

THE PALAEOENVIRONMENT OF *SAMBURUPITHECUS KIPTALAMI* BASED ON ITS ASSOCIATED FAUNA

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ABSTRACT This paper analyzes the palaeoenvironment of the Late Miocene large hominoid, *Samburupithecus kiptalami* by using the mammalian faunal assemblages. It is based on the mammal fauna found at the hominoid sites, using the habitat preferences of extant mammals, the probable feeding preferences based on morphology of the teeth, the footprint fauna and the relative abundance of each mammal taxon. The habitat preferences of extant mammals and the probable feeding preferences in relative abundances of each mammal taxon suggest that the Upper Member of the Namurungule Formation is likely to have been open whereas the Lower one is likely to have included both open and wooded components. In fact, the faunal components are different at various places in the lower part of the formation. Near the hominoid bearing site, SH 22, the palaeoenvironment seems to have been more wooded. Several places are likely to have been open environments. The footprints suggest a swampland surrounded by savanna. *Samburupithecus kiptalami* was likely to have inhabited woodland surrounded by an open environment such as savanna and grassland.

Key Words: Hominoid; Late Miocene; Mammalian fauna; Northern Kenya; Palaeoenvironment.

INTRODUCTION

The Samburu Hills Area is situated on the eastern margin of the Gregory Rift Valley, Northern Kenya (Sawada *et al.*, 1984). The Samburu Hills form a belt about 30 km wide and about 80 km long trending in a north-south direction and form the eastern wall of the Suguta Valley (Nakaya, 1994). The Namurungule Formation, of Upper Miocene age, crops out extensively in the Samburu Hills and consists mainly of mudstone, sandstone, and gravel intercalated with beds of mud flow deposits and tuff. The Namurungule Formation overlies the Aka Aiteputh Formation and is covered by the Kongia Formation (Sawada *et al.*, 1998).

The Namurungule Formation is the only one that yielded a hominoid fossil from the early Late Miocene (7.5-10.5 Ma) in East Africa. It is dated as ca. 9.5 Ma by the K-Ar dating method. In biostratigraphy, it is equivalent to Faunal Set VI (7.5-10.5 Ma) (Pickford, 1981; Pickford *et al.*, 1984b). The Namurungule Formation is one of the richest deposits yielding numerous mammal fossil remains of this period in East Africa. For example, the Ngorora upper E, Ngerengerwa, Nakali Formations, Kenya and the Ch'orora Formation, Ethiopia, are similar age. However, they have yielded few mammal fossils. The Ngorora upper E Formation dated 11-10.5 Ma yields 6 species of mammals (Benefit & Pickford, 1986; Pickford, 2002). The Ngerengerwa Formation dated ca. 9.5-10 Ma yields 8 species (Benefit & Pickford, 1986; Pickford, 2002). The Nakali Formation being equivalent to Faunal Set VI yields 12 species (Aguirre & Guérin, 1974; Aguirre & Leakey, 1974; Pickford & Fischer, 1987). The Ch'orora Formation dated 9-10.5 Ma yields 12 species (Geraads, 2001; Geraads *et al.*, 1997; Jacobs *et al.*, 1980; Kalb *et al.*, 1982a; 1982b; 1982c). In contrast, the Namurungule Formation has yielded at least 27 species.

This study investigates the palaeoenvironment of the Namurungule Formation based on its

abundant mammal fossil specimens. The palaeoenvironment of the Namurungule Formation is important for the study of human evolution because of the presence of *Samburupithecus kiptalami* (Ishida & Pickford, 1997). *Samburupithecus kiptalami* is chronologically positioned between the Middle Miocene hominoids such as *Kenyapithecus africanus*, *K. wickeri*, *Nacholapithecus kerioi* and *Equatorius africanus* and the Latest Miocene hominids such as *Orrorin tugenensis* and *Sahelanthropus tchadensis* (e.g. Brunet *et al.*, 2002; Ishida *et al.*, 1999; Senut *et al.*, 2001; Ward *et al.*, 1999). Thus, *S. kiptalami* is likely to be close in age to the common lineage of the humans and African apes (Ishida & Pickford, 1997; Pickford & Ishida, 1997). Clarifying its palaeoenvironment greatly enriches our understanding of environmental context of the hominid-African ape divergence. Palaeoenvironments of the earliest hominids are advocated as including closed components (e.g. Pickford & Senut, 2001). The palaeoenvironment of the Namurungule Fauna is crucial for clarifying the environmental polarity of protohominids. *S. kiptalami* is known only by a maxilla fragment. Thus, other approaches to the analyses of the palaeoenvironment are necessary. The analyses using the mammalian faunal assemblages contribute to an understanding of the palaeoenvironment of *S. kiptalami*.

