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Research paper

Brachypotherium (Perissodactyla, Rhinocerotidae) from the late Miocene of Samburu Hills, Kenya☆

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ABSTRACT

Several isolated cheek teeth and mandibular specimens of Rhinocerotidae (Mammalia, Perissodactyla) from the upper Miocene Namurungule Formation in Samburu Hills, Kenya, are redescribed. Previously, these specimens had been identified as *Chilotheridium pattersoni*, *Chilotheridium* sp., *Paradiceros mukirii*, and *Paradiceros* sp. They are reidentified here as documenting the genus *Brachypotherium* based on their bucco-lingually broad molariform upper premolars with short crochet and flattened buccal walls on both upper and lower molars, the latter having a shallow external groove. Comparisons with other *Brachypotherium* species suggest that the present specimens belong to *Brachypotherium* sp. cf. *B. minor*. The presence of *Brachypotherium* in the Samburu Hills, at *ca.* 9.5 Ma, is concordant with the paleoenvironment (presence of lacustrine and river environments) known for this locality during the early late Miocene.

1. Introduction

The Teleoceratini (*sensu* Heissig, 1973, 1989; = Teleoceratina in Antoine, 2002; Antoine et al., 2010) is one of the tribes of the Rhinocerotidae (Perissodactyla, Mammalia); it was widely distributed in Eurasia, Africa, and North America during Neogene times (Heissig, 1989). In sub-Saharan Africa several species of the teleoceratine genus *Brachypotherium* were recorded during the Miocene. In particular, there are fossil records of *B. snowi* and *B. minor* between *ca.* 20 to 15 Ma, and *B. lewisi* has been found after 7 Ma (Geraads, 2010). However, the fossil record of *Brachypotherium* for the early late Miocene in sub-Saharan East Africa remains scarce (Geraads, 2010).

The Kenya-Japan joint expedition has carried out fieldworks in the early late Miocene (*ca.* 10 Ma) of the Samburu Hills from 1982 to 1999 (Ishida, 1984, 1987). Abundant vertebrate fossils have been discovered from this locality. Of these, many specimens of Rhinocerotidae were reported by Nakaya et al. (1984, 1987) and Tsujikawa (2005), and identified as *Chilotheridum pattersoni*, *Chilotheridum* sp., *Brachypotherium* sp., *Kenyatherium bishopi*, *Paradiceros mukirii*, and *Paradiceros* sp. Geraads (2010) reviewed the rhinocerotid fossil record from Africa and pointed out that it is in need of taxonomic revision. The taxonomy of several specimens from the Samburu Hills was updated, leaving three valid species: *Chilotheridium pattersoni*, *Samburuceros ishidai*, and *Diceros* sp. (Fukuchi et al., 2008; Handa et al., 2015, 2017). However, the taxonomic revision of other specimens has not been undertaken since their initial descriptions. Here we redescribe several isolated teeth and mandibular fragments of rhinocerotids from the Samburu Hills, ascribing them to the genus *Brachypotherium*.

2. Geological setting

The Samburu Hills are located 50 km south of Lake Turkana (Fig. 1). The Miocene succession (including the Nachola, Aka Aiteputh, Namurungule, and Kongia formations) and the Pliocene Tirr Tirr Formation are distributed in this area (Saneyoshi et al., 2006; Sakai et al., 2010). The Namurungule Fm. conformably overlies the Aka Aitheputh Fm. and unconformably underlies the Kongia Fm. The Namurungule Fm. is about 200 m thick and is divided into an upper and a lower member which consist of alluvial fans and fluvio-lacustrine deposits, and fluvio-lacustrine delta and fluvial deposits, respectively (Saneyoshi et al., 2006; Sakai et al., 2010). There is a lahar deposit between the lower and upper members. A large hominoid, *Samburupithecus kiptalami* was found

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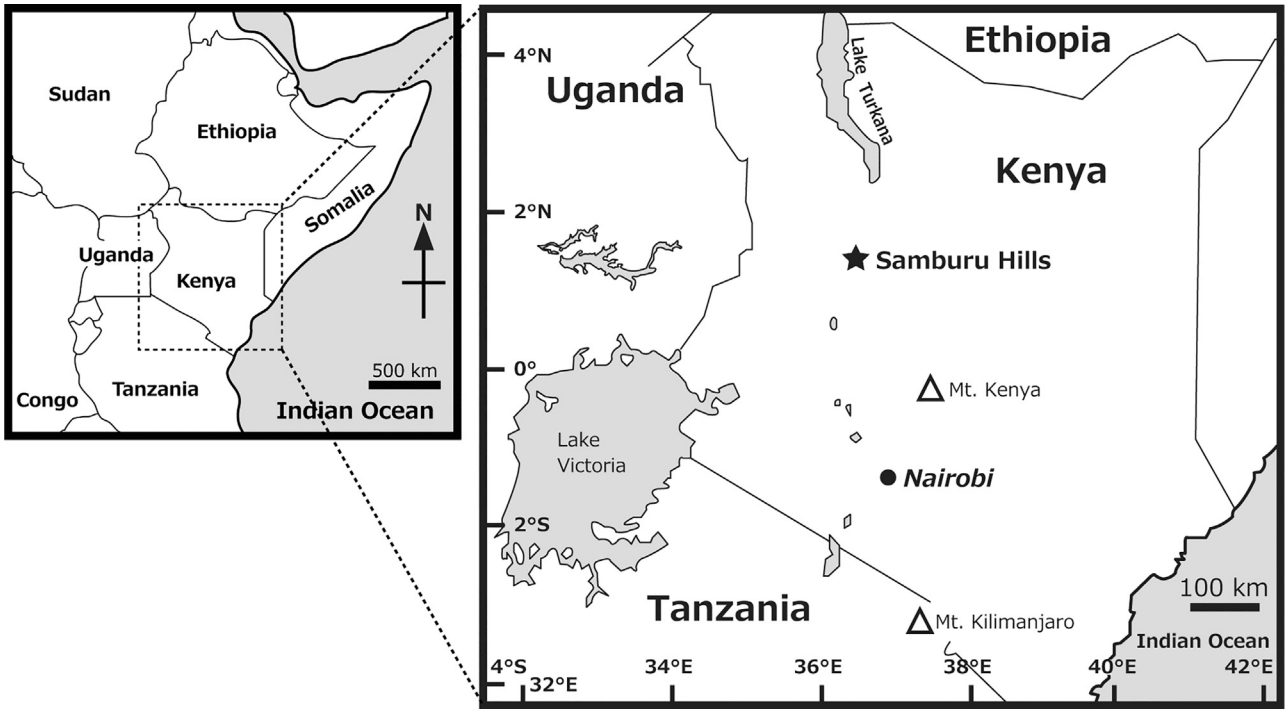

