A new cane rat (Rodentia, Thryonomyidae) from the Upper Miocene Nakali Formation, northern Kenya

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Introduction

The extant cane rats (Rodentia, Thryonomyidae) are represented by two species, Thryonomys swinderianus (greater cane rat) and T. gregorianus (lesser cane rat), in Sub-Saharan Africa (Woods and Kilpatrick, 2005; Mondjem et al., 2015; López-Antoñanzas, 2016). Thryonomyids were widely distributed over continental Afro-Eurasia during the Miocene but their distribution has been limited to Sub-Saharan since the Pliocene (Winkler, 1994; Flynn and Winkler, 1994; Winkler et al., 2010). In previous studies, it has been considered that the extant genus Thryonomys appeared during the Late Miocene (Winkler et al., 2010; Kraatz et al., 2013), based on the oldest fossil from Lemudong’o, Kenya (Thryonomys sp., ~6 Ma; Manthi, 2007).

The Japan-Kenya Expedition team has conducted palaeontological field-work in Nakali since 2002 and has remarkably expanded Late Miocene (~10 Ma) mammalian fossil collections (Kunimatsu et al., 2007; Nakatsukasa et al., 2010; Handa et al. 2015, 2017a, b; Tsubamoto et al., 2015, 2017, 2020). Of the current ~3,500 specimens, approximately 45% are fossil rodents (Tsubamoto et al., 2020). Onodera et al. (2011) and Tanabe et al. (2013) reported additional specimens of Thryonomys sp. from the Nakali Formation. We re-examined the specimens and determined that they belong to a new Thryonomys species. Here we describe the new species and discuss the temporal range of the genus Thryonomys.

Geologic setting

The Nakali Formation is distributed in the Nakali area along the eastern shoulder of the central Kenyan Rift (Fig. 1). The Nakali Formation is unconformably covered by the Nasorut Formation and characterized by lacustrine, fluvio-lacustrine, and pyroclastic flow deposits (Kunimatsu et al., 2007; Sakai et al., 2013). The majority of fossils have been unearthed from the volcanic mud flow deposits of the Upper Member, e.g., at site NA39 (1°12’6.6″N, 36°22’23.2″E), which yielded Nakalipihecus, and site NA60 (1°11’57”N, 36°23’14.9”E), where the bulk of rodent fossils have been recovered. The 40Ar/39Ar 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 part of the Lower Member and the lowermost part of the Upper Member are correlated with Chron C5n.1r.
Materials and methods

The Nakali *Thryonomy* fossils are housed at the National Museums of Kenya, Nairobi. A total of 17 specimens were collected from the Nakali Formation from 2003 to 2012. Most were recovered by sieving using a 1.0 × 1.0 mm mesh screen at locality NA60. The taxonomic determination was completed based on cheek tooth morphology because cheek teeth are relatively well preserved and morphologically diversified in rodent taxa. The thryonomyid dental terminology and measurements used here are based on Winkler (1992), Marivaux et al. (2002), López-Antoñanzas et al. (2004), López-Antoñanzas and Sen (2005) and Kraatz et al. (2013). Occlusal measurements were taken using photogrammetry.

Abbreviations—maxi. maxilla; mandi. mandible; frag. fragment; I incisor; DP/dp upper/lower deciduous premolar; M/m upper/lower molar; w with; KNM the National Museums of Kenya, Nairobi, Kenya; NA Nakali; SH Samburu Hills; OM specimens of the Osteology section in the KNM; BM the Natural History Museum, London, England (formerly the British Museum [Natural History]); EP specimens collected by the Eyasi Plateau Expedition, Tanzania; F, L. and P. specimens collected by the Omo Expedition, Ethiopia (housed in the National Museum of Ethiopia); LAET specimens from Laetoli collected by Mary Leakey; ALA-VP-2 the Alayla Vertebrate Locality 2 (housed in the National Museum of Ethiopia); and NHM Natural History Museum, London, England.

Systematics

Order Rodentia Bowdich, 1821
Suborder Hystricomorpha Brandt, 1855
Infraorder Hystricognathi Brandt, 1855

Fig. 1. Sketch map of eastern-central Africa, showing the location of Nakali (modified from Kunimatsu et al., 2007).

(9.88–9.92 Ma) (Kunimatsu et al., 2007).

