New Specimens of *Chilotheridium* (Perissodactyla, Rhinocerotidae) from the Upper Miocene Namurungule and Nakali Formations, Northern Kenya

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Source: Paleontological Research, 19(3):181-194.
Published By: The Palaeontological Society of Japan
URL: http://www.bioone.org/doi/full/10.2517/2014PR035

Paleontological Research, vol. 19, no. 3, pp. 181–194, July 1, 2015

doi:10.2517/2014PR035

New specimens of *Chilotheridium* (Perissodactyla, Rhinocerotidae) from the Upper Miocene Namurungule and Nakali Formations, northern Kenya

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Received May 27, 2014; Revised manuscript accepted October 7, 2014

Abstract. Rhinocerotid fossils from the lower upper Miocene Namurungule and Nakali Formations, northern Kenya, are described. These materials reveal the following diagnostic characters of *Chilotheridium pattersoni*: a strongly constricted protocone with a flattened lingual wall, a hypocone groove, a developed crochet, and an antecrochet curved toward the entrance of the medisinus. Specimens previously described from the Namurungule Formation as rhinocerotids are re-identified as *C. pattersoni*. The Nakali Formation specimens presented in this study are the first discovery of *C. pattersoni* from this locality. In addition, deciduous teeth of *C. pattersoni*, which were unknown previously, are reported for the first time. This discovery of *C. pattersoni* extends its temporal range to the early late Miocene.

Key words: *Chilotheridium*, Kenya, Late Miocene, Nakali, Rhinocerotidae, Samburu Hills

Introduction

The lower upper Miocene Namurungule and Nakali Formations are distributed in the Samburu Hills and Nakali fossil localities on the eastern shoulder of the Kenya Rift, northern Kenya (Figure 1). These early late Miocene localities are important for understanding the evolution of human beings and extant African apes, because two great apes, which may be related to the last common ancestor of humans and extant African apes, were discovered in these localities: *Samburupithecus kiptalami* was discovered from the Namurungule Formation in the Samburu Hills (Ishida and Pickford, 1997), and *Nakalipithecus nakayamai* from the Nakali Formation at Nakali (Kunimatsu *et al*., 2007).

Abundant non-primate mammalian fossils have also been discovered from these localities (e.g. Aguirre and Guérin, 1974; Aguirre and Leakey, 1974; Nakaya, 1994; Morales and Pickford, 2006; Kunimatsu *et al*., 2007). Among these, Aguirre and Guérin (1974) described a few rhinocerotid specimens from Nakali as *Kenyatherium bishopi* gen. et sp. nov., and many rhinocerotid fossils from the Samburu Hills were preliminarily reported by Nakaya *et al*. (1984, 1987). Since then, the Kenya-Japan Joint Expedition recovered more mammalian fossils from the Samburu Hills through fieldwork in the 1990s (Tsujikawa, 2005). Moreover, the Kenyan-Japan Joint Expedition has carried out new fieldwork at Nakali since 2002, and has collected plenty of additional mammalian fossils including rhinocerotids (Kunimatsu *et al*., 2007; Fukuchi *et al*., 2008; Handa *et al*., 2012).

This study describes new rhinocerotid specimens from the Samburu Hills and Nakali, and redescribes some rhinocerotid specimens from the Samburu Hills. It demonstrates that cheek teeth and mandibular fragments from the Samburu Hills and Nakali are identifiable as *Chilotheridium pattersoni*. The Nakali specimens in the present study are the first reported *Chilotheridium* from this locality. Moreover, this is the first description of the deciduous premolars of *C. pattersoni*. The temporal

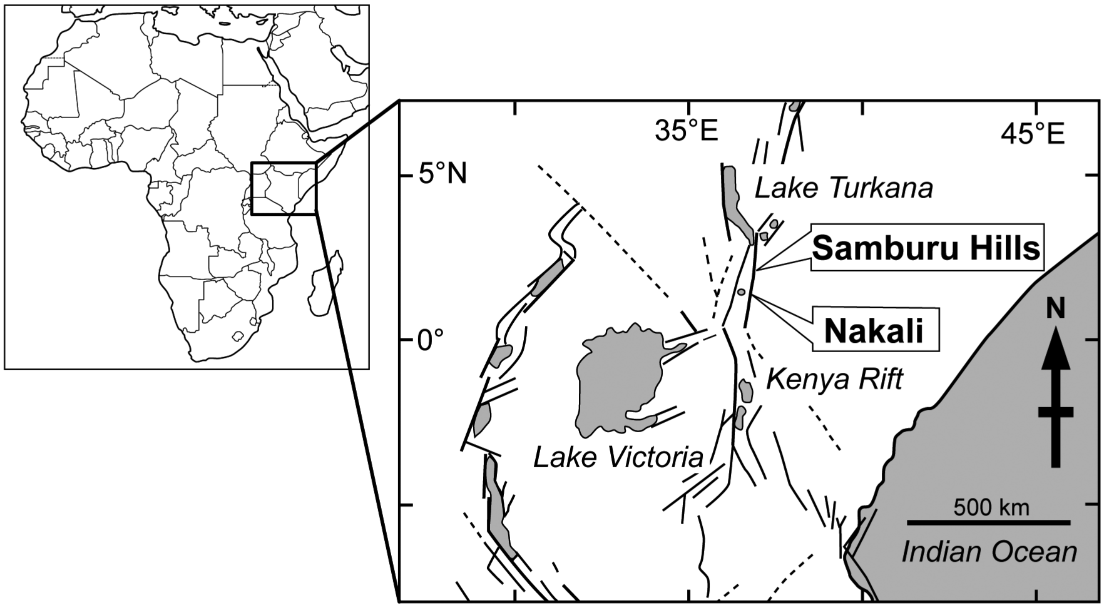

Figure 1. Map of Africa showing the fossil localities (modified from Kunimatsu *et al.*, 2007).

range of *C. pattersoni* is also discussed.

Materials and methods

The present specimens are stored in the National Museums of Kenya, Nairobi, Kenya. Measurements were taken using a digital caliper. The taxonomy used in the present study follows Heissig (1973, 1989), and tooth terminology and measurements follow Guérin (1980). Measurements are shown in Table 1.

Abbreviations.—M, upper molar; m, lower molar; P, upper premolar; p, lower premolar; dP, upper deciduous premolar; dp, lower deciduous premolar; Mc, metacarpal; KNM, National Museums of Kenya, Nairobi, Kenya; BN, Ngorora; FT, Fort Ternan; MB, Maboko; NA, Nakali; NC, Nyakach; RU, Rusinga; SH, Samburu Hills.

Geological setting

The Namurungule Formation is distributed in the Samburu Hills, which are located 50 km south of Lake Turkana (Figure 1). The Namurungule Formation is divided into the Upper and Lower members. It consists of alluvial fan, lacustrine delta and lahar deposits (Saneyoshi *et al*., 2006; Sakai *et al*., 2010). K−Ar age of the hominoid-fossil-bearing horizon of the Lower Member is estimated to be 9.57±0.22 Ma and 9.47±0.22 Ma, and the paleomagnetic stratigraphy of the Lower Member is correlated with Chron C4Ar.2n (9.64 to 9.58 Ma) and Chrons C4Ar.2r to C4Ar.1n (9.58 to 9.31 Ma) (Sawada *et al*., 1998, 2006).

