Brachypotherium minor n. sp., and other Rhinocerotidae from the Early Miocene of Buluk, Northern Kenya

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ABSTRACT

A new species of Rhinocerotidae, *Brachypotherium minor* n. sp., from the Early Miocene of Buluk, northern Kenya, is described. The new species shares with other members of the genus large sexually dimorphic incisors, flattened buccal walls on its molars, and a low astragalus, but differs from other species of *Brachypotherium* Roger, 1904 in its small size, placement of the orbit, having widely separated temporal lines, and more simple molar crown morphology. A comparison of the new species with other brachypotheres suggests that the new species may be present at a small number of other sites, and that the brachypothere group may contain more than one African lineage, adding to our understanding of the diversity of African rhinoceroses.

KEY WORDS
Mammalia,
Perissodactyla,
Rhinocerotidae,
Early Miocene,
Kenya,
new species.

RÉSUMÉ

Brachypotherium minor *n. sp., et autres Rhinocerotidae du Miocène inférieur de Buluk, nord du Kenya.*
Nous décrivons une nouvelle espèce de Rhinocerotidae, *Brachypotherium minor* n. sp., du Miocène inférieur de Buluk, nord du Kenya. Cette nouvelle espèce partage avec les autres formes du genre de grandes incisives à dimorphisme sexuel marqué, des murailles buccales des molaires aplaties, et un astragale bas, mais diffère des autres espèces de *Brachypotherium* Roger, 1904 par sa petite taille, la position de l'orbite, ses lignes temporales largement séparées, et une morphologie dentaire plus simple. La comparaison de cette nouvelle espèce avec d'autres brachypthères suggère qu'elle pourrait être présente dans quelques autres sites, et que ce groupe pourrait comprendre plus d'une lignée africaine, accroissant encore la diversité connue des rhinocéros africains.

MOTS CLÉS
Mammalia,
Perissodactyla,
Rhinocerotidae,
Miocène inférieur,
Kenya,
espèce nouvelle**.**

INTRODUCTION

Buluk is located in a remote part of northern Kenya (Fig. 1). Fossiliferous deposits at Buluk are part of the Buluk Member, Bakate Formation; and the Buluk Member is composed of claystones with coarse sandstone and conglomerate channel fill. Fossils are retrieved from the channel deposits. A potassium/argon (K/Ar) date for a layer just above the fossiliferous deposits gives an age for the Buluk fauna of < *c.* 17 Ma (McDougall & Watkins 1985).

The occurrence of fossil mammals at Buluk was first noted in 1974 and the geochronology was reported in 1985 (McDougall & Watkins 1985). Also in 1985, R. Leakey and A. Walker announced the recovery of a sizable collection of early Miocene mammals (*c.* 20 species in 17 genera; see Leakey & Walker 1985). This material included remains of a hominoid, as well as 16 specimens of a catarrhine monkey which were described by M. Leakey in the same year (Leakey 1985). Owing largely to the remoteness of the locality, no fossil collecting was then done at Buluk for almost thirty years, until work in the area was re-initiated beginning in 2004 (E. Miller and colleagues).

Because of the recovery of fossil primates, Buluk has been well known as an important site for paleoanthropology (Leakey 1985; Miller *et al.* 2009). In addition, preliminary work on the paleoecology of Buluk contributes to a more comprehensive understanding of regional ecologies in the Rift Valley system (e.g., Miller & Wood 2010). This research is important because habitat fragmentation occurring during the Miocene, generated in part by the initial phases of East African rifting, may be at the root of later Miocene ape diversity. Information from Buluk helps document the transition from an archaic to a modern African fauna by contributing to a more complete understanding of the important faunal turnover events of the Early Miocene. This includes the timing and extent of contact between African and Eurasian faunas, as immigrant taxa, such as rhinocerotids, deployed across the African landscape.

The rhinoceroses from Buluk were briefly mentioned recently (Geraads 2010). A full description of the whole collection housed in the National Museums of Kenya, Nairobi, is provided here.

TERMINOLOGY

The names of the various components of rhino cheek-teeth follow Geraads (2010: fig. 34.1). In the descriptions, the tooth-rows are supposed to be horizontal. Upper teeth are in uppercase, lower teeth in lowercase. All measurements are in mm.

ABBREVIATIONS
Anatomy
APD   antero-posterior dimension;
L   length;
TD   transverse dimension;
W   width.

Institutions
HLMD   Hessisches Landesmuseum, Darmstadt;
KNM   National Museums of Kenya, Nairobi;
NHML   Natural History Museum, London;
NME   National Museum of Ethiopia, Addis Ababa;
UCBL   Université Claude Bernard, Lyon;

Collections (prefix for fossils)
DIN   Dinotherien-Sanden, Germany;
LT   Lothagam;
MI   Mwiti, Kajong;
NL   Nabwal;
RU   Rusinga;
WS   Buluk, also called West Stephanie.

SYSTEMATIC PALAEONTOLOGY

Family RHINOCEROTIDAE Gray, 1821

Genus *Brachypotherium* Roger, 1904

DIAGNOSIS. — Large rhinos with broad and low skull, short nasals, nasal horn(s) absent or small, orbit far forward, powerful anterior dentition and especially large I1s with a short root, brachyodont cheek-teeth and short but broad premolars. Upper and lower molars tend to have flattened buccal walls and the latter have shallow ectoflexids. Gonial area of the mandible expanded. Short massive terminal limb segments, with a characteristically low talus. Three digits.

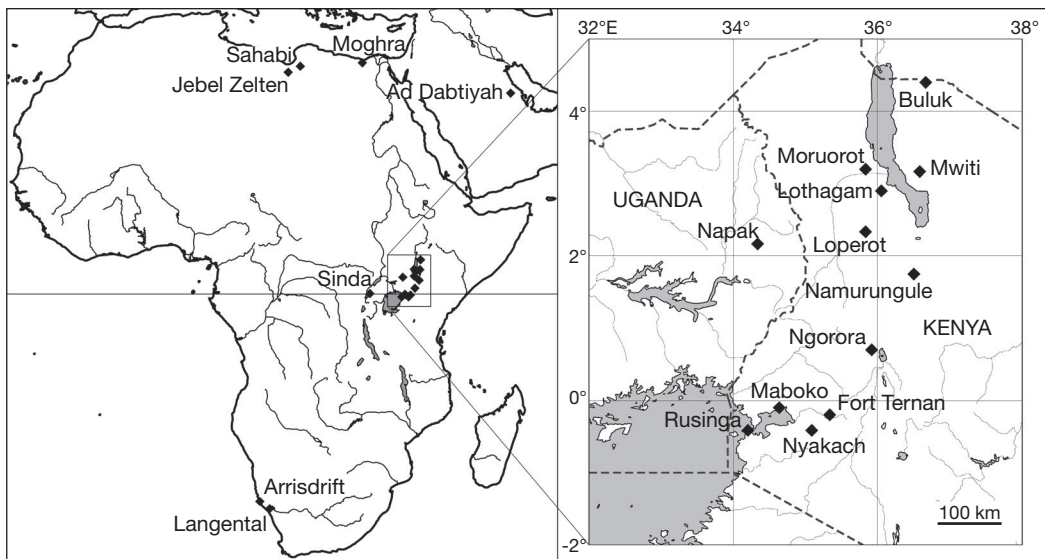TYPE SPECIES. — *Rhinoceros goldfussi* Kaup, 1834 by original designation.