Fig. 2. Thryonomyid dental terminology and measurements used for upper (A, KNM-NA 50198) and lower (B, KNM-NA 54957) teeth, based on Winkler (1992), Marivaux et al. (2002), López-Antoñanzas et al. (2004), López-Antoñanzas and Sen (2005), and Kraatz et al. (2013). Anterior is to the left. *Al* Anteroloph, *Prl* Protoloph, *Pol* Posteroloph, *Mu* Mure, *Pr* Protocune, *Pa* Paracune, *Hy* Hypocone, *Mt* Metacone, *Si* Sinus, *ASI* Anterosinus, *Psi* Posterosinus, *Mld I* Metalophulid I, *Mld II* Metalophulid II, *Hyld* Hypolophid, *Pold* Posterolophid, *Ecd* Ectolophid, *Prd* Protoconid, *Mtd* Metaconid, *Hyd* Hypoconid, *End* Entoconid, *Sid* Sinusid, *ASid* Anterosinusid, *MSid* Mesosinusid, *PSid* Posterosinusid, *A* Anterior, *L* Labial.
Family Thryonomyidae Pocock, 1922
Genus *Thryonomys* Fitzinger, 1867

*Thryonomys kamulai*, sp. nov.  
(Figs. 3–6)

*Paraphiomys*, Kawamura and Nakaya, 1984. p.133–139.

**Etymology.**—In commemoration of the late Jackson Kamula, who was a veteran field assistant at Nakali and other fossil localities in Kenya.

**Holotype.**—KNM-NA54957, Rt. mand. frag. w/ dp4–m1 (Figs. 5f, 6f)

**Paratypes.**—Lt. maxi. frag. w/ DP4–M2 (KNM-NA 50312), Lt. maxi. frag. w/ DP4–M1 (Field No. 2668’ 11), Rt. maxi. frag. w/ DP4–M1 (KNM-NA 52402), Lt. maxi. frag. w/ M2–3 (KNM-NA 52431), Lt. mand. frag. w/ 11(broken)–dp4–m2 (KNM-NA 50313), Rt. mand. frag. w/ Rt. m1–3 (KNM-NA 50311), Rt. mand. frag. w/ dp4–m1 (KNM-NA 46295), Lt. mand. frag. w/ m1–2 (KNM-NA 52480), Lt. isolated M1 or M2 (KNM-NA 50198, 52657), Rt. isolated M1 or M2 (KNM-NA 50199, 52410, NA60-2646’ 11), Lt. isolated m1 or m2 (KNM-NA 50197), Rt. isolated m1 or m2 (NA60-2778’ 11, NA60-2815’ 11)

**Referred material.**—Lt. mand. frag w/ dp4–m2 (KNM-SH 10524 in Kawamura and Nakaya, 1984)

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

**Diagnosis.**—Smaller than the other species of the genus. Upper cheek teeth lacking mesoloph and metaloph and with shallower and wider sinuses. Lower cheek teeth lacking anterolabial cusp. dp4 longer than that of the lower molars. dp4 with four lophids (metalophulid I, metalophulid II, hypolophid, and posterolophid) and well developed crescent-shaped metalophulid I with spur on the posterior side. Anterosinusid on dp4 closed lingually closed. m1–3 with relatively straight metalophulid I and hypolophid.

**Differential diagnosis.**—*Thryonomys kamulai* differs from any known species of Miocene thryonomyids such as *Paraphiomys*, *Paraulacodus*, and *Protohummus* in having the upper molars without mesoloph, lower molars lacking the anterolabial cusp, and the presence of four transverse lophids on dp4. *T. kamulai* is different from the two extant thryonomyids, *T. swinderianus* and *T. gregorianus*, in being smaller, in having lower hypsodonty, less transversely expanded M1–2, and in the presence of a well developed metalophulid I on dp4. *T. kamulai* is distinct from *T. asakomae* in being its smaller, in having shallower and wider sinuses on the upper cheek teeth, relatively oblique anteroloph, in lacking the metaloph on M1–2, in having a well developed crescent-shaped metalophulid I with a spur and a closed anterosinusid on dp4, a slightly straight hypolophid and an inclined posterolophid on the lower molars. *T. kamulai* differs from *T. wesselmani* in being smaller, shallower and wider sinuses on the upper cheek teeth with straight anteroloph, in lacking a metaloph on M1–2, and in hav-

