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# Additional specimens of *Diceros* (Perissodactyla, Rhinocerotidae) from the Upper Miocene Nakali Formation in Nakali, central Kenya

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**ABSTRACT**
An upper incisor and upper and lower cheek teeth of Rhinocerotidae from the Upper Miocene of Nakali in central Kenya are described. Those specimens are identified as *Diceros* sp. The present study confirms the presence of *Diceros* in sub-Saharan East Africa during Vallesian as noted by several studies. The present result and the fossil records of *Diceros* in Africa and Eurasia suggest that *Diceros* might have migrated to Eurasia from Africa by Vallesian, although more fossil records and detailed phylogenetic analysis of *Diceros* are needed to discuss this hypothesis.

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*Diceros*; Kenya; Late Miocene; Nakali; Rhinocerotidae; Samburu Hills

## Introduction

The extant species of African Rhinocerotidae, *Diceros bicornis* (black rhino) and *Ceratotherium simum* (white rhino), belong to the tribe Dicerotini (Heissig 1989). The fossils of this tribe have been described from early Miocene to Pleistocene localities of Africa and Eurasia so far (e.g. Deng and Qiu 2007; Giaourtsakis et al. 2009; Geraads 2010). In Africa, many fossil records of the species of the Dicerotini were known from Plio-Pleistocene localities (e.g. Geraads 2010). In contrast, early late Miocene (Vallesian; The European Mammal Neogene zones: Steininger 1999) fossil records of them were limited. Especially, in sub–Saharan East Africa, Vallesian records are poorly known.

Since 2002, a Japan-Kenya joint expedition team has been conducting research in Vallesian locality of Nakali in central Kenya (Nakatsukasa 2009). Various terrestrial mammal fossils have been discovered from this locality, including diverse primate taxa such as two large hominoids (*Nakalipithecus nakayamai* and another different hominoid), cercopithecoids, non-cercopithecoid small catarrhines and a prosimian (Aguirre and Guérin 1974; Aguirre and Leakey 1974; Flynn and Sabatier 1984; Morales and Pickford 2006; Kunimatsu et al. 2007, 2016, 2017; Nakatsukasa et al. 2010, Tanabe et al. 2013; Handa et al. 2015, 2017; Tsubamoto et al. 2015; Tsubamoto et al. Forthcoming). Rhinocerotid fossils have been found from Nakali since 1970s. Aguirre and Guérin (1974) described a few isolated upper cheek teeth as *Kenyathreium bishopi*. Recently, several new materials have been described from Nakali such as *Chilotheridum pattersoni* and *Samburuceros ishidai* (Handa et al. 2015, 2017).

Kunimatsu et al. (2007) listed *Diceros* sp. in their faunal list of Nakali. Fukuchi et al. (2008) referred to some rhinocerotid specimens from Nakali as *Diceros* sp., but this is a conference abstract without any figures and detailed descriptions. Accordingly, the majority of rhinocerotid specimens newly collected from Nakali by the Japan-Kenya joint expedition team have yet to be described.

The fossil records from Nakali will contribute to the discussion of the paleobiogeography of *Diceros* in sub-Saharan East Africa during Vallesian. Here, we describe the additional specimens of *Diceros* from Nakali and discuss the paleobiogeography of *Diceros*.

## Geological setting

Nakali is situated in the northeast part of Baringo County, 50 km west of Mararal (Figure 1). It is 60 km south of the Samburu Hills, another Vallesian locality which yielded a large hominoid species, *Samburupithecus kiptalami* (Ishida and Pickford 1997). The Upper Miocene Nakali Formation is distributed in this locality (Kunimatsu et al. 2007; Sakai et al. 2013). The thickness of this formation is about 340 m and is divided into the Lower, Middle, and Upper Members in ascending order (Kunimatsu et al. 2007; Sakai et al. 2013). The Lower and Upper members are composed of lacustrine and fluvio-lacustrine deposits. The Middle Member consists of a pyroclastic flow deposit. *Nakalipithecus nakayamai* was collected from the Upper Member (Kunimatsu et al. 2007). The rhinocerotid specimens described in this article were found in both 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 correlates with Chron C5n.1r (9.88–9.92 Ma) (Kunimatsu et al. 2007).

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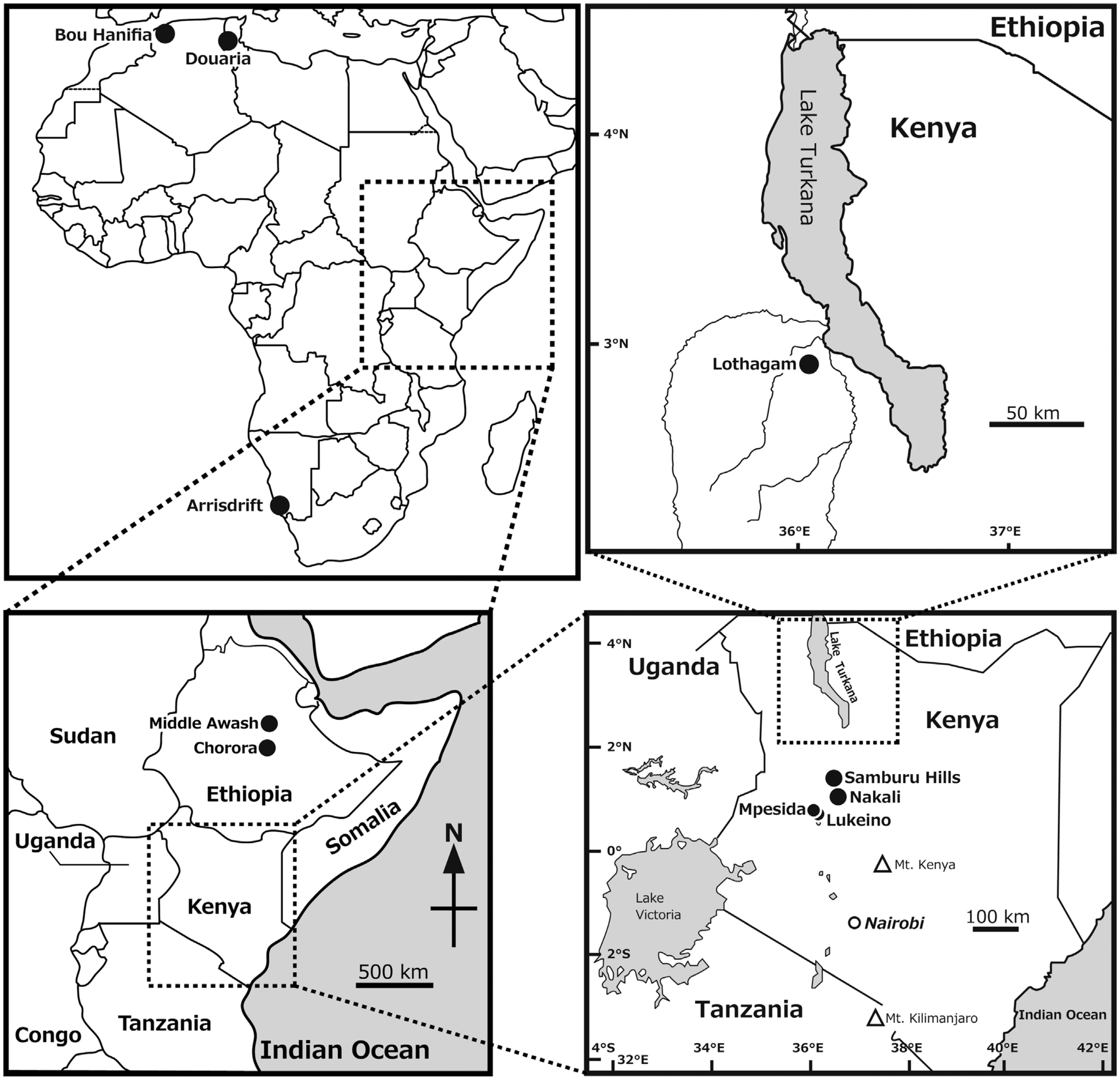


**Figure 1.** Map showing the selected localities of Miocene fossil records of *Diceros* in Africa (modified after Leakey et al. 2011; Handa et al. 2015).

