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Listriodontine suid and tragulid artiodactyls (Mammalia) from the upper Miocene Nakali Formation, Kenya

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Abstract. Two rare artiodactyl mammals from the basal upper Miocene Nakali Formation (*ca.* 10 Ma) of central Kenya are described. They are cf. *Listriodon* sp. (Suidae, Listriodontinae) and *Dorcatherium* cf. *pigotti* (Ruminantia, Tragulidae), which are the first discoveries of a listriodontine and a tragulid in the formation. Cf. *Listriodon* sp. is represented by a talonid of a lower molar that has a strongly lophodont hypolophid. Although this listriodontine material is fragmentary, it is comparable in morphology and size to large and fully lophodont species of the genus *Listriodon*, such as *L. splendens* and *L. pentapotamiae theobaldi*. If the Nakali specimen proves to be phyletically closely related to these two species, it indicates that a highly derived lineage of *Listriodon* existed in East Africa around 10 Ma, implying a possible migration of this lineage from Europe/Asia to East Africa during the middle or earliest late Miocene. *Dorcatherium* cf. *pigotti* is represented by DP4 (or M1) and a mandible with p3–m3, which are comparable in size to those of *D. pigotti* among the African species of the genus. Although the genus *Dorcatherium* and species *D. pigotti* are common taxa in the early to middle Miocene of Africa, they are rarely found in the late Miocene. This is the second record of the genus in the late Miocene of Africa, reinforcing evidence that *Dorcatherium* existed until the basal late Miocene in East Africa.

Key words: Africa, *Dorcatherium*, *Listriodon*, Ruminantia, Tortonian, Vallesian

Introduction

The upper Miocene Nakali Formation of central Kenya is an important fossil-bearing deposit particularly for anthropology and primatology because the formation has yielded several taxa of colobine, small non-cercopithecoid catarrhine, and hominoid primates (Nakatsukasa *et al*., 2006, 2010; Kunimatsu *et al*., 2007, 2016). Among these fossil primates, a new great ape, *Nakalipithecus nakayamai*, attracted much attention because it is a candidate for the latest common ancestor of the extant African great apes and humans (Kunimatsu *et al*., 2007). The fossil mammals including primates, a rodent, carnivores, proboscideans, perissodactyls, and artiodactyls from the formation were first reported by Aguirre and Leakey (1974). Since then, additional fossil mammalian specimens have been described and mentioned from the formation by several researchers (Aguirre and Guérin, 1974; Pickford, 1983, 1986; Flynn and Sabatier, 1984; Fischer, 1986; Morales and Pickford, 2006). However, the Nakali fossil mammal fauna has still not been well documented.

Since 2002, a joint research team from Kyoto University and the National Museums of Kenya has been conducting geological and paleontological field research in the Nakali Formation (Nakatsukasa *et al*., 2006; Nakatsukasa, 2009; Sakai *et al*., 2013) and has described some mammalian fossil specimens from the formation (Kunimatsu *et al*., 2007, 2016; Nakatsukasa *et al*., 2010; Handa *et al*., 2015; Tsubamoto *et al*., 2015). This article describes two rare artiodactyls from the Nakali Formation, a listriodontine suid and a tragulid ruminant, collected by the joint research team. These two artiodactyl taxa are rare in terms of collection size in the formation and are important for clarifying the Nakali fossil mammal fauna.

Repository.—The specimens described here are stored

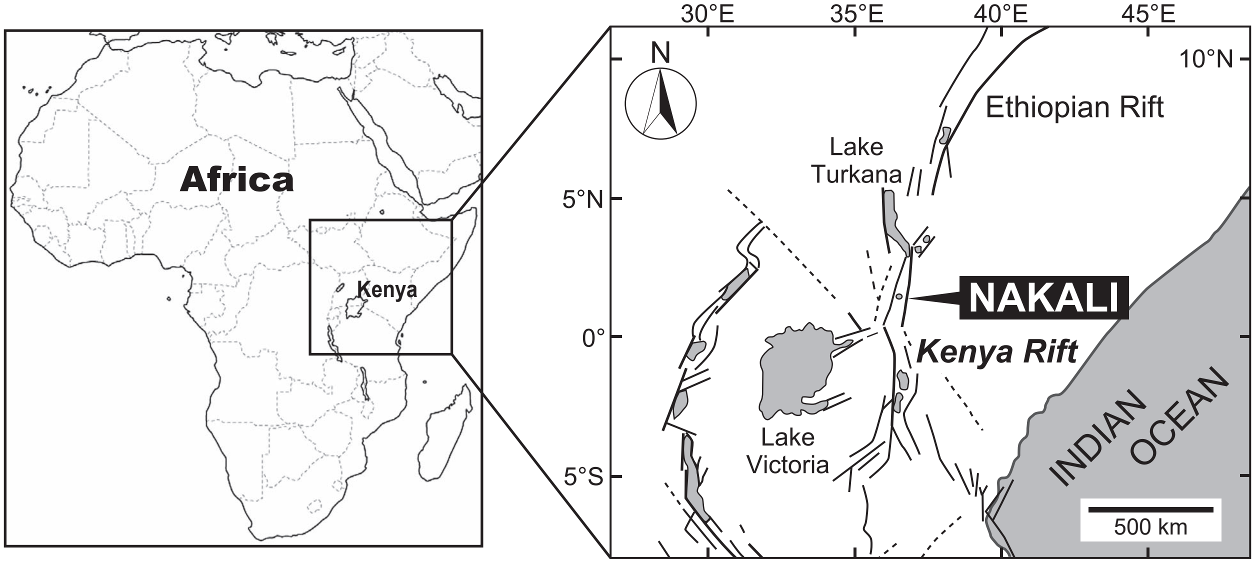

Figure 1. Map of Africa, showing the Nakali fossil locality in central Kenya (after Kunimatsu *et al.*, 2007).

in the Palaeontology Section, National Museums of Kenya, Nairobi, Kenya.

Taxonomy and terminology.—Generic taxonomy of the Listriodontinae generally follows van der Made (1996). Dental terminology for the Tragulidae generally follows Sánchez *et al*. (2015). The trigonid stands for a homologous part to the triangle formed by the protoconid, metaconid, and paraconid in the lower molars of primitive tribosphenic mammals, while the talonid stands for a homologous part to the dental crown distal to the trigonid in the lower molars of primitive tribosphenic mammals (Hershkovitz, 1971; Kielan-Jaworowska *et al*., 2004).

