



Taxonomic status and paleoecology of *Rusingoryx atopocranion* (Mammalia, Artiodactyla), an extinct Pleistocene bovid from Rusinga Island, Kenya

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ABSTRACT

Rusingoryx atopocranion is a poorly known extinct alcelaphine bovid, documented in Pleistocene deposits associated with Middle Stone Age artifacts on Rusinga Island, Kenya. Following its initial description, *Rusingoryx* was subsumed into *Megalotragus*, which includes the extinct giant wildebeests, on the basis of its cranial architecture. Renewed investigations of the Pleistocene deposits on Rusinga Island recovered a large sample of *Rusingoryx* specimens that provide new taxonomic and paleoecological insight. This study (1) reviews the morphological and phylogenetic evidence concerning the taxonomic status of *Rusingoryx* and (2) evaluates its paleoecology and dietary habits. The morphology and phylogenetic data indicate that *Rusingoryx* is distinct from *Megalotragus*; they likely shared a common ancestor in the late Pliocene. Ecomorphology and mesowear analysis point to a specialized grazing adaptation, and its association with arid-adapted ungulates suggests a preference for arid grasslands. The confirmation of *Rusingoryx* as a valid taxonomic entity, together with the presence of other extinct taxa (including *Megalotragus*) on Rusinga Island, suggests an increasingly complex pattern of ungulate biogeography and extinctions in the late Quaternary of East Africa. *Rusingoryx* appears to have been part of an arid-adapted faunal community that potentially persisted in East Africa until the onset of the Holocene.

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Introduction

Pickford and Thomas (1984) described a new genus and species (*Rusingoryx atopocranion*) of alcelaphine bovid on the basis of a partial cranium recovered from the Pleistocene Wasiriya Beds on Rusinga Island, Kenya (Fig. 1; 0°25.5'S, 34°10.5'E). *Rusingoryx* was subsequently subsumed by Harris (1991) into the genus *Megalotragus* van Hoepen, 1932, which includes the largest known extinct alcelaphines (Gentry and Gentry, 1978), on the basis of similarities in cranial architecture. Vrba's (1997) phylogenetic analysis of fossil alcelaphines supported this assessment by showing *Rusingoryx* to fall within the *Megalotragus* clade. Since then, *Rusingoryx* has been generally regarded as a junior synonym of *Megalotragus* (Geraads et al., 2004; Brink, 2005; Gentry, 2010).

Renewed investigations into the archaeology, paleontology, and paleoenvironments of the Wasiriya Beds (Tryon et al., 2010), including at the *Rusingoryx* type locality (Wakondo), have yielded a large sample of this extinct alcelaphine that provides valuable taxonomic and

paleoecological insight. Our examination of this expanded fossil assemblage, in addition to the *Rusingoryx* type specimen, calls into question the placement of *Rusingoryx* within the genus *Megalotragus*. This paper (1) provides morphological and phylogenetic information indicating that *Rusingoryx* is taxonomically distinct from *Megalotragus* and (2) assesses the paleoecology of *Rusingoryx* and its relevance to late Quaternary extinctions in East Africa.

The Wasiriya Beds of Rusinga Island

Rusinga Island is located in Lake Victoria and separated from the mainland by a passage ~350 m wide and ~5 m deep (Whitehouse and Hunter, 1955; Fig. 1). The fossiliferous and artifact-bearing deposits overlying the Miocene strata on the island have been noted since L.S.B. Leakey's paleoanthropological exploration in the 1930s (Kent, 1942; MacInnes, 1956; Van Couvering, 1972; Leakey, 1974; Pickford and Thomas, 1984; Pickford, 1986). Pickford and Thomas (1984) proposed the term Wasiriya Beds to describe those sediments mapped by Van Couvering (1972) as the Wasiriya Terrace, following terminology introduced by Kent (1942). The deposits are primarily fluvial, recording a complex cut-and-fill system composed of silts, sands,

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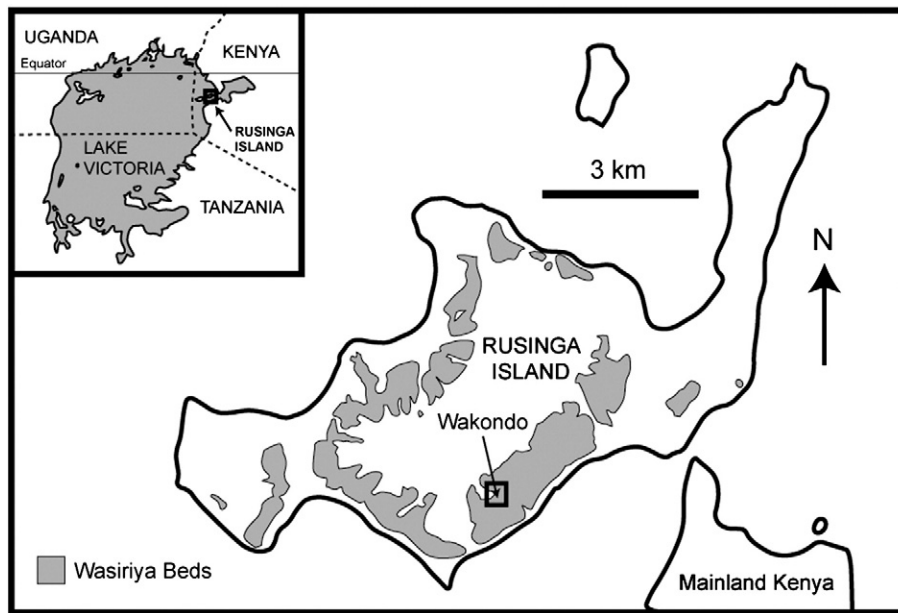


Figure 1. Outcrops of the Pleistocene Wasiriya Beds on Rusinga Island, Kenya. Wakondo is the type locality for *Rusingoryx atopocranion*.

conglomerates, and variably reworked tephra (Tryon et al., 2010). Radiocarbon dates on fossil gastropods from the Wasiriya Beds provide a minimum age estimate of between $28,670 \pm 600$ (AA-85426) and $41,700 \pm 1400$ (AA-85425) ^{14}C yr BP (32,475–33,765 and 43,899–46,811 cal yr BP) (Tryon et al., 2010). The stone artifacts recovered from the Wasiriya Beds include small unifacial and bifacial points and Levallois flakes and cores, typical of the Middle Stone Age (MSA) in East Africa (Tryon et al., 2010). In turn, this suggests a maximum age of ~285 ka for the Wasiriya Beds based on sites elsewhere in the region (Tryon and McBrearty, 2006; Morgan and Renne, 2008). Together, the archaeology and radiometric dates suggest that the Wasiriya Beds are of late–middle to late Pleistocene in age.

The faunal assemblage recovered from the Wasiriya Beds is dominated by alcelaphine bovids (Tryon et al., 2010), suggesting the predominance of open grassland vegetation (Vrba, 1980). Also present are arid-adapted ungulates including oryx (*Oryx gazella*) and Grevy's zebra (*Equus grevyi*). In addition to *Rusingoryx*, several extinct bovids are also documented, including the giant long-horn buffalo (*Syncerus antiquus*), a small unnamed alcelaphine (cf. *Damaliscus* sp.) also known from late Pleistocene contexts at Lukenya Hill in south-central Kenya (Marean and Gifford-Gonzalez, 1991; Marean, 1992), and an exceptionally large alcelaphine attributed to *Megalotragus* (Tryon et al., 2010). The extinct bovids are associated elsewhere with faunas indicative of dry and open habitats (Klein, 1980; Vrba, 1987; Marean and Gifford-Gonzalez, 1991; Marean, 1992). Together, these faunal indicators suggest an open and grassy environment that is substantially drier than at present.

