Title	Fossil rhinoceroses from the Late Miocene of Kenya: Miocene faunal changes of the Rhinocerotidae (Mammalia, Perissodactyla) in sub-Saharan East Africa(博士論文要約)
Author(s)	半田, 直人
Citation	
Issue Date	2016-04-22
URL	http://hdl.handle.net/10232/26924

学位論文の要約

氏名	HANDA Naoto（半田直人）
学位論文題目	Fossil rhinoceroses from the Late Miocene of Kenya –Miocene faunal changes of the Rhinocerotidae (Mammalia, Perissodactyla) in sub-Saharan East Africa-

CHAPTER 1

Introduction

1-1. Historical review of the paleontological studies in Samburu Hills and Nakali, northern Kenya

The fossil records in Africa show that there are no records of large bodied hominoids and primitive hominids during ca. 13 to 7 Ma. Therefore, the middle Middle to early Late Miocene (ca. 13 to 7 Ma) localities are important for understanding the evolution of human beings and extant African apes.

The lower Upper Miocene (ca. 10 Ma) Namurungule and Nakali Formations are distributed in the Samburu Hills and Nakali fossil localities on the eastern shoulder of the Kenya Rift, northern Kenya (Figures 1 and 2). The Kenya-Japan joint expedition has carried out fieldworks in the Samburu Hills during 1982 to 1999 (Ishida, 1984, 1987). In contrast, during late 1960s to early 1970s, Spain-Kenya excavation team firstly researched in Nakali (Aguirre and Guérin, 1974; Aguirre and Leakey, 1974). In 2002, Japan-Kenya joint expedition team started research in Nakali and the excavation continues at present (Nakatsukasa, 2009).

Two fossil great apes, which may be related to the last common ancestor of humans and extant African apes, were discovered in these localities by the Kenya-Japan Joint expedition team: *Samburupithecus kiptalami* was discovered from the Namurungule Formation in the Samburu Hills (Ishida and Pickford, 1997), and *Nakalipithecus nakayamai* was from the Nakali Formation in the Nakali (Kunimatsu *et al.*, 2007). Abundant non-primate mammalian fossils have also been discovered from these localities.

1-2. Miocene Rhinocerotidae in sub-Saharan East Africa

Family Rhinocerotidae (Mammalia, Perrisodactyla) is a major group of the African mammals. In Africa, many species of Rhinocerotidae were diversified during the Miocene (e.g. Geraads, 2010). In particular, there are many fossil localities in sub-Saharan East Africa (Kenya, Ethiopia, Uganda and Tanzania: Figure 3).

Many specimens of Rhinocerotidae were reported from Samburu Hills by Nakaya *et al.* (1984, 1987) and Tsujikawa (2005). In Nakali, there are a few reports of rhinocerotid fossils. Aguirre and Guérin (1974) first reported a new species, *Kenyatherium bishopi*.

Moreover, *K. bishopi* and *Diceros* sp. were reported by the Kenya-Japan joint expedition, though there are no any descriptions and illustrations (Kunimatsu *et al*., 2007; Fukuchi *et al*., 2008).

1-3. Aim of this study

Taxonomic revision of Rhinocerotidae from the Namurungule and Nakali Formations.—The fossil records of the early Late Miocene (ca. 10 Ma) in sub-Saharan East Africa are scarce. In contrast, hundreds specimens of rhinocerotid have been found from the Namurungule and Nakali Formations. Therefore, Rhinocerotid fauna from the Namurungule and Nakali Formations are the richest fauna in the early Late Miocene in sub-Saharan East Africa. However, the taxonomic revision of those specimens has not been undertaken since their initial descriptions. Additionally, there are many undescribed specimens from the both formations. Thus, It needs that the revision of the specimens from the Namurungule and Nakali Formations.

Miocene rhinocerotid faunal change in sub-Saharan East Africa.—In Eurasia, the relationships between the rhinocerotid fauna and paleoenvironment changes are discussed (Cerdeño and Nieto, 1995; Deng and Down, 2002). In contrast, these studies in Africa are poorly known. The paleoenvironmental study of the Miocene localities in Sub-Saharan East Africa has been carried out based on the various methods (e.g. Jacobs *et al*., 2010). According to these studies, the forest-dominated environments were developed in sub-Saharan East Africa during the Early to Middle Miocene, and more open environments were dominated by the Late Miocene (Jacobs *et al*., 1999, 2010; Jacobs, 2004). Therefore, it is expected that these paleoenvironmental changes would affect the faunal composition of the rhinocerotid in sub-Saharan East Africa.

In Africa, fossil records during the Early Miocene to early Middle Miocene (ca. 18 to 15 Ma) and late Late Miocene (7 Ma ~) are well known, whereas, there are a few records between these ages (Geraads, 2010). Recently, Geraads (2010) reviewed the rhinocerotid fossils from Africa, and preliminary revised the taxonomy of them. Later, additional descriptions of new taxa or new specimens have also reported by several researchers (Guérin, 2011; Leakey *et al*., 2011; Geraads *et al*., 2012; Geraads and Miller, 2013). Those studies and the rhinocerotids from the Namurungule and Nakali Formations fill in the gap of the fossil records, and contribute the discussion of the relationship between the diversification of African rhinocerotid fauna and paleoenvironment changes during the Miocene Period.

In this study, I first revise the taxonomy of the rhinocerotid specimens from the Namurungule and Nakali Formations, and also describe the undescribed specimens from the both formations. Then, the characteristics of the rhinocerotid fauna of the Namurungule and Nakali Formations are discussed. Finally, the relationships between the Miocene rhinocerotid fauna and environment changes in sub-Saharan East Africa are discussed.

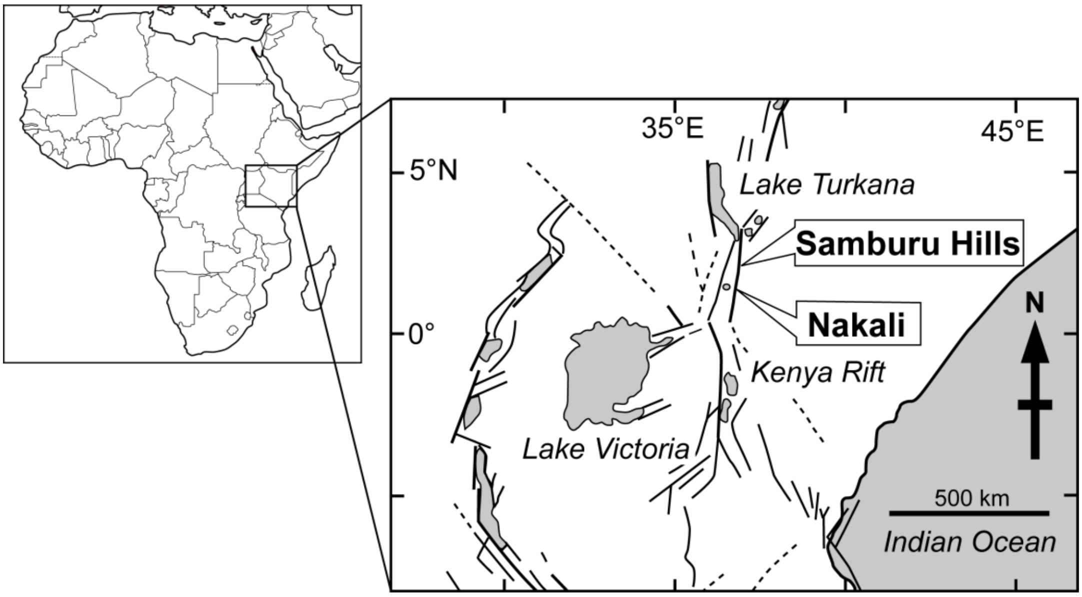


Figure 1. Map showing the localities of Samburu Hills and Nakali in northern Kenya (modified from Kunimatsu *et al*., 2007).