Dental abbreviations.—**M/m**, upper/lower molars; **P/p**, upper/lower premolars; **DP**, upper deciduous premolars.

Institutional abbreviations.—**KNM**, National Museums of Kenya, Nairobi, Kenya; **KU**, Kyoto University, Kyoto, Japan; **NMNS**, National Museum of Nature and Science, Tsukuba, Japan.

Other abbreviations.—**ELMA**, European Land Mammal Age; **MN**, European Neogene Mammal Chron; **NA**, Nakali fossil locality, central Kenya.

Locality, formation, and age

The specimens described here are from the basal upper Miocene Nakali Formation at the Nakali locality (approx. 01°11´N, 36°22´E), which is located on the eastern margin of the central Kenya Rift, about 40 km west of Maralal, central Kenya (Figure 1; Kunimatsu *et al*., 2007; Sakai *et al*., 2013). It is underlain by the Alengerr Tuffs (Golden, 1978), and is unconformably overlain by the Nasorut Formation, which is composed of basalt and trachyte lava, pyroclastics, and conglomerate (Figure 2).

The Nakali Formation (*ca.* 340 m in thickness) is stratigraphically subdivided into the "Lower," "Middle," and "Upper" members, and is characterized by tuffaceous sandstones and mudstones with conglomerate interbeds, a thick pyroclastic flow deposit, and tuff beds (Figure 2; Kunimatsu *et al*., 2007; Sakai *et al*., 2013). The basal part of the "Lower" Member consists mainly of lacustrine turbidite and debrite of lake delta front origin, grading upwards into fluvio-lacustrine deposits. The "Middle" Member consists of a thick pyroclastic flow deposit. The lower half of the "Upper" Member consists mainly of fluvio-lacustrine deposits and the upper half is represented by muddy sediments of lake slope origin (Sakai *et al*., 2013).

The age of the mammalian and other vertebrate fossils from the Nakali Formation is estimated to be around 10.0–9.8 Ma, that is, early Tortonian (basal late Miocene), based on the anorthoclase ^{40}Ar-^{39}Ar datings and magnetostratigraphy (Figure 2; Kunimatsu *et al*., 2007). It ranges within the period from Chron C5n.2n (11.06–9.98 Ma) to C5n.1n (9.94–9.79 Ma), with Chron C5n.1r (9.98–9.94 Ma) corresponding to the horizon from the upper part of the "Lower" Member to the basal part of the "Upper" Member (Kunimatsu *et al*., 2007; Hilgen *et al*., 2012; Tsubamoto *et al*., 2015). Therefore, the Nakali vertebrate fossil fauna is correlated to the uppermost part of MN9 or lowermost part of MN10, and to the Vallesian ELMA (McKenna and Bell, 1997; Hilgen *et al*., 2012).

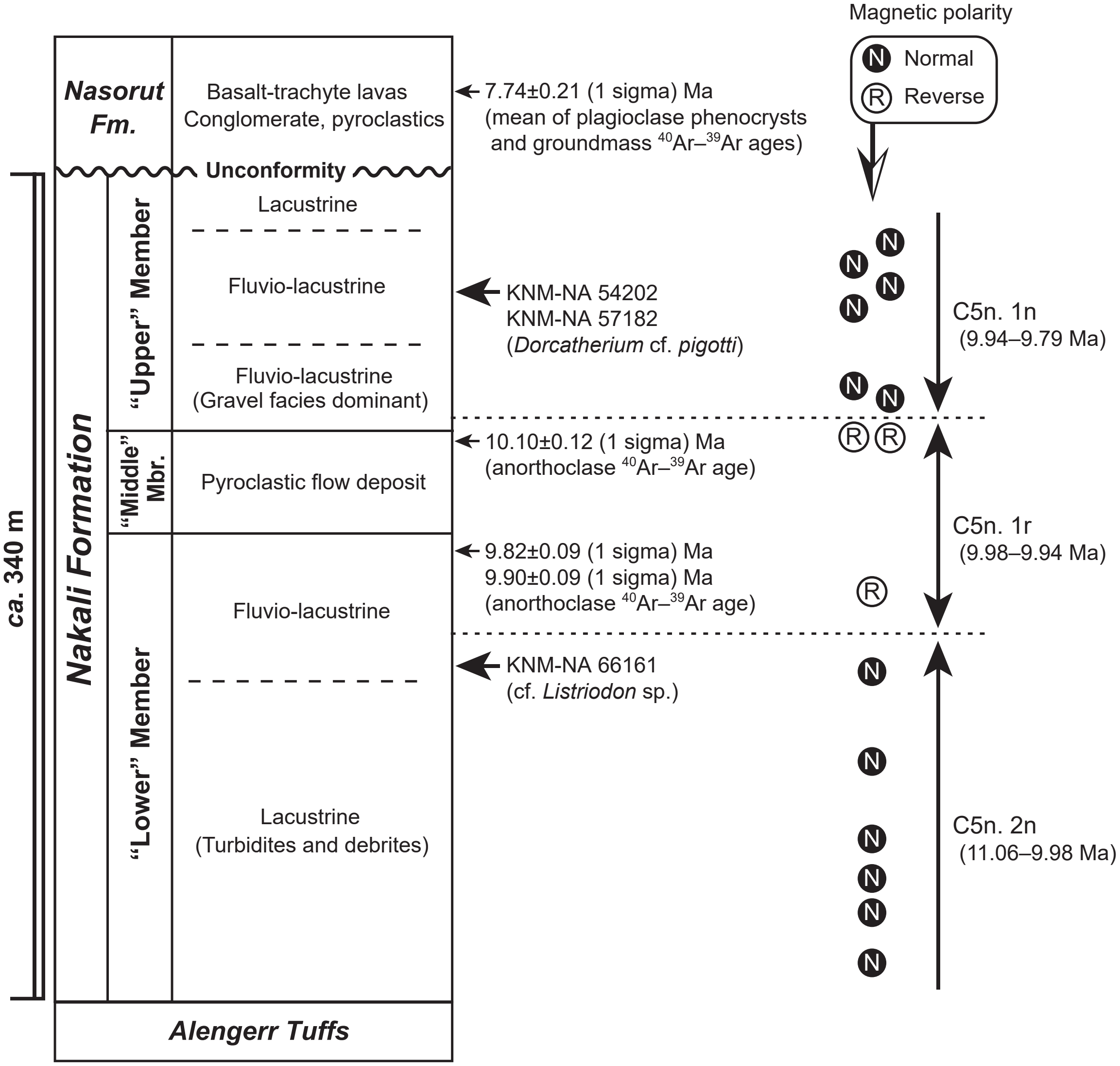

Figure 2. General stratigraphy and geological information of the Miocene Nakali Formation of central Kenya, showing the stratigraphic horizon of the specimens described here (after Kunimatsu *et al*., 2007; Hilgen *et al*., 2012).