The arid conditions inferred from the fauna, together with the fluvial nature of the sedimentary deposits and the proximity of Rusinga Island to the mainland, strongly suggest that the Wasiriya Beds document a period when the island was connected to the mainland. This is further supported by sedimentary cores and seismic profiles, which indicate drought-induced desiccation of Lake Victoria between 18 and 14 ka and during earlier periods of the Pleistocene (Johnson et al., 1996; Stager and Johnson, 2008), as well as historic records that document ~4 m of lake level fluctuations in response to changes in precipitation over the last approximately 200 yr (Nicholson, 1998). Given the shallow depth (~5 m) of the channel separating Rusinga Island from the mainland and the evidence for repeated lake level fluctuations, it follows that the Wasiriya Beds faunal assemblage, of which *Rusingoryx* was part,

was not an insular community and should be regarded as a mainland fauna. This precludes the Wasiriya Beds fauna from being isolated for sufficient time intervals to allow for endemic evolutionary change and speciation.

The cranial configuration of *Rusingoryx atopocranion*

Collected by M. Pickford at the Wakondo locality in 1983 (Fig. 1), the type specimen (Fig. 2) of *R. atopocranion* is curated at the National Museums of Kenya (KNM-RU 10553A). Also included with the type specimen, although unpublished by Pickford and Thomas (1984), is a right maxilla preserving the $\text{dP}^3\text{-M}^1$ and a mandible including the $\text{P}_4\text{-M}_3$, both of which are from the same locality as the cranium. The contrast in dental eruption between these two specimens indicates that they belong to separate individuals. Whether or not the mandible or maxilla belonged to the individual represented by the partial cranium is uncertain, although we concur with Harris (1991) that the three specimens are conspecific.

Pickford and Thomas (1984) point out numerous features of the *Rusingoryx* cranium, many concerned with the anatomy of the braincase and its orientation with respect to the facial region, that are unusual among alcelaphines and other bovids. Orienting the cranium as in Figure 2A, they note that the nuchal surface of the *Rusingoryx* cranium is almost in line with the roof of the skull, with a cranio-nuchal angle of 152° . They also observe substantial flexing of the base of the skull and that the sphenoid is located behind the orbits, as opposed to beneath them. Further, the temporal condyle is inclined downwards and thus oriented perpendicular to, rather than parallel to, the cranio-facial axis (Fig. 2). This unusual orientation of the temporal condyle relative to the facial axis would require dramatic reorganization of the mandible to allow for dental occlusion (Pickford and Thomas, 1984). Lastly, the jugular (paroccipital) processes and the foramen magnum are positioned nearly parallel to the facial axis rather than perpendicular (Fig. 2).

Harris (1991) observed that the *Rusingoryx* cranium shares a number of similarities with *Megalotragus* specimens recovered from Koobi Fora. For example, the upward doming of the posterior nasal bones and the positioning of the orbits are consistent with that of *Megalotragus* from Koobi Fora and elsewhere (Gentry and Gentry, 1978; Harris, 1991; Gentry et al., 1995; Vrba, 1997). In most respects,

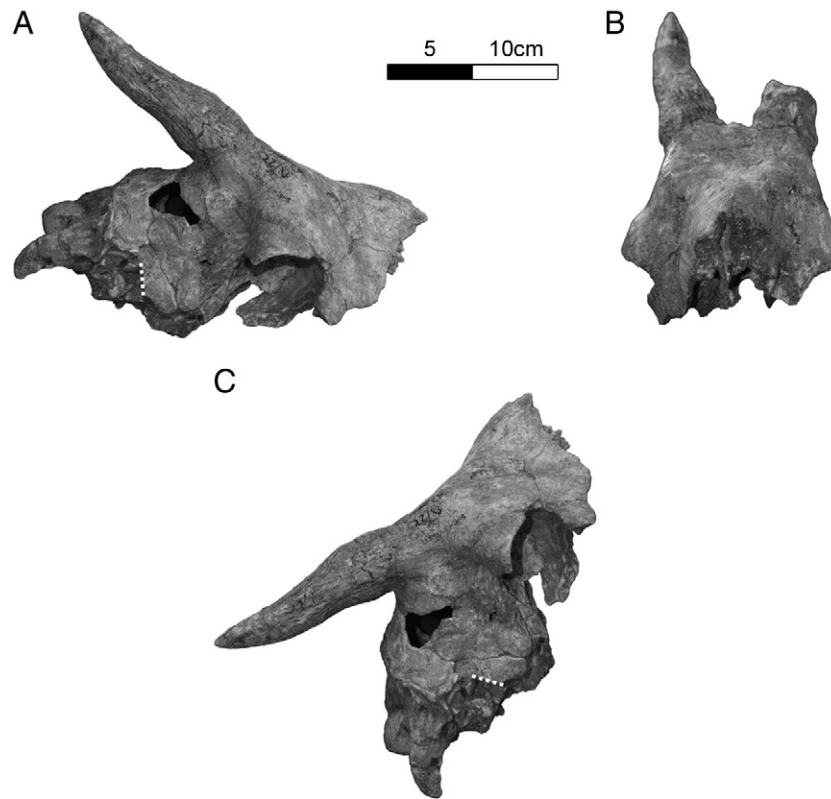


Figure 2. The type specimen of *Rusingoryx atopocranium* in (A) right lateral view, (B) anterior view, and (C) right lateral view with occiput oriented vertically. The dashed lines in A and C correspond to the plane of the temporal condyle.

we agree with his assessment of the cranial architecture of *Rusingoryx* and of its morphological affinities to *Megalotragus*. However, regarding the unusual angulation between the axes of the braincase and the facial region and the orientation of the temporal condyles, Harris (1991) suggests that reorientation of the cranium to match that of *Megalotragus* resolves the issue. As illustrated in Figure 2C, however, if one were to orient the cranium so that the plane of the occiput was positioned vertically, as is typical of *Megalotragus* (Harris, 1991:188; Vrba, 1997:149), the horns would project downwards and the facial region would project upwards. This orientation is extreme, even taking into account the upward doming of the nasal bones that characterizes *Megalotragus* and *Rusingoryx*. Our inspection of the *Rusingoryx* type specimen suggests that a more plausible explanation for the apparently unusual orientation of the cranium is that the type specimen has been subject to substantial *postmortem* deformation.

Pickford and Thomas (1984) note that the base of the skull, particularly the subphenoidal region, has undergone some *postmortem* deformation. They also note a minor amount of transverse compression. We suggest that the deformation observed by Pickford and Thomas (1984) at the base of the skull reflects substantial *postmortem* deformation that resulted in the complete reconfiguration of the braincase. Recent finds at the *Rusingoryx* type locality provide evidence supporting this argument. In 2010, we collected a block of sediment from Wakondo containing two partial skulls, with horn cores and dentitions indistinguishable from the *Rusingoryx* material collected by Pickford (Pickford and Thomas, 1984). The specimens are extremely fragmented, and the cranial bases are unfortunately not preserved. Although we lack more complete cranial material, the configuration of the mandible in the specimens we have recovered, particularly the orientation of the mandibular condyle relative to the horizontal ramus, is similar to that of other alcelaphine bovids (Fig. 3); it fails to show any drastic anatomical reconfiguration, as predicted by Pickford and Thomas (1984), to accommodate the unusual orientation of temporal condyles seen on the *Rusingoryx* type specimen.

