Geobios 50 (2017) 197–209

Available online at
ScienceDirect
www.sciencedirect.com

Elsevier Masson France
EM|consulte
www.em-consulte.com

Original article

A new Elasmotheriini (Perissodactyla, Rhinocerotidae) from the upper Miocene of Samburu Hills and Nakali, northern Kenya[☆]

Naoto Handa[a,*], Masato Nakatsukasa[b], Yutaka Kunimatsu[c], Hideo Nakaya[d]

[a] *Museum of Osaka University, 1-20 Machikaneyama-cho, Toyonaka, Osaka 560-0043, Japan*
[b] *Laboratory of Physical Anthropology, Graduate School of Science, Kyoto University, Kitashirakawa-oiwakecho, Sakyo-ku, Kyoto 606-8502, Japan*
[c] *Faculty of Business Administration, Ryukoku University, 67 Tsukamoto-cho, Fukakusa, Fushimi-ku, Kyoto 612-8577, Japan*
[d] *Graduate School of Science and Engineering, Kagoshima University, 1-21-35 Korimoto, Kagoshima 890-0065, Japan*

ARTICLE INFO

Article history:
Received 15 August 2016
Accepted 20 April 2017
Available online 8 May 2017

Keywords:
Elasmotheriini
Rhinocerotidae
Late Miocene
Samburu Hills
Nakali
Kenya

ABSTRACT

Several rhinocerotid cheek teeth and mandibular fragments from the upper Miocene of the Samburu Hills and Nakali in northern Kenya are described. These specimens show characteristics that place them in the Tribe Elasmotheriini such as a constricted protocone, a developed antecrochet, and coronal cement. The present specimens are compared with other Elasmotheriini species from Eurasia and sub-Saharan East Africa. They are found to be morphologically different from the previously known species of Elasmotheriini. Morphologically, they are most similar to *Victoriaceros kenyensis* from the middle Miocene of Kenya, but differ from *V. kenyensis* in having the upper molars with the simple crochet, lingual groove of the protocone and enamel ring in the medisinus. Therefore, the present specimens are assigned to a new genus and species of Elasmotheriini: *Samburuceros ishidai*. A cladistic analysis tentatively places *S. ishidai* nov. gen., nov. sp. as a sister taxon of *V. kenyensis*. However, questions remain regarding a further detailed discussion of the phylogenetic relationship between the African Elasmotheriini and other Eurasian taxa because of the incompleteness of the specimens from Africa, as already noticed by several researchers.

1. Introduction

The Tribe Elasmotheriini (Heissig, 1973, 1989; = Elasmotheriina *in* Antoine, 2002, 2003), an extinct group of Rhinocerotidae (Mammalia, Perissodactyla), was widely distributed in Europe, Asia and sub-Saharan East Africa, especially during the early to middle Miocene of Europe (Cerdeño and Nieto, 1995; Heissig, 1996, 1999), early to middle Miocene of Pakistan (Heissig, 1972; Antoine and Welcomme, 2000), early Miocene to late Pleistocene of China (Tong and Moigne, 2000; Deng and Downs, 2002; Antoine, 2003), and Pleistocene of Russia (Schvyreva, 2015). The first known Elasmotheriini are from the early Miocene of Pakistan (Antoine and Welcomme, 2000). This tribe diversified during the early to middle Miocene in Eurasia and became extinct during the Pleistocene in Europe and Asia (Heissig, 1989).

In contrast, only a few species have been reported so far from sub-Saharan East Africa (Fig. 1). *Kenyatherium bishopi* was first discovered in the late Miocene locality of Nakali in Kenya (Aguirre and Guérin, 1974), and later in the late Miocene locality of the Samburu Hills in Kenya (Nakaya et al., 1987). *Ougandatherium napakense* was discovered in the early Miocene (20–19 Ma) locality of Napak in Uganda (Guérin and Pickford, 2003). Geraads et al. (2012) described *Victoriaceros kenyensis* from the middle Miocene locality (*ca.* 15.5 Ma) of Maboko in Kenya. Recently, Geraads et al. (2016) described a skull from the early Miocene (> 17.7 Ma) locality of Karungu in western Kenya, and tentatively assigned it as a second species of *Victoriaceros*, *V. hooijeri*.

The Kenya–Japan joint expedition carried out fieldwork in the Samburu Hills during the 1980s and 1990s (Ishida and Pickford, 1997) and has been working in Nakali since 2002 (Kunimatsu et al., 2007). Abundant mammal fossils, including the large hominoid fossils *Samburupithecus kiptalami* and *Nakalipithecus nakayamai*, have been discovered in these localities. Rhinocerotid fossils were also discovered through fieldwork in those localities (Nakaya et al., 1987; Kunimatsu et al., 2007; Fukuchi et al., 2008; Handa et al., 2015; Handa, 2016). Nakaya (1994) reported a taxon of rhinocerotid from the upper Miocene Namurungule Formation in the Samburu Hills as "Iranotheriinae sp. nov.". This taxon was first reported as Rhinocerotidae gen. et sp. indet. (Nakaya et al., 1987). Tsujikawa (2005) cited the identification of Nakaya (1994) as the

---

[☆] Corresponding editor: Pierre-Olivier Antoine.
[*] Corresponding author.
E-mail address: k1552325@kadai.jp (N. Handa).

http://dx.doi.org/10.1016/j.geobios.2017.04.002
0016-6995/

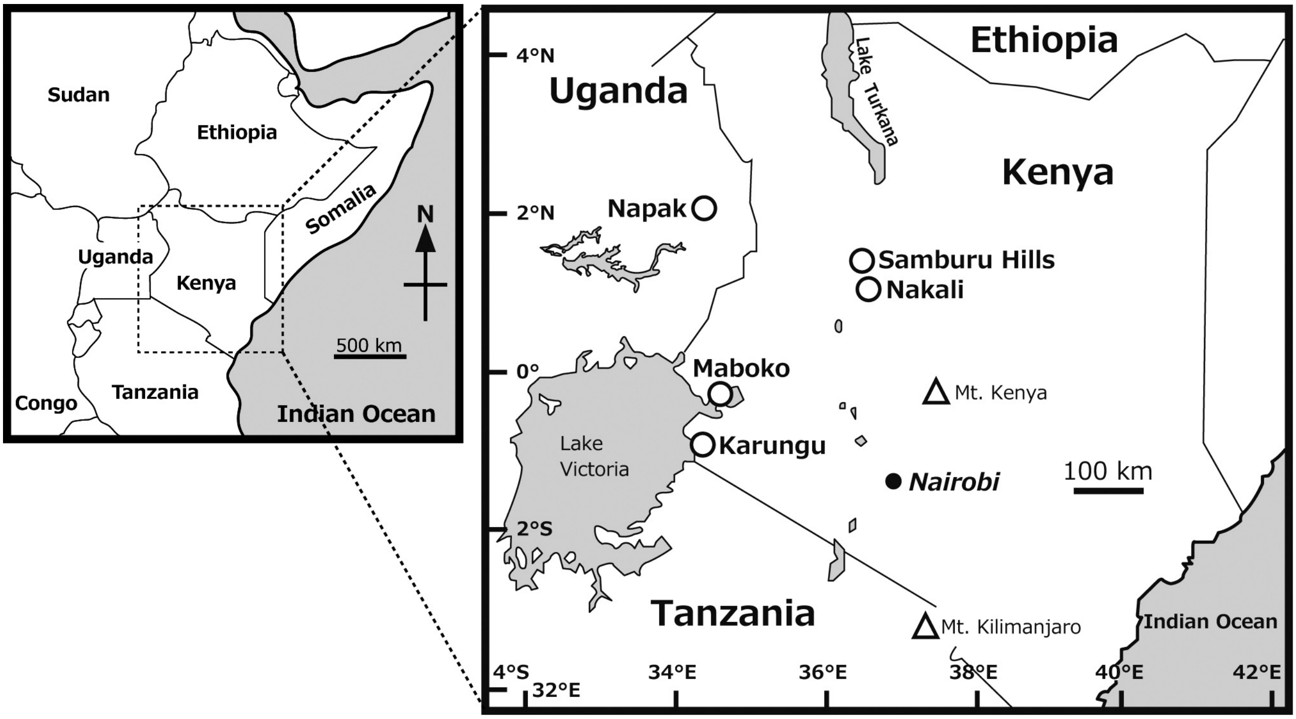

Fig. 1. Map showing the African Elasmotherhiini-bearing localities.
Modified from Sawada et al., 1998.

number of species of rhinocerotids from the Namurungule Formation. However, a detailed taxonomic description of those specimens has not been undertaken since Nakaya (1994). Furthermore, a few undescribed specimens that would belong to "Iranotheriinae sp. nov." were also found in the Nakali Formation in Nakali. Here, we describe those specimens as a new genus and species of Elasmotheriini.

2. Geological setting

The Samburu Hills is located 50 km south of Lake Turkana (Fig. 1). The Miocene succession (including the Nachola, Aka Aiteputh, Namurungule, and Kongia formations) and Pliocene succession (corresponding to the Tirr Tirr Formation) are distributed in this area (Saneyoshi et al., 2006; Sakai et al., 2010). Among them, the Namurungule Formation overlies the Aka Aitheputh Formation conformably and underlies the Kongia Formation unconformably. Some parts of the boundary between the Aka Aiteputh and Namurungule formations are local faults. The Namurungule Formation is about 200 m thick and is divided into the Upper and Lower Members, which consist of alluvial fan and fluvio-lacustrine, and fluvio-lacustrine delta and fluvial deposits, respectively (Saneyoshi et al., 2006; Sakai et al., 2010). *Samburupithecus kiptalami* was found from the Lower Member (Ishida and Pickford, 1997). There is a lahar deposit between the Lower and Upper Members. The studied rhinocerotid specimens from the Namurungule Formation were discovered from the Lower Member. The 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 (Sawada et al., 1998, 2006). In the paleomagnetic stratigraphy, the Upper and Lower Members are correlated with Chron C4Ar.2n (9.64 to 9.58 Ma) and Chrons C4Ar.2r to C4Ar.1n (9.58 to 9.31 Ma), respectively (Sawada et al., 1998, 2006).