Fig. 1. Map locating the Miocene localities of Samburu Hills, Kenya (modified after Handa et al., 2017).

from the lower member (Ishida and Pickford, 1997). The rhinocerotid specimens studied in this paper were also discovered from the lower member. The K-Ar age of the hominoid fossil-bearing horizon of the lower member is estimated to 9.57 ± 0.22 Ma and 9.47 ± 0.22 Ma (Sawada et al., 1998, 2006). Regarding the paleomagnetic stratigraphy, the upper and lower members are correlated with Chron C4Ar.2n (9.64 to 9.58 Ma) and Chrons C4Ar.2r to C4Ar.1n (9.58 to 9.31 Ma), respectively (Sawada et al., 1998, 2006).

3. Material and methods

The specimens described in the present study are stored in the paleontology section of the Earth Sciences Division, the National Museums of Kenya in Nairobi, Kenya. Measurements were taken using a digital caliper. The taxonomy used in the present study follows Heissig (1973, 1989), and the anatomical terminology and measurements follow Guérin (1980).

The studied specimens were compared with previously-known species of *Brachypotherium* from Eurasia and Africa. Comparisons were carried out with the collections held by the following institutions: National Museums of Kenya, Nairobi, Kenya and Natural History Museum London, UK. Several rhinocerotid materials for comparison were based on the references listed in Table 1.

Abbreviations: **P**, upper premolar; **p**, lower premolar; **m**, lower molar; **MNHN**, Muséum Nationale d'Histoire Naturelle, Paris, France; **NHML**, Natural History Museum London, UK; **KNM**, National Museums of Kenya, Nairobi, Kenya; **NMNS**, National Museum of Nature Science, Tsukuba, Japan; **SH**, Samburu Hills, Kenya; **WS**, Buluk (Western Stephanie), Kenya.

4. Systematic paleontology

Class Mammalia Linnaeus, 1758
Order Perissodactyla Owen, 1848
Suborder Ceratomorpha Wood, 1937
Family Rhinocerotidae Owen, 1845
Subfamily Aceratheriinae Dollo, 1885
Tribe Teleoceratini Hay, 1902
Genus ***Brachypotherium*** Roger, 1904

Included species: *B. brachypus*, *B. goldfussi*, *B. perimense*, *B. snowi*, *B. lewisi*, *B. minor*, and *B. pugnator*.

Diagnosis (cheek teeth only; Heissig, 1972; Geraads, 2010): Brachydont cheek teeth and short but broad molariform premolars with short crochet. Upper and lower molars tend to have flattened buccal walls and the latter have a shallow external groove.

Brachypotherium sp. cf. *B. minor* Geraads et Miller, 2013
Figs. 2–4
1984. *Brachypotherium* sp. - Nakaya et al., p. 127, pl. 7, figs. 2–5.
1987. *Chilotheridium* sp. - Nakaya et al., p. 96.
1987. *Paradiceros* sp. - Nakaya et al., p. 121, pl. 6, figs. 2–3.
2005. *Paradiceros mukirii* - Tsujikawa, p. 19, p. 20, fig. 5A.

Table 1
Comparative material of *Brachypotherium* from Afro-Eurasia.

Species	Age	Type locality	Direct observation	Reference
Brachypotherium snowi	Early to middle Miocene	Moghara, Egypt	KNM, NHML	Hamilton (1973)
Brachypotherium lewisi	Late Miocene	Lothagam, Kenya	KNM	Hooijer and Patterson (1972), Harris and Leakey (2003)
Brachypotherium minor	Middle Miocene	Buluk, Kenya	KNM	Geraads and Miller (2013)
Brachypotherium brachypus	Early to middle Miocene	Simorre, France	MNHN	Ginsburg and Bulot (1984), Cerdeño (1993), Heissig (2012)
Brachypotherium perimense	Early to late Miocene	Perim Island, India		Colbert (1935), Heissig (1972)
Brachypotherium pugnator	Early Miocene	Kani, Japan	NMNS (cast)	Fukuchi and Kawai (2011)