Articulation of the mandible with the temporal condyle of the *Rusingoryx* type specimen would make dental occlusion effectively impossible, since the plane of the occlusal surface would be situated roughly perpendicular to the facial region and presumably to the plane of the maxillary teeth. Considering the morphology of the mandible, it is most likely that the temporal condyles of the *Rusingoryx* cranium were originally oriented more or less parallel to the facial axis, as is typical of other bovids. It follows that the perpendicular orientation of the temporal condyles and the unusual orientation of the braincase with respect to the facial region are in all likelihood exaggerated by severe *postmortem* deformation.

A proboscis in Rusingoryx?

Pickford and Thomas (1984) interpret the size and shape of the nasal bones as evidence that *Rusingoryx* had an extremely short face and a very large nasal aperture, leading them to suggest that *Rusingoryx* developed a proboscis. However, as also noted by Harris (1991), only the posterior portions of the nasal bones are preserved, making any inferences about the length of the face and the size of the nasal aperture extremely speculative. The preserved portion of the nasal region on the type specimen recalls that of *Megalotragus*, and we agree with Harris (1991) that it is very unlikely that *Rusingoryx* had a proboscis.

The taxonomic status of *Rusingoryx atopocranium*

It is generally agreed that all exceptionally large African alcelaphines belong within the genus *Megalotragus* and that all species of this genus are closely related (Gentry, 1978, 2010; Gentry and Gentry, 1978; Vrba, 1979; Klein, 1980; Harris, 1991; Brink et al., 1995; Gentry et al., 1995; Vrba, 1997; Brink, 2005; Gilbert, 2008). Gentry and Gentry (1978:356) provide the generic diagnosis for *Megalotragus*: “Very large alcelaphines, including the largest known, with narrow

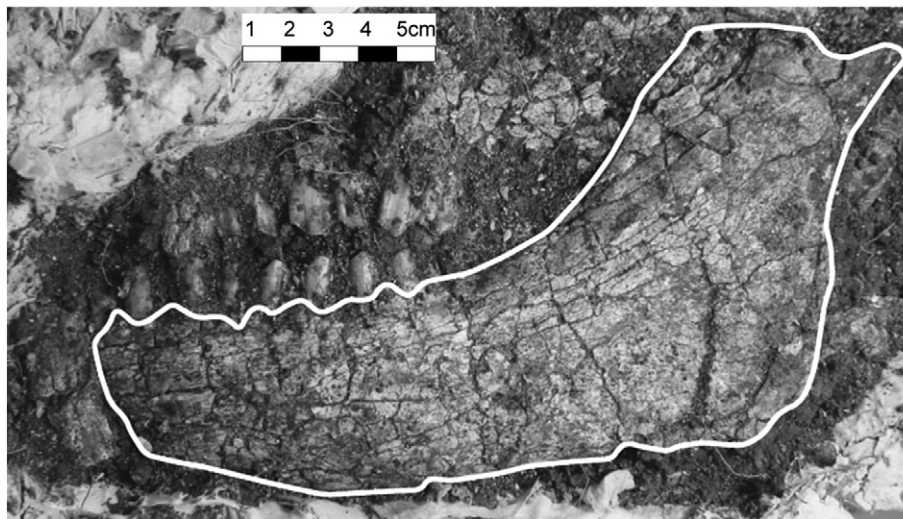


Figure 3. A nearly complete mandible of *Rusingoryx atopocranium* (outlined in white) in dental occlusion with a partial maxilla.

skulls and horn cores inserted obliquely in side view, behind the level of the orbits and close together, and with torsion that is clockwise from the base upwards on the right side; molar teeth tending to have a simple occlusal pattern; very short premolar rows; long legs.”

Harris (1991) first subsumed *Rusingoryx* into *Megalotragus*, arguing that the cranial architecture suggests congeneric affinity. This opinion was later supported by Vrba's (1997) phylogenetic analysis of fossil alcelaphines, which placed *Rusingoryx* within the *Megalotragus* clade. Below, we provide morphological evidence and a revised phylogenetic analysis suggesting that *Rusingoryx*, although closely related to *Megalotragus*, should be retained as a valid genus.

The horn cores of *Rusingoryx*

The horn cores of *Rusingoryx* exhibit a number of morphological characteristics that diverge from those of *Megalotragus*. These are outlined below.

1. *Horn-core length*: the horn cores of *Megalotragus* have been described as ranging from short to moderately long. Vrba (1997) reports horn-core lengths of 400 and 490 mm for two specimens of

M. isaaci from Koobi Fora. Five horn cores of *M. kattwinkeli* from Olduvai Gorge range from 240 to 385 mm (Gentry and Gentry, 1978), while a specimen from Bouri reaches an estimated 420 mm (Vrba, 1997), and two from Shungura measure 430 and 498 mm (Gentry, 1985). The right horn core of the *Rusingoryx* type specimen falls well outside the range of *Megalotragus*, measuring only 120 mm. Additional horn cores of *Rusingoryx* have been recovered during the course of our fieldwork on Rusinga Island ($n=8$), and seven previously accessioned Rusinga Island specimens at the National Museums of Kenya have also been identified as *Rusingoryx* (Fig. 4). The largest horn core (Fig. 4A) measures 160 mm in length, once again falling well below the range of *Megalotragus*. The remaining specimens lack the bases or tips, precluding additional measurements. However, there is nothing to suggest that they would differ substantially in size from those of the *Rusingoryx* type specimen or approach the size range of *Megalotragus*.

2. *Horn-core torsion and compression*: Gentry and Gentry (1978) note that the horn cores characterizing *Megalotragus* exhibit clockwise torsion from the base upward on the right side. This feature characterizes both *M. kattwinkeli* and *M. isaaci* (Harris, 1991;

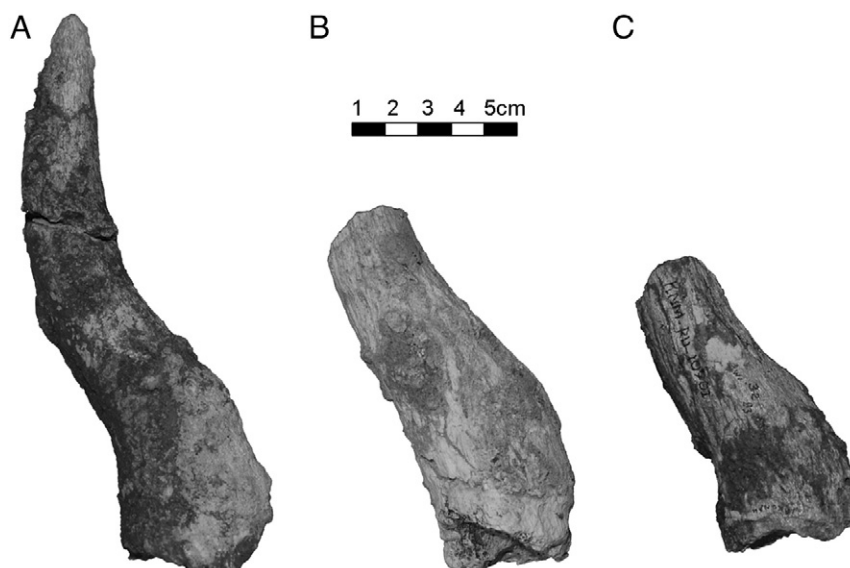


Figure 4. Horn cores of *Rusingoryx atopocranium* in right lateral view: (A) KNM-RU 49739, (B) RUP10-278, (C) KNM-RU 10701.

