A SKULL OF *PLESIACERATHERIUM GRACILE* (RHINOCEROTIDAE, PERISSODACTYLA) FROM A NEW LOWER MIOCENE LOCALITY IN SHANDONG PROVINCE, CHINA, AND THE PHYLOGENETIC POSITION OF *PLESIACERATHERIUM*

XIAOKANG LU,[*,1] XIAOTING ZHENG,[2] CORWIN SULLIVAN,[1] and JIN TAN[3]

[1]Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China, luxiaokang@ivpp.ac.cn;
[2]Tianyu Museum of Natural History, Pingyi, Shandong 273300, China, ty4291666@163.com;
[3]Shanwang National Geopark of China, Linqu, Shandong 262600, China

ABSTRACT—A well-preserved fossil skull from a new locality in Jijiazhuang, Changle County, Shandong Province, China, is attributable to *Plesiaceratherium gracile*. Other rhinoceroses from the nearby Shanwang Basin of Linqu County, Shandong, formerly described as *Aceratherium* sp. and *Plesiaceratherium shanwangensis* are also referable to *P. gracile*. The new skull demonstrates the presence in *P. gracile* of the following characters: continuous labial cingula on lower cheek teeth; skull roof with nearly flat profile; and external auditory pseudomeatus ventrally closed, proceeding dorsocaudally in a shallow groove. Comparison of *Plesiaceratherium* with *Brachypotherium pugnator* Matsumoto, 1921, suggests that referral of the latter to *Plesiaceratherium* should be reconsidered. A phylogenetic analysis based on 314 characters scored for 39 terminal taxa places *Plesiaceratherium mirallesi* in a basal position within Rhinocerotidae, and recovers other species of *Plesiaceratherium* as a clade that is well separated from *B. pugnator* and is sister to the [*Subchilotherium* [*Acerorhinus* [*Shansirhinus, B.* pugnator [*Chilotherium*]]]] grouping. Based on this result and a reevaluation of the anatomy of '*P.*' *mirallesi*, we propose that the genus *Dromoceratherium* should be revived to accommodate this species as *D. mirallesi*. The occurrence of *P. gracile* at Jijiazhuang indicates that the fossiliferous diatomaceous shales of this locality were deposited during the lower Miocene.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

INTRODUCTION

China has a rich fossil record of perissodactyls and other Cenozoic mammals, whose remains were traditionally regarded as 'dragon bones' and used in traditional medicine but have been objects of paleontological study since the end of the 19th century. The genus *Plesiaceratherium* and its type species *P. gracile* are based on crushed teeth and well-preserved limbs from the lower Miocene Shanwang Formation in the Shanwang Basin of Shandong Province, China, which consists of diatomaceous lacustrine shales and volcanic and volcaniclastic rocks (Young, 1937; Yan et al., 1983; Deng et al., 2003; He et al., 2011). *Plesiaceratherium* is traditionally regarded as an aceratheriine rhinocerotid, and indeed the only aceratheriine known from the lower Miocene of China. Material referable to this genus has been reported from Shandong, Hebei, and Tibet (Young, 1937; Chen and Wu, 1976; Deng et al., 2011), as well as from western Europe and probably South Asia and Africa (Mermier, 1895; Heissig, 1972; Antunes and Ginsburg, 1983; Yan and Heissig, 1986; Antoine and Welcomme, 2000; Geraads, 2010). Putative fossils of *Plesiaceratherium* from Pakistan and Africa are not considered in this paper because detailed descriptions and accessible illustrations are lacking for these specimens.

Revisions of *Plesiaceratherium* have been proposed by some authors (Wang, 1965; Yan, 1983; Yan and Heissig, 1986; Cerdeño, 1992). Wang (1965) referred a partial skull with badly worn upper cheek teeth from the lower Miocene of Kani District, Japan (Matsumoto, 1921), originally described as *Brachypotherium pugnator*, to *Plesiaceratherium* as *P. pugnator*. Wang (1965) similarly reassigned other isolated cheek teeth described as *Brachypotherium pugnator* from the Miocene of Sihong, China (Chow and Wang, 1964), to the species *Plesiaceratherium shanwangensis*. However, Yan (1983) and Yan and Heissig (1986) assigned both the specimens of *P. shanwangensis* from the Shanwang Basin described by Wang (1965), and additional material from the same basin identified by Hu (1957) and Xie (1982) as *Aceratherium* sp., to *Brachypotherium* as *B. shanwangensis*. Cerdeño (1992) considered *Plesiaceratherium* to be a synonym of *Protaceratherium*, but other authors have continued to regard these genera as distinct (Heissig, 1999; Antoine, 2002; Becker et al., 2013).

Surprisingly, phylogenetic analyses by Antoine et al. (2003, 2010) recovered *Plesiaceratherium mirallesi* as a basal rhinocerotid that was placed as the sister taxon of the clade comprising Rhinocerotinae and Aceratheriinae. This unexpected result called into question the previously accepted view that *Plesiaceratherium* was an aceratheriine. *Plesiaceratherium gracile*, the type species of *Plesiaceratherium*, is known from many well-preserved skeletons reported by Yan (1983) and Yan and Heissig (1986), but to date no analysis of rhinoceros phylogeny has included this species and discussed the phylogenetic position of the genus as a whole.

This paper describes a newly collected skull that represents the first record of *P. gracile* from near Jijiazhuang Village in Changle County, Shandong Province, China. Jijiazhuang is located near the Linqu County border, and lies about 5 km east of the famous Shanwang Basin in Linqu (Fig. 1). Specifically, the fossil was collected on Hanjiashan (Hanjia Hill), in an interval of diatomaceous lacustrine shale about 2 m thick and sandwiched between underlying and overlying basalts. For a time, local residents worked quarries located high on the east and north faces of the hill, about 230 m above sea level, and recovered numerous fossils from the shale beds. Most of these specimens, particularly some large mammal fossils, are better preserved than those from the Shanwang Basin (Qiu and Qiu, 2013). Previous studies of Jijiazhuang fossils (Roček et al., 2011; Qiu and Qiu, 2013) did not discuss the stratigraphy of the site, and an adequate description is impossible because the quarry pits have now been filled with clay and pieces of volcanic rock.

The newly discovered skull of *Plesiaceratherium gracile* displays a well-preserved occipital area, and many features can be observed on the cheek teeth that add to current understanding of intraspecific variation within *P. gracile*. After documenting the novel morphological information provided by the specimen, we conducted detailed comparisons among species of *Plesiaceratherium* and revised the species-level taxonomy of the genus. In addition, a more comprehensive phylogenetic analysis was performed as part of the present study in order to reevaluate the affinities of *P. mirallesi*, other species of *Plesiaceratherium*, and *Brachypotherium pugnator*. This analysis is the first to include any species of *Plesiaceratherium* other than *P. mirallesi*.

Terminology follows conventions established by previous authors (Sisson, 1953; Guérin, 1980; Qiu and Wang, 2007). Measurements were performed according to the protocol universally applied to rhinocerotids and developed by Guérin (1980).

Institutional Abbreviations—IVPP V, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **STM**, Shandong Tianyu Museum of Natural History, Pingyi, China.

SYSTEMATIC PALEONTOLOGY

Order PERISSODACTYLA Owen, 1848
Family RHINOCEROTIDAE Owen, 1845
Subfamily ACERATHERIINAE Dollo, 1885
PLESIACERATHERIUM Young, 1937

Type Species—*Plesiaceratherium gracile* Young, 1937, from the Shanwang Basin of Linqu County, Shandong Province, China.

Included Species—*P. fahlbuschi* (Heissig, 1972); *P. lumiarense* (Antunes and Ginsburg, 1983); *P. platyodon* (Mermier, 1895).