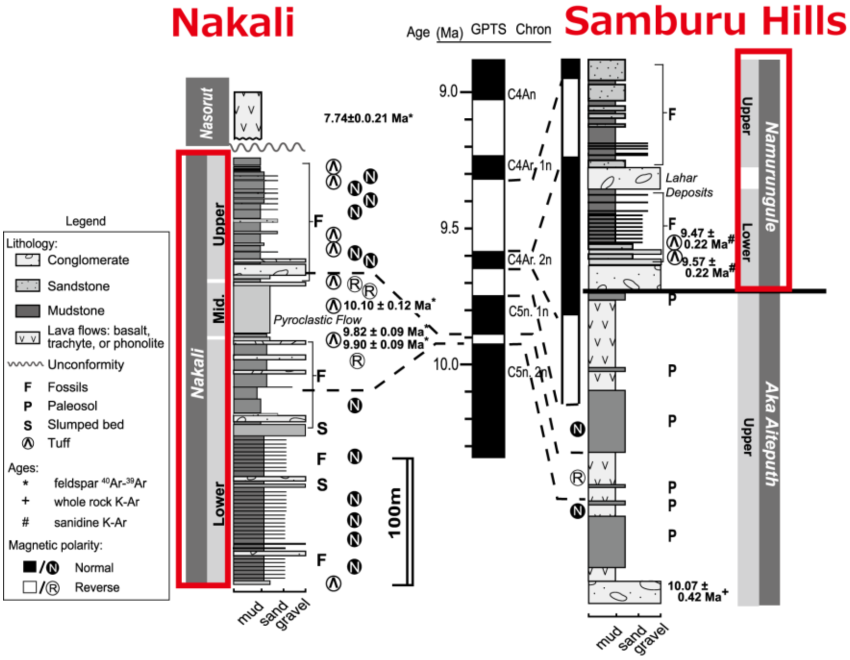


Figure 2. Columnar sections of the Namurungule and Nakali Formations (modified from Uno *et al*., 2011).

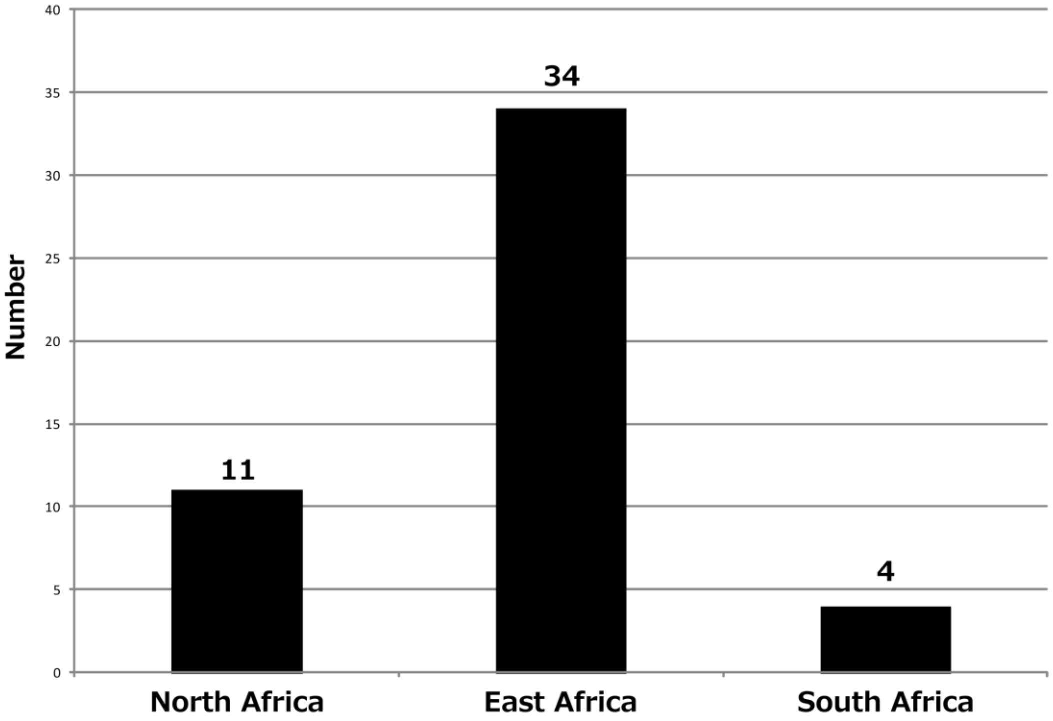


Figure 3. Numbers of fossil record of the Miocene rhinocerotid fossil from Africa (based on Geraads, 2010).

CHAPTER 2

Geological setting

Samburu Hills is located 50 km south of Lake Turkana (Figure 1). In this area, the Namurungule Formation is overlying the Aka Aithepus Formation conformably, and is overlied the Kongia Formation unconformably, respectively. This formation about 200 m thick and is divided into the Upper and Lower Members, which are consists of alluvial fan and fluvio-lacustrine, and fluvio-lacustrine delta and fluvial deposits, respectively (Saneyoshi *et al*., 2006; Sakai *et al.*, 2010). *Samburupithecus kiptarami* was found from the Lower Member (Ishida and Pickford, 1997). There is lahar deposit between the Lower and Upper Members. The studied specimens from the Namurungule Formation were discovered from the Lower member. 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 the Upper Member is correlated with Chrons C4Ar.2r to C4Ar.1n (9.58 to 9.31 Ma) (Sawada *et al*., 1998, 2006 in Nakatsukasa and Kunimatsu, 2009, not seen) (Figure 2).

Nakali is situated 60 km south of the Samburu Hills (Figure 1). The Upper Miocene Nakali and Nasorut Formations are distributed in this area (Sakai *et al*., 2013). The Nakali Fomation is unconformably overlied the Nasorut Formation, which is composed of trachitic or basaltic lava and volcaniclastics. The thickness of the Nakali Formation is about 340 m. This formation is divided into three units: the lower, middle and upper in ascending order (Kunimatsu *et al*., 2007; Sakai *et al*., 2013). The Lower Member is composed mainly of lacustrine and fluvio-lacstrine deposits. The Middle Member consisted of pyloclastic flow deposit, which thickness is ca. 40 m. The Upper Member is characterized fluvio-lacstrine and lacustrine deposits. *Nakalipithecus nakayamai* was corrected from the Upper Member (Kunimatsu *et al*., 2007). The studied specimens from the Nakali Formation were found from the Upper and Lower Members. ^{40}Ar/^{39}Ar dating provided ages of 9.82 ± 0.09 and 9.90 ± 0.09 Ma for the uppermost part of the Lower Member of this 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) (Figure 2).

CHAPTER 3

Taxonomic revision of Rhinocerotidae from the Namurungule and Nakali Formations

In this study, the rhinocerotid from the Namurungule and Nakali Formations (early Late Miocene), northen Kenya, were revised. As a result, the following taxa are recognized: *Chilotheridium pattersoni*, *Brachypotherium* cf. *minor*, *Diceros* cf. *primaevus*, *Kenyatherium bishopi* and Rhinocerotidae gen. et sp. indet.

3-1. Materials and methods

The specimens described here are stored in the National Museums of Kenya, Nairobi, Kenya. The specimens from the Namurungule Formation and the Nakali Formation were discovered during 1980 to 1999 and from 2002 to 2012, respectively. The specimens number of African materials is composed of institutional abbreviation (KNM: National Museums of Kenya, Nairobi), locality abbreviation (e.g. SH=Samburu Hills, NA=Nalali, see also below) and accession number. Measurements were taken using a digital caliper. The taxonomy used in the present study follows Heissig (1973, 1989), and anatomical terminology and measurements follow Guérin (1980) and Made (2010).

Comparisons with Eurasian and African rhinocerotids carried out in the collections of the following institutions: National Museums of Kenya, Nairobi, Kenya; Natural History of Museum, London, UK; Museo National de Ciencias Naturales, Madrid, Spain; Muséum National d'Histoire Naturelle, Paris, France; Université Claude Bernard-Lyon I, Lyon, France; Kanagawa Prefectural Museum of Natural History, Odawara; Osaka Museum of Natural History, Osaka. Some rhinocerotid materials for comparison were based on the references.

Locality abbreviations.—BN, Ngorora, Kenya; NA, Nakali, Kenya; SH, Samburu Hills, Kenya.

Anatomical abbreviations.—dP, upper deciduous premolar; dp, lower deciduous premolar; M, upper molar; m, lower molar; Mc, metacarpal; Mt, metatarsal; P, upper premolar; p, lower premolar.

3-2. *Chilotheridium pattersoni*

Upper and lower cheek teeth, and several mandibular fragments from the Namurungule and Nakali Formations were described as *Chilotheridium pattersoni* in this study (Figure 4).

