

# *Homo erectus*

Pleistocene Evidence from the Middle Awash, Ethiopia

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## Rhinocerotidae

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Living rhinos are extremely rare and threatened with extinction, but they are the survivors of a once broadly distributed and extremely diverse clade. Rhinos are known from North America and the Old World and have a well-documented fossil record (Prothero et al. 1989). Rhinocerotidae is first reported from the Eocene, and representatives of the family persist through the remaining Cenozoic. Different rhino taxa occupied many different niches. Taxa included small, cursorial forms as well as giraffe-like canopy browsers (Prothero et al. 1989). Modern genera have not changed dramatically since their first appearances in the Pliocene. Data Member rhinos are attributed to *Ceratotherium* (the white rhino) and *Diceros* (the black rhino).

Tougaard et al. (2001) estimate the divergence of Rhinocerotidae from other Perissodactyla to have occurred around 29.0 Ma based on analysis of mitochondrial cytochrome *b* and 12S rRNA genes. The earliest known fossil rhinos, genus *Tetartarhinus*, occur in the early Eocene of North America and, debatably, Asia (Cerdeño 1998). This genus is present in Asia by later Eocene times. Numerous genera appear in the Oligocene of North America and Eurasia. The first African rhinos occur in the early Miocene, and the lineage that would eventually lead to the modern African genera is first recorded in the middle Miocene with the genus *Pseudodicerus*. The two modern African lineages, genera *Diceros* and *Ceratotherium*, are first reported from the late Miocene, and they are suggested to have diverged close to this time (Geraads 1988, 2005). The modern species may have already been established in the Pliocene (Cerdeño 1998).

There are five modern rhino species. The grazing, square-lipped "white" (*Ceratotherium simum*) and the browsing, pointed-lipped "black" (*Diceros bicornis*) rhinoceroses are African. The Indian (*Rhinoceros unicornis*), Javan (*R. sondaicus*), and Sumatran (*Diceros bicornis nematensis*) rhinoceroses are Asian. Molecular phylogenetic analyses indicate that the African rhinos are more closely related to each other than either is to Asian genera (Tougaard et al. 2001), a claim supported by morphological data (Hooijer 1969).

### ***Ceratotherium* and *Diceros***

The first appearance of *Ceratotherium* is in the upper Miocene of Pikermi, Greece (Geraads 1988, 2005). The earliest African *Ceratotherium* is *C. neumayri* from Sahabi (Bernor et al. 1987). *Ceratotherium* is the sole grazer among living rhinos. Morphological differences



FIGURE 10.1

Dolichorhinocerotidae.  
 A. BOU.VP.4/36, *Dicotyles*  
 sp. RM<sup>1</sup> or RM<sup>2</sup>. B. BOU.  
 VP.4/55, *Ceratotherium*  
*simum* maxilla with R  
 dp<sup>3</sup>-M<sup>1</sup> and L dp<sup>3</sup>-M<sup>2</sup>  
 (exposed LM<sup>1</sup> or LM<sup>2</sup>).  
 C. BOU.VP.1/89,  
*C. simum* RM<sup>2</sup>. D. BOU.  
 VP.1/116, *C. simum* left  
 mandible with M<sub>3</sub> and M<sub>2</sub>.

between it and *Dicotyles* have been associated with its unique ecology (Kingdon 1989a). *Ceratotherium* has a broad, less prehensile lip, a wide mouth, a longer head, and more hypsodont teeth. *Ceratotherium* further differs from *Dicotyles* in the following dental features: The first upper premolar is shed early and is not present in mature individuals; upper premolars differ strikingly from upper molars; the premolar mediavallum is rapidly enclosed with wear by fusion of the protocone and hypocone; premolar protoloph is arcuate and curved posteriorly; the parastyle is more pointed and not apparently grooved; the postfossette becomes isolated with wear; and the metaflexid is persistent through wear (Cooke 1950).

One *Ceratotherium simum* (KNM-ER 2320) is first recognized in the sub-KBS units at Koobi Fora (Harris 1983). It is distinguished from its closest sister species, *C. praecox*,