Vrba, 1997). Furthermore, the basal horn-core cross-sections of *Megalotragus* are compressed on the posterior aspect, with dorsoventral compression increasing towards the middle of the horn core (Harris, 1991; Vrba, 1997). Later *M. priscus* from southern Africa is also characterized by dorsoventral compression at the base of the horn core and clockwise torsion on the right (Broom, 1909; Brink, 2005). The horns cores of *Rusingoryx*, however, lack the torsion characterizing *Megalotragus* and the basal horn-core cross-section ranges from circular to sub-circular and lack compression throughout its length (Fig. 4).

3. *Width across horn-core bases*: the width across the horn-core bases of the *Rusingoryx* type specimen measures 62 mm, compared to a range of 139 to 147 mm for four specimens of *M. isaaci* from Koobi Fora (Harris, 1991), a range of 129 to 130 mm for three specimens of *M. kattwinkeli* from Olduvai (Gentry and Gentry, 1978), and widths of 115.5 and 170 mm for two specimens of *M. kattwinkeli* from Bouri (Vrba, 1997). This reflects the much smaller size of *Rusingoryx* compared to *Megalotragus*, consistent with the shorter length of the horn cores.

The dentition of Rusingoryx

The dental remains of like-sized fossil alcelaphines can be difficult to distinguish from one another. Indeed, Pickford and Thomas (1984) note that the dentitions assumed to belong to *Rusingoryx* had been previously misidentified as *Connochaetes*, and we initially encountered similar difficulties. In our previous report of the Wasiriya Beds fauna (Tryon et al., 2010), based on collections in 2009, many of the specimens now identified as *Rusingoryx* were attributed to Alcelaphini indeterminate or Alcelaphini cf. *Alcelaphus/Damaliscus*. Owing to the 2010 recovery of two partial skulls yielding horn cores and dentitions indistinguishable from the *Rusingoryx* material collected by Pickford, we are now able to confidently link the dentition of *Rusingoryx* (absent from the type specimen) to the diagnostic horn cores. Further surface collections on Rusinga Island in 2010 allow us to identify a number of dental features that set *Rusingoryx* apart from *Megalotragus* and from extant medium-sized alcelaphines, including the wildebeest (*C. taurinus*), hartebeest (*Alcelaphus buselaphus*), and topi (*Damaliscus lunatus*).

A number of partial mandibles ($n=82$) recovered from the Wasiriya Beds have been assigned to *Rusingoryx*. They are similar to those of *Megalotragus* in that the P_2 is consistently absent (15/15 specimens), the P_3 is substantially reduced, and the horizontal ramus is deep (Table 1). However, the teeth of *Rusingoryx* are substantially smaller than those of *Megalotragus*, which consistently yields dental measurements well beyond the range of extant alcelaphines (Harris, 1991; Klein and Cruz-Urbe, 1991; Vrba, 1997; de Ruiter, 2003). Figure 5 compares the occlusal length of the mandibular M_3 of *Rusingoryx* to that of extant alcelaphines and *Megalotragus* from Bouri and Koobi Fora. Also included are two very large alcelaphine teeth from the Wasiriya Beds that almost certainly belong to *Megalotragus* (a horn-core fragment that resembles *M. isaaci* further confirms the presence of *Megalotragus* on Rusinga Island). The teeth of *Rusingoryx* fall well below the range of *Megalotragus* and instead fall between

Table 1
Mandibular characters distinguishing *Rusingoryx* from *Megalotragus* and like-sized extant alcelaphines.

| Taxon | Tooth size | Mandibular depth | P2 presence/absence | P3 size |
|------------------------------|--------------|------------------|---------------------|------------|
| <i>R. atopocranium</i> | Medium–large | Large | Absent | Very small |
| <i>M. kattwinkeli/isaaci</i> | Very large | Large | Absent | Very small |
| <i>C. taurinus</i> | Large | Large | Absent | Small |
| <i>A. buselaphus</i> | Medium | Medium | Present | Medium |
| <i>D. lunatus</i> | Medium | Medium | Present | Medium |

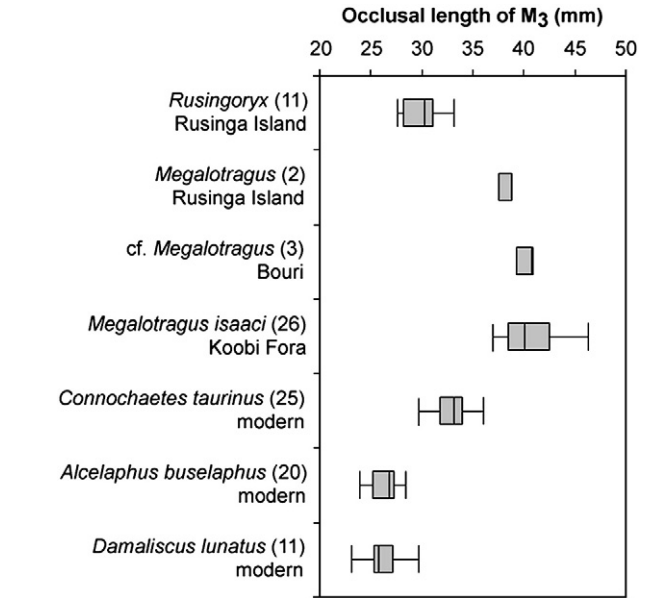


Figure 5. Box plots illustrating occlusal length of *Rusingoryx* mandibular M_3 s compared to extant alcelaphines and *Megalotragus* from Rusinga Island, Bouri, and Koobi Fora. Sample size in parentheses. Modern specimens are from the National Museums of Kenya.

modern wildebeest and hartebeest/topi. Although the *Rusingoryx* M_3 s overlap in size with extant alcelaphines, Bonferroni-corrected Mann–Whitney *U*-tests shows median occlusal lengths to differ significantly from those of wildebeest ($p=0.001$), hartebeest ($p<0.001$), and topi ($p=0.001$).

Rusingoryx can be further distinguished from like-sized extant alcelaphines in that the premolar row is exceptionally reduced (owing to the loss of the P_2 and reduction of the P_3), resulting in a markedly low premolar:molar row ratio (Fig. 6). We lack comparable measurements of *Megalotragus*, although its much larger size allows it to be readily distinguished from *Rusingoryx* (Fig. 5). Bonferroni-corrected Mann–Whitney *U*-tests show the premolar rows of *Rusingoryx* to be significantly smaller than extant wildebeest ($p<0.001$), hartebeest ($p<0.001$), and topi ($p<0.001$). Similarly, the premolar:molar row ratio of *Rusingoryx* is also significantly lower than wildebeest ($p=0.015$), hartebeest ($p=0.013$), and topi ($p=0.03$). The average premolar:molar row ratio characterizing *Rusingoryx* (0.29) falls below the range of 19 species of extant grazing bovids reported by Spencer (1995a, 1995b), suggesting a highly specialized grazing adaptation in *Rusingoryx*.