Emended Diagnosis—(Based on Yan and Heissig, 1986.) Medium-sized to large aceratheriine; limb bones more slender than in other Miocene aceratheriine genera; upper incisor I1 medium-sized (sagittal length of the crown about 30 mm); labial cingulum always present on upper premolars, and protocone constriction usually absent on P3 and P4.

Horizon and Localities—Lower Miocene. Shandong, Hebei, and Tibet, China; Bavaria, Germany; Lisbon, Portugal; Gers, Drôme, Orléanais, and Touraine, France; Bugti Hills, Pakistan.

PLESIACERATHERIUM GRACILE Young, 1937

Plesiaceratherium gracile Young, 1937:214, text-figs. 4(2–6), 5–9, pls. 1, 2 (original description).
Aceratherium sp.: Hu, 1957:163, pl. 1(2–7).
Plesiaceratherium gracile Young, 1937: Hu, 1957:163, pl. 1(8).
Plesiaceratherium shanwangensis Wang, 1965:109, pl. 1.
Plesiaceratherium gracile Young, 1937: Chen and Wu, 1976:6, pl. 1(3).
Aceratherium sp.: Xie, 1982:146, pl. 1(1).
*Plesiaceratherium shanwangensis*Wang, 1965: Xie, 1982:146, pls. 1(2), 2.
Plesiaceratherium gracile Young, 1937: Yan, 1983:134, pl. 1.
Plesiaceratherium gracile Young, 1937: Yan and Heissig, 1986:81, text figs. 2, 3(a, c), 4, 5(a)–9(a), 11(a)–15(a), 16, 17(a)–25(a), pl. 1.
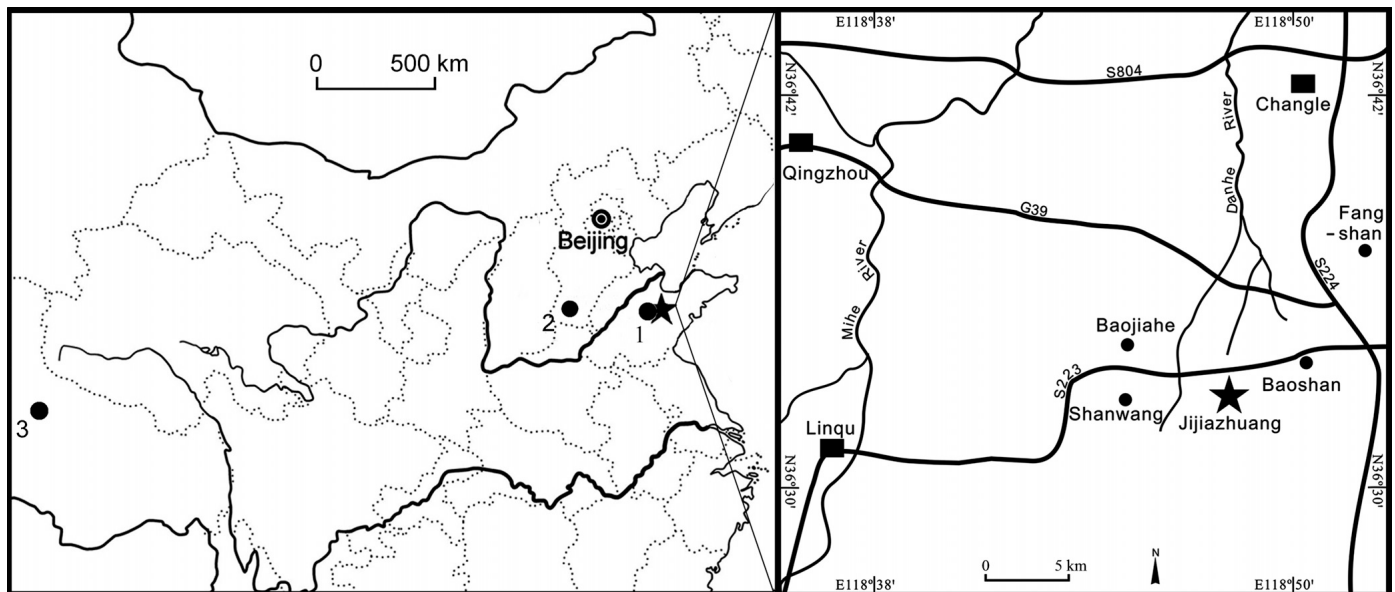

FIGURE 1. Location of Jijiazhuang in Changle County, Shandong Province, China. **1**, lower Miocene, Shanwang Basin, Shandong Province (Young, 1937); **2**, middle Miocene, Jiulongkou locality, Hebei Province (Chen and Wu, 1976); **3**, lower Miocene, Lunpola Basin, northern Tibet (Deng et al., 2011).

Lectotype—RV37084, forefoot, including well-preserved carpals, metacarpals, and digits.

Emended Diagnosis—(Based on Yan and Heissig, 1986.) Larger than other three *Plesiaceratherium* species (M1–M3 length of 118–144 mm); sagittal crest present; caudal end of dorsal edge of zygomatic arch bears posterior process; crista and medifossette present on upper premolars; lower incisor i2 triangular in cross-section.

Type Horizon and Locality—Shanwang Formation, lower Miocene Shanwangian Stage of China, corresponding to MN 4 (Orleanian) of Europe; Shanwang Basin in Linqu County, Shandong Province, China.

Included Material—STM 44–68, nearly complete skull with slightly crushed right zygomatic arch and skull roof, lacking the nasal bones, from Hanjiashan in Jijiazhuang Village, Changle County, Shandong Province, China. This skull remains embedded in a slab of diatomaceous shale with only the right side exposed, making it difficult to adequately examine, describe, or illustrate some features on the dorsal and ventral surfaces. The specimen is somewhat laterally compressed, bringing the left row of upper cheek teeth closer to the right one, and tilting the former so that the occlusal surfaces of the teeth are visible in right lateral view (Fig. 1).

DESCRIPTION

Skull

The skull roof of STM 44-68 is nearly parallel to the occlusal line in lateral view. The nuchal crest protrudes slightly above the surface formed by the parietals and frontals, and is inclined slightly caudally, but does not overhang the occipital condyle. The nuchal surface is nearly vertical. The zygomatic arches are dorsoventrally deep (depth about 73 mm at level of orbit), and their ventral edges are slightly recessed anterior to the temporal condyles. The rostral end of the zygomatic arch is high above the alveolar margin of the upper cheek teeth. The caudal end of the dorsal edge of the zygomatic arch bears a single process that overhangs the external auditory pseudomeatus (outlined in Fig. 2). The nasal notch is retracted to the level of the posterior border of P4 and rather closely approaches the anterior rim of the orbit, which lies dorsal to the posterior border of M1 (Fig. 2). The nasal notch has a 'U'-shaped outline in lateral view. Only a single infraorbital foramen is present, and it lies below the nasal notch and dorsal to P4, opening rostrally. The postorbital processes on the frontal are very rough and bulbous, but do not form ventrally curving tubercles. The zygomatic arch does not bear a postorbital process. The lacrimal tubercle is located on the upper half of the anterior rim of the orbit. The premaxilla bears the upper incisor I1 and extends posteriorly to reach the level of P2.

Various features of the occipital region of STM 44–68 are well preserved (Fig. 2). The lateral expansion of the posttympanic process is flush with the lateral edge of the postglenoid process and anteriorly covers the posterior edge of the latter, which is laterally flattened. The paroccipital process is distinct from the posttympanic process (a dashed line indicates the boundary between these structures in Fig. 2), and the ventral end of the paroccipital process extends caudally and ventrally beyond that of the postglenoid process. The external auditory pseudomeatus is closed ventrally, and a groove (delineated with white lines in Fig. 2) extends dorsally from the pseudomeatus to the lower half of the lateral edge of the nuchal face.