The Nakali Formation is distributed at Nakali, which is situated 60 km south of the Samburu Hills (Figure 1). The Nakali Formation is divided into three members: the Lower, Middle and Upper in ascending order (Kunimatsu *et al*., 2007). The formation is composed of lacustrine, fluvio-lacustrine and pyroclastic flow deposits. $^{40}Ar/^{39}Ar$ dating provided ages of 9.82±0.09 Ma and 9.90±0.09 Ma for the uppermost part of the Lower Member of the formation (Kunimatsu *et al*., 2007). The paleomagnetic stratigraphy of the uppermost level of the Lower Member and the lowermost level of the Upper Member is correlated with Chron C5n.1r (9.88−9.92 Ma) (Kunimatsu *et al*., 2007).

Systematic paleontology

Family Rhinocerotidae Owen, 1845
Subfamily Aceratheriinae Dollo, 1885
Tribe Aceratheriini Dollo, 1885
Genus ***Chilotheridium*** Hooijer, 1971

Type and only known species.—*Chilotheridium pattersoni* Hooijer, 1971.

Holotype.—A skull (70-64K, B12) discovered from Loperot, Kenya, stored in the National Museums of Kenya, Nairobi.

Table 1. Cheek teeth measurements (in mm) of the specimens from the Namurungule and Nakali formations. Abbreviations: *L*, length; *W*, width; *H*, height; *E*, enamel thickness of the ectoloph.

Specimen number	Element	*L*	*W*	*H*	*E*	Remarks
KNM-NA257B	right dP3	39.6	36.5	29.0	1.0	with coronal cement
KNM-NA257A	right dP4	48.2	>42.0	>41.4	0.8	with coronal cement
KNM-SH40128	left P3	38.0	43.8	37.7	1.3	with coronal cement
KNM-SH15828	right M2	>65.3	>60.1	–	1.7	
KNM-SH15828	right M3	>53.2	>57.1	–	1.9	with coronal cement
KNM-SH15840	right M3	–	–	>40.1	2.5	
KNM-SH15832	right M3	>45.7	55.3	–	1.9	
KNM-SH15833	right M3	50.4	>51.4	–	1.7	
KNM-SH40792	right M3	–	–	>66.0	1.8	
KNM-SH15831	left M3	62.5	>53.5	74.6	1.8	
KNM-SH15840	left M3	75.9	52.3	–	2.1	
KNM-SH15861	left M3	>54.6	>58.8	>48.9	2.2	
KNM-SH38404	left M3	60.8	66.0	>52.5	1.6	
KNM-NA47409	left M3	>56.6	>54.1	>63.9	1.8	with coronal cement
KNM-SH15866C	left p3	>32.0	>15.5	14.4		
KNM-SH15866B	left p4	>45.9	21.2	–		
KNM-SH15749	right m1	36.0	–	–		
KNM-SH15866A	right m1 or m2	52.1	29.5	31.0		
KNM-SH15769	right m3	43.0	28.5	–		

Diagnosis.—Upper molars with paracone fold fading away basally and a flattened ectoloph; constricted protocone, flattened lingually; developed hypocone groove; basally prominent antecrochet, curving inward to medisinus entrance; typically long crochet and weak or absent crista; metacone bulge at base in M3; strong anterior cingulum; lingual cingulum weak and usually forming cusp at medisinus entrance in M3 (Hooijer, 1971).

Chilotheridium pattersoni Hooijer, 1971

Figures 2–4

Chilotheridium pattersoni Hooijer, 1971, p. 342–357, pls. 1–8; Tsujikawa, 2005, p. 20, fig. 5.
Chilotheridium sp. Nakaya *et al*., 1987, p. 96, 122, pl. 7, figs. 4, 5.

Diagnosis.—As for the genus.

Material.—The following are undescribed specimens: right dP3 (KNM-NA257B); right dP4 (KNM-NA257A); left M3 (KNM-NA47409); fragments of left M1 or M2 (KNM-SH12137, 12140). The following specimens have been tentatively described by Nakaya *et al*. (1987) and Tsujikawa (2005): left P3 (KNM-SH40128); a right maxillary fragment with M2–M3 (KNM-SH15833); maxillary fragments with right M2–M3 and left M3 (KNM-SH15840); right M3 (KNM-SH15828, 40792); left M3 (KNM-SH15831, 15832, 15861, 38404); a right mandibular fragment with dp4 and m1–m2 (KNM-SH15749); left p3 (KNM-15866C); left p4 (KNM-SH15866B); right m1 or m2 (KNM-SH15866A); a right mandibular fragment with m1–m2 (KNM-SH15751); a right mandibular fragment with m1 or m2 (KNM-SH15757); a right mandibular fragment with m2–m3 (KNM-SH15769); a right mandibular fragment with dp2–dp4 (KNM-SH15753); a left mandibular fragment with m1–m3 (KNM-SH15774); a left mandibular fragment with m1–m2 (KNM-SH15752); right mandibular fragments (KNM-SH15764, 15772); left mandibular fragments (KNM-SH15758, 15761, 15765, 15770, 15771, 15773, 15775).

