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STUDIES ON THE PLEISTOCENE RHINOCEROS COELODONTA ANTIQUITATIS (BLUMENBACH)

(BADANIA NAD PLEJSTOCEŃSKIM NOSOROŻCEM COELODONTA ANTIQUITATIS (BLUMENBACH)

BY

MAGDALENA BORSUK-BIAŁYNICKA

(WITH 13 TEXT-FIGURES, 50 TABLES AND 23 PLATES)



WARSZAWA - KRAKÓW 1973

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ABSTRACT

The anatomy of the woolly rhino — Coelodonta antiquitatis (Blumenbach) was studied on the basis of rich bone material from Poland, USSR and Czechoslovakia. The rate of fusing of the cranial sutures and the development of some other craniological character in the ontogenesis of the woolly rhino were investigated. The results of the investigations allowed to establish four ontogenetic groups of skulls, each of them characterised by a number of characters such as state of sutures, degree of ossification of the nasal septum, shape of nasals, state of dentition. Each of these characters, apart from the others, made, to some extent, a basis for determination of individual age of a given specimen.

The investigation of variability of the craniometric features in woolly rhino, based on about 110 specimens from Poland and USSR revealed the existence of two breeds within the range of this species. One breed characterised by a stocky skull (mean skull proportion coefficient 3.0) is the only breed represented in Poland and the one predominating in European Russia; the other one, with a more slender skull (mean skull proportion coefficient approaching 3.2) is presumably a stratigraphically older variety of Siberian origin. Partial sex dimorphism in some linear dimensions of skull in *Coelo-donta antiquitatis* is shown as well as some correlations between the following pairs of characters, i.e.: maximum length of skull — angle between foramen magnum axis and palate, the same angle — degree of the ossification of nasal septum, maximum length of skull — skull proportion coefficient. An analysis of the muscle-bone system of *Coelodonta antiquitatis*, in comparison with those of the Recent rhinoceros species, gives some new data on the degree of flexibility of the vertebral column of woolly rhino, which is shown to be similar to the Recent white rhino in this respect. Some morphological characters of limb bones fo the woolly rhino are proved to represent graviportal adaptations, which are combined in this species with the anatomical type common to most of the late Pleistocene and Recent rhinos, that is with the mediportal type of Gregory (in OSBORN 1929). Detailed description of the skeleton of the woolly rhino, including the interpretation of muscle scars, is given, on the basis of the material from Polish collections, including a complete skeleton of this species from Podbaba (Czechoslovakia).

INTRODUCTION

The present paper makes up a study of *Coelodonta antiquitatis* (BLUMENBACH), based on materials from Poland, Czechoslovakia and Soviet Union. In the collection described a prominent role is played by an almost complete skeleton of the woolly rhino from Czechoslovakia which has for several scores of years been housed as a museum exhibit in the collection of the Jagiellonian University in Cracow. In addition, here studied collection includes about a hundred skulls of the woolly rhino (most of them from the teritory of the USSR and sixteen from Poland) and a total of more than two hundred specimens of long bones of this species.

The remains of this rhino, abundant in Poland, are known from almost entire Europe and a vast area in Northern Asia, where their range reaches about 45° of latitude (for accurate geographical distribution see FLEROW *et al.*, 1955). In Asia, the woolly rhino appears in the Early Pleistocene (BELAYEVA, 1966), preceded by early forms of the genus *Coelodonta* known from the Eopleistocene of the Transbaykal Region (*l. c.*) and occurs throughout the Pleistocene. In Europe, the main period of its occurrence is the Würm, but few earlier findings are also known



Fig. 1

The distribution of *Coelodonta antiquitatis* (BLUM.) in Poland. The localities of the woolly rhino given by KOWALSKI (1959) (black spots). The localities from which the materials come described in the present paper (circles).

from the Riss glaciation in Saxony (WOLDSTEDT, 1954) and even from the Mindel glaciation in Thuringia Frankenhausen (KAHLKE, 1963) and Harz, Neuekrug, Bornhausen (SICKEN-BERG, 1962). The findings of the woolly rhino in Poland are on the whole dated from the Würm or undated at all. The only unquestionable finding of older age is skull MZ No VIII/Vm-452 from Konin dated from the Eemian interglacial. The allegedly still older finding from the Krowodrza suburb of Cracow, dated from the Riss (KOWALSKI, 1959) is uncertain.

The Polish materials here studied come from several localities, the northernmost being the findings from the Konin Coalfield and most of them from Southern Poland (cf. Text-fig. 1). Part of them are postwar findings and part — prewar, not studied materials, mostly without labels. The lack of information on the geological conditions of the findings and even a complete lack of detailed data on the locality where most specimens were found deprive the materials of a stratigraphic value. On the other hand, they represent a valuable material for morphological studies. The same is true for the specimens coming from the Soviet Union.

The woolly rhino is one of the best known Pleistocene animals. The skull of this species has as early as 1849 been described in detail by BRANDT and later by GIEBEL (1851) and NIE-ZABITOWSKI (1914). These authors' works also contain the descriptions of the wolly rhino's mandible. GROMOVA (1935) presents a detailed comparison of such mandible with those of

7

other Pleistocene rhinos and FRIANT (1961) describes the details of the structure of the maxillary joint. The structure of the postcranial skeleton of the woolly rhino is known from GIEBEL'S (1851), BRANDT'S (1877) and NIEZABITOWSKI'S (1914) works. Much information on the bones of limbs is given by SCHROEDER (1930), KRYSIAK (1938), BELAYEVA (1939) and GROMOVA (1950).

An extensive study of the variability of the woolly rhino's craniological characters is given by BRANDT (1849). It mostly concerns some immeasurable features of the skull, in particular certain characters of the occiput. In addition, BRANDT (1849) ascertains the existence of two types of the woolly rhino's skull, one of them more slender and the other rather stocky. According to NIEZABITOWSKI (1914), this differentiation is connected with the sexual dimorphism. This supposition has not, however, been confirmed by the present writer's studies (see below). The characteristics of the variability of some craniometric features (cranial angles) of the woolly rhino and other fossil and Recent rhinos are given by ZEUNER (1934).

The present paper contains a detailed description and interpretation of muscle scars on the woolly rhino's bones. The writer seeks to explain certain characters of the animal's musculo-skeletal system as compared with those of the Recent species *Diceros bicornis* and *Rhinoceros sondaicus*. Certain parts of the osteological description, concerning so far less known morphological details such as, the structure of the osseous connection between the nasal and intermaxillary bones and their contact with the nasal septum, have been dealt with more extensively.

In addition, the paper contains an analysis of the variability of craniological features, connected with individual age as seen from the viewpoint of their suitability for determining such age. A statistical study of the variability of craniological characters, given in the final part of the paper, allows one to characterize the Polish population of the woolly rhino and to compare it with East-European and Siberian populations.

The materials under study are housed at the following scientific institutions (the abbreviations quoted below):

Chair of Geology of the University of Leningrad.

- GI Mining Institute of the USSR.' Academy of Sciences in Leningrad.
- IG Geological Institute in Warsaw.
- KGU Museum of the Geological Department of the University of Kazan, USSR.
- MG Regional Museum in Gliwice.
- Mining Institute of the USSR.' Academy of Sciences in Moscow.
- MIZ Museum of the Polish Academy of Sciences' Zoological Institute in Wrocław.
- Moravske Museum in Brno, Czechoslovakia.
- MP Palaeontological Museum of the USSR.' Academy of Sciences in Moscow.
- MSE Museum of the Polish Academy of Sciences' Institute of Systematic and Experimental Zoology in Cracow.
- M. Wiś Regional Museum in Wiślica.
- MZ Museum of the Earth, Polish Academy of Sciences.
- Narodni Museum in Prague, Czechoslovakia.
- PS Technical University in Gliwice.
- RS Regional Museum in Sandomierz.
- RZ Regional Museum in Rzeszów.
- UL Zoological Museum, University of Łódź.
- Wet. Veterinary Faculty of the Warsaw Agriculture University.
- Wrocł. Department of Palaeontology, University of Wrocław.
- ZAPUJ Zoological Museum, Jagiellonian University.
- ZG Department of Geology, Jagiellonian University.
- ZIN Zoological Institute of the USSR.' Academy of Sciences in Leningrad.
- ZK Museum of the Konin Coalfield.

Other abbreviations used in the paper:

- YM, a young skull from the collections of the Palaeontological Museum of the USSR.'s Academy of Sciences in Moscow, probably coming from the environs of Voronezh, without catalogue number;

- St I, a skull of the first rhinoceros, excavated at Starunia and described by NIEZABITOWSKI (1914), without catalogue number.

The measurement methods used by the writer are mostly based on the principles given by DÜRST (1926), while the measurements of the bone of an anterior limb also on BELAYEVA (1939). The cranial angles were measured according to ZEUNER (1934).

ACKNOWLEDGEMENTS

The writer's heartfelt thanks are extended to all persons by whose courtesy the bones of fossil and Recent rhinos were made available to her for investigation or comparison, in particular to Professor Z. GRODZIŃSKI (Laboratory of Comparative Anatomy of the Jagiellonian University in Cracow) and Professor A. HALICKA (Museum of the Earth, Polish Academy of Sciences in Warsaw). The writer's gratitude is also due to Dr. K. Świeżyński (Warsaw Agriculture University) and Professors A. URBANEK, K. KRYSIAK and K. KOWALSKI for reading the manuscript and valuable critical remarks.

Palaeozoological Laboratory of the Warsaw University Warszawa, April 1972

GENERAL PART

CHANGES IN CRANIOLOGICAL CHARACTERS CONNECTED WITH INDIVIDUAL AGE

During the ontogenetic development of the woolly rhino, gradual changes are observed in its craniological characters such as, the degree of fusion of the sutures, development of nasal bones and nasal septum, degree of a posterior inclination of the upper part of occiput and sculpture of the surface of bones. These changes are more distinct and occur faster in early development stages and become slower or completely disappear in older individuals.

The dentition changes throughout an individual's life and although the changes are considerably faster and stronger in juvenile individuals, those occurring in the adults and consisting in a gradual abrasive wear of permanent teeth are also distinct. The generally known fact that the state of dentition is the best index of individual age result from it. Since fossil skulls are, however, frequently devoid of dentition, establishing criteria of determining individual age, based on craniological characters, is much desired. In this respect, the most important of these characters is the state of sutures, which fuse during the ontogenetic development in a certain, fixed order (see below) and rate in relation to the rate of changes in dentition. The importance of this character as a basis for determining individual age is somewhat decreased by a relatively early completion of the process of fusing sutures. Yet more limited is the range of such characters as the development of nasal bones and the inclination of occiput, which change perceptibly only in the early development stages, and of the sculpture of the surface of bones, whose strong development characterizes old individuals and whose gradual changes are imperceptible in younger stages of ontogenetic development.

The rate of development of the bony nasal septum is subject to a relatively strong individual variability. As a matter of fact, the rate of changes in dentition, sutures and other characters, connected with individual age, is also subject to a certain, if smaller, individual variability. To obtain as reliable determination of individual age as possible it is advisable to base the determinations simultaneously on several characters of the skeleton.

The order of the erupting of the deciduous and permanent teeth in *C. antiquitatis* is known from literature (GIEBEL, 1851; NIEZABITOWSKI, 1914; and others). The observations of the specimens MZ No. VIII/Vm-453, KGU No. 748, YM, KGU No. 729 and KGU No. 736 in principle confirm the results obtained by previous authors.

The deciduous teeth are replaced in the order from DP^2 to DP^4 and the process of replacement starts after the use of M^1 has begun. M^2 may erupt still before the loss of DP^2 and DP^2 (which is indicated by the state of skull YM), after the loss of DP^2 and before the loss of DP³ (specimen MZ No. VIII/Vm-453 and GIEBEL's observations, 1851), or after the loss of DP³ as NIEZABITOWSKI (1914) maintains on the basis of the skull from Starunia (the state of dentition in the last-named skull does not, however, entitle one to such a statement). DP¹ was probably lost before DP² as in skull KGU No. 748. According to NIEZABITOWSKI (*l. c.*), DP¹ falls out after DP⁴. He bases this statement on the state of dentition of skull St I, which, however, indicates that DP¹ (height of crown, 15 mm) fell out rather after DP² (height of crown, 8 mm) more or less simultaneously with the loss of DP³ (height of crown, 15 mm) and decidedly before that of DP⁴ (height of crown, 30 mm). As a vestigial tooth, not replaced by a permanent tooth, DP¹ was, however, subject to a considerable variability in regard to the period of its falling out.

The erupting and growth of P^4 and P^3 more or less coincide, as indicated by the dentition of skulls ZAPUJ No. 683, ZG No. II-b-13-1 and others. P^4 wedges in between already grown P^3 and M^1 . The growing of P^4 and M^3 as the last ones is observed in so many specimens, that any departures from this principle should be considered as an anomaly.

The order of growing deciduous teeth could not be observed for the lack of material. According to NIEZABITOWSKI (1914), they grow from DP^1 to DP^4 and are subsequently followed by M^1 .

In respect to changes, occurring in them, the cranial sutures are considerably less variable than the dentition. Only four groups of them, varying in the rate of fusing, may be distinguished.

Group I includes sutures situated mostly in the neural part of skull (Table 1). They fuse prior to the completion of the replacement of deciduous dentition.

The sutures of group II (Table 2), situated mostly in the preorbital part of skull, fuse somewhat later. In addition, the moment at which they fuse seems to be more variable than that in group I. Mostly, they do not fuse until M³ is fully grown. Sometimes, it happens earlier, but always after a complete replacement of the deciduous dentition. The greatest variability in this respect is displayed by the occipito-squamous sutures and the sagittal suture near the boundary between the frontals and nasals.

Group III mostly includes the sutures of bones surrounding the posterior part of oral cavity and those in parts of skull less important from the mechanical viewpoint (e.g., between the paramastoid and posttympanic process, etc.). These sutures, fusing mostly during the initial period of the abrasion of M³, are as a rule (with few exceptions) fused in aged individuals (M³ worn-off halfway down or even more). The spheno-squamosal suture and the sutures between the processes of the region of skull base (Table 3) are marked by a particularly large variability.

The only suture which frequently does not fuse to the extreme old age is, in its posterior part, the palato-maxillary suture. This is an only suture assigned to group IV.

Thus, the following four age groups may be distinguished on the basis of the state of dentition and sutures:

Young — individuals having deciduous dentition and those in the stage of replacement of such dentition up to the loss of DP^4 . Sutures not fused. This is a period of a strong growth of skull which, as we may suppose on the basis of analogy to Recent rhinoceroses, corresponds to the first eight months of life (NIEZABITOWSKI, 1914). Completely preserved happen to be only older representatives of this group immediately prior to a complete fusion of the sutures of group I and completion of growth. This is indicated by large dimensions of young skulls. In the initial phase of the replacement of dentition, there takes place a fusion of the sutures surrounding the neural part of skull and those situated on the skull roof.

Young-adult. This group includes individuals in the stage of growing P^4 and M^3 and prior to M^3 coming into use. During this period, the skull only slightly increases lengthwise in the region of the naso-frontal suture and across in the region of the preorbital part of skull. A pre-

Ta	ble	1
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The rate of fusing of the cranial sutures of the Group I as compared with that of changes in dentition in Coelodonta antiquitatis (BLUM.)

Skull, Cat. No. Type of suture	St I	ХW	KGU No. 748	KGU No. 736	ZAPUJ No. 683	ZG No. II-b-13-1	ZIN No. 10707	KGU No. 729	MPŁ No. IV-3	Wet No. 4053
Sphenooccipital	_	+	+	+	+	+	+	+	+	+
Parietal	+	+	+	+	+	+	+	+	+	+
Frontal	+	+	+	+	+?	+	+	+	+	+
Nasal	_		+	+	+	+	+	+	+	+
Parietointerparietal	_	_	+	+	+	+	+	+	+	+
Frontoparietal			+	+	+	+	+	+	+	+
Synchondrosis interoccipitalis interlateralis			+	+	+	+	+	+	+	+
Synchrondrosis interoccipitalis squamolateralis	_	-	+	+	+	+	+	+	+	+
Parietotemporal			trace	+	+	+	+	+?	+	+
Frontotemporal			trace	+	+	+	+	+?	+	+
Sphenofrontal		_	+	+	+?	+	?	+	+	+
State of dentition	M ¹ c	deciduous coming into	o use	P	¹ not yet us M ³ getti	sed or com ng out of	iing into u alveolus	se	M ³ fully grown, not yet used	M ³ not fully grown

Table 2	Ta	ble	2
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Skull, Cat. No. Type of suture	StI	ЖW	KGU No. 748	KGU No. 736	ZAPUJ No. 683	ZG No. II-b-13-1	ZIN No. 10707	KGU No. 729	MPL No. IV-3	Wet No. 4053	KGU No. 734, 732, 747	MZ No. VIII/Vm-234	ZG No. II-b-13-3
Occipitosquamous		_	+?	`+-		_	+	+	+	trace	+	+	+
Frontonasal		_	trace	trace	trace	_	+	trace	+	+	+	+	+
Sagittal suture on the boundary be- tween frontals and nasals		_	+	+	+?		?	+	+	+	+	+	+
Lacrimal surrounding bones				_	trace	_	trace	trace	+	+	+	+	+
Nasomaxillary				?	trace?				+	.+	+	+	+
Zygomaticomaxillary	_	_	?	?	trace	_	?		+	+	+	trace	+
Incisivomaxillary		?	?	?	+?	trace	_	?	+	+	+	+	+
State of dentition	d M ¹ co	eciduous ming into	o use	P⁴ n	ot yet use M ³ gettin	ed or cor ig out of	ning into alveolus	use	M ³ lar not ye	rge but et used	beg	inning of vear of M	the 1 ³

The rate of fusing of the cranial sutures of the Group II as compared with that of changes in dentition of Coelodonta antiquitatis (BLUM.)

PLEISTOCENE	
RHINOCEROS	
COELODONTA	
ANTIQUITATIS	

Table 3

The rate of fusing of the cranial sutures of the Group III as compared with that of changes in dentition of Coelodonta antiquitatis (BLUM.)

Skull, Cat. No.	St I	МХ	KGU No. 748	ZAPUJ No. 683	ZG No. II-b-13-1	ZIN No. 10707	KGU No. 729	MPŁ No. IV-3	KGU No. 734	KGU No. 732	KGU No. 747	KGU No. 726	ZG No. II-b-13-3	MZ No. VIII/Vm 146	ZIN No. 10693	ZIN No. 10694	MZ No. VIII/Vm-173
Temporozygomatic						—	-	partly	+	+	+	+	trace	+	+	+	+
Sphenopalatine			?	—?	_		_	trace	+		+	+		+	+	+	+
Vomeropalatine			—?	?	_	—	-	trace	+	+	+	+	_	+	+	+	+-
Median palatine	_	?		?	_		_	trace	+		+	+		trace	+	+	+
Intermaxillary		?	_	?	-	_		trace	+	poste- riorly	+	+	-	+	+	+	+
Sphenosquamosal	-		trace	trace	+	trace	+	+	+	+	+	+	+	+	+	+	+
A suture between paramastoid and posttympanic process			trace			?	+	+		+	+	+		+	+	+	-+-
A suture between posttympanic and postglenoid process	_	trace	+?		+		+		+	+	+	+	+	+	+	+	+
State of dentition deciduous M ¹ coming into use			M ³ get of the	ting out alveolus		beginning of the wear of M ³ Worn-off half dow the height of crown even more								own 1 or			

servation of the possibility of growth in this region of skull is connected with the growth of permanent teeth, in particular of the molars which, on the one hand cut in the palate and thus narrow it and, on the other, cause an outward growth of the maxillae. In this connection, the sutures of group II and those fusing later (group III and the palato-maxillary suture) remain not yet fused.

Old-adult — individuals with M³ in the process of wearing-off down to two-thirds of the height of crown (one-third worn-off). In this stage, the sutures of the posterior border of oral cavity usually remain not yet fused which is connected with the fact that M³, considerably wider and longer at the root than at the tip, gets out of its alveolus. In addition, other sutures of group III may remain not fused.

Old. M³ worn-off halfway down or more (the boundary between age groups III and IV is conventional). A loss of completely worn-off anterior cheek teeth and an anterior displacement of the posterior molars. Sutures fused, except for the palato-maxillary one, which mostly persists to extreme old age and, sporadically, other ones, e.g. median palatine suture in its posterior part.

As shown in Tables 1—3, here studied characters are subject to a certain individual variability. In this connection, combinations of the state of teeth and that of sutures, which may determine particular age groups, should be recognized as the most likely ones and not as unquestionably valid.

Particular difficulties may occur in determining the age of certain individuals of the group of old-adults, whose sutures of group III fused earlier, which, with a simultaneous lack of dentition, causes their obvious assignment to the old group. If such is the case, that is, in determining age of toothless individuals with fused sutures, observations of the surface of bone, which in old individuals is strongly tuberous, with distinctly marked muscle scars and emphasized sculpture, may be helpful.

The development of the bony nasal septum, along with the outline of nasal bones, change with the individual age, much the same as the state of sutures and teeth. In young individuals (skull St I, according to NIEZABITOWSKI, 1914, as well as the specimen MZ No. VIII/Vm-453), the nasal bones are pointed in the anterior part (Text-fig. 2A) and neither project anteriorly from the anterior part of the intermaxillary bones, nor reach down to the level of their upper margins.

In this stage, the bony nasal septum is in the form of a triangular bony plate with its tip wedged in between the nasal and intermaxillary bones and projecting anteriorly of them. The posterior margin of the bony nasal septum is concave posteriorly (in the rhinoceros from Starunia it reaches to about halfway the length of the nares in its lower and to about one-third this length at a point halfway its height; NIEZABITOWSKI, *l. c.*, Pl. 8, Fig. 27). Its lateral parts, corresponding to ossified parietal cartilages (according to HOYER, 1914), bend anteriorly and downwards, projecting anteriorly of the nasal bones and downwards as far as the level of the upper margins of intermaxillary bones. In this stage, the anterior margin of the skull is formed by a bent dorsal surface of the parietal parts of the nasal septum and, at the bottom between the maxillary bones, by its vertical part (Text-fig. 3*A*, according to NIEZABITOWSKI, 1914, Pl. 13, Fig. 31).

The further development of nasal bones consists in their anterior and downward growth and in all extension of their anterior part, while the development of the nasal septum takes place by a more and more posteriorly progressing ossification and by a fusion of the septum to the surrounding bones.