Concerning the maxillary teeth, the infundibula of the molars are simple compared to those of extant alcelaphines (Fig. 7). This simple occlusal pattern recalls those of *Megalotragus* (Gentry and Gentry, 1978), although in terms of size, they are intermediate between *Connochaetes* and *Alcelaphus/Damaliscus* (Fig. 7). The occlusal length of maxillary M_2 s belonging to *Rusingoryx* range from 22.0 to 26.8 mm ($n=13$), while those of *Megalotragus* from Koobi Fora and Bouri range from 29.4 to 35.3 mm ($n=6$) and 31.9–32.3 ($n=2$), respectively (Harris, 1991; Vrba, 1997), and a single specimen from Olduvai measures 31.6 mm (Gentry and Gentry, 1978). This further highlights the substantial reduction in size that distinguishes *Rusingoryx* from *Megalotragus*.

Phylogenetic analysis

In light of our expanded sample of *Rusingoryx* material, we provide a revised phylogenetic analysis of *Rusingoryx* and other fossil alcelaphines, drawing upon Vrba's (1997) phylogenetic study of alcelaphine cranial anatomy. The taxa included ($n=38$) and the

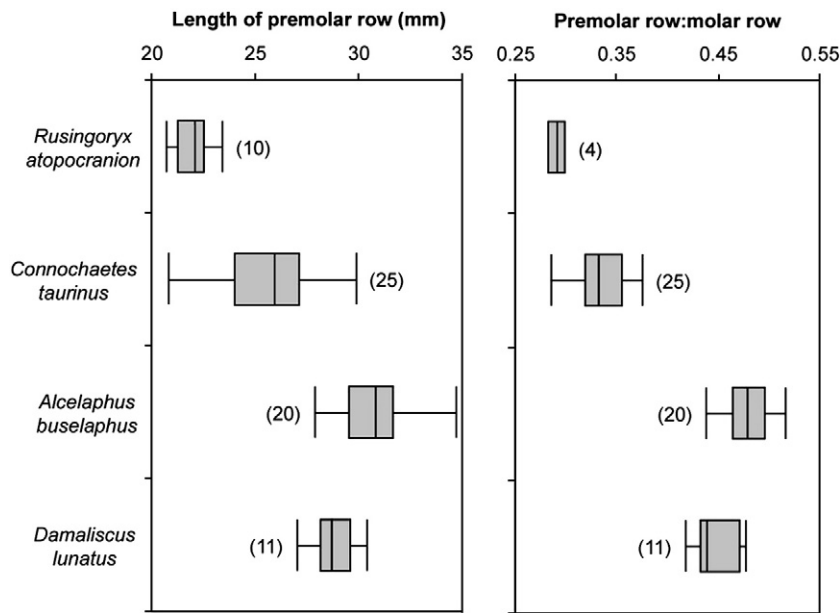


Figure 6. Box plots illustrating the length of the premolar row and the premolar to molar row ratio for *Rusingoryx* and extant alcelaphines. Sample size in parentheses.

phylogenetic characters used here ($n = 40$) are reported in detail by Vrba (1997).

Our study of the *Rusingoryx* material leads to the following additions and revisions to the *Rusingoryx* character states reported by Vrba (1997):

Character 7: the basal horn-core cross-section shows pronounced flattening laterally but not posteriorly (0), neither laterally nor posteriorly (1), or posteriorly but not laterally (2). Vrba (1997) assigned *Rusingoryx* a character state of 2, indicating posterior flattening of the basal horn core. However, our examination of the type specimen

and newly recovered horn cores indicates that the basal horn-core cross-section of *Rusingoryx* is nearly circular and lacks flattening on any aspect. This is consistent with Pickford and Thomas' (1984) description of the horn cores, and accordingly, we have re-assigned a character state of 1 for *Rusingoryx*.

Character 13: clockwise torsion of the right horn core is absent (0), incipient (1), or strong (2). For this character, Vrba (1997) assigned *Rusingoryx* an indeterminate value. We assign *Rusingoryx* a value of 0, noting that the type specimen and our sample of *Rusingoryx* horn cores lack clockwise torsion.

Character 19: the angle of forehead to braincase, or craniofacial angle, is low (0), moderately high (1), high (2), or very high (3). Vrba (1997) assigned *Rusingoryx* a value of 2. In light of the evidence that braincase of the *Rusingoryx* type specimen was likely subject to substantial *postmortem* deformation (Figs. 2–3), we conservatively assign *Rusingoryx* an indeterminate value.

Character 38: the $P_{2-4}:M_{1-3}$ ratio is markedly low with P_2 absent and P_3 very reduced (0), moderately low with P_3 less reduced (1), or higher with P_2 present in most specimens (2). The mandibular anatomy of *Rusingoryx* was previously unknown, and Vrba (1997) assigned it an indeterminate value. Our expanded sample of *Rusingoryx* material allows us to confidently assign *Rusingoryx* a value of 0.

Reanalysis of Vrba's (1997) character matrix with the amended character codings for *Rusingoryx* was performed in the phylogenetic software package TNT (Goloboff et al., 2000). Our analytical protocol consisted of the following: 10,000 Wagner tree builds using random addition of taxa; heuristic search of the Wagner trees for most-parsimonious topologies (MPTs) using tree bisection and reconnection (TBR), holding two MPTs per search, and a final round of TBR on the held trees. This heuristic search yielded 219 trees with lengths of 154 steps, ensemble consistency index of 0.46 and ensemble retention index of 0.78. The strict consensus of these trees is shown in Figure 8.

Rusingoryx was recovered outside of *Megalotragus* in all MPTs, placed sister to the clade composed of (*Megalotragus* (*Connochaetes* + *Oreonagor*), hereafter referred to as the "*Megalotragus* clade." Three characters support the monophyly of the *Megalotragus* clade to the exclusion of *Rusingoryx*: the presence of incipient or clockwise torsion of the right horn core (character #13; absent in *Rusingoryx* and plesiomorphic for the Alcelaphini); large to very large body size (character #20; *Rusingoryx* is medium bodied, which is the plesiomorphic condition); and high brain width across the parietal-

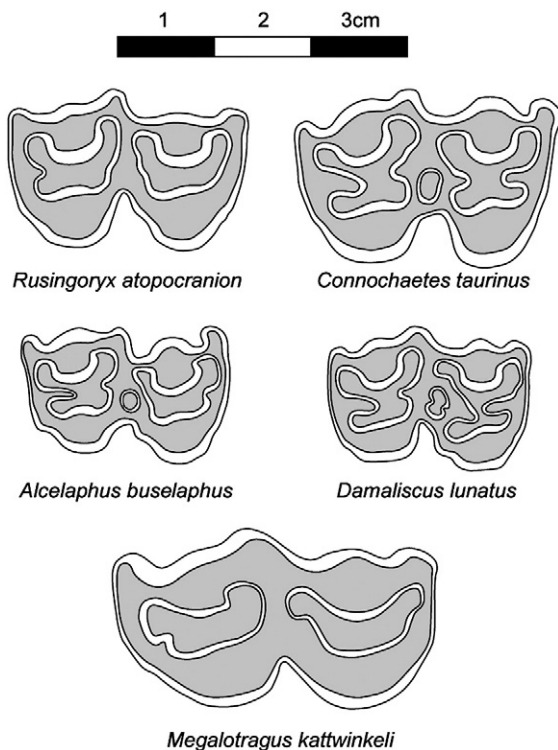


Figure 7. Occlusal view of the right maxillary M_2^2 of fossil *Rusingoryx atopocranion*, *Megalotragus kattwinkeli*, and modern *Connochaetes taurinus*, *Alcelaphus buselaphus*, and *Damaliscus lunatus*. Scale bar in centimeters.