Systematic paleontology

Order Artiodactyla Owen, 1848
Family Suidae Gray, 1821
Subfamily Listriodontinae Gervais, 1859
Genus ***Listriodon*** von Meyer, 1846

Type species.—*Listriodon splendens* von Meyer, 1846.

cf. ***Listriodon*** sp.

Figure 3

Material.—KNM-NA 66161, a talonid fragment of a left lower molar.

Sublocality.—KU Sublocality Number NA22.

Horizon.—"Lower" Member of the Nakali Formation (Figure 2).

Measurement.—Talonid (or distal lophid in the Suidae) width = 17.6 mm.

Description.—This lower molar talonid (or distal lophid in the Suidae) is lophodont and is moderately worn. The mesial and distal margins are broken (Figure 3F, G), and the root is poorly preserved (Figure 3E). The hypoconid and entoconid are sharp and are connected to each other by the buccolingually oriented hypolophid. The hypolophid is well developed and high for the family. The entoconid is mesiodistally compressed in lingual view (Figure 3C). The entoconid is higher than the hypo-

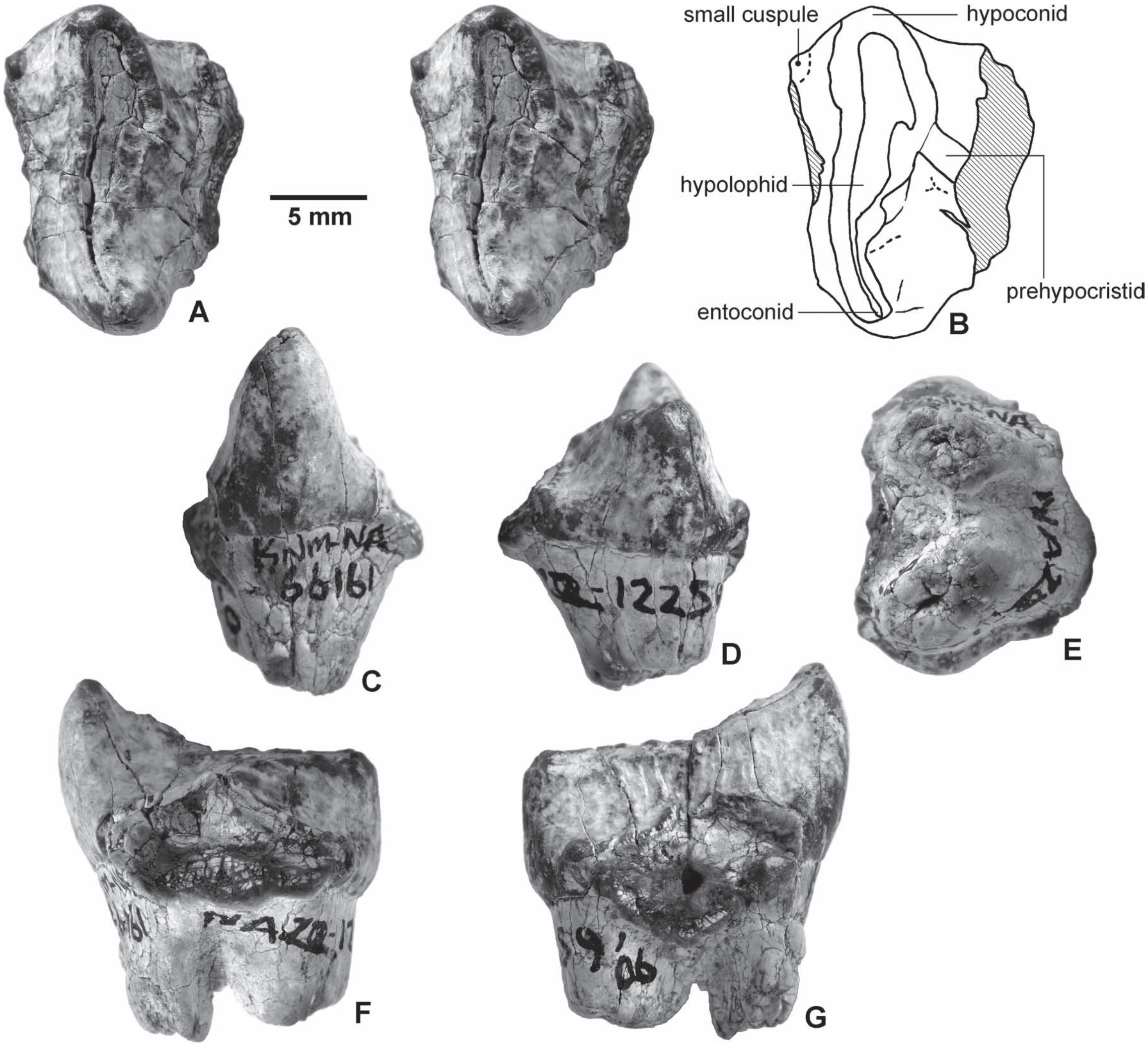

Figure 3. Cf. *Listriodon* sp. from the Miocene Nakali Formation of Kenya, KNM-NA 66161, a talonid (or distal lophid in the Suidae) fragment of a left lower molar. **A,** occlusal view (stereo pair); **B,** schematic drawing of occlusal view; **C,** lingual view; **D,** buccal view; **E,** ventral view; **F,** mesial view; **G,** distal view.

conid at this wear stage: the hypoconid is more worn than the entoconid. The prehypocristid (= cristid obliqua) is weak and originates at the mesial face of the hypolophid, extending mesiolingually. It is much more lingually located compared to the preserved tip of the hypoconid. There is no cristid on the distal face of the hypolophid. There is a small cuspule at the distal base of the hypoconid. No cingulid is observed. The root for the talonid is buccolingually bifurcate (Figure 3E–G). The enamel is not crenulated.

