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A NEW SPECIES OF *ACERATHERIUM* (RHINOCEROTIDAE, PERISSODACTYLA) FROM THE LATE MIOCENE OF NAKHON RATCHASIMA, NORTHEASTERN THAILAND

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ABSTRACT—A new species of the genus *Aceratherium*, *A. porpani* sp. nov., from the Tha Chang sand pits in Nakhon Ratchasima Province, northwestern Thailand, is described. It is a mid-sized rhinocerotid in the subfamily Aceratheriinae, and represents the first discovery of *Aceratherium* in Thailand. The material includes a well-preserved skull and mandible. *A. porpani* has broadly separated parietal crests, slightly expanded zygomatic arches, a straight nuchal crest, moderate supraorbital tuberosities, a flat skull roof, a deep nasal notch above the P4/M1 boundary, a moderately wide mandibular symphysis with a posterior border at the p3/p4 boundary, a short diastema between i2 and p2, absence of DP1 and dp1, strong crochets, constricted molar protocones, and long metalophs. This new species has a mixture of primitive and derived characters that differ from the known species of *Aceratherium*, *A. incisivum*, and *A. depereti*. The evolutionary stage of *A. porpani* is consistent with the latest Miocene age of the associated fauna and flora in the Tha Chang sand pits.

INTRODUCTION

In the Tha Chang area, Nakhon Ratchasima Province, Thailand, several sand pits previously have yielded fossils (Chaimanee et al., 2004; Hanta et al., 2008). The area is 220 km northeast of Bangkok, and the sand pits are located next to the Mun River (15°05'N and 102°20'E) (Fig. 1A, B). The sedimentary sequence of these sand pits consists of unconsolidated mudstone, sandstone, and conglomerate (Fig. 1C), deposited by the ancient Mun River. Unfortunately, almost all the fossils have been found and collected by local villagers working in these sand pits, and only later were brought to public institutions such as the district office, library, or Nakhon Ratchasima Rajabhat University (Hanta et al., 2008). Consequently, precise field information is unavailable for most of the fossils from the Tha Chang area, including the type mandible of the recently described new hominoid *Khoratpithecus piriyai* (Chaimanee et al., 2004). The skull of a new anthracothere species *Merycopotamus thachangensis* was a rare exception in that it was discovered and collected directly by scientists (Hanta et al., 2008).

It is difficult to estimate precisely the geological age of the fossils discovered in the Tha Chang sand pits. Until now, only the skull of *M. thachangensis* and some stegolophodonts have ever been collected with reliable locality information. The stegolophodonts are more primitive than *Stegodon* in northern China, suggesting that the sand pits are older than 6 Ma. Based on other mammalian fossils from the Tha Chang area, the age of the fossiliferous deposits in Tha Chang Sand Pit 8 has been estimated to be 9–7 Ma (Chaimanee et al., 2004), and later, 7.4–5.9 Ma (Chaimanee et al., 2006). Apart from the locality problem, however, the mammalian fossils stored in the public institutions in Nakhon Ratchasima and in some private collections can be largely sorted into three assemblages of different geological ages,

that is, the middle Miocene, late Miocene, and early Pleistocene faunas (Nakaya et al., 2003; Saegusa et al., 2005).

The fossils described in this paper were collected and donated by Mr. Porpan Watchajitpan. Now they are preserved in the Northeastern Research Institute of Petrified Wood and Mineral Resources. Terminology and taxonomy follow Heissig (1972, 1999), Guérin (1980), and Qiu and Wang (2007). The measurements are according to Guérin (1980) and given in mm.

Institutional Abbreviation—PRY, Northeastern Research Institute of Petrified Wood and Mineral Resources

Other Abbreviations—H, height; L, length; MN, Neogene Mammal Zone; W, width.

SYSTEMATIC PALEONTOLOGY

Order PERISSODACTYLA Owen, 1848
Family RHINOCEROTIDAE Owen, 1845
Subfamily ACERATHERIINAE Dollo, 1885
Tribe ACERATHERIINI Dollo, 1885
ACERATHERIUM Kaup, 1832

Type Species—*Aceratherium incisivum* Kaup, 1832, from Eppelsheim, Germany.

ACERATHERIUM PORPANI, sp. nov.
(Figs. 2–5; Tables 1–3)

Holotype—An adult skull (PRY 142) without premaxillae and the anterior portion of nasals, keeping cheek teeth from P4 to M3 (Figs. 2, 3, 5A; Tables 1, 3).

Paratype—An almost complete mandible (PRY 141), missing tusks of i2 (Figs. 4, 5B; Tables 2, 3).

Etymology—In honor of Porpan Vachajitpan, who donated the studied holotype and paratype specimens of this new species.

Type Horizon and Locality—Latest Miocene (corresponding to MN 12 in Europe) at Tha Chang, Nakhon Ratchasima Province, Thailand. The locality and horizon (Fig. 1C) was determined on the basis of the collector's description for the

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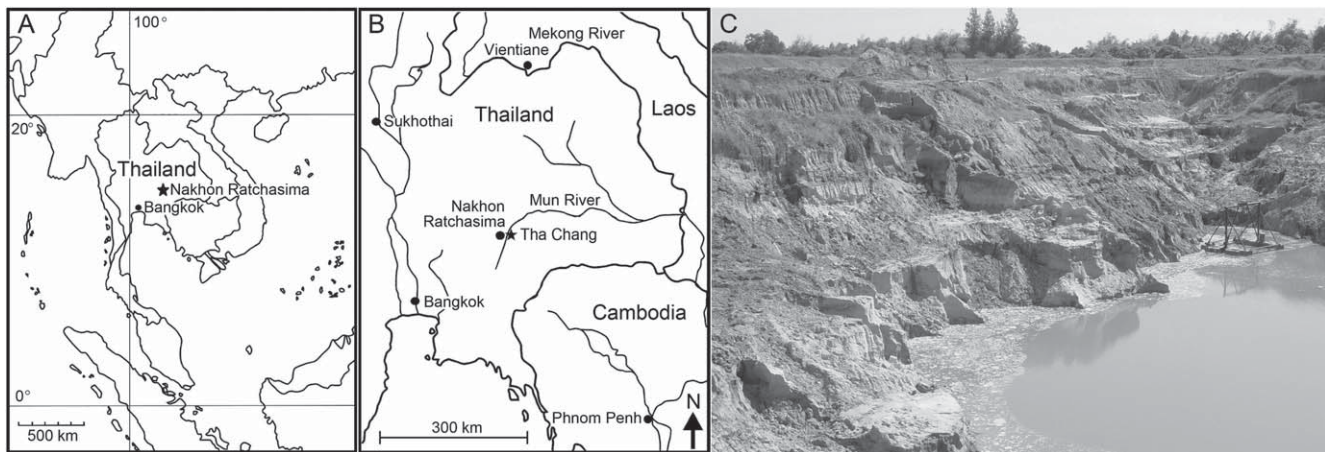


FIGURE 1. Location and section of Tha Chang in Chalem Prakieat District, Nakhon Ratchasima Province, Thailand. **A**, Southeast Asia with location of Nakhon Ratchasima; **B**, Thailand with location of Tha Chang; **C**, sequence of Miocene fluvial deposits at a Tha Chang sand pit. (Color figure available online.)

discovery and our personal examination of the site, and the age of the fossiliferous horizon in this sand pit was judged by the correlation to Tha Chang Sand Pit 8 (Hanta et al., 2008:fig. 4).