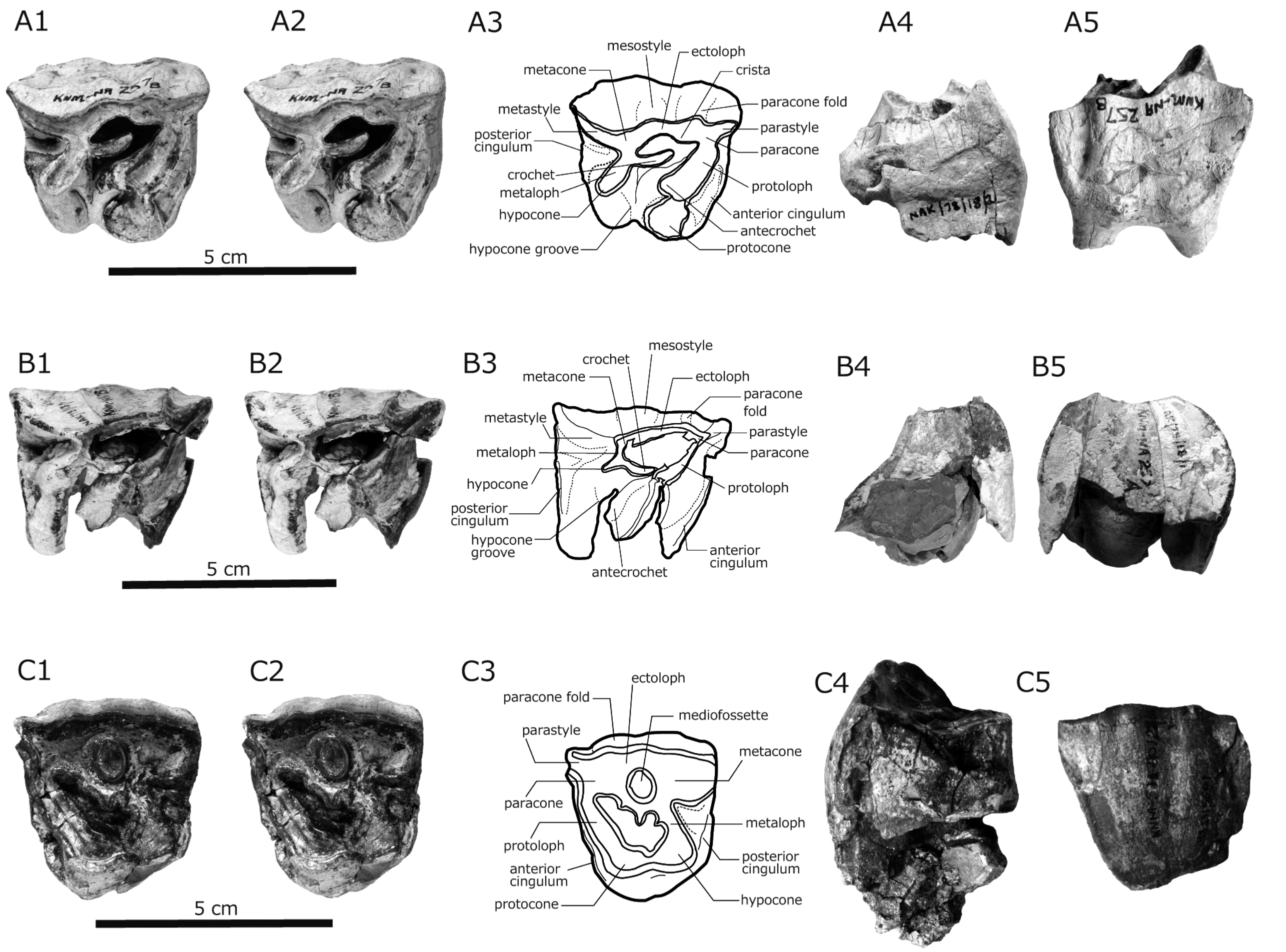

Figure 2. Upper premolar and deciduous premolars of *Chilotheridium pattersoni* Hooijer from the lower upper Miocene Namurungule and Nakali Formations, Kenya. **A**, KNM-NA257B (right dP3); **B**, KNM-NA257A (right dP4); **C**, KNM-SH40128 (left P3). For A−C: 1 and 2, stereo pairs in occlusal view; 3, schematic drawing; 4, mesial view; 5, buccal view.

Description

Upper cheek teeth

KNM-NA257B (Figure 2A) is a dP3 that lacks a part of the protocone. The tooth is heavily worn with a thin coronal cement. The enamel of the ectoloph is thinner than that of the premolar (Table 1). The protoloph and metaloph extend disto-lingually. The protocone is constricted. The parastyle projects mesially. A weak paracone fold is present. The mesostyle is weak. The hypocone groove is located on the mesial surface of the hypocone. The crochet is strongly projected mesially. The antecrochet bends toward the entrance of the medisinus. There is a trace of the crista. The anterior cingulum is low and continues from the parastyle to the protocone. The posterior cingulum is short and low. There are no buccal or lingual cingula.

KNM-NA257A is a dP4 (Figure 2B) that lacks the lingual side of the protocone. It is at an early stage of wear, with a thin coronal cement. The enamel of the ectoloph is relatively thin as in KNM-NA257B (Table 1). The protoloph bends disto-lingually. The paracone fold is weak. The parastyle and metastyle are distinct. The metaloph extends disto-lingually and bulges at the base. The hypocone groove is located on the mesial side of the hypocone. The mesostyle is developed slightly. The crochet projects mesially but does not contact the protoloph. The antecrochet curves toward the entrance of the medisinus. The anterior cingulum continues along the mesial margin of the protoloph. The posterior cingulum is short and indented at its mid-point.

KNM-SH40128 (Figure 2C) is an isolated left P3. It is well worn. Coronal cement is present. The protoloph bends disto-lingually, and the metaloph extends lin-

