

# A New Rhinoceros, *Victoriaceros kenyensis* gen. et sp. nov., and Other Perissodactyla from the Middle Miocene of Maboko, Kenya

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**Abstract** The middle Miocene site of Maboko (Lake Victoria, Kenya), dated to ca. 15 Ma, has yielded one of the best collection of rhinos in Africa. The most common taxon, *Victoriaceros kenyensis* n.gen., n.sp., is represented by an almost perfect skull (whose main features are the large nasal horn, an orbit located very anteriorly and with a prominent border, and very broad zygomatic arches) and numerous limb bones, probably belonging to only a few individuals. Characters of the teeth and skull support an assignment to the subfamily Elasmotheriinae, a group best known in the middle and upper Miocene, but whose monophyly is disputable, as some of their tooth characters could be adaptations to a grazing diet (in agreement with their distribution in the Maboko beds). In any case, *Victoriaceros* clearly differs from other East African middle Miocene rhinos, whose diversity is far greater than currently assumed. A few other specimens attest to the occurrence at Maboko of at least one other species, perhaps close to the brachypotheres; a single calcaneum is tentatively assigned to the Chalicotheriidae.

**Keywords** Mammalia · Perissodactyla · Rhinocerotidae · Middle Miocene · Kenya

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## Introduction

Middle Miocene deposits on Maboko Island preserve the oldest strata (Beds 1–16) of the Maboko Formation, which includes localities at Majiwa and Kaloma (Pickford 1981). Laser fusion  $^{40}\text{Ar}/^{39}\text{Ar}$  dating of alkali feldspars from the Maboko phonolite overlying the entire sequence yields a youngest and therefore minimum age of  $13.8 \pm 0.04$  Ma for the formation (Feibel and Brown 1991). A large majority of fossils from Maboko derives from Beds 3–5 at the site of Maboko Main located in a saddle-shaped depression on the northwest of the island. Radiometric dating of the Bed 8 tuff occurring uphill and immediately east of Maboko Main at the locality of Maboko Cliffs yields a  $14.71 \pm 0.16$  Ma maximum age for these fossils. Unfortunately, no absolute dates were obtainable for the base of the sequence. The presence of *Choerolophodon*, the giraffoid *Climacoceras*, horned bovids, and listriodontid suids at Maboko Main suggests the Maboko fauna is significantly more recent than Rusinga and is usually considered to be closer to 15 Ma, but could theoretically be as old as 16 Ma (Pickford 1981; Andrews et al. 1981). A smaller sample of fossils from the surface of localities at Maboko South and Southeast approximately 300 m south of Maboko Main, where Beds 12–16 are exposed, are constrained to between 14.7 and 13.8 Ma. The absence of *Victoriapithecus* monkeys from Beds 12–16, the dominant taxon at Maboko Main, suggests a faunal change has taken place between the southern and Main localities (Benefit 1999).

A small number of fossil rhinocerotids were first collected at Maboko during the 1930s by Archdeacon Owen and sold to the British Museum (Andrews et al. 1981). Circumstantial evidence suggests that many of the fossils he collected derive from Bed 3 at Maboko Main, including the 1992 discovery of bones that attach to specimens Owen collected (McCrossin and Benefit 1994). Rhinocerotid collections were

also made during the 1940s by L.S.B. Leakey (Clark 1952) and in 1973 by the Yale-Kenya Expedition (Andrews et al. 1981). Andrews et al. (1981) attribute eight specimens collected at Maboko before 1973 to *Rhinocerotidae* indet., one specimen collected in 1973 to *Dicerorhinus* sp., and another one to *Brachypotherium heinzlini*. It is only recently, as a result of surface collections and the wet-screening of backdirt from quarries made in the 1930s and 40s at Maboko Main by Pickford (1982–1983) and the excavation of Maboko Main fossils by Benefit and McCrossin (1987–1997), that taxonomic diagnosis of the Maboko rhinocerotids is possible. The new sample of 235 rhinocerotid fossils includes nearly complete crania, mandibles, and postcrania that are critical to interpreting their phylogenetic relationships.

A majority of the new Maboko rhinocerotid fossils ( $n=186$ ) comes from in situ excavation of two stratigraphic levels, Beds 3 ( $n=178$ ) and 5 ( $n=8$ ), as well as from the surface ( $n=18$ ) at Maboko Main, and from Maboko South and Southeast ( $n=7$ ). Rhino fossils excavated from Beds 3 and 5 were mapped in place, with a distribution of the most common species shown in Fig. 1. Bed 3 sediment consists of a yellow sand overlying an uneven surface of bentonite. Fossils in this level tend to be well preserved and fairly complete. The diversity of rhinocerotid skeletal elements in Bed 3 includes most of the lower limb and upper limb, minus some phalanges and metacarpals, indicating that a small number of fairly complete skeletons are represented in the stratum. Such high levels of skeletal completeness indicate the stratum may have been laid down in a fairly short amount of time and experienced limited disturbance. At least three individuals of the most common species are preserved in Bed 3 based on the presence of three left mandibles. The artiodactyl fauna in Bed 3 includes more giraffoids than tragulids, indicative of more open country. In contrast, in large areas of Bed 5 brown clay surrounding Pit 183 on the map, where rhinocerotids are absent, tragulids greatly outnumber giraffoids indicating a more closed country and/or swampy environments. This is in agreement with data from the paleosols (Retallack et al. 2002), which show that the rhinos are far more common in the nyika bushland (ratong) than in the riparian woodland (dhero), in sharp contrast to the distribution of tragulids.

## Terminology

The names of the various components of rhino cheek teeth are well known (e.g., Heissig 1969: fig. 4; Antoine 2002: fig. 72; Geraads 2010: fig. 34.1; Antoine et al. 2010: fig. 3) and need not be repeated here. However, we are not using the terms ‘premolariform,’ ‘paramolariform,’ or ‘semimolariform’ because we believe that the distinction between them, based upon the presence and position of a connection between the

protocone and the metacone, is more a matter of degree than of kind. In the descriptions, the tooth rows are supposed to be horizontal. Upper teeth are in uppercase, lower teeth in lowercase. All material from Maboko is housed in the Department of Paleontology, Kenya National Museums, Nairobi, and in the Natural History Museum, London.

**Abbreviations** APD: antero-posterior dimension; L: length; TD: transverse dimension; W: width; KNM: Kenya National Museum, Nairobi; MB: prefix for Maboko specimens in the KNM; MNHN: Muséum National d’Histoire Naturelle, Paris; NHML: Natural History Museum, London; NME: National Museum of Ethiopia, Addis Ababa.

## Systematic Paleontology

Order Perissodactyla Owen, 1848  
Family Rhinocerotidae Gray, 1821  
Subfamily Elasmotheriinae Bonaparte, 1845

Genus *Victoriaceros*, nov. gen.

**Derivatio nominis**— From Lake Victoria, where Maboko Island is located.

**Type species**—*Victoriaceros kenyensis*, nov. sp.

**Diagnosis**—That of the type species.

***Victoriaceros kenyensis* nov. sp.**

**Holotype**— MB-29179, virtually complete skull, with greatly worn teeth, and lacking all teeth anterior to P4 (Figs. 2, 3a–b). It was found in 1994.

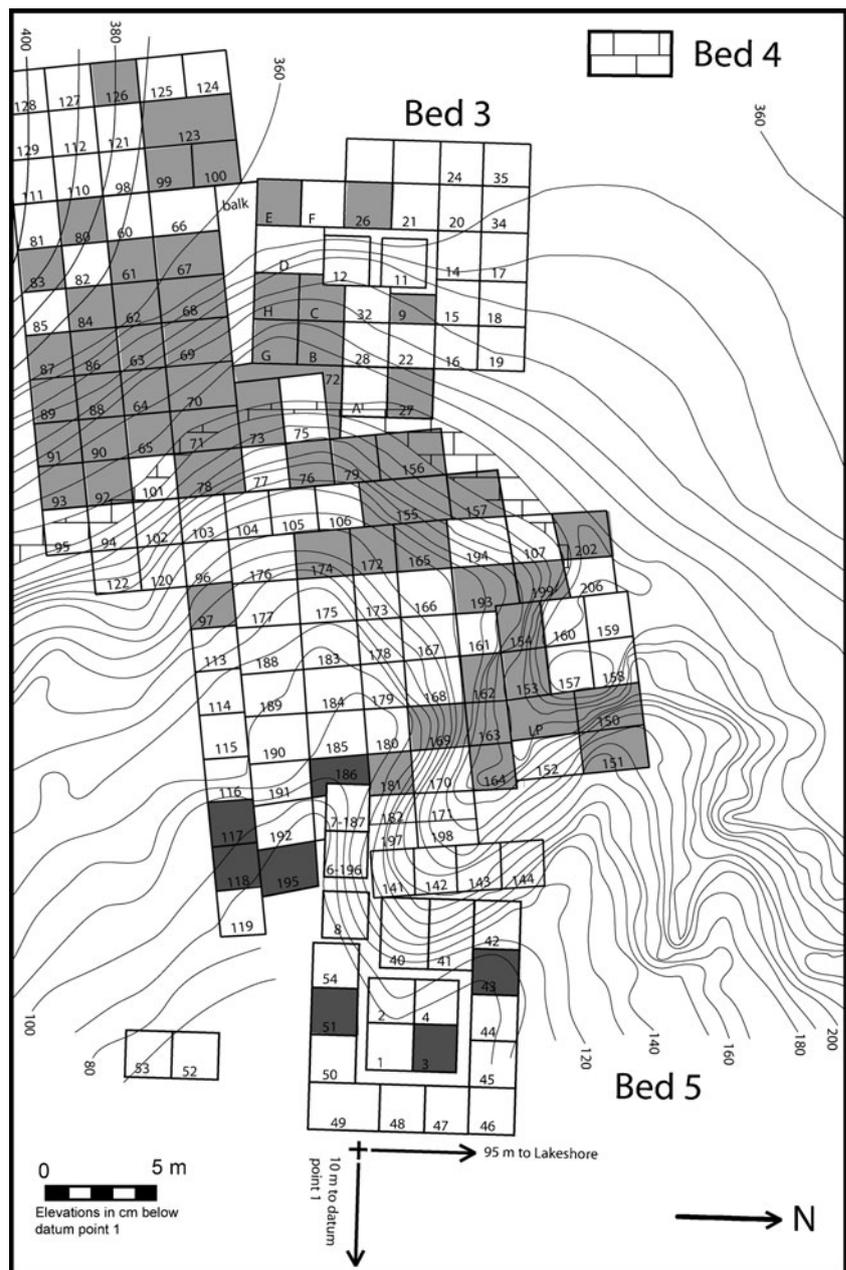
**Diagnosis**— A rhinoceros with a brachycephalic skull, large nasal horn boss (at least in the male), deep nasal notch, orbit located far anteriorly and with prominent border, concave fronto-parietal profile, occiput vertical, zygomatic arches very broad. Premolar row short; cement present; P4 with a small subdivided crochet, a bridge connecting the anterochet to the metaloph at some distance from the lingual border and not very high, a transversely elongated postfossette, upper molars with a strongly constricted protocone, a thick anterochet. Mandible with a long, straight ventral border, gonial area expanded, i2s present but probably not very large.

