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A preliminary report on the Pliocene rhinoceros from Udunga, Transbaikalia, Russia

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Abstract

Over 500 rhinoceros fossils were collected from Udunga (MN15–16a), Transbaikalia, Russia and housed at the Southern Scientific Center, Rostov-on-Don, Russia. Both qualitative and statistic analyses applied for the fossils indicate that they are composed of a single species. 16 individuals are recognized in the collection. The Udunga rhinoceros is allocated into the tribe Rhinocerotini based on the anteriorly extended articulation between the ulna and the semilunar. Although the ossification of nasal septum is unknown, it can be assigned to *Stephanorhinus* based on the loss of the functional anterior dentition. In addition to the reduced incisor, the quantitative analyses for the dental and the postcranial materials show the similarities between the Udunga materials and *S. megarhinus*. The quantitative analyses for the central metapodials strongly suggest that the former species is more closely related to the European species than to the Turkish one. It also implies that the rhinoceroses were migrated to Transbaikal area directly from Europe.

Introduction

The Transbaikal area is rich in the Late Cenozoic mammalian fossil localities. The Udunga, one of the localities, has yielded a plenty of mammalian fossils including rodents, lagomorphs, carnivores, proboscideans, perissodactyls, artiodactyls and primates (Kalmykov, 1999; Erbajeva et al., 2003; Egi et al., 2007). Based on the mammalian fossil associations, the age of the Udunga fauna is correlated to the European mammal faunal zone MN 15-16a (Vislobokova et al., 2000; Alexeeva et al., 2001; Erbajeva et al., 2003).

Although the persissodactyls such as the three-toed horse (*Hipparion houfenese* and *H. tchicoicum*) and the chalicotherid (*Postschizotherium* cf. *chardini*) have been studied well, the rhinoceros (*Dicerorhinus* sp.) has rather poorly studied in spite of the rich occurrences from the locality (Kalmykov, 1999). The large samples from the locality enable us to examine these rhinoceros fossils qualitatively and quantitatively. This report is the first step

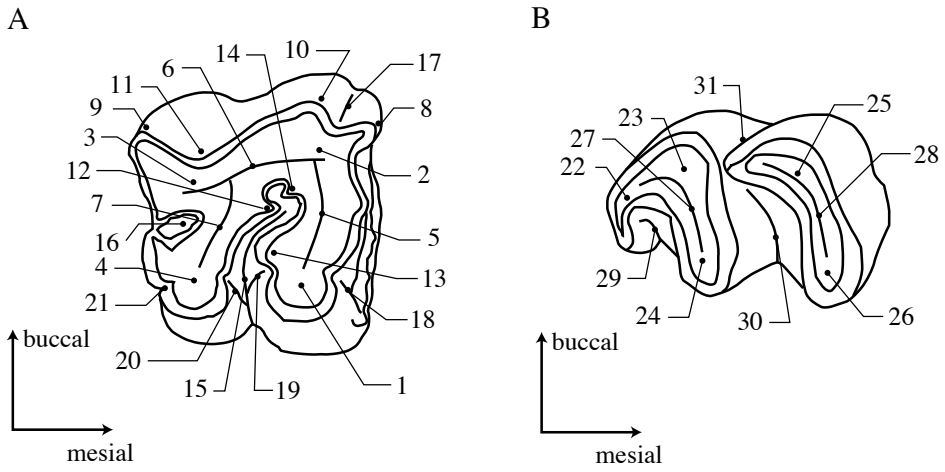

Figure 1. Dental terminology of rhinoceroses after Heissig (1969), Hamilton (1973), Guérin (1980), and Peter (2002). Upper dentition: 1, protocone; 2, paracone; 3, metacone; 4, hypocone; 5, protoloph; 6, ectoloph; 7, metaloph; 8, parastyle; 9, metastyle; 10, paracone rib; 11, metacone rib; 12, crochet; 13, antecrochet; 14, crista; 15, medisinus; 16, mediofossette; 17, postfossette; 18, parastyle fold; 19, anterior protocone groove; 20, posterior protocone groove; 21, anterior hypocone groove. Lower dentition: 22, paraconid; 23, protoconid; 24, metaconid; 25, hypoconid; 26, entoconid; 27, paralophid; 28, metalophid; 29, hypolophid; 30, trigonid basin; 31, talonid basin; 32, labial groove.

to understand the Pliocene rhinoceros in Udunga.

Controversy on '*Dicerorhinus*'

Dicerorhinus is a primitive member of the tribe Rhinocerotini *sensu* Heissig (1973) and Groves (1983). It is a general agreement among the researchers, but this is a controversial genus in the rhinoceroses from the Mio-Pliocene localities. Two genera, *Lartetotherium* and *Stephanorhinus*, are proposed for Mio-Pliocene rhinos that are formerly called '*Dicerorhinus*', whereas the classification of these fossil rhinoceroses is quite far from the agreement even among the specialists. Before we describe the Pliocene rhinoceros from Udunga, we need to summarize those previous works briefly.

The generic type of *Dicerorhinus* (or *Didermocerus*) is the extant Sumatran rhino (Asian two-horned rhino or hairy rhinoceros). This species possesses two horns and the functional anterior dentition. The latter trait is definitely primitive character in the family (e.g., Guérin, 1989; Cerdeño, 1995). The direct ancestor of the species has never been reported and its phylogeny is still in mystery (recently, Zin-Maung-Maung-Thein et al. (2008) reported *D. gwebinensis* from the Upper Irrawaddy Formation (Pliocene to early Pleistocene) of Myanmar, and suggested that this species is more closely related to *D. sumatrensis* than other known species are). Groves (1983) argued that the usage of '*Dicerorhinus*' is restricted only to the living Sumatran rhino and accepted *Lartetotherium* and *Stephanorhinus* for fossil rhinoceroses. He also acknowledged the generic name *Dihoplus* for '*D.*' *schleiermacheri* from the Middle Miocene of the western Europe (Groves, 1983). Giaourtsakis (2003) also

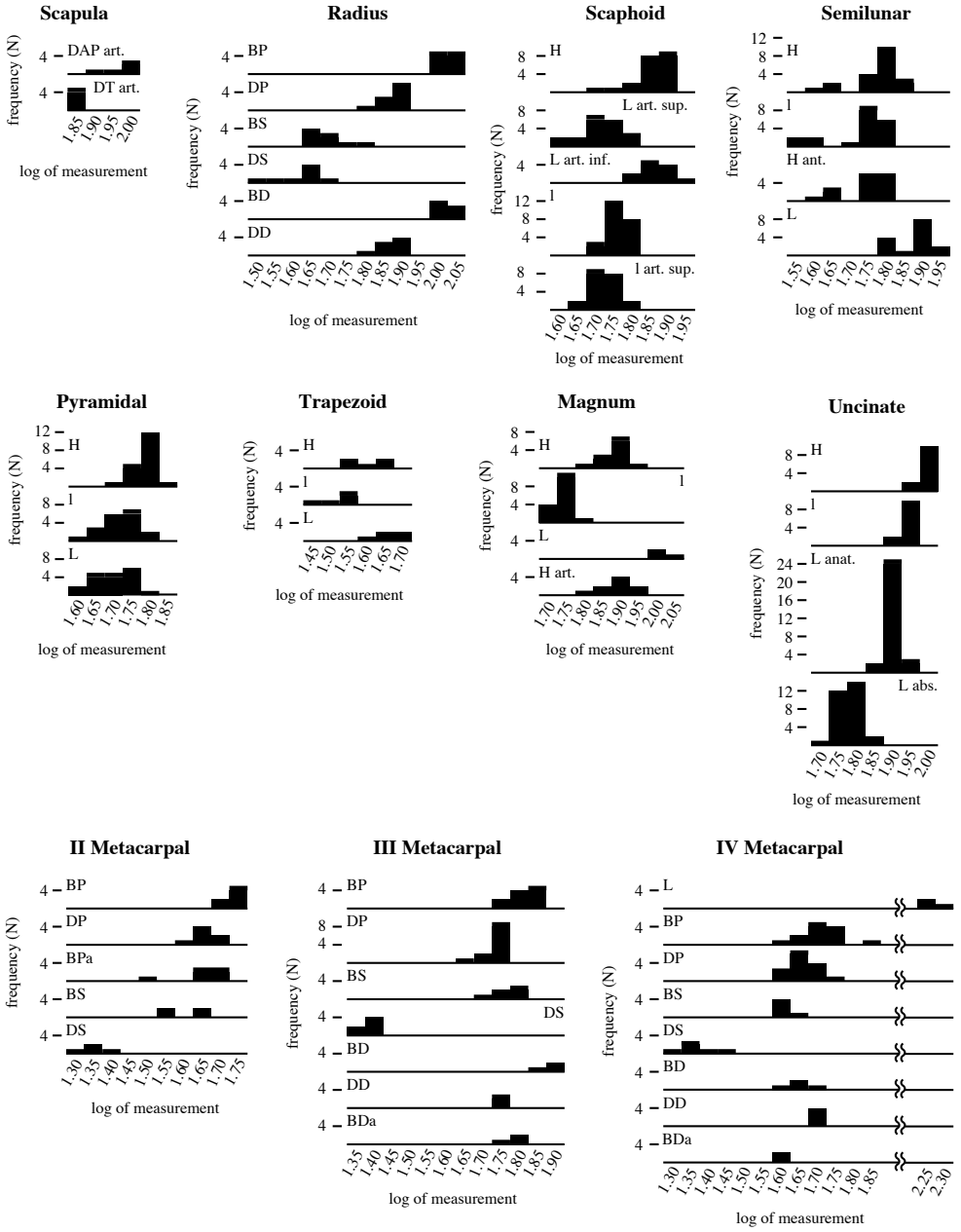

Figure 2. The frequency histograms of the skeletal elements of the forelimb. They show the unimodal distribution, except those of the semilunar.

reviewed the Mio-Pliocene European rhinoceroses with an emphasis on the rhinos of Greece, and recommended the usage of the generic name *Dihoplus* for the fossil large-sized Miocene '*Dicerorhinus*'. Geraads (1988) made a critical revision on the Miocene rhinoceroses from Pikermi and clarified that *Dicerorhinus orientalis* is the junior synonym of *D. pikermiensis*. Giourtsakis (2003) followed this concept and also assigned *pikermiensis* into *Dihoplus*. However, the Chinese *D. orientalis* described by Rinström (1924) cannot be included to *D. pikermiensis* because of the presence of the crista on DP^3 and DP^4 (Ringström, 1924: Pl. 1, Fig. 1 and 2), as stated by Geraads (1988). The large Pliocene rhinoceros *miguelcrusafonti* from the southwestern Europe is tentatively kept in the genus *Dicerorhinus* in this report

Table 1. Measurements (mm) of vertebrae. See Appendix 2 for abbreviations.

		La	Bcra	Hvb
Axis	Udg-880	123.1	143.1	-
Cervical vertebra	Udg-966	94.7	50.0	62.8
	Udg-1798	-	48.1	62.7
Thoracic veretbra	Udg-900	65.9	54.9	53.8
	Udg-1743	68.0	49.6	54.7
	Udg-1746	-	52.8	58.1
	Udg-1857	67.2	64.0	63.6
	Udg-2213	62.0	62.1	58.2
Thoracic vertebra(juvenile)	Udg-1723	>62	44.5	>55
	Udg-1724	>51	47.0	47.0
Lumber vertebra	Udg-1745	-	74.5	39.5

because of the lack of the information of the anterior dentition. The further study and discussion on the classification of '*Dicerorhinus*' are definitely required.

Lartetotherium was established by Ginsburg (1974) for *Rhinoceros sansaniensis* from Sansan. The comments on the genus are abbreviated in this report because this is the western European Miocene genus.

Stephanorhinus was erected by Kretzoi in 1942 for the European Plio-Pleistocene incisorless rhinoceroses. Kretzoi (1942) also established the new genus *Procerhinus* for '*D.*' *hemitoechus* based on the absence of the frontal horn. Guérin (1980) regarded that both genera (*Stephanorhinus* and *Procerhinus*) are invalid and established the subgenus *Brandtorhinus* under the genus *Dicerorhinus* instead of the genus *Stephanorhinus*, however his new subgenus is virtually equivalent with *Stephanorhinus*. This subgenus includes not only *etruscus* but also *hemitoechus* and *kirchbergensis* (Guérin, 1980). Fortelius et al. (1993) made a critical revision of *Stephanorhinus* based on the materials stored in the museums in western Europe, especially from the Pleistocene time. The authors included *hemitoechus* and *kirchbergensis* into *Stephanorhinus* and abandoned *Procerhinus*. We accepted the concept for *Stephanorhinus* shown by Fortelius et al. (1993) in this report: *S. megarhinus*, *S. kirchbergensis*, *S. jeanvireti*, *S. etruscus*, *S. hundsheimensis*, and *S. hemitoechus*. In the view of the loss of functional incisors, the Chinese '*Dicerorhinus orientalis*' is also possibly allocated to *Stephanorhinus* (Ringström, 1924: Pl. 1, Fig. 4). However, this taxonomic name is tentatively retained in this paper because we have never observed it.

Pliocene Eurasian rhinoceroses

In contrast to the flourish of rhinoceroses in Miocene, the only one species *Stephanorhinus megarhinus* is known from the basal Pliocene of Europe (Heissig, 1996). The second species of the Upper Ruschinian is *D. miguelcrusafonti*, which was found only from Iberian Peninsula and southern France (Guérin, 1980). *S. jeanvireti* emerged from the beginning of the late Pliocene and coexisted with *S. etruscus* for a short time (Heissig, 1996). Only the latter species survived into Pleistocene.

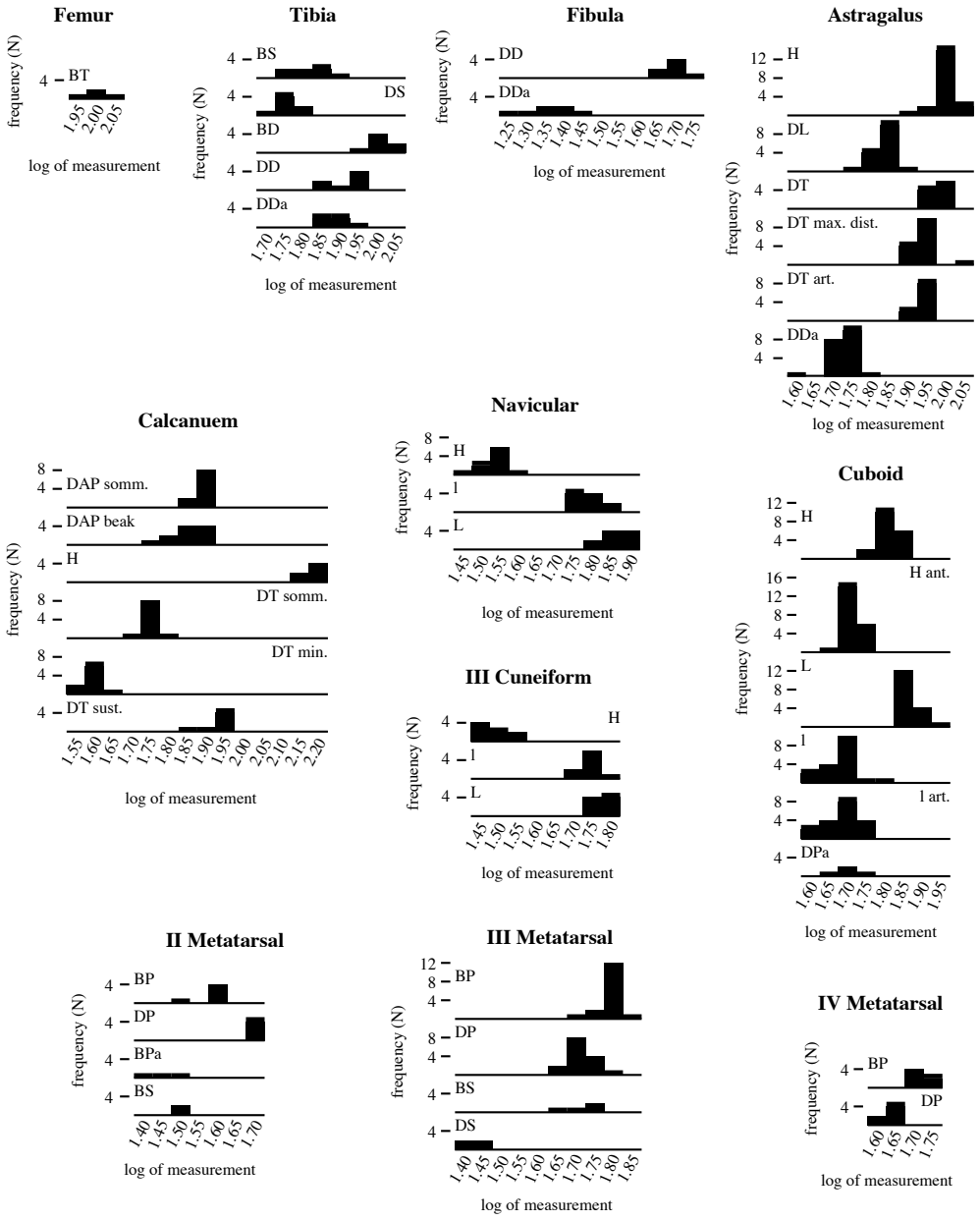

Figure 3. The frequency histograms of the skeletal elements of the hindlimb, showing the unimodal distribution.