In the young-adult stage, the nasal bones are strongly extended anteriorly and the lateral margins of the base of nasal horn are slightly concave, uneven and sharp (Text-fig. 2B and

Table 4

	Ye	oung	Young adult	Old adult	Old
Number of individuals Cat. Nos.	MZ No. VIII/Vm- -453 (YM), (StI)	4 KGU No. 748	5 KGU No. 736, ZAPUJ No. 683, ZG No. II-b-13-1,ZIN No. 10707, KGU No. 729	45	25 —
Dentition	Deciduous (KG a loss of the No. VIII/Vm-45 DP ¹ and DP ² , M	U No. 748 after right DP ¹ , MZ 3 after a loss of coming into use)	P ⁴ and M ³ not yet used in KGU No. 736 and ZAPUJ No. 683, P ⁴ just coming into use in ZIN No. 10707 KGU No. 729 and ZG No. II-b-13-1	M ³ in the process of abrasion, worn-off not more than down to 2/3 of the height of crown	M ³ worn-off down to about half the height of crown or more
State of sutures	All sutures not fused	Some sutures of Group I not fused	Sutures of Group I fused, of Group II not fused in ZG No II-b-13-1, partly fused (about 35% of them) in KGU No. 729 and ZIN No. 10707	Sutures of Group II fused, of Group III not fused in 44—46% of individuals; the palatomaxillary suture not fused	All sutures fused in 70% of in- dividuals. The palatomaxillary suture not fused in 30% of in- dividuals
Nasal bones (Ty- pes I, II and III, Text-fig. 4 <i>A-C</i> accordingly)	Туре І	?	Three individuals — type II; two individuals (ZIN No. 10707 and KGU No. 729) type III	Type III	Type III
The fusion of nasal and inter- maxillary bones	Lacking	Present	Present	Present	Present
Osseous nasal septum (Types A-F, Text-fig. 3A-F)	Туре А	Туре В	Type B — ZG No. II-b-13-1, Type C — KGU No. 736, Type C" — KGU No. 729	Type E — 56% of individuals (including 44% dama- ged in the posterior part of septum), Type F — 44% of individuals	Type F — 80% of individuals Type E — or F (with damaged posterior part of sep- tum) — 16% of in- dividuals Type E — 4% of individuals

A comparison of craniological and dental characters in four ontogenetic groups in Coelodonta antiquitatis (BLUM.)



Changes in the shape of nasal bones in the ontogenetic development of *Coelodonta antiquitatis* (BLUM.) *A* the shape of nasal bones in young individuals; drawn on the basis of the specimen MZ No VIII/Vm — 453; the right side reconstructed;

B the shape of nasal bones in young adults (on the basis of the specimen ZG No IIb-13-I);

C the shape of nasal bones in old adults.

Pl. V, Fig. 1). In this stage, the anterior margin of nasal bones has already a shape typical of the woolly rhino, that is, wide, rectilinearly truncate and with a projecting process halfway its length. It is situated somewhat above the level of the upper margin of intermaxillary bones, but is already connected with them by a bony bridge (Pl. III, Fig. 1). No traces of sutures occur on the bridge, which indicates that it was surely formed in the youngest age group, but probably after the beginning of the replacement of dentition, as shown by the skulls from Starunia (St I) and MZ No. VIII/Vm-453. (A complete lack in the collection of specimens with visible sutures of this region is connected with a rare occurrence in fossil state of such young individuals, in particular of the anterior parts of their skulls).

In old-adult individuals, the base of nasal horn yet more extends so that its lateral margins become convex (Text-fig. 2C). At the same time, the apex of nasal bones shifts further towards the intermaxillary bones and anteriorly. Consequently, the profile of the anterior part of skull takes an S shape.

In the young-adult group, the posterior range of the bony nasal septum is undoubtedly subject to a certain individual variability, which, due to a frequently very poor state of preservation of the posterior margin of the nasal septum, is, however, difficult to determine. It seems that in this stage the middle part of this margin is on the whole situated in the lumen of external nares, while its lower and upper part reach further posteriorly (Text-fig. 3*B*, *C*). In utmost cases, the bony nasal septum is, in this stage, complete, as in the skull of a woolly rhino from Białocerkiew, mentioned by HOYER (1914). An intermediate position is taken by skull KGU No. 729 with a completely ossified nasal septum, which is, however, somewhat damaged in its posterior and middle part and skull KGU No. 741 whose septum reaches beyond the posterior margin of nares. In skull ZIN No. 10707, the posterior margin of the septum, which halfway its height reaches a level midway the length of nares, is damaged. Judging from the length of the upper part of septum, which reaches much further posteriorly, the extent of the bony nasal septum might be considerably.

In the group of old adults, the nasal septum is mostly subject to a complete ossification and the individual variability undoubtedly occurring in this case is much lower in the rate of ossification than that in the previous age group. A fusion of the bony nasal septum with adjacent bones takes place simultaneously with its posterior growth. The fusion of the septum with skull bones is limited in the least advanced young-adult individuals (ZG No. II-b-13-1) to the lower part of the naso-intermaxillary bridge (Text-fig. 3B). Thus limited fusion of the nasal septum with adjacent bones is charactetistic of the group of young individuals, although it appears only in older representatives of this group, that is, those in which a connection has already been developed between the nasal and intermaxillary bones.

In older representatives of the group of young adults, this fusion extends along the lower surface of the nasal bones more or less to about one-third of the length of nares (Text-fig.



Fig. 3

Changes in the bony nasal septum occurring in the ontogenetic development of Coelodonta antiquitatis (BLUM.)

- A a type of the bony nasal septum characteristic of young individuals; drawn according to NIEZABITOWSKI, 1914, Pl. 8;
- B, C types of the bony nasal septum characteristic of young-adult individuals;
- D a type of the bony nasal septum characteristic of older representatives of the group "young adults" or younger representatives of the group "old adults";
- E, F types of the bony nasal septum characteristic of old adult and old (=gerontic) individuals.

The heavy line indicates the areas of fusion between the bony nasal septum and surrounding bones.

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3C, C', C'') and not including the outer margins of the nasal bones. Since lateral parts of the nasal septum closely adhere to the lower surface of the nasal bones and their fusion along the outer margins of these bones takes place considerably later, frequently it is difficult to determine how far they are fused with the nasal bones. A degree of the movability of the nasal septum may serve as an index in this respect. In the earliest development stages the septum is movable and after the fusion with the nasal bones becomes immovable. A nasal septum ossified in the anterior part of the nasal cavity (as above) and fused to the bony naso-intermaxilliary bridge and to the lower surface of the nasal bones over about one-third of the length of nares (Text-fig. 3C) is typical of the group of young adults.

The posteriorly extended bony nasal septum at first fuses neither with the bones of skull roof, nor with the maxillae and vomer, on which it only rests. Its fusion with the bones of skull roof does take place in the group of young adults but relatively late and reaches from the posterior part to the region between the orbit and the posterior margin of the external nares (Text-fig. 3D). The presence or absence of this fusion is difficult to find on account of its situation. It seems, however, that even in the skulls so advanced in the development of the nasal septum as skull KGU No. 729 there was no such fusion or, if any, it was situated very far posteriorly. Likewise, no such fusion is observed in skull KGU No. 741. On the other hand, in skull ZIN No. 10707 the upper part of the nasal septum is fused in the region between about halfway the orbit-external nare sector up to the level of the choanae, at which the fusion abruptly terminates. A double connection between the bony nasal septum and the bones of skull (in the anterior part of skull and in the middle of the skull roof, Text-fig. 1 D), also occurs in some younger individuals of the group of old adults, which is visible in skulls with the broken off nasal septum and destroyed palate, such as M. Wiś No. (10) and GI No. 54/1, which in regard to age are on the boundary between the young and old adults, as well as Wet No. 4053 and MG No. (7). In the last-named skull, probably belonging to a specimen somewhat older than skull Wet No. 4053, fused lateral parts of the nasal septum have been preserved on the lower surface of the nasal bones over the anterior one-third of the length of nares, along with a distinct trace of the fusion line running posteriorly over the skull roof from halfway the orbit-nare distance. A barely perceptible, double trace of a slight growth of the nasal septum runs sagittally through the nasal bones which connects both traces mentioned above. On the whole, in the stage of old adults, a complete fusion takes place, however, between the bony nasal septum and the lower surface of the skull roof, while its lower margin rests for a long time yet on the vomer and maxillary bones without fusing with them (Text-fig. 3E). The fusion of the nasal septum in this region takes place in older or, in this respect, more advanced individuals of the group of old adults. Of about 60 individuals of this group, more than 50% have nasal septa fused completely and on all sides, but nearly a half of them (15 individuals) are, in regard to age, on the boundary between the groups of old-adult and old individuals. Of 25 old individuals, 20 have a completely fused nasal septa and one - a septum resting on the vomer. The septa of the remaining specimens are destroyed which precludes the determination of their degree of fusion.

The rate of fusing the bony nasal septum with the surrounding bones is undoubtedly subject to a certain individual variability as, for instance, in skulls MZ No. VIII/Vm-452 and MZ No. VIII/Vm-234 which, in regard to age, are indistinguishable by the available methods (see above). The former has a nasal septum fused completely and without any traces, while the latter's septum is divided by a suture over its entire length, even in the upper part and destroyed halfway its height and at the bottom over a sector of the posterior one-third of the nares. Such a state of preservation may be indicative of the fragility of this septum or even of its incompleteness in the posterior part. It may be explained by an indeterminable but ne-

vertheless existent difference in age between the two skulls, or by a different constitution of particular individuals, which determines the differences in the rate of ossification.

As shown by a list of characters of the skull and dentition (Table 4), varying with age, a certain correlation occurs between them. This correlation is incomplete and rather statistical in character since the rate of changes in particular features may more or less vary in different development stages. The degree of the correlation is, however, sufficient for forming age groups which may be characterized by a definite development of such characters as, the state of dentition and sutures, shape of the nasal bones, their connection with intermaxillary bones or a lack of such connection and the development of the nasal septum. The most strongly variable is the rate of the development of the nasal septum, but this variability is mostly displayed in the stage of young adults and, to a smaller extent, old adults. In the two groups, the variability is emphasized by differences in the state of preservation.

VARIABILITY IN THE CRANIOMETRIC CHARACTERS

CHARACTERISTICS OF THE SAMPLES STUDIED A PROBLEM OF THE LONG- AND SHORT-HEADED FORM

Of eighteen skulls of the woolly rhino from Polish collections, fifteen (fourteen from Poland and one from Podolia, U. S. S. R.) have been adopted as a group representative of the Polish population of this species. The remaining three (ZG No. II-b-13-3, Wrocł. No. M. 369 and ZAPUJ No. 683), as coming from other geographical regions, have been excluded from the Polish group.

The studies on the variability in the craniometric characters within the Polish group of skulls, indicate a racial homogeneity of the Polish population of the woolly rhinos. This is expressed in the value of variability coefficients $V\left(V=100\frac{\sigma}{M}\right)$, which for most linear dimensions fluctuates between 4 and 7 (cf. Table 5), representing the most frequent values of V for homo-

genous samples (SIMPSON, ROE & LEWONTIN, 1960)¹. Slightly higher values of coefficient V, obtained in three cases (cf. Table 5), amounting to 7.2 (for the width of frontal bones), 8 (for the width of nasal bones) and 8.9 (for the orbit-naris distance) are indicative of a higher degree of individual variability in these characters, not contradicting the homogeneity of the population. The homogeneity of the Polish group is also confirmed by the distributions of the values of cranial angles ² and skull proportion coefficients.

They are marked by a unimodality characteristic of homogeneous samples (Tables 6-8). The three skulls mentioned above, which have been excluded from the Polish group (Wrocł. No. M 369 from Siberia, ZG No. II-b-13-3 from Rumania and ZAPUJ No. 683 from Czechoslovakia), do not deviate in linear dimensions from the skulls of this group and remain within the observed range of their variability. On the other hand, in regard to the skull proportion coefficient two of them, that is, the Czechoslovak and Rumanian skulls (with coefficients of 3.35 and 3.31 resp.) exceed the upper limit (3.27) of the theoretical range and the more so of the observed range of this coefficient for the Polish group.

¹ According to these authors (*l. c.*), the values of coefficients V for linear dimensions fluctuate, in the case of homogeneous samples, between 4 and 10 (which has been found empirically). Lower values indicate that the sample is inadequate to show the variability and higher ones reveal its heterogeneity.

² Cranial angles measured according to ZEUNER, 1934. For definition see Table 7.

Table 5

Characters (in mm)	Maximum length	Basal length	Orbit — nuchal crest distance	Orbit — nare distance	Length of nares	Width of occiput **	Width of nasal bones	Width of frontal bones	Spacing of zygomatic arches
Number of observations N	15	14	14	14	13	15	14	14	13
Mean M	741.5	631.7	390	152.8	218.8	247.9	154.2	241.1	334.1
Variance S	1551.05	716.35	438.14	188.52	77.41	134.86	155.5	303.29	378.2
Standard deviation σ	39.38	26.77	20.93	17.73	8.8	11.6	12.47	17.42	19.44
Variability coefficient V = $100 \frac{\sigma}{M}$	5.3	4.2	5.4	8.9	4.02	4.7	8.08	7.22	5.8
Observed range of variability	672—807	580—685	352-422	116-180	209—238	230-268	135—186	2 16—291	306—366
Theoretical range of variability*	622860	551—712	327-453	112—194	192—245	213—282	117—192	189—293	276—392

Statistical data for the group of skulls of Coelodonta antiquitatis (BLUM.) from the territory of Poland

* The theoretical range of variability is assumed to correspond to the actual range or variability of a given characters within the population under study, better than the observed range of variability which depends to a considerable extent on the number of observations. This range is calculated from values M and σ on the basis of the fact that, in the case of normal distributions, 99% of observations are contained within the interval of between M — 3σ and M + 3σ and 95% between M — 2σ and M + 2σ . An actual range of variability of approximately normal distributions met with in nature, is usually smaller than thus calculated range of normal distributions with identical parameters. However, due to the possibility of considerable deviations from normal distributions that may occur in nature and to the possibility of errors in calculating M and σ the theoretical range should be calculated as for normal distributions, that is, with a certain margin for errors. This is of a particular importance in the case of small samples (about 14—15 elements), in which, due to an increased possibility of error, a theoretical range of between M — 3σ and M + 3σ is used.

In larger samples (about 50 elements) a range of $M - 2.8\sigma$ to $M + 2.8\sigma$ may be used.

** Width of occiput above the external acoustic meatus.

This suggests the existence of another breed, which differs from Polish rhinos in a more slender skull. A certain light is thrown on the dimensions and on the character of these differentiations by a comparative study of the collection of the woolly rhino's skulls from the territory of the U. S. S. R. As compared with that from Poland, the Soviet collection is characterized primarily by a markedly greater variability which is quite understandable in view of its coming from an incomparably more extensive territory and perhaps of its greater differentiation in regard to the stratigraphic occurrence. Separating from this collection approximately homogenous groups similar to natural populations is very difficult on account of the lack of any data on the provenance of 50% of the specimen and the absence of stratigraphic data on the rest (in the east, there is probably a larger amount of the specimens older stratigraphically). The specimens of an approximately known origin have been divided into two groups, one of them from the European part of the U. S. S. R. and the other from Siberia. In further considerations, these groups are considered separately. Specimens from the U. S. S. R. but coming from an unknown locality make up the third group.

Table 6

Frequency distribution of the skull proportion coefficients for Coelodonta antiquitatis (BLUM.) from the territory of Poland

Values of coefficient	2.86—2.9	2.91-2.95	2.96—3.0	3.01-3.05	3.06—3.1	3.11—3.15
Frequency	2	5	3	2	2	2

Table 8

Frequency distribution of the value of angle m for the skulls of Coelodonta antiquitatis (BLUM.) from the territory of Poland

Angle values	39°—42°	43°—46°	47°—50°	51°—54°	55°—58°	59°—62°
Number of observations	1	0	2	6	2	0

Table 9

Frequency distribution of the value of angle o for the skulls of Coelodonta antiquitatis (BLUM.) from the territory of Poland

Angle values	44°47°	48°51°	52°—55°	56°—59°	60°—63°
Number of observations	1	2	6	3	0

The sample of skulls from the European part of the Soviet Union is in many respects similar to a homogeneous group which does not differ racially from the Polish population. It is, however, more variable than the Polish population as primarily indicated by the values of variability coefficients V (Table 11) for all the characters under study larger than for the Polish group, although remaining within limits of a standard for homogeneous samples (see page 19). The distributions of the values of the skull proportion coefficient (Table 10) and the distributions of angles o, m and y (Tables 12—14) are unimodal which confirms the hypothesis on an approximate homogeneity of the group from the European Russia.

Table 10

Frequency distribution of the skull proportion coefficient for Coelodonta antiquitatis (BLUM.) from the European Russia

Values of coefficient	2.71—2.8	2.81—2.9	2.91-3.00	3.01—3.1	3.11-3.2	3.21—3.3	3.31—3.4
Number of observations	3	5	14	6	2	2	1

Table 11

Comparison of variability coefficients V for various craniometric characters in the Polish group, in the group from European Russia, in the mixed group from the entire USSR and in the Siberian group

Character	Length of nares	Basal length	Width of occiput *	Maximum length	The orbitnuchal crest distance
Poland	4.02	4.2	4.7	5.3	5.4
European Russia	7.8	5.2	6.1	6.8	6.3
The entire USSR	6.5	4.6	7.2	6.8	7:3
Siberia	6.65	3.4	7.0	3.7	7.2

Country	Character	Spacing of zygomatic arches	Width of frontals	Width of nasals	The orbit-nare distance
Poland		5.8	7.22	8.08	8.9
European Russia		5.9	6.84	9.7	8.8
The entire USSR		5.75	9.56	11.4	8.31
Siberia		4.75	5.59	5.55	6.33

* Above the external acoustic meatus.

Table 12

Frequency distribution of the values of angle o for the skulls of Coelodonta antiquitatis (BLUM.) of the European Russia

Values of angle	40°44°	45°—49°	50°—54°	55°—59°	60°—64°
Number of observations	1	10	15	2	1

Table 7

Inv. No. No. ŝ ∞ ZAPUJ No. MZ No. VIII/Vm 3 MZ No. VIII/Vm ZG No. II-b-13-3 ZG No. 11-b-13-2 MZ No. VIII/Vm MZ No. VIII/Vm No. MZ No. VIII/Vm MPL No IV-3-IA No. ZG No. 11-b-13-1 No. No. Š. No. MG MG ZZ Dimensions RS Rz Σ Maximum length (acrocranion-rhinion measured along the upper surface of skull) Basal length (basion-position, measured parallel to palate Length of external nares ----Distance from lacrimal tubercule to nuchal crest Distance from lacrimal tubercule to the posterior margin of external nares Length of palate -___ ____ Length of choanae (to pterygoid process) --------_ ____ Distance from basion to posterior alar foramen -Width of occiput just above the external acoustic meatus Maximum width of nasal bones ok. 162 Maximum width of frontal bones Maximum width on zygomatic arches ____ ok. 336 ok. 356 Height of occiput Maximum height of skull in the region of the nasal horn _ Angle γ between the axis of the foramen magnum and palate 98.5 ____ _ Angle *m* between the axis of the foramen magnum and the parietal part of the skull roof 39.5 53.5 49.5 50.5 53.5 52.5 ____ Angle p between the parietal part of the 51.5 skull roof and occiput 45.5 48.5 56.5 57.5 --2 7.5 -2.5 —3 --6 -0.5 ---3.5 -0.5-17.5x = m - o_ Skull proportion coefficient (maximum length to width of occiput above the external acoustic meatus) 3.14 3.04 3.02 2.96 2.86 3.35 3.31 3.01 2.86 2.91 2.98 2.93 3.15 2.93

Dimensions of the skulls of Coelodonta antiquitatis (BLUM.) from Polish collections (linear dimensions in mm)

Table 13

Frequency distribution of the values of angle m for the skulls of Coelodonta antiquitatis (BLUM.) of the European Russia

Values of angle	36°—40°	41°—45°	46°—50°	51°—55°	56°—60°	61°—65°
Number of observations	2	3	6	15	6	0

Table 14

Frequency distribution of the values of angle y for the skulls of Coelodonta antiquitatis (BLUM.) of the European Russia

Values of angle	85°—89°	9 0° —94°	95°—99°	100°—104°	105°—109°	110°—114°	115°—119°
Number of observations	1	1	6	13	8	1	0

In regard to linear dimensions, the sample of skulls from the European Russia differs from the Polish sample in larger values of the means of these dimensions (cf. Table 16). This is accompanied by an extension of the variability range for these dimensions and for same characters (maximum length, width of occiput, width of frontals and length of nares) the upper limit of this range is shifted upwards beyond the limit of the theoretical variability range of the Polish population.

The group of skulls, known to come from Siberia, consists of only nine specimens, which to a certain extent makes its representative character questionable. The low representative qualities of this group is also indicated by very low values of the variability coefficient, in particular that of the maximum length (cf. Table 11). The data obtained from this group of specimens indicate a larger mean length of the skull, which is probably connected with an upward shift in variability range as compared with the sample from European Russia. These data also indicate a higher mean coefficient of skull proportions (Table 16).

Table 15

Frequency distribution of the skull proportion coefficient in *Coelodonta antiquitatis* (BLUM.) in the mixed group from the entire USSR

Value of coefficient	2.71-2.8	2.81—2.90	2.913.0	3.01—3.1	3.11—3.2
Frequency	2	4	15	6	12
	·				
Value of coefficient		3.21—3.3	3.31—3.4	3.41—3.5	3.51—3.6
Frequency		6	2	2	1

In the case of the skull proportion coefficient, the question is not shifting both limits of variability upwards, but only an increase in the part of skulls with very high values of this coefficient as compared with the sample from European Russia and in particular that from Poland. The extensive variability range and very large standard deviations with so small a number of individuals may be indicative of a non-homogeneity of the Siberian sample in this respect.

A certain light is thrown on the shaping of skull proportions in the woolly rhino by the results of studies on skull proportion coefficients in the mixed group, whose representatives



Fig. 4

Frequency polygons of the skull proportion coefficient in the mixed group from the entire territory of the U. S. S. R. (continuous line), in the group from the European part of the U. S. S. R. (dotted line) and in the Polish group (dotted and dashed line). Cf. Tables 6, 10, 15.

come from the entire territory of the Soviet Union. In regard to the proportion coefficient, the mixed group displays a conspicuous non-homogeneity, which is manifested by the presence of two modes in the frequency distribution of this coefficient (Table 15, Text-fig. 4).

As follows from this frequency distribution, two forms of the woolly rhino, one with a more slender and the other with a more stocky skull, occurred in the mixed group. They undoubtedly correspond to the long- and short-headed forms of the woolly rhino, whose existence was first found by BRANDT (1848) and which, according to this author (l. c.) were supposed to differ in skull proportions. These differences were interpreted by NIEZABITOWSKI (1914) as an expression of sexual dimorphism, but his hypothesis was not confirmed by the studies on the frequency distribution of skull proportion coefficient in the group from Poland and European Russia. These distributions do not display a bimodality characteristic for those concerning the

Table 16

Measurements		Number of observations	Mean M	Standard deviation σ	Observed range of variability	Theoretical range of variability *
Maximum length (in mm)	Р	15	741.5	39.38	672-807	622—860
	ER	34	768.5	52.25	650—874	622—915
	USSR	53	762.8	52.04	675—871	_
	S	9	787.2	28.93	755—859	—
Basal length (in mm)	Р	14	631.7	26.77	580-685	551—712
	ER	30	645.5	33.84	579—710	_
	USSR	43	641.8	28.59	589—708	
	S	6	649.5	21.81	629694	—
Width of occiput above the external	Р	15	247.9	11.6	230268	213-282
acoustic meatus (in mm)	ER	33	257.8	15.82	219—295	
	USSR	53	247.5	17.8	212-283	
	S	9	254.4	17.84	228283	—
Width of nasal bones (in mm)	P	14	154.2	12.47	135—186	117—192
	ER	34	161.5	15.67	135—200	_
	USSR	52	157.5	17.92	128—191	_
	S	9	164	9.11	146177	
Skull proportion coefficient	Р	15	3.0	0.09	2.86-3.15	2.73-3.27
	ER	33	3.0	0.137	2.78-3.34	
	USSR	51	3.09	0.17	2.76-3.55	
	S	9	3.1	0.16	2.83-3.37	

Comparison of statistical data for the groups of skulls of *Coelodonta antiquitatis* (BLUM.) from Poland (P.), European Russia (ER), Siberia (S) and for the mixed group from the entire territory of the U. S. S. R. (USSR)

* This range for the fifteen elements Polish sample amounts to between M-3 σ and M+3 σ and for the 50-elements group of skulls from European Russia – M-2.8 σ and M+2.8 σ .

features which are subject to sexual dimorphism. Hence, the differentiation observed in the mixed group has to be connected with differences of another type, probably racial ones. On the basis of the frequency distribution of the skull proportion coefficient in the mixed group, one may suppose that on the territory of the Soviet Union there occurred two breeds of the woolly rhino, but it is not yet known whether or not this differentiation was more complex. The variability ranges of the skull proportion coefficient in the two stocks overlap each other to a considerable extent, so that no distinct boundary occurs between them (Text-fig. 4). In the undivided mixed group, the mode of this coefficient for "short-headed" forms is contained within an interval of 2.91 and 3.0 and for "long-headed" forms between 3.1 and 3.2. Actually, the theoretical mode for "long-headed" forms may be higher and for "short-headed" ones this value may be lower than those given above.