Diagnosis—Mid-sized species of *Aceratherium* with broadly separated parietal crests, slightly expanded zygomatic arches, a straight nuchal crest, moderate supraorbital tuberosities, a flat skull roof, a deep nasal notch above the P4/M1 boundary, a moderately wide mandibular symphysis with a posterior border at the p3/p4 boundary, a short diastema between i2 and p2, absence of DP1 and dp1, strong crochets, constricted molar protocones, and long metalophs.

DESCRIPTION

Skull

The skull is dolichocephalic, with a distance of 451 mm between the incisive foramen and the intercondylar notch. The suture between the nasal and frontal bones is clear with a wide and shallow 'V'-shaped valley; and its base oriented anteriorly (Fig. 2A). The premaxillary bones are narrow and thin, with a thickness of 9.5 mm and a height of 23.5 mm in front of the maxillary bones. The supraorbital tuberosities are moderate, so the lower orbital rims are completely seen in dorsal view. The zygomatic arches, nearly vertical laterally, are not expanded. The skull roof is flat, with a high occiput (Fig. 2B), and its maximum width is between the supraorbital tuberosities. The braincase is rounded. The frontal surface is very smooth. The parietal crests are strong and broadly separated with a minimum width of 59.4 mm, between which there is a depression posteriorly (Fig. 2A).

There are two infraorbital foramina, the anterior one of which is triangular in shape, with a vertical diameter of 16 mm, and a wide, deep, and short front groove, and the posterior one is oval in shape and slightly smaller than the anterior one. Both are located above P4 and near the lower margin of the nasal notch. The nasal notch is 'U'-shaped, with a height of 47 mm, and it extends to a point above the P4/M1 boundary. The orbits are not projecting and near the skull roof, and their anterior rims are situated above the M1/M2 boundary. The zygomatic process of the maxillary bone begins above the P4/M1 boundary and has a distance of 23 mm from the alveolus border. The facial crest is strong and oblique upward. The maxillary surface in front of the orbit is flat. There are two lacrimal tubercles, the lower one of which is big and the upper one is tiny. The postorbital process is strong on

the frontal bone, but very weak on the terminal of the zygomatic process of the squamosal. The broad zygomatic arch is 49.5 mm wide in front of the temporal condyle. The zygomatic processes of the zygomatic and squamosal bones join in a smooth suture. Its posterior surface bears a transverse groove. The very large external auditory pseudomeatus is closed ventrally and inversely triangular in shape, above which the temporal crest is straight (Fig. 2B).

The nuchal crest is straight in both dorsal and occipital views with a very weak median groove. Its lateral margins are inclined anteriorly and divergent inferiorly. The occipital surface is trapezoid in shape and slightly inclined posteriorly. In occipital view, the median and exterior crests are weak, and the lateral crests are strong. The tip of the exterior crest extends to the posttympanic process. The foramen magnum is ellipsoidal, and its upper border is much higher than the upper margin of the occipital condyle. The nuchal ligament fossa is shallow, rough, and inversely triangular in shape (Fig. 3).

In ventral view, the intercondylar notch is wide, with a minimum width of 17.4 mm. The posterior margin of the pterygoid bone is vertical. The sulcus between the pterygoid bones is wide and deep. The anterior border of the temporal fossa is at the level of the M2/M3 boundary. The articular surface behind the temporal condyle is smooth and has a marginal ridge. The postglenoid processes are slightly compressed, robust, straight, and convergent anteriorly. The hypoglossal foramen is anteroexternally displaced. The basal tuberosity is less rough, with a narrow and sharp sagittal crest. The posterior part of the basioccipital bone is wide, short, and smooth. The posttympanic process is thin, inclined anteriorly, and weakly expanded laterally, the lower end of which is 10.5 mm thick and fused to the lower 1/3 of the postglenoid process. The paroccipital process is moderately developed and nearly vertical, and it is pyramidal in shape. The posttympanic and paroccipital processes are fused to each other at their bases. The palate is concave and moderately wide, with a distance of 74 mm between M3s, and its posterior border is 'U'-shaped and moderately wide, ending opposite the M2/M3 boundary, and with a distinct sagittal crest, and a small central tubercle. The anterior palatine foramen is at the level of the M2 hypocone, and the alar canal can be seen in ventral view (Fig. 2C). The maxillary tuberosity is strong. The zygomatic arch is thin, with a somewhat rough lower margin, and its anterior tip is progressive (see Antoine, 2002:fig. 46), with a wide and deep groove from the maxillary bone.

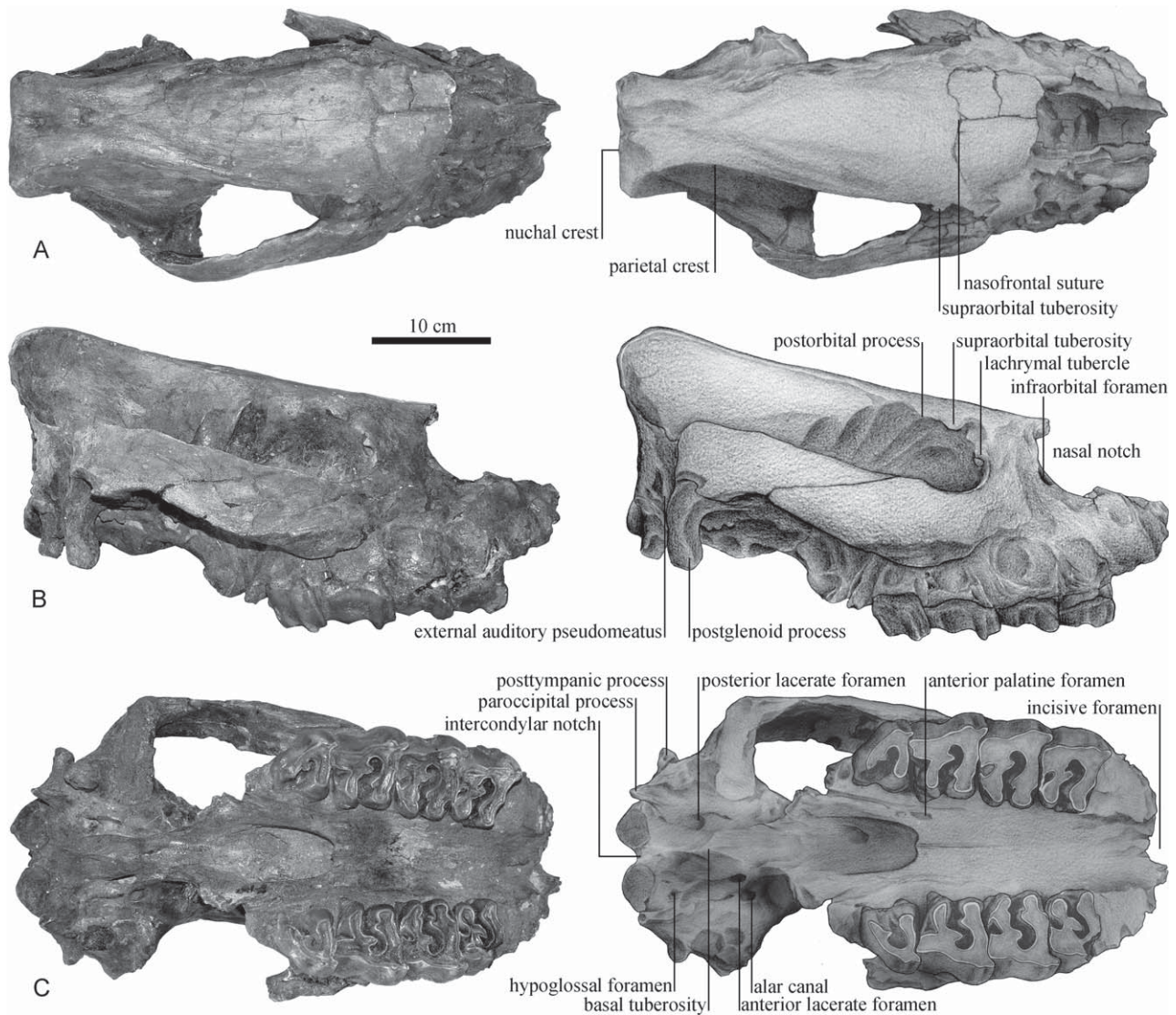


FIGURE 2. Holotype skull of *Aceratherium porpani*, sp. nov., from Tha Chang in Nakhon Ratchasima, Thailand, PRY 142. Photographs to the left and interpreted drawings to the right. **A**, dorsal view; **B**, lateral view; **C**, ventral view. (Color figure available online.)

