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Taxonomic revision of a late Miocene rhinoceros from Japan with an overview of *Brachypotherium* from East Asia

Naoto Handa [a] and Hajime Taru [b]

[a]Lake Biwa Museum, Kusatsu, Japan; [b]Kanagawa Prefectural Museum of Natural History, Odawara, Japan

ABSTRACT

The genus *Brachypotherium* is an extinct rhinoceros that has been mainly found in the Miocene in Eurasia and Africa. Among of them, the taxonomic status of the East Asian *Brachypotherium* is controversial. Here, the study re-describes tooth fragments of rhinoceros from the Upper Miocene locality in Japan. This specimen (KPM-NNV 50) has been previously identified as *Brachypotherium* sp. Compared with the Asian Miocene rhinoceros, KPM-NNV 50 is re-identified as Aceratheriinae gen. et sp. indet. in this study. Both previous studies and the present study suggest that the Late Miocene Japanese rhinoceroses are ranging from about 10 Ma to 5.5 Ma, indicating that a large gap of the rhinocerotid fossil records (16 Ma to 10 Ma) between the Early and Late Miocene. We summarise the taxonomic status of *Brachypotherium* in East Asia, resulting that the East Asian '*Brachypotherium*' are possibly different species. The present study confirms that the genus *Brachypotherium* existed throughout the Miocene in Europe, South Asia, and Southeast Asia, and possibly persisted into the African Pliocene.

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Introduction

The genus *Brachypotherium* is an extinct widely distributed rhinoceros of the tribe Teleoceratini. This genus has been mainly found in the Miocene in Eurasia and Africa (e.g. Handa et al. 2021 and references therein). The type species of this genus, *Brachypotherium brachypus*, has been found from the Middle Miocene in Europe (e.g. Heissig 1999). In Africa, four species of the genus (*Brachypotherium heinzelini*, *Brachypotherium snowi*, *Brachypotherium lewisi*, and *Brachypotherium minor*) were found from the Miocene sediments (e.g. Geraads 2010; Geraads & Miller 2013). Of these, *B. lewisi* has been known from the Early Pliocene locality in Lothagam, Kenya (Geraads 2010 and references therein). South to Southeast Asian species *Brachypotherium perimense*, *Brachypotherium fatehjagensis*, and *Brachypotherium gajense* have been known from the Miocene (Colbert 1935; Heissig 1972, Zin-Maung-Maung-Thein et al. 2010; Antoine et al. 2013; Handa et al. 2021; Rafeh et al. 2020; Longuet et al. 2023).

In contrast to these regions, the East Asian records are scarce. *Brachypotherium shangwangensis* has been described from the Early Miocene Shanwang Basin in China (Wang 1965). In Japan, *Brachypotherium*? *pugnator* and *Brachypotherium* sp. were described from the Early Miocene and the Late Miocene localities, respectively (Fukuchi & Kawai 2011; Zin-Maung-Maung-Thein et al. 2009).

Of these, *Brachypotherium* sp. (specimen number: KPM-NNV 50) was collected from the conglomerate layer in the middle unit of the Oiso Fomation near the Oiso coast in Kanagawa Prefecture, Japan (Zin-Maung-Maung-Thien et al. 2009) (Figure 1). The geological age of this formation is estimated as the late Late Miocene based on the calcaneus planktonic nannofossil Zone (CN9: 8.29–5.59 Ma) and planktonic foraminiferal Zone (N17: 8.58–5.57 Ma) (Ishihama et al. 2012). Beside rhinocerotid fossil, an isolated upper molar of Suinae gen. et sp. indet., cf. *Propotamochoerus hyotherioides*, bone fragments and ear bones of cetacean, the teeth of pinniped, and abundant shark teeth have been collected from this formation (see Tanaka et al. 2023; Tsubamoto & Taru 2022).

Recently, the taxonomic status of East Asian *Brachypotherium* has been revised based on the newly discovered specimens (e.g. Lu et al. 2016, 2021). Therefore, the taxonomic position of Japanese species also requires re-examination. Here, we re-describe KPM-NNV 50 that was identified as *Brachypotherium* sp. and discuss the generic assignment of this specimen. Additionally, we summarise the taxonomic status of *Brachypotherium* in East Asia.

Material and methods

The taxonomic framework in the present study follows Lu et al. (2023). The dental terminology of rhinocerotid follows Antoine et al. (2010). KPM-NNV 50 is compared with the species within *Brachypotherium* and Asian Miocene species of the Teleoceratini, Rhinocerotinae, Elasmotheriinae, and Aceratheriinae (Table 1).