MATERIALS

Geology

Eighty-four fossiliferous sites are known in the Namurungule Formation (Ishida *et al.*, 2001). The formation is divided into two members: “upper” and “lower”, by the mud flow deposits situated in the middle of the formation. The Lower Member of the formation is mudstone and includes localities : SH 8, 9, 20, 21-24, 27, 34, 50-54, 59 and 61-63. The Upper Member consists of a mudstone-dominant part and a brown-coloured conglomerate part which interfinger with each other. The Upper Member with fine lithology includes localities: SH 4, 5, and 28 and the conglomerate (coarse facies) part includes localities: SH 11-16, 19, 25, 38 and 41 (Pickford *et al.*, 1984a). The Upper and Lower Member are not different each other in age (ca. 9.5 Ma) based on the K-Ar dating (Sawada, *et al.*, 1998). In addition, SH 6, 17, 31, 45-46 belong to the Uppermost Limestone Member of the Aka Aiteputh Formation. The member was dated as being younger than 9.9 Ma and older than 9.6 Ma by the K-Ar dating method (Pickford *et al.*, 1984b; Sawada *et al.*, 1998). However, the positions of new fossiliferous sites, SH 65-84, are unknown.

The Namurungule Fauna

Since the 1980 field season, the Japan-Kenya Expedition Team has continued with palaeoanthropological, palaeontological and geological researches in the Sumburu Hills Area, Northern Kenya. During the 1982, 84, 86, 98 and 99 field seasons, numerous fossils were collected from excavations, mainly in the hominoid bearing site, SH 22 and by surface collections. The large mammal fauna during the 1982 and 1984 collections were described by Nakaya *et al.* (1984, 1987). A Late Miocene large hominoid, *Samburupithecus kiptalami*, was collected during the 1982 field season and was described by Ishida & Pickford (1997). The rodent remains, *Paraulacodus* sp. and *Paraphiomys* sp. were described by Kawamura & Nakaya (1984, 1987). Furthermore, footprint remains consisting of aves, carnivores, rhinocerotids and artiodactyls at site SH 23 were described by Nakano *et al.* (2001). Nakaya (1994) summarized the Namurungule Fauna of the 1982 to 1986 collections. Tsujikawa

Table 1. Quantity of fossil specimens and minimum number of individuals in each taxon.

Taxon	Lower Member		Upper Member	
	N (%)	MNI (%)	N (%)	MNI (%)
<i>Samburupithecus kiptalami</i>	1 (0.2)	1 (0.6)	-	-
<i>Paraphiomys</i> sp.	1 (0.2)	1 (0.6)	-	-
<i>Paraulacodus</i> sp.	2 (0.5)	2 (1.3)	-	-
?Felidae	2 (0.5)	2 (1.3)	-	-
Hyaenidae spp.	5 (1.2)	5 (3.2)	2 (1.4)	2 (3.1)
<i>Tetralophodon</i> sp. nov.	3 (0.7)	2 (1.3)	6 (4.1)	3 (4.7)
<i>Choerolophodon</i> sp.	1 (0.2)	1 (0.6)	-	-
<i>Deinotherium</i> sp.	9 (2.1)	6 (3.8)	8 (5.4)	1 (1.6)
Proboscidea indet.	12 (2.8)	3 (1.9)	1 (0.7)	1 (1.6)
Pliohyracidae indet.	1 (0.2)	1 (0.6)	-	-
<i>Hipparion africanum</i>	107 (25.2)	24 (15.3)	44 (29.9)	15 (23.4)
<i>Paradicerus mukirii</i>	19 (4.5)	9 (5.7)	7 (4.8)	3 (4.7)
<i>Chilotheridium pattersoni</i>	21 (5.0)	12 (7.6)	-	-
<i>Kenyatherium bishopi</i>	3 (0.7)	3 (1.9)	-	-
<i>Iranotheriinae</i> sp. nov.	10 (2.4)	7 (4.5)	-	-
Rhinocerotidae indet	29 (6.8)	5 (3.2)	10 (6.8)	3 (4.7)
Chalicotheriidae	-	-	1 (0.7)	1 (1.6)
<i>Nyanzachoerus</i> cf. <i>devauxi</i>	16 (3.8)	7 (4.5)	6 (4.1)	6 (9.4)
<i>Kenyapotamus corydoni</i>	9 (2.1)	3 (1.9)	2 (1.4)	2 (3.1)
Tragulidae indet.	-	-	1 (0.7)	1 (1.6)
<i>Palaeotragus</i> cf. <i>germaini</i>	84 (19.8)	21 (13.4)	12 (8.2)	8 (12.5)
? <i>Samotherium</i> sp.	15 (3.5)	6 (3.8)	6 (4.1)	5 (7.8)
<i>Tragoportax</i> sp.	5 (1.2)	3 (1.9)	-	-
<i>Boselaphini</i> sp. small	47 (11.1)	20 (12.7)	-	-
<i>Gazella</i> sp.	-	-	12 (8.2)	7 (10.9)
? <i>Antidorcas</i> sp.	1 (0.2)	1 (0.6)	2 (1.4)	1 (1.6)
<i>Pachytragus</i> sp.	16 (3.8)	10 (6.4)	-	-
Bovidae indet.	9 (2.1)	2 (1.3)	27 (18.4)	4 (6.3)
Total	424(100.0)	157(100.0)	147(100.0)	63(100.0)

N: number of fossils; MNI: minimum number of individuals.