Comparisons.—KNM-NA 66161 is assigned to the Listriodontinae, which are bilophodont suids. It has a lophodont hypolophid and a relatively sharp and high entoconid. This morphology and size are reminiscent of the lower molars of some bilophodont suoid artiodactyls (such as the listriodontine suids and some palaeochoerids), tapirid perissodactyls, and macropodid marsupials. KNM-NA 66161 is distinguished from the molariform teeth of the pyrotheriids (South American mammals) and Neogene proboscideans, which have lophodont teeth, in being much smaller and in having much thinner enamel and a cristid/crista extending diagonally from the buccolingually oriented lophid/loph. It is distinguished from the upper molars of the above-mentioned mammals in having much less buccolingually separated roots. It differs from the lower molars of the tapirids in having a much more lingually shifted prehypocristid and a much more mesiodistally compressed entoconid. It also differs from the lower molars of the macropodids in having a much more mesiodistally compressed entoconid and a much more diagonally oriented prehypocristid at the central position. Furthermore, it differs from the lower molars of some palaeochoerids that have a lophodont dentition such as *Schizoporcus* and *Yunnanochoerus* in having a much more lingually shifted prehypocristid, a much more mesiodistally compressed entoconid, and more lophodont teeth with a lack of a deep V-shaped notch on the hypolophid in distal view. Therefore, it is identified as a fragmentary lower molar of the Listriodontinae.

KNM-NA 66161 is comparable in morphology to the lower molars of *Listriodon* and *Lopholistriodon*, which have a very derived degree of lophodonty among the subfamily. It differs from the lower molars of the other listriodontine genera such as *Nguruwe*, *Kubanochoerus*, *Bunolistriodon*, and *Eurolistriodon* in having a much more lophodont dentition (van der Made, 1996; Orliac, 2009; Orliac *et al*., 2009). *Listriodon* and *Lopholistriodon* are the most lophodont and most derived genera among the subfamily. These two genera are distinguished from each other mainly based on size and morphology of the upper canines (van der Made, 1996). The upper canine morphology cannot apply to the identification of KNM-NA 66161 because this specimen lacks upper canines. The species of *Listriodon* are much larger than those of *Lopholistriodon*.

KNM-NA 66161 is likely assignable to *Listriodon* rather than to *Lopholistriodon*. It has a talonid width of 17.6 mm, which is comparable in size to m2 of *Listriodon*, is much larger than m1 of *Listriodon* and the lower molars of *Lopholistriodon*, and is smaller than m3 of *Listriodon* (van der Made, 1996). Even when compared to the species of *Listriodon* and *Lopholistriodon*, KNM-NA 66161 has relatively well developed lophodonty with a mesiodistally compressed entoconid, which is a derived characteristic. In this morphology, it is comparable to the lower molars of the more lophodont species such as *Lopholistriodon kidogosana* (Pickford and Wilkinson, 1975), *Listriodon splendens*, *Li. pentapotamiae theobaldi* (Lydekker, 1878), and *Li. bartulensis* (Pickford, 2001b) (including '*Listriodon akatikubas*' (Wilkinson, 1976) from the Fort Ternan locality of Kenya reported by Pickford, 1986) (van der Made, 1996; Pickford, 2001b). KNM-NA 66161 is larger than the lower molars of *Lo. kidogosana* and *Li. bartulensis*, so that it is most comparable to the lower molars of *Li. splendens* and *Li. pentapotamiae theobaldi* in morphology and size. Therefore, it is likely assignable to the genus *Listriodon*. However, the possibility that KNM-NA 66161 is derived from the lineage of *Lopholistriodon* with an increased size and therefore belongs to the genus *Lopholistriodon* cannot be completely excluded because the present material from the Nakali Formation is poor. KNM-NA 66161 appears to have a more compressed entoconid than the lower molars of *Li. splendens* and *Li. pentapotamiae theobaldi*. Therefore, this specimen might represent a new species of *Listriodon* (or perhaps *Lopholistriodon*), although it is not confirmed due to the scarcity of the material.

Suborder Ruminantia Scopoli, 1777
Family Tragulidae Milne-Edwards, 1864
Genus **Dorcatherium** Kaup, 1833

Type species.—*Dorcatherium naui* Kaup, 1833.

Dorcatherium cf. **pigotti** Whitworth, 1958

Figures 4–7

Material.—KNM-NA 54202, a right mandible with p3–m3; KNM-NA 57182, left DP4 or M1.

Sublocality.—KU Sublocality Number NA39.

Horizon.—"Upper" Member of the Nakali Formation (Figure 2).

Dental measurements.—Shown in Table 1.

Description.—KNM-NA 57182 is a left upper molariform tooth and is moderately worn (Figure 4). The crown is low and brachyodont with conical buccal main cusps (paracone and metacone) and selenodont lingual main cusps (protocone and metaconule). There are interstitial wear facets on the mesial face of the crown lingual to the parastyle and on the distal face of the crown near the distal base of the metacone, indicating that the tooth is not M3, but M1, M2, or DP4. The buccal rib of the paracone is stronger than that of the metacone. The parastyle is located mesially to the paracone. The mesostyle is located distobuccally to the paracone and mesiobuccally to the metacone. The ectoloph connects the parastyle, paracone, mesostyle, metacone, and distobuccal base of the crown. The metastyle is absent. The preprotocrista extends mesiobuccally, connecting to the parastyle. The postprotocrista extends distally and connects to the mesial wall of the metaconule. The premetaconule crista extends mesiobuccally, fading out at the valley between the paracone and the metacone: it does not connect to either the mesostyle or the ectoloph. The postmetaconule crista extends distobuccally and connects to the postmetacrista at the distal base of the metacone (= at the distobuccal corner of the crown). The paraconule is absent. The mesial cingulum exists at the mesial base of the protocone. The lingual cingulum exists between the protocone and the metaconule. The distal cingulum originates at the distal base of the metaconule and is continuous to the lingual base of the metaconule: it does not connect to the lingual cingulum but is located buccally to the lingual cingulum at the lingual base of the metaconule. There is no buccal cingulum. The roots for the paracone and metacone are well separated from each other. The root for the metaco-