Institutional abbreviations

KPM-N, Kanagawa Prefectural Museum of Natural History, Japan; MNHN, Muséum National d'Histoire Naturelle Paris, France; KNM, National Museum of Kenya, Nairobi, Kenya; NHMUK, Natural History Museum, London, UK, NRRU, Northeastern Research Institutes of Petrified Wood and Mineral Resources, Nakhon Ratchasima Rajabhat University, Nakhon Ratchasima, Thailand; SNSB-BSPG, Staatliche Naturwissenschaftliche Sammlungen Bayerns-Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany.

Other abbreviations

M, upper molar; P, upper premolar.

CONTACT Naoto Handa k1552325@kadai.jp Lake Biwa Museum, 1091, Oroshimo-Cho, Kusatsu 525-0001, Japan

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Figure 1. The map showing the Late Miocene rhinocerotid fossil localities in Japan (modified after Handa 2020).

Systematic palaeontology

Family Rhinocerotidae Gray, 1821
Subfamily Aceratheriinae Dollo, 1885
Aceratheriinae gen. et sp. indet.

Synonymy. *Brachypotherium* sp.: Zin-Maung-Maung-Thein et al., 2009, p. 208, fig. 2.

Specimen. KPM-NNV 50 (right upper molar fragments).

Repository. Kanagawa Prefectural Museum of Natural History, Japan.

Description. KPM-NNV 50 is composed of four pieces of right upper molar (M1 or M2) (Figure 2). The occlusal surface is worn down. The paracone rib is weak. The parastyle is short. The unfolded crochet is long and its tip is near the protoloph. The short crista is on the lingual side of the ectoloph. Additional folds are also present on the crochet. The protocone is moderately constricted. The anterior cingulum is near the protocone. There is no protocone lingual groove. There is white-coloured coronal cement in the medisinus and the groove between the anterior cingulum and anterior protocone groove.

Comparisons

Comparison with the species of the genus *Brachypotherium*

The upper molar of the type species of *Brachypotherium*, *B. brachypus*, has a short crochet, weak constricted protocone, wide medisinus, and lacking coronal cement (e.g. Cerdeño 1993). The same characteristics are also seen on the molars of African, South Asian and South East Asian species such as *B. lewisi*, *B. minor*, and *B. perimense* (e.g. Colbert 1935; Geraads & Miller 2013; Handa et al. 2021; Heissig 1972; Hooijer & Patterson 1972; Longuet et al. 2023; Rafeh et al. 2020). In contrast to these characteristics, KPM-NNV 50 has long crochet, moderately constricted protocone, and coronal cement on the medisinus.

KPM-NNV 50 is also different from three Asian species of *Brachypotherium* remains. KPM-NNV 50 is different from the molar of *B. shanwanensis* from China (Wang 1965) in having a weaker constricted protocone and no coronal cement. It also

Table 1. The compared Miocene species in this study.

Taxon	Reference	Direct observation
Brachypotherium brachypus	Cerdeño (1993)	MNHN
Brachypotherium fatehjangense	Pilgrim (1912)	SNSB-BSPG
Brachypotherium heinzelini	Hooijer (1963)	
Brachypotherium lewisi	Hooijer & Patterson (1972)	KNM
Brachypotherium minor	Geraads & Miller (2013)	KNM
Brachypotherium perimense	Colbert (1934, 1935), Heissig (1972), Zin-Maung-Maung-Thein et al. (2010), Rafeh et al. (2020), Handa et al. (2021), Longuet et al. (2023)	SNSB-BSPG, NRRU
Brachypotherium? *pugnator*	Fukuchi & Kawai (2011)	
Brachypotherium shanwangensis	Wang (1965)	
Brachypotherium snowi	Hamilton (1973)	KNM, NHMUK
Aceratherium incisivum	Hünermann (1989)	
Aceratherium porpani	Deng et al. (2013)	NRRU
Acerorhinus yuanmouensis	Lu (2013), Lu et al. (, 2023)	
Chilotherium andersoni	Ringström (1924)	
Chilotherium habereri	Ringström (1924)	
Chilotherium licenti	Sun et al. (2018)	
Chilotherium persiae	Mecqenem (1908)	MNHN
Chilotherium wimani	Ringström (1924)	
Diceros gansuensis	Deng & Qiu (2007)	
Elasmotherium primigenium	Sun et al. (2021)	
Gaindatherium browni	Colbert (1934, 1935), Heissig (1972)	SNSB-BSPG
Iranoherium morgani	Mecqenem (1908), Deng (2005)	MNHN
Lartetotherium cixianensis	Li & Deng (2023)	
Parelasmotherium linxiaense	Deng (2007)	
Parelasmotherium schansiense	Kampouridis et al. (2022)	
Persiatherium rodleri	Pandolfi (2016)	
Prosantorhinus yei	Sun et al. (2023)	
Rhinoceros sp.	Longuet et al. (2023)	
Shansirhinus ringstroemi	Deng (2005)	
Sinotherium lagrelii	Ringström (1924)	