Mandible

The symphysis is moderately wide (68.7 mm at the anterior margin) and deeply concave, with nearly parallel lateral margins and a maximum width between the lateral borders of i2. The alveolar margins at the diastema are ridge-like and extend laterally to reach the posteroexterior corner of i2. The labial surface of the symphysis is slightly concave, with a few tiny nutrient foramina. The symphysis is shifted posteriorly, with a posterior border at the level of the p3/p4 boundary and a short diastema (49.4 mm) between i2 and p2 (Fig. 4A). In lateral view, the symphysis is moderately elevated from the horizontal ramus (Fig. 4B).

The mental foramen, located under p2 and at the lower part of the horizontal ramus, is narrow, horizontal, and long (22.2 × 7.5 mm). On the right side, there is a small foramen under the mental foramen and below the p2/p3 boundary. The horizontal ramus is moderately high and thick, with a height of 77 mm and a thickness of 41.5 mm at the p4/m1 boundary. Here its lower margin is slightly curved. There is a wide and moderately deep groove on the lingual surface of the horizontal ramus, corre-

sponding to the sulcus mylohyoideus. The mandibular angle is rounded and thick, with a strong ridge at the lower part and a minimal thickness of 22.3 mm. The vascular impression is conspicuous (Fig. 4B).

The ascending ramus is oblique anteriorly and dorsally. Its anterior margin is 38 mm from m3. The condyle is long, with a strong constriction at its inner half, a wide and deep groove, and a wide and rounded ridge behind it. The lateral and median surfaces of the ascending ramus are broadly and deeply depressed, and the anterior surface is wide (34 mm at the base), deeply concave and sharp superiorly. The mandibular foramen is large and circular. The coronoid process is broken, but its base occupies more than one-half of the ascending ramus in lateral view.

Teeth

The upper cheek tooth rows are straight and slightly convergent anteriorly (Fig. 2C). The lower tooth rows are almost parallel (Fig. 4A). Both DP1 and dp1 are absent (Fig. 5). The dental formula is ?I/3P/3M and 2i/3p/3m. The premolars are long, with a

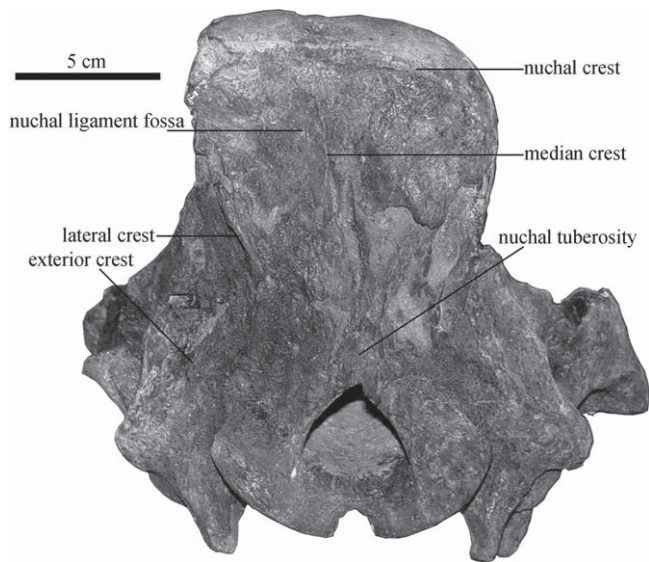


FIGURE 3. Occipital surface of *Aceratherium porpani*, sp. nov., from Tha Chang in Nakhon Ratchasima, Thailand, PRY 142. (Color figure available online.)

p2–p4/m1–m3 ratio of 0.76. The tooth crowns are subhypsodont (Table 3), without cement cover and labial cingulum. The two lower second incisors (i2) are lost, but their huge alveoli (transverse diameter: 26.5 mm) imply that they are large tusks. There are two alveoli of di1 with an anteroposterior diameter of 14 mm.

P4—The crochet is robust and long, with a sharp and labially pointed end. The protoloph is ‘S’-shaped, slightly oblique posterolingually, and the metaloph is posterolingually inclined and centrally constricted. There is a pillar on the open entrance of the median valley. The posterior valley is large and closed after heavy wear. The protocone is not constricted, with a rounded lingual border. The labial wall is shallowly undulated, with a weak parastyle fold and a wide, low paracone rib. The parastyle is weak. The crista and antecrochet are absent. The hypocone is larger and more rounded than the protocone (Fig. 5A).

Upper Molars—The antecrochet is short and posteriorly pointed on M1 and M2, but absent on M3. The crochet is robust, simple, and moderately long, and the crista is absent. The lingual cingulum is absent on M1 and M2, and pillars are present on the entrance of the median valley of M3. The lingual border of the protocone is rounded on M1 and flat on M2 and M3, without a lingual groove. The parastyle projects strongly, and it is moderately wide on M1 and M2, but narrow on M3. The anterior groove is weak on M1 and M2, and absent on M3. The posterior valley is nearly closed on M1, but open on M2. The metastyle is long and wide, with a flat posterior margin. The protoloph is slightly oblique, and the metaloph is long and nearly transverse, so the hypocone is more lingually positioned than the protocone on M2. The protocone is strongly constricted on M1 and M2, but weakly on M3. There is a small plication in the posterior groove of the protocone of M1. The hypocone is constricted, with an anterior fold on M1, but not constricted on M2. The labial wall undulates weakly. The paracone rib is weak on M1, and moderate on M2 and M3. The metacone fold is shallow. The posterior cingulum is reduced on M1 and M2, and ridge-like on M3. The median valley is open. The posterior valley is large and closed near the crown base. The ectoloph and metaloph merge completely on M3 so that the occlusal outline of this tooth is triangular (Fig. 5A).

