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Perissodactyla (Rhinocerotidae and Equidae) from Kanapoi

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Abstract

The Kanapoi collection of Rhinocerotidae, first studied by Hooijer and Patterson (1972), now consists of 25 specimens and substantial reinterpretation of their affinities is made here. Kanapoi post-dates the extinction of *Brachypotherium* and the whole collection belongs to the Dicerotini. It is important because it includes the type-specimen of *Diceros praecox*, a species that remains poorly known, but looks slightly larger and more primitive than the modern 'black' rhino *Diceros bicornis*. A second species is probably ancestral to the modern 'white' rhino *Ceratotherium simum*; it looks identical with the Pleistocene North African *Ceratotherium mauritanicum*, of which *Ceratotherium efficax* is probably a synonym. The evolution of the Dicerotini in Africa can be regarded as an increasing divergence in diet and related morphofunctional adaptations in the two lineages. The co-occurrence at Kanapoi of both *Diceros* and *Ceratotherium*, with distinct dietary preferences, suggests some habitat heterogeneity, although the low sample size prevents robust paleoecological conclusions.

The Equidae are also rare and consist mostly of isolated teeth. I take the most parsimonious option of tentatively including all of them in a single species, whose identification is left open. Dental features of eastern African Pliocene to Pleistocene hipparions may reflect increasing adaptation to grazing.

Introduction

The Perissodactyla do not make up a high proportion of the Kanapoi large mammals, and no previous publication specifically deals with them, although Hooijer and Patterson (1972) and Hooijer (1975), respectively, studied the Rhinocerotidae and Equidae known at that time, together with fossils from other sites. Since then, renewed research at Kanapoi has significantly increased the faunal sample. The following revision is based upon the study of the material in the National Museums of Kenya (KNM) during several visits between 2002 and 2016, and takes into account all the material of Perissodactyla known to date. It includes no remain of the Chalicotheriidae, although this family was present in Africa from the Early Miocene until the Early Pleistocene with a sparse fossil record (Coombs and Cote, 2010.

Materials and methods

The comparisons of the Equidae are mostly based upon published literature, but the Rhinocerotidae have been extensively compared with the rich collections from other Pliocene and Pleistocene Kenyan sites in the KNM, as well as with the Hadar and Omo material in the National Museum of Ethiopia, Addis Ababa (NME). Late Miocene rhinos were principally examined in the Muséum National d'Histoire Naturelle, Paris (MNHN); Faculté des Sciences, Lyon (FSL); Naturhistorisches Museum, Basel (NHMB); Natural History Museum, London (NHMUK); Natural History Museum, Sofia and Asenovgrad (NHMSA); Geologisch-Paläontologisches Museum, Münster (GPMM); Staatliches Museum für Naturkunde, Karlsruhe (SMNK); Staatliches Museum für Naturkunde, Stuttgart (SMNS); Naturhistorisches Museum, Wien; and Natural History Museum, Skopje (NHMMS). Modern specimens were examined in the KNM and MNHN.

Systematic paleontology

Family Rhinocerotidae Gray, 1821

Description Hooijer and Patterson (1972) assigned all the Rhinocerotidae material known from Kanapoi at this time to a new species that they called *Ceratotherium praecox*, assuming that it was ancestral to the modern 'white' rhinoceros, *Ceratotherium simum*. No other study devoted to the Kanapoi rhinos has been published since then, although Harris et al. (2003), Geraads (2005, 2010), Giaourtsakis et al. (2009), and Hernesniemi et al. (2011) discussed them briefly.

Whereas a few Pliocene specimens from Chad and Tunisia have been assigned to *'Dicerorhinus'* (Arambourg, 1970; Likius, 2002), the only tribe present in East Africa after the extinction of *Brachypotherium*, last recorded in the Apak Member of Lothagam (specimen KNM-LT-90; Hooijer and Patterson, 1972), is that of the Dicerotini, with two lineages leading to the seriously threatened modern African rhinos *Diceros bicornis* ('black' rhino) and *C. simum* ('white' rhino). As they are closely related and often co-occur in the same sites, determining to which of these branches each fossil belongs is not always easy; the Kanapoi material is critical in reconstructing their histories.

Genus *Ceratotherium* Gray, 1868

Ceratotherium mauritanicum (Pomel, 1888)

Type: MNHN TER-2261, upper M2 from Tighennif, Algeria, Late Early Pleistocene. I refer all Pliocene to lowermost Pleistocene East African representatives of *Ceratotherium* to this species (see below and Geraads, 2005, 2010).