Mandible

The symphysis of the lower jaw is upturned and extends caudally to the level of p2. The mental foramen opens anterior to p2. The posterior rim of the ascending ramus is inclined rostrodorsally in lateral view.

Teeth

Incisors—The left and right I1s converge slightly as they protrude rostrally, and in both teeth the facet for i2 is uneven. The
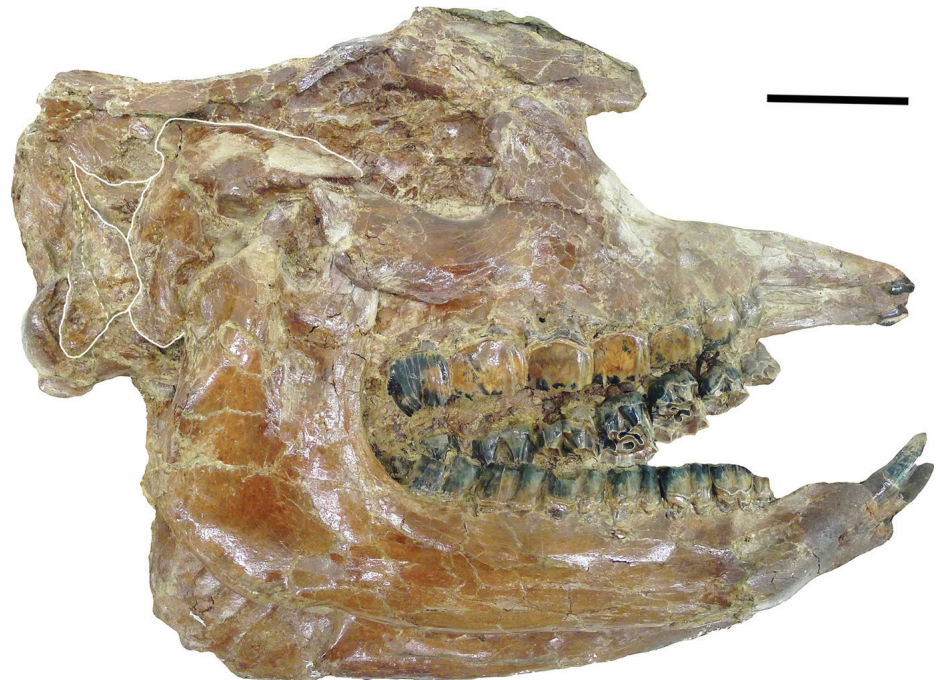

FIGURE 2. Skull of *Plesiaceratherium gracile*, STM 44-68 from the lower Miocene of Jijiazhuang in Changle County, Shandong Province, China. Right lateral view. The following structures are outlined in white: process on caudal end of dorsal edge of zygomatic arch; external auditory pseudomeatus; paroccipital process; posttympanic process; and postglenoid process. Dashed line marks external boundary between posttympanic process and paroccipital process. Scale bar equals 100 mm.

crown length of the left I1 is 32 mm, whereas that of the right I1 is 33 mm.

The i2 is tusk-like, with a badly worn crown (crown height of the left i2 42 mm, of the right one 41 mm). The mesial edge of i2 is not upturned apically. The lingual occlusal surface of i2 bears some transverse, undulating wear marks resulting from contact with I1. The i2 has a triangular cross-section with a sharp mesial edge, and its distolabial face is narrower than the lingual and mesiolabial faces.

Upper Cheek Teeth—The tooth in the first premolar position is unusual, and we examined many juvenile and adult skulls of *Plesiaceratherium gracile* from the Shanwang Basin in order to understand its structure and ontogeny. Although this tooth erupts later than DP2–DP4, and is not replaced, its enamel is thinner than that of the permanent premolars and molars, and instead similar in thickness to that of DP2–DP4. Accordingly, we regard this 'first premolar' as a DP1 that is never replaced, rather than as a P1 with no precursor. The tooth in question is double-rooted, and in STM 44–68 it is slightly worn. The parastyle is reduced and slightly curved lingually. The protocone and protoloph are less well developed than the hypocone and metaloph, respectively. The lingual cingulum is continuous with both the mesial and distal cingula. The protocone and the hypocone are separated. An unusually short enamel process (7 mm) is present on the mesiolingual side of the ectoloph, anterior to the protoloph, and does not contact the protoloph or the lingual cingulum. This structure has never been recorded in previously described material of *P. gracile* or any other aceratheriine.

On all premolars, the parastyle and paracone rib are present, and the groove between these structures extends to the base of the crown. The lingual cingulum is continuous, with an incision at the entrance of the median valley (Fig. 3). The remains of the labial cingulum are visible around the base of the crown. The crochet always meets the crista to form a medifossette, except on the left P3. A metacone rib is present on P2. The lingual cusps of P3 and P4 are slightly constricted. Rather than an antecrochet, P2–P4 each bear a complete bridge connecting the protocone to the hypocone. The ectoloph of P3 bears a mesostyle, but this structure is absent on P4.

The M1 and M2 also each bear a parastyle and paracone rib. The crochet is slightly longer than on P4 but much longer than on the other premolars. A crista is present, but fails to contact the crochet (Fig. 3). Each lingual cusp is deeply constricted. The antecrochet is long, extending to the entrance of the median valley. The lingual cingulum is continuous with the distal cingulum, but fails to contact the mesial cingulum at the lingual base of the protocone. The metastyle is more elongated in M1 and M2 than in the premolars. The posterior part of the ectoloph is concave.

Lower Cheek Teeth—We here identify the first lower cheek tooth in STM 44-68 as dp1 rather than p1, for the same reason as given above in the case of DP1. The dp1 is slightly worn and has only one root and a laterally flattened crown. Vertical rugosities are present at the bases of the labial walls of both the talonid and trigonid on p2–m3, but fade out near the upper rim of the crown due to wear. Although rounded on p2–p3, the labial wall of the trigonid is angular on p4–m3, causing the ectoflexid to become narrower. Remnants of the labial cingulum are present at the base of the ectoflexid. The ectoflexid vanishes above the root.

COMPARISONS AND DISCUSSION

The well-preserved skull from Jijiazhuang has features traditionally considered diagnostic of Aceratheriinae, a group of rhinocerotids with a wide distribution in the Miocene of Eurasia and North America. These features include nasal notch greatly retracted; posttympanic processes in contact with the postglenoid processes; symphysis moderately upturned; i2 tusk-like; metacone rib and mesostyle on upper premolars weak or absent; and lingual cusps on upper cheek teeth constricted. Comparisons of the new skull with previously described Old World aceratheriines follow.

The new skull differs from those of other Old World aceratheriines in the degree of specialization of the incisors and cheek teeth, and in some other aspects of cranial morphology. In *Alicornops*, which has been recovered from the middle to upper Miocene around the Old World, I1 is larger than in the new skull; the distance from the nasal notch to the orbit is longer; and the nuchal crest is elevated far above the parietal and frontal surfaces, giving the skull roof a sloping profile rather than a nearly horizontal one (Cerdeño and Sanchez, 2000; Deng, 2004). In *Mesaceratherium*, which is known from the upper Oligocene to lower Miocene of the Old World, I1 is also larger, i2 is upturned, and the occlusal pattern of the upper cheek teeth is much simpler. The new skull is particularly distinct from those of advanced Eurasian aceratheriines, including *Hoploaceratherium, Chilotherium, Acerorhinus, Subchilotherium,* and *Shansirhinus,* in having an I1 (Borissiak, 1915; Ringström, 1924; Colbert, 1935; Deng, 2005; Heissig, 2012).