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

A right M1 or M2 and a right molar fragment (Hooijer, 1966) 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 right P2 to M3 (Walker, 1968: un-numbered specimens) from Bukwa in Uganda (Early Miocene) as *C. pattersoni*, while Geraads (2010) pointed out that the specimens are attributed 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 protocone constriction and a flattened lingual wall, a presence of the 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 a fragment of the right maxilla with the tooth row (dP1, P2, P3, P4 and M1) in *C. pattersoni* (KNM-BN133) from Ngorora E, Kenya (Late 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 contrast, as mentioned above, Geraads *et al*. (2012) noted that the specimens from the Namurungule Formation are possibly *Kenyatherium* based on the characters such 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 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 many dental and mandibular specimens from the 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).

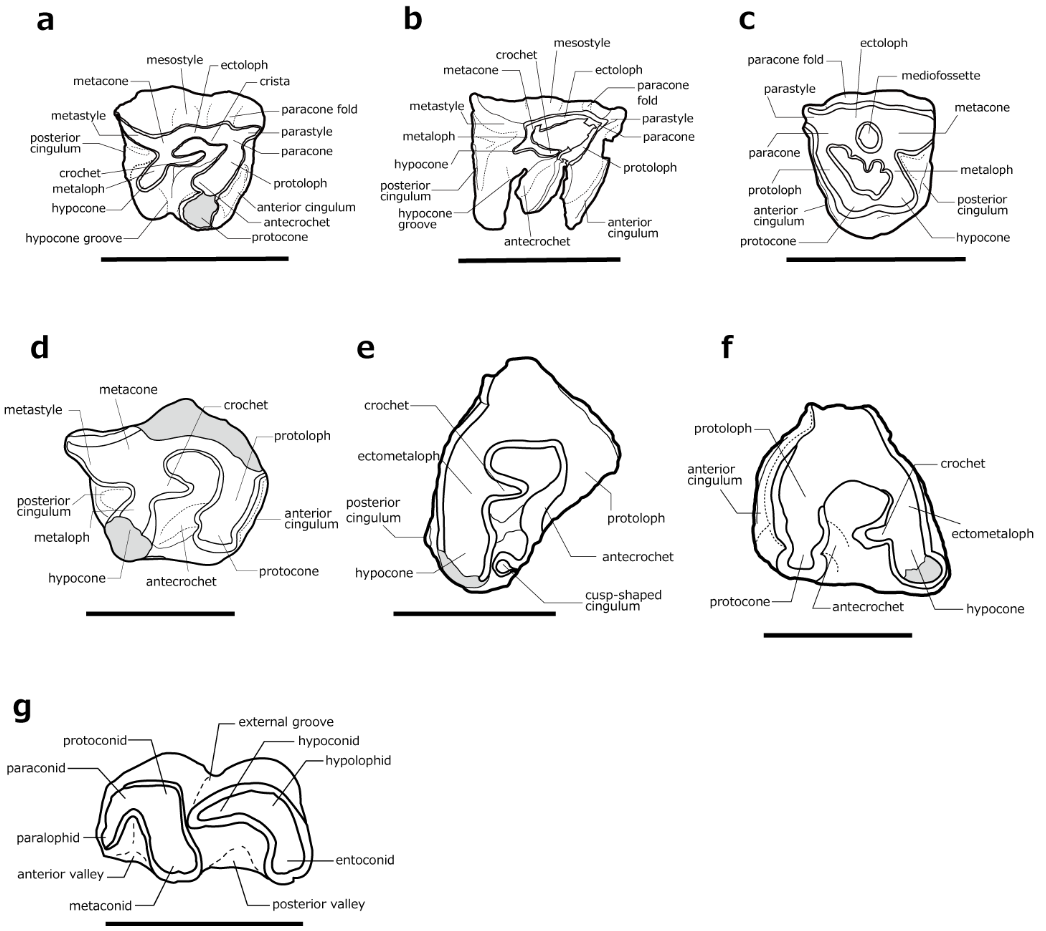
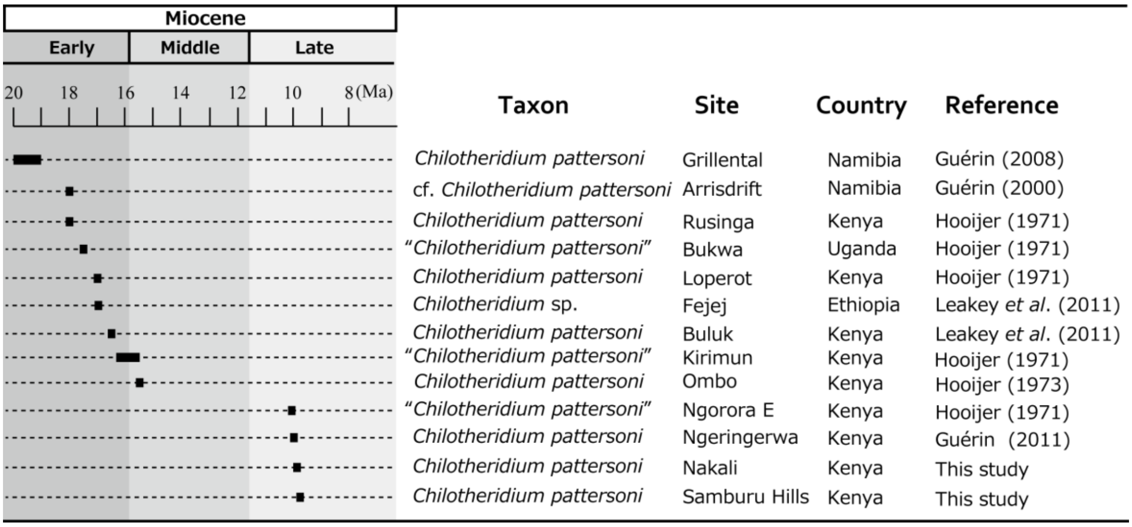


Figure 4. Schematic drawing of the teeth of *Chilotheridium pattersoni*.

a, KNM-NA257B (right dP3); **b**, KNM-NA257A (right dP4); **c**, KNM-SH40128 (left P3); **d**, KNM-SH15840 (right M2); **e**, KNM-SH15828 (right M3); **f**, KNM-SH47409 (left M3); **g**, KNM-SH15866A (right m1 or m2). Gray shaded indicates that damaged portion. Scale bar = 5 cm.



Taxon	Site	Country	Reference
Chilotheridium pattersoni	Grillental	Namibia	Guérin (2008)
cf. *Chilotheridium pattersoni*	Arrisdrift	Namibia	Guérin (2000)
Chilotheridium pattersoni	Rusinga	Kenya	Hooijer (1971)
“*Chilotheridium pattersoni*”	Bukwa	Uganda	Hooijer (1971)
Chilotheridium pattersoni	Loperot	Kenya	Hooijer (1971)
Chilotheridium sp.	Fejej	Ethiopia	Leakey *et al*. (2011)
Chilotheridium pattersoni	Buluk	Kenya	Leakey *et al*. (2011)
“*Chilotheridium pattersoni*”	Kirimun	Kenya	Hooijer (1971)
Chilotheridium pattersoni	Ombo	Kenya	Hooijer (1973)
“*Chilotheridium pattersoni*”	Ngorora E	Kenya	Hooijer (1971)
Chilotheridium pattersoni	Ngeringerwa	Kenya	Guérin (2011)
Chilotheridium pattersoni	Nakali	Kenya	This study
Chilotheridium pattersoni	Samburu Hills	Kenya	This study

Figure 5. Temporal range of *Chilotheridium pattersoni* 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).

3-3. *Diceros* cf. *primaevus*

In this study, several upper and lower cheek teeth, and an upper incisor from the Nakali Formation were described as *Diceros* cf. *primaevus* (Figure 6).

Early dispersal and migration patterns of *Diceros* are controversial so far. Geraads (2005) discussed the early dispersal pattern of Dicerotini. He noted that *Ceratotherium neumayri* (="*Diceros*" *neumayri* in Giaourtsakis *et al*., 2009) is a common ancestor of both *Diceros* and *Ceratotherium* (white rhino), and considered that, *Diceros primaevus* which is a Late Miocene taxon from Tunisia, was closely related taxon with *C. neumayri*. Additionally, *Diceros douariensis*, which is an African species in the early Late Miocene, was considered that conspecific of *C. neumayri*. In his context, however, the detail reason of these identifications is not mentioned. Moreover, "*D.*" *australis*, which were discovered from Namibia (Guérin, 2000, 2003) is excluded in those discussions as noted by Giaourtsakis *et al*., (2009). According to Geraads (2005), *C. neumayri* was migrated into Africa from Eurasia in the Late Miocene, and the both extant lineage (*Diceros* and *Ceratotherium*) split after the Miocene/Pliocene boundary. In contrast, Giaourtsakis *et al*. (2009) and Deng and Qiu (2007) suggest that the migration of *Diceros* were occurred in Africa during the Late Miocene, and the genus were migrated from Africa to Eurasia by the early Late Miocene. Giaourtsakis *et al*. (2009) also suggest that "*D.*" *neumayri* (=*C. neumayri* in Geraads, 2005) is considered as a paraphyletic taxon in Dicerotini.