## Materials and methods

All the studied specimens are stored in the paleontology section of the Earth Sciences Department, 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) and Antoine et al. (2010) (Figure 2).

The studied specimens were compared with previously known species of *Diceros* from Africa and Eurasia. Comparisons were carried out with the collections housed in some museums and a university, and with the literature (Table 1).

The European Mammal Neogene zones are based on Steininger (1999): Agenian (MN1–2, early/lower Miocene), Orleanian (MN3–5, middle Miocene), Astaracian (MN6, MN7/8, middle Miocene), Vallesian (MN9–10, late/upper Miocene), and Turolian (MN11–13, late/upper Miocene).

*Abbreviations*. I, upper incisor; M, upper molar; m, lower molar; P, upper premolar; p, lower premolar; DP, upper delicious premolar; FT, Fort Ternan, Kenya; KP, Kanapoi, Kenya; NA, Nakali, Kenya; RU, Rusinga, Kenya; SH, Samburu Hills, Kenya; MN, the European Neogene Mammal Zones; FSL, Faculté des Sciences, Lyon, France; KNM, National Museums of Kenya in Nairobi, Kenya; MNHN, Muséum National d'Histoire Naturelle, Paris, France; OMNH, Osaka Museum of Natural History, Osaka, Japan; UCBL, Université Claude Bernard-Lyon I, Lyon, France.

## Systematic paleontology

Family **Rhinocerotidae** Owen, 1845

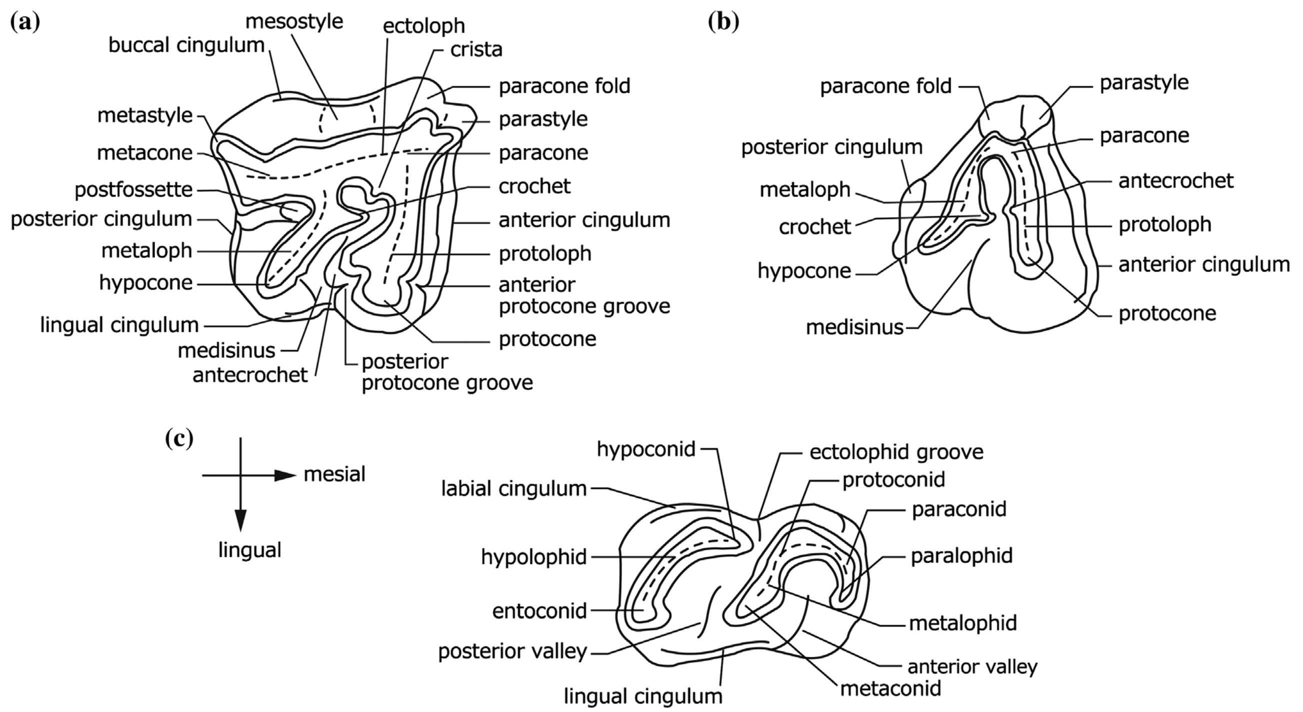


**Figure 2.** Terminology of the teeth of Rhinocerotidae (Terminology follows Guérin 1980 and Antoine et al. 2010. Illustrations are modified after Fukuchi 2003). a, upper molar (M1 and M2); b, upper molar (M3); c, lower cheek tooth.

**Table 1.** Comparative materials of *Diceros* from Afro-Eurasia.

| Species | Age | Direct observation | Reference |
|---|---|---|---|
| *Diceros australis* | Early Miocene | | Guérin (2000, 2003) |
| *Diceros primaevus* | Late Miocene | MNHN | Arambourg (1959) |
| *Diceros douariensis* | Late Miocene | UCBL | Guérin (1966); Giaourtsakis et al. (2009) |
| *Diceros praecox* | Late Miocene to Late Pliocene | KNM | Hooijer and Patterson (1972); Geraads (2005) |
| *Diceros bicornis* | Late Miocene to Recent | OMNH | |
| *Diceros neumayri* | Late Miocene | | Geraads (1988); Giaourtsakis et al. (2006); Giaourtsakis (2009); Antoine et al. (2012) |
| *Diceros gansuensis* | Late Miocene | | Deng and Qiu (2007) |
| *Diceros* sp. | Late Miocene | KNM | Fukuchi et al. (2008) |

Subfamily **Rhinocerotinae** Owen, 1845
Tribe **Dicerotini** Groves, 1983
Genus ***Diceros*** Gray, 1821

## *Type species*

*Diceros bicornis* (Linnaeus 1758)

## *Diagnosis*

Upper cheek teeth with concave occlusal surface and irregular enamel thickness; premolars with developed paracone fold and occasionally present faint metacone fold; molars with no medifossette, presence of the paracone fold, sharp buccal apices of the metacone, paracone cusps; anterior protocone groove, no posterior protocone groove and simple crochet; M3 with triangular shape and lacking crista and medifossette (Giaourtsakis et al. 2009; Geraads 2010).

*Diceros* sp. indet.
(Figures 3–5; Tables 2–3)

## *Materials*

left I1 (KNM-NA 52139), right P3 (KNM-NA 52150), right P4 (KNM-NA 52149), right M1 (KNM-NA 52143), left M1 (KNM-NA 52139), left M1 or M2 fragment (KNM-NA 52151), right M3 (KNM-NA 52139), left M3 (KNM-NA 52139), left p2 (KNM-NA 52146; KNM-NA 52147), left p4 (KNM-NA 52144), left m1–m3 (KNM-NA 52139).

