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NEW RHINOCEROTIDAE FROM THE KISINGIRI LOCALITIES (LOWER MIOCENE OF WESTERN KENYA)

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ABSTRACT—We describe new material of Rhinocerotidae recently collected in western Kenya. A skull from Karungu is one of the best-preserved Miocene skulls in Africa. It differs substantially from that of *Rusingaceros leakeyi*, the only other relatively well-known rhino from this region and age, in its degree of brachycephaly, possession of a deep nasal notch, and long nasal bones that probably carried a horn of moderate size. Miocene African rhinos are still too poorly known to resolve their phylogenetic relationships, but we tentatively assign this skull to a new species of *Victoriaceros*, a genus whose type species comes from the younger site of Maboko, although the Karungu skull has a much smaller nasal horn. A parsimony analysis resolves them as sister species within the Elasmotheriini, close to the other African genera *Turkanatherium* and *Chilotheridium*, but we consider this result debatable, as *Victoriaceros* differs considerably from them. Still, they might all be descended from European forms. A partial skull from Gumba is assigned to the Aceratheriini, making it one of the earliest representatives of this group and suggesting that the origin of this tribe could be African.

<http://zoobank.org/urn:lsid:zoobank.org:pub:2B1E8135-CCD4-43EB-826B-6DF7176DC74E>

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

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INTRODUCTION

The Kisingiri Volcano, which formed at the western extent of Kenya's Nyanza Rift, is associated with some of the richest fossil assemblages from the early Miocene in East Africa (Fig. 1; Pickford, 1986; Drake et al., 1988; Peppe et al., 2009; Michel et al., 2014; Driese et al., 2016). The best-known Kisingiri locality, Rusinga Island, has been the focus of extensive paleontological and geological research, spanning more than eight decades and producing tens of thousands of fossil remains. With expeditions driven primarily by the discovery of early fossil apes (Leakey, 1943; MacInnes, 1943; Le Gros Clark and Leakey, 1950, 1951; Andrews, 1974; Andrews and Simons, 1977; Teaford et al., 1988), the Miocene deposits on Rusinga have yielded more than 100 species of vertebrate animals (Pickford, 1986; Werdelin and Sanders, 2010), exquisitely preserved invertebrate fauna (Verdcourt, 1963; Wilson and Taylor, 1964; Paulian, 1976; Thackray, 1994), and abundant paleobotanical remains (Chesters, 1957; Collinson et al., 2009; Maxbauer et al., 2013; Michel et al., 2014). For this reason, Rusinga is a critical reference assemblage for

studies of lower Miocene paleobiology and of East African floral and faunal succession.

Despite being geographically close to Rusinga, the Kisingiri fossil sites near Karungu have received relatively little attention. These deposits flank the southwestern extent of Kisingiri and were the focus of some of the earliest paleontological investigations in East Africa (Andrews 1911, 1914; Newton, 1914; Oswald, 1914). Nevertheless, a nearly complete lack of primate specimens at Karungu resulted in its relative obscurity, with only sporadic excavations taking place there in the intervening years (see Pickford, 1986). Based on the early paleontological work at Karungu, the assemblages have typically been compared with Rusinga's Hiwegi Formation fauna (Pickford, 1981) and are thought to be approximately the same age (e.g., Drake et al., 1988). If so, faunal differences between Rusinga and Karungu—notably the dearth of primates and small mammals at the latter—could be the result of subtle variations in habitat and/or differences in depositional environment. The relative lack of research at Karungu, however, has made such conclusions tentative.

Recent field work on Rusinga Island (McNulty et al., 2007; Peppe et al., 2009; Michel et al., 2014) and now at Karungu as part of the REACHE (Research on East African Catarrhine and Hominoid Evolution) project (Driese et al., 2016; Lehmann

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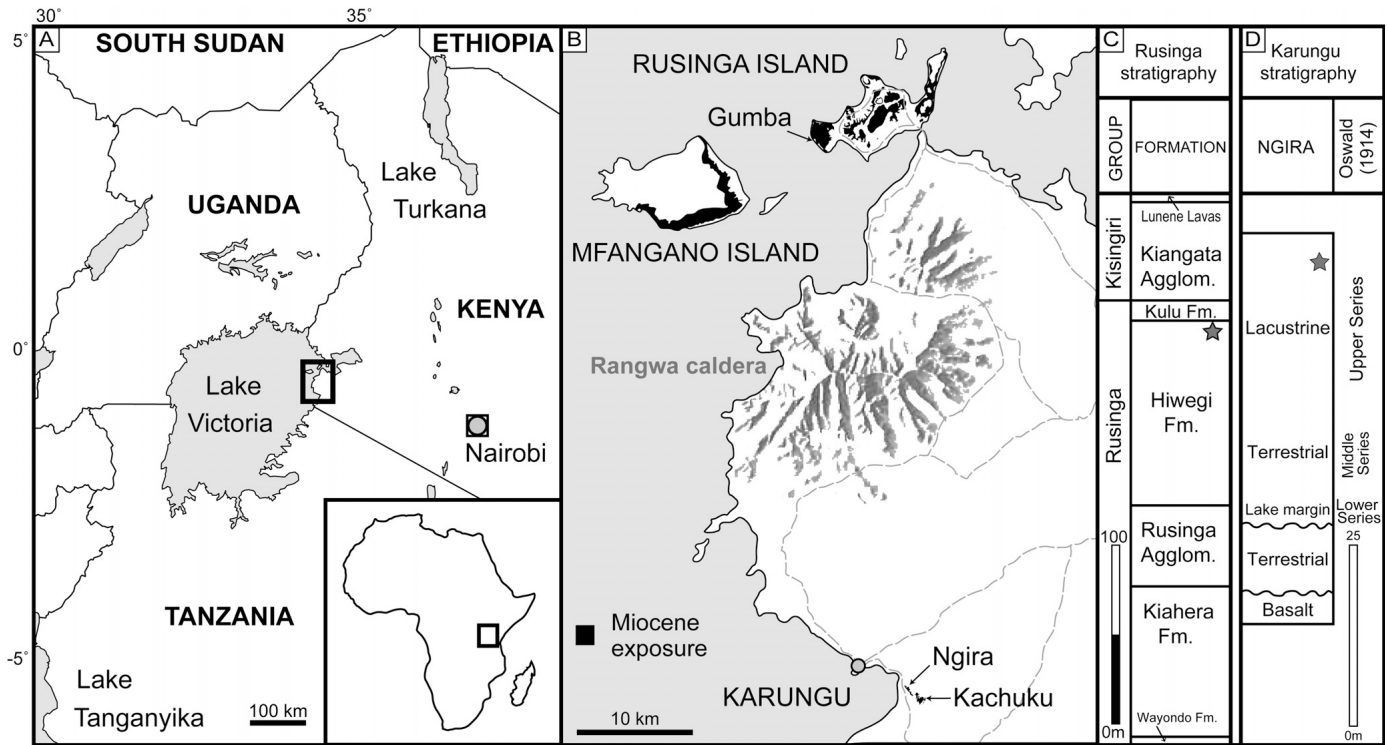