The present study supported migration hypothesis by Giaourtsakis *et al*. (2009), and Deng and Qiu (2007), because *Diceros* cf. *neumayri* was discovered from the early Late Miocene localities of Nakali in northern Kenya, namely genus *Diceros* was already presented in the sub-Saharan East Africa during the early Late Miocene. Geraads *et al*. (2002) and Suwa *et al*. (2015) noted that *Ceratotherium* sp. was found from the Late Miocene (ca. 8 Ma) locality of Chorora in Ethiopia. The preservation of these specimens, however, is too incomplete to identify as the genus. Therefore, the specimens from Chorora are treated as Dicerotini gen. et sp. indet. in this study.

In Eurasia, "*D.*" *neumayri* was presented during MN10 to MN13 (early Late Miocene to late Late Miocene) (Figure 7). In China, *D. gansuensis* was recorded from the early Late Miocene (MN10, middle Vallesian) locality in Ganus (Deng and Qiu, 2007). Thus, the present study is the earlist record of *Diceros* in Afro-Eurasia during Late Miocene. In the latest Middle Miocene (MN7-8; 13.5~10.7 Ma), a landbridge had connected between Africa and Eurasia continents (Koufos *et al*., 2005) (Figure 8). Thus, Ancestors of "*D.*" *neumayri* and *D. gansuensis* were possibly migrated into Eurasia during this period via this landbridge and "*D.*" *neumayri* was distributed in the eastern Mediterranean such as Greece (Giaourtsakis, 2003, 2009), Turky (Alçiçek, 2010) and Iran (Thenius, 1955) among Vallesian to Turolian (MN9-MN12) as noted by Giaourtsakis *et al*. (2009). Additionlly, due to the mammal faunal exchange had occurred between eastern Meditteranean and East Asia in during the Late Miocene (Koufos *et al*., 2005), the lineage of *Diceros gansuensis* could reach in China.

According to Senut *et al*., (2009), development of Sahara desert had began to about 7-6 Ma. Futhermore, earian sediment reported from late Late Miocene (7 Ma) locality in Chad (Schuster *et al*., 2006). Therefore, the distribution of *Diceros* in Africa might be limitted in sub-Saharan Africa because the Sahara desart block their expansion to North in the late Late Miocene (~7 Ma). The extant *Diceros bicornis* is distributed in present sub-Saharan Africa (Rookmaaker and Antoine, 2012). The fossil records of *Diceros* suggest that the restricted distribution of the *Diceros* in present sub-Saharan Africa had already appeared during the Late Miocene (ca. 7 Ma).

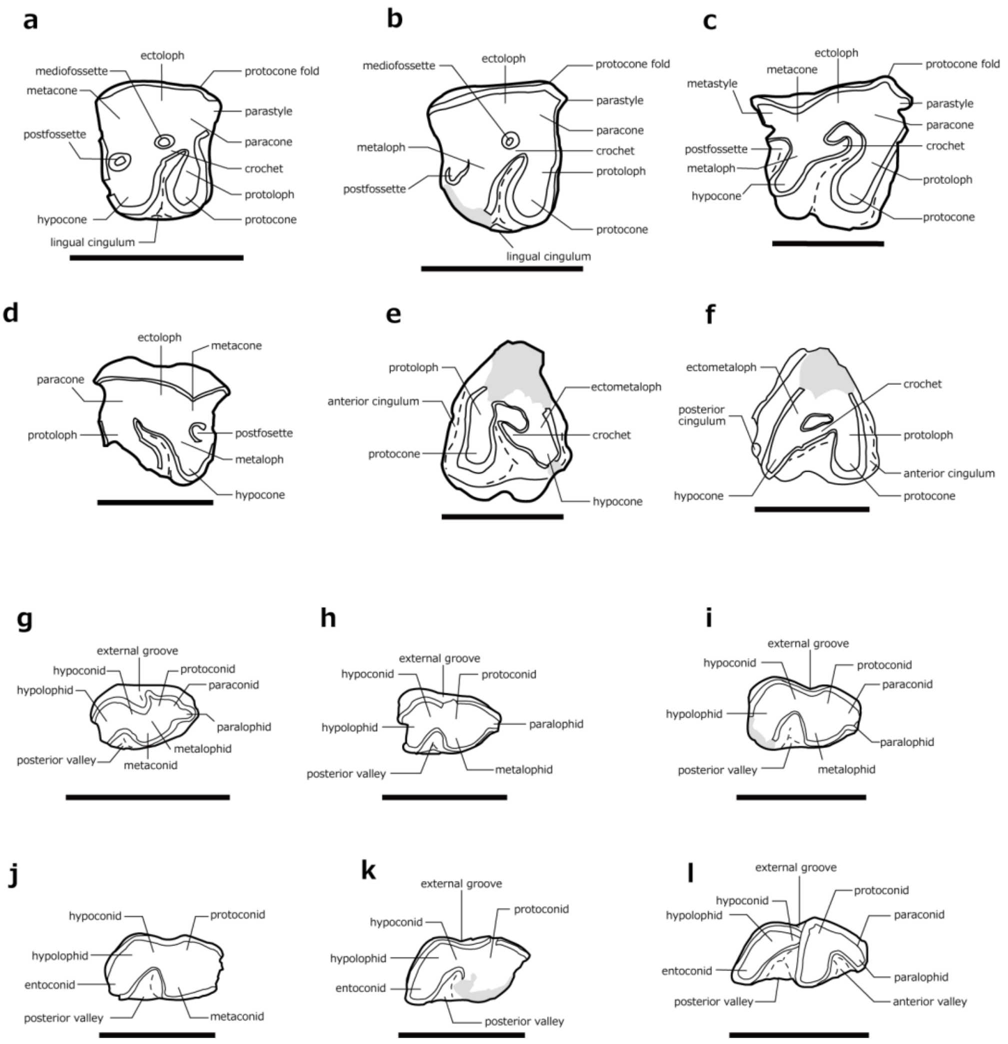


Figure 6. Schematic drawing of the cheek teeth of *Diceros* cf. *primaevus*.
a, KNM-NA52150 (right P3); **b**, KNM-NA52149 (right P4); **c**, KNM-NA52143 (rigtht M1 or M2); **d**, KNM-NA52139 (left M1 or M2); **e**, KNM-NA52139 (left M3); **f**, KNM-NA52139 (right M3); **g**, KNM-NA52147 (left p2); **h**, KNM-NA52146 (left p4); **i**, KNM-NA52144 (left p4); **j**, KNM-NA52139 (left m1); **k**, KNM-NA52139 (left m2); **l**, KNM-NA52139 (left m3). Gray shaded indicates that damaged portion. Scale bar = 5 cm.

