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ARTICLE

Brachypotherium perimense (Perissodactyla, Rhinocerotidae) from the Miocene of Nakhon Ratchasima, Northeastern Thailand, with comments on fossil records of *Brachypotherium*

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ABSTRACT

The cranio-dental and postcranial remains of the Rhinocerotidae collected from the sand pit no. 8 at Nakhon Ratchasima in northeastern Thailand, are described in this study. The remains show cheek teeth that tend to have flattened buccal walls, bucco-lingually broad molariform premolars with short crochet, and brachypodal limb bones, suggesting that these remains belong to genus *Brachypotherium*. Compared with Afro-Eurasian *Brachypotherium*, the remains are identified as a South Asian species, *Brachypotherium perimense*. The result reveals that *B. perimense* was distributed in Southeast Asia during the Late Miocene. The fossil records of *Brachypotherium* in Afro-Eurasia show that the genus *Brachypotherium* was already present in the Indian Subcontinent by the earliest Miocene. This genus then became widely distributed and diversified in Afro-Eurasia during the late Early Miocene and Middle Miocene. Its diversity seems to have decreased before it became extinct by the end of the Miocene, with only the African species, *B. lewisi*, surviving.

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Introduction

The family Rhinocerotidae (Mammalia, Perissodactyla) had been widely distributed in Eurasia, Africa and North America from the Eocene to the Quaternary (Heissig 1989; Antoine et al. 2003a; Prothero 2005), although only five species have survived in Asia and Africa. During that geological age, tectonic events and palaeoenvironmental changes affected the diversity and distribution of Rhinocerotidae (e.g. Cerdeño and Nieto 1995; Cerdeño 1998).

Genus *Brachypotherium*, a group of the subtribe Teleoceratina (*sensu* Antoine et al. 2010 = tribe Teleoceratini in Heissig 1973), is a cosmopolitan extinct rhinocerotid. The fossil records of *Brachypotherium* have been found mainly from the Miocene sediments in Eurasia and Africa (Colbert 1935; Heissig 1972, 1999; Guérin 1980; Geraads 2010). Thus, an investigation of the palaeobiogeography of *Brachypotherium* would be a fine example to study the relationship between dispersal of rhinocerotid and palaeogeographic or palaeoenvironmental changes in Afro-Eurasia. *Brachypotherium* has been well documented from Europe, and its chronostratigraphic and palaeobiogeographical implications (e.g. Heissig 1996, 1999; Becker et al. 2009) have been discussed in the literatures. In Asia, the fossil records of *Brachypotherium* are still contended, although several fossil records of *Brachypotherium* from the Indian Subcontinent have been discussed (e.g. Antoine et al. 2013; Nanda et al. 2018). However, a detailed description of *Brachypotherium* from Southeast Asia is lacking, and this study aims to address this gap.

In Thailand, there are the latest Early to earliest Late Miocene localities in the northern part. In contrast, the Middle to Late Miocene and Quaternary ones are in northeastern part (e.g. Nakaya et al. 2002; Pickford et al. 2004; Suganuma et al. 2006; Nagaoka and Nakaya 2014). The numerous sand pits along the Mun River at Nakhon Ratchasima in northeastern Thailand (Figure 1) yield abundant vertebrate fossils, which have been collected by the workers at the sand pits. Especially, the sand pit no. 8 (= Somsak Sand Pit in Chaimanee et al. 2006) in Tha Chang area yielded a large hominoid fossil, *Khoratpithecus piriyai* (Chaimanee et al. 2004, 2006). Various other land mammal remains have also been found in the sand pit. A South Asian taxon of *Brachypotherium*, *Brachypotherium perimense* is one among those included with this fauna, but a detailed systematic description of this taxon from the pit is lacking.

In this study, we describe the remains of *B. perimense* derived from sand pit no. 8 and discuss its palaeoenvironmental and palaeobiogeographical implication. Additionally, we briefly summarise the chronostratigraphy and palaeobiogeography of other Afro-Eurasian *Brachypotherium*.

Geological setting

More than 10 sand pits have been opened along the Mun River at Nachon Ratchasima and have exposed Neogene and Quaternary fluvial deposits (e.g. Nagaoka and Nakaya 2014; Duangkrayom et al. 2017). The mammalian fossil assemblages from Tha Chiang sand pits are chronologically categorised as the Middle Miocene, Late Miocene and Pleistocene faunas (e.g. Saegusa et al. 2005; Nagaoka and Nakaya 2014). Four species of rhinocerotids (*Alicornops complanatum*, *Acerorhinus palaeosinensis*, *Aceratherium porpani*, and *Brachypotherium perimense*) were obtained from the Miocene horizon on the sand pit no. 8 (after Chaimanee et al. 2004, 2007; Deng et al. 2013; the present study). *Brachypotherium* sp. was listed as a member of the Middle Miocene fauna of the sand pit (Nagaoka and Nakaya 2014), although precise pit number is uncertain. Chaimanee et al. (2004, 2006) described a Miocene hominoid

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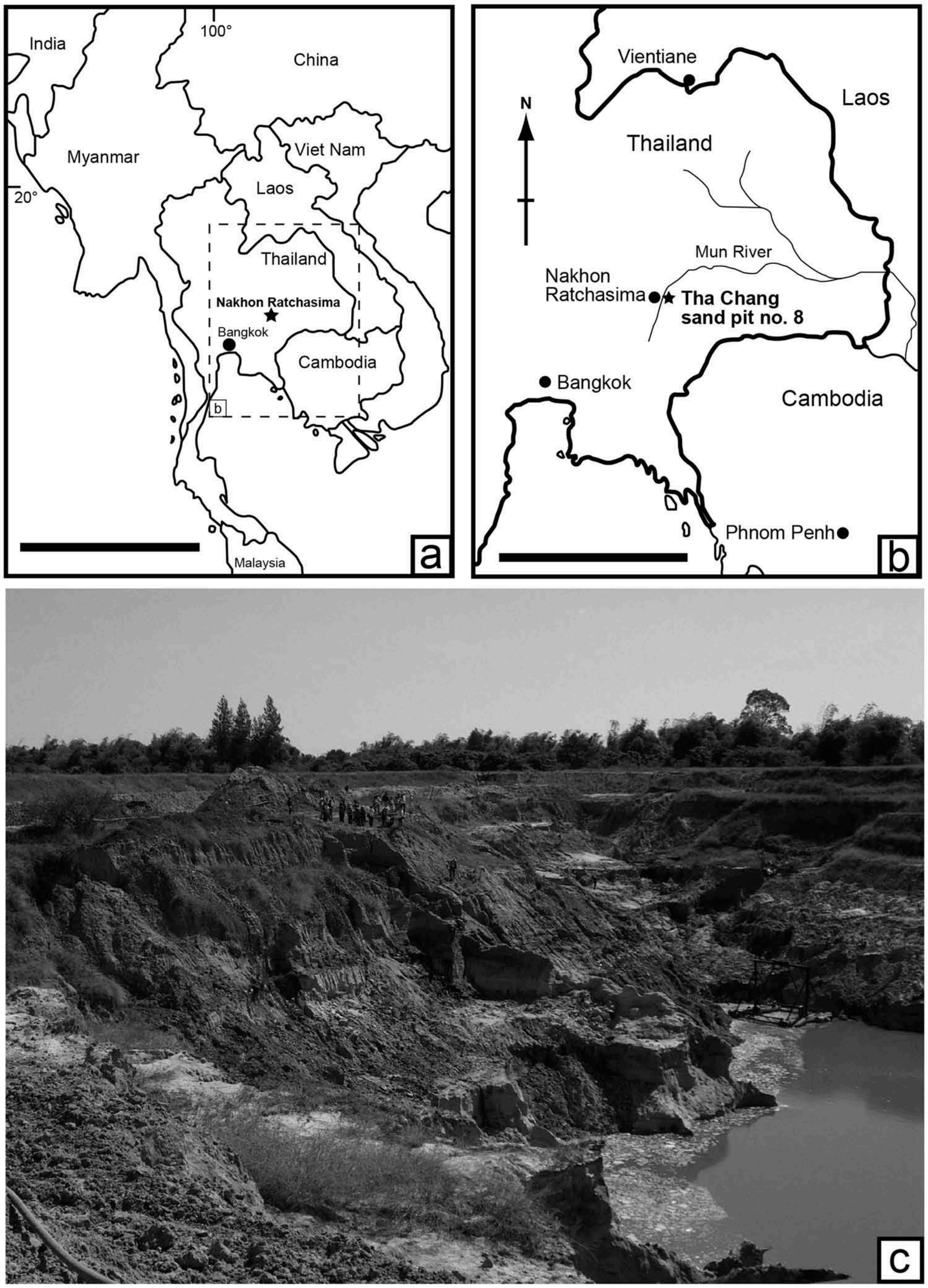

Figure 1. Map showing the fossil locality of rhinocerotid specimens from Nakhon Ratchasima city, northeastern Thailand (modified after Hanta et al. 2008). (a) The locality of Nakhon Ratchasima, (b) The locality of sand pit no. 8, (c) The landscape of sand pit no. 8 (photo courtesy: Yusuke Ozawa). Scale bars represent 500 km (a) and 300 km (b).

(*Khoratpithecus piriyai*) from the sand pit no. 8 (= Somsak sand pit). They also listed the following terrestrial mammal fossils besides the rhinocerotids: proboscideans (*Deinotherium* cf. *indicum, Gomphotherium* sp., *Stegolophodon* sp. and a primitive *Stegodon*), an equid (*Hipparion*), suids (*Hippopotamodon* cf. *sivalense* and *Propotamochoerus* cf. *hysudricus*), anthracotheres (*Merycopotamus medioximus* and *Microbunodon milaensis*), giraffids, and several bovids. Hanta et al. (2008) described a skull of anthracotheres from the sand pit no. 8 as a new species *Merycopotamus thachangensis*. Nishioka et al. (2014) described several dental and postcranial remains of giraffid from the sand pit no. 8 as *Bramatherium* sp. Nishioka and Vidthayanon (2018) described a calvarium with right and left horn cores of *Duboisia* aff. *santeng* from the sand pit no. 8. Thasod et al. (2011) summarised the proboscidean fossils from Tha Chang sand pits as follows: *Prodeinotherium pentapotamiae, Gomphotherium* sp., *Tetralophodon* sp., *Sinomastodon* cf. *yangziensis, Sinomastodon* sp., cf. *Protanancus macinnesi, Stegolophodon*/*Stegodon* spp., and *Elephas* sp. In addition, two dental remains of *Zygolophodon* sp. were recovered from the sand pit no. 10 (Duangkrayom et al. 2017).

The stratigraphy and geological age of the sediments in Tha Chiang sand pits are debatable (e.g. Chaimanee et al. 2006; Nagaoka and Nakaya 2014). The specimens studied here were collected from Tha Chang sand pit no. 8 (Figure 1). The sand sediments at this sand pit had exposed about 30 m depth from the ground to the bottom when the sandpit was first mined (e.g. Thasod et al. 2011). According to Chaimanee et al. (2006), the sediments at this sand pit are divided into lower and upper units in ascending order. The lower and upper units are composed mainly of organic greyish sand and gravel, and yellowish sand, respectively. The lower unit is about 50 m thick and overlies on the Mahasarakham Formation. The upper unit is less than 7 m and overlain by topsoil. The sandstone in the lower unit shows intense crossbedding, and has yielded fish, turtle and crocodile fossils, suggesting channel deposits (Chaimanee et al. 2006). Mammal fossils by Chaimanee et al. (2006) would have collected from the lower unit. Abundant tree trunk and leaves have also found this unit. The upper unit consists of sand and gravel, with some clay lenses. The lowermost part of this unit includes reworked tektites, with abundant tree trunk.

Nagaoka and Nakaya (2014) noted that there are differences of fossil mammal fauna at each sand pit and the geological age of the sediments in Tha Chiang is different at each sand pits. They also carried out a sedimentological analysis of seven sand pits in Tha Chiang and proposed a sediment model as follows. The sediments in the sand pits were derived from different aged fluvial ones and were deposited by the erosion of Mun River and supply from the hinterland. Contrary, the basement rock, such as the Cretaceous Khorat Group, was almost not affected by tectonic deformation. Therefore, the sediments in the sand pits in Tha Chiang would have been deposited eroding the older sediments and the basement rock.