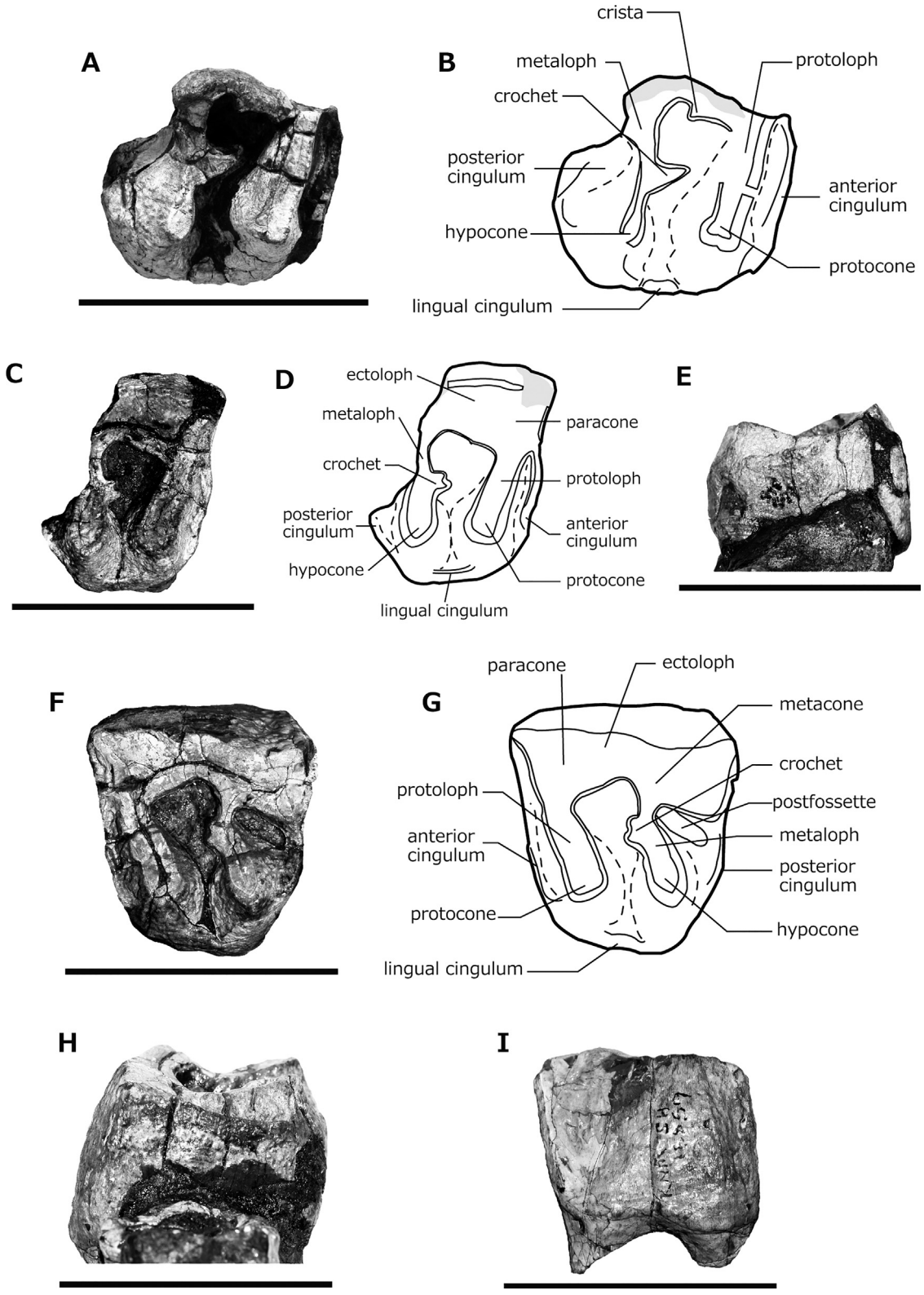

Fig. 2. Upper cheek teeth of *Brachypotherium* sp. cf. *B. minor* from Samburu Hills. **A, B.** KNM-SH 37910, right P3 or P4. **C–E.** KNM-SH 15859B, right P3 or P4. **F–I.** KNM-SH 15859A, left P3 or P4. A, C, F: buccal view; E, H: mesial view; I: buccal view; B, D, G: schematic drawing; shaded surface: damaged portion. Scale bars: 5 cm.

2005. *Chilotheridium pattersoni* - Tsujikawa, p. 22, fig. 6C–E.

Material: right P3 or P4 (KNM-SH 15859B; KNM-SH 37910), left P3 or P4 (KNM-SH 15859A), left mandibular fragment with m1? (KNM-SH 15754), left mandibular fragment with p4 to m2 (KNM-SH 38405), isolated left m1 or m2 (KNM-SH 12143), isolated right m3 (KNM-SH 40120).

Measurements: See Tables 2 and 3.

Description: Three upper premolars are described in this study. The upper premolars KNM-SH 15859A and KNM-SH 15859B pertain to the same individual because these were found together. KNM-SH 15859A and KNM-SH 15859B are left and right P3 or P4, respectively. The parastyle and distal part of KNM-SH 25859B are

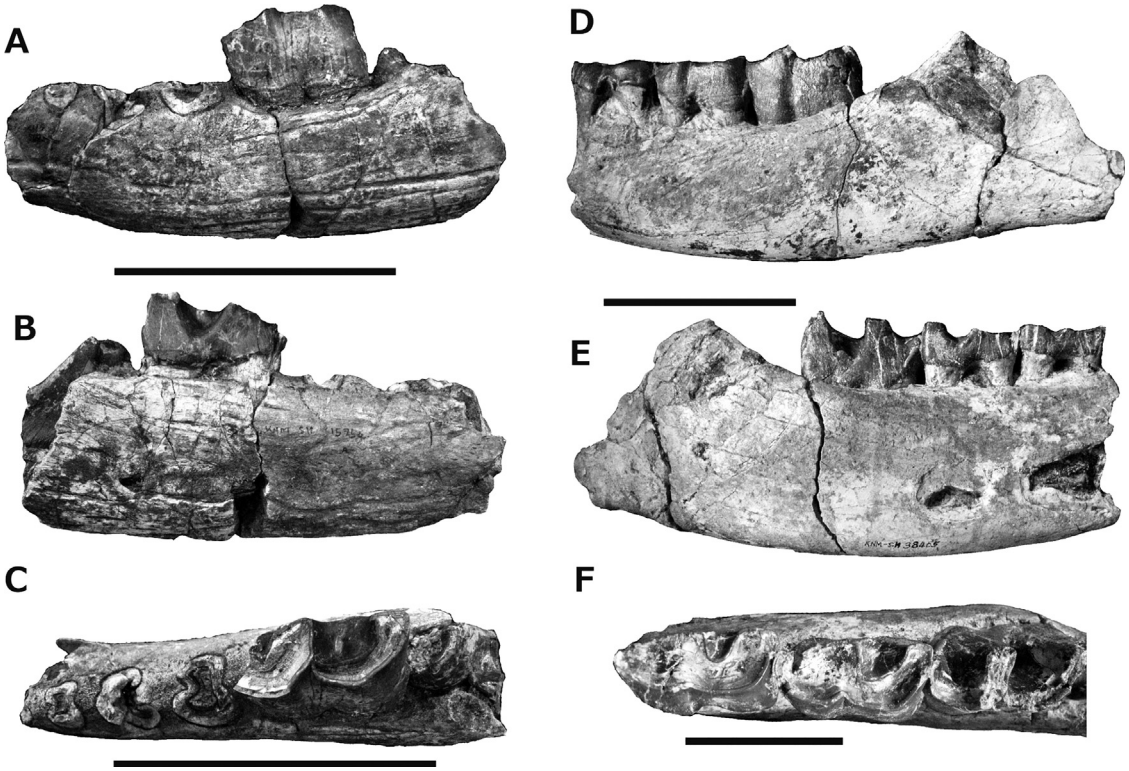

Fig. 3. Mandibular fragments of *Brachypotherium* sp. cf. *B. minor* from the late Miocene of Samburu Hills. **A–C.** KNM-SH 15754, left mandibular fragment with ?m1. **D–F.** KNM-SH 38405, left mandibular fragment with p4 to m2. A, D: buccal view; B, E: lingual view; C, F: occlusal view. Scale bars: 10 cm.

broken. KNM-SH 37910 is a well-worn right P3 or P4. The ectoloph and distal part of KNM-SH 37910 are missing.