FIGURE 1. Location maps and stratigraphy of Rusinga Island and Karungu, Kenya. **A**, location map of Rusinga Island and Karungu in the north-eastern corner of Lake Victoria, Kenya. Solid black box indicates location shown in **B**; **B**, location of Rusinga Island, Mfangano Island, Karungu, and the remnant of the Kisingiri Volcano, the Rangwa caldera. Miocene exposures indicated in black; **C**, local stratigraphy for Miocene deposits on Rusinga Island. The Gumba Beds are likely younger than the Kiahera Formation. Rusinga stratigraphy from Peppe et al. (2009). Gray star indicates stratigraphic position of an ash dated to ca. 18 Ma (McCollum et al., 2013); **D**, stratigraphy for the Karungu Miocene localities. Depositional environments interpreted for Karungu stratigraphy at the Ngira locality from Driese et al. (2016) and Lehmann et al. (2014) and related to the stratigraphy of Oswald (1914). Gray star indicates the approximate stratigraphic position of an ash deposit dated to ~17.5–17.7 Ma (Drake et al., 1988).

et al., 2014; McNulty et al., 2014a, 2014b) is helping to provide much better resolution to these faunal communities through new fossil collection and excavations, as well as revisions of stratigraphic and geochronological relationships both within and among localities. Here, we report the discovery of two important new rhinocerotid cranial specimens that resulted from those projects. The first is a nearly complete cranium discovered in 2012 at the Karungu locality of Kachuku (Fig. 1B). The second, a palatal specimen preserving most of the cheek teeth, was discovered in 2007 in the Gumba Beds on Rusinga at locality R74 (Fig. 1B). Both specimens add important new information about this relatively underrepresented group in the early Miocene of East Africa and aid in developing a more detailed understanding of the relationship between the faunas of Rusinga and Karungu.

Geological Context

Kisingiri fossil localities are found within a sequence of primarily volcanic and volcanoclastic deposits that accumulated over the course of as much as a few million years during the development and eruptive history of the carbonatite-nephelinite Kisingiri Volcano (McCall, 1958; Van Couvering, 1972; Drake et al., 1988). Volcanic activity in this area resulted from intense East African rifting starting in the early Miocene (Ebinger, 2005), and the Rangwa dome that underlies the remnants of the Kisingiri Volcano sits at the terminus of the failed Nyanza Rift arm (Fig. 1). Rusinga Island likely formed during faulting as part of the post-eruptive graben wall to the north of Kisingiri, whereas the Karungu deposits formed just beyond the southern graben wall (Drake et al., 1988).

Deposits on Rusinga record a long section of Kisingiri's eruptive history, from the volcanoclastic Wayando Formation at the base of the stratigraphic sequence to the volcanic Lunene Lavas that cap it (Fig. 1C). Fossils have been found throughout the stratigraphic formations in the Rusinga Group, with the majority deriving from a variety of fluvial, alluvial, and volcanoclastic deposits in the Hiwegi Formation (e.g., Van Couvering, 1972; Pickford, 1986; Conrad et al., 2013; Jenkins, 2013; Maxbauer et al., 2013; Michel et al., 2014). Despite being the focus of some of the earliest K-Ar studies (Evernden et al., 1964; Bishop et al., 1969; Van Couvering and Miller, 1969), the age of deposits on Rusinga has been difficult to constrain due to the unique chemistry of volcanic materials and, in many cases, the significant post-depositional alteration of dateable minerals, such as biotite (see Drake et al., 1988). Dates published by Drake et al. (1988) suggested that the base of the Hiwegi Formation was ~17.8 Ma, and those authors interpreted the entire Rusinga Group sequence to have accumulated quickly, in at most a few hundred thousand years. More recent analyses, however, indicate that Rusinga's mammalian faunas were deposited over as much as a few million years, beginning ~20 Ma in the Wayando Formation until ca. 17 Ma in the Kulu Formation (Peppe et al., 2009; McCollum et al., 2013). It is important to note that these new age constraints are still preliminary, but they indicate a much longer depositional time during the early Miocene of Rusinga.

Unfortunately, the Gumba Beds cannot be reliably situated within Rusinga's otherwise well-documented stratigraphy. The Gumba Beds sit in a fault-bounded, down-dropped block, surrounded by discontinuous exposures of the Kiahera Formation that dip in the opposite direction to the Gumba Beds, which prevents any correlation between the fossil deposits and the

surrounding stratigraphy. Additionally, the Gumba Beds lack any of the diagnostic features of Rusinga's other stratigraphic formations, making lithostratigraphic correlation impossible. Previous workers have suggested that deposits at locality R74 may be related to the Wayando or Kulu Formations (Drake et al., 1988), but in both cases the evidence is weak. The latter correlation was based in part on the supposed presence of the rhinocerotid *Chilotheridium pattersoni* in the Gumba Beds and the Kulu Formation, but in fact this species can only be definitively identified at its type locality Loperot (Geraads, 2010). Alternatively, if one looks at the stratigraphic dip of the Gumba Beds within the fault-bounded block compared with that of the surrounding beds of the Kiahera Formation outside the fault block, it seems likely that the Gumba Beds were down-dropped below the Kiahera Formation. If verified, this would suggest that the Gumba Beds postdate deposition of the Kiahera Formation and therefore cannot be correlative with the older Wayando Formation. Therefore, we interpret the specimen from Gumba to have been deposited between ~19 and ~17 Ma. However, additional geochronological work is necessary to test this interpretation.

The age of the early Miocene deposits near Karungu are likewise relatively poorly constrained. Biostratigraphic evidence suggests a close similarity between Karungu assemblages and those from Rusinga's Hiwegi Formation (Van Couvering and Van Couvering, 1976; Pickford, 1981), and this is consistent with lithostratigraphic correlations between localities (Van Couvering and Van Couvering, 1976). Unfortunately, neither of Karungu's primary collecting sites, Ngira and Kachuku, has volcanic deposits among the fossiliferous beds. Ash layers become somewhat more common stratigraphically above the fossil-bearing units (i.e., the Upper Series of Oswald, 1914; Driese et al., 2016; Lehmann et al., 2014), and one near the top of the sequence at Ngira was dated by Bishop et al. (1969) to 23.1 ± 0.4 Ma (Fig. 1D). Like Rusinga, however, post-depositional alteration of dateable minerals is problematic at Karungu and indicates that the dates reported by Bishop et al. (1969) are likely to be incorrect. Drake et al. (1988) re-dated the same ash bed to 17.7 ± 0.06 and 17.5 ± 0.2 Ma using total-fusion K-Ar methods (Fig. 1D). Yet, even these age estimates may not be accurate, as has been shown by recent reanalysis of Rusinga's geochronology (Peppe et al., 2011; McCollum et al., 2013). Hence, a precise age of the Karungu faunas awaits further geochronological testing.

Within Karungu, the stratigraphic correlations of Ngira and Kachuku are still based primarily on Oswald's (1914) original stratigraphic work, but seem reasonable based on our geologic surveys. The rhinocerotid cranium reported here was found at Kachuku within a poorly lithified sandstone from Oswald's (1914) Middle Series, which we interpret to be primarily fluvial deposits (Driese et al., 2016). Based on this correlation, we hypothesize that this specimen is older than ~17.7 Ma.