The precise geological age of Tha Chang sand pit no. 8 is unclear due to lack of informative key strata and the precise provenance of the almost-mammal remains. The mammal fauna from sand pit no. 8 have been correlated roughly with the Late Miocene (ca. 9–7 Ma) based on a comparison with the land mammal fauna of Siwalik and China (e.g. Chaimanee et al. 2004; Hanta et al. 2008). Chaimanee et al. (2006) proposed a slightly younger age, ranging from possibly 7.4 to 5.9 Ma, if the fossil assemblage from the sand pit no. 8 contains hippo (*Hexaprotodon*) remains. According to Deng et al. (2013), the evolutionary grade of *Acera. porpani* found from sand pit no. 8 supports those estimated chronological ranges of the sand pit. The occurrence of *Bramatherium* sp. suggests that the biochronogical age of the sand pit is correlated with at least before 6 Ma (Nishioka et al. 2014). Nagaoka and Nakaya (2014) proposed six mammalian biostratigraphy (Zone I to Zone VI) in the Neogene localities in Thailand and they recognised that the age of Tha Chiang sand pit no. 8 is Zone V (the Late Miocene; 9 to 5? Ma). In contrast, proboscidean fossils (e.g. *Elephas*) which imply the Pleistocene in age have also recovered from this sand pit (Thasod et al. 2011). In addition, Howard et al. (2003) estimated that the tektites collected from the lowermost part of the upper unit are originated from the widespread tektite debris field at 0.8Ma in northeastern Thailand. Haines et al. (2004) also reported the tektites from the lower unit, and suggested that the sediments of Tha Chiang sand pits are dated in Quaternary. Therefore, the fossil mammal assemblage from the sand pit no. 8 suggests the Late Miocene in age, but it sometimes includes several faunas from different ages (Nishioka and Vidthayanon 2018).

Materials and methods

The specimens described in the present study are stored in the Northeastern Research Institutes of Petrified Wood and Mineral Resources (or Khorat Fossil Museum), Nakhon Ratchasima Rajabhat University, Nakhon Ratchasima, northeastern Thailand. The taxonomy and anatomical terminology used in the present study follow Antoine et al. (2010) (Figure 2) and the measurements follow Guérin (1980).

The specimens studied here were compared with previously known species of *Brachypotherium* from Eurasia and Africa, and Miocene rhinocerotids from Thailand. Comparisons were carried out from among collections of the following institutions: National Museums of Kenya, Nairobi, Kenya, Muséum National d'Histoire Naturelle Paris, France and Natural History Museum, London, UK. Several rhinocerotid remains used for comparison were based on the references.

Anatomical abbreviations

Teeth: I, upper incisor; i, lower incisor; P, upper premolar; p, lower premolar; M, upper molar; m, lower molar; Mt, metatarsal.

Postcrania: cie, central intercondylar eminence; ct, collum tali; e.g. extensor groove; fc, facet for the cuboid; ff, fibula facet; fIV, facet for MtIV; f1c, facet 1 for the calcaneus; f2c, facet 2 for the calcaneus; f3c, facet 3 for the calcaneus; gmec, gutter for the m. extensor carpi; if, intercondylar fossa; imi, insertion of m. interossei; ir, intermediate relief; imbb, insertion of the m. biceps brachii; lg, ligamental groove; lt, lesser trochanter; pa, posterior apophysis; pbpt, proximal border of the patella trochlea; pesf, posterior expansion of the scaphoid-facet; pfII, posterior facet for MtII; puf, proximal-ulna facet of radius; sdau, Second distal articulation for the ulna; sf, supracondylar fossa; tibt, tibial tuberosity; tt, third trochanter.

Institutional abbreviations

MNHN, Muséum National d'Histoire Naturelle Paris, France; KNM, National Museum of Kenya, Nairobi, Kenya; NHML, Natural History Museum, London, UK, NRRU-RIN (hereafter abbreviated as RIN), Nakhon Ratchasima Rajabhat University, Nakhon Ratchasima, Thailand.

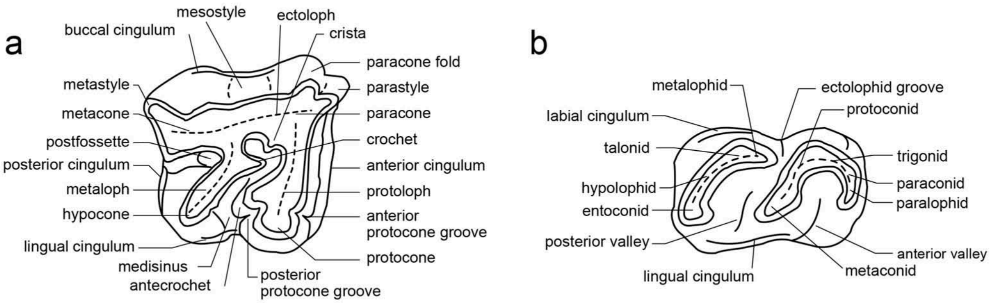

Figure 2. Dental terminology of the cheek teeth of Rhinocerotidae (terminology follows Antoine et al. 2010. Illustrations are modified after Fukuchi 2003). (a) upper cheek tooth, (b) lower cheek tooth.

Systematic palaeontology

Order Perissodactyla Gray, 1821
Family Rhinocerotidae Gray, 1821
Subfamily Rhinocerotinae Gray, 1821
Tribe Rhinocerotini Gray, 1821
Subtribe Teleoceratina Hay, 1902
Geuns *Brachypotherium* Roger, 1904

Diagnosis

Large-sized taxon of the Teleoceratina with massive skull and short nasals. Mandibular symphysis is not broadened. Upper and lower incisors are extremely developed. Molars are brachydont with moderately developed secondary folding and strong cingula. Usually secondary reduction of the antecrochet and constrictions. Lower molars with a strong, shallow ecotolophid groove. Greatly shortened limb bones (Heissig 1972).

Brachypotherium perimense (Falconer and Cautrey 1847)
(Figures 3–9, Tables 1–2, S1–5)

Diagnosis

Large species of the genus *Brachypotherium* with relatively high crown cheek teeth. Upper molar with slight constriction of the protocone and hypocone. Antecrochet mostly reduced, but still present. Molariform upper premolar with usually a strongly convex outer wall. Lower cheek teeth are almost without ectolophid groove. Cingula are usually reduced (Heissig 1972).

Materials

RIN 1220, a right premaxilla and maxilla fragment with I1 and P1, a left premaxilla and maxilla fragment with I1 and P1 to P4, and a right maxilla with P2 to P3; RIN 1220, a right maxilla with P2 to P3; RIN 1222, a right maxilla with M1 to M3; RIN 83, a left maxilla with M2 to M3; RIN 1225, a right mandible with p4 and m1; RIN 34, a right mandible with m2 and m3; RIN 355, a left mandible with p2 and p3; RIN 291, a right i2; RIN 1228, a right P4; RIN 395, a left P4; RIN 1201, a right M1; RIN 1225, a right mandible with p4 to m1; RIN 1211, a left p1; RIN 292, a right lower molar; RIN 1217 and RIN 1218, left lower molars; RIN 267, a right radius; RIN 155, a left femur; RIN 166, a right tibia, RIN 288, a right astragalus; RIN 800, a right MtIII.

Locality and age

Tha Chang sand pit no. 8, Nakhon Ratchasima, northeastern Thailand. Probably the Late Miocene based on the mammal fauna from sand pit no. 8 (Nagaoka and Nakaya 2014).

Description

Skull. The three remains (RIN 1220, RIN 1222, RIN 1228; Figure 3) belong to the same individual. The premaxillae are long. In the lateral

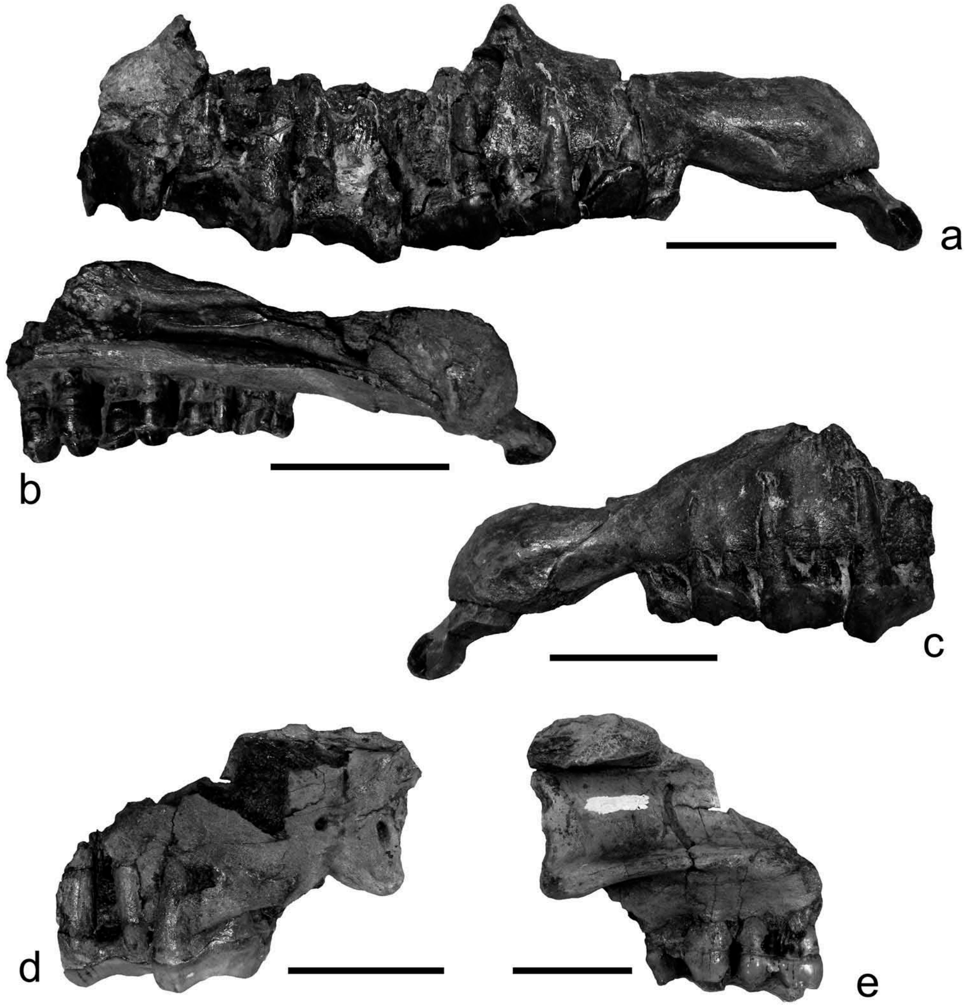

Figure 3. *Brachypotherium perimense* from Nakhon Ratchasima, Northeastern Thailand. Skull fragments. (a) RIN 1220, (b–c) RIN 1222, (d–e) RIN 1228. (a, c and e) lateral view, (b and e) lingual view. All scale bars represent 10 cm.