(2005) updated the mammal fauna from the Namurungule Formation based on the 1986, 1998 and 1999 collections. The Namurungule Fauna includes at least 27 species (Table 1). The fauna occurs in three members, the Lower and Upper Members of the Namurungule Fauna and the Uppermost Limestone Member of the Aka Aiteputh Fauna. *Samburupithecus kiptalami* was collected from the Lower Member of the Namurungule Formation with numerous mammal fossil remains. The fauna from the Uppermost Limestone Member of the Aka Aiteputh Formation is not used in this study because it is fairly poor and fragmentary. The palaeoenvironment of the Namurungule Formation is analyzed in three ways, habitat preferences of equivalent extant mammals, feeding preferences based on morphology of the teeth and footprints at site SH 23. Before analyses, the number (N) of the fossils and minimum number of individuals (MNI) are counted in the Upper and Lower Member of the Namurungule mammal fauna. Each member is respectively analyzed for MNI.

Habitat Preferences of Equivalent Extant Mammals

At present, in Africa, there are various environments ranging from rainforest to desert, and aquatic to montane. Various mammals inhabit these environments. Some mammals confined to special environments and others are more wide ranging. These recent data are useful for the study of palaeoenvironments and probable habitat preferences of fossil mammals.

Using the habitat preferences of equivalent extant mammals, habitat preferences of the plaeospecies were estimated using two data sets - number of fossils and minimum number of individuals.

Probable Feeding Preferences Based on Morphology of the Teeth

Since numerous mammalian teeth were collected from the Namurungule Formation and morphology of the teeth is correlated with their feeding preferences, the relative abundance of browsing to grazing species can be estimated. The estimation of the feeding preferences are based mainly on brachydonty or hypsodonty and occurrence or absence of cementum. This study is based on the minimum number of individuals.

The Footprint Fauna

In addition to the hard tissue fossils, numerous footprints were found at site SH 23 (Nakano *et al.*, 2001; Pickford *et al.*, 1984a). The footprint fauna is informative for the palaeoenvironment reconstruction because it provides direct *in situ* evidence of the palaeofauna. This study is investigated with reference to habitat preferences of equivalent extant species and their probable feeding preferences.

RESULTS

Number of Fossils and Minimum Number of Individuals (Table 1)

Number of fossils (N) and minimum number of individuals (MNI) in the Lower and Upper Member of the Namurungule mammal fauna are given in Table 1. In the mammal fauna from the Lower Member of the Namurungule, the dominant species is *Hipparion africanum* both in N (25.2 %) and MNI (15.3 %). *Palaeotragus cf. germaini* (N = 19.8 %; MNI = 13.4 %) and *Samburucerus ethekoni* (N = 11.1 %; MNI = 12.7 %) are also abundant in the Lower Member. In the mamal fauna from the Upper Member of the Namurungule, the dominant species is also *H. africanum* (N = 29.9 %; MNI = 23.4 %). *P. cf. germaini* (N = 8.2 %; MNI = 12.5 %) and *Gazella* sp. (N = 8.2 %; MNI = 10.9 %) are also abundant in the Upper Member.

Habitat Preferences of Equivalent Extant Mammals (Table 2)

Habitat preferences of the extant mammals were obtained from Kingdon (1971, 1974, 1977, 1982a, 1982b, 1982c, 1997). For graduating importance between habitat preferences, it is considered that a habitat inhabited by several species of the taxon is a strong preference and a habitat that a single species inhabits is a weak preference.

The dominant species in the mammal fauna of the Lower Member of the Namurungule both in number of fossils and minimum number of individuals is the equid, *H. africanum*. Extant equids are represented by *Equus* species. Several *Equus* species inhabit open environments such as bushland, grassland, savanna and semi-desert. The second most dominant species in the Lower Member is the giraffid, *P. cf. germaini*. Extant giraffids are represented by *Okapia johnstoni* and *Giraffa camelopardalis*. *O. johnstoni* lives in thick forest and *G. camelopardalis* inhabits bushland to savanna. Boselaphini sp. small is also abundant in the mammal fauna from the Lower Member of the Namurungule (TsujiKawa, 2005). However, today no boselaphines occur in Africa. The tribe Tragelaphini present in Africa is thought to have been derived from Boselaphini (e.g. Gentry, 1978, 1990). Thus

Table 2. Habitat preferences of equivalent extant mammals (from Kingdon, 1971, 1974, 1977, 1982a, 1982b, 1982c, 1997).

Taxon	F	W	B	G	SA	SD	D	A	M
Thryonomyidae				**	*		*	*	
Hyaenidae				**	**	*	*		*
Hyracoidea	*	*	*	*	**			*	*
Proboscidea	*	*	*	*	**	*			
Equidae		*	**	**	**	**			*
Rhinocerotidae			*	**					
Hippopotamidae	*							**	
Suidae	**	**	**	**	**	*	*	*	
Tragulidae	*							*	
Giraffidae	*		*	*	*				
Tragelaphini	*	**	**	**	*			*	**
<i>Gazella</i>			*	**	**	**	*		
<i>Antidorcas</i>			*	*	*				
Caprini							*		**

F: forest; W: woodland; B: bushland; G: grassland; SA: savanna; SD: semi-desert; D: desert; A: aquatic; M: montane; *: single species present; **: plural species present.

tragelaphines are used as extant African equivalent of *S. ethekoni*. The extant tragelaphines are *Tragelaphus*, *Taurotragus* and *Boocerus* species. Many species prefer woodland, bushland, grassland and swamp forest as their habitats.