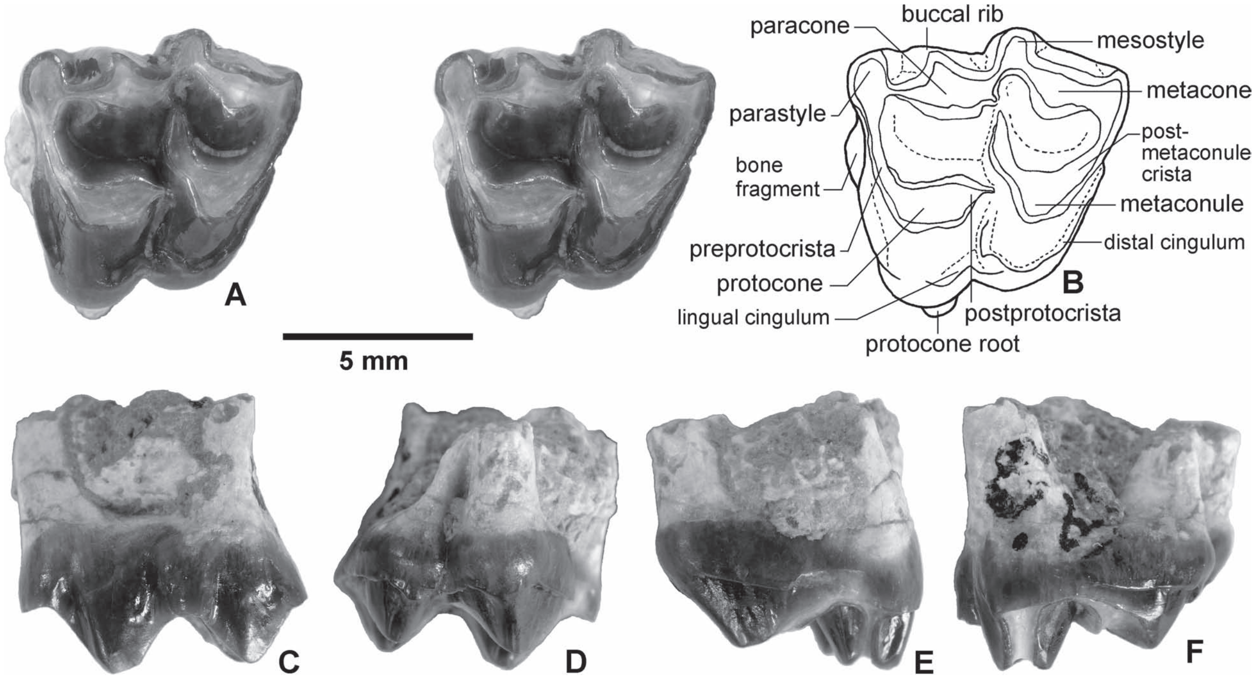

Figure 4. *Dorcatherium* cf. *pigotti* Whitworth from the Miocene Nakali Formation of Kenya, KNM-NA 57182, left DP4 or M1. **A,** occlusal view (stereo pair); **B,** schematic drawing of occlusal view; **C,** lingual view; **D,** buccal view; **E,** mesial view; **F,** distal view.

nule is smaller than that for the protocone (Figure 4D). These two lingual roots are located close to each other and are fused with each other near the cervix of the tooth.

KNM-NA 54202 is a right mandible with p3–m3 (Figures 5–7). The ventral border of the mandibular corpus is convex and its deepest part is below the trigonid of m3 (Figure 5). The mandibular depth is: 13.7 mm below m2 at the lingual side; 13.5 mm below m2 at the buccal side; 15.4 mm below m3 trigonid at the lingual side; and 14.5 mm below m3 trigonid at the buccal side. The teeth are brachyodont.

The p3 is simple and mesiodistally elongated (Figures 6, 7). Its mesial part is broken. There is a small cusp (= hypoconid?) distal to the main large cusp (= protoconid). There are buccal and lingual grooves between these two cusps. A cristid extends from the protoconid to the distal margin of the crown, connecting the protoconid to the distal cuspid. There is a cingulid at the distolingual base of the distal cuspid. There is no buccal cingulid. Judging from the size and position of the p3 mesial root, p3 appears to be longer than p4.

The p4 is also simple and mesiodistally elongated (Figures 6, 7). It is wider than p3. There is a tall protoconid. The preprotocristid is oriented mesiolingually rather than mesially, bearing a small swelling at the paraconid position. The postprotocristid extends distally, bearing a small cuspule or cristid at the lingual side of the basal position, and connects to the distal margin of the crown, where a low hypoconid appears to occur. The postprotocristid is more heavily worn than the preprotocristid. The lingual postprotocristid appears to be absent. There are mesial and distal cingulids. There are no buccal or lingual cingulids.

The lower molars are basically tetracuspidate with a hypoconulid on m3 (Figure 6). The lower molar size gradient is: m1 < m2 < m3. The buccal cusps (protoconid and hypoconid) are selenodont, and the lingual cusps (metaconid and entoconid) are conical and are somewhat buccolingually compressed. The m1 is heavily worn and m2 is moderately worn. On m1–m2, there are mesial and distal cingulids, lacking buccal and lingual cingulids, and the posthypocristid extends distolingually, fading out at the distal base of the entoconid.

