Earliest Man and Environments in the Lake Rudolf Basin

Stratigraphy, Paleoecology, and Evolution

3157

Edited by

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18. RHINOCEROTIDAE AND CHALICOTHERIIDAE (MAMMALIA, PERISSODACTYLA) FROM THE SHUNGURA FORMATION, LOWER OMO BASIN
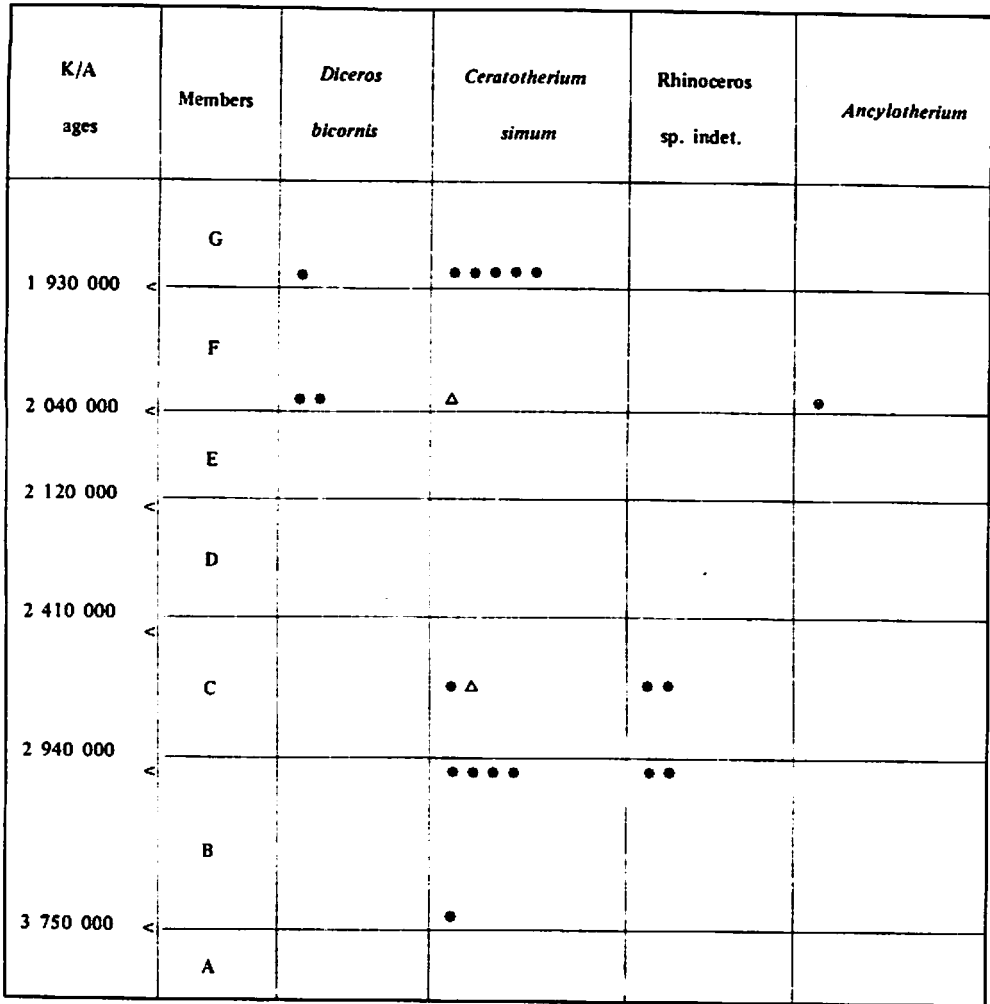
C. Guerin

Remains of rhinoceros and chalicotheres collected from the Shungura Formation, lower Omo basin, under the direction of Yves Coppens and the late C. Arambourg are briefly discussed here. Only specimens from the 1967, 1968, and 1973 field seasons have been examined thus far. Hooijer (1969, 1973, and this symposium) provides additional information on perissodactyls from the Mursi, Usno, and Shungura formations collected under the direction of F. Clark Howell.

Like most African mammalian localities of Pliocene and Pleistocene age the Omo succession has afforded faunal associations which have permitted continentwide correlation and the definition of a series of eight biozones (Coppens 1973). Most localities yield remains of Rhinocerotidae, but remains of Chalicotheriidae rarely occur. Although these perissodactyls have not yet played much of a role in the biozonation of African mammal faunas, they probably will do so once more extensive collections are available. Moreover, these large herbivores must have been dependent on well-defined plant communities which should afford indications of the paleoecology of the particular localities in which they occur.