Lower Miocene Rhinocerotidae

The entire sample of Rhinocerotidae collected at Rusinga prior to 1963 was described by Hooijer (1966), but no further study of this or of more recently collected material has been published since, with the exception of the brief review by Geraads (2010). Prior to this review, lower and middle Miocene African Rhinocerotidae were all assigned to a few genera, namely, *Aceratherium* Kaup, 1832, *Dicerorhinus* Gloger, 1841, *Brachypotherium* Roger, 1904, *Paradicerus* Hooijer, 1968, and *Chilotheridium* Hooijer, 1971, to which was more recently added *Ougandatherium* Guérin and Pickford, 2003. It is obvious, however, that this group is in need of revision, and that some of these genera have been incorrectly identified (Geraads, 2010). The main source of confusion is that, relative to their taxonomic diversity, rhinos do not display many clearly diagnostic features

(Heissig, 1981); hence, building a systematic scheme upon incomplete remains is risky. Teeth are the most commonly found remains, but clear differences between the modern *Ceratotherium simum* and the closely related *Diceros bicornis* or even the congeneric *C. mauritanicum* demonstrate that variation in dental traits should be interpreted cautiously. By contrast, nasal and horn characters conform to genetic studies suggesting a close relationship between these two modern African forms; the same is true of the two Asian one-horned forms of the genus *Rhinoceros*—whose teeth are also markedly different—showing that rostral features are much more reliable than dental characters, at least with regard to modern and recent taxa.

Thus, we believe that the first step towards understanding rhinocerotid phylogeny should be the identification of well-defined groups, based upon complete, well-preserved remains: the Kachuku skull is one such specimen; the Gumba palate, although less well preserved, nevertheless provides important new information on the diversity of Lower Miocene rhinocerotids in East Africa.

Institutional Abbreviations—KA, Karungu; KNM, National Museums of Kenya, Nairobi, Kenya; NHMUK, Natural History Museum, London, U.K.; RU, Rusinga.

Anatomical notes—Measurements are in mm. Open nomenclature follows Bengtson (1988).

SYSTEMATIC PALEONTOLOGY

Order PERISSODACTYLA Owen, 1848

Family RHINOCEROTIDAE Gray, 1821

Genus *VICTORIACEROS* Geraads, McCrossin, and Benefit, 2012

Type Species—*Victoriaceros kenyensis* Geraads, McCrossin, and Benefit, 2012.

Diagnosis—A rhinoceros with a short, deep skull, long nasal bones (at least in the male), deep nasal notch reaching the level of P2/P3, orbit located far anteriorly and not far from the nasal notch, and concave frontoparietal profile. Premolar row short; upper molars with a strongly constricted protocone and a thick anterochet. Anterior teeth unknown, but certainly present.

VICTORIACEROS HOOIJERI, sp. nov.

Holotype—KNM-KA 57652.

Type Locality—Karungu (Kachuku sub-locality; UTM Arc 1960: 36 M 0634120 9904535), Kenya, lower Miocene.

Derivation of the Name—In acknowledgment of the pioneering work of D. A. Hooijer on African rhinoceroses and other Perissodactyla.

Differential Diagnosis—A species of *Victoriaceros* with a narrow skull, narrow nasals, moderately concave frontoparietal profile, orbit with incipient inflation of the supraorbital processes, occiput slightly inclined forwards, and 'V'-shaped choanae. This species differs from *V. kenyensis* in its shallower dorsal concavity of the skull (with the deepest point located more rostrally), less brachycephalic skull, laterally expanded nuchal crest, slightly inclined occiput, narrower nasals, less prominent supraorbital processes, 'V'-shaped and less rostrally expanded choanae, probably larger I1s, and absence of lingual basal expansion from the hypocone towards the protocone on the molars.

Description

The skull KNM-KA 57652 from the Kachuku sub-locality near Karungu is one of the best-preserved specimens of African rhinos (Figs. 2A–C; S2). It lacks only the anterior end of the premaxillae, the left DP1–M1, and the right DP1 and P3. Although not perfectly symmetrical, the skull shows no evidence of significant crushing or distortion, as shown, e.g., by the complete

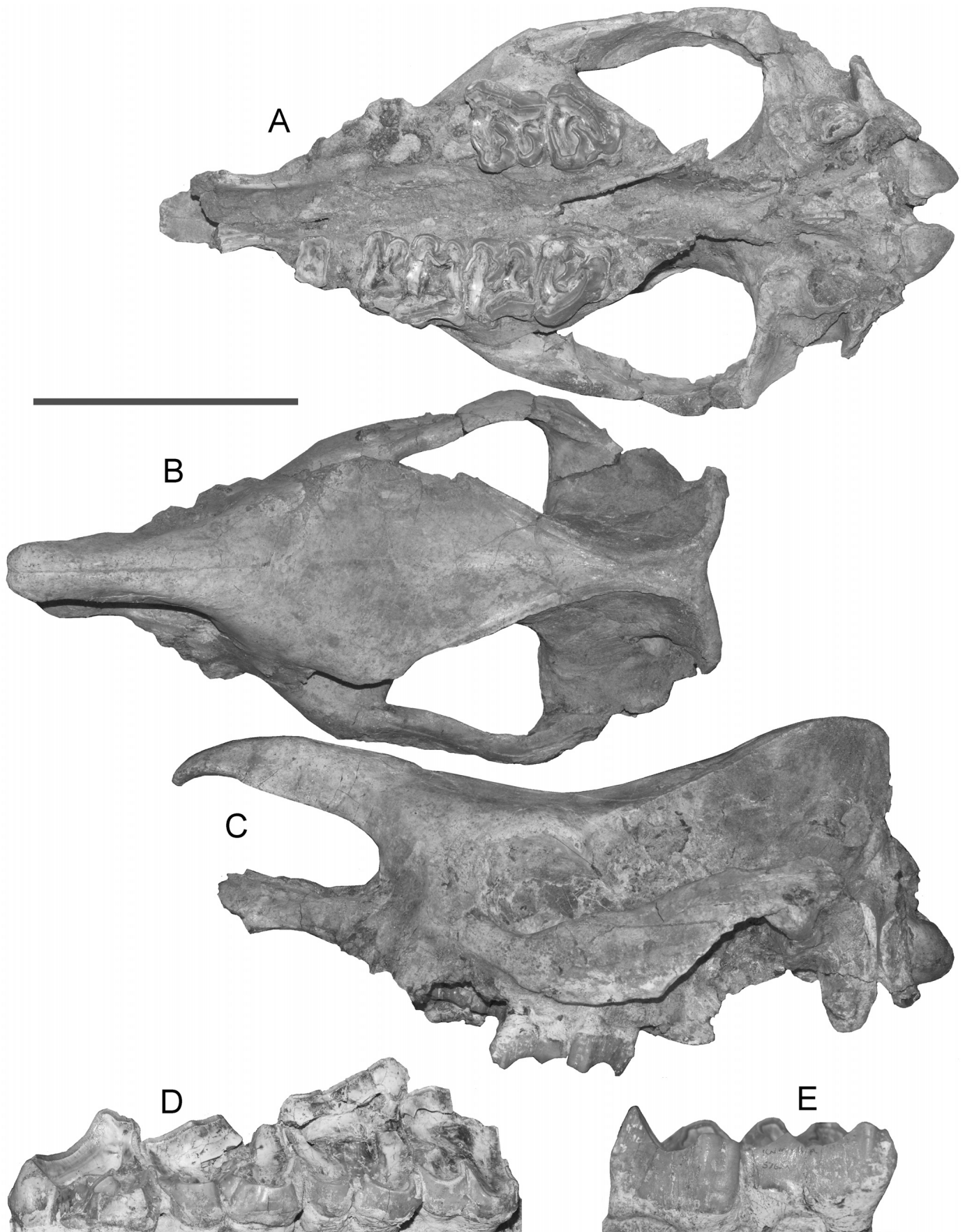


FIGURE 2. *Victoriaceros hooijeri*, holotype cranium KNM-KA 57652 from Karungu-Kachuku, in **A**, ventral view; **B**, dorsal view; and **C**, lateral view; **D**, oblique view of right P4–M3; **E**, buccal view of left M2–M3. Scale bar equals 20 cm (**A–C**) and 10 cm (**D, E**).

