学 位 論 文 の 要 約

氏　　名	TANABE Yoshiki (田邉佳紀)
学位論文題目	Systematics and paleobiogeography of the Late Miocene rodents from the Nakali Formation, Northern Kenya

Chapter 1. Introduction

Africa, particularly North, East, and South Africa, has provided important rodent fossil records. Lavocat (1973) summarized the past diversity of rodents in Africa, and recorded at least 54 genera (excluding extant murines) dating from the Oligocene through the Pleistocene. Lavocat (1978) discussed the evolutions and the Miocene immigrants based on rodent fossil records from Africa. Winkler et al. (2010) recorded approximately 133 named genera. In addition, they summarized the distribution and ecology of the extant families of African rodents and focused on the fossil records, including discussing systematics, biochronology, and paleobiogeography.

According to these and other studies (e.g., Winkler, 1994; Wesselman et al., 2009), diverse rodent lineages originated in either Europe or Asia, migrating subsequently into Africa, particularly around the Early to Middle Miocene, and the modern rodent fauna of Africa developed from the Late Miocene. However, the Late Miocene is represented poorly in East Africa, compared to the Early to Middle Miocene. The early Late Miocene (around 10 Ma) rodent fauna is especially poor, and rodents have been found only in three localities (Fig. 1): the Chorora Formation (ca. 8.5–7.0 Ma), Chorora, Ethiopia (Jaeger et al., 1980; Geraads, 1998a, 2001; Suwa et al., 2015), the Namurungule Formation (9.6–9.3 Ma), Samburu Hills, Kenya (Kawamura and Nakaya, 1984, 1987) and the Nakali Formation (ca. 10 Ma), Nakali, Kenya (Flynn and Sabatier, 1984). These localities have yielded the discoveries of three great apes that may be the common ancestor of humans and extant African apes. *Chororapithecus abysynicus* was discovered in the Chorora Formation (Suwa et al., 2007), *Samburupithecus kiptarami* was discovered in the Namurungule Formation (Ishida and Pickford, 1997), and *Nakalipithecus nakayamai* was discovered in the Nakali Formation (Kunimatsu et al., 2007). These localities have also yielded abundant non-primate mammalian fossils.

To date, only a single rodent species, *Nakalimys lavocati* (Rhizomyinae, Spalacidae) has been described for Nakali (Flynn and Sabatier, 1984). Similarly, only a few families have been reported in East Africa. The Japan–Kenya Expedition team has been conducting paleontological field-work in Nakali since 2002 and has expanded the mammalian fossil collection remarkably [e.g., Kunimatsu et al. (2007); Nakatsukasa et al. (2010); see Chapter 2]. Rodent specimens constitute approximately 45% of Nakali mammals. Onodera et al. (2011) described new rodent fauna, with five families and eight taxa, recovered from the Nakali Formation by the team from 2003 to 2009. The paleoenvironments of the Nakali Formation have been reconstructed based on these faunas. Tanabe et al. (2013, 2014) described the rodent fauna from 2010 to 2012, adding one family and two taxa.

This article summarizes these studies of the rodent fauna recovered by Japan–Kenya Expedition team from the Nakali Formation from 2003 to 2012. The Nakali rodent fauna greatly enriches our understanding of the evolution and paleobiogeography of rodents of the early Late Miocene in East Africa, updating the FAD (First Appearance Datum)/LAD (Last Appearance Datum) of various rodent taxa and providing clues to help refine the phylogeny of fossil rodents from Africa. The paleobiogeography of the Neogene rodent taxa related to taxa from the Nakali Formation is discussed herein.

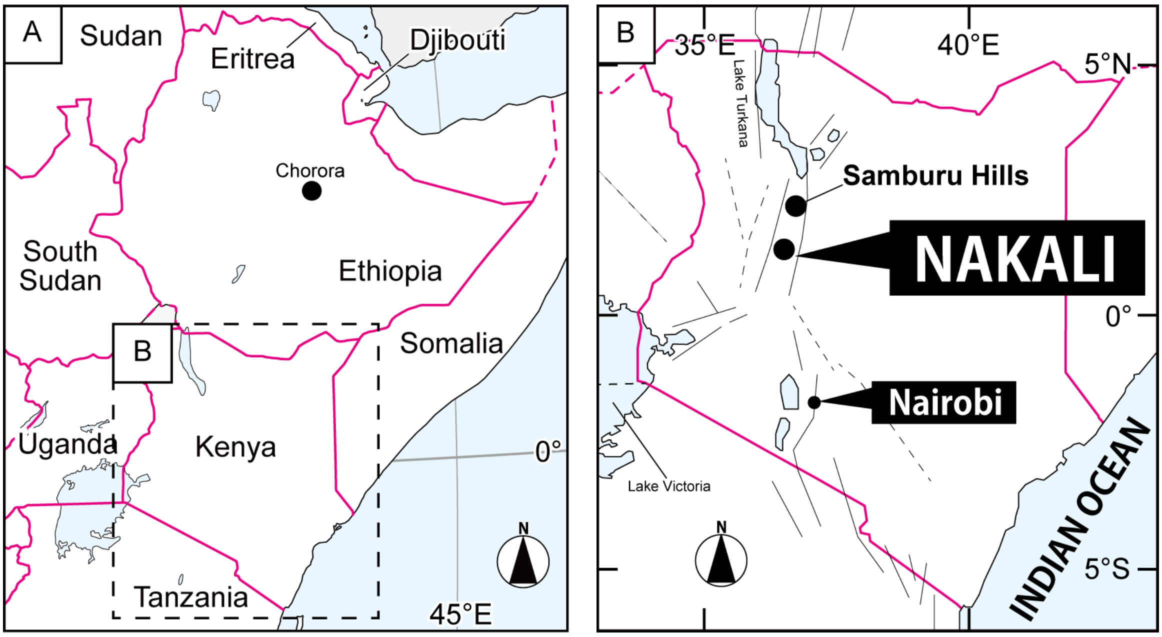

Fig. 1. Map showing the localities of Chorora, Samburu Hills and Nakali (modified from Kunimatsu et al., 2007 and Tanabe et al., in press)

Chapter 2. Geological setting

2.1. Geology and Dating

The Upper Miocene Nakali Formation is distributed in the Nakali area (Baringo, Samburu, and Turkana Counties) and located at the eastern shoulder of the central Kenya Rift (Fig. 1). The Nakali Formation is covered unconformably by the Nasorut Formation, which is composed of trachitic or basaltic lava and volcaniclastics and is characterized by lacustrine, fluvio-lacustrine, and pyroclastic flow deposits (Kunimatsu et al., 2007). The Nakali Formation is divided stratigraphically into the Lower, Middle, and Upper Members. Most of the fossils derive from the volcanic mud flow deposits of the Upper Member, e.g., NA39 (1° 12′ 6.6″ N, 36° 22′ 23.2″ E), the site yielding Nakalipithecus, and the site NA60 (1° 11′ 57″ N, 36° 23′ 14.9″ E), from which the bulk of rodent fossils have been recovered. ^{40}Ar/^{39}Ar ages of the uppermost part of the Lower Member are 9.82 ± 0.09 and 9.90 ± 0.09 Ma (Kunimatsu et al., 2007). The paleomagnetic stratigraphy of the uppermost level of the lower Member and the lowermost level of the Upper Member is correlated with Chron C5n. 1r (9.88–9.92 Ma) (Kunimatsu et al., 2007). This formation is estimated to date from approximately 10.0–9.8 Ma (early Tortonian: basal late Miocene), which is correlated with either the uppermost part of MN9 or the lowermost part of MN10, and to the Vallesian ELMA (Kunimatsu et al., 2007; Tsubamoto et al., 2017).

2.2. Nakali mammalian fauna

The Nakali Formation has yielded an abundance of vertebrate fossils (Aguirre and Leakey, 1974; Aguirre and Guérin, 1974; Pickford, 1983, 1986; Flynn and Sabatier, 1984; Fischer, 1986; Morales and Pickford, 2006; Nakatsukasa et al., 2006, 2010; Saegusa et al., 2006; Kunimatsu et al., 2007, 2016, 2017a, 2017b; Nakatsukasa, 2009; Onodera et al., 2011; Tanabe et al., 2013, 2014, in press; Handa et al., 2015, 2017a, 2017b; Tsubamoto et al., 2015, 2017, 2020; this study). Currently, the fossil specimens collected by the Japan–Kenya Expedition team from Kyoto University and the National Museums of Kenya during the 2002 to 2016 field seasons consist of approximately 3,500 identifiable mammalian specimens. Approximately 45% of these specimens are rodents, approximately 24% are artiodactyls, approximately 14% are primates, approximately 11% are perissodactyls, and approximately 6% consist of other orders (Tsubamoto et al., 2020). The fossil great ape *Nakalipithecus nakayamai* and other primate fossils, such as *Microcolobs*, have been discovered in this Formation. Moreover, non-primate terrestrial mammalian fossils have been corrected. Currently, the record consists of 9 orders, 30 families, and 49 species. Fishes, crocodiles, chelonians, snakes, and birds have been recognized in the Formation.

2.3. Paleoenvironment

Matsui et al. (2008) provided a preliminary report of fossil pollens; however, they found fossil pollens only from the Lower Member of the Nakali Formation. They discovered Podocapaceae, Taxodiaceae, and Poaceae, indicative of wet forest habitat. Nakatsukasa et al. (2010) reported the discovery of a colobine monkey (*Microcolobus*) from the Nakali Formation. The fossil has characters of an arboreal quadruped (distal joint of the humerus and capitulum), which is indicative of forest habitat in Nakali. Uno et al. (2011) estimated the paleodiet of herbivores in the Late Miocene to the Early Pliocene localities (i.e., Samburu Hills, Nakali, and Lothagam) in Kenya by analyzing the stable carbon isotope ratios from fossil tooth enamel. Their findings indicate that, though some herbivores (e.g., equids) from the Nakali Formation had C4-dominated diets, most herbivores from the Formation had either C3-dominated or mixed C3/C4 diets. Mesowear analysis of *Hipparion* and bovids from the Nakali Formation suggest that they were mix-feeders, indicating that woodland was the dominant environment in Nakali (Nakaya et al., 2012).

As described above, the paleoenvironment of the Nakali Formation is estimated as forest with woodland, rivers, and lakes under a seasonal climate.

Chapter 3. Systematic paleontology of rodents from the Nakali Formation

In this study, the rodents from the Nakali Formation (ca. 10 Ma), Northern Kenya, were revised. As a result, the following taxa are recognized: *Vulcanisciurus africanus*, Sciuridae gen. et sp. indet., *Nakalimys lavocati*, *Afrocricetodon* cf. *songhori korui*, *Abudhabia* sp., *Paraulacodus johanesi*, Thryonomyidae gen. et sp. indet. (small), Thryonomyidae gen. et sp. indet. (large), Hystricidae gen. et sp. indet.

3.1. Materials and methods

The Nakali rodent fossils are housed at the National Museums of Kenya, Nairobi. From 2003 to 2012, a total of 1,513 rodent specimens was collected from the Nakali Formation (Table 1). Most of these fossils were recovered by sieving, using a 1.0 mm x 1.0 mm mesh screen, at the locality NA60. The numbers of recovered elements are as follows: cheek teeth and cheek tooth fragments (1176 specimens), incisors (165 specimens), and bones and bone fragments (182 specimens) (Table

1). Taxonomic determination was carried out based on cheek tooth morphology, as cheek teeth are relatively well preserved and morphologically diversified in rodent taxa. Bones and incisors are still being studied (Tanabe, in preparation). Measurements were obtained using photogrammetry.

3.2. Anatomical abbreviations

A, anterior; ***B,*** buccal; ***L***, antero-posterior length; ***W***, bucco-lingual width; ***Lt.***, left; ***Rt.***,right; ***I/i,*** upper/lower incisor; ***DP/dp***, upper/lower deciduous premolar; ***P/p***, upper/lower premolar; ***M/m***, upper/lower molar; ***maxi.***, maxilla; ***mand.***, mandible; ***w/,*** with; ***frag***., fragmentary specimens

Table 1. Number of identified specimens from 2003–2012 sample.

Specimens	Number of specimens	%
Cheek tooth	1176	77.7
Incisor	165	10.9
Scapla	3	0.2
Humerus	11	0.7
Ulna	3	0.2
Pelvis	3	0.2
Vertebra	29	1.9
Femur	36	2.4
Tibia	7	0.5
Astragalus	9	0.6
Calcaneus	9	0.6
Phalange	10	0.7
Bone fragment	52	3.4
Total number of identified specimens	1513	

3.3. Systematic paleontology

3.3.1. *Vulcanisciurus africanus*

Upper and lower cheek teeth, and several maxilla and mandible fragments from the Nakali Formation were described as *Vulcanisciurus africanus* in this study (Fig. 2–3; Table 2).

The current specimens exhibit the dental characteristics of Sciuridae (Ungar, 2010): tiny P3, with a series of four moderately developed transverse ridges (lophs) on the upper cheek teeth, deeply basined (= the posterior basin). Known Miocene sciurid taxa from Africa are *Vulcanisciurus, Kubwaxerus*, *Xerus*, *Atlantoxerus*, *Paraxerus*, *Helioxerus* (Winkler et al., 2010). As discussed in this study, the current specimens show the characters of *V. africanus.*

The size and lophodonty recall the dentition of *Vulcanisciurus,* which includes only one species, *V. africanus.* This species has a strong protocone, a weak hypocone and a small metaconule on the upper cheek teeth, and an undeveloped entoconid. These characters of *V. africanus* are consistent with those of the current specimens from the Nakali Formation. Thus, the current specimens are identified as *V. africanus.*

V. africanus has been recovered from Early Miocene [Songhor, Rusinga, and Koru, in Kenya, and Napak, in Uganda, Lavocat (1973)], Middle Miocene [14 Ma: Fort-Ternan, Kenya, Denys and Jeager (1992)], and late Middle Miocene (12.5 Ma: Ngorora Formation, Tugen Hills, Winkler (1990, 2002) localities. The record from Nakali Formation updates the latest occurrence of the genus *Vulcanisciurus*.

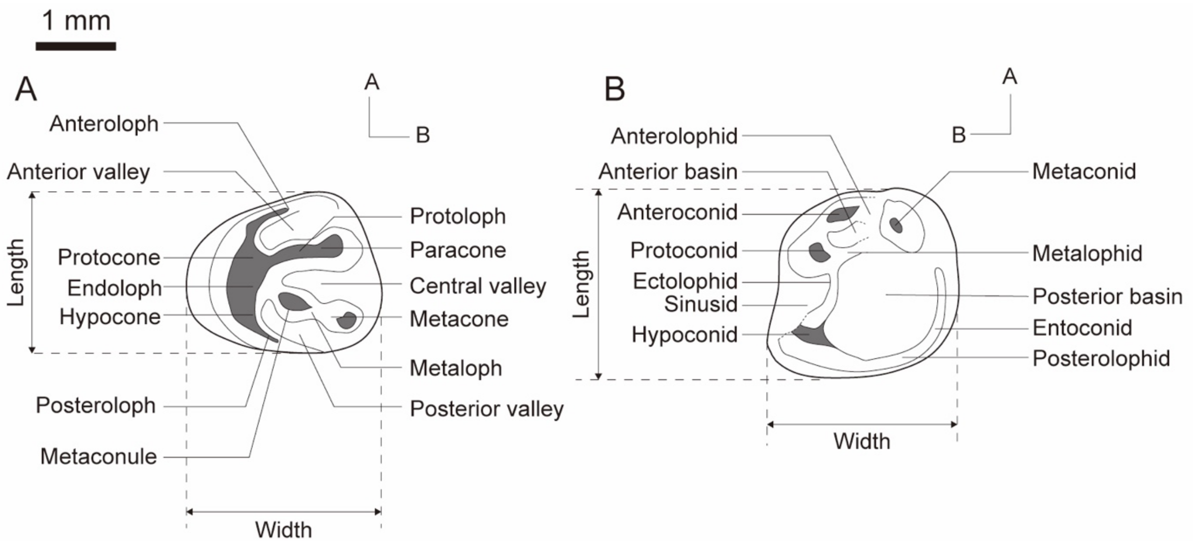

Fig. 2. Sciurid dental terminology and measurements used in text of upper (A, KNM-NA 52660) and lower teeth (B, KNM-NA 50912), based on Casanovas (2007).

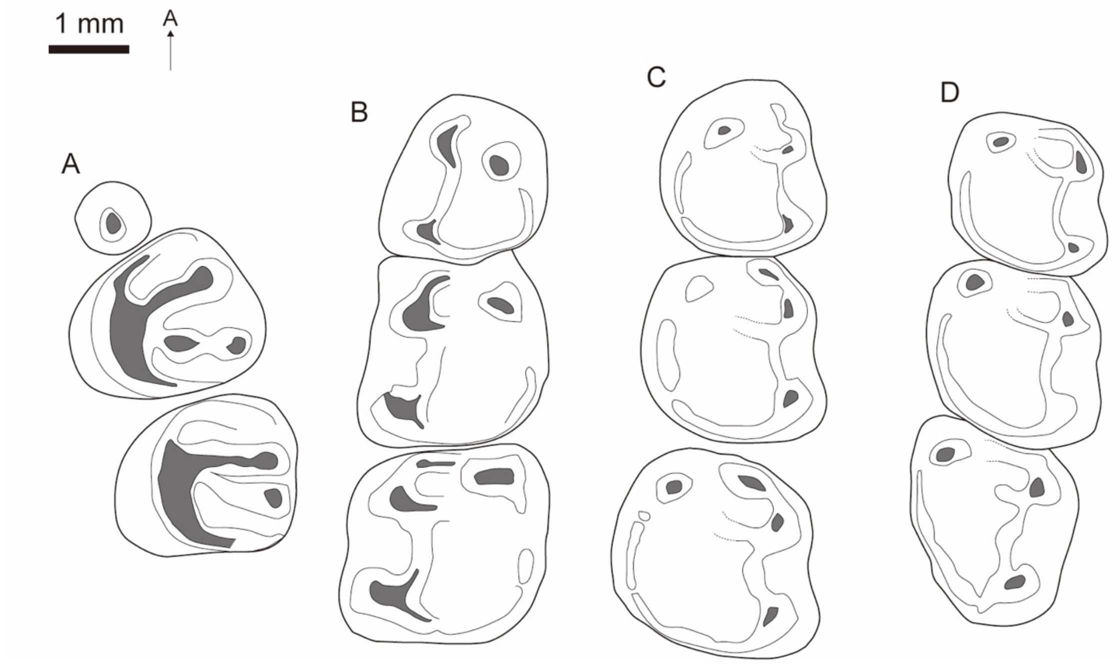

Fig. 3. Schematic drawings of the occlusal surfaces of cheek teeth of *Vulcanisciurus africanus* from the Nakali Formation. A, KNM-NA 52660. Lt. P3–M1. B, KNM-NA 52409, Lt. p4–m2. C, KNM-NA 52424, Rt. p4–m2. D, KNM-NA 50910, Rt. m1–m3. The scale bar indicates 1 mm, anterior (A) denoted by the arrow.