The m3 is also worn, but the precise structure of the cristids can be observed (Figure 6). The preprotocristid and premetacristid are connected to each other at the mesial margin of the crown. These two cristids do not protrude much mesially and make a *Dorcatherium*-platform (Sánchez *et al*., 2015). The postprotocristid and postmetacristid are connected with each other, making a V-shaped notch at the distal trigonid wall. There is a *Dorcatherium*-fold at the distolingual face of the metaconid. A cristid that is located buccally to the postprotocristid exists on the distal face of the protoconid. This cristid appears to

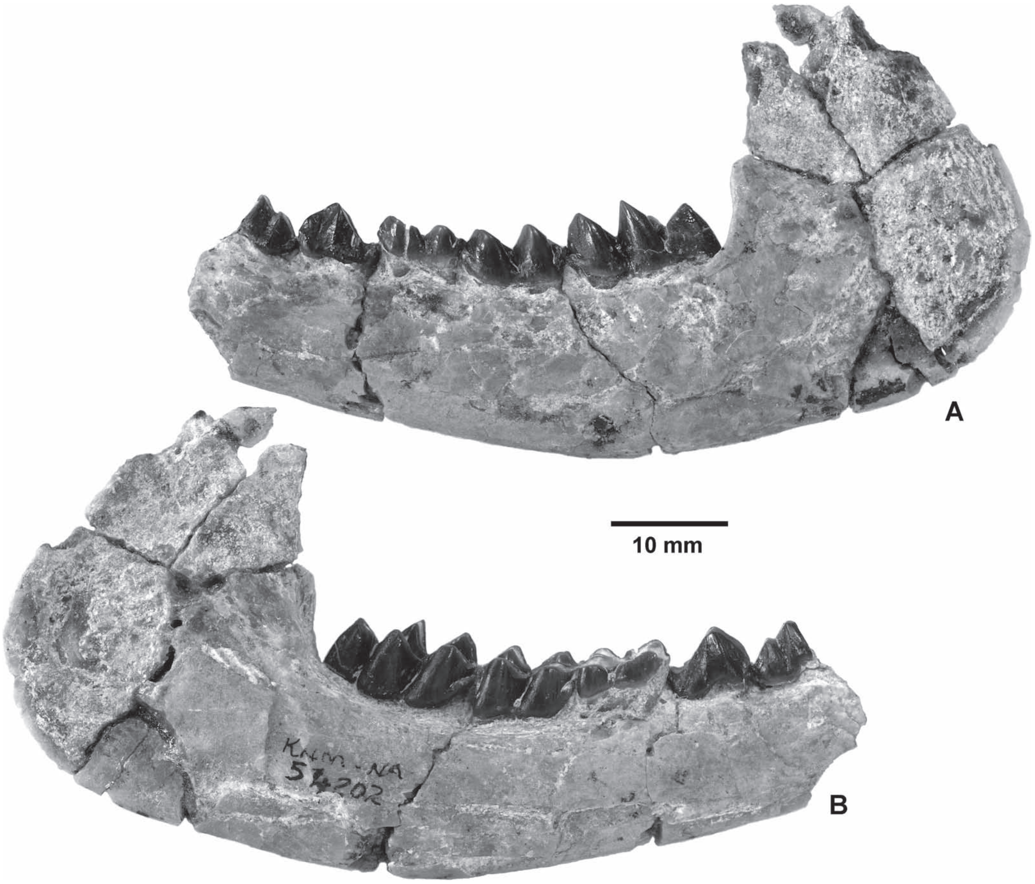

Figure 5. *Dorcatherium* cf. *pigotti* Whitworth from the Miocene Nakali Formation of Kenya, KNM-NA 54202, a right mandible with p3–m3. **A,** lingual view; **B,** buccal view.

originate from the tip of the protoconid and extends distolingually, approaching the mesial tip of the prehypocristid (= cristid obliqua). Therefore, this cristid is identified as a *Tragulus*-fold, not as a *Palaeomeryx*-fold (Geraads, 2010). The *Dorcatherium*-fold, postmetacristid, postprotocristid, and *Tragulus*-fold make an M-structure (Métais *et al*., 2001) on the distal trigonid wall. The prehypocristid extends mesiolingually and reaches the distal wall of the protoconid. It does not connect to the preentocristid. The posthypocristid extends distolingually. The preentocristid connects to the notch of the distal trigonid wall. The postentocristid is absent or very weak. The hypoconulid is single-cusped with only one cristid, lacking a hypoconulid basin and a hypoconulid loop. The cristid on the hypoconulid extends mesiolingually from the tip of the hypoconulid and connects to the posthypocristid. There is a mesial cingulid. The lingual cingulid only exists at the lingual base of the hypoconulid. There are no buccal or distal cingulids.

Comparisons.—The present specimens have a dental morphology typical of small primitive ruminants, such as a brachyodont dentition, a relatively weakly developed selenodonty, no paraconule on the upper molar/DP4, and no molar paraconid. They are assigned to the Tragulidae in having an M-structure with *Dorcatherium*- and *Tragulus*-folds on the distal trigonid wall of the lower molars and morphologically simpler premolars than those of the pecorans, and in lacking a *Palaeomeryx*-fold.

Among the Tragulidae, the present specimens are assigned to *Dorcatherium*, which is a wastebasket genus in the family, mainly defined as having a *Dorcatherium*-platform on the lower molars. The specimens are distinguished from *Dorcabune* and *Krabitherium* in having a much less bunodont dentition. They are distinguished from *Archaeotragulus* in lacking a paralophid on the lower molars, any trace of the hypoconulid on m2, and a *Zhailimeryx*-fold (= ‘entoconidian groove’ in Métais *et al*., 2001) on the mesial face of the molar entoconid. They are distinguished from *Afrotragulus* and *Yunnanotherium* in being much larger. They are also distinguished from *Afrotragulus*, *Siamotragulus*, *Moschiola*, *Hyemoschus*, and *Tragulus* in having a less mesially protruded preprot-

Table 1. Dental measurements (in mm) of *Dorcatherium* cf. *pigotti* Whitworth from the Miocene Nakali Formation, Kenya. The p3 length of KNM-NA 54202 was estimated based on the position of the mesial root. Abbreviations: *L*, mesiodistal length; *W*, buccolingual width; *W-m*, width of the mesial part; *W-d*, width of the distal part; *W-trd*, trigonid width; *W-tad*, talonid width.