Nakali is located 60 km south of the Samburu Hills (Fig. 1). The upper Miocene Nakali and Nasorut formations are distributed in this area (Kunimatsu et al., 2007; Sakai et al., 2013). The Nakali Formation is unconformably overlaid by the Nasorut Formation, which is composed of trachytic 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 Members in ascending order (Kunimatsu et al., 2007; Sakai et al., 2013). The Lower Member is composed mainly of lacustrine and fluvio-lacustrine deposits. The Middle Member consists of a pyroclastic flow deposit, whose thickness is *ca.* 40 m. The Upper Member is characterized by fluvio-lacustrine and lacustrine deposits. *Nakalipithecus nakayamai* was collected from the Upper Member (Kunimatsu et al., 2007). The studied rhinocerotid specimens from the Nakali Formation were found in the Upper and Lower Members. $^{40}\mathrm{Ar}/^{39}\mathrm{Ar}$ 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 to 9.92 Ma; Kunimatsu et al., 2007).

3. Review of the Rhinocerotidae from the Namurungule and Nakali formations

Nakaya et al. (1984, 1987) reported abundant specimens of the Rhinocerotidae from the Samburu Hills. After that, additional mammalian fossils were recovered through the fieldwork sessions in 1990s (Tsujikawa, 2005). Nakaya et al. (1984) preliminarily reported several rhinocerotid fossils from the Namurungule Formation, such as *Brachypotherium* sp. and Rhinocerotidae gen. et sp. indet. Nakaya et al. (1987) reported additional specimens, which were preliminarily identified as *Chilotheridium* sp., *Paradiceros* sp., *K. bishopi*, and Rhinocerotidae gen. et sp. indet. Later, Nakaya (1994) discussed the faunal changes among the late Miocene terrestrial mammals in sub-Saharan East Africa. In this context, Rhinocerotidae gen. et sp. indet., reported by Nakaya et al.

(1987) was transferred to Iranotheriinae sp. nov. (Nakaya, 1994: p. 17). Tsujikawa (2005) described additional rhinocerotid fossils discovered from the Namurungule Formation in 1986, 1998 and 1999; he reported *Chilotheridium pattersoni*, *Paradiceros mukirii*, and Rhinocerotidae gen. et sp. indet. Fukuchi et al. (2008) noted a cheek teeth row specimen of *P.*sp. from the Namurungule Formation as *Diceros* sp. There are a few reports of rhinocerotid fossils from Nakali. Aguirre and Guérin (1974) first reported a new species, *K. bishopi*, based on material collected in the 1960s. Since 2000, a great amount of additional mammalian fossils was recovered from new fieldwork, and the presence of *Diceros* sp. was reported but without description and illustration (Kunimatsu et al., 2007; Fukuchi et al., 2008).

Recently, Handa et al. (2015) and Handa (2016) revised all the rhinocerotid specimens from the Namurungule and Nakali formations and re-identified all of them. As a result, several specimens previously described by Nakaya et al. (1987) and Tsujikawa (2005) were described as *C. pattersoni* (Handa et al., 2015). Handa (2016) identified several isolated cheek teeth of *Diceros* in the recent collection from the Nakali Formation, as well as an upper molar of *K. bishopi* and isolated cheek teeth and mandibular specimens of *Brachypotherium*. Moreover, many postcranial specimens from both formations were identified as Rhinocerotidae gen. et sp. indet. (Handa, 2016). Thus, the following taxa were recognized from both the Namurungule and Nakali Formations prior to the present study: *C. pattersoni*, *Brachypotherium* sp., *K. bishopi*, and *Diceros* sp.

4. Material and methods

The specimens described in the present study are stored in the paleontology Section of the National Museums of Kenya in Nairobi, Kenya (KNM). Measurements were taken using a digital caliper. The taxonomy used in the present study follows Heissig (1973, 1989), and the anatomical terminology and measurements follow Guérin (1980). The studied specimens were compared to previously known taxa of Elasmotheriini from Eurasia and Africa (Table 1), based on the collections held by the following institutions: **KNM**: National Museums of Kenya, Nairobi, Kenya; **NHML**: Natural History Museum, London, UK; **MNCN**: Museo National de Ciencias Naturales, Madrid, Spain; **MNHN**: Muséum National d'Histoire Naturelle, Paris, France. Other comparisons are based on published references.

Abbreviations: M: upper molar; m: lower molar; P: upper premolar; p: lower premolar; MB: Maboko, Kenya; NA: Nakali, Kenya; NC: Nyakach, Kenya; SH: Samburu Hills, Kenya; MN: European Neogene Mammal Zones.

5. Systematic paleontology

Class Mammalia Linnaeus, 1758
Order Perissodactyla Owen, 1848
Family Rhinocerotidae Owen, 1845
Subfamily Rhinocerotinae Dollo, 1885
Tribe Elasmotheriini Bonaparte, 1845
Genus ***Samburuceros*** nov. gen.

1987. Rhinocerotidae gen. et sp. indet. – Nakaya et al., p. 98–99, pl. 8, figs. 2–5.

1994. Iranotheriinae sp. nov. – Nakaya, p. 17.

2005. Iranotheriinae sp. nov. – Tsujikawa, p. 44.

Derivation of the name: From the Samburu Hills, where the holotype was discovered, and '*ceros*', the Greek word for horn.

Occurrence: Samburu Hills and Nakali, northern Kenya.

Diagnosis: Medium-sized species of Elasmotheriini with upper molars that have simple crochet, lingual groove on the protocone on M2 and M3, and the presence of the enamel ring in the medisinus on M2 and M3.

Samburuceros ishidai nov. gen., nov. sp.
Figs. 2–4

Derivation of the name: Species named in honor of Hidemi Ishida, professor emeritus of Kyoto University, who organized the Kenya–Japan expedition in the Samburu Hills.

Holotype: KNM-SH 15826 (a left maxillary fragment with M2 and M3) from the Namurungule Formation, Samburu Hills, Kenya.

Paratype: KNM-NA 47407 (an isolated right M3) from the Nakali Formation, Nakali, Kenya.

Referred specimens: a right maxillary fragment with M3 (KNM-SH 15825), an isolated right M1 or M2 (KNM-SH 15829), an isolated left M1 or M2 (KNM-NA 47340 and KNM-NA 47406), an isolated right M3 (KNM-SH 15824), a right mandibular fragment with p3 to m2 (KNM-SH 15767), and a left mandibular fragment with p4 (KNM-SH 15768).

Locality and horizon: Namurungule Formation in the Samburu Hills, and Nakali Formation in Nakali, northen Kenya; both early late Miocene (*ca.* 10 Ma) in age.

Measurements: See Tables 2 and 3.

Table 1
Specimens of African and Eurasian species of Elasmotheriini discussed in this work.

Taxa	Locality	Age	Direct observation	Reference
Bugtirhinus praecursor	Pakistan	Early Miocene	NHML	Antoine and Welcomme (2000)
Caementodon oettingenae	Pakistan	Middle Miocene		Heissig (1972); Antoine (2003)
Elasmotherium sibiricum	Russia	Early to Late Pleistocene		Brandt (1878); Schvyreva (2015)
Elasmotherium caucasicum	Russia	Early Pleistocene		Borissiak (1914); Schvyreva (2015)
Elasmotherium peii	China	Early Pleistocene		Schvyreva (2015)
Hispanotherium beonense	France	Early Miocene		Antoine et al. (2002)
Hispanotherium matritense	Western Europe, China	Early to Middle Miocene	MNCN	Antoine et al. (2002); Deng (2003); Sanisidro et al. (2012)
Hispanotherium corcolense	Spain	Early Miocene		Iñigo and Cerdeño (1997); Antoine et al. (2002)
Huaqingtherium lintungense	China	Middle Miocene		Zhai (1978); Antoine (2003)
Iranotherium morgani	Iran, China	Late Miocene	MNHN	de Mecqenum (1908); Deng (2005)
Kenyatherium bishopi	Kenya	Late Miocene	KNM	Aguirre and Guérin (1974); Nakaya et al. (1984, 1987)
Ninxiatherium euryrhinus	China	Late Miocene		Deng (2008)
Ougandatherium napakense	Kenya	Early Miocene		Guérin and Pickford (2003)
Parelasmotherium linxiaense	China	Late Miocene		Deng (2007)
Procoelodonta mongoliense	China, Mongolia	Middle Miocene		Antoine (2003)
Sinotherium lagrelii	China, Mongolia, Kazakhstan	Late Miocene		Ringström (1924); Kondrashov (2000); Deng et al. (2013)
Victoriaceros hooijeri	Kenya	Early Miocene		Geraads et al. (2016)
Victoriaceros kenyensis	Kenya	Middle Miocene	KNM	Geraads et al. (2012)