It should be emphasized that the skull proportion coefficient is an only character displaying a distinct bimodality of the frequency distribution in the mixed group and, therefore, an only character distinctly differentiated racially. Other characters, both linear and angular, display in this group of specimens — a considerable and fairly irregular variability, which, however, does not exceed the standards for homogenous groups. Thus, they are not subject to a direct racial differentiation.

Of interest is the fact that the diagram of the skull proportion coefficient for the group from European Russia is almost identical with the left-hand side of the diagram for the mixed group. This side of the diagram is also resembled by that for the Polish skulls which, in regard to the mode, is in conformity with it and with the frequency distribution of the group from European Russia. The high mean value of the skull proportion coefficient for the Siberian group mentioned above may indicate (under the stipulation that this sample is not representative enough) that the long-headed forms were numerously represented in Siberia and perhaps even were a race of the Siberian origin. Since, however, short-headed forms are also relatively numerous in the Siberian group, one may suppose that the long-headed form represents not a geographical race but a variety older stratigraphically. Such a variety would be most frequent in Siberia, a region of a possible origin of *Coelodonta antiquitatis* (BELAYEVA, 1966). Its numerous representatives were also recorded, as an admixture, in European Russia and single specimens are known from Czechoslovakia, Rumania and Sub-Carpathian region (ZAPUJ No. 368, ZG No. II-b-13-3, St I).

In view of the scarcity of information on the origin of skulls from Soviet collections, in particular the lack of stratigraphic data, the interpretation of the "long- and "short-headed" forms as stratigraphic varieties cannot be supported by any weighty argument. It may be backed up only by slenderer proportions of bones recorded in the early representatives of this species (BOULE *et al.*, 1928; TEILHARD DE CHARDIN *et al.*, 1930 — after BELAYEVA, 1966).

SEXUAL DIMORPHISM IN THE DEVELOPMENT OF SOME CRANIOMETRIC CHARACTERS

In the group of Polish skulls homogenous racially, the frequency distribution values of some of the craniometric characters display an undoubtful, although due to a small number of specimens, not always distinct bimodality. This concerns the width of occiput (measured above the external acoustic meatus), maximum length, the orbit-nuchal crest and orbit-nares lengths (Table 5, measurements 4 and 7 respectively) and the width of skull in the region of zygomatic arches.

The differentiation, seen in Tables 17-21, is most likely to be connected with the sexual dimorphism. The correctness of such a supposition is supported by sexual dimorphism shown

Table 17

Frequency distribution of maximum lengths of the skulls of Coelodonta antiquitatis (BLUM.) from the territory of Poland

Length (in mm)	671—690	691—710	711—730	731—750	751—770	771790	791—810
Number of observations	2	2	2	3	1	2	3

in the length and width of skulls, found by HELLER (1913) in the white rhinoceros Ceratotherium simum. This dimorphism is manifested by the bimodality in frequency distribution (Table 22), much the same as that observed in C. antiquitatis.

Table 18

Frequency distribution of the orbit-nares lengths in the skulls of Coelodonta antiquitatis (BLUM.) from the territory of Poland

Length (in mm)	113—124	125—134	135—144	145—154	155—164	165—174	175—184
Number of observations	1	0	4	3	1	3	2

Table 19

Frequency distribution of the orbit-nuchal crest lengths in the skulls of *Coelodonta antiquitatis* (BLUM.) from the territory of Poland

Length (in mm)	350—369	370—389	390409	410—429	430—449
Number of observations	1	7	2	4	0

Table 20

Frequency distribution of the width of occiput above the external acoustic meatus in the skulls of *Coelodonta antiquitatis* (BLUM.) from the territory of Poland

Width (in mm)	225234	235—244	245—254	255—264	265—274
Number of observations	1	4	6	1	3

Table 21

Frequency distribution of the width of skull in the region of zygomatic arches in the specimens of *Coelodonta antiquitatis* (BLUM.) from the territory of Poland

Width (in mm)	301—310	311—320	321—330	331—340	341—350	351—360
Number of observations	1	3	0	5	2	2

Table 22

Frequency distribution in maximum length of the skull of *Ceratotherium simum cottoni* (on the basis of Heller's 1913 measurements)

Lengths (in mm)	670699	700—729	730—759	760—789	790819	820—849
Number of observations	0	1 ♀	1 ♀	6 (5♀+1♂)	1 ठ	4 đ

The sexual dimorphism here is not, however, complete (complete sex dimorphism sensu KURTEN, 1955), but partial (partial sex dimorphism, *l. c.*). Its ranges for male and female animals overlap to a considerable extent, which slightly obliterates the bimodal character of the distribution and causes that the sexual dimorphism does not reflect fundamentally in the value of coefficient V. Since, however, in the case of the white rhinoceros we have to do with specimens of a definite sex, it is easy to divide each of the distributions under study into two ones, of which the distribution for the female animals is marked by the shifting of the variability range downwards as compared with that for the males.

In the light of these facts, the occurrence of sexual dimorphism, expressed in the differentiation in length and width of skulls in *Coelodonta antiquitatis* (Tables 17—21) seems to be very likely. The fairly strong overlapping of the range of variability for males and females decreases the possibility of a correct sex determination on this basis. In practice, the sex determinability of the specimens of the woolly rhino is limited to the individuals included in the extreme intervals of frequency distributions, provided that these are specimens of the same population for which the distribution is prepared. On the basis of this consideration the sex of specimens MPŁ No. IV-3, M No. (3) and MZ No. VIII/Vm-452 may be determined as male. These specimens are, in all the four distributions under study, in the intervals of the highest values (except for skull MZ No. VIII/Vm-452 in respect to the nuchal crest — orbit length). On the other hand, specimens RS No. (14), ZG No. IIb-13-2 and MZ No. VIII/Vm-146 are probably females, although the meaning of the frequency distributions is not so unequivocal as in the case of the males.

Table 23

Frequency distribution of the width of nasal bones in Ceratotherium simum cottoni (on the basis of Heller's measurements 1913)

Width (in mm)	140—159	• 160179	180—199	200-219
Number of observations	3 ♀	5 (4♀+1 ♂)	2 చి	4 ठ

Table 24

Frequency distribution of the width of nasal bones in Coelodonta antiquitatis (BLUM.) from the territory of Poland

Width (in mm)	130—139	140—149	150—159	160—169	170—179	180—189
Number of observations	1	4	7	0	1	1

Table 25

Frequency distribution of the width of frontal bones in Coelodonta antiqitatis (BLUM.) from the territory of Poland

Width (in mm)	210—229	230—249	250—269	270—289	290—309
Number of observations	2	9	2	0	1

The undoubtful correlation between the width of nasal and frontal bones (that is, the size of the nasal and frontal horn) and the sex in rhinos, which may be observed in the Recent rhinos (cf. Table 23) is not distinct in frequency distributions of these characters for the woolly rhino (Tables 24 and 25). This is probably caused by the mutual overlapping of the variabilities of different types, connected with the sexual dimorphism, individual age and individual features of particular specimens.

The studies on the variability of craniometric features in the group of skulls from European Russia confirm the occurrence of the sexual dimorphism in the development of such characters as, the maximum length of skull, the orbit-nares distance and the spacing of zygomatic arches (cf. Tables 26–28). Other craniometric characters subject to dimorphism such as, the nuchal crest — orbit distance, width of occiput and of nasal bones, do not display distinct bimodality probably as the result of a considerable variability in this group of skulls (see above).

Table 26

Frequency distribution of the maximum length of skulls of Coelodonta antiquitatis (BLUM.) from European Russia

Length (in mm)	650—669	670689	690—709	710—729	730—749	750—769
Number of observations	1	1	2	4	5	6
Length (in mm)	770—789	790—809	810—829	830—849	850869	870—889
Number of observations	3	5	2	2	2	1

Table 27

Frequency distribution of the orbit-nares length in the skulls of Coelodonta antiquitatis (BLUM.) from European Russia

Length (in mm)	115—124	125—134	135—144	145—154	155—164	165—174	175—184
Number of observations	1	0	6	9	5	9	2

Table 28

Frequency distribution of the width of skulls in the region of zygomatic arches in Coelodonta antiquitatis (BLUM.) from European Russia

Width (in mm)	295—304	305—314	315—324	325—334	335344
Number of observations	1	2	3	6	3
Width (in mm)	345—354	355—364	365—374	375—384	385394
Number of observations	6	4	- 1	1	1

CORRELATIONS BETWEEN CRANIOLOGICAL CHARACTERS IN COELODONTA ANTIQUITATIS (BLUM.)

The studies on craniometric characters of the groups of skulls from Poland and the Soviet Union allowed the writer to find the existence of certain correlations between these characters, as well as between craniometric and some of the craniological characters such as, the development of the bony nasal septum.

The strongest positive correlation occurs between the maximum length of skull and the angle of the inclination of the axis of the foramen magnum to palate (y). This correlation is observed both in the Polish collection and, more distinctly, in the more numerous, although less homogenous, skull collection from the USSR. It is most strongly manifested for extreme values of length and cranial angles and becomes obliterated near the mean values.

In the Polish collection, the skulls with extreme values of angle y 91° and 111° have maximum lengths amounting to 684 and 807 mm respectively, which make up extreme values of these dimensions for this collection. The same is observed in the case of mean values of maximum lengths of the skulls, calculated for the groups of specimens with various values of angle y in both the Polish and Soviet material (Table 29).

Та	ble	29
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Correlations between craniometric characters of Coelodonta antiquitatis (BLUM.) from Poland and the USSR.

Specimens		Mean values of maxi- mum length of skulls (in mm)		
s	kulls from Poland with:			
angle y between 91° and 103°		717		
a	ngle y between 104° and 113°	770		
s	kulls from the USSR. with:			
angle y below 100°		745		
angle y more than 100°		790		
s	kull proportion coefficient below 3.01	752		
s	kull proportion coefficient more than 3.11	782		
1				

The biomechanical significance of this correlation is distinctly visible. The tendency to the inclination of the skull in relation to the neck and, consequently, to an increase in angle y is the stronger the larger is the load of the anterior part of skull and the longer is the distance from the point thus loaded to the atlanto-occipital joint (that is, the longer is the arm of acting force). Obviously, some role is here also played by the size of the nasal horn and length of skull. This correlation is decreased by the influence of neck musculature which tends to keep the equilibrium in the atlanto-occipital joint without changing angle y, which is a character stabilized specifically (ZEUNER, 1934) and marked by a small range of variability.

A certain correlation is also observed between the maximum length and the value of the skull proportion coefficient. In the Polish group, this correlation is most strongly manifested in extreme parts of the frequency distribution so that in the case of the longest five skulls, whose mean length amounts to 787.6 mm, a mean skull proportion coefficient is 3.06 and of the shortest five skulls, whose mean length amounts to 695 mm, a mean coefficient is 2.93.

This correlation also occurs in the group of skulls from the USSR. (cf. Table 29). Despite this fact, it seems that there is no actual causal nexus between the length of skull and the coefficient of its proportions. A dependence of the two values on some other factor common for both of them, seems more likely.

The correlation between the length of skull and the coefficient of its proportions is not strong enough to cause the manifestation of sexual dimorphism concerning skull proportions in such a not very variable group as the Polish population of the woolly rhino. On the other hand, the fact that the individuals representing the long-headed form of the woolly rhino are longer statistically and vice-versa distorts the picture of the sexual dimorphism as concerns the length of skull in the mixed group (Table 30).

Table 30

Frequency distribution of the maximum lengths of the skulls of *Coelodonta antiquitatis* (BLUM.) from the entire territory of the Soviet Union

Length (in mm)	660—679	680—699	700—719	720—739	740—759	760—779
Number of observations	1	5	5	9	4	10
Length (in mm)	780799	800—819	820—839	840—859	860879	-
Number of observations	7	2	6	1	2	_

It is likely that a certain correlation also occurs between the degree of ossification of the nasal septum and the value of angle y. Due to a large number of factors affecting the development of the nasal septum, in particular the individual age and state of the specimen's preservation, this correlation is rather elusive.

The observations were conducted in a group of old adult specimens, in which the differences in the development of the nasal septum give evidence of the actual differences in the degree of ossification. It was assumed at the same time that the state of preservation of the nasal septum is connected with the degree of its development in the individual's lifetime.

From the studies on the correlation between the value of angle y and the development of nasal septum, it follows that 44% of old-adult individuals with angle y larger than 101° (mean value 105°) had an incomplete or less strongly developed (damaged in fossil state) nasal septum, while only 18 per cent of the individuals of the same age but with angle y lesser than 101° (mean value 96°) had an incomplete or probably less strongly developed (destroyed) nasal septum.

The essence of this correlation probably consists on the one hand in the manner of mounting the horn on the skull with various cranial angles and on the other in the effect of the function of horn on the process of ossification of the nasal septum. With larger values of angle y the skull was more strongly inclined in relation to the ground level and the nasal horn, placed in the woolly rhino almost parallel to this level, was in a more perpendicular position to the axis of skull than in the case of lower values of angle y. The smaller angle y the more conspicuous was a decrease in the value of an angle between the axis of horn and the longitudinal axis of skull. This caused an extension of the range of forces acted on the horn deep into the nasal cavity. The action of these forces, compressing and stretching the horn base, as well as of the shocks, passing from the horn base onto the nasal septum, was probably a factor exerting its influence on the ossification of the septum. Thus, in the case of a small range of the forces in the nasal cavity and with high values of angle y, the ossification might be smaller than in the case of a low value of angle y accompanied by an increased range of forces acting through the horn on the nasal septum. This explains the correlation discussed above.

AN ANALYSIS OF THE MUSCULO-SKELETAL SYSTEM OF THE WOOLLY RHINO AS COMPARED WITH THOSE OF THE RECENT RHINO

The comparison of the structure of the postcranial skeleton of the woolly rhino from Podbaba (Cat. No. ZAPUJ 683) with those of the Recent rhinos reveals many differences. The greatest of them are observed in the development and position of spinous processes which is connected with certain differences in musculature and functions of vertebral column.

In regard to the position of spinous processes in the posterior part of the thoracic and lumbar regions of the vertebral column, the woolly rhino's position is transitional between the black and the Javanese rhinos on the one hand and the white rhino on the other. Like the Recent species, mentioned above, it is characterized by the lack of an anticlinal arrangement of spinous processes, but, in contrast to D. bicornis and Rh. sondaicus, its spinous processes do not incline caudad in the postdiaphragmatic region but are arranged more or less perpendicularly to the axis of vertebral column. The vertebral column of the white rhino, apparently differing from those of the species mentioned above, in particular of the woolly rhino, in the presence of anticline, has actually much the same as the last-named species, its spinous processes arranged vertically beginning with the 17th thoracic vertebra. The difference in relation to the woolly rhino here consists mainly in a stronger caudal inclination of the spinous processes of the 11th to 16th thoracic vertebrae and in their shape (longer, slenderer and caudally bent on the apex). C. simum and D. bicornis are similar to each other both in shape and strong inclination of the processes of this region, which is probably connected mostly with a similar development in the two species of the multifidus and the submultifidus muscles. On the other hand, the arrangement of spinous processes in the postdiaphragmatic sector of the vertebral column is connected (according to SLIJPER, 1946) with the position of caudal attachments of the longissimus dorsi muscle. Their posterior turn is indicative of a shift of these attachments towards the sacrum, which is connected with the disappearance of the mobility of the postdiaphragmatic sector of vertebral column (l. c., p. 104), especially characteristic of heavy representatives of the Ungulata.

Adopting a structural model in the form of the epaxial spinal musculature in D. bicornis (l. c., Fig. 46) in which the caudal muscle attachments of m. longissimus dorsi begin with the 19th thoracic vertebra (according to SLIJPER, 1946, the number of thoracic vertebrae in the black rhino amounts to 21 and in the specimen of D. bicornis Inv. No. MIZ there are 19 of them), we may suppose that these attachments started in both the woolly (cf. p. 57) and white rhino more cranially. The fact that the two species are similar to each other in the degree of the flexibility of the postdiaphragmatic part of vertebral column may be either explained by their relatively smaller adaptation to running or, in view of the well known similarities in their mode of life (herbivorous, steppe forms, ZEUNER, 1934), the preservation of this flexibility may be related to the necessity of lowering the vertebral column during grazing (according to SLIJPER,
1946, p. 57, in the horse, the point of an increased flexibility is located just before the diaphragmatic vertebra).

In regard to the structure of limbs, the strongest differences are observed in the proportions of particular bones (Table 20) and in the morphology of some of them, in particular of the scapula, humerus and femur.

The scapula of the woolly rhino is characterized by the caudal angle more strongly extended posteriorly than in the black rhino (Pl. VIII, Fig. 1a, b; Pl. 1X, Fig. 2a, b), by a more deeply concave posterior and a more convex anterior margin. The curve of the posterior margin of scapula is caused in part by a posterior shift of the glenoid cavity and in part by the caudad development of the posterior angle of scapula which may be explained by the tendency of here attached muscles, in particular m. teres major and m. deltoideus, to decreasing the angles of muscular inclination by a posterior shift of their initial attachments. The lower scars of these muscles are indicative of an equal degree of development in both species.

Despite the curve of the posterior margin of scapula in *C. antiquitatis*, the width of the infraspinous fossa is not smaller in this species than in *D. bicornis*. The convexity of the anterior margin of scapula in the woolly rhino is connected with the extensiveness of the attachment of m. pectoralis profundus, whose maximum width amounts in this place to about 28 mm, that is, 21 per cent of the width of scapula at this level and in the black rhino to 6 mm equalling about 4 per cent of the width of scapula. Below the attachment of the pectoralis profundus muscle, the margin of scapula in the woolly rhino is more strongly concave than in *D. bicornis* and consequently, the attachment of m. supraspinatus strongly contracts in this region.

The scapula of *Rh. sondaicus* differs from that of *C. antiquitatis* in its posterior margin which is more concave in the supraglenoid region. Near the posterior angle of scapula, the posterior margin is less concave in *Rh. sondaicus* than in *C. antiquitatis*, which is connected with a stronger development of the posterior angle of scapula in the last-named species. The strongly convex anterior margin of scapula is indicative of the extensiveness of the attachment of the pectoralis profundus muscle. The area of this attachment is here, however, differently shaped than in the woolly and black rhinos. It does not form a depression near the margin of outer surface, but it is situated on the margin of scapula of the Javanese rhino is marked by a very strong (as compared with that of the woolly rhino) scapular spine with an apical angle smaller than 90°, as well as an extensive scar of m. trapezius. This spine is bent posteriorly onto the infraspinous fossa which is larger than the supraspinous fossa. This is particularly distinct in its upper part and not recorded in either the woolly or black rhino.

The humerus of the woolly rhino differs from that of the Recent, black and Javanese rhinos in the following morphological details:

The degree of the medial inclination of the head to the axis of the shaft. In the woolly rhino, it is inclined at an angle of 73° , which results in a slight downward convergence of the humeri — a character unadaptative from the viewpoint of fast running. In the black and Javanese rhinos the transverse diameter of caput humeri is perpendicular to the shaft.

The longitudinal diameters of caput humeri in all the three species are arranged at a more or less identical angle (about 40° to 50°) to the shaft. This might indicate an identical value of the scapulo-humeral angle in the species compared and, consequently, a certain extent of adaptation to running. Since the differences found in the morphology of the skeleton are small and contained within limits of one and the same, principal, adaptable type, these angles might actually be identical. It is not unlikely, however, that the ranges of variability of this feature, not yet known at present, differed from each other to a certain extent. If such would be the case,

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we might expect that the inclination of caput humeri to the shaft would be smaller in the woolly rhino.

The lesser tubercle in the woolly rhino is bifid with its anterior part higher than posterior. The major tubercle of this species is similarly developed as that in the Javanese rhino. On the other hand, in the black rhino, this tubercle is indivisible and its anterior part is even slightly lower than posterior. This character is bound to be related with the development of the terminal, external attachment of m. supraspinatus. It is difficult, however, to interpret it more accurately.

The tuberculum intermedium, which sustains the tendon of the biceps brachii in the horse, is lacking in the woolly rhino. It is, however, substituted by the medial bend of the apex of the lateral tuberosity, which prevents the tendon of the biceps brachii from shifting. The tuberculum intermedium occurs in the black, Javanese and white rhinos. It is situated in the intertubercular groove on the lateral wall of the medial tuberosity and is somewhat flatter than in the horse.

The development of the curved line and tuberculum tereticum. In the woolly rhino, the curved line is on the whole very strongly developed, which results in a considerable width of the lower part of a muscle area, contained between the lateral and deltoid tuberosity. In the studied specimens of the black and Javenese rhinos (Cat. No. MIZ), this area is strongly narrowed ventrally as the result of a poor development of linea anconea. They also lack tuber-culum tereticum which may be connected with a poor development of the teres minor. It is not unlikely, however, that the degree of the development of a scar of the last-named muscle and the curved line is subject to the individual variability and it certainly depends on the individual age.

The ulna of the woolly rhino differs from that of the black rhino mostly in a stronger elongation of the olecranon. In the woolly rhino, the length of this process varies within limits of 140 and 180 mm and in the black rhino - of 112 and 123 mm, the shaft of ulna being in the latter somewhat longer. The significance of such an elongation of the ulnar process is obvious. On the one hand, it shifts the attachment of muscles (caput longum m. tricipitis) frcm the rotation axis of the joint which they operate and, on the other, it increases the angle of insertion of scme muscles (this may concern also the remaining heads of the triceps). It seems that the elongation of the olecranon in the woolly rhino took place mostly by the dorsal growth of a tuber destined for the long head of the triceps. On the other hand, the position of the lateral and medial heads of the triceps do not differs at all, or differs to a very small extent only, from the arrangement of these muscles in the black and Javanese rhinos. The comparison of the olecranons, in particular the morphology of the tuber olecranii, of the woolly and black rhinos, reveals, however, a considerably stronger development of the bony attachments of muscles in the former animal. This concerns both the long and the remaining heads of the triceps brachii (cf. the thickness of the tuber olecranii, Table 42). This fact distinctly corresponds to the stronger development of the linea anconea and elongation of the posterior angle of scapula in the woolly rhino. Keeping an angle between the humerus and the forearm is one of the tasks of the triceps brachii. The development of this muscle and increase in the efficiency of its long head in the woolly rhino was probably connected with difficulties in keeping this angle with an increased body weight. These are, therefore, graviportal adaptations.