FIG. 1. — Location of the main Afro-Arabian sites with *Brachypotherium* Roger, 1904. Right: detail of Eastern Kenya and Western Uganda.

Brachypotherium minor n. sp.

Brachypotherium sp. Geraads, 2010: 670.

HOLOTYPE. — KNM WS-46072, relatively complete skull, lacking the premaxillae and right cheek teeth, but preserving the left P2–M3. Housed in the National Museums of Kenya, Nairobi.

ETYMOLOGY. — In reference to its small size.

EXAMINED MATERIAL. — Except for the specimens mentioned below under "Rhinocerotidae gen. et sp. indet.", we assign all the Rhinocerotidae material from Buluk to this new species.

TYPE HORIZON. — Buluk Member, Bakate Formation.

TYPE LOCALITY. — Buluk, Northern Kenya, Early Miocene (*c.* 17 Ma), 4°15'N, 36°36'E.

DIAGNOSIS. — A *Brachypotherium* of relatively small size. Skull short and broad, dorsal profile almost flat, temporal lines far apart, nasals not much shortened, perhaps bearing (a) small terminal horn(s), orbit does not reach very far anteriorly. No sub-aural contact between postglenoid and post-tympanic processes. Upper teeth with poor development of accessory crests, protoloph and metaloph of premolars directed transversely and of even thickness, protocone of molars not much constricted, antecrochet moderate. Upper I1 and lower i2 sexually dimorphic.

DESCRIPTION
Skull
The holotype skull KNM WS-46072 (Fig. 2) is the most instructive specimen. It is not much crushed, but is slightly affected by what White (2003) called "expanding matrix distortion" (EMD), i.e. the skull consists of a mosaic of fragments that are not contiguous, but are separated by intervening matrix, resulting in some inflation of the specimen and increasing its apparent size.

Measurements (in mm): length from condyle to front of P2 = 460 ; bizygomatic width 2 × 175- (width increased by EMD); maximum occipital width = *c.* 240; length from condyle to rear of M3 = 250; bicondylar width = 112; length from tip of nasals to top of occipital = 520- (length increased by EMD).

In lateral view, the top of the skull is slightly concave from the top of the occipital to the anteorbital area, where preservation is not very good, and it is likely that the anterior part of this profile, to the tip of the nasals, was approximately straight. The occipital plane is distinctly inclined forwards, so that the nuchal crest is more anterior than the occipital condyles. The zygomatic arch is robust, but not extremely so, and has a gentle

TABLE 1. — Measurements (in mm) of the upper I1s of *Brachypotherium minor* n. sp. from Buluk.

	KNM WS-11 male	KNM WS-147 male	KNM WS-139 female	KNM WS-12860 female	KNM WS-12862 female
Length of the crown	c. 83	68	40.8	34	48.5
Width	22.5	20.8	14.4	14.5	14.3

sigmoid curvature; its ventral border has a large notch behind the orbit. The latter is not well preserved; its anterior border is above the rear part of M1. The nasals have been somewhat crushed down into the nasal notch; therefore, the outline of the latter is not clear, but its bottom was above P2/P3. The nasals show a hint of dorsal convexity and of longitudinal swellings that suggest that they might have born some kind of small horn, but this is far from certain, as the preserved part of their surface is smooth.

In dorsal view, the skull is broadest at orbital level; behind this, the transverse diameter of the fronto-parietal roof, between the temporal lines, decreases slowly caudally, but it remains broad even in its narrowest part. The occipital has a flat top border between the temporal lines. Rostrally, the decrease in width is not abrupt either, as the nasals are well anterior to the orbit.

In ventral view, the well preserved sub-aural region shows that the postglenoid process remains separated by several millimeters from the transversely elongated paroccipital process, but the rest of the cranial base is poorly preserved. We do not know whether the vomer and basioccipital were rounded or keeled. The location of the condylar foramen is not quite clear, but it is probably rather close to the condyles. The choanae reach the level of the metaloph of M2.

Upper teeth
The cheek-teeth are well-worn, but their main features remain visible. There is an alveolus for a P1 or DP1. All teeth have a flat or very slightly concave buccal wall behind the moderate paracone fold. The metaloph of P2 is directed slightly mesially and comes into contact with the protoloph. On P3, the protoloph and metaloph are long and transverse, without accessory crests (save

perhaps for a vestigial crochet) or constriction, so that their thickness is regular for most of their length; the lingual cingulum is faint, except at the opening of the central valley, where it is stronger. P4 displays the same features, except that it has a small crochet and a hint of protocone constriction. On the much worn M1, constriction of the protocone is distinct but remains shallow, as on M2 and M3, which have a small crochet. M3 is triangular, with a robust paracone fold.

Its premaxillae being absent, the upper incisors are unknown in the holotype, but there is no doubt that they were present, as they are represented by several isolated specimens. Two of them are much larger than the other three (Table 1; Fig. 3A-E), and we assume that they represent two male and three female individuals, because such sexual dimorphism (or rather "dimetrism", as there is no major morphological difference between the male and female upper incisors) is well known in brachypotheres (e.g., Roger 1900; Heissig 1972b; Cerdeño 1993), and because the non-brachypothere rhino of Buluk (see below) is a rare form that is unlikely to be represented by three upper incisors. On the male specimens, the root is shorter than the mesio-distal length of the crown. KNM WS-11 is unworn; in occlusal view, the crown is long and of regular width; in WS-147, instead, the central part of the crown is distinctly broader, but none of these specimens match any of the types illustrated by Antoine (2002: fig. 82). In both male and females, wear first affects the buccal part of the crown in the mesial half, and then proceeds distally and buccally.