| Table 1. Measurements (in millimeters) of cheek teeth of *Thryonomys kamulai*, sp. nov., collected from the Nakali Formation. * = where tooth identification is uncertain, the measurement is repeated, in parentheses. |  |
|---|---|---|---|---|---|---|---|---|
|  | DP4 / dp4 | M1 / m1 | M2 / m2 | M3 / m3 |
|  | L | W | L/W | L | W | L/W | L | W | L/W |
| **Upper Dentition** |  |  |  |  |  |  |  |  |  |
| KNM-NA 50198* | Lt. | — | — | — | 2.75 | 2.75 | 1.00 | (2.75) | (2.75) | (1.00) |
| KNM-NA 50199* | Rt. | — | — | — | 2.61 | 2.73 | 0.96 | (2.61) | (2.73) | (0.96) |
| KNM-NA 50312 | Lt. | 2.46 | 2.78 | 0.88 | 2.36 | 2.93 | 0.81 | 2.37 | 3.09 | 0.77 |
| KNM-NA 52402 | Rt. | 2.56 | 2.72 | 0.94 | 2.56 | 2.83 | 0.90 | — | — | — |
| KNM-NA 52410* | Rt. | — | — | — | 2.23 | 2.58 | 0.86 | (2.23) | (2.58) | (0.86) |
| KNM-NA 52431 | Lt. | — | — | — | 2.36 | 3.01 | 0.78 | 2.18 | 2.81 | 0.78 |
| KNM-NA 52657* | Lt. | 2.58 | 2.69 | 0.96 | (2.58) | (2.69) | (0.96) |
| NA60-2646’11 | Lt. | 2.27 | 2.70 | 0.84 | (2.44) | (2.82) | (0.87) |
| **Lower Dentition** |  |  |  |  |  |  |  |  |  |
| KNM-NA 46295 | Rt. | 3.15 | 2.35 | 1.34 | 2.90 | 2.83 | 1.02 | — | — | — |
| KNM-NA 50197* | Lt. | — | — | — | 2.59 | 2.54 | 1.02 | (2.59) | (2.54) | (1.02) |
| KNM-NA 50311 | Lt. | 2.96 | 2.72 | 1.09 | 2.79 | 2.66 | 1.05 | 2.71 | 2.33 | 1.16 |
| KNM-NA 50313 | Lt. | 3.01 | 2.34 | 1.29 | 2.36 | 2.55 | 0.93 | 2.17 | 2.46 | 0.88 |
| KNM-NA 52480 | Rt. | 2.83 | 2.59 | 1.09 | 2.79 | 2.88 | 1.08 | — | — | — |
| KNM-NA 54957 | Lt. | 3.41 | 2.77 | 1.23 | 3.13 | 3.21 | 0.98 | — | — | — |
| NA60-2778’11* | Rt. | — | — | — | 2.59 | 2.40 | 1.08 | (2.59) | (2.40) | (1.08) |
| NA60-2815’11* | Lt. | — | — | — | 2.77 | 2.21 | 1.25 | (2.77) | (2.21) | (1.25) |
ing well developed crescent-shaped metalophulid I and closed anterosinid on dp4.

Measurements. – See Table 1.

Description. – Tooth terminology is shown in Fig. 2A (upper molars) and Fig. 2B (lower molars).

Upper dentition (See Figs. 3–4)

DP4 is the smallest tooth in the upper cheek tooth row. The outline is rectangular with round corners, with the anterior margin shorter than the posterior margin. Three transverse lophs (anteroloph, protoloph, and posteroloph) are developed and buccally run from the entoloph. The anteroloph obliquely runs toward the molar anterior margin. The tip of the anteroloph becomes sharp. The anteroloph is narrower than the other two lophs. The protoloph is nearly straight, reaching the buccal margin of the tooth. The metaloph is lacking. There is no mesoloph, which projects buccally from anterior arm of the hypocone. The protoloph is slightly nearer the anteroloph than the posteroloph. The posteroloph is oblique along the posterior margin and it meets the posterior arm of the hypocone. The posteroloph is the thickest of the three lophs, swelling midway. There is no metaloph, which bucco-anteriorly projects from the midpoint of the posteroloph. There are four main cusps (protocone, paracone, hypocone and metacone). The crown is lower hypsodonty. The protocone and hypocone are connected to one another by the mure on the lingual side. These cusps are large. The buccal ends of the protoloph and posteroloph meet the paracone and metacone, respectively. The paracone and metacone are smaller than the protocone and hypocone. The sinuses are shallow and wide, and the anterosinus is smaller than the posterosinus.

M1–2 resemble the DP4 in the morphology of the oc-
A new *Thryonomys* from the Nakali Formation

The occlusal surface but they are much wider. The occlusal outline is rectangular with rounded corners. M2 is wider than M1. The three transverse lophs are relatively more transversely directed and longer than those of DP4. In early wear (KNM-NA50199, Figs. 3b, 4b; KNM-NA52410, Figs. 3e, 4e; KNM-NA52657, Figs. 3g, 4g), the wear facet of the posterior arm of the protocone is absent or weak, but after moderate wear (the other specimens) the wear facet is developed.