The temporal distribution in the Shungura Formation of the remains studied thus far is shown in figure 1. They include a single chalicothere tooth and 20 specimens of rhino (4 of which are so worn or fragmentary that the genus cannot be determined). The chalicothere is referred to *Ancylotherium hennigi* (Dietrich). The rhinos represent the present species *Diceros bicornis* (black rhino) and *Ceratotherium simum* (white rhino). These are the usual rhinoceros species found in most African fossil localities of Pliocene to middle Pleistocene age, exceptions being *Brachypotherium lewisii* from the Pliocene of Lothagam, Kenya (Hooijer and Patterson 1972) and *Dicerorhinus africanus* from the "Villafranchian" of Lake Ichkeul, Tunisia (Arambourg 1968). *Ceratotherium* is more common than *Diceros* (13:3), as is usually true in Africa until the Upper Pleistocene, at which time the proportions are reversed (Hooijer and Singer 1960; Arambourg, Chavaillon, and Coppens 1967). On the other hand, in his recent discussion of Rhinocerotidae from the Omo succession, Hooijer (1973) notes that *Diceros* is more common than *Ceratotherium*.

Both genera show evolutionary changes during the Pleistocene, particularly in respect to increasing hypsodonty and certain variations in size (Hooijer 1969). However, Pleistocene representatives of the genus *Diceros* have never been separated specifically, or even subspecifically, from extant *Diceros bicornis*, in which six subspecies, one recently extinct, have been recognized (Zukowsky 1964; Groves 1967). The genus *Ceratotherium*, on the

214

K/A ages	Members	*Diceros bicornis*	*Ceratotherium simum*	*Rhinoceros* sp. indet.	*Ancylotherium*
	G	●	●●●●●		
1 930 000 <					
	F	●●	△		●
2 040 000 <					
	E				
2 120 000 <					
	D				
2 410 000 <					
	C		● △	●●	
2 940 000 <			●●●●	●●	
	B		●		
3 750 000 <					
	A				

● teeth
△ postcranials

Figure 1. Stratigraphic distribution of rhinoceros and chalicothere remains in the Omo succession (collections of Y. Coppens and C. Arambourg).

other hand, is considered to have two living subspecies (*C. simum simum, C. simum cottoni*) and two extinct Pleistocene subspecies (*C. simum mauritanicum, C. simum germanoafricanum*) regarded as very different by Arambourg (1968). Hooijer and Patterson (1972) have also recognized a primitive ancestral species, *Ceratotherium praecox*, of Pliocene age, which also occurs in the earliest part of the Omo succession (Hooijer, this symposium).

All the Rhinocerotidae reported here derive from Shungura Formation members B, C, F, and G. There are no specimens from members D and E, but Hooijer (1973; this symposium) records three specimens of *Ceratotherium* from Member E (and none of *Diceros*) and lists both genera in Member D. Member G has afforded the most specimens of both rhinos and *Ancylotherium* (see also Hooijer 1973; this symposium).

The dentition is more often represented than the postcranial skeleton (although the latter is represented among collections made in years other than those discussed here). The postcranial skeleton is often neglected, and Dietrich (1945), Hooijer and Singer (1960) and Hooijer (1969) have suggested that such skeletal parts (in contrast to craniums and elements of the dentition) may not be specifically determinable. My own work on the "Pontian," Pliocene, and Pleistocene rhinos of western Europe has involved some detailed studies of the postcranial skeleton. A number of criteria (including size, proportions, and morphology of limb bones, carpals, tarsals, and metapodials) do permit separation of different species. The basis for the criteria has been a detailed comparative study of individual, sexual, and geographic variability in the five extant species of rhinoceros. However, a major problem is the general lack of postcranial skeletal parts in museum collections. (For example, there is only one mounted skeleton of *Ceratotherium simum* in France, and only two, one mounted and the other juvenile, in the British Museum of Natural History in London!) Nevertheless it has been possible to distinguish between the three species of *Dicerorhinus* in the Plio-Pleistocene of Western Europe (Guerin 1972) and the three species of rhinoceros in the Middle and Upper Pleistocene (Guerin 1973). Hooijer (1973), who has until recently considered it almost impossible to make specific differentiations on the basis of postcranial parts, now feels that it is possible, though difficult, to do so.

Diceros bicornis

The black rhino is represented by only three specimens of M^3, one of which is unworn. Figure 2 shows the breadth (taken parallel to the protoloph) to length (taken along the greatest length of the ectoloph) relations of this tooth in comparison with a modern *D. bicornis* sample (*N*=24). There are no differences between the samples either in dimensions or proportions.