Qiu and Qiu (1995) summarized the Chinese Neogene mammalian faunas and described two Pliocene faunas: Gaozhuang Fauna (MN14-15) and Mezegou Fauna (MN16), both from Shanxi Province. The Gaozhuang Fauna includes *D. orientalis* and *Acerorhinus* sp, and only '*D.*' sp. is listed in the Mezegou Fauna (Qiu and Qiu, 1995). Deng et al. (2004) made a revision of the Cenozoic mammalian fossil localities and their stratigraphic sequence of the Linxia Basin in Gansu Province. The authors added the Chinese Pliocene mammalian fauna, which comes from the basal Pliocene Hewangjia Formation (MN14), including *Shansirhinus ringstromi* (Deng et al., 2004). Previous works reported the Pliocene *Chilotherium* species from Inner Mongolia, Gansu and Yunnan (Chan and Tung, 1961; Hu, 1962; Tang et al., 1974; Qiu,

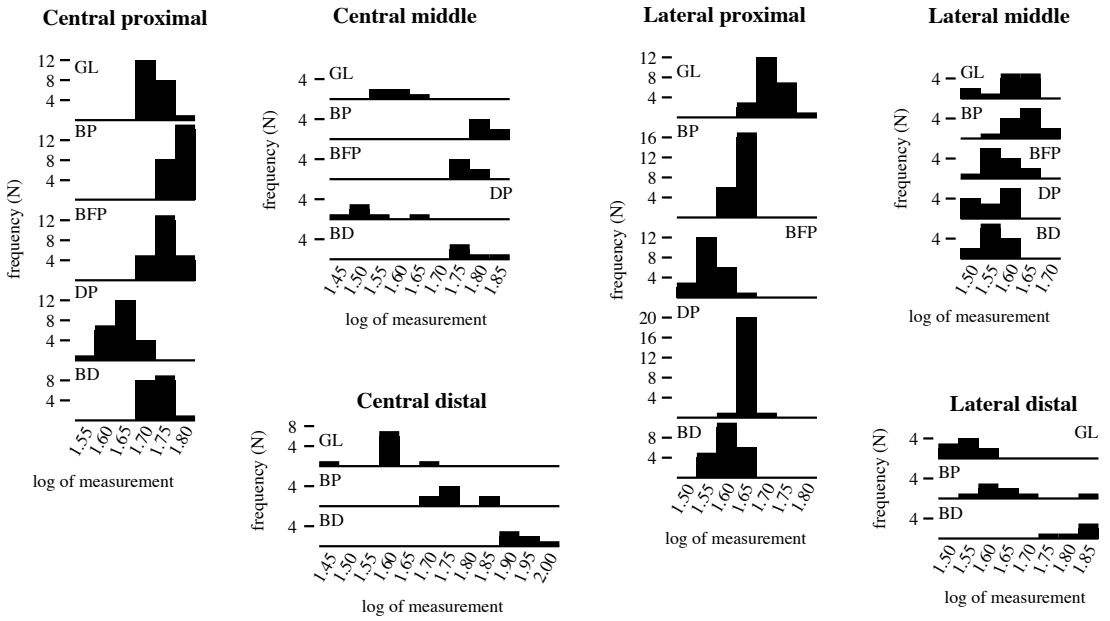

Figure 4. The frequency histograms of the phalanges. They roughly indicate a unimodal distribution.

1979; Zong, 1987), however this genus was disappeared after the Mio-Pliocene boundary in the current revision of the Chinese Neogene stratigraphy (Qiu and Qiu, 1995). Huang and Yan (1983) described a primitive member of Elasmotherini rhinoceros *Shennogtherium hypsodontus* from Hubei.

From the Upper Siwaliks (Pinjor Type, ranging in age from 3.2-1.0 Ma (Plbeam et al., 1996)), *Coelodonta platyrhinus*, *Rhinoceros sivalensis* and *R. paleindicus* were described (Colbert, 1935).

Dicerorhinus continued to the basal Pliocene (MN14-15) in northern Eurasia, while it was replaced by *Stephanorhinus* after MN16 in Europe. On the other hand, in China the former genus continued to MN16 and the latter genus emerged from the Pleistocene.

Material and methods

Materials from Udunga are stored in the Southern Scientific Center, Rostov-on-Don, Russia. The fossil materials examined are listed in Appendix 1. Dental terminologies are after Heissig (1969), Hamilton (1973), Guérin (1980), and Peter (2002) and illustrated in Figure 1. For cheek teeth, the greatest mesiodistal length (L), the mesial buccolingual diameter (Wa), the distal buccolingual diameter (Wp), and the greatest height of the crown (H) were measured. The postcranial bones were measured by the following standard methodology (Appendix 2).

Rhinoceros of Udunga

In the observation for 516 rhinoceros fossil specimens from Udunga stored in the South Scientific Center there is no significant difference in the morphology among them, suggesting

Table 2. Measurements (mm) of teeth. See Appendix 2 for abbreviations

Upper left teeth

		P^2	P^3	P^4	M^1	M^2	M^3	DP^1	DP^2	DP^3	DP^4
	L								37.1		
Udg	Wa								35.5		
-201	Wp								35.9		
	H								23.8		
	L								41.1		
Udg	Wa								36.9		
-202	Wp								38.5		
	H								23.6		
	L								39.0		
Udg	Wa								36.6		
-203	Wp								37.3		
	H								24.2		
	L				52.5						
Udg	Wa				48.4						
-204	Wp				44.1						
	H				32.5						
	L								40.6	44.9	49.5
Udg	Wa								35.4	45.5	49.2
-207	Wp								36.2	41.9	44.7
	H								27.8	27.9	36.0
	L							28.2			
Udg	Wa							-			
-213	Wp							23.0			
	H							22.0			
	L				53.7						
Udg	Wa				50.1						
-215	Wp				44.4						
	H				34.6						
	L			47.8							
Udg	Wa			45.1							
-216	Wp			40.2							
	H			29.1							
	L							31.1	-	44.7	
Udg	Wa							-	-	43.4	
-218	Wp							22.6	-	37.9	
	H							22.6	-	26.9	
Udg	L							27.6			
-	Wa							-			
1027	Wp							22.3			
	H							22.1			
Udg	L							25.6			
-	Wa							-			
1028	Wp							24.5			
	H							22.8			
Udg	L	43.6									
-	Wa	42.5									
1030	Wp	37.7									
	H	26.5									
Udg	L			47.0							
-	Wa			46.1							
1031	Wp			41.4							
	H			34.2							
Udg	L					58.8					
-	Wa					61.2					
1032	Wp					53.2					
	H					54.9					
Udg	L				52.4						
-	Wa				-						
1892	Wp				-						
	H				38.7						
Udg	L					58.5					
-	Wa					-					
1901	Wp					-					
	H					50.1					
Udg	L					59.3					
-	Wa					-					
2554	Wp					-					
	H					55.4					

Upper right teeth

		P^2	P^3	P^4	M^1	M^2	M^3	DP^1	DP^2	DP^3	DP^4
	L							28.7			
Udg	Wa							-			
-205	Wp							24.1			
	H							23.1			
	L									45.0	
Udg	Wa									44.5	
-207	Wp									41.3	
	H									28.9	
	L								40.1		
Udg	Wa								37.0		
-214	Wp								37.7		
	H								23.4		
	L				49.1	54.0					
Udg	Wa				49.9	47.7					
-217	Wp				45.6	-					
	H				34.9	34.9					
	L							31.1			
Udg	Wa							-			
-218	Wp							22.6			
	H							22.6			
	L							27.1			
Udg	Wa							-			
-886	Wp							24.5			
	H							23.7			
Udg	L								39.3		
-	Wa								35.9		
102	Wp								38.1		
9	H								24.8		

Lower left teeth

		P_2	P_3	P_4	M_1	M_2	M_3
	L						52.0
Udg	Wa						-
-206	Wp						31.4
	H						32.6
	L				40.8	51.9	
Udg	Wa				-	-	
-208	Wp				-	32.5	
	H				30.1	32.1	
Udg	L	30.0					
-	Wa	-					
199	Wp	14.1					
0	H	21.8					
Udg	L	29.7					
-	Wa	-					
199	Wp	15.5					
1	H	26.2					

Lower right teeth

		P_2	P_3	P_4	M_1	M_2	M_3
	L	29.8		39.7	40.9	52.0	54.9
Udg	Wa	-		-	-	-	-
-208	Wp	18.1		26.1	28.0	33.1	31.6
	H	24.8		28.8	28.4	33.0	34.2

that the rhinoceros fossils we examined are composed of a single species.

The frequency histograms of the skeletal elements (Figure 2-4) indicate a unimodal distribution, except those of the semilunar that show the bimodal distribution (Figure 2). In the bivariate plot for the semilunar (Figure 5), it is evident that the lesser group is proportionally smaller than the larger one is. These two groups may suggest a difference

Table 3. Descriptive statistics of dental measurements from dentitions.

Upper dentition

		N	Mean	St. Dev.
DP^1	L	7	28.63	2.270
	W	7	23.30	1.044
DP^2	L	6	39.53	1.426
	W	6	37.28	1.040
DP^3	L	3	44.87	0.153
	W	3	44.47	1.050
DP^4	L	1	(49.50)	-
	W	1	(49.20)	-
P^3	L	1	(43.60)	-
	W	1	(42.50)	-
P^4	L	2	47.40	-
	W	2	45.60	-
M^1	L	4	51.93	1.974
	W	3	49.47	0.929
M^2	L	4	57.65	2.456
	W	2	54.45	-

Lower dentition

		N	Mean	St. Dev.
P_2	L	3	29.83	0.153
	W	3	15.90	2.030
P_3	L			
	W			
P_4	L	1	(39.70)	-
	W	1	(26.10)	-
M_1	L	2	40.85	-
	W	1	(28.00)	-
M_2	L	2	51.95	-
	W	2	32.80	-
M_3	L	2	53.45	-
	W	2	31.50	-

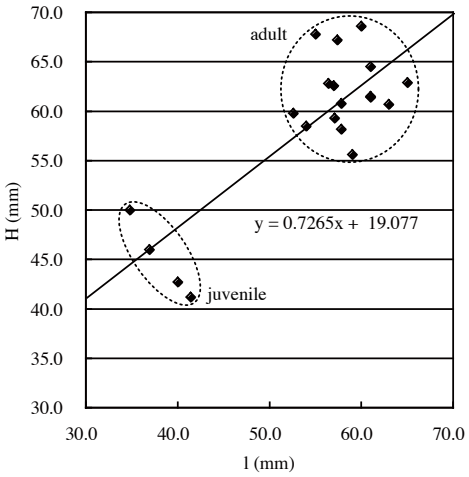

Figure 5. The graph of the height vs. transverse diameter of the semilunar. See Appendix 2 for the abbreviations. The lesser group is proportionally smaller than the larger one is.

in the growth, i.e. the larger one is composed of the adult individuals and the smaller one consists of the juveniles. The numerical analyses support the idea that the fossil specimens we observed in the center consist of a single species.

Vertebrae (Figure 6, Table 1)

Only an incomplete axis was available for us. The dens and vertebral body are preserved, but the vertebral arch and the spinous process is missing. In dorsal view the dens appears cylindrical and tapers cranially. Two other cervical vertebrae are also incomplete and the exact identification for them is impossible. Seven thoracic vertebrae are kept at the center. They are also badly preserved. Thoracic vertebrae are cranio-dorsally shorter and rather transversely wider than cervical ones. The caudal articular surface was not fused in two specimens (Udg-1723, 1724). We could observe only one lumber vertebra, which typically has proximodistally flat vertebral body.

Skull and mandibular fragments (Figure 6)

We could examine two fragments of the occipital condyle. They appear a roughly triangular shape in caudal view. The premaxillary fragment (Udg-1967) has a trace of alveolus for an upper incisor, possibly DI^1. Unfortunately the incisors are not kept in the collection, however they are thought to be non-functional because of the small-sized alveolus. In dorsal view no traces of the ossification between the premaxilla and nasal could be observed. But it cannot mean the absence of the partial ossification of nasal septum. It just indicates that the nasal septum was not fully ossified.

Three fragments of the mandibular corpus were available. They are shallow in lateral view. The ventral border of the symphyseal portion upraised antero-dorsally. There are two

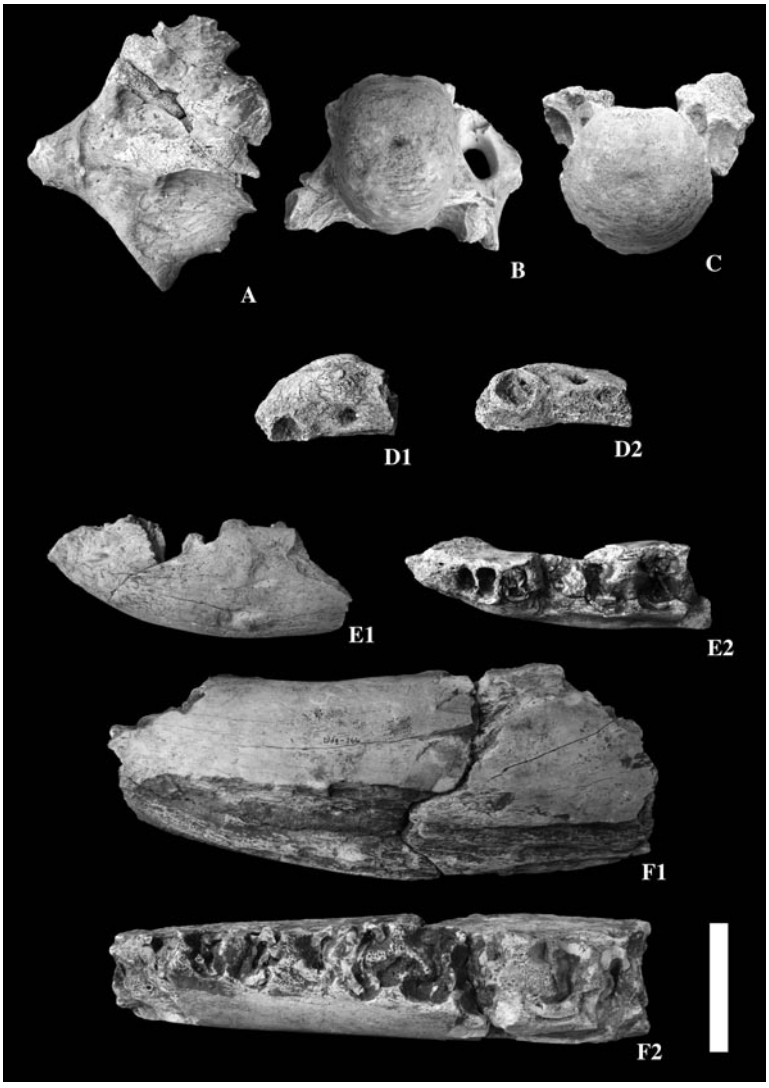

Figure 6. Vertebrae, skull, and mandibular fragments. **A**, Udg-880, axis, ventral view. **B**, Udg-966, cervical vertebra, cranial view. **C**, Udg-2213, thoracic vertebra, cranial view. **D**, Udg-1967, a fragment of left premaxilla with alveoli for an upper incisor. **D1**, lateral view. **D2**, occlusal view. **E**, Udg-878, a fragment of left mandible: **E1**, lateral view. **E2**, occlusal view. **F**, Udg-264, a fragment of left molar portion: **F1**, lateral view. **F2**, occlusal view. Scale bar equals 5 cm.

fragments of the condyloid process recognized.

Teeth (Figures 7-8, Table 2-3)

All dental materials reported herein are isolated. The isolated cheek teeth were identified by matching with the neighboring teeth and wear facets between them. The wear-profiles of the ectoloph of the deciduous cheek teeth show the subhypsodont, whereas those of the permanent teeth are brachydont.

Upper dentition (Figure 7, Table 2)

There are seven specimens of DP^1 recognized. The DP^1 shows a triangular shape with a strong parastyle in occlusal view. Three materials have a weak protoloph that does not connect to the ectoloph. The buccal wall is rounded. The internal enamel folds were formed in four specimens. The lingual cingulum is formed in three.

We could observe six materials of DP^2. The metacone rib is positioned rather mesially.

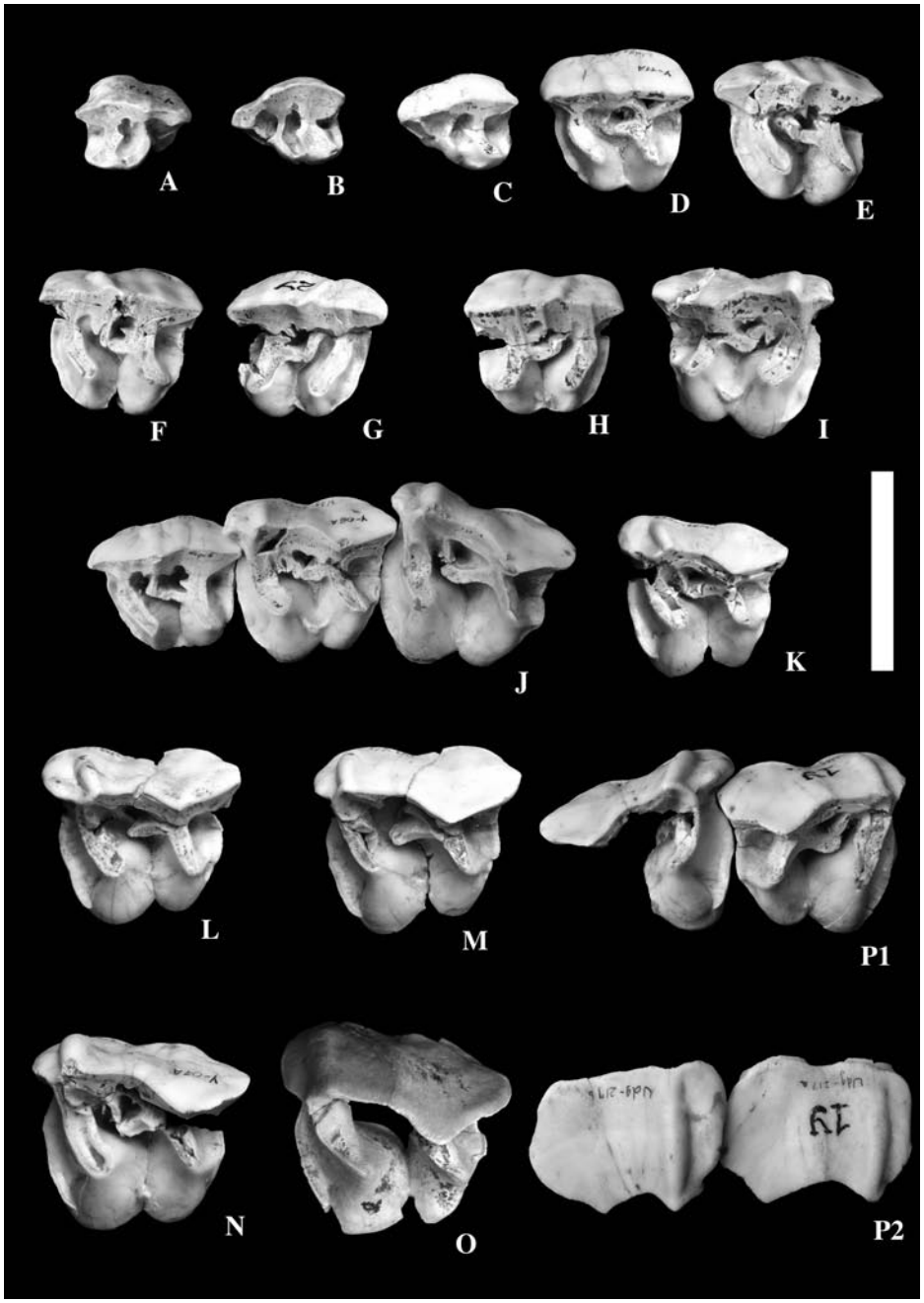

Figure 7. Upper cheek teeth in occlusal (**A**-**P1**) and buccal (**P2**) views. **A**, Udg-205, right DP^1. **B**, Udg-213, left DP^1. **C**, Udg-1028, left DP^1. **D**, Udg-201, left DP^2. **E**, Udg-202, left DP^2. **F**, Udg-203, left DP^2. **G**, Udg-214, right DP^2. **H**,. Udg-1029, right DP^2. **I**, Udg-207d, right DP^3. **J**, Udg-207a-c, right DP^2-DP^4. **K**, Udg-1030, left P^3. **L**, Udg-216, left P^4. **M**, Udg-215, left M^1. **N**, Udg-204, left M^1. **O**, Udg-1032, left M^2. **P1** and **P2**, Udg-217a-b, right M^1-M^2. Scale bar equals 5 cm.