Upper cheek teeth are represented by a number of other specimens, so that the morphological and metric variations can be estimated (Table 2; Fig. 3F-I). None bears cement. KNM WS-12633 (Fig. 3H) is a left maxilla including the rounded
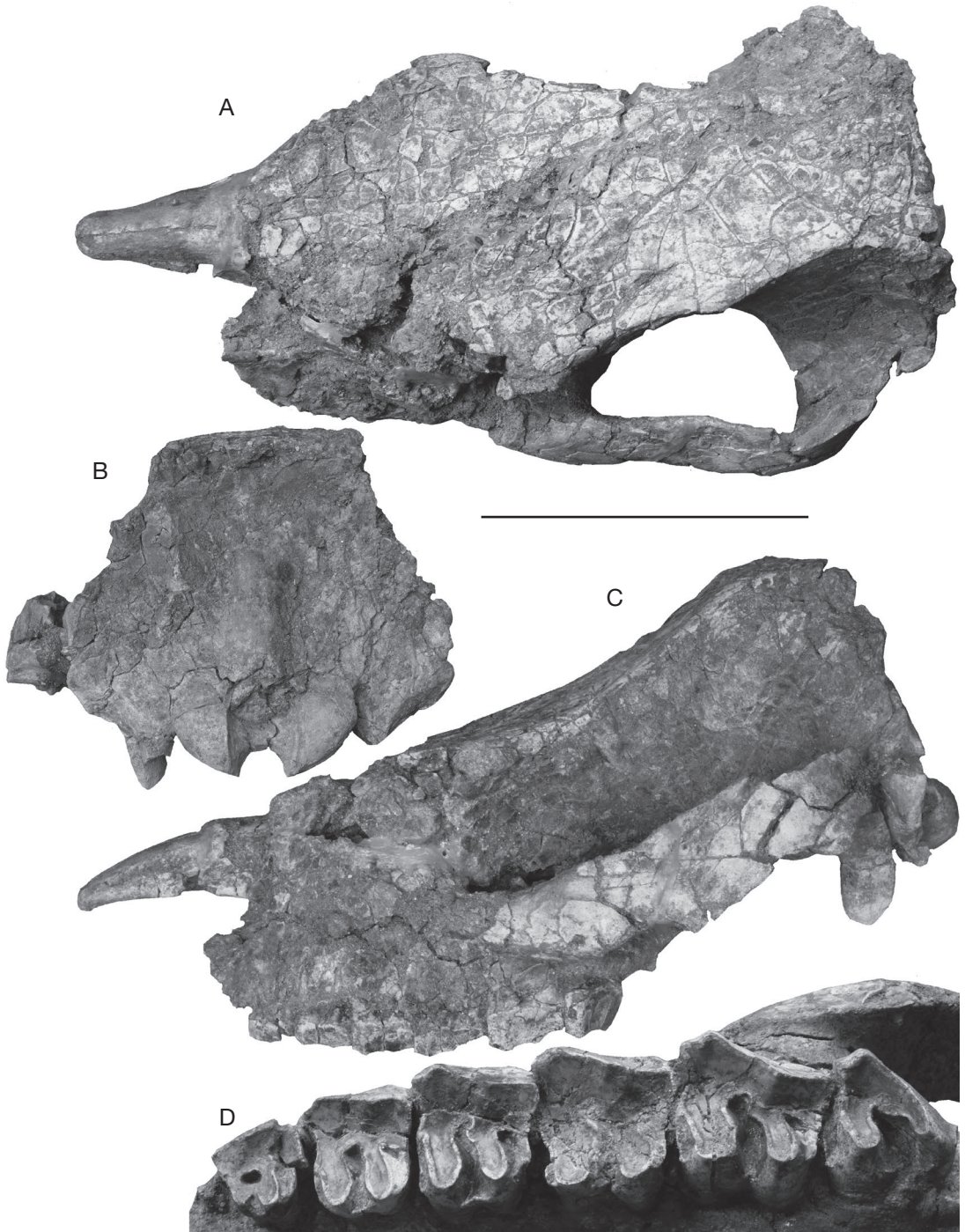
Fɪɢ. 2. — *Brachypotherium minor* n. sp., holotype skull KNM WS-46072 from Buluk in: **A**, dorsal; **B**, occipital; **C**, left lateral views; **D**, occlusal view of left P2-M3. Scale bar: A-C, 20 cm; D, 10 cm.

TABLE 2. — Measurements of upper cheek teeth of *Brachypotherium minor* n. sp. and of Rhinocerotidae indet. (specimens marked with a *) from Buluk.

Specimens from KNM	DP2		P2		P3		P4		M1		M2		M3		M1-M3
	L	W	L	W	L	W	L	W	L	W	L	W	L	W	
WS-13*							44.5	56.4							
WS-14													57.4	51.5	
WS-15													51.7	50.8	
WS-98											48.8	53.2			
WS-133									47		50	52.7	54.5	48.8	
WS-141					35.5	42.6									
WS-143	25	23.4													
WS-12633					32.8	42.8	35.3	49.2	45.4	53.3	50.5	58.4		49.7	131
WS-12843*											56				
WS-12844											56.6	53.4			
WS-12848													49.4	47.2	
WS-12849			29.2	31.8	33	41.3									
WS-12851							36	47							
WS-12855	32	30													
WS-12858					30	39.5	34.2	45							
WS-30722							40	53.1							
WS-30726							38.3	45.2							
WS-46072			27.5	32	34	42.3	39.6	47.5	45	48	48.3	50.6	49.5	46.3	131
WS-49467					39.2	46	41.9	53.3	51.8	53	54.5	55.5			

ventral orbital border; its mesial border reached farther rostrally than in the type, above the mesial part of M1. The P3-M3 series shows almost exactly the same features as the holotype, except that the lingual cingulum is better indicated, especially on the molars, and that the metaloph is slightly longer than the protoloph on P4, instead of slightly shorter. WS-12858 (Fig. 3G) is a series P3-M1 in medium wear. The well-preserved premolars have a stronger lingual cingulum than in the previous specimens, but are otherwise similar in their long, simple, parallel lophs showing no indication of a constriction or lingual connection, and with a small crochet as the only accessory spur. It is also present on M1, of which, unfortunately, the protocone is broken off; the distal part of the ectoloph is directed somewhat disto-buccally, so that the buccal wall is more concave than in the previous M1s. WS-12849 is a series P2-P4 (buccal part of P4 missing), again with the same characters, but completely lacking the lingual cingulum. WS-133 (Fig. 3I) is a series M1-M3, moderately worn; the buccal walls of M1 and M2 also have a paracone fold and a concave distal part; all molars have a small

crochet and a robust but short antecrochet, less distinct on M3. WS-49467 (Fig. 3F) is a tooth-row P4-M2; on P4, the protoloph and metaloph are slightly convergent lingually, but remain far from each other; the antecrochet is poorly indicated on the molars.

KNM WS-143 is a very small incompletely cleaned DP2, with a poor central buccal rib and no other buccal fold, and short crochet and crista that remain far from each other, no prefossette, a transverse metaloph and a long, oblique protoloph. WS-12851 is a P4 similar to those of WS-46072 and WS-12633 in its parallel lophs and some indication of an incipient antecrochet. WS-30722 is another P4 on which the antecrochet is better indicated, but remains moderate; the lingual cingulum is weak. WS-30726 is still another P4, unworn, also with a weak lingual cingulum and poorly expressed antecrochet; its height (42 mm) is intermediate between its length and width and the tooth can therefore be qualified as mesodont.