The carpus of the woolly rhino differs from those of the black and Javanese rhinos only in a few minor details, such as, the proportions of the magnum and development of the posterior process of this bone. In the woolly rhino, the height of the anterior wall of magnum is to its width as 1:2, while in the black rhino this ratio amounts to 1:1.5 and in the Javanese to 1:1.3. The posterior process of magnum in the black rhino has the form of a thin rod, provided posteriorly with a tuberosity and projecting posteriorly and slightly ventrally from the ventroexternal angle of the posterior wall of this bone. In the woolly rhino, this process is much more robust and having at its end a strong, bony muscle attachment scar. In the Javanese rhino, this process, almost equally robust, is, however, devoid of a distinct muscle scar at its end which is pointed and slightly turned ventrally.

The above mentioned features of the carpi in the species compared seem to indicate a more graviportal character of the limbs of the woolly rhino. However, in view of the lack of data on the intraspecific variability in the development of these features of carpus and of accurate indications concerning the attachment place of the interosseus medius and, possibly, other short flexors of the manus, it is difficult to interpret accurately these differences.

The pelvis of the woolly rhino differs from those of the black and Javanese rhinos primarily in larger dimensions (cf. Table 45). With such a large size of pelvis, conspicuous becomes a small length of the ischium in the woolly rhino, which results in considerably less favorable conditions to the operation of muscles attached to the tuber ischii (GREGORY, *in* OSBORN, 1929), that is, m. semitendinosus, m. semimembranaceus and m. biceps femoris, than those in the case of Recent species compared. This is indicative of a relatively poorer adaptation of this rhino to fast running.

Remarkable is also a relatively small width of the shaft of the ilium, but the interpretation of this fact encounters certain difficulties. It might seem that the small width of the shaft of the ilium indicates a poorer development of m. gluteus profundus in the woolly rhino. This is, however, contradicted by the development of the distal attachments of this muscle, situated on the upper surface of the trochanter major (Text-fig. 11*d*). These muscle scars are much more strongly developed in the woolly rhino (Pl. XXII, Figs. 1*b*, 2, 3), which, however, concerns only its anterior part, while the posterior part is developed in both Recent species to a similar extent as in the woolly rhino or even somewhat better (in *D. bicornis*). It is not unlikely that in the black rhino this muscle was actually strong but it was attached to the trochanter major more posteriorly than in the wcolly rhino.

The comparison of femora of the woolly, Javanese and black rhinos reveals in addition the following differences.

The trochanter minor in the woolly rhino is situated lower than in the two Recent species. The apex of this trochanter is slightly above the level of the third trochanter, while in the black rhino it is situated more or less halfway between the third and major trochanter. In the Javanese rhino (Cat. No. MIZ), it is situated just below the level of the trochanter major, but, due to the fact that the skeleton studied belongs to a young individual, this may be not a final position, much the same as a relatively high situation of the third trochanter (Table 46).

A great massivity of the femur in the woolly rhino (Table 31), is particularly distinctly visualized in posterior view and emphasized by a perimedial concavity of the medial border of the shaft (Pl. XX, Fig. 1 b, 2) relatively slight as compared to that of the black rhino, in which this concavity is very strong and causes a considerable decrease of the area of muscle scars on the posterior side of the bone. This concerns in particular the attachment of the quadratus femoris and adductor femoris. On the anterior side of the bone, it is accompanied by a distinct reduction in the attachment area of the vastus medialis.

In regard to absolute lengths, the long bones of the Recent, Javanese and black rhinos do not depart very much (cf. Tables 40—42 and 46, 47) from the dimensions of such bones in the woolly rhino. The variability ranges were probably shifted in them, as compared with the woolly species, slightly downwards, but, on account of too scant a comparative material it cannot be stated with a certainty.

Table 31 presents the indexes of the proportions of long bones in the woolly rhino and

3 .

the Recent species *D. bicornis* and *Rh. sondaicus* compared with it. It follows from these comparisons that the long bones in the woolly rhino were more massive than those of the Recent species.

Table 31

Widths of the bones of limbs expressed as a percentage of the length of bones * in C. antiquitatis (BLUM.), D. bicornis L. and Rh. sondaicus DESM.

Species			
Bone. Kind of width	C. antiquitatis	D. bicornis	Rh. sondaicus
Humerus the minimum width of shaft	16%—18%	15%	14%
the width of shaft at the level of the tuberosites deltoidea	34%-39%	32%35%	33%
Radius the minimum width of shaft the width of distal end	15%—18% 31%—33%	14% 25%—26%	 below 29%
Ulna the minimum width of shaft the anteroposterior dimension of the	13%—14%	9%-11%	_
shaft (as in Table 42) Femur	12%—14%	11%-12%	_
the minimum width of shaft Tibia	18%-21%	13%—15%	15%
the width of proximal end the smallest width of shaft the width of distal end	42%—46% 22%—25% 35%—37%	36%—40% 19%—20% 30%—36%	44% 20% 36%

* Maximum length of humerus and radius, length of the shaft of ulna, length of femur on the medial side and length of tibia on the lateral side.

In regard to the indexes of proportion of the limbs the woolly rhino is almost identical with the black and does not depart much from the studied representatives of the genus *Rhinoceros*. All the rhinos make up a fairly uniform group most similar in their anatomy to the mediportal and subcursorial type of GREGORY (*in* OSBORN, 1929) (cf. Table 32). In contrast to other types, the limbs of the woolly and black rhinos are marked by a stronger elongation of the radius and the metacarpus, which makes them similar to the cursorial type and by a slight opposite tendency in the hind limb expressed by a relative shortening of the tibia. The graviportal adaptations, observed in the woolly rhino, should be understood as characters connected with the massiveness of skeleton and increase in body mass which are combined with the characters of the anatomical type common to all or most of the late-Pleistocene and Recent rhinos and corresponding to the mediportal type with a slight deviation to the cursorial type.

The data listed in Table 32 may suggest that the anatomical type of the woolly rhino was inherited from distant ancestors of the genus *Coelodonta* and Recent African rhinos, which should be looked for among the early representatives of the subfamily Dicerorhininae and that

Table 32

Coefficient *				
Species	Tibio-femoral	Metatorso-tibial	Radio-humeral	Metacarpo-radial
C. antiquitatis				
(ZAPUJ 683)	72	_	91	49
D. bicornis				
(ZIN 24729)	73	48	97	45
(ZIN 615)	72	_	96	
Rh. unicornis			· ·	
(ZIN)	68	52	86	56
Rh. sondaicus	about 70		about 86	
C. simum				
(ZIN)	—		81	50
Phenacodus primaevus	· · · · · · · · · · · · · · · · · · ·			
(primitive ancestral type)	84	31	87	42
Tapirus terrestris	79	41	86	50
Tapirus indicus	80	37	91	48
Palaeosyops leidyi	78	30	72	34
(mediportal ungulates)				
Teleoceras fossiger	57	25	78	37
Matamynodon planifrons	58	24	81	39
(graviportal digitigrades)				
Sue serofa		· · · · · · · · · · · · · · · · · · ·		·
(subcursorial artiodactyls)	86	34	80	37
Folionus (cursorial primitive)	100	50	90	53
Mesohinnus sp. (cursorial intermediate)	108	68	100	68
Neohipparion whitneyi (cursorial)	117	101	130	116
Eauus kiang (cursorial)	99	88	127	100
Equus caballus "Elmer Weeks" (cursorial)	92	73	119	78
Hippidion neogeum (cursorial, retrogressive)	89	62	105	72

Proportions of limbs in C. antiquitatis (BLUM.) and some of the Recent rhinos as compared with those in various adaptive types of limbs according to GREGORY (in OSBORN, 1929)

* The tibio-femoral coefficient = the ratio of the length of tibia to the length of femur \times 100. The remaining coefficient express analogous ratios.

this type was not subject to major changes, except for those connected with an increase in body weight which, however, did not cause any conspicuous regress in the adaptation to running. However, as indicated by the structure of the early representatives of the species C. antiquitatis,

known from China (BOULE et al., 1926; TEILHARD & PIVETEAU, 1930, after BELAYEVA, 1966) and the anatomy of C. tologoiensis, a species of the genus Coelodonta from the Eopleistocene of the Trans-Baykal Region, described not long ago (BELAYEVA, 1966), the woolly rhino was a regressive form in regard to its running adaptation. Since only the ranges of variability of the long bones are available, it was impossible to calculate accurate coefficients of the proportions of limbs for these early forms. Approximate values of these coefficients are as follows: for C. cf. antiquitatis from China, the radio-humeral coefficient amounts to between 94 and 100 and the tibio-femoral coefficient to between 81 nad 85, while for C. tologoiensis they are respectively about 110 (certainly more than 100) and between 87 and 105. A considerably larger slenderness of bones in these forms than in later representatives of C. antiquitatis has also been found by BELAYEVA (l. c.).

In the history of the stock of rhinos, from which the woolly species descends, there occur, therefore, phenomena similar to that found by GREGORY (in OSBORN, 1929) in the Equidae. In the development of the Equidae, a strong progression is observed of the cursorial characters, expressed in an increase in limb proportion coefficients (cf. Table 32), which reach their peak values in the Lower Pleistocene species *Hipparion (Neohipparion) whitneyi*. GREGORY (*l. c.)* also observed a regression in cursorial characters, combined with an increase in body weight which takes place in Recent representatives of the Equidae of the genus *Equus*.

The occurrence of certain inadaptive characters, concerning running capabilities, in the woolly rhino may be explained by a similar process of regression.

DESCRIPTIVE PART

Family RHINOCEROTIDAE Owen, 1845 Subfamily DICERORHININAE SIMPSON, 1945

Genus COELODONTA BRONN, 1831

Coelodonta antiquitatis (BLUMENBACH, 1807)

- 1849. Rhinoceros tichorhinus FISCHER; J. F. BRANDT, Observationes, pp. 161-412, Pls. 1-24.
- 1877. Rhinoceros (Tichorhinus) antiquitatis BLUMENBACH; J. F. BRANDT, Versuch einer Monografie..., pp. 8-17. (A detailed synonymy up to 1877 is given in BRANDT'S work 1877).
- 1880. Rhinoceros Mercki JAEG.; L. v. SCHRENCK, Der erste Fund...
- 1914. Rhinoceros antiquitatis BLUM., tichorhinus FISCH.; E. LUBICZ-NIEZABITOWSKI, Starunia fossils, pp. 181-267.
- 1922. Tichorhinus antiquitatis (BLUMENBACH, 1807) (== tichorhinus FISCH.; 1814); E. WÜST, Beiträge zur Kenntnis..., pp. 641-656, 680-688.
- 1924. Rhinoceros antiquitatis BLUM.; M. HILZHEIMER, Eine neue Rekonstruktion ...
- 1934. Tichorhinus antiquitatis (BLUMENBACH); F. ZEUNER, Beziehungen zwischen..., pp. 21-80.

MATERIAL

The material studied includes an almost complete skeleton of one individual, 19 well--preserved skulls, several long bones and various, fragmentary bones of the skeleton.

- (1) ZAPUJ No. 683. An almost complete skeleton. Skull preserved complete, together with a mandible. The nasal septum, nasal bones, orbits and the temporal process of mandible are damaged. These parts are supplemented by plaster with a slight deformation of the shape of nasal bones. Dentition complete. The axial skeleton lacks caudal vertebrae and two thoracic vertebrae. The latter, very poorly preserved, have not been mounted in the skeleton. In the limbs, the following bones are lacking; the naviculare, the endocuneiform and the mesocuneiform in both limbs, the ectocuneiform in the right limb and the cuboideum in the left limb. Both limbs are lacking metatarsal bones and phalanges. Scapulae and spinous processes are supplemented by plaster. Young adult. Sex indeterminable. Stratigraphic age: unknown. Podbaba, Prague, Czechoslovakia.
- (2) MZ No. VIII/Vm-234. A skull preserved complete except for the posterior part (two-thirds) of the nasal septum and left P². Old adult, male (?), Würm, Góra Puławska.
- (3) MZ No. VIII/Vm-137. A complete skull except for P²-M² on both sides. M⁸ worn down to a half of the height of crown and shifted anteriorly. Old, female, Würm, Pyskowice, Rzeczyca.
- (4) MZ No. VIII/Vm-146. A complete skull except for the left zygomatic arch. The right M² and M³ strongly worn; alveoli of P² and P³ overgrown with a spongy bone. Traces of fracture and fusion of the nasal septum and the palatine processes of maxilla. Bone losses above the right condyle and on the sides of condyles, probably connected with a purulent condition in the region of occiput. Old, female. Stratigraphic age: unknown. Drawn out of the Vistula River in the environs of Warsaw (?).
- (5) MZ No. VIII/Vm-452. A complete skull with all teeth. Old adult, male. Eemian interglacial. Konin Coalfield; Kazimierz outcrop of Konin mine; depth, 9.5 m.

- (6) MZ No. VIII/Vm-139. A skull roof with the anterior part of nasal septum, anterior part of palate, intermaxillary bones and the right zygomatic arch. Old adult, female, Würm, Pyskowice Rzeczyca.
- (7) MZ No. VIII/Vm-235. A skull minus the left zygomatic arch and left maxilla. Old adult (?), male (?), Würm, Góra Puławska.
- (8) ZG No. II-b-13-1. A complete skull. Left P² lacking. Young adult. Sex: indeterminable. Stratigraphic age: unknown. Wola Przemykowska, drawn from the bed of the Vistula.
- (9) ZG No. II-b-13-2. A poorly preserved skull, here and there (the right zygomatic arch) supplemented by plaster. The borders of occiput, anterior part of nasal bones, posterior palate and right maxillary bone damaged. Premolars lacking. Old adult. Female. Stratigraphic age: unknown. Buchach, Podolia, U. S. S. R.
- (10) ZG No. II-b-13-3. A complete skull. The left and right P² and P³ and the left M² lacking. Old adult. Sex: indeterminable. Stratigraphic age: unknown. Transylvania, Hammersdorf near Hermanstadt, Sibiu, Rumania.
- (11) MPŁ No. IV-3, IA 857. A complete skull. Except for the left and right M³, all teeth lacking. Old adult. Male. Stratigraphic age unknown. Łódź.
- (12) MG. Provisonal number M-3. A skull lacking maxillae, bony palate and the left zygomatic arch. Old adult. Male. Stratigraphic age unknown. Silesia.
- (13) Wet. No. 4053. A skull lacking the bony nasal septum, anterior parts of palate and alveolar processes of maxillary bones. The upper and both lateral borders of occiput damaged by beasts of prey; traces of teeth visible on the bones. The right P² and left P² and P³ lacking. Individual age on the boundary between young adult and old adult. Sex indeterminable. Origin unknown.
- (14) Provisional number RZ-30. Cat. No. lacking. Now, housed at the Polish Academy of Sciences' Institute of Palaeozoology in Warsaw. A skull lacking maxillae, bony palate and zygomatic arches. Old adult or old. Sex indeterminable. Stratigraphic age unknown. The Wislok River near Lisia Góra, Rzeszów Region.
- (15) Provisional number ZK-32. Cat. No. lacking. Skull complete, but damaged in many places, including the broken-off left half of nasal bones. Right P² and M³ and left P²-P⁴ and M³ lacking. Individual age: a younger representative of old adults. Male (?). Stratigraphic age unknown. Konin, Jóźwin outcrop.
- (16) Provisional number RS-14. Cat. No. lacking. A complete skull. Origin unknown.
- (17) Wrocl. No. M/369. A complete skull with all teeth. Old adult. Sex indeterminable. Stratigraphic age unknown. Siberia.
- (18) MG. Provisional number M-8. Cat. No lacking. A cast of skull with part of dentition preserved. Old (?). Sex indeterminable. Origin unknown.
- (19) M. S. E. A skull described by STACH (1956). Old. Sex indeterminable. Stratigraphic age unknown. Wadowice.
- (20) MZ No. VIII/Vm-233. A cranium. Young, sex indeterminable. Würm, Góra Puławska.
- (21) MZ No. VIII/Vm-453. The left half of the visceral part of skull with DP⁸, DP⁴ and P²-P⁴ in the maxilla. Young, sex indeterminable. Würm, Pyskowice.
- (22) Provisional number ZK-33 Fragments of anterior part of skull with a bony bridge between the intermaxillary and nasal bones. Nasal septum and nasal bones lacking except for the latter's most anterior part. The right P² and M¹ and left P³-P⁴ and M¹ preserved. Young adult. Sex indeterminable. Stratigraphic age unknown. Konin.
- (23) Provisional number M. Wiś.-10. Five larger and several smaller fragments of a skull. Considerable bone losses preclude reconstruction. Part of dentition preserved. A younger representative of the old adult group, sex indeterminable, loess, Pleistocene (Würm?). Czarkowy on the Nida.
- (24) PS Nos. 1804 MZB and 892/1. Two fragmentary skulls and several smaller fragments without Cat. Nos. Silesia.
- (25) MG. Cat. Nos. lacking. Two fragmentary skulls with provisional Nos. MG-7 and MG-9 and several smaller, unnumbered fragments of skulls. Silesia.
- (26) MZ No. VIII/Vm-236. A mandible from Góra Puławska preserved complete except for articular processes. MZ Nos. VIII/Vm-142, 230b, 143 and 231a. Four, partly preserved mandibles.
- (27) IG. No. 256-II-12. A complete humerus. Kubekowo.
- (28) PS No. 374 MZB. A fragmentary humerus without its proximal part. Silesia.
- (29) UŁ. No. IA 858/1. A complete femur. Łódź.

In addition, the material includes 60 specimens of humerus, mostly without proximal extremities, 51 specimens of femur, mostly without both extremities, 40 of radius, 28 of ulna, 41 of tibia, 2 of fibula, about 30 poorly preserved fragmentary scapulae, 27 fragmentary innominates, 7 sacra and about 30 vertebrae (cf. BORSUK-BIALYNICKA, 1965).

The writer has also used in her paper comparative measurements of about 90 skulls of the woolly rhino from the territory of the U. S. S. R. and the measurements of the skeletons

of the Recent rhinos Diceros bicornis L. and Rhinoceros sondaicus DESM. MIZ (unnumbered) D. bicornis ZIN No. 24,749 and ZIN No. 615, Rhinoceros sondaicus ZIN No. 1918 and Ceratotherium simum BURCH, ZIN (a specimen from the exhibition).

DESCRIPTION

SKULL

Maximum length between acrocranion and rhinion (cf. Table 7). During the ontogenetic development, nasal septum gradually ossifies anteroposteriorly. It is completely ossified in at least 65 per cent of old adult and in 100 per cent of old individuals.

Occipital view of the skull (norma occipitalis). Trapezoidal nuchal surface is strongly extended in its upper part. The ratio of maximum width of occiput (above the external auditory meatus) to the width of its upper part (on the nuchal crest) fluctuates between about 1.6 in young to about 1.3 in old skulls. The height of occiput approximately equals its width measured directly above the external auditory meatus, slightly exceeding it in young and being smaller in old skulls.

The squamous part of the occipital bone is withdrawn from the foramen magnum (Pl. VI, Fig. 5) in a manner characteristic of the Rhinocerotidae (also of most of the Artiodactyla; STARCK in GRASSÉ, 1967). The synchrondrosis interoccipitalis squamolateratis runs slightly below than halfway the height of the occiput. It occupies the medial three-fifths of the width of occiput at this level, while the remaining two-fifths are taken by the sutures between the squamous part of the occipital bone and the temporal bones running up- and outwards. The lateral parts of the occipital bone are laterally fused directly with strongly developed posttympanic processes of the left and right side, since the mastoid parts of the temporal bones do not project here on the outer surface of skull, much the same as in the pig and some other mammals (in the Cetacea and in the many Artiodactyla; in the *Tapirus*, they are visible on the surface only to a small extent; STARCK in GRASSÉ, 1967). The suture between the lateral part of the occipital bone and the posttympanic process runs (beginning with the end of synchondrosis interoccipitalis squamolateralis) down- and outwards parallel to the outer border of the occiput. A small mastoid foramen is as a rule situated on the line of the suture at the level of the upper border of the external auditory meatus. This foramen does not occur in young skulls (MZ No. VIII/Vm-233), probably becoming perceptible only after the fusion of the suture. Below the level of the external auditory meatus, the line of suture slightly bends medially, turning downwards into a suture between the posttympanic process and the paramastoid processs of the occipital bone.

The paramastoid process, rarely preserved complete, is slender, tapering, pointed, triangular in transverse section and reaching about 70 mm in height. The posttympanic process reaches more or less to halfway the paramastoid process with which it fuses tightly (the two processes were jointly described by NIEZABITOWSKI, 1914, under the name of posttympanic process).

The suture situated in the sagittal plane between the left and right lateral part of the occipital bone is serrate. As a suture of group I (cf. Table 1) it fuses relatively early, but sometimes incompletely at the bottom. Thus formed cleavage is connected in young skulls with the foramen magnum, forming a narrow incurve in its upper part. In older individuals, this incurve is frequently cut off from the foramen magnum and forms an independent foramen.

Lateral and dorsal surfaces (Norma lateralis et frontalis). — In the parietal region, the dorsal surface of the skull is slightly convex transversally and slightly convex or flat longitudinally. Due to a strong pneumatization of the parietal bones and the development of a spongy substance

of the occipital bone, this surface ascends posteriorly and upwards, forming an angle of, on the average, about 150° with the surface of horn bases.

In the region of the frontoparietal suture, parietal crests are spaced on the average at 80 mm. They diverge posteriorly and join temporal crests. The parietotemporal suture runs horizontally about 30 mm above the dorsal border of the external auditory meatus. Two foramina are situated below this suture. The slightly concave temporal crest gently turns into the upper border of the zygomatic arch.

The posterior process of the temporal bone fuses with the postglenoid process, forming an external auditory meatus, whose length equals the width of the posterior process of the temporal bone. This duct contains a troughlike, dorsally concave process of the tympanic part, reaching approximately halfway the length of this duct.

Caudally of the base of the zygomatic arch and below the temporal crest, there occurs an oval outlet of the external auditory meatus about 30 mm (hirozontal) by about 25 mm (vertical diameter). The postorbital process, only slightly separated from the dorsal border of the orbit and not curved ventrally, turns anteriorly into a border of the orbit, which is strongly nodular, particularly so in older individuals. A sharp pterygoid crest, turning at the level of the sphenoid bone anteriorly, ventrally and approximately along the suture between the palatal bone and the pterygoid process of the sphenoid bone, runs from the postorbital process ventrally and posteriorly. The following foramina, covered by the pterygoid crest, are situated on its medial side: an ethmoidal foramen in the form of a wide, horizontal fissure about 1 cm (or less) long occurs about 50 to 60 mm below the supraorbital process; below it, an optic foramen, slightly narrower but similar in shape and, finally, a large foramen deeply concealed below the crest and including a common inlet of the orbito-rotundum (the foramen rotundum is not separated) foramen and the alar canal.

An anteriorly tapering crest (crista endoorbitalis; POPLEWSKI, 1948), which makes up a boundary between the pterygo-palatine fossa and the orbit, runs from the last-named foramen towards the ventral border of the lacrimal bone. The pterygo-palatine fossa is situated completely over the maxillary tuberosity, so that the latter makes up its lower (and not lateral) wall. At the same time, this fossa is situated medially and slightly ventrally of the orbit. Medially, the pterygo-palatine fossa is limited by a perpendicular part of the palate bone, whereas no bony limitation occurs from outside and dorsally. The anterior part of the fossa is completely occupied by a large, round maxillary foramen.