TABLE 10.1 Daka Rhino Dental Metrics

Specimen	Element	Wear (1-5)	Anterior Labiolingual		Metastatal Length	Etioloph Height	Posterior Labiolingual Breadth
			Breadth				
BOU-VP-4/96	M <sup>1+2</sup>	4 1/2	61.3		52.2	32.5	49.7
BOU-VP-4/55	R. dP <sup>4</sup>	5	37.6e		51.5e		50.8e
BOU-VP-4/55	R. M <sup>1</sup>	2	42.7e		44.6	49.3e	30.3
BOU-VP-4/55	R. M <sup>2</sup>	2	33.8		47.4	62.3e	22.9
BOU-VP-4/55	R. M <sup>3</sup>	1	22.8				
BOU-VP-4/55	L. dP <sup>4</sup>	5	54.6		41.4		41.8e
BOU-VP-4/55	L. M <sup>1</sup>	2	43.1		44	48.2e	32.6
BOU-VP-4/55	L. M <sup>2</sup>	2	32		48.4e	61e	26.8
BOU-VP-1/89	R. M <sup>1</sup>	2	57.9		66.8	70.6e	44.1e
BOU-VP-1/89	R. M <sup>3</sup>	2	37.4		44.4	85.4e	
BOU-VP-1/72	L. M <sub>1</sub>	2	23.8		57.4		
BOU-VP-1/116	L. M <sub>1</sub>	2	21.2		52.7		

NOTE: Metrics are in millimeters. e = estimate.

by the following features: presence of medifossettes, rounded corners of upper teeth, no fossitids in the lower dentition, less hypsodont cheek teeth, and variable internal cingula on uppers (Hooijer and Patterson 1972). Four subspecies of *C. simum* have been named. Two are prehistoric: *C. s. germanoaffricanum* from eastern and southern Africa, and *C. s. mauritanicum* from the Maghreb. Two subspecies are extant, *C. s. cottoni* of central Africa and *C. s. simum* of southern Africa (Prothero et al. 1989).

#### *Carototherium simum* (Burchell, 1817)

DIAGNOSIS "Skull markedly dolichocranial, with backwards leaning occipital crest; no incisors or canines; jaws abbreviated in front; mandibular symphysis broad, spatulate; nasal bones broad, short, high; ascending ramus of mandible backwards-leaning; no marked angulation at gonion. Cheek teeth hypsodont; protoloph and metaloph strongly curved back, showing early fusion with wear; much cement on crown" (Harris 1983, 132).

DESCRIPTION Nonjoining right and left halves of maxilla BOU-VP-4/55 (Figure 10.1 B) preserve dP<sup>4</sup>-M<sup>3</sup> on the right and dP<sup>5</sup>-M<sup>2</sup> on the left. Alveolar and palatal bone is preserved on both sides, and unerupted premolars are detectable below the broken alveoli. Partial mandible BOU-VP-1/116 (Figure 10.1D) preserves the M<sub>1</sub>, part of the M<sub>2</sub>, and much of the corpus. Dental specimen BOU-VP-1/89 (Figure 10.1C) consists of associated right and left upper molars. Other specimens are isolated teeth.

DISCUSSION These specimens are placed in *Carototherium* because of their isolated postfossettes, enclosed medivali, pronounced metaflexids, and overall morphological similarity to the modern form. They are placed in *C. simum* based on the presence of medifossettes and rounded corners in upper molars and premolars. Dental metrics (Table 10.1) are similar to those reported for Koobi Fora *C. s. germanoaffricanum* and recent *C. simum* (Harris 1983). Morphological features diagnosing *C. simum* subspecies, many of which pertain to cranial vault metrics (Harris 1983), are not preserved in the small Daka sample.

*Diceros* Gray, 1821

GENERIC DIAGNOSIS "Premaxilla absent or vestigial; cranium short and relatively broad; neurocranium tilted anterodorsally relative to splanchnocranium, resulting in more vertically oriented occipital plane or even one inclined anterodorsally, nuchal crest less expanded posteriorly, more deeply concave cranial profile, basioccipital angled relative to basisphenoid, shortened face with orbits more anteriorly positioned and closer to nasal notch, and often nasolacrimal contact" (Geraads 2005).

*Diceros* sp.

*Diceros* upper molars and premolars differ from those of *Ceratotherium* in being less hypsodont. *Diceros* protoloph and metaloph do not join lingually, even in late stages of wear. The prefossette, medifossette, and medivallum are connected, opening lingually. The metacone forms a posterior projection that makes no lingual connection with the hypcone, as occurs with moderate wear in *Ceratotherium*. The *Diceros* occlusal outline of the protoloph, ectoloph, and metaloph presents a pattern similar to the Greek letter pi. Upper third molars are less mesiodistally elongate than in *Ceratotherium*.

Only one specimen from the Daka Member is referred to *Diceros*. Upper molar BOU-VP-4/36 (Figure 10.1A) is very highly worn. It has a separated protoloph and metaloph with prefossette, medifossette, and medivallum that open lingually. These characters are typical for *Diceros*.

### Conclusion

*Ceratotherium simum*, a grazer, and *Diceros bicornis*, a browser, are both present in the Daka Member. *Ceratotherium simum* is represented by a mandible, a maxilla, and several dental specimens and is not demonstrably different from Pleistocene and recent *C. simum*. Daka Member *Diceros* is represented by a single upper molar.