**Hypodigm**— MB-34843 is a second skull, but lacking most of the antorbital part, and all teeth; MB-36189 is a maxilla with P4-M2 (Fig. 3d); MB-24459, MB-24460, MB-25721, and MB-25922 are more or less complete mandibles; there are also a number of postcranials, but few isolated teeth.

**Type locality**— Maboko, Kenya, ca. 15 Ma.

**Description** The holotype skull MB-29179 (measurements: Table 1) is one of the most complete and best preserved

**Fig. 1** Distribution of *Victoriaceros kenyensis* within excavations at Maboko. Elevations are given of the surface, prior to excavation, and are relative to a principal datum point situated 756 cm above the 1987 level of Lake Victoria. Fossils from Bed 3 are shown in lighter and from Bed 5 darker gray. A large majority of the specimens were mapped in place within the numbered, predominantly 2×2 m, excavation units. Bed 3 fossils are concentrated within the 50 cm above the base of the uneven bentonite floor, with depth below PI 1 increasing from 440 cm below in northern pits to 580 cm in pits to the south. The southeast trending trench was quarried by L.S.B. Leakey during the 1940s and the mouth of the trench by Archdeacon Owen during the 1930s

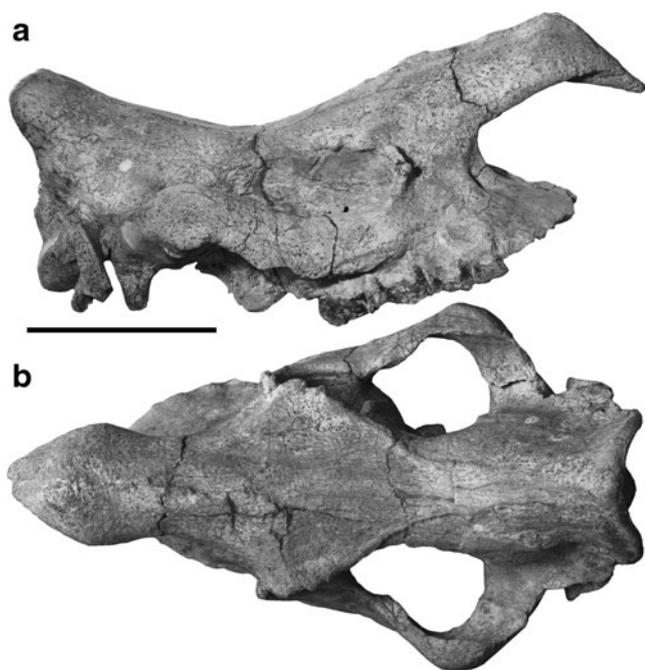


rhino skulls from the African Miocene. It lacks only the premaxillae and teeth anterior to P4, and is only very slightly crushed transversely, as shown by the slightly asymmetrical occipital. The greatly worn teeth indicate an old individual.

The lateral aspect is reminiscent of the modern Sumatran rhino, *Dicerorhinus sumatrensis*. The dorsal profile is strongly concave, but most of this concavity is localized above the anterior part of the temporal fossa, the parietal and frontal profiles being almost straight. However, the strongly convex nasals form a large horn base that obviously carried a median horn located far anteriorly, more rostrally than the cheek teeth. The nasals are long, pointed rostrally, incompletely fused at their tips, and show no trace of a nasal

septum. A slight convexity of the dorsal profile anterior to the orbit might suggest the occurrence of a second frontal horn, but it was in fact caused by a slight postmortem transverse crushing of this area, raising the bone along the sagittal plane, and we deduce that there was no second horn.

The nasal notch is very deep; its bottom is above the mesial part of the (missing) P3, and the infra orbital foramen is only slightly more caudal, above the distal part of the same tooth. Unfortunately, the premaxillae are missing (as is often the case in fossil rhinos), so that the occurrence of upper incisors is not definitely known, but the palate was broad in front of the cheek teeth, and is unlikely to have sharply narrowed rostrally, so that the premaxillae were



**Fig. 2** *Victoriaceros kenyensis* from Maboko, skull MB-29179 (holotype). **a** lateral view. **b** dorsal view. Scale bar equals 15 cm

probably not much reduced. This is confirmed by the long nasals that cannot have been much longer than the premaxillae. Long premaxillae must have borne large upper I1s, and these teeth were almost certainly present, although none has been retrieved.

The orbit is located quite anteriorly, as its rostral border reaches the level of the limit between M1 and M2, not very far from the nasal notch. This anterior border is raised into a strong, dorsoventrally elongate lachrymal process, and there are also large supraorbital processes. Its ventral border is a well-marked ridge. All together, these prominent processes give the orbit a somewhat tubular shape. The well-preserved zygomatic arches rise sharply from the maxillary surface, not far above the tooth row. They are robust and rugose laterally, and arched dorsad, reaching the level of the dorsal orbital border. They bear a very small postorbital process. Behind the teeth, the pterygoid wings have a rather long ventral border, before sharply turning dorsad.

The posttympenic process is widely separated from the postglenoid; the latter is but slightly longer than the paroccipital process. The occipital surface is approximately vertical but, in lateral view, its dorsal part is hidden by the caudally-stretched nuchal crest. In caudal view, the occipital is rather broad at the mastoid level, but much narrower across the dorsal part of the nuchal crest. The mandibular articulation is concave transversely, and not very salient.

In dorsal view, the zygomatic arches are symmetrical and free from crushing. Their anterior part is almost parasagittal, but they curve outwards behind the orbits, and widely expand laterally, so that the maximum bi-zygomatic width

of the skull is almost 2/3 its maximum length. The skull is also broad across the protruding orbits and, remarkably, across the nasals, confirming the large size of the nasal horn; there is a clear constriction between the nasals and the orbit. The temporal lines closely approach each other but remain distinct for their whole length. The nuchal crest is concave, as the parietals are splayed caudolaterally.

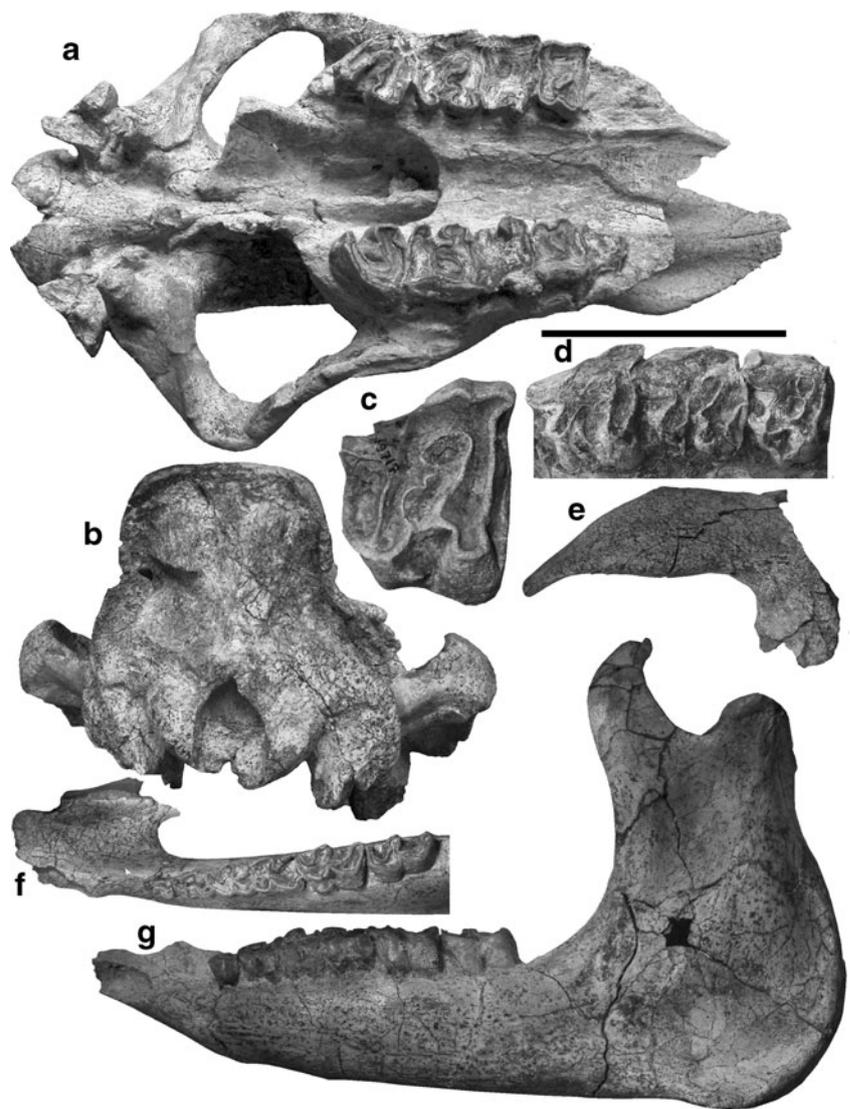
Further features observable in ventral view are the shortness of the basicranium; sharp vomer; rather narrow occipital condyles; and thick, craniocaudally short postglenoid processes with both anterior and lateral articular surfaces. Details of the foramina are not distinct, except that the condylar (hypoglossal) foramen occupies a central position in the middle of the condylar fossa.

The second skull MB-34843 is less complete and somewhat crushed transversely. It is slightly larger but displays basically the same characters, the only differences being that the postglenoid processes are somewhat compressed transversely and that the basioccipital bears a pair of anterior swellings that might almost be called tuberosities (but none of the basioccipitals has a median crest).

MB-29400 (Fig. 3e) is an isolated left nasal with part of the maxilla. The nasal notch is as deep as that of the holotype, showing that it certainly came from an adult or sub-adult individual. Still, there is no sagittal fusion with the right nasal. The dorsal part of the notch, instead of being straight or concave as in most other horned rhinos, is distinctly convex for most of its length.

