
Polarity Chron
NALMA
ALMA
Number of Genera
2 4 6 8 10 12 14 16
30 35 40 45 50 55
Oligocene
Eocene
Pa.
Repelian
Priabonian
Bartonian
Lutetian
Ypresian
Th.
33.9
37.8
41.2
47.8
56.0
C11 C12 C13 C15 C16 C17 C18 C19 C20 C21 C22 C23 C24 C25
Wt.
Or.
Chadronian
Du.
Uintan
Bridgerian
Wasatchian
Ck.
Ch3 Ch2 Ch1 Du2 Du1 Ui3 Ui2 Ui1 Br3 Br2 Br1b Br1a
Ta.
Hs.
Ergilian
Ul.
Shara.
Irdinmanhan
Arshantan
Bumbanian
Ga.
EECO
PETM
δ18O (‰)
3 2 1 0
0° 4° 8° 12°
Temperature (°C)

mals from the lower fossil-bearing horizon of the Hetaoyuan Formation in the Liguanqiang Basin, Tong (1997) suggested that Irdinmanhan can be correlated to the early Uintan NALMA.

The Sharamurunian and Ulangochuan are complex issues to address. As discussed above, the perissodactyls from the upper member of the Shara Murun Formation and "Lower White" of the Erden Obo are more similar to those from the overlying Ulan Gochu Formation and "Middle Red," respectively, than to those from their underlying strata. However, previously the Sharamurunian probably was based largely on the entire fauna from both the lower and upper members of the Shara Murun Formation, although most fossils likely were found in the lower member (Russell and Zhai, 1987). On the other hand, previously the Ulangochuan mainly was based on the fauna from East Mesa and Erden Obo rather than those from the type Baron Sog Mesa (Russell and Zhai, 1987), and was a mixture of faunas from various ages and horizons. The following discussion on the Sharamurunian and Ulangochuan is based on the perissodactyls from Baron Sog Mesa and Erden Obo. However, the material from Twin Obos, Jhama Obo and nearby localities, and Nom Khong Obo were excluded, pending further investigation and correlation.

Perissodactyls from the lower member of the original Shara Murun Formation and "Lower Red" of the Erden Obo (both may represent restricted Sharamurunian) are dominated by amynodontids (figs. 4, 10, 11), comprising five genera and six species: *Sharamynodon mongoliensis*, *Sianodon ulausuensis*, *Lushiamynodon sharamurenensis*, *Gigantamynodon promisus*, *Caenolophus promissus*, and *C. obliquus* (Matthew and Granger, 1925b; Osborn, 1936; Xu, 1966). However, Wall (1989) suggested that *Lushiamynodon* and some species of *Sianodon* should be placed in *Sharamynodon*, and *Gigantamynodon* likely is a nomen dubium. Tapiroidea is restricted to two species: the lophialetid *Rhodopagus*? *minimus* and the deperetellid *Deperetella cristata* (Radinsky, 1965). The hyracodontid *Triplopus*? *progressus* and the paraceratheriid *Juxia sharamurenensis* also are known (Radinsky, 1967; Qiu and Wang, 2007). The brontotheriidae is represented by *Rhinotitan kaiseni* and *R. andrewsi* (Granger and Gregory, 1943; Mihlbachler, 2008). The Sharamurunian is usually correlated to the late Uintan and Duchesnean NALMAs (Wang et al., 2007; Vandenberghe et al., 2012). However, Wang (1982) correlated the Sharamurunian with the late Uintan NALMA (Ui3) based on the similar evolutionary stage between *Rhinotitan andrewsi* and the late Uintan (Ui3) *Protitanotherium* (Robinson et al., 2004; Mihlbachler, 2008; Gunnell et al., 2009).

Regarding the perissodactyls from the upper member of the original Shara Murun Formation, overlying Ulan Gochu Formation, and the "Lower White" and "Middle Red" of the Erden Obo (all may represent restricted Ulangochuan), the diversity of tapiroids radically decreased over time with

←

FIG. 11. The diversity of perissodactyl fossils in the Erlian Basin from the early Eocene to the early Oligocene with superimposed reconstructed temperature curves, and revised correlation between the Eocene Asian Land Mammal Ages (ALMA) and North American Land Mammal Ages (NALMA). The left column showing magnetic Polarity Chrons and NALMAs modified from Vandenberghe et al. (2012). The average global temperature curve was derived from stable oxygen isotopes and is modified from Zachos et al. (2001). The gray, blue, green, and orange areas represent Tapiroidea, Rhinocerotoidea, Brontotheriidae, and Chalicotherioidea, respectively. Abbreviations: **Ck.**, Clarkforkian; **Du.**, Duchesnean; **EECO**, Early Eocene Climatic Optimum; **Ga.**, Gashatan; **Hs.**, Hsandagolian; **Or.**, Orellan; **Pa.**, Paleocene; **PETM**, Paleocene-Eocene Thermal Maximum; **Shara.**, Sharamurunian; **Ta.**, Tabenbulakian; **Th.**, Thanetian; **Ul.**, Ulangochuian; and **Wt.**, Whitneyan.

only the deperetellid *Teleolophus magnum* remaining. The hyracodontid *Ulania wilsoni* and abundant amynodontid *Amynodontopsis parvidens* were present (figs. 4, 10, 11). Paraceratheres are represented by the more advanced *Juxia shoui and Urtinotherium parvum* rather than the underlying *Juxia sharamurenensis* (Qiu and Wang, 2007). Brontotheres are slightly more diverse than those from the restricted Sharamurunan, including *Pachytitan ajax*, *Titanodectes minor*, and *Embolotherium grangeri* (Granger and Gregory, 1943; Mihlbachler, 2008). Among perissodactyls from the restricted Ulangochuan, only *Amynodontopsis* is distributed in North America as the genotype *A. bodei* (Stock, 1933; Wall, 1989). Ulangochuan is usually correlated to the early Chadronian NALMA (Wang et al., 2007; Vandenberghe et al., 2012). However, considering that *Amynodontopsis* is known only from the Duchesnean NALMA (Lucas, 1992; Robinson et al., 2004), we tentatively correlate the restricted Ulangochuan with the whole Duchesnean NALMA.