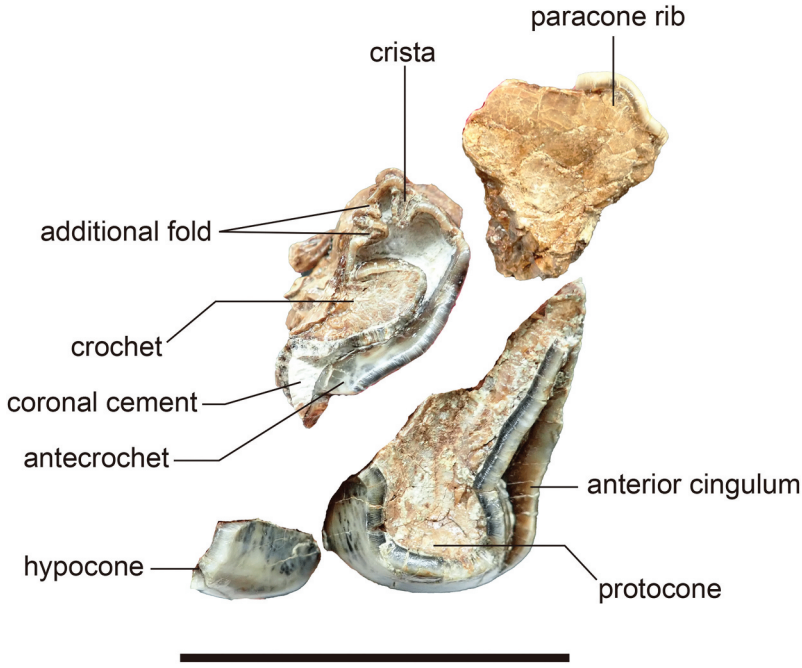

Figure 2. Upper molar (M1 or M2) of Aceratheriinae gen. et sp. indet. (KPM-NNV 50) from the Upper Miocene Oiso formation in Oiso coast, Kanagawa Prefecture.

differs in the molar of *B.*? *pugnator* from the Lower Miocene Japan (Fukuchi & Kawai 2011) in having a weaker constricted protocone, long crochet, and coronal cement. It is distinguished from the molar of the Early Miocene South Asian species, *B. fatehjangense* by Pilgrim (1912), in having a long crochet, crista, and additional folds. Antoine et al. (2013) listed *B. gajense* from the Miocene Siwalik Group in Pakistan, but there are no descriptions or figures. Therefore, we cannot compare with KPM-NNV 50 and this species.

Comparison with other Late Miocene species

KPM-NNV 50 is different from the molar of Late Miocene Asian species of the tribe Teleoceratini, *Prosantorhinus yei* described by Sun et al. (2023), in having much developed paracone rib, crista, additional folds, and the weaker constricted protocone.

KPM-NNV 50 is distinguished from the upper molar of the Miocene Asian taxa of the Rhinocerotinae (*Gaindatherium*, *Lartetotherium*, *Dihoplus*, *Rhinoceros* and *Diceros*) in having the constricted protocone, antecrochet, long crochet, crista and additional folds (Colbert 1934; Deng & Qiu 2007; Li & Deng 2023; Longuet et al. 2023; Shi et al. 2023).

The coronal cement is also seen in the molar of the subfamily Elasmotheriinae (= Elasmotheriina *sensu* Antoine 2002, 2003), but KPM-NNV 50 is distinguished from this group, especially the Late Miocene species (e.g. Deng 2005, 2007; Kampouridis et al. 2022; Mecqenem 1908; Ringström 1924; Sun et al. 2021), in having long unfolded crochet, simple enamel folding, weak constricted protocone and the developed paracone rib.