## *Description*

KNM-NA 52139 is composed of an upper incisor (possibly left I1), left M1–M2, both side of M3, and left m1–m3 (see below). Of these, this incisor is triangular shape in both mesio-distal view. The crown is covered with dark brown colored enamel. The presence of wear facet is uncertain. The cross section of the tooth is mesio-distally compressed oval shape.

KNM-NA 52150 is a well worn right P3. The tooth is molariform. The buccal wall of the ectoloph is almost flat at this wear stage. There is a weak paracone fold. The protoloph connects

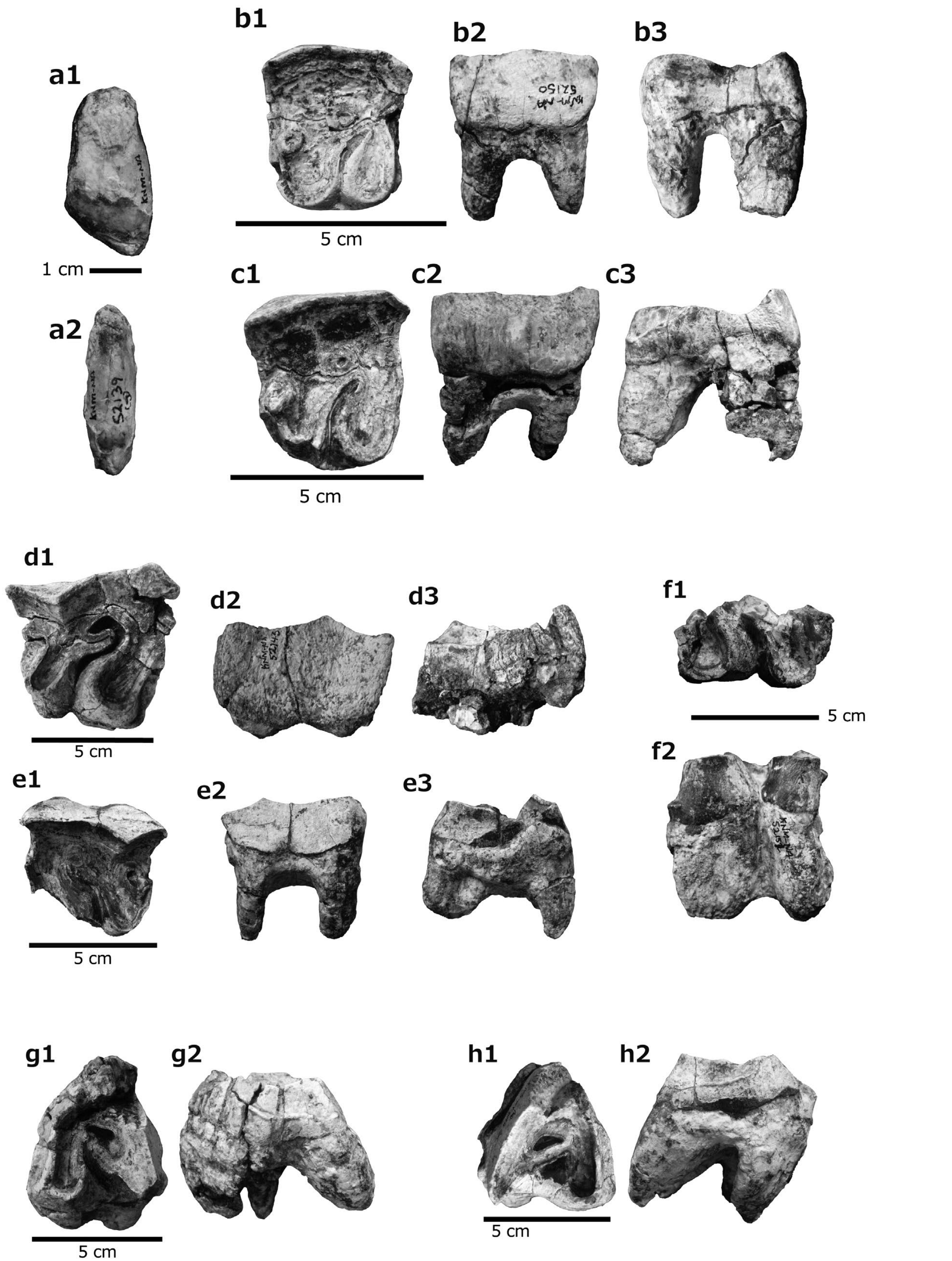


**Figure 3.** The upper incisor and upper molars of *Diceros* sp. from the Nakali Formation. a, KNM-NA 52139 (possibly left I1). a1, lingual view; a2, labial view; b, KNM-NA 52150 (right P3). b1, occlusal view; b2, buccal view; b3, mesial view; c, KNM-NA 52149 (right P4). c1, occlusal view; c2, buccal view; c3, mesial view; d, KNM-NA 52143 (rigtht M1). d1, occlusal view; d2, buccal view; d3, mesial view; e, KNM-NA 52139 (left M1). e1, occlusal view; e2, buccal view; e3, mesial view; f, KNM-NA 52151 (left M1 or M2). f1, occlusal view; f2, lingual view; g, KNM-NA 52139 (left M3). g1, occlusal view; g2, mesial view; h, KNM-NA 52139 (right M3). h1, occlusal view; h2, mesial view.