Specimen	DP4/ M1	DP4/ M1	DP4/ M1	p3	p3	p4	p4	m1	m1	m1	m2	m2	m2	m3	m3	m3	m1–m3 row
KNM-NA	*L*	*W-m*	*W-d*	*L*	*W*	*L*	*W*	*L*	*W-trd*	*W-tad*	*L*	*W-trd*	*W-tad*	*L*	*W-trd*	*W-tad*	*L*
57182	7.5	7.1	7.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—
54202	—	—	—	> 7.4	3.5	7.2	3.7	7.9	4.7	5.0	8.8	5.7	6.2	12.8	6.4	6.6	29.6

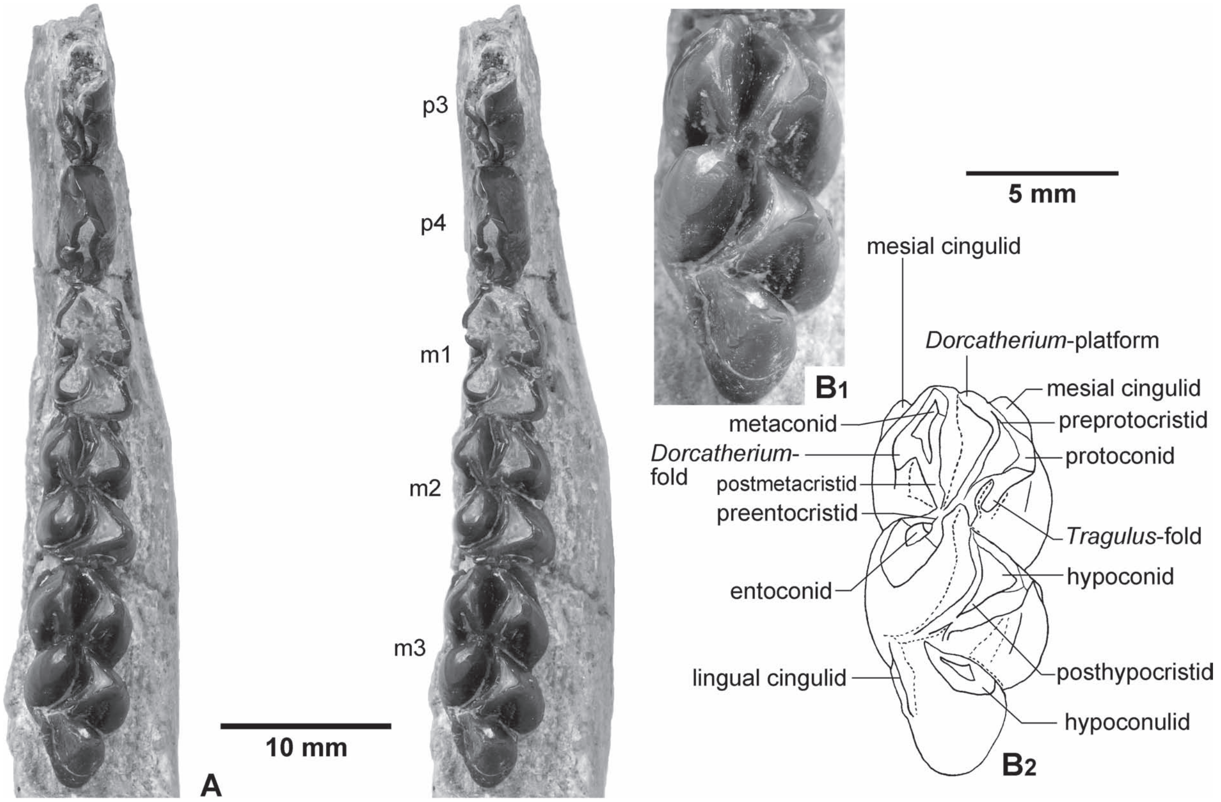

Figure 6. *Dorcatherium* cf. *pigotti* Whitworth from the Miocene Nakali Formation of Kenya, dentition (right p3–m3) of KNM-NA 54202. **A,** occlusal view (stereo pair) of right p3–m3; **B,** disto-occlusal view of right m3; B1, photo; B2, schematic drawing. Left scale corresponds to A, and right scale corresponds to B.

ocristid and premetacristid with a *Dorcatherium*-platform on the lower molars. They differ from *Afrotragulus* in having a cingulum on the metaconule on the upper molar/DP4, a stronger M-structure on the distal trigonid wall on the lower molars, a mesiodistally shorter central valley between the trigonid and the talonid without an interlobular bridge (Sánchez *et al*., 2010) on the lower molars. They differ from *Moschiola* in having a *Tragulus*-fold. They differ from *Hyemoschus* in having a distally oriented postprotocrista (distobuccally oriented in *Hyemoschus*) and weaker buccal ribs of the paracone and metacone on the upper molar/DP4. They differ from *Tragulus* in having a stronger mesostyle and parastyle on the upper molar/DP4 and a less buccolingually compressed metaconid and entoconid on the lower molars (Figure 8).

The genus *Dorcatherium* includes many species and is recorded in the Miocene of Africa and Europe and in the Miocene and early Pliocene of Asia (Pickford, 2001a, 2002; Rössner, 2007; Geraads, 2010; see also Sánchez *et al*., 2010, 2015). The species identification within each continent has been mainly based on the size (Colbert, 1935; Whitworth, 1958; Pickford, 2001a, 2002). The

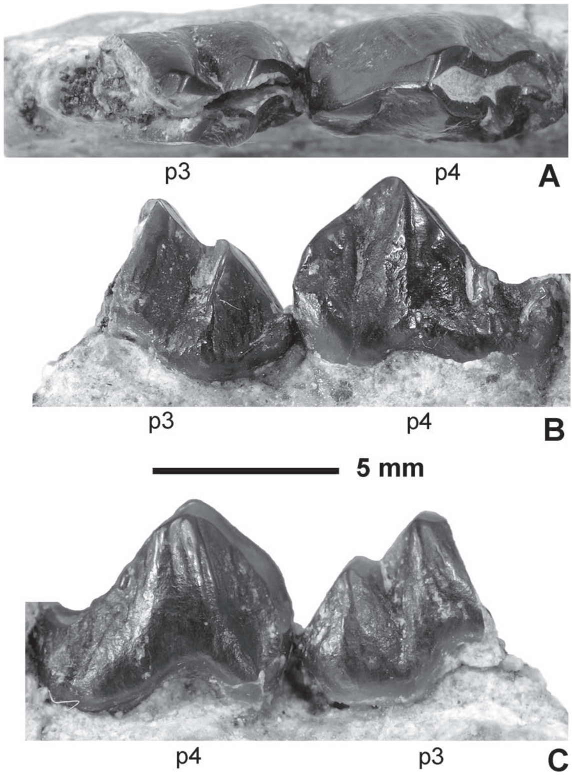

Figure 7. *Dorcatherium* cf. *pigotti* Whitworth from the Miocene Nakali Formation of Kenya, p3–p4 of KNM-NA 54202. **A,** occlusal view; **B,** lingual view; **C,** buccal view.