The skull STM 44–68 shares some key diagnostic features with the genus *Plesiaceratherium* (Young, 1937; Yan, 1983; Yan and Heissig, 1986), supporting its referral to this genus: the nuchal crest is narrow and slightly higher than the frontal part of the skull roof; the zygomatic arches are dorsoventrally deep; the nasal notch is retracted to the level of P4; I1 is medium-sized; i2 is tusk-like and in a horizontal orientation; the postorbital
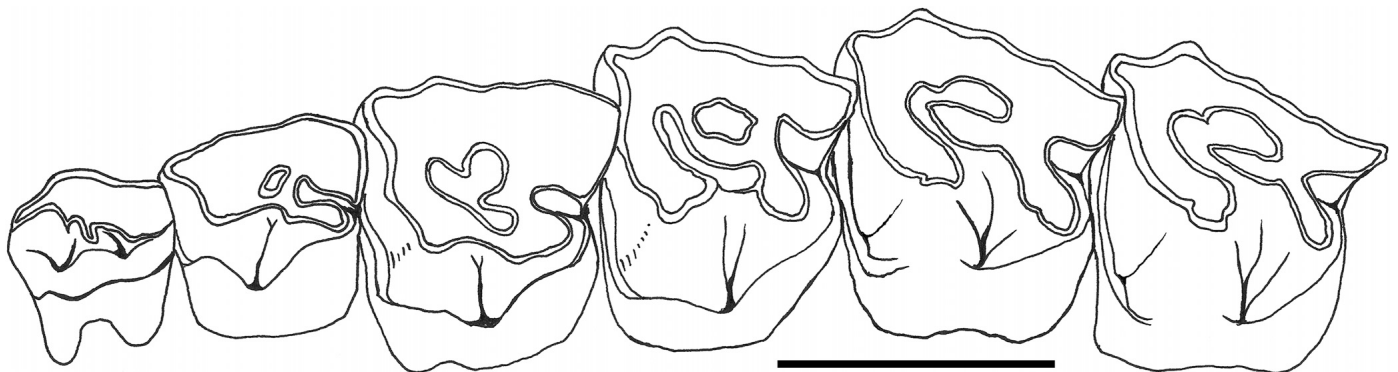

FIGURE 3. Drawing of occlusal surface of left upper cheek teeth (DP1–M2) of *Plesiaceratherium gracile*, STM 44-68 from the new early Miocene locality of Jijiazhuang in Changle County, Shandong Province, China. Scale bar equals 50 mm.

processes are swollen; and the metacone rib and mesostyle of P2 and P3 are weak.

Plesiaceratherium is the only aceratheriine genus known from the lower Miocene of China, in which it is represented by the type species *P. gracile*. Other species, namely, *P. fahlbuschi* (Heissig, 1972), *P. lumiarense* (Antunes et Ginsburg, 1983), *P. mirallesi* (Crusafont et al., 1955), and *P. platyodon* (Mermier, 1895), are known from Europe (Yan and Heissig, 1986; Deng et al., 2011). The new skull STM 44–68 differs from each of these European species. In *P. fahlbuschi*, the metaloph on P3 and P4 is elongated and nearly flush with the lingual wall of the protoloph, and the upper cheek teeth are labiolingually narrower than in the new skull (Heissig, 1972). In *P. lumiarense*, the labial cingula of the lower cheek teeth are restricted to the bases of the ectoflexid (Antunes and Ginsburg, 1983). In *P. platyodon*, the parietal crests are moderately well separated, the nuchal crest extends farther laterally, and the caudal end of the dorsal edge of the zygomatic arch does not bear a process (Mermier, 1895).

However, the skull STM 44–68 displays the key diagnostic features of the species *P. gracile*: the nuchal crest is even narrower than in other species of the genus; the parietal crests are fused to form a single sagittal crest; the metaloph on P3 and P4 is much shorter than the protoloph; and the base of the antecrochet on each upper molar extends toward the entrance of the median valley. These similarities allow us to refer the skull to *P. gracile*.

Yan and Heissig (1986) noted numerous intraspecific, as well as interspecific, variations in *Plesiaceratherium*. The new material differs from other known specimens of *P. gracile* in the following morphological details of the cheek teeth: the protocone and the hypocone are separated on DP1; a crista is present on some of the upper molars; the lingual cingulum on each upper premolar is notched by an incision; and the lingual cingula on the upper molars are reduced. The most obvious difference, however, is that the new skull is larger than all previously reported specimens of *P. gracile* (Young, 1937; Yan, 1983; Yan and Heissig, 1986) (Table 1), having a DP1–P4 length of 139 mm and an M1–M3 length of 144 mm (Table 2). However, the size difference is small enough to be most plausibly interpreted as the result of intraspecific variation.

Yan (1983) and Yan and Heissig (1986) stated that, in *Plesiaceratherium*, the lingual cusps of the upper cheek teeth are only slightly constricted. However, in the skull STM 44-68, and in the material described by Wang (1965), the upper cheek teeth have strongly constricted lingual cusps, and the base of the antecrochet extends to the entrance of the median valley. Furthermore, in specimens assigned to other species of *Plesiaceratherium*, the lingual cusps are strongly constricted, but the presence of the crista and medifossette is variable (Mermier, 1895; Heissig, 1972; Antunes and Ginsburg, 1983). These observations indicate that the occlusal surfaces of the upper cheek teeth are complex in at least some individuals of *P. gracile*, and that the lingual cusps are strongly constricted in most known specimens of *Plesiaceratherium*.

Yan and Heissig (1986) considered the presence of vertical rugosities on the lower premolars to be a diagnostic feature of *Plesiaceratherium*. However, this feature is universally present in

aceratheriines (Ringström, 1924; Deng, 2005). Accordingly, the vertical rugosities are not useful in differentiating *Plesiaceratherium* from other aceratheriines and cannot be considered diagnostic of this genus.

The swelling on the orbital margin of *Plesiaceratherium* was described as a 'supraorbital tuberosity' by Yan (1983) and Yan and Heissig (1986), but the appropriateness of this term is doubtful. The swelling around the posterior border of the orbit seen in *Plesiaceratherium* ends at the midpoint of the supraorbital rim, never extending rostrally to the anterodorsal corner of the orbit (Yan and Heissig, 1986). Therefore, it should be called a postorbital process instead of a supraorbital tuberosity.

REVISION OF RHINOCEROSES FROM THE SHANWANG BASIN

Plesiaceratherium gracile is the first rhinoceros represented by abundant material from the lower Miocene strata of the Shanwang Basin (Young, 1937; Yan, 1983; Yan and Heissig, 1986). Other rhinoceros specimens from this area are fragmentary and have been assigned to *Plesiaceratherium shanwangensis* and *Aceratherium* sp. (Hu, 1957; Wang, 1965; Xie, 1982).

Hu (1957) mistakenly identified an isolated rhinoceros P4 (IVPP V 895) as an M1 and assigned it and other isolated teeth to *Aceratherium* sp. because the lingual cusps were only weakly constricted. Xie (1982) subsequently described more teeth from the same locality. Xie (1982) referred them to *Aceratherium* sp. together with one astragalus and one calcaneus, on the basis of the crown height of the i2 and the configuration of the calcaneal facets of the astragalus. The crown height of i2 is in fact too easily affected by wear to be taxonomically informative. Xie (1982) further assumed that the second and third calcaneal facets of the astragalus in his material were directly adjacent, as in *Aceratherium*, but the two facets are in fact separated by a crest. However, the astragalus described by Xie (1982) matches that of the lectotype of *P. gracile* in that the anterior edge of the distal cuboid facet is narrow. Furthermore, the teeth described by Hu (1957) and Xie (1982) share with those of *Plesiaceratherium* the following characteristics: the incisors are medium-sized; the cheek teeth are low-crowned; the lingual cusps of the upper molars are strongly constricted; and P2 and P3 have metacone ribs and mesostyle. In contrast, the upper cheek teeth of *Aceratherium* lack the metacone rib and mesostyle (Hünermann, 1989). We therefore refer the specimens from the Shanwang Basin previously identified as *Aceratherium* sp. by Hu (1957) and Xie (1982) to *P. gracile*.