The best preserved mandible is MB-24460+MB-25922 (Fig. 3f–g). The complete ramus is very large and high by comparison with the corpus, and slightly inclined dorso-rostrally, an unusual feature in rhinos; the mandibular foramen is well below the tooth row. The gonial area is expanded (the distance from the rear of m3 to the rear of the mandible is greater than the length p2–m3). The ventral border of the corpus is slightly convex, and the symphyseal area is but slightly upturned; there is no lingual groove (present in several species, and perhaps homologous with the sulcus mylohyoideus, according to Antoine 2002). The caudal border of the symphysis is at the level of p3, and the mental foramen is just rostral to this tooth. Unfortunately, none of the mandibles has a well-preserved symphysis, and none preserves any incisor. The occurrence of i1s is unknown; the alveoli for the i2s are far apart enough for the central incisors to have been present (but the upper Miocene *Chilotherium* has no central incisors even though its i2s are very far apart). The i2s were certainly tusk-like, but not very large; unfortunately, no isolated incisor is preserved in the collection (showing that the absence of upper I1s in the collection cannot be used to infer their absence in the skull). We know nothing of sexual dimorphism in *Victoriaceros kenyensis*, and it may be that the male incisors were larger than suggested by the symphysis MB-24460, if the latter is

**Fig. 3** *Victoriaceros kenyensis* from Maboko. **a–b** skull MB-29179 (holotype). **a** ventral view. **b** occipital view. **c** P4 MB-19717, occlusal view. **d** P4–M2 MB-36189, occlusal view. **e** left nasal MB-29400, left lateral view. **f–g** mandible MB-24460. **f** occlusal view. **g** lateral view. Scale bar equals 15 cm for **a–b** and **e–g**, 5 cm for **c**, 10 cm for **d**



from a female individual. However, we consider this as unlikely, because the postcranials (see below) show that

very few individuals are represented, and it would be surprising that the collection includes male cranium and nasal

**Table 1** Skull measurements (measurements of Guérin 1980 in brackets)

	MB-29179	MB-34843	MB-29400
Length from nuchal crest to front of orbit	320	340	–
Length from nuchal crest to tip of nasals [3]	500		
Length condylo-M3 [13]	230		
Length condylo-P2	ca. 420		
Depth of nasal notch [4]	145		142
Bizygomatic width [21]	300		
Maximum occipital width [16]	187	194	
Width over nasals	98+		ca. 75
Maximum bi-orbital width [19]	182		
Minimum width between temporal lines [17]	23		
Occipital height (from top of for. magnum) [23]	125		
Occlusal length M1-M3	119		

(as shown by the large size of the horn boss), and a female mandible.

Few features are visible on the much worn cheek teeth of the holotype. The alveolar region of the premolars shows that they were short compared to the molars. P4 is significantly shorter and narrower than M1; at this advanced wear stage, the protocone is connected to the hypocone. M1 is worn almost to the roots. M2 is also greatly worn. The labial wall of the ectoloph is gently undulating. The lingual wall of the protocone is flattened, and this cusp is sharply demarcated from the rest of the protoloph by deep mesial and distal grooves; a thick, rounded antecrochet contacts the metaloph, without fusion; at this wear stage, no crochet or crista is visible; on the metaloph, not far from its lingual end, a deep mesial groove isolates the hypocone (or only part of it, in the form of a mesially-curved appendix) from the rest of the metaloph. M3 has no distolabial expansion, and is thus rather triangular, with the protoloph and ecto-metaloph only slightly divergent distolingually; the protoloph is pinched like that of M2, but the ecto-metaloph is simple, with only a hint of crochet.

MB-36189 is a maxilla with P4-M2. The teeth are imperfectly preserved labially, but are much less worn than those of the holotype. At this early wear stage, the protoloph and metaloph of P4 are already connected by a longitudinal bridge that is about as broad as the metaloph; mesiolingually, the protocone is distinct, but not pinched; a strong cingulum blocks the central valley lingually. There is a weak, digitate crista, and a minute crest opposite it on the protoloph. From the ectoloph, the metaloph arises first distolingually, but its lingual half is almost transverse, so that the postfossette, closed distally by a high cingulum, is broader than long, and that the protoloph and metaloph are slightly convergent lingually. M1 and M2 are similar to those of the holotype, especially showing the mesially-curved hypocone, but the antecrochet is weaker, and there is even a slight groove on the lingual walls of M1 and M2. Thanks to the moderate wear, the crochet remains visible; it is long and bifid on M2. All valleys are filled with thick cement.

MB-19717 (Fig. 3c) is probably a P4, slightly less worn than that of MB-36189. It differs only in that, at occlusal level, the antecrochet does not extend distally as far as the metaloph, the full connection occurring only lower down. The paracone fold is present, but weak, confirming that the ectoloph is rather flat.

MB-28462 is a M1 or M2, showing the same characters as the previous ones. The antecrochet is strong, and there is a slight groove on the lingual side of the protocone.

*Victoriaceros* offers no exception to the rule that rhino lower cheek teeth are less distinctive than upper ones. The premolars are short compared to the molars (Table 2); the tooth row of the mandible MB-24460 is remarkable for the strong convexity of the occlusal surface in lateral view, especially at the level of p4-m1; the incomplete upper tooth

**Table 2** Lower tooth measurements

	L m1-m3	L p2-p4	L p2-m3
MB-25721	113	–	
MB-24459	128	–	
MB-24460/25922	113	70	182

row of the holotype is too worn for its curvature to be reliably assessed, but it is only slightly convex, if at all. The lower teeth have no cingulid; in lingual view, the mesial valleys are more V-shaped than the distal ones, but all are filled with cement. On m3, the least worn tooth, the metalophid is distinctly pinched, and the top of the metaconid was probably distinct on unworn teeth.

The cranial and dental remains described above are homogeneous in size and morphology, and nothing suggests that they represent more than one species (measurements: Tables 3, 4 and 5). Therefore, most postcranial remains must also belong to this species, but a few specimens differ too much to be assigned to *Victoriaceros*, and will be discussed separately. Most of the main bones are represented, and their relative abundances are more equal than in most other sites, suggesting that most of them belong to a very low number of individuals; the MNI is only three (right astragali). In the descriptions, we will pay special attention, whenever possible, to the characters listed by Antoine (2002) and used in his cladistic analysis, as well as in several other papers (Antoine et al. 2002, 2003, 2010; Deng 2008); their numbers are indicated between brackets. However, as discussed further down, it is often hard to decide unambiguously the character states.

*Humerus* MB-24461 (Fig. 4a) and NHML M32755 lack the proximal end. The fossa olecrani is low [193]; the distal articulation is only moderately constricted centrally [194], and lacks a non-articular surface [195]; a marked groove separates it from the lateral epicondyle [196].

*Radius* MB-28453 (Fig. 4d) and MB-28454 (Fig. 4c), both from the left side, have slightly concave lateral borders [198]; the ulnar facets are distinct [199]. The area of insertion of the biceps brachii [200] is depressed; at the distal end, the groove for the carpal extensors is deep [202]. The radius and ulna are distinct but were certainly firmly united [201] and lack a second distal articular facet [203].

*Ulna* MB-28455 and MB-28457 (Fig. 4b) are almost complete specimens that match quite well MB-28453 or MB-28454. The olecranon process is strongly angled with respect to the diaphysis [205]. There is no articular facet for the lunate [211].

**Table 3** Measurements of long bones (in this table and the following ones, specimens marked with a \* are probably not *Victoriaceros*; see text)

Number	Anatomy	Max. length	Prox. W	W shaft	Dist. W	Dist. APD
MB-24461	Humerus			61	139	95
M 32755	Humerus				100	81
MB-24463*	Radius	285	82.5	49.3	66	
MB-28453	Radius	280	76	39.5	62	
MB-28454	Radius	278	76	38	73	
MB-25715	Ulna	317	76.5			
MB-28455	Ulna	315				
MB-28457	Ulna	325				
MB-28499	McII		33		23.1	
MB-29984*	McII	112.5	40	30.8	31.5	
MB-21585	McIII	139.5	40.8	34.2	31.5	
M 32779*	McIII				46	
MB-21584*	McIV	102.2	39.3	29.6	35.3	
MB-28494	McIV	100.7	31.8	22.3	29.5	
MB-36345	McIV	108.4	36	23.8	28.4	
MB-25713	Femur				117	
MB-25716	Femur	445	152	58		
MB-29399	Femur			51	115	
MB-24458	Tibia	305	101	51		62.5
MB-25719*	Tibia	233	95.5	53.5	77.5	
MB-28449	Tibia	302	92.5	44.3	74	59
MB-29401	Tibia	353	103.5	50	74	59.5
M 32780*	MtII	153		19.6	30	
MB-25546	MtIV		31			
MB-26172	MtIV	119.9	34.1	22.4	29.3	
MB-45006	MtIV		36.3			

*Carpals* All are represented, most of them by several specimens (measurements: Table 5; character states listed here are the most common ones). The scaphoid (Fig. 4i) has a proximopalmar facet for the lunate [207], a concave facet for the magnum [209], and is deeper posteriorly than anteriorly [210]. The lunate is rounded on its anterior face [213] and anterodistally [212]. The pyramidal (one specimen only) has a low distal lunar facet [214] and a triangular distal articulation [215]. The trapezoid usually has an

asymmetrical anterior face [215]. The magnum (Fig. 4k) has a straight anteroproximal border [217], no notch on the medial face [218], and a rather short [220] and straight [221] palmar process. On the unciform (Fig. 4m), the pyramidal facet has no palmar extension [223] and remains far from the McV facet. [222]. According to Antoine (2002), the orientation of the latter is indicative of the development of the lateral metacarpal: rhinos with a functional McV have a less vertical facet; this observation is clearly verified in

**Table 4** Measurements of astragali and calcanei

Number	Anatomy	Max. APD	Width (TD)	Medial height	Dist artic. W	Tuber
MB-12525	Astragalus	45.5		59		
MB-20192	Astragalus			57	59	
MB-26168	Astragalus	50.5	78	61.5	63.5	
MB-29498	Astragalus	48	66	60	59	
MB-408	Astragalus			61	61	
M 18882	Astragalus		87.5	71		
MB-26171	Calcaneum	103.5	66			59×39.5
MB-29405*	Calcaneum	115.5	65			54.5×40.5
MB-29406	Calcaneum	96.2	53			55.5×37.8
MB-29989	Calcaneum	99	58.5			62×37.5

**Table 5** Measurements of carpals and other tarsals

	Anatomy	APD	Width (TD)	Anterior height	Posterior height
MB-21860	Scaphoid	54	39.2	40.4	49.7
MB-26170*	Scaphoid	64	42	44	36.5
MB-26176	Scaphoid	54.5	39	41.5	49
MB-36344	Scaphoid	48	30	34.2	41.5
M 18896	Scaphoid	57.5	39	41.5	50
M 18898	Scaphoid	64	43	49	65.5
MB-12518	Lunate	54			
MB-21583	Lunate	52.3	38.5	38.2	
MB-21933	Lunate	52.5	34.7	38.5	
MB-25510	Lunate	60	43.5	45	
MB-28481	Lunate	53.5	39	40.5	
MB-33347	Lunate	52.5	35	38	
M 32777	Lunate	50		38	
MB-25561	Pyramidal	49		42	
MB-25559	Trapezoid	35		25	
MB-29972	Trapezoid	36.8		24.4	
MB-29974	Trapezoid	32.3		23.5	
MB-29982	Trapezoid	33.5		27.4	
MB-28500*	Magnum	77	45	49	
MB-29496	Magnum	68.7	28.8	40	
MB-28484	Unciform	62	47.5	40.5	
MB-33357	Unciform	49	42	43.2	
MB-21877	Cuboid	51.5	30	31.5	
MB-25568	Cuboid	53.5		29.2	
M 32775	Cuboid	47.5		28	
MB-12522*	Navicular	65	54		
MB-28480	Navicular	48	35		
MB-28491*	Navicular	44.5	30.3		
MB-29408	Navicular	46	34.8		
MB-29971	Navicular	50	36		
MB-29979	Navicular	51.3	33.5		
MB-25923	Cuneiform lat	42	33		
MB-21907	Cuneiform lat.	45	32.5		
MB-28489	Cuneiform lat.	40	32.5		
MB-29970	Cuneiform lat.	46.3	34.4		
MB-28482	Cuneiform med.			37.5	
MB-28492	Cuneiform med.	34			

*Chilotheridium* from Loperot, but both Maboko unciforms have a McV facet whose orientation is intermediate between both states for this character [231]; we assume that the McV (not found at Maboko) was not extremely reduced.