zygomatic arches. The most distinctive features are described below; for an exhaustive character states description, see our data matrix in Supplementary Data. Among modern forms, it most resembles the Sumatran rhino, *Dicerorhinus sumatrensis*, in overall shape. The dorsal profile of the skull is markedly and regularly concave, but not extremely so; the deepest part of the concavity is located above the postorbital processes. The most remarkable feature of the skull is the shape of the nasal bones, which are unfused—in spite of the considerable ontogenetic age of the specimen—and bear no incipient nasal septum. Their free part (rostral to the bottom of the nasal notch) is extremely long and slender; in dorsal view, they first narrow sharply but remain of almost uniform width for most of their length, terminating in a rounded rostral tip; in lateral view, their dorsal convexity increases rostrally, and their lateral borders are somewhat expanded into vertical flanges that reinforce this otherwise weak structure. There is no doubt that these nasal bones bore a horn, the presence of which is confirmed by slight rugosities on their dorsal surface; however, even allowing for a possible minor transverse crushing, it is clear that the horn was small, as these bones are quite narrow. There is no evidence of a second horn farther posteriorly on the skull. The orbit is located far rostrally with respect to the tooth row, because its front border is above M1; it is remarkably close to the bottom of the nasal notch, located above the distal part of the (missing) P2. A small, slit-like infraorbital foramen opens just behind the nasal notch. The ventral border of the orbit is rounded, so that its limit is not sharp. On the left side of the skull, a small postorbital process is preserved, and on both sides the supraorbital area is inflated without forming a true supraorbital process or tubercle. Behind the orbit, the zygomatic arch is quite deep, but is not much expanded laterally, so that the temporal fossa is not very broad. The temporal lines are strong, almost ridge-like, and sharply delimit the temporal fossae from the dorsal skull roof; they first converge gently behind the orbits but remain clearly separated; caudally, they abruptly diverge to form a broad occipital crest. The trapezoidal occipital surface is slightly inclined forward, so that its top is distinctly less caudal than the occipital condyles. It is much broader in its ventral part, where its breadth is increased by laterally expanded posttympanic flanges that curve only slightly rostrally to meet the postglenoid processes but without fusing with them. On their rostral side, these postglenoid processes bear an extension of the articular surface for the lower jaw, but this surface does not extend to their lateral side. The basioccipital bears a strong but short median crest. The 'V'-shaped choanae almost reach the level of the mesial border of M3. Cranial measurements are provided in Table 1.

Unfortunately, the anterior ends of the premaxillae are missing, but because their size sharply increases towards the break, large incisors were certainly present. The cheek teeth are incompletely preserved and rather worn; the molar row is much longer than the premolar row (see Table 2 for measurements). A DP1 is represented by its alveolus only; P2 is extremely worn; P3 is missing on both sides. The P4 is also extremely worn, which certainly decreased its length, but it must have been broad, with a protoloph broader than the metaloph; the lingual notch between them is deep in spite of the heavy wear, and these lophs were unconnected by a lingual bridge (molariform structure of

TABLE 1. Main cranial measurements (in mm) of KNM-KA 57652.

Length of the nasal notch (4) = 175
Distance from orbit to occipital crest (8) = 320
Distance from orbit to nasal notch (9) = 95
Distance between temporal lines (17) = 34
Supraorbital width (19) = 205
Bizygomatic breadth (21) = ca. 310
Skull length, from occipital crest to tip of nasals (27) = 550
Length from occipital condyle to M3 = 272

Numbers in parentheses refer to Guérin, 1980:table 1.

Heissig, 1969). The M1, preserved on the right side, is much broader than P4; the protocone is rounded lingually and bordered by a slight mesiolingual cingulum, but nothing is visible of the central part of the tooth. The right M2 shows abnormal wear in the area of the paracone, but the left one is well preserved. The labial paracone fold is moderate, the parastyle is short, and the remaining part of the ectoloph labial wall is flat. The protoloph is clearly pinched, so that the protocone, slightly flattened lingually, is distinct; there is a clear but short antecrochet, but the crochet and crista, if present, must have been quite small and restricted to the apical part of the crown. The metaloph is short. There is a slight mesiolingual cingulum, as on M1, plus a weak distolabial one. The M3 is triangular, with the distolingual part of the ectometaloph almost parallel to the protoloph, which is more flattened lingually than on M1, and has a weaker antecrochet.

Comparisons

Hooijer (1966) described the Rhinocerotidae from Rusinga under the names *Aceratherium acutirostratum* (Deraniyagala, 1951), *Dicerorhinus leakeyi* Hooijer, 1966, and *Brachypotherium heinzlini* Hooijer, 1963. These identifications were mostly based upon isolated teeth and postcranials, except for the second species, which Geraads (2010) made the type of a new genus, *Rusingaceros*.

The type skull of *Rusingaceros leakeyi* (Hooijer, 1966), KNM-RU 2821, is relatively complete but weathered and transversely crushed. In sharp contrast to the Kachuku skull, it is long and narrow, with its dorsal concavity restricted to the parietal area. The bottom of the nasal notch is located above the mesial part of DP1 and the anterior border of the orbit above M2; the face is extremely long and totally unlike that of the Kachuku skull; the nasal horn was probably stronger, but the premaxillae are slender and the incisors of moderate size only; the zygomatic arch is strikingly robust, especially in its caudal part. All known premolars are substantially worn. They are about as large as those of Kachuku, long relative to their breadth, and their transverse lophs fuse basally near the lingual border. The molars are much smaller than in the Kachuku cranium (thus, they are also smaller relative to the premolars), and their protoloph is not constricted. On the whole, the skull of *R. leakeyi* is extremely different from KNM-KA 57652.

Among the fossils from Rusinga that Hooijer (1966) described and figured as *A. acutirostratum*, a pair of nasal bones (KNM-RU 3012; Hooijer, 1966:pl. 9, fig. 3) are much less curved than

TABLE 2. Dental maximum measurements (in mm) of the new Kenyan rhinoceroses.

Dimension	P2	P3	P4	M1	M2	M3	P2–P4	M1–M3
KNM-RU 58954								
Length	25.6	30.7	37.9	43.3	54.8	63.3	88	145
Width	35.6	48.5	53.4	62.2	65.8	62.7	—	—
KNM-KA 57652								
Length	—	—	c. 39	52.2	60	64.7	—	158
Width	—	—	57	67.7	66.5	62.3	—	—