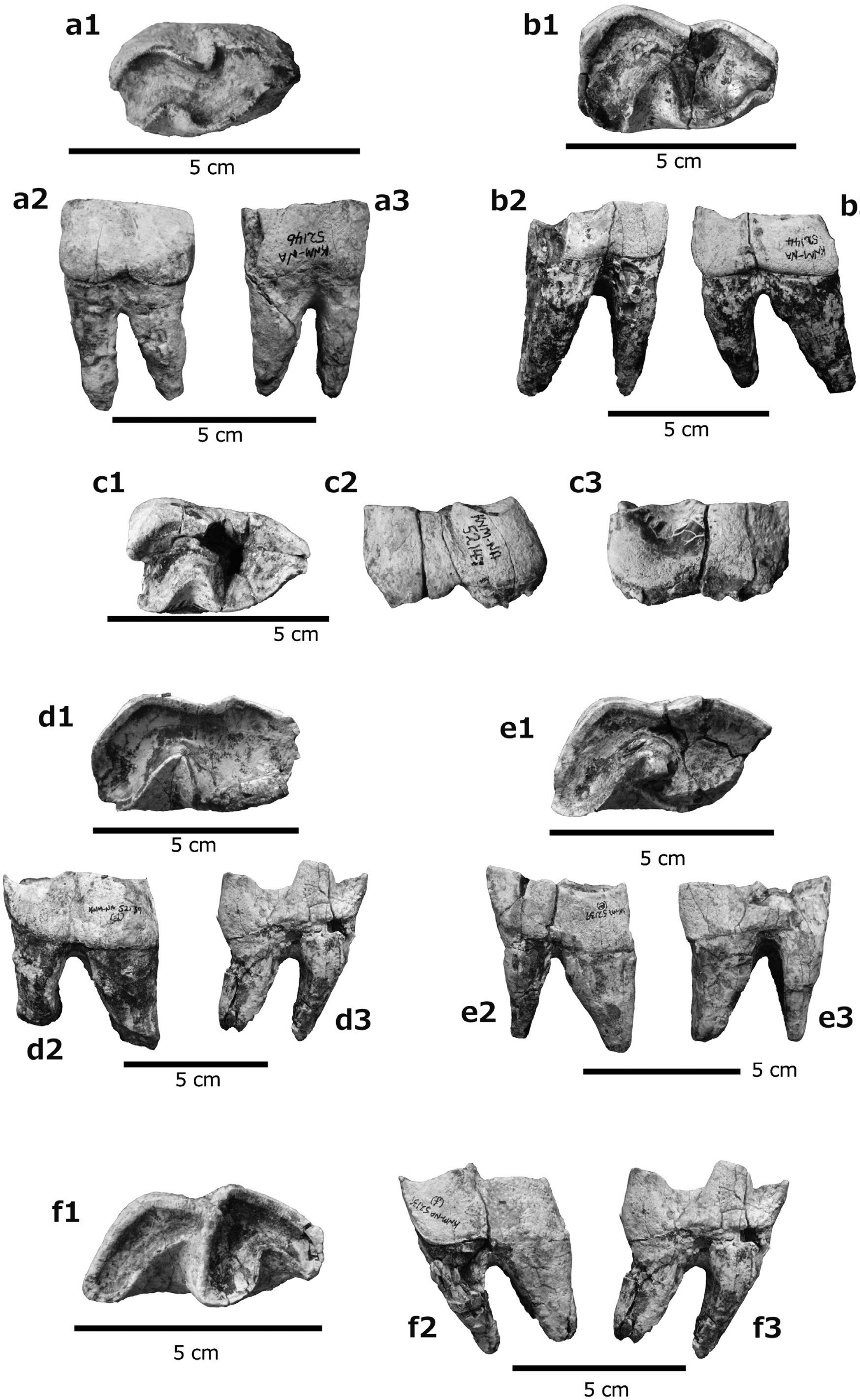


**Figure 4.** The lower cheek teeth of *Diceros* sp. from the Nakali Formation. a, KNM-NA 52146 (left p2); b, KNM-NA 52144 (left p4); c, KNM-NA 52147 (left p2); d, KNM-NA 52139 (left m1); e, KNM-NA 52139 (left m2); f, KNM-NA 52139 (left m3). 1, occlusal view; 2, buccal view; 3, lingual view.

the ectoloph, and is oriented lingually. The lingual side of the protocone and metacone is rounded. The crochet connects the protoloph at this wear stage. The anterior cingulum is low. There is no buccal cingulum, whereas the short lingual cingulum is on the entrance of the medisinus. The occlusal surface is weakly concave in both mesio-distal views.

KNM-NA 52149 is a well worn right P4, which belongs to the same individual as KNM-NA 52150. Like P3, it is molarifom. The tooth has an almost flat ectoloph as in KNM-NA 52150. The protoloph is directed lingually. The protocone is not constricted, and its lingual wall is rounded. A slightly developed paracone fold is preserved at this wear stage. The parastyle is short. The crochet extends mesially and connects the protoloph as in KNM-NA 52150. There is a trace of the postfossette. The low anterior cingulum is on the mesial margin of the protocone. There is no buccal cingulum. The lingual cingulum is short. The occlusal surface is concave.

KNM-NA 52143 is a well worn isolated right M1. There is no coronal cement. The ectoloph is weakly concave behind the paracone fold. The paracone fold developed and faded out basally. Protoloph and metaloph are oriented disto-lingually. The mesio-distal width of the protoloph is wider than that of the metaloph. The lingual wall of the cusps is rounded. The anterior protocone groove is weak. There is no posterior protocone groove. The hypocone is not constricted. The cusp shape of the metacone is sharp in buccal view. The parastyle is weak. The metastyle is short. The simple crochet projects mesially, and is not in contact with the protoloph at this wear stage. There are no antecrochet and crista. The low anterior cingulum extends from the mesial side of the paracone to protocone. The posterior cingulum is also low. The postfossette is narrow at this wear stage. There are no buccal and lingual cingula. The occlusal surface of the tooth is concave.

The cheek teeth of KNM-NA 52139 include left M1, right and left M3s, and lower m1–m3, of which are same individual. Left M1 is missing a part of the protoloph and mesio-buccal portions of the crown. The tooth is well worn down. Thus, the presence of the crochet is uncertain. The medisinus is very narrow at this wear stage. Both lophs extend disto-lingually. The lingual wall of the hypocone is rounded. The metacone is distinct. The small postfossette is preserved. The buccal and lingual cingula are absent. The right M3 lacks the buccal part. The tooth is triangular in occlusal view. The protoloph is straight and extends lingually. The ectometaloph is directed disto-lingually. The protocone is not constricted, and its lingual wall is rounded. The crochet projects mesially, and connects the protoloph at this wear stage. The low anterior cingulum runs along the protoloph. The tubercle-like posterior cingulum is on the disto-lingual margin of the ectometaloph. There is no lingual cingulum. The left M3 lacks the buccal part; its morphology is similar to that of right M3.

KNM-NA 52151 is a lingual part of left M1 or M2. The lingual wall of both cusps is rounded. The protocone and hypocone are not constricted. There is a part of the crochet. The lingual cingulum is absent. The lingual part of the posterior cingulum is preserved. There is no coronal cement.

KNM-NA 52146 and KNM-NA 52147 are left p2s. These are similar to each other in having a reduced paralophid, shallow ectolophid groove, and no buccal and lingual cingula. There is no coronal cement.

KNM-NA 52144 is probably left p4, which is well worn down. Its morphology is very similar to those of other lower cheek teeth from Nakali described here in having no coronal cement, reduced paralophid, shallow ectolophid groove, and no labial and lingual cingula.

KNM-NA 52139 includes m1–m3. These teeth are very similar in morphology to each other. The hypolophid is directed disto-lingually. The ectolophid groove is relatively shallow at this wear stage. The posterior valley is V-shaped in occlusal view. There is weak mesio-labial cingulum. In contrast, the lingual cingulum is absent.

## Comparisons

The upper premolars described here are molarifom and the upper molars have no constricted protocone. In this regard, these cheek teeth are distinct from those of the tribes Aceratheriini, Teleoceratini and Elasmotheriini from Africa (e.g. Deraniyagala 1951; Hooijer 1971; Hooijer and Patterson 1972; Geraads 2010; Geraads et al. 2012, 2016; Geraads and Miller 2013), eliminating a possibility that the present specimens belong to these tribes.

The specimens described here are also different from tribe Rhinocerotini from Africa such as *Rusingaceros leakeyi* and *Paradiceros mukirii*. A species of the tribe Rhinocerotini, *Rusingaceros leakeyi* has been found in several Orleanian to Astaracian localities in Africa (Hooijer 1966; Geraads 2010). Originally, this species was described as *Dicerorhinus leakeyi* (Hooijer 1966), then transferred to *Rusingaceros* on the basis of the skull and dental morphology by Geraads (2010). The present specimens discriminated from *R. leakeyi* (KNM-RU 2821) in having smaller upper incisor, molarifom upper premolars, and the long crochet and narrow medisinus on the upper cheek teeth.

Another species of the Rhinocerotini in Africa, *Paradiceros mukirii*, had been considered as a close relative of *Diceros*. Many specimens, which include skulls, mandible, and postcrania, have been found from middle Miocene locality of Fort Ternan in Kenya (Hooijer 1968; Geraads 2010). Giaourtsakis et al. (2009) pointed out that majority of specimens of *P. mukirii* could belong to a taxon of the Rhinocerotini (possibly '*Dicerorhinus*' *leakeyi* in his context = *Rusingaceros leakeyi*) based on the skull and mandibular morphology. The present specimens are distinguished from *P. mukirii* from Fort Ternan (KNM-FT 2870, KNM-FT 2873, and KNM-FT 3328) in having reduced lingual cingulum on the upper premolars, long crochet on both the upper premolar and molars, and the absence of the protocone constriction of the upper cheek teeth.