KNM-KP 30187 is the most complete remains of this species at Kanapoi (Fig. 1A). It consists of several parts of a skull, unfortunately without connections between them: a posterior part (occipital and auditory region), a central (orbito-frontal) part, and a piece of the left maxilla with P^3–P^4 (measurements: Supplementary Online Material [SOM] Table 1). The skull was certainly long, with a poorly concave dorsal profile. The teeth are almost unworn, but much broken. They are very high-crowned. They both have a crochet, but P^3 has no visible crista, unlike P^4 in which a closed medifossette would probably have formed in later wear. The protoloph is much longer than the metaloph and curved backwards so that the protocone occupies most of the lingual part of the tooth. The cingulum is well developed anteriorly, but is interrupted between the base of the protocone and the base of the hypocone. The bottom of the nasal notch is above the anterior part of P^3, as in *C. simum,* but the infra-orbital foramen, above the anterior part of P^4, is more anterior than in the modern form and more like in fossil *Ceratotherium* from the Mediterranean late Miocene or from the African Plio-Pleistocene. The orbit also reached farther anteriorly than in average *C. simum*; its ventral border is rounded and slanting ventro-laterally, as in other African Dicerotini. In front of the orbit, the lacrymal, nasal, maxillary, and frontal bones have an X-shape connection, as in *D. bicornis,* whereas the maxilla has a suture with the frontal in adult *C. simum*. The nuchal crest is broad and has a deep central notch, as in fossil forms but unlike *C. simum*. The occipital, whose ventral part is missing, was certainly broader than in *Diceros*. Although it is hard to orientate this cranial piece in respect to the tooth row, it is clear that this occipital was stretched caudally and that the nuchal crest overhung the condyles to some extent.

KNM-KP 38 (Fig. 1B) is a right premolar, probably P^4, lacking the buccal enamel and part of the protocone. It is not heavily worn, but the crochet and crista meet to fully enclose the medifossette. The lingual part of the protoloph curves distally but fails to meet the inflated hypocone. The width of the metaloph also greatly increases lingually.

KNM-KP 32 is a partial mandible with P_3-M_3, with P_4 and M_3 in the process of erupting (Hooijer and Patterson, 1972:Fig. 9B-C). The unworn M_2 is at least as tall as it is long, but its base is still concealed in bone. This specimen was described as *Ceratotherium praecox* by Hooijer and Patterson (1972), who noted that it is distinctly more hypsodont than *D. bicornis*; Harris et al. (2003) also identified it as *C. praecox*, but Hernesniemi et al. (2011) considered it to be less derived than the *Ceratotherium* KNM-KP 30217 and consequently assigned it to *Diceros*. In fact, it does not differ significantly, neither in morphology nor in hypsodonty, from KNM-KP 30217, meaning that either the lower teeth of these genera were undistinguishable at that time or, more likely, that both specimens belong to *Ceratotherium*.

KNM-KP 30217 is probably a P_4, about as hypsodont as that of KNM-KP 32. KNM-KP 40 is a very incomplete upper milk tooth, probably DP^3; it is only tentatively assigned here, because at Hadar no robust feature distinguishes the DP^3 of *Diceros* from that of *Ceratotherium*. KNM-KP 32868 is a very worn lower tooth, probably a P_4. KNM-KP 33 is an isolated, unworn lower molar, probably M_2. It is taller than long, thus about as hypsodont as the M_2 KNM-KP 32. KNM-KP 30554 is a well-worn lower tooth, probably M_1. KNM-KP 49386 is a lower molar, probably M_1, in mid-wear and with a tall crown. These lower teeth are not so long as those of Pleistocene and modern *C. simum*, and there is no tendency for the prefossettid to close lingually, unlike in this species.

KNM-KP 30195 (Harris et al., 2003:Fig.14B) is a complete, robust humerus. Its size (SOM Table 2) exceeds the maximum recorded size of *C. simum* (cf. Guérin, 1980:Table 8); it is similar to the largest Hadar *Ceratotherium* in this regard (Geraads, 2005).

There is no doubt that the Kanapoi *Ceratotherium* is markedly more primitive than *C. simum* in its dental morphology and that it belongs to a distinct species, but its name is disputable. It is obviously not *C. praecox* (see below). Hernesniemi et al. (2011) called it *Ceratotherium efficax*

Dietrich, 1942, but the differences between this species, whose type is from Laetoli, and the North African Pleistocene *Ceratotherium mauritanicum* (from Tighennif, Aïn Hanech, and Grotte des Rhinocéros; Geraads, 2005) are quite subtle. In contrast to Hernesniemi et al. (2011), I fail to see any difference in the shape of the upper M3 ectoloph or in the wear stage at which the lingual valley closes in the upper premolars; it may be true that these teeth have a more reduced lingual cingulum in *C. mauritanicum*, but this is weak support for species distinction. Choosing between these names for the Kanapoi species is a matter of preference; in age and morphology, it is certainly close to the Laetoli form, but calling it *C. efficax* hides the remarkable stability of the North African lineage and I prefer to keep calling it *C. mauritanicum*, of which I regard *C. efficax* as a junior synonym.

Genus *Diceros* Gray, 1821

Diceros praecox (Hooijer and Patterson, 1972)

Type: KNM-KP 36 (see below); I refer to this species Early to Middle Pliocene African representatives of *Diceros*.