**Metacarpals** There are only a few metapodials (Table 3), rather slender [279], with weak proximal tuberosities [232], weak central keels [280], and no distal tuberosity [281]. The imperfect McII has a curved facet for the magnum [224] and probably an anterior McIII facet [225], certainly distinct [227] from the posterior one, if any. On the McIII

(Fig. 4r), the magnum facet is visible in anterior view [229]. Both McIVs (Fig. 4s) have a very triangular proximal facet [230].

**Femur** MB-25716 (Fig. 4f) is a complete, slender femur; the trochanter is low [234], the head is spherical [235], and the third trochanter is remarkably weak for a rhino, although it is more salient on other specimens [239].

**Tibia** MB-24458 is a tibia that is fused to the fibula for most of its length [245], but other specimens are more distinct



**Fig. 4** *Victoriaceros kenyensis* from Maboko, except e, h, j, l, u, v (specimens marked with \*): Rhinocerotidae gen. et sp. indet. **a** right humerus MB-24461. **b** left ulna MB-28457. **c** left radius MB-28454. **d** left radius MB-28453. **e** right radius MB-28463\*. **f** right femur MB-25716. **g** left tibia and fibula MB-29401. **h** left tibia MB-25719\*. **i** right scaphoid MB-21860, medial view. **j** right scaphoid MB-26170\*, medial view. **k** right magnum MB-29496, medial view. **l** right magnum

MB-28500\*, medial view. **m** left unciform MB-33357. **n–q**, right astragalus MB-29498. **n** front view. **o** plantar view. **p** distal view. **q** medial view. **r** left Mc III MB-21585. **s** left Mc IV MB-28494. **t** left Mt IV MB-26172. **u** right Mc II MB-29984\*. **v** right Mc IV MB-21584\*. **w–x** left calcaneum MB-26171. **w** dorsal view. **x** lateral view. Scale bar equals 20 cm for **a–h** 10 cm for **i–x**

(Fig. 4g); in all of them, there is no anterodistal groove [242], the mesiodistal groove is shallow [243, 244], and the distal posterior process is high [246] and rounded [247].

**Fibula** Its proximal end articulates below the tibial plateau [248]; its distal end is slender [249], with a deep [250], posterior [251] lateral groove.

**Astragalus** The four complete specimens differ somewhat in their size (Table 4; Fig. 4n–q) and in the development of the distal medial tuberosity, but their other features are homogeneous, and they can all be referred to *Victoriaceros*. They are moderately high compared to their width [252], thick [253], have a rather oblique, flat fibular facet [254, 255], a short neck [256], and a stop facet on the cuboid surface [257]. The trochlea has a rather straight plantar limit [258] and is very oblique in respect to the distal face [259]. The proximolateral calcaneal facet (Cc1) is deeply concave [262], and has a long, narrow [261] distal expansion [260]. The distal facets (Cc2 and Cc 3) are connected [263], on three out of four specimens.

**Calcaneum** The calcanea (Fig. 4w–x) have fibular [264] and tibial [265] facets, a robust tuber [266], and a salient tubercle for the insertion of the m. fibularis longus [267]; as on the astragali, the distal facets are connected.

**Other Tarsals** The naviculars have a clearly lozenge-shaped outline [268], the cuboid has an oval proximal surface [269], and the ectocuneiform has a weak plantar process [270].

**Metatarsals** The only known metatarsal is the MtIV, of which MB-26172 (Fig. 4t) is a complete specimen that matches the metacarpals in size and slenderness. The MtIII facets are distinct [273], and the plantar tuberosity is long [267].

**Comparisons** Middle Miocene African rhinos are still poorly known, as most of the recent finds are as yet unpublished, and most of the earlier collections were studied within a systematic frame that is now outdated in the northern continents (see review in Geraads 2010). We will briefly compare the Maboko rhino with the most significant published finds, starting with the earliest ones.

The earliest rhinos of Africa could be those from Napak IIC (Iriiri Member) described by Hooijer (1966, 1973) as *Brachypotherium heinzelini*, but this name is probably a synonym of *B. lewisi* (see discussion in Pickford et al. 1993 and Geraads 2010). Brachypotheres are a long-lasting lineage, as they survive in Africa until the Pliocene. They are known, mostly in the middle Miocene, from a number of sites throughout Africa, and are quite distinctive in their broad and low skull bearing at most a minute horn,

rather simple teeth, short but broad premolars, and massive distal limb elements, with especially a characteristic low astragalus. All these features are totally unlike those of *Victoriaceros*.

*Ougandatherium napakense* Guérin and Pickford, 2003, also from Napak, is another early African rhino. A cranial piece shows that the nasal notch is shallow, and that the nasals are shorter than the premaxillae; their width decreases regularly towards the rostral acute end, showing that the nasal horn, if present, was certainly quite small. The premolars have a well-marked paracone fold, a metaloph whose labial half is directed disto-lingually, and a transverse lingual half that fuses lingually with the protoloph; on the Maboko P4s, this connection is definitely more labial. The upper molars also have a well-marked paracone fold, and a moderately constricted protocone with a rather short antecrochet. The metapodials are of similar proportions as those from Maboko, but larger; the astragalus is said to have a very strong distal medial tuberosity, and is thus unlike the Maboko ones. All these differences leave no doubt as to the distinctness of the Maboko rhino from *Ougandatherium*.

*Diceros australis* Guérin, 2000, is a poorly known species from the lower/middle Miocene of Arrisdrift in Namibia (see also Guérin 2003). It is of very large size for its age, and much larger than the Maboko rhino. Although assignment to *Diceros* can be disputed, the P4 indeed resembles that of the modern *Diceros* in its fully molariform pattern, with a protoloph lacking antecrochet and unconnected to the metaloph, quite unlike the Maboko P4s. Furthermore, the astragalus has a very deep central groove, a medial lip that is very short distally, and a very rounded lateral lip; all these features are also very different from those of the Maboko astragali.

The rhinos from the various formations of Rusinga Island, in the 17–18 Ma range (Werdelin 2010), were mostly described by Hooijer (1966, 1973) as belonging to *Brachypotherium heinzelini*, *Dicerorhinus leakeyi*, and *Aceratherium acutirostratum*. In addition, two incomplete teeth were first assigned to the Eurasian genus *Chilotherium*, but were later (Hooijer 1973) referred to *Chilotheridium pattersoni* Hooijer, 1971. As mentioned above, *Brachypotherium* is quite peculiar, but the distinction between the other forms is not straightforward. “*Dicerorhinus*” *leakeyi* has been assigned to a new genus, *Rusingaceros*, by Geraads (2010); it is represented by a rather complete (albeit imperfectly preserved) skull, a few teeth and worn tooth rows, and mandibles. “*Aceratherium*,” instead, is represented by only a pair of nasals, a few teeth, less worn than those of *Rusingaceros*, and perhaps some limb bones that Hooijer felt unable to tell from those of “*Dicerorhinus*.” Full discussion of this issue is beyond the scope of this paper, but it might well be that all specimens assigned to *Aceratherium* belong in fact to other taxa, and we will center the comparison on

*Rusingaceros*. The Maboko rhino resembles *Rusingaceros* in its long curved nasals certainly bearing a large horn, in the strongly concave dorsal profile of the cranium above the temporal fossa, in the general shape of the mandibular corpus bearing rather large incisors, but it widely differs in its much shorter preorbital part, with the nasal notch reaching much farther posteriorly above the tooth row and coming close to the orbit, in the salient orbital border, and in the much more divergent zygomatic arches. Even if some of the teeth of “*Aceratherium*” from Rusinga belong in fact to *Rusingaceros*, the upper molars of the latter have a weaker antecrochet, less constricted protocone, non-constricted hypocone, and smaller crochet than at Maboko; on P4, as far as can be seen from the worn teeth, the hypocone was more mesiodistally expanded and more distinct from the rest of the metaloph, and connected to the protocone by a bridge that is more lingual. There is no doubt that the Maboko rhino is not closely related to *Rusingaceros*.

Another middle Miocene rhino showing some resemblance to the Maboko form is *Paradiceros mukirii* Hooijer, 1968, from Fort Ternan. Both the adult specimen described by Hooijer (1968: pl. 2, fig. 3) and a more complete skull briefly mentioned by Geraads (2010: fig. 34.5) bear a nasal horn, but there is also a supraorbital horn, the nasal bones are much shorter than at Maboko, the nasal notch is shallower (it reaches only the level of the back of P2) and remains far from the orbit, the ventral orbital border slopes ventrally in the adult skull (as in modern African rhinos), the orbital border is not salient, the dorsal skull profile is only slightly concave, and the occipital was inclined posterodorsally. The mandible bears no front teeth. The upper molars have at most a vestigial antecrochet and a very weak crista, the central part of the P4 metaloph is narrow, the hypocone is large and has a late connection with the protocone. It is thus clear that the relationship of the Maboko rhino with *Paradiceros* is very distant. The same is true of the late Miocene to Recent Dicerotini (modern African rhinos and their fossil relatives) that share with *Paradiceros* molarized premolars and simple molars, even though they may not be closely related to it (Giaourtsakis et al. 2009; Geraads 2010).

Hooijer (1971) described as *Chilotheridium pattersoni* a rather large rhino sample from the middle Miocene of Loperot in Kenya, a locality dated to ca. 17 Ma, thus somewhat older than Maboko. Unfortunately, all cranial and mandibular remains are distorted and highly fragmented, consisting of a puzzle of small pieces, making their original shape hard to reconstruct, and few features can be reliably ascertained. The main obvious difference from *Victoriaceros* is the small size of the nasals, which remain narrow anteriorly, even though they certainly carried a small horn. The extent of the nasal notch cannot be estimated, as the position of its bottom, as reconstructed, differs by as much as 10 cm on the left and right sides. As at Maboko, the

temporal lines come rather close together but do not meet; the shape of the nuchal crest and the inclination of the occipital were also similar. However, although the Loperot skulls are crushed, it is unlikely that they were so remarkably broad at the supraorbital level, and over the zygomatic arches. The shape of the lower jaw is similar, although the condyle is not so high above the ventral border and the gonial area is not so expanded. Hooijer stated that there are no upper incisors, but there is no basis for that assumption, and he was probably misled by his belief in the similarity with Eurasian *Chilotherium*. As at Maboko, lower i2s of moderate size were present, and there is no evidence that the symphyses differed from the Maboko ones, but they are much distorted. On P4, the paracone fold is better marked than at Maboko, but there is a similar bifid crochet; with wear, the protocone becomes separated from the rest of the protoloph by anterior and posterior grooves (Hooijer 1971: pl. 3, fig. 1 and pl. 4, fig. 1), as it is on MB-19717, and the antecrochet connects the hypocone through a bridge located at some distance from the lingual border, as at Maboko again. However, the metaloph does not converge lingually with the protoloph, and is expanded at its lingual end into a large hypocone, whereas it remains of regular width on MB-19717 and MB-36189, and the lack of lingual expansion is also clear on the type skull MB-29179. The Loperot molars also have a stronger paracone fold, but the protoloph is similar, with a strong antecrochet, and a protocone well demarcated by vertical grooves. The lingual end of the metaloph is less clearly curved forward, with a less distinct hypocone. As at Maboko, the lower premolars are small compared to the molars, but the entoconid and metaconid are less distinct from the lophids. The radius is about as long as at Maboko, but the epiphyses are distinctly more robust. As at Maboko, none is fused with the ulna, which has no facet for the lunate. On the femur, the third trochanter is smaller than at Maboko, but the main trochanter is higher than the head, in contrast to Maboko. The astragalus of *Chilotheridium* is so different from that of *Victoriaceros* that this single bone, represented by several specimens both at Loperot and Maboko, warrants generic distinction. They are roughly of the same size, but the Loperot astragali are lower, the collum is shortened, the navicular facet is more saddle-shaped, the trochlea is more deeply excavated, its lips are much more unequal in height (proximodistally), and the whole trochlea is remarkably shifted laterally in respect to the distal articulation, producing a very strong medial process, unmatched in any other rhino. It may be that this very peculiar morphology was related to some special architecture of the distal part of the autopodium, with more weight bearing on the lateral digits, and a parallel can perhaps be found in the forelimb, with the occurrence of a McV. So, even though *Chilotheridium* does show some significant resemblances with the Maboko

rhino, there are some major differences that certainly preclude generic identity.