The buccal wall is undulated with a strong metacone rib. The protoloph and the metaloph are completely separated. The internal enamel folds are remarkably developed. The mediofossette is totally isolated from the medisinus in three specimens. The lingual cingulum is developed as a tubercle at the lingual end of the medisinus in three.

Three specimens of DP^3 are recognized in the collection. The protocone is slightly constricted. The buccal wall is strongly undulated with the paracone rib and the metacone rib.

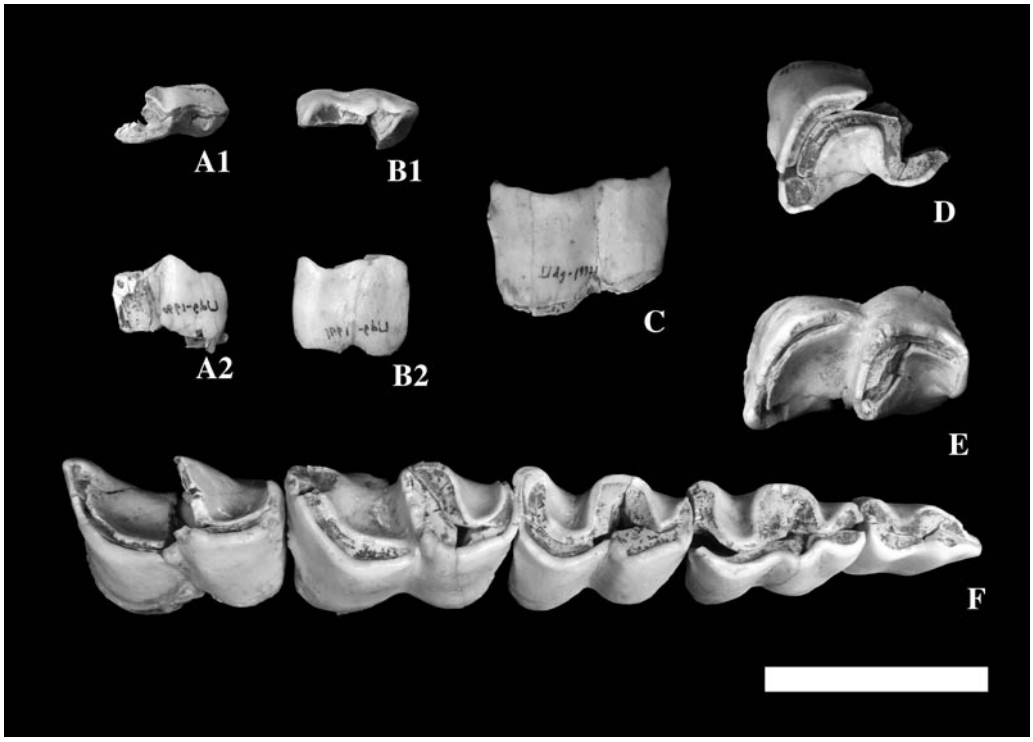

Figure 8. Lower cheek teeth. **A**, Udg-1990, left P_2 fragment: occlusal (**A1**) and buccal (**A2**) viewes. **B**, Udg-1991, left P_2 fragment: occlusal (**B1**) and buccal (**B2**) views. **C**, Udg-1992, right lower cheek tooth fragment (only buccal wall is preserved, buccal view). **D**, Udg-1993, distal half of a lower cheek tooth (occlusal view). **E**, Udg-206, left M_3 (occlusal view). **F**, Udg-208, right P_4-M_3, occlusal view. Scale bar equals 5 cm.

The medisinus opens lingually. The parastyle fold does not reach to the base of the crown. The internal enamel folds are strongly developed in two specimens. In both specimens the mediofossette is totally isolated. The tubercle-like lingual cingulum is formed at the lingual end of the medisinus in one of three.

Only one material of DP^4 was identified. The protocone is slightly constricted with the anterior protocone groove and the shallow posterior one. The medisinus opens lingually. The buccal wall is undulated. The parastyle fold is evident in occlusal view, but is obscure at the base of the crown. The internal enamel folds are simple in contrast to other deciduous upper cheek teeth. The single crista entends lingually toward the crochet. The mediofossette is isolated by the connection between the crista and the crochet. The lingual cingulum is absent.

Only one material of P^3 is kept in the collection. The protoloph and the metaloph are completely separated. The protocone is slightly constricted. The posterior protocone groove is shallower than the anterior one. The buccal wall is strongly undulated with the paracone rib and the metacone rib. The parastyle is evident, but it is indistinct at the base of the crown. The internal enamel folds are simple. The mediofossette is isolated by the connection of the crista and the crochet. The lingual cingulum cannot be observed because the lingual end of the medisinus is damaged.

Two specimens of P^4 are almost completely preserved. They are slightly worn. The medisinus is widely open at its lingual end. The protocone is slightly constricted by the

Table 4. Measurements (mm) of scapulae and humerii. See Appendix 2 for abbreviations.

Scapula

	DAP art.	DT art.	DAP tub.
Udg-1021	96.0	71.5	-
Udg-1752	95.0	70.6	-
Udg-1812	101.1	73.0	149.4
Udg-1956	90.0	73.8	-
Udg-1978	76.0	67.2	-
N	*5*	*5*	*1*
Mean	*91.6*	*71.2*	*(149.4)*
St. Dev.	*9.58*	*2.57*	-

Humerus

	BS	DS	BD	DD
Udg-265	66.0	64.0	158.9	120.8
Udg-865	-	-	154.4	114.6
Udg-1754	-	-	-	>99
Udg-1804	-	-	-	100.9
Udg-1813	-	-	-	101.5
Udg-1880	-	-	-	118.0
Udg-1904	-	-	-	99.5
Udg-1941	-	-	-	>84
Udg-1977	67.2	83.5	-	-
N	*2*	*2*	*2*	*6*
Mean	*66.6*	*73.8*	*156.7*	*109.2*
St. Dev.	-	-	-	*9.63*

anterior protocone groove and the shallow posterior one. The single crista extends lingually and slightly distally toward the crochet. The mediofossette seems to be totally isolated if the tooth was moderately worn. The lingual cingulum is absent.

There are four specimens of M^1. The protocone is slightly constricted in M^1. The internal part of the tooth was lacked or heavily damaged in two specimens. The paracone rib is strongly developed. The parastyle fold is evident, but does not reach to the base of the crown. The mediofossette is isolated in two observable materials. The double crista is observed in one of the two. The lingual cingulum is developed as a tubercle at the lingual end of the medisinus in one of four.

Only one of four specimens of M^2 is nearly complete, however it lost the internal part. Two specimens preserve only the buccal wall. The protocone is slightly constricted in one of two observable specimens. The paracone rib is prominent and the metacone rib is weak. The parastyle fold is evident even at the base of the crown in one of four specimens.

Fragmentary upper cheek teeth show a low-crowned dentition. The protocone is constricted in Udg-1988, Udg-2555, Udg-2556 and possibly in Udg-1985, which lost the mesial part of the protocone. The posterior protocone groove is absent in Udg-1989.

Lower dentition (Figure 8, Table 2)

There are three specimens of P_2. P_2 is roughly triangular in occlusal view. The paralophids typically extends just mesially, not mesio-lingually. The metalophid is buccolingually narrower than the hypolophid. The buccal walls of both lophids are rounded. A shallow vertical groove is recognized between the paraconid and the protoconid. The labial groove is shallow. The cingula are absent.

There is no P_3 specimens in the collection.

We could observe only one material of P_4. The metalophid is buccolingually narrower

Table 5. Measurements (mm) of radii and ulnae. See Appendix 2 for abbreviations,

Radius

	BP	DP	BS	DS	BD	DD
Udg-261	-	-	-	-	107.5	82.5
Udg-800	97.6	75.7	-	-	-	-
Udg-813	108.1	69.4	53.0			
Udg-814	96.1	72.0	46.8	41.8	-	-
Udg-815	110.6	79.8	-	-	-	-
Udg-878	-	-	-	-	110.7	78.4
Udg-898	-	-	-	-	97.6	69.0
Udg-899	-	-	-	-	102.1	62.4
Udg-920	105.1	82.0	47.3	43.2	-	-
Udg-962	-	-	-	-	115.2	70.7
Udg-967	109.1	78.1	-	-	-	-
Udg-968	104.9	78.1	-	-	-	-
Udg-969	109.4	80.6	-	-	-	-
Udg-998	106.9	68.4	-	-	-	-
Udg-1014	-	-	-	-	97.9	72.0
Udg-1772	-	-	60.7	43.5	-	-
Udg-1848	-	-	56.0	47.0	-	-
Udg-1861	-	-	47.4	34.7	-	-
Udg-1922	-	-	46.6	43.8	-	-
Udg-1935	-	-	50.0	52.0	102.8	75.3
Udg-1937	-	-	-	-	-	75.8
Udg-1938	105.0	66.8	-	-	-	-
Udg-1954	-	-	-	-	-	>46
Udg-1979	-	-	47.0	33.0	-	-
N	*10*	*10*	*9*	*8*	*7*	*8*
Mean	*105.3*	*75.1*	*56.4*	*42.4*	*104.8*	*73.3*
St. Dev.	*4.88*	*5.52*	*5.02*	*6.15*	*6.60*	*6.17*

Radius (Juvenile)

	BP	DP	BS	DS	BD	DD
Udg-1751	108.3	74.9	-	-	-	-
Udg-1943	81.2	59.1	-	-	-	-
N	*2*	*2*	-	-	-	-
Mean	*94.8*	*67.0*	-	-	-	-
St. Dev.	-	-	-	-	-	-

Ulna

	DD	Bo	Do	Hsiu	Bpau
Udg-1764	57.3	-	-	-	-
Udg-1830	64.4	-	-	-	-
Udg-1915	-	-	-	>82	68.3
Udg-1925	-	62.6	92.1	-	-
Udg-1939	-	-	-	93.0	-
Udg-1942	80.0	-	-	-	-
Udg-1950	-	-	-	-	>64
N	*3*	*1*	*1*	*1*	*1*
Mean	*67.2*	*(62.6)*	*(92.1)*	*(93.0)*	*(68.3)*
St. Dev.	*11.6*	-	-	-	-

than the hypolophid. The buccal wall of the metalophid is rather flatter than that of the hypolophid. A vertical groove between the paraconid and the protoconid is shallow. The labial groove is shallow. The cingula are absent.

There are two specimens for each molar (M_1 – M_3). The lower molars are similar in the morphology. The metalophid and the hypolophid are similar in size. The buccal walls of both lophids are rounded. In M_3 the buccal walls are rather flatter than those of others. The labial groove is sharp in four of five molars. The cingula are absent.

A right lower cheek tooth fragment (Udg-1992) has a rather sharp labial groove. A moderately worn left tooth fragment (Udg-1993) shows the rounded buccal wall of the hypolophid.

Postcrania (Figures 9-12, Tables 4-15)

Scapula (Figure 9, Table 4)

Five distal ends of the scapula are kept at the center. The supraglenoid tubercle is

Table 6. Measurements (mm) of scaphoids and semilunars. See Appendix 2 for abbreviations.

Scaphoid

	H	L art.sup.	L art inf.	l	l art.sup.
Udg-253	74.3	55.5	78.1	60.8	58.8
Udg-254	64.5	49.9	69.6	52.0	48.0
Udg-827	78.0	58.1	73.5	64.4	57.0
Udg-835	76.4	48.5	-	53.3	52.7
Udg-841	70.2	48.5	73.1	58.0	-
Udg-856	71.6	49.6	63.4	55.9	52.0
Udg-922	72.8	51.2	70.6	55.1	50.8
Udg-923	-	-	-	58.0	52.9
Udg-924	78.9	47.7	68.0	59.5	55.8
Udg-925	77.3	54.7	76.3	60.6	56.1
Udg-926	75.3	40.5	-	-	47.3
Udg-939	72.1	61.5	76.9	60.4	55.3
Udg-950	78.0	39.7	66.3	59.6	48.6
Udg-976	58.9	-	-	54.7	-
Udg-979	53.0	-	-	58.1	-
Udg-982	78.5	-	-	65.1	60.7
Udg-986	74.2	61.5	79.4	61.3	58.2
Udg-991	77.3	57.4	87.7	64.2	59.1
Udg-1026	80.3	53.7	-	59.8	53.7
Udg-1803	66.0	46.0	-	47.5	44.8
Udg-1870	-	54.0	-	53.1	50.9
Udg-1871	74.0	49.3	-	57.4	51.7
Udg-1874	-	59.7	-	58.8	57.0
Udg-1875	72.0	46.0	-	55.2	52.9
N	*21*	*20*	*12*	*23*	*21*
Mean	*72.6*	*51.7*	*73.6*	*57.9*	*53.5*
St. Dev.	*6.91*	*6.27*	*6.64*	*4.23*	*4.26*

Semilunar

	H	l	H ant.	L
Udg-243	42.7	40.0	44.2	65.6
Udg-244	46.0	36.9	46.0	66.1
Udg-249	50.0	34.8	42.5	66.5
Udg-250	41.2	41.4	40.0	61.7
Udg-833	62.8	56.4	60.6	86.4
Udg-834	59.8	52.6	58.9	73.6
Udg-918	59.3	57.1	59.8	78.7
Udg-919	60.7	63.0	60.3	78.7
Udg-1004	67.2	57.4	63.2	82.0
Udg-1006	60.8	57.8	58.0	80.4
Udg-1007	61.8	-	60.0	83.0
Udg-1008	58.2	57.8	54.8	81.8
Udg-1009	61.5	61.0	60.9	-
Udg-1749	64.5	61.0	-	-
Udg-1759	58.5	54.0	-	-
Udg-1766	55.6	59.0	-	-
Udg-1828	68.6	60.0	-	-
Udg-1877	61.4	61.0	59.0	83.3
Udg-1881	67.8	55.0	57.5	86.5
Udg-1887	62.6	57.0	-	-
Udg-1945	62.9	65.0	59.6	81.3
N	*21*	*20*	*16*	*15*
Mean	*58.8*	*54.4*	*55.3*	*77.0*
St. Dev.	*7.68*	*8.86*	*7.55*	*8.21*

evident, but the coracoid process is much reduced. The glenoid cavity appears elliptical in distal view.

Humerus (Figure 9, Table 4)

There are nine specimens of the humerus, but we could not examine their proximal parts in the collection. They are badly damaged and only two materials show the complete distal ends. The lateral distal epiphysis is massive, whereas the medial one is reduced. Only one humeral shaft was available. The shaft is the rounded triangular shape in a cross section.

Radius (Figures 9, Table 5)

We could observe twenty-five materials including two juvenile radii, however a complete radius was not kept in the collection. In adult specimens, the proximal facet for ulna is separated in posterior view. The bicipital rugosity is broad in anterior view. The proximal border of the radius is blunt in both anterior and posterior view. The shaft is triangular shape in a cross section. The styloid process of the radius is strong.

Table 7. Measurements (mm) of pyramidals, pisiforms, trapeziums, and trapezoids. See Appendix 2 for abbreviations.

Pyramidal

	H	l	L
Udg-293	62.7	53.5	58.4
Udg-294	60.6	51.3	48.1
Udg-295	66.6	62.9	46.6
Udg-296	57.9	41.9	44.5
Udg-297	60.3	56.3	52.7
Udg-298	59.0	53.4	54.6
Udg-299	64.7	53.5	44.4
Udg-300	56.6	53.0	48.4
Udg-808	56.0	45.6	56.3
Udg-845	63.7	47.8	61.7
Udg-860	65.2	52.5	49.0
Udg-902	66.2	54.3	51.6
Udg-957	60.6	54.3	59.5
Udg-972	59.8	49.3	55.2
Udg-974	61.3	65.6	45.2
Udg-976	58.9	45.9	41.6
Udg-977	52.9	45.9	41.9
Udg-993	61.9	51.8	54.5
Udg-1987	71.6	54.8	44.5
N	*19*	*19*	*19*
Mean	*61.4*	*52.3*	*50.5*
St. Dev.	*4.35*	*5.72*	*6.15*

Pisiform

	H	l	L
Udg-850		50.0	63.3

Trapezium

	H	l	L
Udg-931	31.5	26.1	34.4

Trapezoid

	H	l	L
Udg-804	33.6	27.9	40.2
Udg-824	36.4	35.5	51.6
Udg-839	42.0	30.5	45.4
Udg-901	42.6	34.4	49.8
Udg-903	43.2	35.5	46.3
N	*5*	*5*	*5*
Mean	*39.6*	*32.8*	*46.7*
St. Dev.	*4.30*	*3.41*	*4.41*

Ulna (Table 5)

The fragmentary six ulnae were identified. The distal end is damaged and the facet for the semilunar cannot be observed.

Scaphoid (Figures 9, Table 6)

We could examine twenty-four specimens of the scaphoid. The posterior distal border is protruding distally in five of eleven complete materials. The proximal articular surface is deeply concave in lateral view. In proximal view the lateral border of the proximal facet is slightly convex and the medial one is pointed medially.