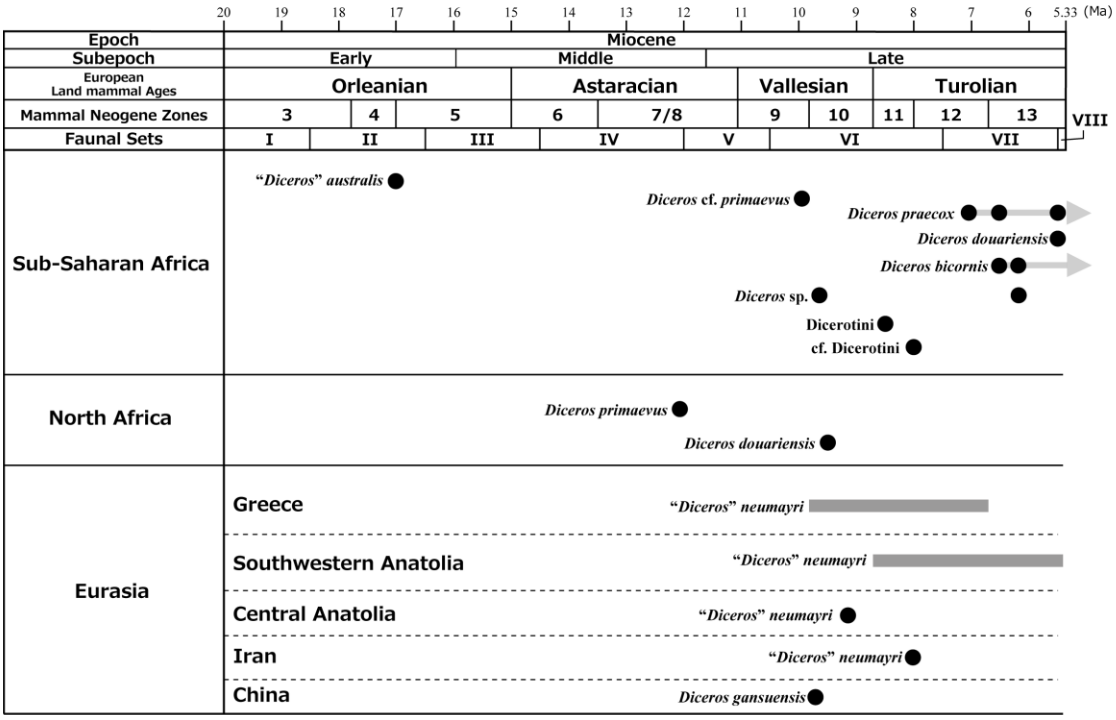


Figure 7. Temporal ranges of the species of *Diceros* in Africa and Eurasia. The fossil records follow Guérin (1966, 2000); Hooijer and Patterson (1972); Harris and Leakey (2003); Deng and Qiu (2007); Fukuchi *et al.* (2008); Giaourtsakis *et al.* (2009); Alçiçek (2010); Suwa *et al.* (2015); this study.

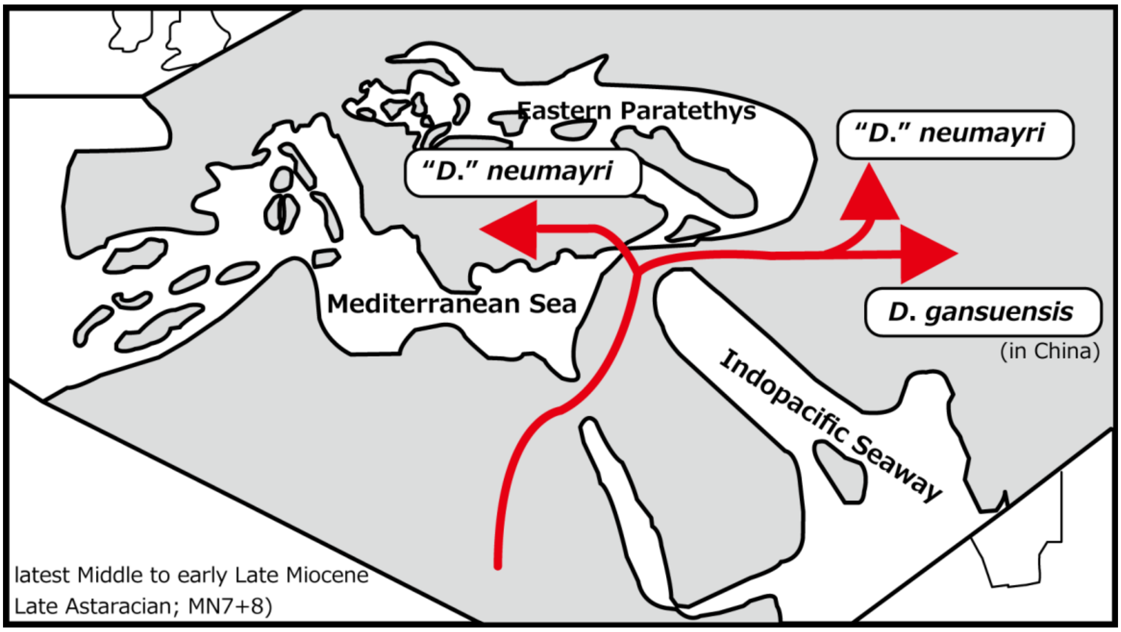


Figure 8. Paleogeographic map of eastern Mediterranean area during the latest Middle Miocene (modified from Koufos *et al.*, 2005).

3-4. Other rhinocerotid specimens

Additional specimens of *Brachypotherium* cf. *minor*, *Kenyatherium bishopi* and Rhinocerotidae gen. et sp. indet. were described in this study.

Brachypotherium* cf. *minor Geraads and Miller, 2013

Several cheek teeth and mandibular specimens were identified as *B*. cf. *minor* (Figure 9). These specimens had reported as *Chilotheridium* sp. or *Paradiceros mukirii* by Nakaya *et al*. (1987) and Tsujikawa (2005). However, the present specimens show the characteristics of *Brachypotherium* such as molarized upper premolars, flat ectoloph of the upper premolars and shallow external groove of the lower cheek teeth. Additionally, the dementions of the present specimens are similar to those of *B. minor*. Therefore, these are recognised as *B*. cf. *minor.* This result indicates that the temporal range of *B. minor* extends up to the early Late Miocene.

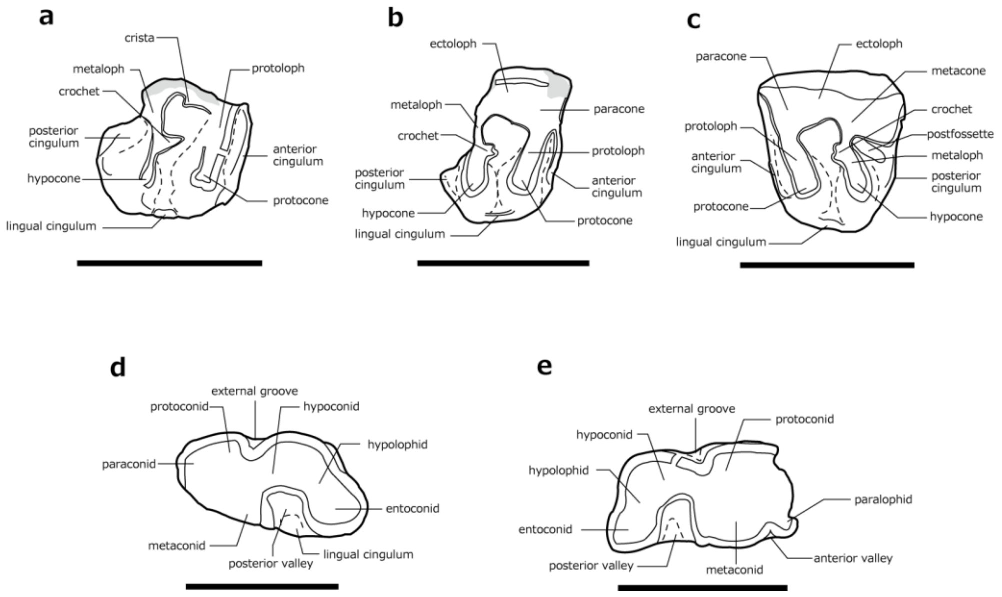


Figure 9. Schematic drawing of the cheek teeth of *Brachypotherium* cf. *minor*.

a, KNM-SH37910 (right P4); **b**, KNM-SH15859B (right P4); **c**, KNM-SH15859A (left P4); **d**, KNM-SH40120 (right m3); **e**, KNM-SH12143 (left m1 or m2). Gray shaded indicates that damaged portion. Scale bar = 5 cm.

Kenyatherium bishopi Aguirre and Guérin, 1974

An isolated upper molar (KNM-SH15869: Figure 10) is the following combination of the characters of the upper molar of *K. bishopi*: the coronal cement, constricted protocone, triangle shaped postfossette and lingual cingulum. Although, the present specimen is poorly preserved, its size is relatively similar to that of *K. bishopi*. The present specimen differs from *Victoriaceros kenyensis* (Geraads *et al*., 2012) in having the simple crochet and the connection of the protocone and hypocone. The present specimen differs from *Ougandatherium napakense* (Guérin and Pickford, 2003) in having the lingual cingulum. Therefore, the present specimen belongs to *K. bishopi*.