In 1951, Deraniyagala described as *Turkanatherium acutirostratus* [sic] a skull found by H.B.S. Cooke at Moruorot (also known as Losodok), a locality he thought to be Pliocene, but that in fact is about 17.2 Ma (Werdelin 2010). Hooijer (1963: 43, 1966: 136) moved this species to *Aceratherium*, the type-species of which is usually (Giaourtsakis and Heissig 2004) considered to be *A. incisivum* Kaup, 1832, from the upper Miocene of Eppelsheim, Germany. However, the Moruorot skull is sharply different from that of *A. incisivum* (Geraads 2010: 681), and we consider *Turkanatherium* a valid genus. We have not seen the Moruorot skull, still preserved in the Colombo Museum, Sri Lanka, but M. Goonatilake kindly provided us with useful photos. It is about as large as the Maboko skulls but, even allowing for transverse crushing, was more dolichocephalic. The nasals do not taper rostrally, meaning they probably carried a small horn (contra Hooijer 1966), and are much shorter and narrower than at Maboko. The premaxillae are long and certainly carried incisors. The supraorbital margin is not prominent; the orbit reaches less far anteriorly than at Maboko and remains farther from the nasal notch, which is less deep and has a remarkable rectangular outline, unlike the parabolic shape seen at Maboko. However, the cheek teeth display significant similarities to those from Maboko. The P4 has a stronger paracone rib than MB-19717 (this region is not preserved on other Maboko teeth), but it resembles both this tooth and MB-36189 in the presence of a crochet and of a bridge, at some distance from the lingual border, connecting the protoloph and the metaloph (this connection is more lingual on P3). The metaloph is directed transversally and converges lingually with the protoloph, so that the postfossette is transversally elongated. The molars are also very similar; they share a strong antecrochet, a protocone well demarcated by deep mesial and distal grooves and flattened lingually, and a metaloph that ends lingually at a narrow hypocone, demarcated from the rest of the metaloph by a groove on its mesial flank. The weaker paracone fold and the bifid crochet are the only noticeable dental differences between the Maboko form and *Turkanatherium acutirostratum*, but the skull characters are sharply different.

Hooijer (1968) referred to “*A.*” *acutirostratum* a mandible (now KNM-MO-43) from the same area as the type skull, but this identification is hard to demonstrate; it differs greatly from the Maboko mandibles in its slender ramus with non-expanded gonial area, almost straight ventral border that does not turn upward below p2, probably denoting a more robust (missing) symphysis, and less reduced premolars compared to the molars. Hooijer (1966) also referred to “*Aceratherium*” *acutirostratum* several fragmentary specimens from Rusinga. The well-preserved nasals (Hooijer

1966: pl. 9, fig. 3), long and of the same regular width as at Moruorot, may have been correctly identified; as seems to be true of the molars (Hooijer 1966: pl. 5, figs. 4–5), but the illustrated P4s (Hooijer 1966: pl. 6, figs. 1–4) are probably not of this species, as they lack a closed medifossette in spite of their heavy wear. An imperfectly preserved P4 from Kiahera, mentioned by Hooijer (1966: 138) as N° 187 (now RU-3009) shows instead a high bridge between protoloph and metaloph, and could be of this species.

The upper teeth from Bukwa, Uganda, described by Walker (1968) and Hooijer (1966), of which we have seen casts in the KNM, are also very similar to those from Maboko. The M2 has a clear groove, of which there is only a hint at Maboko and Moruorot, on the lingual side of the protocone.

From Majiwa, a site geographically and chronologically close to Maboko, there are two teeth in the KNM. MJ-13261 is probably a M1, much worn, and MJ-13254 is a M2. They both have a strong antecrochet and a protoloph deeply constricted by anterior and posterior grooves, defining a lingually flattened protocone with a hint of lingual groove. The metaloph becomes more transverse lingually, and terminates into a narrow hypocone. All these features are strongly reminiscent of those observed at Maboko and Moruorot, except for the labial paracone rib which is weaker at Majiwa. An incomplete upper molar (M2 ?), from Locherangan (Anyonge 1991), KNM-LC-17680, has a well-marked paracone rib, as in the Moruorot skull.

*Kenyatherium bishopi* Aguirre and Guérin, 1974, was based on a P4 and an incomplete upper molar from the early late Miocene of Nakali, Kenya, and was the first African rhino assigned to the “Iranotheriinae.” The holotype P4 KNM-NA-198 is rather hypsodont, being taller than it is long; has an almost flat labial wall; a narrow protoloph and metaloph that converge lingually and are united by a bridge at some distance from the lingual border; a protocone and hypocone that are quite distinct; and a postfossette that is transversely elongated. The tooth is also remarkable for the numerous enamel spurs projecting from the protoloph and metaloph into the central valley. An upper molar lacking the labial wall, NA-199, also has narrow lophs, a strong antecrochet, a distinct protocone and a small distinct hypocone, a large postfossette, and a thick cement cover. The main feature distinguishing these teeth from those previously mentioned is the narrowness of the lophs, which is obviously linked to their hypsodonty, greater than in middle Miocene forms.

From the Namurungule Formation in the Samburu hills, roughly contemporaneous with Nakali, Nakaya et al. (1987) described both *Chilotheridium* sp. and *Kenyatherium bishopi*, and Tsujikawa (2005) referred some other teeth to *Chilotheridium pattersoni*, but we believe that most of the fossils described under these names are of the same species.

An upper premolar KNM-SH-40128 (Tsujikawa 2005: fig. 5c) differs from the type P4 of *K. bishopi* in much the same characters as the P3 of *T. acutirostratum* differs from its P4: the bridge between protoloph and metaloph is more lingual, and the protocone is less distinct from the protoloph. The complete closure of the medifossette is a unique feature among African rhinos of this age, but may not have taxonomic significance (see *Parelasmotherium* below). The molars have an extremely constricted protocone, a long antecrochet and a pinched hypocone; these features are definitely less marked in *Chilotheridium*, but can be expected in the (unknown) molars of *Kenyatherium*.

Outside Africa, most middle and late Miocene rhinos have slender, narrow nasals and certainly lacked large nasal horns. Most taxa that do have a well-developed nasal horn, such as *Gaiotherium* in Asia or the *Ceratotherium-Diophylus* group in Europe, are phylogenetically close to the modern and recently extinct forms and have modern-looking (“molariform”) cheek teeth. In addition, a number of fossil forms, ranging from the early Miocene to the Pleistocene, which share some similarities in their cheek tooth morphology and the presence of a variably developed horn, have been assigned to a single taxonomic group, the Elasmotheriina (or to a higher taxonomic category within the subfamily Elasmotheriinae; e.g., Heissig 1974; Fortelius and Heissig 1989; Deng 2001, 2005, 2008; Antoine et al. 2002, 2010).

The type genus, *Elasmotherium* Fischer von Waldheim, 1808, from the Pleistocene of central Asia and China (Antoine 2002: fig. 312), is highly derived in its huge frontal horn (e.g., Antoine 2002: fig. 6) and very hypsodont cheek teeth with much folded enamel, which are obviously an extreme adaptation to grazing. The cheek teeth are remarkable because of the narrowness of the lophs, the long crista, and the high distal cingulum that closes the post-fossette. The same features are found in *Sinootherium* Ringström, 1923, an earlier, poorly known related form from China (Ringström 1923, 1924), and are all more derived than in the Maboko rhino. The different nature of the main horn rules out any close relationship between *Victoriaceros* and *Elasmotherium*.

*Iranotherium* Ringström, 1924, from the late Miocene of Maragha, Iran (Mecquenem 1908) and central China (Deng 2005) has a large nasal horn, at least in males, but is dolichocephalic, with the whole tooth row set anterior to the orbit, and in the males, the zygomatic arches have a rugose inflated posterolateral angle, much as in some suids. These differences rule out any identity with the Maboko form, but the cheek teeth display interesting similarities. The protocone forms a very distinct cusp, limited by deep anterior and posterior grooves; on P4 and on worn molars, the protoloph connects the metaloph through a bridge mostly formed by the antecrochet, and the hypocone is a narrow lingual expansion of the metaloph. Features more derived

than at Maboko, but reminiscent of *Elasmotherium* and *Sinootherium*, are the more hypsodont teeth, the higher distal cingulum, and the tendency for the molars to become longer relative to their width (especially clear in the Maragha skull: Mecquenem 1908: pl. 8, fig. 3) so that the protoloph and metaloph are farther apart, and the central valley is longer.

Other Chinese late Miocene taxa to be considered are *Parelasmotherium schansiense* Killgus, 1923, *Ninxiatherium longirhinus* Chen, 1977, and *Parelasmotherium linxiaense* Deng, 2001. The last two names were considered by Antoine (2002) as synonyms of the first. *Ninxiatherium euryrhinus* Deng, 2008, is a recent addition to this group. They share with the Maboko rhino a well-developed nasal horn, a concave cranial profile, a prominent orbital border and, on the molars: an antecrochet connecting the metaloph in late wear, a deeply constricted protocone that may have a lingual vertical groove, and a small distinct hypocone. However, they differ greatly in their long dolichocephalic skull, with non-expanded zygomatic arches, and a tooth row that is fully anterior to the orbit. The hypsodont cheek teeth are also distinctly more derived than at Maboko: the P4 has a much expanded central valley that appears circled by completely fused protoloph and metaloph with the protocone distinct only as a small appendix; the P4 of *P. linxiaense* has a closed medifossette; the molars have an expanded central valley with narrow lophs, a crista, and a closed postfossette in medium wear.