Table 2. Measurements (mean and range; in mm) of teeth of *Vulcanisciurus africanus*. Abbreviations: N, number of specimens; M, mean; OR, observed range.

	P3 (N=2)			P4 (N=2)			M1 (N=2)		
	L	W	L /W	L	W	L / W	L	W	L / W
M	0.83	0.82	1.03	1.71	2.25	0.76	1.96	2.41	0.81
OR	0.75–0.90	0.68–0.95	0.95–1.10	1.50–1.92	2.04–0.74	0.74–0.78	1.81–2.11	2.31–2.51	0.78

	p4 (N=2)			m1 (N=4)			m2 (N=5)			m3 (N=3)		
	L	W	L /W	L	W	L /W	L	W	L /W	L	W	L /W
M	2.22	2.09	1.06	2.27	2.26	1.00	2.46	2.49	0.99	2.66	2.22	1.20
OR	2.12–2.07	2.07–2.11	1.00–1.12	2.01–2.39	1.98–2.38	0.99	1.7-2.8	2.0-2.7	0.93–1.02	1.7-2.8	1.7-2.7	1.04–1.30

3.3.2. Sciuridae gen. et sp. indet.

The current specimens are identified as a small-sized species of *Vulcanisciurus* characterized by closeness between the protoconid and the metaconid and either weak or absent entoconid. The occlusal pattern displays an affinity to the genus *Vulcanisciurus*. However, the current specimens are much smaller. As it is difficult to determine the taxonomic allocation from just a few specimens, I leave it as Sciuridae gen. et sp. indet.

3.3.3. *Nakalimys lavocati*

Upper and lower molars, incisors, and several maxilla and mandible fragments from the Nakali Formation were described as *Nakalimys lavocati* in this study (Fig. 4–5; Table 3).

The current specimens are assigned to the Rhizomyinae (Spalacidae) in the following respects: 1) three upper molars and three lower molars; 2) The molars are lophodont; 3) High unilateral hypsodonty (upper molars are higher crowned internally than externally and lower molars are higher crowned externally); 4) Four or five transverse lophs; and 5) M3 is oval and lacks a hypocone (Flynn, 1982a).

The morphology of the molars (low crowns, anterocone on M1 being bilobed until advanced wear stages, large m3 longer than either m1 or m2) is similar to that of *Nakalimys lavocati*, a tachyoryctine reported previously by Flynn and Sabatier (1984) from the same locality.

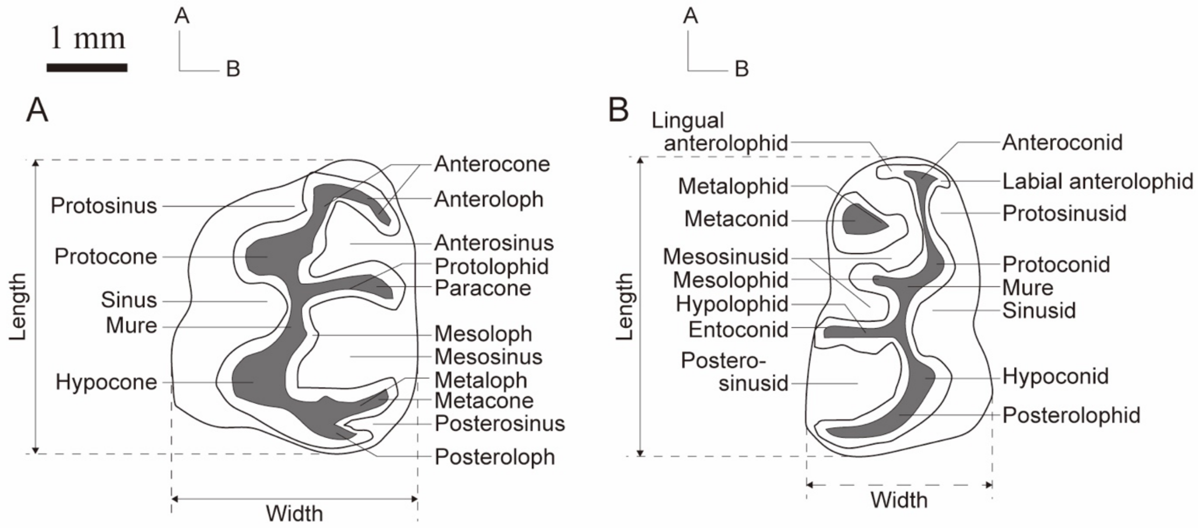

Fig. 4. Rhizomyine dental terminology and measurements used in text of upper (A, KNM-NA 52196) and lower teeth (B, KNM-NA 50123), based on Lopez-Antonanzas et al. (2013).

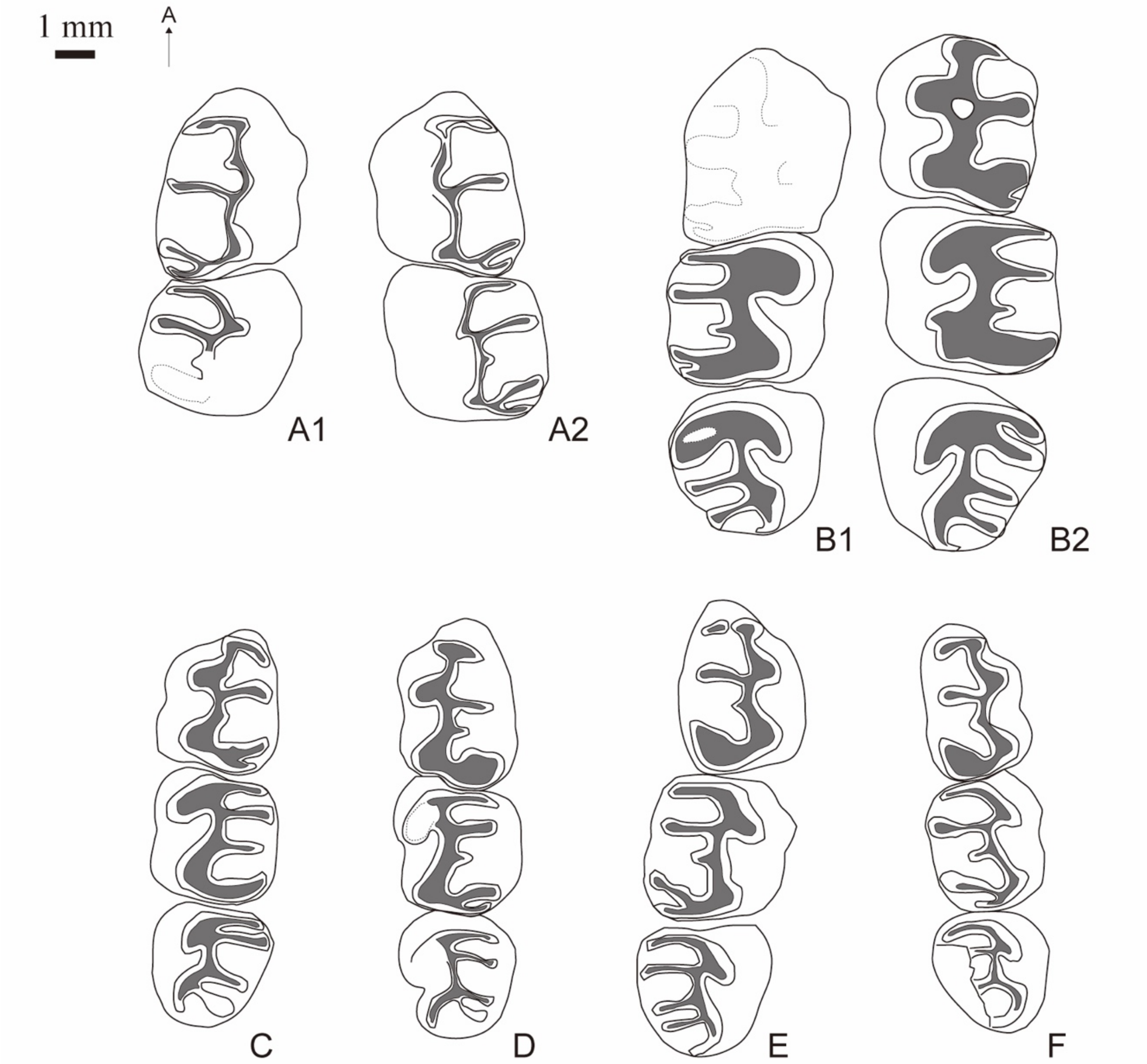

Fig. 5. Schematic drawings of the occlusal surfaces of cheek teeth of *Nakalimys lavocati* from the Nakali Formation. A, KNM-NA 52576. A1, Rt. M1–M2. A2, Lt. M1–M2. B, KNM-NA 52564. B1, Lt. M1–M3. B2. Rt. M1–M3. C, KNM-NA 52196, Lt. M1–M3. D, KNM-NA 52576 (a), Lt. M1-M3. E, KNM-NA 52197, Rt. M1–M3. F, KNM-NA 52360, Rt. M1–M3. The scale bar indicates 1 mm, anterior (A) denoted by the arrow.

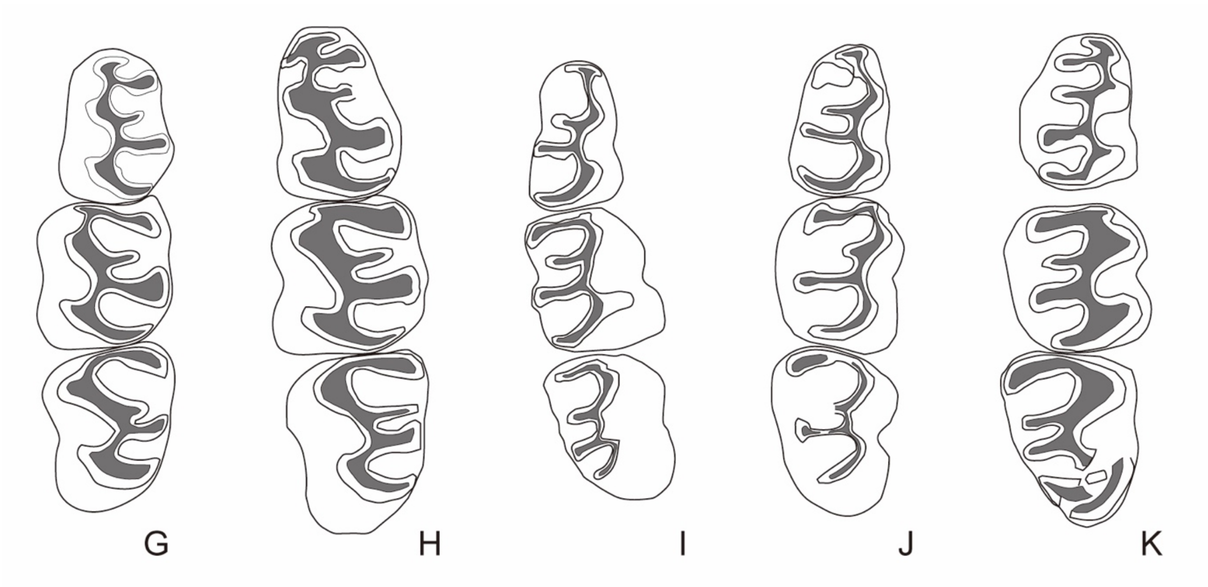

Fig. 5. Continued. G, KNM-NA 52573, Lt. m1–m3. H, KNM-NA 52576, Lt. m1–m3. I, KNM-NA 50123, Rt. m1–m3. J, KNM-NA 50701, Rt. m1–m3. K, KNM-NA 50892, Rt. m1–m3. The scale bar indicates 1 mm, anterior (A) denoted by the arrow.

Table 3. Measurements (mean and range; in mm) of teeth of *Nakalimys lavocati*, collected from the Nakali Formation. Abbreviations as in Table 2.

	M1 (N=153)			M2 (N=119)			M3 (N=74)		
	L	W	L / W	L	W	L / W	L	W	L / W
M	4.08	3.13	1.32	3.45	3.21	1.08	3.27	3.07	1.07
OR	3.33–5.03	2.23–3.96	1.06–1.70	2.62–4.49	2.25–4.27	0.81–1.50	2.48–4.54	2.29–4.15	0.83–1.43

	i1 (N=8)			m1 (N=115)			m2 (N=214)			m3 (N=131)		
	L	W	L / W	L	W	L / W	L	W	L / W	L	W	L / W
M	2.64	1.77	1.49	3.80	2.71	1.41	3.60	3.19	1.13	3.96	3.13	1.27
OR	2.14–3.07	1.5–2.14	1.37–1.69	2.95–4.69	1.85–3.69	1.01–1.77	1.85–4.75	1.66–4.34	0.85–1.54	1.48–4.93	1.59–4	0.93–1.54

3.3.4. *Afrocricetodon* cf. *songhori korui*

Upper and lower molars, and several maxilla and mandible fragments from the Nakali Formation were described as *Afrocricetodon* cf. *songhori korui* in this study (Fig. 6–7; Table 4).

Dental characteristics of the Afrocricetodontinae include the presence of three upper/lower molars, cheek teeth with four main cusps and connecting crests between them, and strongly-developed anterocone and anteroconid on M1 and m1. All these are present in the current specimens (Lavocat. 1973).

Among the Afrocricetodontinae, the Nakali specimens most resemble the genus *Afrocricetodon,* of which one species and two subspecies are known: *A. songori songhori* and *A. S. korui* (Lavocat, 1973). *A. S. korui* has a strong anterocingulum and a bilobed anterocone on M1, and a weak posterocingulum on M2 relative to *A. S. songhori*. The current specimens exhibit a greater affinity with *A. S. korui* than with *A. S. songhori*, though the width on M1 is slightly smaller than is that of *A. S. korui* and the lingual side is constricted inward. Otherwise, size is comparable, and we assign the Nakali specimens as *Afrocricetodon* cf. *songhori korui*.

To date, *Afrocricetodon* is known only from the Early Miocene [Songhor, Rusinga, and Koru, Kenya, and Napak, Uganda; (Lavocat and Mein, in Lavocat, 1973)]. The current specimens from the Nakali Formation suggest that the genus survived until the early Late Miocene.

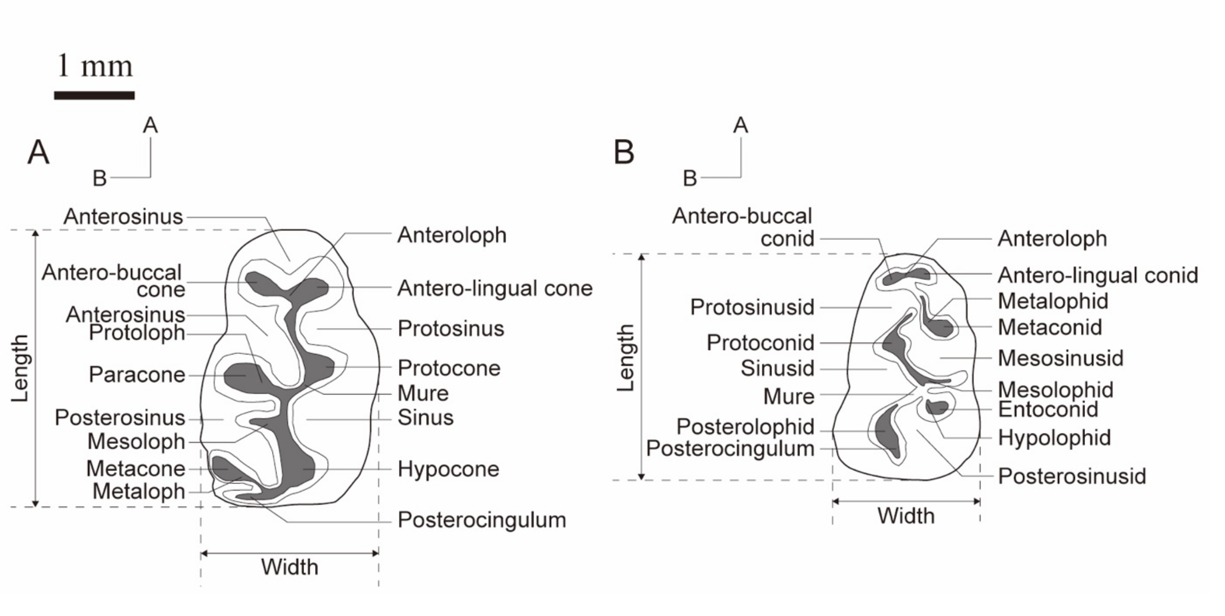

Fig. 6. Murid dental terminology and measurements used in text of upper (A, KNM-NA 52519) and lower teeth (B, NA60-2879’11), based on Wood and Wilson (1936), Mein and Freudenthal (1971), and Costa et al. (2019).