The fauna from the Baron Sog Formation and the equivalent the "Middle White" of Erden Obo contain roughly equally diverse perissodactyl faunas as those from the Ulangochuan (figs. 4, 10, 11), including brontotheriids (*Embolotherium andrewsi* and *Parabrontops gobiensis*), abundant specimens of the amynodontid *Zaisanamynodon borisovi*, hyracodontids (*Ardynia praecox* and *Proeggysodon qiui*), and the paraceratheriid *Urtinotherium intermedium*. Since *P. gobiensis, Z. borisovi*, and *A. praecox* are indicative of late Eocene Ergilian (Dashzeveg, 1991; Dashzeveg, 1993), the Baron Sog Formation can be correlated to the Ergilian, which in turn can be correlated to the Chadronian NALMA.

Both brontotheres and amynodontids disappeared in the Oligocene Hsandagolian, as represented by the fauna from the "Upper White" at Erden Obo and its equivalent bed at Nom Khong Obo (Wang, 2003) (figs. 10, 11). The perissodactyl diversity decreases considerably, and consists of the hyracodontid *Ardynia kazachstanensis*, the paraceratheriid *Paraceratherium grangeri*, some rhinocerotids, and the chalicothere *Schizotherium* (fig. 11). The age of the "Upper White" at Erden Obo is considered late early Oligocene, as discussed above.

On the basis of the distribution of the general numbers of perissodactyls from the Erlian Basin from the early Eocene through the early Oligocene, we inferred that the changes in perissodactyl diversity that occurred over that time were in relation to coincedent paleoclimatic change (fig. 11). The biodiversity greatly increased during the Arshantan as compared to the early Bumbanian, which is probably attributable to the Early Eocene Climatic Optimum (EECO) (Zachos et al., 2001, 2008; Vandenberghe et al., 2012). Although global temperatures decreased after EECO, perissodactyls reached their greatest diversity in the Irdinmanhan. Alternatively, the underestimated diversity of perissodactyls in the Arshantan may account for its relatively lower diversity than in the Irdinmanhan. The gradual decrease in perissodactyl diversity from the middle Eocene Irdinmanhan to the late Eocene Ergilian likely can be attributed to the steady cooling trend of global temperature as indicated by a 7° C drop in deep-sea temperatures during the middle and late Eocene (Zachos et al., 2001; Prothero, 2006). In the early Oligocene Hsandogolian, the diversity of perissodactyls distinctly declined, and may be the result of the dramatic 5°–6° C drop in deep-sea temperatures across the Eocene-Oligocene boundary (Prothero, 2006). After the Eocene-Oligocene transition, the perissodactyl-dominant fauna in a warm, humid Eocene "greenhouse" was replaced by a rodent/lagomorph-dominant fauna in a dry, cold Oligocene "icehouse" (Meng and McKenna, 1998; Sun et al., 2014).

CONCLUSIONS

We clarify and discuss the temporal and spatial distributions of the dominant perissodactyl fossils from the Erlian Basin at the species level from the early Eocene to the early Oligocene, spanning about 26 million years. Over the past decade, our investigations in the Erlian Basin have resolved some long-standing problems, particularly in the Huheboerhe area, and have produced many new mammalian fossils, including perissodactyls from various localities and stratigraphic horizons. On the basis of this present paper, future study of these new materials may improve or alter our understanding of the evolutionary history of perissodactyls. Furthermore, although we propose a correlation of the fossiliferous sedimentary deposits at Erden Obo with other formations/faunas from type localities, evidence from our new discoveries of perissodactyls and other mammalian fossils may support or augment the present argument. Most importantly, the Eocene Asian Land Mammal Ages, which are based primarily on the faunas from the Erlian Basin, are in need of a more finely calibrated definition, subdivision, and intercontinental correlation that will be accomplished in future studies of the entire mammalian fauna and magnetostratigraphy.

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APPENDIX 1

List of Perissodactyl Fossils from the Ulan Shireh Formation at North Mesa
Asterisks indicate the holotype discovered from the North Mesa.

Perissodactyla
 Tapiroidea
  Lophialetidae
   Zhongjianoletes chowi Ye, 1983
   **Simplates ulanshirehensis* Qi, 1980
   **Breviodon acares* Radinsky, 1965
   **Rhodopagus pygmaeus* Radinsky, 1965
   Lophialetes expedius? Matthew and Granger, 1925c
   Lophialetes sp.
  Deperetellidae
   Teleolophus medius? Matthew and Granger, 1925c
 Rhinocerotoidea
Hyracodontidae
 Triplopus proficiens (Matthew and Granger, 1925c)
Paraceratheriidae
 **Forstercooperia ulanshirehensis* Wang, Bai, Meng, and Wang, 2018
Brontotheriidae
  **Microtitan mongoliensis* (Osborn, 1925)
  **Desmatotitan tukhumensis* Granger and Gregory, 1943
  **Acrotitan ulanshirhensis* Ye, 1983
  **Epimanteoceras formosus* Granger and Gregory, 1943
  **Metatitan primus* Granger and Gregory, 1943

APPENDIX 2

Field Records of Paleogene Perissodactyl Fossils by the CAE, SSPE, and IVPP from the Erlian Basin of Inner Mongolia, China

The field numbers of CAE expeditions in 1922, 1923, 1925, 1928, and 1930 include 32–107, 130–404, 507–616, 631–812, and 813–937, respectively. Abbreviations: **AM,** AMNH FM; **BSL,** Baron Sog Lamasery; **EMM**, Erenhot Dinosaur Museum, mammal fossils; **SS**, Sino-Soviet Paleontological Expedition specimens; **TLC,** Telegraph Line Camp; **TKL,** Tukhum Lamasery; and **V**, IVPP V.