The dominant species both in number of fossils and minimum number of individuals in the mammal fauna from the Upper Member of the Namurungule is also *H. africanum* suggesting an open environment such as bushland, grassland and savanna. The second most dominant species in the Upper Member is *P. cf. germaini* suggesting forest or open woodland to savanna. However, *Gazella* sp. (one specimen was collected from an unknown level) that is not confirmed in the Lower Member is abundant in the Upper Member. The genus *Gazella* is abundant in Africa today and is represented by numerous species. *Gazella* species are relatively specialized living in open environments ranging from grassland to semi-desert.

From the habitat preferences of the extant mammals, the palaeoenvironment of the mammal fauna from the Upper Member of the Namurungule is likely to have been an open environment such as savanna or grassland because the dominant species, *H. africanum* and *Gazella* sp. are represented by equivalent extant mammals which live in open environments.

In contrast, the palaeoenvironment of the Lower Member of the Namurungule mammal fauna seems to have been a more wooded environment because of presence of numerous boselaphines. However several species represented by a few specimens suggest a more open environment. Hyaenidae spp. (N = 1.2 %; MNI = 3.2 %) represented at present in Africa by *Hyaena* spp., *Crocuta crocuta* and *Proteles cristata* suggest savanna. *Antidorcas* sp. (N = 0.2 %; MNI = 0.6 %) also suggests an absence of forest and woodland. There are no species which suggest forest specialization in the Lower Member. In conclusion, the palaeoenvironment of the Lower Member seems to include both wooded environments and open ones such as savanna and grassland.

Probable Feeding Preferences Based on Morphology of the Teeth (Table 3; Fig. 1)

From the Namurungule Formation, numerous mammalian teeth were collected. Dental morphology correlates with diet. For example, hypsodont teeth indicate grazing habitats and open environments whereas brachydont teeth indicate browsing or frugivorous habitats and

Table 3. Morphology of the teeth and probable feeding preferences of the Namurungule large mammals and minimum number of individuals (MNI).

Taxon	Morphologies of the tooth	Feeding preferences	MNI (Lower Mb)	MNI (Upper Mb)
<i>Tetralophodon</i> sp. nov.	without thick cementum	browser	2	3
<i>Choerolophodon ngorora</i>	thick cementum	grazer	1	-
<i>Deinotherium</i> sp.	bilophodont, brachyodont	browser	6	1
Pliohyracidae	?brachyodont	?browser	1	-
<i>Hipparion africanum</i>	moderately hypsodont with cementum	grazer	24	15
<i>Paradicerus mukirii</i>	brachyodont	browser	9	3
<i>Chilotheridium pattersoni</i>	hypsodont	grazer	12	-
<i>Kenyatherium bishopi</i>	hypsodont with cementum	grazer	3	-
Iranotheriinae sp. nov.	hypsodont with cementum	grazer	7	-
<i>Nyanzachoerus</i> cf. <i>devauxi</i>	potamochoerus-like cheek teeth but more hypsodont	omnivore	7	6
<i>Kenyaipotamus coryndoni</i>	more brachyodont than recent hippos	?browser	3	2
<i>Palaeotragus</i> cf. <i>germaini</i>	brachyodont	browser	21	8
<i>Boselaphini</i> sp. large	brachyodont	browser	3	-
<i>Boselaphini</i> sp. small	brachyodont	browser	20	-
<i>Gazella</i> sp.	hypsodont	grazer	-	7
<i>Antidorcas</i> sp.	hypsodont	grazer	1	1
<i>Pachytragus</i> sp.	hypsodont	grazer	10	-

wooded environments. The presence of cementum in teeth also suggests grazing. Feeding preferences of each large mammal species from the Namurungule Formation based on morphology of the teeth are given in Table 3.

For example, *H. africanum* has moderately hypsodont teeth with thick cementum. Although a few *Hipparion* species are thought to have been browsers (e.g. MacFadden *et al.*, 1999), *Hipparion* is usually thought to be a grazing and cursorial equid and suggests an open environment. *Choerolophodon ngorora* is thought to be a grazing proboscidean based on the thick cementum on its teeth.

In the Lower Member, relative abundances of the browsers (MNI = 44.9 %) and grazers (MNI = 47.1 %) are not different from each other in the minimum number of individuals. In this fauna, both browsers such as *S. ethekoni* and grazers such as *H. africanum* are abundant.

In the Upper Member, grazers (MNI = 54.7 %) are more common than browsers (MNI = 30.2 %). The palaeoenvironment of the Upper Member seems to have been more open than that of the Lower Member in accordance with the study of habitat preferences of equivalent extant mammals. The palaeoenvironment of the Lower Member based on probable feeding preferences seems to include both open and wooded environments.

Footprint fauna (Table 4)

At site SH 23, numerous footprints were found (Nakano *et al.*, 2001; Pickford *et al.*, 1984a). It includes aves, Hyaenidae 2 spp., Rhinocerotidae sp., Artiodactyla 4 spp.. The footprint fauna is also informative for the palaeoenvironment although its stratum belongs to a different facies from that of *Samburupithecus kiptalami* (Saneyoshi, 2001).

The avian footprints are similar to those of wading birds such as extant cranes and plovers. These birds occur in swampland. In fact, the sediments accumulated in a (back-) swamp or floodplain (Saneyoshi, 2001).