Lower Cheek Teeth—The absence of a contact facet in front of p2 indicates the absence of dp1. The labial valley is deeply

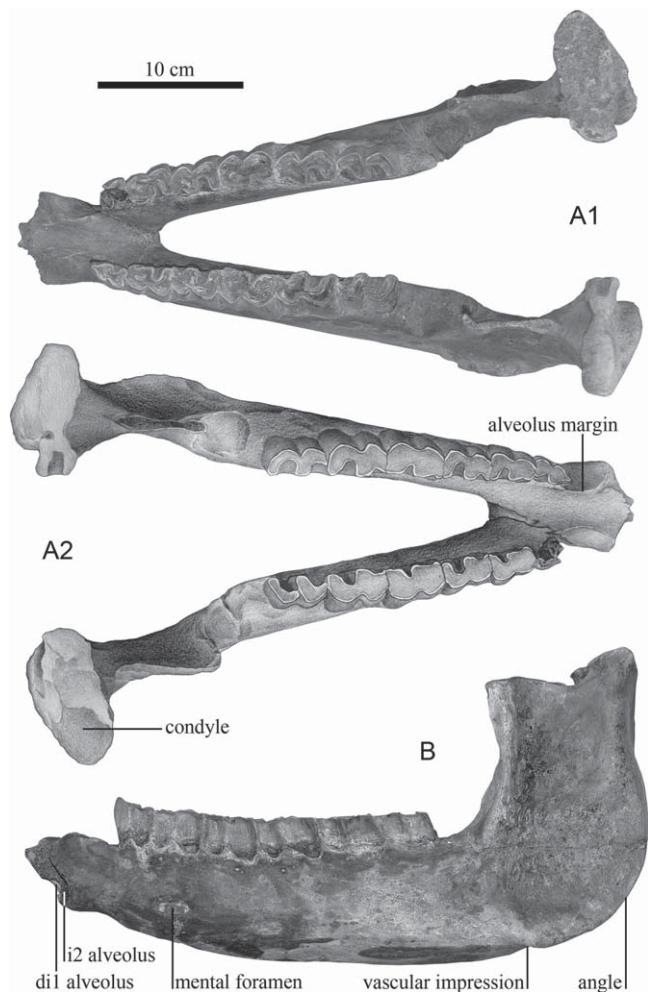


FIGURE 4. Mandible of *Aceratherium porpani*, sp. nov., from Tha Chang in Nakhon Ratchasima, Thailand, PRY 141. Photograph to the top; interpreted drawing and photograph to the middle and bottom. **A**, occlusal view; **B**, lateral view. (Color figure available online.)

‘V’-shaped until the crown base. The anterior lobe is angular in shape, with an acute angle between the protolophid and the metalophid. The paralophid is present on the premolars, but absent on the molars (totally worn out on m1 and m2 and pointing forward on m3). The posterior valley is widely U-shaped in occlusal view but ‘V’-shaped in lingual view. The entolophid is slightly oblique. The lingual cingulum is absent, but there is a pillar on the entrance of the posterior valley of m1. On p2, the paralophid is narrow and sharp, the paraconid is reduced, and the posterior valley is open lingually (Fig. 5B). The m3 is much narrower than m1 and m2.

Because only one skull and one mandible have been assigned to *Aceratherium porpani*, individual variation in these cranial, mandibular, and dental characters cannot yet be assessed for this new species. However, the broadly separated parietal crests, the narrow symphysis, and the short diastema are probably characters indicative of a female individual.

COMPARISON AND DISCUSSION

Cuvier (1822) named the species *Rhinoceros incisivus* based on an isolated first upper incisor of large size from the middle Miocene locality of Weisenau in Germany, but the tooth

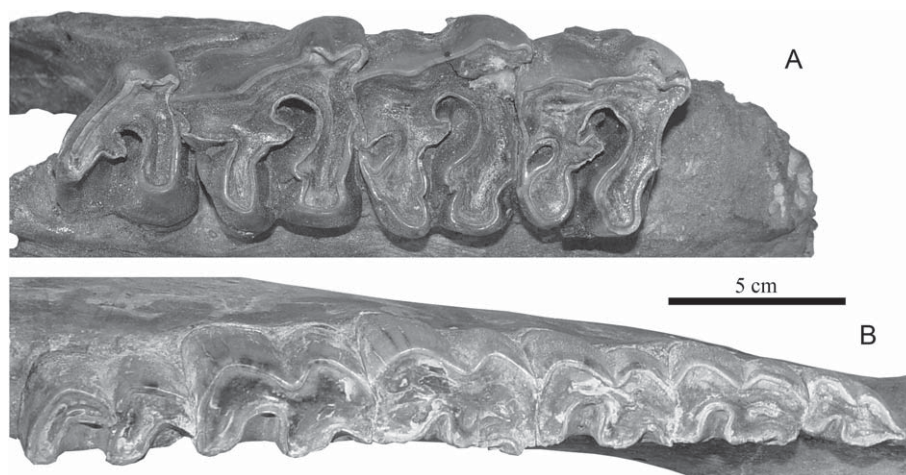


FIGURE 5. Cheek teeth of *Aceratherium porpani*, sp. nov., from Tha Chang in Nakhon Ratchasima, Thailand. **A**, upper right cheek teeth, PRY 142; **B**, lower left cheek teeth, PRY 141. (Color figure available online.)

unambiguously belongs to a representative of the tribe Teleoceratini. Kaup (1832) described two skulls of a hornless rhinoceros from the late Miocene locality of Eppelsheim in Germany, and he erected a new genus *Aceratherium* for them, but used Cuvier's species name. The prevailing usage of *Aceratherium incisivum* Kaup, 1832, is conserved in fact (Giaourtsakis and Heissig, 2004). Since Kaup (1832), many rhinoceroses, at least 83 species, have been described as species of *Aceratherium*, relegating this genus to a wastebasket taxon. As Prothero (2005) indicated, the paleontologists of the late 19th and early 20th centuries were typological 'splitters,' who recognized new taxa based on every slight variation in teeth. Later, however, most of the species were referred to other genera within the subfamily Aceratheriinae or to other rhinocerotoid suprageneric taxa, such as *Acerorhinus*, *Alicornops*, *Amphicaenopus*, *Aphelops*, *Aprotodon*, *Brachypotherium*, *Chilotherium*, *Diaceratherium*, *Diceratherium*, *Didermoceros*, *Eggysodon*, *Hoploaceratherium*, *Hyracodon*, *Menoceras*, *Mesaceratherium*, *Paraceratherium*, *Peraceras*, *Plesiaceratherium*, *Pleuroceros*, *Protaceratherium*, *Rhinoceros*, *Ronzotherium*, *Subhyracodon*, and *Teleoceras*. For example, in South Asia, *Aceratherium perimense* Falconer and Cautley, 1847, *A. planidens* (Lydekker, 1876), *A. iravadicus* (Lydekker, 1876), and *A. lydekkeri* Pilgrim, 1910, were reviewed and combined into the teleoceratine species *Brachypotherium perimense* (Colbert, 1935); in North America, *Aceratherium occidentalis* (Leidy, 1850), *A. quadriplicatum* (Cope, 1873), *A. trigonodum* Osborn and Wortman, 1894, and *A. exiguum* Lambe, 1908, were referred to *Subhyracodon occidentalis* (Leidy, 1850) (Prothero, 2005); and in Europe, *Aceratherium tetradactylum* (Lartet, 1837) typified *Hoploaceratherium* as *H. tetradactylum* (Ginsburg and Heissig, 1989). Now the genus *Aceratherium* includes *A. incisivum* and *A. depereti* Borissiak, 1927, which are distributed across Eurasia, although Heissig (1999) proposed that *Aceratherium* is a monospecific genus with the sole species *A. incisivum*. On the other hand, Geraads and Saraç (2003) have suggested that most acerathere 'genera' correspond to poorly defined evolutionary grades rather than to clades. Antoine et al. (2010) made a preliminary cladistic analysis including the acerathere clades.

Aceratherium huadeensis has not been discussed or revised since it was established from the late Miocene of Inner Mongolia, China (Qiu, 1979). The original author correctly indicated that this species was not similar to *Aceratherium incisivum*, but was very similar to *Aceratherium zernowi* from Sevastopol, Ukraine (Borissiak, 1914). Kretzoi (1942) had referred *Aceratherium zernowi* to as the type species of the new genus *Acerorhinus* still in use today. Accordingly, '*Aceratherium huadeensis* Qiu, 1979',

should be referred to as *Acerorhinus huadeensis* (Qiu, 1979) based on its expanded protocones and hypocones, weak antecrochets, flat labial walls, and slightly oblique protoloph and metalophs.