Wang (1965) established *Plesiaceratherium shanwangensis* on upper cheek teeth from the Shanwang Basin that she considered to be larger, higher-crowned, and more advanced in their morphology than those of *P. gracile*. However, the teeth assigned to *P. shanwangensis* are in fact similar to teeth of *P. gracile* in crown height and morphology. The two species can be considered synonymous, and *P. gracile* has priority.

Chow and Wang (1964) referred some crushed cheek teeth from the Miocene of Sihong, Jiangsu Province, China, to

TABLE 1. Measurements (in mm) of skull of *Plesiaceratherium gracile* STM 44–68 and other specimens of *Plesiaceratherium*.

Dimension	*P. gracile* STM 44–68	*P. gracile* IVPP V 6880	*P. fahlbuschi* type	*P. platyodon* type
Distance between occipital condyle and premaxillary tip	642	—	—	—
Distance between occipital crest and nasal tip	—	590	516	563
Distance between nasal notch and nasal tip	—	184	185	206
Distance between nasal notch and orbit	75	66	43	51
Distance between M3 and occipital condyle	274	—	—	—

Measurements of *P. gracile* and *P. fahlbuschi* are from Yan and Heissig (1986); measurements of *P. platyodon* were taken on the figures of Ballesio et al. (1965).

TABLE 2. Measurements (in mm) of upper cheek teeth of *Plesiaceratherium gracile* STM 44–68 and other specimens of *Plesiaceratherium*.

| Tooth | *P. gracile* | | *P. fahlbuschi* | *P. mirallesi* | *P. platyodon* |
	STM 44–68	IVPP V 6880	Type	Geor.	Type
DP1	28/—	—/—	—/—	21/19	20/18
P2	34/—	31/36	24/33	—/—	30/35
P3	42/—	34/42	29/39	35/44	28/43
P4	44/—	37/43	32/43	37/48	34/45
M1	50/—	46/48	32/44	41/47	35/43
M2	54/—	48/50	36/47	45/51	38/46
M3	52/—	43/45	41/42	41/45	37/42
P2–P4	114	110	87	102	91
M1–M3	144	121	109	126	115

The measurements are presented as length/width. All the measurements except those of STM 44–68 are from Yan and Heissig (1986). **Abbreviation**: **Geor.**, means Georgensgmünd in Bavaria, Germany.

Brachypotherium pugnator Matsumoto, 1921. Wang (1965) reassigned these specimens to *P. shanwangensis*, but we believe that they belong to *Brachypotherium* because of two critical features: P3 and P4 each have a broad crown outline, their metaloph is long and nearly flush with the protocone lingually; and the distal cingulum of P3 forms a slender pseudometaloph when badly worn (Chow and Wang, 1964; Wang, 1965; Cerdeño, 1993).

Wang (1965) reassigned *B. pugnator*, which Matsumoto (1921) had established for material from the early Miocene Hiramaki Formation of Kani District, Japan, to *Plesiaceratherium* as *P. pugnator*. She believed that *B. pugnator* was similar to *Plesiaceratherium* in that a ridge connected the protocone to the hypocone on P3. The lingual cusps of P3 of *B. pugnator* described by Matsumoto (1921) indeed appear connected, but this tooth is heavily worn on both sides of the skull. In the less worn P4, an antecrochet is present but is separated from the hypocone by a conspicuous gap (Matsumoto, 1921:pl. 14), suggesting that the apparent connection between the protocone and hypocone in P3 is probably an artifact of heavy wear combined with limited contact between the antecrochet and the base of the hypocone. In contrast, the apices of the lingual cusps of both P3 and P4 of *Plesiaceratherium* are connected by a tall ridge, so that this feature distinguishes *Plesiaceratherium* from *B. pugnator* (Yan, 1983; Yan and Heissig, 1986).

PHYLOGENETIC AFFINITIES OF *PLESIACERATHERIUM*

Methods

A phylogenetic analysis was carried out in order to evaluate the affinities of *P. gracile* and other species assigned to *Plesiaceratherium*. A total of 314 characters (Table S1) modified from those used in previous studies by Antoine (2002), Antoine et al. (2003, 2010), Deng (2008), and Lu (2013) were included in our data matrix (Table S2), of which 282 characters were from Antoine (2002) and the other 32 were added by Lu (2013). All characters were equally weighted. Twelve characters (2, 3, 8, 31, 65, 94, 123, 131, 170, 219, 246, 262) were treated as 'unordered.' The present phylogenetic analysis included 39 terminal taxa, five of which were newly added: *Brachypotherium pugnator*, *P. gracile*, *P. platyodon*, *P. fahlbuschi*, and *P. lumiarense*. Four terminal taxa were used as outgroups: the extant tapirid *Tapirus terrestris* Linnaeus, 1758, the Eocene hyrachyid *Hyrachyus eximius* Leidy, 1871, and the Eocene stem rhinocerotids *Trigonias osborni* Lucas, 1900, and *Ronzotherium filholi* (Osborn, 1900). Codings for most of the Chinese taxa, including *Acerorhinus yuanmouensis*, *Shansirhinus ringstroemi*, *Chilotherium wimani*, *C.*

anderssoni, and *Plesiaceratherium gracile*, were based on direct observation of specimens. However, *Acerorhinus zernowi* and *Subchilotherium intermedium* were coded partly from the literature. Scorings for other taxa were taken from Antoine (2002), Antoine et al. (2003, 2010), Lu (2013), and other relevant literature. The matrix was analyzed with PAUP 4.0b10 (heuristic search, branch-swapping tree bisection and reconnection [TBR], 1000 replications with random addition of taxa). The character list and data matrix are given in Supplementary Data Files 1 and 2, respectively.

Results

The results of the present analysis coincide in many respects with those of recent studies by Antoine et al. (2003, 2010) and Becker et al. (2013). However, the present analysis found the subfamily Aceratheriinae, as normally conceived, to be polyphyletic. A major clade approximating the traditional taxonomic content of Aceratheriinae (Fig. 4, Node A) was recovered, but *Aceratherium* itself and two other taxa usually regarded as aceratheriines were recovered well outside Node A and formed a separate grouping (Fig. 4, Node B) that was found to be the sister group of a clade approximating Rhinocerotinae (Fig. 4, Node C). In our analysis, '*B*.' pugnator was recovered far from *B. brachypus* and indeed other rhinocerotines, implying that '*B*.' pugnator is not a member of *Brachypotherium*. However, '*B*.' pugnator was also clearly separated from all *Plesiaceratherium* species, a result confirming our suggestion based on cheek tooth morphology (see above) that Wang's (1965) referral of '*B*.' pugnator to *Plesiaceratherium* was unjustified.

The sister group relationship between Nodes B and C (Node D) is supported by seven synapomorphies: foramen magnum subtriangular; protocone of P2 less strong than hypocone; posterior part of ectoloph of M1 and M2 straight; vertical external rugosities on p2 and p3 absent; lingual cingulum on lower premolars usually absent; lingual cingulum on lower molars usually absent; and magnum facet of Mc II straight. Only two of these synapomorphies, namely, the absence of a lingual cingulum on the lower premolars and on the lower molars, are scored as occurring in all three aceratheriines. However, these two features are known to be quite variable in rhinocerotid upper cheek teeth, raising the possibility that the closeness of Node B to rhinocerotines rather than to the larger group of aceratheriines (Node A) may be a spurious result. The phylogenetic interrelationships of aceratheriines clearly require further investigation.