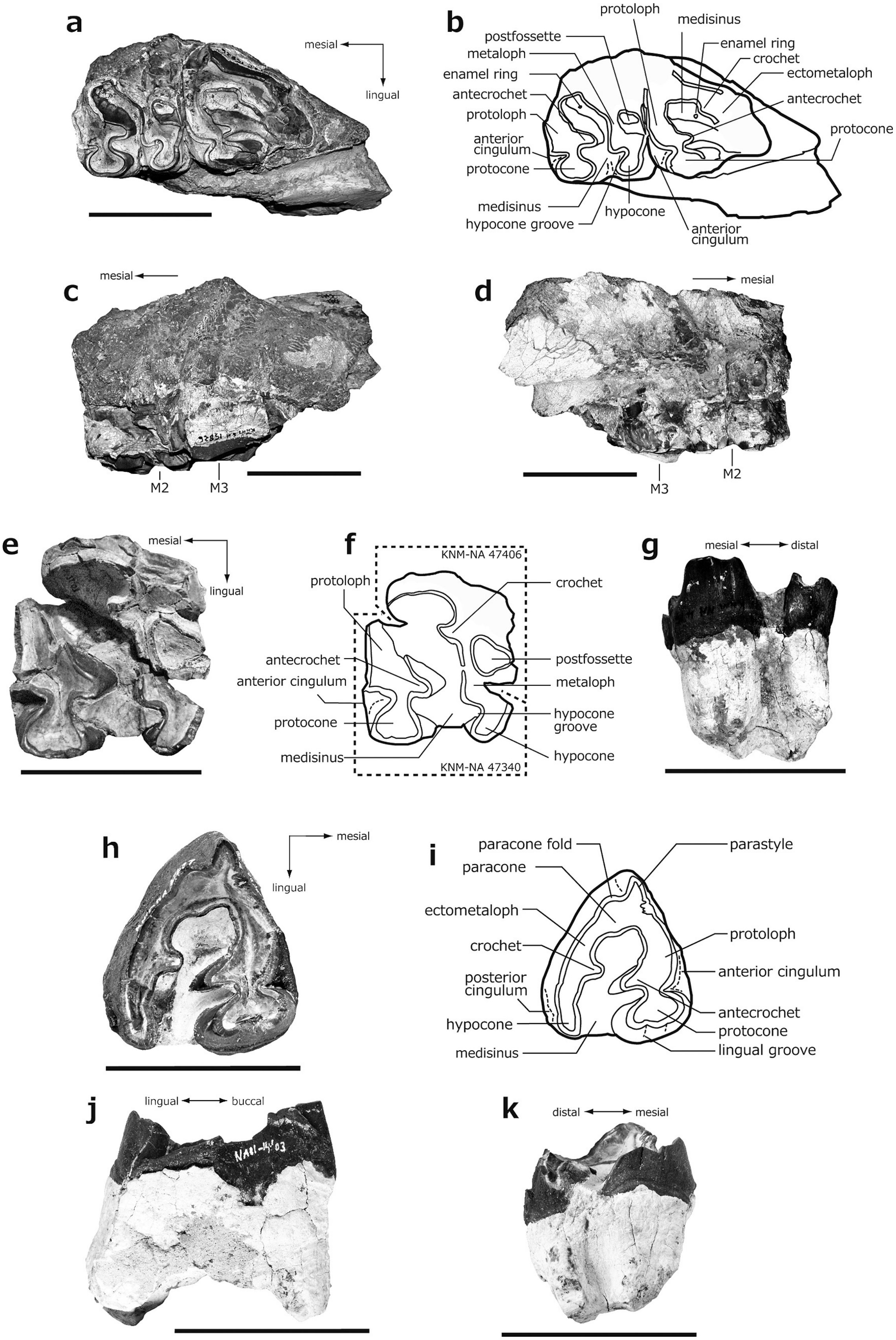

Fig. 2. Maxillary fragment and upper cheek teeth of *Samburuceros ishidai* nov. gen., nov. sp. from the Namurungule and Nakali formations: **a–d**: left maxillary fragment with M2 and M3 (KNM-SH 15826: holotype); a: occlusal view; b: schematic drawing; c: buccal view; d: lingual view; **e–g**: isolated left M1 or M2 (KNM-NA 47340 and KNM-NA 47406); e: buccal view; f: schematic drawing; g: lingual view; **h–k**: isolated right M3 (KNM-NA 47407: paratype); h: occlusal view; i: schematic drawing; j: mesial view; k: lingual view. Scale bars: 10 cm (a, c, d), 5 cm (e, g, h, j, k).

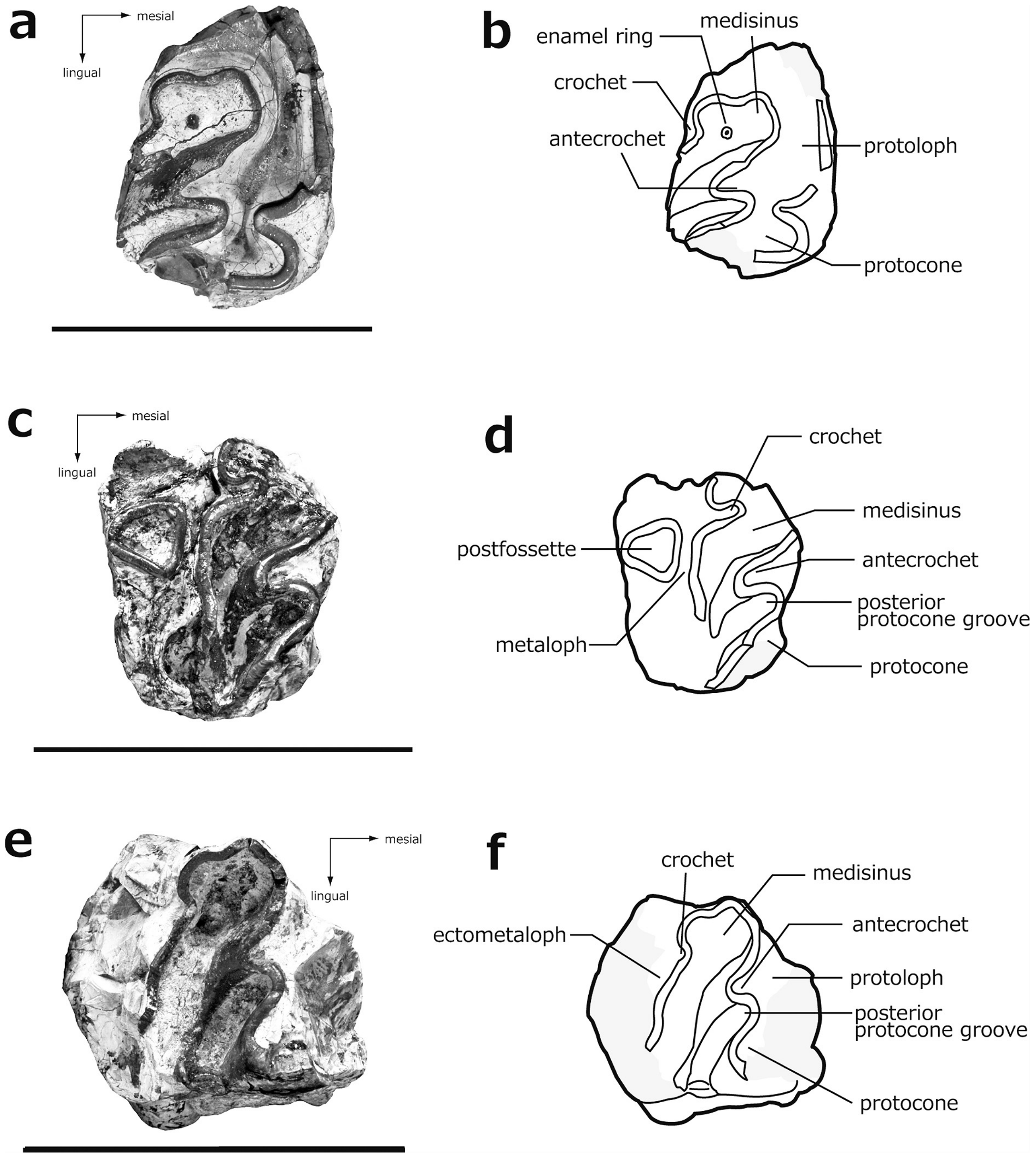

Fig. 3. Maxillary fragment and upper cheek teeth of *Samburuceros ishidai* nov. gen., nov. sp. from the Namurungule and Nakali formations: **a, b**: right maxillary fragment with M3 (KNM-SH 15825); a: occlusal view; b: schematic drawing; **c, d**: right isolated M1 or M2 (KNM-SH 15829); c: occlusal view; d: schematic drawing; **e, f**: right isolated M3 (KNM-SH 15824); e: occlusal view; f: schematic drawing. Scale bars: 5 cm.

Diagnosis: As for the genus, by monotypy.

Description: KNM-SH 15826 is a left maxillary fragment with M2 and M3 (Fig. 2(a–d)). The ventral margin of the orbit is preserved in the lateral view. The molars are covered with the coronal cement and the enamel folding is not developed at this wear stage. The occlusal surface is almost flat in the mesio-distal view. M2 is moderately worn, and the ectoloph and mesial margin of the protoloph are broken. Its protoloph and metaloph extend lingually. The protocone is strongly constricted, and its lingual wall is flattened. The lingual protocone groove is shallow. There is a deep hypocone groove. The lingual wall of the hypocone is rounded. At this wear stage, neither the crochet nor crista is visible. The antecrochet extends distally and does not contact the metaloph. The anterior cingulum on the mesial margin of the protocone is low and short. The short posterior cingulum is on the distal side of the hypocone. There is a small enamel ring in the medisinus. The entrance of the medisinus is open. There is no lingual cingulum. M3 is moderately worn; its outline is triangular in the occlusal view. The distal end of the ectometaloph is lacking. The protoloph extends lingually. The protocone is strongly constricted, similar to M2. There is a trace of the crochet at this wear stage. The antecrochet is developed basally, curving inward toward the entrance of the medisinus. A small enamel ring is visible in the medisinus, as for M2.

KNM-SH 15825 is a right maxillary fragment with M3 (Fig. 3(a, b)). The detailed characteristics of the maxilla are unknown