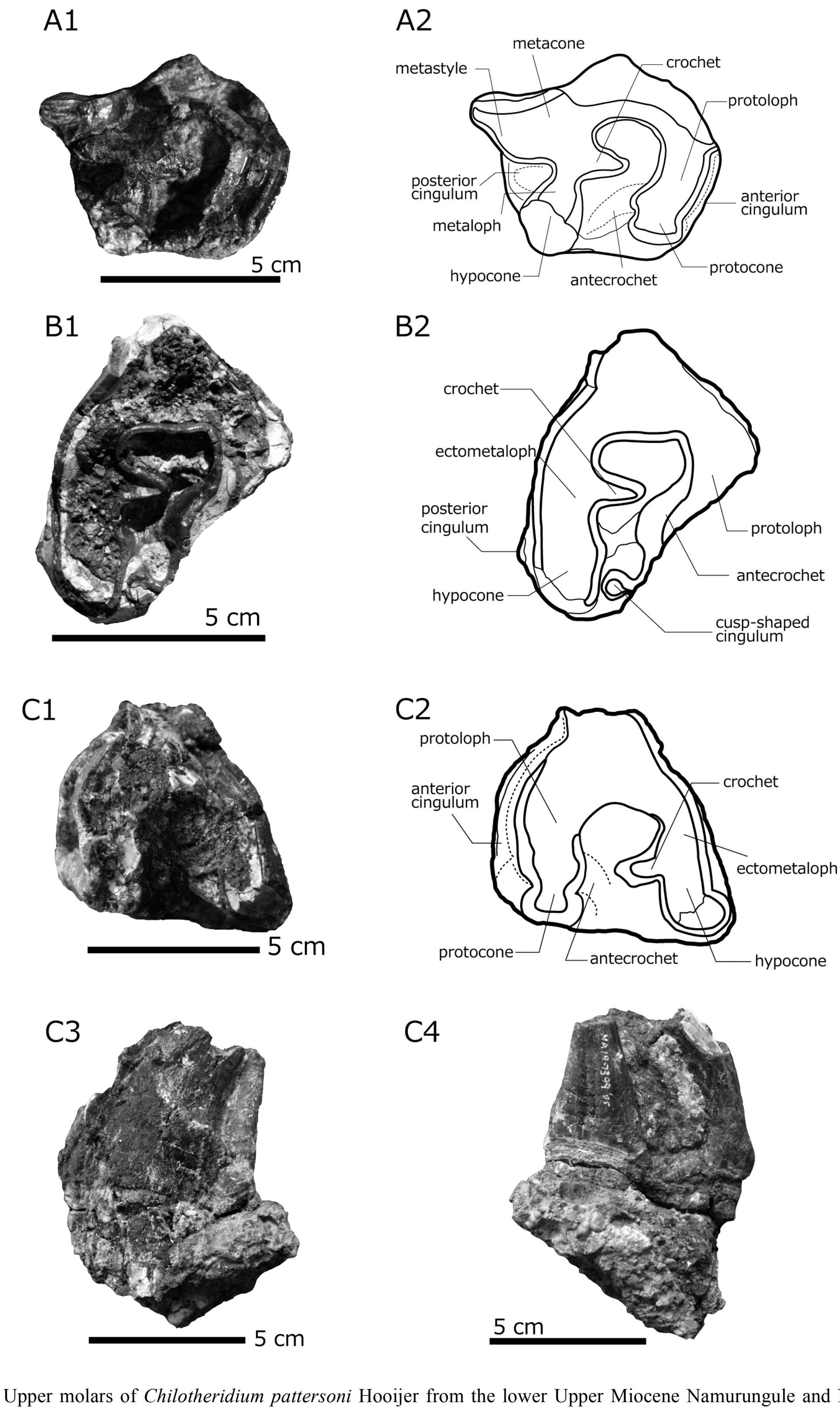

Figure 3. Upper molars of *Chilotheridium pattersoni* Hooijer from the lower Upper Miocene Namurungule and Nakali Formations. **A**, KNM-SH15840 (right M2); **B**, KNM-SH15828 (right M3); **C**, KNM-NA47409 (left M3). For A−C: 1, occlusal view; 2, schematic drawing; 3, mesial view; 4, lingual view.

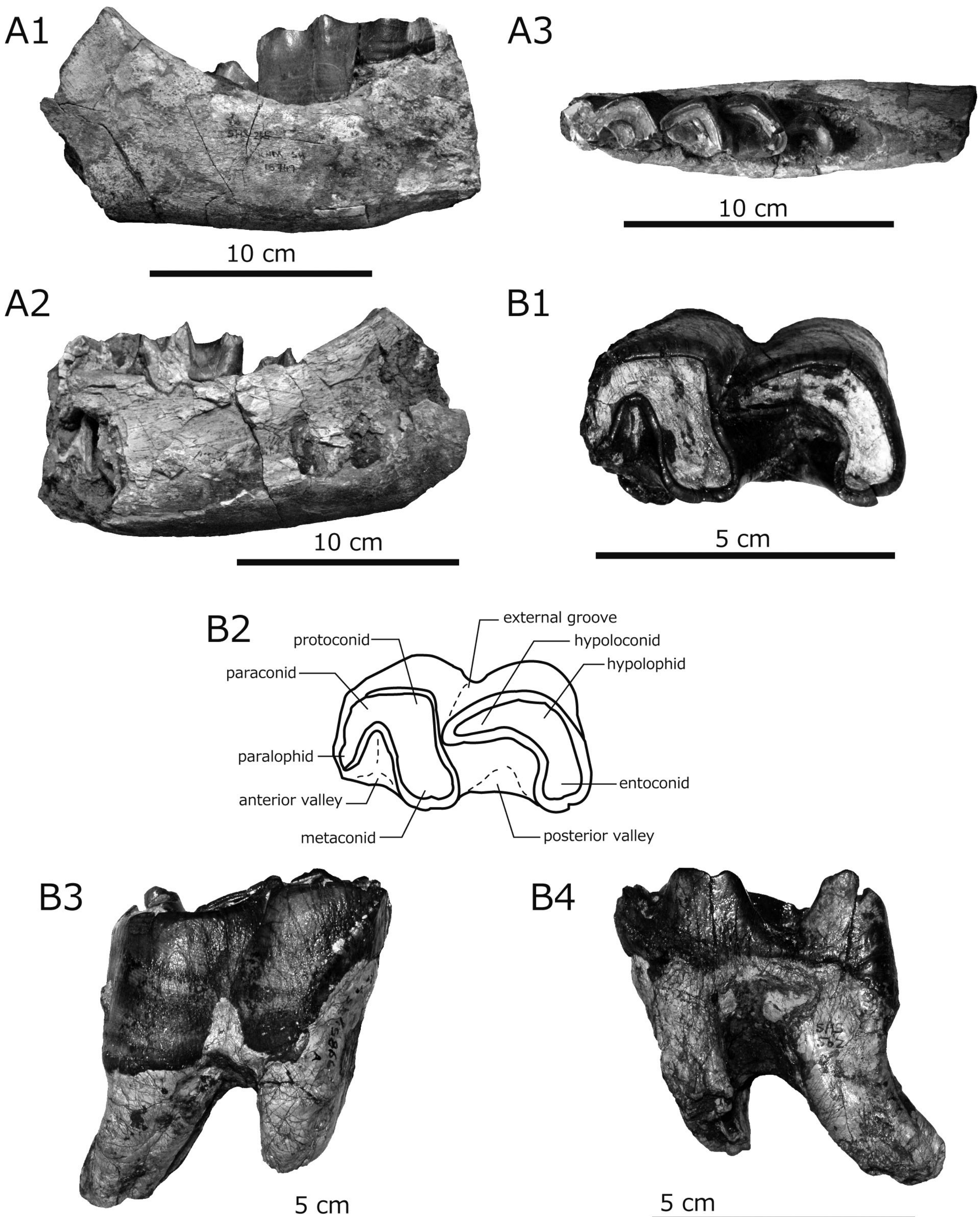

Figure 4. Mandible and lower molars of *Chilotheridium pattersoni* Hooijer from the Miocene Namurungule and Nakali Formations. **A**, KNM-SH15749 (right mandible); A1, buccal view; A2, lingual view; A3, occlusal view; **B**, KNM-SH15866A (right m1 or m2); B1, occlusal view; B2, schematic drawing of the occlusal view; B3, buccal view; B4, lingual view.

gually. There is a weak paracone fold. The crochet and crista are developed, and form an oval-shaped mediofossette. The lingual margin of the crochet is undulate. The entrance of the medisinus is closed by the connection of the protocone and hypocone. The anterior cingulum extends from the parastyle to the protocone. The posterior cingulum is short. There are no buccal or lingual cingula. The occlusal surface is concave in mesial view.

The protoloph and metaloph on M2 (KNM-SH15840) extend disto-lingually (Figure 3A). The protocone is constricted, and its lingual wall is flattened. The metastyle extends distally. The crochet is developed. The antecrochet is prominent, curving toward the entrance of the medisinus. The crista is absent. Anterior and posterior cingula are present. The postfossette is small.

The protoloph on M3 extends lingually (Figure 3B−C). Coronal cement is present in some specimens (Table 1). The ectometaloph extends lingually. The protocone is constricted, with a flat lingual wall and a shallow groove on its surface. The crochet projects mesially. The antecrochet is developed and curves toward the entrance of the medisinus. The crista is absent. There is a cusp-shaped cingulum at the entrance of the medisinus on the M3 (KNM-SH15828). The anterior cingulum extends to the protoloph. A short cingulum is present on the distal surface of the ectometaloph.