In this place, a thin wall of the maxillary bone is frequently subject to destruction in the fossil state and, consequently, the lumen of the infraorbital canal fuses with that of the maxillary sinus, making observations difficult. The same concerns the wall of the infraorbital canal on the side of the nasal cavity. The round sphenopalatine foramen is situated on the perpendicular part of the palate bone over the maxillary tuberosity and under the endorbital crest, in a depression extending as far as the maxillary foramen. A tiny (about 4 mm in diameter) posterior palatine foramen occurs directly behind the sphenopalatine foramen. In the anterior corner of the orbit, on the border of the lacrimal bone, there occurs a thick lacrimal tubercle and behind it, on the orbital surface of the lacrimal bone, a small fossa for lacrimal sac with a lacrimal foramen. Another lacrimal foramen is situated ventrally of the lacrimal tubercle (on the facial surface or on the border of orbit) and is connected with the first foramen directly under the lacrimal tubercle. The third lacrimal foramen occurs just over the maxillary foramen on the lacrimal wall of some sufficient with the naso-lacrimal duct about 4 cm from the orbit. The ventral wall of the orbit, formed by a bilaterally extended zygomatic bone, about 35 mm thick and about 60 mm

In its anterior part, the zygomatic arch is more or less parallel to the surface of palate. The ventral border (which makes up an extension of the facial crest), about 10 cm from the anterior border of the orbit (Pl. II, Figs. 1-3; Pl. III, Fig. 1; Text-fig. 5*A*) suddenly bends dorsally at an angle of about 150° to 155° , turning posteriorly into an arcuate margin, whose concavity faces ventrally and which terminates in a convex temporal condyle. Posteriorly of the temporal condyle, the ventral border of the zygomatic arch runs slightly upwards and medially towards the base of the postglenoid process. The ventral border of the zygomatic arch, running more or less parallel to the dorsal, forms in the posterior part a convexity (geniculum processi zygomatic; POPLEWSKI, 1948) with its apex situated above the temporal condyle. This convexity turns in the form of a gentle, wide arc into the temporal crest and, anteriorly, into a horizontal ventral border of the zygomatic arch.

Ventral surface (Norma ventralis). — The ventral surface of the basilar part of the occipital bone has the form of a flat plate narrowing towards the sphenoid bone. The occipital condyles only to a relatively small extent overlap the ventral surface of skull. The length of the ventrally facing surfaces of occipital condyles amounts to about 50 mm or somewhat less. The anterior borders of the condyles are arranged nearly in a straight line perpendicular to skull axis or inclined to each other at an angle slightly larger than 180° (converging anteriorly).

The hypoglossal foramen, situated posteromedially of the paramastoid process, extends in the form of a deep groove on the posteromedial surface of the latter. The hypoglossal canal turns medially.

The posterior lacerated foramen is divided into two notches by a crest which makes up an extension of the medial border of the paramastoid process (Pl. III, Fig. 3). A small hiatus canalis facialis situated outwards and anteriorly of the auditory tube extends in the form of a groove onto the temporal wing of the sphenoid bone.

The tympanic part of the temporal bone in gerontic individuals usually fuses with the basal part of occiput. The anterior lacerated foramen is divided into two notches by a small spine extended onto the temporal wing of the sphenoid bone as a crest running towards the medial surface of the pterogoid process of the sphenoid bone. Sometimes, the anterior lacerated foramen in gerontic individuals is completely divided by a bony beam into two parts, the medial corresponding to the carotid notch and the external one formed by the oval notch.

The basilar tubercle on the sphenooccipital suture is sharp, unpaired, having muscle scars on both sides and crestlike postriorly. At the base of the pterygoid process of the sphenoid bone there occurs the oval posterior alar foramen about 10 mm in sagittal and about 7 mm in transverse diameter.

The body of the sphenoid bone is situated more or less in the same plane as the base of the occipital bone and, consequently, does not form any angle with it. The width of the body of the sphenoid bone between its pterygoid processes amounts to about 20 to 30 mm. Anteriorly, the body slightly extends and turns, without any distinct boundary, into the bony nasal septum. The width of the choanae between the apexes of pterygoid processes amounts to about 85 mm.

The palatal length makes up 45 to 47 per cent of the basal length of skull.

The anterior part of skull is marked by a ventral curve and expansion of the nasal bones down to the level of the upper border of the intermaxillary bones which they reach in the group of old adults and by their fusion with the last-named bones. This fusion is direct and not through the mediation of nasal septum. Thus a wide bony bridge is formed to which the posterior surface the bony nasal septum is fused, as it has first been observed by SCHROEDER (1899) in a skull from Pössneck. As noticed by the present writer in a young adult specimen (ZK No. 33), this bridge 40 to 60 mm wide is, in its dorsal part, rhomboidal in transverse section, with its shorter diagonal line running sagittally, lenticulate in transverse section halfway its height and biconvex. In its ventral part, it is semilunar and having posteriorly a concavity in which its fusion with the nasal septum is started. In adult individuals, a sagittally situated keel, running from prosthion to nasion and forming an anterior border of the skull, occurs in the anterior part of the bridge. This border is oblique with its ventral end directed posteriorly which is connected with an anterior projection of nasal bones before the intermaxillary bones and with anterior development of the last-named bones in their dorsal part.

The intermaxillary bones occur in the form of bony beams (Pl. II, Figs 1-3, Pl. III, Fig. 1) about 10 cm in maximum length measured along the dorsal border (measurements taken on the skulls with fused sutures) and about 45 to 55 mm high. In the posterior sector (about 50 mm long), they slightly converge anteriorly at an angle of about 25°. More anteriorly, they bend medially and fuse at an angle of about 80°. Due to this bend, the anterior parts of the intermaxillary bones turn anteriorly forming a wide front of the rostral part of skull (Pl. VII, Fig. 3), characteristic of the woolly rhino.

A longitudinal groove runs, near a suture with the maxillary bone, along the ventral border of the intermaxillary and maxillary bone up to an alveolus of P2. In young individuals, the appearance of this groove, in particular the situation of its deepest part near the intermaxillary suture, seems to indicate its connections with a vestigial dental alveolus of a canine. About 50 mm from this suture, the ventral border of the intermaxillary bone becomes swollen. The vestigial alveoli of the incisors are 15 to 18 mm from the anterior border of this swelling and about 15 mm further posteriorly. Of these two pairs of alveoli, whose homology is unknown (probably the alveoli of I² and I³), the posterior pair sporadically contains (KGU No. 738, ZIN No. 10 707, ZIN No. 10,690) vestigial incisors, usually on one side only. The anterior pair is developed in the form of round cavities 5 mm in diameter or, sometimes, it is not preserved at all. In some cases, there are traces of only anterior alveoli, while the posterior ones completely disappear. The dorsal border of the intermaxillary, together with the dorsal border of the maxillary bone, form a ventral limitation of the external nares which converges slightly anteriorly with the ventral borders of these bones (Pl. II, Figs 1-3; Text-fig. 5A). In the region of the incisivomaxillary suture, the ventral border of the intermaxillary bone forms a more or less strongly marked, sharp projection and - close to nasal bones - a rounded notch, limited posteriorly by an elevation which the lateral part of the bony nasal septum is wedged in.

Medially, the premaxillary bones form processes which, projecting towards skull axis (Pl. IV, Fig. 1), are situated above the plane of palate. Their ventral surface is smooth, tubelike and concave in transverse section. It makes up a dorsal limitation of incisive foramina and is situated in the extension of a groove (but on its dorsal side) running over the dorsal surface of the maxillary bone and destined for the naso-palatine duct. Blindly terminating and posteriorly wedged canals run along the bases of these processes. The apertures of these canals open medially. In their shape and spongy substance, filling them in part, the canals slightly resemble the vestigial alveoli, but they are situated above the alveolar border and they face almost straight ahead. In adult individuals, the canals fuse completely and are hidden by the spongy bone which fills the space between distal parts of the intermaxillae and the nasal septum.

As a result of the fusion of medial processes of intermaxillary bones in skull axis, which starts in the young adults, a beamlike ossification is formed which covers ventrally the border of the bony nasal septum and is wedged in with its posterior part between the palatine processes of maxillary bones. This ossification corresponds to the palatine processes of intermaxillary bones. Its original twin character is preserved in the anterior part, developed in the form of twin tubercles ventrally projecting down to the level of the alveolar border and anteriorly reaching the level of the anterior alveoli of incisors. This twin character is also emphasized by two to three axially situated apertures occurring in this region and leading to sinuous canals opening into the nasal cavity near the wall of nasal septum.

In young and young-adult individuals, there are no palatine processes proper of the intermaxillary bones and the incisive foramina are fused together to form a single large, triangularly outlined foramen with its base turned anteriorly. This triangle, about 60 mm high and 7 mm in base, is divided only inside by the nasal septum.

The nuchal surface of the wooly rhino is marked by a poor development of the external occipital protuberance. This protuberance is better visible in young skulls (MZ No. VIII/Vm-233) in which it has the form of a small, slightly projecting, about 15 mm wide convexity situated in the medial part of the nuchal crest and turning ventrally into a hardly perceptible sagittal crest (Pl. VI, Fig. 5, Text-fig. 5B ln). In older skulls, it completely fuses with adjoining muscle scars or forms a depression between them. A relatively high situation of the external occipital protuberance and its posterodorsal turn are probably connected with a low, but not very strongly inclined position of the head. The size of this attachment is indicative of a small role of the nuchal ligament in supporting the head. Muscle attachments, directly adjoining the external occipital protuberance, form, together with it, a semilunar, about 90 mm wide protuberance projecting posterodorsally and with its concavity turned ventrally. (Text-fig. 5B, ln, a). In a young skull (MZ No. VIII/Vm-233, Pl. VI, Fig. 5), subround (about 25 mm in horizontal and about 18 mm in vertical diameter), concave areas, situated on both sides of the external occipital protuberance, correspond to these muscle attachments. On the basis of an analogy to the skull of horse (SISSON, 1953, Fig. 30), one may suppose that these were the attachments of the complexus.

Outside the attachments of the complexus, the splenius was attached on lateral tuberosities of the nuchal crest reaching as far as the suture with the temporal bone (Text-fig. 5 B, b). According to ZEUNER (1934) this most important of the nuchal muscles, exerting an influence on the extension of the nuchal crest in herbivorous animals, was bound to be extended in the woolly rhino over the entire width of the nuchal crest so that it was connected in skull axis with a corresponding muscle of the other side and was thus responsible for the lack of the excavatio occipitalis in this species. It follows from the development of muscle scars near nuchal crest of the woolly rhino that the lack of the excavatio occipitalis should be ascribed rather to the complexus whose strong development is connected with the weight of head and horns, as well as the function of the latter (cf. NICKEL, SCHUMMER & SEIFERLE, 1968, p. 281, a function of the semispinalis capitatis) and whose dorsal development is related to a low position of the head only slightly inclined to the neck. Nevertheless, since a connection between their attachments exists anterodorsally of the attachment of the complexus, the left and right splenii seem to be connected with each other by a thin aponeurosis. The attachment of the splenius does not extend ventrally on the temporal part of the nuchal surface, disappearing at the level of its suture with the squamous part of the occipital bone. Part of its fibers might, however, be attached below, that is, in the region of the posttympanic process (Text-fig. 5Bg), by means of a common tendon of the cleidomastoideus, sternomastoideus and longissimum capitatis, as is the case in domestic mammals (NICKEL, SCHUMMER & SEIFERLE, 1968). The rectus capitatis dorsalis major was probably attached, much the same as in the horse, directly below the attachment of the complexus on the surface of the fossa of the squamous part of the occipital bone (Text-fig. 5B,c).













А







Fig. 5

A depression (Text-fig. 5 B, e), in old individuals separated externally by a dorsally running crest (Pl. VI, Fig. 6), is situated above the occipital condyle outside of the roller-like convexity running obliquely towards the foramen magnum. This place corresponds to the attachment of the rectus capitis dorsalis minor situated directly (e.g., in the dog, l. c.) over the condyle and covered dorsally by the rectus capitis dorsalis major.

Strongly concave, oval depressions on both sides of the nuchal surface, outside of the roller-like convexities running towards the foramen magnum (Text-fig. 5B, d), contained the attachments of the obliquus capitis anterior which, judging from the extensiveness of the fossae, was a relatively strong muscle. It is difficult to estimate how far it stretched ventrally.

A longitudinal depression running from the lateral part of the condyle to the base of the paramastoid process was probably destined for the attachment of the rectus capitis lateralis.

The remaining muscles attaching in the ventrolateral part of nuchal surface, such as, the jugulo-mandibularis, the digastricus and the jugulohyoideus, were probably attached onto or in the region of a rough convexity between the attachment of the rectus capitis lateralis and the posttympanic process, which also might be an attachment place of a common tendon of the brachio-cephalicus the sterno-mastoideus, the longissimus capitis and the splenius.

The attachment of the temporalis on the surface of the temporal fossa is limited by a low situation of the parietal crest from which results a relatively small length of its fibers. A considerable degree of concavity of the temporal fossa indicates, on the other hand, a large physiological cross section of this muscle. The temporal fossa is covered, in particular in individuals older ontogenetically, with bony crests, mostly parallel to the axis of temporal fossa and converging anteroventrally in the ventral part of fossa, which also indicates the direction of muscle fibers.

The parietal, frontal and temporal crests, limiting the temporal muscle, at the same time are attachments for the temporal part of a deep fascia of the head and attachment of the muscles which move the auricular concha. Posteriorly of the postorbital process, there are small elevations or crests (Text-fig. 5A, h), running below the external frontal crest and parallel to it. They were probably attachments of the frontal part of the frontoscutularis. The temporal part of this muscle was most likely attached to rough surfaces of the dorsal border of the zygomatic arch in its medial part (Text-fig. 5A, h), while a convexity in the basal part of the zygomatic

Fig. 5

A Skull, lateral view: a m. levator labii superioris proprius, b m. levator naso-labialis, c m. dilatator naris lateralis, d m. masseter, f m. buccinatorius, g m. malaris, h m. fronto-scutularis, i m. zygomatico-auricularis;

B Skull, occipital view; a m. complexus, b m. splenius, c m. rectus capitis dorsalis major, d m. obliquus capitis cranialis, e m. rectus capitis dorsalis minor, f m. capitis lateralis, g common tendon of m. brachio-cephalicus, m. sternomastoideus, m. longissimus capitis and m. splenius, ln ligamentum nuchae;

C Axis, cranial view;

D Axis, caudal view;

E Axis, lateral view; a membrana atlanto-epistrophica, b ligamentum dentis internum, c ligamentum interspinale, d m. obliquus capitis caudalis, e lamina nuchae;

F Atlas, dorsal view;

G Atlas, ventral view; a m. rectus capitis dorsalis minor, b m. obliquus capitis caudalis, c. m. longus colli, d m. rectus capitis lateralis, e m. rectus capitis ventralis, f m. obliquus capitis cranialis;

H Pisiform, lateral view;

I Pisiform, medial view; c articular surface for cuneiform, ul articular surface for ulna, ex groove for tendon of m. extensor carpi ulnaris; fl m. flexor carpi ulnaris; lg ligaments.

process of the temporal bone on its dorsal side (geniculum processi zygomatici) was probably connected with the attachment of the zygomatico-auricularis (Text-fig. 5A, i).

The scutularis muscles, attaching themselves on the frontal and parietal crests converge in skull axis in animals whose crests are strongly convergent and form a sagittal crest (horse, carnivores). In the case of parietal crests situated low (pig), the scutularis muscles do not converge in skull axis. In the pig, the cervicoscutularis muscles are shifted behind the occiput, which results from a short skull and a notch in the nuchal crest. In the woolly rhino, such a shift probably did not take place as a result of a strong extension of the posterior part of skull. A strong sculpture of the parietal surface of skull, observed in particular in older individuals, may be indicative of a shift of the scutularis and auricular muscles from the frontal and parietal crests towards skull axis. It is in particular in skull axis that a longitudinal, a few centimeter long and 1.5 cm wide convexity (Text-fig. 5A, h) which might be connected with the bilateral attachments of the parieto-auricularis, occurs posteriorly of the fronto-parietal suture. This convexity is bilaterally bordered by strips of a rough surface posteriorly slightly diverging and almost parallel to the parietal crests but nearer skull axis. They also diverge anteriorly towards the frontal crests, with which they fuse at the level of the bend of frontal bones. These roughnesses may be caused by the attachments of the interscutularis, the cervicoscutularis and, posteriorly, may be also the cervicoauricularis superficialis.

Anteriorly of the temporal fossa and posteriorly of the pterygoid crest, there occur strong muscle scars, starting at the level of the ethmoidal foramen about 2 cm behind the pterygoid crest and extending ventrally down to the end of the pterygoid process of the sphenoid bone. In the dorsal part, these scars are probably related with the attachment of the straight muscles, the levator palpebrae superioris and the retractor oculi. They reach to about halfway of the common inlet of the orbito-rotundum foramen and the alar canal. Lower situated muscle scars either partly fuse with those described above or are separated from them by a smooth, concave area. They belong to the pterygoideus lateralis and, along the posterior border of the pterygoid process, to the pterygoideus medialis.

A slightly concave muscular depression square in outline, about 1.5 cm wide, containing the attachment of the obliquus ventralis, is visible inside the orbit.

Facial crest not very conspicuous. Below it, there occurs a distinct, strongly sculptured attachment of the masseter about 20 mm in maximum width and facing ventrolaterally. This attachment stretches over about 15 cm up to a geniculate bend of the zygomatic arch and then runs further on the ventral surface of the arch.

Several other, distinct muscle attachments are also visible on the lateral surface of the visceral part of skull. The largest of them is shaped like a shallow depression irregular in outline, having a rough surface and including approximately the entire surface of lacrimal bone (Text-fig. 5A, a). This attachment probably belonged to the levator labil superioris proprius (in the pig, it is attached in fossa canina). Above this depression, the levator naso-labialis was attached on a crest (Text-fig. 5A, b), running from the anterodorsal angle of orbit anteriorly and slightly medially and limiting the depression dorsally.

Behind the infraorbital foramen, there occurs a slightly concave, reniform muscle scar 75 mm high, 35 mm long and probably belonging to the caninus (according to SISSON, 1938 m. dilatator naris lateralis).

The lateral surface of the maxillary bone over the posterior half of diastema is covered with roughnesses, frequently separated from each other by a horizontal prominence, extending towards the facial crest and probably connected with the buccinatorius (Text-fig. 5A, f).

The tuberosities which surround the orbit may be related with the attachments of the

superciliaris (dorsally), with the orbicularis oculi on the border of the lacrimal bone and with the malaris anteriorly and ventrally of the orbit. Judging by the dimensions of a tuber adjoining the anteromedial border of the orbit (Text-fig. 5A, g), the last named muscle was relatively strongly developed.

The longus colli was attached to the skull base on both sides of the muscular tubercle. Bony roughnesses undoubtedly related with the attachments of the rectus capitis ventralis are situated externally and posteriorly of the longus colli.

MANDIBLE

In regard to structure the mandibles of *Coelodonta antiquitatis* under study are on the whole in conformity with the specific characters of *C. antiquitatis* given by GROMOVA (1935), namely: the ventral border of the ramus is strongly convex, particularly so in young individuals, in the adults becoming parallel to the occlusion surface of teeth between M_1 and M_3 and a few

Cat. No. Measurement	ZAPUJ No. 683		Z No.	IN 10725	ZIN No. 16948	GI No. $\frac{83}{112}$	ZIN No. 10735	
Infradentale-gonion caudale length	507 517		527	524	605	500	465	
Infradentale-condylion mediale length	533	537	_	_				
Length of ramus from the posterior border of M ₃ to infradentale	315 320		309	308	351	288	273	
Length of tooth row	229	229	207	206	259	193	183	
Length of symphyseal part	1	26	1	.75	165	141	102	
Width of the vertical part of ramus from the posterior border of M ₃ alveolus	176	190	210	213	249	257	190	
Maximum width of symphyseal part		84	90		90 69			
Minimum width of symphyseal part		79	90		71	83		
Width between lingual walls of P_2		48		67	65	50		
Width of articular surface of the articular process	98	99	97	96	132	123	_	
Width of ramus posteriorly of M ₃	108	110	105	114	129	105	97	
Height of ramus anteriorly of P ₂	68	70	81	82	95	_	66	
Height of the vertical part of ramus up to the apex of the articular process	2	24	249 244		298	240	241	

Table 33

Dimensions of mandibles in Coelodonta antiquitatis (BLUM.) in mm

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centimeters behind M_3 , but strongly curving dorsally anteriorly and posteriorly of this sector. The symphysis mandibulae reaches posteriorly to a boundary between P_2 and P_3 . The dorsal surface of the symphysis is at this level V-shaped in transverse section, flattening anteriorly. The symphysis widens anteriorly. A longitudinal depression occurs on its ventral surface. Vestigial alveoli of the incisors, if preserved at all, are directed anterodorsally. The anterior part of the symphysis is wide, rounded and with a slight concavity in sagittal axis. No external crests occur along the interalveolar borders.

The mandibular angle rounded, not projecting posteriorly. Mostly, it also does not project laterally, except for the mandibles of old individuals (M.G. No. 11), in which a laterally projecting, strongly sculptured crest, connected with the development of the masseter, is formed along the border of the mandibular angle. The alveolar border is not limited externally by a crest. The anterior border of the vertical part of the ramus mandibulae is arranged at an angle of about 115° to the alveolar border. It is blunt, except for a short sector near the center of its height in which it sharpens. In the dorsal part, it once again becomes blunt as a result of a medial bend of the anterior part of the coronoid process. The coronoid process is poorly developed, triangular, rounded at the apex.

The mental foramina mostly occurred as two pairs, the posterior one below P_4 , the anterior at the level of the interalveolar border. The mandibular foramen large, slitlike, situated in the anterior part of the concavity for the pterygoid muscles.

The largest thickness of the horizontal ramus occurs in its ventral part below P_4 and M_1 (according to GROMOVA, 1935, below M_1 and M_2).

The masseter fossa slightly concave, on the whole (except for old individuals, as above not limited ventrally by a crest, including the entire ventral part of the outer surface of the vertical part of ramus, reaching anteriorly to the level of M_3 and dorsally somewhat higher than a half of the anterior border of mandible. The dorsal part of the attachment of the masseter, situated above the alveolar border, is frequently more distinctly sculptured than the ventral part and in old individuals (in which the entire surface of the masseter fossa is strongly sculptured) separated from the ventral part by horizontal furrows. Such a division of the attachments of the masseter would presumably correspond to the division of this muscle into two parts, of which the dorsal one would include muscle bundles whose trace might be nearly horizontal.

The fossa for the pterygoid muscles on the medial surface of the ramus of mandible in its ventral part has anterodorsally a slightly smaller range than the masseter fossa, but is much deeper and limited posteriorly by a medially projecting bony protuberance.

The surface of the temporal process is on the whole smooth and, therefore, does not allow one to imagine the size of the temporal muscle attached to it. The size of the process is, however, indicative of a poor development of this muscle.

The ventral surface of the ramus of mandible and the posterior border of the mandibular symphysis are covered with roughnesses, probably connected with the muscles which lower the mandible, that is, the mylchyoideus and with the anterior venter of the digastricus.