KNM-KP 36 (Fig. 1C; Hooijer and Patterson, 1972:Fig. 9A) is the type-specimen of *Ceratotherium praecox* Hooijer and Patterson, 1972. It consists of a large portion of the skull of a relatively old adult, unfortunately in very poor condition and lacking the anterior part, so that few features can be observed. Size is larger than in *D. bicornis*. The bottom of the nasal notch is more posterior than in *D. bicornis*; the ventral orbital border is rounded, as in other Dicerotini. The temporal fossa was certainly long. As far as the preservation allows, it seems that the occipital was broad and intermediate in orientation between those of the modern forms, i.e., less vertical than that of *D. bicornis*, but less stretched caudally than in *C. simum*. This orientation is in agreement with a marked angle between the basisphenoid and basioccipital, again intermediate between those of modern forms. In *C. simum*, the cranial base is almost straight, the long neurocranium being in line with the basicranium; in *D. bicornis* instead, the basicranial angle is even stronger than in KNM-KP 36, and the neurocranium is rotated so that the occipital is vertical or even inclined rostro-dorsally with respect to the occlusal plane. The teeth are much worn and very imperfectly preserved. On P^4-M^2 (Fig.1C), the protoloph is only slightly curved distally, so that the protocone does not occupy much more than half of the lingual part of the tooth. The crochet is present but small, perhaps because of heavy wear. The poor preservation of the specimen forbids precise measurements, but it was certainly large, with an estimated M^2 width of c. 73 mm, thus slightly above the maximum recorded by Guérin (1980) for *D. bicornis*.

KNM-KP 35 is an incomplete, much worn P^2. The lophs are transverse, without any crochet or crista. The postfossette is completely enclosed by the metaloph and distal cingulum. There is a continuous lingual cingulum. KNM-KP 30216 (Fig. 1E) is another well preserved, moderately worn P^2. It has lophs that are almost transverse, a strong crochet but no crista, and a strong cingulum completely circling the lingual part of the tooth. KNM-KP 58726 (Fig. 1F) is still another P^2, similar to the previous ones, except that the broken crochet might have been slightly smaller. KNM-KP 30472 (Fig. 1D) is an upper premolar, probably P^3, lacking the mesiobuccal corner. Its main characters are similar to those of KNM-KP 30216; the cingulum is complete all around the lingual part of the tooth. The crochet is stronger than in modern *D. bicornis* or than in Plio-Pleistocene representatives of this genus, such as WT-41576. KNM-KP 57018 is a fragment of a rather brachyodont lower molar.

KNM-KP 39 (Harris et al., 2003:Fig.14A) is a complete humerus; I follow Harris et al. (2003) in assigning it to *Diceros* on the basis of size, assuming that *D. praecox* is smaller than *Ceratotherium* (SOM Table 2).

In addition, there are some isolated teeth and various fragments that are unidentifiable to genus: KNM-KP 30 are cranial fragments including nasal and occipital pieces; KNM-KP 32556 and KNM-KP 57014 are tooth fragments; KNM-KP 504 is also a tooth fragment, but is very ^{13}C depleted (Cerling et al., 2015) and is therefore probably of *Diceros*; KNM-KP 36520 is a mandibular piece with two much worn teeth; KNM-KP 31 is a fragment of mandible with the condyle; KNM-KP 57007 and KNM-KP 59726 are isolated, much worn lower molars; KNM-KP 540 is a sesamoid; and KNM-KP 538 is a distal MT III.

Comparisons and discussion One of the main reasons of interest in the Kanapoi Rhinocerotidae is that they include the type of *Ceratotherium praecox* Hooijer and Patterson, 1972. I had previously shown (Geraads, 2005) that this type specimen belongs in fact to *Diceros*, and this generic assignment has gained general acceptance among researchers working on these rhinos (Giaourtsakis et al., 2009; Hernesniemi et al., 2011). Unfortunately, over the years '*Ceratotherium praecox*' had become synonymous with 'primitive *Ceratotherium*,' leading to much confusion (e.g., Harris, 1983; Hooijer and Churcher, 1985; Guérin, 1987). It is clear, anyway, that there are two lineages in the