Mandibles and lower cheek teeth

Many mandibular specimens were discovered in the Namurungule Formation. Of these, KNM-SH15749 (Figure 4A) is a relatively well preserved right mandible. The anterior portion of the mandibular body and ascending ramus are missing. The dp4 and m1 are erupted, while m2 is partially erupting, suggesting a juvenile individual. The anterior end of dp4 is broken and the lingual portion of m1 is missing. In lingual view, p4 is not yet fully erupted below the dp4. The external groove of the teeth is deep, continuing to the neck of each tooth. There are no cingula on the buccal or lingual sides. Anterior and posterior valleys are V-shaped in lingual view, and on m1, the posterior valley is also wide in occlusal view. There is a groove on the lingual surface of the entoconid (Figure 4A).

The lower molar (Figure 4B) is similar to that of the lower molar of KNM-SH15749. It is hypsodont in that the lower molar has lophids with relatively flattened buccal walls, which is characteristic of the hypsodont teeth of Rhinocerotidae (Fortelius, 1982). The coronal cement is missing, and the external groove is deep. There are no buccal or lingual cingula. The posterior valley is wide in occlusal view and V-shaped in lingual view.

Comparisons and specific identification

The present specimens show a combination of characters of Aceratheriini (Heissig, 1973; Cerdeño, 1995; Antoine *et al*., 2010): a constricted protocone, an extended metastyle and a prominent antecrochet. Three taxa of Aceratheriini (*Chilotheridium pattersoni*, *Plesiaceratherium* sp. and *Turkanatherium acutirostratum*) were discovered from Africa. As discussed below, the present specimens have the characters of *C. pattersoni*.

Chilotheridium pattersoni was originally reported from the early Miocene locality of Loperot in Kenya (Hooijer, 1971). The species is characterized by a strongly constricted protocone with flattened lingual wall, a hypocone groove, a developed crochet, an antecrochet that curves toward the entrance of the medisinus and a cusp-shaped lingual cingulum on M3. These characters of the present specimens are consistent with those of *C. pattersoni* (Hooijer, 1971). In addition, the following characters of the lower cheek teeth are similar to those of *C. pattersoni* (see Appendix): a deep external groove, the absence of buccal and lingual cingula, and a V-shaped posterior valley in lingual view. Thus, these specimens from the Namurungule and Nakali formations are identified as *C. pattersoni*.

Until now, no detailed description existed of the deciduous premolars of *C. pattersoni* from other localities. The enamel thickness of the present deciduous premolars is thinner than that of the permanent premolar (Table 1). In addition, the mesostyle is weak, and there is no connection between the protocone and hypocone, unlike the permanent premolar. They have the following characters in common with the molars of *C. pattersoni*: a strongly constricted protocone with flattened lingual wall, a mesially projected crochet, an antecrochet, curving toward the entrance of the medisinus and a hypocone groove. Therefore, we consider that the present deciduous premolars belong to *C. pattersoni*.

The present specimens differ from *Plesiaceratherium* sp., which is composed of two incomplete skulls with tooth row (P2 to M3), discovered from the Middle Miocene locality of Nyakach in Kenya (Geraads, 2010). The present specimens have a connection between the protocone and hypocone in the upper premolar, strong constriction of the protocone, a crochet, and no lingual cingulum in the upper molars. In contrast, the upper cheek teeth of *Plesiaceratherium* sp. (KNM-NC10486) are characterized by lack of connection between the protocone and hypocone in the premolars, a weakly constricted protocone with rounded lingual wall, a weak or absent crochet, and a short lingual cingulum on the upper molars.

The present specimens are discriminated from *Turka-*

natherium acutirostratum, which was from the middle Miocene locality of Moruorot in Kenya and originally described by Deraniyagala (1951). Later, Arambourg (1959) and Hooijer (1963, 1966) re-identified it as *Aceratherium acutirostratum*. Recently, Geraads (2010) re-identified *A. acutirostratum* as *T. acutirostratum* based on the characters of the skull and teeth. The present premolar differs from that of *T. acutirostratum* (Deraniyagara, 1951, pl. 1) in that it has a weak paracone fold and a crista. The present molars have a cusp-shaped cingulum on M3, which is not observed on M3 of *T. acutirostratum*. Additionally, the upper molar of *T. acutirostratum* is much smaller (M2: length = 62 mm, width = 57 mm: Deraniyagara, 1951).

Several taxa of the Aceratheriini were also reported in Eurasia; for example, *Aceratherium*, *Alicornops*, *Plesiaceratherium*, *Hoploaceratherium* and *Chilotherium*. However, the present specimens can also be discriminated from these taxa. They differ from *Aceratherium* (Hünermann, 1989; Deng *et al*., 2013) in having a connection of the protocone and hypocone on the upper premolar, lingually curved antecrochet on the molars, a short metaloph, and the teeth in general are much larger. They are distinguished from *Alicornops* (e.g. Cerdeño and Sánstez, 2000) in having a connection between the protocone and hypocone in the upper premolar, no lingual cingulum on the premolar, and much larger teeth. They differ from *Plesiaceratherium* from Eurasia (Yan and Heissig, 1986) in that they show a strong protocone constriction with flattened lingual wall, absence of a labial cingulum on the upper premolar, and a deep external groove on the lower cheek teeth. They are discriminated from *Hoploaceratherium* (Heissig, 2012) in that they show a connection of the protocone and hypocone on the upper premolar, there is no lingual cingulum on the upper premolar, and the upper molars are much larger. Compared with *Chilotherium* (Ringström, 1924; Deng, 2006), a connection of the protocone and hypocone on the upper premolars, the strongly constricted protocone on the molars, a projected parastyle on the upper cheek teeth, and a nearly flattened ventral surface of the mandible (Ringström, 1924; Deng, 2006), are the distinguishing characters of the present specimens.

They can also be distinguished from other rhinocerotid groups (including Teleoceratini, Dicerotini, Rhinocerotini, and Elasmotheriini) (Appendix).

The present specimens differ from Teleoceratini (including *Brachypotherium*). Several species of *Brachypotherium* were found from the Miocene to Pliocene of Africa (Hooijer, 1963, 1966; Hooijer and Patterson, 1972; Hamilton, 1973; Geraads, 2010; Geraads and Miller, 2013). The present specimens differ from *Brachypotherium* from Africa in having a disto-lingually oriented protoloph, a weak crista, a connection between the protocone and hypocone, no lingual cingulum on the upper premolar, a strong protocone constriction, a long metastyle, and a cusp-shaped cingulum on M3.

The present specimens also differ from Dicerotini (including *Diceros* and *Ceratotherium*). The present specimens are distinguished from *Diceros* (Arambourg, 1959; Hooijer, 1959; Guérin, 1966, 2000; Hooijer and Patterson, 1972; Geraads, 2005; Giaourtsakis *et al*., 2009) in having a protocone constriction, an antecrochet, and a hypocone groove on the upper cheek teeth. Additionally, the present premolar has a connection between the protocone and hypocone, whereas the premolars of *Diceros* lack this condition. The present specimens also differ from the species of *Ceratotherium* (Hillman-Smith *et al*., 1986; Antoine, 2002; Geraads, 2005; Giaourtsakis *et al*., 2009) in having a lingually directed metaloph on the premolar, a connection between the protocone and hypocone on the premolar, and a weak paracone fold on the premolar. The present specimens also lack the following upper cheek tooth characters of *Ceratotherium*: protocone constriction, a rounded lingual wall of the protocone, hypocone groove, a short metastyle, antecrochet, and cusp-shaped cingulum on M3.