The hypsodonty index[1] of the unworn M^3 (from Member G) is 100, compared with 120, 103.1, and 97.9 for three modern samples. Unfortunately, there are few comparative values of this index for modern rhinos (which would be most readily obtained with X ray in order not to damage specimens). At any rate there is no significant difference between the Omo value and that of modern samples of *D. bicornis*. Variability of this index on the order of 20% for M^3 is normal for European Pleistocene species.

Ceratotherium simum

The white rhino is represented by 13 specimens, 8 of which can be measured. They are two upper and three lower premolars, an upper molar, a fragment of metacarpal, and an astragalus.[2] The two teeth from Member B are too fragmentary to determine whether these represent *C. praecox* rather than *C. simum*. From Member C upward the specimens are clearly *C. simum*.

An unworn P^4 has a hypsodonty index of 138.8 compared with 185.1 in a recent specimen of *C. simum*. An M^3, very slightly worn, has an index of 118.

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1. This index is 100 x H/L, where length (L) is along the greatest extent of the ectoloph and the height (H) is the maximum height of the ectoloph, perpendicular to the length. The length at the level of the neck is not used, since it is too imprecise when taken between two points of inflection.

2. One lower molar, collected in 1972, derives from a still undefined part of the uppermost Shungura Formation in the Kalam area. Arambourg (1947) described three upper and four lower cheek teeth and a fragmentary mandible from his collecting from the Shungura Formation in 1933.
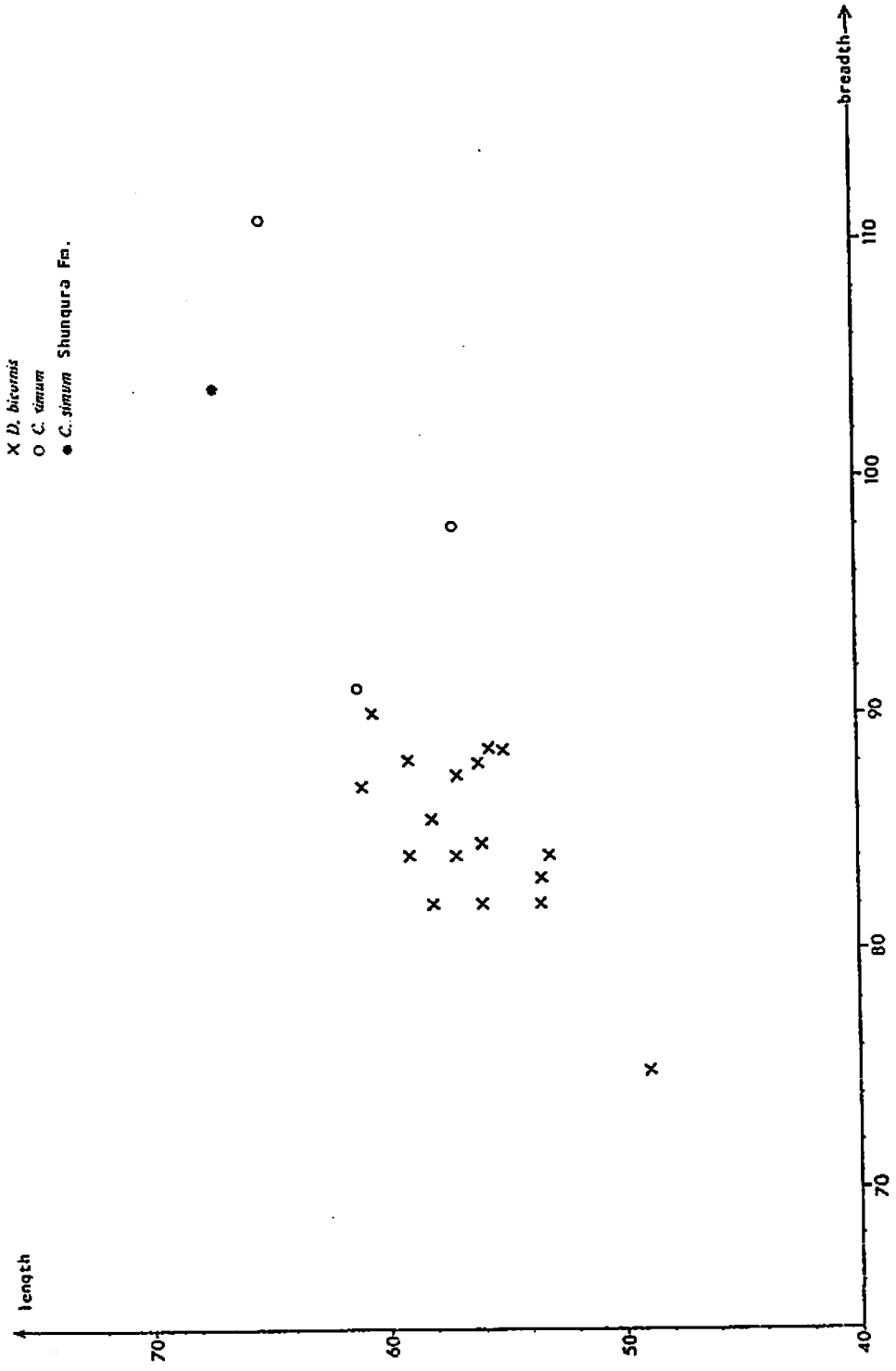
Figure 2. Length and breadth measurements of M^3 in *Diceros bicornis*