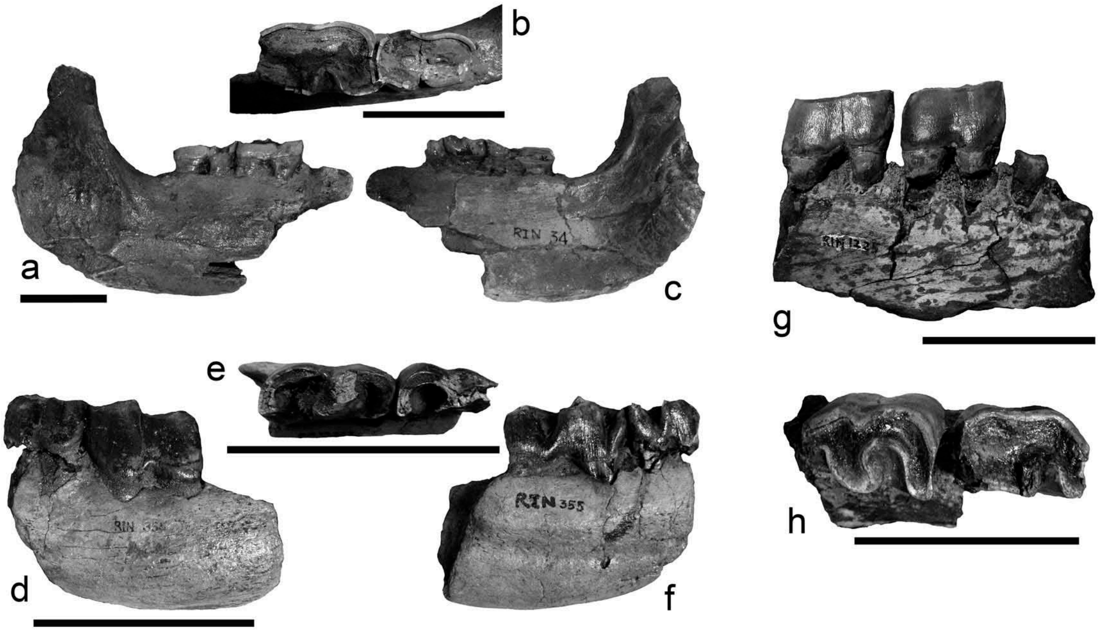

Figure 4. *Brachypotherium perimense* from Nakhon Ratchasima, Northeastern Thailand. Mandibles. (a–c) RIN 54, (d–f) RIN 355, (g–h) RIN 1235. (a, b and g) buccal view, (c and f) lingual view, (b, e and h) occlusal view. All scale bars represent 10 cm.

view, the suture between the premaxilla and maxilla is visible. The posterior end of the nasal notch lies above the mesial end of P3. The infraorbital foramen is large and located above the middle part of P3. The P1 to M3 and P1 to P4 erupt on the right and left maxillae, respectively. Both sides I1s erupt in the premaxillae (RIN 1220, RIN 1222; Figure 3(a–c)). These are extremely worn on the lingual side and its occlusal surface is well concaved. A dark grey-coloured enamel covers the apex of the teeth.

Mandible. Three mandibular remains were collected (RIN 34, RIN 355, RIN 1225). RIN 34 is large-sized right mandible with m2 and m3 (Figure 4(a–c)). The rostral side and dorsal part of the mandible corpus are missing. The mandible ramus is massive and its ventral margin curves gently. RIN 355 is a left mandibular fragment with p2 and p3 (Figure 4(d–f)). The mandibular body is relatively shallow dorsoventrally. RIN 1225 is right mandibular fragment with p4 and m1 (Figure 4(g–h)). There is no lingual groove on the lingual side of the mandible on RIN 34 and RIN 355.

Upper premolar. On both sides, the small P1 (RIN 1220, RIN 1228) are preserved (Figure 5(c–d)). The ectoloph is convex buccally. There is no buccal cingulum. A lingual cingulum continues. The medisinus is open lingually. Small posterior fossette is preserved at this wear stage.

P2 to P4 shows similar morphology (Figure 5). All teeth are molariform. There is no coronal cement. The occlusal surface is concave in the mesiodistal view. There is no crista and antecrochet. The lingual wall of the protocone and hypocone is rounded. The hypocone is not constricted. The paracone fold and parastyle are weak. The metastyle is short. The medisinus is narrow. The posterior valley is small and narrow at this wear stage. The buccal cingulum is weak. The ectoloph is convex on P2 and flattened behind the paracone fold on P3-P4, respectively. A short crochet is developed on P3 and P4. The hypocone is more developed than the protocone on P2. The protocone is weakly constricted on P4. The lingual cingulum continues with the anterior cingulum on P2 and P3. In contrast, the cingulum is connected with the anterior cingulum on P4.

Two isolated upper premolars are also collected (Figure 5(f–m)). RIN 395 has moderately worn P4. Its morphology is similar to that of RIN 1220 and RIN 1228. There is no cement on the tooth. The crochet, paracone fold, and parastyle of RIN 395 are more prominent than that of other P4 at this wear stage. The anterior and posterior protocone grooves are faint. The buccal cingulum is short at the mesiobuccal side of the ectoloph. The anterior, posterior and lingual cingula are continued. RIN 1221 (a right P4) is extremely worn. There is no crochet, crista, and antecrochet at this wear stage. The paracone fold and parastyle are lacking. There is no buccal cingulum, while the anterior, posterior and lingual cingula are preserved. The postfossette is oval-shaped at this wear stage.

The M1 and M2 on the maxilla (RIN 1222; Figure 5(a)) share similar characteristics such as a flattened ectoloph, constricted protocone, weak crochet and antecrochet, shallow hypocone groove, weak paracone fold and parastyle, no crista, short metastyle, shallow lingual groove on the protocone, no buccal cingulum, reduced lingual cingulum, and no coronal cement. The ectoloph of the M2 is more inclined than that of M1. The anterior cingulum on M1 is longer than that of M2. The M3 (RIN 1222) has a triangular outline in occlusal view. Its size is smaller than M1 and M2. The protocone is not clearly constricted at this wear stage, but there is a shallow posterior protocone groove at the base. The lingual wall of the protocone is rounded. The simple crochet is projected. The antecrochet is not developed. A pillar is present in the medisinus. There is no hypocone groove. The paracone fold and parastyle are developed. The anterior cingulum is low. The short posterior cingulum is near the distal side of the hypocone. The tubercle-shaped lingual cingulum is on the lingual end of the protocone.

A left maxilla fragment (RIN 83; Figure 5(e)) has M2 and M3. These teeth are moderately worn as in those of RIN 1222. They are almost similar to those of RIN 1222 except for M2, which has a more reduced lingual cingulum, and M3 with reduced lingual cingulum and flatter lingual wall of the protocone.

An isolated M2 (RIN 1201; Figure 5(n–q)) is less worn than the molars of RIN 1222. This tooth shows characteristics similar to that of other M2 remains. The crochet, antecrochet, paracone and

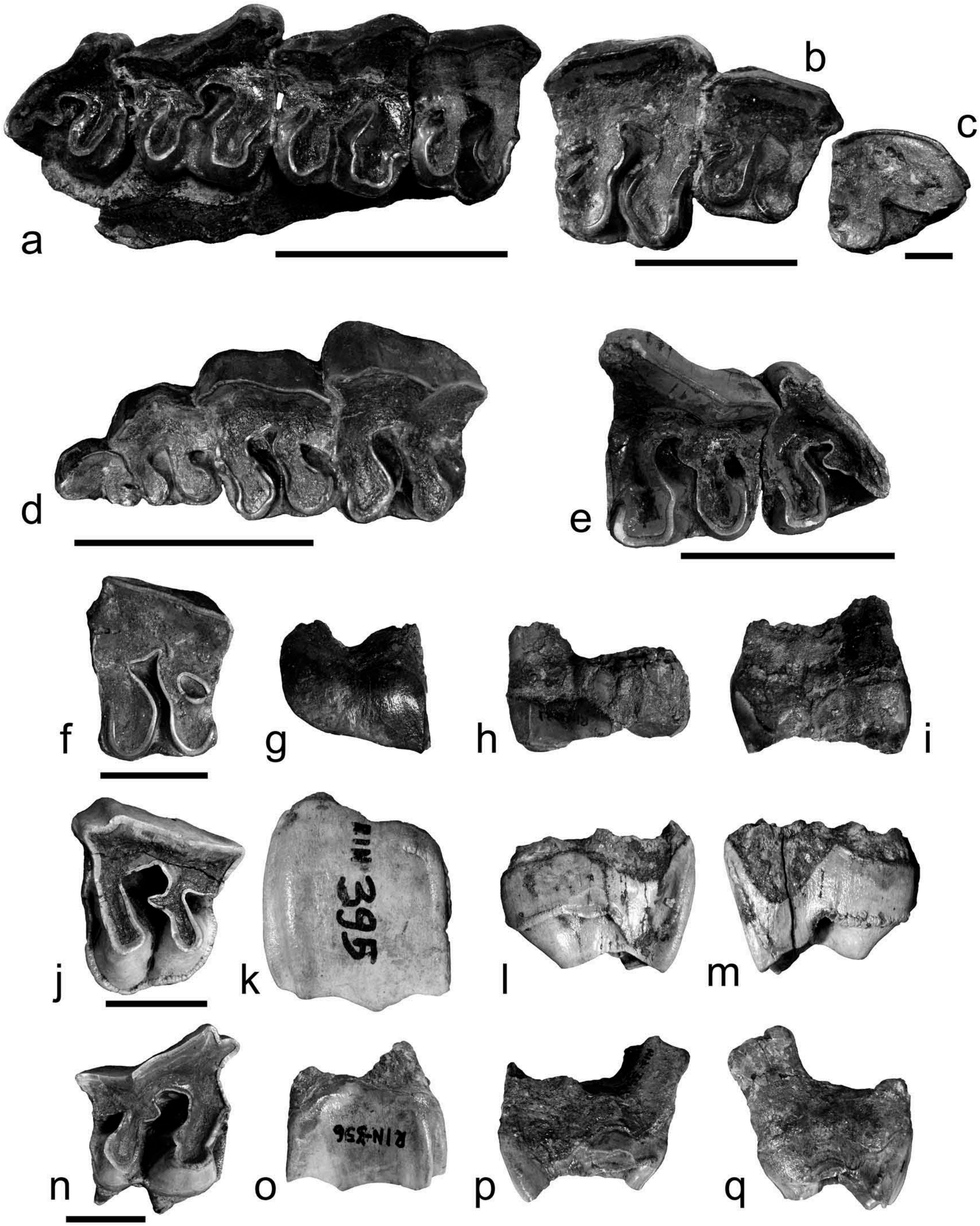

Figure 5. *Brachypotherium perimense* from Nakhon Ratchasima, Northeastern Thailand. Upper cheek teeth. (a) RIN 1222, (b–d) RIN 1220, (e) RIN 83, (f–i) RIN 1221, (j–m) RIN 395, (n–q) RIN 1201. (a–f, j and n) occlusal view, (g, k and o) buccal view.(h, i and p) mesial view; (i, m and p) distal view. Scale bars represent 10 cm (a, d, e), 5 cm (b, f, j, n) and 1 cm (c).

parastyle are more developed than the M2 of RIN 1222. The protocone constriction is distinct. The medisinus is wide at this wear stage. There is no lingual groove on the protocone. The anterior and posterior cingula are low and continued. The lingual cingulum is reduced.

Lower incisor. A right i2 (RIN 291; Figure 6) was found. The root end and most of the lingual part are missing. The tooth curves lingually. The enamel covers the lingual side of the tooth. The cross-section of the tooth is oval-shaped; it is mesiodistally wider than labio-lingually.

Lower cheek teeth. The m2 and m3 erupt in the mandible of RIN 34 (Figure 4(b)). Both teeth are extremely worn, and hence, a detailed morphology is uncertain. The disto-lingual part of the m3 is missing. The ectolophid of both teeth are almost flat. There is no buccal cingulum on both teeth. The posterior valley of the m2 is V-shaped in occlusal view. The p2 and p3 erupt in the mandible of RIN 355 (Figure 4(e)). The ectolophid groove is shallow on both teeth. The anterior and posterior valleys are V-shaped on both teeth in lingual view. There is a buccal cingulum on p3. In occlusal view, the posterior valley is wide U-shaped on both teeth. There is no lingual cingulum. The p4 and m1 erupt in the mandible of RIN 1225 (Figure 4(h)). The