Aceratheres sensu lato (i.e., including *Mesaceratherium*) are a widespread group of hornless or small-horned rhinoceroses. They are considered to be a paraphyletic group, mostly defined by symplesiomorphies (e.g., Antoine et al., 2003, 2010). The earliest known acerathere is *Mesaceratherium gaimersheimense* Heissig, 1969, from the late Oligocene in Gaimersheim, Germany (Heissig, 1999). In the Miocene, aceratheres became very common in Eurasia, and they also dispersed into North America and Africa (Prothero et al., 1989). The narrow skull, the moderately broad mandibular symphysis with tusk-like lower incisors, and the high crowned cheek teeth with constricted protocones indicate that the Tha Chang specimens belong to the subfamily Aceratheriinae. The highly molariform premolars and the moderately developed molar antecrochets indicate that the Tha Chang rhino belongs to the genus *Aceratherium* (Heissig, 1989, 1999).

In Eurasia, there are many genera included within the subfamily Aceratheriinae (e.g., Prothero and Schoch, 1989). DP1 is absent in the Tha Chang skull, which is contrary to what is observed in *Aceratherium incisivum*, *A. depereti*, *Hoploaceratherium tetradactylum*, and most 'aceratheres.' The concave ventral side of the symphysis, the strong subvertical facial crest, and the very short distance of the nasal notch to the orbit are characters hitherto unknown in the genus *Aceratherium* but present in *Acerorhinus* (Heissig, 1999). On the other hand, the Tha Chang skull narrows from the frontals to the nasals, not abruptly as in *Acerorhinus* (Kretzoi, 1942), but gradually. Moreover, the molar protocones of *Acerorhinus zernowi* are not constricted (Borissiak, 1914), the posttympanic processes of *A. hezhengensis* and *A. fuguensis* are strongly expanded laterally (Qiu et al., 1988; Deng, 2000), and the maxillary surface of *A. tsaidamensis* is deeply depressed (Bohlin, 1937). As a result, the species of the genus *Acerorhinus* are easily distinguished from the Tha Chang form.

The weakly posteriorly narrowing frontal bones and slightly laterally expanded zygomatic arches of the Tha Chang skull are different from those of *Alicornops*, which are strongly narrowing and expanded respectively (Deng, 2004). The nuchal crest is straight in dorsal view, and the antecrochet is absent on P4 in the Tha Chang skull, but the nuchal crest is concave, and the antecrochet is strong in *Pleuroceros* (Antoine et al., 2010). The crochets are strong, the metalophs are long, the bridge is absent on P4, and the paracone rib is weak on M1 in the Tha Chang rhino, whereas

the crochets are weak, the metalophs are short, the bridge is present on P4, and the paracone rib is strong on M1 in *Mesaceratherium* (Heissig, 1969). Compared with *Hoploaceratherium* (Ginsburg and Heissig, 1989), the absence of DP1, the stronger crochet on P4, and the more reduced paralophid on p2 are the distinguishing characters of the Tha Chang rhino. Compared with *Plesiaceratherium* from the early and middle Miocene of Eurasia (Yan and Heissig, 1986), the broad braincase, the broadly separated parietal crests, the long metalophs, and the strongly constricted protocones are the most important features of the Tha Chang skull.

Chilotherium is easily distinguished from the Tha Chang rhino, because the former has a strongly expanded mandibular symphysis, a long diastema between i2 and p2, strong antecrochets, posteriorly oblique metalophs, and weak paracone ribs (Ringström, 1924). Geraads and Koufos (1990) described the new species *Aceratherium kiliasi* from the upper Miocene at Pentelophos-1 in Macedonia, Greece, but Heissig (1999) referred it to the genus *Chilotherium* based on its strongly expanded mandibular symphysis. *Ch. kiliasi* is different from the Tha Chang form in having highly curved zygomatic arches and separated posttympanic processes from the postglenoid process. *Shansirhinus* is characterized by elaborate enamel plications, moderately separated parietal crests, and a posterior border of the mandibular symphysis at the p2/p3 boundary (Deng, 2005), which are different from those of the Tha Chang rhino.

Heissig (1972) established a new subspecies, *Chilotherium intermedium complanatum*, from Siwalik deposits in Pakistan, with reduced and flattened antecrochet and weaker or absent posterior groove of the protocone. Heissig (1975) referred *Ch. intermedium* to a new subgenus, *Subchilotherium*, i.e., *Ch. (Subchilotherium) intermedium*. Heissig (1989) promoted *Subchilotherium* as a genus, and Deng and Gao (2006) described a skull and three mandibles of *Subchilotherium intermedium* from Yuanmou, Yunnan, in China. *Subchilotherium* is different from the Tha Chang rhino in the absence of antecrochets, and having a narrow sagittal crest, short metalophs, strong paracone ribs, an anteriorly shifting mandibular symphysis, and a long diastema between i2 and p2 (Heissig, 1972; Deng and Gao, 2006). Antoine et al. (2003) revised *Chilotherium intermedium complanatum* as *Alicornops complanatum*, but their new material was only a lower tooth row from Bugti Hills in Pakistan, without new characters to add the original diagnosis of Heissig (1972).

The genera of the subfamily Aceratherinae are few in North America. On the upper cheek teeth of the Tha Chang rhino, the crochets are strong, the metalophs are long, and the antecrochets are marked on M1 and M2, but *Floridaceras* lacks antecrochets, and has short metalophs and weak crochets (Wood, 1964). The Tha Chang rhino is distinguished from *Aphelops* by its broadly separated parietal crests, deeper nasal notch at the level of the P4/M1 boundary (*Aphelops* at anterior P4), flat skull roof, constricted molar protocones, and weakly expanded zygomatic arches. The Tha Chang rhino is distinguished from *Peraceras* by its dolichocephalic skull, constricted molar protocones, long metalophs, and absence of lingual cingulum (Prothero, 2005).

Africa has only two endemic acerathere genera, i.e., *Chilotheridium* Hooijer, 1971, and *Turkanatherium* Deraniyagala, 1951 (Geraads, 2010). *Chilotheridium* is different from the Tha Chang rhino in having moderately separated parietal crests, a narrow mandibular symphysis, short metalophs, and a lower position of the orbit far from the skull roof (Hooijer, 1971). *Turkanatherium* is different from the Tha Chang rhino in having a vertical occipital surface, a concave skull roof, a sagittal crest met by parietal crests, and a shallow nasal notch anterodorsal to P3 (Deraniyagala, 1951).

In South Asia, the non-acerathere *Brachypotherium* is very common (Heissig, 1972), and includes the late Miocene '*Aceratherium*' *lydekkeri* and the middle Miocene '*Aceratherium*'

TABLE 1. Measurements (in mm) and comparison between skulls of *Aceratherium porpani* and other species of *Aceratherium*.