Antoine (2002) lumped in the same species *Huaqingtherium lintungense* (Zhai, 1978), *Caementodon tongxinensis* Guan, 1988, *Huaqingtherium qiui* Guan and Zhang in Guan, 1993 (*H. giui* [sic] Guan, 1988 is a nomen nudum), and *Hispanotherium tungureense* Cerdeño, 1996, all from the late middle Miocene of China. The skull is dolichocephalic, but the tooth row is less rostrally shifted than in the previously mentioned late Miocene forms of the same area, although more so than at Maboko: the orbit reaches only the level of the limit M1-M2, and is much farther from the shallower nasal notch. The molars are at about the same evolutionary grade as the Maboko ones, with a moderate antecrochet, a central valley that is not expanded, and a postfossette that remains open distally. Their strongly folded labial wall differs from the much flatter ectoloph of the complete Majiwa molar MJ-13254 that is certainly of the same species as the Maboko teeth (which are all much worn or incomplete labially). The labial wall is also strongly folded on P4, which is also higher crowned than at Maboko, with a higher bridge between protoloph and metaloph, and some expansion of the central valley resulting in a more reduced postfossette. Remarkably, the metaloph is interrupted lingually or labially of the strong crochet.

Ten other middle Miocene Eurasian species were included by Antoine (2003) in the genera *Caementodon*,

*Hispanotherium*, and *Procoelodonta*, which are all paraphyletic according to his cladogram (Antoine 2003: fig. 3). They are mostly known by teeth and some postcranials, but their skulls remain very poorly known, which probably explains why the systematic arrangement of these species varies so much between authors. *Procoelodonta mongoliense* (Osborn, 1924), included in *Gobitherium* by Deng (2008), has extremely long nasals, so that the nasal notch is deep but probably remains fully anterior to the tooth row, and therefore far from the orbit (Beliajeva 1971: fig. 1a). It may be that the lateral downward flange of the nasals acted as a reinforcement for these long, free bones. The zygomatic arch is also more slender but much higher caudally than at Maboko. The skull of *Hispanotherium beonense* (Antoine, 1997), is known by an incomplete crushed specimen from France; the caudal half is not unlike that of *Victoriaceros* but the nasals are missing and the nasal notch looks shallow, according to Antoine (1997). The skull of *Rhinoceros caucasicum* Borissiak, 1935, type species of the genus *Beliajevina* Heissig, 1974, which was included in *Procoelodonta* by Antoine (2002, 2003), but in *Caementodon* by Deng (2008), remains very incompletely described. The nasal horn is said to rest on the dome-shaped caudal part of the nasal bones, their rostral part being narrow; it would therefore differ greatly from *Victoriaceros*, and resemble *Elasmotherium* instead. The P3 has a bridge that is not far from the lingual border, a strong crista, a well-folded labial wall, and on all upper premolars the protoloph is but loosely connected to the ectoloph, as in *H. beonense*. *Begertherium borissiakii* Beliajeva, 1971, from the middle Miocene of Mongolia, is known by a poorly preserved anterior skull portion, with rather short horn-bearing nasals, and a shallow nasal notch certainly not close to the orbit. Finally, *Hispanotherium matritense* (Lartet in Prado, 1864), is known from numerous dental and postcranial remains from the Iberian peninsula (Antunes and Ginsburg 1983; Cerdeño and Alberdi 1983), but its cranial remains are known only from a single nasal (Cerdeño and Iñigo 1997), said to be slender and straight, and therefore not bearing a horn. It is clear that no member of this poorly known paraphyletic group has a special resemblance to *Victoriaceros*.

In late middle Miocene forms (Paşalar, Çandır, Loh, Beger Nur, but perhaps also in *Tesselodon fangxianensis* Yan, 1979, said by Antoine (2002: 69) to be of early middle Miocene age), the teeth are more derived than in earlier forms. The P4 is very hypsodont, the distal cingulum is high, the protocone and hypocone are closely appressed along their whole height, the crista is variably present, the postfossette is transversely elongated and closed distally. The molars have a well-distinct protocone, a moderate anterochet that contacts the metaloph in late wear, a small crista may be present, and the postfossette is not closed distally. The labial walls are gently undulating (Beliajeva 1971: fig.

1a; Heissig 1972: pl. 6; Heissig 1974: pl. 2; Yan 1979: fig. 1-2; Fortelius 1990: fig. 3; Geraads and Saraç 2003: pl. 1).

Antoine (2002, 2003) and Antoine et al. (2003, 2010) addressed the issue of elasmotherine relationships by means of parsimony analysis, using 282 cranial, dental, and postcranial characters. Their matrix was slightly revised and enlarged by Deng (2008), who used somewhat different search options, ending up with a slightly different cladogram. Antoine et al. (2010) modified a number of character states for various taxa, but did not specifically address the elasmotherine issue.

The matrices published by P.-O. Antoine and Deng Tao are based upon careful and detailed study of a large number of fossil remains stored in many museums, and carry a wealth of information seldom found in other rhino papers. We owe much to these authors for making their data available, but we express doubts about the reliability of their results. Our reservations do not arise so much because we noticed some mistakes in the matrix (obviously, a matrix of more than 15,000 character scores cannot be expected to be fully approved by all) or because we disagree with some of the search options used (additive vs. non-additive characters). More importantly, there are two major issues that are hidden by the rigorous treatment of the data matrix:

- 1) First, most of the characters are in fact hard to score objectively, because few quantitative character states (usually two or three) are included. This is obvious for states like “high” vs. “low,” “short” vs. “long,” “narrow” vs. “wide,” “angular” vs. “rounded,” “small” vs. “large,” but this is also true of many “binary-looking” characters, often coded as “absent” vs. “present,” “above premolars” vs. “above molars,” “flat” vs. “concave,” as rather different conditions can in fact be united under the same state. In these cases, some taxa can easily be scored because they display an extreme condition, and were therefore those chosen by Antoine (2002) to illustrate the character states, but intermediate conditions are more common. Our attempt to score the East African forms (*Victoriaceros*, *Chilotheridium*, *Turkanatherium*) showed how often choosing between 0, 1, and 2 is a difficult task. Indeed, no fewer than 748 character scores (not including the replacement of a “?” by another value, and non-applicable characters) for several taxa, including the three living forms considered in both papers, have been modified between Antoine et al. (2003) and Antoine et al. (2010). Even though the latter authors did not state the reasons for these changes, this demonstrates how the scoring of characters, far from being an objective task, can be tricky; this is particularly true of the carpals, which can be highly variable (Harrison and Manning 1983).

Of course, changes in character states lead to changes in the resulting cladograms and upset taxonomic conclusions. It is beyond the scope of this paper to explore the extent to which different scorings affect the whole phylogenetic tree, but we notice that, in the consensus tree resulting from the matrix published by Antoine et al. (2010), augmented by our observations, the genus *Rhinoceros*, whose living members are so similar, is poorly supported, and that the modern African rhinos do not form a monophyletic group, a result that no one would admit.

- 2) Second, the alleged neutral option of not weighting the characters, which in fact means weighting them all equally (as acknowledged by Antoine et al. 2010: 175), is unsupported. We know nothing of the genetic determinants, but there is no basis for giving to presence vs. absence of a nasal horn the same weight as any of the five characters observed on the magnum. Furthermore, a number of important characters are missing, such as the shape of the occipital, the proportions of the basicranium, the shape and position of the nasal notch, of the orbital border, the proportions of limb bones, etc. As a whole, major features of the skull architecture are given little consideration compared to many details. The result is that the cladograms rest mostly upon the many dental and postcranial characters, which are given overwhelming importance.

Our two major areas of reservation amount to a single fact: we usually do not know what a morphological character and an evolutionary event are, and the sophistication of the parsimony programs used hides the basic point that the coding, scoring, and equal weighting of the characters and states remain highly arbitrary.

Many rhinocerotid taxa remain very incompletely known, especially in their skull morphology, and we believe that it is premature to attempt a cladistic analysis of the whole family. We prefer to restrict our interpretation to a tentative evolutionary scenario. One can probably recognize, in the Neogene and Quaternary of the Old World, a group of rhinos whose upper premolars did not follow the same evolution as most others towards molarization. We hypothesize that instead of acquiring a  $\pi$ -shape, they retained and reinforced the primitive lingual connection between the protoloph and metaloph. In Africa, the earliest of them is *Ougandatherium* from Napak (Guérin and Pickford 2003); its premolars are still much like those of the European *Ronzotherium*, but they are already higher and cement is present. Later, these rhinos acquired more and more grazing adaptations, including an increase in crown height. In the more derived forms, presumably for mechanical reasons, the transverse lophs became narrower, and enclosed an enlarged central valley. Convergent evolution can be observed in those rhinos with molariform premolars

that become grazers, such as *Ceratotherium*, *Coelodonta*, and some *Chilotherium* (especially *Ch. kowalewskii*).

Whether this group, the elasmotherines, is monophyletic is hard to tell. Dental features are certainly highly subject to parallel evolution and it is likely that unrelated lineages developed similar adaptations to grazing, which culminated in upper Miocene forms, both in Africa and Asia. By contrast, the diversity of cranial shapes is perhaps even greater than in other rhinos. The skull may be dolichocephalic or quite broad, and the relative positions of the orbit, tooth row, and nasal notch are greatly variable. The most conspicuous diversity lies in the horn: some skulls bear a large frontal horn, several others a large nasal one, sometimes with an ossified nasal septum, and some others none or only a minute one. It is hard to imagine *Elasmotherium* deriving from a form with a strong nasal horn, so it must have branched lower than suggested by the cladogram, but this does not imply that those species with a nasal horn form a natural group. On biogeographic grounds, it is more parsimonious to assume that the East African forms are closely related, with *Chilotheridium*, with its weak horn and functional McV, branching first, followed by *Turkanatherium*.

Subfamily indet.

Rhinocerotidae gen. et sp. indet. A

A few rhinocerotid limb bones and teeth are too different from those assigned to *Victoriaceros kenyensis* to be confidently assigned to the same taxon, and they must belong to at least two other species, but sorting them is not easy. A first group includes mostly specimens that are only doubtfully distinct from *Victoriaceros*. These are a radius MB-24463 (Fig. 4e), which differs from the others in being more robust, having a less rounded lateral edge, and in the bicipital insertion not being depressed. A calcaneum MB-29405 is long and slender, and lacks the tibial and fibular facets. A navicular MB-28491 is more rectangular and the distal facet is distinctly convex rather than flat in lateral view. A MtII M 32780 in NHML is certainly too long and slender for *Victoriaceros*, being reminiscent of the metapodials from Gebel Zelten assigned by Hamilton (1973) to *Aceratherium campbelli*, but we will not attempt a generic identification.

Rhinocerotidae gen. et sp. indet. B, aff. *Brachypotherium* sp.