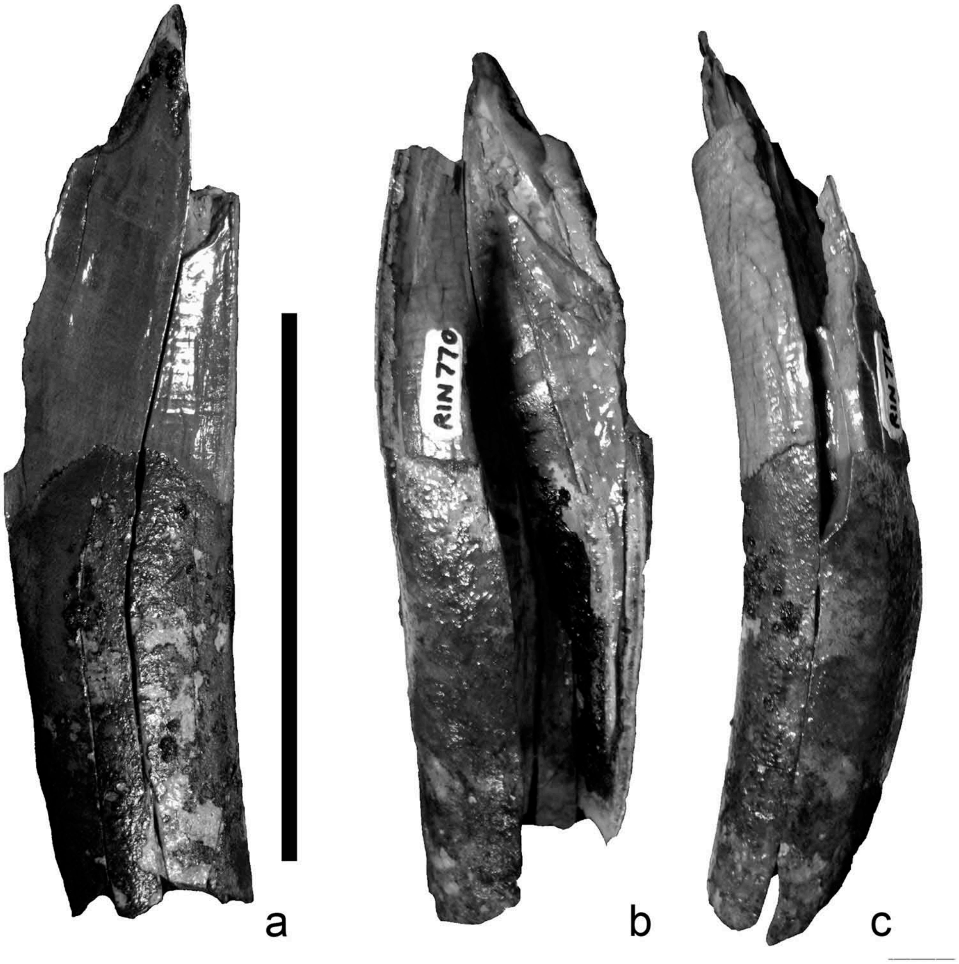

Figure 6. *Brachypotherium perimense* from Nakhon Ratchasima, Northeastern Thailand. Lower second incisor (RIN 770). (a) lingual view, (b) labial view, (c) mesial view. Scale bar represents 10 cm.

p4 is more worn than m1. Both teeth have a shallow ectolophid groove. There is no buccal cingulum on both teeth. The short paralophid extends lingually on p4. The metalophid is oriented disto-lingually on p4. The hypolophid on p4 bends lingually. The posterior valley on p4 is U-shaped on occlusal view. The posterior valley of m1 is U-shaped. The hypolophid of m1 is oriented lingually as in p4.

Four isolated lower cheek teeth (RIN 1211, RIN 1218, RIN 292, RIN 1217; Figure 7) are found. All teeth are extremely worn and have no cement. The ectolophid groove is almost flat at this wear stage except for p1. The ectolophid groove is almost flat at this wear stage in the occlusal view. The right p1 (RIN 1211; Figure 7(a–c)) lacks a root of the proximal side. The buccal cingulum is on the proximal side, whereas the lingual cingulum is absent. The anterior groove of the ectolophid, the ectolophid groove and the lingual groove of the entoconid are lacking at this wear stage.

A left lower premolar (RIN 1218; Figure 7(d–f)) was found with its roots partially missing. The characteristic of the anterior valley is uncertain due to wear. The posterior valley is U- and V-shaped in occlusal and lingual views, respectively. There are no cingula. A straight shallow groove is seen on the buccal side of the tooth surface.

A right lower molar (m1 or m2) (RIN 292; Figure 7(g–i)) is missing both roots. There are no buccal and lingual cingulum. The hypolophid bends disto-lingually. The anterior valley is almost missing at this wear stage. The posterior valley is V-shaped in occlusal and lingual views.

A left lower molar (m1 or m2) (RIN 1217; Figure 7(j–l)) lacks both roots and mesial and distal margin of the crown are damaged. A short mesial cingulum is seen on the mesiobuccal side of the tooth. There are no cingula. The posterior valley is V-shaped in lingual view whereas it is U-shaped in the lingual view. The hypolophid bends disto-lingually as in RIN 292.

Radius. RIN 267 is completely preserved (Figure 8(a–f)). This radius is independent for an ulna. The proximal-ulna facet is fused. Second distal articulation for the ulna is present. The anterior border of the proximal articulation is straight. In proximal view, the medial articular surface is sub-circular and the lateral is square. Both surfaces are shallow concave. The medial border of the diaphysis is concave, whereas the lateral border is curved. The insertion of the *m. biceps brachii* is deep. The gutter for the *m. extensor carpi* is weak. The posterior expansion of the scaphoid-facet is low. In distal view, the lateral articular surface is small and circular and the medial part is well swollen.

Femur. The femur (RIN 155; Figure 8(g–k)) lacks the proximal part. The tip of the third trochanter and the proximal half of the lesser trochanter are damaged. The third trochanter is well projected laterally. Between the medial rip of the trochlea and the diaphysis is a rupture. In posterior view, the supracondylar fossa is slightly concave and its surface is rugose. In distal view, the patella trochlea is asymmetrical, and the medial trochlea is higher than the lateral one. The proximal border of the patella trochlea is straight. The intercondylar fossa is deep. Its medial and lateral condyles are

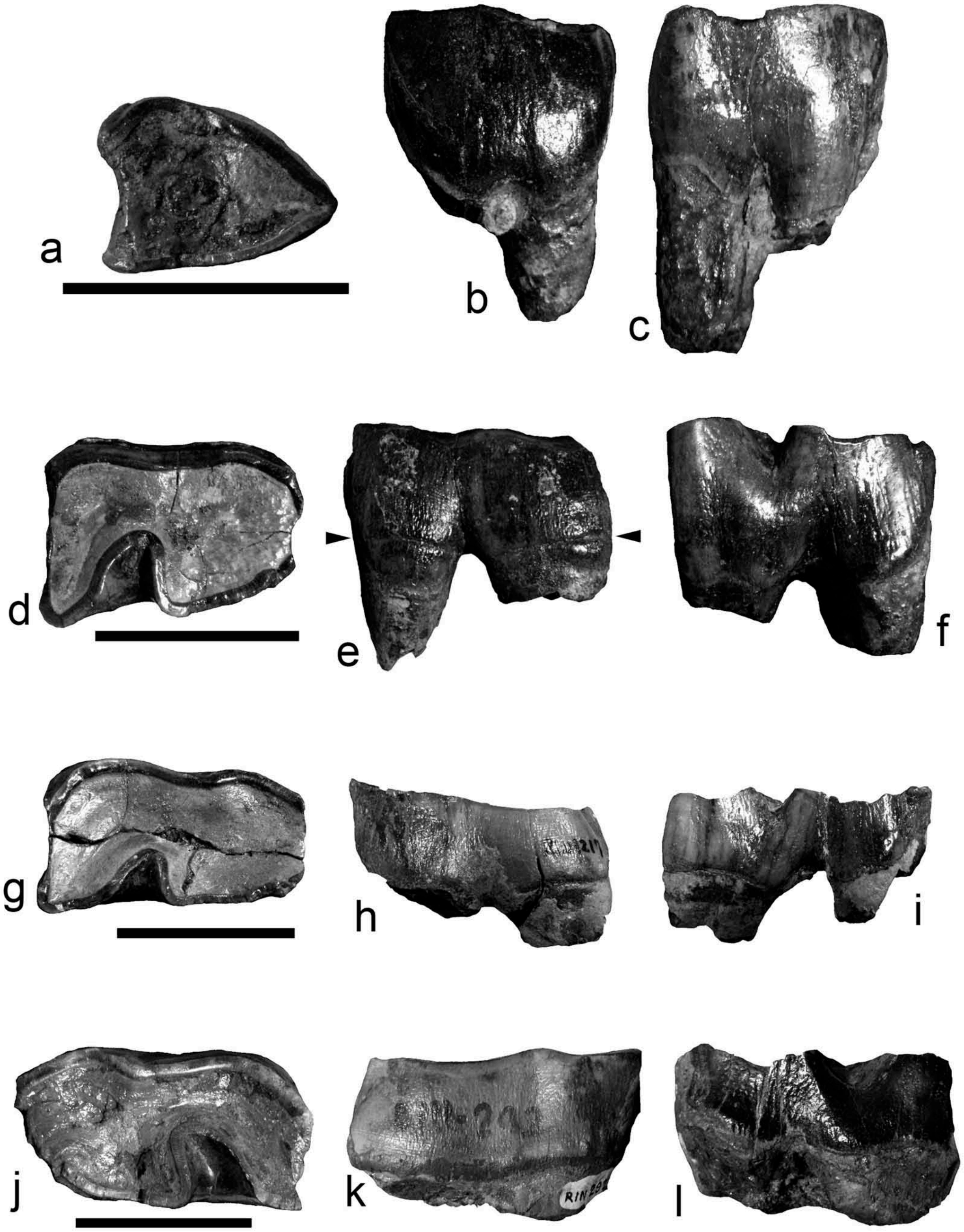

Figure 7. *Brachypotherium perimense* from Nakhon Ratchasima, Northeastern Thailand. Lower cheek teeth. (a–c); RIN 1211, (d–f) RIN 1218, (g–i) RIN 1217, (j–l) RIN 292. (a, d, g and j) occlusal view, (b, e, h and k) buccal view, (c, f, i and l) lingual view. All scale bars represent 5 cm.

oval in shape. The lateral epicondyle is more projected than the medial one.

Tibia. The tibial tuberosity and distal epiphysis are damaged (RIN 166; Figure 8(l–q)). In the proximal view, the ligamental groove is shallow. The central intercondylar eminence is shallow. The cranial border of the tibial tuberosity runs down to the medial margin in cranial view. The antero-distal groove is absent. The medio-distal gutter is shallow. The posterior apophysis is low and rounded. In the posterior view, the extensor groove is shallow at the preserved part. There is a small foramen is on the middle part of the shaft. In the distal view, the articular surface is oval-shape and shallow concave.

Astragalus. This element is completely preserved (RIN 288; Figure 9(a–f)). The ratio of its transverse diameter/height is 1.51. The ratio of its anteroposterior diameter/height is 0.79. The fibula facet is flat. The orientation of the facet for the fibula is oblique in dorsal view. The *collum tali* is high. The posterior stop on the facet for cuboid is absent. The caudal border of the trochlea is sinuous. The orientation of the trochlea/posterior articulation is oblique. The expansion of facet 1 for the calcaneus is wide and low. Facet 1 for calcaneus is almost flat in lateral view. Facets 2 and 3 for the calcaneus are fused.

MtIII. The distal-palmer side of the MtIII is partially damaged (RIN 800; Figure 9(g–k)). The shaft is of brachypodal proportion. The proximal articular surface is triangular and its proximal border