Measures	<i>A. porpani</i>	<i>A. incisivum</i>	<i>A. depereti</i>
5. Minimal width of braincase	75	—	—
6. Distance between nuchal crest and postorbital process	224.5	282	247
7. Distance between nuchal crest and supraorbital tuberosities	251.5	313	296
8. Distance between nuchal crest and lachrymal tubercle	282	336	313
9. Distance between nasal notch and orbit	49	58	60
13. Distance between occipital condyle and M3	201	251	240
15. Width of nuchal crest	110	180	101
16. Width between mastoid processes	161	270	—
17. Minimal width between parietal crests	59.4	21	11
18. Width between postorbital processes	114.2	—	—
19. Width between supraorbital tuberosities	126.5	237	200
20. Width between lachrymal tubercles	131.5	—	—
21. Maximal width between zygomatic arches	~ 250	395	—
22. Width of nasal base	70.6	116	117
23. Height of occipital surface	107	110	—
26. Cranial height in front of M1	158.5	187	187
27. Cranial height in front of M3	154	165	198
29. Palatal width in front of M1	55	99	—
30. Palatal width in front of M3	74	100	—
31. Width of foramen magnum	41.3	56	—
32. Width between occipital condyles	95.2	143	—

Numbers (5–32) follow the protocol of Guérin (1980). *A. incisivum* and *A. depereti* are measured on the figures (Hünemann, 1989; Borissiak, 1927).

perimense, both known in central Myanmar (Zin-Maung-Maung-Thein et al., 2010) near Thailand, and they should be *Brachypotherium perimense* as Colbert (1935) indicated. *B. perimense* is different from the Tha Chang acerathere in having narrowly separated parietal crests, laterally expanded zygomatic arches, strong supraorbital tuberosities, a deep nasal notch above the P4/M1 boundary, and short metalophs on molars (Heissig, 1972).

The skull and especially the teeth of *Aceratherium porpani* resemble those of *A. incisivum* from Eppelsheim (Kaup, 1932) and Höwenegg (Hünemann, 1989). Their common characters include an elongated skull, non-projecting orbits, moderate supraorbital tuberosities, nearly vertical zygomatic arches, a rounded braincase, a narrow nuchal crest, a wide intercondylar notch, compressed and straight postglenoid processes, thin and weakly expanded posttympanic processes, a wide U-shaped choana reaching the M2/M3 boundary, subhypsodont teeth, tusk-like i2, strong crochets, shallowly undulated labial walls, weak paracone ribs, narrow parastyles, constricted molar protocones, short and posteriorly pointed molar antecrochets, absent lingual cingulum on molars, a well-developed labial cingulum on the lower premolars, a weak or absent crista on the upper molars, a molar protocone with a rounded lingual margin, a strong molar parastyle fold, and a slightly constricted protocone on the molars. On the other hand, there are some differences between the Tha Chang specimens and *A. incisivum* from Eppelsheim and Höwenegg. *A. incisivum* is much larger than *A. porpani* (Tables 1, 2). The skull of *A. incisivum* has converging parietal crests, but the Tha Chang skull has very broadly separated ones. The posterior parts of the zygomatic arches are more expanded in *A. incisivum* than in the Tha Chang skull. The nuchal crest is concave in

TABLE 2. Measurements (in mm) and comparison of mandibles between *Aceratherium porpani* and other species of *Aceratherium*.

Measures	<i>A. porpani</i>	<i>A. incisivum</i>	<i>A. depereti</i>
1. Length	431	486.5	> 460
2. Distance between symphysis and angular process	338.5	377.5	—
3. Height of horizontal ramus in front of p3	64.5	70.5	—
4. Height of horizontal ramus in front of p4	68	72	—
5. Height of horizontal ramus in front of m1	77	75.8	65
6. Height of horizontal ramus in front of m2	81.4	80.7	—
7. Height of horizontal ramus in front of m3	84.5	84.9	85
8. Height of horizontal ramus posterior to m3	87.4	91.1	—
9. Distance between horizontal rami in front of m1	54.8	38.5	—
10. Distance between horizontal rami in front of m3	71.8	40.4	—
11. Length of symphysis	107.5	125.5	—
12. Maximum width of symphysis	68.7	—	—
13. Anteroposterior diameter of ascending ramus	123	143.2	125
14. Transverse diameter of condyle	81	84.4	—
15. Height at condyle	211	234.3	210

Numbers (1–15) follow the protocol of Guérin (1980). The measurements of *A. incisivum* and *A. depereti* are from Guérin (1980) and Borissiak (1927), respectively.

A. incisivum, but straight in the Tha Chang rhino. The anterior tip of the maxillary zygomatic process is abrupt in *A. incisivum*, but progressive in the Tha Chang rhino. The crista and medifossette on P4 are developed in *A. incisivum*, but absent in the Tha Chang form. The metalophs on M1 and M2 are short and transverse or slightly oblique posteriorly in *A. incisivum*, but long and slightly oblique anteriorly in the Tha Chang form. The hypocone on M1 is rounded in *A. incisivum*, but constricted in the Tha Chang form.

The skull of *A. porpani* is similar to that of *A. incisivum* from Yulafli in Turkey (Kaya and Heissig, 2001). They share the weakly expanded posterior parts and almost vertical lateral surfaces of zygomatic arches. Although the parietal crests are

TABLE 3. Measurements (in mm) and comparison of cheek teeth between *Aceratherium porpani* and other species of *Aceratherium*.

Teeth	<i>A. porpani</i>	<i>A. incisivum</i>	<i>A. depereti</i>
P4	43.0 × 53.0 × 28.0	43.9 × 53.2 × 44.5	44.8 × 58.8 × 28.1
M1	45.3 × 57.3 × 25.3	50.1 × 53.7 × 44.0	47.4 × 57.5 × 25.4
M2	51.1 × 55.3 × 33.5	53.9 × 52.7 × —	51.4 × 59.1 × 27.1
M3	37.7 × 48.3 × 38.2	51.3 × 48.7 × 46.0	56.3 × 55.1 × 31.4
p2	25.7 × 16.6 × 24.5	30.0 × 19.3 × 27.3	34.0 × 24.5 × 30.0
p3	35.4 × 23.7 × 21.6	41.1 × 26.2 × 38.5	37.0 × 33.0 × 28.0
p4	35.7 × 26.0 × 24.0	41.9 × 27.9 × 40.5	38.5 × 34.0 × 29.0
m1	40.3 × 28.6 × 18.0	45.5 × 29.3 × —	40.0 × 31.0 × 24.0
m2	43.0 × 28.0 × 20.8	50.7 × 27.2 × 39.2	47.0 × 32.5 × 25.0
m3	42.3 × 24.3 × 17.2	48.3 × 26.7 × 32.0	50.0 × 32.0 × 26.0
M1–M3	131.3	137.6	131.2
p2–p4	104.5	101.9	108.0
p2–m3	247.2	233.1	250.0
m1–m3	143.2	131.3	142.0

Length × width × height. Length of M3 is the length of the ectometaloph. The measurements of *A. incisivum* and *A. depereti* are from Guérin (1980) and Borissiak (1927), respectively.

more widely separated in *A. incisivum* from Yulafli than from Höwenegg, they are still narrower than those of the Tha Chang form.

The upper cheek teeth of *A. incisivum* from Montredon (Guérin, 1980:pl. 8, fig. A) have many common characters with those of *A. porpani*, such as weakly undulated labial walls, strong crochets, moderate antecrochets, long metalophs, and enlarged protocones. On the other hand, differences between the two species are the longer metalophs of *A. porpani*, which are flush with or longer than the protolophs.

Aceratherium porpani and *A. depereti* from Jilančik in Turgai, Kazakhstan (Borissiak, 1927), are similar with respect to their nearly vertical and weakly expanded zygomatic arches. However, in *A. depereti*, the parietal crests unite posteriorly to form a narrow and high sagittal crest, the metaloph is slightly oblique posteriorly on M1 and M2, the crista is well developed and connects with the crochet to form a medifossette on premolars, and the crochet is distinctly shifted labially.

Aceratherium porpani is different from *Aceratherium* sp. from Çandır, Turkey (Geraads and Saraç, 2003). In the latter, P4 has a continuous cingulum, a closed median valley, and a weak crochet, which are primitive features; the mandible has a rather long diastema between i2 and p2, which is longer than that of *A. porpani*, and a posterior border of the symphysis at the level of the anterior lobe of p3, which is more anterior than that of *A. porpani*.