The metacarpal fragment represents the distal half. It shows characteristics distinctive of *C. simum*, including the shaft cross-section, which is thicker and more irregular than that of *D. bicornis*, with greater dimensions (even compared with the Cape subspecies of the latter) and the posterior face less depressed and the distal end more shortened.

An astragalus has the same dimensions and proportions (table 1; fig. 3) of a large *C. simum* individual and is very different from *D. bicornis*. It is also distinctive in its broader superior articular process and in the marked development and very different shape of the distal articular process.

Table 1

Comparative Dimensions of Rhinoceros Astragali

Dimension	Shungura Formation	Modern Ceratotherium simum			Modern Diceros bicornis		
		n	Mean	Range	n	Mean	Range
Breadth	104	3	100	91-111	17	84.91	75.90
Height	94	3	86	80-92	15	77.53	66-88
A-p diameter internal lip	67	3	61	57-65	17	56.29	49-61
Transverse diameter, distal articular surface	91.5	2	79.5	74-85	15	68.20	63.5-73
A-p diameter, distal articular surface	50.5	2	44.75	44-45.5	15	44.13	41-49.5
Trochlear width	76	2	67.5	67-68	15	63.37	57-70
Transverse diameter, distal portion	95.5	3	87.67	83-93	17	74.24	55-78

The relatively low hypsodonty index is typical of the subspecies *C. simum germanoafricanum*.

Ancylotherium hennigi

An unworn right lower molar, from Member F, is attributed to this chalicothere. It measures 52 mm (length), 24.5 mm (breadth), 35.5 mm (height), and has a hypsodonty index of 68.27. Dietrich (1942), Butler (1965), and Hooijer (1972) do not figure this tooth of this species, which appears to be the only such known from this time range. The morphology of the specimen is remarkably similar to an M_2 of *Phyllotillon* aff. *naricus*, described and figured by Viret (1961, pl. V, fig. 8), from La Grive-Saint-Alban. It also shows the two distinct points on the lingual face of the crown at the junction of the two lobes. However, the latter specimen is smaller (45 x 20.5 x 25.5 mm) and clearly more brachyodont (index 56.57) than the Omo specimen.

Conclusions

The Shungura Formation affords evidence of a chalicothere and of two species of rhino. The chalicothere is a very rare element of the fauna. The two rhinos are more common, the black being rarer than the white. It is impossible to distinguish the former from the living species, whereas the latter is represented by the extinct subspecies *C. simum germanoafricanum*.

These two rhinos clearly have (now) different biotopes. *Diceros bicornis* favors more or less wooded or bushy savannas or open woodland, whereas *C. simum* favors open savanna or

Figure 3. Breadth/length relationships in rhinoceros astragali

X *R. bicornis*
□ *R. bicornis* Shungura Fm.

length

breadth →

grassland. The frequency of each species throughout the Omo Group formations should re-
flect, in some way, the general nature of the vegetation cover at that time and place.
Thus it is probable that the coexistence of these two species, as well as chalicothere, in
Member G, should correspond to a more "closed" vegetation pattern than in other members of
the Shungura Formation in which *Ceratotherium simum* is thus far the only species repre-
sented. However, this is not confirmed by the palynological evidence (Bonnefille, this
symposium) or the microfaunal evidence (Jaeger and Wesselman, this symposium).

The two living species of African rhinoceros have existed for 3 or 4 m.y. without
significant morphological change. Each species is both ancient and remarkably stable. By
comparison, during the same range of time in western Europe six species of rhino appear
and vanish, to be replaced or to evolve rapidly over some hundreds of thousands of years;
only one persisted over some 2.5 m.y., and none of the other species persisted more than
1 m.y.

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