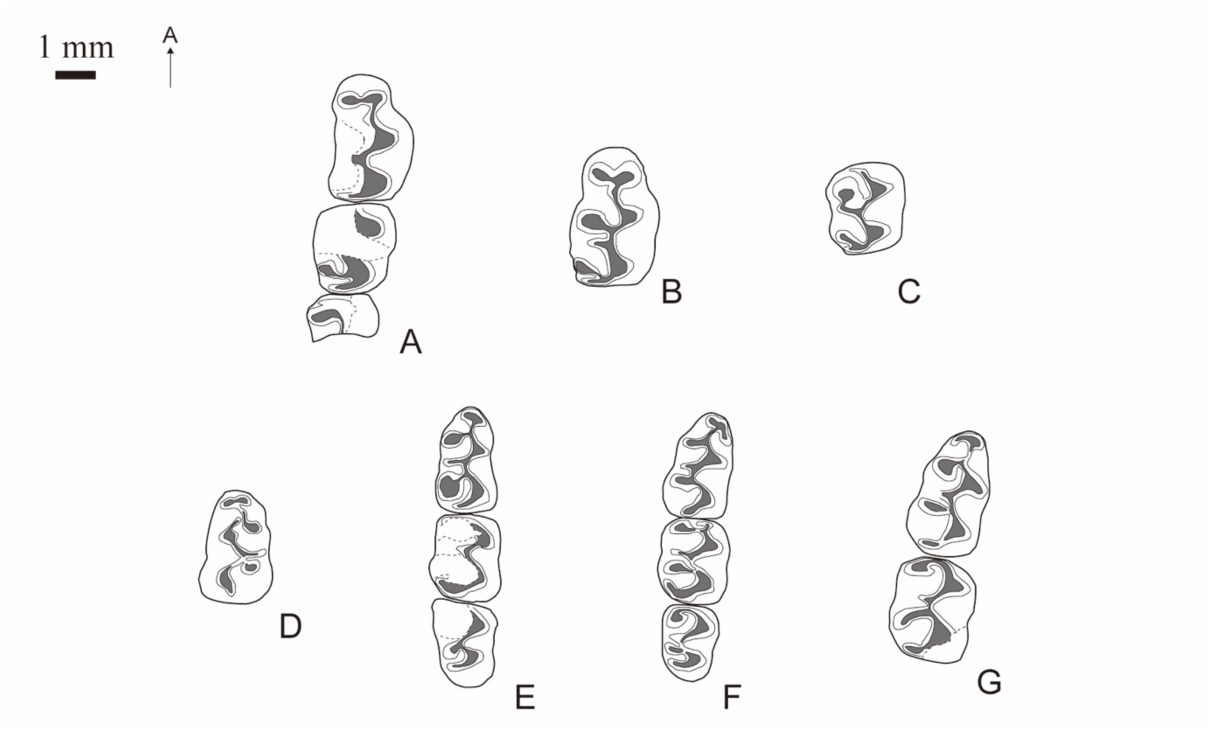

Fig. 7. Schematic drawings of the occlusal surfaces of cheek teeth of *Afrocricetodon* cf. *songhori korui* from the Nakali Formation. A, KNM-NA 52509, Rt. M1–M3. B, KNM-NA52519 (a), Rt. M1. C. KNM-NA 52539, Rt. M2. D, NA60-2879’11, Lt. m1. E, KNM-NA 50296, Rt. m1–m3. F, KNM-NA 50303, Rt. m1–m3. G, KNM-NA 52376, Rt. m1–m2. The scale bar indicates 1 mm, anterior (A) denoted by the arrow.

Table 4. Measurements (mean and range; in mm) of teeth of *Afrocricetodon* cf. *songhori korui*. Abbreviations as in Table 2.

	M1 (N=5)			M2 (N=11)			M3 (N=8)		
	L	W	L / W	L	W	L / W	L	W	L / W
M	3.01	1.92	1.50	2.07	1.79	1.16	1.95	1.77	1.10
OR	2.7–3.29	1.57–2.14	1.37–1.61	1.89–2.3	1.49–2.02	0.95–1.36	1.4–2.29	1.52–2.09	0.88–1.35

	m1 (N=14)			m2 (N=12)			m3 (N=9)		
	L	W	L / W	L	W	L / W	L	W	L / W
M	2.91	1.84	1.59	2.19	1.81	1.21	2.07	1.77	1.21
OR	2.39–3.35	1.5–2.23	1.47–1.79	1.95–2.48	1.55–1.94	1.14–1.28	1.8–2.4	1.42—2.12	1.03–1.32

3.3.5. *Abudhabia* sp. indet.

Upper and lower molars, and several maxilla and mandible fragments from the Nakali Formation were described as *Abudhabia* sp. indet. in this study (Fig. 8–9; Table 5).

African Late Miocene Gerbillinae (Muridae) show a simple anterocone on M1 and cusp-pairs (transverse rows) with no longitudinal crest on M1–2. Fossil Taterillinae consist of *Protatera* and *Abudhabia* (Wessels. 2009). Although there are few molar specimens, there are distinct characteristics that indicate that the current material can be assigned to *Abudhabia*. These characteristics include the disappearance of the longitudinal loph and the formation of three transverse ridges by the fusion of opposing cusps (anterior loph, medial loph, and posterior loph) (de Brujin and Whybrow, 1994).

The genus *Abudhabia* comprises six species. These species, known from south of the Sahara and Eurasia, are *A. baynunensis* (de Brujin and Whybrow, 1994), *A. pakistanensis* (Flynn and Jacobs, 1999), *A. kabulense* (Sen, 1983; Wessels, 1998), *A. radinskyi* (Flynn et al., 2003), *A. yardangi* (see Flynn and Jacobs, 1999; de Brujin, 1999), and *A. baheensis* (Qiu et al., 2004). *Abudhabia* is also known from the Late Miocene of Lothagam, Kenya [5.23 Ma: Winkler (2003)], but this is a single Rt. m1, and the species cannot be determined.

The Nakali material can, in many characteristics, be attributed to *Abudhabia*, but it is distinct from the known species in possessing a unique combination of features (an anterior cusp on the anterior margin and a dentine lake in the posterior loph, representing a reduced posterior cingulum, and a much narrower occlusal outline). I will refrain from naming a new species until additional specimens, particularly lower dentition, are obtained.

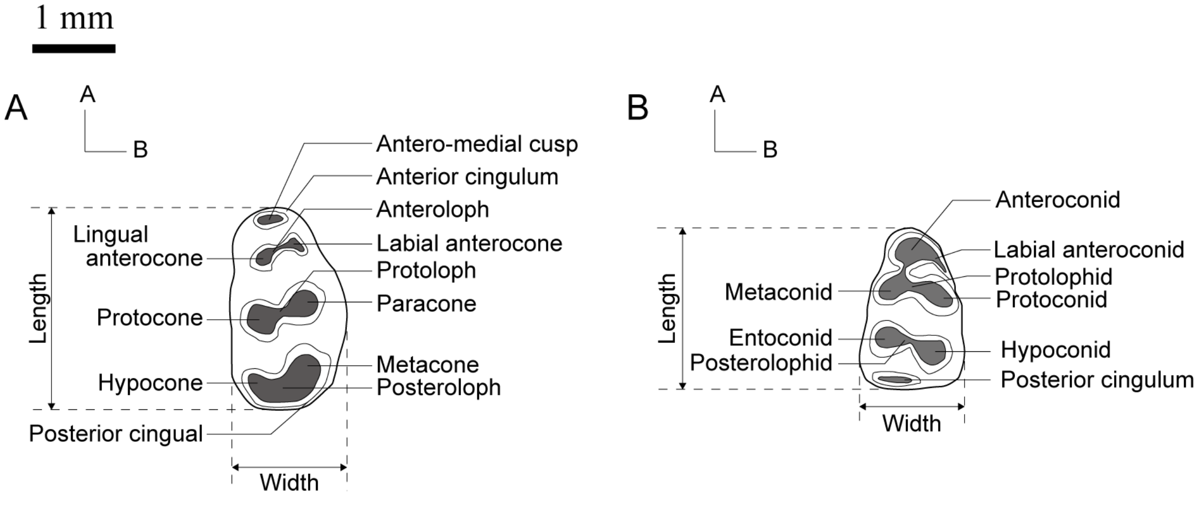

Fig. 8. Gerbilline dental terminology and measurements used in text of upper (A, KNM-NA 50302) and lower teeth (B, KNM-NA 54903), based on Jacobs (1978) and Flynn et al. (2003).

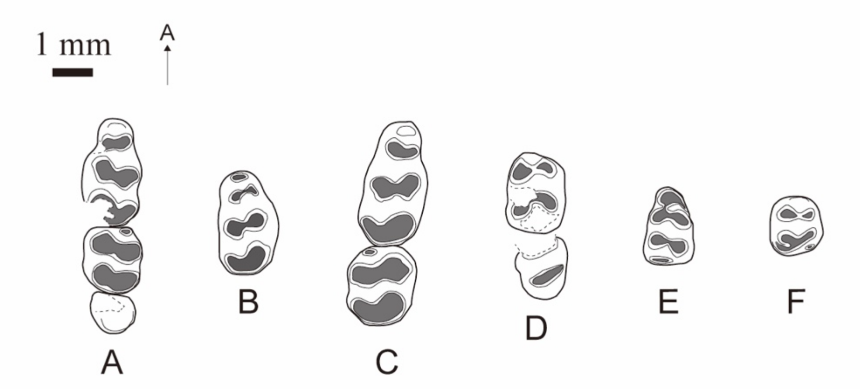

Fig. 9. Schematic drawings of the occlusal surfaces of cheek teeth of *Abudhabia* sp. from the Nakali Formation. A, KNM-NA 52653, Lt. M1–M3. B, KNM-NA 50302, Rt. M1. C. KNM-NA 52511, Rt. M1–M2. D, NA60-2664’11, Lt. m2–m3. E, KNM-NA 54903 (a), Rt. m1. F, KNM-NA 54903, Rt. m2. The scale bar indicates 1 mm, anterior (A) denoted by the arrow.

Table 5. Measurements (mean and range; in mm) of cheek teeth of *Abudhabia* sp., collected from the Nakali Formation. Abbreviations as in Table 2.

	M1 (N=3)			M2 (N=2)			M3 (N=1)		
	L	W	L / W	L	W	L / W	L	W	L / W
M	2.74	1.44	1.90	1.80	1.56	1.15	—	—	—
OR	2.57–2.89	1.41–1.46	1.82–1.98	1.75–1.84	1.55–1.56	1.13–1.18	1.00	1.11	0.90

	m1 (N=1)			m2 (N=2)			m3 (N=1)		
	L	W	L / W	L	W	L / W	L	W	L / W
M	—	—	—	1.64	1.38	1.18	—	—	—
OR	1.84	1.24	1.48	1.33–1.94	1.22–1.53	1.09–1.27	1.49	1.35	1.10

3.3.6. *Paraulacodus johanesi*

Upper and lower cheek teeth, upper incisors, and several maxilla and mandible fragments from the Nakali Formation were described as *Paraulacodus* sp. in this study (Fig. 10–11; Table 6).

The Nakali specimens are assigned to the Thryonomyidae because they have well-developed lophs/lophids (Winkler et al., 2010), upper cheek teeth with two labial and one lingual enamel infoldings (=sinus, anterosinus, posterosinus), and lower cheek teeth with the opposite pattern (=sinusid, mesosinusid, posterosinusid) (Woods, 1984; Ungar, 2010).

Of the presently recognized six genera of the Thryonomyidae, the Nakali material is most similar to *Paraulacodus* in terms of the three transverse lophs on all cheek teeth, the molar size gradient increasing from P4 to M2 (Jaeger et al., 1980; de Brujin and Hussain, 1985), the entoflexus on P4, and a spur on the posteroloph of P4 and M1. Along with *Paraulacodus*, *Thryonomys* also resembles the current specimens in the m1 lophodonty. However, *Thryonomys* lacks entoflexus on P4 and an anterolabial cuspid on the lower molars, and has four transverse lophs on p4.

Paraulacodus contains two known species: *P. indicus* (Hinton, 1933), and *P. johanesi* (Jaeger et al., 1980). *P. indicus* is from the Middle Miocene of the Chinji Formation, Northern India (Hinton, 1933), and *P. johanesi* is from the Upper Miocene of the Ch'orora Formation, Ethiopia (Jaeger et al., 1980). The Nakali material resembles *P. johanesi* in having inconspicuous and unisolated anterolabial cuspids on the lower molars. *P. indicus* has a stronger anterolabial cusp on the lower molars. I assign the Nakali species to *P. johanesi*.

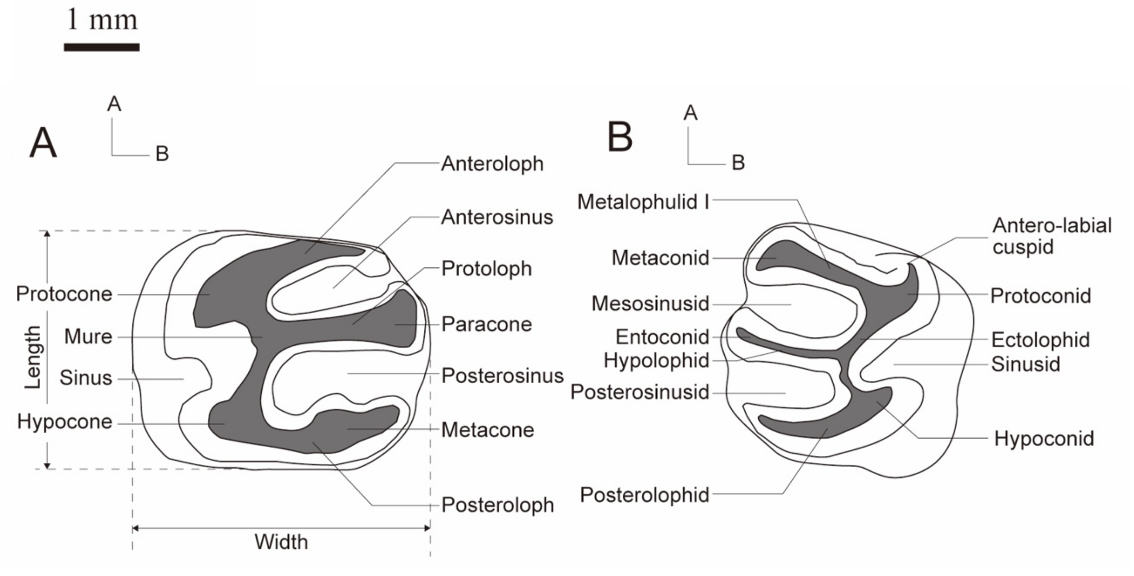

Fig. 10. Thryonoyid dental terminology and measurements used in text of upper (A, KNM-NA 50312), lower teeth (B, KNM-NA 54904), based on Marivaux et al. (2002), López-Antoñanzas et al. (2004), López-Antoñanzas and Sen (2005) and Kraatz et al. (2013).

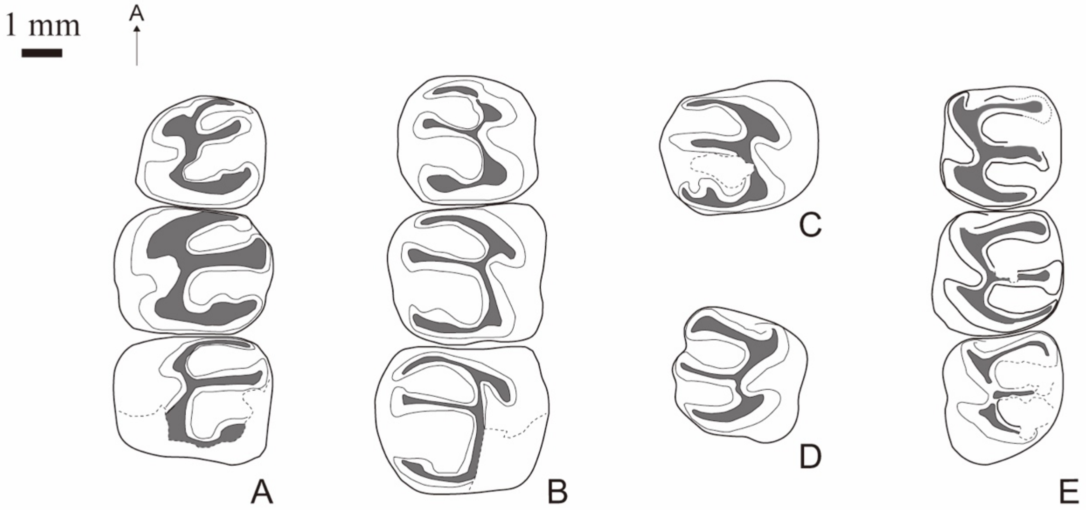

Fig. 11. Schematic drawings of the occlusal surfaces of *Paraulacodus johanesi* from the Nakali Formation. A, KNM-NA 50312, Lt. P4–M2. B, NA60-12460’07, Rt. P4-M2, C, NA60-3055’11, Rt. M1 or M2. D, KNM-NA 54904, Rt. m1 or m2. E. KNM-NA 56080, Lt. M1–M3. The scale bar indicates 1 mm, anterior (A) denoted by the arrow.

Table 6. Measurements (in mm) of cheek teeth of *Paraulacous johanesi*, collected from the Nakali Formation (when tooth identification uncertain, the measurement is repeated in parentheses).

		I1 / i1			P4 / p4			M1 / m1			M2 / m2			M3 / m3		
No.		L	W	L / W	L	W	L / W	L	W	L / W	L	W	L / W	L	W	L / W
Upper Dentition																
KNN-NA 54912	Lt.	3.40	2.49	1.37	—	—	—	—	—	—	—	—	—	—	—	—
KNN-NA 54914	?	—	2.82	—	—	—	—	—	—	—	—	—	—	—	—	—
KNN-NA 50314	Lt.	—	—	—	2.72	3.20	0.85	3.13	4.06	0.77	2.74+	4.14	—	—	—	—
NA60-3055'11*	Rt.	—	—	—	—	—	—	3.54	3.95	0.90	3.54	3.95	0.90	—	—	—
NA60-12160'07	Rt.	—	—	—	2.92	3.12	0.94	3.25	3.62	0.90	3.17	3.67	0.86	—	—	—
Lower Dentition																
KNM-NA 54904*	Rt.	—	—	—	—	—	—	3.11	3.16	0.98	3.11	3.16	0.98	—	—	—
KNM-NA 56080	Lt.	—	—	—	—	—	—	2.73	2.64	1.03	2.76	2.93	0.94	2.98	2.65	1.12

3.3.7. Thryonomyidae gen. et sp. indet. (small)

An isolated molar (KNM-NA 50310) from the Nakali Formation were described as Thryonomyidae gen. et sp. indet. (small) in this study.

In the advanced groups of the Thryonomyidae (for example, *Paraulacodus* and *Thryonomys*), the upper molars tend to show simple patterns similar to those of the lower molars (Kawamura and Nakaya, 1987).

The present specimen is similar to both *Paraulacodus* and *Thryonomys* in having three transverse lophs, but it differs from them in terms of posteroloph morphpology. Unlike *Paraulacodus*, it does not have a spur, and, unlike *Thryonomys*, its posteroloph is straight. The possibility that it belongs to *Paraphiomys* cannot be dismissed completely, as three to four transverse lophs appear on the upper molars of *Paraphiomys* depending on either dental wear or individual variation. The specimen is smaller than are the other Thryonomyid specimens (see below). The single worn specimen does not allow any definite conclusion, and we assign it tentatively to Thryonomyidae gen. et sp. indet. (small).

3.3.8. Thryonomyidae gen. et sp. indet. (large)

An isolated molar (KNM-NA 55875) from the Nakali Formation were described as Thryonomyidae gen. et sp. indet. (large) in this study.