Semilunar (Figures 9, Table 6)

There are twenty-two semilunars recognized in the collection. The semilunar is stretched anteroposteriorly and appears rather trapezoidal shape with the wider proximal border in dorsal view. The distal border is transversely blunt in dorsal view. The facet for the ulna is visible in dorsal view. The proximo-medial corner of the anterior wall is strongly protruding medially.

Pyramidal (Figures 9, Table 7)

Table 8. Measurements (mm) of magnums and uncinates. See Appendix 2 for abbreviations.

Magnum

	H	l	L	H art.
Udg-906	73.2	53.8	-	74.9
Udg-907	76.7	52.0	98.5	77.1
Udg-908	81.6	53.3	-	86.6
Udg-909	-	59.3	105.4	-
Udg-910	66.6	52.6	-	76.3
Udg-911	72.9	58.9	-	83.8
Udg-985	81.3	57.2	-	82.6
Udg-990	85.4	-	-	62.3
Udg-1005	82.9	58.1	114.4	85.3
Udg-1010	75.6	59.0	-	74.4
Udg-1714	-	55.6	-	-
Udg-1715	78.0	56.2	-	-
Udg-1716	78.0	60.4	-	-
Udg-1747	-	52.8	-	-
Udg-1820	-	56.4	-	-
Udg-1831	72.0	54.1	-	-
Udg-1832	ca 69	ca 46	-	-
Udg-1900	-	51.1	-	-
N	*12*	*16*	*3*	*9*
Mean	*77.0*	*55.7*	*106.1*	*78.1*
St. Dev.	*5.34*	*2.94*	*7.97*	*7.54*

Uncinate

	H	l	L anat.	L abs.
Udg-251	63.1	81.0	92.4	105.9
Udg-252	61.3	80.2	86.6	102.4
Udg-826	61.7	75.6	90.6	99.6
Udg-828	60.0	77.3	88.0	102.5
Udg-829	61.9	76.7	90.3	103.7
Udg-830	59.4	79.8	92.4	101.3
Udg-831	58.9	80.0	90.8	103.2
Udg-832	55.1	73.8	84.0	93.4
Udg-836	58.0	78.5	-	-
Udg-838	59.5	78.6	-	-
Udg-840	57.5	78.4	-	-
Udg-842	58.3	77.9	-	-
Udg-866	69.1	78.5	-	-
Udg-869	66.8	82.1	-	-
Udg-870	69.1	86.4	-	-
Udg-887	62.9	83.9	-	-
Udg-888	62.2	81.0	-	-
Udg-889	61.9	84.3	-	-
Udg-893	58.6	77.1	-	-
Udg-894	59.0	77.4	-	-
Udg-912	62.9	88.7	-	-
Udg-913	-	84.2	91.4	105.8
Udg-914	60.2	79.0	-	-
Udg-915	54.3	77.5	-	-
Udg-916	62.3	82.2	-	-
Udg-921	60.2	82.7	85.4	95.8
Udg-960	52.4	70.7	81.3	92.9
Udg-978	60.4	76.4	87.4	100.7
Udg-1793	58.9	84.0	-	-
Udg-1947	58.1	76.0	-	-
N	*29*	*30*	*12*	*12*
Mean	*60.5*	*79.7*	*88.4*	*100.6*
St. Dev.	*3.74*	*3.83*	*3.55*	*4.41*

Nineteen specimens of the pyramidal are kept at the center. In medial view the proximal facet for the semilunar has a valiability on its anteroposterior length. It terminates at the middle of the proximo-medial border of the bone in five materials. The distal facet for the semilunar continues to the posterior tuberosity. It has a depression on the proximal border of the facet in fourteen.

Pisiform (Table 7)

Only one pisiform was available to us. It is almost completely preserved and appears a pear-shaped.

Trapezium (Table 7)

We could examine only one material of the trapezium. It is the smallest bone in the carpals.

Trapezoid (Figures 9, Table 7)

There are seven trapezoids recognized in the collection. The trapezoid is rather prismatic

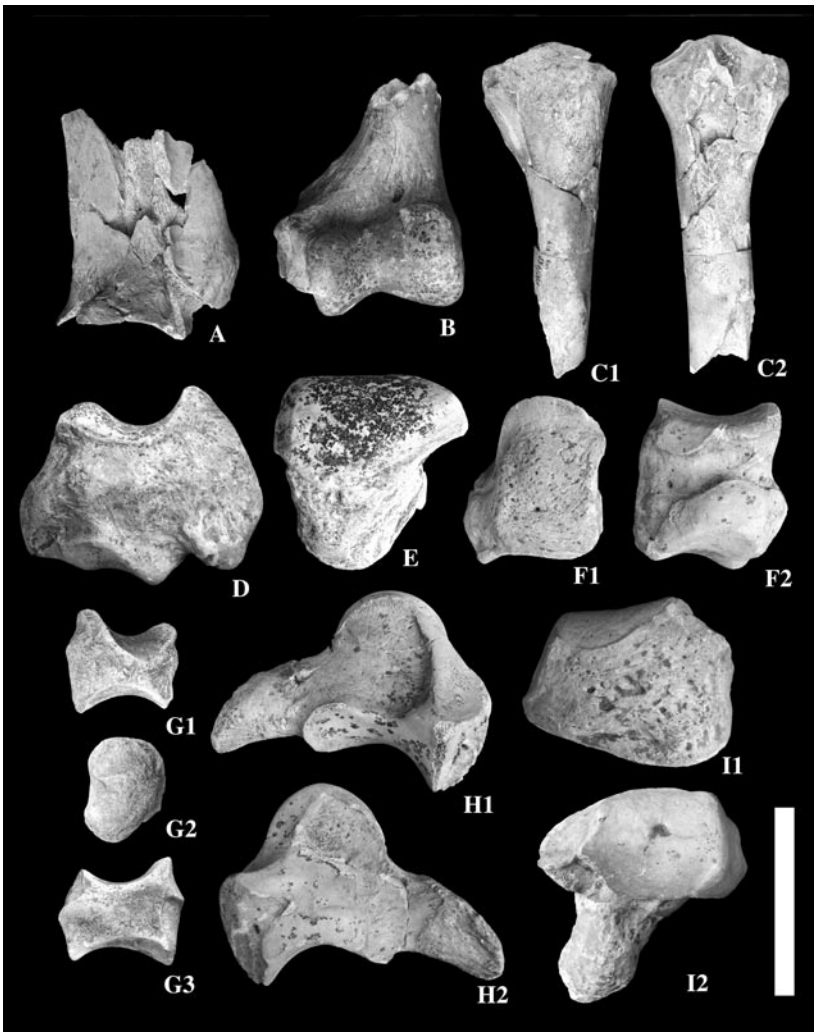

Figure 9. Forelimb fragments. **A**, Udg-1812, a distal end of the scapula, lateral view. **B**, Udg-265, a distal end of the humerus, anterior view. **C**, Udg-814, a proximal part of the radius: **C1**, anterior view; **C2**, posterior view. **D**, Udg-856, scaphoid, lateral view. **E**, Udg-833, semilunar, dorsal view. **F**, Udg-902, pyramidal: **F1**, dorsal view; **F2**, medial view. **G**, 903, trapezoid: **G1**, medial view; **G2**, dorsal view; **G3**, lateral view. **H**, Udg-1005, a magnum: **H1**, lateral view; **H2**, medial view. **I**, Udg-830, uncinate, **I1**, dorsal view; **I2**, distal view. Scale bar equals 5 cm. Scale bar for A- C equals 10 cm and for D – I equals 5 cm.

in dorsal view. The proximal articular surface is more concave than the distal one.

Magnum (Figures 9, Table 8)

We could observe eighteen materials of the magnum. It appears an anteroposteriorly long form with a thumb-like posterior projection. In dorsal view the distal border of the anterior wall is smoothly convex distally in six of ten obeservable materials. In medial view a notch between the facets for the trapezoid and the second metacarpal is deep. The posterior end of the proximal articular surface is not overhung.

Uncinate (Figures 9, Table 8)

There are thirty specimens of the uncinate, including sixteen left ones and fourteen right ones. It is the most abundant skeletal element in the fossil rhinoceros materials from Udunga. The uncinate is a massive bone with a thumb-like posterior projection like the magnum. In dorsal view the facet for the pyramidal is visible in all examined specimens. Proximally the facet appears a quadrangular shape.

Figure 10. Metapodials in dorsal view. **A**, Udg-219, a right third metacarpal. **B**, Udg-220a, a left third metacarpal. **C**, Udg-970, a right third metacarpal. **D**, Udg-988, a proximal part of the left third metacarpal. **E**, Udg-220b, a left fourth metacarpal. **F**, Udg-231, a left fourth metacarpal. **G**, Udg-232, a right fourth metacarpal. **H**, Udg-807, a right fourth metacarpal. **I**, Udg-825, a left third metatarsal. Scale bar equals 10 cm.

II Metacarpal (Figure 10, Table 9)

We could observe seven specimens of the second metacarpal. There is no distal parts in the collection. In lateral view the facet for the third metacarpal terminates at the middle of the proximo-lateral border of the bone in three. In proximal view the bone appears rather a triangular shape. The facet for the trapezium is absent.

III Metacarpal (Figures 10, Table 9)

We could examine eleven materials of the third metacarpal. The third metacarpal is proximodistally long and straight. The shaft is somewhat widened distally. The facet for the magnum is visible in all specimens examined in dorsal view. Its articular surface is deep in three materials. In lateral view the facet for the fourth metacarpal is anteroposteriorly separated.

IV Metacarpal (Figures 10, Table 9)

Table 9. Measurements (mm) of metacarpals. See Appendix 2 for abbreviations.

IIMc

	BP	DP	BPa	BS	DS
Udg-238	56.4	45.3	48.0	-	-
Udg-241	52.4	44.3	42.9	36.2	22.3
Udg-242	56.7	47.2	46.3	-	-
Udg-273	49.5	39.2	31.9	34.3	21.0
Udg-951	55.1	47.1	51.1	43.1	25.2
Udg-952	54.2	47.5	46.8	44.7	21.7
Udg-954	58.1	51.9	49.8	-	-
N	*7*	*7*	*7*	*4*	*4*
Mean	*54.63*	*46.07*	*45.26*	*39.58*	*22.55*
St. Dev.	*2.920*	*3.858*	*6.452*	*5.096*	*1.845*

IIIMc

	L	BP	DP	BS	DS	BD	DD	BDa
Udg-219a	234.2	68.5	58.2	63.4	24.4	77.3	54.3	60.1
Udg-220a	230.3	65.3	54.0	58.6	25.7	72.5	53.9	55.5
Udg-266	-	67.7	56.1	-	-	-	-	-
Udg-801	-	67.6	56.1	64.0	26.5	-	-	-
Udg-806	-	66.3	53.9	-	-	-	-	-
Udg-810	-	67.0	54.1	-	-	-	-	-
Udg-867	-	58.0	49.6	-	-	-	-	-
Udg-872	-	62.2	44.5	54.7	23.7	-	-	-
Udg-949	-	-	55.3	-	-	-	-	-
Udg-970	232.0	69.9	55.5	65.0	24.8	75.5	57.1	60.1
Udg-988	-	58.5	52.5	50.8	23.0	-	-	-
Udg-1765	-	65.1	55.2	-	-	-	-	-
N	*3*	*11*	*12*	*6*	*6*	*3*	*3*	*3*
Mean	*232.00*	*62.74*	*52.10*	*56.83*	*23.83*	*75.50*	*57.10*	*60.10*
St. Dev.	*1.955*	*3.938*	*3.605*	*5.748*	*1.283*	*2.425*	*1.744*	*2.656*

IVMc

	L	BP	DP	BS	DS	BD	DD	BDa
Udg-219b	-	48.2	44.0	-	-	-	-	-
Udg-220b	-	-	-	39.6	24.0	41.6	48.6	-
Udg-231	187.7	53.5	39.5	41.4	23.1	48.2	52.3	40.6
Udg-232	181.1	53.2	39.5	38.8	28.2	46.9	49.8	38.3
Udg-237	-	45.3	45.9	-	-	-	-	-
Udg-239	-	55.3	46.8	44.3	23.5	-	-	-
Udg-268	-	51.6	45.6	-	-	-	-	-
Udg-807	194.4	52.0	52.4	40.1	23.6	43.8	51.9	-
Udg-811	-	59.0	51.2	-	-	-	-	-
Udg-812	-	57.6	46.1	-	-	-	-	-
Udg-885	-	47.3	46.7	-	-	-	-	-
Udg-904	-	49.2	52.2	-	-	-	-	-
Udg-1796	-	42.0	44.8	38.9	19.7	-	-	-
Udg-1797	-	-	47.7	-	-	-	-	-
Udg-1808	-	67.3	53.2	-	-	-	-	-
Udg-1817	-	51.6	40.0	-	-	-	-	-
N	*3*	*14*	*15*	*6*	*6*	*4*	*4*	*2*
Mean	*187.71*	*52.36*	*46.37*	*40.52*	*23.68*	*45.13*	*50.65*	*39.45*
St. Dev.	*6.660*	*6.305*	*4.522*	*2.082*	*2.711*	*2.988*	*1.752*	*1.626*

Fifteen specimens of the fourth metacarpal are kept in the collection. The fourth metacarpal appears disto-laterally arched in dorsal view. The proximal articular surface is slightly transversely concave. In proximal view the anterior border of the proximal facet is rather flat and the posterior one is pointed posteriorly. The proximal facet has a shorter anterior border and longer medial border.

Femur (Figure 11, Table 10)

Table 10. Measurements (mm) of femora, patellae, tibiae, and fibulae. See Appendix 2 for abbreviations.

Femur

	BC	DC	BD	DD	BT
Udg-881	96.0	101.4	-	-	-
Udg-1019	-	-	130.6	137.8	-
Udg-1741	-	-	-	-	101.1
Udg-1824	91.9	85.9	-	-	-
Udg-1823	-	-	-	-	89.6
Udg-1838	-	-	-	-	106.1
Udg-1974	-	-	-	-	97.0
N	*2*	*2*	*1*	*1*	*4*
Mean	*94.0*	*93.7*	*(130.6)*	*(137.8)*	*98.5*
St. Dev.	-	-	-	-	*6.98*

Patella

	H	DT
Udg-961	125.7	94.7
Udg-965	117.0	92.8
N	*2*	*2*
Mean	*121.4*	*93.8*
St. Dev.	-	-

Tibia

	BS	DS	BD	DD	DDa
Udg-260	-	-	98.8	93.5	84.5
Udg-871	-	-	115.3	91.4	70.0
Udg-917	-	-	90.3	75.6	78.5
Udg-997	74.1	60.4	106.7	85.7	78.8
Udg-1018	64.3	47.9	-	-	-
Udg-1806	-	-	-	-	-
Udg-1809	67.0	54.0	96.0	67.0	73.5
Udg-1855	-	-	103.0	94.0	76.7
Udg-1869	-	-	97.0	74.7	70.0
Udg-1883	54.3	59.5	-	-	-
Udg-1884	77.4	59.5	-	-	-
Udg-1885	61.5	55.6	-	-	-
Udg-1899	57.1	56.1	-	-	-
Udg-1946	72.7	66.6	-	-	-
N	*8*	*8*	*7*	*7*	*7*
Mean	*66.1*	*57.5*	*101.0*	*83.1*	*76.0*
St. Dev.	*8.29*	*5.47*	*8.18*	*10.71*	*5.25*

Tibia(Juvenile)

	BS	DS	BD	DD	DDa
Udg-1918	44.1	41.8	79.6	-	71.2

Fibula

	BS	DS	BD	DD	DDa
Udg-1806	-	-		49.9	21.7
Udg-1864	-	-		56.7	29.1
Udg-1866	19.7	21.6		52.5	24.6
Udg-1919	-	-		47.6	23.7
Udg-1926	-	-		46.4	18.6
Udg-1957	-	-		45.0	24.3
Udg-1959	-	-		50.1	20.9
N	*1*	*1*		*7*	*7*
Mean	*(19.7)*	*(21.6)*		*49.7*	*23.3*
St. Dev.	-	-		*3.97*	*3.34*

The femora stored in the center are all fragmentary specimens. Two materials of the femoral head were identified. It is hemispherical and has a relatively shallow *fovea capitis*. Only one distal ends of the right femur is kept in the collection. The distal lateral epiphysis protrudes more strongly than does the medial one. The trochlea trough is rather shallow. There are four femoral shafts recognized.

Patella (Figure 11, Table 10)

There are three patellae in the collection. The bone appears roughly trapezoidal in anterior view. The distal border protrudes distally.

Tibia (Figure 11, Table 10)

We could examine thirteen specimens of the tibia, including eight distal ends and five shafts. There is no proximal parts of the tibia recognized. In distal view the medial articular surface is deep and the lateral one is transversely wide.

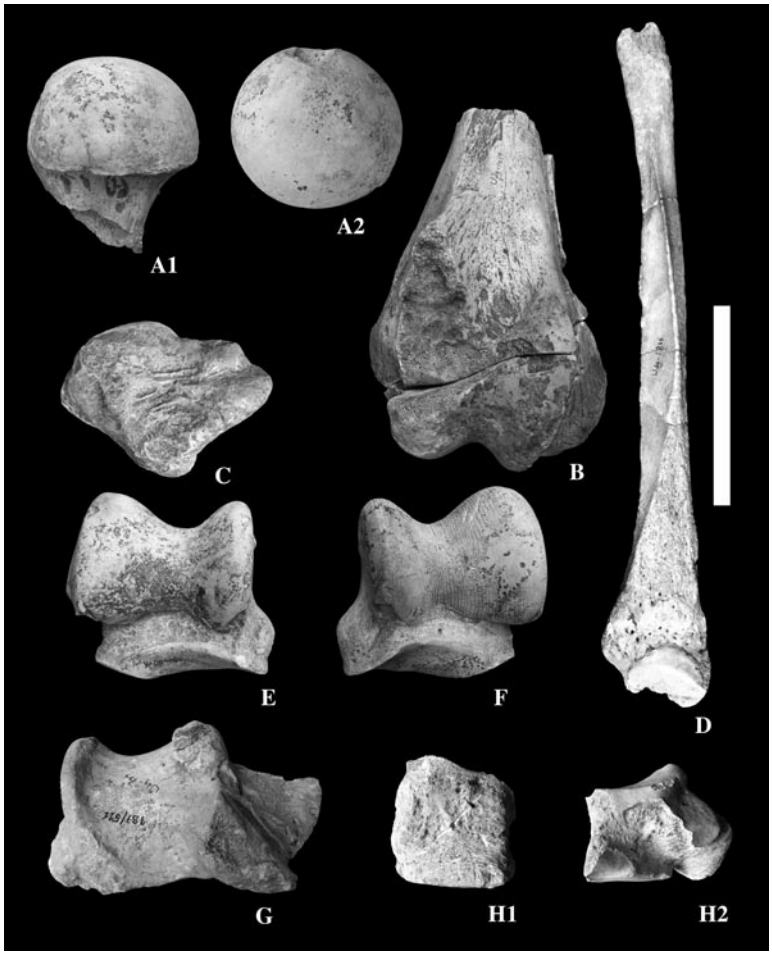

Figure 11. Hindlimbs. **A**. Udg-881, a head of the femur: **A1**, posterior view; **A2**, proximal view. **B**, Udg-1019, a distal end of the femur, anterior view. **C**, Udg-965, patella, anterior view. **D**, Udg-1866, a distal part of the fibula, medial view. **E**, Udg-229, astragalus, dorsal view. **F**, Udg-230, astragalus, dorsal view. **G**, Udg-989, calcaneum, medial view. **H**, Udg-245, cuboid: **H1**, dorsal view; **H2**, medial view. Scale bar equals 10 cm.