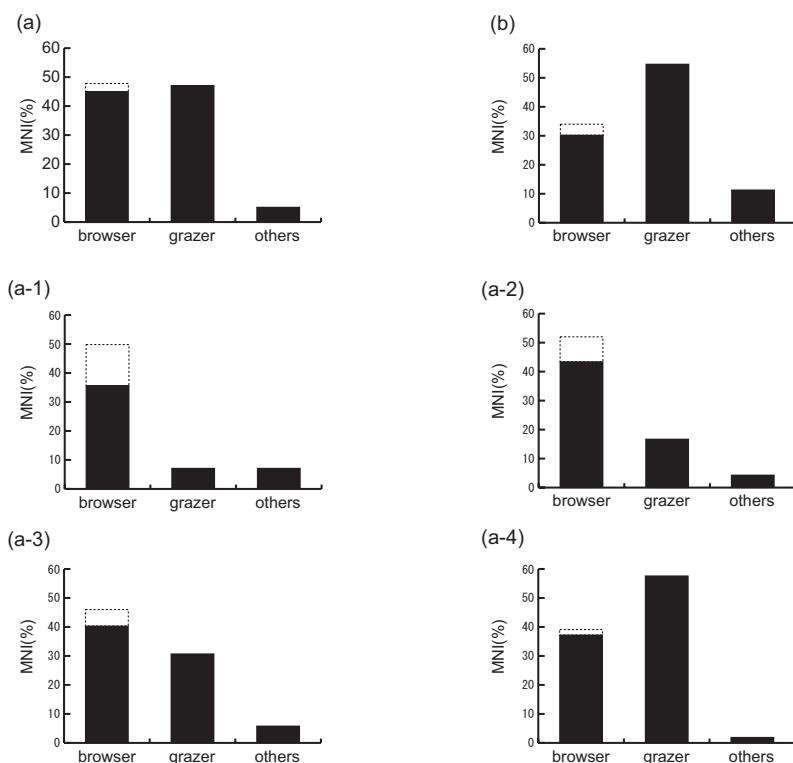


Fig. 1. Probable feeding preference of the faunas from the Lower (a) and Upper (b) Members of the Namurungule Formation; Regional probable feeding preference of the fauna at the site SH 22 (a-1), the area within 1 km (a-2) and 2 km (a-3) and Moru Abenyo Area (a-4) of the Lower Member.

The hyaenid footprints are most abundant ($N = 43$) and include two size groups. Hyaenidae spp. (at least 3 spp.) are known in the Namurungule fossil fauna. The extant hyaenid species strongly prefer open environments such as savanna, grassland and semi-desert (Table 2; Kingdon, 1977, 1997).

The artiodactyl footprints include at least 4 species of ruminants. The largest one, sp. A seems to be consistent with the Namurungule giraffid, *?Samotherium* sp. based on the size of the talus. The hypsodont teeth of *Samotherium* suggest an open environment. The small tracks, sp. B seem to be consistent in size with the Namurungule bovid, *Gazella* sp. *Gazella* sp. also suggests an open environment on the basis of extant habitats and hypsodonty. The other two track types differ from sp. A and B but precise identification is not possible.

The perissodactyl footprints include at least one rhinocerotid species smaller than the extant black rhino. These footprints are possibly those of the grazing and browsing rhinocerotid, *Paradiceros mukirii*, *Chilotheridium pattersoni* and *Iranotheriinae* gen. et sp. indet. The extant rhinocerotids prefer grassland.

It is remarkable that no hipparionine footprints were found at site SH 23 because *Hipparion* is the most common fossil in the Namurungule Formation.

In conclusion, the footprints suggest swampland surrounded by open environment such as savanna or grassland.

Table 4. Fauna and estimated habitat preference of the taxa represented by footprints at site SH 23 (Nakano *et al.*, 2001).

Aves	sp. or spp.	swampland
Hyaenidae	small sp.	savanna
	large sp.	savanna
Rhinocerotidae	sp. (small black rhino)	savanna/woodland
?Giraffidae	sp. (? <i>Samotherium</i>)	?savanna
Bovidae	sp. A (? <i>Gazella</i>)	savanna
	sp. B	?
	sp. C	?

Table 5. Minimum number of individuals in each taxon of the fauna at site SH 22, and the areas within 1 km and 2 km from SH 22 and the Moru Abenyo Area of the Lower Member of the Namurungule mammal Formation.