Although the occlusal pattern of the M3 resembles that of the other upper molars, the occlusal outline is triangular. The posteroloph obliquely runs toward the posterior margin of the tooth, and the crown posteriorly narrows.

**Lower dentition** (See Figs. 5–6)

dp4 is rectangular in occlusal outline, anteriorly narrowing. The crown is lower hypsodonty. dp4 has four distinct transverse lophids (metalophulid I, metalophulid II, hypolophid, and posterolophid). The crescentic metalophulid I has a posterior spur and obliquely runs toward the anterior margin from the metaconid. The metalophulid II lingually runs straight from the protococonid. The hypolophid is straight, reaching the lingual margin of the tooth. The posterolophid obliquely runs toward the posterior margin of the tooth. The protococonid is at the junction of the labial end of the metalophulid I

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**Fig. 4.** Occlusal view of the upper cheek teeth of *Thryonomys kamulai*, sp. nov., from the Nakali Formation. a. KNM-NA 50198, Lt. M1 or M2. b. KNM-NA 50199, Rt. M1 or M2. c. KNM-NA 50312, Lt. maxilla fragments with DP4–M2. d. KNM-NA 52402, Rt. maxilla with DP4–M1. e. KNM-NA 52410, Rt. M1 or M2. f. KNM-NA 52431, Lt. maxilla fragment with M2–3. g. KNM-NA 52657, Lt. M1 or M2. h. NA60-2646’11, Rt. M1 or M2. i. NA60-2668’11, Lt. DP4–M1. The scale bar is 1 mm; anterior is to the left.
and II, and the metaconid is at the junction of the lingual ends of these lophids. The hypoconid is at the labial end of the posterolophid, and the entoconid is at the lingual end of the hypolophid. The lingual cuspids are larger than the labial cuspids. The sinuses are shallow and the anterosinusid is lingually closed with metalophulid I and II, while the mesosinusid and posterosinusid lingually open.

The occlusal pattern of the lower molars is similar to that of the upper molars. m1–2 generally resemble dp4, but they are rather square in outline and have only three lophids (metalophulid I, hypolophid, and posterolophid) without metalophulid II. m1 is longer than m2. The mesosinusid of m1–2 is slightly wider than the posterosinusid. Metalophulid I runs straight along the anterior margin of the tooth. The hypolophid runs straight toward the lingual side and is slightly postero-lingually directed. The posterolophid obliquely runs toward the posterior margin of the crown.

m3 differs from the m1–2 in being posteriorly reduced. The posterolophid runs obliquely toward the posterior margin of the tooth and the lingual end of the
Remarks. – 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, anter sinus, poster sinus), and lower cheek teeth with the opposite pattern (=sinusid, mesosinusid, poster sinusid) except for dp4 which has an extra lingual infolding (=anterosinusid) (Woods, 1984; Ungar, 2010).

Among other genera of Thryonomyidae, they closely resemble Paraphiomys, Paraaulacodus, Protohummus, and Thryonomys. Paraphiomys differs from the Nakali

Fig. 6. Occlusal view of the lower cheek teeth of Thryonomys kamulai, sp. nov., from the Nakali Formation. a. KNM-NA 46295, Rt. mandible with dp4–m1. b. KNM-NA 50197, Lt. m1 or m2. c. KNM-NA 50311, Rt. mandible with m1–3. d. KNM-NA 50313, Lt. mandible with dp4–m2. e. KNM-NA 52480, Lt. mandible with m1–2. f. KNM-NA 54957, Rt. mandible with dp4–m1. g. NA60-2778 11, Rt. m1 or m2. h. NA60-2815 11, Rt. m1 or m2. The scale bar is 1 mm; anterior is to the left.
species in having the mesoloph on M1–2, in the absence of the metalophulid II on dp4 and in the presence of the anterolabial cuspid on the lower molars (López-Antoñanzas, 2004; López-Antoñanzas and Sen, 2005; Kraatz et al., 2013). *Paralacodus* differs from the Nakali specimens in the absence of the metalophulid II on dp4 and presence of the anterolabial cuspid on the lower molars (López-Antoñanzas et al., 2004; López-Antoñanzas and Sen, 2005; Kraatz et al., 2013). *Protohummus* differs from the Nakali specimens in the absence of the metaloph on the M1–2 and the metalophulid II on dp4 (Kraatz et al., 2013). The Nakali specimens most closely resemble the genus *Thryonomys* in having upper molars without a mesoloph, lower molars lacking the anterolabial cuspid, and the presence of four transverse lophids on dp4 (Winkler et al., 2010; Kraatz et al., 2013). *Thryonomys* is characterized by the presence of two or three-grooved upper incisor (Winkler et al., 2010; Kraatz et al., 2013); however, we have not found a grooved upper incisor in *T. kamulai* from the Nakali Formation.