The tribe Dicerotini includes two genera, namely *Diceros* and *Ceratotherium*. The present specimens show several affinities with the extinct and modern species of genus *Diceros* in having the following dental morphologies: upper cheek teeth with concave occlusal surface, molars with no medifossette, presence of the paracone fold, sharp buccal apices of the paracone and metacone cusps; anterior protocone groove, no posterior protocone groove and simple crochet; M3 with triangular shape and lacking crista and medifossette (Giaourtsakis et al. 2009).

In contrast, the present specimens differ from modern *Ceratotherium* (Giaourtsakis et al. 2009) in having the upper teeth with no coronal cement, transversely oriented proto- and metalophs, absence of the medifossette, undeveloped mesostyle, the presence of the paracone fold, the lower premolars without medifossette. Thus, we conclude that the specimens described here are identified as *Diceros*.

Fukuchi et al. (2008) reported a few specimens from the Vallesian localities of Nakali and Samburu Hills as *Diceros*: an adult skull with DP1 to M3 (KNM-NA 46987) and a fragment of maxilla with tooth row (KNM-SH 15835) whose are under study by Dr. Fukuchi. KNM-NA 46987 is a well-preserved skull that has the following characters of *Diceros*: wide and rounded rostral tip of nasals; frontals with strong supraorbital processes; absence of the postorbital processes; lower borders of the orbit sloping downwards. Fukuchi et al. (2008) noted that this specimen is distinguished from *D. praecox* and *D. douariensis*. The present upper cheek teeth are very similar to those of KNM-NA 46987 in having the premolars with the crochet, weakly developed paracone fold that fade away basally, rounded protocone and hypocone, absence of the protocone constriction, and the molars with distolingually oriented proto- and metalophs, developed crochet, absence of the crista and antecrochet, no lingual protocone groove, and absence of coronal cement. However, the lingual cingulum of the upper cheek teeth of KNM-NA 46987 is more developed than those of the present specimens. The present specimens closely resemble the teeth of *Diceros* sp. from Nakali reported by Fukuchi et al. (2008). Although there are several differences of the dental dimensions, development of paracone fold and lingual cingulum on the upper cheek teeth, they will not exceed the range of individual variation within a species.

As noted above, seven species of *Diceros* are know from Miocene localities in Afro-Eurasia, namely *D. primaevus*, *D. praecox*, *D. douariensis*, *D. australis*, *D. bicornis*, '*D*'. *neumayri* and *D. gansuensis*. *Diceros primaevus* have been originally described as *Dicerorhinus primaevus* from Vallesian locality of Bou Hanifia in Algeria (Arambourg 1959) and was transferred to the species as the genus *Diceros* by Geraads (1986). The present molars share the following features with *D. primaevus* (MNHN1951-9-219 and MNHN1951-9-222): no crown cement, no lingual protocone groove, straight ectoloph in the premolars, and rounded lingual wall of the protocone. However, the present specimens differ from *D. primaevus* in having weak paracone fold, reduced lingual cingulum in the upper cheek teeth.

*Diceros praecox* has been found from Turolian to the Pliocene localities of sub-Saharan East Africa. This species was originally erected as *Ceratotherium praecox* based on the materials of the Pliocene locality of Kanapoi in Kenya (Hooijer and Patterson 1972). Geraads (2005), however, proposed to transfer *C. praecox* to *Diceros praecox* based on his investigation of new materials from the Pliocene locality of Hadar in Ethiopia. While the present specimens share the following dental features with the holotype of *D. praecox* (KNM-KP 36): no crown cement, absence of the lingual protocone groove on the molars, and the rounded lingual wall of the protocone and hypocone, they differ from KNM-KP 36 in having the reduced lingual cingulum of the premolars, less developed anterior groove of the protocone on the upper molar, and more developed crochet on the upper cheek teeth. The present specimens are similar to *D. praecox* from Hadar in having the upper cheek teeth with strong crochet, no crista, paracone fold that fade away basally, rounded lingual wall of the protocone, and no coronal cement, whereas they differ from Hadar specimens in having reduced lingual cingulum on the premolars, and smaller dental dimensions (Geraads 2005; Table 2).

*Diceros douariensis* was originally called as *Rhinoceros pachygnathus* (Roman and Solignac 1934) and revised as *D. douariensis* by Guérin (1966). The age of Douaria in Tunisia, the type locality of this species, was estimated ca. 9.5 Ma (Guérin 2003), although the age is still controversial (e.g. 7 Ma: Geraads 2010). The present specimens are clearly distinguished from the holotype of *D. douariensis* (FSL16749) in having no crown cement on the upper cheek teeth, absence of lingual protocone groove on the premolar, straight ectoloph, rounded lingual wall of the protocone on the molar, developed metastyle and lingual protocone groove of the M3 (Guérin 1966; Giaourtsakis et al. 2009). Giaourtsakis et al. (2009) described a cranium, a mandible and several cheek teeth of *D. douariensis* from Turolian locality of Kuseralee, Middle Awash in Ethiopia. *D. douariensis* from Kuseralee has the cheek teeth with thin coronal cement layer and weak paracone fold, faint metacone fold and continued lingual cingulum on the upper premolars, and presence of the lingual groove of the protocone on M3 (Giaourtsakis et al. 2009). None of these characters are seen in the present specimens. The present specimens, therefore, are clearly different from the specimen of *D. douariensis* from Kuseralee.

*Diceros australis* was reported from Orleanian locality (ca. 17.5–17.0 Ma: Pickford and Senut 2003) of Arrisdrift in Orange River Valley, Namibia (Guérin 2000, 2003), although this taxonomic affinity is controversial by some researchers (e.g. Geraads 2010). The specimens of *D. australis* include a small occipital, a few mandibles, several isolated teeth and postcranial elements. The present specimens differ from *D. australis* in having the upper premolars with long crochet, lesser developed the paracone fold and reduced lingual cingulum, the upper molars with developed crochet, no lingual cingulum, the presence of short posterior cingulum, no constricted protocone and absence of the lingual cingulum on M3. The dental dimensions of the present specimens are smaller than that of *D. australis*.

*Diceros bicornis* is an extant species of African rhinocerotid. Harris and Leakey (2003) described the oldest fossil record of this species from the Upper Nawata and Apak Members (Turolian) in Lothagam, Kenya, although the Apak specimens are also referred to as *D. praecox* by Geraads (2005). Abundant specimens of this species have been discovered from the Plio-Pleistocene localities of sub-Saharan Africa (Geraads 2010). Compared with the extant specimen (a skeleton stored in OMNH), the present specimens resemble *D. bicornis* in having molariform premolars, rounded both cusps on the molar, presence of the paracone fold, and absence of the antecrochet on the molar. However, they differ from *D. bicornis* in having weak paracone fold of the premolars, absence of the continuous lingual cingulum, no crown cement on the premolars, weak anterior protocone groove and no lingual cingulum on the upper molars, more developed crochet on M1, and weak paracone fold on M1.