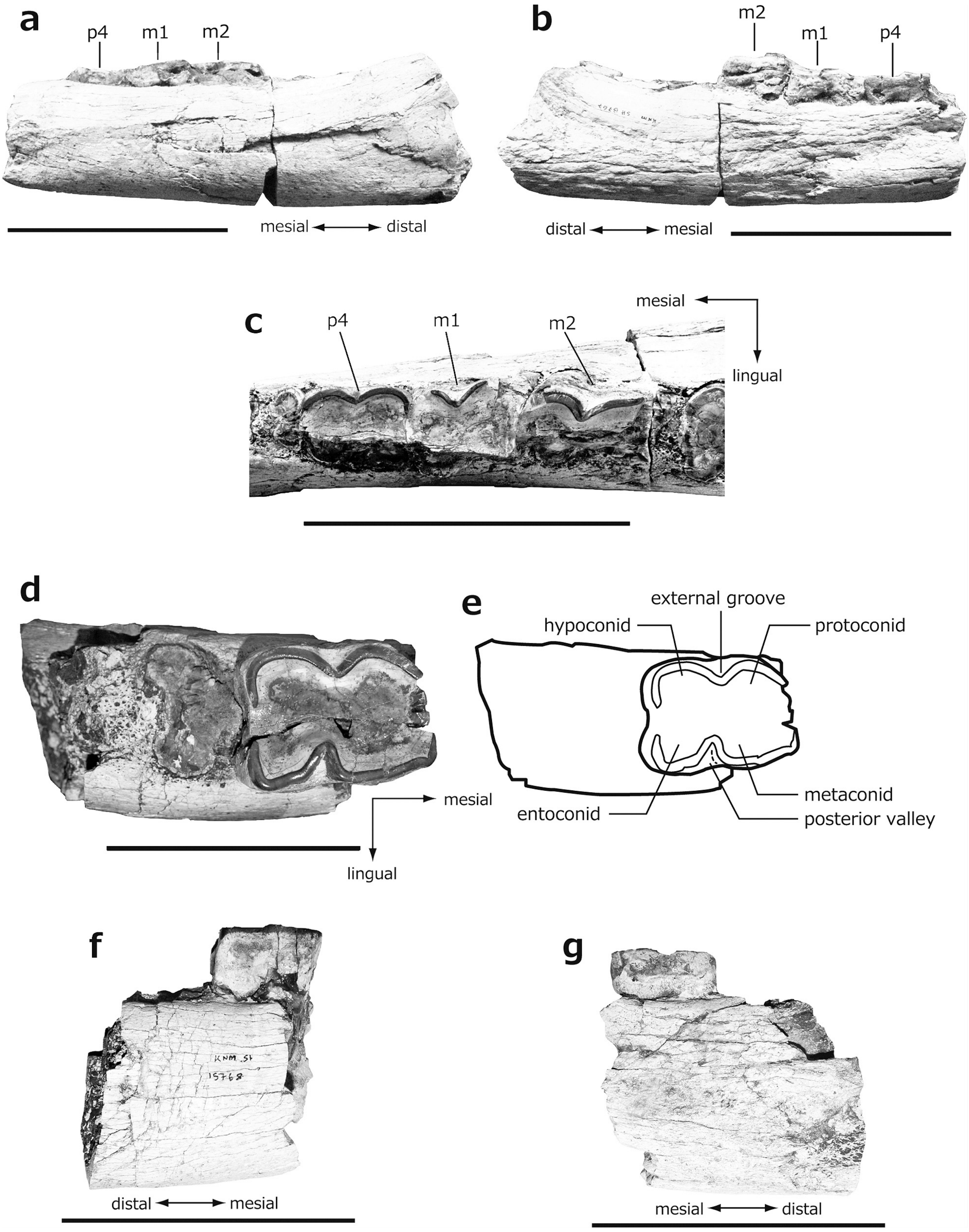

Fig. 4. Mandibular fragments of *Samburuceros ishidai* nov. gen., nov. sp. from the Namurungule and Nakali formations: **a–c**: right mandibular fragment (KNM-SH 15767) in lingual (a), buccal (b) and occlusal (c) views; **d–g**: left mandibular fragment (KNM-SH 15768); d: occlusal view; e: schematic drawing; f: lingual view; g: buccal view. Scale bars: 10 cm (a, b), 5 cm (c, d, f, g).

because the element is not well-preserved. The preserved tooth is moderately worn. The ectometaloph is missing. The medisinus and protocone are covered with coronal cement. The protoloph extends lingually. The protocone is strongly constricted. The lingual wall of the protocone is flattened. The crochet is weakly developed. The antecrochet projects and extends toward the entrance of the medisinus at the base. There is a small enamel ring in the medisinus, which is similar to M3 in KNM-SH 15826.

Table 2
Upper cheek teeth measurements of *Samburuceros ishidai* nov. gen., nov. sp. and comparative material.

Specimen number/species name	Remarks		M2			M3		
			L	W	H	L	W	H
KNM-SH 15826	This study	Left	40.9	> 41.3	21.3	44.4	52.8	–
KNM-NA 47406	This study	Left	–	–	20.9			
KNM-NA 47407	This study	Right				50.8	56.5	25.1
Kenyatherium bishopi	KNM-NA199	Left	> 33.8	> 39.0	–			
	KNM-SH15827	Right	> 28.4	> 33.3	–			
Ougandatherium napakense	Guérin and Pickford (2003)	Min.	42	45.5	–	43	39.5	–
		Max.	45	42	–	43.5	39	–
		Mean	43.5	43.75	–	43.25	39.25	–
Victoriaceros kenyensis	KNM-MB29179	Right	> 38.6	51.5	10.9	46.5	47.6	20
	KNM-MB29179	Left	41.7	51	13	44.7	50.3	18.7
	KNM-MB36189	Right	46.4	54	34.9			
Victoriaceros hooijeri	KNM-KA57652		60	66.5	–	64.7	62.3	–
Bugtirhinus praecursor	Antoine and Welcomme (2000)		36.5	32	–	34	39	> 34.0
Caementodon’ (*Beliajevina*) *fangxianense*	Yan (1979)		–	44	–			
Hispanotherium matritense	Sanisidro et al. (2012)	Right	52.1	59.4	23.4	57.7	41.8	28.4
		Left	51.9	57.4	23.9	56	37.5	27.7
	Deng (2003)	Min.	49	55	44	47	49.5	30
		Max.	56	57	63.6	49.5	47	70
		Mean	53.2	56.2	55.4	48.2	48.2	50
Hispanotherium beonense	Antoine (1997)		57	56	53	56	–	50
Hispanotherium corcolense	Iñigo and Cerdeño (1997)	Min.	44	46.8	–	44.7	45.8	–
		Max.	47.5	51.4	–	46	50	–
		Mean	45.8	49.22	–	45.17	47.23	–
Procoelodonta mongoliense	Antoine (2003)	Min.	48	45	–	49	36	–
		Max.	49	45	–	50	37	–
		Mean	48.5	45	–	49.5	36.5	–
Huaqingtherium lintungense	Antoine (2003)-Lengshuigou	Min.	48	58	–	48	52	–
		Max.	49	60	–	48	54	–
		Mean	48.5	59	–	48	53	–
	Antoine (2003)-Tunggur	Min.	64.4	60.9	–	46.4	59.8	–
		Max.	64.4	64.6	–	60	67.5	–
		Mean	64.4	69.1	–	52.3	61.3	–
	Antoine (2003)-Tongxin	Min.	47	51	–	40	46	–
		Max.	49	56	–	43	52	–
		Mean	48	53.5	–	41.6	48.4	–
Iranotherium morgani	Deng (2005)	Min.	63.5	60.5	30	62	50.5	43
		Max.	76.5	84	99	79	66	51
		Mean	70	72.25	64.5	70.5	58.25	47
Parelasmotherium lingxiaense	Deng (2007)	Min.	89.3	70.4	100	88.8	61	96.5
		Max.	100	80	132	90	77.5	109
		Mean	94.65	75.2	116	89.4	69.25	102.75
Ningxiatherium euryrhinus	Deng (2008)		82	70	81	69	64	> 72.0
Sinotherium lagrelii	Deng (2007)		70	71	185	106	60	90
Elasmotherium pelii	Tong et al. (2014)	Min.	70	58	–	66	51	–
		Max.	84	63	–	70	62	–
		Mean	75.3	56.7	–	68	56.5	–
Elasmotherium caucasicum	Tong et al. (2014)	Min.	69	64	–	77	113	–
		Max.	86	76	–	77	113	–
		Mean	79.3	67.6	–	77	113	–
Elasmotherium sibiricum	Tong et al. (2014)	Min.	60	49	–			
		Max.	74.6	72	–			
		Mean	67.4	60.5	–			
	Teryaev (1929)	Min.				65	107	–
		Max.				70	110	–
		Mean				67.5	108.5	–

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

Table 3
Lower cheek teeth measurements of *Samburuceros ishidai* nov. gen., nov. sp.

Specimen number	Side	p4			m1			m2		
		L	W	H	L	W	H	L	W	H
KNM-SH 15768	Left	36.1	28.2	10.3						
KNM-SH 15767	Right	32.8	–	8.7	39.3	–	–	35.0	–	15.8

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

KNM-SH 15829 (an isolated right M1 or M2) is not well-preserved (Fig. 3(c, d)). There is coronal cement in the medisinus and postfossette. The simple crochet projects mesially. The antecrochet extends distally. There is no connection between the antecrochet and metaloph. The posterior protocone groove is well-developed. At this wear stage, the postfossette is triangular in shape.

An isolated left M1 or M2 (Fig. 2(e–g)) is composed of two fragmentary specimens: KNM-NA 47406 is the buccal part, and

KNM-NA 47340 is the lingual part. The ectoloph is missing. The medisinus and postfossette are filled with coronal cement. The protocone and hypocone are strongly constricted. The lingual wall of the protocone is flattened, whereas that of the hypocone is round. The lingual groove of the protocone is shallow, as with KNM-SH 15826. A simple crochet extends mesially. The antecrochet projects distally, and its tip does not contact the metaloph. There is an anterior cingulum on the mesial side of the protocone. The entrance of the medisinus is open. There is no lingual cingulum.

KNM-NA 47407 is a right M3 (Fig. 2(h–k)). In the occlusal view, its outline shape is triangular. The tooth is covered with coronal cement. The protoloph extends lingually. The protocone is strongly constricted. The lingual wall of the protocone is flattened, and there is a shallow lingual protocone groove on its surface. The simple crochet is developed. As in the other M3 specimens, the antecrochet extends toward the entrance of the medisinus. The paracone fold and parastyle are developed. In particular, the parastyle strongly projects buccally. There is an anterior cingulum near the anterior protocone groove. The short posterior cingulum is developed on the distal surface of the ectometaloph.

KNM-SH 15824 is a poorly preserved isolated right M3 (Fig. 3(e, f)). There is coronal cement in the medisinus. The protocone is strongly constricted, and its lingual wall is flattened. There is a trace of the crochet at this wear stage. The antecrochet is strong and extends toward the entrance of the medisinus, as with other M3 specimens.

KNM-SH 15767 is a partially preserved right mandible with p3 to m3, but the crowns of the p3 and m1 are missing (Fig. 4(a–c)). The mandibular body is slender and its ventral margin is almost straight in lateral view. The cross section of the mandibular body is oval-shaped. The detailed dental morphology is uncertain because the teeth are worn out and partially broken. The crown is covered with coronal cement. The external groove is distinctive.

KNM-SH 15768 is a left mandibular fragment with p4 (Fig. 4(d–g)). As with KNM-SH 15767, the cross section of the mandibular body is oval-shaped. The mesial end of the p4 is broken. This tooth is moderately worn. The crown is covered with coronal cement. The lingual surface of the entoconid is slightly concave. The anterior valley is uncertain because the tooth is worn out. The posterior valley and external groove are relatively deep in the occlusal view.

6. Comparisons

The present specimens share the following synapomorphies of the Tribe Elasmotheriini (Heissig, 1972; Fortelius and Heissig, 1989; Antoine, 2002): a constricted protocone, a developed antecrochet, and coronal cement. Conversely, they are distinct from other rhinocerotid tribes such as Aceratheriini, Teleoceratini, Rhinocerotini, and Dicerotini.