Taxon/specimen number	Material	Field no.	Horizon	Locality
Tapiroidea				
Lophialetidae				
Minchenoletes				
M. erlianensis				
V 14683 (holotype)	Right maxilla with M1–2		NM-3	Nuhetingboerhe
V 14686	Right M3		NM-3	Nuhetingboerhe
Schlosseria				
S. magister				
AM 20241 (holotype)	Upper and lower jaws, fore and hind feet	172	Arshanto beds	About 7 mi N of TL
AM 81787	Left p2–m3, right p3–m3		? “Houldjin gravels”	10 mi SW of Camp Margetts
AM 81788	P3–M3		? “Houldjin gravels”	10 mi SW of Camp Margetts
V 16573	Right part of skull with P2–M2		“Basal White”	Erden Obo
?*Schlosseria*				
AM 26139	Mandible with p2–m2	734	? “Shara Murun” beds	Erden Obo
Lophialetes				
L. expeditus				
AM 19163 (holotype)	Maxilla with P4–M3	41	Irdin Manha beds	23 mi S of Iren Dabasu
L.expeditus ?				
AM 22091–22095	Crushed skulls, jaws, and foot bones	572	Lower red beds (= Tukhum F.)	W of main pocket at Ula Usu
Lophialetes sp.				
AM 26138	Mandible with p2–m2	734	“Shara Murun” beds	Erden Obo
Zhongjianoletes				
Z. chowi				
V 6671 (holotype)	Mandible with partial symphysis and p2–m3	SS 01533	Ulan Shireh F.	Wulanhuxiu
Simplaletes				
S. sujiensis				
V 6508 (holotype)	Mandible with i1, i3, c, and p2–m3	SS 03010	Irdin Manha F.	Irdin Manha
S. ulanshirehensis				

Taxon/specimen number	Material	Field no.	Horizon	Locality
V 6509 (holotype)	Mandible with left m1–2 and right p2–m3	SS 01526	Ulan Shireh F.	Ulan Shireh
Breviodon				
B. acares				
AM 26113 (holotype)	Mandible with p3–m3	637	Buckshot's Quarry	Chimney Butte
Cf. *Breviodon acares*				
AM 81751	Fragmental skull with all cheek teeth	892	"Irdin Manhan beds"	7 mi 235° from Camp Margetts
B.? minutus				
AM 20139 (holotype)	Left upper molar	156	Irdin Manha	TLC
V 5757	Maxilla with DP3–4, M1	77027	Arshanto F.	Huheboerhe
V 5758	DP3–4	77027	Arshanto F.	Huheboerhe
V 5759	Mandible with m1–2	$1P_{25}H_8$	Arshanto F.	Wulanboerhe
V 5760	Mandible with dp4, m1	$1P_{25}H_8$	Arshanto F.	Wulanboerhe
Rhodopagus				
R. pygmaeus				
AM 21554 (holotype)	Maxilla with P3–M3	606	"Shara Murun" beds	4 mi N of TKL
AM 20331	Mandible with p3–m3		Ulan Shireh F.	4 mi N of TKL
R.? minimus				
AM 20310 (holotype)	Mandible with m1–2	191	"Irdin Manha" Eocene	Ula Usu
Pataecops				
P. parvus				
V 14630	Maxillae with P3–M3 and a mandible with p4		NM-3	Wulanboerhe
Deperetellidae				
Teleolophus				
T. primarius				
V 5761 (holotype)	Mandible with p2–m2	$1P_5H_7$	Arshanto beds	Wulanboerhe
T.? rectus				
V 5766 (holotype)	Two mandibles with left p4 and m1, right p4	$1P_5H_8$	Arshanto beds	Wulanboerhe
T. medius				
AM 20166 (holotype)	Mandible with p1–m3	177	Irdin Manha Eocene	TLC, 2 mi N of Line
AM 20163	p4–m3		Irdin Manha beds	Irdin Manha escarpment
AM 20164	DP4–M1		Irdin Manha beds	Irdin Manha escarpment
AM 20165	Isolated upper and lower molars		Irdin Manha beds	Irdin Manha escarpment
AM 20168A	M2		Irdin Manha beds	Irdin Manha escarpment
T. medius?				
AM 21559	Fragmentary maxilla	598	Presumably of "Shara Murun" age	4 mi N of TKL