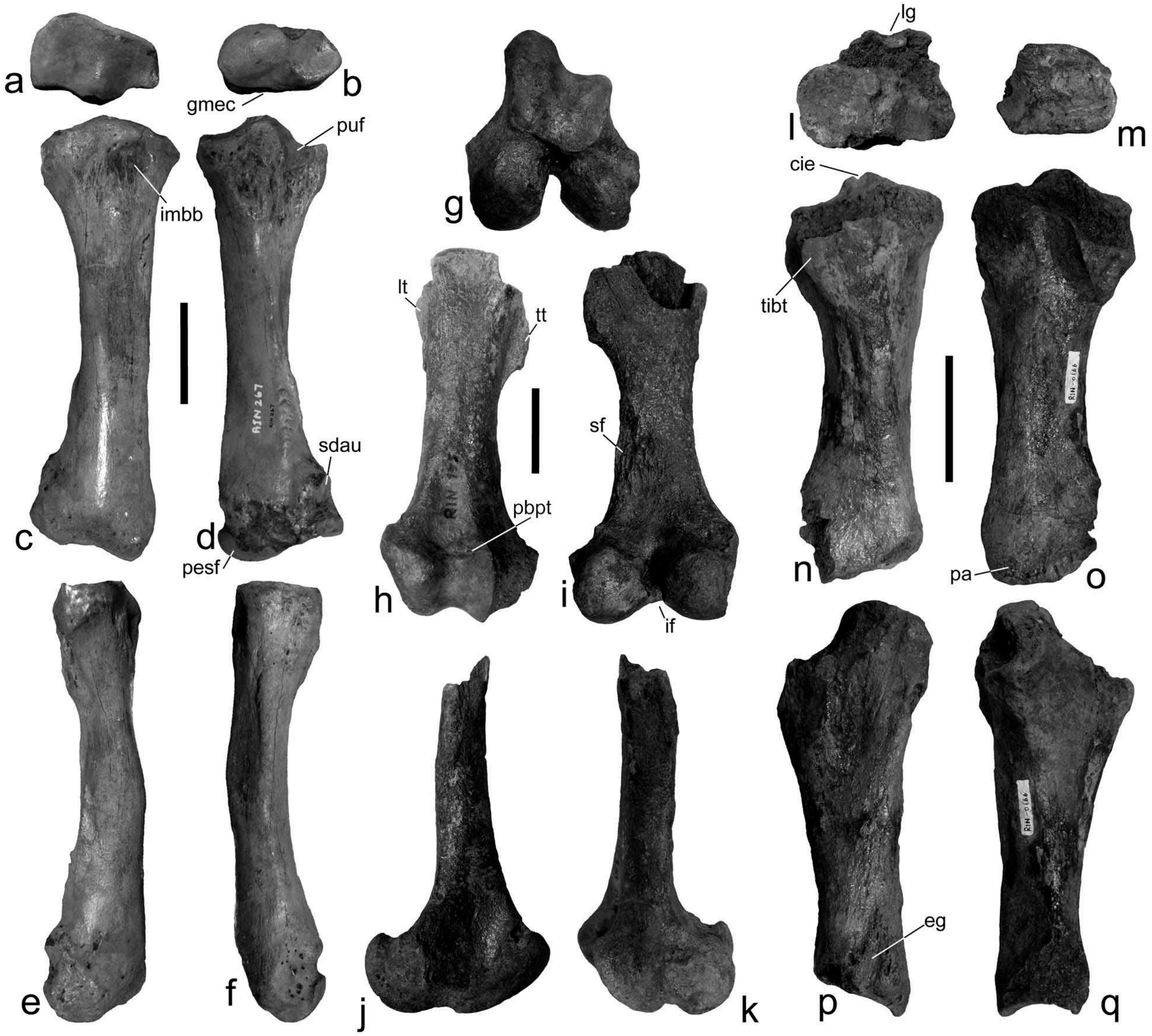

Figure 8. *Brachypotherium perimense* from Nakhon Ratchasima, Northeastern Thailand. Limb bones. (a–f) radius (RIN 267), (g–k) femur (RIN 155), (l–q) tibia (RIN 166). (a and l) proximal view, (b and m) distal view, (c, h and n) dorsal view, (d, i and o) posterior view, (e, j and p) mesial view, (f, k and q) lateral view. All scale bars represent 10 cm. Abbreviations are shown in the text.

on the dorsal side is slightly concave in proximal view. The posterior facet for MtII is present. The facet for MtIV is distinct. The medio-distal width of the diaphysis widens towards distally. The facet for the cuboid is large. The intermediate relief is low and smooth. The postero-distal tubercle on the diaphysis is absent. The insertion of *m. interossei* is long.

Comparison

Comparison with the Afro-Eurasian species of *Brachypotherium*

The present specimen shows several characteristics of the genus *Brachypotherium* such as having bucco-lingually broad molariform premolars with short crochet. Cheek teeth tend to have flattened buccal walls and brachypodal limb bones (Heissig 1972; Geraads 2010).

The type species of *Brachypotherium*, *B. brachypus*, was found from the Lower to Middle Miocene of Central and Western Europe, and Eastern Mediterranean region (e.g. Guérin 1980; Cerdeño 1993; Heissig 1999, 2012). Another European species, *Brachypotherium goldfussi* has also been known from the Late Miocene in Europe (Heissig 1999), but the remains of the latter species are scarce compared to that of *B. brachypus* (e.g. Guérin 1980). Heissig (2012) implied the possibility of synonymy of *B. goldfussi* with *B. brachypus*. This study follows Heissig's opinion. The present specimen is similar to *B. brachypus* in having a large tusk-like i2, upper premolar with molariform, short crochet, and continued lingual cingulum; M1 and M2 with flat or concaved ectoloph profile, weak constricted protocone, short crochet and antecrochet; lower cheek teeth with shallow ectolophid groove, and flat buccal wall; and no coronal cement on the upper and lower cheek teeth (Guérin 1980; Ginsburg and Bulot 1984; Cerdeño 1993; Antoine 2002; Heissig 2012). In addition, the present postcrania is similar to that of *B. brachypus* in terms of the radius, with a straight medial border of the diaphysis, weak gutter for the *m. extensor carpi*, low posterior expansion of the facet for the scaphoid, presence of second distal articulation for ulna, and facet for the pyramidal on distal margin. The present specimens also resemble the femur of *B. brachypus* (MNHN.F.SML.1209) in having a small third

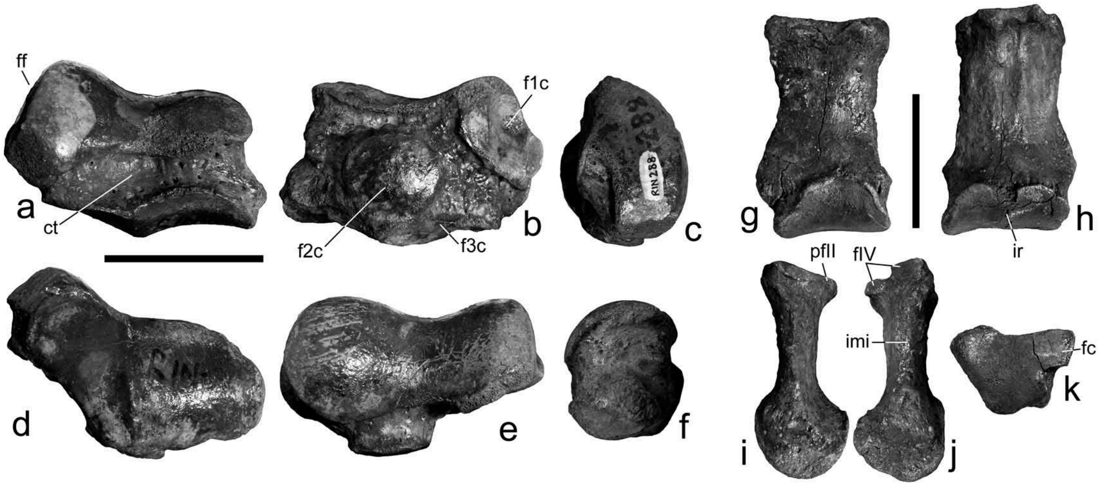

Figure 9. *Brachypotherium perimense* from Nakhon Ratchasima, Northeastern Thailand. Pes elements. (a–f) astragalus (RIN 288), (g–k) MtIII (RIN 800). (a and g) dorsal view, (b and h) palmar view, (g and j) mesial view, (c and i) lateral view, (e and k) proximal view, (d) distal view. All scale bars represent 10 cm. Abbreviations are shown in the text.

trochanter; the tibia with similar dimensions (Table S3), a robust shaft, shallow medio-distal gutter, and absence of the antero-distal groove; a proximo-distally low astragalus; and brachypodal MtIII. Metrically the present astragalus is similar to that of *B. brachypus* except for the measurement of height (Table S4).

However, several differences can be identified between the present specimen and *B. brachypus*. The present M1 has a lingual protocone groove which is not seen in *B. brachypus*. The present radius has a straight margin of the proximal articular facet of radius, whereas that of *B. brachypus* (MNHN.F.SML.331) is M-shaped. The insertion for the *m. biceps brachii* of the present radius is more depressed than that of *B. brachypus*. Metrically, the present radius is larger than that of *B. brachypus* (Table S1). The dimensions of the present femur are larger than that of *B. brachypus* (Table S2). The present tibia differs from that of *B. brachypus* in having a more rounded and low posterior apophysis. The present astragalus differs from that of *B. brachypus* in having a more circular-shaped and larger facet 2 for the calcaneus, a shallower facet 1 for the calcaneus, and an oval-shaped facet for the navicular. The present MtIII is different from *B. brachypus* (e.g. MNHN.F.SML.332) in having a more robust shaft, trapezoidal-shaped proximal facet, and a wider antero-posterior distal part. The dimensions of the present MtIII are larger than those of *B. brachypus* (Table S5).

As noted earlier, Chaimanee et al. (2004) noted the occurrence of *B. perimense* from the Late Miocene fauna in Nakhon Ratchasima in northeastern Thailand without any descriptions and figures. *Brachypotherium perimense* was originally reported from the Miocene in Pakistan and India (e.g. Lydekker 1884; Colbert 1935; Heissig 1972; Khan et al. 2012; Antoine et al. 2013). Falconer and Cautrey (1847) first reported *Aceratherium perimense* from India. Lydekker (1884) and Colbert (1935) also reported additional remains of *A. perimense* from India. Later, Heissig (1972) described the cranio-dental and postcrania remains of *A. perimense* from Pakistan and considered this genus as *Brachypotherium*. A mandibular fragment of this species was also reported from the middle Miocene in central Myanmar (Zin-Maung et al. 2010).

The present specimen has several diagnostic features of *B. perimense* such as upper molar with weak constriction of the protocone and hypocone, reduced antecrochet, molariform upper premolar with a convex outer wall, lower cheek teeth with shallow ectolophid groove, and cingula usually reduced or short (Heissig 1972).

The cheek teeth of the specimen are similar to those of *B. perimense* described by Falconer and Cautrey (1847) as in having upper premolars with weak convex ectoloph profile; M3 with weak protocone constriction and short crochet; and a shallow ectolophid groove on the lower cheek teeth. The present M2 is similar to that of *B. perimense* as described by Lydekker (1884, plate 1, fig 5) in having a concave ectoloph profile, short crochet and antecrochet, a weak constricted protocone, and a reduced lingual cingulum. The present specimen is similar to *B. perimense* described by Colbert (1935) in having an almost flat ectoloph profile on the molars and similar molar size. Compared with *B. perimense* as described by Heissig (1972), the present specimen is similar to the following features of the species: the positions of the nasal notch and the infraorbital foramen are near P3 in lateral view; robust premaxillae; molariform premolars; slightly developed paracone folds, no metacone fold, short crochet and continued lingual cingulum on the upper premolars; convex buccal wall on P2; the upper molars with concave ectoloph profile, weak constriction of the protocone, weak paracone fold, no metacone fold, thick and short crochet and antecrochet, missing crista, narrow medisinus, and reduced lingual cingulum. The present lower cheek teeth are similar to those of *B. perimense* as described by Heissig (1972) in having a shallow ectolophid groove and a flat buccal wall, and no buccal cingulum. Khan et al. (2012) described a few mandibles and the lower cheek teeth of *B. perimense*. The present mandibular fragments and lower cheek teeth are similar to those of *B. perimense* by Khan et al. (2012) in having a slightly curved ventral margin of the mandibular ramus, a shallow ectolophid groove on the cheek teeth, flat buccal wall on the cheek teeth, V-shaped anterior and posterior valleys on the lower cheek teeth in lingual view, U-shaped posterior valley on the premolar in occlusal view, and no buccal and lingual cingula. The present lower molars are also similar to that of *B. perimense* as described by Zin-Maung et al. (2010) in having shallow ectolophid groove, flat buccal wall and V-shaped posterior valley in lingual view, and the absence of lingual cingulum.

In contrast, several differences are seen between the present specimen and *B. perimense*. The mandible body is more robust than that of *B. perimense* (Heissig 1972, plate 11, fig. 12). The angle margin of the mandible is rounded, whereas that of *B. perimense* is projected. The present P4 has a deeper constricted protocone. The present M3 has a pillar in the medisinus, which is not seen in *B. perimense* by Heissig (1972). Compared with the

Table 1. Measurements of upper cheek teeth of *Brachypotherium perimense* from Nakhon Ratchasima, Northeastern Thailand and compered specimens (in mm). Abbreviations: L, length; W, width; H, height.