Chaimanee et al. (2004) listed *Chilotherium palaeosinense* in the fauna associated with the hominoid *Khoratpithecus piriyai* from Tha Chang. Ringström (1924) established *Diceratherium palaeosinense*, and Heissig (1975) revised it as *Chilotherium (Acerorhinus) palaeosinense*. Qiu et al. (1988) revived *Acerorhinus* as a genus according to the original definition of Kretzoi (1942) and assigned *Ch. (A.) palaeosinense* to *Acerorhinus palaeosinensis*. Later, Heissig (1989) accepted *A. palaeosinense* and recognized it as belonging in the genus *Acerorhinus*. Compared with the Tha Chang rhino, *A. palaeosinensis* of northern China differs in its narrowly separated parietal crests, small premolars, well-developed cristae, shorter metalophs, strong lingual cingula, and shallow nasal notch above the P3/P4 boundary (Ringström, 1924).

In the region adjacent to Thailand, late Miocene rhinocerotid fossils were found from Yunnan Province, China. Deng and Qi (2009) reported the late Miocene rhinocerotid fossils from Lufeng in Yunnan, China, including two acerathere species, *Acerorhinus lufengensis* and *Shansirhinus* cf. *S. ringstroemi*. The Lufeng materials have only isolated teeth of these rhinoceroes. *S. ringstroemi* was also recognized at Banguo in Yuanmou, Yunnan (Tang et al., 1974; Deng, 2005). Zong (1998) established *Acerorhinus yuanmouensis* in Yuanmou, Yunnan. *A. lufengensis* differs from *A. porpani* in having unconstricted protocones, absence of antecrochet, weak crochets, and shorter and more oblique metalophs. *S. ringstroemi* differs from *A. porpani* in having rich enamel plications, well-developed medifossettes, very short and oblique metalophs, and expanded hypocones. *A. yuanmouensis* differs from *A. porpani* in having narrowly separated parietal crests and strongly constricted protocones.

Aceratherium porpani has several characters that are more derived than in *A. incisivum* and *A. depereti*, such as very broadly separated parietal crests, a straight nuchal crest, and longer metalophs on M1 and M2. But *A. porpani* also has some more primitive characters than *A. incisivum*, such as narrow zygomatic arches, a progressive anterior tip of the maxillary zygomatic process, and absence of the medifossette on P4.

The very broadly separated parietal crests, an important derived character in the morphological evolution of acerathere, indicate that the age of *A. porpani* may be later than the ages of *Aceratherium depereti* and *A. incisivum*. *A. depereti* came from the lower Miocene deposits of the Turgai region (Borissiak, 1927),

and *A. incisivum* was distributed in MN 9–10 of the early late Miocene of western Europe (Heissig, 1999). As a result, the age of *A. porpani* should be the late late Miocene, corresponding to the European Turolian, which is consistent with the age estimation of the fossiliferous deposits in Tha Chang Sand Pit 8 (Chaimanee et al., 2004, 2006).

The occipital surface of *A. depereti* is vertical or apparently weakly deflected backward (Borissiak, 1927), which is a primitive character compared with the posteriorly inclined occiput of *A. incisivum* (Hünemann, 1989). The occipital surface of the Tha Chang rhino is slightly inclined posteriorly or nearly vertical, and the cheek teeth are subhypsodont, both indicating a woodland habitat (Zeuner, 1934). This result is consistent with the paleobotanical evidence for the Tha Chang sand pits, which indicates the occurrence of wet and tropical forest environments (Chaimanee et al., 2004, 2006).

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LITERATURE CITED

- Antoine, P.-O. 2002. Phylogénie et évolution des Elasmotheriina (Mammalia, Rhinocerotidae). Mémoires du Muséum National d'Histoire Naturelle 188:1–359.
- Antoine, P.-O., F. Duranthon, 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.
- Bohlin, B. 1937. Eine tertiäre Säugetier-Fauna aus Tsaidam. *Palaeontologia Sinica, Series C* 14(1):1–111.
- Borissiak, A. 1914. Mammalian fossils of Sebastopol, I. *Trudy Geologicheskogo Komiteta, Novaya Seriya* 87:1–154. [Russian with French abstract]
- Borissiak, A. 1927. *Aceratherium depereti* nov. sp. from the Jilančik beds. *Bulletin de l'Académie des Sciences de l'URSS* 21:769–786.
- Chaimanee, Y., V. Suteethorn, P. Jintasakul, C. Vidthayanon, B. Marandat, and J.-J. Jaeger. 2004. A new orang-utan relative from the late Miocene of Thailand. *Nature* 427:439–441.
- Chaimanee, Y., C. Yamee, P. Tian, K. Khaowiset, B. Marandat, P. Tafforeau, C. Nemoz, and J.-J. Jaeger. 2006. *Khoratpithecus piriya*, a late Miocene hominoid of Thailand. *American Journal of Physical Anthropology* 131:311–323.
- Colbert, E. H. 1935. Siwalik mammals in the American Museum of Natural History. *Transactions of the American Philosophical Society New Series* 26:1–401.
- Cope, E. D. 1873. On some new extinct Mammalia from the Tertiary of the Plains. *Palaeontological Bulletin* 14:1–2.
- Cuvier, G. 1822. *Recherches sur les Ossements Fossiles*, Nouvelle Édition, Tome II. Dufour et d'Ocagne, Paris, 684 pp.
- Deng, T. 2000. A new species of *Acerorhinus* (Perissodactyla, Rhinocerotidae) from the late Miocene in Fugu, Shaanxi, China. *Vertebrata Palasiatica* 38:203–217. [Chinese 203–211; English 211–217]
- 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., and F. Gao. 2006. Perissodactyla; pp. 334–335 in G.-Q. Qi and W. Dong (eds.), *Lufengpithecus hudienensis* Site. Science Press, Beijing.
- Deng, T., and G.-Q. Qi. 2009. Rhinocerotids (Mammalia, Perissodactyla) from *Lufengpithecus* site, Lufeng, Yunnan. *Vertebrata Palasiatica* 47:135–152. [Chinese 135–146; English 146–152]
- Deraniyagala, P. E. P. 1951. A hornless rhinoceros from the Miocene deposits of East Africa. *Spolia Zeylanica* 26:133–135.
- Dollo, L. 1885. Rhinocéros vivants et fossiles. *Revue des Questions Scientifiques* 17:293–300.
- Falconer, H., and P. T. Cautley. 1847. *Fauna Antiqua Sivalensis*, Being the Fossil Zoology of the Sewalik Hills, in the North of India. Atlas, Smith, Elder and Co., London, 90 pp.
- 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.
- Geraads, D., and G. Koufos. 1990. Upper Miocene Rhinocerotidae (Mammalia) from Pentalophos-1, Macedonia, Greece. *Palaeontographica Abteilung A* 210:151–168.
- Geraads, D., and G. Saraç. 2003. Rhinocerotidae from the middle Miocene hominoid locality of Çandır (Turkey). *Courier Forschungsinstitut Senckenberg* 240:217–231.
- Giaourtsakis, I. X., and K. Heissig. 2004. On the nomenclatural status of *Aceratherium incisivum* (Rhinocerotidae, Mammalia); pp. 314–317 in A. A. Chatzipetros and S. B. Pavlides (eds.), *Proceedings of 5th International Symposium on Eastern Mediterranean Geology*, Volume 1, 14–20 April 2004, Thessaloniki, Greece. Aristotle University, Thessaloniki.
- Ginsburg, L., and K. Heissig. 1989. *Hoploaceratherium*, a new generic name for "*Aceratherium*" *tetradactylum*; pp. 418–421 in D. R. Prothero and R. M. Schoch (eds.), *The Evolution of Perissodactyls*. Oxford University Press, New York.
- Guerin, C. 1980. Les rhinocéros (Mammalia, Perissodactyla) du Miocène terminal au Pleistocène supérieur en Europe occidentale: comparaison avec les espèces actuelles. *Documents du Laboratoire de Géologie de la Faculté des Sciences de Lyon* 79: 1–1182.
- Hanta, R., B. Ratanasthien, Y. Kunimatsu, H. Saegusa, H. Nakaya, S. Nagaoka, and P. Jintasakul. 2008. A new species of Bothriodontinae, *Merycopotamus thachangensis* (Cetartiodactyla, Anthracotheriidae) from the late Miocene of Nakhon Ratchasima, northeastern Thailand. *Journal of Vertebrate Paleontology* 28: 1182–1188.
- Heissig, K. 1969. Die Rhinocerotidae (Mammalia) aus der oberoligozänen Spaltenfüllung von Gaimersheim bei Ingolstadt in Bayern und ihre phylogenetische Stellung. *Bayerische Akademie der Wissenschaften Mathematisch-Naturwissenschaftliche Klasse, Abhandlungen, Neue Folge* 138:1–133.
- Heissig, K. 1972. Paläontologische und geologische Untersuchungen im Tertiär von Pakistan, 5. Rhinocerotidae (Mamm.) aus den unteren und mittleren Siwalik-Schichten. *Bayerische Akademie der Wissenschaften Mathematisch-Naturwissenschaftliche Klasse, Abhandlungen, Neue Folge* 152:1–112.
- Heissig, K. 1975. Rhinocerotidae aus dem Jungtertiär Anatoliens. *Geologisches Jahrbuch, Reihe B* 15:145–151.
- Heissig, K. 1989. Rhinocerotidae; pp. 399–417 in D. R. Prothero and R. M. Schoch (eds.), *The Evolution of Perissodactyls*. Oxford University Press, New York.
- 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.
- Hooijer, D. A. 1971. A new rhinoceros from the late Miocene of Loperot, Turkana district, Kenya. *Bulletin of the Museum of Comparative Zoology* 142:339–392.
- Hünemann, K. A. 1989. Die Nashornskellette (*Aceratherium incisivum* Kaup, 1832) aus dem Jungtertiär vom Höwenegg im Hegau (Südwestdeutschland). *Andrias* 6:5–116.
- Kaup, J. J. 1832. Über *Rhinoceros incisivus* Cuvier und eine neue Art, *Rhinoceros schleiermacheri*. *Isis* 8:898–904.
- Kaya, T., and Heissig, K. 2001. Late Miocene rhinocerotids (Mammalia) from Yulafli (Çorlu-Thrace/Turkey). *Geobios* 34:457–467.