Pliocene and Pleistocene of Africa, one ending in the modern *C. simum*, the other in *D. bicornis*, although side branches may of course have arisen and gone extinct (SOM Fig. 1). Geraads (2005) regarded the late Miocene Western Mediterranean *Ceratotherium neumayri* (Osborn, 1900), previously known as *'Diceros pachygnathus'* or *'Diceros' neumayri*, as the last common ancestor of these lineages, whereas Giaourtsakis et al. (2006, 2009) and Hernesniemi et al. (2011) believed that this species is in fact a side branch, because of some derived postcranial characters that bar it from the ancestry of modern forms, whose last common ancestor would be in fact *'Dicerorhinus' primaevus* Arambourg, 1959 from the Vallesian (early late Miocene) of Algeria, first recognized as a Dicerotini by Geraads (1986). Unfortunately, those purportedly specialized postcranial features remain unpublished. Antoine and Saraç (2005) listed some characters of the postcranials that they also assumed to be autapomorphic. A full discussion would be beyond the scope of this paper, and I shall only mention that the absence of a trapezium facet on MC II is in fact shared by both modern forms (Guérin, 1980), that there is no evidence that the fusion of tibia and fibula occurred early in life and that it is based upon a single specimen, and that some of their other features are inconsistent with their descriptions (distal keels on central metapodials said to be acute but described and figured by Giaourtsakis [2009] as smooth; medial calcanear facet on the astragalus said to be low but described and figured as tall; it is also tall in most Plio-Pleistocene *Ceratotherium*). Therefore, the assumption of Giaourtsakis et al. (2009) that the similarities of *C. neumayri* with later *Ceratotherium* are in fact "early convergences" remains unsubstantiated. Still, the idea of the derivation of both lineages from *'D.' primaevus* is acceptable, although our poor knowledge of the anatomy of this species prevents a full appraisal of its phylogenetic position. In any case, *C. neumayri* is certainly not far removed from this common ancestry, and its cranial anatomy is much better known (Osborn, 1900; Weber, 1904; Arambourg and Piveteau, 1929; Thenius, 1955; Geraads, 1988; Geraads and Koufos, 1990; Antoine and Saraç, 2005; Giaourtsakis et al., 2006, 2009; Geraads and Spassov, 2009; Spassov et al., in press), allowing the reconstruction of evolutionary trends in these two lineages. All available evidence shows that its dental morphology is primitive and closer to that of *D. bicornis*; the tooth crown is low, the protoloph is only moderately curved disto-lingually on the molars, and the crista is usually absent and at most weak (SOM Fig. 1). By contrast, the skulls differ from those of *D. bicornis* in being long, with an orbit located more posteriorly. Undistorted ones have a gently concave dorsal profile and an occipital that is essentially vertical, with a nuchal crest whose caudal extension is intermediate between those of the modern species, although there is variation in all these forms. The skull is, on the average, certainly less lengthened than that of *C. simum*, but they share the same overall shape; this is why I prefer to include *C. neumayri* in *Ceratotherium* rather than in *Diceros* (but this is not a central issue). In the *Ceratotherium* lineage, the nuchal crest becomes more stretched backwards, but the most conspicuous changes affect the cheek teeth. From the Late Pliocene to the Pleistocene, they increased their hypsodonty and plagiolophodonty (e.g., Geraads, 2010), so that those of the Pleistocene and modern *C. simum* much differ from those of their ancestors. These changes are obviously adaptations to a grazing diet (and parallel those that occur in the Asian *Rhinoceros unicornis* as opposed to the browser *R. sondaicus*).

By contrast, the cheek teeth of modern *D. bicornis* are little changed over those of *C. neumayri*, but the orbit is located more anteriorly, the dorsal profile is more concave, and the occipital is vertical, or even inclined forwards in old individuals (although not to the extent of modern *Rhinoceros*). As first analyzed by Zeuner (1934), these differences are linked to a different head posture, that of *C. simum* being held more vertically, in relation with its grazing habits, *D. bicornis* being instead a browser or at most a mixed feeder. There is every reason to believe that this cranial morphology of *D. bicornis* is derived: first, because no late Miocene potential ancestor displays it; and second, because Zeuner (1934) showed that, during the ontogeny of the 'black' rhino, the plane of the occipital changes from vertical to forwardly inclined. Unfortunately, well preserved cranial elements that would document the evolution from *D. praecox* to *D. bicornis* are rare; there is a poorly preserved skull from Laetoli (Guérin, 1987) and some incomplete specimens from Hadar (Geraads, 2005). This evolution involves some decrease in size, at least in most populations, because Pliocene forms are close to, or slightly above, the maximum size of the modern species. The tooth row is located slightly more posteriorly in *D. bicornis*, and this can probably be related to increased cranial flexure. It is clear, anyway, that differences are slight and species assignment of Pliocene specimens is often difficult.

Giaourtsakis et al. (2009) described a skull from Kuseralee in the Middle Awash, dated to 5.2 Ma, which they ascribed to '*Diceros*' *douariensis* Guérin, 1966 and placed in the ancestry of *Ceratotherium* on the basis of an oblique protoloph on M1 and the presence of a lingual protocone groove on the same tooth. This species was first described from Douaria in Tunisia, a locality whose age is poorly constrained, but a very large giraffid suggests the latest Miocene, thus roughly contemporaneous with Kuseralee. The diagnosis of this species provided by Giaourtsakis et al.

(2009) is a mixture of features common to all Dicerotini and to the Kuseralee cranium. In fact, there is no significant difference between the teeth of the Kuseralee cranium, those of '*D.*' *douariensis*, and those of *C. neumayri*, as exemplified by the skull and dentitions from Maragha (Thenius, 1955), Pikermi (Geraads, 1988), Samos (NHMB), Akkaşdağı (Antoine and Saraç, 2005), or Kalimantsi (Geraads and Spassov, 2009). Giaourtsakis et al. (2009:455) believed that the Kuseralee cranium is "close to the ancestral stock of the *Ceratotherium* clade" because of its M^1 with oblique protoloph and lingual protocone groove, but the protoloph is certainly not more oblique than on the type specimen of *C. neumayri* (NHMW A4791); the flattened lingual wall of the protocone can hardly be called a groove and the difference with some *C. neumayri* is quite subtle. What is quite clear in the Kuseralee skull is its shape, with its raised neurocranium forming a strong angle with the facial part, resulting in a deeply concave dorsal profile of the neurocranium and a vertical occipital plane. These are all features shared by *D. bicornis* and the Kuseralee cranium definitely belongs to its lineage. However, both the nasal notch and the orbit are located more posteriorly than in *D. bicornis* and more like in *C. neumayri*. Thus, the Kuseralee cranium is a good morphological intermediate between earlier *C. neumayri*, preserving a similar dental morphology and facial pattern, and later *Diceros*, of which it already has the upwardly tilted neurocranium. It does differ in some features from *D. bicornis*, including a slightly larger overall size, but most of those noted by Giaourtsakis et al. (2009) are quite subtle, if not non-existent; it is not true, for instance, that the protoloph is more inclined than in the modern species, but it seems that the lingual protocone wall is indeed more flattened, and overall size is larger. These are differences that are also found in the Kanapoi material, and I can see no reason for not including the Kuseralee cranium in *D. praecox*.