The premolars are molariform. The morphology of KNM-SH 15859A and KNM-SH 15859B is similar. The ectoloph is almost flat. The protoloph and metaloph are directed disto-lingually. The protocone and hypocone are not constricted. The lingual walls of the protocone and hypocone are rounded. The short crochet is projected and is slightly bifid. There is no antecrochet. The metastyle is short. There is no buccal cingulum. The short lingual cingulum is present on the entrance of the medisinus. The anterior cingulum extends from the parastyle to the lingual side of the protocone. The posterior cingulum is low. The paracone fold of KNM-SH 25859A is slightly developed at this wear stage, whereas that of KNM-SH 25859B is apparently lacking. The posterior valley of KNM-SH 25859A is narrow in mesio-distal view.

KNM-SH 37910 is similar in shape to the former two specimens, with disto-lingually oriented proto- and metalophs, rounded lingual wall of both cusps, not constricted hypocone, mesially projected crochet, low and continued anterior cingulum on the mesial margin of the protoloph, reduced lingual cingulum, and concave occlusal surface. In contrast, there are a few differences in those specimens such as a slightly constricted protocone, simple crochet, and a trace of a crista.

Two mandibular fragments are described here: KNM-SH 15754 and KNM-SH 38405. KNM-SH 15754 is composed of right and left mandibular fragments. Right mandibular fragment has no tooth crown. Only m1? erupted on the left mandibular fragment. KNM-SH 38405 is a left mandibular fragment with p4 to m2. The dorso-ventral height of these specimens is low. There is no lingual groove on the medial surface of the specimens. The ventral margin of both mandibular bodies is gently curved ventrally. The presence of the *foramen mentale* and *foramen mandibulare* is uncertain because the anterior and ramus parts are lacking.

Generally, the lower cheek teeth described here have a similar morphology. The external groove is shallow. The buccal wall of the teeth is flattened. There is no coronal cement. The hypolophid extends disto-lingually. There is a weak mesial cingulum. There is no buccal cingulum. The posterior valley of the molars is U-shaped in occlusal and lingual views.

The p4 (KNM-SH 38405) is heavily worn. The anterior valley is uncertain because the tooth is worn down. Lower molar morphology is consistent and monotonous. The m1? of KNM-SH 15754 is moderately worn. The metalophid extends disto-lingually. The anterior valley is V-shaped in lingual view. The m1 of KNM-SH 38405 is relatively worn. There is a small paralophid. The anterior valley is narrow in the occlusal view. The m2 (KNM-SH 38405) is also relatively worn. The paralophid is oriented lingually. The metaconid is not constricted. A small tubercle shaped lingual cingulum is on the lingual side of the posterior valley. The anterior and posterior valleys are wide and deep in the occlusal view.

KNM-SH 12143 is an isolated left m1 or m2. The tooth is well worn. The mesial part is lacking. The lingual cingulum is restricted to the mesial side. The distal surface of the hypolophid is concave in occlusal view. The m3 (KNM-SH 40120) is also well worn. The mesio-lingual part is broken. The distal surface of the hypolophid is concave as in KNM-SH 12143. A tubercle appears on the lingual side of the posterior valley.

Remarks: Previously, the upper premolars KNM-SH 15859A and KNM-SH 15859B have been assigned to *Paradiceros* sp. (Nakaya et al., 1987) based on characters such as: brachydont teeth, curved ectoloph, and development of the crochet and crista. Tsujikawa (2005) also identified an upper premolar (KNM-SH 37910) as belonging to *Paradiceros mukirii* on the basis of the presence of crochet and crista, and weakly constricted protocone. The premolars of *P. mukirii* (KNM-FT 2870; Hooijer, 1968) from the middle Miocene in Fort Ternan in Kenya, however, have neither crochet nor crista. Therefore, those upper premolars are distinguished from *Paradiceros*.