	P1			P2			P3			P4			M1			M2			M3		
Specimen number	L	W	H	L	W	H	L	W	H	L	W	H	L	W	H	L	W	H	L	W	H
NRRU-RIN 1220 (right)	34.19	28.62	21.90	40.13	47.42	31.92	48.30	74.26	26.54	63.84	83.47	38.61									
NRRU-RIN 1220 (left)	35.15	28.74	21.77	37.00	47.69	29.87	51.85	72.36	31.74												
NRRU-RIN 395										59.46	90.24	75.37									
NRRU-RIN 1201										57.84	63.81	31.42									
NRRU-RIN 1228										58.77	86.41	33.27									
NRRU-RIN 1222													61.74	84.10	24.76	70.16	87.40	35.22	56.91	73.45	39.92
NRRU-RIN 350																78.89	93.84	57.97			
NRRU-RIN 83																>75.79	98.32	30.57	72.56	88.14	41.94

Table 2. Measurements of lower cheek teeth of *Brachypotherium perimense* from Nakhon Ratchasima, Northeastern Thailand and compered specimens (in mm). Abbreviations: L, length; W, width; H, height.

	p1			p2			p3			p4			m1			m2			m3		
Specimen number	L	W	H	L	W	H	L	W	H	L	W	H	L	W	H	L	W	H	L	W	H
NRRU-RIN 1211	27.90	23.42	26.04																		
NRRU-RIN 355				>33.54	21.31	27.69	50.65	26.20	36.40												
NRRU-RIN 1225										56.37	39.35	41.55	59.62	37.71	33.27						
NRRU-RIN 34																75.95	44.64	18.97	>67.02	>34.37	16.72
Isolated lower premolar	L	W	H																		
NRRU-RIN 1218	58.50	41.11	36.74																		
Isolated lower molar	L	W	H																		
NRRU-RIN 292	68.69	41.06	33.64																		
NRRU-RIN 1217	74.50	46.02	28.88																		

description of Colbert (1935), the present maxilla differs in having a more rostrally (near P3) situated nasal notch, and a more developed paracone fold on the molar.

In the postcrania, the present astragalus is also similar to that of *B. perimense* by Heissig (1972), although it has a more proximodistally low body and a projected medial tuberosity. The present astragalus is metrically similar to that of *B. perimense* by Heissig (1972) (Table S4). The present MtIII resembles that of *B. perimense* in having a similar sized proximodistal length and transverse width of the diaphysis (Table S5), brachypodal shape, but the proximal outline is more trapezoidal in shape (Heissig 1972).

Brachypotherium fatehjangense was found from the Miocene in Pakistan and Myanmar (Chavasseau et al. 2006; Khan et al. 2010; Zin-Maung et al. 2010), although several researchers used *Aprotodon fatehjangense* instead of the former genus name (Heissig 1972; Deng 2006). The present specimens differ from *B. fatehjangense* from the Siwalik Group in Pakistan (Heissig 1972) in their cheek teeth by having molariform premolars and lack the mesostyle on the molars. The present lower cheek teeth are different from that of *B. fatehjangense* from Chaungtha in Myanmar (Chavasseau et al. 2006) in having a deep ectolophid groove on the lower cheek teeth and larger dental size. The present astragalus differs from that of *B. fatehjangense* as described by Heissig (1972) in having larger size (Table S4), an invisible of facet for the navicular in medial view, shorter medial tuberosity, circular-shaped facet 2 for calcaneus, and a shallower facet for the navicular.

Brachypotherium gajense was reported from the Lower Miocene in Pakistan (Pilgrim 1912; Antoine et al. 2010, 2013), although the taxonomic status of this species is debated (e.g. Geraads and Miller 2013). This species was originally described as *Aceratherium gajense* by Pilgrim (1912). Antoine et al. (2010, 2013) was identified this species as genus *Brachypotherium*, although without providing any detailed explanation. The present specimen differs from *B. gajense* by Pilgrim (1912) in having P3 with a flat ectoloph profile, open entrance of the medisinus, no tubercle at the entrance of the medisinus, weaker protocone constriction and antecrochet; M1 with a more concave ectoloph profile, flattened lingual wall of the protocone with a lingual groove, and no tubercle at the entrance of the medisinus.

There have been arguments about a Chinese species, *Brachypotherium shanwangensis*, for its taxonomic status. Wang (1965) first described *Plesiaceratherium shanwangensis*. Later, Yan et al. (1983) reported this species as *Brachypotherium shanwangensis*. Recently, Lu et al. (2016) made the phylogenetic analysis of *Plesiaceratherium*, and they suggested that *P. shanwangensis* is a junior synonym of *Plesiaceratherium gracile*. Therefore, this species excluded from the comparison in this study.

A few upper cheek teeth of *Brachypotherium*? *pugnator* were described from the Early Miocene locality of Kani area in Japan (Fukuchi and Kawai 2011), which was previously identified as *Chilotherium pugnator* by Okumura et al. (1977). The present specimen is different from *B.*? *pugnator* in having a larger dental size, no bridge between the proto- and metalophs on P4, and continued lingual cingulum on P4; a flat lingual wall of the protocone and weak protocone constriction, and antecrochet on M1.

Several upper cheek teeth of *B. pugnator* have been reported from the Middle Miocene locality Hsiachaohwan in Shiong, China (Chow and Wang 1964). This specimen was reconsidered by Wang (1965) as *Plesiaceratherium pugnator*. Qiu and Qiu (2013) listed this species as *Plesiaceratherium gracile*. In contrast, Lu et al. (2016) noted that they are part of *Brachypotherium*. The present specimen differs from those in having a premolar with weak constricted protocone and continued lingual cingulum; and the upper molars with weak protocone constriction and a short antecrochet.

Zin-Maung et al. (2009) described a few upper molar fragments found from the Late Miocene locality of Oiso, Japan, as *Brachypotherium* sp. The present upper molars differ in that specimen in having a short crochet, no enamel folding and absence of coronal cement.

Several species of *Brachypotherium* are also known from Africa, namely *B. snowi*, *B. lewisi* and *B. minor* (e.g. Hooijer and Patterson 1972; Hamilton 1973; Geraads 2010; Geraads and Miller 2013; Handa et al. 2018). Another African Early to Middle Miocene *Brachypotherium*, *B. heinzelini*, is considered to be preferred to *B. snowi* except for that type specimen (Geraads 2010).

Brachypotherium snowi has been known from the Early to Middle Miocene in Africa (Geraads 2010). In addition, numerous remains of *Aceratherium campbelli* from the Early Miocene locality in North Africa have been considered synonymy of *B. snowi* (Geraads 2010). The present specimen differs from *B. snowi* as described by Hamilton (1973) (include *A. campbelli* and *B. heinzelini*) in having more a posteriorly situated nasal notch (Hamilton 1973, NHML-M 29250), continued lingual cingulum on the upper premolars, much convex ectoloph profile on P2, bulged hypocone on P4, lingual protocone groove on M1 and M2, and a pillar in the medisinus on M3. Hooijer (1966) described well-preserved upper cheek teeth of *B. snowi* (= *B. heinzelini* in the reference) from Rusinga in Kenya, which are similar to the present premolars in having a flat ectoloph profile beyond the paracone fold, a weak paracone fold and antecrochet, and lingual cingulum. The present radius differs from that of *B. snowi* by Hooijer (1966, NHML-M 18908) in having a more robust shaft, a shallower postero-lateral margin of the proximal facet, and much lower posterior expansion of the scaphoid-facet. The present radius is also different from that of *B. snowi* (= *A. campbelli*) by Hamilton (1973, NHML-M 29274) in being much longer and slender proportions (Table S1), a straight anterior border of the proximal articulation, much deeper insertion of the *m. biceps brachii*, and a weak gutter for the *m. extensor carpi*. The present astragalus is different from that of *B. snowi* (= *B. heinzelini* in Hooijer 1966, plate. 14, fig. 3, KNM-RU 3021) in having larger size (Table S4), a lower the proximo-distal height, a more circular-shaped facet 2 for the calcaneus. The present astragalus is similar to that of *B. snowi* by Hamilton (1973) but is much larger in size. The astragalus of *B. snowi* (= *A. campbelli* in Hamilton 1973) is different from that of the present specimen in having much taller proximo-distal height.

The holotype (an isolated P4) of *B. heinzelini* is from the Late Miocene locality of Sinda in Congo (Hooijer 1963; the age of this locality follows Geraads 2010); it has a buccal cingulum and lacks the lingual cingulum. In contrast, the present P4s have a trace of the buccal cingulum or a lack of it and a continued lingual cingulum. Additionally, the dental size of the present P4 is larger than that of *B. heinzelini* described by Hooijer (1963).

Brachypotherium lewisi was found within the Late Miocene to Early Pliocene localities from Africa (Hooijer and Patterson 1972; Harris and Leakey 2003; Harris et al. 2003; Geraads 2010; Pandolfi and Rook 2019). The present cheek teeth are similar to that of *B. lewisi* in having premolars with short crochet, continued lingual cingulum; constricted protocone on P4; molars with a flat lingual wall of the protocone, weak constricted protocone, short crochet and antecrochet, and reduced lingual cingulum; and a hypocone groove on M1 and M2. However, the present specimen differs from *B. lewisi* in having more anteriorly situated infraorbital foramen, a bulging hypocone on P4, lingual protocone groove on M1 and M2, a pillar in the medisinus on M3, and a much larger dental size. The present lower cheek teeth differ in that of *B. lewisi* (Hooijer and Patterson 1972; KNM-LT 91) in having shallower ectolophid groove on the cheek teeth and absence of buccal cingulum.

Geraads and Miller (2013) described the Middle Miocene rhinocerotid remains from Buluk in northern Kenya as *B. minor*. The present specimen is distinguished from *B. minor* in having a clearly larger dental size, a more anterior situated nasal notch, always a continued lingual cingulum on the upper premolars, weak constricted protocone on P4, lingual protocone groove on M2, a pillar in the medisinus on M3; slightly curved ventral margin of the corpus of mandible, larger sized astragalus (Table S4), and a circular shaped facet 2 for calcaneus on astragalus.

Compared with the dental dimensions of the present specimens with those of other species of *Brachypotherium*, almost both upper and lower cheek teeth of the present specimens are larger size than those of other species or closer to those of the *B. perimense* and *B. lewisi* (Figures S1, 2).

Comparison with Miocene rhinocerotids from Thailand

The following Miocene rhinocerotids have been known from Thailand beside *Brachypotherium perimense; Gaindatherium* sp., *Chilotherium intermedium, Acerorhinus palaeosinensis*, and *Aceratherium porpani*.

Several fossil records of *Gaindatherium* sp. were reported from the Early to Middle Miocene localities of Thailand (Ducrocq et al. 1995; Kunimatsu et al. 2005). These studies, however, have no descriptions or figures. The type species of *Gaindatherium, G. browni* was described from the Middle Miocene Chinji Formation in India (Colbert 1934, 1935). The present specimens are distinguished from *G. browni* in having a more posteriorly located nasal notch, a further anteriorly situated infraorbital foramen, rather thick premaxilla, upper premolar without the metacone fold, and lingually directed lophs on upper premolars; a weak constricted protocone on P4; the upper molars with constricted protocone, short crochet, short antecrochet, concave or flattened ectoloph and short lingual cingulum; lower cheek teeth with shallow ectolophid groove and flat buccal wall.

In Pickford et al. (2004), *Chilotherium* (*Subchilotherium*) *intermedium* was listed as fauna of the latest Middle to earliest Late Miocene in Chiang Muan (Nakaya et al. 2002; Pickford et al. 2004; Suganuma et al. 2006; Nagaoka and Nakaya 2014) without any description. Originally, Matthew (1929) revised *Rhinoceros sivalensis* var. *intermedius* reported by Lydekker (1884) from Siwalik into *Chilotherium*. Later, Heissig (1975) revised this genus as the new subgenus *Chilotherium Subchilotherium intermedium*. Heissig (1989) changed subgenus *Subchilotherium* to the genus rank, namely *Subchilotherium intermedium*. Deng (2006) reviewed all species of *Chilotherium*, and he followed Heissig (1989)'s opinion. Recently, Khan et al. (2011) considered *S. intermedium* a synonym of *C. intermedium* based on the new remains of this species found from Pakistan. This discussion is far beyond the scope of the current work; we followed the latest study, namely Khan et al. (2011). The present upper cheek teeth are different from that of *C. intermedium* described by Matthew (1929) in having continued lingual cingulum on the premolars, weaker constricted protocone on the molar, and weak paracone fold. The present specimen is different from *C. intermedium* by Khan et al. (2011) in having larger sized upper and lower cheek teeth, convex ectoloph profile on the upper premolar, concaved ectoloph profile on M1 and M2, reduced lingual cingulum on M1, and a much wider posterior valley of the lower cheek teeth. The present astragalus differs from that of *C. intermedium* as described by Heissig (1972) in having a proximodistally higher dimension, shallow trochlea groove, a smaller and shallower facet for the navicular, and a larger facet 2 for calcaneus.