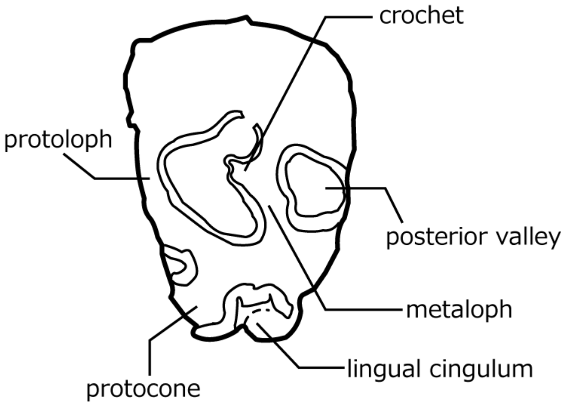


Figure 10. Schematic drawing of the tooth of *Kenyatherium bishopi* (KNM-SH15869, left M1 or M2).

Rhinocerotidae gen. et sp. indet.

Abundant fragmentary or isolated specimens of rhinocerotid have been obtained from the Namurungule and Nakali Formation. These specimens were described Rhinocerotidae gen. et sp. indet. A to D in this study.

Rhinocerotidae gen. et sp. indet. A is composed of right femora (KNM-SH15763, SH40136), left femur (KNM-SH15750) from the Namurungule Formation. Rhinocerotidae gen. et sp. indet. B is a right astragalus (KNM-SH15762) from the Namurungule Formation. Rhinocerotidae gen. et sp. indet. C is a left astragalus (KNM-SH14765) from the Namurungule Formation. Rhinocerotidae gen. et sp. indet. D is composed of other all materials from the Namurungule and Nakali Formations.

3-5. Characteristic of the rhinocerotid fauna of the Namurungule and Nakali Formations

Rhinocerotid faunal composition of the Namurungule and Nakali Formations.—The rhinocerotid fauna of the Namurungule and Nakali Formations is composed of "Early to Middle Miocene" and "Late Miocene" forms. "Early to Middle Miocene" form is characterized as the Early to Middle Miocene dominated taxa (*C. pattersoni* and *B.* cf. *minor*) or having morphologically primitive characters (*K. bishopi*). *Chilotheridium pattersoni* was dominant during the Early to Middle Miocene. *Brachypotherium minor* has also been found from the Middle Miocene. *Kenyatherium bishopi* is morphologically similar to that of the Early Miocene taxa, such as *O. napakense* from Napak in Kenya (Guérin and Pickford, 2003) and *Bugtirhinus praecosor* from Bugti in Pakistan (Antoine and Welcomme, 2000) as noted by Antoine (2002). In contrast, "Late Miocene" form is composed of *Diceros* cf. *primaevus*. Genus *Diceros* was diversified in late Late Miocene to Pliocene period.

Relationship with the rhinocerotid fauna and paleoenvironment in Samburu Hills and Nakali.— The paleoenvironmental studies of the fossils localities in Samburu Hills and Nakali have been conducted various methods.

The paleoenvironment of Nakali is estimated as forest with woodland and river and lake under seasonal climate. Nakatsukasa *et al*. (2010) reported colobine monky, *Microcolobus* from the Nakali Formation, which has characters of an arboreal quadruped (distal joint of of the humerus and capitulum). This suggests that forest habitat in Nakali. The faunal composition of the rodent fossils from the Nakali Formation suggests that the paleoenvironment of the Nakali was forest on upland with watery environment under seasonal climate (Onodera *et al*., 2011). Uno *et al*. (2011) estimated the paleodiet of the large mammal fauna in the early Late to late Late Miocene localities (Samburu Hills, Nakali and Lothagam) in Kenya based on the analysis of the carbon stable isotope in the enamel of the cheek teeth of mammals. According to the study, the carbon stable isotope analysis of an equid, *Hipparion*, from the Nakali Formation shows C_4-dominated habitat. In contrast, rhinocerotids from the Nakali Formation shows C_3-dominated habitat as well as the result of bovid from this Formation. Mesowear analysis of *Hipparion* and bovids from the Nakali Formation indicate that they were mix-feeder, suggesting that there was woodland dominant environment in Nakali (Nakaya *et al*., 2012). Matsui *et al*. (2008) preliminary reported fossil pollens such as Podocapacea, Taxodiaceae and Poaceae, suggesting that there was wet forest habitat.

The paleoenvironment of Samburu Hills (the Namurungule Formation) is more open and wooded habitat with lakes and rivers under dry climate. Nakaya (1994) noted that the presence of abundant equid and bovids fossils from the Namurungule Formation indicates that the open country and/or woodland environment. The results of mesowear analysis of *Hipparion* and bovids from this formation suggest that grazer and mix-feeder, respectively (Nakaya *et al*., 2012). This result suggests that there were woodland and savanna environments. According to Uno *et al*. (2011), the results of carbon isotope analysis of equids, rhinocerotids, bovids, hippopotamids, suids and gomphotheriids from the Namurungule Formation show the increasing of C_3/C_4-mixed or C_4-dominated habitats, suggesting there were more open habitats in Samburu

Hills than Nakali. Many aquatic vertebrate fossils such as Pices, Crocodylia and Tetsudines, have been found from the Namurungule Formation. This result indicates that the presence of lacustrine and river environments. Based on the sedimentological analysis, the Namurungule Formation would be deposited at lowland with lakes under ths strong seasonality (Sakai *et al*., 2010).

The rhinocerotid fauna of the Namurungule and Nakali Formations confirm the estimated paleoenvironments in Samburu Hills and Nakali. Genus *Brachypotherium* is considered to be a swampy habitat based on the barrel shaped body and garavipodal short legs, whose are similar to that of hippopotamid (e.g. Heissig, 1989). Based on the sedimentological study, the Lower Member of the Namurungule Formation, which yielded *Brachypotherium*, includes the lacustrine deposits (Sakai *et al*., 2010). Therefore, the habitat of *B.* cf. *minor* concordants with the sedimentological study of the Namurungule Formation.

The dental morphology of the rhinoceorids exhibits the paleoecological characters. The cheek teeth of *D.* cf. *primaevus* show the following features: concave occlusal surface, convergent of the labial and lingual walls, presence of the paracone folds that are more developed than the mesostyle, and absence of the crista and enamel folding. These morphologies are considered a browsing diet (Fortelius, 1982). The extant *Diceros* (Black rhino) distributed in the wide range habitats such as montane forest, through savanna woodland, bush and thicket, medium grassland－woodland ecotones, scattered tree grassland and semi-desert, to desert (Hillman-Smith and Groves, 1994). Therefore, the discovery of *Diceros* from the Nakali and Namurungule Formations coincide with the paleoenvironment of the Nakali and Samburu Hills during the early Late Miocene as noted by Fukuchi *et al*. (2008). In contrast, *C. pattersoni* shows the features that grazer habitat (Fortelius, 1982) such as relatively high crown height, coronal cement and flattened occlusal surface.

Both browsing (*Diceros* and *Brachypotherium*) and grazing (*Chilotheridium*) dwellers are co-existed from the same formations. According to Uno *et al*. (2011), the stable carbon isotope analysis shows that bimodal number of the carbon isotope of rhinocerotids, namely C_3 -dominated and C_4-dominated during the early Late Miocene, suggesting that there would be the niche partitioning at the period. The present study confirms this hypothesis.

CHAPTER 4

Miocene rhinocerotid faunal change in the sub-Saharan East Africa

In this chapter, the rhinocerotid fossil records and the paleoenvironments in sub-Saharan Africa during the Miocene are reviewed. Additionally, the relationships between the faunal changes of rhinocerotid and paleoenvironmental transition are discussed.

4-1. Materials and methods

In this study, the Miocene rhinocerotid fossil records in sub-Saharan East Africa are compiled (Figures 11 and 12). These are followed by direct observation or many references. The paleoenvironmental studys of sub-Saharan Africa are follwed by the references. Geological age is followed by Gradstein *et al*. (2012). The Faunal Sets, which is the African mammalian biostratigraphy, is based on Pickford (1981) and Pickford and Morales (1994).

4-2. Discussion

The Miocene rhinocerotid fauna in Sub-Saharan East Africa are classified three phases proceeded by "Early-Middle Miocene fauna" and followed by "faunal renewal period" and by "Late Mio.-Pliocene fauna" in this study (Figure 12).