The four species *P. fahlbuschi*, *P. gracile*, *P. lumiarense*, and *P. platyodon* form a monophyletic group (Fig. 4, Node E) within Node A, corresponding to the genus *Plesiaceratherium* and supported by two unambiguous synapomorphies: labial cingulum always present on the upper premolars, and protocone constriction usually absent on P3 and P4. Both features can be scored as present in all the species included in the *Plesiaceratherium* clade, with one exception: in *P. platyodon*, the protocone constriction is usually present on P3 and P4. These features have been added to the diagnosis of *Plesiaceratherium* given above. We provisionally retain in the diagnosis two other characteristics of *Plesiaceratherium* that were not coded in our phylogenetic analysis, namely, very slender limbs and a medium-sized I1, because of their value in distinguishing *Plesiaceratherium* from other aceratheriine genera.

The monophyletic clade *Plesiaceratherium* (Fig. 4, Node E) is sister to the group [*Subchilotherium* [*Acerorhinus* [*Shansirhinus*, *Brachypotherium pugnator* [*Chilotherium*]]]] within the major aceratheriine clade (Fig. 4, Node A). However, '*P*.' mirallesi is placed well outside the *Plesiaceratherium* clade as a stem rhinocerotine (Fig. 4, Node F), as in previous analyses by Antoine et al. (2003, 2010). These results suggest that it is necessary to reconsider the generic assignment of '*P*.' mirallesi, particularly given
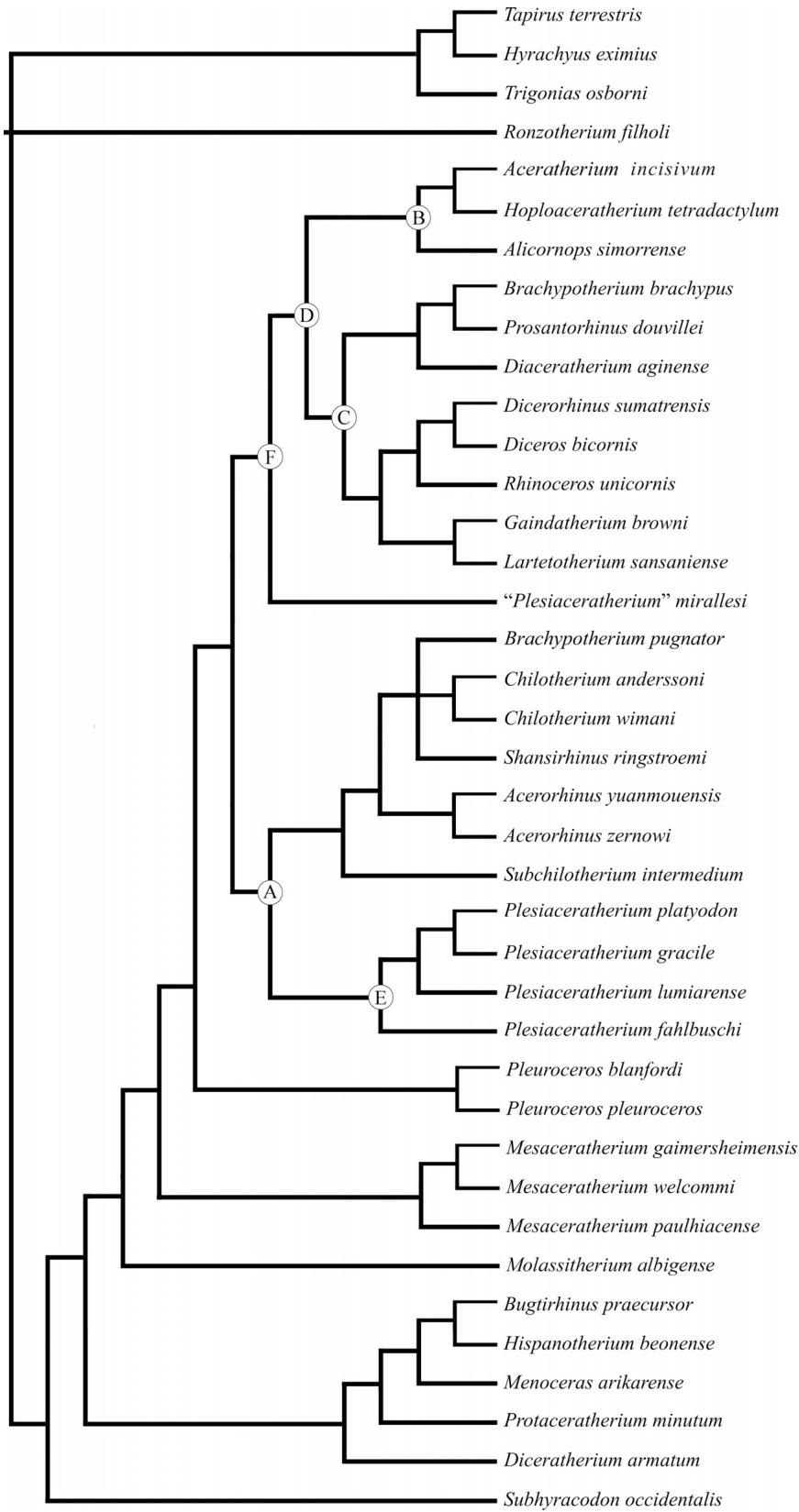
FIGURE 4. Single most parsimonious tree (1473 steps, CI = 0.26, RI = 0.49) obtained by using PAUP 4.0b10 (heuristic search, branch-swapping TBR, 1000 replications with random taxa addition; Swofford, 2001) to analyze a matrix containing 314 characters and 39 taxa, with *Tapirus terrestris, Hyrachyus eximius, Trigonias osborni*, and *Ronzotherium filholi* as outgroups. Twelve characters are treated as 'unordered': 2, 3, 8, 31, 65, 94, 123, 131, 170, 219, 246, and 262. Node E is supported by transitions to the derived state in characters 40 and 134.

that both synapomorphies supporting the *Plesiaceratherium* clade can be scored as absent in '*P.*' *mirallesi*.

Crusafont et al. (1955) established *Dromoceratherium* and its type species *D. mirallesi* on material including an isolated i2, some isolated lower cheek teeth, and some crushed limb bones from the lower Miocene of Can Julia, Barcelona, Spain. Yan (1983) and Yan and Heissig (1986) referred *D. mirallesi* to *Plesiaceratherium* as '*P.*' *mirallesi*, considering the genus *Dromoceratherium* to be a synonym of *Plesiaceratherium*.

The original description and illustration of i2 in '*P.*' *mirallesi* stated that i2 was large, and described the cross-section of the crown as teardrop-shaped in the basal half of the tooth and semilunar in the apical half (Crusafont et al., 1955). However, the i2 of *Plesiaceratherium gracile, P. platyodon,* and *P. fahlbuschi* are clearly distinct from '*P.*' *mirallesi* in having a triangular cross-section, although admittedly the shape of the cross-section of i2 in *Plesiaceratherium lumiarense* remains unknown.

In '*P.*' *mirallesi,* the lower cheek teeth are narrow, exhibiting a larger length-to-width ratio than in any other species currently assigned to *Plesiaceratherium* (Crusafont et al., 1955; Yan and Heissig, 1986). Furthermore, in contrast to '*P.*' *mirallesi,* the lower cheek tooth with the highest length-to-width ratio in other species of *Plesiaceratherium* is m3 rather than m2 (Table 3) (Mermier, 1895; Ballesio et al., 1965; Heissig, 1972; Yan and Heissig, 1986). At least in *Chilotherium,* the length-to-width ratios of the lower cheek teeth appear to be largely unaffected by wear (unpublished data), so we believe that this metric might be taxonomically significant.