The weak constricted protocone, coronal cement, developed paracone rib and long crochet are seen in the upper molars of several Asian Late Miocene species of the subfamily Aceratheriinae, such as *Aceratherium incisivum*, *Shansirhinus ringstroemi* and *Acerorhinus yuanmouensis* (e.g. Deng 2005, Lu 2013; Lu et al. 2015; Hünermann 1989). Additionally, the crista often develops on the molars of *Acerorhinus*.

KPM-NNV 50 is different from the molars of the genus *Chilotherium*, in having developed paracone rib and lacking the mesostyle and mediofossette (Mecqenem 1908; Ringström 1924; Sun et al. 2018). It also differs in the molar of *Aceratherium porpani* from the Upper Miocene fauna in Thailand (Deng et al. 2013) in having a long crochet, narrow medisinus, and coronal cement. It is also distinguished from the molar of *Persiatherium* from the Upper Miocene in Iran (Pandolfi 2016) in having a crista, additional folds, developed paracone rib, and lacking coronal cement.

In conclusion, KPM-NNV 50 is similar to the dental morphology of several species of the Aceratheriinae, such as *Acera. incisivum*, *Acero. yuanmouensis* and *S. ringstroemi*, although its detailed taxonomic status is unclear due to the poor preservation. Thus, we identified that KPM-NNV 50 is Aceratheriinae gen. et sp. indet. in this study.

Discussion

The fossil records of Late Miocene Japanese rhinoceros

In Japan, only two specimens have been reported from the Late Miocene localities beside KPM-NNV 50 (Figure 1). Yoshida et al. (1989) reported skull fragments with cheek teeth and a mandible with incisors and cheek teeth from the Upper Miocene in Kawamoto, Saitama Prefecture (the Yagii Formation, 9.8–8.4 Ma; Kobayashi et al. 2011), and temporally identified them as 'Teleoceratinae' gen. et sp. indet. based on the Jean's (1958) classification that includes *Brachypotherium*, *Chilotherium* and *Teleoceras*. Asano (1996) also described an isolated lower molar from the Aoso Formation in Taiwa, Miyagi Prefecture (10–8.9 Ma; Suzuki et al. 2019) and reported it as 'Teleoceratinae' gen. et sp. indet. based on the comparison with the specimen described by Yoshida et al. (1989).

In sum, the Japanese fossil record of Late Miocene rhinoceroses including the present study ranges from ca. 10 Ma to 5.5 Ma, although detail taxonomy of those specimens is unclear (Table 2). In Japan, many rhinocerotid fossils have been found from the Early

Table 2. List of Japanese late Miocene rhinocerotid records.

Taxon	Locality	Age	Reference
'Teleoceratinae' gen. et sp. indet.	Taiwa	10–8.9 Ma	Asano (1996), Suzuki et al. (2019)
'Teleoceratinae' gen. et sp. indet.	Kawamoto	9.8–8.4 Ma	Yoshida et al. (1989), Kobayashi et al. (2011)
Aceratheriinae gen. et sp. indet.	Oiso	CN9 (8.29–5.59 Ma); N17 (8.58–5.57 Ma)	Zin-Maung-Maung-Thien et al. (2009), Ishihama et al. (2012); present study

Table 3. Proposed new taxonomic status for East Asian *Brachypotgherium*.

Taxa	Locality	Currently proposed taxonomic status	Reference
Brachypotherium shanwangensis	China	*Plesiaceratherium gracile*, *Diaceratherium shanwangense* or *Brachydiceratherium shanwangense*	Lu et al. (2016, 2021), Sizov et al. (2024)
Brachypotherium pugnator	China	*Diaceratherium shanwangense* or *Brachydiceratherium shanwangense*	Lu et al. (2021), Sizov et al. (2024)
Brachypotherium? *pugnator*	Japan	*Brachydiceratherium shanwangense*	Sizov et al. (2024)
Brachypotherium sp.	Japan	Aceratheriinae gen. et sp. indet.	present study

Miocene (ca. 20–16 Ma; Handa 2020). In contrast, there is no description of the Middle Miocene rhinocerotid fossil record officially (Tomida et al. 2013). These records and the present study indicate that there is a large gap of the rhinocerotid fossil records between the Early and Late Miocene (16 Ma to 10 Ma).