KNM WS-12844 is a slightly worn M1 or M2 with distinct pinching of the protocone, moderate antecrochet, and small crista; as on the molar series mentioned above, the parastyle is short and
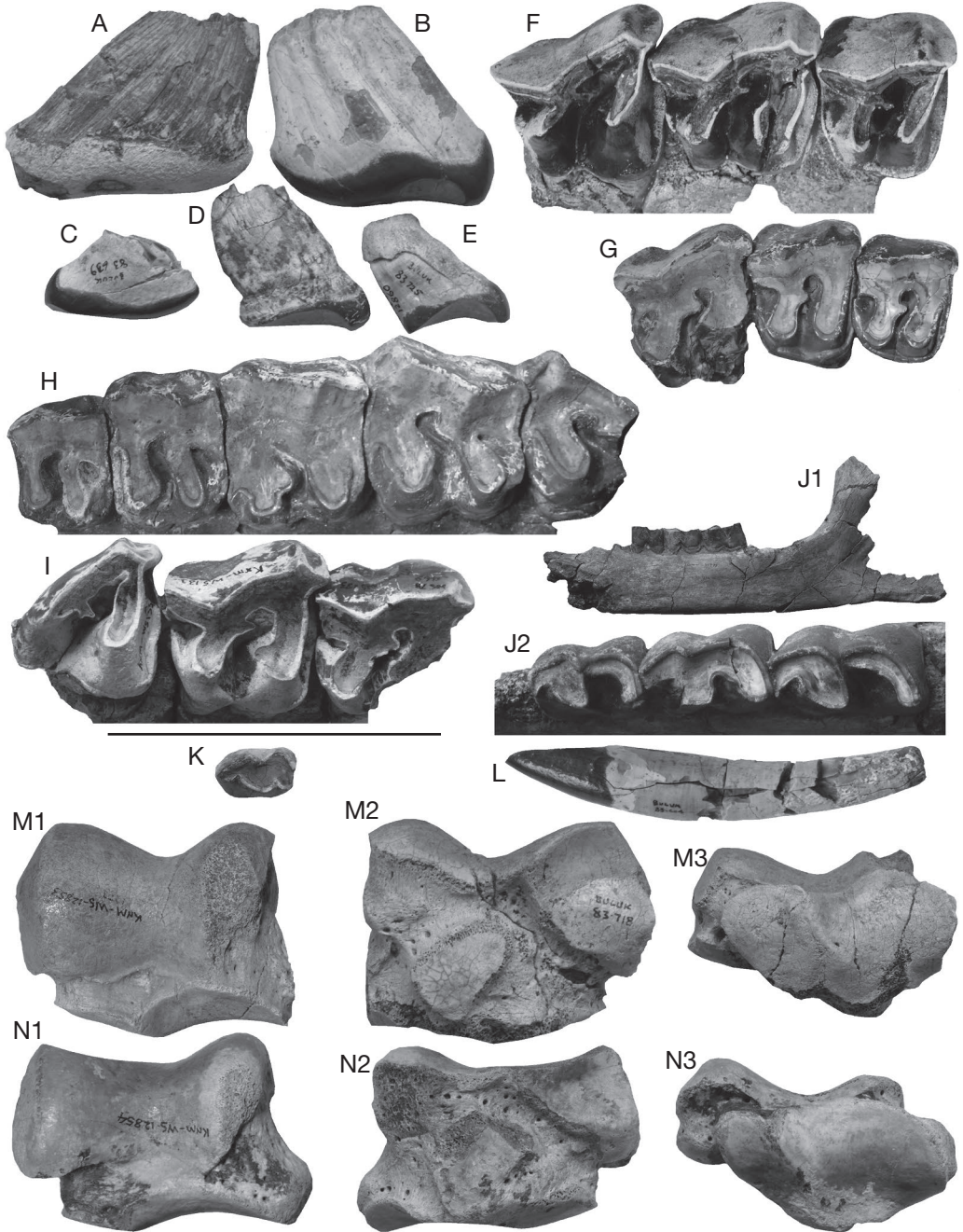
Fig. 3. — *Brachypotherium minor* n. sp. from Buluk: **A-E**, upper I1s in labial view; **A**, WS-11 (male ?); **B**, WS-147 (male ?); **C**, WS-12862 (female ?); **D**, WS-139 (female ?); **E**, WS-12860 (female ?); **F**, P4-M2, WS-49467; **G**, P3-M1, WS-12858; **H**, P3-M3, WS-12633; **I**, M1-M3, WS-133; **J1**, mandible WS-45979, medial view; **J2**, same, occlusal view of p4-m2; **K**, p2 WS-12850; **L**, left female i2 WS-12864, lateral view; **M**, right astragalus WS-12853; **N1**, right astragalus WS-12854, cranial view; **N2**, same, plantar view; **N3**, same, distal view. Scale bar: A-I, J2-N, 10 cm; J1, 1.25 cm.

much less buccal than the robust paracone rib. The tooth is about as high as it is broad. WS-99 is another upper molar, in medium wear, with the same characters; the distal part of the buccal wall is distinctly concave. There are three M3s (KNM WS-14, WS-15 and WS-12848) that are clearly triangular but with some basal disto-buccal expansion, a weak crochet, and a poorly expressed antecrochet.

On the whole, these upper cheek-teeth are notable for their simplicity, mesodonty, poor development of accessory structures, variable cingulum, transverse orientation of the pro-toloph and metaloph, and lack of lingual contact between them.

Mandible

The best mandibular specimen is KNM WS-45979 (Fig. 3J); it lacks the rostral part and most of the ascending ramus, but the large size and great depth of the corpus anterior to the cheek-teeth leave no doubt as to the presence of large incisors. The ventral border of the corpus is virtually straight for its entire length. The mental foramen is below the mesial root of p3. From what remains of the posterior part, it is likely that the gonial area was at least somewhat expanded. The mandible preserves p4-m2 in me-dium wear (Fig. 3J2). Rhinoceros lower teeth are less distinctive than upper ones, but these ones display some typical features: on the molars, the paralophid is short lingually, the protolophid is oblique rather than transverse, the hypolophid is more crescent-shaped than L-shaped, and the ectoflexid (buccal groove) is shallow. The premo-lars were certainly short compared to the molars; from its alveoli, p2 was quite small, and there was certainly no p1.

Lower teeth

KNM WS-12850 (Fig. 3K) and WS-12861 are p2s; they are small, simple, with a reduced par-alophid and shallow valleys. WS-146 consists of several mandibular pieces with unworn p3, p4, m1, and partial m2, showing the same characters; like the upper ones, they are mesodont, being about as high as they are long. The oblique lophids

and shallow ectoflexid are also quite clear on the m1-m2 WS-23 and on the large m2, WS-136. A few isolated lower cheek-teeth display similar features. Measurements of lower cheek-teeth are given in Table 3.

KNM WS-12866 is a large fragment of the crown of a large lower i2 (diameters: 42 × 24). In its unworn part, the cross-section is amyg-daloidal, i.e., the dorsal face is as convex as the enamel-covered ventral one. It is likely from a male individual, while the much worn i2 WS-12864 (Fig. 3L), which preserves its very long root, is much smaller (26.5 × 17) and therefore probably represents a female.

Post-cranials

Rhinocerotid post-cranial remains are rare at Buluk. KNM WS-13021A and WS-13021B are two distal ulnae. The latter is more robust and the radial facet is more vertical; there is a strong tuberosity on the anterior face but no lunar facet, as in European *Brachypotherium* (Antoine 2002) and no accessory facet for the radius is visible; we tentatively assign it to *Brachypotherium*.