The present specimens differ from the African Aceratherhiini, which includes *C. pattersoni*, *Turkanatherium actirostratum*, and *Plesiaceratherium* sp. (Deraniyagara, 1951; Hooijer, 1971; Geraads, 2010). The holotype of *C. pattersoni* was found in the lower Miocene of Loperot in Kenya (Hooijer, 1971). The present specimens differ from *C. pattersoni* in having a more constricted protocone on the upper molars, a lingually directed metaloph on M2, the presence of protocone grooves on M2 and M3, no enamel folding in the medisinus, and no cusp-shaped cingulum on M3. A well-preserved skull with cheek teeth of *Turkanatheirum acutirostratum* was reported from the middle Miocene of Moruorot in Kenya (Deraniyagara, 1951). The upper molars of the present specimens differ from those of *T. acutirostratum* in having a lingual groove in the protocone, deeper hypocone grooves, an absent lingual cingulum, no enamel ring in the medisinus, and a more developed antecrochet that curves toward the entrance of the medisinus on M3. Geraads (2010) tentatively assigned the partial skulls from the middle Miocene locality of Nyakach in Kenya to *Plesiaceratherium* sp. The upper molars of *Plesiaceratherium* sp. (KNM-NC 10486; Geraads, 2010) are moderately worn down. These upper molars differ from the present specimens in having a weakly constricted protocone, a rounded lingual surface of the protocone, no crochet at this wear stage, the presence of the reduced lingual cingulum, an undeveloped antecrochet and no enamel ring in the medisinus.

The present specimens also differ from the Teleoceratini. Three species of this tribe (*Brachypotherium snowi*, *B. lewisi*, and *B. minor*) have been reported so far from early Miocene to early Pliocene localities in Africa (Hooijer and Patterson, 1972; Harris and Leakey, 2003; Geraads, 2010; Geraads and Miller, 2013). *Brachypotherium heinzelini*, which was discovered from the lower Miocene in Africa, was considered by Geraads (2010) to be synonymous with *B. snowi*. All the species of *Brachypotherium* from Africa have upper molars with a weakly constricted protocone, a short or continued lingual cingulum, a short antecrochet, an undeveloped hypocone groove, no coronal cement, and lower cheek teeth with a flat buccal wall and shallow external groove. These characteristics are not found in the present specimens.

The present specimens are distinguished from the Rhinocerotini such as *Rusingaceros leakeyi* and *Paradiceros mukirii*. *Rusingaceros leakeyi* is an early to middle Miocene species discovered from sub-Saharan Africa (Hooijer, 1966, 1973; Geraads, 2010; Guérin, 2011). Although the upper cheek teeth of the holotype of *R. leakeyi* are worn down (KNM-RU 2821A; Hooijer, 1966), this specimen shows the following characteristics: no protocone constriction, a rounded lingual wall of the protocone, the absence of the antecrochet and hypocone groove, and no coronal cement. These characteristics are not seen in the present specimens. Many materials of *P. mukirii*, including the holotype, have been reported from the middle Miocene locality of Fort Ternan in Kenya (Hooijer, 1968). The present specimens also differ from *P. mukirii* described by Hooijer (1968) in having the upper molars with protocone constriction, a flattened lingual surface of the protocone, a developed antecrochet, a simply developed crochet, and coronal cement.

The present specimens are also discriminated from the Dicerotini. This tribe includes two taxa: *Diceros* and *Ceratotherium*. Five species of *Diceros* (*D. australis*, *D. primaevus*, *D. douariensis*, *D. praecox*, and *D. bicornis*) have been found from the Miocene localities in Africa (Arambourg, 1959; Guérin, 1966, 2000, 2003; Hooijer and Patterson, 1972; Harris and Leakey, 2003; Geraads, 2005; Giaourtsakis et al., 2009). These species have no protocone constriction and hypocone groove, a rounded lingual wall of the protocone, an undeveloped antecrochet and the presence of the lingual cingulum. These characters are not seen in the upper molars of the present specimens. *Ceratotherium simum*, *C. mauritanicum* and *C. efficax* have been reported from several Plio-Pleistocene localities in Africa (Geraads, 2005, 2010; Hernesniemi et al., 2011). These species have upper molars with a mediofossette and distally oriented proto- and metalophs, which are not seen in the present specimens. Additionally, the present specimens differ from the three species of *Ceratotherium* in having protocone constriction, the development of the antecrochet, and the presence of a hypocone groove.

6.1. Morphological comparison with the Rhinocerotidae from the Namurungule and Nakali formations

As mentioned above, the Rhinocerotidae from the Samburu Hills and Nakali have been previously revised by Fukuchi et al. (2008), Handa et al. (2015), and Handa (2016). According to those studies, the following taxa are recognized from the Namurungule and Nakali formations: *K. bishopi*, *C. pattersoni*, *Brachypotherium* sp., and *Diceros* sp. The present specimens differ morphologically from these four taxa.

K. bishopi was found from both the Namurungule and Nakali formations (Aguirre and Guérin, 1974; Nakaya et al., 1987). Aguirre and Guérin (1974) described the upper P4 (holotype: KNM-NA 198) and M1 (paratype: KNM-NA 199) from the Nakali Formations as a new Elasmotheriini species: *K. bishopi*. The present specimens differ from the upper molar of *K. bishopi* (KNM-NA 199) for the following reasons. The entrance of the medisinus in the present specimens is open while that of KNM-NA 199 is closed by the connection of the protocone and hypocone. The protocone and hypocone of the present specimens are more strongly constricted than those of KNM-NA 199. There is no lingual cingulum on the molars of the present specimens, whereas KNM-NA 199 has a reduced lingual cingulum. Unlike *K. bishopi*, the present specimens have the enamel ring in the medisinus of the upper molars. The present specimens have no enamel folding; in contrast, KNM-NA 199 shows a weakly developed enamel folding.

Nakaya et al. (1987) described an isolated upper molar of *K. bishopi* (KNM-SH 15827) from the Namurungule Formation. The present specimens differ from KNM-SH 15827 in having a more strongly constricted protocone and hypocone, disconnection between the antecrochet and metaloph, and the enamel ring in the medisinus. In addition, the present specimens have larger dimensions than those of *K. bishopi* (Table 2). Handa (2016) also identified an isolated upper molar fragment (M1 or M2; KNM-SH 15869) as *K. bishopi*. The present specimens depart from KNM-SH 15869 in having a lingually oriented protoloph, an opened entrance of the medisinus, and the presence of the enamel ring in the medisinus.

The lower cheek teeth on the mandibular specimens described here (Fig. 4) are covered with coronal cement, which is a characteristic of the Elasmotheriini. These teeth are metrically smaller to that of the upper cheek teeth of *K. bishopi* (Tables 2 and 3). Therefore, the mandibular specimens described here are assigned to the same taxon of the present upper teeth.

Handa et al. (2015) described as *C. pattersoni* several isolated cheek teeth (KNM-NA 257A, NA 257B, NA 47409) from the Nakali Formation. They also redescribed the specimens of *C. pattersoni* from the Namurungule Formation that have been previously reported by Nakaya et al. (1987) and Tsujikawa (2005). The present specimens differ from *C. pattersoni* as described by Handa et al. (2015) in having abundant coronal cement on both the upper and lower cheek teeth, a lingually directed metaloph on M2, more constricted protocone, no lingual cingulum in M3, and the enamel ring in the medisinus of the upper molars. In addition, the dental dimensions of the present specimens are smaller than those of *C. pattersoni* from the Namurungule and Nakali Formations.

Three specimens with cheek teeth and isolated lower cheek teeth from the Namurungule Formation, which were described as *Paradiceros* and/or *Chilotheridium* by Nakaya et al. (1987) and Tsujikawa (2005), were considered as possibly *Brachypotherium* by Handa (2016). Those specimens (KNM-SH 12143, SH 38405, and SH 40120) show characters of *Brachypotherium* such as the flattened buccal wall of the lower teeth, a character not seen in the present specimens. Therefore, the present specimens are clearly different from the material of *Brachypotherium* from both the Namurungule and Nakali formations.

Upper molars of possibly *Diceros* (KNM-NA 52143, NA 52139, NA 52151) have been reported from the Nakali Formation (Handa, 2016). Those specimens show the following characters: no coronal cement on the cheek teeth, absence of the constriction of the protocone, long crochet, absence of the antecrochet and hypocone groove, and no enamel ring in the medisinus of the upper cheek teeth. These are not seen here, suggesting that the present specimens differ from *Diceros* from the Nakali Formation.

Fukuchi et al. (2008) reported a skull of *Diceros* sp. (KNM-NA 46987) from the Nakali Formation. They also considered an upper cheek teeth row (KNM-SH 15839, assigned to *Paradiceros* sp. by Nakaya et al., 1987) to belong to *Diceros* sp. The present specimens differ from those specimens in showing a constriction of the protocone on M1 and M2, coronal cement, the hypocone groove, and the enamel ring in the medisinus of the upper molars.

6.2. Morphological comparison with African species of the Elasmotheriini

Aside from the differences with *K. bishopi*, the present specimens are also distinguished from the previously known African Elasmotheriini species, namely *O. napakense*, *V. kenyensis*, and *Victoriaceros hooijeri*. The present specimens differ from the early Miocene species *O. napakense*, which was reported from Napak in Uganda (Guérin and Pickford, 2003). The dimensions of M2 in the present specimens are similar to those of *O. napakense* (Table 2; Fig. 5(a)). However, the metaloph of the present specimens extends lingually, whereas that of *O. napakense* extends distolingually (Guérin and Pickford, 2003). Unlike *O. napakense*, there is a small enamel ring in the medisinus of the present specimens.

Two species of *Victoriaceros*, *V. kenyensis* and *V. hooijeri*, have been reported from Miocene localities in Kenya (Geraads et al., 2012, 2016). An almost completely preserved skull of *V. kenyensis* was found from Maboko in Kenya (Geraads et al., 2012). The following features of the present specimens are similar to *V. kenyensis*: a strongly constricted protocone in the upper molars, a projected antecrochet, absence of the crista, a hypocone groove, and an almost straight ventral margin of the mandible. In addition, the dimensions of M3 in the present specimens are also similar to those of *V. kenyensis* (Table 2; Fig. 5(b)). However, the following features differ between the present specimens and *V. kenyensis*: the crochet of the present specimens is simple whereas that of *V. kenyensis* is bifid (KNM-MB 36189), the lingual wall of the protocone of M2 in the present specimens is more flattened, the present specimens have the lingual groove of the protocone on M3, which is not seen in *V. kenyensis*, the antecrochet of the present specimens does not contact the metaloph, and unlike *V. kenyensis* the present specimens have an enamel ring.

Geraads et al. (2016) tentatively assigned a skull from the lower Miocene of Karungu in western Kenya to another species of *Victoriaceros*, *V. hooijeri*. The present specimens also differ from *V. hooijeri* in having a developed antecrochet that curves toward the entrance of the medisinus, no lingual cingulum in the upper molars, stronger protocone constriction on the upper molars, a lingual groove of the protocone on M2 and M3, the enamel ring in the medisinus, the presence of the hypocone groove on M2, a more developed paracone fold on M3, and abundant coronal cement.