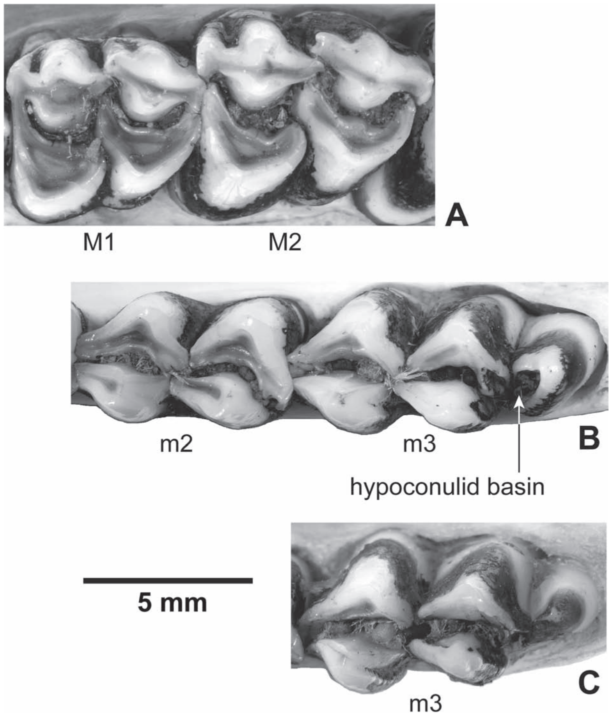

Figure 8. Upper and lower molars of a living tragulid species, *Tragulus javanicus* (Osbeck), in occlusal view. **A,** left M1–M2 of NMNS M31096 (male); **B,** right m2–m3 of NMNS M31096 with a hypoconulid basin on m3 (normal condition); **C,** right m3 of NMNS M31085 (male) without a hypoconulid basin (rare condition).

present specimens are comparable in size to *Dorcatherium pigotti* among the African species of the genus. The length of the lower molar row of KNM-NA 54202 is 29.6 mm, which is comparable to that of *D. pigotti* (Pickford, 2001a, 2002; Geraads, 2010). The size of the upper molariform tooth (KNM-NA 57182) is comparable to or slightly smaller than M1 of this species (Whitworth, 1958), implying that KNM-NA 57182 appears to be M1 or DP4 of the same species as the mandibular specimen KNM-NA 54202. KNM-NA 57182 appears to be DP4 because its mesiobuccal corner projects out somewhat mesially, which is often seen in DP4 but is not seen in the upper molars among the species of *Dorcatherium*.

The mandibular specimen KNM-NA 54202 differs from *Dorcatherium pigotti* and is unique in the genus *Dorcatherium* in lacking a lingual postprotocristid on p4 and a hypoconulid basin on m3. *D. pigotti* and other species of *Dorcatherium* have a lingual postprotocristid on p4, making a groove on the distal face of the protoconid between the postprotocristid and the lingual postprotocristid (Colbert, 1935; Whitworth, 1958; Ginsburg *et al*., 2001; Pickford, 2002; Aiglstorfer *et al*., 2014). Also, *Dorcatherium* usually has a hypoconulid basin with two (mesial and buccal) cristids (or a hypoconulid loop) on m3, whereas KNM-NA 54202 has only a single cristid on the m3 hypoconulid without a hypoconulid basin. We should note that this m3 character might be an individual variation within a species because the same morphological variation is observed in the specimens of the living tragulid species *Tragulus javanicus* (Osbeck, 1765) stored in NMNS (Figure 8): most specimens have a hypoconulid basin on m3, while one specimen (NMNS M31085) lacks it. Because the material from the Nakali Formation is poor, it is impossible to determine whether these two characteristics indicate intraspecific variation in *D. pigotti* or interspecific differences. Therefore, although there is a possibility that the Nakali *Dorcatherium* could be a new species based on the morphology of p4 and the m3 hypoconulid, this is not clear due to the scarcity of the fossil material from the Nakali Formation.

Discussion and conclusions

The two taxa described here (cf. *Listriodon* sp. and *Dorcatherium* cf. *pigotti*) are the first discoveries of a listriodontine and a tragulid in the Nakali Formation, adding two taxa to the faunal list of the formation (Kunimatsu *et al*., 2007).

The discovery of a listriodontine lower molar (KNM-NA 66161; Figure 3) indicates that a *Listriodon*-like very lophodont and large listriodontine suid existed in the Nakali area at the time of deposition. The genus *Listriodon* (*sensu* van der Made, 1996) has not been recorded in Africa except for a small and highly lophodont species of *Listriodon*, *Li. bartulensis* from the Member A (*ca.* 13 Ma) of the Ngorora Formation (Tugen Hills) and from the Fort Ternan locality (*ca.* 14 Ma), Kenya (Pickford, 2001a). If the Nakali listriodontine is phyletically closely related to the large and lophodont species of *Listriodon*, *Li. splendens* (recorded in Europe, Turkey, and East Asia; van der Made, 1996) and/or *Li. pentapotamiae theobaldi* (recorded in South Asia; van der Made, 1996), it indicates that a highly derived lineage of *Listriodon* existed in East Africa around 10 Ma and also implies that this lineage might have migrated from Europe/Asia to East Africa during the middle or earliest late Miocene.

Dorcatherium cf. *pigotti* discovered in the Nakali Formation is the second record of the genus in the late Miocene of Africa (Pickford, 1991; Geraads, 2010). Although the genus *Dorcatherium* and species *D. pigotti* are common taxa in the early to middle Miocene of Africa, they are rarely found in the late Miocene (Geraads, 2010). In the Pliocene (*ca.* 5.0 Ma), the living tragulid genus of Africa, *Hyemoschus*, appeared in East Africa (Pickford *et al*., 2004; Geraads, 2010; *contra* Rössner, 2007). This study reinforces the observation that an archaic tragulid *Dorcatherium* survived until the base of the late Miocene in East Africa before the appearance of the living tragulid genus of Africa, *Hyemoschus*.

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