Taxon/specimen number	Material	Field no.	Horizon	Locality
AM 21560	Fragmentary maxilla	598	Presumably of "Shara Murun" age	4 mi N of TKL
AM 26128	Molar teeth	637	Buckshot's Quarry	Chimney Butte
AM 26286	Maxilla with P1–M3	637	Buckshot's Quarry	Chimney Butte
AM 26287	Maxilla	637	Buckshot's Quarry	Chimney Butte
AM 81796	Mandible with p3–m1	637	Buckshot's Quarry	Chimney Butte
AM 81797	p3, M1		Ulan Shireh F.	
Teleolophus cf. *T. medius*				
AM 81851, 81799, 81850, 81800	Maxilla and mandibles	892	"Irdin Manha beds"	7 miles 235° from Camp Margetts
AM 81853	M2–3		Upper gray layer (Arshano F.)	10 mi SW of Camp Margetts
AM 81854	i2–m3	931	? "Houldjin gravels"	10 mi SW of Camp Margetts
AM 81855	p3–m2		"Houldjin gravels"	10 mi SW of Camp Margetts
AM 81798	p2–4		Irdin Manha F.	5 mi E of Camp Margetts
T. magnum				
AM 26063 (holotype)	Maxilla with C–P1, P3–M2, mandible with c–m2	763	Base of the "Middle Red"	Erden Obo
Deperetella				
D. cristata				
AM 20290 (holotype)	Skull fragments with P2, P4–M3	210	"Irdin Manha" Eocene	Ula Usu
AM 20291, 20192	Mandible with c–m3; mandible with p1–m3	217	"Irdin Manha" Eocene	Ula Usu
AM 20293–20295, 20300, 20301, 20306	Fragmentary maxillae and mandibles, postcrania	210	"Irdin Manha" Eocene	Ula Usu
AM 20302	Mandible with dp4–m3	191	"Irdin Manha" Eocene	Ula Usu
Deperetella cf. *D. cristata*				
AM 26027	Mandible with dp3–m1	669	"Shara Murun beds"	Twin Obos
Deperetella sp.				
AM 81807	Mandible with p2–m3	904A	?"Houldjin gravels"	7 mi W of Camp Margetts
Helaletidae				
Heptodon				
H. minimus				
V 5732 (holotype)	Associated mandible with left p1–m3 and right p2–m2	77036-2	Layer 10 of Arshanto bed	Huheboerhe
V 5733	Mandible with p2–m3	77036-2	Layer 10 of Arshanto bed	Huheboerhe
V 5731	M3	77027	Arshanto bed	Huheboerhe

Taxon/specimen number	Material	Field no.	Horizon	Locality
Desmatotherium				
D. mongoliense				
AM 19161 (holotype)	Premaxilla and maxilla with I1–P1 alveoli and P2–M2	40	Irdin Manha beds	23 mi S of Iren Dabasu
AM 20155	Mandible with p3–m3	156	Irdin Manha Eocene	TLC
V 14692	Maxilla with DP1, P2–M2		Irdin Manha F.	Chaganboerhe
Paracolodon				
P. fissus				
AM 20161 (holotype)	Maxilla with P2–4	147	Irdin Manha F.	Camp Margetts
AM 81802	Mandible with c–m3	865	"Irdin Manha beds"	Camp Margetts
AM 81804	Mandible with p4–m3	839	"Houldjin gravels"	Camp Margetts
V 22640	Associated skull and mandible lacking rostral part		Irdin Manha F.	Duheminboerhe
Rhinocerotoidea				
Hyrachyus				
H. neimongoliensis				
V 5721 (holotype)	Incomplete skull with left P2, P4, and M1–3	77036-2	Layer 10 of Arshanto bed	Huheboerhe
H. crista				
V 5722 (holotype)	Maxilla with P4–M3	77031	Layer 4 of Arshanto bed	Bayan Ulan
V 5723	Maxilla with P4–M2	77031	Layer 4 of Arshanto bed	Bayan Ulan
Hyracodontidae				
Triplopus				
T.? proficiens				
AM 20141 (holotype)	Right mandible with p1–m3	171	Irdin Manha Eocene	TLC, 2 mi S of Line
AM 21552	Maxilla with P1–M3	605	"Shara Murun" beds	4 mi N of TKL
AM 21561	Mandible		Ulan Shireh F.	8 mi N of TKL
AM 21562	Maxilla		Ulan Shireh F.	8 mi N of TKL
AM 26124	Mandible with p1–m3	658	Buckshot's Quarry	Chimney Butte
AM 26285	Mandible			1 mi N of the main Ulan Shireh Quarry at Chimney Butte
AM 26674, 26675	Mandible		"Irdin Manha beds"	Camp Margetts
AM 26673	Maxilla with P1–M2		"Irdin Manha beds"	7 mi SW of Camp Margetts
T.? progressus				
AM 20298 (holotype)	Maxilla with M1–3	191	"Irdin Manha" Eocene	Ula Usu
Teilhardia				
T. pretiosa				
AM 20299 (holotype)	Right mandible with p2–m3	191	"Irdin Manha" Eocene	Ula Usu

Taxon/specimen number	Material	Field no.	Horizon	Locality
Ulania				
U. wilsoni				
V 8922 (holotype)	Maxilla, mandibles, manus, and phalanges	$1P_{14}H_{17}$	Lower part of the “Ulan Gochu F.”	Erden Obo
Ardynia				
A. praecox				
AM 26039	Skull, mandible, and a few postcrania	747	“Middle Gray layer”	Erden Obo
A. kazachstanensis				
AM 26183	Mandible with i1–m3	776	“Baron Sog” beds	Nom Khong Obo
Proeggysodon				
P. qiui				
V 18099 (holotype)	Mandible with i1–m3		Upper part of “Middle White”	Erden Obo
Paraceratheriidae				
Pappaceras				
P. confluens				
AM 26660 (holotype)	Skull and mandible	915	“Upper Gray clays” of the “Irdin Manha”	10 mi SW of Camp Margetts
AM 26666	Mandible with p3–m3	920	? “Irdin Manha beds” (top)	7 mi W of Camp Margetts
P. minuta				
AM 26672 (holotype)	Maxilla and mandible	925	“Upper Gray clays” of “Irdin Manha”	10 mi SW of Camp Margetts
AM 26668	Mandible with p1–m3	852	“Irdin Manha beds”	Overnight Camp
AM 26670	Fragmental skull with P2–M1	924	“Upper Gray layer” of “Irdin Manha”	10 mi SW of Camp Margetts
AM 26643	Skull with C, M1–3	913	“Irdin Manha beds”	7 mi W of Camp Margetts
AM 26056	Mandible	724	“Shara Murun” beds	6 mi E of Spring Camp
P. meiomenus				
V 20254 (holotype)	Nearly complete skull	AS-5	upper part of the Arshanto F.	Huheboerhe
AM 107851	Mandible with i2, c, p2–3	931	?“Houldjin gravels”	10 mi SW of Camp Margetts
AM 107852	Mandible with c, p2–m3	924	“Upper Gray layer” of “Irdin Manha”	10 mi SW of Camp Margetts
AM 107856	Mandible with i2–3, c, p2–m3	924	“Upper Gray layer” of “Irdin Manha”	10 mi SW of Camp Margetts
AM 26677	Mandible with p3–m3		“Irdin Manha”	Camp Margetts
P. sp.				
AM 26671	Partial skull with M3			
AM 107848	Juvenile mandible with dp2–4		“Irdin Manha beds”	10 mi SW of Camp Margetts