6.3. Morphological comparison with Eurasian species

Many species of Elasmotheriini have been discovered from outside of Africa. Morphologically, the Eurasian species most similar to the present specimens is *Huaqingtherium lintungense* from the middle Miocene (MN6-8) of China and Mongolia (Zhai, 1978; Antoine, 2003). The present specimens and *H. lintungense* described by Zhai (1978) share the following features: the lingually directed proto- and metalophs; an undeveloped enamel folding; a flattened lingual wall of the protocone; a hypocone groove on M2; and the absence of the crista. The dimensions of M3 of the present specimens are also similar to those of *H. lintungense* (Table 2; Fig. 5(b)). The present specimens, however, differ from *H. lintungense* in having the lingual protocone groove on M2, and the enamel ring in the medisinus of the upper molars. The

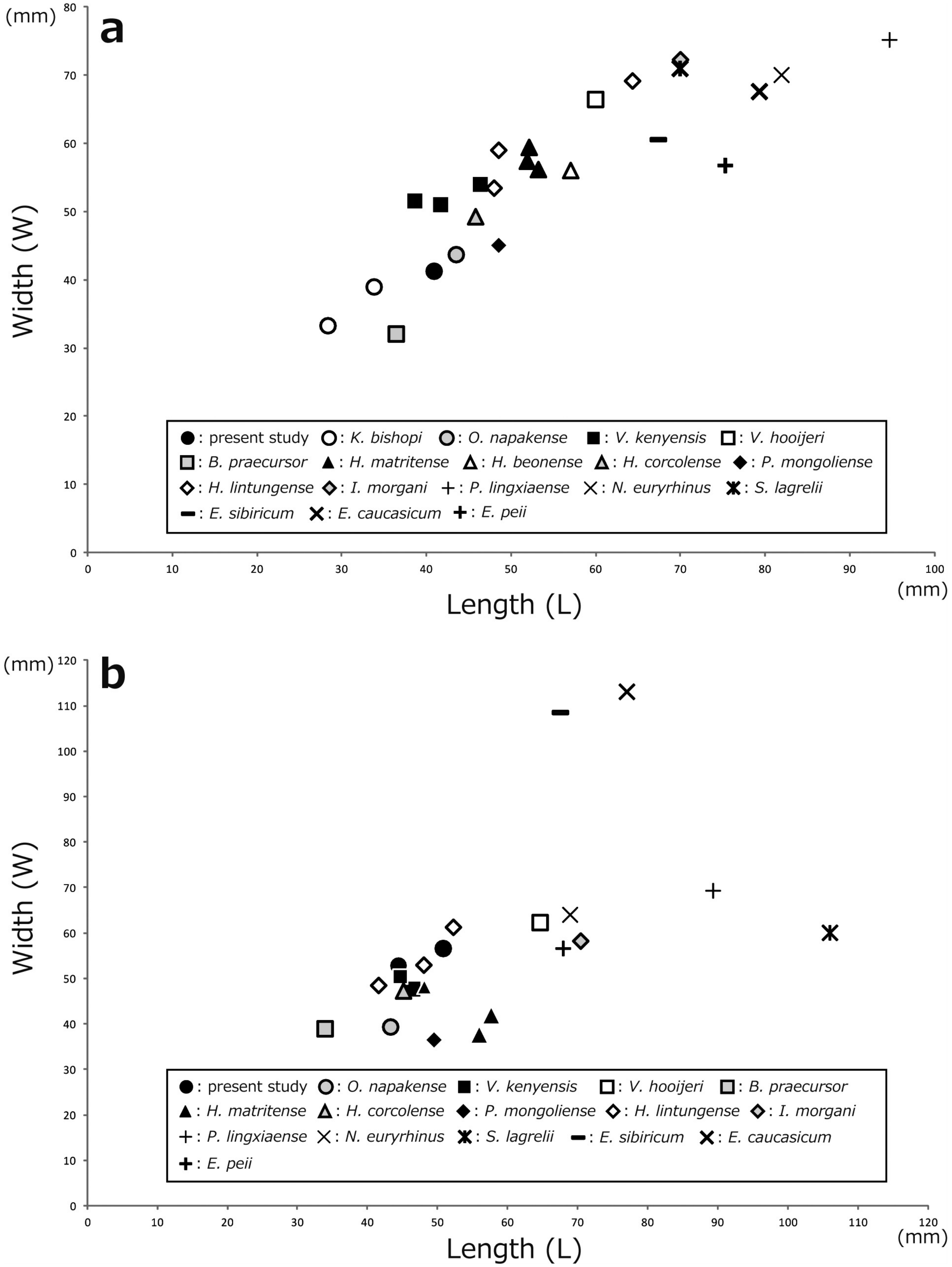

Fig. 5. Scatter diagrams of the tooth measurements of *Samburuceros ishidai* nov. gen., nov. sp. from the Namurungule and Nakali formations and comparative material: **a**: scatter diagram of the measurements of M2; **b**: scatter diagram of the measurements of M3. Data are from Table 2. The measurements of *O. napakense*, *H. matritense*, *H. corcolense*, *P. mongoliense*, *H. lintungense*, *I. morgani*, *P. linxiaense*, *E. sibiricum*, *E. caucasicum*, and *E. peii* are based on mean values.

tooth size of M2 in the present specimens is smaller than that of *H. lintungense* (Table 2; Fig. 5(a)). Therefore, the present specimens differ from *H. lintungense*.

The present specimens differ from other early to middle Miocene taxa in Eurasia (including the genera *Bugtirhinus*, *Hispanotherium*, *Procoelodonta*, and *Caementodon*; Antoine and Welcomme, 2000; Antoine, 2003; Sanisidro et al., 2012). The present specimens are discriminated from *Bugtirhinus praecursor*, which is known from the early Miocene (MN3) locality of the Bugti Hills in Pakistan (Antoine and Welcomme, 2000), in having a lingual groove on the protocone, a wide postfossette, a reduced anterior cingulum, the absence of the tubercle on the entrance of the medisinus of M3, and larger-sized teeth (Table 2; Fig. 5).

In the early to middle Miocene localities of Eurasia, several species of *Hispanotherium* have been described, such as those from Western Europe and China (MN4-MN6; *H. matritense*), from Pellecahus in France (MN4-MN5; *H. beonense*), and from Córcoles in Spain (MN4; *H. corcolense*) (Iñigo and Cerdeño, 1997; Antoine et al., 2002; Deng, 2003; Sanisidro et al., 2012). The present specimens differ from all *Hispanotherium* species by the lingually directed metaloph, lingual groove of the protocone on M3, undeveloped crista, and simple crochet in M3.

Procoelodonta mongoliense from the early middle Miocene of Mongolia and China (Antoine, 2003) shows characters such as the connection of the antecrochet to the metaloph, wrinkled enamel folding, absence of the lingual groove of the protocone, and posterior vertical groove on the ectometaloph of M3 (Antoine, 2003). These are not seen in the upper cheek teeth of the present specimens. In addition, the size of M3 of the present specimens is larger than that of *P. mongoliense* (Table 2; Fig. 5(b)). Therefore, the present specimens differ from *P. mongoliense*. The present specimens also differ from *Caementodon oettingenae* from middle Miocene (MN7/8) localities of Pakistan (Heissig, 1972; Antoine, 2002, 2003) in having lingually oriented lophs, a simple crochet, no labial cingulum on the upper molars, well-developed hypocone groove, and the presence of the enamel ring in the entrance of the medisinus.

The present specimens obviously differ from all the late Miocene taxa in Eurasia (including the genera *Iranotherium*, *Parelasmotherium*, *Ningxiatherium*, and *Sinotherium*). Overall, these Eurasian late Miocene taxa have upper molars with distally directed proto- and metalophs, indented protocone constriction, and developed crista and/or cristella (de Mecqenum, 1908; Killgus, 1923; Ringström, 1924; Antoine, 2002, 2003; Deng, 2005, 2007, 2008). These characters are not seen in the present specimens. Moreover, these Eurasian taxa are larger than the present specimens (Table 2; Fig. 5). The present specimens differ from *Iranotherium morgani*, which has been found in Iran (MN11) and China (MN10-12) (de Mecqenum, 1908; Deng, 2005), in having no pillar-shaped lingual cingulum in the M1 and M2, the presence of an anterior cingulum, the lingually elongated protoloph of M3, and the more distally elongated metaconid on the lower molars. The present specimens differ from *Parelasmotherium linxiaense* from late Miocene localities in China (MN9; Deng, 2007) in having upper molars with lingually elongated protoloph and metaloph, constricted hypocone, and a developed anterior cingulum. The present specimens also differ from *Ningxiatherium euryrhinus*, which was discovered from the upper Miocene (MN9) of Linxia Basin in Gansu, China (Deng, 2008). The molars of the holotype of *N. euryrhinus* have the connection of the antecrochet and hypocone and weakly wrinkled enamel around the medisinus on M1, no lingual groove on M2, quadrangular-shaped upper molars in occlusal view, and a short antecrochet on M3 (Deng, 2008). These characters are not seen in the present specimens. Finally, the present specimens differ from *Sinotherium lagrelii* from late Miocene localities (*ca.* 7 Ma) of China, Mongolia and Kazakhstan (Ringström, 1924; Kondrashov, 2000; Deng et al., 2013), in having undeveloped enamel folding, lingually elongated lophs, no postcrista in the upper molars, and an almost straight ventral margin of the mandible (Ringström, 1924; Kondrashov, 2000).

The most derived taxon of the Elasmotheriini, *Elasmotherium*, has been found from the early to late Pleistocene localities of Eurasia (Schvyreva, 2015). *Elasmotherium sibiricum*, *E. caucasicum* and *E. peii* have abundant coronal cement, corrugated enamel folding, more distally bending protoloph in the upper molars, and a convex ventral margin of the mandible (Brandt, 1878; Borissiak, 1914; Schvyreva, 2015). These characters distinguish the present specimens from all known species of *Elasmotherium*. The tooth dimensions of the present specimens are obviously smaller than those of *Elasmotherium* (Table 2; Fig. 5).