Fibula (Figure 11, Table 10)

There are seven specimens of the fibula in the collection, however their proximal parts are not recognized. The distal facet for the ulna appears a semicircular shape. The fibulae were not fused with the tibiae.

Astragalus (Figures 11, Table 11)

Twenty-four astragali were identified. The trochlea of the astragalus has a broad and deep trough. It is assymetrical and the lateral lip is much larger than the medial one. A tubercle on the medial wall of the *caput tali* is slightly protruding. In distal view the facet for the navicular is broad and rhomboidal. The facet for the cuboid appears rather a rectangular shape.

Calcaenum (Figures 11, Table 11)

We could observe seventeen materials of calcaneum, including four juvenile ones. The calcaenum is a massive bone like the astragalus. In both medial and lateral view the tuberosity summit appears an anteroposteriorly bilobed shape. The posterior summit is protruding stronger than the anterior one. The bone has a weakly concave posterior border.

Table 11. Measurements (mm) of astragali and calcanei. See Appendix 2 for abbreviations.

Astragalus

	H	DL	DT	DT max.dist.	DT art.	DDa
Udg-221	100.3	66.3	101.9	83.0	-	52.2
Udg-222	101.7	70.3	108.0	91.5	-	57.3
Udg-223	101.1	73.8	110.4	90.5	86.3	58.2
Udg-224	98.3	71.2	-	89.8	>78	49.7
Udg-225	101.3	72.3	112.3	92.1	91.1	56.8
Udg-226	89.6	71.0	-	107.6	-	53.7
Udg-227	96.6	61.0	99.9	87.1	85.5	54.6
Udg-228	98.5	68.9	105.3	87.9	85.3	59.7
Udg-229	101.6	68.7	109.8	92.0	88.0	53.2
Udg-230	106.2	66.9	104.9	93.0	89.7	55.2
Udg-882	104.7	63.3	101.4	89.2	85.0	49.7
Udg-897	-	70.3	-	-	-	-
Udg-987	80.3	70.5	-	79.1	77.1	59.9
Udg-999	95.5	69.9	-	-	-	-
Udg-1000	100.5	72.2	112.1	-	92.1	56.3
Udg-1756	95.0	61.8	-	-	-	49.0
Udg-1829	-	-	-	82.8	80.8	48.5
Udg-1905	98.3	-	-	-	-	40.0
Udg-1906	98.7	59.3	-	79.0	-	50.2
Udg-1907	92.0	-	-	92.4	88.9	53.3
Udg-1908	108.0	77.0	108.0	79.0	-	53.6
Udg-1909	107.0	-	-	-	-	52.0
Udg-1948	-	-	-	-	75.2	51.4
Udg-1975	101.0	-	-	-	-	-
N	*21*	*18*	*11*	*16*	*12*	*21*
Mean	*98.9*	*68.6*	*106.7*	*88.5*	*85.4*	*53.1*
St. Dev.	*6.26*	*4.69*	*4.36*	*7.19*	*5.31*	*4.53*

Calcaneum

	DAP somm.	DAP beak	H	DT somm.	DT min.	DT sust.
Udg-877	73.3	78.6	154.4	57.3	41.5	-
Udg-938	76.8	76.6	163.2	53.9	42.9	84.3
Udg-989	82.0	82.6	157.5	56.2	40.1	91.9
Udg-992	81.6	74.3	147.7	52.1	36.1	79.9
Udg-1020	73.0	79.2	160.0	55.4	40.6	92.8
Udg-1841	79.0	68.0	142.0	57.8	39.8	-
Udg-1826	-	66.6	-	-	-	88.6
Udg-1840	-	57.1	>123	-	36.4	71.3
Udg-1893	-	67.4	-	-	41.7	-
Udg-1933	75.8	61.0	-	54.2	39.5	-
Udg-1936	78.4	-	-	53.5	-	-
Udg-1951	77.6	-	-	61.2	-	-
Udg-1968	80.8	74.0	-	54.7	41.4	90.0
N	*10*	*11*	*6*	*10*	*10*	*7*
Mean	*77.8*	*71.4*	*154.1*	*55.6*	*40.0*	*85.5*
St. Dev.	*3.18*	*8.02*	*7.96*	*2.62*	*2.22*	*7.73*

Calcaneum(Juvenile)

	DAP somm.	DAP beak	H	DT somm.	DT min.	DT sust.
Udg-1760	-	63.4	-	-	38.1	79.6
Udg-1761	-	60.9	-	-	35.3	65.0
Udg-1762	-	71.1	>118	-	41.8	73.0
Udg-1911	75.7	66.1	-	-	39.8	-
N	*1*	*4*			*4*	*3*
Mean	*(75.7)*	*65.4*			*38.8*	*72.5*
St. Dev.	-	*4.37*			*2.75*	*7.31*

In dorsal view the *sustentaculum tali* is rather transversely long and curved slightly distally. Four juvenile materials were excluded from the ratio diagrams.

Navicular (Figure 11, Table 12)

We could observe eleven specimens of navicular. It is a proximodistally flat and transversely wide bone.

Cuboid (Figures 11, Table 12)

There are twenty-two specimens of the cuboid in the collection. The cuboid appears a solid cube with the posterior apophysis that protrudes weakly distally.

I Cuneiform

It is absent in the collection.

II Cuneiform (Table 12)

Only one material of the second cuneiform was available. It is a small flat bone.

III Cuneiform (Figure 11, Table 12)

Table 12. Measurements (mm) of cuboids, naviculars, second cuneiforms, and third cuneiforms. See Appendix 2 for abbreviations.

Cuboid

	H	H ant.	L	l	l art.	DPa
Udg-245	66.9	56.2	77.4	51.5	50.3	-
Udg-246	70.4	54.0	71.5	49.7	48.3	-
Udg-247	65.7	54.0	78.0	50.4	56.8	-
Udg-248	67.4	48.5	67.2	48.8	56.7	-
Udg-289	64.8	54.0	85.9	49.2	56.3	-
Udg-290	63.3	51.4	69.5	47.5	48.2	-
Udg-291	64.4	53.8	72.3	46.5	47.8	-
Udg-292	58.9	51.8	68.8	42.2	44.0	-
Udg-837	68.3	54.6	78.2	44.2	44.5	47.8
Udg-843	58.5	50.1	70.3	43.8	40.1	46.2
Udg-844	60.0	51.0	-	48.4	48.5	57.0
Udg-862	67.3	48.8	74.8	46.3	51.7	-
Udg-863	64.5	47.4	71.6	>50	50.5	-
Udg-890	65.8	50.6	69.0	40.6	45.2	-
Udg-891	64.4	50.1	68.4	40.6	42.0	-
Udg-892	65.5	48.6	68.5	-	41.7	-
Udg-930	68.6	52.5	78.8	50.9	51.5	-
Udg-933	-	49.0	-	48.0	-	-
Udg-981	70.1	48.9	-	54.8	51.9	48.0
Udg-1017	66.4	50.4	70.2	-	-	-
Udg-1888	-	47.2	-	50.2	45.5	-
Udg-1890	-	48.7	-	57.5	54.7	-
N	*19*	*22*	*17*	*19*	*20*	*4*
Mean	*65.3*	*51.0*	*73.0*	*48.0*	*48.8*	*49.8*
St. Dev.	*3.36*	*2.56*	*5.10*	*4.43*	*5.06*	*4.90*

Navicular

	H	l	L
Udg-857	35.7	58.4	67.5
Udg-858	31.6	58.0	73.2
Udg-861	33.3	67.6	77.7
Udg-864	27.4	58.7	65.3
Udg-865	34.2	63.4	74.8
Udg-975	39.6	62.9	77.9
Udg-1025	35.1	61.9	77.8
Udg-1755	33.8	56.8	-
Udg-1811	33.4	67.0	63.1
Udg-1886	35.4	60.0	70.5
Udg-1927	33.7	57.4	76.4
N	*11*	*11*	*10*
Mean	*33.9*	*61.1*	*72.4*
St. Dev.	*2.96*	*3.77*	*5.52*

II Cuneiform

	H	l	L
Udg-809	26.8	53.5	53.2

III Cuneiform

	H	l	L
Udg-283	28.0	57.7	54.7
Udg-284	32.7	57.8	60.2
Udg-285	30.6	54.5	58.5
Udg-859	35.2	58.6	62.6
Udg-940	33.9	60.6	66.6
Udg-958	28.3	51.3	59.7
Udg-971	28.3	57.8	64.3
Udg-973	29.8	55.1	56.3
Udg-1011	31.1	52.8	55.0
N	*9*	*9*	*9*
Mean	*30.9*	*56.2*	*59.8*
St. Dev.	*2.60*	*3.00*	*4.15*

We could observe nine materials of the third cuneiform. The third cuneiform is proximodistally flat and transversely wide. In both proximal and distal view it appears a L-shaped.

II Metatarsal (Table 13)

There are five second metatarsals in the collection. Three specimens preserve only their proximal parts. In dorsal view the proximal articular surface appears a crescent shape.

III Metatarsal (Figures 10, Table 13)

We could observe sixteen materials of the third metatarsal. Eleven specimens are just proximal parts. Udg-825, the complete third metatarsal, has a slightly curved shaft. The proximal articular surface is rather straight in dorsal view. In proximal view the facet for the third cuneiform appears a L-shaped, corresponding to the facet in the cuboid.

IV Metatarsal (Table 13)

Table 13. Measurements (mm) of metatarsals. See Appendix 2 for abbreviations.

IIMt

	L	BP	DP	BPa	BS	DS	BD	DD	BDa
Udg-905	-	33.3	50.8	-	-	-	-	-	-
Udg-956	-	37.7	50.4	33.2	-	-	-	-	-
Udg-996	189.0	37.9	50.9	25.5	33.4	32.5	44.1	45.5	39.3
Udg-1795	-	38.5	50.3	-	-	-	-	-	-
Udg-1932	-	37.7	48.9	27.1	31.7	-	-	-	-
N	*1*	*5*	*5*	*3*	*2*	*1*	*1*	*1*	*1*
Mean	*-189*	*37.02*	*50.26*	*28.60*	*32.55*	*(32.5)*	*(44.1)*	*(45.5)*	*(39.3)*
St. Dev.	-	*2.105*	*0.802*	*4.063*	*1.202*	-	-	-	-

IIIMt

	L	BP	DP	BPa	BS	DS	BD	DD	BDa
Udg-233	-	64.5	-	-	57.7	27.5	-	-	-
Udg-1785	-	58	43	-	-	-	-	-	-
Udg-995	-	59.7	47.7	-	50.5	25.1	-	-	-
Udg-825	212.4	62.5	50.5	-	57.7	27.9	68.2	47.5	58.2
Udg-955	-	64.4	49.5	-	-	-	-	-	-
Udg-803	-	63	50.9	-	-	-	-	-	-
Udg-234	-	63.6	51.3	-	-	-	-	-	-
Udg-802	-	64.5	52.2	-	-	-	-	-	-
Udg-1012	-	70.7	49.9	-	-	-	-	-	-
Udg-240	-	50.4	45.7	-	42.6	24.2	-	-	-
Udg-267	-	58.2	50.9	-	-	-	-	-	-
Udg-805	-	62.2	59.8	-	-	-	-	-	-
Udg-959	-	61.5	53.9	-	-	-	-	-	-
Udg-994	-	61.3	58.8	-	-	-	-	-	-
Udg-1807	-	60.3	53.8	-	-	-	-	-	-
Udg-1986	-	61.8	54.2	-	-	-	-	-	-
N	*1*	*16*	*15*	-	*4*	*4*	*1*	*1*	*1*
Mean	*(212.4)*	*61.66*	*51.47*	-	*52.13*	*26.18*	*(68.2)*	*(47.5)*	*(58.2)*
St. Dev.	-	*4.242*	*4.389*	-	*7.200*	*1.806*	-	-	-

IVMt

	L	BP	DP	BPa	BS	DS	BD	DD	BDa
Udg-235	-	53.1	45.2	-	-	-	-	-	-
Udg-236	-	55.8	47	-	-	-	-	-	-
Udg-269	-	48.2	41.5	-	-	-	-	-	-
Udg-270	-	48.7	42.6	-	-	-	-	-	-
Udg-271	-	57.4	41.4	-	-	-	-	-	-
Udg-884	-	56.7	44.7	-	-	-	-	-	-
Udg-953	-	49.5	42.7	-	33.6	26.6	-	-	-
N	-	*7*	*7*	-	*1*	*1*	-	-	-
Mean	-	*52.77*	*43.59*	-	*(33.6)*	*(26.6)*	-	-	-
St. Dev.	-	*3.965*	*2.097*	-	-	-	-	-	-

Six materials of the fourth metatarsal were identified. There is no distal parts of the fourth metatarsal in the collection. The proximal lateral tuberosity is protruding laterally, but a considerable variation was recognized in its anteroposterior length. In dorsal view the facet for the cuboid appears a subtriangular shape.

Fragmentary central metapodial (Table 14)

There are six materials of the shaft of the central metapodial. They are straight and transversely wide. Seven distal ends of the central metapodial are also recognized in the collection. They are transversely broad and symmetrical in dorsal view.

Fragmentary lateral metapodial (Table 14)

Table 14. Measurements (mm) of fragmentary metapodials. See Appendix 2 for abbreviations.

Fragmentary central metapodial

	BS	DS	BD	DD	BDa
Udg-868	-	-	-	63.7	60.7
Udg-896	-	-	77.1	56.9	56.3
Udg-1013	-	-	-	58.2	49.4
Udg-1727	51.0	24.4	-	-	-
Udg-1728	50.8	25.4	-	-	-
Udg-1768	64.0	24.5	-	-	-
Udg-1771	54.4	29.0	-	-	-
Udg-1839	-	-	-	55.7	47.3
Udg-1876	51.5	24.3	-	-	-
Udg-1916	-	-	-	54.8	49.4
Udg-1917	50.7	24.9	-	-	-
Udg-1929	-	-	71.3	53.0	52.4
Udg-1930	-	-	-	52.1	50.2

Fragmentary lateral metapodial

	BP	DP	BS	DS	BD
Udg-272	47.1	41.5	25.9	-	41.1

Fragmentary miscellaneous metapodial

	BP	DP	BS	DS	BD
Udg-1732	-	-	36.5	21.2	-
Udg-1774	-	-	38.1	23.9	-
Udg-1783	-	-	43.6	23.9	-

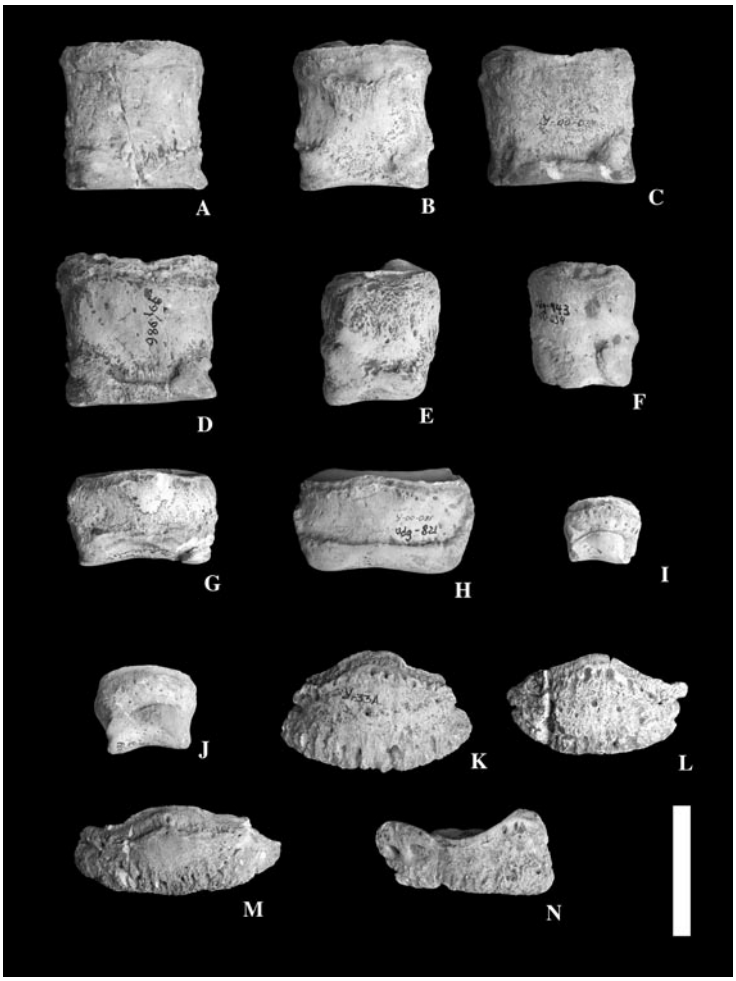

Figure 12. Phalanges in dorsal view. **A**, Udg-275, central proximal phalange. **B**, Udg-276, central proximal phalange. **C**, Udg-816, central proximal phalange. **D**, Udg-817, central proximal phalange. **E**, Udg-277, lateral proximal phalange. **F**, Udg-943, lateral proximal phalange. **G**, Udg-820, central middle phalange. **H**, Udg-821, central middle phalange. **I**, Udg-944, lateral middle phalange. **J**, Udg-1298, lateral middle phalange. **K**, Udg-823, central distal phalange. **L**. Udg-875, central distal phalange. **M**, Udg-879, central distal phalange (robust form). **N**, Udg-874, lateral distal phalange. Scale bar equals 5 cm.