It seems that the reluctance of some authors to admit that the *D. bicornis* cranial shape is derived is linked to the change of diet with which it is correlated. In the interpretation favored here, ancestors of the modern African rhinos, with their intermediate cranial morphology, were likely mixed feeders. Later, while the representatives of the *Ceratotherium* lineage became more grazers (an evolutionary trend that is easily accepted), the lineage leading to *D. bicornis*, with its flexed cranium, must have shifted to a more browsing diet. This is an evolution that is less easily conceivable, as it seems to be a reversal to an ancestral condition; however, Cerling et al. (1999) showed that it occurred in elephants. A plot of $\delta\ ^{13}C$ isotopic values of late Miocene to modern African rhinos (Fig. 3) shows that, for most of the Pliocene, many rhinos, although they were certainly already part of either the *Diceros* or *Ceratotherium* lineage, still had mixed-feeder habits that are no longer found today (δ ^{13}C between -3 and -7‰). Some of the specimens are certainly of *Ceratotherium* that had not fully shifted to a grazing diet (Harris and Leakey, 2003). Others, such as KNM-LT-28762 and LT-23971 from the Apak Member of the Nachukui Formation, are definitely of *Diceros*, but their δ ^{13}C (respectively -3.6 ‰ and – 2.5‰) are clearly above values of modern *D. bicornis*, showing that their diet certainly incorporated a significant grass component. It also seems that no fossil reached such very low ^{13}C values as some modern *Diceros*, but it remains to be confirmed that this is not just an effect of smaller sample size. At Kanapoi, however, the distinction is clear-cut (Cerling et al., 2015) and we may assume that in this site at least, the rhinos had already adopted their modern dietary preferences, perhaps also testifying to the presence of various habitats, including both grassland/savannas and bushland/woodland, but sample size is far too low for estimating their relative importance.

Family Equidae Gray, 1821

Description It seems that the dispersal of hipparionines into the Old World is a virtually instantaneous event at the geological scale, as their first appearance in Africa at >10 Ma (Pickford, 2001) might well be contemporaneous with their FAD in Europe. However, in contrast to what occurs in the well-known 'hipparion faunas' of the Western Mediterranean, their fossil documentation in Africa is very patchy, and in many of the famous hominid bearing East African Pliocene and Pleistocene sites, they are mostly represented by incomplete bones and isolated teeth. Kanapoi is no exception, and the whole equid collection, reviewed here, consists of only about 50 specimens, among which there are only a few partial tooth rows (tooth measurements: SOM Table 3) and a single complete bone. Given the difficulties of equid systematics, even when dealing with far better preserved material, definite conclusions cannot be reached.

Hipparioninae Gen. et sp. indet.

Hooijer and Maglio (1974) described and/or figured the following specimens: KNM-KP 42, said to be a set of three lower teeth but what I have seen with this number is an M_3 with an ectostylid reaching about half of the crown height; KNM-KP 43, an upper tooth series P^3-M^3 (Hooijer, 1975:Pl. 6, his Fig.1 also illustrated a P^2 with the same accession number; it could well be of the same specimen, but I have not seen this tooth); KNM-KP 44, a mandible with P_3-M_2 and part of M_3; KNM-KP 45, a distal metatarsal; KNM-KP 46, tooth fragments; KNM-KP 47, a poorly preserved upper molar; and KNM-KP 48 (Fig. 2E), a much worn upper molar.

According to Hooijer and Maglio (1974:18), the last three specimens "have the characters of *Hipparion turkanense*," and they also tentatively assigned KNM-KP 45 to the same species, while KNM-KP 42, KNM-KP 43, and KNM-KP 44 would belong to *H. primigenium*. In addition, they referred two upper M^3s, KNM-KP 490 and KNM-KP 496, to *H.* cf. *sitifense*, but these accession numbers are erroneous and they probably meant KNM-KP 49, a set of poorly preserved upper molars. I shall mention below the main specimens that were not described by Hooijer and Maglio (1974).

KNM-KP 51 (Fig. 2C) is certainly an M^2, not much worn. The mesostyle is narrow; the central part of the tooth bears several long folds, especially in the distal part of the prefossette; the protocone is flattened lingually; the pli caballin is double; and the hypocone is pinched and almost isolated, obviously because of the early wear stage.