VERTEBRAL COLUMN

Atlas. — The length of the wing of atlas makes up less than a half of the width of vertebra and the length of the neural arch less than one-sixth of this width. The ventral arch is yet shorter than the neural, but it is extended by a ventral tubercle projecting caudally from the caudal border and whose length exceeds a half of that of ventral arch. The dorsal tubercle thick, low and blunt (Pl. VIII, Fig. 2b). The ventral arch equals the neural arch in the degree of arcuation due to a deep fovea dentis, which indents by a wide, rounded notch for about 27 mm below the ventral wall of the vertebral canal. In this connection, the wings are arranged halfway the height of a vertebra. Wings are flat. Their surface gradually turns into the surface of arches. The fossa atlantis lacking (Pl. VIII, Fig. 2a; Text-fig. 5G), the same as the transverse foramen. The alar foramen is replaced by a deep, semicircular alar notch (incisura alaris), connected with the intervertebral foramen by a wide, groovelike concavity. The intervertebral foramina are oval, large (about 12 mm long, 19 mm wide) and situated in the cranial half of the neural arch, on its both sides, 54 mm from each other.

The cranial articular surfaces are oval (60×90 mm), with their longitudinal axes directed strongly externally, cranially and dorsally. The axis of concavity runs more or less horizontally. The degree of arcuation of the cranial articular surfaces is lower than in the horse. The distance between cranial articular surfaces amounts ventrally to about 32 and dorsally to about 73 mm.

The caudal articular surfaces are oval (about 65×34 mm), situated approximately in the frontal plane, slightly converging cranioventrally and turning into the articular surface of a wide (about 30 mm) and deep fovea dentis. The axis of the fovea dentis is arranged horizon-tally and in the sagittal plane.

Cat. No.	ZAPUJ No. 683	PS No. 1	PS No. NIZ 1116	ZIN No. 4160	ZIN No. 4716
Total length in projection, without the ventral tubercle	136	142	110	139	111
Total width	320	385	327	369	
Width between alar notches	165	164	149	188	169
Length of neural arch in sagittal axis	53	68	56	71	63
Length of ventral arch in sagittal axis together with ventral tubercle	70	72	65		61
Length of wing	119	137	105	123	
Distance between intervertebral foramina	55	59	55	60	57

Table 34

Dimensions of atlas in Coelodonta antiquitatis (BLUM.) in mm

The following ligamental attachments may be observed on the surface of the atlas:

Attachments of the ligaments reinforcing the atlanto-occipital and atlanto-axial articulations. A bony protuberance for the dorsal atlanto-occipital membrane and for the left and right lateral atlantal ligaments occurs sometimes along the cranial border of the dorsal arch between alar notches and a trace of the dorsal atlanto-axial ligament is visible posteriorly of this arch. The cranial border of the ventral arch is, except for a sector located in the extension of the fovea dentis, also slightly swollen, which is connected with the presence of the ventral atlanto-occipital membrane. Strong, cranially convergent crests for the ventral atlanto-axial ligament are situated on the dorsal surface of the ventral tubercle. Tuberosities for the ligament of dens, cranially contacting the fovea articularis cranialis atlantis, occur on the inner surface of the ventral arch laterally of the fovea dentis.

On the dorsal surface of the atlas, only the attachments of the rectus capitis dorsalis minor are visible on the ventral tubercle, where they occur in the form of a tuberosity turned craniodorsally, as well as the left and right (running from the epistropheus attachment of the obliquus capitis caudalis in the form of rough surfaces situated caudally of alar notches, which — without a distinct boundary — turn into the surface of wing (Text-fig. 5F, b).

Strongly developed, rough fossae, situated in the external parts of the ventral arch and which reach as far as the boundary between the arch and the wing, probably made up the attachments of the rectus capitis lateralis.

The cranial border of wing forms a usually swollen attachment projecting ventrally in the form of a crest, sometimes lacking in young specimens. Truncate on the side of the alar notch, this attachment makes up a plane facing craniomedially (Text-fig. 5G, f). It probably served for the obliquus capitis cranialis which ran cranially.

The longus colli was probably attached to the lateral, flattened surfaces of the ventral tubercle.

The writer did not succeed in identifying the position of other muscular and ligamental attachments (the longissimus atlantis, the brachiocephalicus and the interspinal ligament).

Axis. — Short, with a high spinous process. Its total height equals more than one and a half length of its body (the dens included).

The apex of the spinous process is shaped like a quadrangular tuber with its longer diagonal running in sagittal plane.

The cranial border of the spinous process is sharp and, in its ventral part over the vertebral canal, terminating in a ventrally facing tuber to which the interspinal ligament is attached.

The caudal border of the spinous process, nearly perpendicular to the axis of vertebral canal, is about 34 mm wide and limited laterally by blunt crests which pass onto the dorsal surface of caudal articular processes. A sagittally arranged, sharp crest, that is, an attachment of the lamina nuchae, runs through the middle of the caudal border.

Cranial articular surfaces are flat, oval, slightly convergent cranioventrally and fusing with each other on the ventral surface of the dens.

The dorsal surface of the dens is convex, with an oval scar of the ligament of dens situated on it. A bony swelling is located caudally of this scar and cranially of a late fusing suture between the body and dens.

The vertebral canal has an outline of a ventrally flattened oval whose height equals approximately three quarters of its width.

The cranial intervertebral notches tend to close and form intervertebral foramina. Processes, extended in a crest-like manner towards the spinous process and slightly turned ventrally, are situated in their dorsal part. These processes, along with a crest occurring between them, make up an attachment of the dorsal atlanto-epistrophical membrane (Pl. VIII, Fig. 3; Text-fig. 5C, a).

Articular surfaces of the caudal articular processes are wide, flat, pear-shaped and turned extroventrally. The caudal surface of the body is subround and 74 mm (height) by 60 mm (width).

Transverse processes short, narrow, directed laterally and somewhat caudally, a maximum distance between them amounting to 140 mm. Their ventral borders are medially extended on the ventral surface of the body and take the form of crestlike projections.

Table 35

Cat. No.	ZAPUJ No. 683	IG No. 1791N	IG No. 1657
Length of body with dens (from below)	about 116	131	127
Height width of the caudal articular surface	74/60		
Total height of vertebra	171		
Width of cranial articulation	140	170	152
Width of caudal articulation	149		_
Minimum width of body	120	137	122
Length of arch in sagittal axis	99		_
Length of arch at the base	75		_

Dimensions of the axis in Coelodonta antiquitatis (BLUM.) in mm

Ventral crest distinct. Tubercles for the ventral atlanto-axial ligament usually occur on both sides of its cranial part.

Lateral surfaces of the spinous process are covered with roughnesses. A crest, running from the apex of the process to the dorsal part of the intervertebral notch, subsequently turns towards the transverse foramen and passes on the dorsal border of the transverse process. In the dorsal part, this crest might be an attachment place of the obliquus capitis caudalis and in the ventral part, that is, at the base and along the dorsal border of the transverse process, an attachment of the intertransversalis. A bony protuberance on the ventral border of the transverse process and at its base, might probably serve as an attachment of part of the brachiocephalicus. Rough parts of some specimens' dorsal surfaces of caudal articular processes were attachments places of the complexus.

The writer did not succeed in identifying other muscle attachment (the rectus capitis dorsalis major on the epistrophical spinous process and the longus colli on the ventral crest).

Cervical vertebrae (III-VII). — Cervical vertebrae relatively short and high, the height length ratio of its body amounting to about 1.3.

The length of the bodies of cervical vertebrae III-VII does not change over the entire length of neck and does not differ from the length of thoracic vertebrae. The length of arch is, on the other hand, considerably smaller than in the thoracic vetebrae (cf. Table 37), the arch of vertebra VII being somewhat longer.

Much the same as in the axis, the vertebral canal is shaped like a ventrally flattened oval (width height ratio amounting approximately to 4:3).

Articular surfaces of the cranial and caudal articular processes are oval and strongly deflected from the horizontal position. The cranial ones are turned dorsomedially and caudal ones — extroventrally.

Mammillary processes, strongly developed on vertebrae III-VII (slightly less so on vertebra IV), are situated externally of the caudal part of the articular surfaces of cranial articular

Table 36

Serial number of vertebra	m	IV	v	VI	VII
Dimensions					
Length of body	55	54	50	50	50
Width of caudal articular surface	60	59	58	63	65
Height of caudal articular surface	73	77	77	70	64
Length of arch	41	40	37	37	51
Height of spinous process	30	27	75	95	more than 142
Inclination of spinous process			90	90	89
Maximum width between transverse processes	179	159	157	139	145

Dimensions of cervical vertebrae (III-VII) in Coelodonta antiquitatis (BLUM.), ZAPUJ No. 683. Linear dimensions in mm

processes. On vertebra III, mammillary processes are situated externally and below the dorsal borders of articular surfaces and towards the posterior part of the vertebral column they shift caudally and slightly dorsally, placing themselves at the level of these borders (such processes, not so robust but also prominent, are marked on thoracic vertebra I, see below).

Spinous processes of vertebrae III and IV are underdeveloped. In the remaining vertebrae, they are shaped like triangular lamellae with sharp borders (except for the ventral part of the border in vertebra VII) and their height increasing from vertebra V to VII (cf. Table 36). In vertebrae V and VI, they are arranged perpendicularly to the axis of the vertebral column, the process of vertebra VII being deflected caudally (cf. Pl. I).

The transverse process of vertebra III is shaped like a lamella slightly inclined cranioventrally and divided into two parts by an oblique crest. In vertebra IV, the cranial part of the process is more strongly developed than that in vertebra III, more strongly extended ventrally and arranged in a different plane (approximating a sagittal one) than the caudal (dorsal) part. Vertebrae V and VI have transverse processes similar to those of the plate-like type of the ruminants (the ventral lamella shaped like a sledge runner).

Ligamental attachments of the cervical part of the vertebral column are poorly visible.

Muscle attachments of cervical vertebrae, similarly as in the vetebrae of further sectors of the column, are hardly identifiable due to a large number of here attached bundles of segmentally built muscles of the vertebral column and, finally, the lack of sufficient comparative data.

Mammillary processes, situated outside of cranial articular processes, probably made up of attachments of bundles of the multifidus cervicis running towards spinous processes of cranially situated vertebrae. These bundles would correspond to the cranial part of the multifidus cervicis of the horse ("der vordere Teil", NICKEL, SCHUMMER & SEIFERLE, 1968), while the lateral part and the deep part attached to caudal articular processes would be much weaker (although swellings, which might be attachments of these parts of the multifidus cervicis, occur on the dorsal surfaces of caudal articular processes in cervical vertebrae VI and VII). Fascicles of the longissimus capitis et atlantis might also attach themselves near the articular processes of cervical vertebrae, as is the case in some domestic animals (cow, pig). (Mammillary processes of cervical vertebrae in *Brontopus robustus*, developed much the same as those in the woolly rhino, were interpreted by GREGORY & CHRISTMAN (*fide* OSBORN, 1929), as the attachments of the longissimus capitis et atlantis).

The attachments of the bundles of the longus colli are situated on the ventral surface of cervical vertebrae which are covered ventrally by these bundles. The tubers, occurring in the caudal part of the ventral spine, were probably — similarly as the ventral tubercle of the atlas (see above) — cranial attachments of cervical bundles of this muscle, whereas the tubers, situated on the last two cervical vertebrae on the medial side of the ventral lamella of the transverse process near its caudal border, might be cranial attachments of the thoracic part of the longus colli.

The scars of the remaining muscles which are attached to the cervical vertebrae could not be identified. In particular, there are no distinct traces of the cranial attachments of the multifidus cervicis and the spinalis cervicis, which should be situated on caudal borders of the spinous processes of cervical vertebrae. Next, the purpose of some distinct muscle scars is not clear. They are: depressions on both sides of the ventral spines of vertebral bodies (perhaps also connected with the longus colli) and some more or less distinctly individualized attachments situated on vertebra VI, such as the dorsal part of the transverse process, the caudal corner of this process and a deep depression developed caudally between the dorsal and ventral lamella of this process.

Thoracic and lumbar vertebrae. — The thoracic part of the vertebral column probably includes 18 and the lumbar part 4 vertebrae³.

The bodies of the thoracic and lumbar vertebrae do not differ in length and width from those of cervical vertebrae, but they are higher (cf. Tables 36, 37) and have less domed articular surfaces.

The ventral spine, visible on the first four thoracic vertebrae, dwindles away caudally.

The vertebral canal is shaped like a ventrally flattened oval, lower in cervical vertebrae and provided with a troughlike notch whose width equals about a half of that of the canal and which is situated axially in the dorsal wall.

The arches, longer than in cervical vertebrae, are the largest in the thoracic region, which is connected with a stronger development and oblique position of the spinous processes, whose bases they form and with the position of the articular processes converging in the thoracic region (these processes are widely spaced in the cervical region).

The articular surfaces of articular processes are oval and, in the cranial sector of the thoracic part, situated subhorizontally with a cranioventral deflection only. Beginning with thoracic vertebra XIV and up to lumbar vertebra IV, they are situated vertically (parallel to the frontal plane), which is probably related with a larger degree of sagittal mobility of the vertebral column in the diaphragmatic region. Posteriorly, the articular surfaces take a horizontal position. No roller-like articular surfaces are here observed stiffening the lumbar vertebrae as those characteristic of the Ungulata.

³ Due to the losses in the vertebral column of the woolly rhino from Podbaba (ZAPUJ No. 683, cf. p. 39), the number of vertebrae of particular regions of the vertebral column has been given on the basis of the skeleton of the woolly rhino from Starunia (MSE). This number is in conformity with BRANDT'S (1877) data for the skeleton of the woolly rhino from Munich. In the Recent rhinos *D. bicornis, Rh. sondaicus* and *C. simum* the number of lumbar vertebrae amounts to four and that of thoracic vertebrae 19, 18 and 18 respectively. The data mentioned above also served as a basis for the identification of two vertebrae not mounted into the skeleton from Podbaba.

Mammillary processes are developed on all thoracic and lumbar vertebrae. On thoracic vertebra l, they occur externally of the articular surfaces of cranial articular processes. In farther thoracic vertebrae, they are situated over the articular surfaces for costal tubercles. They become more and more robust caudally, forming strong, cranially facing tubers over the facets of costal tubercles and at the level of the dorsal parts of articular processes. In the caudal part of the thoracic sector, the mammillary processes diminish and shift ventrally. In the lumbar vertebrae they are shaped like sharp elevations and are situated below and externally of the articular processes.

The transverse processes of thoracic vetebrae are short, stocky and provided with a round facet for the costal tubercle, at first concave and, beginning with vertebra VII, flat and facing laterally and slightly ventrally. The cranial facet for the head of rib is squeezed cranioventrally into the base of transverse process. It is oval, strongly concave and does not adhere to the cranial articular surface of the body. Another, similarly developed facet for the head of rib, situated in the caudal part of the body adheres to its caudal articular surface. Caudally, the facets for the head of rib diminish and take a higher position. They disappear on thoracic vertebra XV.

The transverse processes of lumbar vertebrae have the form of strongly tapering lamellae. Their caudal borders are perpendicular to the axis of the vertebral column, while cranial ones are directed posterolaterally. Swellings, which turn on the last vertebra into articular surfaces for the wing of sacrum, are situated on caudal borders of the transverse processes near the vertebral canal. The presence of this surface and a corresponding lumbar surface for the wing of sacrum express a tendency typical of the Ungulata to stiffen the vertebral column, in this case, in particular laterally.

The spinous processes reaching in the first four thoracic vertebrae about 34 cm in height, diminish gradually as far as vertebra XI on which they are about 8 cm high. Caudally of vertebra XI their height does not change. A strong caudal inclination of spinous processes, observed in the region of thoracic vertebrae I-X, considerably decreases in the caudal thoracic vertebrae, beginning approximately with vertebra XI. Remarkable is a certain degree of cranial deflection of the spinous process of thoracic vertebra I in relation to subsequent processes (cf. Pl. I, Table 37). The way in which the specimen (ZAPUJ No. 683) has been assembled may arouse certain doubts concerning the correctness of such a disposition of the spinous process, but a similar deflection is observed in the skeleton of the woolly rhino from Starunia (MSE).

The spinous processes of lumbar vertebrae are perpendicular to the axis of vertebrae. A typical anticline is lacking.

The spinous processes in both the thoracic and lumbar part are approximately rectangular, but in the caudal part of the thoracic region and in the lumbar region, their cranial and caudal ridges are concave, which is related with the anteroposterior extension of the dorsal ends of spinous processes, particularly strong in this region. The apexes of spinous processes in vertebra I-VI are terminated in rough, flat surfaces to which the cartilage adheres. In older specimens, these cartilages became ossified and they fused to the spinous processes in the form of a spongy substance.

The cranial borders of spinous processes are sharp. The caudal ones vary from each other in thickness and in the development of muscle scars occurring on them over the entire length of the vertebral column. More or less strongly developed sagittal crests serving for the interspinal ligament run along the caudal borders of spinous processes. On both sides of such a crest, two muscles were attached: ventrally the multifidus dorsi and dorsally the spinalis dorsi. The multifidus dorsi forms prominent, crestlike scars running on both sides of the sagittal crest for the interspinal ligament and more strongly projecting posteriorly than this crest. Their

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M. Borsuk-Bialynicka, Table 37

Table 37

Dimensions of thoracic and lumbar vertebrae of the skeleton of Coelodonta antiquitatis (BLUM.) from Podbaba, ZAPUJ No. 683. Linear dimensions in mm

Serial number of vertebra	I	п	ш	IV	v	VI	VII	VIII	IX	x	XI	хп	xiii	xıv	xv	xvi	хүн х	(VIII	I	п	ш	IV
Dimensions																						
Length of body	45	43	45	50	50	52	52	53	53	52	53	54	48	50	48	48	48	48	49	45	45	49
Width of the posterior articular surface	65	-			_	63	63	59	58	58	58	57	57	54	52	57	74	72	66	64	71	63
Height of the posterior articular surface (approximate)	61	_	_	_	-	65	65	59	59	67	65	61	66	64	63	62	52	48	60	55	48	48
Length of arch (near the base)	73	83	88	89	84	76	84	83	77	82	84	85	81	83	79	76	68	68	75	72	70	69
Maximum width (between transverse processes)	157	150	140	_	141	138	126	116	106	96	101	100	103	103	99	100	-		-	232	223	190
Height of spinous process	360	360	340	330	320	290	240	200	170	110	80	80	80	75	_	80	-		75	70	65	80
Angle of posterior inclination of spinous process	61	51	60	65	61	61	51	56	69	75	78	76	80	84	84	83	_		86	85	90	89

presence causes an extension of the caudal border. These are anterior attachments of the multifidus dorsi. On thoracic vertebra I, these crests are observed over the ventral four cm of the height of spinous process. The rest of the border is sharp. The range of the multifidus dorsi on the caudal borders of the spinous processes extends more and more dorsally while passing towards the posterior part of the thoracic region. On vertebra V, it occupies about three-quarters of the height of spinous process and, beginning with vertebra IX, the entire caudal border of this process. Consequently, this border is provided over its entire length with two posterolateral crests separated by a sagittal groove with a crest for the interspinal ligament running inside it. On vertebra XIV and posteriorly of it, the crests converge and fuse with each other approximately halfway the height of the crest, ventrally diverging towards the articular processes. The spinous processes of lumbar vertebrae have sharp border bifurcating ventrally and provided with paired tuberosities dorsally. The distribution of the attachments of the multifidus dorsi is in this region somewhat less clear. The posterior scars of this muscle occur on the mammillary processes. (A higher position of these processes on thoracic vertebrae (see above) may be connected with, among other things, a larger dorsal range of the anterior scars of this muscle in the thoracic sector and it would be an expression of the tendency of muscle bundles to an as horizontal position as possible and thus to increase the component of the pressing force of the muscle).

Cranial attachments of the spinalis dorsi, situated on the borders of the spinous processes of thoracic vertebrae over the attachments of the multifidus are poorly developed. They are most distinctly visible on thoracic vertebrae II and III, where they form posterolateral crests running as a continuation of the crests which serve for the multifidus dorsi. Posteriorly, the attachments of the spinalis dorsi reach thoracic vertebra VIII. The situation of caudal attachments has not been determined.

The vertebrae also lack distinct traces of the longissimus dorsi. According to SLIPER (1946), this muscle attaches in the rhinos only to the spinous processes and has no accessory attachments on transverse, articular and mammillary processes. The arrangement of spinous processes in the lumbar region is indicative of the attachments of this muscle on these processes. A caudal inclination or vertical position of the processes of lumbar region and a lack of a distinct anticline in the diaphragmatic region is, according to SLIJPER (l. c.) connected with shifting the attachments of the longissimus dorsi from the lumbar region onto the sacral bone (by a decrease in muscle bundles attaching themselves in the lumbar region in favour of those attaching themselves onto the sacral bone), which in turn is connected with the limitation of the flexibility of the lumbar region. According to this author (l. c.), the lack of anticline is also a feature of several other heavy representatives of the Ungulata, including D. bicornis and Rh. sondaicus, but the spinous processes of these rhinos are markedly inclined caudally. The vertical position of the spinous processes in the lumbar region of the vertebral column in the woolly rhino indicates that the process of shifting the attachments of the longissimus dorsi was not very advanced in this species and that this sector preserved a certain sagittal flexibility as also shown by the development of articular processes (see above) and the adaptation to the horse-gallop (SLIJPER, 1946) is manifested only by the development of a short lumbar sector.

In the lumbar and thoracic vertebrae, beginning with vertebra VIII, a depression occurs on each side of the spinous process laterally of its base. These depressions are most strongly developed on thoracic vertebrae XIII and XIV. Their assignment is not clear, but they might be connected with part of the fibers of the multifidus dorsi.

On the ventral side of the vertebral column, noteworthy are bony swellings on the last thoracic vertebra, as well as in lumbar, cranial and caudal parts of the ventral spine. The situation of these swellings at the end of the thoracic sector and in the lumbar sector on the ventral side of the vertebral bodies leads one to suppose that they are connected with the psoas minor, but it is not unlikely that they served for attaching the ventral longitudinal ligament.

A bony prominence running over the entire width of the transverse process of lumbar vertebra I, was probably connected at its base with the psoas major running from the trochanter minor of the femur to the ventral surface of the vertebral column externally of the psoas minor.

Sacrum. — The sacrum (Pl. XIX, Figs. 2a, b) consists of four vertebrae.

The transverse processes of sacral vertebrae II, III and IV are reduced to a small extent and fused with strongly developed transverse processes of sacral vertebra I. Since the posterior border of the last transverse process is situated at an angle smaller than 180° to the lateral border of the sacrum, the latter is subpentagonal in shape.

The auricular surface stretches over the entire length of the lateral border and, consequently, the pelvis closely adheres three sacral vertebrae and also contacts the fourth.

The auricular surface is oval, 144 mm long and 75 mm wide. The ventral, most medial part of this surface is concave, uneven, but not as rough as the external part, from which it is separated by a crest. Medially, the auricular surface is also bounded by a prominent crest, related with the attachment of a ligament (ligamentum sacroilicum suspensorium).

Table 38

Cat. No. Dimensions	ZAPUJ No. 683	ZIN No. 4118	ZIN No. 24729	ZIN No. 673		
Length of body	152	155	182	206		
Width of the wings of sacrum	208		203	201		
Width (height) of the anterior articular surface	62/38	78/42	60/29	54/34		
Height of the first spinous process	83	_	87	96		
Height of the last spinous process	68	46	37	41		
Angle of the inclination of spinous processes	about 60					
Dimensions of auricular surface — length, maximum width	144 75	158 161 78 82	185 185 76 72	183 185 70 75		

Dimensions of the sacrum (in mm) in Coelodonta antiquitatis (BLUM.)