Udg-272 preserves only the antero-proximal part of the lateral metapodial. The anteroposterior diameter of the shaft is longer than the transverse diameter.

Fragmentary miscellaneous metapodial (Table 14)

Three shafts of the miscellaneous metapodial are kept in the collection. The transverse

Table 15. Measurements (mm) of phalanges. See Appendix 2 for abbreviations.

Central proximal

	GL	BP	BFP	DP	BD
Udg-256	54.1	64.6	60.6	48.2	59.0
Udg-274	53.0	57.2	55.2	39.8	49.1
Udg-257	49.0	60.7	56.2	44.4	58.9
Udg-258	49.6	61.3	53.6	43.0	57.8
Udg-275	55.4	58.3	54.1	40.2	51.6
Udg-276	53.4	54.4	49.6	40.4	50.5
Udg-796	51.2	55.9	54.7	37.3	50.8
Udg-797	53.1	62.7	56.1	44.0	47.9
Udg-816	50.0	60.4	60.4	43.9	58.5
Udg-817	52.7	64.1	64.1	49.0	56.7
Udg-847	48.8	-	-	46.1	53.3
Udg-848	53.6	54.5	52.1	40.9	-
Udg-934	50.3	57.4	48.1	43.4	-
Udg-936	-	65.4	58.9	46.6	-
Udg-937	-	63.9	56.8	42.7	-
Udg-945	55.7	59.7	56.3	39.1	50.1
Udg-947	53.1	66.9	61.8	49.6	60.0
Udg-983	58.0	57.6	53.6	43.7	51.7
Udg-984	54.1	64.7	59.8	44.4	58.5
Udg-1001	-	61.9	57.3	41.6	-
Udg-1002	48.2	62.4	57.7	47.2	-
Udg-1016	56.0	53.8	52.3	41.3	52.1
Udg-1023	47.6	64.0	55.0	50.6	54.0
Udg-2211	61.5	59.7	49.2	44.6	54.2
N	*21*	*23*	*23*	*24*	*18*
Mean	*52.8*	*60.5*	*55.8*	*43.8*	*54.2*
St. Dev.	*3.45*	*3.82*	*4.07*	*3.48*	*3.92*

Central middle

	GL	BP	BFP	DP	BD
Udg-795	38.2	64.8	54.6	32.6	54.6
Udg-819	35.5	61.7	54.8	28.7	56.2
Udg-820	37.3	61.9	53.6	30.8	54.3
Udg-821	39.0	71.6	64.3	35.2	66.9
Udg-935	-	61.4	58.1	46.0	-
Udg-946	42.6	70.1	61.8	32.5	67.6
N	*5*	*6*	*6*	*6*	*5*
Mean	*38.5*	*65.3*	*57.9*	*34.3*	*59.9*
St. Dev.	*2.63*	*4.53*	*4.36*	*6.12*	*6.73*

Central distal

	GL	BP	BD
Udg-818	27.0	56.6	84.9
Udg-823	49.5	56.4	81.5
Udg-846	37.9	54.6	-
Udg-849	40.7	69.0	-
Udg-853	39.5	48.8	-
Udg-873	40.1	54.6	83.6
Udg-875	41.0	51.9	76.3
Udg-876	41.2	67.3	104.7
Udg-942	40.6	57.3	92.9
N	*9*	*9*	*6*
Mean	*39.7*	*57.4*	*87.3*
St. Dev.	*5.77*	*6.65*	*10.08*

Lateral proximal

	GL	BP	BFP	DP	BD
Udg-277	55.6	46.0	38.7	43.1	42.8
Udg-278	56.2	42.6	36.0	43.3	40.7
Udg-279	50.8	44.8	40.0	44.1	39.6
Udg-280	50.7	46.5	35.7	43.0	40.9
Udg-883	52.0	46.4	38.3	44.0	46.3
Udg-927	47.0	45.9	34.9	45.9	39.4
Udg-928	50.1	41.6	34.8	41.3	-
Udg-932	50.1	42.3	36.6	45.3	40.6
Udg-941	59.8	45.0	35.3	43.5	36.9
Udg-964	53.7	45.5	38.2	44.8	42.4
Udg-1015	50.8	41.4	37.3	42.5	35.7
Udg-1996	49.7	37.7	31.7	42.7	35.2
Udg-1997	57.6	42.6	39.8	43.8	40.8
Udg-1998	50.0	44.9	33.8	45.0	38.0
Udg-2000	44.2	40.6	32.8	44.8	37.9
Udg-2201	49.3	40.1	35.4	43.2	35.7
Udg-2202	47.9	42.8	36.7	43.0	40.8
Udg-2203	46.0	46.8	36.5	48.6	43.1
Udg-2204	51.3	42.5	36.9	46.0	40.3
Udg-2206	55.4	47.2	37.9	48.6	42.4
Udg-2207	59.3	45.7	43.2	45.2	44.0
Udg-2208	47.7	39.4	32.8	44.7	36.0
Udg-2212	54.3	44.0	34.7	43.9	40.4
N	*23*	*23*	*23*	*23*	*22*
Mean	*51.7*	*43.6*	*36.4*	*44.4*	*40.0*
St. Dev.	*4.16*	*2.63*	*2.63*	*1.76*	*2.95*

Lateral middle

	GL	BP	BFP	DP	BD
Udg-259	43.4	48.6	46.9	41.4	39.4
Udg-281	38.9	39.8	35.5	33.7	34.1
Udg-798	37.8	40.8	36.8	33.6	35.5
Udg-799	41.7	46.5	39.6	37.7	41.3
Udg-851	46.7	47.4	36.1	40.8	30.6
Udg-929	45.0	45.0	42.9	30.5	35.1
Udg-944	33.2	36.4	32.4	33.3	33.8
Udg-963	46.4	47.2	40.5	39.2	37.1
Udg-1298	43.2	44.8	40.9	39.7	40.0
Udg-1994	42.0	44.7	39.5	39.2	38.6
Udg-2205	39.7	42.6	34.3	36.1	36.7
Udg-2210	32.6	39.4	35.3	33.4	35.0
Udg-2298	34.3	41.6	37.6	33.2	32.0
N	*13*	*13*	*13*	*13*	*13*
Mean	*40.4*	*43.4*	*38.3*	*36.3*	*36.1*
St. Dev.	*4.81*	*3.67*	*3.93*	*3.55*	*3.16*

Lateral distal

	GL	BP	BD
Udg-855	34.0	-	-
Udg-948	40.0	41.2	-
Udg-1003	34.7	39.8	-
Udg-1944	37.6	41.0	58.0
Udg-262	40.2	68.9	68.9
Udg-282	33.5	47.4	68.7
Udg-822	33.3	44.9	64.4
Udg-874	36.0	34.6	71.9
Udg-852	31.0	43.1	-
N	*4*	*4*	*4*
Mean	*35.8*	*49.0*	*68.5*
St. Dev.	*3.21*	*14.41*	*3.09*

diameters of the shaft are longer than the anteroposterior ones.

Central proximal phalange (Figure 12, Table 15)

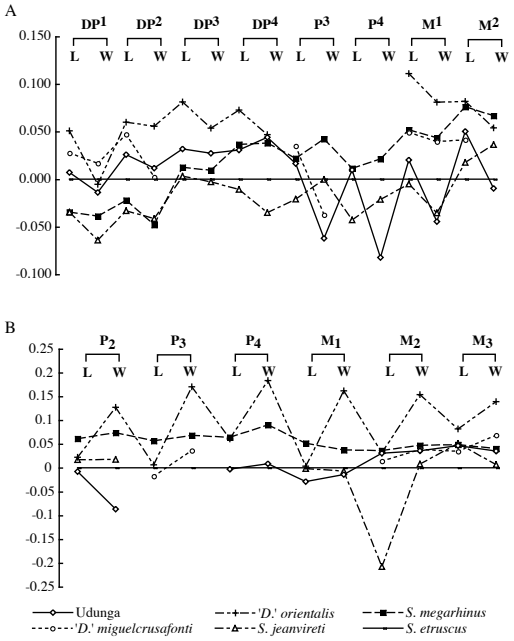

Figure 13. Ratio diagram of the dentitions of the rhinoceros from Udunga, '*D.*' *orientalis*, *S. megarhinus*, '*D.*' *miguelcrusafonti* and *S. jeanvireti* versus *S. etruscus* (standard). Data of '*D.*' *orientalis* are from Ringström (1924). Measurements of the last four species were taken from Guérin (1980). Data from table 3. **A**, upper dentitions. **B**, lower dentitions.

There are twenty-four central proximal phalanges recognized. It appears a solid cube. The transverse diameter decreases distally. The distal border is rather straight in both dorsal and plantar view. The distal articular surface is invisible in dorsal view.

Lateral proximal phalange (Figure 12, Table 15)

Twenty-three materials of the lateral proximal phalanges were available. The lateral proximal phalanges are more slender than the central ones. Like the central proximal phalange, the transverse diameter decreases distally. The distal border is slightly concave in both dorsal and plantar view.

Central middle phalange (Figure 12, Table 15)

Six central middle phalanges are kept in the collection. Like the central proximal phalange the central middle phalange appears rather cubic, and they are proximodistally short. The distal border is concave in both dorsal and plantar view. The distal facet is visible in dorsal view.

Lateral middle phalange (Figure 12, Table 15)

There are thirteen lateral middle phalanges recognized. The lateral middle phalanges are quite smaller than the central ones. The distal facet is visible in dorsal view. It is stretched to the distal half of the anterior wall.

Central distal phalange (Figure 12, Table 15)

Nine materials of the central distal phalanges were available. Six are broad, flat, and nearly symmetrical. They are nearly symmetrical and appear a proximodistally flat and

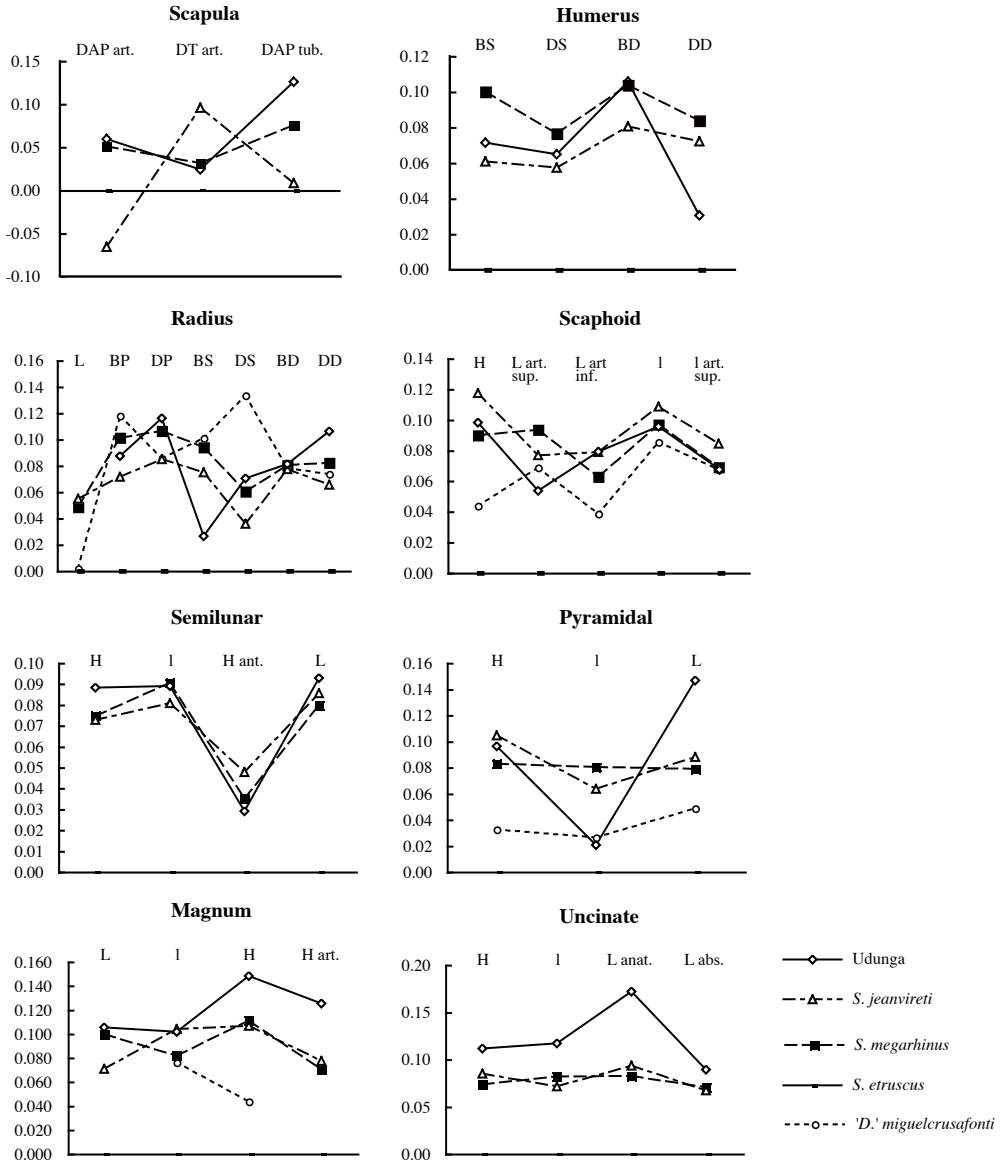

Figure 14. Ratio diagram of the skeletal elements of the forelimb of the rhinoceros from Udunga, *S. megarhinus*, '*D.*' *miguelcrusafonti* and *S. jeanvireti* versus *S. etruscus* (standard). Measurements of the last four species were taken from Guérin (1980). Data from table 4 - 8 (juvenile materials were excluded).

transversely wide shape.

Lateral distal phalange (Figure 12, Table 15)

There are nine materials of the lateral distal phalange recognized. The lateral distal phalange is an assymetrical bone with the rather straight distal border. The proximal articular surface is deeply concave.

Comparisons

The fossil rhinoceros from Udunga is assigned into the tribe Rhinocerotini based on the anteriorly expanded articulation between the ulna and semilunar, the dental characters such as

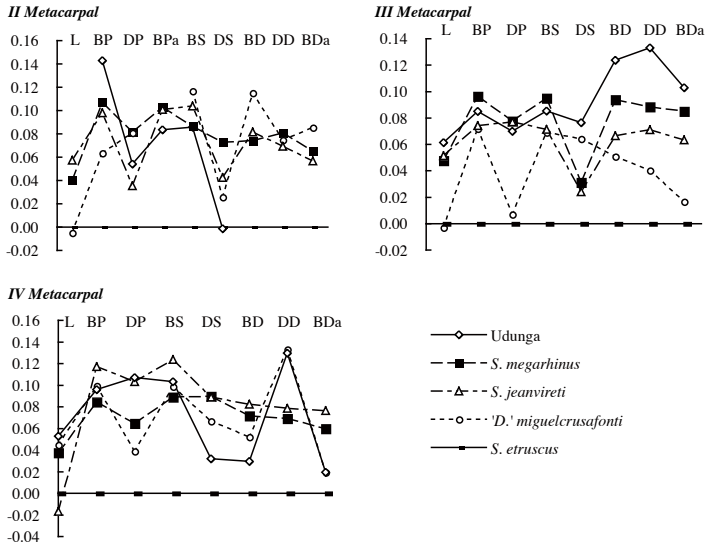

Figure 15. Ratio diagram of the metacarpals of the rhinoceros from Udunga, *S. megarhinus*, '*D.*' *miguelcrusafonti* and *S. jeanvireti* versus *S. etruscus* (standard). Measurements of the last four species were taken from Guérin (1980). Data from table 9.

the weakly conctricted protocones in upper cheek teeth, and the absence of the demarcation of the hypoconid in the lower molars (Heissig, 1973; Fortelius & Heissig, 1989). In addition to the dental morphologies and the geological ages, the non-functional incisor of the Udunga rhino leads us an idea that this species belongs to *Stephanorhinus* (Fortelius et al., 1993). Therefore, the comparisons were especially made with the Pliocene *Stephanorhinus* and some poorly known '*Dicerorhinus*' species.

Quantitative analysis for dental materials (Figure 13)

The dimensions of the deciduous teeth of the Udunga materials are intermediate between '*D.*' *orientalis* and *S. megarhinus*. Their patterns in the ratio diagram are similar to *S. megarhinus*. The upper permanent cheek teeth from Udunga are characterized by the relatively narrow buccolingual width. The mesiodistal length of premolars is similar to that of *S. megarhinus*. The molars of the Udunga materials are intermediate in the mesiodistal length between *S. megarhinus* and *S. jeanvireti*.

The lower premolars are small, which are similar in size to *S. etruscus*. However the lower molars, especially M_2 and M_3, are similar in dimensions and patterns to *S. megarhinus*.