A second group includes specimens that are larger and/or more robust than *Victoriaceros*. A scaphoid MB-26170 (Fig. 4j) resembles the other specimens, except that it is long and distinctly deeper anteriorly than posteriorly, a very unusual feature in rhinos; only the scaphoid from the lower/middle Miocene of Artenay (France) assigned to *Diaceratherium aurelianense* by Cerdeño (1993: pl. 2, fig. 6) approaches this shape. A magnum MB-28500 (Fig. 4l) is

much broader than that assigned to *V. kenyensis*, and has a relatively shorter palmar process but a very salient proximal one. A McII MB-29984 (Fig. 4u) and a McIV MB-21584 (Fig. 4v) are more robust than the other metapodials; on the McII there is probably no McIII facet, but probably one for the trapezium. The tibia MB-25719 (Fig. 4h) is too imperfectly preserved to assess its characters, but is decidedly shorter and more massive than the others. In the NHML there are a very large distal McIII M 32779 and a very large lower molar M 32782 (L=51.5; W=35), with a shallow labial groove, as in *Brachypotherium*.

If these specimens are all of the same species, the tooth would prompt us to assign it to *Brachypotherium*, but the scaphoid goes against this identification, and the metapodials are not short enough. An alternative possibility is that this group includes in fact two species, but we are reluctant to accept four rhino species at Maboko. MB-12522 is a navicular of large size, and MB-12536 is a fragment of a large lower tooth with a shallow labial groove, but the field numbers of these two specimens show that they are not from Maboko.

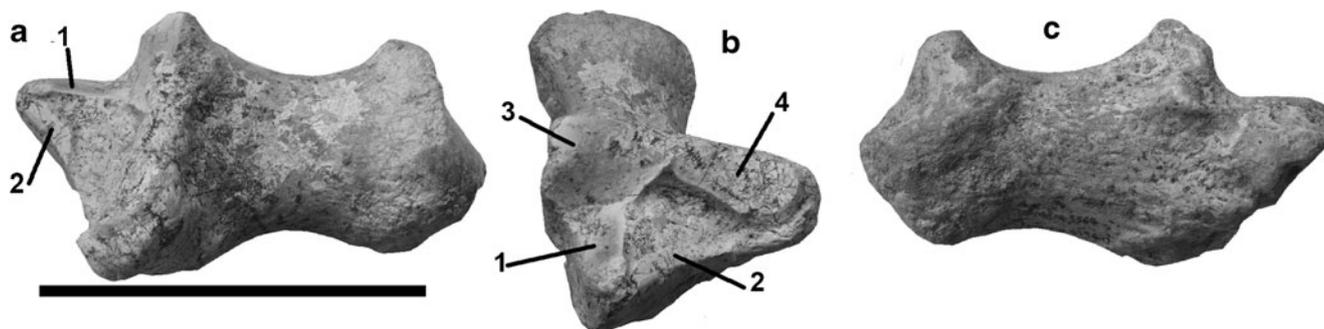
#### Perissodactyla, family indet., cf. Chalicotheriidae

A calcaneum from bed 3, MB-33349 (Fig. 5), is definitely of a perissodactyl, but hard to assign to a family. The tuber calcis has a strong waist, both in lateral and dorsal views. The main talar (ectal) facet (Fig. 5b, 3) is rather small and only slightly convex, unlike that of rhinos; it extends as a narrow flat calcaneal facet to the distal tip of the bone (Fig. 5a–b, 1); both facets make an angle of about 100°. Medially, the main facet is continuous with a transversely elongated ental facet (Fig. 5b, 4), borne by a weak sustentaculum that narrows medially. The distal facet, for the cuboid, is rather small, transversely concave and elongated. There is no facet for the tibia or fibula. This calcaneum differs from that of rhinos in the extension of the ectal facet to the tip of the lesser (distal) process, and in the triangular rather than quadrangular outline of this process in lateral view. Brachypotheres have a distal process that is less quadrangular than in other rhinos, but

its tip is not so far from the plantar border of the bone, and the ectal facet is more convex and has only a short distal extension. Still, as the less common Maboko rhino could be close to this group, we cannot completely discard the possibility that this bone is an extreme brachypothere variant.

Alternatively, this bone could belong to the Chalicotheriidae, whose calcanea are poorly known. It differs from that of the known calcanea of the Chalicotheriinae (Colbert 1935: fig. 76; Zapfe 1979: fig. 116) in its weak sustentaculum, but assignment to the Schizotheriinae cannot easily be rejected. In this subfamily, the calcaneum is known in the middle Miocene *Metaschizotherium* (Coombs 2009: fig. 10D), in the late Miocene Eurasian *Ancylotherium pentelicum* (Zapfe 1979: fig. 117; Roussiakis and Theodorou 2001: fig. 28; Saraç and Sen 2005: fig. 3 – the skull described by these authors is obviously not of this genus, but identification of the calcaneum looks correct; there are also three specimens from Pikermi in the MNHN and NHML), in the African Plio-Pleistocene *A. hennigi* (Guérin 1985, 1987), in the late Miocene *A. cheboitense* (Guérin and Pickford 2005) and *Chemositia tugenensis* (Pickford 1979; NMK-MP-229), and in the North American *Moropus* (Coombs 1978: fig. 14) and *Tylocephalonyx* (Coombs 1979: fig. 20). However, members of this subfamily differ in that:

- the ectal talar facet is more convex; this is the only character that can be verified on all specimens, but the difference with the Maboko fossil is quite clear.
- the ental facet is distinct from the ectal facet and rounded in *A. pentelicum*, oval in *Moropus* (Coombs 1978: 35), elliptical in the Laetoli *A. hennigi* (Guérin 1987:318) but definitely absent at Omo (NME, Omo 210–1973) and probably also in *A. cheboitense*, whose astragalus lacks the ental facet. None has a transversely elongated facet as at Maboko.
- the cuboid facet is seldom described, but was “elliptical” at Laetoli (Guérin 1987), “pear-shaped” in *Moropus* and *Tylocephalonyx* (Coombs 1978, 1979), “moon-shaped” in *A. pentelicum* (Saraç and Sen 2005), and



**Fig. 5** Perissodactyla family indet. Calcaneum MB-33349. **a** medial view. **b** distal view. **c** lateral view. 1: distal extension of the ectal facet, 2: distal talar facet, 3: ectal facet, 4: ental facet. Scale bar equals 10 cm

almost circular at Omo, so that its is never transversely elongated as at Maboko.

On the astragalus of *Butleria* from Rusinga (Butler 1965; NHML M 32567), the ectal facet is only slightly concave, so that it may be that its unknown calcaneum was more like the Maboko one in this regard than those of later forms. Other resemblances with MB-33349 are that this facet has a distal expansion, and is close to the ental facet.

Neither assignment (to the Rhinocerotidae or Chalicotheriidae) is fully satisfactory, and we prefer to leave this bone as incertae sedis. Future discovery of early African schizotheriines, still unknown (Coombs and Cote 2010) may help settle its affinities.

## Conclusion

The rhinocerotid material from Maboko is abundant, well preserved, and especially valuable because almost all of it belongs to a single taxon, *Victoriaceros kenyensis*. We include it in the Elasmotheriinae, although the monophyly of this subfamily is questionable, as most of its shared features could have been acquired through parallel adaptation to a similar diet. At Maboko, its presence is a clear indicator of an open environment, in agreement with paleosol analyses (Retallack et al. 2002).

*Victoriaceros* adds to the knowledge of Miocene African rhinos, but much remains to be learned about them, as several have been incompletely studied, and significant discoveries have recently come to light. The middle Miocene clearly marks the climax of their diversity there, before the Dicerotini became dominant.

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## References

- Aguirre E, Guérin C (1974) Première découverte d'un Iranotheriinae (Mammalia, Perissodactyla, Rhinocerotidae) en Afrique : *Kenya-therium bishopi* nov. gen. sp. de la formation vallésienne (Miocène supérieur) de Nakali (Kenya). *Estud geol* 30: 229–233
- Andrews P, Meyer GE, Pilbeam DR, Van Couvering JA, Van Couvering JAH (1981) The Miocene fossil beds of Maboko Island, Kenya: geology, age, taphonomy and palaeontology *J Hum Evol* 10: 35–48
- Antoine PO (1997) *Aegyrcitherium beonensis* n.g. n.sp., nouvel élasmothère (Mammalia, Rhinocerotidae) du gisement miocène (MN4b) de Montréal du Gers (Gers, France). Position phylogénétique au sein des Elasmotheriini. *N Jahrb Geol Paläontol Abh* 204: 399–414
- Antoine PO (2002) Phylogénie et évolution des Elasmotheriina (Mammalia, Rhinocerotidae). *Mém Mus Nat Hist Nat* 188: 1–359
- Antoine PO (2003) Middle Miocene elasmotheriine Rhinocerotidae from China and Mongolia: taxonomic revision and phylogenetic relationships. *Zool Scripta* 32: 95–118
- Antoine PO, Alférez F, Iñigo C (2002) A new elasmotheriine (Mammalia, Rhinocerotidae) from the early Miocene of Spain. *C R Palevol* 1: 19–26
- Antoine PO, Downing K, Crochet JY, Duranthon F, Flynn LJ, Marivaux L, Métais G, Rajpar AR (2010) A revision of *Aceratherium blanfordi* Lydekker, 1884 (Mammalia: Rhinocerotidae) from the early Miocene of Pakistan: postcranials as a key. *Zool J Linn Soc* 160: 139–194
- Antoine PO, Duranthon F, Welcomme JL (2003) *Alicornops* (Mammalia, Rhinocerotidae) dans le Miocène supérieur des collines Bugti (Balouchistan, Pakistan): implications phylogénétiques. *Geodiversitas* 25: 575–603
- Antunes MT, Ginsburg L (1983) Les Rhinocérotidés du Miocène de Lisbonne. Systématique, écologie, paléobiogéographie, valeur stratigraphique. *Ciências da Terra* 7: 17–98
- Anyonge W (1991) Fauna from a new lower Miocene locality west of Lake Turkana, Kenya. *J Vertebr Paleont* 11: 378–390
- Beliajeva EI (1971) On some rhinoceroses of Rhinocerotidae family from Neogene of western Mongolia. Mesozoic and Cenozoic fauna of western Mongolia. The joint Soviet-Mongolian scientific research geological expedition. *Akademia Nauk USSR* 3: 78–97
- Benefit B (1999) *Victoriapithecus*, the key to Old World monkey and catarrhine origins. *Evol Anthropol* 7: 155–174
- Borissiak AA (1935) Neue Materialien zur Phylogenie der Dicerorhinae. *C R Acad Sci URSS* 3: 381–384
- Butler PM (1965) East African Miocene and Pleistocene chalicotheres. *Bull Br Mus (Nat Hist) Geol* 10: 163–237
- Cerdeño E (1993) Etude sur *Diaceratherium aurelianense* et *Brachypotherium brachypus* (Rhinocerotidae, Mammalia) du Miocène moyen de France. *Bull Mus Nat Hist nat* 15, C: 25–77
- Cerdeño E (1996) Rhinocerotidae from the middle Miocene of the Tung-Gur Formation, Inner Mongolia (China). *Am Mus Novitates* 3184: 1–43
- Cerdeño E, Alberdi MT (1983) Estudio descriptivo del esqueleto post-craneal de *Hispanotherium* del yacimiento mioceno de Torrijos (Toledo). *Estud geol* 39: 225–235
- Cerdeño E, Iñigo C (1997) *Hispanotherium matritense* (Rhinocerotidae) de la ciudad de Madrid. *Rev Esp Paleontol* 12: 80–90
- Clark WE Le Gros (1952) Report on fossil hominoid material collected by the British-Kenya Miocene Expedition. *Proc Zool Soc London* 122: 273–286
- Chen G (1977) A new genus of Iranotheriinae of Ningxia. *Vert PalAsiat* 15: 143–147
- Colbert EH (1935) Siwalik mammals in the American Museum of Natural History. *Trans Am Phil Soc NS* 26: 1–401
- Coombs MC (1978) Reevaluation of early Miocene North American *Moropus* (Perissodactyla, Chalicotheriidae, Schizotheriinae). *Bull Carnegie Mus Nat Hist* 4: 1–62
- Coombs MC (1979) *Tylocephalonyx*, a new genus of North American dome-skulled chalicotheres (Mammalia, Perissodactyla). *Bull Am Mus Nat Hist* 164: 1–64
- Coombs MC (2009) The chalicotheres *Metaschizotherium bavaricum* (Perissodactyla, Chalicotheriidae, Schizotheriinae) from the Miocene (MN5) Lagerstätte of Sandelzhausen (Germany):