The cranial borders of wings are slightly oblique diverging anteriorly and consequently the base of the sacrum is concave anteriorly. The anterior articular surface of the body is oval (38 mm high, 62 mm wide), the same as the surfaces for articulation with the transverse processes of the last lumbar vertebra which are 22 mm high and 27 mm (right) or 32 mm (left) wide.

The dorsal and ventral sacral foramina are the largest between sacral vertebra I and II (the dorsal 10 mm and the ventral 18 mm in diameter), diminishing and becoming slitlike

posteriorly. The body of vertebra I is not as strongly fused with the whole of the sacrum as those of the remaining vertebrae, between which only transverse lines are visible, while a fissure occurs between the bodies of vertebrae I and II. The body of the sacrum is separated from its wings by two notches situated on the sides of the cranial articular surface of the body and on the ventral side by oblique crests (lineae terminales).

The spinous processes of the sacrum are similar in shape to those of the lumbar region, but more strongly extended anteroposteriorly and laterally in their dorsal parts. The spinous process of sacral vertebra I is not fused with the remaining ones, the same as the arch of this vertebra, which is separate from the next arch by an interarcual space. The spinous processes of the remaining sacral vertebrae are fused together to form a crest provided dorsally with a very strong tuberosity. Boundaries between successive processes are visible in the form of groovelike depressions.

The articular surfaces of cranial articular processes are oval, horizontal and bounded by mammillary processes of the same type as those of the lumbar region. Further articular processes, occurring in a vestigial form, are distinctly outlined only over the dorsal sacral foramen between vertebra 1 and II, where convexities are also visible undoubtedly corresponding to mammillary processes. The traces of articular processes disappear posteriorly.

The vertebral canal is triangular in transverse section.

The sacrum is an attachment place of many important ligaments related with the sacro--iliac articulation and those forming a dorsolateral limit of the pelvis.

Strongly widened tubers on the spinous processes of the sacrum make up an attachment of the dorsal sacro-iliac ligament, running from the sacral tuber, of the supraspinous ligament, probably very strongly developed in the woolly rhino and, in addition, of the gluteal fascia and, through its mediation, of the fibers of the gluteus medius and superficialis, the biceps femoris and the semitendinosus. Moreover, these tubers might serve, much the same as in the horse (the tubers of the last three spinous processes of the sacrum) for the attachment of the sacro coccygeus dorsalis medialis, while the sacro coccygeus dorsalis lateralis was presumabely inserted on the lateral surfaces of the spinous processes. The traces of the latter are, however, lacking.

The lateral sacro-iliac ligament, usually attaching on an extensive area of the lateral border of the sacrum, in the woolly rhino was attached — due to the length of the auricular surface (see above) — much more posteriorly on the caudal border of the wing (= of the last transverse process). Directly below, the sacro-sciatic ligament was attached along the caudal border of the sacrum. This border is, however, sharp and does not display any traces of attachments.

The posterior inclination of the spinous processes of the sacrum is caused by the gluteal muscles, biceps femoris and semitendinosus, whose caudal action is much stronger than the cranial one of the longissimus dorsi, irrespective of the strength of its fibers attached to the sacrum.

The following remarks result from the observation of the axial skeleton of the woolly rhino:

The position of the spinous processes of the cervical region, vertical in vertebrae V and VI and a caudal bend of the process of vertebra VII, is probably connected with a low position of the head and inclination of the neck. These processes are influenced by the spinalis cervicis, spinalis dorsi (the last two vertebrae), multifidus cervicis and the lamellar part of the ligamentum nuchae which is attached to the tips of spinous processes. However, the position of these processes, depends almost entirely on the spinalis cervicis (SLIJPER, 1946). The most advantageous from the viewpoint of the action of this muscle is on the whole the cranial inclination of the spinous processes of cervical vertebrae, observed in most mammals (all domestic mammals, l. c.). The inclination of the head and neck causes a decrease in an angle of insertion and, conse-

quently, a decrease in a component force suspending the cervical vertebrae to the thoracic part of the vertebral column. The caudal turn of the spinous processes of cervical vertebrae in the woolly rhino would serve for a compensative increase in the value of this angle. Here may be also involved a relative decrease in the role of the spinalis cervicis and increase in that of the multifidus cervicis, which, however, cannot be ascertained.

A similar sense (the compensation of the angle of insertion) may be ascribed to the deflection of the spinous process of thoracic vertebra I from the direction of the remaining thoracic vertebrae (Pl. I). Here would be involved the muscles spinalis cervicis and splenius, as well as the nuchal ligament, whose posterior attachments are situated on this process. In addition, a certain influence on the position of this process is exerted by the spinalis dorsi and multifidus dorsi, which, however, act in opposite direction.

The woolly rhino, as a hoofed animal with a large body weight, could certainly trot or gallop as a horse (horse gallop, SLIJPER, 1946). In these types of movement, only the limbs make up a driving organ, while the vertebral column remains stiffened, except for the lumbo-sacral articulation, which preserves a small degree of flexibility playing a certain role in one of the phases of horse gallop. The stiffening of the vertebral column in its thoracic sector is caused by high spinous processes and their ligaments (SLIJPER, *l. c.*) and in the lumbar region mostly by its shortness and by the articular surfaces occurring between the transverse processes. A certain degree of flexibility before the diaphragmatic vertebra was also found in herbivorous Ungulata, which is connected with the lack of ventral flexibility (concave ventrally) in the cervical sector (found by SLIJPER, *l. c.*) which is replaced, by lowering of the entire vertebral column beginning with the diaphragmatic vertebra. This is accompanied of course by a bend of the atlanto-occipital articulation.

In the woolly rhino, an increased flexibility of probably the same type is observed in the region from thoracic vertebra XVI to lumbar vertebra III, which is expressed by a vertical position of articular surfaces of articular processes parallel to the articular surfaces of the bodies and theoretically enabling a slight shift of the vertebrae in vertical plane. An incomplete shift of the bundles of the longissimus dorsi from the lumbar region may probably be also referred to the preservation of a certain flexibility in this region.

BONES OF THE THORACIC LIMB

Scapula. — Scapula (Pl. VIII, Figs. 1a-c) of the mediportal type, with its vertebral and anterior borders slightly convex and posterior somewhat concave. The posterior angle extended posteriorly. Maximum width of the scapula, recorded near the vertebral border, amounts to -about a half of the physiological length ⁴.

The spine of the scapula is shaped like an isosceles triangle with its base stretching from the region of the neck of scapula to the vertebral border and an obtuse (about 130°) apical angle. The spine is bent posteriorly towards the infraspinous fossa. The supra- and infraspinous fossae are developed to an approximately equal degree. At the level of the spinal tuber, slightly wider is the supra- and near the spinal border the infraspinous fossa.

The neck of scapula is elongate but not very strongly contracted. The spinal tuber is robust, the glenoid cavity oval and anteroposteriorly elongate. The glenoid notch vestigial.

⁴ The proportions of the scapula were undoubtedly subject to a certain variability which, however, due to the scarcity of material, could not be accurately studied. In the specimen from Podbaba, the width-length ratio, amounting to 1:2 is in conformity with BRANDT'S (1877) data. The scapula of the rhino from Starunia I is relatively wider (about 3:5 according to NIEZABITOWSKI, 1914), which may be caused by its young individual age.



A Scapula, medial view;

B Scapula, lateral view; a m. rhomboideus, b m. trapezius, c m. deltoideus, d caput longum m. tricipitis, e m. teres major, f m. teres minor, g m. pectoralis profundus, h m. serratus ventralis, i m. subscapularis, k m. biceps brachii.

C Humerus, proximal view; a m. infraspinatus, b m. supraspinatus

The following traces of muscle attachments are observed on the surface of scapula (Text-fig. 6A, B).

The trace of the rhomboideus occurs in the form of tubers situated on the vertebral border of scapula and on its medial surface about 2 cm from the vertebral border (Text-fig. 6A, a).

The serrate line, a trace of the attachment of the serratus ventralis, runs at a distance equalling about two-thirds of the length of scapula from the glenoid cavity. It is indented by wide, shallow bends.

The subscapular fossa, an attachment place of the subscapularis muscle is wide and shallow. Its surface is smooth, except for the lowest part. A longitudinal convexity, taking about one-third of the width of scapular neck, separates it from the posterior border of scapula.

The posterior border of scapula is the region in which the caput longum musculi tricipitis is attached. At the lower one-third of its length, it is thickened to about 30 mm and, above this place, bent externally. The trace of the attachment of the long head of the triceps is shaped like a crest beginning with a tubercle above the glenoid cavity and running dorsally along the outer margin of the posterior border (Text-fig. 6B,d). The crest disappears dorsally.

MAGDALENA BORSUK-BIAŁYNICKA

Table 39

Cat. No.	C. antiquitatis		Rh. son-				
	ZAPUJ	ZIN N	No. 615	ZIN NO	o. 24729	MIZ	daicus
Dimension	No. 683	left	right	left	right		MIZ
Physiological length	457	431	431	400	395	408	344
Length measured along the an- terior border	480	421	421	394	390	395	347
Length of the base of spine	350	335	342	325	302	352	252
Width of supraspinous fossa *	123	74	80	74	79	83	47
Width of infraspinous fossa *	147	120	110	110	113	87	132
Maximum antero-posterior di- mension of the neck	113	89	91	103	101	82	84
Maximum antero-posterior di- mension of the glenoid part	142	137	135	133	134	120	139
Anteroposterior diameter of the glenoid fossa	88	84	84	78	83	73	72
Height of spine, together with thickness of scapula	95	113	114	99	82	82	95
Thickness of scapula in the region of the acromion	47	33	39	35	36	36	34

Dimensions (in mm) of the scapula of Coelodonta antiquitatis (BLUM.) as compared with those of Diceros bicornis L. and Rhinoceros sondaicus DESM.

* The largest near the vertebral border, perpendicular to the spine.

The posterior projection of the posterior angle of scapula is caused by the activity of the dorsal part of the caput longum musculi tricipitis, the teres major and the dorsal part of the deltoideus, but the scars of these muscles are indistinct.

The coracoid process is very poorly developed in the form of a slight roughness.

The spinal tuber extends on both borders of the scapular spine. Its apex and the dorsal border of the scapular spine serve as attachment places for the trapezius. The lower extension of the spinal tuber was an attachment place of the deltoideus. A longitudinal tubercle situated in the ventral part of the scapular spine (Text-fig. 6c) is most likely to be related with the last-named muscle.

The areas of the infra- and supraspinatus, having smooth or almost completely smooth surfaces, are approximately identical in extent. The area of the supraspinatus is limited anteriorly by a muscle scar of the pectoralis profundus (or, higher up by the levator scapulae), developed in the form of a longitudinal depression, 25 mm wide and running along the anterior border of scapula. The area of the infraspinatus is limited in the dorsal part by attachments traces of the teres major, deltoideus and of the long head of the triceps.

A crest running posterodorsally of the acromial end of the scapular spine (Text-fig. 6B, f) is a trace of the teres minor. Part of this muscle is attached to a flat tubercle situated just over the posteroexternal border of the glenoid cavity.

The strongly developed scar of the biceps brachii on the external surface of the scapular tuber projects ventrally and externally.

Humerus. — The humerus (Pl. X, Fig. 2; Pl. XI, Figs. 1, 4a, b; Pl. XII, Fig. 3) is characterized by a strong, external extension of its extremities and upper part of shaft, with a simultaneous external shift of the medial muscular part of the upper extremity and a reduction of the medial epicondyle.

The head of humerus, slightly separated from the muscular part, round, slightly convex, is inclined posteriorly, at an angle of about 44° , to the axis of shaft and somewhat to the medial surface of the humerus (about 107° to the axis of shaft).

The lateral tuberosity is bifid. It projects above the level of head anteriorly for about 25 mm and posteriorly for about 15 mm. The notch of the lateral tuberosity is situated anteriorly and ventrally of the anterior border of head.

The medial tuberosity is also bifid. Its anterior part is shifted before the head and exceeds it in height by about 35 mm. The posterior part is situated on the medial side directly below the head. The bicipital groove, with a smooth, concave surface, is about 65 mm wide.

A strong development of the muscular part, limited by the crest of the lateral tuberosity, the curved line and the deltoid tuberosity, results in an extension of the proximal part of the shaft of the order of about 0.6 of the physiological length of the bone and about twice as wide as the minimum width of shaft, as well as in its anteromedial and posterolateral flattening.

A turn of the distal extremity of humerus in relation to the proximal one amounts to about 30° .

The oleocranon fossa is deep, with its borders running obliquely, ventrally and medially.

The medial condyle is larger and extends towards the medial surface of the humerus and the lateral smaller, becomes rounded towards its epicondyle. The distal extremity of humerus is inclined posteriorly and externally forming, together with the axis of shaft, an angle of about 120°.

The lateral epicondyle (Pl. XI, Fig. 1; Text-fig. 7B) has the form of a bony protuberance with a round $(90 \times 90 \text{ mm})$ strongly tuberculate lateral wall. In the anterior part, it does not project externally outside the level of condyle; in the posterior part, its thickness reaches about 50 mm and the dorsal border projects about 60 mm outside of the border of condyle. Ventrally, the lateral epicondyle is oviform and narrowing anteriorly (Text-fig. 9E).

The medial epicondyle (Pl. XII, Fig. 3; Text-fig. 7C) is shaped like an oval bony protuberance (90×60 mm), not very strongly projecting over the surface of condyle and reaching posteriorly about 45 mm in thickness. Its posterior part overlaps the oleocranon fossa contracting its inlet.

The traces of the following muscles may be recognized on the humerus (Text-fig. 7A-D).

Two flat oval areas (about 65×40 mm), making up attachments of the infraspinatus occur on the lateral surface of the lateral tuberosity. One of them, situated about 20 mm below the notch of the lateral tuberosity, is arranged with its longer diameter parallel to the axis of the shaft, the other occurring on the posterior part of the lateral tuberosity, has its longer diameter approximately perpendicular to the bone axis.

The anterior parts of the lateral and medial tuberosities, separated by a wide bicipital groove are attachment places of the supraspinatus. The lateral scar of this muscle is probably formed by an oval area (50 mm long and 26 mm wide), situated before the notch

Table 40

Cat. No.		Coelodonta antiquitatis						Diceros	bicorni	C. simum	Rh. sondaicus	
Dimensions	MG-1	PS-2	PS-3	ZA No.	PUJ 683	, Z No.	24729	ZIN N	No. 615	MIZ	ZIN exhibition	MIZ
Physiological length *	356	376	380	350	344	340	339	350	364		_	
Maximum length	394	415	424	433	429	400	400	410	422	_	478	_
Width of shaft at the level of the deltoid tuberosity	150	167	_	161	161	158	165	193	173	147	197	170
Minimum width of shaft	73	74	. 77	70	70	60	58	60	59	59	79	58
Minimum diameter of shaft	72	84	88	70	71	61	67	68	65	50	75	66
Maximum width of distal end **	155	159	156	143	143	145	152	149	146	143	170	141
Width of the trochela humeri (measured from below)	97	106	104	100	101	93	95	93	86	89	114	102
Transverse diameter of the caput humeri	103		108	105	107	101	95	100	82	89	110	101
Longitudinal diameter of the caput humeri	106	_	99	98	103	89	81	95	85	77	115	96
Medial diameter of the distal end	112	130	126	119	118	102	105	103	103	98	106	118
Lateral diameter of the distal end	115	120	112	100	113	99	108	110	108	93	109	109

Dimensions (in mm) of the humeri of Coelodonta antiquitatis (BLUM.) as compared with those in Diceros bicornis L., Rhinoceros sondaicus DESM. and Ceratotherium simum BURCH.

* According to DÜRST (1926).

** Parallel to the axis of the distal extremity of humerus.





The right humerus of *Coelodonta antiquitatis* (BLUM). with muscle and ligament attachment areas marked; \times ca 1/6, *A* anterior view, *B* lateral view, *C* medial view, *D* posterior view, *a* m. infraspinatus, *b* m. supraspinatus, *c* m. subscapularis, *d* m. pectoralis profundus, *e* m. teres minor, *f* m. deltoideus, *g* caput laterale m. tricipitis, *h* caput mediale m. tricipitis, *i* m. brachiocephalicus, *k* m. latissimus dorsi and m. teres major, *l* m. coracobrachalis, *m* m. flexor digitalis superficialis, *n* m. extensor digitalis communis, *o* m. extensor digitalis lateralis, *p* m. extensor carpi ulnaris, *r* m. extensor carpi radialis, *l*. c. m. lig. collaterale mediale, *l*. c. l., lig. collaterale laterale

of the lateral tuberosity (Text-fig. 7B, b) and does not reach its most anterior part. The attachment place of the medial part of this muscle was probably the apex of the anterior part of the medial tuberosity, while the lateral surface of this part of the tuberosity might be connected with part of the fibers of the pectoralis profundus (Text-fig. 7A, d). Posteriorly of these muscles, the subscapularis was undoubtedly attached to the posterior part of the medial tuberosity. Its scar, turning without a distinct boundary, into those of the pectoralis profundus and the supraspinatus, is shaped like a smooth area, 83 mm long and 34 mm wide, under the head of humerus.

A depression (impressio teretica), limited by a tubercle near the curved line and provided with a small bony protuberance on its surface (Text-fig. 7*B*, *e*), that is, a trace of the teres minor (poorly developed in young individuals) occurs on the lateral side of the bone directly posteriorly and distally of the anterior attachment of the infraspinatus. The deltoid tuberosity, connected with the attachment of m. deltoideus, has the form of an elongate bony protuberance ($68 \times$ about 28 mm) with its longer axis slightly ascending posteriorly. Frequently, it projects posteriorly and externally of the muscle area.

The curved line and a rough area adhering to it posteriorly make up an attachment of the lateral head of the triceps brachii.

The wide, flat crest of humerus, running parallel to the axis of shaft, is cut by longitudinal grooves on both its external (anteriorly of the anterior attachment of the infraspinatus) and anteromedial surface. The brachiocephalicus and probably part of the fibers of the pectoralis 5 - Palaeontologia Polonica No. 29

superficialis were attached in this region. Both these muscles were probably attached also below the deltoid tuberosity on the above mentioned crest running towards the medial condyle. Their traces, starting about 30 mm below the deltoid tuberosity, discontinue directly above the coronoid fossa. They border a wide groove of the brachial muscle (sulcus m. brachialis). The trace of the brachial muscle, which on the whole starts posteriorly of the head of humerus, has not been identified in this place. On the other hand, quite distinct is the distal attachment of this muscle to the anteromedial surface of the radius (see below).

A sharp, short (about 30 mm) crest runs from the medial tuberosity over the anteromedial surface of humerus. A convex, teres tuberosity about 20 mm wide and varying in length (about 30 to about 70 mm) is situated, in continuation of this crest, more or less halfway the length of humerus. The crest and the tuberosity form an attachment area of the latissimus dorsi and the teres major. Another small, longitudinal tuberosity occurs (Text-fig. 7 D, h) above the teres tuberosity, posteriorly of it and, at the same time, in continuation of the crest of lateral epicondyle. It makes up an attachment place for the medial head of the triceps brachii. Near the teres tuberosity, a not very distinctly separated attachment of the coraco-brachialis (Text-fig. 7 A, l) is formed by the anterior surface of humerus above the medial condyle.

The epicondyles of humerus make up places of origin of numerous muscles moving the distal part of the limb and attachment places of ligaments.

An attachment, probably related with the flexor digitalis profundus, is situated in the posterior part of the medial epicondyle on its distal surface slightly inclined medially. It is difficult to interpret the remaining attachments of this epicondyle (Text-fig. 7C). A smooth area in its central part is limited anteriorly by a rough convexity, resembling in development an attachment place of the medial ligament in the ruminants and the horse, but situated considerably more posteriorly than in these mammals. With such a position of the ligament, it is difficult to imagine the situation of the attachments of the flexor capri radialis and the flexor carpi ulnaris (or, of a common tendon of these muscles which, according to BEDDARD & TREVES, 1889, occurs in D. sumatrensis), since they are on the whole situated posteriorly of the ligament. Perhaps, they were situated anteromedially of the attachment of the flexor digitalis superficialis, on the posterior surface of the epicondyle, which is, however, marked by relatively small dimensions for a supposed attachment area of the three important muscles.

An oval, smooth area $(50 \times 37 \text{ mm})$, situated in the anterior part of the lateral epicondyle and whose longer axis is arranged perpendicularly to the axis of shaft, is a trace of the lateral ligament of the elbow joint. Dorsally of it, a tuberculate attachment scar of the extensor digitalis communis (Text-fig. 7B, n) occurs in the lateral part of the coronoid fossa and on the surface of the epicondyle adhering to this fossa. A rhomboidal, tuberculate area (Text-fig. 7B, o) is situated posteriorly of the last-named scar and posterodorsally of the trace of the ligament. This area probably belonged to the humeral part of the lateral digital extensor, whose venter is situated in the limb directly behind the common digital extensor. The humeral part of the lateral digital extensor occurs in the Sumatran rhino (BEDDARD & TREVES, 1889) in contrast to the horse in which this muscle begins on the forearm bones.

A ventrally facing ovate surface and part of laterodistal surface of the epicondyle formed attachment areas of the ulnaris lateralis, a strong flexor of the forearm.

A longitudinal sharp about 85 mm long crest runs along the lateral condyloid crest, changing in its upper part into a longitudinal tuberosity directed towards the coronoid fossa. The crest and the tuberosity are attachment places of two muscles: the extensor carpi radialis and the supinator longus. However, it is impossible to separate accurately the traces of the two

muscles. Judging from its position in *D. sumatrensis* (cf. BEDDARD & TREVES, 1889) the origin of the supinator longus was probably situated more proximally.

The humeral head of the extensor carpi obliquus 5, whose occurrence in *C. antiquitatis* may be expected by analogy to *D. sumatrensis*, was certainly also attached in this region. In the horse, this muscle begins on the external side of the radius.

Radius (Pl. XII, Figs. 1, 2a-c; Pl. XIII, Figs. 1a, b). — A massive bone. The strongest contraction of the shaft, amounting to about 16 to 19% of the physiological length, occurs just above a point halfway of this length. The width of the distal extremity is twice as large and that of the proximal one slightly less than twice as large as the minimum width of the shaft.

The proximal articular surface is bifid. Its medial part (about 70 mm long and about 60 mm wide) strongly projects anteriorly. The external part is about 40 mm long and about 45 mm wide. A distinct, sharp protuberance occurs on the posterior border of the articular surface of the head.

The tuberosites for the attachment of ligaments are prominent, oval, about 25 mm high and about 40 mm (the external one) and about 52 mm (the medial one) long. The external tuberosity overlaps the anterior surface of the radius (Text-fig. 8A, c, l).

The radial tuberosity oval (about 49 mm high and 32 mm wide) and covered with crests parallel to its longer axis. It is situated more or less in the middle of the anterior surface of radius and frequently fuses, by a barely perceptible crest (Pl. XII, Fig. 2c), with the external ligamental tuberosity which gives it the shape of a triangle with an obtuse apex turned distally. Posteriorly of the external ligamental tuberosity, there occurs a tubercular crest, running down from the border of the humeral articular surface and making up a lateral limit of the surface for articulating with the ulna.