Quantitative analyses for skeletal elements (Figure 14-17)

The quantitative analysis is not conducted for vertebrae because the exact position of the disarticulated vertebra is hardly identified. In the log ratio diagram of the scapula, the pattern of the Udunga rhino is very similar to that of *S. megarhinus*. But the anteroposterior diameter of the supraglenoid tubercle of the former species is longer that that of the latter. The dimensions of the humerus of the Udunga rhino are intermediate between *S. megarhinus*

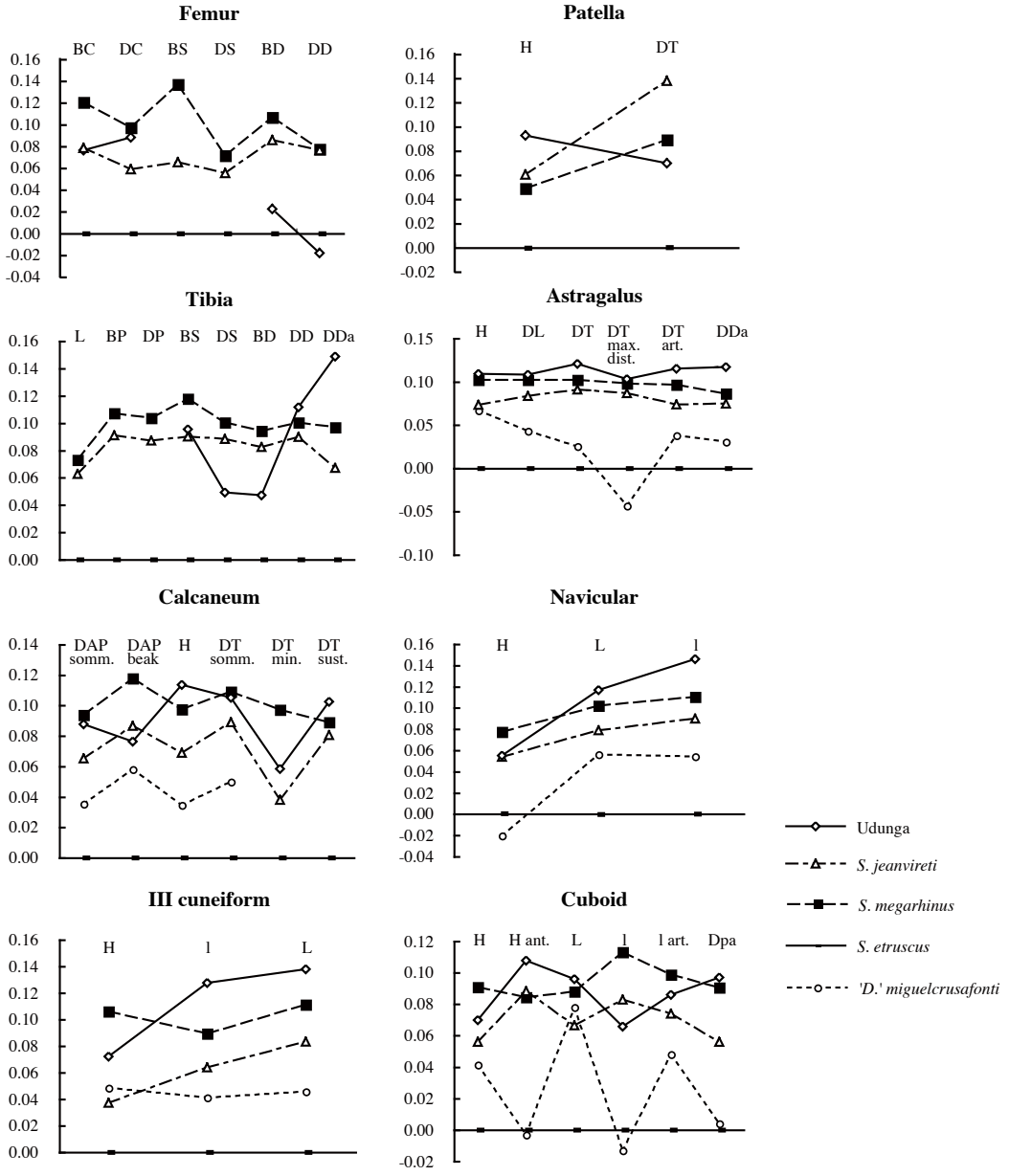

Figure 16. Ratio diagram of the skeletal elements of the hindlimb of the rhinoceros from Udunga, *S. megarhinus*, '*D.*' *miguelcrusafonti* and *S. jeanvireti* versus *S. etruscus* (standard). Measurements of the last four species were taken from Guérin (1980). Data from table 10-13.

and *S. jeanvireti*, except the anteroposterior diameter of the distal end. It is thinner than that of the latter two species. Compared with the radius of *S. megarhinus*, '*D*'. *miguelcrusafonti*, *S. jeanvireti*, and *S. struscus*, the diaphysis of the Udunga rhino is transversely narrower than the first three species, and its distal end is anteroposteriorly thicker than the species compared. The patterns of the scaphoid of the Udunga specimens in the ratio diagram are rather similar to those of *S. jeanvireti* than to those of *S. megarhinus*. The log ratio diagram of the semilunar does not indicate significant differences among *S. megarhinus*, *S. jeanvireti*, '*D.*' *miguelcrusafonti,* and the Udunga rhino. The pyramidal of the Udunga materials is more slender than that of *S. megarhinus*, *S. jeanvireti*, and '*D.*' *miguelcrusafonti*. The

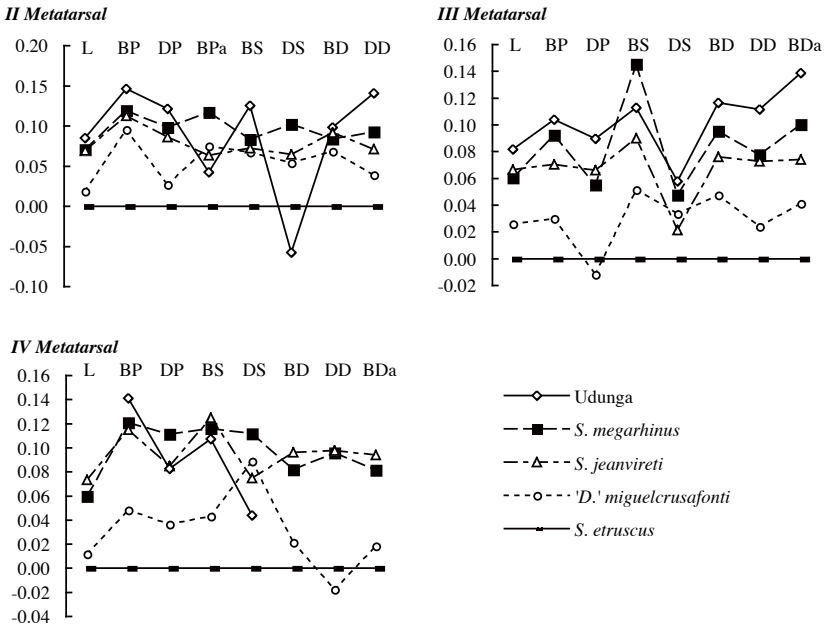

Figure 17. Ratio diagram of the metatarsal of the rhinoceros from Udunga, *S. megarhinus*, '*D.*' *miguelcrusafonti* and *S. jeanvireti* versus *S. etruscus* (standard). Measurements of the last four species were taken from Guérin (1980). Data from 14.

magnum and uncinate of the Udunga rhino is larger than *S. megarhinus*, *S. jeanvireti*, '*D.*' *miguelcrusafonti*, and *S. etruscus*. In the log ratio diagram, the patterns of these two bones suggest a similarity between *S. megarhinus* and the Udunga species. The second metacarpal of the Udunga rhino is different from that of the species compared in having the transversely wider proximal end and the anteroposteriorly thin diaphysis. Compared with the third metacarpal of *S. megarhinus*, *S. jeanvireti*, '*D.*' *miguelcrusafonti*, and *S. etruscus,* that of the Udunga rhino is similar to that of *S. megarhinus*, but the distal end of the former species is evidently larger than that of the other species. The fourth metacarpal of the Udunga rhino is rather similar to '*D.*' *miguelcrusafonti* than to that of the other species, but the proximal end of the former species is anteroposteriorly thicker than that of the other species in the comparison. The distal end of the femur of the Udunga materials is smaller than that of *S. megarhinus* and *S. jeanvireti*, and it is anteroposteriorly thinner than that of *S. etruscus*. Compared with *S. megarhinus* and *S. jeanvireti*, the patella of the Udunga rhino shows the opposite pattern in the ratio diagram. The diaphysis of the tibia of the Udunga specimens is anteroposteriorly thinner than that of *S. megarhinus* and *S. jeanvireti*, whereas the distal end of the former is anteroposteriorly thicker than that of the latters. The astragalus of the Udunga rhino is very similar to that of *S. megarhinus*, while the calcaneum of the former species is proximodistally longer than that of the latter. The navicular and third cuneiform of the Udunga materials are proximodistally shorter than those of *S. megarhinus*, but those of the former are anteroposteriorly and transversely bigger than those of the latter. The anterior height of the cuboid of the Udunga rhino is taller than that of *S. megarhinus*, *S. jeanvireti*, '*D.*' *miguelcrusafonti*, and *S. etruscus*. On the other hand, it is transeverly narrower than that of

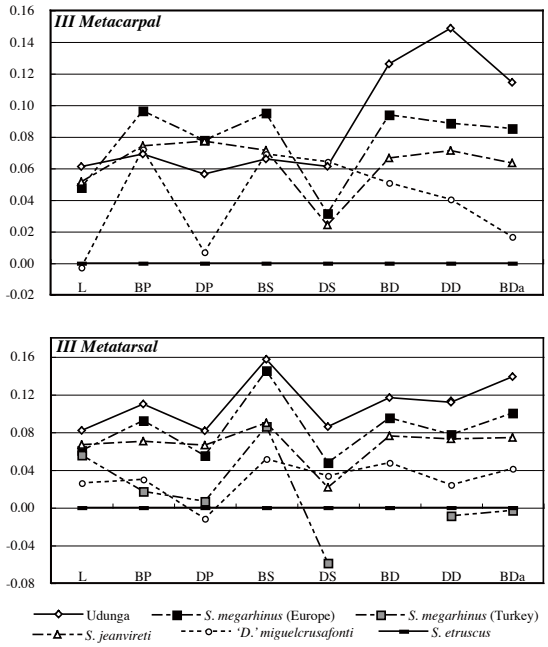

Figure 18. Ratio diagram of the central metapodials of the rhinoceros from Udunga, *S. megarhinus* (from Turkey), *S. megarhinus* (from Europe) and *S. jeanvireti* versus *S. etruscus* (standard). Measurements of the last three species were taken from Guérin (1980). Measurements of *S. megarhinus* from Turkey and the last four species were taken from Guérin and Sen (1998) and Guérin (1980), respectively.

S. megarhinus and *S. jeanvireti*. The second metatarsal of the Udunga rhino is similar in size to that of *S. megarhinus*, but the diaphysis of the former species is anteroposteriorly thinner than that of *S. megarhinus*, *S. jeanvireti*, '*D.*' *miguelcrusafonti*, and *S. etruscus*. The third metatarsal of the Udunga rhinoceros is very similar to that of *S. megarhinus*. It is slightly larger than that of the latter in all dimensions. The fourth metatarsal of the Udunga rhino appears rather similar to that of *S. jeanvireti* than to that of *S. megarhinus*.

Discussion

Fortelius et al. (1993) showed that the quantitative analyses on the postcranial bones of *Stephanorhinus* species, especially on the central metapodials, could provide us the significant specific information. The log ratio diagrams of the central metapodials (Figure 15, 17) indicate that the Udunga rhino is more similar to *S. megarhinus* than to other Pliocene Rhinocerotini. The quantitative analyses on the dental materials also show the similarities between them.

S. megarhinus has been reported not only from Europe but also from East Europe and Turkey (Guérin and Sen, 1998; and cited therein). In the log ratio diagrams of the central metapodials, including the data of *S. megarhinus* from Turkey, it is evident that the Udunga species is more closely related to European *S. megarhinus* than to Turkish one (Figure 18). It suggests a hypothesis that *S. megarhinus* migrated directly from Europe to Transbaikal area, not via East Mediterranean.

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References

Cerdeño, E. (1995) Cladistic analysis of the family Rhinocerotidae (Perissodactyla). *American Museum Novitates* 3143:1-25.

Chan, Y. and Tung, Y. (1961) Pliocene mammalian fossils from Chingning, Kansu. *Vertebrata PalAsiatica* 5(4): 380-384, 1 pl.

Colbert, E.H. (1935) Siwalik mammals in the American Museum of Natural History. *Transactions of the American Philosophical Society* new series 26: 1-401.

Deng, T., Wang, X., Ni, X., Liu, L., and Liang, Z. (2004) Cenozoic stratigraphic sequence of the Linxia Basin in Gansu, China and its evidence from mammal fossils. *Vertebrata PalAsiatica* 42(1): 41-66.

Egi, N., Nakatsukasa, M., Kalmykov, N.P., Mashenko, E.N., and Takai, M. (2007). Distal humerus and ulna of Parapresbytis (Colobinae) from the Pliocene of Russia and Mongolia: phylogenetic and ecological inplications based on elbow morphology. *Anthropological Science* 115: 107-117.

Erbajeva, M., Alexeeva, N., and Khenzykhenova, F. (2003) Pliocene small mammals from the Udunga site of the Transbaikal area. *Coloquios de Paleontologia* 1: 133-145.

Fortelius, M. and Heissig, K. (1989) The phylogenetic relationships of the Elasmotherini (Rhinocerotidae, Mamm.). *Mittelungen der Bayerischen Staatssammlung für Paläontologie und Hisorische Geologie* 29: 227-233.

Fortelius, M., Mazza, P., and Sala, B. (1993) *Stephanorhinus* (Mammalia, Rhinocerotidae) of the western European Pleistocene, with a revision of *S. etruscus* (Falconer, 1868). *Palaeontographia Italica* 80: 63-155.

Geraads, D. (1988) Révision des Rhinocerotinae (Mammalia) du Turolien de Pikermi. Comparaison avec les formes voisines. *Annales de Paléontologie* 74(1): 13-41.

Giaourtsakis, I. X. (2003) Late Neogene Rhinocerotidae of Greece: distribution, diversity and stratigraphical range. *Deinsea* 10: 235-253.

Ginsburg, L. (1974) Les Rhinocérotidés du Miocène de Sansan (Gers.). *Comptes rendus de l'Académie des Sciences* 278(5): 597-600.

Guérin, C. (1980) Les Rhinocéros (Mammalia, Perissodactyla) du Miocène terminal au Pléistocène supérieur en Europe occidentale. *Comparaison avec les espèces actuelles. Documents des Laboratoire de Géologie de Lyon* 79, 1-1185.

Guérin, C. (1989) La famille des Rhinocerotidae (Mammalia, Perissodactyla): systematique, histoire, évolution, paléoécologie. *Cranium* 6(2): 3-14.

Guérin, C. and Sen, S. (1998) Le gisement de vertébrés pliocène de Çalta, Ankara, Tarquie. 6. Rhinocerotidae. *Geodiversitas* 20(3): 397-407.

Groves, C. P. (1983) Phylogeny of the living species of rhinoceros. *Zeitschrift fur zoologische Systematik*

und Evolutionforschung 21(4): 293-314.

Hamilton, W.R. (1973) North African Lower Miocene rhinoceroses. *Bulletin of the British Museum (Natural History) Geology* 24(6): 351-395, 8 pls

Heissig, K. (1969) Die Rhinocerotidae (Mammalia) aus der oberoligozanen Spaltenfullung von Gaimersheim bei Ingolstadt in Bayern und ihre phylogenetische Stellung. *Bayerische Akademie der Wissenschaften Mathematishc-Naturwissenschaftliche Klasse Abhandlungen* neue falge 138: 1-133, 5 pls.

Heissig, K. (1972) Die obermiozäne Fossil-Lagerstätte Sanderzhausen. 5. Rhinocerotidae (Mammalia), Systematik und Ökologie. *Mittelungen der Bayerischen Staatssammlung für Paläontologie und Hisorische Geologie* 12: 57-81.

Heissig, K. (1973) Die Unterfamilien und Tribus der rezenten und fossilen Rhinocerotidae (Mammalia). *Säugetierkundliche Mitteilungen* 21: 25-30.

Heissig, K. (1996) The stratigraphical range of fossil rhinoceroses in the late Neogene of Europe and the Eastern Mediterranean. p. 339-347. In "*The Evolution of Western Eurasian Neogene Mammal Faunas*." Bernor, R.L., Fahlbusch, V., and Mittmann, H.-W. (eds.) Columbia University Press: New York.

Hu, C. (1962) Pliocene and Pleistocene mammalian fossils from Kansu. *Vertebrata PalAsiatica* 6(1): 88-108, 5 pls.

Huang, W. and Yan, D. (1983) New material of elasmotherini from Shennongjia, Hubei. *Vertebrata PalAsiatica* 21(3): 223-229, 1 pl.

Kalmykov, N.P. (1999) *Ecosystem Evolution of the Lake Baikal Basin in the Late Cenozoic*. Russian Academy of the Sciences: Ulan-Ude. 112 pp. (in Russian).

Kretzoi, M. (1942) Bemerkungen zum System der Nachmiozänen Nashorn-Gattung. *Földtani Közlöny* 72(4-12): 309-318.

Peter, K. (2002) Odontologie der Nashornverwandten (Rhinocerotidae) aus dem Miozän (MN5) von Sandelzhausen (Bayern). *Zitteliana* 22: 3 – 168.

Pilbeam, D., Morgan, M., Barry, and J.C., Flynn (1996) European MN units and the Siwalik Faunal Sequence of Pakistan. P. 96-105. In "*The Evolution of Western Eurasian Neogene Mammal Faunas*." Bernor, R.L., Fahlbusch, V., and Mittmann, H.-W. (eds.) Columbia University Press: New York.

Qiu, Z. (1979) Some mammalian fossils from the Pliocene of Inner Mongolia and Gansu (Kansu), *Vertebrata PalAsiatica* 17(3): 222-235, 4 pls.

Qiu, Z. and Qiu, Z. (1995) Chronological sequence and subdivision of Chinese Neogene mammalian faunas. *Palaeogeography, Palaeoclimatology, Palaeoecology* 116: 41-70.

Ringström, T. (1924) Nashörner der Hipparion-Fauna Nord-Chinas. *Palæontologia Sinica* 1(4): 1-156, 12 pls.

Tang, Y., You, Y., Liu, H., and Pan, Y. (1974) New materials of Pliocene mammals from Banguo Basin of Yuanmou, Yunnan and their stratigraphical significance. *Vertebrata PalAsiatica* 12(1): 60-67, 1 pl.

Vislobokova, I., Sotnikova, M., and Dodonov, A. (2001) Late Miocene – Pliocene mammalian faunas of Russia and neighbouring contries. *Bollettino della Società Paleontologica Italiana* 40(2): 307-313.

Zin-Maung-Maung-Thein, Takai, M., Tsubamoto, T., Thaung-Htike, Egi, N., and Maung-Maung (2008) A new species of Dicerorhinus (Rhinocerotidae) from the Plio-Pleistocene of Myanmar. *Paleontology* 51(6): 1419 – 1433.

Zong, G. (1987) Note on some mammalian fossils of Yanyuan, Sichuan. *Vertebrata PalAsiatica* 25(2): 137-145.