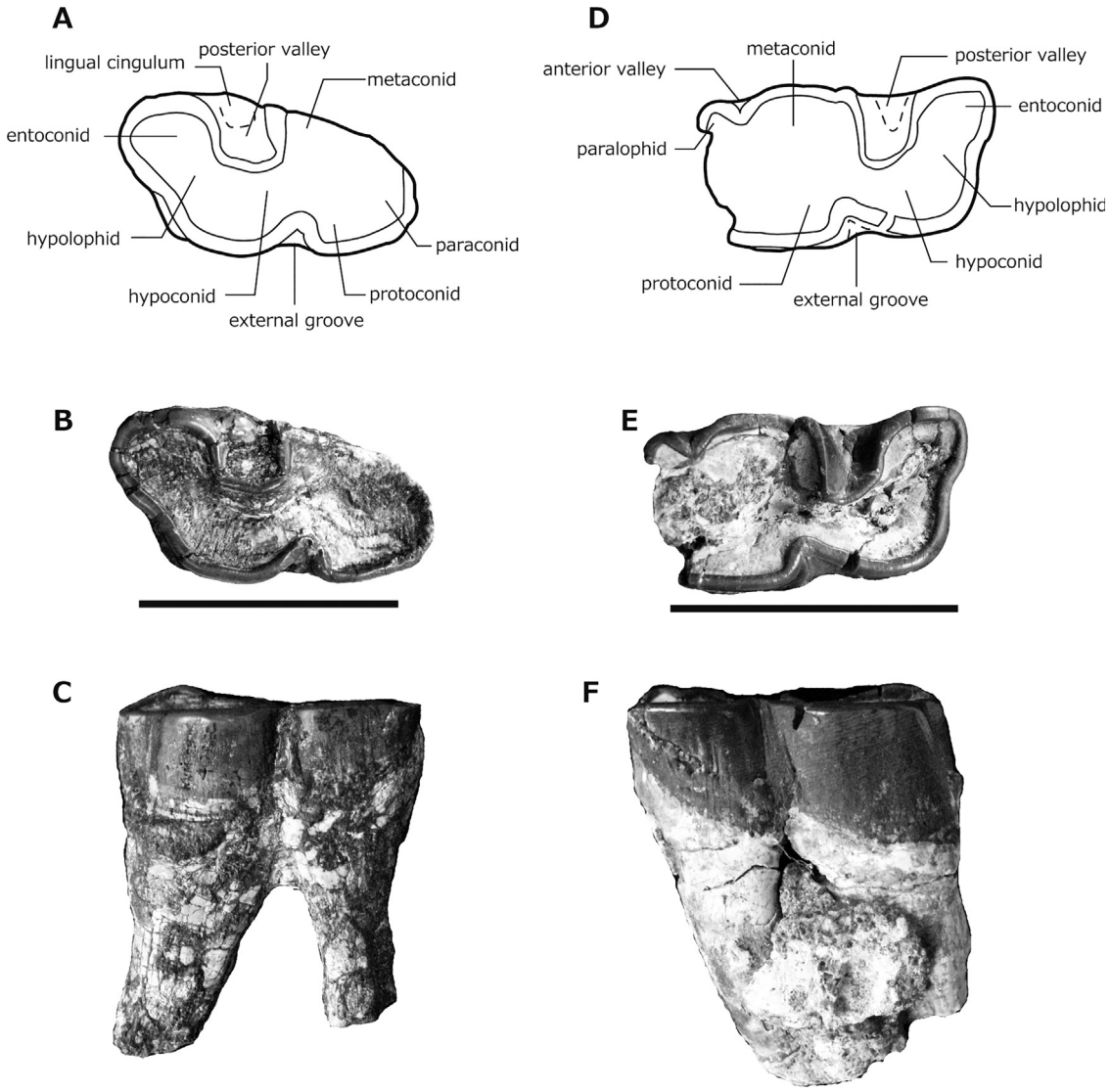

Fig. 4. Lower cheek teeth of *Brachypotherium* sp. cf. *B. minor* from the late Miocene of Samburu Hills. **A–C.** KNM-SH 40120, right m3. **D–F.** KNM-SH 12143, left m1 or m2. B, E: occlusal view; C, F: buccal view; A, D: schematic drawing. Scale bars: 5 cm.

KNM-SH 15754 was described as a mandibular fragment of *Chilotheridium* sp. by Nakaya et al. (1987) without any diagnostic features. KNM-SH 38405 was formerly reported as a mandibular fragment of *Chilotheridium pattersoni* (Tsujikawa, 2005), although nothing was characteristic of this species in the detailed description of this specimen. Holotype of *C. pattersoni* (including several lower cheek teeth) was reported from Loperot in Kenya (Hooijer, 1971). Mandibular specimens with lower cheek teeth of *C. pattersoni* have also been found from the Namurungule Fm. (Handa et al., 2015). The present remains differ from those specimens in that they have a shallow external groove and smaller dental dimensions. KNM-SH 40120 was identified as a mandible of *P. mukirii* (Tsujikawa, 2005). However, the detailed reasons for such specific identification was not provided. Compared with lower cheek teeth of *P. mukirii* (KNM-FT 2869 and KNM-FT 2874; Hooijer, 1968), the present specimens have a shallower external

Table 2
Measurements (in mm) of the upper premolar (P3 and P4) of *Brachypotherium* sp. cf. *B. minor*.

Specimen number	L	W	H	Remarks
KNM-SH 15859-A	38.5	45.8	35.3	Nakaya et al. (1987)
KNM-SH 15859-B	>39.0	47.9	37.3	Nakaya et al. (1987)
KNM-SH 37910	–	42.3	>29.6	Tsujikawa (2005)

Abbreviations: L: length; W: width; H: height.

Table 3
Measurements (in mm) of the lower cheek teeth of *Brachypotherium* sp. cf. *B. minor*.

	p4			m1			m2			m3			Remarks
Specimen number	L	W	H	L	W	H	L	W	H	L	W	H	
KNM-SH 15754				42.6	25.6	28.2							Nakaya et al. (1987)
KNM-SH 38405	41	23.2	11.2	42.6	28	27.5	49.4	32.6	-				Tsujikawa (2005)
KNM-SH 12143							46.3	28.4	20.5				Nakaya et al. (1984)
KNM-SH 40120										55.9	30.5	15.6	Tsujikawa (2005)

Abbreviations: L: length; W: width; H: height.

groove and flattened buccal wall of the teeth, suggesting that those remains are distinguished from *P. mukirii*.

In the present work, we identified on the studied specimens the following characters diagnostic of *Brachypotherium*: upper premolars with molariform, flat ectoloph and short crochet, and lower cheek teeth with a shallow external groove and oblique lophids (Heissig, 1972). In addition, the present specimens are similar to the type species of *Brachypotherium*, *B. brachypus*, in having the following features (Guérin, 1980; Cerdeño, 1993; Antoine, 2002): brachydont teeth, no coronal cement, upper premolars with presence of a crochet, absence of crista and antecrochet, undeveloped metacone constriction, presence of a lingual cingulum, hypocone posterior to the metacone, and lower cheek teeth with rounded anterior valley, no constriction of metaconid and entoconid, and oblique hypolophid. Therefore, the present specimens can be confidently assigned to *Brachypotherium*.

In Africa, three species of *Brachypotherium* have been recognized so far; *B. snowi* (Fourtau, 1920), *B. lewisi* Hooijer et Patterson, 1972, and *B. minor* Geraads et Miller, 2013. *Brachypotherium snowi* was reported from the early Miocene locality of Moghara, Egypt (Fourtau, 1920). Hamilton (1973) also reported *B. snowi* from the early Miocene locality of Gebel Zelten, Libya. According to Geraads (2010), *Brachypotherium heinzelini*, which has been discovered in early to middle Miocene localities in Africa, must be restricted to the type specimen which was reported from the early Miocene locality of the Western Rift in Congo (Hooijer, 1963), whereas other assigned specimens can be included in *B. snowi*. Geraads (2010) also reassigned *Aceratherium campbelli* from the early Miocene locality of Gebel Zelten (Hamilton, 1973) to *B. snowi* based on the characters of the skull. Compared with numerous remains of *B. snowi* from Gebel Zelten, the present mandibular specimens are similar to the lower cheek teeth of *B. snowi* (NHML-M 26260; Hamilton, 1973) in having oblique lophids and a small tubercle on the lingual side of the posterior valley. The present upper premolars are distinguished from those of *B. snowi* (NHML-M 29252; Hamilton, 1973) in having more developed crochet and smaller dimensions (Figs. 5, 6). Heissig (1971) described a mandibular fragment of *B. heinzelini* (= *B. snowi*) from the early Miocene locality of Langental in Namibia. The present specimens are similar to the Langental specimen in having a shallow external groove and no buccal cingulum. In contrast, the length of the present lower cheek teeth is smaller than that in Langental (p4: 48 mm; m1: 50 mm; m2: 55 mm).