7. Discussion

The morphological and metrical characters of the present specimens from the Namurungule and Nakali formations differ from all known taxa of the tribe Elasmotheriini. Therefore, those specimens are considered here to belong to a new taxon, namely *Samburuceros ishidai* nov. gen., nov. sp. Nevertheless, dental characters of the Rhinocerotidae often show intra- or interspecific variability and homoplasy. In order to further discuss the diagnostic characters of the new genus and species from the Namurungule and Nakali Formations, we preliminarily conducted a phylogenetic analysis using PAUP4.0α152 (Swofford, 2002). The character matrix and character states analyzed here were adapted from Antoine (2003) and Sanisidro et al. (2012). Twenty-six terminal taxa were included in the analysis, using *Tapirus terrestris* and *Hyrachyus eximius* as the outgroup. All characters were equally weighted and unordered. Parsimony analysis was performed with 1000 starting addition sequences and a tree-bisection-reconnection (TBR) swapping algorithm. As a result, a strict consensus tree (697 steps, CI = 0.488, RI = 0.604) was obtained from two equally parsimonious trees (Supplementary data, Appendix A). *Samburuceros ishidai* nov. gen., nov. sp. is situated as a sister taxon of *V. kenyensis* and is separated from *K. bishopi*. According to this analysis, the autapomorphic character of *S. ishidai* nov. gen., nov. sp. is the presence of the lingual groove on the protocone on the M2 (Supplementary data, Appendix B: char. #128: 2). In addition, direct comparison between the present specimens and *V. kenyensis* showed that the following characters of *S. ishidai* nov. gen., nov. sp. differ from *V. kenyensis* as mentioned above: the simple crochet, the lingual groove on the protocone on M3, and the enamel ring in the medisinus on M2 and M3. Thus, those differences are considered as the diagnostic character combination of *S. ishidai* nov. gen., nov. sp.

The phylogenetic relationships between the African species and the other species of the Elasmotheriini remain controversial. Several cladistic analyses of the Elasmotheriini have been already achieved and discussed by Antoine (2002, 2003), Deng (2008), Sanisidro et al. (2012), and Geraads et al. (2016). However, the taxa used in these analyses vary among authors, leading to different cladograms supporting distinct phylogenetic hypotheses. According to Antoine (2002), *K. bishopi* is the most basal taxon in the clade Elasmotheriini, and is phyletically closely related to *B. praecursor* (Supplementary data, Appendix A; see also Antoine, 2003; Deng, 2008; Sanisidro et al., 2012; Geraads et al., 2016). Guérin and Pickford (2003) suggested that *O. napakense* is closely related to *K. bishopi* based on the morphological comparison of their cheek teeth. Geraads et al. (2016) analyzed the phylogeny of the Rhinocerotidae to discuss the phylogenetic position of *V. hooijeri*, based on Lu's (2013) data matrix. According to their analysis, *O. napakense* was separated from *K. bishopi* and was situated as a more derived species than *K. bishopi* within the clade Elasmotheriini, departing from Guérin and Pickford's (2003) hypothesis. In addition, *V. hooijeri* was the sister taxon of *V. kenyensis* and these two species were closely related to *C. pattersoni* which has been previously included in the Tribe Aceratheriini.

Geraads et al. (2012, 2016) noted that the phylogenetic positions of African elasmotheres within the Elasmotheriini were debatable because of the incompleteness of the specimens and the poor state of preservation of the available fossil record from Africa. Therefore, additional well-preserved specimens need to be discovered from Africa in order to further discuss phylogenetic relationships of African elasmotheres with other Eurasian taxa. Nevertheless, *S. ishidai* nov. gen., nov. sp. is the fifth described taxon of the Tribe Elasmotheriini in sub-Saharan East Africa. *K. bishopi* was already described from the Namurungule and Nakali formations (Aguirre and Guérin, 1974; Nakaya et al., 1987). The present study indicates that two species of Elasmotheriini existed in East Africa during the early late Miocene.

Acknowledgements

We thank the Government of Kenya and the National Museums of Kenya for research permission, and the staff of the National Museums of Kenya for assistance in the museum. The first author is grateful to Emma Bernard (Natural History Museum, London, UK), Patricia Pérez Dios (Museo Nacional de Ciencias Naturales, Madrid, Spain), Christine Argot (Muséum National d'Histoire Naturelle, Paris, France), Abel Prieur and Emmanuel Robert (Laboratoire de Géologie de Lyon : Terre, Planètes, Environnement and Observatoire des Sciences de l'Univers de Lyon, Université Claude-Bernard–Lyon I, Lyon, France), and Hiroyuki Taruno (Osaka Museum of Natural History, Osaka, Japan) for providing access to specimens for the comparative works. The authors thank the associate-editor P.-O. Antoine and three anonymous reviewers, who made constructive suggestions for improving the original manuscript. This study was partly supported by grants from the Fujiwara natural History Foundation, Japan in 2012, by the Sasakawa Research Grant from the Japan Science Society No. 24-622, and by the JSPS KAKENHI grants No. 22255006, 25257408, and 16H02757.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.geobios.2017.04.002.

References

Aguirre, E., Guérin, C., 1974. Première découverte d'un Iranotheriinae (Mammalia, Perissodactyla, Rhinocerotidae) en Afrique : *Kenyatherium bishopi* nov. gen. nov. sp. de la formation vallésienne (Miocene supérieur) de Nakali (Kenya). Estudios Geológicos 30, 229–233.

Antoine, P.-O., 2002. Phylogénie et évolution des Elasmotheriina (Mammalia, Rhinocerotidae). Memoire du Muséum National d'Histoire Naturelle 188, 1–359.

Antoine, P.-O., 2003. Middle Miocene elasmotheriine Rhinocerotidae from China and Mongolia: taxonomic revision and phylogenetic relationships. Zoologica Scripta 32, 95–118.

Antoine, P.-O., Welcomme, J.-L., 2000. A new rhinoceros from the Lower Miocene of the Bugti Hills, Baluchistan, Pakistan: the earliest elasmotheriine. Palaeontology 43, 795–816.

Antoine, P.-O., Alférez, F., Iñigo, C., 2002. A new elasmotheriine (Mammalia, Rhinocerotidae) from the Early Miocene of Spain. Comptes Rendus Palevol 1, 19–26.

Arambourg, C., 1959. Vertébrés continentaux du Miocène supérieur de l'Afrique du Nord. Publication du Service de la Carte géologique de l'Algérie (nouvelle série), Paléontologie 4, 1–159.

Borissiak, K.K., 1914. Sur la dentition d'Elasmotherium *caucasicum* n. sp. Bulletin de l'Académie Impériale des Science, Saint-Pétersbourg 6, 555–584.

Brandt, J.F., 1878. Mittheilumgen ueber die Gattung *Elasmotherium* besonders den Schaedelbau derselben. Bulletin de l'Académie Impériale des Science, Saint-Pétersbourg 26, 1–36.

Cerdeño, E., Nieto, M., 1995. Changes in Western European Rhinocerotidae related to climatic variations. Palaeogeography, Palaeoclimatology, Palaeoecology 114, 325–338.

Deng, T., 2003. New material of *Hispanotherium matritense* (Rhinocerotidae, Perissodactyla) from Laogou of Hezheng County (Gansu, China), with special reference to the Chinese Middle Miocene elasmotheres. Geobios 36, 141–150.

Deng, T., 2005. New discovery of *Iranotherium morgani* (Perissodactyla, Rhinocerotidae) from the Late Miocene of the Linxia Basin in Gansu, China, and its sexual dimorphism. Journal of Vertebrate Paleontology 25, 442–450.

Deng, T., 2007. Skull of *Parelasmotherium* (Perissodactyla, Rhinocerotidae) from the Upper Miocene of in the Linxia Basin (Gansu, China). Journal of Vertebrate Paleontology 27, 467–475.

Deng, T., 2008. A new elasmotheres (Perissodactyla, Rhinocerotidae) from the Late Miocene of the Linxia Basin in Gansu, China. Geobios 41, 719–728.

Deng, T., Downs, W., 2002. Evolution of Chinese Neogene Rhinocerotidae and its response to climatic variations. Acta Geologica Sinica 76, 139–145.

Deng, T., Wang, S., Hou, S., 2013. A bizarre tandem-horned elasmothere rhino from the Late Miocene of northwestern China and origin of the true elasmotheres. Chinese Science Bulletin 58, 1811–1817.

Deraniyagara, P.E.P., 1951. A hornless rhinoceros from the Mio-Pliocene deposits of East Africa. Spolia Zeylanica 26, 133–135.

Fortelius, M., Heissig, K., 1989. The phylogenetic relationships of the Elasmotherini (Rhinocerotidae, Mamm.). Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie 29, 227–233.

Fukuchi, A., Nakaya, H., Kunimatsu, Y., Nakatsukasa, M., 2008. Rhinoceros fossils from the Late Miocene mammalian localities (Nakali and Samburu Hills) in Kenya. Abstracts of the Regular Meeting of the African Study Society of Japan 7, (in Japanese).

Geraads, D., 2005. Pliocene Rhinocerotidae (Mammalia) from Hadar and Dikika (Lower Awash, Ethiopia), and a revision of the origin of modern African rhinos. Journal of Vertebrate Paleontology 25, 451–461.

Geraads, D., 2010. Rhinocerotidae. In: Werdelin, L., Sanders, W.J. (Eds.), Cenozoic Mammals of Africa. University of California Press, Berkeley, pp. 669–683.

Geraads, D., Miller, E., 2013. *Brachypotherium minor* n. sp., and other Rhinocerotidae from the Early Miocene of Buluk, Northern Kenya. Geodiversitas 35, 359–375.

Geraads, D., McCrossin, M., Benefit, B., 2012. A new rhinoceros, *Victoriaceros kenyensis* gen. et sp. nov., and other Perissodactyla from the Middle Miocene of Maboko, Kenya. Journal of Mammal Evolution 19, 57–75.

Geraads, D., Lehman, T., Peppe, D.J., Mccnulty, K.P., 2016. New Rhinocerotidae from Kisingiri localities (lower Miocene of Western Kenya). Journal of Vertebrate Paleontology 36, e1103247, http://dx.doi.org/10.1080/02724634.2016.1103247.

Giaourtsakis, I.X., Pehlevan, C., Haile-Selassie, Y., 2009. Rhinocerotidae. In: Haile-Selassie, Y., WoldeGabriel, G. (Eds.), Ardipithecus kadabba Late Miocene evidence from the Middle Awash. Ethiopia. The Middle Awash Series, vol. 2, University of California Press, Berkeley, pp. 429–468.

Guérin, C., 1966. Diceros douariensis nov. sp., un rhinocéros du Mio-Pliocène de Tunisie du Nord. Documents des Laboratoires de Géologie de la Faculté des Sciences de Lyon 16, 1–50.

Guérin, C., 1980. Les Rhinocéros (Mammalia, Perissodactyla) du Miocène terminal au Pléistocène supérieur en Europe occidentale : comparaison avec les espèces actuelles. Documents des Laboratoires de Géologie de la Faculté des Sciences de Lyon 79, 1–1185.