KNM-KP 55 (Fig. 2G) is a lower cheek tooth, probably a P_4, not much worn, with a relatively large ectostylid reaching the occlusal level. KNM-KP 56 is probably also a P_4, poorly preserved, with a very small ectostylid.

KNM-KP 58 (Fig. 2I) are an associated P_2 and $M_{?1}$; the ectostylid is minute; it reaches the occlusal surface on P_2, but not on $M_{?1}$. On this tooth, both the lingual and buccal flexids are deep and come into contact with each other; the metastylid is angular and pointed.

KNM-KP 532 (Fig. 2L) is a partial mandible, with teeth in medium wear, somewhat larger than those of KNM-KP 44. They include P_2, half of P_3, and the series M_1-M_3. The double knot is clearly of caballine type, with a pointed metastylid, and a broad, U-shaped lingual flexid that comes into contact with the buccal flexid on the molars; this lingual flexid is more V-shaped in other specimens, such as KNM-KP 44. The molars have a pli caballinid, stronger on M_2. None of the teeth display an ectostylid; since the teeth are still embedded in bone, nothing is missing on the buccal side of the teeth, the cement layer is rather thin, and we can therefore assume that this stylid was at most extremely small.

KNM-KP 30555 (Fig. 2H) are associated $P_{?4}$ and M_3, moderately worn. On $P_{?4}$ the ectostylid is rather large and reaches the occlusal level, whereas it is smaller and is only about 35 mm tall on M_3, therefore failing to reach this level. The lingual flexid is V-shaped and the metastylid angular. The hypoconulid of M_3 is divided by a deep lingual groove.

KNM-KP 30556 (Fig. 2D) are three successive teeth, probably P^4-M^2, very similar in size and morphology to KNM-KP 43 (Hooijer and Maglio, 1974:Pl. 3); the long folds in the central part of the tooth are especially noticeable. Slight differences are that the protocone is more flattened lingually and that the pli caballin is single.

KNM-KP 50797 (Fig. 2F) is an $M_{?1}$ with a tall, much compressed ectostylid; the double knot is caballine, with a wide lingual flexid.

KNM-KP 50822 (Fig. 2J) is an M_2 that is not much worn and is 51 mm tall; a small ectostylid fails to reach the occlusal level, but there is also a long pli caballinid and a small protostylid. The double knot and lingual flexid are similar to those of KNM-KP 50797.

KNM-KP 51005 is an associated set of three upper teeth. Two of them, that I identify as M^1 and M^2, are slightly worn, but their occlusal surfaces are blurred; the third one is unworn and I regard it as a P^4. M^2 is 24 mm long and 54.5 mm high, and thus distinctly less hypsodont than later Pliocene teeth, such as those from Omo (Hooijer, 1975; Eisenmann, 1985; Hooijer and Churcher, 1985).

KNM-KP 56934 is a mandible fragment with P_2 and P_3; there is no evidence of an ectostylid, but the teeth are very little worn and are covered by a thick cement coating, so that it might be concealed in it. There is a long pli caballinid on both teeth and an accessory fold in the lingual flexid, which is quite wide, and the metaconid has a complex shape; these latter features would probably have disappeared with wear.

KNM-KP 57003 (Fig. 2K) is a P_3 in medium wear, also with a wide lingual flexid, but the metastylid is more rounded than in the previous specimens. There is no evidence of an ectostylid on the occlusal surface, and the cement layer is too thin to hide it lower down so that it was almost certainly absent.

KNM-KP 58730 (Fig. 2B) is a $P^{?3}$ similar to the teeth KNM-KP 43 in its long folds in the central part of the tooth and digitate pli caballin; the protocone is also flattened lingually.

In summary, the Kanapoi teeth can be characterized by: hypsodonty moderate; premolars distinctly larger than the molars; narrow, lingually flattened protocones; moderately incised hypoglyph; long, numerous folds in the central part of upper cheek teeth; mesostyle narrow; pli caballin varying from simple to complex; ectostylids small and low, rarely reaching the occlusal level of slightly worn teeth; pli caballinid frequent; double knot caballine but with lingual flexid of variable width; and/or buccal flexid rather shallow. It should be stressed that these features are observed on a small number of teeth only.

The distal metatarsal KNM-KP 45, already mentioned above, is smaller than the Lothagam specimen (Bernor and Haile-Selassie, 2009:Fig.13.21) or than the Hadar ones (Bernor et al., 2005); the articular keel is more salient than in the Höwenegg reference sample (Bernor et al., 1997).

The most complete equid fossil from Kanapoi is a humerus KNM-KP 246 (Fig. 2A) not mentioned by Harris et al. (2003), probably because it was stored with the Suidae. Unfortunately, no other hipparionine humerus has been reported from the East African Pliocene. There is a distal humerus in the Moroccan site of Ahl al Oughlam, close to the Plio-Pleistocene boundary (Eisenmann and Geraads, 2007); it is slightly larger than the Kanapoi one and, in contrast to the latter, the distal articulation is not perpendicular to the long axis of the bone, but slightly slanting disto-laterally.