The present specimens are distinguished from the African Rhinocerotini (including *Paradiceros mukirii* and *Rusingaceros leakeyi*). *Paradiceros mukirii* has been reported from the middle Miocene locality of Fort Ternan in Kenya (Hooijer, 1968b). This species was previously thought to be closely related to *Diceros* (Hooijer, 1968b). Recently, *P. mukirii* was assigned to a taxon of Rhinocerotini based on its cranial and dental morphology (Giaourtsakis *et al*., 2009). The present deciduous premolars have disto-lingually directed lophs, a constricted protocone, a mesostyle, and a hypocone groove. In contrast, the dP3 and dP4 of *P. mukirii* (KNM-FT2866) show the following characters: a lingually directed protoloph and metaloph, no protocone constriction, no mesostyle and no hypocone groove. The present premolar also differs from that of *P. mukirii* (KNM-FT2870) in having a disto-lingually directed protoloph, a mediofossette, a connection between the protocone and hypocone and no lingual cingulum. The present molars have a long metastyle and a cusp-shaped cingulum on M3. These characters are not seen in the molars of *P. mukirii* (KNM-FT3328: Geraads, 2010). The present specimens are also distinguished from *Rusingaceros leakeyi*, which was discovered from early Miocene localities in sub-Saharan Africa (e.g. Hooijer, 1966). *Rusingaceros leakeyi* was originally described as *Dicerorhinus leakeyi* by Hooijer (1966). Recently, this taxon was transferred from *Dicerorhinus* to the new genus *Rusingaceros* by Geraads (2010). The present upper deciduous premolars differ from those of *R. leakeyi* (Hooijer, 1966, pl., 5, fig. 1) in having a weak paracone fold, a mesostyle and an antecrochet. Moreover, the present molars show a strongly constricted protocone, a developed antecrochet, and a cusp-shaped cingulum, whereas *R. leakeyi* lacks the constricted protocone and an antecrochet in the upper molars, and has no cusp-shaped cingulum in the M3 (KNM-RU2821A, RU2822).

The present specimens differ from Elasmotheriini (including *Kenyatherium bishopi*, *Ougandatherium napakense* and *Victoriaceros kenyensis*). *Kenyatherium bishopi* has been described from the late Miocene localities of Nakali and the Samburu Hills. An upper premolar and an upper molar were discovered from the Nakali Formation (Aguirre and Guérin, 1974), and an upper molar from the Namurungule Formation was described by Nakaya *et al*. (1987). The present premolar (KNM-SH40128) has no wrinkled enamel folding, a disto-lingually orientated protoloph, a crista, and no lingual cingulum. In contrast, these characters are not seen in the premolar of *K. bishopi* (KNM-NA198). Additionally, the connection between the protocone and hypocone of the present premolar is situated more lingually and the occlusal surface is more concave than that of *K. bishopi*. The present molars show a strong protocone constriction, a flattened lingual wall in the protocone and no lingual cingulum, whereas these characters are not seen in the upper molars of *K. bishopi* (KNM-NA199, KNM-SH15827). Therefore, the present specimens are distinguished from *K. bishopi*. The present specimens are discriminated from *Ougandatherium napakense*, which was discovered from the early Miocene locality of Napak, Uganda (Guérin and Pickford, 2003). The present premolar has a crista, a mediofossette, and no lingual cingulum. In contrast, the premolars of *O. napakense* have a lingual cingulum, and no crista or mediofossette. The present molars also differ from *O. napakense* in having a strongly constricted protocone with a flattened lingual wall, a hypocone groove and a cusp-shaped lingual cingulum on M3. The present specimens differ from *Victoriaceros kenyensis*, which was discovered from the middle Miocene locality of Maboko, Kenya (Geraads *et al*., 2012). The present premolar has a simple crochet, a mediofossette, a disto-lingually directed protoloph, and no lingual cingulum. In contrast, the premolars of *V. kenyensis* (KNM-MB19717, MB36189) have a bifid crochet, a lingually directed protoloph, and a short lingual cingulum. The present molars have a simple crochet and a cusp-shaped cingulum on M3, whereas these characters are not seen in the upper molars of *V. kenyensis* (KNM-MB29179, MB36189).

***Chilotheridium* and its temporal range in sub-Saharan Africa**

Cheek teeth of *C. pattersoni* have been reported from many Miocene localities in sub-Saharan Africa, although identification of some of the specimens remains controversial (Figure 5). The characters of the present specimens conform to those of *C. pattersoni* from other localities (Appendix).

A right M1 or M2 and a right molar fragment (Hooijer, 1966, pl. 6, figs. 10, 11) of *C. pattersoni* have been reported from the early Miocene locality of Rusinga, Kenya (Hooijer, 1971). The present specimens are similar to these Rusinga specimens in that they have a strongly constricted protocone with a flattened lingual wall, an antecrochet and a hypocone groove and no lingual cingulum. Hooijer (1971) described a right P2 to M3 (Walker, 1968: unnumbered specimens) from Bukwa in Uganda (early Miocene) as *C. pattersoni*, while Geraads (2010) pointed out that the specimens are attributable to Elasmotheriini gen. et sp. indet. The upper cheek teeth of the Bukwa specimens have the characters of *C. pattersoni* such as a protocone that has strong constriction and a flattened lingual wall, presence of an antecrochet and a hypocone groove. These characters are also seen in the present molars. Hooijer (1973) described right M2 and M3, and a fragment of the right upper molar of *C. pattersoni* from Ombo, Kenya (middle Miocene). The molars from Ombo show a strong protocone constriction, a flattened lingual wall in the protocone, a developed antecrochet and a hypocone groove. These characters are also seen in the present specimens. Hooijer (1971) described as *C. pattersoni* a fragment of the right maxilla (KNM-BN133) with the tooth row (dP1, P2, P3, P4 and M1) from Member E of the Ngorora Formation, Kenya (upper Miocene: Geraads, 2010). However, as noted by Geraads (2010), this specimen is too worn to identify as *C. pattersoni*. An isolated P3 of *C. pattersoni* from Ngeringerwa in Kenya (late Miocene) was reported by Guérin (2011). This specimen has a crochet, a crista and no buccal or lingual cingula. These characters are similar to those of the present specimens. Nakaya *et al*. (1987) reported *Chilotheridium* sp. and Tsujikawa (2005) reported *C. pattersoni* from the Namurungule Formation in the Samburu Hills (lower upper Miocene). Geraads *et al*. (2012), however, pointed out that the specimens from the Namurungule Formation are possibly *Kenyatherium* based on such characters as a constricted protocone, a long antecrochet, and a pinched hypocone. The present specimens from the Namurungule Formation, however, lack the upper cheek teeth characters of *Kenyatherium* such as lingually oriented lophs, wrinkled enamel folding, a short lingual cingulum, and a flattened occlusal