Guérin, C., 2000. The Neogene rhinoceroses of Namibia. Palaeontologia Africana 36, 119–138.

Guérin, C., 2003. Miocene Rhinocerotidae of the Orange River Valley, Namibia. In: Pickford, M., Senut, B. (Eds.), Geology and Palaeobiology of the Central and Southern Namib, vol. 2, Palaeontology of the Orange River Valley, Memoir of the Geological Survey of Namibia, Windhoek, Namibia 19, pp. 257–281.

Guérin, C., 2011. Les Rhinocerotidae (Mammalia, Perissodactyla) miocènes et pliocènes des Tugen Hills (Kenya). Estudios Geológicos 67, 333–362.

Guérin, C., Pickford, M., 2003. Ougandatherium napakense nov. gen. nov. sp. Le plus ancien Rhinocerotidae Iranotheriinae d'Afrique. Annales de Paléontologie 89, 1–35.

Handa, N., 2016. Fossil Rhinoceroses From the Late Miocene of Kenya – Miocene Faunal Changes of the Rhinocerotidae (Mammalia, Perissodactyla) in Sub-Saharan East Africa (Ph. D. thesis). Kagoshima University (unpubl.).

Handa, N., Nakatsukasa, M., Kunimatsu, Y., Tsubamoto, T., Nakaya, H., 2015. New specimens of Chilotheridium (Perissodactyla, Rhinocerotidae) from the Upper Miocene Namurungule and Nakali Formations, northern Kenya. Paleontological Research 19, 181–194.

Harris, J.M., Leakey, M.G., 2003. Lothagam Rhinocerotidae. In: Leakey, M.G., Harris, J.M. (Eds.), Lothagam – The Dawn of Humanity in Eastern Africa. Columbia University Press, New York, pp. 371–385.

Heissig, K., 1972. Paläontologische und geologische Untersuchungen im Tertiär von Pakistan–5. Rhinocerotidae (Mammalia) aus den unteren und mittleren Siwalik-Schichten. Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Klasse, München 152, 1–112.

Heissig, K., 1973. Die Unterfamilien und Tribus der rezenten und fossilen Rhinocerotidae (Mammalia). Säugetierkundliche Mitteilungen 21, 25–30.

Heissig, K., 1989. The Rhinocerotidae. In: Prothero, D.R., Schoch, R.M. (Eds.), The Evolution of Perissodactyls. Oxford University Press, New York, pp. 399–417.

Heissig, K., 1996. The stratigraphical range of fossil rhinoceroses in the Late Neogene of Europe and the Eastern Mediterranean. In: Bernor, R.L., Fahlbusch, V., Mittmann, H.-W. (Eds.), The Evolution of Western Eurasian Neogene Mammal Faunas. Columbia University Press, New York, pp. 339–347.

Heissig, K., 1999. Family Rhinocerotidae. In: Rössner, G.E., Heissig, K. (Eds.), The Miocene Land Mammals of Europe. Verlag Dr. F. Pfeil, Munich, pp. 175–188.

Hernesniemi, E., Giaourtsakis, I.X., Evans, A.R., Fortelius, M., 2011. Chapter 11: Rhinocerotidae. In: Harrison, T. (Ed.), Paleontology and Geology of Laetoli: Human Evolution in Context, Vol. 2: Fossil Hominins and the Associated Fauna, Vertebrate Paleobiology and Paleoanthropology. Springer Science+Business Media B. V., Springer, Netherlands, pp. 275–294.

Hooijer, D.A., 1966. Miocene rhinoceroses of East Africa. Bulletin of the British Museum (Natural History), Geology 13, 119–190.

Hooijer, D.A., 1968. A rhinoceros from the Late Miocene of Fort Ternan, Kenya. Zoologische Mededelingen 43, 77–92.

Hooijer, D.A., 1971. A new rhinoceros from the Late Miocene of Loperot, Turkana district, Kenya. Bulletin of the Museum of Comparative Zoology 142, 339–392.

Hooijer, D.A., 1973. Additional Miocene to Pleistocene rhinoceroses of Africa. Zoologische Mededelingen 59, 151–191.

Hooijer, D.A., Patterson, B., 1972. Rhinoceroses from the Pliocene of northwestern Kenya. Bulletin of the Museum of Comparative Zoology 144, 1–26.

Iñigo, C., Cerdeño, E., 1997. The Hispanotherium matritense (Rhinocerotidae) from Córcoles (Guadalajara, Spain): its contribution to the systematics of the Miocene Iranotheriina. Geobios 30, 243–266.

Ishida, H., Pickford, M., 1997. A new Late Miocene hominoid from Kenya: Samburupithecus kiptalami gen. et sp. nov. Comptes Rendus de l'Académie des Science, Series IIA, Sciences de la terre et des planètes 325, 823–829.

Killgus, H., 1923. Unterpliozäne Säuger aus China. Paläontologisches Zeitschrift 73, 251–257.

Kondrashov, P.E., 2000. Sinotherium (Mammalia, Rhinocerotidae) the Early Pliocene of Mongolia. Paleontological Journal 6, 74–79 (in Russian).

Kunimatsu, Y., Nakatsukasa, M., Sawada, Y., Sakai, T., Hyodo, M., Hyodo, H., Itaya, T., Nakaya, H., Saegusa, H., Mazurier, A., Saneyoshi, M., Tsujikawa, H., Yamamoto, A., Mbua, E., 2007. A new Late Miocene great ape from Kenya and its implications for the origins of African great apes and humans. Proceedings of the National Academy of Sciences, United States of America 104, 19220–19225.

Lu, X., 2013. A juvenile skull of Acerorhinus yuanmouensis (Mammalia: Rhinocerotidae) from the Late Miocene hominoid fauna of the Yuanmou Basin (Yunnan, China). Geobios 46, 539–548.

Mecqenum, R., 1908. Contribution à l'étude du gisement de vertébrês de Maragha et de ses environs. Annales d'Histoire Naturelle, Paris 1, 27–79.

Nakaya, H., 1994. Faunal change of Late Miocene Africa and Eurasia: mammalian fauna from the Namurungule Formation, Samburu Hills, northern Kenya. African Study Monographs suppl. issue 20, 1–112.

Nakaya, H., Pickford, M., Nakano, Y., Ishida, H., 1984. The Late Miocene large mammal fauna from the Namurungule Formation. African Study Monographs, Samburu Hills, northern Kenya (Suppl. issue 2, 87−131).

Nakaya, H., Pickford, M., Yasui, K., Nakano, Y., 1987. Additional large mammalian fauna from the Namurungule Formation, Samburu Hills, northern Kenya. African Study Monographs suppl. issue 5, 79–129.

Ringström, T.J., 1924. Nashörner der Hipparion-Fauna Nord-Chinas. Geological Survey of China, Series C 1, 1–156.

Sakai, T., Saneyoshi, M., Tanaka, S., Sawada, Y., Nakatsukasa, M., Mbua, E., Ishida, H., 2010. Climate shift recorded at around 10 Ma in Miocene succession of Samburu Hills, northern Kenya Rift, and its significance. Geological Society, London, Special Publications 342, 109–127.

Sakai, T., Saneyoshi, M., Sawada, Y., Nakatsukasa, M., Kunimatsu, Y., Mbua, E., 2013. Early continental rift basin stratigraphy, depositional facies and tectonics in volcaniclastic system: examples from the Miocene successions along the Japan Sea and in the East African rift valley (Kenya). In: Itoh, Y. (Ed.), Mechanism of Sedimentary Basin Formation-Multidisciplinary Approach on Active Plate Margins. Intech, Rijeka, Croatia, pp. 83–108.

Saneyoshi, M., Nakayama, K., Sakali, T., Sawada, Y., Ishida, H., 2006. Half graben filling processes in the early phase of continental rifting: the Miocene Namurungule Formation of the Kenya Rift. Sedimentary Geology 186, 111–131.

Sanisidro, O., Alberdi, M.T., Morales, J., 2012. The first complete skull of Hispanotherium matritense (Plado, 1864) (Perissodactyla, Rhinocerotidae) from the Middle Miocene of the Iberian Peninsula. Journal of Vertebrate Paleontology 32, 446–455.

Sawada, Y., Pickford, M., Itaya, T., Makinouchi, T., Tateishi, M., Kabeto, K., Ishida, S., Ishida, H., 1998. K−Ar ages of Miocene Hominoidea (Kenyapithecus and Samburupithecus) from Samburu Hills, Northern Kenya. Comptes Rendus de l'Académie des Science, Series IIA, Sciences de la terre et des planètes 326, 445–451.

Sawada, Y., Saneyoshi, M., Nakayama, K., Sakai, T., Itaya, T., Hyodo, M., Mukokya, Y., Pickford, M., Senut, B., Tanaka, S., Chujo, T., Ishida, H., 2006. The ages and geological backgrounds of Miocene Hominoids Nacholapithecus, Samburupithecus, and Orrorin from Kenya. In: Ishida, H., Tuttle, R.H., Pickford, M., Ogihara, N., Nakatsukasa, M. (Eds.), Human Origins and Environmental Backgrounds. Springer, New York, pp. 71–96.

Schvyreva, A.K., 2015. On the importance of the representatives of the genus Elasmotherium (Rhinocerotidae, Mammalia) in the biochronology of the Pleistocene of Eastern Europe. Quaternary International 379, 128–134.

Swofford, D.L., 2002. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods) Version 4. Sinauer Associates, Sunderland, Massachusetts.

Teryaev, V.A., 1929. [On the structure of teeth and synonymy of Elasmotherium Fisch. and Enigmatherium M. Pavlov] Bulletin de la Société des Naturalistes de Moscou, Section Géologique 7, 465–496 (in Russian).

Tong, H., Moigne, A.-M., 2000. Quaternary Rhinoceros of China. Acta Anthropologica China Suppl. 19, 257–263.

Tong, H., Wang, F., Zheng, M., Chen, X., 2014. New fossils of Stephanorhinus kirchbergensis and Elasmotherium peii from the Nihewan Basin. Acta Anthropologica Sinica 33, 369–388.

Tsujikawa, H., 2005. The updated Late Miocene large mammal fauna from Samburu Hills, northern Kenya. African Study Monographs suppl. issue 32, 1–50.

Yan, D.-F., 1979. Einige der fossilen Miozänen Säugetiere der Kreis von Fangxian in der Provinz Hupei. Vertebrata PalAsiatica 17, 189–199 (in Chinese).

Zhai, R., 1978. A primitive Elasmothere from the Miocene of Lintung, Shensi. Professional Papers of Stratigraphy and Palaeontology 7, 122–126.