Chaimanee et al. (2004) listed *Chilotherium palaeosinese* and *Alicornops complanatum* as well as *B. perimense* in members of Late Miocene mammalian fauna from Tha Chang sand pit no. 8 at Nakhon Ratchasima, without any figures and description. *Chilotherium palaeosinese* was originally described as *Diceratherium palaeocinense* by Ringstöm (1924). Heissig (1975) considered this species to a subgenus of *Chilotherium, Chilotherium* (*Acerorhinus*) *palaeosinensis*. Qiu et al. (1987) and Deng (2006) revised the taxonomic status of this species, and they considered *C.* (*Acero.*) *palaeosinense* to *Acero. palaeosinensis* based on the differences of skull morphology between *Acerorhinus* and *Chilotherium*. The present specimen differs in that of *Acero. palaeosinensis* (= *D. palaeosinense*) by Ringstöm (1924) in having a further anteriorly situated nasal notch and infraorbital foramen; absence of the medifossette on the upper premolars; less constricted protocone on upper molars; short crochet and antecrochet on the upper molars, shallower hypocone groove on M1 and M2, triangular-shaped M3; shallower ectolophid groove on the lower cheek teeth; flattened buccal wall of the lower cheek teeth; more robust-shaped radius; lower height of the proximo-distal height of the astragalus, circular-shaped facet 2 for the calcaneus of the astragalus; separation of the facets 2 and 3 for the calcaneus.

Heissig (1972) described a subspecies of *Chilotherium, C. intermedium complanatum* from Siwalik in Pakistan. Antoine et al. (2003b) described a lower tooth row from Bugti Hills in Pakistan and proposed *C. intermedium complanatum* as a new combination *Alicornops complanatum*. Khan et al. (2012) also described additional remains of *Al. complanatum* from lower to middle Siwalik in Pakistan. The present specimen is different from *Al. complanatum* by Antoine et al. (2003b) in lacking the lingual cingulum on the lower cheek teeth, in having a rounded buccal wall and deep ectolophid groove on the lower cheek teeth and larger tooth size of the lower cheek teeth. The present specimens are different from *Al. complanatum* by Heissig (1972) in having an open entrance of the medisinus on the premolars, short paracone fold on the premolar, flatter ectoloph profile on the premolar, lingually oriented lophs on the premolars, short crochet on the upper molars, a much concaved ectoloph profile on the M1 and M2, more developed parastyle on the upper molars, long metastyle on the M1 and M2, weak constricted protocone on the upper molars, and a shallower ectolophid groove on the lower cheek teeth. The present specimens are different from *Al. complanatum* by Khan et al. (2012) in having M3 with simple crochet, no pillar-like tubercle on the entrance of the medisinus, and a larger dental size; lower cheek teeth with shallow ectolophid groove, flat buccal wall, and much larger dental size.

Deng et al. (2013) described a skull and mandible from the Late Miocene fauna in Tha Chang sand pit no. 8 as a new species, *Aceratherium porpani*. The present specimen differs from *Acera. porpani* in having a more anterior positioned nasal notch, an upper premolar with short crochet, continued lingual cingulum; upper molar with concave ectoloph profile, weak paracone fold, short antecrochet, short crochet and shallow hypocone groove; and lower cheek teeth with a deep ectolophid groove and a rounded buccal wall.

Saegusa et al. (2000) reported an incomplete skeleton of an unidentified rhinocerotid from the Middle Miocene locality of Ban Na Sai (Nagaoka and Nakaya 2014) in northern Thailand. Based on the description and figures by Saegusa et al. (2000), the present specimens differ from those specimens in having molariform premolars, M1 and M2 with weak paracone fold, flatter ectoloph profile; constricted protocone on the upper cheek teeth; and larger-sized cheek teeth with a shallow ectolophid groove and an almost flat buccal wall.

In sum, the present specimens have several characteristics of genus *Brachypotherium*, and they are distinguished from other Miocene Thai rhinocerotids. Compared with Afro-Eurasian species of *Brachypotherium*, the present specimens are identified as a South Asian species, *B. perimense* based on the similarities of the diagnostic characteristics and dental dimensions.

Discussion

Morphological differences between the Thai specimen and other specimens of B. perimense

As noted above, the present specimens differ in other specimens of *B. perimense* in having a more rostrally situated nasal notch; P4 with a deeper constricted protocone; a more developed paracone fold on the molar; M3 with a pillar in the medisinus. The position of the nasal notch frequently changes between in range of two teeth in the same species of both extant and extinct taxa (Guérin 1980; Geraads 2005). Although the protocone constriction is a character for *Brachypotherium*, its development is various (Heissig 1972; Cerdeño 1993). Thus, the development is also an intraspecific variation. The paracone fold on the upper cheek teeth of the *Brachypotherium* become weak near the tooth neck. The teeth of compared specimens of *B. perimense* are more worn down than those of the Thai specimens. Therefore, the differences in the development of the fold are owing to different wear stage. The pillar in the medisinus on M3 presents only one specimen (RIN 1222), whereas other M3 (RIN 83) has no pillar. This result indicates that the characteristic would be intraspecific variation.

Metrically, several specimens of the studied upper premolars, M3, p3, p4, m1 and m2 are larger than those of previously known specimens of *B. perimense* (Figures S1, 2). Several other extinct species of Eurasian rhinocerotid frequently show the tendency of the increasing size (Cerdeño 1998). The size differences between the present specimens and other ones, therefore, would be a same tendency.

Palaeoenvironmental significance

Sepulchre et al. (2010) analysed the pollen assemblages from the Late Oligocene to Late Miocene sites in Thailand, which includes the Somsak sand pit (= sand pit no. 8). According to their study, the environment was forested-dominated in northern Thailand (Mae Moh and Chiang Muan) during the Middle Miocene. In the Late Miocene, the palaeoenvironment at Khorat (= Nakhon Ratchasima) was dominated by thermophilous trees and grasslands, and this period would be a transition of the environment from woodlands to grassland-dominated landscapes. Duangkrayom et al. (2017) noted that these environmental changes would be correlated with the Eurasian palaeoclimatic change that occurred from the Middle to Late Miocene when tropical and forested environments changed to dryer and savanna environments (Cerling et al. 1994; Zachos et al. 2001). Deng et al. (2013) noted that *Acera. porpani* collected from sand pit no. 8 would have been in a woodland habitat based on the cranio-dental characters of this species such as the vertical or almost vertical angle of the occipital part and the subhypsodont cheek teeth. This suggestion confirms the hypothesis of the estimated paleoenvironment by pollen analysis, as mentioned earlier.

The habitat of genus *Brachypotherium* was estimated by body proportion, tooth morphology and tooth enamel isotope analysis. Traditionally, genus *Brachypotherium* is considered a swampy dweller based on its large body and a hippo-like body proportion (Guérin 1980; Heissig 1989; Antoine 2002), although Fortelius et al. (2003) noted that there is no direct support for the estimated habitat. Dental morphology of *B. brachypus* suggests a mix-feeder habitat (Fortelius 1990). The tooth enamel carbon and oxygen isotope analysis of *Brachypotherium* implies that this taxon would have preferred a closed woodland habitat (Aiglstofer et al. 2014a). According to Heissig (1972), *B. perimense* from Pakistan would have preferred a drier medium than swampy forests, but a wetter than a dry bush, based on the associated Miocene fossil mammal fauna in Pakistan. These results suggest that *Brachypotherium* would have been in forests or woodland habitats and possibly was a semiaquatic dweller. If *B. perimense* from Nakhon Ratchasima was in the same habitat with other ones, these suggestions confirm the palaeoenvironment of Nakhon Ratchasima during the Late Miocene.

Straight shallow grooves are on the buccal surface of the p1 of the present specimen (RIN 1225: Figure 7(e)). The shallow groove on the enamel surface has often been recognised as enamel hypoplasia (EH), which was caused by environmental or physiological stresses (e.g. Mead 1999; Roohi et al. 2015). Roohi et al. (2015) described EH on the cheek teeth of rhinocerotids from the Miocene to Pleistocene Siwalik Group in Pakistan and India. They suggested that the EH of rhinocerotids (including *B. perimense*) in the Middle to Late Miocene (12 to 8 Ma) would be caused by increasing seasonality and climatic changes including the appearance and expansion of C4 plants. The present specimen might also have been the same condition in Thailand during the Late Miocene. However, only one tooth with EH was found from sand pit no. 8 so far. Further teeth materials with EH from the sand pit are needed to discuss this hypothesis.

Palaeobiogeography of B. perimense in the Indian Subcontinent and Southeast Asia

Four rhinocerotids have been recognised in the Late Miocene fauna from sand pit no. 8 in Nakhon Ratchasima: *B. perimense, Al. complanatum, Acero. palaeosinensis*, and *Acera. porpani* (Chaimanee et al. 2004, 2006; Deng et al. 2013). *Brachypotherium perimense* and *Al. complanatum* have been found mainly from the Miocene in Pakistan (e.g. Colbert 1935; Antoine et al. 2003b). *Acerorhinus palaeosinensis* has been reported from the Upper Miocene in northern China (Ringstöm 1924). *Aceratherium porpani* has been only known from sand pit no. 8 in Nakhon Ratchasima (Deng et al. 2013). Therefore, the Late Miocene rhinocerotid assemblage of sand pit no. 8 comprises South Asian, Chinese and Thai endemic species, suggesting interchanges of rhinocerotids between Thailand, South Asia and/or China.

Regarding *B. perimense*, this species has presented in Pakistan since the earliest Miocene (Antoine et al. 2013; Nanda et al. 2018). *Brachypotherium perimense* was also distributed in India and Nepal during the Middle to Late Miocene, and Middle Miocene, respectively (e.g. West et al. 1991; Patnaik 2013). In addition, *B.* cf. *perimense* was reported from the Late Miocene of Iraq (Thomas et al. 1980). *Brachypotherium perimense* was also found from the Middle to Upper Miocene parts of the Irrawaddy sediments in central Myanmar (e.g. Zin-Maung et al. 2010; Nishioka et al. 2018), implying that this species spread into southeast Asia from the Indian Subcontinent by the Middle Miocene.

In the earliest Miocene, the rhinocerotid assemblages between Pakistan and Vietnam show high similarity (Prieto et al. 2018). In the Middle Miocene, similar land mammal fauna was distributed between the Indian Subcontinent and Myanmar, suggesting that both areas had a similar biogeographic province (Ducrocq et al. 1995; Zin-Maung et al. 2010; Nanda et al. 2018). These studies imply that the dispersal of rhinocerotids between the Indian Subcontinent and Southeast Asia happened during the Early to Middle Miocene. Handa et al. (2019) pointed out that a few cheek teeth of *Brachypotherium* from the latest Middle to earliest Late Miocene locality, Chiang Muan (Suganuma et al. 2006; Nagaoka and Nakaya 2014) in northern Thailand, were morphologically similar to those of *B. perimense*. If so, this species would have migrated into Thailand by the late Middle Miocene, then distributed in Nakhon Ratchasima by the Late Miocene.

In sum, *B. perimense* would have presented in Pakistan since the Early Miocene. Its distribution expanded into the east (India, Nepal, Myanmar and Thailand) and probably west (Iraq) during the Middle to Late Miocene (Figure 10); *B. perimense* would therefore have migrated to Southeast Asia by the late Middle Miocene at least. As mentioned earlier, the palaeoenvironment of the south to southeastern Asia during the Early to Middle Miocene would be a similar condition (tropical forest dominated habitat), which was preferred by *Brachypotherium*. Therefore, *B. perimense* may have been distributed along the palaeoenvironmental regions.