- Kretzoi, M. 1942. Bemerkungen zum System der nachmiozänen Nashorn-Gattungen. *Földtani Közlöny* 72:4–12.
- Lambe, L. M. 1908. The Vertebrata of the Oligocene of the Cypress Hills, Saskatchewan. *Contributions to Canadian Paleontology* 3:1–65.
- Lartet, E. 1837. Sur les débris fossiles trouvés à Sansan et sur les animaux antédiluviens en général. *Comptes Rendus de l'Académie des Sciences* 5:158–159.
- Leidy, J. 1850. Remarks on *Rhinoceros occidentalis*. *Proceedings of the Academy of Natural Sciences of Philadelphia* 5:119.
- Lydekker, R. 1876. Molar teeth and other remains of mammalia. *Palaeontologia Indica* 10(1):19–87.
- Nakaya, H., H. Saegusa, B. Ratanasthien, Y. Kunimatsu, S. Nagaoka, P. Jintasakul, Y. Sukanuma, and A. Fukuchi. 2003. Neogene mammalian biostratigraphy and age of fossil ape from Thailand. *Asian Paleoprimatology* 3:66–67.
- Osborn, H. F., and J. H. Wortman. 1894. Fossil mammals of the lower Miocene White River beds. Collection of 1892. *Bulletin of the American Museum of Natural History* 7:199–228.
- Owen, R. 1845. A History of British Fossil Mammals and Birds. J. van Voorst, London, 560 pp.
- Owen, R. 1848. On the Archetype and Homologies of the Vertebrate Skeleton. J. van Voorst, London, 203 pp.
- Pilgrim, G. E. 1910. Notices of new mammalian genera and species from the Tertiaries of India. *Records of the Geological Survey of India* 15:63–71.
- Prothero, D. R. 2005. *The Evolution of North American Rhinoceroses*. Cambridge University Press, Cambridge, U.K., 218 pp.
- Prothero, D. R., and R. M. Schoch. 1989. Classification of the Perissodactyla; pp. 530–537 in D. R. Prothero and R. M. Schoch (eds.), *The Evolution of Perissodactyls*. Oxford University Press, New York.
- Prothero, D. R., C. Guérin, and E. Manning. 1989. The history of the Rhinocerotidae; pp. 322–340 in D. R. Prothero and R. M. Schoch (eds.), *The Evolution of Perissodactyls*. Oxford University Press, New York.
- Qiu, Z.-D. 1979. Some mammalian fossils from the Pliocene of Inner Mongolia and Gansu (Kansu). *Vertebrata Palasiatica* 17:222–235. [Chinese 222–233; English 234–235]
- Qiu, Z.-X., and B.-Y. Wang. 2007. Paraceratherium fossils of China. *Palaeontologia Sinica, New Series C* 29:1–396. [Chinese 1–248; English 249–396]
- Qiu, Z.-X., J.-Y. Xie, and D.-F. Yan. 1988. A new chilotere skull from Hezheng, Gansu, China, with special reference to the Chinese '*Diceratherium*.' *Scientia Sinica, Series B* 41:494–502.
- Ringström, T. 1924. Nashörner der *Hipparion*-Fauna Nord-Chinas. *Palaeontologia Sinica, Series C* 1(4):1–159.
- Saegusa, H., Y. Thasod, and B. Ratanasthien. 2005. Notes on Asian stegodontids. *Quaternary International* 126–128:31–48.
- Tang, Y.-J., Y.-Z. You, H.-Y. Liu, and Y.-R. Pan. 1974. New materials of Pliocene mammals from Banguo Basin of Yuanmou, Yunnan and their stratigraphical significance. *Vertebrata Palasiatica* 12:60–67. [Chinese 60–66; English 66–67]
- Wood, H. E., II. 1964. Rhinoceroses from the Thomas Farm Miocene of Florida. *Bulletin of the Museum of Comparative Zoology* 130:361–386.
- Yan, D. F., and K. Heissig. 1986. Revision and autopodial morphology of the Chinese-European rhinocerotid genus *Plesiaceratherium* Young 1937. *Zitteliana* 14:81–109.
- Zeuner, F. E. 1934. Die Beziehungen zwischen Schädelform und Lebensweise bei den rezenten und fossilen Nashörnern. *Berichte der Naturforschenden Gesellschaft zu Freiburg* 34:21–79.
- Zin-Maung-Maung-Thein, M. Takai, T. Tsubamoto, N. Egi, Thaing-Htike, T. Nishimura, Maung-Maung, and Zaw-Win. 2010. A review of fossil rhinoceroses from the Neogene of Myanmar with description of new specimens from the Irrawaddy sediments. *Journal of Asian Earth Sciences* 37:154–165.
- Zong, G. F. 1998. A new evidence of dividing in the Neogene stratigraphy of Yuanmou Basin. *Memoirs of Beijing Natural History Museum* 56:159–178. [Chinese 159–171; English 172–178]

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