The genus *Thryonomys* contains four species as previously named. Two of them (*T. swinderianus* and *T. gregorius*) are extant (Musser and Carleton, 2005; Monadjem et al., 2015; López-Antoñanzas, 2016), and two others are extinct: *T. asakomae* from the Adu-Asa Formation, Middle Awash, Ethiopia (5.7–5.6 Ma; Wesselman et al., 2009) and *T. wesselmani* from the Upper Ndolanya Beds of Laetoli, Tanzania (2.66 Ma; Denys, 1987, 2011).

The only two extant species are similar in terms of molar morphology; however, *T. gregorius* generally has a smaller dentition than that of *T. swinderianus* (Figs. 7, 8 and Tables 2, 3). In comparison with these species, the Nakali specimens are smaller yet (Figs. 7, 8 and Tables 2, 3), with lower hypsodonty and a rather anteriorly short M3. Both extant species have a straighter metalophulid I on the dp4 than that of *T. kamulai*, and the outline of the occlusal surface of m3 is not reduced.

*Thryonomys asakomae* is intermediate in dental size. It is smaller than the extant species but is larger than the Nakali specimens (Figs. 7, 8 and Tables 2, 3). The sinus on the upper cheek teeth of *T. asakomae* are deeper and narrower than those of *T. kamulai*. M1–2 have a metaloph on the midpoint of the posteroloph. dp4 has a spur on metalophulid I, which is not well developed and crescent-shaped, and an open anterolabial cuspid. The lower molars have a slightly inclined hypolophid and a relatively straight posterolophid. These characteristics are not found in the present specimens. *T. asakomae* has an upper incisor with two grooves in the labial enamel surface (Wesselman et al., 2009). This characteristic is also seen in the Miocene thryonomyids *Paralacodus* and *Protohummus* and is considered a primitive characteristic (Kraatz et al., 2013). *T. asakomae* is considered morphologically intermediate between *Paralacodus* or *Protohummus* (having an upper incisor with two grooves) and the other *Thryonomys* (having three grooves) (Kraatz et al., 2013). However, as no upper incisor of *Thryonomys* is known from the Nakali Formation, comparisons are not possible.

*Thryonomys wesselmani* is large in dental size, as large as *T. gregorius* and larger than the Nakali specimens (Figs. 7, 8 and Tables 2, 3). The sinuses on the upper cheek teeth of *T. wesselmani* are deeper and narrower than those of *T. kamulai*. The buccal end of the anteroloph obliquely runs toward the posterior on the upper cheek teeth, and M1–2 have a metaloph on the midline of the posteroloph. The occlusal surface of the lower molars of *T. wesselmani* resembles that of *T. kamulai*; however dp4 has the metalophulid I, which is neither well developed nor well developed and crescent-shaped, and an open anterolabial cuspid.

Kawamura and Nakaya (1984) described a lower tooth row (KNM-SH 10524, left mandibular fragment with dp4 [broken]–m2) from the Namurungule Formation of the Samburu Hills in Kenya (~9.5 Ma) as *Paraphiomys* sp. An important characteristic of the specimen is the absence of the anterolabial cuspid (as “anteroconid” in Kawamura and Nakaya, 1984). Furthermore, it has three transverse lophids and the metalophulid I (“metalophid” in Kawamura and Nakaya, 1984) and hypolophid run straight toward the lingual side and are slightly postero-lingually directed. The posterolophid extends from the hypoconid along the posterior margin of the crown. The specimen is slightly larger than the Nakali specimens. However, based on morphological similarities, we consider that the Samburu Hills specimen (KNM-SH 10524) is a *T. kamulai*.

**Discussion**

According to previous studies, *Thryonomys* fossil records are reported from the uppermost Miocene of Sub-Saharan Africa. Fossils assigned to *Thryonomys* sp. (Manthi, 2007) were collected from Lemudong’o, Kenya (6.12–6.08 Ma; Deino and Ambrose, 2007); this material has been considered the oldest representative of the genus (Winkler et al., 2010). However, the present findings from Nakali change the first appearance datum of *Thryonomys* to ~10 Ma.

