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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.

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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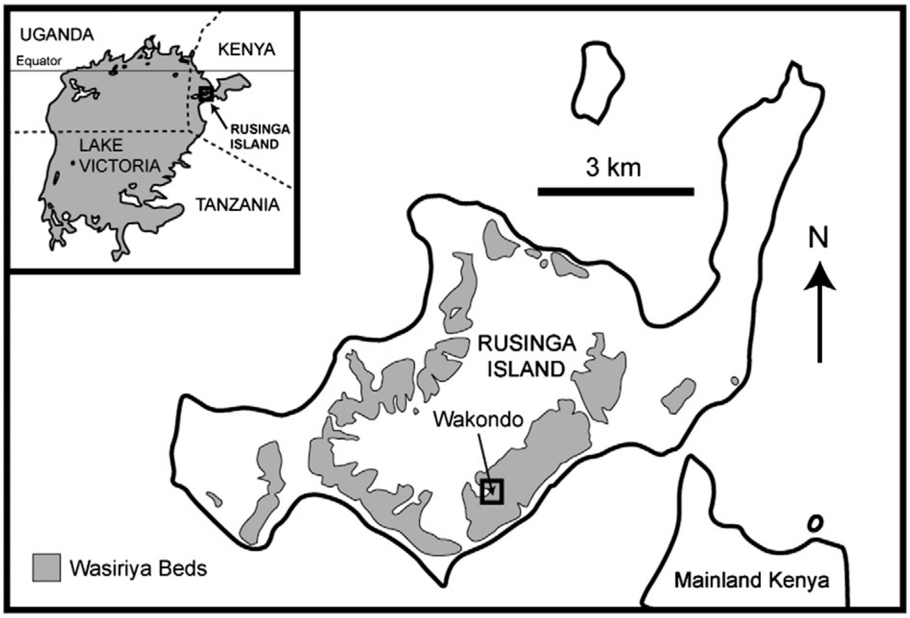

Figure 1. Outcrops of the Pleistocene Wasiriya Beds on Rusinga Island, Kenya. Wakondo is the type locality for *Rusingoryx atopocranion*.

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 ± 600 (AA-85426) and 41,700 ± 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 dP^3–M^1 and a mandible including the P$_4$–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,