Brachypotherium lewisi was found from late Miocene to early Pliocene localities in Kenya. The holotype of this species comes from Lothagam in Kenya (Hooijer and Patterson, 1972; Harris and Leakey, 2003). Hooijer (1973) reported this species from Ngorora in Kenya, but without detailed description or figures. Therefore, this record was assigned to *Brachypotherium* sp. and excluded from this comparison. The present upper premolars are distinguished from *B. lewisi* of Lothagam in having slightly disto-lingually oriented lophs in the upper cheek teeth (Hooijer and Patterson, 1972; Harris and Leakey, 2003), and smaller upper and lower cheek tooth dimensions (Figs. 5, 6).

Brachypotherium minor was reported from the middle Miocene of Buluk in Kenya (Geraads and Miller, 2013). The dental morphology of the present specimens is almost similar to that of *B. minor* from Buluk, especially the isolated upper premolars of this species (KNM-WS 12851 and KNM-WS 30722) which show a rounded lingual wall of the protocone and hypocone, a slightly or not constricted protocone, and a reduced lingual cingulum. However, the present upper premolars have slightly bifid crochet, whereas the upper premolars of *B. minor* have simple crochet (Geraads and Miller, 2013: p. 363, fig. 2(D)). The dimensions of the present specimens are also close to those of *B. minor* (Figs. 5, 6).

Several species of *Brachypotherium* were also discovered from Eurasia, such as *B. brachypus*, *B. perimense*, and *B. pugnator* (Kaup, 1834; Heissig, 1972, 2012; Cerdeño, 1993; Fukuchi and Kawai, 2011). *Brachypotherium goldfussi* has been reported from the late Miocene in Europe (e.g., Heissig, 1999). The specimens of this species, however, remain poorly known (Guérin, 1980). In addition, Heissig (2012) implies the possibility of synonymy of *B. goldfussi* with *B. brachypus*. Thus, this species is excluded from the comparison in this study. The generic assignment of "*Brachypotherium*" *fatehjangense* and "*Brachypotherium*" *shanwangense*, both found from early and middle Miocene localities in Asia,

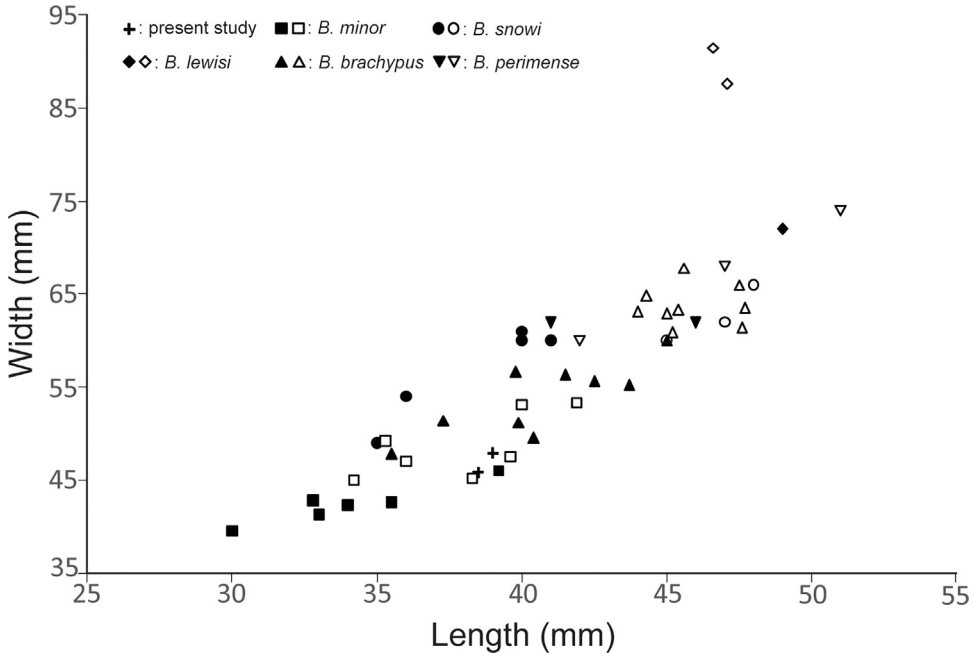

Fig. 5. Scatter diagram of the upper cheek teeth measurements of *Brachypotherium* sp. cf. *B. minor* from the late Miocene of Samburu Hills and comparative material. Black symbol: P3; White symbol: P4. Data from the following references: *B. snowi*: Hooijer (1966), Hamilton (1973), N. Handa, pers. obs.; *B. lewisi*: Hooijer and Patterson (1972), Harris and Leakey (2003), N. Handa, pers. obs.; *B. minor*: Geraads and Miller, 2013; *B. brachypus*: Cerdeño (1993); *B. perimense*: Colbert (1935), Heissig (1972).