Some authors claim that *Thryonomys* was derived
Table 2. Measurements (in millimeters) of upper cheek teeth of *Thryonomys* species.

|                     | DP4 | M1 | M2 | M3 | Reference          |
|---------------------|-----|----|----|----|--------------------|
| *Thryonomys kamalai*| N=3 |    |    |    |                    |
| Mean                | 2.43| 2.73| 0.89| 2.50| 2.76 | 0.91 | 2.48| 2.69 | 0.92 | 2.18| 2.81 | 0.78 |
| Range               | 2.27-2.56| 2.70-2.78| —  | 2.23-2.75| 2.58-2.93| —  | 2.23-2.75| 2.58-3.09| —  | —   | —    | —    |
| *T. wesselmani*     |     |    |    |    |                    |
| EP1324/05           |     |    |    |    |                    |
| LAET 73-73A         |     |    |    |    |                    |
| LAET 73-73B         |     |    |    |    |                    |
| Mean                | 3.70| 3.70| 1.00| —   | —    | —    | —   | —   | —    | —    | —    | —    |
| Range               | 3.56-3.63| 4.92-4.93| —  | 3.18-3.89| 4.44-5.13| —  | 3.14-3.69| 3.73-4.61| —  | —   | —    | —    |
| *T. asakomae*       |     |    |    |    |                    |
| ALA-VP-2/181        |     |    |    |    |                    |
| Various             |     |    |    |    |                    |
| Mean                | 3.25| 4.00| 0.81| —   | —    | —    | —   | —   | —    | —    | —    | —    |
| Range               | 3.56-3.63| 4.92-4.93| —  | 3.18-3.89| 4.44-5.13| —  | 3.14-3.69| 3.73-4.61| —  | —   | —    | —    |
| *T. swinderianus* (fossil) |     |    |    |    |                    |
| F.197-73            |     |    |    |    |                    |
| Mean                | 4.45-4.80| 4.90-5.39| —  | 4.75-5.01| 5.91-6.35| —  | 4.70-5.58| 5.76-6.70| —  | 4.70-6.00| 5.94-6.70| —  |
| Range               | 4.45-4.80| 4.90-5.39| —  | 4.75-5.01| 5.91-6.35| —  | 4.70-5.58| 5.76-6.70| —  | 4.70-6.00| 5.94-6.70| —  |
| *T. gregorianus* (fossil) |     |    |    |    |                    |
| L.1-374             |     |    |    |    |                    |
| Mean                | 3.70| 4.28| 0.86| —   | —    | —    | —   | —   | —    | —    | —    | —    |
| Range               | 3.70| 4.28| 0.86| —   | —    | —    | —   | —   | —    | —    | —    | —    |
| *T. gregorianus* (extant) |     |    |    |    |                    |
| OM6435              |     |    |    |    |                    |
| OM7595              |     |    |    |    |                    |
| BM30.3.4.4          |     |    |    |    |                    |
| BM32.8.6.4          |     |    |    |    |                    |
| Various Localities  |     |    |    |    |                    |
| Various (coll. NHM) |     |    |    |    |                    |
| Mean                | 4.12| 4.84| 0.85| —   | —    | —    | —   | —   | —    | —    | —    | —    |
| Range               | 3.7-4.67| 4.4-6.1| —  | 3.6-4.20| 4.4-5.02| —  | 4.01-4.45| 5.1-5.66| —  | 3.96-4.47| 4.27-5.22| —  |
| Reference           | 4.12| 4.84| 0.85| —   | —    | —    | —   | —   | —    | —    | —    | —    |

Denys (2011)  Wesselman et al. (2009)  Wesselman et al. (2011)  Winkler (2003)
### Table 3. Measurements (in millimeters) of lower cheek teeth of *Thryonomys* species.