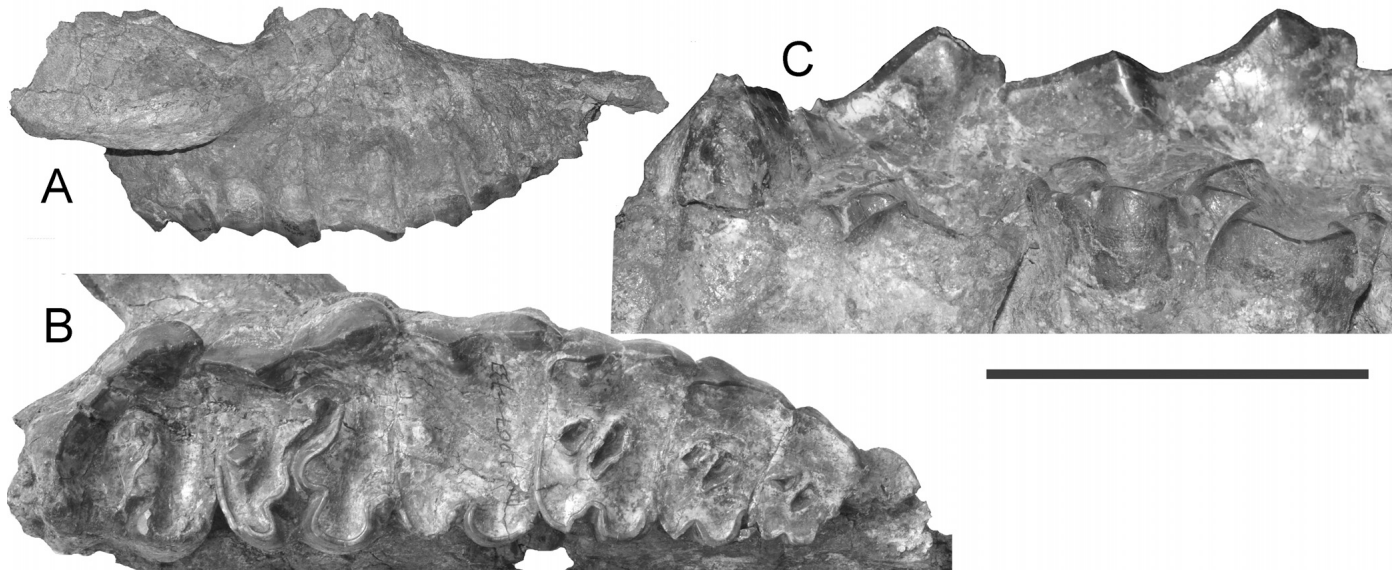


FIGURE 3. *Aceratheriini?*, gen. et sp. indet., maxilla KNM-RU 58954 from Gumba. **A**, lateral view; **B**, occlusal view of P1–M3; **C**, oblique view of right M2–M3. Scale bar equals 20 cm (**A**), 10 cm (**B**), and 5 cm (**C**).

those of *R. leakeyi*; they are even straighter than those of the Kachuku skull but could belong to a similar form, or to *Turkanatherium* Deraniyagala, 1951, as was suggested by Geraads (2010). Most of the other fossils assigned to *A. acutirostratum* are isolated teeth. Because of the presence of a clear antecrochet, the molars resemble those from the Kachuku cranium more than those of *R. leakeyi*, but a positive identification of every single one would be difficult. All premolars (in addition to the specimens figured by Hooijer, 1966, we have seen KNM-RU 3009, NHMUK-M32950, and NHMUK-M32952) are less worn than those of *R. leakeyi* but also broader relative to their length, showing that the distinction is well founded. The P4s are distinctly broader across the protoloph than across the metaloph, which is short and narrow, and usually connected to the antecrochet by a bridge located some distance from the lingual border; in the Kachuku skull, the metaloph is instead nearly as long and as thick as the protoloph. Lastly, there are a few teeth identified by Hooijer as *Brachypotherium*. An upper incisor, KNM-RU 3016, is very large, as usually assumed for this genus; an M3 is only slightly larger than the Kachuku one and similar in its clearly triangular outline and distinct protocone with flattened lingual wall. In short, although it may be that some of the fragmentary material described by Hooijer (1966) belongs to the same taxon as the Kachuku cranium, they do not help us determine its relationships.

Several other African sites have also yielded fragmentary material. Hooijer (1966, 1973) described some teeth from Songhor and Napak, and Guérin and Pickford (2003) named *Ougandatherium napakense* from the latter site. Assuming that all the material described under this name is from the same species, it differs from KNM-KA 57652 in its much smaller size, triangular and much shorter nasal bones, and premolariform (sensu Heissig, 1969) premolars, from which Guérin and Pickford (2003) inferred a relationship with what they called Iranotheriinae (= *Elasmotheriina* sensu Becker et al., 2013). In any case, *Ougandatherium* is too imperfectly known to contribute significantly to the phylogeny of African rhinos.

Arrisdrift in Namibia is probably roughly contemporaneous with Kachuku, and the site has yielded isolated teeth and limb bones described by Guérin (2000, 2003) as *Diceros australis*. This generic assignment, based upon the purportedly short

mandibular symphysis, small lower incisors, morphology of P4, and large size of the metapodials, is questionable (and very unlikely), but what can be inferred from the Kachuku skull, especially the rostral region, differs substantially in these features.

In younger African sites, the first important group to consider consists of the species usually included in *Brachypotherium*, a genus that is, as is the case with many other rhino genera, badly in need of revision. It is best known from Jebel Zelten in Libya, from which Hamilton (1973) described '*Aceratherium campbelli*,' and from Buluk (West Stephanie) in Kenya (Geraads and Miller, 2013), both sites presumed to be slightly younger than Kachuku. They have short, broad skulls with a low occipital, very large upper incisors, and molariform premolars, in addition to lower molars with shallow ectoflexids and short, stout astragali and metapodials. These few features are probably insufficient to define a clade, however. In any case, the Kachuku skull shows no special resemblance to them, because it is long, narrow, and rather tall by comparison.

Turkanatherium acutirostratum Deraniyagala, 1951, is based upon a skull from Moruorot, preserved in the Colombo Museum, Sri Lanka, of which we have seen only photographs; these show that it is transversely crushed and seemingly heavily coated with varnish, but otherwise rather well preserved. No other specimen can be confidently assigned to the same species. It is more dolichocephalic than the Kachuku skull, with the deepest point of the dorsal concavity located more rostrally. The occiput is vertical and the orbit located more caudally so that it is farther away from the nasal notch. The nasals, although incomplete, were certainly shorter; the choanae reach farther caudally and are 'U'-shaped. The teeth are hard to compare with those of Kachuku because they are much less worn, but P4 was relatively broader, the lophs are connected by a bridge located not far from the lingual border, and the crochet is stronger on the molars (and very strong on M2). The skulls resemble each other in the presence of a dorsal concavity, nasals that are neither very short nor much expanded, the location of the bottom of the nasal notch, and molars with a constricted protoloph and rather flat labial wall behind the paracone fold. They are certainly not of the same species, and the differences in skull and tooth shape at similar stratigraphic levels (Moruorot is dated to ca. 17.2 Ma) preclude ancestor-descendant and other close relationships. The dental

characters of *T. acutirostratum* are reminiscent of those found in the rhinos commonly included in the Elasmotheriina.

Chilotheridium pattersoni Hooijer, 1971, from Loperot is based upon a large sample, but the cranial material consists of mosaics of fragments, making skull shape hard to figure out; no serious estimate can be made of the depth of the nasal notch (contra Hooijer, 1971), except that it was not very deep. In general shape, the skull might have been little different from that of *Turkanatherium*, but the nasal bones, which bear a distinct boss for a small horn, were certainly much shorter than at those of the Kachuku skull. We know nothing of the upper incisors (contra Hooijer, 1971). The premolars are small relative to the molars (and especially narrow buccolingually) and lack the transverse lengthening of the metaloph, but the molars do not much differ from those of *Turkanatherium*. They also differ from the Kachuku ones in their strong crochet and in the trapezoidal outline of M3. The Loperot taxon is relatively well defined by the peculiar features of its limb bones (Hooijer, 1971; Geraads, 2010), features that have not hitherto been recognized elsewhere, so that it cannot reliably be identified at other sites and is certainly absent from Rusinga and Karungu.