The presence of three transverse lophs support a Thryonomyidae status of KNM-NA 55875, particularly with an affinity to *Paraulacodus* and *Thryonomys*. However, it differs from these genera in respect of the valley morphology. This specimen is very large compared with thryonomyid rodents, such as extant *Thryonomys.* In these species, the crown outline is rectangular, it is elongated bucco-lingually, and it has no robust loph in this specimen. The corresponding valley of *Thryonomys* is shallower than is valley in this specimen. The size of this specimen is larger, although all crests are straight. The current specimen is either as large or larger than is the extant *T. swinderianus*, and it may be possible to assign it to a new species. As the specimen is only one isolated molar, further determination is difficult. Thus, we assign the specimen tentatively as Thryonomyidae gen. et sp. indet. (large).

3.3.9. Hystricidae gen. et sp. indet.

An isolated premolar (KNM-NA 52956) from the Nakali Formation were described as Hystricidae gen. et sp. indet. in this study (Fig. 12; Table 7).

The hystricid status of this specimen is supported by its many curved crests and strong unilateral hypsodonty. Precise identification of Hystricidae from an isolated tooth is difficult because the complexity of the occlusal pattern changes with continuing wear (Masini and Rook, 1993; Sen and Kovatchev, 1987; Winkler, 2003).

The current specimen is smaller than both *Xenohystrix* and *Hystrix* and slightly larger than *Atherurus*. As it is not possible to distinguish clearly between *Hystrix* and *Atherurus* molars, we leave the present specimen as Hystricidae gen. et sp. indet.

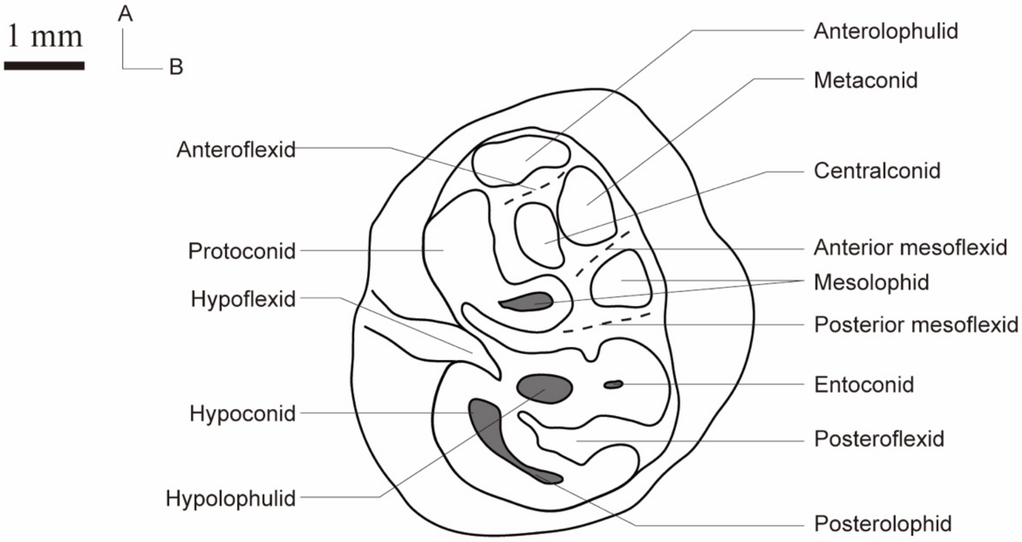

Fig. 12. Hystricid dental terminology and measurements used in text of lower teeth (KNM-NA 54956), based on Sen (2001a).

Table 7. Measurements (in mm) of cheek teeth of Hystricidae gen. et sp. indet., collected from the Nakali Formation.

No.			L	W	L /W
Hystricidae gen. et sp. indet.					
KNM-NA 54956	Lt.	Lower	5.70	4.81	1.19

3.4. Discussion

3.4.1. Composition of Nakali rodent fauna

Through identifying the Nakali rodent fauna, we have recognized six families and 9 species (Table 8). The dominant taxon in the six families (total 680 classified specimens) is the Rhizomyinae (615 specimens); the remainder are Afrocricetodontinae (37 specimens), Sciuridae (13 specimens), Thryonomyidae (8 specimens), Gerbillinae (6 specimens), and Hystricidae (1 specimen) from the Nakali Formation. Most of the rodent fossil remains from site NA39 are fragmented strongly. The following taxa are recognized: *Vulcanisciurus africanus* (Sciuridae), Sciuridae gen. et sp. indet., *Nakalimys lavocati* (Rhizomyinae, Spalacidae), *Afrocricetodon* cf. *songhori korui* (Afrocricetodontinae, Nesomyidae), *Abudhabia* sp. indet. (Gerbillinae, Muridae), *Paraulacodus johanesi* (Thryonomyidae), Thryonomyidae gen. et sp. indet. (small), Thryonomyidae gen. et sp. indet (large), Hystricidae gen. et sp. indet.

Table 8. Rodent fauna based on cheek teeth from Nakali Formation.

Family	Taxa
Sciuridae	*Vulcanisciurus africanus*
	Sciuridae gen. et sp. indet.
Spalacidae (Rhizomyinae)	*Nakalimys lavocati*
Nesomyidae (Afrocricetodontinae)	*Afrocricetodon* cf. *songhori korui*
Muridae (Gerbillinae)	*Abudhabia* sp.
Thryonomidae	*Paraulacodus johanesi*
	Thryonomyidae gen. et sp. indet. (small)
	Thryonomyidae gen. et sp. indet. (large)
Hystricidae	Hystricidae gen. et sp. indet.

Reference: Onodera (2011), Tanabe (2013, 2014), this study.

3.4.2 Reconstruction of paleoenvironments based on Nakali rodent fauna

The environmental interpretations arrived at from the Nakali rodent fauna are based on the use of modern analogs and the assumption that ecological requirements and/or behavior have remained constant for both the rodents and the accumulating agency (e.g., Avery, 1982).

The dominant taxon in the Nakali rodent fauna, *Nakalimys lavocati,* belongs to the subfamily Rhizomyinae (Spalacidae). Extant rhizomyines are fossorial rodents that live in Southern Asia and Eastern Africa. The African rhizomyine, the 'mole rat,' includes only one genera (*Tachyoryctes*), which inhabits wet uplands (700–4000 m), and prefers either wet grassland or open forest (Kingdon, 1974, 1997; Nowak, 1999; Monadjem et al., 2015; Norris, 2017). The same may be said of *N. lavocati*.

As most genera among the Gerbillinae (Muridae) are restricted to arid areas and open landscapes (Kingdon, 1997; Nowak, 1999; Wesssels, 2009), Nakali *Abudhabia* also likely indicates mainly dry environments. However, as these specimens are very rare from the Nakali Formation. It may be possibile that dry environments were not the dominant habitat. Nakali was likely to have temporary dry environments (e.g., rainy–dry seasons).

The extant African Hystricidae have two genera: *Atherurus* (brush-tailed porcupine) and *Hystrix* (porcupine). *Hystrix* occurs in nearly all habitats (apart from extensive wet forests and very arid regions), but it is found most often in hilly, rocky country (Kingdon, 1997). *Atherurus* lives exclusively in forests (Kingdon, 1997).

The ecological requirements of *Vulcanisciurus* and *Afrocricetodon* are unknown. However, both taxa are known generally from the Upper–Middle Miocene East African sites sampling forest habitats (Ungar et al., 2012; Pickford et al., 2014; Coste et al., 2019). *Vulcanisciurus* has been recovered from the Lower Miocene [Koru-Songhor (20–19 Ma) and Rusinga (18–15 Ma) in Kenya, and Napak (20–19 Ma), in Uganda, e.g., Lavocat (1973)], the Middle Miocene [Fort-Ternan (14 Ma), Kenya, Denys and Jeager (1992)], and the late Middle Miocene [Ngorora Formation (12.5 Ma), Tugen Hills, Winkler (1990, 2002)]. *Afrocricetodon* has been known only from the Early Miocene [Koru-Songhor ([20–19 Ma) and Rusinga (18–15 Ma) in Kenya, and Napak (20–19 Ma), in Uganda, e.g., Lavocat (1973)].

From what has been stated thus far, it follows that Nakali should have had a watery environment and forested uplands, with rainy–dry seasons during the early late Miocene. This reconstruction is in accordance with the previously reconstructed paleoenvironment of the Nakali Formation (as mentioned in chapter 2.3).

3.4.3 Comparison to other localities of the upper lower Miocene in Eastern Africa

The early late Miocene rodent fauna have been found in Kenya (Nakali and Samburu Hills) and Ethiopia (Chorora) in sub-Saharan Eastern Africa.

The Chorora Formation (8.5–7.0 Ma) is located along the southeastern margin of the transition zone of the Afar and the Main Ethiopian Rifts (Suwa et al., 2015). Based on the mammalian fauna, the paleoenvironments of the Chorora Formation have been estimated to be wooded with more open (savanna-like) habitat (Geraads et al., 2002; Cote, 2004). Seven families and 11 taxa of rodent fauna from the Chorora Formation have been reported by Jaeger et al. (1980), Geraads (1998a, 2001), and Suwa et al. (2015) (Table 9). The fauna are characterized by a diverse array of Murids and a resemblance to the Nakali rodent fauna (i.e., *Nakalimys lavocati* and *Paraulacodus johanesi* from the type locality). From the upper Chorora (7.5–7.0 Ma, the upper upper Miocene), *Abudhabia* has been known. The Murid records represent the earliest occurrence in Eastern Africa (Winkler et al., 2010); they did not occur during the age of the Nakali Formation (ca. 10 Ma). And the similarity of some taxa from the Nakali Formation and the Chorora Formation is connected to the similarity of the paleoenvironments of each.

The Samburu Hills are situated 60 km north of the Nakali (Fig. 1). The Namurungule Formation (9.6–9.3 Ma) is distributed in this area (Saneyoshi et al, 2006; Sakai et al., 2010). The paleoenvironments of the Namurungule Formation are more open and wooded habitat with lakes and rivers in a dry climate (Nakaya, 1994; Sakai et al., 2010; Uno et al., 2011; Nakaya et al., 2012). Sedimentological study has shown that the Namurungule Formation would have been deposited in lowlands with lakes under strong seasonality (Sakai et al., 2010). The known rodent fauna from the Namurungule Formation include only three reports of thryonomyids by Kawamura and Nakaya (1984, 1987) (Table 9). As mentioned above, thryonomyids indicate watery environments; this is in accordance with the sedimentological study findings (Sakai et al., 2010). Though the ages and locations of the Nakali Formation and the Namurungule Formation are nearly the same, fewer rodents are known from the Namurungule Formation. This difference may arise from depositional and environmental differences. The drier environments and lower lands of the Samburu Hills compared to Nalali during the Miocene may not have been suitable for rodents.

Table 9. Faunal list of rodents from the Chorora and Namurungule Formation.

Chorora Fm. (ca. 8.5–7.0 Ma) of Ethiopia				
Order / Family-Level	Taxa	Type Locality (ca. 8.5 Ma)	Beticha (ca. 8.0 Ma)	Upper Chorora (ca. 7.5–7.0 Ma)
Thryonomyidae	*Paraulacodus johanesi*	X	X	X
	Paraphiomys chororensis	X		
Spalacidae (Rhizomyinae)	*Nakalimys lavocati*	X		
Gerbillidae (Gerbillinae)	cf. *Abudhabia* sp.			X
Cricetidae	*Afaromys gillemoti*	X		
Nesomyidae	"*Dendromus* " (?*Saccostomus*) spp.	X		
Muridae	*Preacomys kikiae*	X		
	aff. *Stenocephalomys* sp.	X		
	cf. *Parapelomys* sp.	X		
	cf. *Tectomys* sp.	X		
Sciuridae	*Xerus* sp.	X		

Reference: Jaeger et al. (1980), Geraads (1998a, 2001), and Suwa et al. (2015)

Namurungule Fm. (ca. 9.5 Ma) of Kenya	
Order / Family-Level	Taxa
Rodenia	
Thryonomyidae	*Paraphiomys* sp.
	Paraulacodus sp.
	Thryonomyidae gen. et sp. indet.

Reference: Kawamura and Nakaya (1984, 1987), and this study.

Chapter 4. Paleobiogeography of the Neogene Rodents from Afro-Eurasia

As discussed in the previous chapter, rodent fauna from the Nakali Formation have renewed the FAD/LAD of different rodent taxa. Following this updating, this chapter reviews fossil records of some rodent groups in Afro-Eurasia during the Neogene. Further, the relationships between migrations, faunal changes, and paleoenvironmental transitions are discussed.

4.1. Materials and Methods

This study focuses on the fossil records of the genus *Vulcanisciurus*, the genus *Afrocricetodon*, the genus *Abudhabia*, and the Family Hystricidae in Afro-Eurasia during the Neogene. *Vulcanisciurus* and *Afrocricetodon* from the Nakali Formation are the latest records, and *Abudhabia* and hystricid from the Formation are the oldest records in Eastern Africa. These are followed by either direct observations or numerous references (see the following sections). Geological age is followed by Gradstein et al. (2012) and Ogg et al. (2016). The Faunal Sets, which is the African mammalian biostratigraphy, is based on Pickford (1981) and Pickford and Morales (1994). The "European Land Mammalian Ages" (ELMA) and the "Neogene Mammal-Zones" (MN-Zones) are followed by Steininger (1999).

4.2. Results and Discussions

4.2.1. Genus *Vulcanisciurus* (Sciuridae) and genus *Afrocricetodon* (Afrocricetodontinae)

Vulcanisciurus is the oldest fossil sciurid from Africa. Its fossil records are known from the lower [20–19 Ma: Rusinga, Songhor, and Koru, Kenya; Lavocat (1973); 20–19 Ma: Napak, Uganda; Lavocat (1973); Coste et al. (2019)] to the middle [14 Ma: Fort Ternan, Kenya; Denys and Jaeger (1992)] and the upper–middle Miocene [12.5 Ma: Ngorora Formation, Tugen Hills Kenya; Winkler (1990, 2002)]. Although Senut et al. (1992) previously listed *Vulcanisciurus* from Harasib 3a, Namibia (ca. 10Ma), Mein et al. (2000a) described it as *Heteroxerus*, as *Vulcanisciurus* was the only genus described from eastern Africa during the early–middle Miocene. *Afrocricetodon* is the only known genus from eastern Africa, and it has been reported from the lower Miocene [20–19 Ma: Rusinga, Songhor, and Koru, Kenya; Lavocat (1973); 20–19 Ma: Napak, Uganda; Lavocat (1973); Coste et al. (2019)]. Its occurrence was limited in the early Miocene. Both taxa from the Nakali Formation (ca. 10Ma) suggest that the genus survived until the early Late Miocene.

Both taxa are known from the Upper–Middle Miocene East African sites, including the Nakali Formation, generally sampling forest habitats (see section 3.4.2). The taxa, which became extinct after this period, suggest dominance of more open habitas (e.g., either woodland or savanna).

4.2.2. Genus *Abudhabia* (Gerbillinae; see Appendix 1)

Abudhabia is distributed widely in the Neogene. There are groups known from Eastern Africa to Western and Southern Asia and to Eastern Asia (Figs. 13–14).

Their first occurrence is from Turkey, Kenya (the Nakali Fm.) and China during the Vallesian (11.1–8.7 Ma: the early late Miocene). The *Abudhabia* reported from the late Miocene Turkey [MN9 (11.1–9.8 Ma); de Bruijn et al. (2013)] is inferred as being the oldest record of the genus. However, de Bruijn only listed the species and did not describe it in detail. The Nakali *Abudhabia* reported in this study is the oldest record in Africa. At least, it inhabited in Africa by this period. The occurrence of Chinese *Abudhabia* [*A. baheensis*; Bahe Fm. (9.98–8.07 Ma); Qui et al., 2004] indicates the close biogeographical affinity of Eastern Asia with Eastern Africa. It also implies that there was a xeric open region between Eastern Asia and Eastern Africa in this period that enabled interchange of small mammals through the Arabian Peninsula (Qui et al., 2004; this study). These old *Abudhabia*, which are distributed widely from East Africa to East Asia, are reported from similar ages. Therefore, it is difficult to determine their origin.

In the Turolian (8.7–4.9 Ma: the late Tortonian to the early Zanclean), the genus is known from Eastern and Northern Africa, Western and Southern Asia, and possibly China. *A. radinskyi* is named from the early–middle Tulorian Kabul, Afghanistan (Flynn et al., 2003). The oldest fossil Gerbillid from Africa is *Abdhabia*, which has been reported previously from the upper Miocene of Ethiopia [Chorora Fm. (Upper Chorora; ca. 7.5–7.0 Ma: Suwa et al. (2015)], Libya [Sahabi Fm. (ca. 7 Ma): described as *Protatera yardangi* by Manthe (1987), and discussed as *A. yardangi* by Flynn et al. (2003)] and Kenya [Lukeino Fm. (6.2–5.6 Ma): Mein and Pickford (2006)], and the lower Pliocene of Kenya (Lothagam [5.23 Ma]: Winkler (2003)]. The *Abudhabia* from the Nakali Formation (ca. 10Ma) mean that the temporal range of *Abudhabia* dates to ca. 10Ma in Africa. The fossil records indicate that more open environments (e.g., woodland, savanna, or arid zones) developed in Eastern Africa during the Vallesian to the Turolian. Moreover, the last fossil records of *Abudhabia* in Africa and of other extinct (*Protatera, Pseudmeriones,* and *Mascaramys*) and extant (*Gerbilliscus*, *Desmobillus*, *Gerbillurus*, *Meriones*) gerbillids in Africa begun to occur at the end of the Turolian (e.g., Winkler et al., 2010).

The last records of *Abudhabia* are from the Ruscinian and the Vilanyian. *A.* cf. *A. kabulense* is known from India (4.18–2.58 Ma: Patnaik, 1997). *Abudhabia* disappeared at the end of this period and interchanged with modern gerbillids.