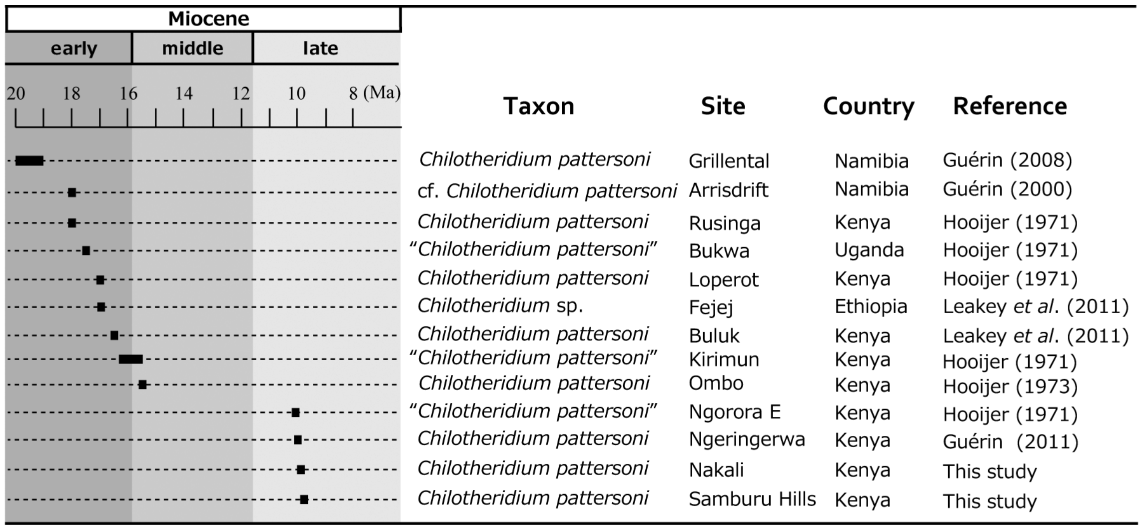

Figure 5. Temporal range of *Chilotheridium* in sub-Saharan Africa. Taxa in quotation marks indicate those whose identification has been disputed by Geraads (2010) and Geraads *et al*. (2012). The age of each fossil locality follows Sawada *et al.* (1998), Kunimatsu *et al.* (2007), Geraads (2010) and Tsujikawa *et al*. (2011).

surface in mesial view. Additionally, the present specimens have the diagnostic characters of *C. pattersoni* such as a flattened lingual wall in the protocone, a hypocone groove, a developed crochet, and an antecrochet that curves toward the entrance of the medisinus. Therefore, the specimens from the Namurungule Formation are identified as *C. pattersoni*.

In addition to the cheek teeth, several other specimens of *Chilotheridium* have also been reported from the following five Miocene localities in sub-Saharan Africa. Hooijer (1971) described a left lower second incisor from Kirimun in Kenya (late early Miocene to early middle Miocene), although Geraads (2010) suggested that the incisor belongs to *Brachypotherium*. Leakey and Walker (1985) and Leakey *et al*. (2011) reported *C. pattersoni* from the early Miocene locality of Buluk in Kenya, though descriptions and illustrations were not given. Guérin (2000, 2003) reported a left magnum of cf. *C. pattersoni* from the early Miocene locality of Arrisdrift, Namibia. Guérin (2008) reported a left Mc IV of *C. pattersoni* from the early Miocene of Grillental in Namibia. Leakey *et al*. (2011) listed *Chilotheridium* sp. from the early Miocene locality of Fejej in Ethiopia, although it was not described or illustrated.

Geraads (2010) and Geraads *et al*. (2012) implied that the temporal range of *C. pattersoni* is from the early Miocene to the middle Miocene. However, the present specimens from the lower upper Miocene Namurungule and Nakali formations were identified as *C. pattersoni*. Therefore, the present discovery confirms that the temporal range of *C. pattersoni* extends up to the early late Miocene (Figure 5) as noted by Guérin (2011).

Acknowledgements

The authors wish to thank the Government of Kenya and the National Museums of Kenya for research permission. The first author thanks Naomichi Ogihara (Keio University, Tokyo) for assistance in the National Museums of Kenya. He also thanks Akira Fukuchi (Hanshin Consultants Co., Ltd., Satsumasendai) for providing references and Hiroshi Tsujikawa (Tohoku Bunka Gakuen University, Sendai) for providing his helpful comments. We are grateful to Emma Bernard (Natural History Museum, London), Patricia Pérez Dios (Museo Nacional de Ciencias Naturales, Madrid), Christine Argot (Muséum National d'Histoire Naturelle, Paris), Mitsuharu Oshima and Hiroko Hirotani (Kanagawa Prefectural Museum of Natural History, Odawara), and Hiroyuki Taruno (Osaka Museum of Natural History, Osaka) for providing access to specimens for the comparative work. This research was supported in part by grants from the Fujiwara Natural History Foundation, by a Sasakawa Research Grant from the Japan Science Society, and by the JSPS KAKENHI grant (22255006 and 25257408) award to M. Nakatsukasa.

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Appendix. Comparison of *Chilotheridium pattersoni* specimens from the Namurungule and Nakali formations with other rhinocerotids from Africa.