Taxon	SH22 (MN = 14)	<1km from SH22 (MN=23)	<2km from SH22 (MN=52)	MoruAbenyo (MN=54)
<i>Samburupithecus kiptalami</i>	1 (7.1%)	1 (4.3%)	1 (1.9%)	-
<i>Paraphiomys</i> sp.	1 (7.1%)	1 (4.3%)	1 (1.9%)	-
?Felidae	1 (7.1%)	1 (4.3%)	1 (1.9%)	-
Hyaenidae	1 (7.1%)	1 (4.3%)	1 (1.9%)	1 (1.9%)
<i>Tetralophodon</i> sp. nov.	-	-	1 (1.9%)	1 (1.9%)
<i>Deinotherium</i> sp.	-	1 (4.3%)	1 (1.9%)	1 (1.9%)
Pliohyracidae	1 (7.1%)	1 (4.3%)	1 (1.9%)	-
<i>Hipparion africanum</i>	1 (7.1%)	3 (13.0%)	12 (23.1%)	7 (13.0%)
<i>Paradiceros mukirii</i>	1 (7.1%)	2 (8.7%)	4 (7.7%)	4 (7.4%)
<i>Chilotheridium pattersoni</i>	-	-	-	11 (20.4%)
<i>Kenyatherium bishopi</i>	-	-	1 (1.9%)	1 (1.9%)
<i>Iranotheriinae</i> sp. nov.	-	-	-	5 (9.3 %)
<i>Nyanzachoerus</i> cf. <i>devauxi</i>	1 (7.1%)	1 (4.3%)	3 (5.8%)	1 (1.9%)
<i>Kenypotamus coryndoni</i>	1 (7.1%)	1 (4.3%)	2 (3.8%)	1 (1.9%)
<i>Palaeotragus</i> cf. <i>germaini</i>	2 (14.3%)	4 (17.4%)	8 (15.4%)	7 (13.0%)
? <i>Samotherium</i> sp.	1 (7.1%)	2 (8.7%)	5 (9.6%)	-
<i>Boselaphini</i> sp. large	-	1 (4.3%)	2 (3.8%)	1 (1.9%)
<i>Boselaphini</i> sp. small	2 (14.3%)	2 (8.7%)	5 (9.6%)	6 (11.1%)
<i>Antilocapra</i> sp.	-	-	1 (1.9%)	-
<i>Pachytragus</i> sp.	-	1 (4.3%)	2 (3.8%)	7 (13.0%)

DISCUSSION AND CONCLUSIONS

Habitat preferences of equivalent extant mammals, and feeding preferences based on dental morphology indicate that the palaeoenvironment of the fauna of the Lower Member of the Namurungule comprised both wooded and open components. A swampland surrounded by savanna is suggested at the footprint site (Table 4). The Upper Member is likely to have been somewhat more open on the basis of both the species diversity and dental morphological analysis. *Samburupithecus kiptalami* was collected from the Lower Member of the Namurungule Formation that likely included both open and wooded components.

Several researchers studied and discussed the palaeoenvironment of the Namurungule Formation based on the terrestrial mollusc fauna, sedimentology and taphonomy. Pickford (1987) described the terrestrial mollusc fauna from the Lower Member of the Namurungule Formation and compared their extant habitats in Africa. The Namurungule molluscs suggest an open environment such as grassy savanna at 1400 to 1600 metres above the sea level similar to the Serengeti plains, Tanzania. Saneyoshi (2001) indicated that *S. kiptalami* was

obtained from sediment consisting of crevasse splay deposits (Facies E). He also examined the taphonomy and indicated that vertebrate fossil remains from the hominoid bearing site, SH 22, must have been transported less than a few kilometres and therefore reflect the fauna around *S. kiptalami* even though they were subjected to some hydraulic sorting.

The minimum number of individuals of each taxon at site SH 22, and the areas within 1 km and 2 km from SH 22 and the Moru Abenyo Area of the Lower Member are given in Table 5. The Moru Abenyo Area including localities SH 53-55 and 62-64 is situated about 5 km southwest of SH 22 and yields numerous, well preserved specimens (MNI = 54 in total) (Fig. 1). Near site SH 22 which yielded *S. kiptalami*, *Hipparion africanum* which suggests an open environment is reduced in MNI in comparison with the entire fauna of the Lower Member, 7.1 % at site SH 22 and 13.0 % in the area within 1 km of SH 22 including SH 20-22 and 58. However, in the area within 2 km of SH 22 including SH 7-9, 20-24, 27, 30 and 58, the minimum number of individuals of *Hipparion* increases (MNI = 23.1 %), more than that of the entire fauna (MNI = 15.3 %) of the Lower Member. In the Moru Abenyo Area, *Hipparion* is not so abundant (MNI = 13.0 %) but *Chilotheridium pattersoni* is dominant (MNI = 20.4 %). Feeding preferences of those areas are also examined and given in Fig. 1. Near site SH 22, browsers are more common than grazers on the basis of minimum number of individuals. However, apart from SH 22, the area within 2 km from SH 22 has more grazers and fewer browsers. In the Moru Abenyo Area, grazers are more common than browsers as in the Upper Member. Therefore, it seems to have been a relatively wooded environment near the site yielding the hominoid. The other areas such as Moru Abenyo Area are likely to have been open environments such as savanna or grassland. Although this analysis neglects problems of taphonomy and sampling biases, it does reveal the presence of both wooded and open components in the Lower Member of the Namurungule.

Recent apes inhabit wooded environments such as forest and woodland. Only humans have adapted to a broad spectrum of habitats including open environments such as savanna (e.g. Coppens, 1994). The Late Miocene hominoid, *S. kiptalami* as a creature presumed to be close to the common lineage of the humans and African apes is thought to have inhabited wooded environments such as woodland near open environments.