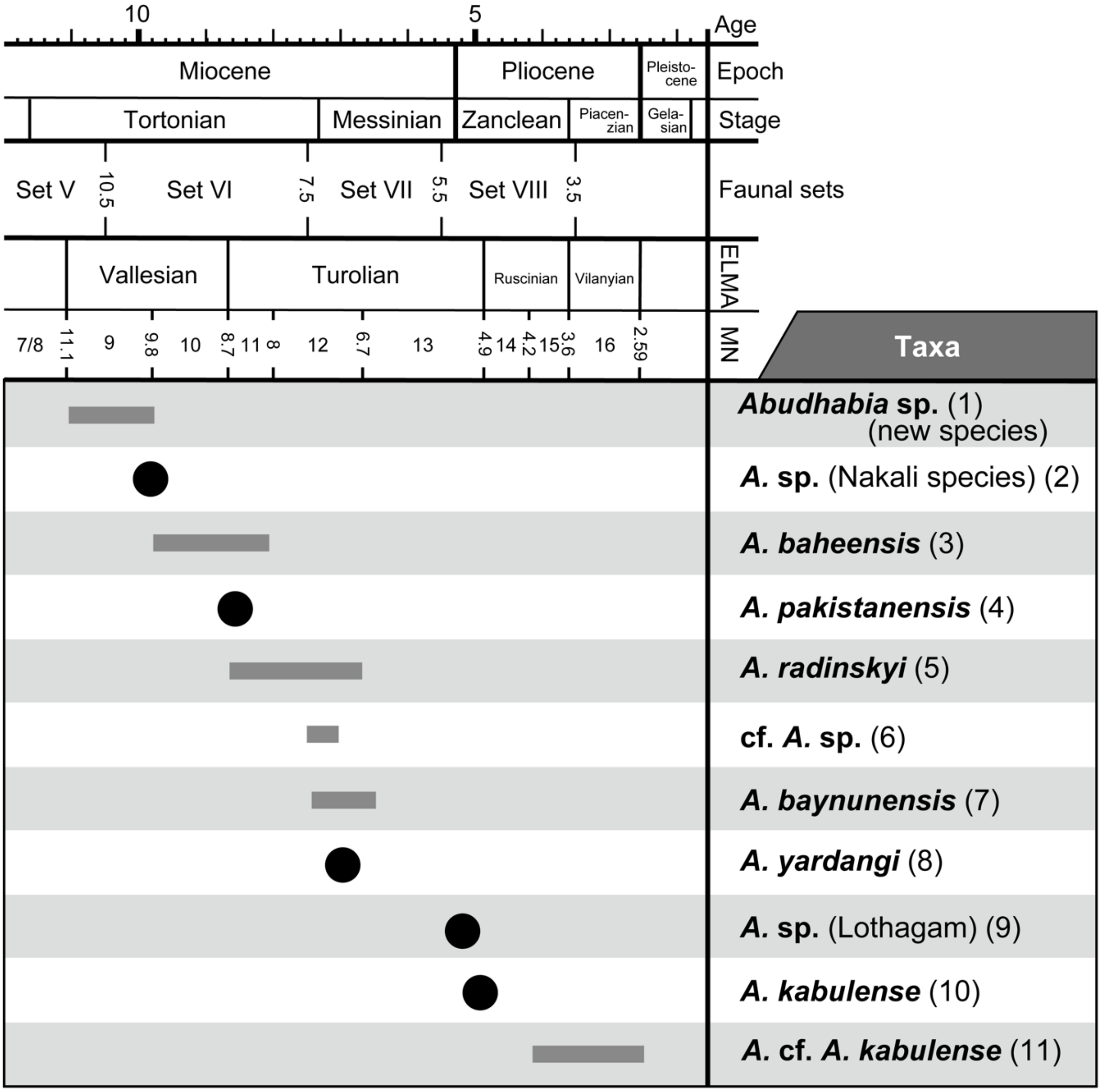

Fig. 13. Temporal ranges of *Abudhabia*. For detail fossil records see Appendix 1.

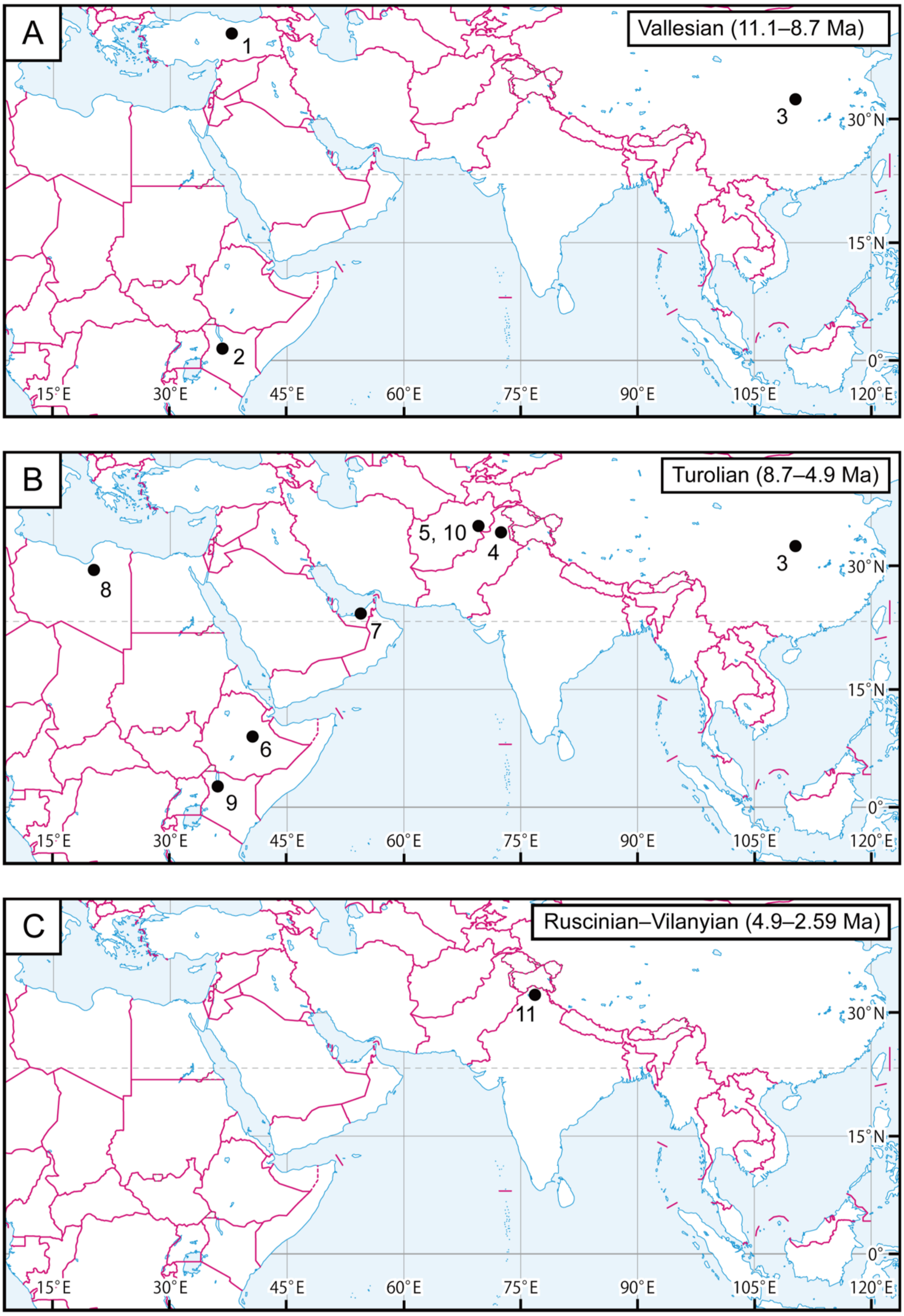

Fig. 14. Paleogeographic map of *Abudhabia* in Afro–Eurasia during Vallesian to Vilanyan (MN 9–16; early late Miocene–Pliocene). A, Vallesian (11.1–8.7Ma; MN9–10); B, Turolian (8.7–4.9 Ma); C; Ruscinian–Vilanyan (4.9–2.59 Ma). See appendix 1 for the numbers in this figure.

4.2.4. Family Hystricide (see Appendix 2)

The earliest occurrence of hystricids is *Atherurus karnuliensis*, known from the Chinji Formation of the lower Siwalik, India (14.3–11.5 Ma: Colbert, 1993; Landry, 1957; Van Weers, 2002, 2005). The oldest record in Europe is *Hystrix parvae* from Cskvar, Hungary (MN10; 9.8–8.7 Ma; Kretzoi, 1951; Weers and Montoya, 1996). This is also the oldest occurrence of *Hystrix*.

The family is represented by three genera, *Atherurus*, *Hystrix*, and *Xenohystrix,* in Africa during the Neogene. Only the last of these is extinct. The oldest African Hystricidae is 11–10Ma, from Sheikh Abdallah, Egypt (*Atherurus* sp.; Pickford et al., 2008). The Nakali specimen is one of the oldest records of this family in Africa. The hystricids are likely Vallesian, particularly MN9 (11.1–9.8 Ma), immigrants from Eurasia to Africa, distributed throughout eastern Africa by the early Late Miocene (Fig. 16, 21-A).

In the MN12 (8–6.7 Ma: the Middle Turolian; Fig. 21-B), the earliest occurrences of *Hystrix* are represented from Northern and Eastern Africa. The earliest record of *Hystrix* in Northern Africa is known from Manacer, Algeria (*H*. sp.; 7.1–5.3? Ma; Aramboug, 1959) and Tros-Menalla, Chad (*H*. sp.; 7–6 Ma; Vignaud et al., 2002), and in Eastern Africa is known from Lothagam, Kenya (*H*. sp.; ca. 7.44 Ma; Winkler, 2003). The *Hystrix* is likely MN12 (8–6.7 Ma) immigrants from Eurasia to Africa, distributed throughout Northern and Eastern Africa by the early Late Miocene.

Moreover, in the MN13 (6.7–4.9 Ma; Late Turolian; Fig. 21-C), the earliest occurrences of *Atherurus* and *Xenohystrix* are represented from Eastern Africa. The earliest records of *Atherurus* and *Xenohystrix* in Eastern Africa are known from Lemdong'o, Kenya (*A*. sp.; 6.12–6.08 Ma: Hlusko, 2007). During this period, *Atherurus* ingressed to Eastern Africa, and *Xenohystrix* appeared in Eastern Africa. However, these are their last records from Eastern Africa. After this period, the fossil records of *Hystrix* are increase.

In the Ruscinian to the Vilanyian (MN14–16; 4.9–2.59 Ma), Neogene African hystricids were the most diversified, and they expanded to Southern Africa. The extant species, *H. cristata* and *H. africaeaustralis*, appeared for the first time.

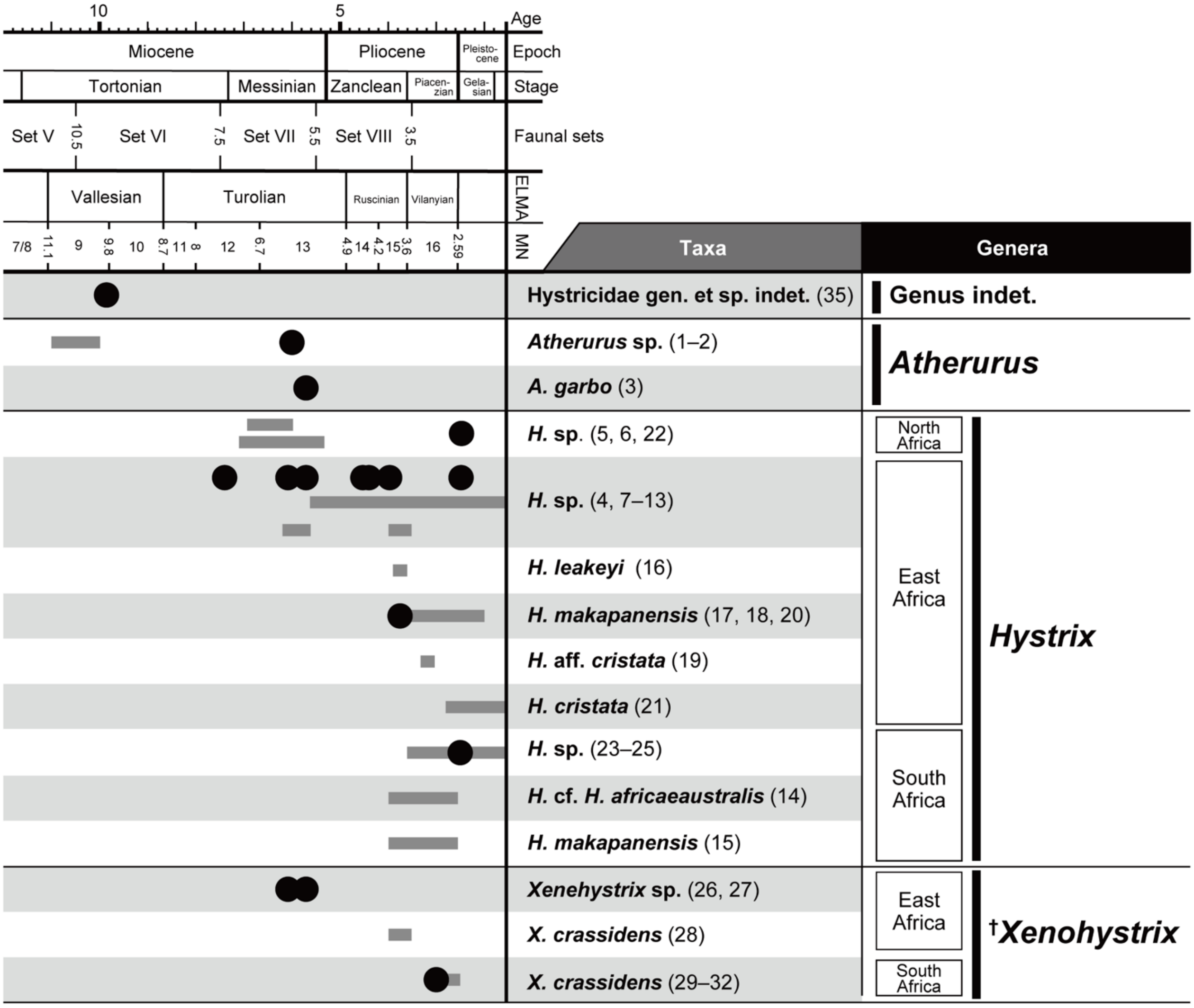

Fig. 15. Temporal ranges of the species in Africa. For detail fossil records see Appendix 2.

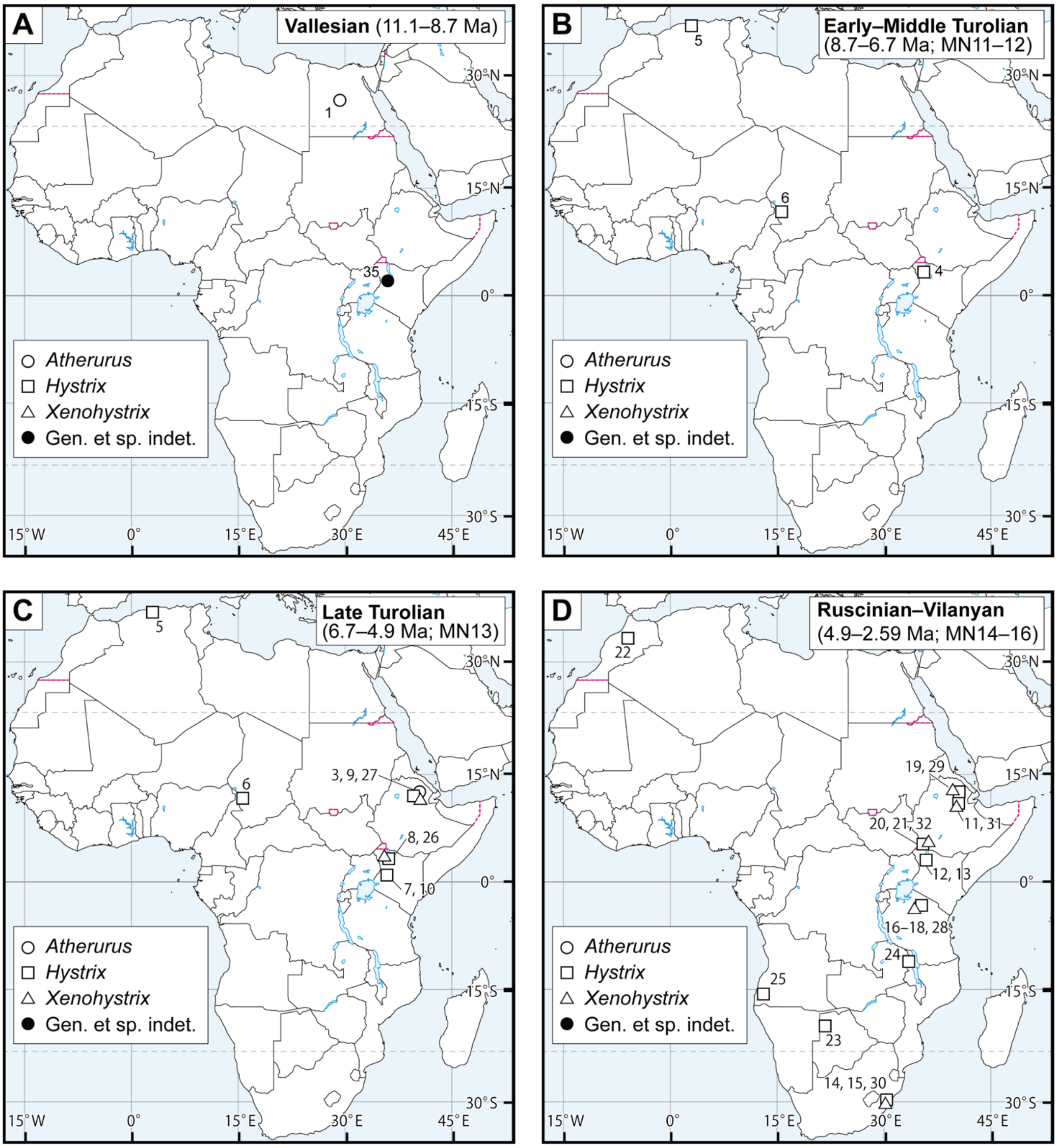

Fig. 16. Paleogeographic map of African hystricids during Vallesian to Vilanyan (MN 9–16; early late Miocene–Pliocene). A, Vallesian (11.1–8.7Ma; MN9–10); B, Early–Middle Turolian (8.7–6.7 Ma; MN11–12); C; Late Turolian (6.7–4.9 Ma; MN13); D, Ruscinian–Vilanyan (4.9– 14–16). See appendix 2 for the numbers in this figure.

Chapter 5. Conclusion

In this study, the Late Miocene rodent fauna from Nakali Formation (ca. 10 Ma), Northern Kenya, were revised and described. As a result, the following taxa are recognized: *Vulcanisciurus africanus* (Sciuridae), Sciuridae gen. et sp. indet., *Nakalimys lavocati* (Rhizomyinae, Spalacidae), *Afrocricetodon* cf. *songhori korui* (Afrocricetodontinae, Nesomyidae), *Abudhabia* sp. indet. (Gerbillinae, Muridae), *Paraulacodus johanesi* (Thryonomyidae), Thryonomyidae gen. et sp. indet. (small), Thryonomyidae gen. et sp. indet (large), Hystricidae gen. et sp. indet. From identifying the Nakali rodent fauna, this study recognized six families and 9 species (Table 8). The dominant taxon among the six families (total 680 classified specimens) is the Rhizomyinae (615 specimens); the remainder are the Afrocricetodontinae (37 specimens), the Sciuridae (13 specimens), the Thryonomyidae (8 specimens), the Gerbillinae (6 specimens), and the Hystricidae (1 specimen).