| Species                  | dp4             | m1               | m2             | m3             | Reference     |
|--------------------------|-----------------|------------------|----------------|----------------|---------------|
|                          | L (N=3)         | W (N=8)          | L (N=6)        | W (N=1)        |               |
| *Thryonomys kamalai*     | 3.19            | 2.49             | 2.77           | 2.63           | 1.05          | 2.62          | 2.48           | 1.06          | 2.71          | 2.33           | 1.16          | Denys (2011) |
|                          | 3.01-3.41       | 2.34-2.77        | 2.36-3.13      | 2.21-3.21      | 2.17-2.79     | 2.21-2.66     |                |               |               | Denys (2011) |
| **T. wesselmani**        |                 |                  |                |                |               |               | Denys (2011) |
| EP 1251/00               | Lt              | 4.55             | 3.85           | 1.18           | 4.89          | 4.17          | 1.17           | 4.71          | 4.18          | 1.13          | Denys (2011) |
| EP 464/05                | Lt              | 5.00             | 4.66           | 1.07           | 4.81          | 4.96          | 0.97           | 4.52          | 4.56          | 0.99          | Denys (2011) |
| EP 814/01                | Lt              | 4.9              | 3.1            | 1.58           | 4.7           | 4.8           | 0.98           | 4.4           | 5.2           | 0.85          | Denys (1987)  |
| LAET 75-32               | Lt              | 4.8              | 3.6            | 1.33           |                |                |                |               |               | Denys (1987)  |
| LAET 75-700              | Lt              | 4.9              | 3.1            | 1.55           |                |                |                |               |               | Denys (1987)  |
| LAET 75-117              | Lt              | 4.8              | 3.6            | 1.33           |                |                |                |               |               | Denys (1987)  |
| LAET 74-31               | Lt              | 4.8              | 3.6            | 1.33           | 4.7           | 4.8           | 0.98           | 4.4           | 5.2           | 0.85          | Denys (1987)  |
| **T. asakomeae**         |                 |                  |                |                |               | Denys (2011) |
| Various                  | 4.19-4.55       | 3.30-3.55        | 3.25-4.24      | 3.40-4.30      | 4.00-4.10     | 3.73-4.27     | 4.14-4.32      | 3.84-4.07     | Wesselman et al. (2009) |
| **T. swindernianus (fossil)** |                 |                  |                |                |               | Denys (2011) |
| P.994-1                  | Lt              | 6.15             | 4.56           | 1.35           |                |                |                |               | Wesselman (1984) |
| **T. swindernianus (extant)** |                 |                  |                |                | Denys (2011) |
| Central African Republic |                 |                  |                |                |               |               | Denys (2011) |
| 1974-35 Gabon            | 6.42            | 4.18             | 1.54           | 4.66           | 5.45          | 0.86           | 4.76           | 5.49          | 0.87           | 4.75           | 5.14          | 0.93           | 4.59           | 5.54          | 0.83          | Denys (2011) |
| 1991-200b Congo          | 6.30            | 4.22             | 1.49           | 4.75           | 5.47          | 0.87           | 4.77           | 5.14          | 0.93           | 4.59           | 5.54          | 0.83          | Denys (2011) |
| Various (coll. NHM)      | 5.44-5.99       | 4.30-4.70        | 5.06-5.40      | 5.37-5.81      | 5.08-5.85     | 5.88-6.35     | 5.95-6.50      | 5.01-6.43     | Wesselman et al. (2009) |
| **T. gregorianus (extant)** |                 |                  |                |                | Denys (2011) |
| OM6435                   | 5.32            | 3.73             | 1.43           | 4.23           | 4.29          | 0.99           | 4.31           | 4.62          | 0.93           | 4.35           | 3.79          | 1.15           | Denys (2011)  |
| OM7595                   | 5.65            | 3.64             | 1.55           | 4.45           | 4.46          | 1.00           | 4.45           | 4.31          | 1.03           | —             | —             | Denys (2011)  |
| BM303.3.4.4              | 5.84            | 4.70             | 1.24           | 4.50           | 4.94          | 0.91           | 4.94           | 4.72          | 1.05           | —             | —             | Denys (2011)  |
| BM322.8.6.4              | 5.40            | 4.10             | 1.32           | 4.60           | 4.92          | 0.93           | 4.94           | 5.36          | 0.92           | —             | —             | Denys (2011)  |
| Various (coll. NHM)      | 5.18-5.44       | 3.95-4.34        | 4.12-4.60      | 4.40-5.18      | 4.45-4.80     | 5.00-5.45     | 4.45-5.29      | 4.40-4.83     | Wesselman et al. (2009) |
from a *Paraulacodus*-like ancestor based on cladistic analysis of thryonomyid dental morphology (Flynn and Winkler, 1994; López-Antoñanzas et al., 2004; López-Antoñanzas and Sen, 2005). *Paraulacodus* has a two-grooved upper incisor, lower cheek teeth with an anterolabial cuspid, no metalophulid II on dp4, and was known two taxa *Pa. johanesi* (Middle–Late Miocene, East Africa; i.e., from ~8.5 to ~7.5 Ma, Chorora, Ethiopia; Geraads, 1998; Suwa et al., 2015) and *Pa. indicus* (12.9–12.5 Ma, Potwar Plateau, Pakistan; Hinton, 1933; Black, 1977; Flynn and Winkler, 1994). Kraatz et al. (2013) reported a new genus and species of thryonomyids, *Protohummus dango*, from the upper Miocene (7.5–6.5 Ma, Bibi et al., 2013) of the United Arab Emirates. *Pr. dango* has the two-grooved upper incisor, lower cheek teeth without the anterolabial cuspid, and no metalophulid II on dp4. They conducted a cladistic analysis of thryonomyids, including *Pr. dango* and recently de-
scribed thryonomyids (i.e., *T. asakomae*, Wesselman et al., 2009; *T. wesselmani*, Denys, 1987, 2011), and concluded that *Pr. dango* fills the phylogenetic and morphological gap between *Paraulacodus* (i.e., *Pa. johanesi*) and the fossil and extant species of *Thryonomys* (i.e., *T. asakomae*). Thus, Kraatz et al. (2013) claimed that the age of divergence between *Pr. dango* and *T. asakomae* predates \(~5.6\) Ma, which is the age of *T. asakomae*. Ac-