KNM WS-12857 is a distal central metapo-dial, with a marked plantar concavity above the articulation

KNM WS-12853 and WS-12854 are two right astragali (Fig. 3M, N) that share the same low and broad proportions (Table 4), a poorly concave ectal calcanear facet with a marked distal extension, and a much reduced or absent distal calcanear facet. WS-12854 differs in that, unlike in most rhinos, the proximal profile of the lateral lip of the trochlea is flat or even slightly concave in front view, and the cuboid facet is much narrower compared to the navicular one. It is likely that these differences reflect a different dispatching of the weight on the digits, but the similar size and proportions of these astragali prompt us to assign both of them to *Brachypotherium*.

Although a second rhino species is certainly pre-sent at Buluk (see below), we assign all specimens described above to a single species. Features of the upper teeth, as well as those of the lower ones, are homogeneous, and there is no reason to doubt their association.

TABLE 3. — Measurements of lower permanent cheek teeth of *Brachypotherium minor* n. sp. and of Rhinocerotidae indet. (specimens marked with a *) from Buluk.

Specimens from KNM	p2		p3		p4		m1		m2	
	L	W	L	W	L	W	L	W	L	W
WS-23							44	28	49	30
WS-130			33.3	23.5	37	27.6				
WS-136									52	28
WS-144*			32.6	22					43.9	29
WS-146			36	21			43	24.4		
WS-12842*							40.7	26.1		
WS-12846*					36.2	25.4				
WS-12850	24.5	15.3								
WS-12852			33	24.5						
WS-12856			34	25						
WS-12861	25.7	17.3								
WS-31253								26		
WS-45979					36.2	28.3			46	31

COMPARISONS AND DISCUSSION

Early and Middle Miocene rhinos of Africa are still very imperfectly known (see review in Geraads 2010), but several groups can be distinguished, although they may well not have taxonomic value:

1) the elasmotheres and related forms include *Ougandatherium napakense* Guérin & Pickford, 2003 from Napak, *Turkanatherium acutirostratum* Deraniyagala, 1951 from Moruorot (Hooijer 1968; Geraads 2010), a rhino from the Samburu Hills (Nakaya *et al.* 1987; Tsujikawa 2005), *Victoriaceros kenyensis* Geraads, McCrossin & Benefit, 2012 from Maboko, and perhaps the poorly known *Chilotheridium pattersoni* Hooijer, 1971 from Loperot (this author thought it was related to the Eurasiatic *Chilotherium* Ringström, 1924, a relationship rejected by Geraads 2010 and Antoine *et al.* 2010). The diversity of their cranial morphology casts doubts on the monophyly of this group, but they have a distinctive upper cheek tooth morphology, with a tendency to hypsodonty, lingual fusion of the lophs of the upper premolars, and strongly pinched protoloph on the molars, with a robust antecrochet. Overall, this morphology may be called the opposite of that of the Buluk most common rhino; therefore, the latter is certainly not closely related to the elasmotheres *s.l.*;

TABLE 4. — Measurements of rhinocerotid astragali from Buluk. Those marked with * are not of *Brachypotherium* Roger, 1904. Abbreviations: see Material and methods.

Specimens from KNM	max. TD	distal articular TD	medial height
WS-1*	73	–	65
WS-7*	73	59	58
WS-12853	88	71.5	64.3
WS-12854	91	71	60.5

2) rhinoceroses that, at least superficially, resemble the modern forms (but a phyletic connection is far from certain) first appear at Arrisdrift (Guérin 2000, 2003) with the poorly known "*Diceros*" *australis* Guérin, 2000; they seem to be well represented at Rusinga by *Rusingaceros leakeyi* (Hooijer, 1966) Geraads, 2010, and in the Late Middle Miocene of Fort Ternan by *Paradiceros mukirii* Hooijer, 1968. Their simple cheek tooth morphology is reminiscent of the Buluk rhino, but they have a strong nasal horn. *Paradiceros* Hooijer, 1968 further differs in its vestigial or absent incisors, and *Rusingaceros* Geraads, 2010 differs in the completely different cranial shape and proportions;

3) still another group, perhaps related to *Plesiaceratherium* Young, 1937, might be represented by the undescribed material from Nyakach (Pickford 1986), but it is also certainly distinct from the Buluk rhino;

and 4) last, the brachypotheres are rhinos of large size, hornless or virtually so, with a short and broad skull, and short distal limb segments; commonly included here (Cerdeño 1995; Antoine 2002; Antoine *et al.* 2010) are the American *Teleoceras* Hatcher, 1894, the European *Prosantorhinus* Heissig, 1974 and *Diaceratherium* Dietrich, 1931 and *Brachypotherium*, widespread in the Old World, with several African representatives (Fig. 1). It is probably present as early as Napak (Hooijer 1966), it is definitely present at Rusinga (Hooijer 1966), but it is best known from Moghra (= Moghara) in Egypt (Fourtau 1920; Miller 1996) and Gebel Zelten in Libya (Hamilton 1973), two sites that are roughly contemporaneous with Buluk (although Moghra might be slightly earlier), and in the much later Nawata and Apak Formations of Lothagam in Kenya (Hooijer & Patterson 1972; Harris & Leakey 2003). There is also a nice unpublished mandible from the Middle Miocene of Mwiti (Kajong), KNM MI-3. Fragmentary remains from several other Afro-Arabian sites can be assigned to *Brachypotherium* with reasonable confidence. These include material from Langental in Namibia (Heissig 1971; Hooijer 1973; Guérin 2000), Ad Dabtiyah in Saudi Arabia (Gentry 1987), Nyakach (a single unpublished I1), perhaps Maboko (Geraads *et al.* 2012), Ngorora (Nakaya 1993) in Kenya, Sinda in Congo (Hooijer 1963), and Sahabi in Libya (d'Erasmo 1954).

In the characters of the skull, upper and lower dentition, and astragali, the Buluk most common rhino clearly aligns with brachypotheres but differs from all previously described forms.

It differs from American *Teleoceras* (reviewed in Prothero 2005) in the short and narrow nasals probably lacking horn(s), in the straight ventral mandibular corpus, in the brachyodont cheek-teeth lacking cement, in the weaker antecrochet on upper molars.

The Buluk rhinoceros differs from *Diaceratherium aurelianense* (Nouel, 1866) in its shorter and narrower nasals, less concave dorsal skull profile, lower and broader occipital, straight ventral border of the mandible, broader lower teeth with a shallower ectoflexid, much weaker antecrochet on the premolars and flatter buccal walls on the upper cheek-teeth

(Mayet 1908; Cerdeño 1993). *Diceratherium aurelianense* from the European MN 3 is also earlier in time than the Buluk Brachypotherium.

Prosantorhinus Heissig, 1974, from the European early and middle Miocene, is about the same size as the Buluk form. Sexual dimorphism in the incisors is more marked than at Buluk (Peter 2002), the ectoflexid is much deeper on the lower cheek teeth, upper cheek teeth have very strong paracone fold and parastyle, the protocone is better distinguished from the protoloph on P4 and on the molars (Heissig 1972a; Ginsburg & Bulot 1984; Cerdeño 1996; Petter 2002). Photographs of the cranial remains from Sandelzhausen, described by Heissig (1972a) but not illustrated by him, were kindly provided by I. Giaourtsakis, and a skull from Langenau was illustrated by Heizmann *et al.* (1996). The skulls from both sites are broad and low, but differ from the Buluk form in the slightly deeper nasal notch and more anterior orbit (so that they are closer to each other), in the presence of a well-marked sagittal crest, in the concave cranial profile (especially so at Sandelzhausen), and in the presence of small nasal horns. There is no reason to connect the Buluk rhinoceros to *Prosantorhinus*, which remains unknown in Africa.