The taxonomic identifications by this study represent important new data for early Late Miocene biogeography. It suggests that Nakali presents 1) the latest records for *Vulcanisciurus* and *Afrocricetodon,* 2) the oldest records in Africa for *Abudhabia*, 3) the oldest records in Sub-saharan Africa for Hystricidae. These suggest that faunal changes of some rodent taxa of Eastern African bugun to occurred from around 10 Ma. It is quite likely that the changes would be related to the land connection of Afro–Eurasia and paleoenvironmental change in Africa.

The rodent fauna from the Nakali Formation fill a paleobiogeographic gap during the early Late Miocene. Nontheless, the Late Miocene is represented poorly in East Africa, compared to the Early to Middle Miocene. More fossil records and detailed phylogenetic analysis of each rodents are needed to discuss this hypothesis

REFERENCES

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

Aguirre, E., and P. Leakey. 1974. Nakali, nueva fauna de *Hipparion* en del Rift Valley de Kenya. Estudios Geológicos, vol. 30:219– 227. (in Spanish with English abstract)

Arambourg, C. 1959. Vertébrés continentaux du Miocène supérieur de l'Afrique du Nord.

Publications du Service de la Carte Geologique de l'Algérie (nouvelle série). Paléontologie, Mémoire 4:1–161. (in French)

Avery, 1982. Micromammals as palaeoenvironmental indicators and an interpretation of the late Quaternary in the southern Cape Province, South Africa. Annals of the South African Museum, 85:183–374.

Bibi, F., A. Hill, M. Beech, and W. Yasin. 2013. Late Miocene Fossils from the Baynunah Formation, United Arab Emirates; pp. 583–894 in X. Wang, L. J. Flynn, and M. Fortelius (eds.), Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology. Columbia University Press, New York.

Boaz, N. T. 2008. A view of the south: Eo-Sahabi palaeoenvironments compared and implications for hominid origins in Neogene North Africa. Circum-Mediterranean geology and biotic evolution during the Neogene period: The perspective from Libya. Garyounis Scientific Bulletin, Special 5:291–308.

Boaz, N. T., A. El-Arnauti, J. Agustí, R. L. Bernor, P. Pavlakis, and L. Rook. 2008. Temporal, lithostratigraphic, and biochronologic setting of the Sahabi Formation, North-Central Libya. Geology of East Libya, 3:959–972.

Bobe, R. 2011. Fossil Mammals and Paleoenvironments in the Omo-Turkana Basin. Evolutionary Anthropology, 20:254–263.

Boisserie, J. R., A. Souron, H. T. Mackaye, A. Likius, P. Vignaud, and M. Brunet. 2014. A new species of *Nyanzachoerus* (Cetartiodactyla: Suidae) from the late Miocene Toros-Ménalla, Chad, central Africa. PLoS ONE, vol. 9(8) e103221:1–22.

Brandy, L. D. 1979. Rongeurs Nouveaux du Néogène d'Afghanistan. Comptes Rendus des séances l'Academie des Sciences (Paris), Series D, 289:81–83.

———. 1981. Rongeurs muroïdés du néogène supérieur d'afghanistan. Evolution, Biogeographie, Correlations. Palaeovertebrata, Montpeller, 11(4):133–179.

Bromage T. G., F. Schrenk, and Y. M. Juwayeyi. 1995. Palaeobiogeography of the Malawi Rift: age and vertebrate paleontology of the Chiwondo Beds, northern Malawi. Journal of Human Evolution, 28:37–59.

de Brujin H. 1999. A Late Miocene Insectivore and Rodent Fauna from the Baynunah Formation, Emirate of Abu Dhabi, United Arab Emirates; pp. 186–197 in P. J. Whybrow, and A. Hill (eds.), Vertebrate fossils of the Arabian Peninsula, Yale University Press., New Haven and London.

de Bruijn, H., and S. T. Hussain. 1985. Thryonomyidae from the Lower Manchar Formation of

Sind, Pakistan. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen B 88 (2):155–166.

de Bruijn, H., and P. J. Whybrow. 1994. A late Miocene rodent fauna from baynunah Formation, Emirate of Abu Dhabi, United Arab Emirates. Proceedings Koninklijke Nederlandse Akademie van Wetenschappen, 97:407–422.

de Bruijn, H. E. Ünay, and K. Hordijk. 2013. A review of the Neogene succession of the Muridae and Dipodidae from Anatolia with special reference to taxa known from Asia and/or Europe; pp. 566–582 in X. Wang, L. J. Flynn, and M. Fortelius (eds.), Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology. Columbia University Press, New York.

Casanovas, I. V. 2007. The rodent assenmlages from the late Miocene Aragonian and the Vallesian (middle to late Miocene) of the Valles-Penedes basin (Catalonia, Spain). Ph.D. dissertation, Université autonoma de Barcelona, 282 pp.

Colbert, E. H. 1933. Two new rodents from the lower Siwalik Beds of India. American Museum Novitates, 633:1–6.

Costa, L. B., B. Senut, D. Gommery, and M. Pickford. 2019. Dental remains of Lower Miocene small rodents from Napak (Uganda): Afrocricetodontidae, Myophiomyidae, Kenyamyidae and Sciuridae. In Annales de Paléontologie, Elsevier Masson, 105:155–167.

Cote, S. M., 2004. Origins of the African hominoids: an assessment of the paleobiogeographical evidence. Human paleontology and Preghistory (Paleoanthropology), vol. 3:323− 340.

Deino, A. L. and S. H. Ambrose. 2007. ^{40}Ar/^{39}Ar dating of the Lemudong'o late Miocene fossil assemblages, southern Kenya Rift. Kirtlandia, 56:65–71.

Deino, A. 2011. ^{40}Ar/^{39}Ar dating of Laetoli, Tanzania; pp. 77–97 in Harris, T. (ed.), Paleontology and Geology of Laetoli: Human Evolution in Context. Volume 1: Geology, geochronology, paleoecology and Paleoenvironment, Springer, New York,

Dennell, R. W. 2004. Early Hominin landscape in northern Pakistan. Investigations in the Pabbi Hills. BAR International Series, 1265:1–454.

Dennell, R. W., R. Coard, and A. Turner. 2006. The biostratigraphy and magnetic polarity zonation of the Pabbi Hills, northern Pakistan: An Upper Siwalik (Pinjor Srage) Upper Pliocene–Lower Pleistocene fluvial sequence. Palaeoecology, Palaeoclimatology, Palaeogeography, 234:168–185.

Denys, C. 1987. Fossil rodents (other than Pedetidae) from Laetoli; pp. 118–170 in M. D. Leakey and J. M. Harris (eds.), Laetoli: A Pliocene Site in Northern Tanzania. Oxford University Press, New York.

———. 2011. Rodents; pp. 15–53 in Harris, T. (ed.), Paleontology and Geology of Laetoli: Human Evolution in Context. Volume 2: Fossil Hominins and the Associated fauna, Springer, New York.

Denys, C., and J. J. Jaeger. 1992. Rodents of the Miocene site of Fort Ternan (Kenya) first part: Phiomyids, bathyergids, sciurids and anomalurids. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, 185:63–84.

Denys, C., O. Sandrock, O. Kullmer, F. R. Rozzi, T. G. Bromage, F. Schrenk. 2011. Note on the presence of *Hystrix* (Mammalia, Rodentia) in the Malawi Chiwondo Beds (Plio-Pleistocene): taphonomical and palaeoecological implications. Geodiversitas, 33(4):729–738.

Feibel, C. S., F. H. Brown, and I. McDougall. 1989. Stratigraphic context of fossil hominids from the Omo Group deposits: Northern Turkana Basin, Kenya and Ethiopia. American Journal of Physical Anthropology, 78:595–622.

Fischer, M. S. 1986. Die Stellung der Schliefer (Hyracoidea) im phylogenetischen System der Eutheria. Zugleich ein Beitrag zur Anpassungsgeschichte der Procaviidae. Courier Forschungsinstitut Senckenberg, no. 84:1–132.

Flynn, L. J. 1982. Systematic revision of Siwalik Rhizomyidae (Rodentia). Geobis, 15, fasc. 3:327–389.

Flynn, L. J., and L. L. Jacobs. 1999. Late Miocene small-mammal faunal dynamics: the crossroads of the Arabian Peninsula; pp. 410-419 in P. J. Whybrow, and A. Hill (eds.), Vertebrate fossils of the Arabian Peninsula, Yale University Press., New Haven and London.

Flynn, L. J. and M. Sabatier. 1984. A muroid rodent of Asian affinity from the Miocene of Kenya. Journal Vertebrate Paleontology, 3:160–165.

Flynn, L. J. and W. Wessels. 2013. Paleobiogeography and South Asian Small Mammals; pp. 445–460 in X. Wang, L. J. Flynn, and M. Fortelius (eds.), Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology. Columbia University Press, New York.

Flynn, L. J., A. J. Winkler, L. L. Jacobs, and W. Downs. 2003. Chapter 23: Tedford's Gerbils from Afghanistan. Bulletin of the American Museum of Natural History, 603–624.

Geraads, D. 1995. Rongeurs et insectivores (Mammiferes) du Pliocene final d'Ahl al Oughlam (Casablanca, Moroc). Geobios, 28:99–115.

———. 1998a. Rongeurs de Miocene superieur de Chorora (Ethiopie): Cricetidae, Rhizomidae, Phiomyidae, Thryonomyidae, Sciuridae. Paleovertebrata, 27:203–216, 2pl.

———. 1998b. Rongeurs du Moi-Pliocene de Lissasfa (Casablanca, Moroc). Geobios, 31:229–245

———. 2001. Rongeurs du Miocène sup ’rieur de Chorora (Ethiopie): Murinae, Dendromurinae et conclusions. Paleovertebrata, 30:89–109.

———. 2006. The Late Pliocene locality of Ahl al Oughlam, Morocco: Vertebrate fauna and interpretation. Transactions of the Royal Society of South Africa, 61:97–101.

Geraads, D., Z. Alemseged, and H. Bellon. 2002. The Late Miocene mammalian fauna of Chorora, Awash basin, Ethiopia: systematic, biochronology and the ^{40}K-^{40}Ar ages of the associated volcanics. Tertialy Research, vol. 21:113− 122.

Greenwood, M. 1955. Fossil Hystricoidea from the Makapan Valley, Transvaal. Palaeontologica, Africana 3:77–85.

———. 1958. Fossil Hystricoidea from the Makapan valley, Transvaal. *Hystrix makapanensis* nom. nov. for *Hystrix major* Greenwood. Annals and Magazine of Natural History, 13:365.

Gradstein, F. M., F. M. Ogg, M. D. Schmitz, and G. M. Ogg (eds.). 2012. The Geological Time Scale 2012. Elsevier, Boston, 1578 pp.

Haile-Selassie, Y., G. Woldegabriel, T. D. White, R. L. Bernor, D. Degusta, P. R. Renne and F. C. Howell 2004. Mio-Pliocene mammals from the Middle Awash, Ethiopia. Geobios, 37:536–552.

Handa, N., M. Nakatsukasa, Y. Kunimatsu, and H. Nakaya. 2017a: A new Elasmotheriini (Perissodactyla, Rhinocerotidae) from the upper Miocene of Samburu Hills and Nakali, northern Kenya. Geobios, vol. 50:197–209.

———. 2017b: Additional specimens of *Diceros* (Perissodactyla, Rhinocerotidae) from the Upper Miocene Nakali Formation in Nakali, central Kenya. Historical Biology, DOI: 10.1080/08912963.2017.1362560.

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

Harris, J. M., M. G. Leakey, T. E. Cerling, and A. J. Winkler. 2003. Early Pliocene tetrapod remains from Kanapoi, Lake Turkana Basin, Kenya; pp. 39–113 in J. M. Harris and M. G. Leakey (eds.), Contributions in Science, 498.

Harrison, T. 2011. Introduction: The Laetoli Hominins and Associated Fauna; pp. 1–14 in Harris, T. (ed.), Paleontology and Geology of Laetoli: Human Evolution in Context. Volume 2: Fossil Hominins and the Associated fauna, Springer, New York,

Hill, A. 1999. The Barongo Basin, Kenya: From Bill Bishop to BPRP; pp. 85–97 in P. Andrews, and P. Banham (eds.), Late Cenozoic Environments and Hominid Evolution: A Tribute to

Bill Bishop, London: Geological Society.

Hinton, M. A. C. 1933. Diagnoses of new genera and species of rodents from IndianTertialy deposits. Annals and Magazine of Natural History, 10:620–622.

Hlusko, L. J. 2007. Earliest evidence for *Atherurus* and *Xenohystrix* (Hystricidae, Rodentia) in Africa, from the late Miocene site of Lemudong'o, Kenya. Kirtlandia, 56:86–91.

Hopley, P. J., A. G. Latham, and J. D. Marshall. 2006. Palaeoenvironments and palaeodiets of mid-Pliocene micromammals from Makapansgat Limeworks, South Africa: a stable isotope and dental microwear approach. Palaeogeography, Palaeoclimatology, Palaeoecology, 233(3-4):235-251.

Ishida, H., and 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 planétes, vol. 325:823− 829.

Jacobs, L. L., L. J. Flynn, W. R. Downs and J. C. Barry 1990. Quo vadis, *Antemus*? the Siwalik muroid record; pp. 573–586 in E. H. Lindsay, V. Fahlbusch and P. Mein (Eds.), European Neogene mammal chronology. Plenum Press, New York.

Jaeger, J. J., J. Michaux and M. Sabatier. 1980. Premiers donnees sur les rongeurs de la formation de Ch'orora (Athiopie) d'age Miocene superior. I : Thryonomyides. Paleovertebrata, Montpellier, mémoire Jubilaire R. Lavocat, 365–374.

Kaakinen, A. 2005. A long terrestrial sequence in Lantian : A Window into the late Neog ene palaeoenvironments of northern China. Ph. D. diss., Unibersity of Helsinki, 49 pp.

Kaakinen, A. and J. P. Lunkka. 2003. Sedimentation of the late Miocene Bahe formation and its implications for stable environments adjacent to Qinling mountains in Shaanxi, China. Journal of Asian Earth Sciences 22 :67–78.

Katoh, S., Y. Beyene, T. Itaya, H. Hyodo, M. Hyodo, K. Yagi, C. Gouzu, G. WoldeGabriel, W. K. Hart, S. H. Ambrose, H. Nakaya, R. L. Bernor, J. -R. Boisserie, F. Bibi, H. Saegusa, T. Sasaki, K. Sano, B. Asfaw, and G. Suwa, 2016. New geological and palaeontological age constraint for the gorilla–human lineage split. Nature, vol. 530:215–218.

Kawamura, Y. and H. Nakaya, 1984. Thryonomyid rodent from the Late Miocene Namurungule Formation, Samburu Hills, northern Kenya. African Study Monographs, Supplementary Issue 2:133–139.

———. 1987. Additional materials of the Late Miocene rodents from the Namurungule Formation in the Samburu Hills, northern Kenya. African Study Monographs, Supplementary Issue, 5:131–139.

Kingdon. J. 1974. East African Mammals: Vol. IIB. Hares and Rodents. University of Chicago, 704 pp.

———. J. 1997. The Kingdon Field Guide to African Mammals. Academic Press, San Diego, 464 pp.

Kingston, J. D. 1999. Isotopes and environments of the Baynunah Formation, Emirate of Abu Dhabi, United Arab Emirates; pp. 354–372 in P. J. Whybrow, and A. Hill (eds.), Vertebrate fossils of the Arabian Peninsula, Yale University Press., New Haven and London.

Kraatz, B. P., F. Bibi, A. Hill, and M. Beech. 2013. A new fossil thryonomyid from the Late Miocene of the United Arab Emirates and the origin of African cane rats. Naturwissenschaften, 100:437–449.

Kretzoi, M. 1951. The *Hipparion* fauna from Csákvár. *Földtani Közlöny*, 81:384–417.

Kunimatsu, Y., M. Nakatsukasa, T. Sakai, M. Saneyoshi, Y. Sawada, and H. Nakaya. 2017a. A newly discovered galagid fossil from Nakali, an early Late Miocene locality of East Africa. Journal of Human Evolution, vol. 105, p. 123–126.

Kunimatsu Y., M. Nakatsukasa, Y. Sawada, T. Sakai, M. Hyodo, T. Itaya, H. Nakaya, H. Saegusa, A. Mazurier, M. Saneyoshi, H. Tsujikawa, A. Yamamoto and E. Mbua. 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 of the United States of America, 104:19220–19225.

Kunimatsu, Y., M. Nakatsukasa, Y. Sawada, T. Sakai, M. Saneyoshi, H. Nakaya, A. Yamamoto, and E. Mbua. 2016. A second hominoid species in the early Late Miocene fauna of Nakali (Kenya). Anthropological Science, vol. 124:75–83.

Kunimatsu, Y., Y. Sawada, T. Sakai, M. Saneyoshi, H. Nakaya, A. Yamamoto, and M. Nakatsukasa. 2017b. The latest occurrence of the nyanzapithecines from the early Late Miocene Nakali Formation in Kenya, East Africa. Anthropological Science, vol. 125:45–51.

Kullmer, O. 2008. The fossil Suidae from the Plio-Pleistocene Chiwondo Beds of northern Malawi Africa. Journal of Vertebrate Palaeontology 28:208–216.

Landry, S. O. 1957. The interrelationships of the New and Old World hystricomorph rodents. University of Califolnia Publications, Zoology, 56 (1):1–118.

Lavocat, R. 1973. Les Rongeurs du Miocene d'Afrique Orientale. I. Miocene Inferieur. Memoires et Travaux de l'Ecole Pratique des Hautes Etudes, Institut de Montpellier. 1:1–284.

———. 1978. Rodentia and Lagomorpha; pp. 69–89 in V. J. Maglio and H. B. S. Cooke (eds.), Evolution of African Mammals. Harvard University Press, Cambridge.

Leakey, M. G., C. S. Feibel, R. L. Bernor, J. M. Harris, T. E. Cerling, K. M. Stewart, G. W. Storrs, A. Walker, L. Werdelia, A. J. Winkler. 1996. Lothagam: A record of faunal change in the Late Miocene of East Africa. Journal of Vertebrate Paleontology, 16(3):556–570.

Leakey, M. G., C. S. Feibel, I. McDougall, A. Walker. 1995. New four-million-year-old hominid species from Kanapoi and Allia Bay, Kenya. Nature, 376:565–571.