Appendix 1. List of the Udg rhinoceros specimens examined

Udg-	part	side
201	DP2/	L
202	DP2/	L
203	DP2/	L
204	M1/	L
205	DP1/	R
206	m/3	L
207	DP2/-DP4/, (DP3/)	L, (R)
208	m/1-m/2, (p/2, p/4-m/3)	L, (R)
213	DP1/	L
214	DP2/	R
215	M1/	L
216	P4/	L
217	M1/-M2/	R
218	DP1/-DP3/, (DP1/)	L, (R)
219	McIII (a) and McIV (b)	R
220	McIII (a) and McIV (b)	L
221	astragalus	L
222	astragalus	R
223	astragalus	R
224	astragalus	L
225	astragalus	R
226	astragalus	R
227	astragalus	L
228	astragalus	R
229	astragalus	R
230	astragalus	L
231	McIV	L
232	McIV	R
233	MtIII proximal end to schaft	L
234	MtIII proximal end	R
235	MtIV proximal end	L
236	MtIV proximal end	R
237	McIV proximal end	R
238	McII proximal end	L
239	McIV proximal end to schaft	L
240	MtIII proximal end to schaft	L
241	McII proximal end to schaft	R
242	McII proximal end	L
243	semilunar	R
244	semilunar	R
245	cuboid	R
246	cuboid	L
247	cuboid	R
248	cuboid	L
249	semilunar	L
250	semilunar	R
251	uncinate	R
252	uncinate	R
253	scaphoid	R
254	scaphoid	R
256	central proximal phalanx	-
257	central proximal phalanx	-
258	central proximal phalanx	-
259	lateral middle phalanx	-
260	tibia distal end	L
261	radius distal end	L
262	lateral distal phalanx	-
263	mandibular fragment without teeth	R
264	mandibular fragment without teeth	L
265	humerus distal end	R
266	McIII proximal end	L
267	MtIII proximal end	L
268	McIV proximal end	L
269	MtIV proximal end	L
270	MtIV proximal end	L
271	MtIV proximal end	L
272	lateral metapodial schaft	-
273	McII proximal end to schaft	L
274	central proximal phalanx	-
275	central proximal phalanx	-
276	central proximal phalanx	-
277	lateral proximal phalanx	-
278	lateral proximal phalanx	-
279	lateral proximal phalanx	-
280	lateral proximal phalanx	-
281	lateral middle phalanx	-
282	lateral distal phalanx	-
283	3rd cuneiform	R
284	3rd cuneiform	L
285	3rd cuneiform	R
289	cuboid	L
290	cuboid	R
291	cuboid	L
292	cuboid	L
293	pyramidal	L
294	pyramidal	L
295	pyramidal	L
296	pyramidal	L
297	pyramidal	R
298	pyramidal	L
299	pyramidal	L
300	pyramidal	L
795	central middle phalanx	-
796	central proximal phalanx	-
797	central proximal phalanx	-
798	lateral middle phalanx	-
799	lateral middle phalanx	-
800	radius proximal end	L
801	McIII proximal to schaft	L
802	Mt III proximal end	R
803	MtIII proximal end	L
804	trapezoid	R
805	Mt III proximal end	R
806	McIII proximal end	R
807	McIV	R
808	pyramidal	R
809	2nd cuneiform	R
810	McIII proximal end	L
811	McIV proximal end	R
812	McIv proximal end	L
813	radius proximal end	R
814	radius proximal end to shaft	R
815	radius proximal end	L
816	central proximal phalanx	-
817	central proximal phalanx	-
818	central distal phalanx	-
819	central middle phalanx	-
820	central middle phalanx	-
821	central middle phalanx	-
822	lateral distal phalanx	-
823	central distal phalanx	-
824	trapezoid	R
825	MtIII	L
826	uncinate	R
827	scaphoid	L
828	uncinate	R
829	uncinate	R
830	uncinate	L
831	uncinate	R
832	uncinate	L
833	semilunar	R
834	semilunar	L
835	scaphoid	L
836	uncinate	R
837	cuboid	L
838	uncinate	L
839	trapezoid	L
840	uncinate	L
841	scaphoid	L
842	uncinate	R
843	cuboid	R
844	cuboid	L
845	pyramidal	R
846	central distal phalanx	-
847	central proximal phalanx	-
848	central proximal phalanx	-
849	central distal phalanx	-
850	pisiform	R
851	laterla middle phalanx	-
852	lateral distal phalanx	-
853	central distal phalanx	-
854	sesamoid	-
855	lateral distal phalanx	-
856	scaphoid	R
857	navicular	L
858	navicular	L
859	3rd cuneiform	R
860	pyramidal	L
861	navicular	R
862	cuboid	R
863	cuboid	R
864	navicular	L
865	navicular	R
865	humerus distal end	R
866	uncinate	L
867	McIII proximal end	R
868	central metapodial distal end	-
869	uncinate	R
870	uncinate	L
871	tibia distal end	R
872	McIII proximal end to schaft	R
873	central distal phalanx	-
874	laterla distal phalanx	-
875	central distal pahalnx	-
876	central distal phalanx	-
877	calcaneum	L
878	radius distal end	L
879	mandible fragment without teeth	L
880	axis	-
881	head of femur	L
882	astragalus	L
883	lateral proximal phalanx	-
884	MtIV proximal end	L
885	McIV proximal to schaft	R
886	DP1/	R
887	uncinate	L
888	uncinate	R
889	uncinate	R
890	cuboid	L
891	cuboid	L
892	cuboid	L
893	uncinate	L
894	uncinate	L
896	central metapodial distal end	-
897	astragalus	R
898	radius distal end	L
899	radius distal end	L
900	thoracic vertebra	-
901	trapezoid	L
902	pyramidal	R
903	trapezoid	L
904	McIV proximal end	L
905	MtII proximal end	R
906	magnum	R
907	magnum	R
908	magnum	R
909	magnum	L

Appendix 1. (continued)

Udg-	part	side
910	magnum	L
911	magnum	R
912	uncinate	L
913	uncinate	R
914	uncinate	L
915	uncinate	R
916	uncinate	L
917	tibia distal end	L
918	semilunar	R
919	semilunar	R
920	radius proximal end	R
921	uncinate	L
922	scaphoid	L
923	scaphoid	L
924	scaphoid	R
925	scaphoid	L
926	scaphoid	L
927	lateral proximal phalanx	-
928	lateral proximal phalanx	-
929	lateral middle phalanx	-
930	cuboid	R
930	sesamoid	-
931	trapezium	L
932	lateral proximal phalanx	-
933	cuboid	R
934	central proximal phalanx	-
935	central middle phalanx	-
936	central proximal phalanx	-
937	central proximal phalanx	-
938	calcaneum	R
939	scaphoid	L
940	3rd cuneiform	R
941	lateral proximal phalanx	-
942	central distal phalanx	-
944	lateral middle phalanx	-
945	central proximal phalanx	-
946	central middle phalanx	-
947	central proximal phalanx	-
948	lateral distal phalanx	-
949	McIII	L
950	scaphoid	R
951	McII proximal end to schaft	L
952	McII proximal end to schaft	L
953	MtIV proximal end to schaft	L
954	McII proximal end to schaft	L
955	MtIII proximal end	L
956	MtII proximal end	L
957	pyramidal	R
958	3rd cuneiform	R
959	MtIII proximal end	L
960	uncinate	L
961	patella	R
962	radius distal end	R
963	lateral middle phalanx	-
964	lateral proximal phalanx	-
965	patella	R
966	cervical vertebra	-
967	radius proximal end	R
968	radius proximal end	L
969	radius proximal end	L
970	McIII	R
971	3rd cuneiform	R
972	pyramidal	L
973	3rd cuneiform	R
974	pyramidal	R
975	navicular	R
976	scaphoid	L
977	pyramidal	L
978	uncinate	L

Udg-	part	side
979	scaphoid	L
981	cuboid	L
982	scaphoid	R
983	central proximal phalanx	-
984	central proximal phalanx	-
985	magnum	L
986	scaphoid	L
987	astragalus	L
988	McIII proximal end to schaft	R
989	calcaneum	L
990	magnum	L
991	scaphoid	R
992	calcaneum	L
993	pyramidal	L
994	MtIII proximal end	L
995	MtIII proximal end to schaft	L
996	MtII	L
997	tibia schaft to distal end	R
998	radius proximal end	R
999	astragalus	R
1000	astragalus	R
1001	central proximal phalanx, proximal end	-
1002	central proximal phalanx	-
1003	lateral distal phalanx	-
1004	semilunar	L
1005	magnum	R
1006	semilunar	R
1007	semilunar	L
1008	semilunar	L
1009	semilunar	R
1010	magnum	L
1011	3rd cuneiform	L
1012	MtIII proximal end	L
1013	central metapodial distal end	-
1014	radius distal end	R
1015	laterla proximal phalanx	-
1016	central proximal phalanx	-
1017	cuboid	L
1018	tibia schaft	-
1019	femur distal end	R
1021	scapula fragment	R
1023	cantral proximal phalanx	-
1024	central proximal phalanx	-
1025	navicular	L
1026	scaphoid	R
1027	DP^1	L
1028	DP^1	L
1029	DP^2	R
1030	calcaneum	R
1030	P^3	L
1031	P^4	L
1032	M^2	L
1298	lateral middle phalanx	-
1714	magnum	L
1715	magnum	L
1716	magnum	R
1723	thoracic vertebra	-
1724	thoracic vertebra	-
1727	central metapodial shaft	-
1728	central metapodial shaft	-
1732	metapodial shaft fragment	-
1741	femur distal end	R
1743	thoracic vertebra	-
1745	lumbar vertebra	-
1746	vertebral fragment	-
1747	magnum	L
1749	semilunar	L
1750	lateral metapodial shaft to distal end	-
1751	radius proximal part	R

Udg-	Material	side
1752	scapula fragment	L
1754	humerus distal end	R
1755	navicular	R
1756	astragalus	R
1759	semilunar	L
1760	calcaneum	L
1761	calcaneum	L
1762	calcaneum	R
1764	ulna distal end	R
1765	McIII proximal end	L
1766	semilunar	R
1768	central metapodial shaft	-
1770	lateral metapodial shaft	-
1771	central metapodial shaft	-
1772	radius shaft	-
1774	metapodial shaft fragment	-
1779	lateral metapodial distal end	-
1782	lateral metapodial shaft	-
1783	metapodial shaft fragment	-
1784	lateral metapodial shaft	-
1785	MtIII proximal end	R
1786	central metapodial shaft	-
1793	uncinate	R
1795	MtII proximal end	L
1796	McIV	R
1797	McIV proximal end	R
1798	cervical vertebra	-
1803	scaphoid	L
1804	humerus distal end	L
1805	mandible , condyloid process	L
1806	fibula distal end	L
1807	MtIII proximal end	L
1808	McIV proximal end	R
1809	tibia distal end	L
1811	navicular	R
1812	scapula fragment	L
1813	humerus distal end	L
1817	McIV proximal end	L
1820	magnum	L
1822	mandible, condyloid process	R
1823	femur distal end	L
1824	head of femur	L
1826	calcaneum	R
1828	semilunar	R
1829	astragalus distal end	L
1830	ulna distal end	L
1831	magnum fragment	L
1832	magnum fragment	L
1838	femur distal end	L
1839	central metapodial distal end	-
1840	calcaneum	R
1841	calcaneum	L
1843	lateral metapodial shaft to distal end	-
1848	radius shaft	L
1855	tibia distal end	R
1857	thoracic vertebra	-
1861	radius shaft	-
1864	fibula distal end	L
1865	lateral metapodial shaft	-
1866	fibula	L
1867	navicular	L
1868	metapodial shaft fragment	-
1869	tibia distal end	L
1870	scaphoid	R
1871	scaohoid	L
1874	scaphoid	L
1875	scaphoid	L
1876	central metapodial shaft	-
1877	semilunar	R

Appendix 1. (continued)

Udg-	part	side
1880	humerus distal end	R
1881	semilunar	L
1882	upper cheek tooth fragment	L
1883	tibia shaft	-
1884	tibia shaft	-
1885	tibia shaft	-
1887	semilunar fragment	R
1888	cuboid	R
1890	cuboid	R
1892	upper cheek tooth fragment	L
1893	calcaneum fragment	L
1894	lateral metapodial distal end	-
1899	tibia shaft	-
1900	magnum fragment	L
1901	upper cheek tooth fragment	L
1904	humerus distal end	L
1905	astragalus	L
1906	astragalus	R
1907	astragalus	R
1908	astragalus	R
1909	astragalus	L
1911	calcaneum	R
1915	ulna fragment	L
1916	central metapodial distal end	-
1917	central metapodial shaft	-
1918	tibia shaft to distal part	L
1919	fibula distal end	R
1920	patella	-
1921	occpital condyle	R
1922	radius shaft	-
1924	lateral metapodial distal end	-
1925	ulna fragment	L
1926	fibula distal end	-
1927	navicular	L
1929	central metapodial distal end	-
1930	central metapodial distal end	-
1932	MtII proximal end to shaft	R
1933	calcaneum	R
1935	radius shaft to distal end	L
1936	calcaneum fragment	-
1937	radius distal end	R
1938	radius proximal end	R
1939	ulna fragment	L
1941	humerus distal end	L
1942	ulna fragment	L
1943	radius proximal part	R
1944	lateral distal phalanx	-
1945	semilunar	L
1946	tibia shaft	-
1947	uncinate	L
1948	astragalus	R
1950	ulna fragment	R
1951	calcaneum fragment	-
1954	radius distal end	R
1956	scapula fragment	R
1957	fibula distal end	R
1959	fibula distal end	L
1967	premaxilla fragment	L
1968	calcaneum	R
1974	femur distal end	L
1975	astragalus	L
1977	humerus shaft fragment	L
1978	scapula fragment	L
1979	radius shaft	-
1981	lateral metapodial distal end	-
1982	upper cheek tooth fragment	L
1983	upper cheek tooth fragment	R
1984	upper cheek tooth fragment	L
1985	upper cheek tooth fragment	R
1986	MtIII proximal end	L
1987	pyramidal	R
1988	upper cheek tooth fragment	R
1989	deciduous upper cheek tooth	R
1990	P_2 fragment	L
1990	sesamoid	-
1991	P_2 fragment	L
1992	lower cheek tooth fragment	R
1993	lower cheek tooth fragment	L
1994	lateral middle phalanx	-
1995	sesamoid	-
1996	lateral proximal phalanx	-
1997	lateral proximal phalanx	-
1998	lateral proximal phalanx	-
2000	lateral proximal phalanx	-
2201	lateral proximal phalanx	-
2202	lateral proximal phalanx	-
2203	lateral proximal phalanx	-
2204	lateral proximal phalanx	-
2205	lateral middle phalanx	-
2206	lateral proximal phalanx	-
2207	lateral proximal phalanx	-
2208	lateral proximal phalanx	-
2210	lateral middle phalanx	-
2211	central middle phalanx	-
2212	lateral proximal phalanx	-
2213	thoracic vertebra	-
2298	lateral middle pahalanx	-
2554	upper cheek tooth fragment	R
2555	upper cheek tooth fragment	R
2556	upper cheek tooth fragment	L
2557	upper cheek tooth fragment	R
2559	lateral metapodial shaft fragment	-

Appendix 2. Abbreviations of the postcranial measurements.

Vertebra	
La	distance from the cranial to caudal articulation
Bcra	breadth of the cranial articular surface
H	height
Scapula	
DAP art.	anteroposterior diameter of the glenoid cavity
DT art.	transverse dimeter of the glenoid cavity
DAP col.	anteroposterior diameter of the collum scapulae
DAP tub.	anteroposterior diamter of the supraglenoidal tubercle
H	height
DAP max.	greatest anteroposterior diameter
Humerus/Radius/Ulna	
L	greatest length
BP	transverse diameter of the proximal end
DP	anteroposterior diameter of the proximal end
DP1	anteroposterior diameter of the proximal end, from the caput humeri to the greatest tubercle
Bd	transverse diameter of the deltoid tuberosity
BS	smallest transverse diameter of the shaft
DS	smallest anteroposterior diameter of the shaft
BD	transverse diameter of the distal end
DD	anteroposterior diameterof the distal end
Bo	transverse diameter of the olecranon
Do	anteroposterior diameter of the olecranon
Hsiu	height of the sigmoidal incisure of the ulna
Bpau	transverse diameter of the proximal articular surface of the ulna
Scaphoid/ Semilunar/ Pyramidal/ Pisiform/ Trapezoid/ magnum/ Unicinate	
H	height
H ant.	anterior height of semilunar or magnum
L	anteroposterior diamter
L art.sup.	anteroposterior diameter of the proximal articular surface of scaphoid
L art.inf.	anteroposterior diameter of the distal articular surface of scaphoid
L anat.	anatomical anteroposterior diameter of uncinate
L abs.	absolute anteroposterior diameter of uncinate
l	transverse diamater
l art.sup.	transverse diameter of the proximal articular surface of scaphoid
Femur/ Patella/ Tibia/ Fibula	
L	greatest length
BC	transverse diameter of the caput femoris
DC	anteroposterior diameter of the caput femoris
BP	transverse diameter of the proximal end
DP	anteroposterior diameter of the proximal end
Bt	transverse diameter of the third trocanter
BS	smallest transverse diameter of the shaft
DS	smallest anteroposterior diameter of the shaft
BD	transverse diameter of the distal end
DD	anteroposterior diameter of the distal end
DDa	anteroposterior diameter of the distal articular surface
BT	transverse diameter of the trochlea
DT	transverse diameter of patella
H	height of patella
Astragalus	
H	height
DL	distance of the trochanter lips
DT	transverse diameter
DT max.dist.	greatest distal transverse diameter
DDa	anteroposterior diameter of the distal articular surface
Calcaneum	
DAP somm.	anteroposterior diameter of the tuberosity summit
DAP beak	anteroposterior diameter at the beak
H	height
DT somm.	transverse diameter of the tuberosity summit
DT min.	smallest plantar transverse diameter
DT sust.	transverse diameter of at the sustentaculum tali
Navicular/ Cuboid/ 2nd Cunieform/ 3rd Cunieform	
H	height
H ant.	anterior height of cubid
l	transverse diamater
l art.	transverse diameter of the proximal articular surface of cuboid
DPa	anteroposterior diameter of the proximal articular surface of cuboid
L	anteroposterior diameter
Metapodials	
L	greatest length
BP	transverse diameter of the proximal end
DP	anteroposterior diameter of the proximal end
BPa	transverse diameter of the proximal articular surface
BS	smallest transverse diameter of the shaft
DS	smallest anteroposterior diameter of the shaft
BD	transverse diameter of the distal end
DD	anteropsterior diameter of the distal end
BDa	transverse diameter of the distal articular surface
Phalanges	
GL	greatest length
BP	transverse diameter of the proximal end
BFP	transverse diameter of the proximal articular surface
DP	anteroposterior diameter of the proximal end
BD	transverse diameter of the distal end