Taxon/specimen number	Material	Field no.	Horizon	Locality
AM 26669	Juvenile mandible with dp3–4, m1–2	892	"Irdin Manha beds"	7 mi, 235°, from Camp Margetts
AM 107849	M3	133	Irdin Manha beds	25 miles east of Iren Dabasu
Forstercooperia				
F. totadentata				
AM 20116 (holotype)	Rostrum with I3, C, and P1–4	173	Irdin Manha Eocene	TLC, 2 mi N of Line
F. ulanshirehensis				
AM 21608 (holotype)	Nearly complete skull	613	"Shara Murun" beds	8 mi N of TKL
AM 22101	Mandible with p3–m3	602	"Shara Murun" beds	4 mi N of TKL
V 20154–20156	Maxilla and mandibles		Irdin Manha F.	Irdin Manha
Juxia				
J. sharamurenensis				
V 2891 (holotype)	Nearly complete skeleton		Shara Murun F.	Ula Usu
AM 20286–20288	Skull, mandible and post-cranial material	198	"Irdin Manha" Eocene	Ula Usu
AM 26753	Mandible with p2, p4–m3	734	Base of "Lower Gray"	Erden Obo
AM 26750	Mandible with p3–m3	668	"Shara Murun beds"	Twin Obos
J. shoui				
V 8757 (holotype)	Fragmentary skull with C–M2		"Ulan Gochu" F.	Erden Obo
V 3268	Lunar		"Lower White"	Erden Obo
Urtinotherium				
U. intermedium				
V 2769 (holotype)	Complete mandible		"Middle Gray"	Erden Obo
AM 26026	Radius	772	"Middle Gray"	Erden Obo
AM 26032	Mandible	702	"Ulan Gochu beds"	Jhama Obo
AM 26390	Axis	914	"Houldjin gravels"	7 mi W of Camp Margetts
AM 26389	Mc III	840	"Houldjin gravels"	Camp Margetts
V 8803 (holotype of *Dzungariotherium erdenensis*)	Maxilla with right P2–M3 and left P3–M3		"Ulan Gochu F."	Erden Obo
U. parvum				
EMM 0146	Maxilla with P1–M3	199102	"Lower White"	Erden Obo
AM 26190	Postcrania	686	"Baron Sog beds"	Jhama Obo
Paraceratherium				
P. grangeri				
AM 26166	Mandible with i1 and p2–4	745	"Baron Sog beds"	Erden Obo
AM 26179	Calcanei	731	"Baron Sog beds"	Erden Obo
AM 26387	Postcrania	874	"Houldjin gravels"	Overnight Camp
Aralotherium				
Aralotherium sp.				

Taxon/specimen number	Material	Field no.	Horizon	Locality
EMM 0016	Mandible with symphysis and p3–m1		Houldjin F.	Near Erlian Hot
Amynodontidae				
Rostriamynodon				
R. grangeri				
AM 107635 (holotype)	Complete skull and mandible	890	"Irdin Manha beds"	2 mi E of Camp Margetts
Caenolophus				
C. promissus				
AM 20297 (holotype)	Maxilla with P3–M3	191	Shara Murun F.	Ula Usu
AM 20304	Mandible with m1–2	191	Shara Murun F.	Ula Usu
C. obliquus				
AM 20296 (holotype)	Maxilla with DP3–DP4, P3–M2	191	Shara Murun F.	Ula Usu
Sharamynodon				
S. monogoliensis				
AM 20278 (holotype)	Nearly complete skeleton	224	Shara Murun F.	Ula Usu
AM 21601	Partial skeleton	580	Shara Murun, gray beds	4 mi N of BSL
V 3216	Maxilla with M1–3	7073	Shara Murun F.	Ula Usu
Sianodon				
S. ulausuensis				
V 3215 (holotype)	Nearly complete skull	7113	Shara Murun F.	Ula Usu
Lushiamynodon				
L. sharamurenensis				
V 2892 (holotype)	Juvenile cranium with DP1–M1	7123.1	Shara Murun F.	Ula Usu
V 3217	Mandible with m2–3		"Shara Murun F."	"Ulan Shireh Obo" (at North Mesa)
Gigantamynodon				
G. promisus				
V 3218 (holotype)	Mandible with p2–m3	7003	Shara Murun F.	Ula Usu
Cadurcodon				
C. matthewi				
AM 26029 (holotype)	Partial skull and mandible	677	"Ulan Gochu"	Jhama Obo
C. houldjinensis				
EMM 0126 (holotype)	m2	1988 001	Houldjin F.	E of Erenhot Railway Station
Amynodontopsis				
A. parvidens				
AM 26043 (holotype)	Skull and mandible	761	Top of "Lower White"	Erden Obo
AM 26045	Ventral portion of skull with good teeth	768	Base of "Middle Red"	Erden Obo
AM 26046	Anterior portion of skull with worn teeth	771	"Middle Red"	Erden Obo