"Early-Middle Miocene fauna".—In this phase, typical Early to Middle Miocene African endemic species and several immigrant taxa (or its discendant taxa) were appeared. The phase is defined from first fossil occurrencies of *T. actirostratum*, *B. snowi*, *R. leakeyi* and *O. napakense* to the first fossil occurrence of *B. lewisi* and the last fossil occurrence of *R. leakeyi*. During Faunal Set I, the first records of the rhinocerotid in sub-Saharan East Africa are recognized. In this period, both African and Eurasia continents were connectd by the landbridge, which is the event known as "*Gomphotherium* landbridge" or "Proboscidenan datum" (e.g. Bernor, 1983; Rögl, 1999; Koufos *et al*., 2005; Sen, 2013). Several species would migrate from Eurasia into Africa in this period (e.g. Koufos *et al*., 2005; Geraads, 2010; Sen, 2013).

By Faunal Set II, five species in three tribe appeared in sub-Saharan East Africa such as *T. actirostratum*, *C. pattersoni*, *B. snowi*, *R. leakeyi* and *O. napakense*. Antoine *et al*. (2010) pointed out the similarity of the early Miocene rhinocerotid fauna in tribe level between Bugti Hills in Pakistan and sub-Saharan East Africa. Therefore, there was obviously exchange between the Afro-Eurasina continents.

In Faunal Set III, *Plesiaceratherium* sp. was reported from the Middle Miocene (ca. 15 Ma) locality of Nyakach in Kenya (Geraads, 2010). Many species of *Plesiaceratherium* has been reported from the Early to Middle Miocene localities in Eurasia (e.g. Yan and Heissig, 1986; Heissig, 1999; Fukuchi and Kawai, 2011; Antoine and Becker, 2013). The one of the oldest fossil record of genus *Plesiaceratherium* has been reported from the earliest Miocene (MN1-MN2; 23-20 Ma) locality of Pakistan (Antoine *et al*., 2010), and several species of the genus immigrated into Europe during the late Early Miocene (MN4; 18-17 Ma) (Heissig, 1999). There are two hypothesis of immigration timing of *Plesiaceratherium* sp. into Africa.

One is the Middle Orleanian (18.0-17.0 Ma: Koufos *et al*., 2005). A landbridge was appeared between the Afro-Eurasina continents, and faunal exchange occurred (Koufos *et al*., 2005). Made (1999) also proposed a faunal exchange that named "Crenodont event" (17.5 Ma), in which creodont *Hyainailouros* and proboscidean *Gomphotherium* were immigrated from Africa to Europe and Eurasina originated Soricids, the lutrine *Luogale*, the herpestid *Herpestides*, the ursid *Hemicyon*, the suid *Kenyasus*, and the giraffoid *Climacoceras*, were occurred in Africa. Although, there is no fossil record of *Plesiaceratherium* in that time interval, *Plesiaceratherium* would also immigrate into Africa in this timing. Alternative hypothesis of the immigration was occurred in the late Orleanian (17.0-15.0 Ma). According to Koufos *et al*. (2005), the sediments in the eastern Mediterranean of this period yield the African elements fossils. Therefore, it is considered that African continents shortly connected to the Eurasia and faunal change was occurred between both continents (Koufos *et al*., 2005). Made (1999) noted that a hominid *Griphopithecus* ? immigrated from Africa to Europe ("Hominid event"; 15.5 Ma). Ancestral relatives of African *Plesiaceratherium* might come into Africa at this period. Further materials are needed to discuss the timing of the immigration of *Plesiaceratherium* from Eurasia.

The fossil record of *B. snowi* is absent by the end of the Orleanian. In contrast, *B. minor* presented at about 16.5 Ma. Since then, there is a long gap of fossil recorded of *Brachypotherium* between 15 to 12 Ma. Geraads and Miller (2013) noted that *B. minor* is more closely related to *B. lewisi* than *B. snowi* based on the skull morphology, the second immigration of *Brachypotherium* in Africa, although the relationships between the African and Eurasian taxa are not well known yet.

This diversity of the rhinocerotid during the Early to Middle Miocene might also be related to the forested paleoenvironment. The cheek teeth of *T. acutirostratum*, *B. snowi*, *R. leakeyi* and *P. mukirii* have the following features: brachydont teeth, concave occlusal surface, absence of the enamel folding and no coronal cement. These tooth features indicate a browsing habitat (Fortelius, 1982). In sub-Saharan East Africa, forested habitat were dominated in many the Early to Middle Miocene localities (Figure 12). These forest and closed environments confirm that the habitat of the rhinocerotid in the Early to Middle Miocene.

"Faunal renewal period".—This phase is defined by the first fossil records of *B. lewisi* and last fossil records of *R. leakeyi*, *C. pattersoni* and *K. bishopi*. During this period, fossil record of *C. pattersoni*, which is a taxon of "typical Early-Middle Miocene fauna", is absent at around ca. 9.5 Ma. In contrst, *B. lewisi* and *Diceros*, which are the taxa of "typical Late Mio-Pliocene fauna" (see below), appeared during this period. By the late part of Faunal Set IV (13 to 12.5 Ma), the fossil records of *T. actirostratum*, *R. leakeyi* and *P. mukirii*, whose are probably browsing dweller, are absent. It might be due to increase the more open environment (e.g. woodland) in sub-Saharan East Africa. In Astaracian to Vallesian, forest dominant environments in sub-Saharan East Africa changed to open environments and were more seasonally (e.g. Jacobs *et al*., 1999; Feakins *et al*., 2013; Wichura *et al*., 2015). Since faunal Set V, more open habitat taxa were presented in sub-Saharan East Africa as discussed below. Bonnefille (2010) investigated the pollen fossil assemblages in the marine core from the site 231 at the Gulf of Aden (Figure 11A). According to this study, the pollens of Chaenopodiaceae and Amaranthaceae that are widespread in arid lands, were increased

later about 10 Ma. Furthermore, the abundance of pollens of Poaceae which reflect the environment of savanna and open woodland, were recognized at 10 Ma, suggesting that the presence of savanna and open land in the East Africa. Sedimentological evidences suggest that the crimatic shift (from a dry climate with seasonal precipitation to a climate with strong seasonality) was occurred around 10 Ma (Sakai *et al*., 2010). Consequently, the divergence of the open land paleoenvironment and increasing of the seasonality in the sub-Saharan East Africa might be affected the absence of browsing taxa.

"Typical Late Mio.-Pliocene fauna".—This phase is defined by the last occurrencies of *C. pattersoni* and *K. bishopi* to the end of the Late Miocene. The fossil records of the Early to Middle Miocene taxa are absent, wharas, those of genus *Diceros* increse and second rare former *Brachypotherium lewisi* in this phase.

According to the tooth enamel and pedogenic carbon isotopic analysis, the paleodiet of the various large mammlas, including Rhinocerotidae, changed to mix of C_3/C_4 or C_4–dominated habitats by late Late Miocene (Cerling *et al*., 2003; Uno *et al*., 2011). Cerling *et al*. (1997) proporsed that dry climatic condition were expanded globally since the late Late Miocene. Consequently, open environment (woodland or savanna) are developed during the Late Miocene in sub-Saharan East Africa. The diversity of *Diceros* was increased during the Late Miocene. Although, *Diceros* is browsing dweller, extant *D. bicornis* adapted various habitats. Thus, if the habitats of extinct species *Diceros* were similar to those of extant black rhino, their habitats are concordant with the estimatd environment of the localities in sub-Saharan East Africa. The paleoenvironmental changes in the Middle to Late Miocene might have affected the terrestrial mammalian faunal composition of the Late Miocene in sub-Saharan East Africa. For example, Nakaya (1994) analyzed the Neogene East African faunas and suggests that the mammalian faunal assemblage has been changed from woodland fauna to openland fauna during Astaracian to Turolian. Leakey *et al*. (1996) revealed the mammalian fauna in Lothagam (Late Miocene) and compared them with other Late Miocene fauna, suggesting that the Lothagam fauna would be transitional earlier Miocene and the derived Plio-Pleistocene faunas. Sanders *et al*. (2010) summarized the fossils of Proboscidea in Africa and they noted that faunal turnovers during the Late Miocene due to change of the paleoenvironment in Africa. Thus, the rhinocerotid faunal change would also been affected the environmental change as in the case of other terrestrial mammalian fauna.