The limb bones of '*P.*' *mirallesi* are more massive than those of *P. gracile* (Heissig, 1999). The volar edge of the ulna from the olecranon to the upper part of the shaft is nearly straight in '*P.*' *mirallesi,* but concave in *P. gracile* (Young, 1937; Antoine, 2002). The proximal third carpal facet on the third metacarpal of '*P.*' *mirallesi* has a gentle distal-volar inclination. In *P. fahlbuschi* and *P. gracile,* however, this inclination is much steeper (Yan and Heissig, 1986).

Many significant morphological differences exist between '*P.*' *mirallesi* and other species currently assigned to *Plesiaceratherium,* including *P. gracile.* These differences are reflected in the placement of '*P.*' *mirallesi* far outside *Plesiaceratherium* in the phylogenetic analysis given in the present paper. '*P.*' *mirallesi* should be removed from the genus *Plesiaceratherium,* and the genus name *Dromoceratherium* should be revived to accommodate this species.

AGE OF THE JIJIAZHUANG MAMMAL FAUNA

Plesiaceratherium fossils have been found previously at three localities in China: the Shanwang Basin in Shandong Province, Jiulongkou in Hebei Province, and the Lunpola Basin in Tibet (Young, 1937; Chen and Wu, 1976; Deng et al., 2011). The faunas of the Shanwang and Lunpola basins have been determined to be from the early Miocene Shanwangian Age based on paleomagnetic data and biostratigraphic correlations, whereas the

Jiulongkou fauna has been suggested to date from the middle Miocene based on mammalian biostratigraphy (Chen and Wu, 1976; Deng et al., 2003, 2011). The three species of *Plesiaceratherium* known from Europe are all from MN 3–5, within the early Miocene Orleanian Age (Heissig, 1999). Radiometric dating of the basalts beneath the richly fossiliferous diatomaceous lacustrine shales in the Shanwang Basin implied that the diatomite was deposited 17 Ma ago, corresponding to the early Miocene MN 4 interval in Europe (Chen and Peng, 1985; Deng et al., 2003; He et al., 2011). The fossiliferous strata at Jiulongkou and in the Lunpola Basin have not been dated radiometrically. The *Plesiaceratherium*-bearing deposits at Bugti Hills in Pakistan have been dated to around 19 Ma, corresponding to the European early Miocene MN 3 (Welcomme et al., 1997; Antoine and Welcomme, 2000). Currently, nearly all published Eurasian *Plesiaceratherium* specimens are from lower Miocene strata. The occurrence of *P. gracile* in the diatomaceous shales of the Jijiazhuang locality therefore implies that the strata were deposited during the early Miocene.

CONCLUSIONS

A skull recovered from the lacustrine shales of a new locality at Jijiazhuang Village, Shandong Province, China, is assigned to the type species of *Plesiaceratherium, P. gracile.* Morphological comparisons support reassignment to *P. gracile* of the Shanwang Basin specimens previously identified as *Aceratherium* sp. and *P. shanwangensis. Plesiaceratherium* is therefore the only aceratheriine genus known to be present in the Shanwang Basin, and indeed in the entire lower Miocene of China. This fact suggests that early aceratheriines were less diverse in East Asia than in Europe. In addition, the discovery of *Plesiaceratherium* at the new locality of Jijiazhuang implies that the lacustrine shales exposed at this site were deposited in the early Miocene.

Dromoceratherium mirallesi from the lower Miocene of Can Julia, Barcelona, Spain, was reassigned by Yan (1983) to *Plesiaceratherium,* as '*P.*' *mirallesi.* This species was recovered as a stem rhinocerotine in the present analysis, a finding consistent with morphological comparisons and the results of previous analyses. Accordingly, the genus name *Dromoceratherium* should be revived to accommodate the species as *D. mirallesi.* More surprisingly, Aceratheriinae were recovered as a polyphyletic group, with taxa traditionally regarded as aceratheriines assigned to two widely separated clades. This is an unexpected result that will undoubtedly be tested in future analyses of aceratheriine phylogeny.

LITERATURE CITED

Antoine, P.-O. 2002. Phylogénie et évolution des Elasmotheriina (Mammalia, Rhinocerotidae). Mémoires du Muséum national d'Histoire naturelle de Paris 188:1–359.

TABLE 3. Measurements (in mm) of lower cheek teeth of *Plesiaceratherium* and other two aceratheriines.

Taxon	p2	p3	p4	m1	m2	m3
P. gracile IVPP V 6880	28/19	31/20	35/26	38/28	40/26	43/27
P. fahlbuschi 3003	21/15	30/19	32/22	33/21	38/24	39/23
P. mirallesi type	32/18	35/21	39/25	43/23	46/24	47/25
P. platyodon type	27/17	33/23	33/24	35/24	38/24	40/23
H. tetradactylum female	26/19	32/24	36/28	36/26	41/27	42/27
A. simorrense type	26/18	30/23	35/22	37/23	38/24	42/23

The measurements are presented as length/width. All the measurements including the one for *P. gracile* are from Yan and Heissig (1986).

Antoine, P.-O., and J. L. Welcomme. 2000. A new rhinoceros from the lower Miocene of the Bugti Hills, Baluchistan, Pakistan: the earliest elasmotheriine. Palaeontology 43:795–816.

Antoine, P.-O., D. Stéphane, L. Marivaux, Y. Chaimanee, J. Y. Crochet, J. J. Jaeger, and J. L. Welcomme. 2003. *Alicornops* (Mammalia, Rhinocerotidae) dans le Miocène supérieur des collines Bugti (Balouchistan, Pakistan): implications phylogénétiques. Geodiversitas 25:575–603.

Antoine, P.-O., K. F. Downing, J.-Y. Crochet, F. Duranthon, L. J. Flynn, L. Marivaux, G. Métais, A. R. Rajpar, and G. Roohi. 2010. A revision of *Aceratherium blanfordi* Lydekker, 1884 (Mammalia: Rhinocerotidae) from the early Miocene of Pakistan: postcranials as a key. Zoological Journal of the Linnean Society 160:139–194.

Antunes, M. T., and L. Ginsburg, 1983. Les Rhinocérotidés du Miocène de Lisbonne—systématique, écologie, paléobiogéographie, valeur stratigraphique. Ciências da Terra 7:17–98.

Ballesio, R., J. Battetta, L. David, and P. Main. 1965. Mise au point sur *Aceratherium platyodon* Mermier 1895. Documents des Laboratoires de Géologie de la Faculté des Sciences de Lyon 9:51–94.

Becker, D., P.-O. Antoine, and O. Maridet. 2013. A new genus of Rhinocerotidae (Mammalia, Perissodactyla) from the Oligocene of Europe. Journal of Systematic Palaeontology 11:947–972.

Borissiak, A. 1915. Mammifères fossiles de Sebastopol, II. Trudy Geologicheskogo Komiteta, Novaja Seria 137:1–47.

Cerdeño, E. 1992. Spanish Neogene rhinoceroses. Palaeontology 35:297–308.

Cerdeño, E. 1993. Étude sur *Diaceratherium aurelianense* et *Brachypotherium brachypus* du Miocène Moyen de France. Bulletin du Muséum national d'Histoire naturelle de Paris 15:25–77.

Cerdeño, E., and B. Sanchez. 2000. Intraspecific variation and evolutionary trends of *Alicornops simorrense* (Rhinocerotidae) in Spain. Zoologica Scripta 29:275–305.