- description, comparison, and paleoecological significance. *Paläontol Z* 83: 85–129
- Coombs MC, Cote SM (2010) Chapter 33 – Chalicotheriidae. In: Werdelin L, Sanders WJ (eds) *Cenozoic Mammals of Africa*. University of California Press, Berkeley, pp 659–668
- Deng T (2001) New remains of *Parelasmotherium* (Perissodactyla, Rhinocerotidae) from the late Miocene in Dongxiang, Gansu, China. *Vert Palasiat* 39: 306–311
- Deng T (2005) New discovery of *Iranotherium morgani* (Perissodactyla, Rhinocerotidae) from the late Miocene of the Linxia basin in Gansu, China, and its sexual dimorphism. *J Vertebr Paleontol* 25: 442–450
- Deng T (2008) A new elasmothere (Perissodactyla, Rhinocerotidae) from the late Miocene of the Linxia Basin in Gansu, China. *Geobios* 41: 719–728
- Deraniyagala PEP (1951) A hornless rhinoceros from the Mio-Pliocene deposits of East Africa. *Spolia Zeylanica* 26: 133–135
- Feibel CS, Brown FH (1991) Age of the primate-bearing deposits on Maboko Island, Kenya. *J Hum Evol* 21: 221–225
- Fischer von Waldheim G (1808) Notice d'un animal fossile de Sibérie inconnu aux naturalistes. *Progr invit seances publ Soc imp natural Moscou*: 1–28
- Fortelius M (1990) Rhinocerotidae from Paşalar, middle Miocene of Anatolia, Turkey. *J Hum Evol* 19: 489–508
- Fortelius M, Heissig K (1989) The phylogenetic relationships of the Elasmotheriini (Rhinocerotidae, Mammalia). *Mitt Bayer Staatsslg Paläontol hist Geol* 29: 227–233
- Geraads D (2010) Chapter 34 – Rhinocerotidae. In: Werdelin L, Sanders WJ (eds) *Cenozoic Mammals of Africa*. University of California Press, Berkeley, pp 675–689
- Geraads D, Saraç G (2003) Rhinocerotidae from the middle Miocene hominoid locality of Çandir (Turkey). *Cour Forschungs-Inst Senckenberg* 240: 217–231
- Giaourtsakis I, Heissig K (2004) On the nomenclatural status of *Aceratherium incisivum* (Rhinocerotidae, Mammalia). 5<sup>th</sup> International Symposium on Eastern Mediterranean Geology 2004: 1–4
- Giaourtsakis I, Pehlevan C, Haile-Selassie Y (2009) 14 – Rhinocerotidae. In: Haile-Selassie Y, Woldegabriel G (eds) *Ardipithecus kadabba*, Late Miocene Evidence from the Middle Awash, Ethiopia. University of California Press, Los Angeles, pp 429–468
- Guan J (1988) The Miocene strata and mammals from Tongxin, Ningxia and Guanghe, Gansu. *Mem Beijing Nat Hist Mus* 42: 1–21
- Guan J (1993) Primitive elasmotherines from the middle Miocene, Ningxia (northwestern China). *Mem Beijing Nat Hist Mus* 53: 200–207
- Guérin C (1980) Les Rhinocéros (Mammalia, Perissodactyla) du Miocène terminal au Pleistocène supérieur en Europe occidentale. Comparaison avec les espèces actuelles. *Doc Lab Géol Fac Sc Lyon* 79: 1–1185
- Guérin C (1985) Les rhinocéros et les chalicothères (Mammalia, Perissodactyla) des gisements de la vallée de l'Omo en Ethiopie (collections françaises). In: Coppens Y, Howell FC (eds) *Les faunes plio-pléistocènes de la basse vallée de l'Omo*. Tome 1. Editions du CNRS, Paris, pp 67–89
- Guérin C (1987) Chalicotheriidae (Mammalia, Perissodactyla) remains from Laetoli. In: Leakey MD, Harris JM (eds) *Laetoli: A Pliocene Site in Northern Tanzania*. Clarendon Press, Oxford, pp 315–320
- Guérin C (2000) The Neogene rhinoceroses of Namibia. *Palaeontol Afr* 36: 119–138
- Guérin C (2003) Miocene Rhinocerotidae of the Orange river valley, Namibia. *Mem Geol Surv Namibia* 19: 257–281
- Guérin C, Pickford M (2003) *Ougandatherium napakense* nov. gen. nov. sp., le plus ancien Rhinocerotidae Iranotheriinae d'Afrique. *Ann Paléontol* 89: 1–35
- Guérin C, Pickford M (2005) *Ancylotherium cheboitense* nov. sp., nouveau Chalicotheriidae (Mammalia, Perissodactyla) du Miocène supérieur des Tugen Hills (Kenya). *C R Palevol* 4: 225–234
- Hamilton WR (1973) North African lower Miocene Rhinoceroses. *Bull Br Mus (Nat Hist) Geol* 24: 351–395
- Harrison JA, Manning EM (1983) Extreme carpal variability in *Teleoceras* (Rhinocerotidae, Mammalia). *J Vertebr Paleontol* 3: 58–64
- Heissig K (1969) Die Rhinocerotidae (Mammalia) aus der oberoligozänen Spaltenfüllung von Gaimersheim. *Abh Bayer Akad Wiss Math Nat Kl* 138: 1–133
- Heissig K (1972) Paläontologische und geologische Untersuchungen im Tertiär von Pakistan. 5. Rhinocerotidae (Mamm.) aus den unteren und mittleren Siwalik-Schichten. *Abh Bayer Akad Wiss Math Nat Kl* 152: 1–112
- Heissig K (1974) Neue Elasmotheriini (Rhinocerotidae, Mammalia) aus dem Obermiozän Anatoliens. *Mitt Bayer Staatssamm Paläontol hist Geol* 14: 21–35
- Hooijer DA (1963) Miocene Mammalia of the Congo. *Mus R Afr centr, Ann- Sci géol* 46: 1–77
- Hooijer DA (1966) Miocene rhinoceroses of East Africa. *Bull Br Mus (Nat Hist) Geol* 13: 119–190
- Hooijer DA (1968) A rhinoceros from the late Miocene of Fort Ternan. *Zool Meded* 43: 77–92
- Hooijer DA (1971) A new rhinoceros from the late Miocene of Loperot, Turkana district, Kenya. *Bull Mus Comp Zool* 142: 339–392
- Hooijer DA (1973) Additional Miocene to Pleistocene rhinoceroses of Africa. *Zool Meded* 46: 149–178
- Kaup J.-J. (1832) Über *Rhinoceros incisivus* CUV. und eine neue Art, *Rhinoceros schleiermacheri*. *Isis* 8: 898–904
- Killgus H (1923) Unterpliozäne Säuger aus China. *Paläontol Z* 5: 251–257
- McCrossin ML, Benefit BR (1994) Maboko Island and the evolutionary history of Old World monkeys and apes. In: Corruccini RS, Ciochon RL (eds) *Integrative Paths to the Past: Paleoanthropological Advances in Honor of F.C. Howell*. Prentice-Hall, New York, pp 95–122
- Mecquenem R de (1908) Contribution à l'étude du gisement de vertébrés de Maragha et de ses environs. *Ann Hist Nat* 1: 27–79
- Nakaya H, Pickford M, Yasui K, Nakano Y (1987) Additional large mammalian fauna from the Namurungule Formation, Samburu Hills, northern Kenya. *Afr Study Monogr* 5: 79–129
- Osborn HF (1924) *Serridentinus* and *Baluchitherium*, Loh Formation, Mongolia. *Am Mus Novitates* 148: 1–5
- Pickford M (1979) New evidence pertaining to the Miocene Chalicotheriidae (Mammalia, Perissodactyla) of Kenya. *Tertiary Res* 2: 83–91
- Pickford M (1981) Preliminary Miocene mammalian biostratigraphy for western Kenya. *J Hum Evol* 10: 73–97
- Pickford M, Senut B, Hadoto D (1993) Geology and paleobiology of the Albertine rift valley, Uganda-Zaire. Volume I: geology. Centre intern format études géol, Publ occas 24: 1–190
- Retallack GJ, Wynn JG, Benefit BR, McCrossin ML (2002) Paleosols and paleoenvironments of the middle Miocene, Maboko Formation, Kenya. *J Hum Evol* 42: 659–703
- Ringström T (1923) *Sinotherium lagrelii*, a new fossil rhinocerotid from Shansi. *Bull Geol Surv China* 5: 91–93
- Ringström T (1924) Nashörner der *Hipparion*-Fauna Nord-Chinas. *Pal Sinica* C 11: 1–156
- Roussiakis SJ, Theodorou GE (2001) *Ancylotherium pentelicum* (Gaudry & Lartet, 1856) (Perissodactyla, Mammalia) from the classic locality of Pikermi (Attica, Greece), stored in the palaeontological and geological museum of Athens. *Geobios* 34: 563–584
- Saraç G, Sen S (2005) Chalicotheriidae (Mammalia, Perissodactyla) from the late Miocene of Akkasdağı, Turkey. *Geodiversitas* 27: 591–600
- Tsujikawa H (2005) The updated late Miocene large mammal fauna from Samburu hills, northern Kenya. *Afr study monog* 32 suppl: 1–50
- Walker A (1968) The lower Miocene fossil site of Bukwa, Sebei. *Uganda J* 32: 149–156

- Werdelin L (2010) Chapter 3 - Chronology of Neogene Mammal localities. In: Werdelin L, Sanders WJ (eds) *Cenozoic Mammals of Africa*. University of California Press, Berkeley, pp 27–43
- Yan D (1979) Einige der Fossilen Miozänen Säugetiere der Kreis von Fangxian in der Provinz Hupei. *Vert PalAsiat* 17: 189–199
- Zapfe H (1979) *Chalicotherium grande* (Blainv.) aus der miozänen Spaltenfüllung von Neudorf an der March (Devínska Nová Ves), Tschechoslowakei. *N Denkschr naturhist Mus Wien* 2: 1–282
- Zhai RJ (1978) A primitive elasmothere from the Miocene of Lintung, Shensi. *Prof papers stratigr Palaeontol* 7: 122–127