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REFERENCES

- Aguirre, E. & C. Guérin 1974. Première découverte d'un Iranotheriinae (Mammalia, Perissodactyla, Rhinocerotidae) en Afrique: *Kenyatherium bishopi* nov. gen. nov. sp. de la formation vallésienne

- (Miocène supérieur) de Nakali (Kenya). *Estudios Geologicos*, 30: 229-233.
- Aguirre E. & P.H. Leakey 1974. Nakali: nueva fauna de *Hipparion* del Rift Valley de Kenya. *Estudios Geologicos*, 30: 219-227.
- Benefit, B.R. & M. Pickford 1986. Miocene fossil cercopithecoids from Kenya. *American Journal of Physical Anthropology*, 69: 441-464.
- Bishop, L.C. 1994. Pigs and the Ancestors: Hominids, Suids and Environments during the Plio-Pleistocene of East Africa. Ph.D. Dissertation, Yale University (unpublished).
- Brunet, M., F. Guy, D. Pilbeam, H.T. Mackaye, A. Likius, D. Ahounta, A. Beauvilain, C. Blondel, H. Bocherens, J.-R. Boisserie, L. de Bonis, Y. Coppens, J. Dejax, C. Denys, P. Dourner, V. Eisenmann, G. Fanone, P. Fronty, D. Geraads, T. Lehmann, F. Lihoreau, A. Louchart, A. Mahamat, G. Merceron, G. Mouchelin, O. Otero, P.P. Campomanes, M.P. de Leon, J.-C. Rage, M. Sapanet, M. Schuster, J. Sudre, P. Tassy, X. Valentin, P. Vignaud, L. Viriot, A. Zazzo & C. Zollikofer 2002. A new hominid from the Upper Miocene of Chad, Central Africa. *Nature*, 418: 145-151.
- Coppens, Y. 1994. East side story: the origin of humankind. *Scientific American*, 270(5): 88-95.
- Gentry, A.W. 1978. Bovidae. In (V.J. Maglio & H.B.S. Cooke, eds.) *Evolution of African Mammals*, pp. 540-572, Harvard University Press, Cambridge.
- 1990. Evolution and dispersal of African Bovidae. In (G.A. Bubenik & A.B. Bubenik, eds.) *Horns, Pronghorns, and Antlers. Evolution, Morphology, Physiology and Social Significance*, pp. 195-227, Springer-Verlag New York.
- Geraads, D. 2001. Rongeurs du miocène supérieur de Ch'orora (Ethiopie): Dendromuridae, Muridae et conclusions. *Palaeovertebrata*, 30 (1-2): 89-109.
- Geraads, D., Z. Alemseghed & C. Guillemot 1997. L'Ethiopie avant les Hommes: mission de prospection et de fouilles à Ch'orora dans la moyenne vallée de l'Awash. *Maison des Etudes Ethiopiennes, Bulletin*, 11: 79-84.
- Ishida H. & M. Pickford 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.
- Ishida, H., Y. Kunitatsu, M. Nakatsukasa, & Y. Nakano 1999. New hominoid genus from the middle Miocene of Nachola, Kenya. *Anthropological Science*, 107(2): 189-191.
- Ishida H., Y. Kunitatsu & M. Nakatsukasa 2001. Activities of the Samburu Hills/Nachola project in northern Kenya between 1998 and 2000. *Study of Hominoid Evolution and Human Origin in East Africa*, In (H. Ishida ed.) *Research Papers of the Subsidy of Scientific Research Funds during 1998-2000 No. 10041164*, pp. 3-58, the Ministry of Education, Science and Culture of Japan (unpublished).
- Jacobs, L.L., J. Michaux & M. Sabatier 1980. Premières données sur les rongeurs de la formation de Ch'orora (Ethiopie) d'âge Miocène supérieur, I. Thryonomyidae. *Palaeovertebrata, Mémoire jubilaire en hommage à René Lavocat*, pp. 365-374.
- Kalb, J.E., E.B. Oswald, S. Tebedge, A. Mebrate, E. Tola & D. Peak 1982a. Geology and stratigraphy of Neogene deposits, Middle Awash Valley, Ethiopia. *Nature*, 298: 17-25.
- Kalb, J.E., C.J. Jolly, A. Mebrate, S. Tebedge, C. Smart, E.B. Oswald, D. Cramer, P. Whitehead, C.B. Wood, G.C. Conroy, T. Adefris, L. Sperling & B. Kana 1982b. Fossil mammals and artifacts from the Middle Awash Valley, Ethiopia. *Nature*, 298: 25-29.
- Kalb, J.E., C.J. Jolly, S. Tebedge, A. Mebrate, C. Smart, E.B. Oswald, D. Cramer, P. Whitehead, C.B. Wood, T. Adefris & V. Rawn-Schatzinger 1982c. Vertebrate faunas from the Awash Group, Middle Awash Valley, Afar, Ethiopia. *Journal of Vertebrate Paleontology*, 2(2): 237-258.
- Kawamura Y. & H. Nakaya 1984. Thryomyid rodent from the late Miocene Namurungule Formation, Samburu Hills, northern Kenya. *African Study Monographs Supplementary Issue*, 2: 133-139.
- Kawamura Y. & H. Nakaya 1987. Additional materials of the late Miocene Rodents from the Namurungule Formation of Samburu Hills, northern Kenya. *African Study Monographs Supplementary Issue*, 5: 131-139.