Outside Africa, two species of *Diceros* have been reported ('*Diceros*' *neumayri* and *Diceros gansuensis*). '*Diceros*' *neumayri* which taxonomic identification is controversial by some researchers (e.g. in Geraads 2005; the species is assigned as *Ceratotherium neumayri*), has been found in Vallesian to Turolian localities of Eastern Mediterranean area, including Greece (e.g. Geraads 1988; Geraads and Koufos 1990; Giaourtsakis et al. 2006; Giaourtsakis

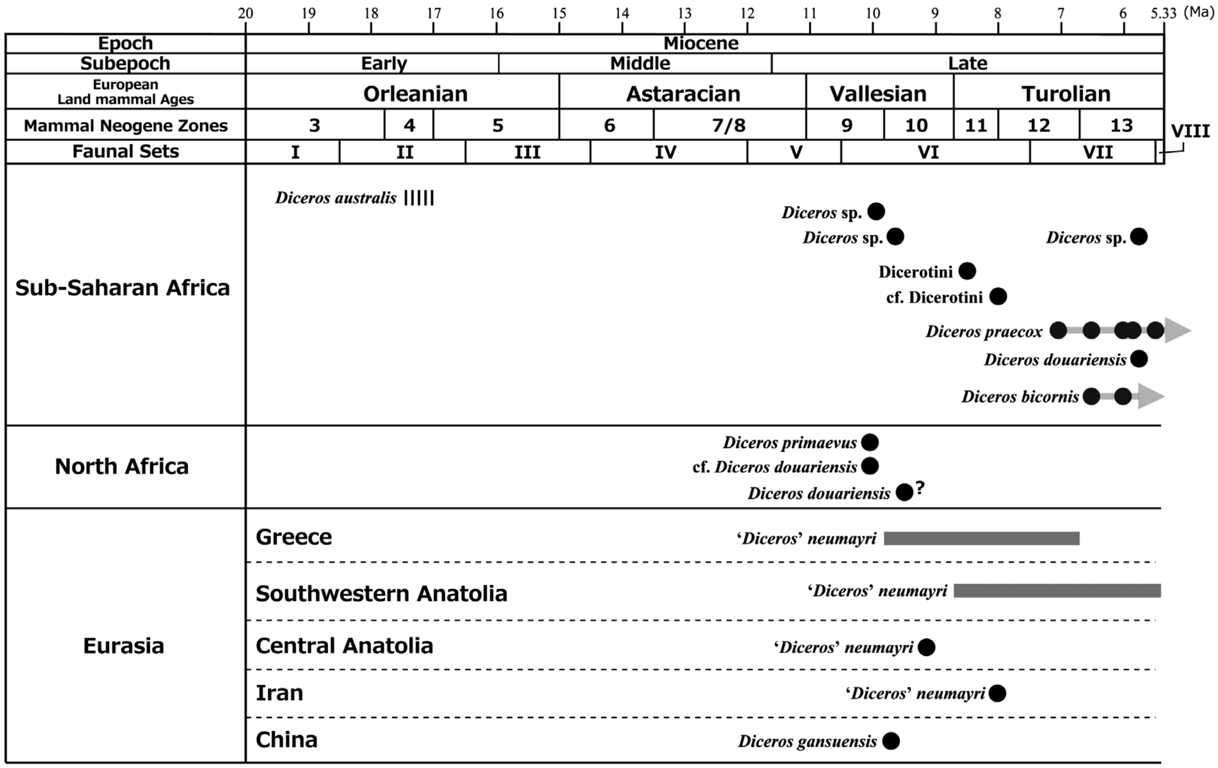


**Figure 5.** Temporal ranges of the species of *Diceros* in Africa and Eurasia during Miocene Period. The fossil records from the following references: *Diceros australis* (Arrisdrift, Namibia: Guérin 2000, 2003); *Diceros primaevus* (Bou Hanifia, Algeria: Arambourg 1959); *Diceros douariensis* (Guérin 1966; Kuseralee (Middle Awash), Ethiopia: Giaourtsakis et al. 2009); cf. *D. douariensis* (Djebel Krechem, Tunisia: Geraads 1989); *Diceros praecox* (Lothagam, Kenya: Hooijer and Patterson 1972, Harris and Leakey 2003; Mpesida, Kenya: Hooijer 1973; Lukeino, Kenya: Pickford and Senut 2001; Manonga-Kiloleli, Tanzania: Geraads 2010; Mabaget, Kenya: Guérin 2011); *Diceros bicornis* (Lothagam, Kenya: Harris and Leakey 2003; Lukeino, Kenya: Guérin 2011); *'Diceros' neumayri* (Greece: Giaourtsakis 2003; southwestern Anatolia, Turkey: Alçiçek 2010; central Anatolia, Turkey: Antoine et al. 2012; Maragheh, Iran: Mirzaie Ataabadi et al. 2013); *Diceros* sp. (Nakali, Kenya: Kunimatsu et al. 2007, Fukuchi et al. 2008, this study; Samburu Hills, Kenya; Fukuchi et al. 2008; Kuseralee (Middle Awash), Ethiopia: Giaourtsakis et al. 2009); *Diceros gansuensis* (Deng and Qiu 2007); Dicerotini (Chorora, Ethiopia: Geraads et al. 2002; Suwa et al. 2015); cf. Dicerotini (Chorora, Ethiopia: Suwa et al. 2015). The fossil locality ages in Africa from the following references: Sawada et al. (1998); Kunimatsu et al. (2007); Geraads (2010). The Faunal Sets is based on Pickford (1981).

2009; Koufos 2016), Turkey (Geraads 1994; Kaya 1994; Antoine and Saraç 2005; Antoine et al. 2012) and Iran (Thenius 1955). The present specimens share the following features with '*D*.' *neumayri* as described by these authors: absence of the lingual protocone groove on the premolars, rounded lingual wall of the proto- and hypocones and no antecrochet of the upper cheek teeth, and absence of buccal cingulum on the upper molars. However, the present specimens differ from '*D*.' *neumayri* in having no crista and lacking coronal cement on the upper cheek teeth, less developed lingual cingulum and lack of the mesostyle on the premolars, weak anterior protocone groove and no mesostyle on M1, no basal pillar on the medisinus of M3 and absence of the mesostyle on the ectometaloph of M3 and smaller dental dimensions (Table 2).

The only East Asian taxon of Dicerotini, *D. gansuensis*, was reported from Vallesian locality of Houshan in Linxia Basin, Gansu, China (Deng and Qiu 2007). The specimens of *D. gansuensis* consist of several crania and mandibles. The present specimens are similar to *D. gansuensis* in having the upper cheek teeth with absence of the antecrochet, no posterior protocone groove, rounded lingual wall of the proto- and hypocones, and absence of the buccal cingulum. The present specimens, however, are different from the cheek teeth of *D. gansuensis* in having the premolars with no crista, long crochet and reduced lingual cingulum, the molars with a lesser developed parastyle, and smaller dental dimensions (Table 2).

The present specimens are clearly different from *D. douariensis*. Contrary, the cheek teeth morphology of other species of *Diceros* are very similar each other. Detailed specific identification of those species has been conducted based on the characteristics of skull (the number of horns, nasal shape, the position of the orbit and angle of the occipital part) and post-crania (e.g. Geraads 2005; Giaourtsakis et al. 2009). Therefore, the present specimens are identified as *Diceros* sp. in the present study. Additional well-preserved materials need to be discovered in order to further discuss specific identification of *Diceros* from Nakali.