Taxon/specimen number	Material	Field no.	Horizon	Locality
AM 26050	Maxilla and mandible	767	Base of "Middle Red"	Erden Obo
AM 26041	Nearly complete skull	758	Base of "Middle Red"	Erden Obo
AM 26042	Ventral portion of skull			Erden Obo
AM 26051	Mandible with p3–m3	766	Base of "Middle Red"	Erden Obo
AM 26044	Front of skull with complete teeth	760	Base of "Middle Red"	Erden Obo
AM 21599	Ventral portion of skull	576	Base of upper red bed (Ulan Gochu)	4 mi N of BSL
AM 26053	Mandible with p3–m3	786	"Ulan Gochu beds"	Nom Khong Obo
AM 26178	Skull with poor teeth	685	Possibly from the "Baron Sog" bed	South of Jhama Obo
AM 26038	Skull and mandible with complete teeth		"Ulan Gochu F."	Jhama Obo
A. tholos				
AM 26035 (holotype)	Skull and mandible	709	Top of gray beds, "Ulan Gochu"	Ulan Shireh Obo (= Ganggan Obo)
AM 26031	Mandibles	684	"Ulan Gochu beds"	South of Jhama Obo
AM 26054	Mandibles	787	"Lower White or Gray (pink)"	Nom Khong Obo
AM 26055	Nearly complete mandibles	789	"Lower White or Gray (pink)"	Nom Khong Obo
AM 26057	Maxilla	788	"Lower White or Gray (pink)"	Nom Khong Obo
Zaisanamynodon				
Z. borisovi				
AM 26034	Skull with C–M3	710	Top of gray, "Ulan Gochu beds"	Ulan Shireh Obo (= Ganggan Obo)
AM 21602	Mandible with i3, c, p2–m3	587	Upper white stratum, Baron Sog	4 mi N of BSL
AM 26052	Mandible with i2, p3–m3	749	"Middle White"	Erden Obo
AM 26170	Symphysis with i2 and c	733	"Baron Sog"	Erden Obo
AM 26049	Right mandible with i2, p3–m3	765	"Middle White"	Erden Obo
AM uncatalogued	m2	840	"Houldjin gravels"	Camp Margetts
Rhinocerotidae				
Aprotodon				
A. lanzhouensis				
EMM 0082	i2	1988001	Houldjin F.	E of Erenhot Railway Station
EMM 0079	Mandible with p3–4	1988001	Houldjin F.	E of Erenhot Railway Station
Symphysorrhachis				
S. sp.				
EMM 0123	Mandible with m2–3	1988001	Houldjin F.	E of Erenhot Railway Station

Taxon/specimen number	Material	Field no.	Horizon	Locality
EMM 0078	M1/2	1988001	Houldjin F.	E of Erenhot Railway Station
AM 19184	M3	36	Houldjin beds	5 mi S of Iren Dabasu
Brontotheriidae				
Microtitan				
M. mongoliensis				
AM 22099 (holotype)	Mandible with p2–m3	602	"Shara Murun beds"	4 mi N of TKL
AM 21611	Maxilla with C–M3	612	"Shara Murun beds"	8 mi N of TKL
AM 20167	Mandible with p4–m1		Irdin Manha	TLC
M.? elongatus				
V 5767 (holotype)	P3–M3	77028 H_2	Arshanto F.	Daoteyin Obo
M. sp.				
V 5768	M2	77027	Arshanto F.	Huheboerhe
Desmatotitan				
D. tukhumensis				
AM 21606 (holotype)	Mandible with i1–c, p2–m3	600	"Shara Murun beds"	4 mi N of TKL
D. sp.				
V 5769	m3	77036-2	Layer 10 of Arshanto bed	Huheboerhe
Acrotitan				
A. ulanshirehensis				
V 6686 (holotype)	Fragmentary mandible with p3–4		Ulan Shireh F.	Wulanhuxiu
Epimanteoceras				
E. formosus				
AM 21613 (holotype)	Complete skull	601	"Shara Murun beds"	4 mi N of TKL
AM 21607 (= holotype of *Dolichorhinoides angustidens*)	Partial skull with P1–M3	610	"Shara Murun beds"	8 mi N of TKL
Hyotitan				
H. thomsoni				
AM 26401 (holotype)	Mandible with i2–c, p1–m3	860	"Houldjin gravels"	Camp Margetts
Metatelmatherium				
M. ultimum				
AM 26411 (holotype)	Skull and mandible	882	"Irdin Manha"	Camp Margetts
M. parvum				
AM 20168 (holotype)	Fragmentary mandible with p3–4		Irdin Manha	TLC
Protitan				
P. grangeri				
AM 20103 (holotype)	Complete skull and mandible	158	Irdin Manha Eocene	0.5 mi S of the TLC