A full revision of the Eurasian material of *Brachypotherium* is badly needed, as a large part of it has not been studied since the XIXth century. The type species, *B. goldfussi* Kaup, 1834, defined in the Vallesian of Eppelsheim, is poorly known (Kaup 1834), as the type-series consist of four teeth only. It differs from the Buluk form in its very large size: a P4 from Eppelsheim (HLMD DIN-1904; Kaup 1834: pl. 12, fig. 12), is 52 mm long and 69 mm broad. Its predecessor, *B. brachypus* (Lartet, 1848) has been reported and described from many sites, mostly in France and Germany, covering part of the early and the whole middle Miocene, although few skulls are known. It is larger than the Buluk form (especially the incisors), hornless, the temporal lines are close to each other and there may be a sagittal crest, the orbits reach farther anteriorly and the forehead narrows abruptly in front of them, the cingulum is usually present, the antecrochet is better indicated and the hypocone more distinct from the metaloph on the premolars, the mandibu-

lar diastema is short, and there may be a small p1 (Roger 1900; Roman & Viret 1934; Heissig 1976; Ginsburg & Bulot 1984; Cerdeño 1993).

Southern Asian forms have been very incompletely described. In the large *Brachypotherium perimense* (Falconer & Cautley, 1847)(see Lydekker 1881; Colbert 1935; Heissig 1972b), the temporal lines are close to each other, the nasal bones are short, the orbit may reach far rostrally and is closer to the nasal notch, the postglenoid and post-tympanic processes fuse below the auditory foramen, the teeth are more hypsodont, the upper premolars have a convex buccal side, their hypocone is more expanded, and a p1 may be present. Antoine *et al.* (2000) assigned *Teleoceras fatehjangense* Pilgrim, 1910 to *Brachypotherium* on the basis that it is "identique en tous points" to *B. brachypus*, but in fact the teeth of the type-specimen of the Asian form (Pilgrim 1912: pl.11, fig. 4) are very different from those of the European species (on P4: extremely folded buccal wall, lingual bridge between the lophs, pinched protoloph); those of other specimens figured by Forster-Cooper (1934: figs 13C, 14) and Heissig (1972b: pl. 9, figs 4, 5, 8, 9) are also quite different, so that we exclude this species from the comparison. Antoine *et al.* (2010) also included in *Brachypotherium* the species *Aceratherium gajense* Pilgrim, 1912, but this is a very poorly known species; the P3 of the type-specimen (Pilgrim 1912: pl. 11, figs 1, 2) differs from those from Buluk in its strong antecrochet, S-shaped metaloph, and strong buccal fold.

Three species of *Brachypotherium* have been identified in Africa; they have been reported from several sites but often on inadequate material, so that it is presently impossible to know with any certainty the morphological characters of the two earlier ones (*B. snowi* and *B. campbelli*), so that only *B. lewisi* is satisfactorily defined.

The two much worn teeth from Napak (Hooijer 1966: pl. 8, figs 1, 2) are significantly larger than the Buluk ones. The same is true of the cheek teeth from Rusinga, but an upper male I1 (Hooijer 1966: pl. 4, fig. 6) is of the same size as the Buluk ones. Postcranially, an astragalus from Rusinga (Hooijer 1966: pl. 14, fig. 3, now KNM RU-3021) is slightly smaller and higher; it is even smaller than those

that Hooijer assigned to *Aceratherium* Kaup, 1832 and *Dicerorhinus* Gloger, 1841. This discrepancy between the sizes of teeth and astragali at Rusinga probably arises from the identification by Hooijer of *Brachypotherium* teeth mainly on the basis of their large size, but his identifications of isolated teeth, often difficult in rhinos, must be treated with caution. The Rusinga astragalus and incisor suggest that a brachypothere similar in size to one at Buluk was present at Rusinga but species identification is impossible.

A mandible from Mwiti indicates the presence of a rhinocerotid slightly larger than the one at Buluk (length p4-m2 = *c.* 130 mm, vs 120 mm on KNM WS-45979, whose teeth are less worn). The shallow ectoflexid and oblique hypolophid unambiguously identify the Mwiti specimen as a brachypothere. The symphysis is deep and broad, the gonial area is expanded, the mental foramen is below the anterior root of p3, the i2s are large (diameters: 42×35 mm), the missing p2 was small and there was certainly no p1. All these features are identical with those of the Buluk form, and there is little doubt that the two are co-specific (and contemporaneous).

From Nabwal, a site geographically and chronologically close to Buluk, there is a lower premolar NL-30962, and associated M2-M3 NL-30736 (M2 : 50.3×51.7; M3: 48.8×48.2), very similar in size and morphology to the Buluk teeth. The M2 is in medium wear, and has a slightly pinched protoloph, and a short antecrochet. We tentatively assign the Nabwal rhino to *B. minor*.

Moghra in Egypt, dated *c.* 21.5-17 Ma, is the type-locality of *Brachypotherium snowi* (Fourtau, 1918), whose type specimen is an upper jaw with the alveolus of a large incisor and worn cheek-teeth that do not significantly differ from the Buluk ones, except in their larger size (length of M1-M3 is 168 mm vs 131 mm at Buluk); these characters are shared by some upper teeth. Fourtau assigned to the same species a mandible (Fourtau 1920: fig. 28) with a long symphysis bearing robust i2s separated by smaller i1s, and with four cheek teeth that are slightly larger than those from Buluk. Although there were small i1s, the i2s are of moderate size only, with a root

diameter of *c.* 22 mm and a root length of 52 mm (Fourtau 1920); accordingly, at the level of the diastema, the symphysis has a clear waist and is much shallower than below the cheek-teeth, whereas rhinos with very large incisors have a broad and deep symphysis of even width. Although the mandibular symphysis is not fully preserved at Buluk, it is clear that the pre-dental portion was not similarly reduced. Also, in contrast to those from Buluk, p2 is large, with a paralophid curving lingually, a deep posterior valley, and p1 was present. If this mandible does belong to *B. snowi*, sexual dimorphism cannot explain the differences with the Buluk and Mwiti mandibles. Indeed, in spite of its much smaller i2s, the female mandibular symphysis of *Chilotherium wimani* Ringström, 1924 is but slightly narrower than that of the male (Chen *et al.* 2010; Fig. 3 and Table 2), and differs much less from it than the Moghra mandible from the Kenyan ones. We conclude that the *Brachypotherium* from Buluk and Mwiti is distinct from *B. snowi*, insofar as the Moghra mandible is indeed of the same species as the type maxilla.