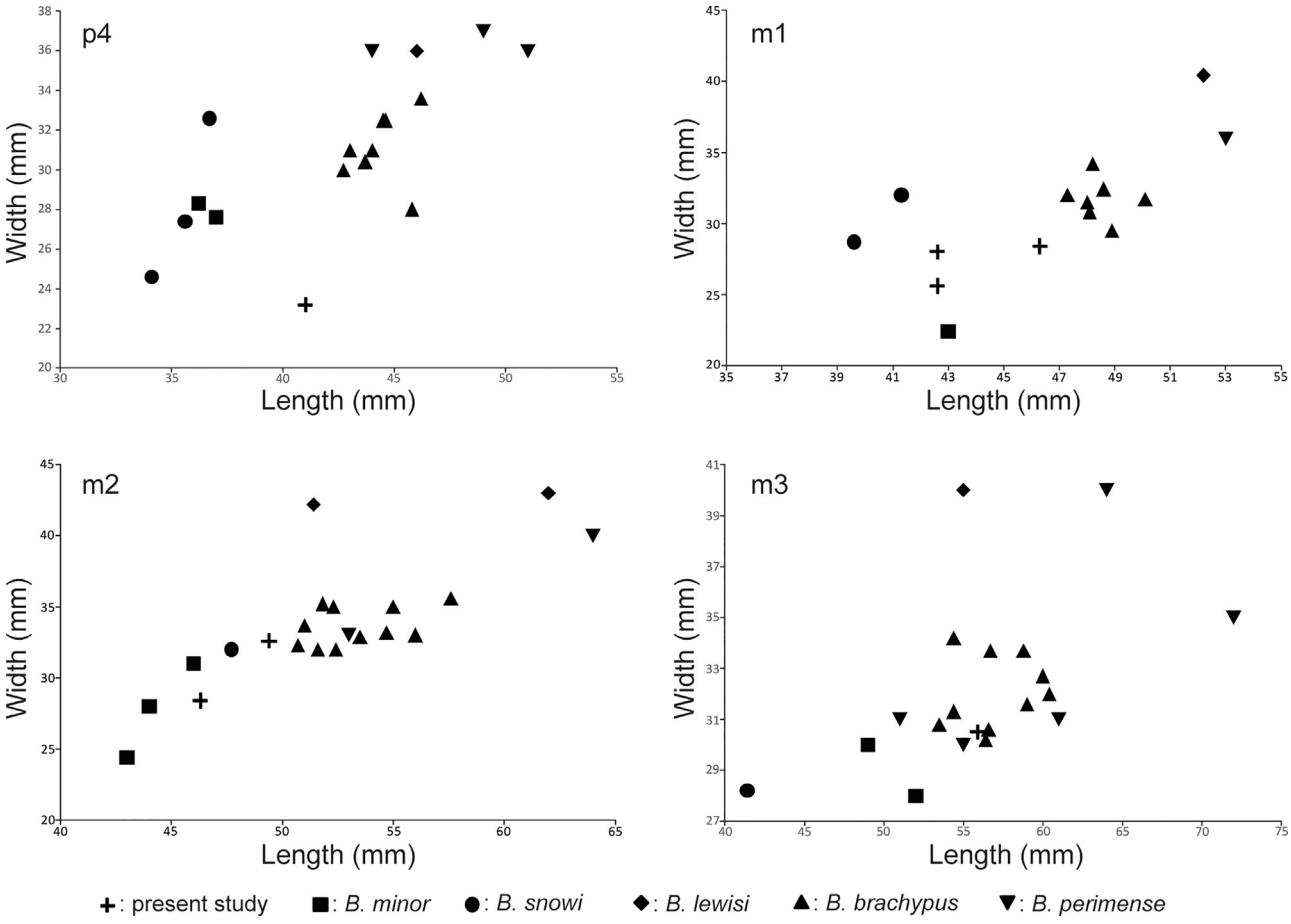

Fig. 6. Scatter diagrams of the lower cheek teeth (p4-m3) measurements of *Brachypotherium* sp. cf. *B. minor* from Samburu Hills and comparative material. Data from the following references: *B. snowi*: Hamilton (1973), N. Handa, pers. obs.; *B. lewisi*: Hooijer and Patterson (1972), Harris and Leakey (2003), N. Handa, pers. obs.; *B. minor*: Geraads and Miller, 2013; *B. brachypus*: Cerdeño (1993); *B. perimense*: Colbert (1935), Heissig (1972).

is debated. "*Brachypotherium*" *fatehjangense* has been used in several studies (Chavasseau et al., 2006; Zin-Maung-Maung-Thein et al., 2010; Fukuchi and Kawai, 2011), whereas other researchers used "*Aprotodon*" *fatehjangense* (Heissig, 1972; Deng, 2006). Wang (1965) first described *Plesiaceratherium shanwangensis*. Later, Yan et al. (1983) reported this species as *Brachypotherium shanwangensis*. In contrast, Lu et al. (2016) analyzed the phylogenetic position of *Plesiaceratherium* and *P. shanwangense* was considered a synonym of *Plesiaceratherium gracile* in their study. Therefore, these two species are excluded from comparison in this study.

The present specimens differ from *B. brachypus*, which has been described from late early and middle Miocene localities of Central and Western Europe, and Eastern Mediterranean region (e.g., Heissig, 1999). Detailed morphological descriptions of the cheek teeth of this species have been reported by several researchers (Guérin, 1980; Ginsburg and Bulot, 1984; Cerdeño, 1993; Antoine, 2002; Heissig, 2012). *Brachypotherium brachypus* has the following characters: a dentary with straight ventral margin, upper premolars with labial cingulum, a continued lingual cingulum, and lower cheek teeth with labial cingulum (MNHN-Si 49; Guérin, 1980; Ginsburg and Bulot, 1984; Cerdeño, 1993; Antoine, 2002; Heissig, 2012); In contrast, the present specimens show weakly convex ventral margin of the dentary, slightly or not constricted protocone, no labial cingulum, reduced lingual cingulum in the upper premolars, and no buccal cingulum in the lower cheek teeth. Additionally, the dental dimensions of the present upper cheek teeth are smaller than those of *B. brachypus* (Fig. 5).

Brachypotherium perimense has been reported mainly from the early to middle Miocene of India, Pakistan, and Southeastern Asia (e.g., Colbert, 1935; Heissig, 1972; Antoine et al., 2013). Falconer and Cautley (1847) first reported *Aceratherium perimense* from Siwalik in India without detailed description. Colbert (1935) reported the detailed description of *A. perimense* from Siwalik in India. Later, Heissig (1972) assigned this species to *Brachypotherium*, and also reported this species from Pakistan. The present specimens differ from *B. perimense* described by Heissig (1972) in having more convex ventral margin of the mandible, more disto-lingually oriented lophs in the upper premolars, a shallower external groove in the lower cheek teeth, and smaller cheek teeth dimensions (Figs. 5, 6). Last, the present specimens differ from the fragmentary upper cheek teeth of *B. pugnator*, which was found from the lower Miocene Nakamura Fm., Kani City, Gifu Prefecture in Japan (Fukuchi and Kawai, 2011) in having premolars with bifid crochet, absence of a small bridge between the proto- and metaloph, no constricted protocone, and no antecrochet.