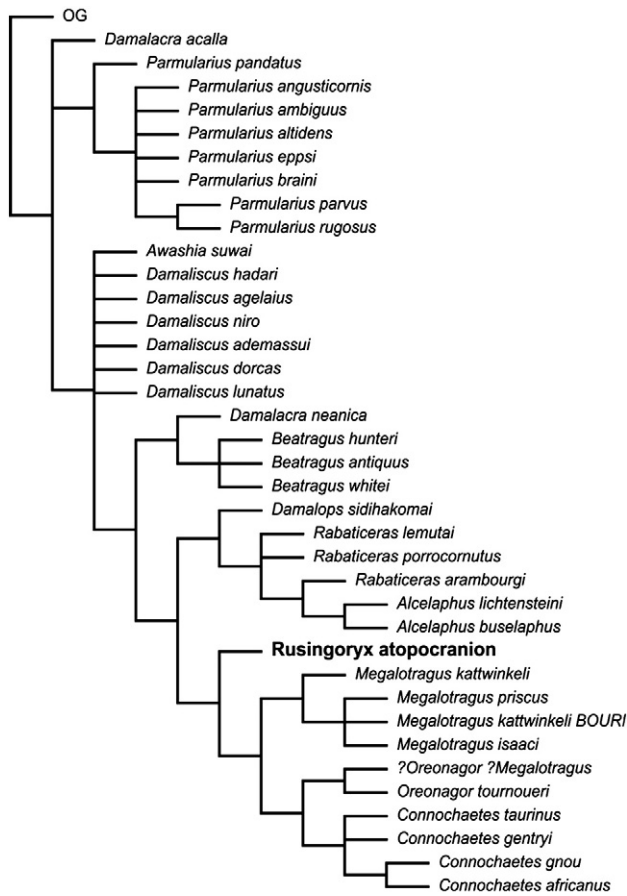


Figure 8. Strict consensus of 219 trees of length 154 steps for fossil Alcelaphini based on amended character codes for *Rusingoryx*. Data from Vrba (1997).

squamosal suture (character #21; *Rusingoryx* has only moderate width across the suture).

Our results differ from Vrba's (1997) phylogenetic analysis, which placed *Rusingoryx* within the *Megalotragus* clade, although it is fully consistent with the differences in horn-core morphology and body size that distinguish *Rusingoryx* from *Megalotragus*. Together, the morphological evidence and phylogenetic analysis supports a genus-level distinction in *Rusingoryx*.

The paleoecology of *Rusingoryx atopocranium*

Our previous discussion of the mandibular dentition of *Rusingoryx* points to a specialized grazing adaptation (Spencer, 1995b; Reed, 1996; Spencer, 1997; Sponheimer et al., 1999), as evidenced by the loss of the mandibular P₂ and the reduced premolar row (Fig. 6). We also note that the teeth of *Rusingoryx* are exceptionally hypsodont. Although the fossil sample lacks unworn mandibular M₃s on which to quantify the hypsodonty index (Janis, 1988), measurements on two specimens in early wear suggest a hypsodonty index >5, which would place *Rusingoryx* among the most hypsodont alcelaphine bovids (Janis, 1988; Marean and Gifford-Gonzalez, 1991; Sponheimer et al., 1999).

Table 2 provides additional ecomorphological data supporting a grazing adaptation in *Rusingoryx*. We compare the mandibular depth and premolar row length of *Rusingoryx* to extant bovid grazers, dicot feeders (browsers), and mixed feeders (Table 2). Extant data are from Spencer (1995b, 1997). The dietary classifications used by Spencer are in close agreement with isotopic observations of modern bovids (Cerling et al., 2003; Sponheimer et al., 2003), with the exception of

Table 2

Size-adjusted mandibular depth and premolar row lengths of *Rusingoryx* compared to extant bovids characterized by different feeding adaptations. Extant data from Spencer (1997).

| Taxon | Mandibular depth | Premolar row length |
|---------------------|------------------------|------------------------|
| <i>Rusingoryx</i> | 0.70–0.82 ^a | 0.28–0.33 ^b |
| Grass feeders | 0.67–0.92 | 0.46–0.69 |
| Dicot feeders | 0.46–0.72 | 0.61–0.78 |
| Mixed grass feeders | 0.59–0.67 | 0.49–0.57 |
| Mixed dicot feeders | 0.54–0.59 | 0.34–0.58 |

^a Range of 6 specimens.

^b Range of 4 specimens.

the lechwe (*Kobus leche*), which is classified as a grazer but may be a mixed feeder (Sponheimer et al., 2003). Following Spencer (1995b, 1997), mandibular depth is measured at the M₂/M₃ junction and standardized by the length of the molar row, which is isometrically correlated with body mass (Janis, 1990). The mandibles of *Rusingoryx* are deep and fully encompassed within the range of extant grazing bovids (Table 2). This deep mandibular corpus allows the mandible to accommodate hypsodont teeth, a feature characteristic of grazing ungulates (Vrba, 1980; Janis, 1988, 1995). The premolar rows, however, are extremely short and fall outside the range of extant bovids (Table 2).

To further explore the dietary habits of *Rusingoryx*, we employ dental mesowear analysis, after Fortelius and Solounias (2000). Mesowear analysis is based on facet development on the occlusal surfaces of ungulate maxillary molars as reflected by the relative amounts of tooth-on-tooth wear (attrition) as opposed to food-on-tooth wear (abrasion). Attrition tends to promote facet development and results in sharp tooth cusps. This type of wear pattern is associated with diets dominated by leafy vegetation (dicots). Alternatively, abrasion tends to generate round or blunt cusps and is associated with grass-dominated diets. The examination of cusp shape and occlusal relief allows one to distinguish ungulate browsers, grazers, and mixed feeders (Fortelius and Solounias, 2000). After Hofmann and Stewart (1972), grazers include those taxa consuming at least 90% grasses (monocots) and browsers include taxa consuming at least 90% dicotyledonous herbage; mixed feeders fall between the extremes and include taxa that alternatively consume monocots and dicots. Mesowear analysis has been successfully applied to reconstruct the dietary habits of a variety of fossil ungulates (Fortelius and Solounias, 2000; Franz-Odenaal and Solounias, 2004; Schubert et al., 2006; Merceron et al., 2007; Rivals et al., 2007; Schubert, 2007; Semperebon and Rivals, 2007; Stynder, 2009; Faith, 2011).

Following Fortelius and Solounias (2000), we rely on occlusal relief and cusp shape of the maxillary M² to reconstruct the dietary preferences of *Rusingoryx*. Occlusal relief was scored as either high or low, depending on the height of the paracone and metacone above the valley between them. Cusp shape along the buccal surface was scored as sharp, round or blunt, according to the degree of facet development. Teeth in early or advanced stages of wear, as well as unworn teeth, are excluded from the analysis.

The *Rusingoryx* fossil sample considered here includes 17 maxillary M²s, 65% of which are characterized by high cusps (11/17) and 100% (17/17) are characterized by round cusps. Hierarchical cluster analysis is used to compare the mesowear signature of *Rusingoryx* with those of 27 extant ungulates (extant data from Fortelius and Solounias, 2000) using the Paleontological Statistics (PAST) package (Hammer et al., 2001). The clustering algorithm used here is the unweighted pair group method with arithmetic mean (UPGMA). This analysis, which takes into account the percentage of high, sharp, and blunt teeth, groups the ungulates according to their feeding niche (grazers, browsers, and mixed feeders). In agreement with the ecomorphological evidence, the mesowear signature of *Rusingoryx* is clearly that of a grazer (Fig. 9).