From Gebel Zelten in Libya, a locality contemporaneous with Buluk and perhaps slightly younger than Moghra, Hamilton (1973) described both *B. snowi* and a new species, "*Aceratherium*" *campbelli*. At least two species are indeed present, but Hamilton (1973) was certainly partly wrong in the sorting of the specimens. The mandibular symphysis assigned to *B. snowi* (Hamilton 1973: pl. 6, fig. 3) is much broader than that of the Moghra specimen referred by Fourtau to this species, and the alveoli of the large i2s always extend much farther posteriorly (Hamilton 1973: 374). A mandibular fragment (Hamilton 1973: pl. 6, fig. 4), definitely of *Brachypotherium* because of the shallow m1 ectoflexid, shows that the missing p2 was certainly small, and p3 is narrow anteriorly. All these features are more reminiscent of the Mwiti and Buluk specimens than of *B. snowi* from Moghra.

The type skull of "*A.*" *campbelli* (Hamilton 1973: pls 1, 2, fig. 3) is large, broad over the zygomatic arches, the cranial basis is short, the cranial profile is deeply concave, and the occipital is broad, even dorsally, high, and rounded. What is preserved of the nasals show they were rather broad, and a pair of isolated nasals certainly carried a horn. Other cranial remains (Hamilton 1973: pl. 3) display the same features, plus large I1s. Upper cheek-teeth are somewhat larger than those from the same site assigned to *B. snowi* but the P4 is similarly broad, with a weak antecrochet. Following the suggestion of Gentry (1987), we take "*A.*" *campbelli* as a brachypothere, and it is likely that most of the specimens assigned by Hamilton to *A. campbelli* and *B. snowi* are in fact of the same species, but it is by no means certain that they really belong to *B. snowi*.

The skull of the Buluk brachypothere differs from that of "*A.*" *campbelli* in its smaller size, much less concave cranial profile, much more widely separated temporal lines, less rounded occipital, shallower nasal notch, absent or much smaller nasal horn, and orbit located less far forward. The two I1s from Gebel Zelten, including the one associated with maxilla NHML-M29252, which bears large cheek teeth, are shorter than those of the male specimens from Buluk; thus, either the Zelten incisors are from male individuals, and this adds another difference between the two forms, or they are from females, confirming that the size difference between the cheek-teeth of the Buluk and Zelten forms is not due to sexual dimorphism.

Some of the differences between the Buluk and Gebel Zelten skulls might be considered to represent sexual dimorphism, but these differences are of far greater magnitude than what has been recorded between males and females of species from elsewhere (*Teleoceras major*: Mead 2000; *Menoceras arikarense*: Mihlbachler 2007; *Chilotherium wimani*: Chen *et al.* 2010; *Rhinoceros unicornis*: Groves 1982). Only the difference in width of the nasals would be compatible with sex dimorphism, as the mean ratio is 75.4/44.3 mm in *M. arikarense* (Mihlbachler 2007), 150/118 mm in *R. unicornis* (Groves 1982) as compared to about 60 mm at Zelten vs about 40 mm at Buluk. All upper cheek teeth from Buluk are smaller than all those from Gebel Zelten, whereas there is always a large overlap between sexes of the same

species (female tooth rows may even be longer than those of males); the depth of the nasal notch is at least 200 mm at Zelten, about 110 mm at Buluk, whereas it is slightly deeper in the females of *Ch. wimani* and *T. major*; the temporal lines fuse into a sagittal crest at Zelten, but remain separated by about 90 mm at Buluk, whereas the difference in the minimum distance between them is only 10% in *Ch. wimani*. Therefore, we conclude that the Buluk brachypothere is distinct from the one present at Gebel Zelten.

From the Western Rift in Congo, Hooijer (1963) described as *Brachypotherium heinzelini* a few isolated teeth and tooth fragments, and an astragalus. The latter is characteristic of the genus, but naming a new species on the basis of these scrappy remains was unfortunate because, since these localities were thought by Hooijer to date from the middle Miocene, this name has been given since then to a number of brachypotheres from the middle and even early Miocene of Africa. In fact, since the Congolese localities are most probably of latest Miocene age (Yasui *et al.* 1992; Pickford 1993: 109), the brachypotheres from Rusinga and other Lower Miocene localities are certainly much earlier than *B. heinzelini*, and should not contribute to the definition of this species. The holotype P4 (Hooijer 1963, pl. 6, figs 4-6) does not morphologically differ from the Buluk ones, but is larger. The astragalus (Hooijer 1963, pl. 5, fig. 10) is also larger (width is 102 mm) and differs in its greater lateral height compared to the medial one; it is otherwise not very different from KNM WS-12854, but lower, especially on the medial side, than WS-12853 or than the Rusinga astragalus RU-3021. However, comparison with a large collection of *B. brachypus* astragali from the early and middle Miocene of France shows that, even though they all share *Brachypotherium* features, and do not greatly vary in size, each population has its own characteristics (concerning the lateral shift of the trochlea with respect to the distal part of the bone, or the relative height, inclination and rounding of its lips), meaning that slight differences may not have taxonomic value, and species identification of African brachypothere astragali is therefore impossible. If *B. heinzelini*
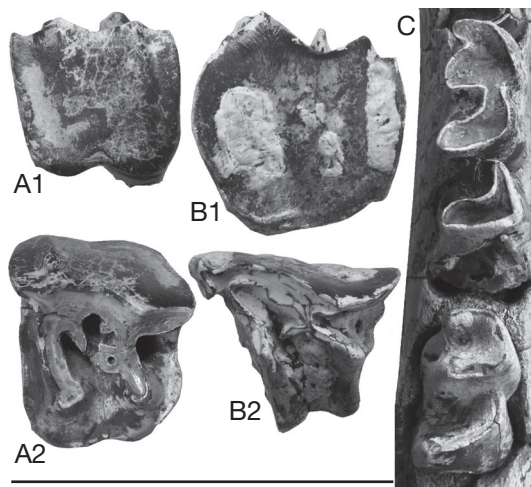

Fig. 4. — Rhinocerotidae gen. et sp. indet. from Buluk: **A1**, P4 WS-13, buccal; **A2**, same, occlusal views; **B1**, M2 WS-12843, buccal; **B2**, same, occlusal views; **C**, right lower dp4-m2, WS-144, occlusal view. Scale bar: 10 cm.

is indeed of latest Miocene age, it should rather be compared to other brachypotheres of this age (whose astragalus is unknown), but the material is so incomplete that this comparison is not very useful. Heissig (1971) assigned to *B. heinzelini* an incomplete lower jaw from the early Miocene of Langental (Namibia); the generic identification is probably correct (although the ectoflexid is deeper than in most African brachypotheres). From the same locality, Guérin (2008) added a few more specimens, but the illustrated upper premolar has an expanded hypocone connecting the protoloph, unlike those of *Brachypotherium*, and his identification must be regarded with caution; this tooth is much more similar to that of the holotype of *Rusingaceros leakeyi* (KNM RU-2821). Given the current state of information, we believe that the species name *B. heinzelini* should be restricted to the material from Sinda 15, the type-locality.