		Aceratheriinae									
		Aceratheriini							Teleoceratini		
		Chilotheridium pattersoni	*Chilotheridium pattersoni*	*Chilotheridium pattersoni*	*Chilotheridium pattersoni*	*Chilotheridium pattersoni*	*Turkanatherium actirostratum*	*Plesiaceratherium* sp.	*Brachypotherium snowi*	*Brachypotherium lewisi*	*Brachypotherium minor*
	Present study	Hooijer (1971) (Loperot specimen)	Hooijer (1966, 1971) (Rusinga specimen)	Walker (1968), Hooijer (1971) (Bukwa specimen)	Hooijer (1973) (Ombo specimen)	Guérin (2011) (Ngeringerwa specimen)	Deraniyagara (1951), Hooijer (1968a), Geraads (2010)	Geraads (2010)	Hamilton (1973)	Hooijer and Patterson (1972)	Geraads and Miller (2013)
Upper deciduous premolar											
coronal cement	present	–	–	–	–	–	–	–	–	–	–
protoloph direction	disto-lingual	–	–	–	–	–	–	–	–	–	–
metaloph direction	disto-lingual	–	–	–	–	–	–	–	–	–	–
protocone constriction	present	–	–	–	–	–	–	–	–	–	–
paracone fold	weak	–	–	–	–	–	–	–	–	–	–
mesostyle	present	–	–	–	–	–	–	–	–	–	–
hypocone groove	present	–	–	–	–	–	–	–	–	–	–
crochet	present	–	–	–	–	–	–	–	–	–	–
antecrochet	present	–	–	–	–	–	–	–	–	–	–
Upper premolar											
coronal cement	present	absent	–	absent	–	–	absent	absent	absent	absent	absent
protoloph direction	disto-lingual	disto-lingual	–	–	–	–	lingual	lingual	lingual	lingual	lingual
metaloph direction	lingual	lingual	–	–	–	–	lingual	disto-lingual	lingual	lingual	lingual
connection of the protocone and hypocone	present	present	–	present	–	–	present	absent	absent	absent	absent
crochet	present	present	–	present	–	present	present	absent	present	present	present
crista	present	present	–	–	–	present	absent	absent	absent	absent	absent
mediofossette	present	present	–	absent	–	–	absent	absent	absent	absent	absent
paracone fold	weak	weak	–	–	–	–	strong	weak	weak	weak	weak
labial cingulum	absent	absent	–	–	–	absent	–	absent	absent	absent	absent
lingual cingulum	absent	absent	–	–	–	absent	present	present	present	present	present
enamel folding	absent	absent	–	absent	–	absent	absent	absent	absent	absent	absent
Upper molar											
protocone constriction	strong	strong	strong	strong	strong	–	strong	weak	weak	weak	weak
lingual wall of the protocone	flat	flat	flat	flat	flat	–	flat	round	round	flat	round
hypocone groove	present	present	present	present	present	–	present	absent	absent	present	absent
metastyle	elongate	elongate	–	short	–	–	elongate	short	short	short	short
crochet	simple	simple	simple	simple	simple	–	simple	simple or absent	simple	simple	simple
antecrochet	present	present	present	present	present	–	present	present	present	present	absent
lingual cingulum	absent	absent	absent	present	–	–	–	present	absent	present	present
cusp-shaped cingulum on the M3	present	present	–	–	–	–	absent	absent	absent	absent	absent
coronal cement	present	present	absent	–	–	–	absent	absent	absent	absent	absent
enamel folding	absent	absent	absent	absent	absent	–	absent	absent	absent	absent	absent
Lower cheek teeth											
buccal walls of the lophids	flat	flat	–	–	–	–	–	round	flat	flat	flat
buccal cingulum	absent	absent	–	–	–	–	–	absent	absent	absent	absent
lingual cingulum	absent	absent	–	–	–	–	–	absent	absent	absent	–
external groove	deep	deep	–	–	–	–	–	deep	shallow	shallow	shallow
posterior valley	V-shape	V-shape	–	–	–	–	–	U-shape	V-shape	V-shape	–
coronal cement	–	absent	–	–	–	–	absent	absent	absent	absent	absent

Appendix. *Continued.*

	Rhinocerotinae											
	Dicerotini							Rhinocerotini		Elasmotheriini		
	Diceros australis	*Diceros primaevus*	*Diceros praecox*	*Diceros douariensis*	*Diceros bicornis*	*Ceratotherium simum*	*Ceratotherium mauritanicum*	*Paradiceros mukirii*	*Rusingaceros leakeyi*	*Kenyatherium bishopi*	*Victoriaceros kenyensis*	*Ougandatherium napakense*
	Guérin (2000)	Arambourg (1959)	Hooijer and Patterson (1972), Geraads (2005)	Guérin (1966), Giaourtsakis *et al.* (2009)	Hooijer (1959), Giaourtsakis *et al.* (2009)	Hilman-Smith *et al.* (1986), Antoine (2002), Giaourtsakis *et al.* (2009)	Geraads (2005), Giaourtsakis *et al.* (2009)	Hooijer (1968b)	Hooijer (1966)	Aguirre and Guérin (1974), Nakaya *et al.* (1987)	Geraads *et al.* (2012)	Guérin and Pickford (2003)
Upper deciduous premolar												
coronal cement	absent	absent	absent	-	absent	present	–	absent	absent	–	–	–
protoloph direction	disto-lingual	disto-lingual	disto-lingual	–	disto-lingual	disto-lingual	–	lingual	disto-lingual	–	–	–
metaloph direction	disto-lingual	disto-lingual	disto-lingual	–	disto-lingual	disto-lingual	–	lingual	disto-lingual	–	–	–
protocone constriction	absent	absent	absent	–	absent	absent	–	absent	present	–	–	–
paracone fold	weak	strong	weak	–	present	absent	–	strong	strong	–	–	–
mesostyle	absent	present	present	–	present	present	–	absent	absent	–	–	–
hypocone groove	absent	absent	absent	–	absent	absent	–	absent	–	–	–	–
crochet	present	present	present	–	present	present	–	present	present	–	–	–
antecrochet	absent	absent	absent	–	absent	absent	–	absent	absent	–	–	–
Upper premolar												
coronal cement	absent	absent	absent	present	absent	present	present	absent	absent	present	present	present
protoloph direction	lingual	lingual	lingual	lingual	lingual	disto-lingual	disto-lingual	lingual	–	lingual	lingual	disto-lingual
metaloph direction	lingual	disto-lingual	disto-lingual	disto-lingual	disto-lingual	disto-lingual	disto-lingual	lingual	-	lingual	disto-lingual	lingual
connection of the protocone and hypocone	absent	absent	absent	absent	absent	absent	absent	absent	present	present	present	present
crochet	present	present	present	present	present	present	present	absent	–	absent	bifid	present
crista	absent	absent	absent	absent	absent	present	present	absent	–	absent	present	absent
mediofossette	absent	absent	absent	absent	absent	present	present	absent	–	absent	absent	absent
paracone fold	weak	weak	weak	weak	weak	absent	absent	weak	–	weak	weak	weak
labial cingulum	absent	absent	absent	absent	absent	absent	absent	absent	–	absent	absent	absent
lingual cingulum	present	present	present	present	present	absent	absent	present	–	present	present	present
enamel folding	absent	absent	absent	absent	absent	absent	absent	absent	absent	present	absent	absent
Upper molar												
protocone constriction	absent	absent	absent	absent	absent	absent	absent	–	absent	weak	strong	weak
lingual wall of the protocone	round	round	round	round	round	round	round	–	round	round	flat	round
hypocone groove	absent	absent	absent	absent	absent	absent	absent	–	absent	present	present	absent
metastyle	–	elongate	elongate	elongate	elongate	short	short	short	short	–	elongate	elongate
crochet	simple	simple	simple	simple	simple	simple	simple	–	simple	simple	bifid	simple
antecrochet	absent	absent	absent	absent	absent	absent	absent	–	absent	present	present	present
lingual cingulum	present	present	present	present	present	absent	present	absent	absent	present	absent	absent
cusp-shaped cingulum on the M3	absent	absent	absent	absent	absent	absent	absent	absent	absent	–	absent	absent
coronal cement	absent	absent	absent	present	absent	present	present	absent	absent	present	present	present
enamel folding	absent	absent	absent	absent	absent	absent	absent	absent	absent	present	absent	absent
Lower cheek teeth												
buccal walls of the lophids	–	round	round	flat	round	flat	flat	round	round	–	flat	–
buccal cingulum	absent	present	absent	absent	absent	absent	–	absent	–	–	absent	–
lingual cingulum	absent	absent	absent	absent	absent	absent	–	absent	–	–	absent	–
external groove	deep	shallow	deep	shallow	shallow	shallow	–	deep	deep	–	deep	–
posterior valley	V or U-shape	V-shape	V-shape	–	V-shape	V-shape	–	V-shape	V-shape	–	U-shape	–
coronal cement	absent	absent	absent	present	absent	present	present	absent	absent	–	present	–