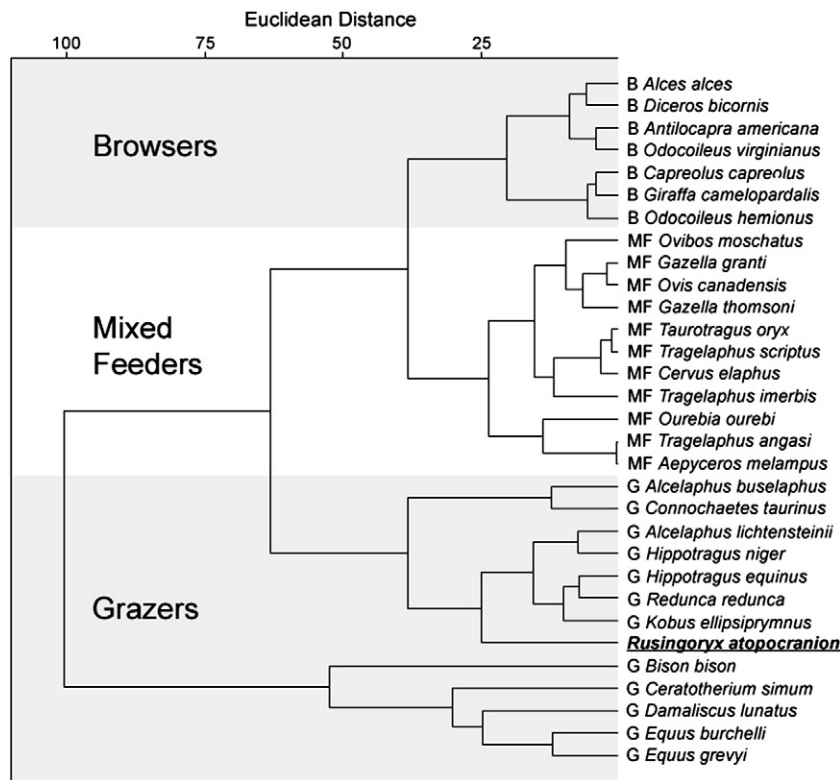


Figure 9. Cluster analysis of mesowear signatures for *Rusingoryx* and 27 extant ungulates (data from Fortelius and Solounias, 2000). Mesowear variables used are %high, %sharp, and %blunt cusps. G = grazers, MF = mixed feeder, B = browser.

Isotopic analysis of *Rusingoryx* and other Wasiriya Beds fauna is currently underway. Stable carbon isotope analysis of a single tooth attributed to *Rusingoryx* (Garret et al., 2010) falls within the range of extant hypergrazers (consuming >95% C₄ grass) (Cerling et al., 2003). Although the sample is limited, this is consistent with our assessment of the dental morphology, mandibular morphology, and mesowear signature of *Rusingoryx*.

Discussion

The taxonomic status of *Rusingoryx*

Our study of the *Rusingoryx* type specimen, supplemented by numerous fossils recovered during recent fieldwork on the Pleistocene Wasiriya Beds of Rusinga Island (Tryon et al., 2010), suggests that *Rusingoryx* is morphologically and systematically distinct from *Megalotragus*. *Rusingoryx* can be distinguished from *Megalotragus* on the basis of its substantially reduced size (Fig. 5) and numerous differences in horn-core morphology. Although the cranial architecture of *Rusingoryx* superficially resembles *Megalotragus* (Harris, 1991), the inclusion of *R. atopocranion* within *Megalotragus* would require substantial revision of the definition of *Megalotragus* (Gentry and Gentry, 1978) to incorporate a broad range of body sizes and horn-core morphologies.

The incorporation of new morphological evidence into Vrba's (1997) study of fossil alcelaphine systematics lends further support for a genus-level distinction between *Rusingoryx* and *Megalotragus*. Our revised phylogenetic analysis places *Rusingoryx* basal to the clade that includes *Megalotragus*, *Connochaetes*, and *Oreonagor*. Thus, not only would placement of *Rusingoryx* within *Megalotragus* require a major expansion to the morphological definition of *Megalotragus*, it would also render the genus *Megalotragus* paraphyletic. It follows that a generic distinction for *Rusingoryx* is supported on both morphological and systematic grounds.

The phylogenetic position of *Rusingoryx* at the base of the *Megalotragus* clade raises interesting questions regarding the origin of *Rusingoryx*. Following Vrba (1997), this clade likely shared a common ancestor some time between 3.0 and 2.5 Ma. If our phylogenetic hypothesis is correct, this would indicate that *Rusingoryx* persisted as a ghost lineage since the late Pliocene. Even if one places *Rusingoryx* within the *Megalotragus* lineage, however, there is no fossil evidence for a reduction in body size or transitional forms that would approach the morphology characterizing *Rusingoryx*. A similar issue also characterizes the small extinct alcelaphine documented in terminal Pleistocene deposits at Lukenya Hill (Marean and Gifford-Gonzalez, 1991; Marean, 1992) and Rusinga Island (Tryon et al., 2010). Both lineages appear fairly late in the Pleistocene, with little indication of their origins. This highlights an important gap in the Pleistocene fossil record of East Africa.

The paleoecology of *Rusingoryx atopocranion*

Consistent with the dietary habits of extant alcelaphine bovids, there is abundant evidence suggesting that *Rusingoryx* was a grazer. This argument is supported by ecomorphological evidence (Fig. 6, Table 2), mesowear analysis (Fig. 8), and stable carbon isotopes (Garret et al., 2010).

From an ecomorphological perspective, the severe reduction of the *Rusingoryx* premolar row is of particular interest as it falls outside the range of extant taxa (Table 2). Spencer (1995b) observed that the premolar row of secondary grassland inhabitants is smaller than inhabitants of edaphic grasslands. Noting that grazers inhabiting edaphic grasslands will at times consume more dicots than those inhabiting secondary grasslands, Spencer (1995b) hypothesized that a longer premolar row may allow bovids that are primarily grass feeders to consume dicots when necessary. If so, the severely reduced premolar row of *Rusingoryx* would preclude it from occasionally consuming dicots, effectively rendering it a hypergrazer.

It is possible that the reduced premolar row is also an adaptation for grazing in relatively arid grasslands, which were evidently abundant in the late Pleistocene of equatorial East Africa (Marean and Gifford-Gonzalez, 1991; Marean, 1992; Tryon et al., 2010). Similar to *Rusingoryx*, the small extinct alcelaphine first documented at Lukenya Hill consistently lacks the mandibular P₂ (Marean and Gifford-Gonzalez, 1991; Marean, 1992), which would contribute to a reduced premolar row. This animal is dominant in the terminal Pleistocene at Lukenya Hill and is also quite abundant on Rusinga Island, both of which have been interpreted as relatively arid grassland environments (Marean, 1992; Tryon et al., 2010). This tentatively suggests that the reduction of the premolar row is an adaptation for grazing in arid grasslands. Although we are unable to offer a functional explanation, this hypothesis is supported by observations of extant antelope and hippotragine bovids. Within these lineages, those taxa with a tendency to inhabit more arid environments, namely the springbok (*Antidorcas marsupialis*) and oryx, have the shortest premolar rows (Spencer, 1995b).