Leakey, M. G., C. S. Feibel, I. McDougall, C. Ward, and A. Walker. 1998. New specimens and confirmation of an early age for *Australopithecus anamensis*. Nature, 393(7):62–66.

López-Antoñanzas, R, L., L. J. Flynn, and F. Knoll. 2013. A comprehensive phylogeny of extinct and extant Rhizomyinae (Rodentia): evidence for multiple intercontinental dispersals. Cladistics 29.3:247–273.

López-Antoñanzas, R. L., and S. Sen. 2005, New species of *Paraphiomys* (Rodentia, Thryonomyidae) from the lower Miocene of As-Sarrar, Saudi Arabia. Palaeontology, 48:223–233.

López-Antoñanzas, R L., S. Sen, and P. Mein. 2004. Systematics and phylogeny of the cane rats (Rodentia: Thryonomyidae). Zoological Journal of the Linnean Society, 142:423–444.

Maguire, J. M. 1976. A Taxonomi and ecological study of the living and fossil Hystricidae with particular reference to southern Africa. Unpublished PhD thesis, University of the Witwatersrand. 1054 pp.

Matsui, T., Konomatsu, M., Sakai, T., Sawada, Y., Nakaya, H., Kunimatsu, Y. and Nakatsukasa, M., 2008: Pollen and paleoenvironments of the early Late Miocene Nakali Formation, central Kenya Rift (preliminary report). Abstracts of the regular meeting of African Study Society of Japan, 8. (in Japanese)

Manthi, F. K. 2006. The Pliocene micromammalian fauna from Kanapoi, northwestern Kenya, and its contribution to understanding theenvironment of Australopithecus anamensis. Unpublished PhD dissertation, University of Cape Town, South Africa, 231 pp.

———. 2007. Preliminary review of the rodent fauna from Lemudong'o, southwest Kenya and its implication to the Late Miocene Paleoemvironments. Kirtlandia, 56: 92–105.

Marivaux, L., M. Vianey-Liaud, J. L. Welcomme, and J. J. Jaeger. 2002. The role of Asia in the origin and diversification of hystricognathous rodents. Zoologica Scripta, 31:225–239.

Masini, F., and L. Rook. 1993. *Hystrix primigenia* (Mammalia, Rodent) from the Late Messinian of the Monticino gypsum quarry (Faenza, Italy). Bollettino della Società Paleontologica Italiana, 32:79–87.

McDougall, I., and F. H. Brown. 2008. Geochronology of the pre-KBS Tuff sequence, Omo Group, Turkana Basin. Journal of the Geological Society, London, 165:549–562.

McDougall, I., and C. S. Feibel. 1999. Numerical age control for the Miocene-Pliocene succession at Lothagam, a hominoid-bearing sequence in the northern Kenya Rift. Journal of the Geological Society (London), 156:731–745.

Mein, P., and M. Freudenthal. 1971. Les Cricetidae (Mammalia, Rodentia) du Néogène Moyen de Vieux-Collonges. Partie 1: Le genre Cricetodomn Lartet, 1851. Scripta Geologica, 5:1–51. (in French)

Mein, P., and M. Pickford. 2006. Lat e Miocene micromammals from the Lukeino Formation (6.1 to 5.8 Ma), Kenya. Bulletin Mensuel de la Societe Linneenne de Lyon, 75 (4):183–223.

———. 2010. Vallesian rodents from Sheikh Abdallah, Western Desert, Egypt. Historical Biology, 22:224–259.

Mein, P., M. Pickford, and B. Senut. 2000. Late Miocene micromammals from the Harasib karst deposits, Namibia: Part 1. Large muroids and non-muroid rodents. Communications of the Geological Survey of Namibia, 12:375–390.

Monadjem, A., P. J. Taylor, C. Denys, and F. P. D. Cotterill. 2015. Rodents of Sub-Saharan Africa; A Biogeographic and Taxonomic Synthesis. Walter de Gruyter GmbH, Germany, 1092p.

Morales, J. and Pickford, M., 2006: A large Percrocutid Carnivore from the Late Miocene (ca. 10–9 Ma) of Nakali, Kenya. Annales de Paléontologie, vol. 92:59‐ 366.

Munthe, J. 1987. Small-mammals from the Pliocene Sahabi Formation of Libya; pp. 135–144 in N. T. Boaz, A. El-Arnauti, A. W. Gaziry, J. de Heinzelin, and D. D. Boaz (eds.), Neogene Paleontology and Geology of Sahabi. Liss, New York.

Nakatsukasa, M., 2009. Paleoanthropological research in Nakali, Kenya. Anthropological Science (Japanese Series), vol. 117:111– 117. (in Japanese)

Nakatsukasa, M., Y. Kunimatsu, Y. Sawada, T. Sakai, H. Hyodo, T. Itaya, M. Saneyoshi, H. Tsujikawa, and E. Mbua. 2006. Late Miocene primate fauna in Nakali, central Kenya. American Journal of Physical Anthropology, vol. 129:136.

Nakatsukasa, M., E. Mbua, Y. Sawada, T. Sakai, H. Nakaya, W. Yano, and Y. Kunimatsu. 2010. Earliest colobine skeletons From Nakali, Kenya. American Journal of Physical Anthropology. 143:365–382.

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

Nakaya, H., M. Onodera, E. Yamada, Y. Kunimatsu, M. Nakatsukasa, and T. Sakai. 2012. Mammalian fauna and its paleoenvironments of the Late Miocene Samburu Hills and Nakali, Rift Valley, Kenya. Abstracts of Japan Geoscience Union Meeting 2012, BPT27-02.

Nanda, A. C. 2002. Upper Siwalik Mammalian faunas of India and associated events. Journal of Asian Earth Sciences, 21:47–58.

Norris, R. W. 2017. The family Spalacidae; pp. 108–143 in Wilson, D. E. and R. A. Mittermeier. (eds.), Handbook of Mammals of the World. Vol. 7. Rodents II. Lynx Edicions, Barcelona.

Nowak, R. M. 1999. Walker's Mammals of the World. 6th ed. Johns Hopkins University Press, Baltimore, 1936 pp.

Ogg. J. G., G. M. Ogg, and F. M. Gradstein. 2016. A Concise Geologic Time Scale 2016. Elsevier, Boston, 234 pp.

Onodera, M., Y. Kunimatsu, M. Nakatsukasa, E. Yamada, and H. Nakaya. 2011. Late Miocene rodent fossils from the Nakali Formation, Kenya and its paleoenvironment. Abstracts with programs of the Palaeontological Society of Japan, 19. (in Japanese)
Available from: http://www.palaeo-soc-japan.jp/events/160_2011.pdf.

Partridge, T.C., A. G. Latham, and D. Heslop. 2000. Appendix on magnetostratigraphy of Makapansgat, Sterkfontein, Taung and Swartkrans; pp.126–129 in T. C. Partridge and R. R. Maud (eds.), The Cenozoic of Southern Africa. Oxford University Press, Oxford.

Patnaik, R. 1997. New Murids and Gerbillids (Rodentia, Mammalia) from Pliocene Siwalik Sediments of India. Palaeovertebrata 26:129–165.

Patnaik, R. 1995. Micromammal-based palaeoenvironment of Upper Siwaliks exposed near Village Saketi, H. P. Journal of the Geological Society of India, 46:429–437.

———. 2013. Indian Neogene Siwalik Mammalian Biostratigraphy, An Overview; pp. 423–444 in X. Wang, L. J. Flynn, and M. Fortelius (eds.), Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology. Columbia University Press, New York.

Pickford, M. 1981. Preliminary Miocene mammalian biostratigraphy for Western Kenya. Journal of Human Evolution, vol. 10:73− 97.

Pickford, M., 1983. Sequence and environments of the Lower and Middle Miocene hominoids of western Kenya; pp. 421− 439 in Ciochon, R. L. and Corruccini, R. S. (eds.), New interpretations of ape and human ancestry, Plenum Press, New York and London.

———. 1986. Cainozoic paleontological sites of western Kenya. Münchner Geowissenschaftliche

Abhandlungen, vol. 8:151.

———. 1990. Some fossiliferous Plio-Pleistocene cave systems of Ngamiland, Botswana. Botswana Notes and Records, 22:1–15.

Pickford, M., T. Fernandes, and S. Aco. 1990. Nouvelles découvertes de remplissages de fissures à primates dans le «Planalto da Humpata», Huíla, Sud de l'Angola, Comptes rendus de l'Académie des Sciences, 310:843–848. (in French with English abstract)

Pickford, M. and P. Mein. 1988. The discovery of fossiliferous Plio-Pleistocene cave fillings in Ngamiland, Botswana. Comptes Rendus de l'Academie des Sciences, Paris, 307:1681–1686.

Pickford, M., P. Mein, and B. Senut. 1992. Primate bearing Plio-Pleistocene cave deposits of Humpata, southern Angola. Human Evolution, 7(1):17–33.

Pickford, M., and J. Morales. 1994. Biostratigraphy and papaeobiogeography of East Africa and the Iberian Peninsula. Palaeogeography, Palaeoclimatology, Palaeoecoloy, vol. 112:297− 322.

Pickford, M., B. Senut, S. Musalizi, E. Musiime. 2014. Osteology of *Afrocricetodon songhori* Lavocat, 1973, from Napak, Early Miocene, Uganda: Keeping a low profile. Geo-Pal Uganda, 9:1–22.

Pickford, M., H. Wanas, P. Mein and H. Soliman. 2008. Humid conditions in the Western Desert of Egypt during the Vallesian (Late Miocene). Bulletin, Tethys Geological Society, 3:63–79.

Qiu, Z. D., S. H. Zheng and Z. Q. Zhang. 2003.Late Miocene micromammals from the Bahe Formation, Lantian, China: pp. 443–453. in J. W. F. Reumer, and W. Wessels (eds.), Distribution and Migration of Tertiary Mammals in Eurasia, DEINSEA 10.

———. 2004. Gerbillids from the Late Miocene Bahe Formation, Lantian, Shaanxi. Vertebrata PalAsiatica 42(7):193–204.

Renne, P. R., G. WoldeGabriel, W. K. Hart, G. Heiken, and T. D. White. 1999. Chronostratigraphy of the Miocene–Pliocene Sagantole Formation, Middle Awash Valley, Afar rift, Ethiopia. Geological Society of America Bulletin, 111(6):869–885.

Sabatier, M. 1978. Un nouveau *Tachyoryctes* (Mammalia, Rodentia) du bassin Pliocene de Hadar (Ethiopie). Geobios, 11(1):95–99.

———. 1982. Les rongeurs du site Pliocene a hominides de Hadar (Ethiopie). Palaeovertebrata 12:1–56.

Saegusa, H., H. Nakaya, Y. Kunimatsu, M. Nakatsukasa, and H. Tsujikawa, 2006. Earliest elephantid remains from Nakali, Kenya. Abstracts with Programs, The 2006 Annual Meeting, The Palaeontological Society of Japan, 19. (in Japanese)

Available from: http://www.palaeo-soc-japan.jp/events/2006.pdf.

Sakai, T., M. Saneyoshi, S. Tanaka, Y. Sawada, M. Nakatsukasa, E. Mbua, and H. Ishida. 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*, vol. 342, p. 109– 127.

Sakai, T., M. Saneyoshi, Y. Sawada, M. Nakatsukasa, Y. Kunimatsu, and E. Mbua. 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); pp. 83– 108 in Y. Itoh (ed.), Mechanism of sedimentary basin formation-multidisciplinary approach on active plate margins. Intech, Rijekla.

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

Sen, S. 1983. Rongeurs et lagomorphes du gisement pliocène de Pul-e Charkhi, bassin de Kabul, Afghanistan. Bulletin du Museum National d'Histoire Naturelle, 5:33–74.

———. 2001a. Early Pliocene porcupine (Mammalia, Rodentia) from Perpignan, France: a new systematic study. *Geodiversitas*, 23(2): 303–316.

———. 2001b. Rodents and Insectivores from the Upper Miocene of Molayan, Afghanistan. Palaeontology, Vol. 44(5):913–932.

Senut, B., M. Pickford, P. Mein, G. Conroy, and J. Van Couvering. 1992. Discovery of 12 new Late Cainozoic fossiliferous sites in paleokarst of the Otavi Mountains, Namibia. Comptes Rendus de l'Academie des Sciences, Paris, Serie II, 314:727–733.

Sen, S. and D. B. Kovatchev. 1987. The porcupine *Hystrix primigenia* (Wagner) from the late Miocene of Bulgaria. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen. Series B. Palaeontology, geology, physics, chemistry, anthropology, 90(4):317–331.

Steininger, F. F. 1999. Chronostratigraphy, Geochronology and Biochronology of the Miocene "European Land Mammal Mega-Zones (ELMMZ)" and the Miocene "Mammal-Zones (MN-Zones)"; pp. 9–24 in: G. Rössner, and K. Heissig (eds.), The Miocene Land Mammals of Europe. Munich, Dr. Friedrich Pfeil, München.

Su, D. F., S. H. Ambrose, D. Degusta, and Y. Haile-Selassie. 2009. Paleoenvironment; pp.521–547 in Y. Haile-Selassie and G. Woldegabriel (eds.), *Ardipithecus kadabba*: Miocene Evidence from the Middle Awash, Ethiopia. University of California Press, Berkeley.

Schrenk F., T. G. Bromage, C. G. Betzler, U. Ring, and Y. Juwayeyi. 1993. Oldest Homo and Pliocene biogeography of the Malawi Rift. Nature, 365:833–836.

Suwa, G., Y. Beyene, H. Nakaya, R. L. Bernor, J. -R. Boisserie, F. Bibi, S. H. Ambrose, K. Sano, S. Katoh, and B. Asfaw. 2015. Newly discovered cercopithecid, equid and other mammalian fossils from the Chorora Formation, Ethiopia. Anthropological Science, vol. 123:19− 39.

Suwa G., R. T. Kono, S. Katoh S, B. Asfaw, and Y. Beyene. 2007. A new species of great ape from the late Miocene epoch in Ethiopia. Nature, 448: 921–924.

Taieb, M., and J. J. Tiercelin. 1979. Sedimentation pliocene et paleoenvironnements de rift; exemple de la formation a Hominides d'Hadar (Afar, Ethiopie). Bulletin de la Société Géologique de France, S7-XXI (3):243–253.

Tanabe, Y., M. Onodera, M. Nakatsukasa, Y. Kunimatsu, and H. Nakaya. 2013. The Late Miocene Rodent Fauna from Nakali Formation, Northern Kenya. *Supplement to Journal of Vertebrate Paleontology*, 33, 223.

Tanabe, Y., M. Onodera, and H. Nakaya, 2014, The Late Miocene rodent fauna from the Nakali Formation, Northern Kenya. Abstracts of the Annual Meeting of the Geological Society of Japan, The 121st Annual Meeting, 284. (*in Japanese*)
Available from: https://www.jstage.jst.go.jp/article/geosocabst/2014/0/2014_554/_pdf.

Tanabe, Y., M. Onodera, M. Nakatsukasa, Y. Kunimatsu, and H. Nakaya. in press. A new can rat (Rodentia, Thryonomyidae) from the Upper Miocene Nakali Formation, northern Kenya. Journal of the Geological Society of Japan.

Tsubamoto, T., Y. Kunimatsu, H. Nakaya, T. Sakai, M. Saneyoshi, E. Mbua, and M. Nakatsukasa, 2015. New specimens of a primitive hippopotamus, Kenyapotamus coryndonae, from the Upper Miocene Nakali Formation, Kenya. Journal of the Geological Society of Japan, vol. 121:153–159.

Tsubamoto, T., Y. Kunimatsu, T. Sakai, M. Saneyoshi, D. Shimizu, N. Morimoto, H. Nakaya, and M. Nakatsukasa. 2017. Listriodontine suid and tragulid artiodactyls (Mammalia) from the upper Miocene Nakali Formation, Kenya. Paleontological Research, vol. 21:347–357.

Tsubamoto, T., Y. Kunimatsu, T. Sakai, M. Saneyoshi, D. Shimizu, N. Morimoto, H. Nakaya, N. Handa., Y. Tanabe, F. K. Manthi, and M. Nakatsukasa, 2020., new species of *Nyanzachoerus* (Mammalia, Artiodactyla, Suidae, Tetraconodontinae) from the upper Miocene Nakali Formation, Kenya. Paleontological Research, vol. 24:41–63.

Tsujikawa, H., 2005. The updated late Miocene large mammal fauna from Samburu Hills, northern Kenya. African Study Monographs, Supplementary Issue, no. 32:1–50.

Ünay, E., H. de Bruijn, and G. sarac. 2003a. Apreliminary zonation of the continental Neogene of Anatolia based on rodents; pp. 539–547 in J. W. F. Reumer, and W. Wessels (eds.), Distribution and Migration of Tertiary Mammals in Eurasia, DEINSEA 10.

———. 2003b. The Oligocene rodent record of Anatolia: review; pp. 531–537 in J. W. F. Reumer, and W. Wessels (eds.), Distribution and Migration of Tertiary Mammals in Eurasia, DEINSEA 10.

Unger, P. S. 2010, Mammal Teeth. Origin, Evolution, and Diversity. Johns Hopkins University Press, Baltimore, MD, 304 pp.

Ungar, P. S., J. R. Scott, S. C. Curran, H. M. Dunsworth, W. E. H. Harcourt-Smith, T. Lehmann, F. K. Manthi, and K. P. McNulty. 2012. Early Neogene environments in east Africa: Evidence from dental microwear of tragulids. Palaeogeography, Palaeoclimatology, Palaeoecology, 342:84–96.

Uno, K., T. E. Cerling, J. M. Harris, Y. Kunimatsu, M. G. Leakey, M. Nakatsukasa, and H. Nakaya. 2011. Late Miocene to Pliocene carbon isotope record of differential diet change among East African herviores. Proceedings of the National Academy of Sciences, United States of America, vol. 108:6509− 6523.

Van Weers, D. J. 2002. *Atherurus karnuliensis* Lydekker, 1886, a Pleistocene brush-tailed porcupine from India, China and Vietnam. Paläontologische Zeitschrift, 76(1):29–33.

———. 2005. A taxonomic revision of the Pleistocene *Hystrix* (Hystricidae, Rodentia) from Eurasia with notes on the evolution of the family. Contributions to Zoology, 74(3/4):301–312.

Van Weers, D. J. and P. Montoya. 1996. Taxonomy and stratigraphic record of the oldest European porcupine *Hystrix parvae* (Kretzoi, 1951). In Proceedings-Koninkijke Nederlandse Akademie Van Wetenssch, 99(1-2):131–141.