Geraads et al. (2012) described *Victoriaceros kenyensis* based on well-preserved skulls and postcranials from Maboko (Kenya), dated to ca. 15.5 Ma. The type skull, KNM-MB 29179, shares with the Kachuku specimen a number of features: the lateral profile is concave dorsally; the face is short, with an orbit located close to the nasal notch; the nasals are long and certainly carried a horn; and the premolars are small relative to the molars, which have a pinched protoloph, isolating the protocone. Differences are that in *V. kenyensis*, the dorsal concavity of the skull is stronger and its deepest point located more caudally; the skull is more brachycephalic and especially broad across the zygomatic arches; the nuchal crest is less expanded laterally, probably as a consequence of the short skull (the same difference can be observed between the dolichocephalic *Ceratotherium* and brachycephalic *Diceros*); the occiput is more vertical; the nasals are much broader and certainly carried a much larger horn; the orbit is tubular; the choanae are 'U'-shaped and reach farther rostrally; the I1s may be smaller; and the hypocone of the molars sends a basal expansion towards the protocone lingually. The brachycephaly and large horn of *V. kenyensis* are certainly derived, but none of these characters rules out a congeneric relationship with the Kachuku specimen.

Two partial skulls collected by M. Pickford at Nyakach, ca. 15 Ma, KNM-NC 10486 and NC 10510, resemble the Kachuku one in their concave dorsal profile, strong temporal crests, short face with the orbit close to the nasal notch, inflated supraorbital region, and long nasals. Their cheek teeth are similar (but much worn) and the I1s probably smaller (as suggested by isolated specimens from Nyakach, compared with the likely size of the Kachuku ones), but the main difference is in their narrow, slender nasals that carried at most a very small horn. This was the primary reason for tentatively assigning these specimens to *Plesiaceratherium* sp. (Geraads, 2010), but the nasal notch is distinctly shallower than in this genus, and even though it was probably hornless, the rostral part of the Nyakach skulls resembles that of horned rhinos more than that of many forms that are either hornless or carry only a small horn, have a very deep nasal notch, and are variously included in *Aceratherium* Kaup, 1832, *Chilotherium* Ringström, 1924, *Plesiaceratherium* Young, 1937, *Acerorhinus* Kretzoi, 1942, *Alicornops* Ginsburg and Guérin, 1979, or *Hoploaceratherium* Ginsburg and Heissig, 1989, and can be called *Aceratheriinae* (or a lower taxonomic category), a group also recognized by, e.g., Antoine et al. (2010). The nasal incision is shallow in early Rhinocerotidae (and other early Perissodactyla), so that there is every likelihood that a deep notch is a derived feature, as also assumed by Heissig (2012b). It follows

that neither the Kachuku nor the Nyakach skulls belong to the aceratheres.

Turning now to those groups that are mostly extra-African, the Elasmotheriina have received much attention in recent years, but remain poorly defined. Antoine et al. (2003) defined them by the shape of the cotyloid cavity, and only a set of homoplastic characters defined them in Antoine (2002, 2003); the list is longer in Antoine et al. (2003) and in Antoine et al. (2010), but these latter papers do not specifically deal with this subtribe, of which only two taxa were analyzed. No analysis including a significant number of elasmotheres, aceratheres, and horned rhino taxa has been performed as yet. Heissig (2012b), using a cladistic but non-parsimonious approach, defined the Elasmotheriina by a long metastyle and 'functional tartar' on the molars, but acknowledged that these characters are lost in the main branch of the clade. He also included as defining characters: a concave dorsal skull profile, perhaps the presence of a single median horn, a short metaloph and long metastyle on M2, plus the presence of an ulna-lunate articulation (linked to the loss of a functional McV), but all these characters are shared by several other taxa outside of this group. Other characters often noted in the cheek teeth of this group are hypsodonty, enamel folding, presence of cement, and broad postfossette on the premolars. All of these features are absent or non-observable on the Kachuku skull, or so common in rhinos that a relationship with the elasmotheres looks, a priori, poorly supported. Among the lower to middle Miocene forms that are represented by some cranial material, *Gobitherium mongoliense* (Osborn, 1924) from Loh in Mongolia (Antoine, 2002) has long nasals that were probably hornless (Antoine, 2002), and its skull pattern is quite different, with a tooth row located much more anteriorly and a strongly upturned zygomatic arch. These latter features are also present in *Hispanotherium tungurensis* Cerdeño, 1996, from Tung Gur; its nasals were certainly horned, but its highly complex cheek teeth with strong labial folds sharply differ from the Kachuku ones.

Molassitherium Becker and Antoine in Becker et al., 2013, from the Oligocene of Europe differs considerably from the Kachuku rhinoceros in its low, broad skull with flat or poorly concave dorsal surface, very short nasals, narrow and backwardly inclined occipital, large premolars, and primitive P4 with pre-molariform pattern (Roman, 1912; Lihoreau et al., 2009; Becker et al., 2013).

Pleuroceros Roger, 1898, is known in Europe by *P. pleuroceros* (Duvernoy, 1853). It differs markedly from the Kachuku form in its shallow nasal notch and short nasals that bear a pair of small horns (Viret, 1958; Bonis, 1973).

Mesaceratherium Heissig, 1969, includes the type species *M. gaimersheimense*, *M. pauliacensis* (Richard, 1937)—incorrectly spelled *paulhiacense* or *paulhiacensis* by most latter authors—and *M. welcommi* Antoine and Downing in Antoine et al., 2010. The skull of this late Oligocene to earliest Miocene genus is said by Antoine et al. (2010) to be hornless, but the types of all species are upper teeth and/or mandibular pieces only. According to Antoine et al. (2010), they are united by a 'strong paracone fold on M1 and M2.' *Mesaceratherium pauliacensis* has simple upper teeth with a broad central valley that differ from the other species, and the monophyly of the genus is perhaps questionable; in any case, there is no basis for assuming a close relationship with the Kachuku skull.

Several species from the lower Miocene of Europe are commonly included in the genus *Diaceratherium*, reviewed by Becker et al. (2009). The best-known are *Diaceratherium lemanceense* Pomel, 1853, and *Diaceratherium asphaltense* (Depéret and Douxami, 1902) from the lowermost Miocene, the slightly younger *D. aginense* (Répelin, 1917), and the Middle Miocene *D. aurelianense* (Nouel, 1866); some of their skulls have also been described and illustrated by Roman (1912), Cerdeño (1993), and Becker et al. (2009). If they really belong to the

same clade, the earliest forms still have a rather long skull and long nasal bones but primitive premolars, whereas *D. aginense* and *D. aurelianense* have broad zygomatic arches and occiput, short nasals, and large, broad P4. These latter taxa are distinctly close to the brachytheres, but early forms are primitive enough to be close to the root of other taxa as well; indeed, no character precludes their being ancestral to African forms, which are all likely to be geologically younger.

Other middle Miocene skulls, such as those of *Plesiaceratherium fahlbuschi* (Heissig, 1972) from Sandelzhausen (MN 5) and '*Aceratherium*' *depereti* Borissiak, 1927, may have long nasals, but they do not extend so far rostrally beyond the maxilla and were probably hornless.