An isolated upper incisor (KNM-NA 52139) has been found with cheek teeth. In general, *Diceros* has no upper and lower anterior teeth. Giaourtsakis et al. (2009), however, described a fossil (*Diceros* sp. from Middle Awash, Ethiopia) and extant (*D. bicornis*) specimens of maxillary bone that have upper incisors. Additionally, possibly the oldest species of *Diceros*, *D. australis*, has lower incisor (Guérin 2000, 2003). The present specimen is consistent with those cases. Further materials are needed to discuss the context of the reduction of incisor of the Dicerotini, although the presence of the incisor of fossil species of the Dicerotini is interesting characteristic.

**Table 2.** Measurements (in mm) of upper cheek teeth of *Diceros* sp. from the Nakali Formation and comparative materials.

| Taxon/Number | | P3 | | | P4 | | | M1 | | | M2 | | | M3 | | | Remarks |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | L | W | H | L | W | H | L | W | H | L | W | H | L | W | H | |
| KNM-NA 52150 | Right | 26.5 | 35.4 | – | | | | | | | | | | | | | Present study |
| KNM-NA 52149 | Right | 26.5 | 35.4 | 15.7 | | | | | | | | | | | | | Present study |
| KNM-NA 52149 | Right | | | | 35.7 | 47.5 | 21.9 | | | | | | | | | | Present study |
| KNM-NA 52143 | Right | | | | | | | 49.1 | 64.1 | 35.7 | | | | | | | Present study |
| KNM-NA 52139 | Left | | | | | | | 49.9 | – | 23.1 | | | | 47.4 | 60.0 | >22.0 | Present study |
| KNM-NA 52139 | Right | | | | | | | | | | | | | 46.8 | 52.6 | >16.0 | Present study |
| *Diceros australis* | *N* | | | | 2 | 2 | | 1 | 1 | | 1 | 1 | | 4 | 4 | | |
| | Mini. | | | | 37.5 | 54.0 | – | 59.0 | 56.5 | – | 58.0 | 62.5 | – | 52.0 | 60.0 | – | Guérin (2000) |
| | Max. | | | | 43.5 | 60.5 | – | | | | | | | 55.0 | 62.0 | – | Guérin (2000) |
| | Mean | | | | 40.5 | 57.3 | – | | | | | | | 53.5 | 61.3 | – | Guérin (2000) |
| *Diceros primaevus* | *N* | | | | | | | 2 | 1 | 1 | 1 | 1 | 1 | | | | |
| | Mini. | – | – | – | – | – | – | 55.0 | 57.5 | 48.0 | 61.0 | 62.5 | 64.0 | – | – | – | Arambourg (1959) |
| | Max. | – | – | – | – | – | – | 56.0 | | | | | | – | – | – | Arambourg (1959) |
| | Mean | – | – | – | – | – | – | 55.5 | | | | | | – | – | – | Arambourg (1959) |
| *Diceros praecox* | *N* | 3 | 3 | | 2 | 2 | | 3 | 3 | | 3 | 3 | | 3 | 3 | | |
| | Mini. | 48.0 | 57.5 | – | 51.0 | 63.0 | – | 59.0 | 67.5 | – | 59.0 | 67.0 | – | 62.0 | 62.5 | – | Geraads (2005) |
| | Max. | 49.5 | 64.5 | – | 51.5 | 72.5 | – | 61.0 | 73.5 | – | 62.0 | 74.0 | – | 70.0 | 68.0 | – | Geraads (2005) |
| | Mean | 48.0 | 60.0 | – | 51.3 | 67.8 | – | 58.8 | 69.0 | – | 60.7 | 71.0 | – | 66.0 | 66.0 | – | Geraads (2005) |
| *Diceros douariensis* (Douaria specimens) | *N* | 2 | 2 | | 2 | 2 | | 2 | 2 | | 2 | 2 | | 2 | 2 | | |
| | Mini. | 42.0 | 56.5 | – | 43.0 | 62.5 | – | 52.0 | 63.0 | – | 53.0 | 67.0 | – | 50.0 | 59.0 | – | Guérin (1966) |
| | Max. | 42.0 | 57.0 | – | 45.0 | 62.5 | – | 55.0 | 64.0 | – | 54.0 | 71.0 | – | 50.0 | 64.0 | – | Guérin (1966) |
| | Mean | 42.0 | 56.8 | – | 44.0 | 62.5 | – | 53.5 | 63.5 | – | 53.5 | 69.0 | – | 50.0 | 61.5 | – | Guérin (1966) |
| *Diceros douariensis* (Kuseralee specimens) | *N* | 1 | | | 2 | 2 | | 2 | 2 | | 1 | 1 | | 2 | 2 | | |
| | Mini. | 45.7 | – | – | 47.8 | 69.9 | – | 56.1 | 69.5 | – | 61.0 | 69.2 | – | 63.1 | 60.2 | – | Giaourtsakis et al. (2009) |
| | Max. | | | | 47.8 | 72.2 | – | 58.8 | 70.0 | – | | | | 63.4 | 60.6 | – | Giaourtsakis et al. (2009) |
| | Mean | | | | 47.8 | 70.1 | – | 57.5 | 69.8 | – | | | | 63.3 | 60.4 | – | Giaourtsakis et al. (2009) |
| *Diceros bicornis* | *N* | 32 | 40 | | 33 | 40 | | 32 | 41 | | 33 | 41 | | 30 | 35 | | |
| | Mini. | 37.0 | 45.0 | – | 39.0 | 53.0 | – | 41.0 | 52.5 | – | 48.0 | 53.5 | – | 47.5 | 43.5 | – | Guérin (1980) |
| | Max. | 51.5 | 63.0 | – | 56.5 | 69.5 | – | 65.0 | 68.0 | – | 71.0 | 71.0 | – | 67.5 | 63.0 | – | Guérin (1980) |
| | Mean | 42.4 | 52.0 | – | 47.8 | 59.6 | – | 54.5 | 59.6 | – | 58.9 | 60.6 | – | 54.5 | 54.6 | – | Guérin (1980) |
| *Diceros neumayri* | *N* | 2 | 2 | | 2 | 2 | | 3 | 3 | | 2 | 2 | | 2 | 2 | | |
| | Mini. | 48.0 | 53.5 | – | 51.0 | 59.0 | – | 48.0 | 62.5 | – | 64.0 | 66.0 | – | 53.0 | 60.0 | – | Antoine and Saraç (2005) |
| | Max. | 49.0 | 54.0 | – | 51.0 | 60.0 | – | 58.0 | 63.0 | – | 65.0 | 67.0 | – | 54.0 | 61.0 | – | Antoine and Saraç (2005) |
| | Mean | 48.5 | 53.8 | – | 51.0 | 59.5 | – | 54.7 | 62.8 | – | 64.5 | 66.5 | – | 53.5 | 60.5 | – | Antoine and Saraç (2005) |
| *Diceros gansuensis* | *N* | 4 | 4 | 4 | 3 | 3 | 3 | 4 | 4 | 4 | 4 | 4 | 4 | 3 | 3 | 3 | |
| | Mini. | 39.8 | 57.5 | 26.6 | 43.5 | 64.5 | 22.6 | 51.3 | 67.2 | 15.0 | 62.0 | 71.0 | 28.0 | 63.8 | 62.5 | 39.5 | Deng and Qiu (2007) |
| | Max. | 48.0 | 63.2 | 52.0 | 54.6 | 70.3 | 52.0 | 67.5 | 78.4 | 68.0 | 73.5 | 75.3 | 70.5 | 67.6 | 69.3 | 61.0 | Deng and Qiu (2007) |
| | Mean | 44.4 | 59.5 | 41.0 | 49.5 | 66.9 | 40.9 | 61.4 | 71.7 | 44.7 | 67.9 | 73.6 | 54.6 | 66.1 | 66.3 | 53.6 | Deng and Qiu (2007) |