<u>Comparisons</u> In their study of the hipparionines from Lothagam, Kanapoi, and Ekora, Hooijer and Maglio (1974) recognized three species at Kanapoi, *Hipparion primigenium* (von Meyer, 1829), *Hipparion turkanense* Hooijer and Maglio, 1973, and *Hipparion* cf. *sitifense* Pomel, 1897. The first species is mostly known from the Vallesian of Europe (and is now assigned to the genus *Hippotherium*), but Hooijer and Maglio (1974), following Forsten (1968), regarded it as a senior synonym of *Hipparion africanum* Arambourg, 1959 from the early late Miocene of Bou Hanifia in Algeria, and it is mostly with this species that Hooijer and Maglio (1974) compared the Kanapoi form. *H. turkanense* is based upon a complete skull from Lothagam. *H. sitifensis* was described on two isolated upper molars and a calcaneum, so that assignment of any other specimen to the same species is problematic and the name is best regarded as a nomen nudum. Bernor and Harris (2003) used a partial anterior limb from Lothagam, assigned to *Hipparion* cf. *sitifense* by Hooijer and Maglio (1974), as the type of their new species *Eurygnathohippus feibeli*, but did not discuss the affinities of the Kanapoi specimens.

Harris et al. (2003) argued against naming Pliocene forms represented by insufficient material; consequently, they listed the Kanapoi hipparionine material known at that time under *Eurygnathohippus* sp. indet., although they observed that some specimens look either smaller or larger than most others. There is indeed no compelling morphological evidence for more than one taxon and the size of almost all teeth can be accommodated within the range of a single species; the only specimen that is really larger is KNM-KP 53, an upper premolar whose occlusal surface is not readable. Thus, I shall hold the more parsimonious option of recognizing only one species. In the absence of cranial remains (in particular, preorbital area and cranial basis) and complete metapodials, identifying it with a previously named species would be too risky, especially implying biogeographic connections that would not be strongly supported.

The Kanapoi hipparion clearly differs from the earlier *'Hipparion' turkanense* from Lothagam in its thinner protocone and more complex enamel folding (Hooijer and Maglio, 1974); in addition, Bernor and Harris (2003:Table 9.10) noted that the pli caballin is usually double, whereas it is often single or complex in the Kanapoi sample. Thus, the latter certainly differs from the Lothagam population, but the material is insufficient to reject species identity.

Bernor and Haile-Selassie (2009) described material from the Middle Awash that is of latest Miocene to earliest Pliocene age. They compared it to *E. feibeli* from Lothagam but noted some differences (e.g., in robustness of the metapodials, size of an astragalus and phalanx I, shape of the double knot, number of protostylids) and accordingly regarded it as more advanced on the lineage leading to *H. hasumense*, a species defined in the lower part of the Koobi Fora Formation (Eisenmann, 1983). Upper teeth are similar to the Kanapoi ones, and the lower ones share the same small ectostylid as the Kanapoi form (although the figured lower p4 KWA-VP-1/2 is an exception), but the metastylid looks on the average more rounded.

The Kanapoi hipparion differs significantly from the recently described *Eurygnathohippus woldegabrieli* Bernor et al., 2013 from the slightly older sites of the Aramis region of the Middle Awash, Ethiopia. This species is more hypsodont, on the upper cheek teeth the protocone is longer, and the hypoglyph is extremely deep. By contrast, lower teeth do not look very different; they also have small ectostylids.

The Kanapoi form differs from the very incompletely published hipparions from the Hadar Formation in their smaller protocone and/or thinner mesostyles, shallower buccal flexid, and smaller ectostylids. It similarly differs from the poorly known *Hipparion hasumense* from the lower part of the Koobi Fora Formation (Eisenmann, 1983) and perhaps the Laetolil Beds (Armour-Chelu and Bernor, 2011) in its smaller ectostylids, less advanced hypsodonty (Armour-Chelu and Bernor [2011] mention teeth more than 75 mm high), and perhaps (there is some variation in this feature) shallower buccal flexid. Armour-Chelu and Bernor (2011) also mention a strong pli caballinid in this species, but it is virtually absent on the type (Eisenmann, 1983:Pl. 5.1I). Only further collecting at Kanapoi and metric and statistical studies on all these samples would allow definite conclusions.

Last, the Kanapoi hipparion differs from the c. 2.5 Ma *Hipparion pomeli* Eisenmann and Geraads, 2007 from Ahl al Oughlam in its narrower mesostyle, less complex pli caballin, much smaller ectostylids, and in the orientation of the distal humerus articulation.