Chen, D.-G., and Z.-C. Peng. 1985. K-Ar ages and Pb, Sr isotopic characteristics of Cenozoic volcanic rocks in Shandong, China. Geochemica 31:293–303. [Chinese 293–303; English 303]

Chen, G.-F., and W.-Y. Wu. 1976. [Miocene mammalian fossils of Jiulongkou of Cixian, Hebei]. Vertebrata PalAsiatica 14:6–15. [Chinese]

Chow, M.-C., and B.-Y. Wang. 1964. Fossil vertebrates from the Miocene of northern Kiangsu. Vertebrata PalAsiatica 8:341–351. [Chinese 341–348; English 348–351]

Crusafont, M., J. F. Villalta, and Y.-J. Truyols. 1955. El Burdigaliense continental de la Cuenca del Vallés-Penedés. Diputación Provincial de Barcelona Memorias y Comunicaciones del Instituto Geológico 12:1–272.

Colbert, E. H. 1935. Siwalik mammals in the American Museum of Natural History. Transactions of the American Philosophical Society 26:1–401.

Deng, T. 2004. A new species of the rhinoceros *Alicornops* from the middle Miocene of the Linxia Basin, Gansu, China. Palaeontology 47:1427–1439.

Deng, T. 2005. New cranial material of *Shansirhinus* (Rhinocerotidae, Perissodactyla) from the lower Pliocene of the Linxia Basin in Gansu, China. Geobios 38:301–313.

Deng, T. 2008. A new elasmothere (Perissodactyla, Rhinocerotidae) from the late Miocene of the Linxia Basin in Gansu, China. Geobios 41:719–728.

Deng, T., W.-M. Wang, and L.-P. Yue. 2003. Recent advances of the establishment of the Shanwang Stage in the Chinese Neogene. Vertebrata PalAsiatica 41:314–323. [Chinese 314–323; English 321]

Deng, T., S.-Q. Wang, G.-P. Xie, Q. Li, S.-K. Hou, and B.-Y. Sun. 2011. A mammalian fossil from the Dingqing Formation in the Lunpola Basin, northern Tibet, and its relevance to age and paleo-altimethy. Chinese Science Bulletin 57:261–269.

Dollo, L. 1885. Rhinoceros vivantset fossiles. Revue des Questions Scientifiques 17:293–300.

Geraads, D. 2010. Rhinocerotidae; pp. 669–683 in L. Werdelin and W. J. Sanders (eds.), Cenozoic Mammals of Africa. University of California Press, Berkeley, California.

Guérin, C. 1980. Les rhinocéros (Mammalia, Perissodactyla) du Miocène terminal au Pléistocène supérieur en Europe occidentale: comparaison avec les espèces actuelles. Documents du Laboratoire de Géologie de la Faculté des Sciences de Lyon 79:1–1182.

He, H.-Y., C.-L. Deng, Y.-X. Pan, T. Deng, Z.-H. Luo, J.-M. Sun, and R.-X. Zhu. 2011. New ^{40}Ar/^{39}Ar dating results from the Shanwang Basin, eastern China: constraints on the age of the Shanwang Formation and associated biota. Physics of the Earth and Planetary Interiors 187:66–75.

Heissig, K. 1972. Die obermiozäne Fossil-Lagerstätte Sandelzhausen, 5. Rhinocerotidae (Mammalia), Systematik und Ökologie. Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie 12:57–81.

Heissig, K. 1999. Family Rhinocerotidae; pp. 175–188 in G. E. Rössner and K. Heissig (eds.), The Miocene Land Mammals of Europe. Verlag Dr. Friedrich Pfeil, Munich.

Heissig, K. 2012. Les Rhinocerotidae (Perissodactyla) de Sansan; pp. 317–485 in S. Peigné and S. Sen (eds.), Mammifères de Sansan. Mémoires du Muséum National d'Histoire Naturelle de Paris 203.

Hu, C.-K. 1957. An antler fragment of *Stephanocemas* and some teeth of *Aceratherium* from Linchü, Shantung. Vertebrata PalAsiatica 1:163–166. [Chinese 163–165; English 165–166]

Hünermann, K. A. 1989. Die Nashornskelette (*Aceratherium incisivum* Kaup, 1832) aus dem Jungtertiär vom Höwenegg im Hegau (Südwestdeutschland). Andrias 6:5–116.

Lu, X.-K. 2013. A juvenile skull of *Acerorhinus yuanmouensis* (Mammalia: Rhinocerotidae) from the later Miocene hominoid fauna of the Yuanmou Basin (Yunan, China). Geobios 46:539–548.

Matsumoto, H. 1921. Descriptions of some new fossil mammals from Kani District, Prov. of Mino, with revisions of some Asiatic fossil rhinocerotids. Science Reports of the Tohôku Imperial University, Sendai, Series 2, Geology 5:75–91.

Mermier, E. 1895. Sur la découverte d'une nouvelle espèce d'*Aceratherium* dans la mollasse burdigalienne du Royans. Annales de la Société Linnéenne de Lyon 42:163–189.

Owen, R. 1845. A History of British Fossil Mammals and Birds. John van Voorst, London, 560 pp.

Owen, R. 1848. On the Archetype and Homologies of the Vertebrate Skeleton. John van Voorst, London, 203 pp.

Qiu, Z.-D., and Z.-X. Qiu. 2013. Early Miocene Xiejiahe and Sihong fossil localities and their fauna, eastern China; pp. 142–154 in X.-M. Wang, L. J. Flynn, and M. Fortelius (eds.), Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology. Columbia University Press, New York.

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

Ringström, T. 1924. Nashörner der *Hipparion*-Fauna Nord-Chinas. Palaeontologia Sinica 1(4):1–156.

Roček, Z., L.-P. Dong, T. Přikryl, C.-K. Sun, J. Tan, and Y. Wang, 2011. Fossil frogs (Anura) from Shanwang (middle Miocene; Shandong Province, China). Geobios 44:499–518.

Sisson, S. B. 1953. The Anatomy of the Domestic Animals. W.B. Saunders Company, Philadelphia and London, 972 pp.

Swofford, D.L. 2001. PAUP* (phylogenetic analysis using parsimony [*and other methods] version 4.0b10). Sinauer, Sunderland, MA.

Wang, B.-Y. 1965. A new Miocene aceratheriine rhinoceros of Shanwang, Shandong. Vertebrata PalAsiatica 9:109–112. [Chinese 109–111; English 112]

Welcomme, J. L., P.-O. Antoine, F. Duranthon, P. Mein, and L. Ginsburg. 1997. Nouvelles découvertes de vertébrés miocènes dans le synclinal de Dera Bugti (Balouchistan, Pakistan). Comptes Rendus de l'Académie des Sciences, Sciences de la Terre et des Planètes 325:531–536.

Xie, W.-M. 1982. New discovery on aceratheriine rhinoceros from Shanwang in Linchu, Shandong. Vertebrata PalAsiatica 20:133–137. [Chinese 133–137; English 137]

Yan, D.-F. 1983. Über die Klassifikation und Morphologie des Schädel von *Plesiaceratherium*. Vertebrata PalAsiatica 21:134–143. [Chinese 134–142; German 143]

Yan, D.-F., and K. Heissig. 1986. Revision and autopodial morphology of the Chinese-European rhinocerotid genus *Plesiaceratherium* Young 1937. Zitteliana 14:81–109.

Yan, D.-F., Z.-D. Qiu, and Z.-Y. Meng. 1983. Miocene stratigraphy and mammals of Shanwang, Shandong. Vertebrata PalAsiatica 21:210–222. [Chinese 210–220; English 220–222]

Young, C.-C. 1937. On a Miocene mammalian fauna from Shantung. Bulletin of the Geological Society of China 17:209–244.