Taxon/specimen number	Material	Field no.	Horizon	Locality
AM 20104 (= holotype of *P. robustus*)	Mandible with i1–m3	159	Irdin Manha Eocene	Irdin Manha
AM 20112	Mandible with i2–c, p2–m3	160	Irdin Manha Eocene	TLC, 1 mi SW of line
AM 19179	Mandible with p2–m2	45	Irdin Manha beds	23 mi S of Iren Dabasu
AM 20109 (= holotype of *Dolichorhinus olseni*)	Mandible with i3–m3		Irdin Manha	TLC, 1 mi N of line
AM 20108	Maxilla with P1–M3	150	Irdin Manha Eocene	TLC, 0.5 mi N of line
AM 20111 (= holotype of "*Manteoceras*?" *irdinensis*)	A mandible with m1–3	183	Irdin Manha Eocene	TLC, 2 mi N of line
AM 20113	Partial cranium with C, P2–M1	164	Irdin Manha Eocene	TLC, 0.5 mi SW of line
AM 20114	Patiral cranium with I2–M3	165	Irdin Manha Eocene	TLC
AM 20119	Mandible with p4–m2	180	Irdin Manha Eocene	TLC, 0.5 mi S of line
AM 20120	Maxilla with M1–3	182	Irdin Manha Eocene	TLC, 2 mi N of line
AM 20123	Maxilla with P4–M2	186	Irdin Manha Eocene	TLC, 2 mi N of line
AM 20125 (= holotype of *P. obliquidens*)	Maxilla with P1–3	188	Irdin Manha Eocene	TLC, 0.5 mi N of line
AM 20126	Mandible with p3–m2	156	Irdin Manha Eocene	TLC
AM 26421	Mandible with p2–m3	859	"Houldjin gravels"	Camp Margetts
AM 26104 (= holotype of *P. bellus*)	Ventral surface of skull with I2–M3	720	"lower red bed" (?Arshanto)	Spring Camp
P. minor				
AM 26416 (holotype)	Nearly complete skull	835	probably top of "Irdin Manha"	0.5 mi W of Camp Margetts
AM 26417	Partial skull with I3, P2–M3	849	"?Irdin Manha beds"	1 mi W of Camp Margetts
Camp Margetts "taxon A"				
AM 26410	Mandible with i1–i3?, p1–4	848	? "Irdin Manha"	1 mi W of Camp Margetts
AM 26415	Mandible with i2–m3	901	"Houldjin gravels"	7 mi W of Camp Margetts
AM 26418	Juvenile mandible with i3, p1–m3	908	"Houldjin gravels"	7 mi W of Camp Margetts
AM 26408	Mandible with p2–m3	842	"Irdin Manha beds"	1 mi W of Camp Margetts
"*P.*?" *cingulatus*				
AM 26412 (holotype)	Mandible with p1–m3	916	"Houldjin gravels"	10 mi SW of Camp Margetts
AM 26403	Mandible with p1–m3	886	"Houldjin gravels"	Camp Margetts
AM 20110	Nearly complete mandible	161	Irdin Manha	TLC, 1 mi SW of line
P. sp.				
V 10104	m3 and postcranina		"Tukhum F." (= Lower Red)	Erden Obo

Taxon/specimen number	Material	Field no.	Horizon	Locality
Gnathotitan				
G. berkeyi				
AM 20106 (holotype)	Mandible with c–m3	163	Irdin Manha Eocene	TLC, 1 mi SW of Line
AM 20107	Mandible with i1–m2	169	Irdin Manha Eocene	TLC, 1 mi S of line
AM 20115	Juvenile mandible with p1, dp2–dp4	170	Irdin Manha Eocene	TLC, 1 mi S of line
AM 20121	Maxilla with P1–M3	184	Irdin Manha Eocene	TLC, 2 mi N of line
AM 141231 (formerly part of AMNH FM 20106)	Maxilla with C–M3	163	Irdin Manha Eocene	TLC, 1 mi SW of Line
AM 20124 (missing)	A mandible	187	Irdin Manha Eocene	TLC, 0.5 mi N of line
AM 20127 (missing)	Premolars and molars	168	Irdin Manha Eocene	TLC, 1 mi S of line
Rhinotitan				
R. kaiseni				
AM 20252 (holotype)	Skull and mandible		Shara Murun F.	Ula Usu
AM 20257	Ventral surface of a skull with complete teeth	223	Shara Murun F.	Ula Usu
FMNH P 14048 (formerly AMNH FM 20260)	Skull and mandible	196	Shara Murun F.	Ula Usu
R. andrewsi				
AM 20271 (holotype)	Skull missing nasal	227	Shara Murun F.	Ula Usu
AM 20254	Skull	200	Shara Murun F.	Ula Usu
AM 20261	Laterally crushed skull	201	Shara Murun F.	Ula Usu
AM 20263	Plate with I2–M3	203	Shara Murun F.	Ula Usu
V 3254-1	Skull and mandible		Shara Murun F.	Ula Usu
V 3254-1	Skull and mandible		Shara Murun F.	Ula Usu
R. sp.				
AM 18653 (= holotype of *R. mongoliensis*)	Mandible with p2–m3		Shara Murun F.	Ula Usu
AM 20251	Mandible with p2–m3	219	Shara Murun F.	Ula Usu
AM 20256	Maxilla with C–M3, mandible with i1–2, c, p1–m3	220	Shara Murun F.	Ula Usu
AM 20262	Mandible with p1–m3, isolated incisors and a canine	202	Shara Murun F.	Ula Usu
AM 20269	Mandible with i1–2, c, p1	221	Shara Murun F.	Ula Usu
AM 20270	Maxilla with P1–M2	225	Shara Murun F.	Ula Usu
AM 20272	Mandible with i2?, c, p2–m3		Shara Murun F.	Ula Usu
AM 20273	Mandible with p2–m3		Shara Murun F.	Ula Usu
AM 20280	Skull with P1–M2	214	Shara Murun F.	Ula Usu
AM 21598	Maxilla with P1–M2	571	Shara Murun F.	Ula Usu
AM 21603	Mandible with i1–m3	590	Shara Murun F., gray beds	4 mi N of BSL