The association of *Rusingoryx* with oryx and Grevy's zebra in the Wasiriya Beds faunal assemblage attests to the relatively arid character of a primarily open grassland faunal community (Tryon et al., 2010). Today, Grevy's zebra is excluded from regions receiving more than 500 mm of rainfall per year and oryx are typically unable to compete with other grazers in regions receiving more than 750 mm of annual rainfall (Lamprey, 1963; Kingdon, 1982; Marean, 1992). *Rusingoryx* is also found in conjunction with *Megalotragus*, *S. antiquus*, and the small alcelaphine, which are elsewhere associated with faunas suggestive of dry and open environments (Klein, 1980, 1994; Vrba, 1987; Marean and Gifford-Gonzalez, 1991; Marean, 1992). This arid-adapted faunal community is replaced at the onset of the Holocene by mammalian faunas more typical of the present (Marean, 1992; Peters et al., 2008), perhaps as the result of increased moisture during the early Holocene (Bonnefille et al., 1990; Taylor, 1993; Bonnefille and Chalie, 2000; Kiage and Liu, 2006). *Rusingoryx* was evidently a component of the arid-adapted Pleistocene faunal community, and although the chronology of its extinction is unknown, it is not likely to have survived beyond the latest Pleistocene.

Was *Rusingoryx* an insular taxon?

Pickford and Thomas (1984) raise the possibility that *Rusingoryx* was an insular taxon restricted to Rusinga Island. As noted above, however, there is good reason to believe that the Wasiriya Beds were deposited at a time when Rusinga Island was connected to the mainland. This is consistent with geological evidence indicating periodic desiccation of Lake Victoria during arid intervals of the Pleistocene (Johnson et al., 1996; Stager and Johnson, 2008) and historic accounts indicating pronounced precipitation-mediated lake-level fluctuations (Nicholson, 1998). Although it is unlikely that *Rusingoryx* was an insular taxon, this raises an interesting question concerning its apparently limited geographic range in the fossil record. *Rusingoryx* has not been reported from equatorial East African sites including Lainyamok (Potts and Deino, 1995), Lukenya Hill (Marean, 1992), Nasera, or Mumba shelters (Mehlman, 1991), all of which include late-middle or late Pleistocene fossil assemblages. There is a reasonable possibility, however, that *Rusingoryx* fossils have been mistakenly attributed to wildebeest or hartebeest, given their similarities in size. The attribution of *Rusingoryx* to *Megalotragus* likely complicates the issue, since one might expect the dental remains of *Rusingoryx* to be of similar size as *Megalotragus*. Future fossil collections at other localities should shed light on the range of *Rusingoryx* and a revisiting of previously reported fossil assemblages is perhaps warranted.

Implications for late Quaternary extinction in East Africa

With respect to late Quaternary extinctions in East Africa, *Rusingoryx* is significant in that it expands the ecological range of the extinct

ungulates. Two members of the arid-adapted Pleistocene faunal community, including *Megalotragus* and *S. antiquus*, were among the largest of their lineages (Klein, 1980, 1994; Marean, 1990, 1992). Enlarged body size allowed them to consume high amounts of low-quality forage (Bell, 1971; Jarman, 1974; Demment and Van Soest, 1985), possibly including dry and tall grasses that were present during arid intervals of the Pleistocene (Marean, 1992). The small extinct alcelaphine is among the smallest of alcelaphine bovids and is characterized by extreme hypsodonty (Marean and Gifford-Gonzalez, 1991; Marean, 1992). Owing to its small body size, which limits it to smaller amounts of higher-quality forage (Bell, 1971; Jarman, 1974; Demment and Van Soest, 1985), it likely focused on the more nutrient-rich portion of grasses nearer to the ground, which would have been exposed by the grazing pressure of larger herbivores (Bell, 1971; Crawley, 1983; McNaughton, 1984, 1985). *Rusingoryx* falls between these extremes and apparently occupied the niche of a specialized medium-bodied grazer.

Following Brink's reconstruction of southern African Pleistocene ungulate communities (Brink, 1987, 1994, 1999; Brink and Lee-Thorpe, 1992), we propose that the later Pleistocene ungulate communities of East Africa followed a grazing succession similar to that documented in the Serengeti (Bell, 1971). In the Serengeti grazing succession, zebras (*E. burchelli*) consume large amounts of the uppermost portion of grass, which is of relatively low quality. Wildebeest follow up, consuming the more nutrient-rich middle portion of the grass. Once the grasses are sufficiently mowed, gazelles selectively consume the highest-quality grasses and shoots closer to the ground. We suggest that in the later Pleistocene of East Africa, the largest ungulates capable of consuming high amounts of low-quality forage (*Megalotragus*, *S. antiquus*, and *E. grevyi*) grazed the upper portion of tall and dry grasses. They were succeeded by medium-bodied ungulates, including *Rusingoryx*, which likely consumed the higher quality middle portion of the grass. Lastly, smaller ungulates, including the small alcelaphine, focused on the highest quality portion of grasses nearer to the ground. Increased moisture at the onset of the Holocene (Bonnefille et al., 1990; Taylor, 1993; Bonnefille and Chalie, 2000; Kiage and Liu, 2006) probably changed the composition of East African grasslands and disrupted this Pleistocene grazing succession. Although the chronology of the extinction for *Rusingoryx* and *Megalotragus* is uncertain, a cascading series of extinctions likely followed, spanning a range of body sizes within the arid-adapted Pleistocene grazing community, and an essentially modern faunal community emerged. Testing this hypothesis will, in part, require an improved chronology of extinctions throughout East Africa (e.g., Faith and Surovell, 2009).

In the global context of late Quaternary extinctions on the continents, the situation in Africa is often considered too poorly resolved to address with any confidence (Barnosky et al., 2004; Koch and Barnosky, 2006). However, our assessment of *Rusingoryx* and its associated faunal community (Tryon et al., 2010), together with evidence from Lukenya Hill (Marean, 1992) and throughout southern Africa (e.g., Klein, 1980; Brink, 1987), points to a geographically widespread pattern of grazer extinctions during the late Quaternary of Africa. Those species to disappear were typically grazers specialized in terms of extreme body size (e.g., *Megalotragus*, *S. antiquus*) and/or hypsodonty (e.g., the small alcelaphine, *Rusingoryx*). Similarities in the ecology of the extinct taxa clearly implicate environmental change as playing a prominent role in African extinctions. This is consistent with a growing body of literature suggesting the late Quaternary extinctions in southern and eastern Africa largely resulted from changes to the structure, availability, or productivity of Pleistocene grasslands (Klein, 1980; Brink, 1987, 1994; Brink and Lee-Thorpe, 1992; Marean, 1992; Faith, 2011).

Conclusion

We provide morphological and systematic evidence showing that *Rusingoryx* is distinct from *Megalotragus*. The confirmation of

Rusingoryx as a valid taxonomic entity, together with the presence of other extinct taxa (including *Megalotragus*) on Rusinga Island, suggests an increasingly complex pattern of ungulate biogeography and extinctions in the late–middle to late Pleistocene of East Africa.

Ecomorphological evidence and mesowear analysis clearly suggest that *Rusingoryx* was a grazer, and this is consistent with our limited observation of stable carbon isotopes (Garret et al., 2010). Further evidence suggests that *Rusingoryx* was specialized for grazing in arid grasslands. These grasslands were evidently abundant in the late–middle to late Pleistocene of equatorial East Africa (Marean and Gifford-Gonzalez, 1991; Marean, 1992; Tryon et al., 2010) and may have favored the development of an arid-adapted grazing succession similar to that observed in the present-day Serengeti. The disappearance of these arid grasslands at the onset of the Holocene would have disrupted the arid-adapted grazing succession, contributing to the extinction of *Rusingoryx* and other ungulates.

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