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

**Table 3.** Measurements (in mm) of lower cheek teeth of *Diceros* from the Nakali Formation.

| | | p2 | | | p4 | | | m1 | | | m2 | | | m3 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Specimen number | Element | L | W | H | L | W | H | L | W | H | L | W | H | L | W | H |
| KNM-NA 53147 | Left | 37.4 | 25.7 | 20.4 | | | | | | | | | | | | |
| KNM-NA 52146 | Left | 25.9 | 18.2 | 18.9 | | | | | | | | | | | | |
| KNM-NA 52144 | Left | | | | >37.8 | 27.9 | 23.4 | | | | | | | | | |
| KNM-NA 52139 | Left | | | | | | | 44.2 | 29.9 | 21.6 | 44.9 | 28.9 | 20.6 | 47.5 | 25.1 | 22.1 |

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

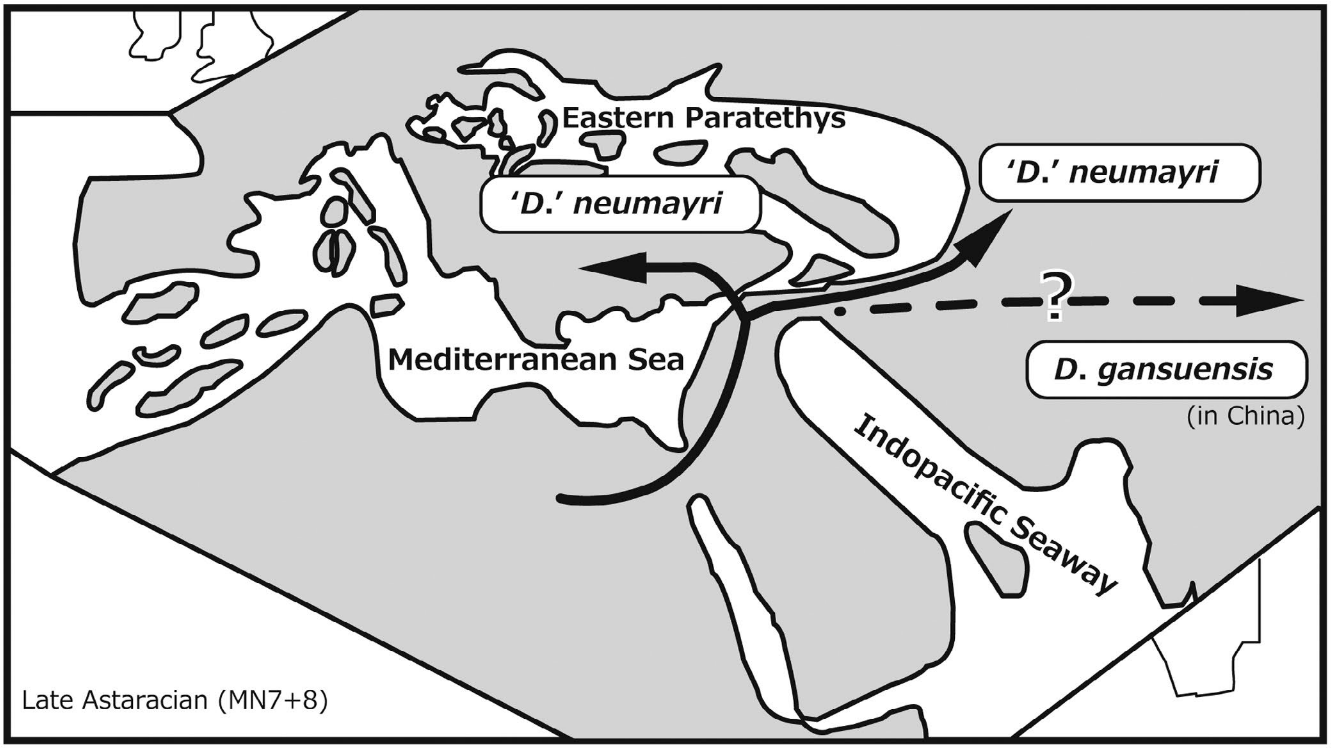


**Figure 6.** Estimated immigration route of *Diceros* between Africa and Eastern Mediterranean area during Astaracian (modified from Koufos et al. 2005).

## Discussion

*Diceros australis* from Orleanian locality of Namibia is the oldest species of *Diceros*, suggesting that this genus had already presented in Africa by the early Miocene. However, Orleanian to Astaracian fossil records of *Diceros* in Africa are scarce so far. Therefore, further materials are needed to discuss the evolutionary scenario of *Diceros* in Africa during this period.

Vallesian fossil records have been described from North Africa, namely *D. primaevus* from Algeria (Arambourg 1959) and *D. douariensis* from Tunisia (Guérin 1966). The present specimens from the Nakali in Kenya confirm that *Diceros* had distributed in sub-Saharan East Africa during Vallesian as already noted by Kunimatsu et al. (2007) and Fukuchi et al. (2008).

History of exchange of *Diceros* between Africa and Eurasia is still controversial. Geraads (2005) proposed the early dispersal pattern of Dicerotini in Africa and Eurasia. He noted that *C. neumayri* (= '*Diceros*' *neumayri* in Giaourtsakis et al. 2009) is a common ancestor of both *Diceros* and *Ceratotherium*, and considered that *D. primaevus* was a closely related taxon with *C. neumayri*. Additionally, *D. douariensis* was considered as conspecific with *C. neumayri*. In his context, however, the detailed reason of those identifications is not mentioned, and *D. australis* is excluded in those discussions as pointed out by Giaourtsakis et al. (2009). According to Geraads (2005), *C. neumayri* entered into Africa from Eurasia in the late Miocene, and both extant lineage (*Diceros* and *Ceratotherium*) split after the Miocene/Pliocene boundary. In contrast, Giaourtsakis et al. (2009), Deng and Qiu (2007) and Hernesniemi et al. (2011) suggested that the *Diceros* evolved in Africa and migrated to Eurasia by the late Miocene. Giaourtsakis et al. (2009) also suggested that '*D*'. *neumayri* (= *C. neumayri* in Geraads 2005) was considered as a paraphyletic taxon in Dicerotini. The present study supports the later migration hypothesis, because the present specimen was discovered in t Vallesian locality of Nakali in northern Kenya.

In Eurasia, '*D*'. *neumayri* presented during MN10–MN13 (Vallesian to Turolian) (Figure 5). *D. gansuensis* was recorded from MN10 (Vallesian) locality in Gansu, China (Deng and Qiu 2007). In Astaracian (MN7–MN8), a land bridge probably connected Africa with the Eurasian continent (Koufos et al. 2005) (Figure 6). The ancestors of '*D*'. *neumayri* and *D. gansuensis* might have dispersed into Eurasia during this period through this land bridge and '*D*'. *neumayri* was distributed in the eastern Mediterranean area among Vallesian to Turolian (MN9–MN12) as noted by Giaourtsakis et al. (2009). However, detailed phylogenetic relationships of *Diceros* are unclear, and there are few fossil records in the area between China and Eastern Mediterranean area. Further materials from Vallesian in Africa and Eurasia are needed to discuss the detailed migration route and its timing.

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## Disclosure statement

No potential conflict of interest was reported by the authors.

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