Taxon/specimen number	Material	Field no.	Horizon	Locality
AM 21605	Mandible with incisors, c, p2–m3	592	Shara Murun F.	4 mi N of BSL
PIN 2198-2	Mandible with p2–m3		Shara Murun F.	4 mi N of BSL
Pachytitan				
P. ajax				
21612 (holotype)	Fragmentary skull with left I3, C, and P2–M3	582	Shara Murun, (gray beds)	4 mi N of BSL
Titanodectes				
T. minor				
AM 26132 (holotype)	Incomplete mandible with front teeth and p2–m1	716	"Shara Murun beds"	Spring Camp
AM 26021 (or *Parabrontops gobiensis*)	Mandible with p1–m3	769	?"Shara Murun beds", "Lower Gray layer"	Erden Obo
AM 26012	Mandible		"Ulan Gochu beds"	Twin Obos
AM 21600	Mandible with i1–3, c, p2–m3	577	Top of the Shara Murun F. (gray beds)	4 mi N of BSL
T. ingens				
AM 26005 (holotype)	Mandible with i1–m3	704	"Ulan Gochu beds"	Jhama Obo
Embolotherium				
E. grangeri				
AM 26002 (holotype)	Complete skull	770	Base of "Middle Red"	Erden Obo
AM 26004	Skull with P2–M3	756	Base of "Middle Red"	Erden Obo
AM 26040	Juvenile skull and mandible	673	Near base of "Ulan Gochu" beds	Twin Obos?
AM 21610 (= holotype of *E. louksii*)	Partial skull with erupting ?M3	595	Base of upper red beds, Ulan Gochu F.	4 mi N of BSL
AM 26018	Mandible with p4–m3 and isolated incisor and canine	730	From surface of plain, possibly Baron Sog beds	2 mi N of BSL
E. andrewsi				
AM 26001 (holotype)	Nearly complete skull	750	"Middle White"	Erden Obo
AM 26003	A skull with C–M3	735	"Ulan Gochu" beds, 1/4 miles north of Obo	Erden Obo
AM 26011	Mandible with p3–m3	751	"Middle White"	Erden Obo
AM 26006	Mandible with p2–m3	755	"Middle White"	Erden Obo
AM 26007	Mandible with p2–m3	746	"Middle Gray"	Erden Obo
AM 26008	Mandible with p2–m3	740	"Middle White"	Erden Obo
V 11959	Skull and mandible		"Ulan Gochu F."	Erden Obo
AM 26009	Skull and mandible	683	Base of "Ulan Gochu beds"	S of Jhama Obo
AM 26010	Crushed skull with I3–M3	688	"Ulan Gochu F."	Jhama Obo
AM 21604 (= holotype of *E. ultimum*)	Crushed basicranium with M2–3	591	"Upper White"	4 mi N of BSL
AM 22114	Maxilla with P3–M1		Baron Sog F.	Baron Sog Mesa

Taxon/specimen number	Material	Field no.	Horizon	Locality
Parabrontops				
P. gobiensis				
AM 26020	Partial skull	742	“Middle White”	Erden Obo
Parabrontops cf. *P. gobiensis*				
AM 26019	Mandible with p1–m3	741	“Middle White”	Erden Obo
AM 26131	Mandible with i1–m3	717	“Shara Murun beds”	Spring Camp
Metatitan				
M. primus				
AM 26101 (holotype)	Partial skull and mandible	650	?Ulan Shireh F.	Big red draw
AM 26102	Mandible with c and m1–3	651	Middle of upper red beds	NW promontory
M. relictus				
AM 26391 (holotype)	Skull and mandible	846	“Houldjin gravels”	1 mi W of Camp Margetts
AM 26395	Fragmentary skull with I1–M3	834	“Houldjin” beds	0.5 mi W of Camp Margetts
AM 26396	Fragmentary skull with P2–M (damaged)	841	“Houldjin gravels”, top of exposures	1 mi W of Camp Margetts
AM 26397	Partial skull with I1–C, P4–M3	845	“Houldjin gravels”	Camp Margetts
AM 26398	Partial skull with I1–M3	866	“Houldjin gravels”	1.5 mi W of Camp Margetts
AM 26399	A partial skull with C, P1–M3	887	“Houldjin gravels”	Overnight Camp
AM 26406	Premaxilla and maxilla with I3–M2	871	“Houldjin gravels”	Camp Margetts
AM 26402	Mandible with i1–m3	868	“Houldjin gravels”	1 mi W of Camp Margetts
AM 26404	Mandible with i1–c, p2–3	867	“Houldjin gravels”	1 mi W of Camp Margetts
AM 26405	Mandible with c, p4–m2	870	“Houldjin gravels”	1.5 mi W of Camp Margetts
AM 26407	Mandible with c, p2–m3	855	“Houldjin gravels”	1 mi W of Camp Margetts
AM 26420	Mandible with p3–m3	879A	“Houldjin gravels”	1 mi W of Camp Margetts
AM 26427	Mandible with i3–m3	856	“Houldjin gravels”	Camp Margetts
AM 26429	Mandible with p4–m3	864	“Houldjin gravels”	Camp Margetts
Camp Margetts “taxa B”				
AM 26400	A partial mandible	854	“Houldjin gravels”	1 mi W of Camp Margetts
M. sp.				
V 15714	Maxilla with P1–3	1988002	Houldjin F.	Houldjin
EMM 0127	m3	1988001	Houldjin F.	E of Erenhot Railway Station

Taxon/specimen number	Material	Field no.	Horizon	Locality
Nasamplus				
N. progressus				
AM 26014 (holotype)	Fragmentary skull with P4–M1	701	“Ulan Gochu” beds	Jhama Obo
Chalicotherioidea				
Litolophus				
L. gobiensis				
AM 26645 (holotype)	Crushed skull and mandible	936	“Irdin Manha” beds	6 mi W of Camp Margetts
V 16139	Skull with C–M3	AS-1	Base of Arshanto F.	Nuhetingboerhe
Schizotherium				
Schizotherium cf. *S. avitum*				
AM 26061	Right maxilla with P2–3, left maxilla with P3–4, M2–3	733	“Ulan Gochu beds”, probably the “Upper Red”	Erden Obo
AM 26061	Right maxilla with P4–M3	738	“Middle White”	Erden Obo
AM 103336	Mandible with p4–m2	732	“Upper White”	Erden Obo
Schizotherium sp.				
AM 26188	Mc III	734	?“Baron Sog beds” (“Upper White”)	Erden Obo

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