Lartetotherium sansaniensis (Lartet, 1851) is best known by a complete but distorted skull from Sansan (France), type locality of zone MN 6 (Heissig, 2012a). Most of the purported characters put forward by Ginsburg (1974) to define his new genus are due to the anteroposterior crushing of this specimen, but it certainly differs from the Kachuku skull in its orbit located farther back, far from a shallower nasal notch, an occipital that is remarkably high and narrow (Heissig, 2012a:fig. 43), a large nasal horn, large premolars, and simple molars without antecrochet.

Besides those already mentioned, one of the most complete skulls from the middle Miocene of Asia is that of *Gaindatherium browni* Colbert, 1934, from the Chinji Formation of the Siwaliks. It resembles that from Kachuku but looks longer, with slender zygomatic arches, fused posttympanic and postglenoid processes below the auditory meatus, an orbit that is more posterior and a nasal notch more anterior, relatively much shorter nasals, and much simpler teeth without antecrochet but with a metacone fold. It is usually considered to be ancestral to *Rhinoceros*, but the species remains poorly known.

The modern *Dicerorhinus sumatrensis* is two-horned, but on the living animal, the second, frontal horn is small, and its area of insertion on the skull is barely distinct, at least in females, so that this second horn can hardly be listed as a difference with the Kachuku skull. However, the Sumatran rhino has a nasal notch located far forward and far from the orbit, slender zygomatic arches, temporal lines remaining far apart, a narrow occiput, simple molars with no posterior groove on the protocone isolating the protocone, no antecrochet, but a crista stronger than in all teeth from Kachuku. At least the rostrally located nasal notch is certainly primitive, and on the whole, the cranial architecture is too different to accept a close relationship.

Discussion

Rhinoceroses are a difficult group to assess systematically because, like other ungulates lacking cranial appendages, they lack clear derived features (Heissig, 1981); for instance, recent diagnoses of middle Miocene European genera (Heissig, 2012a) incorporate many variable or plesiomorphic characters, and the wanderings of many species among various genera attest to the uncertainties in rhino systematics. Furthermore, as already mentioned, well-preserved early and middle Miocene rhino skulls are exceedingly rare in Africa; for instance, only one, the holotype of *Rusingaceros leakeyi*, has its premaxillae fully preserved, so that the major distinctive characters related to the upper incisors are seldom observable. To overcome this dearth of data, the common practice is to convert anatomical features to character states and submit the resulting matrix to parsimony analysis as an objective way of processing the data. Bearing in mind that, by contrast, defining, scoring, and weighting the characters remains a subjective practice; we computed a parsimony analysis using the recent data matrix of Lu (2013), which includes only cranial and dental characters, supplemented with the scores for numerous taxa taken from Antoine (2003), Antoine et al. (2003), Deng (2008), Becker et al. (2013), and our own observations

(supplementary file Geraads&al_TNTmatrix.txt). Using the same character settings as Lu (2013), but without using his new characters because they are not scored for the other taxa (Supplementary Data), TNT (Goloboff et al., 2008) produced two most parsimonious trees, differing only in the position of *Ronzotherium* relative to *Trigonias* + *Hyrachyus*. In the consensus tree (Supplementary Data 1), *V. hooijeri* is the sister taxon of *V. kenyensis*, their next closest relatives being *Chilotheridium pattersoni* and *Turkanatherium acutirostratum*. Together with a number of taxa usually included in this group, they are members of a clade that could be called Elasmotheriini, if not Elasmotheriinae, and is the sister group of most other Rhinocerotidae. However, given the reservations mentioned above, these results should be interpreted cautiously; we believe that although some groups appear in the parsimony analysis, deciphering the relationships of African Miocene rhinos at the species level cannot be achieved at the present time given the poor state of the available record.

As noted, we assume that characters of the horns and nasal shape are more reliable indicators of systematic relationships than dental ones. First, we are confident that the Kachuku skull does not belong to the Aceratheriini because we consider it very unlikely that their derived retracted nasal incision reverted to the much shallower notch found in KNM-KA 57652. Apart from the few features linking them in the parsimony analysis, there is no overt similarity between the Kachuku skull and any of the known Miocene East African genera. Hence, we must be ready to accept significant differences between it and its closest known relative. Even bearing this in mind, the short nasals of *Chilotheridium pattersoni* differ too much from the Kachuku ones for a close relationship to be acceptable, in contrast to the results of the parsimony analysis; this is confirmed by the strong crochet and trapezoidal M3. *Turkanatherium acutirostratum* has nasals that do not greatly differ from the Kachuku ones, but the skull is distinctly more dolichocephalic and, probably as a consequence, the orbit is more posterior and farther from the nasal notch; furthermore, as noted above, there are a number of other cranial and dental differences.

Victoriaceros kenyensis from Maboko differs from the Kachuku skull in its overall brachycephalic shape and other cranial differences. Some of these, however, are probably linked to the short skull, and most, together with the much broader nasals, are probably derived in respect of those observed in the Kachuku skull. This is consistent with the relative ages of the localities. None of these differences necessarily precludes a close relationship between the two, particularly given the genus-level variation found in extant taxa. We therefore tentatively refer the Kachuku skull to *Victoriaceros*, as a new species; fortunately, the generic name is also geographically suitable for it. Like that of other lower Miocene African taxa, its origin must be sought outside this continent; early forms of what is called *Diaceratherium* in Europe are good candidates.

ACERATHERIINI?, gen. et sp. indet.

KNM-RU 58954 (Fig. 3) is a cranial fragment from the Gumba Beds at site R74 consisting of part of a left tooth row, a complete right one plus most of the maxilla, and part of the orbit. The anterior part of the zygomatic arch is very robust; the ventral border of the orbit is rounded; its anterior border is located far caudally, above the middle of M2. The ventral border of the nasal notch is straight and rises regularly from the premental portion to its bottom located high above the limit between P4 and M1, so that the incompletely preserved notch was certainly distinctly 'V'-shaped. The presence of upper incisors cannot be determined; the size of the remaining rostral part of the maxilla suggests that they were not very large; if present, but this rostral part is not extremely reduced either.

The tooth rows are located quite rostrally. All right cheek teeth are preserved, but much worn; no enamel remains in the central part of M1. The cheek teeth are smaller than those of *V. hooijeri* (Table 2) On the premolars, the antecrochet is connected to the hypocone, at some distance from the lingual border. The metaloph is narrow in its central part, so that the hypocone appears as a distinct entity; a vertical groove on its mesial side isolates a mesiolingually directed lingual process. It is also visible on M2, the best-preserved tooth, which has a strongly pinched protoloph isolating the rounded protocone, at most a very small crochet, and a slightly concave ectoloph behind an inconspicuous paracone fold. The M3 is more trapezoidal than that of *V. hooijeri*.

No rhino with well-developed horn has such a deep, 'V'-shaped nasal notch, so that comparisons can be limited to those that are hornless or bear only a small horn, i.e., the brachypotheres, the aceratheres, and some forms of uncertain affinities. African members of the first group have tooth rows that are located less anteriorly, premolars with at most a small antecrochet and a thicker metaloph, and very large upper incisors (Hooijer, 1966; Hamilton, 1973; Geraads and Miller, 2013). No significant feature is shared by KNM-RU 58954 and the brachypotheres, and a close relationship is unlikely.

Ougandatherium napakense is one of the few African rhinos known to have short, pointed nasals and a deep nasal notch, if the cranial fragment illustrated by Guérin and Pickford (2003:pl. 1a, b) does belong to the same species as the type metapodials. As noted above, the cheek teeth are primitive, but the sample consists mostly of isolated teeth. Furthermore, Guérin and Pickford (2003:pl. 2c) illustrated as M2 an M3 that is much larger and more trapezoidal than another M3 (Guérin and Pickford, 2003:pl. 2d), suggesting that two species were perhaps mixed. Only further discoveries can shed light on the affinities of this form.