In the absence of cranial remains and metapodials, species distinction in African hipparions cannot be based upon clear cut features and it is safer not to attempt species identification. Still, and although the Kanapoi material is certainly not a sound basis for revising the phylogeny and taxonomy of African hipparions, I wish to comment again on the use of the name *Eurygnathohippus* van Hoepen, 1930. Bernor et al. (2010:698) diagnose the genus as follows: "…united by the synapomorphy of ectostylids occurring on the permanent mandibular cheek-teeth" and include in it all African hipparionines younger than 6.5 Ma (with the possible exception of the doubtfully valid species *H. sitifensis*). However, it is clear that the ectostylid (whose variations in height and size were first discussed by Eisenmann, 1977) and other structures, such as pli caballinid, ptychostylid, and protostylid (equivalent to the bovid 'goat fold'), increase chewing efficiency and/or reduce rate of wear. They are adaptations to grazing and, as such, are likely to have evolved in parallel in several lineages in response to the expansion of grassland/savanna in the late Cenozoic. Why this particular pillar developed especially in African Pliocene to Pleistocene hipparionines remains unknown, but it likely has to do with a diet consisting mostly of C_4 grasses. In any case, using this single criterion demands inclusion in *Eurygnathohippus* of all specimens (be they African or not) with this structure and exclusion from it of all specimens lacking it (such as several Kanapoi specimens and many other African specimens of early Pliocene age); discarding these specimens as exceptions to the rule simply means that the hypothesis of the monophyly of *Eurygnathohippus* is not falsifiable. It is very likely that many late Pliocene and Pleistocene African forms should indeed be united in a single clade, but the hypothesis that this clade extends back in time to the early Pliocene or even the late Miocene, and includes all African fossils of these ages, remains to be better substantiated.

Paleoecological interpretations

Paleoecological interpretations are hard to draw because of the small size of the collection. For instance, it would not be meaningful to calculate the relative abundance of the browser *Diceros* vs. the grazer *Ceratotherium*, but the presence of both genera and the sharp difference in their isotopic values attest to the presence of grassy plains but also of significant arboreal vegetation.

The Equidae are also rare, and the lack of metapodials or phalanges prevents the ecomorphological analyses that are usually conducted upon these bones. Thanks to their robustness, teeth are better represented but are too few to provide significant mesowear indices; occlusal surfaces have low relief, in agreement with relatively tall crowns suggesting a mostly grazing diet.

Perhaps the most informative aspect of the Kanapoi Perissodactyla is their rarity itself. In the Pliocene, this group had long passed the climax of its diversity and had even sharply declined by comparison with its late Miocene abundance, but it was still common in some African sites younger than Kanapoi, so that this general trend alone does explain its low frequency there. I believe that it speaks against an extensive grass cover, where larger herds of hipparions would have thrived; this interpretation is tentative, but none of the large mammal groups precludes it.

Conclusions

In spite of its small size, the Kanapoi rhino sample is important because it corresponds to a poorly documented time period in the evolution of the lineages leading to the modern forms. Still, only the discovery of well preserved, undistorted skulls could settle the disagreements regarding the evolution of the Rhinocerotidae in Africa, because their rather uniform cranial morphology and the scarcity of complete remains too often leads researchers to over emphasize dental features whose differences between closely related modern forms (*C. simum* vs. *D. bicornis*, but also among the Asian *Rhinoceros*) demonstrate the lability.

Pending elucidation of the relationships of these early forms, I think it is safer to leave the Kanapoi hipparionine unidentified to genus; this is perhaps to be preferred to the option of using *Hipparion* as a 'wastebasket' (as done by Eisenmann and Geraads [2007]). In the development of its hypsodonty and ectostylids, the Kanapoi hipparionine fits well into the general trend towards an increasing reliance on grazing in Pliocene African forms (Melcher et al., 2014).

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Figure legends

Figure 1. A-B) *Ceratotherium mauritanicum*. A) Elements of a skull KNM-KP 30187; A1) lateral view of skull; A2) buccal view of P^3-P^4; A3) occlusal view of P^3-P^4. B) Right P^4 KNM-KP 38. C−F) *Diceros praecox*. C) P^4-M^2 of the type specimen KNM-KP 36; D) left P^3 KNM-KP 30472; E) left P^2 KNM-KP 30216; F) right P^2 KNM-KP 58726. Scale bar = 20 cm for Figure A1, 15 cm for A2 and A3, 10 cm for all others.

Figure 2: Hipparioninae Gen. et sp. indet. A) Right humerus KNM-KP 246, anterior view. B) $P^{?3}$ KNM-KP 58730. C) M^2 KNM-KP 51 in occlusal (C1) and buccal (C2) views. D) P^4-M^2 KNM-KP 30556. E) KNM-KP 48, upper molar. F) $M_{?1}$. G) P_4 KNM-KP 55. H) Associated $P_{?4}$ and M_3 KNM-KP 30555 in occlusal (H1) and buccal (H2) views. I) Associated P_2 and $M_{?1}$ KNM-KP 58 in occlusal (I1) and buccal (I2) views. J) M_2 KNM-KP 50822 in occlusal (J1) and buccal (J2) views. K) P_3 KNM-KP 57003. L) Partial mandible with P_2, part of P_3, and M_1-M_3, KNM-KP 532. Scale bar = 15 cm for Figure A, 5 cm for all others.

Figure 3. $\delta\ ^{13}C$ values of dental enamel of Central and Eastern African fossil rhinos of the Dicerotini tribe. Data (SOM Table 5) from Zazzo et al. (2000), Likius (2002), Semaw et al. (2005), Bedaso et al. (2010, 2013), Kingston (2011), Uno et al. (2011), and Cerling et al. (2015).