An overview of the taxonomic status of *Brachypotherium* in East Asia

Previously, *Brachypotherium shanwangensis* and *Brachypotherium pugnator* have been known from the Miocene in East Asia. *Brachypotherium shanwangensis* was described from the Lower Miocene Shangwang Basin in China (Wang 1965; Yan et al. 1983; see also Fukuchi & Kawai 2011), but the type specimen of this species (Wang 1965) has the molar with much strongly constricted protocone and reduced lingual cingulum than the upper molar of other species of *Brachypotherium*. Lu et al. (2016) recognised this species as a synonym of *Plesiaceratherium gracile*. Later Lu et al. (2021) assigned this specimen to *Diaceratherium shanwangense*. In contrast, Sizov et al. (2024) noted that *D. shanwangense* from Shanwan Basin is the genus *Brachydiceratherium*.

A Japanese rhinocerotid, *Chilotherium pugnator* had been described from the Early Miocene in Kani City (Kamei & Okazaki 1974; Okazaki 1977; Okumura et al. 1977; Takai 1949). Later, Fukuchi & Kawai (2011) re-identified it as *Brachypotherium*? *pugnator* based on a maxillary fragment with upper cheek teeth, P4 and M1 of *C. pugnator*. Fukuchi & Kawai (2011) noted that the characteristics of *B.*? *pugnator* such as strongly constricted protocone on the molar and the bridge between the protoloph and metaloph on the premolar, are similar to that of *Brachypotherium fatehjangense*. The later species was reported from the Miocene in South and Southeast Asia (e.g. Antoine et al. 2013; Chaimanee et al. 2006; Heissig 1972; Khan et al. 2010; Longuet et al. 2023; Pilgrim 1912; Rafeh et al. 2020). However, *B.*? *pugnator* has the characteristics that are different from *Brachypotherium*. There is a bridge between the protocone and hypocone on P4 that is not seen in the premolar of *Brachypotherium* (e.g. Cerdeño 1993). On M1, this molar has a sharp hypocone groove and a narrow medisinus, which are not seen in the molars of the other species of *Brachypotherium*. Additionally, *B. fatehjangense* is revised as *Aprotodon fatehjangense* (e.g. Qiu & Xie, 1997; Deng 2006; Sun et al. 2023). The type specimen of *A. fatehjagense* (= *B. fatehjagense*) by Pilgrim (1912) has the semimolariform premolar and the molar that has a constricted protocone, hypocone groove, but lacks the lingual cingulum, distinct with the upper cheek teeth of Eurasian and African *Brachypotherium*. Therefore, the upper cheek teeth of *B.*? *pugnator* have no morphology of typical *Brachypotherium* from Europe, Africa and South Asia. Sizov et al. (2024) also noted that the Japanese species (*B.*? *pugnatpor*) is close to *Brachydiceratherium shanwangense*.

Chow & Wang (1964) also reported a few cheek teeth of *B. pugnator* from the Miocene Sihong in Jiangsu, China. Indeed, these specimens are similar to *B.*? *pugnator* described by Fukuchi & Kawai (2011) in having the upper cheek teeth with strongly constricted protocone and the molars with a narrow medisinus. However, these specimens were re-identified as *Plesiaceratherium shanwangensis* Wang (1965). Later, Lu et al. (2021) proposed that *P. shanwangensis* is a synonym of *Diaceratherium shanwangense*. Sizov et al. (2024) also proposed *D. shanwangense* as a species of *Brachydiceratherium*.

Besides the above fossil records, Zhang et al. (2013) reported cf. *Brachypotherium* sp., which is a member of the fauna from the Late Miocene Bahe Formation in China, but there is no description and figures.

In sum, the taxonomic status of the Asian *Brachypotherium* have been argued and have been considered as species of *Diaceratherium* or *Brachydiceratherium* (Table 3). Thus, there are no typical *Brachypotherium* in the Miocene localities in East Asia. We propose that the genus *Brachypotherium* has been found from Europe (*B. brachypus*), Africa (*B. snowi*, *B. heinzelini*, *B. lewisi* and *B. minor*) and South-Southeast Asia (*B. perimense* and *B. gajense*) so far.

Heissig (1972) summarised the diagnosis of the genus *Brachypotherium* including the upper cheek teeth, namely, the molars are brachydont with moderately developed secondary folding and strong cingula; usually secondary reduction of the antecrochet and constrictions. We also propose additional characters for upper molar of this genus: short crochet; weak constricted protocone; wide medisinus; lacking coronal cement.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

ORCID

Naoto Handa http://orcid.org/0000-0003-2944-8725
Hajime Taru http://orcid.org/0009-0002-5036-6548

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