**Fig. 8.** Bivariate plot of width versus length of lower cheek teeth for *Thryonomys* species. Measurements taken from previous studies are shown as maximum ranges in rectangles. Measurements are listed in Tables 1 and 3.
tually, in previous studies, the oldest known fossil of *Thryonomys* was from Lemdong’o, Kenya (Manthi, 2007), and the branch age of *Pr. dango* and *Thryonomys* would have been ~6 Ma (instead of ~5.6 Ma). Kraatz et al. (2013) claimed that *Pr. dango* is probably more closely related to *Pa. johanesi* than *Pa. indicus*. It is known that some dispersal events of Thryonomyidae between Africa and southern Asia occurred during the Early–Middle Miocene (e.g., Winkler and Flynn, 1994). *Pr. dango*, being phylogenetically intermediate between *Paraulacodus* (i.e., *Pa. johanesi*) and *Thryonomys*, indicates a dispersal event from Africa to Arabia before ~7 Ma, which was followed by a return of its lineage to Africa at ~6 Ma, evolving into the genus *Thryonomys* (Kraatz et al., 2013). The fossil records of *Thryonomys* have been limited to Sub-Saharan Africa since the Late Miocene (Winkler et al., 2010); no fossils of this genus are known from the Arabian Peninsula. Based on the aforementioned, the presence of *T. kamulai* at Nakali suggests that the divergence of *Protohummus* from a *Paraulacodus*-like ancestor occurred at least by 10 Ma, and most likely in Africa, and that *Protohummus* and *Thryonomys* subsequently diverged. Fossil records of *Protohummus* are unknown from Africa (Kraatz et al., 2013); however, two thryonomyid specimens from the Namurungule Formation of the Samburu Hills in Kenya (~9.5 Ma) described by Kawamura and Nakaya (1987) could belong to a similar taxon of the base of the crown *Thryonomys* near *Pr. dango* or *T. asakomae* (Kraatz et al., 2013), allowing a better understanding of the paleobiogeography. Thus, *T. kamulai* and thryonomyid specimens from the Namurungule Formation favor the possibility that *Protohummus* and *Thryonomys* had diverged in Africa. Cladistic analysis is necessary to strengthen this hypothesis; it is ongoing and will be reported in a separate article in the future.

**Conclusion**

A new species of thryonomyid rodent, *Thryonomys kamulai*, sp. nov., was reported from the Upper Miocene Nakali Formation (~10 Ma), Kenya. A specimen from the Samburu Hills, Kenya (Kawamura and Nakaya, 1984), was also assigned to *T. kamulai*. *T. kamulai* is the oldest species of the genus *Thryonomys*. This study suggests that *Thryonomys* inhabited Africa prior to ~10 Ma.

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田邉典紀 化石の同定記載、原稿執筆を担当。
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腸松 豊 現地での発掘調査。本研究の議論を担当。
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（要 旨）

Tanabe, Y., Onodera, M. Nakatsukasa, M. Kunimatsu, Y. and Nakaya, H., 2020, A new cane rat (Rodentia, Thryonomyidae) from the Upper Miocene Nakali Formation, northern Kenya. J. Geol. Soc. Japan, 126, 167–181. (田邉佳紀・小野寺麻由・中務真人・國松 豊・仲谷英夫. 2020. ケニア中央部上部中新統ナカリ層から産出した新種ヨシネズミ類. 地質雑, 126, 167–181.)

アフリカヨシネズミ（齧歯目. ヨシネズミ科）は2種の現生種がアフリカ・サハラ以南に生息している。先行研究では、現生のヨシネズミ属はその化石記録からアフリカの後期中新世末に出現したと考えられてきた。日本－ケニア調査隊はケニア北部に分布する上部中新統ナカリ層（約10Ma）からヨシネズミ属の新種Thryonomys kamulai, sp. nov. を発見した。筆者らは頑歯化石を基に本種の記載を行い、ヨシネズミ属の中では小型で、また固有の稜線歯（lophodonty）を有することが特徴づけられた。この発見により、ヨシネズミ属の初産出記録が後期中新世の約10Maに更新され、彼らは少なくとも10Ma以前にアフリカに生息していたことが考えられる。