Vignaud, P., P. Duringer, H. T. Mackaye, A. Likius, C. Blondel, J. -R. Boisserie, L. de Bonis, V. Eisenmann, M. –E. Etienne, D. Geraads, F. Guy, T. Lehmann, N. Lopez-Martines, C. Mourer-Chauvire, O. Otero, J. –C. Rage, M. Schuster, L. Viriot, A. Zazzo and M. Brunet. 2002. Geology and paleontology of the Upper Miocene Toros-Menalla hominid locality, Chad. Nature 418:152–155.

Werdlin, L. 2010. Chronology of Neogene Mammal Localities; pp.27–43 in L. Werdelin and W. J. Sanders (eds.), Cenozoic Mammals of Africa, University of Palifornia Press, Berkeley, Los Angeles, London.

Wessels, W. 1998. Gerbillidae from the Miocene and Priocene of Europe. Mitteilungen der

Bayerischen Staatssammlung Fuer Palaeontologie und Historische Geologie 38:187–207.

———. 2003. Miocene small Mammals from Jebel Zelten, libya. Coloquios de Paleontologia, Vol. Ext. 1:699–715.

———. 2009. Miocene rodent evolution and migration —Muroidea from Pakistan, Turkey and Northern Africa—. Geologica Ultraiectina, Mededelingen van de Faculteit Geowetenschappen departement Aardwetenschappen Universiteit Utrecht, No. 307, 290 pp.

Wesselman, H. B. 1984. Omo micromammals: Systematics and Paleoecology of early man sites from Ethiopia. Contributions to Vertebrate Evolution 7:1–219.

Wesselman, H. B., M. T. Black and M. Asnake. 2009. Small mammals; pp.105–133 in Y. Haile-Selassie and G. Woldegabriel (eds.), *Ardipithecus kadabba*: Miocene Evidence from the Middle Awash, Ethiopia. University of California Press, Berkeley.

Winkler, A. J. 1990. Systematics and biogeography of Neogene rodents from the Baringo Distinct, Kenya. Unpublished PhD dissertation, Southern Methodist University, Dallas, 172 pp.

———. 1994. The middle/upper Miocene dispersal of major rodent groups between southern Asia and Africa. National Science Museum Monographs, 8:173–184.

———. 2002. Neogene paleobiogeography and East African paleoenvironments: contributions from the Tugen Hills rodents and lagomorphs. Journal of Human Evolution, 42:237–256.

———. 2003. Rodents and lagomorphs from the Miocene and Pliocene of Lothagam, northern Kenya; pp. 169–198 in M. G. Leakey and J. M. Harris (eds.) Lothogam, the Dawn of Humanity in Eastern Africa. Columbia University Press, New York.

Winkler, A. J., C. Denys, and D. M. Avery. 2010. 17. Rodentia; pp.263–304 in L. Werdelin and W. J. Sanders (eds.), Cenozoic Mammals of Africa, University of Palifornia Press, Berkeley, Los Angeles, London.

WoldeGabriel, G., Y. Haile-Selassie, P. R. Renne, W. K. Hart, S. H. Ambrose, B. Asfaw, G. Helken, and T. White. 2001. Geology and palaeontology of the late Miocene Middle Awash valley, Afar rift, Ethiopia. Nature, 412(6843):175–178.

Wood, A. E. and R. W. Wilson. 1936. A suggested nomenclature for the cusps of the cheek teeth of rodents. *Journal of Paleontology*, 388–391.

Woods, C. A. 1984, Hystricognath Rodents; pp. 389–446 in S. Anderson, and J. K. Jones (eds.), Order and Families of Recent Mammals of the World, John Wiley and Sons, New York.

Woods, C. A. and C. W. Kilpatrick. 2005. Infraorder Hystricognathi; pp. 1538–1600 in D. E. Wilson and D. M. Reeder (eds.), Mammals Species of the World. 3rd ed. Jhons Hopkins University Press, Baltimore.

Zhang, Z. Q., A. W. Gentry, A. Kaakinen. 2002. Land mammal faunal sequence of the late Miocene of China: new evidence from Lantian, Shaanxi Province. Vertebrata PalAsiatica, 40(3) :166–178.

Zhang, Z. Q., A. Kaakinen, L. P. Liu, J. P. Lunkka, S. Sen, W. A. Gose, Z. -D. Qiu, S. -H. Zheng, and M. Fortelius. 2013. Mammalian biochronology of the Late Miocene Bahe formation; pp. 187–202 in X. Wang, L. J. Flynn, and M. Fortelius (eds.), Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology. Columbia University Press, New York.

Appendix 1. List of the fossil localities of *Abudhabia* and its paleoenvironments.

No.	Taxa	Contry	Locality	Horizon	Ma	Dating	Paleoenvironment	References (Fossil record)
1	*A* . sp. (new species)	Turkey	Altinta	—	11.1–9.8 (MN9)	Biostratigraphy (Unay et al., 2003a, b; de Bruijn et al., 2013)	—	de Bruijn et al. (2013) listed only
2	*A.* sp.	Kenya	Nakali	Nakali Fm.	ca. 10 Ma	K/Ar and paleomagnetic data (Kunimatsu et al., 2007)	forest with woodland and river and lake under seasonal climate (Kunimatsu et al., 2007; Nakatsukasa et al., 2010; Sakai et al., 2010, 2013; Uno et al., 2011; Nakaya et al., 2012)	this study
3	*A. baheenensis*	China	Lantian area	Bahe Fm.	9.98–8.07	Paleomagne (Kaakinen and Lunkka, 2003; Kaakinen, 2005; Zhang et al., 2013)	arid and open euvironment (Qiu et al., 2004)	Zhang et al. (2002) as *Abudhabia* sp. nov. Qiu et al. (2003) as *Abudhabia* sp. nov. Qiu et al. (2004)
4	*A. pakistanensis*	Pakistan	Potwar Plateau	Dhok Pthan Fm.	8.6	Paleomagne (Flynn and Jacobs, 1999)	—	Flynn and Jacobs (1999) Flynn and Wessels (2013)
5	*A. radinskyi*	Afghanistan	Kabul	Lataband series	Late Miocene (Early–Middle Turolian)	Biostratigraphy (Sen, 2001b)	—	Flynn et al. (2003)
6	cf. *A.* sp.	Ethiopia	Chorora	Chorora Fm. (Upper Chorora)	ca. 7.5–7.0	K/Ar (Suwa et al., 2015)	wooded with more open (savanna-like) habitat (Geraads et al., 2002; Cote, 2004)	Suwa et al. (2015)
7	*A. baynunensis*	United Arab Emirates	Al Gharba	Baynunah Fm.	7.5–6.5	Biochronology (Bibi et al., 2013)	more woodland environment flanking a river sytem (Paleosol; Kingdon, 1999)/ more open glasslands or wooded grasslands distal to the fluvial environments (enamel isotopic datasets; Kingdon, 1999)	de Bruijn and Whybrow (1994) de Bruijun (1999) (added materials)
8	*A. yardangi*	Libya	As-Sahabi	Sahabi Fm.	ca. 7 Ma	Biostratigraphy (Boaz, 2008; Boaz et al., 2008; Werdlin, 2010)	arid zone behind the better-vegetated and probably forested shoreline (Manthe, 1987)	Manthe (1987) as *Protatera yardangi* Flynn et al. (2003) as *Abudhabia yardangi*
9	*A.* sp.	Kenya	Lothagam	Upper Nawata	5.23 Ma	Sdimentation rate and paleomagne (McDougall and Feibel, 1999)	C4 grass, more open (more grass lands) (Bobe, 2011)	Winkler (2003)
10	*A. kabulense*	Afghanistan	Pul-e Charkhi	—	5	Biochronology (Brandy, 1981; Sen, 1983, 2001b)	open steppe habitat or herbaceous savanna with the presence of gallery forests (Sen, 1983)	Brandy (1979) as *Protatera* sp. Brandy (1981) as *Protatera* sp. Sen (1983) as *Protatera kabalense* Wessels (1998) as *Abudhabia kabalense*
11	*A* cf. *A kabulense*	India	Moginand and Kanthro	—	4.18–2.58	Paleomagne (Nanda, 2002; Dannell, 2004; Dannell et al., 2006; Patnaik, 2013)	pond, pond-bank, bushland and grassland communities (Patnaik, 1995)	Patnaik (1997)

Appendix 2. List of the fossil localities of the Neogene hystricid of Africa and its paleoenvironments.

No.	Taxa	Contry	Locality	Horizon	Ma	Dating	Paleoenvironment	References (Fossil record)
	Atherurus							
1	*A.* sp.	Egypt	Sheikh Abdallar	—	11–10	Biochronology (Pickford et al., 2008)	humid paleoclimate (Pickford et al., 2008)	Pickford et al. (2008, 2010)
2	*A.* sp.	Kenya	Lemudong'o	—	6.12–6.08	^{40}Ar/^{39}Ar (Deino and Ambrose, 2007)	forested and mesic micro-environments dominated over open grassland/woodland habitats (Manthi, 2007)	Hlusko (2007)
3	*A. garbo*	Ethiopia	Middle Awash	Adu-Asa Fm.	5.7	^{40}Ar/^{39}Ar dates, paleomagnetic data, and tephrachemistry (WoldeGabriel et al. 2001; Renne, 1999)	riparian woodland and floodplain grassland/ Arid savanna (vertebrate fossils; Su et al., 2009)	Haile-Salassie et al. (2004) Wesselman et al. (2009)
	Hystrix							
4	*H* . sp. (small)	Kenya	Lothagam	Lower Nawata	ca. >7.44	^{40}Ar/^{39}Ar (McDougall and Feibel, 1999)	mixed woodlands/ open country (Cote, 2004)	Winkler (2003)
5	*H* . sp.	Algeria	Manacer (=Marceau)	—	7.1–5.3? (Cote, 2004)	uncertain	—	Arambourg (1959) Thomas and Petter (1986)
6	*H.* sp.	Chad	Tros-Menalla	—	7–6	Biochronology (Vignaud et al. 2002)	mosaic of environments from gallery forest at the edge of a lake area to a dominance of large savannah and grassland (Vignaud et al. 2002)	Vignaud et al. (2002)
7	*H* . sp.	Kenya	Tugen Hill	Lukeino Fm.	6.2–5.6	K/Ar (Hill, 1999)	a mix of woodlands and more open habitat/ a Savanna habitat (Winkler, 2002)	Winkler (2002) Mein and Poickford (2006)
8	*H* . sp.	Kenya	Lemudong'o	—	6.12–6.08	^{40}Ar/^{39}Ar (Deino and Ambrose, 2007)	forested and mesic micro-environments dominated over open grassland/woodland habitats (Manthi, 2007)	Hlusko (2007)
9	*H* . sp.	Ethiopia	Middle Awash	Adu-Asa Fm.	5.7	^{40}Ar/^{39}Ar dates, paleomagnetic data, and tephrachemistry (WoldeGabriel et al. 2001; Renne, 1999)	riparian woodland and floodplain grassland/ Arid savanna (vertebrate fossils; Su et al., 2009)	Haile-Salassie et al. (2004) Wesselman et al. (2009)
10	*H* . sp.	Kenya	Tugen Hill	Cheneron Fm.	5.6–1.6	K/Ar (Hill, 1999)	a mix of woodlands and more open habitat/ a Savanna habitat (Winkler, 2002)	Winkler (2002)
11	*H* . sp.	Ethiopia	Middle Awash (e.g., Aramis)	Adu-Asa Fm.	4.4 (Wesselman and Black, unpubl.)	—	—	WoldeGabriel et al. (1994) Haile-Salassie et al. (2004) Wesselman et al. (2009)
12	*H* . sp.	Kenya	Kanapoi	Kanapoi Fm.	ca. 4	Tuff (Leakey et al., 1995, 1998; Manthi, 2006)	open and dry savannna grasslands with scattered vegitation, riverine woodlands, and gallery forests (Manthi, 2006)	Harris et al. (2003) Manthi (2006)

Appendix 2. Continued.

No.	Taxa	Contry	Locality	Horizon	Ma	Dating	Paleoenvironment	References (Fossil record)
13	*H* . sp. (large)	Kenya	Lothagam	Kaiyumung Mb.	ca. 4.0–3.5	(Leakey, unpubl. data from Winkler, 2003; Leakey et al. 1996)	—	Winkler (2003)
14	*H* . cf. *H. africaeaustralis*	South Africa, western	Makapansgat	—	4–2.6	Geomorphological, faunal and cultural evidence (Maguire, 1976)	—	Greenwood (1955, 1958)
15	*H. major* (=*H. makapanensis*)	South Africa, western	Makapansgat	—	4–2.6	Geomorphological, faunal and cultural evidence (Maguire, 1976)	—	Greenwood (1955, 1958)
16	*H. leakyi*	Tanzania	Laetoli	Upper Laetoli Beds	3.85–3.6	^{40}Ar/^{39}Ar (Harrison, 2011; Deino, 2011)	mosaic of closed woodland, open woodland, shrubland and grassland (various reason; Harrison, 2011)	Denys (1987a, 2011)
17	*H .makapanensis*	Tanzania	Laetoli	Upper Laetoli Beds	3.85–3.6	^{40}Ar/^{39}Ar (Harrison, 2011; Deino, 2011)	mosaic of closed woodland, open woodland, shrubland and grassland (various reason; Harrison, 2011)	Denys (1987a, 2011)
18	*H. makapanensis*	Tanzania	Laetoli	Upper Ndolanya Beds	3.6–2.66	^{40}Ar/^{39}Ar (Harrison, 2011; Deino, 2011)	greater proportion of grassland / closed or open woodlands (Various reason; Herrison, 2011)	Denys (2011)
19	*H* . aff. *cristata*	Ethiopia	Hadar		3.2–3.1	Paleomagne (Taieb and Tiercelin, 1979)	humid conditions excluding any possibility of arid steppe environments/ closed with buhes and forests (Sabatier, 1982)	Ssbatier (1978, 1982)
20	*H. makapanensis*	Ethiopia	—	Shungura Fm. Mb. C, E, F, G	2.8–2.0	Tuff sequense (Feibel et al., 1989; McDougall and Brown, 2008)	xeric > mesic (Wesselman, 1984)	Wesselman (1984)
21	*H. cristata*	Ethiopia	Omo Valley	Shungura Fm. Mb. B, E, F, G, L	3.4–0.8	Tuff sequense (Feibel et al., 1989; McDougall and Brown, 2008)	xeric > mesic (Wesselman, 1984)	Wesselman (1984)
22	*H* . sp.	Morocco	Ahl al Oughlam	—	ca. 2.5	Biostratigraphy (Geraads, 1998b)	shrubland and bushland (Geraads, 2006)	Geraads (1995, 2006)
23	*H.* sp.	Botswana	NW Botswana (Ngamiland: Gcwihaba and Nqumtsa)	—	ca. 2.5	Biostratigraphy (Pickford, 1990)	arid climate / swampy patches bordered by trees nearby / desertic conditions (Pickford, 1990)	Pickford (1990) Pickford and Mein (1988)
24	*H.* sp.	Malawi	Uraha	Chiwondo Beds	2.5–2.3	Faunal correlation with radiometrically dated biostratigraphic units in eastern Africa (Schrenk et al. 1993; Bromage et al., 1995; Kullmer, 2008)	open / absence of moist dense forest (Denys, 2011)	Denys et al. (2011)
25	*H* . sp.	Angola	Humpata	2, unspecified	The late Pliocene to early Pleistocene	Biostratigraphy (Pickford et al, 1992)	semi- arid steppes or wooded and grassland-savannahs (Pickford et al. 1992)	Pickford et al. (1990, 1992)

Appendix 2. Continued.

No.	Taxa	Contry	Locality	Horizon	Ma	Dating	Paleoenvironment	References (Fossil record)
	†*Xenohystrix*							
26	*X*. sp.	Kenya	Lemudong'o	—	6.12–6.08	$^{40}\mathrm{Ar}/^{39}\mathrm{Ar}$ (Deino and Ambrose, 2007)	forested and mesic micro-environments dominated over open grassland/woodland habitats (Manthi, 2007)	Hlusko (2007)
27	*X*. sp.	Ethiopia	Middle Awash	Adu-Asa Fm.	5.7	$^{40}\mathrm{Ar}/^{39}\mathrm{Ar}$ dates, paleomagnetic data, and tephrachemistry (WoldeGabriel et al. 2001; Renne, 1999)	riparian woodland and floodplain grassland/ Arid savanna (vertebrate fossils; Su et al., 2009)	Haile-Salassie et al. (2004) Wesselman et al. (2009)
28	*X. carassidens*	Tanzania	Laetoli	Upper Laetoli Beds	3.85–3.6	$^{40}\mathrm{Ar}/^{39}\mathrm{Ar}$ (Harrison, 2011; Deino, 2011)	mosaic of closed woodland, open woodland, shrubland and grassland (various reason; Harrison, 2011)	Denys (1987a, 2011)
29	*X.* sp.	Ethiopia	Middle Awash localities (e.g., Aramis)	Haradaso Mb. Sagantole Fm.	3.4	$^{40}\mathrm{Ar}/^{39}\mathrm{Ar}$ (Renne et al., 1999)	—	WoldeGabriel et al. (1994) Haile-Salassie et al. (2004) Wesselman et al. (2009)
30	*X. carassidens*	South Africa, western	Makapansgat	Member 3 and 4	3.2–3.1 Ma for Mb. 3 2.5 Ma for Mb. 4	Magnetostratigraphy (Patridge et al., 2000)	more wooded than present day woodland–savanna mosaic (paleodiet; Hoplay et al., 2006)	Greenwood (1955)
31	*X. carassidens*	Ethiopia	Hadar	Hadar Fm. (SH2: 147, 265; DD2: 133)	3.1–2.9	Paleomagne (Taieb and Tiercelin, 1979)	humid conditions excluding any possibility of arid steppe environments/ closed with buhes and forests (Sabatier, 1982)	Ssbatier (1978, 1982) =1978: *X.* cf. *X. crassidens*
32	*X. carassidens*	Ethiopia	Omo Valley	Shungura Fm. Mb. B	ca. 3	Tuff sequense (Feibel et al., 1989; McDougall and Brown, 2008)	a relic lowland forest (Wesselman, 1984)	Wesselman (1984)
	Hystricidae gen. et sp. indet.							
35	Gen et sp. indet.	Kenya	Nakali	Nakali Fm.	ca. 10 Ma	K/Ar and paleomagnetic data (Kunimatsu et al., 2007)	forest with woodland and river and lake under seasonal climate (Kunimatsu et al., 2007; Nakatsukasa et al., 2010; Sakai et al., 2010, 2013; Uno et al., 2011; Nakaya et al., 2012)	this study