Fossil records of genus *Brachypotherium* in Afro-Eurasia

Asia

According to Antoine et al. (2013), two species of *Brachypotherium, B. fatehjangense* and *B. gajense*, have been found from the Lower Miocene of Sulaiman Province in Pakistan (Zinda Pir and Bugti Hills) (Figure 10). The fossil record of *B. fatehjangense* in Pakistan continues to the Middle Miocene. As noted above, *B. perimense* has been found since the Early Miocene locality in Pakistan. *Brachypotherium fatehjangense* has also been known from the Middle Miocene in Myanmar (Zin-Maung et al. 2010). The ranges of *B. perimense* and *B. fatehjangense* in Pakistan are longer than those of other species (Figure 10). These records might include more than one species or subspecies of the genus; however, additional description and comparison for Pakistan's specimens are required to discuss those possibilities. A few records of *Brachypotherium* sp. (including ?*Brachypotherium* sp.) were recorded from India and Tajikistan. *Brachypotherium brachypus* was found from the Middle Miocene localities such as Sinap, Paşalar, Çandir and Kultak in Turkey (Heissig 1976; Fortelius 1990; Fortelius et al. 2003; Geraads and Saraç 2003; Kayseri Özer et al. 2014), which are the easternmost records of this species.

The fossil records of East Asia are scarce and those taxonomic statuses are debatable (Figure 10). Therefore, the relationship between East Asian taxa and other regions is unclear so far. *Brachypotherium* sp. from the Late Miocene in Japan described by Zin-Maung et al. (2009) shows a different morphology for *Brachypotherium* such as, it has a longer crochet, additional enamel folding and coronal cement (N. Handa, pers. comm. 2019). Fukuchi and Kawai (2011) pointed out that *B.*? *pugnator* from Japan is similar to *B. shanwangensis* and *B. fatehjangense. Brachypotherium pugnator* was also found from the Middle Miocene in China, but its taxonomic status is argued as noted earlier (Wang 1965; Lu et al. 2016). Zhang et al. (2013) listed cf. *Brachypotherium* sp. as a member of the mammal fauna from the Late Miocene Bahe Formation in China; however, there is no detailed description. If these are truly a group of *Brachypotherium*, the ancestral stock of East Asian taxa would have migrated from South Asia by the earliest Miocene (>19 Ma). On the contrary, if *B. shanwangensis* and *B. fatehjangense* had belonged to *P. gracile* and *Ap. fatehjangense* respectively (e.g. Heissig 1972; Deng 2006; Lu et al. 2016), the distribution of truly *Brachypotherium* would have not extended to East Asia. In fact, other species of *Aprotodon* and *Plesiaceratherium* sp. have been found from the Early Miocene in China and Japan, respectively (e.g. Qiu and Xie 1997; Fukuchi and Kawai 2011; Deng 2013). Further remains are needed to discuss the taxonomic status of East Asian forms.

Europe

European species of *Brachypotherium, B. brachypus* and *B. goldfussi*, were distributed in central and western Europe, and eastern Mediterranean regions (Figure 10). A few remains of *B. brachypus* were found from the Miocene in Spain (e.g. Cerdeño 1992), but their taxonomic status is doubtful (Heissig 2012). Those fossil records are, therefore, excluded from the present study. *Brachypotherium* sp. was found from Bulgaria in the late Miocene record (Geraads and Spassov 2009). The stratigraphic range of *B. brachypus* and *B. goldfussi* have been known from MN4 to MN8 and MN9, respectively (Figure 10). *Brachypotherium brachypus* migrated from Asia to Europe during the late Early Miocene (Heissig 1999). The land mammal interchange had occurred in the eastern Mediterranean region via the so-called '*Gomphotherium*-landbridge' which resulted from the collision of the Afro-Arabian plate with the Eurasian plate during the MN4 (e.g. Koufos et al. 2005). Becker et al. (2009) noted that *B. brachypus* migrated from Asia via '*Gomphotherium*-landbridge' during 'Proboscidean Datum Event' (MN4), and the fossil records of an Early Miocene rhinocerotid, *Diaceratherium* were replaced by that of *Brachypotherium* in Western Europe during that period.

Africa and Arabia

The oldest known fossil record of *Brachypotherium* in Africa was from the Early Miocene in sub-Saharan Africa (Figure 10). *Brachypotherium snowi* has been continuously recorded from the Early to Middle Miocene. *Brachypotherium lewisi* has been found from the Upper Miocene to Lower Pliocene. Other fossil records of this group (*B. minor, B. heinzelini* and *B.* sp.) have sporadically been found during the Miocene (Geraads 2010; Geraads and Miller 2013; Handa et al. 2018). Gentry (1987) reported a few teeth fragments and postcranial elements of *Brachypotherium* sp. from the late Early Miocene locality of Ad Dabtiyah in Saudi Arabia.

The interchange of *Brachypotherium* between Africa and Eurasia is still controversial. The first migration of rhinocerotid into Africa would have occurred during 'Proboscidean Datum Event' as well as European ones (e.g. Hooijer 1978; Koufos et al. 2005; Sen 2013). As noted above, Geraads and Spassov (2009) reported *Brachypotherium* from the Late Miocene locality in Bulgaria, and they noted two hypotheses on this record, namely as a refuge for this genus or *Brachypotherium* in Bulgaria from Africa via the Asia Minor. Geraads and Miller (2013) also implied the possibility of several migrations of *Brachypotherium* into Africa. However, details about the period when migration of *Brachypotherium* between Eurasia and Africa is unclear because the phylogenetic relationship between African and Eurasian taxa is uncertain as noted by Geraads and Miller (2013). Therefore, further materials are needed to discuss the exact period of migration between those regions.

Conclusion

The cranio-dental and postcranial remains of the Rhinocerotidae collected from sand pit no. 8 at Nakhon Ratchasima in northeastern Thailand, were described as a South Asian species, *Brachypotherium perimense*.

Brachypotherium has been present in Afro-Eurasia since the Early Miocene. The distribution of this genus was affected by the palaeoenvironment and tectonic events. The oldest fossil record of *Brachypotherium* is known from the earliest Miocene locality of Pakistan. The environment was dominated by forest in Eurasia during the Early to Middle Miocene, which might have been affected the expansion of *B. perimense* eastward. This species would have presented in northern Thailand (Chaing Muan) by the late Middle Miocene at least, then its distribution expanded into northeastern

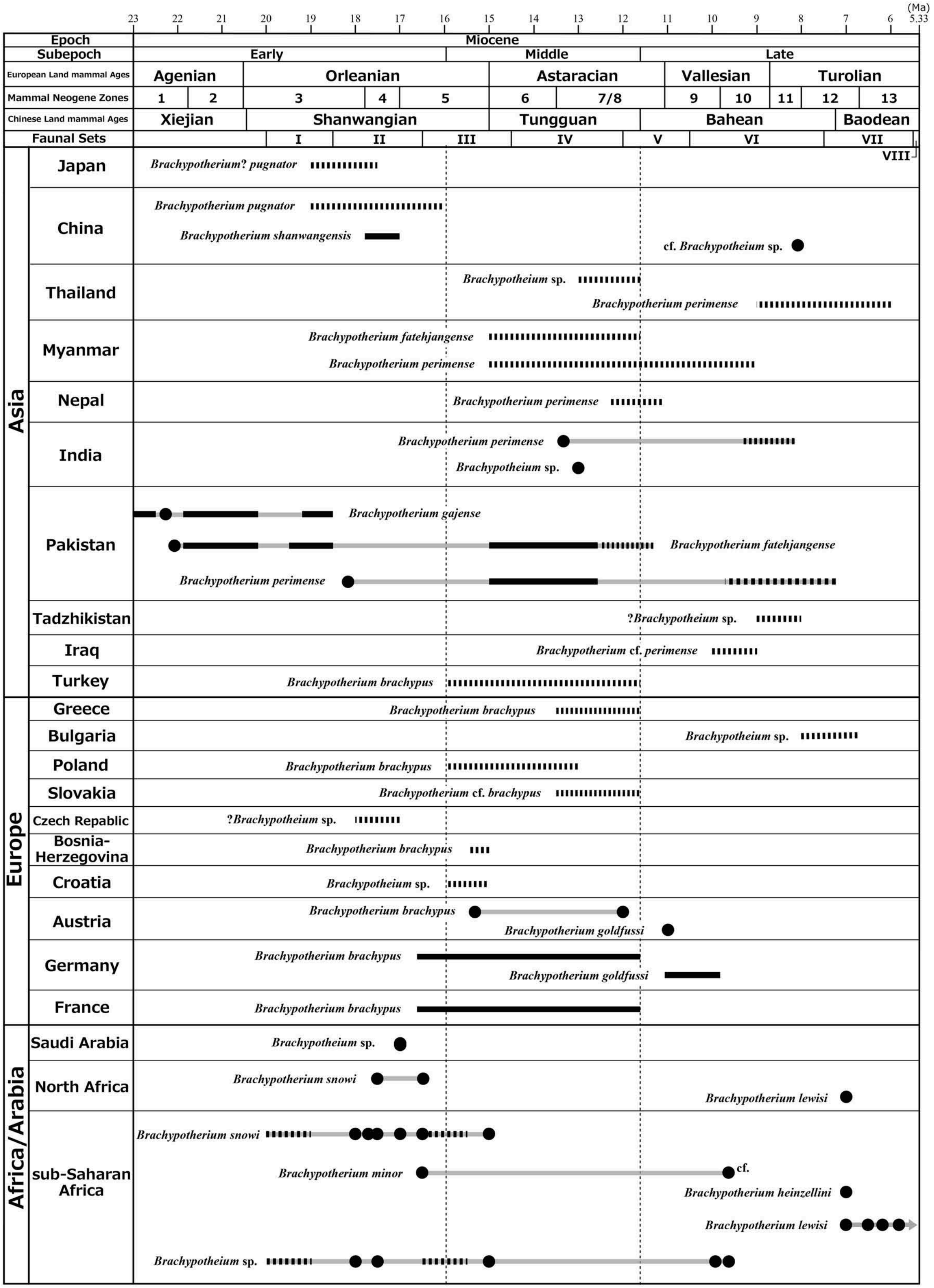

Figure 10. Chronology of species of *Brachypotherium* in Eurasia and Africa. Broken lines indicate uncertain range of the species. Fossil record and locality age from the following references: Japan (Zin-Maung et al. 2009; Fukuchi and Kawai 2011; Tomida et al. 2013); China (Chow and Wang 1964; Qiu and Qiu 2013; Zhang et al. 2013); Thailand (Chaimanee et al. 2004, 2006; Hanta et al. 2008; Deng et al. 2013; present study); Myanmar (Zin-Maung et al. 2010; Nishioka et al. 2018); Nepal (West et al. 1991); India (Patnaik 2013); Pakistan (Antoine et al. 2013); Tazikistan (Forsten and Shaparov 2000); Iraq (Thomas et al. 1980); Turkey (Heissig 1976; Fortelius 1990; Daams et al. 1999; Fortelius et al. 2003; Geraads and Saraç 2003; Kayseri Özer et al. 2014); Greece (Koufos and Kostopoulos 2013); Bulgaria (Geraads and Spassov 2009); Poland (Kowalski 1990), Slovakia (Zervanová et al. 2013); Czech Republic (Ivanov et al. 2006); Bosnia Herzegovina (Becker and Tisser 2019); Croatia (Bernor et al. 2004); Austria (Heissig 2009; Aiglstofer et al. 2014b); Germany (Heissig 1999; von VJ and Heizmann 2001); France (Heissig 1999; Antoine et al. 2000); Saudi Arabia (Gentry 1987; Begun 2007); Africa (Geraads 2010; Geraads and Miller 2013; Handa et al. 2018; Pandolfi and Rook 2019). The European land mammal ages and mammal Neogene zones are based on Steininger (1999). The African faunal sets are based on Pickford (1981). The Chinese land mammal ages are based on Deng et al. (2019).

Thailand (Nakhon Ratchasima) in the Late Miocene. The ancestral stock of African *Brachypotherium* would have entered the African continent from Asia through the '*Gomphotherium*-landbridge'. The migration of *Brachypotherium* into Europe would have occurred at the same timing. Antoine et al. (2010), Antoine et al. (2013) pointed out the similarity of Early Miocene rhinocerotid assemblage which includes *Brachypotherium*, between Eurasia and Africa, implying the interchange between these areas throughout the earliest Miocene. Nanda et al. (2018) also noted a high similarity at the generic level of the land mammal fauna among the fauna of the Himalayan foreland basins, Europe, Turkey, Central Asia and Africa during the Early to Middle Miocene. *Brachypotherium* would be a member of these faunae. In the Middle Miocene, several species of *Brachypotherium* presented in Eurasia. Finally, the diversity of *Bracypotherium* decreased and they became extinct by the end of the Miocene except for the African species, *B. lewisi.*

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