- Kingdon, J. 1971. *East African Mammals: An Atlas of Evolution in Africa I*, pp. 1-446. Academic Press, London.
- 1974. *East African Mammals: An Atlas of Evolution in Africa IIB (Hares and Rodents)*, pp. 343-704. Academic Press, London.
- 1977. *East African Mammals: An Atlas of Evolution in Africa IIIA (Carnivores)*, pp. 1-146. Academic Press, London.
- 1982a. *East African Mammals: An Atlas of Evolution in Africa IIIB (Large Mammals)*, pp. 1-436. Academic Press, London.
- 1982b. *East African Mammals: An Atlas of Evolution in Africa IIIC (Bovids)*, pp. 1-393. Academic Press, London.
- 1982c. *East African Mammals: An Atlas of Evolution in Africa IIID (Bovids)*, pp. 394-746. Academic Press, London.
- 1997. *The Kingdon Field Guide to African Mammals*, pp. 450. Academic Press, San Diego.
- MacFadden, B.J., N. Solounias & T.E. Cerling 1999. Ancient diets, ecology, and extinction of 5-million-year-old horses from Florida. *Science*, 283(5403): 824-827.
- Nakano, Y., H. Tsujikawa, H. Nakaya, M. Nakatsukasa & H. Ishida 2001. The fossil footprints in Samburu Hills, Northern Kenya (in Japanese). *Africa Kenkyu*: 59: 101-114.
- Nakaya, H. 1994. Faunal changes of late Miocene Africa and Eurasia: Mammalian fauna from the Namurungule Formation, Samburu Hills, northern Kenya. *African Study Monographs Supplementary Issue*, 20: 1-112.
- Nakaya, H., M. Pickford, Y. Nakano & H. Ishida 1984. The late Miocene large mammal fauna from the Namurungule Formation, Samburu Hills, Northern Kenya. *African Study Monographs Supplementary Issue*, 2: 87-131.
- Nakaya, H., M. Pickford, K. Yasui & H. Ishida 1987. Additional large mammalian fauna from the Namurungule Formation, Samburu Hills. *African Study Monographs Supplementary Issue*, 5: 79-129.
- Pickford, M. 1981. Preliminary Miocene mammalian biostratigraphy for western Kenya. *Journal of Human Evolution*, 10: 73-97.
- 1987. Fossil terrestrial gastropods from the Namurungule Formation, Kenya. *African Study Monographs Supplementary Issue*, 5: 155-156.
- 2002. *Faunal lists for the Tugen Hills compiled by Martin Pickford*. Abstract Papers of International Workshop at Bogoria, From *Samburupithecus* to *Orrorin*: Origins of Hominids Geological and Palaeontological Background, pp.18-28, Bogoria, Kenya.
- Pickford, M. Ishida, H., Nakano, Y. & Nakaya, H. 1984a. Fossiliferous localities of the Nachola-Samburu Hills Area, Northern Kenya. *African Study Monographs Supplementary Issue*, 2: 45-56.
- Pickford M., H. Nakaya, I. Ishida & Y. Nakano Y. 1984b. The biostratigraphic analyses of the faunas of the Nachola Area and Samburu Hills, Northern Kenya. *African Study Monographs Supplementary Issue*, 2: 67-72.
- Pickford, M. & M.S. Fischer 1987. *Parapliohyrax ngororaensis*, a new hyracoid from the Miocene of Kenya, with an outline of the classification of Neogene Hyracoidea. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 175(2): 207-234.
- Pickford, M. & H. Ishida 1998. Interpretation of *Samburupithecus*, an Upper Miocene hominoid from Kenya. *Comptes Rendus de l'Académie des Science, Series IIA, Sciences de la terre et des planètes*, 326: 299-306.
- Pickford, M. & B. Senut 2001. The geological and faunal context of Late Miocene hominid remains from Lukeino, Kenya. *Comptes Rendus de l'Académie des Science, Series IIA, Sciences de la terre et des planètes*, 332: 145-152.
- Saneyoshi, M. 2001. Depositional processes of the Miocene fluvial-lacustrine sediments in Kenya Rift and its implication to vertebrate fossil taphonomy: an example from the Namurungule Formation in Suguta Valley, Northern Kenya (in Japanese). Master's Thesis, Shimane University.

- Sawada Y., M. Tateishi & S. Ishida 1987. Geology of the Neogene system in and around the Samburu Hills, Northern Kenya. *African Study Monographs Supplementary Issue*, 5: 7-26.
- Sawada, Y., M. Pickford, T. Itaya, T. Makinouchi, M. Tateishi, K. Kabeto, S. Ishida & H. Ishida 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.
- Senut, B., M. Pickford, D. Gommery, P. Mein, K. Cheboi & Y. Coppens 2001. First hominid from the Miocene (Lukeino Formation, Kenya). *Comptes Rendus de l'Académie des Science, Series IIA, Sciences de la terre et des planètes*, 332: 137-144.
- Tsujikawa, H. 2005. The updated Late Miocene large mammal fauna from Samburu Hills, Northern Kenya. *African Study Monographs Supplementary Issue*, 32: 1-50.
- Ward, S., B. Brown, A. Hill, J. Kelley & W. Downs 1999. *Equatorius*: A new hominoid genus from the middle Miocene of Kenya. *Science*, 285: 1382-1386.
- White, T.D., G. Suwa & B. Asfaw 1994. *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia. *Nature*, 371: 306-312.

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