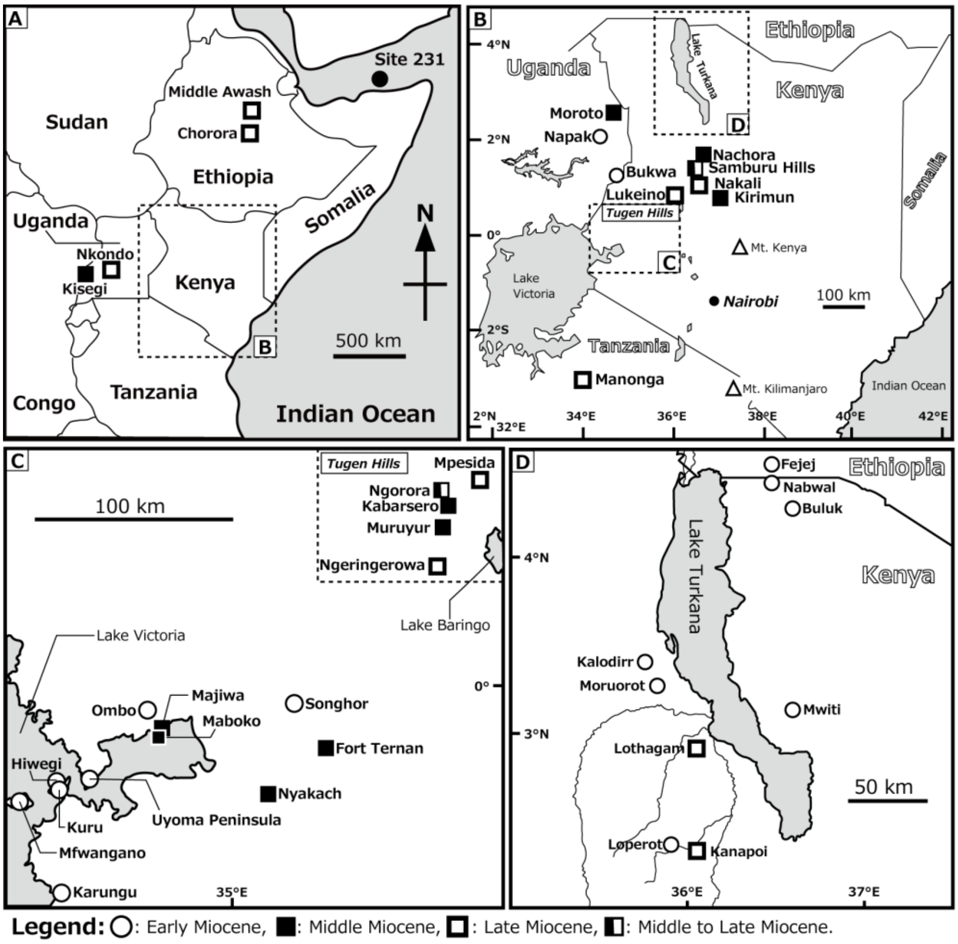


Figure 11. The fossil localities of the Miocene rhinocerotid in sub-Saharan East Africa. **a**, Map showing the around sub-Saharan East Africa; **b**, The fossl localities in Kenya and around area (modified from Sawada *et al*., 1998); **c**, The fossil localities around the eastern part of the Lake Victoria and Tugen Hills (modified from Pickford, 1983); **d**, The fossl localiies around Lake Turkana (modified from Leakey *et al*., 2011).

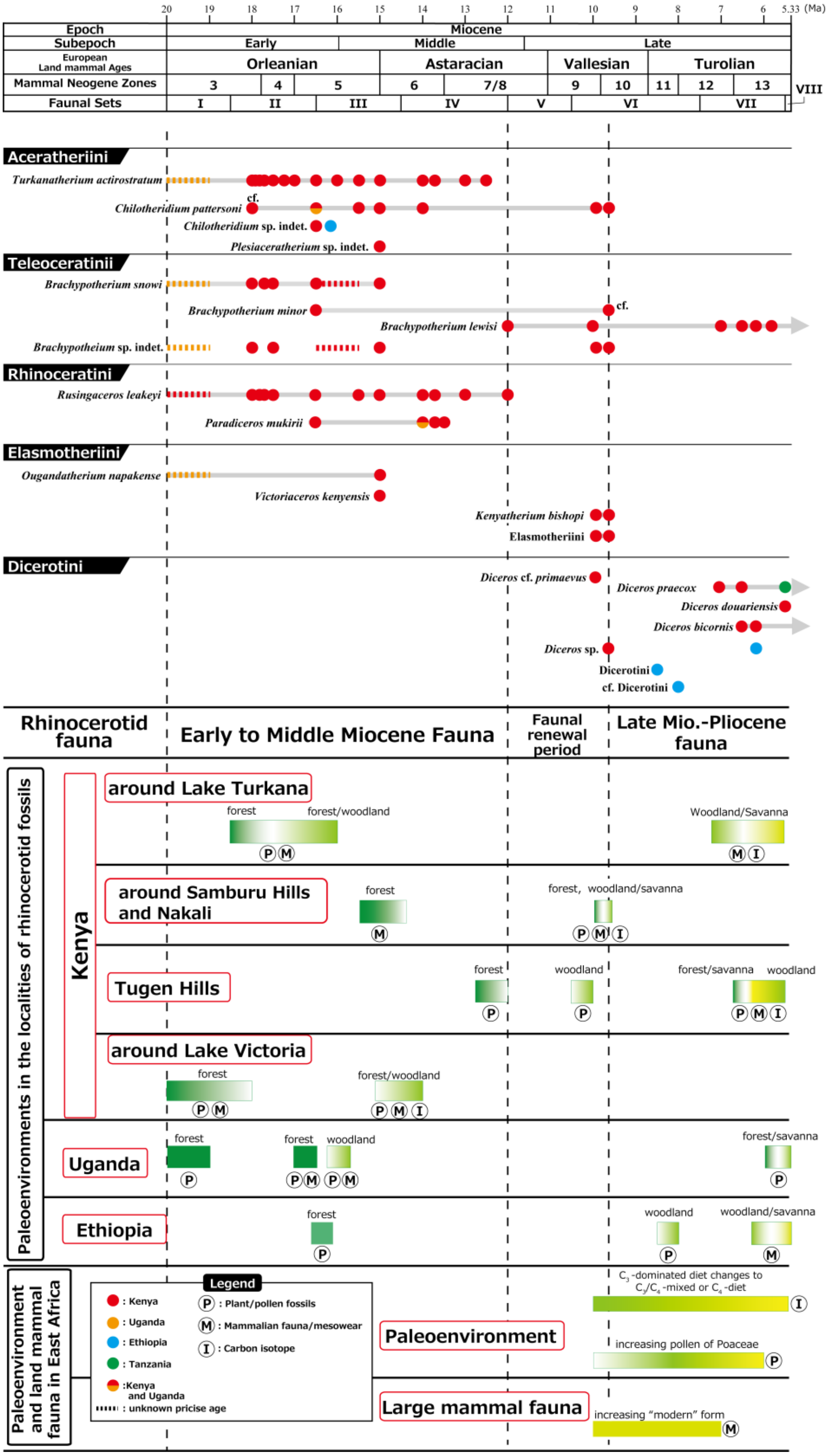


Figure 12. Temporal ranges and paleoenvironments of the Miocene Rhinocerotidae in sub-Saharan East Africa.

CHAPTER 5

Conclusion

The rhinocerotid fauna of the Namurungule and Nakali Formations is composed of "Early to Middle Miocene" and "Late Miocene" forms. The estimated habitats of rhinocerotid fauna from both the Formations confirm the environments of the Namurungule and Nakali Formations.

The faunal change of the Miocene rhinocerotid in sub-Saharan East Africa was also discussed. In the Early Miocene, Africa and Eurasia continents were connected and the first immigration of rhinocerotid was occurred. The forest-dominated environment had expanded in the sub-Saharan East Africa and browsing habitat taxa (including *Rusingaceros leakeyi*, *Turkanatherium acutirostratum*, *Brachypotherium snowi* and *Paradiceros mukirii*) were dominated in the Early Miocene.

During 17-15 Ma, a landbridge developed between the Eurasia and Africa continents, and some Eurasian species such as *Plesiaceratherium* sp. would migrate into Africa.

Since about 15 Ma, the environment in sub-Saharan East Africa would begin to more open habitat. Therefore, browsing habitat taxa were decrease. The latest Middle to early Late Miocene was the translation period of the rhinocerotid fauna in sub-Saharan East Africa. Fossil records of primitive taxa (Early to Middle Miocene taxa) were absent and of derived taxa (Late Miocene to Pliocene taxa) which adapted in more open environment, were presented in this period.

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