Another African brachypothere is *B. lewisi* Hooijer & Patterson, 1972, from the latest Miocene and early Pliocene of Lothagam, Kenya (see also Harris & Leakey 2003), and perhaps also from Sahabi (d'Erasmo 1954); however, if the type of *B. heinzelini* is indeed of late Miocene age, *B. lewisi* might be a synonym. Tooth characters are similar to those of

B. minor, but the transverse lophs of the premolars are more constricted, and the gigantic size readily distinguishes it from the Buluk form. The skull has a similarly flat dorsal profile, but the nasal bones are more retracted, the nasal notch is deeper, the palate is much narrower, and the temporal lines are less wide apart. The mandibles KNM LT-90 and LT-91 have large p1s (and the isolated p1 LT-23962 is as large as the p2s from Zelten and Moghara, and larger than those from Buluk), a remarkably convex ventral border and, from their alveoli, small (LT-90) or very small (LT-91) incisors, contrasting with the huge upper ones, whose measurements are given by Hooijer & Patterson (1972) as 90 × 44 mm. Indeed, it is hard to imagine how these small lower i2s could have produced the heavy wear of the upper ones, unless we assume that the two lower jaws are of female individuals.

The last form to be considered here is the problematic *Diceros douariensis* Guérin, 1966, from Tunisia. Since it is associated with the anthracothere *Libycosaurus* Bonarelli, 1947 and a very large giraffid, *D. douariensis* is certainly younger than the middle Miocene, and probably close to the Mio-Pliocene, as suggested by Guérin. The paratype, a partial juvenile cranium UCBL-16752, is obviously not a representative of the Dicerotini, as discussed by Hernesniemi *et al.* (2011). The molars and deciduous premolars have a pinched protocone and a well-marked antecrochet, the dorsal border of the orbits is at least as high as the frontal between them, and the orbits have marked anterior and ventral rims. A piece of a juvenile symphysis, UCBL-16763, shows a large p2, and unerupted i2s much larger than the vestigial ones that may be found in the Dicerotini, but the symphysis is much narrower than in the contemporaneous Eurasian *Chilotherium*. The characters of the paratype cranium and symphysis match better those of *Brachypotherium*, which is the only non-Dicerotini known at that time in Africa; however, the fossils from Douaria differ from the contemporaneous Lothagam form, *B. lewisi* (Hooijer & Patterson 1972; Harris & Leakey 2003) in the stronger metacone fold on the molars, larger i2s, and perhaps (wear state is different) stronger antecrochet and more pinched protocone on the molars. The Douaria fossils differ

in the same features, and in their larger size and well-marked orbital rim, from the Buluk form, but the young ontogenic age of the specimens limits the comparisons. Several of these features are unlike those of *Brachypotherium*, and UCBL-16752 might in fact represent another genus.

We refer the most common rhinoceros from Buluk to *Brachypotherium* but, admittedly, the list of the most diagnostic features of the genus is short, and it may be questioned whether they suffice to define a natural group. Except for the flattening of the buccal walls, the cheek-teeth lack clearly derived characters, the few shared skull characters are very general, and the low astragali and short distal limb segments could well be convergent (e.g., no one would unite sheep and cattle on the basis of short metapodials). The latter features are also the main ones supporting their traditional union with American *Teleoceras* into the Teleoceratini Hay, 1902 (e.g., Prothero 2005). A full discussion of the systematics of this group is beyond the scope of this paper, but we may note that, in Antoine *et al.* (2003), out of 282 characters, the only non-homoplastic character states defining this group are: 1) the facet for the magnum is not visible in front view on the McIII and 2) the proximo-lateral facet of the astragalus for the calcaneus is almost flat; however, the tooth morphology is different (*Teleoceras* has cement, strong antecrochet, deep ectoflexid, etc.), so that the monophyly of this tribe needs substantiation.

If *Brachypotherium*, or at least its African representatives, are indeed a natural group, it must have included more than one lineage, as the contemporaneous Buluk and Zelten forms are certainly distinct. In its straight lateral profile, high orbit, and low occipital, the much later Lothagam form resembles more *B. minor* than "*Aceratherium*" *campbelli*, although intermediate forms are unknown.

RHINOCEROTIDAE gen. et sp. indet.

KNM WS-12855 is a DP2 that is significantly larger (32 × 30) than the one assigned to *Brachypotherium*; it further differs in that the central buccal rib is

stronger, the buccal cingulum is complete around the hypocone, and the crochet and crista unite to form a medifossette.

KNM WS-13 is a P4 in early-medium wear (Fig. 4A). It differs from those of *Brachypotherium* in its larger size, presence of a complex crochet that would have contacted a long crista in later wear, closing the medifossette (these spurs are much weaker in *Brachypotherium*), and in the parallelism of its mesial and distal borders in buccal view, indicating that is was probably somewhat more hypsodont.

KNM WS-12843 (Fig. 4B) is an incomplete upper molar that can be compared with the *Brachypotherium* molar WS-12844, which is at the same wear stage. The most obvious difference is that WS-12843 bears a thick coat of cement; it is the only tooth from Buluk where cement is preserved. It is also distinctly more hypsodont than WS-12844, as it was certainly higher than long when unworn, whereas these dimensions were roughly identical in WS-12844. Furthermore, the antecrochet is weaker, and the parastyle is curved buccally, being almost as prominent as the moderate paracone fold.

KNM WS-144 is a mandible fragment with p3, dp4 not shed yet, m1 and m2 (Fig. 4C). On the molars, the paralophid is longer lingually, the protolophid is more transverse, and the hypolophid more L-shaped, and the ectoflexid is deeper; m2 is shorter relative to its width. Identification of two other lower cheek teeth, WS-12842 and WS-12846, is less secure, but they are probably also not of *Brachypotherium*.

Comparison of these teeth with most of the other Early and Middle Miocene rhinoceroses in the KNM reveals no satisfactory match. In the lack of lingual connection of the lophs or strong antecrochet, they differ from those of the elasmotherines *s.l.* (including *Chilotheridium*), in the lack of lingual expansion of the lophs, they differ from *Rusingaceros*.

KNM WS-1 and WS-7 are weathered astragali much higher than those of *Brachypotherium*; they lack the characteristic lateral shift of the trochlea of *Chilotheridium* astragali, but have no remarkable feature. We prefer to leave all these specimens as indeterminate, but they definitely point to the occurrence of another species.

CONCLUSION

The diversity of rhinoceroses in the African early and middle Miocene is greater than has been assumed (see recent review in Geraads 2010). Approximately eight or nine genera are now known, including *Brachypotherium*, *Rusingaceros*, *Paradiceros*, *Chilotheridium*, *Turkanatherium*, *Victoriaceros* (Geraads *et al.* 2012), a form akin to *Plesiaceratherium* at Nyakach, plus perhaps *Ougandatherium* (Guérin & Pickford 2003) and "*Diceros*" *australis*. Interestingly, it appears that most African localities yield remains of only two species, typically one predominant taxon along with a second rarer form (e.g., Buluk, Rusinga, Loperot, Maboko, Fort Ternan, Gebel Zelten); Maboko is the only site that has yielded definitive evidence of more than two species. This is in contrast to what has been documented in Europe (mostly in France and Germany), where at least 30 sites have three or four rhinocerotid species present. We think it is unlikely that this difference is only due to better sampling or a tendency of European paleontologists to over split collections. Instead, this disparity between Africa and Europe might reflect more favourable conditions at higher latitudes.

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