5. Discussion

The identification of the species of *Brachypotherium* has been conducted based on the skull morphology as well as cheek tooth characters (Heissig, 1972; Geraads and Miller, 2013). In addition, several features of *Brachypotherium* have also been recognized in the postcranial elements (e.g., Ginsburg and Bulot, 1984; Cerdeño, 1993; Antoine, 2002). Unfortunately, the material studied here does not include any skull or postcranial remain. Therefore, the comparison between the present specimens and other species of

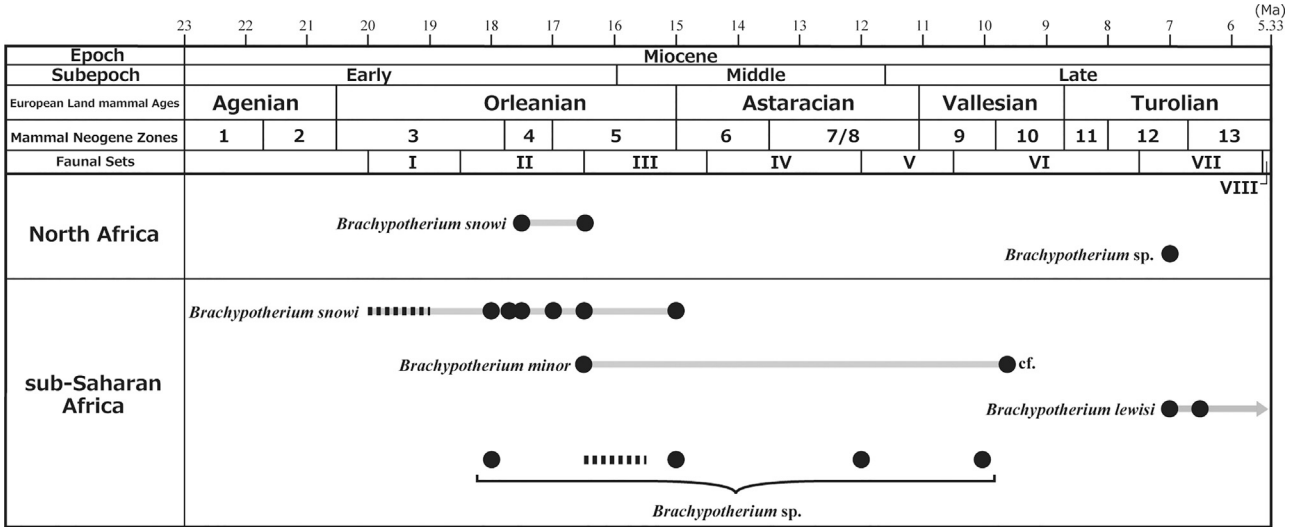

Fig. 7. Temporal range of *Brachypotherium* in Africa during the Miocene. Data from the following references: *B. snowi* from North Africa (Moghara in Egypt: Fourtau, 1920; Jebel Zelten in Libya: Hamilton, 1973); *B. snowi* from sub-Saharan Africa (Rusinga in Kenya: Hooijer, 1966; Langental in Namibia: Heissig, 1971, Guérin, 2000; Bukwa in Uganda: Hooijer, 1971; Maboko in Kenya: Pickford, 1986; Uyoma Peninsula in Kenya: Pickford, 1986; Napak in Uganda: Guérin, 2003); *B. minor* (Buluk in Kenya: Geraads and Miller, 2013, this study); *B. lewisi* (Lothagam in Kenya: Hooijer and Patterson, 1972, Harris and Leakey, 2003; Mpesida in Kenya: Hooijer, 1973); *Brachypotherium* sp. from North Africa (Sahabi in Libya: Geraads, 2010); *Brachypotherium* sp. from sub-Saharan Africa (Ngorora in Kenya: Hooijer, 1971, 1973; Kirimun in Kenya: Ishida and Ishida, 1982; Nyakach in Kenya: Pickford, 1986; Loperot in Kenya: Grossman et al., 2014).

Brachypotherium was carried out based on the cheek tooth morphology only. Although there are few dental characteristics between the present specimens and other species of *Brachypotherium*, they show the closest morphological and metrical similarities with *B. minor* – the only character that differs from *B. minor* is the presence of a slightly bifid crochet. Therefore, the present specimens are assigned to *Brachypotherium* sp. cf. *B. minor*. The present and other taxonomic studies (Fukuchi et al., 2008; Handa et al., 2015, 2017) therefore indicate that the rhinocerotid assemblage of the Namurungule Fm. includes *Chilotheidium pattersoni*, *Brachypotherium* sp. cf. *B. minor*, *Kenyatherium bishopi*, *Samburuceros ishidai*, and *Diceros* sp.

The genus *Brachypotherium* is thought to have preferred a swampy habitat based on its barrel shaped body and brachypodial short legs, whose are similar to that of hippopotamids (Guérin, 1980; Heissig, 1989; Antoine, 2002). Based on the sedimentological analysis, the Namurungule Fm. would have been deposited in a lowland with lakes (Sakai et al., 2010). Indeed, many aquatic vertebrate fossils such as Pisces, Crocodylia and Testudines, have been found from the Namurungule Fm., suggesting the presence of lacustrine and river environments (Nakaya, 1994) and supporting the sedimentological analysis. Therefore, the hypothesized habitat of *Brachypotherium* is concordant with the paleoenvironment of the Namurungule Fm.

The fossil record of *Brachypotherium* in Africa suggests that this genus was already in Africa by the early Miocene (*ca.* 20-19 Ma) (Fig. 7). Ancestral stocks of *Brachypotherium* would have migrated from Eurasia to Africa by the early Miocene through the "*Gomphotherium* landbridge" between Arabo-African and Eurasian landmasses (e.g., Hooijer, 1978; Antoine et al., 2010; Sen, 2013). During the early to early middle Miocene, *Brachypotherium snowi* was in North and sub-Saharan Africa. *Brachypotherium lewisi* was in sub-Saharan Africa during the late Miocene to early Pliocene, whereas *Brachypotherium minor* is found from the middle Miocene. In addition, several records of *Brachypotherium* sp. have been found from sub-Saharan Africa. The present study would update the temporal range of *B. minor*, suggesting that it may have spanned the middle to early late Miocene time interval.

The phylogenetic relationships of those species remain unclear. Geraads and Miller (2013) suggested that the comparison of the skull morphology of *B. minor*, *B. lewisi*, and other members of the brachypothere group may involve the existence of more than a single African lineage. Unfortunately, the present study, based on a fragmentary material, could not reveal any solution to this issue. Additional materials of this genus from Africa, especially skulls and postcranial elements, are needed to further discuss the detailed relationships of *Brachypotherium*.

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