The rhinos that look most similar to KNM-RU 58954 have not hitherto been recorded from Africa but are relatively common in the Palearctic Miocene; they belong to what Antoine et al. (2010) and Becker et al. (2013) called 'aceratheres s. str.' and 'aceratheres s. l.' The late Oligocene *Molassitherium* Becker and Antoine in Becker et al., 2013, and the early Miocene *Pleuroceros* Roger, 1898, had a shallow nasal incision (Roman, 1912:pl. 3, fig. 1; Becker et al., 2013:fig. 3; Viret, 1958:fig. 77), and *Mesaceratherium* is mostly known by teeth (see above). The reviewer P.-O. Antoine suggested close affinities with *M. welcommi* from the lower Miocene of Pakistan (Forster-Cooper, 1934:fig. 9a, c, e, as *Rhinoceros blandfordi*; Antoine et al., 2010:fig. 8). Indeed, there are a number of similarities on the upper cheek teeth, including gently undulating labial wall, protocone connected to hypocone on premolars, strongly pinched protocone, strong antecrochet, and deep mesial groove of the metaloph on molars. Still, we believe that, in spite of these dental similarities, assuming a close relationship would be risky because the skull of *M. welcommi* remains unknown.

Later, lower and middle Miocene forms are better documented. They are known under the names *Plesiaceratherium*, *Acerorhinus*, *Alicornops*, and *Hoploaceratherium* (Bohlin, 1937; Ballésio et al., 1965; Ginsburg and Guérin, 1979; Ginsburg and Heissig, 1989; Cerdeño, 1996; Heissig, 1999, and references therein; Cerdeño and Sánchez, 2000; Deng, 2004; Antoine et al., 2010, and references therein). Systematic relationships within this group that also includes numerous late Miocene forms are still confused, and generic assignments are doubtful, but comparisons can be made at the species level. In Europe, '*Plesiaceratherium*' *platyodon* Mermier, 1895, from France is roughly contemporaneous with Gumba; there are some slight differences in cheek teeth, but, as reconstructed by Ballésio et al. (1965), the nasal notch was much shallower than that of RU

58954, casting doubt on the generic attribution, because it is deeper in *P. gracile* Young, 1937, type species of the genus, from China, and in *P. fahlbuschi* Heissig, 1972, from Germany (MN 5). The dentition of the latter species was studied in detail by Peter (2002); the molars have a shallower groove on the mesial side of the metaloph, and the cingulum and crochet are on the average stronger, but the premolars do not much differ. The nasal notch is deep but 'U'-shaped, and the nasals are long (Heissig, 1972), which is unlikely for the Gumba specimen.

The small *Alicornops simorreense*, type species of its genus, has a wide stratigraphic range (Antoine et al., 2003:fig. 5), assuming that identifications are correct. The skull is poorly known, but the bottom of the nasal notch is located above P4 (Cerdeño and Sánchez, 2000). Upper premolars assigned to this species (Guérin, 1980:pl. 7; Alberdi et al., 1981:pl. 4; Cerdeño and Sánchez, 2000:fig. 4a, b) resemble KNM-RU 2007-733 in their narrow metaloph, conical hypocone, and incipient antecrochet that may connect the metaloph in late wear. The molars have a moderate paracone fold and a robust antecrochet, and may have an anterior metaloph groove, as on KNM-RU 58954. The main difference is that the crochet is stronger, especially at the type locality Simorre. Paradoxically, it may be weaker at later sites, but is probably always better developed than in the Kachuku teeth. The Chinese *Alicornops laougouense* Deng, 2004, displays basically the same dental features as the European form. Cerdeño and Sánchez (2000) assumed that there are large I1s in *Alicornops*, but this seems to be based upon isolated teeth; none of the few known skulls of this genus preserve the rostrum (Deng, 2000; Cerdeño and Sánchez, 2000), and the condition in *Alicornops* is in fact unknown.

Hoploaceratherium tetradactylum (Lartet, 1837) from Sansan is larger than *Alicornops simorreense* (but *A. laougouense* bridges the gap between the genera), but its upper dentition is similar. Heissig (2012a) was positive about the absence of upper incisors at Sansan, in spite of the long premental part of the rostrum. He noted that the nasals carried a horn, but it was certainly so small that one may wonder whether this is really a great difference with *Alicornops*.

Typical forms of the genus *Chilotherium* Ringström, 1924, are only known from the upper Miocene of Asia and eastern Europe. The skull is broad, the nasals are short and almost always hornless, the i2s are large and inserted very far apart, but the upper incisors are absent and the premental portion of the snout is extremely reduced. This set of features is unknown in the middle Miocene; the Tung Gur species described as *Acerorhinus zernowi* by Cerdeño (1996) could be close to the ancestry of *Chilotherium*, but its nasals are longer than those of this genus, its lower incisors are more closely spaced, and the temporal lines close together; nothing is known of its upper incisors. All other forms assigned to *Acerorhinus* are of late Miocene age. '*Diceratherium*' *tsaidamense* Bohlin, 1937, from Tsaidam shows the same characters, but in addition, the premental portion of the snout is extremely reduced, as in *Chilotherium*, in contrast to KNM-RU 58954. However, its cheek teeth (Bohlin, 1937:pl. 8, fig. 1) are virtually identical with those of the Gumba specimen.

It may be that *Acerorhinus*, *Alicornops*, and *Hoploaceratherium*, together with the upper Miocene *Aceratherium* and *Chilotherium*, make up a natural group, the Aceratheriini (or 'aceratheres s. str.'), a conclusion also reached by Antoine et al. (2010) and Becker et al. (2013). It seems that in spite of its very incomplete condition, KNM-RU 58954 can be confidently assigned to it, in which case it would be one of its earliest representatives, but because the relationships of the aceratheres s. l. are still poorly understood, biogeographic conclusions are hard to draw. The Gumba rhino could be close to early Miocene forms from Asia, which would be in agreement with the dispersal hypothesis of Antoine et al. (2013), but whether it represents a

short-lived African branch or a close relative of the ancestor of European taxa cannot be decided at the moment.

CONCLUSIONS

If the identification of the Kachuku skull as a species of *Victoriaceros* is correct, it would increase the resemblance of the Rusingan mammalian fauna to Maboko, which is geographically very close, but thought to be as much as a few million years younger. Grossman et al. (2014) computed the Simpson resemblance indexes between the main early and middle Miocene Kenyan localities. Their table 4 suggests that, although the similarity is not great, Rusinga's Hiwégi fauna is more similar to Maboko than are other early Miocene faunas and is second only to Fort Ternan among all Miocene sites in its similarity to Maboko. Nevertheless, the sharp contrasts between the well-studied faunas from Rusinga and Maboko possibly represent ecological progression driven by climate change associated with the transition into the middle Miocene Climatic Optimum, although there is little fossil evidence documenting the intervening time period. It may be that the Karungu assemblages will help to bridge this gap in the fossil record, but confirmation will require re-dating of the deposits and further analysis of the associated faunas.

The Gumba palate could be close to the root of the Aceratheriini, but obviously not enough is known of the species that it represents to draw any phylogenetic or biogeographic definite conclusion. If it is indeed an Aceratheriini, it documents one of the earliest members of this group, which may therefore have originated in Africa, as did many other mammalian groups.

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