The surface for articulating with the ulna is situated on the posterior proximal side at one-third of the radius and on the posterolateral side at distal two-thirds of the bone. It has the form of two triangles whose bases rest on the articular surfaces of the bone. These triangles are covered with robust tuberosities serving as attachments areas for the interosseous ligaments and provided at their bases with articular surfaces for the ulna. At the proximal extremity, these are two surfaces: the medial one in the form of a narrow strip (about 5 to 8 mm high and 30 to 40 mm long) and the external, triangular one, slightly concave, 30 to 35 mm high and with its base about 60 mm long. The articular surface for the distal extremity of ulna is semilunar and resting with its distal, concave border on the postero-external border of the articular surface of the distal extremity.

The shaft of radius, oval in transverse section in the proximal half of the bone, becomes trapezoidal distally, which is caused by the occurrence — on the anterior surface of the bone — of two longitudinal, blunt crests which limit the tendon groove (for the tendon of the extensor carpi radialis) situated between them and by the sharpening of the posterolateral borders of the bone.

⁵ This muscle is described by BEDDARD & TREVES (1889) as the extensor obliquus metacarpi and designated in their illustration as the extensor carpi radialis, whereas the proper extensor carpi radialis is described as the extensor metacarpi and illustrated as the extensor carpi radialis brevior. It follows from the same illustration that the humeral head of the extensor carpi obliquus was situated between the extensor digitalis communis and the extensor carpi radialis, attaching itself anteriorly below the latter, that is, on the tuberculate surface separating the attachment area of the extensor carpi radialis from the dorsal border of the epicondyle.
Species	Co	elodonta	itatis		Rhino- ceros son- daicus				
Cat. No.	ZAPUJ	No. 683	ZIN	ZIN	MIZ	ZIN N	o. 24729	ZIN	
Dimensions	left	right	17220	No. 5087	WILZ.	left	right	No. 615	
Physiological length	308	312	361	300	_	329	330	336	
Maximum length	347	348	385	343	361	353	358	367	348
Maximum length on the external side	290	295	342	295	333	310	310	312	about 291
Maximum length on the medial side	319	317	351	318	348	325	326	332	309
Width of the head of radius	102	103	117	105	96	99	101	106	107
Width of the proximal articular surface	102	103	114	104	89	92	98	100	106
Minimum width of shaft	54	53	70	53	47	48	49	51	46
Width of the distal extremity	110	110		110	93	62	65	74	about 102
Width of the carpal surface	84	78	106	93	75	81	76	77	89
Diameter of shaft *	39	38	47	35	31	35	34	37	34

 Table 41

 Dimensions (in mm) of the radius in Coelodonta antiquitatis (BLUM.), Diceros bicornis L. and Rhinoceros sondaicus DESM

* At the same level as the smallest width of shaft.

The distal end is irregularly hexagonal due to the presence of the medial tuberosity for the attachment of ligaments and to the occurrence of a posterolaterally facing surface (which makes up the lowermost part of the articular surface for the ulna, see above). This surface is also slightly turned distally thus causing a contraction in this direction.

The articular surface of the distal extremity consists of a medial part, destined for the scaphoideum, anteriorly concave and posteriorly limited by a roller-like concavity, overlapping the posterior surface of the bone, and of a concave external surface for the lunare.

The anterior and posterior walls of the head of radius, as well as the walls of the distal end are covered with many nutrient foramina. A nutrient foramen also as a rule occurs on the radius on the side of the interosseous space. A distant vascular groove runs ventrally of this region along the posteroexternal border of the bone.

The traces of the following muscular and ligamental attachments are visible on the radius: The radial tuberosity — an attachment place of the biceps brachii.

The medial ligamental tuberosity — an attachment place of the medial ligament corresponding to the ligamentum collaterale mediale breve in the horse and the ruminants⁶.

⁶ The other part of the medial ligament of the elbow joint in the horse and the ruminants, that is the long medial ligaments is an equivalent of the vestigial, tendinous muscle called the pronator radii teres (NICKEL, SCHUMMER & SEIFERLE,



Fig. 8

The left radius of *Coelodonta antiquitatis* (BLUM.) with muscle and ligament attachment areas marked; \times ca 1/6. A anterior view, *B* lateral view, *C* posterior view, *D* medial view, *a* m. biceps brachii, *b* m. extensor digitalis communis, *c* m. extensor ossis metacarpi pollicis, *d* m. brachialis, l. c. m., ligamentum collaterale mediale, l. c. l., ligamentum collaterale laterale.

A triangular, rough area, narrowing distally and reaching about halfway the length of shaft, is situated below the attachment of the medial ligament of the elbow joint. This area makes up an insertion of the brachial muscle.

The lateral ligamental tuberosity, as a rule much strongly developed than the medial one, makes up an attachment area of the lateral ligament and a proximal limit of the attachment area of the radial common digital extensor. An oblique crest, which sometimes connects the lateral ligamental tuberosity with the latero-distal border of the radial tuberosity, makes up an anterior limitation and a strong crest parallel to the axis of shaft, running along the external border of the attachment surface for the interosseous ligament, a posterior limitation of the radial attachment area of the common digital extensor. Since the surface of shaft is in this region completely smooth, it is not clear how far the attachment of this muscle reaches down the shaft of the radius (according to BEDDARD & TREVES, 1889, in *D. sumatrensis* this attachment reaches halfway the length of shaft).

In the horse, the tendon of the common digital extensor runs in a lateral tendon groove, limited externally by the styloid process of ulna. In *C. antiquitatis*, in which this groove is poorly developed and limited distally by a strong ligamental tuberosity, connected with the attachment of one of the ligaments of the carpal joints. It seems, therefore, that the tendon of the common

^{1968).} The degree of reduction in this muscle, which rotates the forearm inwards, is connected with the disappearance of the mobility between the forearm bones. The development of the forearm bones in the rhino is most similar, in the mutual ratio of the size of radius and ulna and in their mobility, to the forearm of the pig. Hence, we may expect by analogy that the pronator radii teres in *C. antiquitatis* functioned as a muscle and that the medial ligament was signle as in the pig. BEDDARD & TREVES (1889) do not, however, find the presence of this muscle in *D. sumatrensis*. Likewise, no information in this respect may be obtained from the medial surface of the radius in *C. antiquitatis*.

digital extensor runs over the distal end of ulna externally of the ligamental tuberosity mentioned above.

The longitudinal crest, running along the posterolateral border of radius (Text-fig. 8Bc) separated by the vascular groove from the surface for ulna, might make up an attachment of the radial head of the extensor ossis metacarpi pollicis, corresponding to a single head occurring in the horse and other domestic animals. In *D. sumatrensis*, this muscle also had a radio-humeral head, attached to extensor epicondyle of humerus and to the shaft of radius. It is impossible to ascertain whether or not such a head occurred in *C. antiquitatis* and in which place of the radius it was attached.

The tuberosities occurring on the medial side of radius on the boundary of the shaft and the distal end make up attachments of the medial ligament of the carpal joints. Likewise, the insertion of the supinator longus was probably situated in this region.

The borders of the rough surface for articulating with the ulna serve as attachments of the interosseous ligaments.

The superficial and deep digital flexors, running, in the horse, from the flexor epicondyle of the humerus to the digit, are, in addition, attached to the posterior surface of radius and the deep digital flexor also on the medial side of the olecranon. Such accessory attachments have not been found in D. sumatrensis (BEDDARD & TREVES, 1889) which enables the supposition that they did not occur in C. antiquitatis either. However, irregularities occurring sometimes in the distal half of the medial border of radius and corresponding in position to the radial attachment of the superficial digital flexor in the horse might indicate the presence of such an attachment in C. antiquitatis.

Ulna. — The ulna (Pl. XIII, Figs. 1*a*, *b*, 2*a*, *b*) is about 1.5 times as long as the radius and, consequently, in the life-time position, about one-third of the ulna projects above the level of the proximal articular surface of the radius. The posterior border of ulna is strongly bent with its concavity facing posteriorly. The triangular transverse section of its shaft changes in the region of the olecranon into irregularly quadrangular, which results from a protrusion of the external surface of olecranon. Subsequenty, as a result of a concavity of its anterior and medial walls, it takes an irregularly polygonal shape.

The relatively low tuber olecranii is provided with a thick crest running sagitally through the middle of its anterior part (Text-fig. 9D, a) and then postero-obliquely towards the medial wall of the olecranon.

The narrow anterior wall of the olecranon slightly extends upwards in particular in the medial direction, where a sharp crest (Text-fig. 9D, c), that is, the attachment of the medial head of triceps, runs along it and downwards where it turns into a flattened, dorsal surface of the anconaeus process.

The anterior surface of the shaft, in particular its proximal part, is strongly developed medially. The surface of the semilunar notch is bifid in its lower part, its medial part being oblique and strongly projecting medially, while the external part runs parallel to the sagittal plane of the shaft. The distal borders of the semilunar notch contact each other at an angle which contains a sharp process of the posterior border of the proximal articular surface of radius.

The surfaces for the articulation with the radius closely fit corresponding surfaces on the latter.

A saddle-shaped surface for the cuneiform, with its concavity arranged in the sagittal plane of the bone and with its convexity perpendicular to it, occurs on the distal surface of the distal end of ulna. The articular surface for the accessory carpal bone forms a medial wall

Table 42

Species	Coelo	elodonta antiquitatis Dice			Diceros bicornis		
Cat. No.	ZAPUJ	No. 683	ZIN	MIZ	ZIN	ZIN	MIZ
Dimensions	right	left	No. 4063		No. 24729	No. 615	
Maximum length measured parallel to the axis of shaft	451	451	460	464	444	434	433
Distance from anconaeus process to the distal end *	366	365	362	_		372	_
Length of shaft	366	355	about 383	_	_	398	_
Length of the anterior border of ole- cranon	140	123	160	123	129	112	150
Width of the tuber olecranii	82	68		68	72	72 58	
Width of olecranon at the base (mi- nimum)	25	25	30	32	32	35	23
Minimum anteroposterior dimension of olecranon	86	85	90	80	82	100	83
Anteroposterior dimension in the re- gion of processus anconaeus **	112	110	121	100	102	115	109
Minimum width of the anterior wall of shaft	52	52	53	32	36	42	37
Anteroposterior dimension of shaft (at the same level as the minimum width)	43	42	48	43	40	41	40
Maximum width of semilunar notch ***	93	95	91		89	97	_
Maximum anteroposterior dimension of the distal end	58	58	75	_		61	

Dimensions (in mm) of ulna in Coelodonta antiquitatis (BLUM.), Diceros bicornis L. and Rhinoceros sondaicus DESM.

* In projection on a tangent to the curvature of shaft.

** Perpendicularly to the axis of olecranon.

*** In projection on a straight line perpendicular to the longitudinal axis of shaft.

of the styloid process of ulna, which is shaped like a pyramid with a triangular base and an apex directed distally.

The most important muscle attachments of the ulna are located on the olecranon which makes up a main hypomochlion of the ulnar articulation. It comprises insertions of particular heads of the triceps brachii, origins of the ulnar head of the flexor carpi ulnaris and, perhaps, of the ulnar head of the deep digital flexor and the palmaris longus, or of one of them only.

The medial head of the triceps is attached in the anteromedial part of the tuber olecranii. This attachment is limited posterolaterally by a robust, blunt crest (Text-fig. 9 Ca, d) and extends turning itself into the anteromedial border of the olecranon which, in this connection, takes the shape of a sharp, strongly projecting crest.

The lateral part of the tuber olecranii makes up a bony attachment of the long head of triceps. Extensive and irregularly oval, this attachment turns posteriorly into a rough, oval



Fig. 9

Bones of Coelodonta antiquitatis (BLUM.) with muscle attachment areas and joint surfaces marked; \times ca 1/6. A the right ulna, anterior view; B same bone, lateral view; C same bone, medial view; D olecranon of the right ulna, proximal view; E the right humerus, distal view, right unciforme, medial view; a caput longum m. tricipitis, b caput laterale m. tricipitis, c caput mediale m. tricipitis, d m. flexor carpi ulnaris, e m. flexor digitalis profundus, f m. extensor digitalis lateralis, g mextensor digitalis communis, h m. extensor carpi ulnaris, larticular surface for lunar, m articular surface for magnum, Mc III, articular surface for metacarpale III.

attachment of the ulnar head of the flexor carpi ulnaris with a subvertical longitudinal axis. It is bent medially.

Two tuberosities (Text-fig. 9B, b), which make up an attachment of the lateral head of triceps, usually occur on the lateral side of the olecranon.

The medial side of the olecranon is covered in its proximal half with strong, irregular roughnesses in the form of crests and tubercles intersecting each other. In domestic animals, this region is an attachment place of the ulnar head of the deep digital flexor. According to BEDDARD & TREVES (1889) such head does not occur in *D. sumatrensis*. However, the supposed palmaris longus they mention is excellently matched in regard to its attachments (olecranon — tendon of the deep digital flexor) with the description of the ulnar head of the deep digital flexor. Besides, the occurrence, in the rhino, of the palmaris longus, a muscle typical of the Pri-

mates (it starts on the medial epicondyle), is less probable. In this connection, the attachments visible on the medial surface of the olecranon (Text-fig. 9C, e) are interpreted in the present paper as those belonging to the ulnar head of the deep digital flexor.

A strand of muscle scars (Text-fig. 9B, g) of the ulnar heads of the common digital flexor (situated higher) and the lateral digital extensor (situated lower) occurs on the lateral border of ulna in the medial one-third of its length. This strand is limited proximally by an oblique vascular groove running from the lateral to the anterior surface of the bone and continuing along the surface connecting forearm bones.

An elongate bony protuberance, running from the end of shaft distally and terminating in a smooth, oval area $(20 \times 17 \text{ mm})$ occurs as a continuation of the lateral border of ulna. It probably makes up an attachment of the external ligament of the carpal articulation. The form of this ligament, is however, indeterminable.

Carpal bones (Pls. XV—XVII, Figs. 1*a-d*). — The following traces of muscle and ligament attachments are visible on the carpal bones.

On the dorsal walls of the scaphoideum, lunare and cuneiforme, as well as of the bones of the distal row of carpus, there occur attachments of the dorsal ligaments connecting them. On the scaphoideum this attachment occurs in the form of a convexity running obliquely along the process of this bone formed by os carpi centrale.

Table 43

Dimensions (in mm) of the carpal bones in Coelodonta antiquitatis (BLUM.)

Cat. ZAPUJ No. 683

Bone	Dimension	Maximum anterior width	Maximum anterior height	Total thickness
Scaphoideum		86	60	69
Lunare		52	46	68
Cuneiforme		38	46	46
Pisiforme		27	31	58
Trapezoideum		28	32	43
Magnum		49	25	89
Unciforme		66	48	75

On the lunare, this is a tuberosity limited by two crests slightly convergent distally and running from the proximal to the distal border of the bone (Text-fig. $10B_1$) and on the cuneiform — a vertical crest forming the medial border of the bone. A ligamental tuberosity, situated in the distal and medial corner and markedly corresponding to that situated in the distal lateral part of the dorsal surface of the magnum, occurs on the dorsal surface of the cuneiform. Two tuberosities, facing each other and similarly corresponding to each other (as two attachments of the same ligament), occur near the medial border of the magnum (a tuberosity in the form of a crest) and in the lateral and distal part of the trapezoideum (Text-fig. $10E_1, F$).

The medial surface of the scaphoideum makes up an attachment place of deep part of the ligamentum collaterale mediale. Bony proturbances (Text-fig. $10C_2$), occurring on the

medial surface of this bone anteriorly of its posteromedial tuber, are probably related with this ligament. The anterolateral borders of the cuneiform and unciform (Text-fig. 10 A, D) may in turn be related (judging by analogy to the carpal bones of the horse) with deep part of the ligamentum collaterale ulnare of the carpal joints.

The posterior process of the unciforme (Text-fig. 9F) projecting posteriorly for about 80 mm (measuring from the dorsal surface of the bone) and 34 mm in maximum width is marked by the largest dimensions on the volar surface of the carpus. A robust, oval ligamental tuberosity occurs at the end of this process, which is curved laterally and downward (Pl. XV, Fig. 2c). The magnum has a more delicate (27 mm in width and more strongly contracted at the base) but somewhat longer (90 mm) process, also provided with a tuberosity situated on its proximal, lateral and posterior surfaces (Pl. XV, Figs. 3b-d; Text-fig. 10 E_{2-5}). In the case of the lunare and magnum, these processes form attachments for radiate ligaments connecting particular carpal bones and running to the distal extremity of the radius and to the metacarpal bone. The same concerns the posteromedial tuberosity of the scaphoideum (Text-fig. $10C_2$). Judging by analogy to the horse, only few carpal ligaments were attached to the palmar surface of the unciforme and the purpose of this process was therefore, certainly different. Presumably, together with the posterior process of the magnum and proximal ends of metacarpal bones, it formed an attachment of the interosseus medius. This muscle plays a fundamental role in keeping the metacarpo-digital angle and thus preventing the limb from taking a superextended position typical of the plantigrades. (In connection with this function, this muscle in the horse completely turns into a tendon, forming what is known as the tendo interosseus).

The os carpi accessorium (os pisiforme) (Pl. XVII, Figs. 1a-d) is connected with the adjoining bones by special ligaments (according to SISSON, 1938, ligaments of the accessory carpal bone). The distal ligament connecting this bone with metacarpale IV (Text-fig. 5H, lg) is attached to its swollen distal border in the distal part of the vertical groove for the extensor carpi ulnaris (Text-fig. 5H ex). A robust tuberosity for the ligament connecting the two bones is situated on the medial side of the articular surface for the cuneiforme. The proximal ligament of the accessory bone is attached to its proximal border near the flexor carpi ulnaris, with whose attachment the tuberosities of the posterior surface of this bone (Text-fig. 5H, fl) are probably related.

In regard to the mutual arrangement of its particular bones, the carpus of the woolly rhino displays an alternating type of structure, connected with the cursorial type of the limb and representing a primitive structure, which (according to OSBORN, 1929) is initial in the order Perissodactyla. This structure is marked by a lack of contact or a strongly limited contact between the lunare and the magnum. In the woolly rhino's carpus, this contact is very slight on the dorsal side of limb (limited only to the mediodistal angle of the lunare, Pl. XIV, Fig.1*a*) and its area gradually extends posteriorly (Text-fig. $10E_5$). The proximal articular surface of the magnum, articulates, near the dorsal surface of this bone, almost exclusively with the lateral (central) process of the scaphoideum (Text-fig. $10E_5$, s). Due to the presence of this process, the interosseous space between the scaphoideum and the lunare has the shape of an oblique slit directed distally and laterally and extending directly to form a slit between the magnum and the cuneiforme (Pl. XIV, Fig. 1*a*). This slit seems to divide the carpus into two blocks. Such an oblique division of the carpus is also a primitive character of the carpi in the Perissodactyla, directly connected with the position of the lunare and the magnum.

Some of the features of carpus in the woolly rhino are graviportal in character, which properly corresponds to a considerable body weight of the animal. Here belongs the shape of the magnum (Text-fig. $10E_1$) which grows in width (its height/width ratio amounting to 1 : 2)

Table 44

Dimensions (in mm) of the metacarpal bones in Coelodonta antiquitatis (BLUM.)

Cat. ZAPUJ No. 683

Bone Dimension	Metacarpale II	Metacarpale III	Metacarpale IV
Anterior length in sagittal plane	139	155 (maximum 161)	130
Width of proximal end	46	46	44
Maximum width of proximal end	51	60	44
Width of distal end	36	49	35
Maximum width of distal end	48	57	43

A B_{1} C_{1} C_{2} C_{2}



Fig. 10

The right carpals of *Coelodonta antiquitatis* (BLUM.) with articular surfaces designated by letters; \times ca 1/6. A cuneiform, $B_1 B_2$ lunar, $C_1 C_2$ scaphoid, D uniciform, E_{1-5} magnum, F, trapezoideum. $A B_1 C_1 D_1 E_1$ F anterior views, $B_2 E_2$ posterior views, $C_2 E_3$ medial views, E_4 lateral view, E_5 proximal view, articular surfaces for: c cuneiform, I, lunar, m. magnum, r, radius, s, scaphoid, t, trapezoideum, u, unciform, ul, ulna, Mc II and Mc III, metacarpals II, III.

and, in the present writer's opinion, a strong development of the posterior processes of the distal row of carpus (the unciforme and the magnum). The development of these processes makes up an adaptation to fast running (RADINSKY, 1965, p. 245), since it is connected with the development of here attached palmar flexors. In view of the loss of digits V and I, the interosseus medius only may come into consideration in the rhino. As mentioned above, this muscle is of importance for maintaining the metacarpo-digital angle, which becomes more and more difficult with an increase in body weight. The development of the attachments of muscles which are responsible for this function, is correlated with the development of the muscles themselves and the shift of the muscle attachments from the joint served by them, raises the efficiency of these muscles. The development of the posterior processes of the unciforme and the magnum would be, therefore, a graviportal adaptation, connected, however, with the high degree of the animal's mobility only indirectly, that is, by keeping the limb in an unguligrade position.

BONES OF THE PELVIC LIMB

Pelvic girdle. — Pelvis (Pl. XIX, Fig. 1; Pl. XX, Fig. 1*a-c*) of the subgraviportal type, with a very wide wing, but a relatively elongate shaft of the ilium.

Tuber coxae occupies about a half of the length of the anterior border of the wing of ilium and thus contributes to its swelling. With its convexity it faces anterolaterally. In the posterolateral, thickest part (reaching about 48 mm), the tuber is limited by a triangular surface facing posterolaterally and which makes up the anterior part of the lateral border of wing.

A robust, subtriangular, sacral tuber ascends medially thus causing in this region a deeper concavity of the gluteal surface of ilium, whose more outer part is nearly completely flat.

The crest of ilium slightly concave. The medial, articular part of the pelvic surface of ilium convex. The auricular surface elongate, subhorizontal (in the physiological position of the pelvis), with its longitudinal axis parallel to the sagittal plane. The external part of the pelvic surface of ilium, or iliac part, is developed as a concavity which deepens anteriorly.

The ilio-pectineal line forms a boundary between both parts of the pelvic surface of ilium and, posteriorly, a ventromedial border of the shaft of ilium. It is variously, sometimes fairly strongly, developed. Two vascular grooves ⁷ run externally of the ilio-pectineal line and transversally to the shaft in the place in which the wing turns into the shaft (Pl. XX, Fig. 1c). They are as a rule accompanied by an nutrient foramen.

A distinct, oval, rough psoas tubercle is situated on the shaft of ilium as a continuation of the ilio-pectineal line. Posteriorly of the psoas tubercle, the ilio-pectineal line extends, here and there almost invisible, up to the place somewhat below the level of acetabulum where it terminates in a small swelling.

The dorsal border of ilium is sharp at the level of the auricular surface and in the region of ischiatic spine and blunt in the region of the lesser sciatic notch.

The ventral, external border of ilium begins in the external part of wing with a triangular muscle area facing with its apex posteriorly and occupying slightly more than one-quarter of its length. Further on, it turns into a sharp edge, usually extending up to the anterior border of acetabulum. A triangular muscle area, resting with its base on the margin of acetabulum and overlapping the dorsoexternal surface of ilium, adheres to this border in the region of the shaft of ilium. Sometimes, the border of shaft dwindles away in this region and the muscle area mentioned above overlaps the gluteal surface of the bone.

⁷ In the pelvis of the horse such grooves are located in two places: near the anterior border of the wing (grooves for the iliaco-femoral vessels). A nutrient foramen occurs in the neighborhood of the last-named grooves.

PLEISTOCENE RHINOCEROS COELODONTA ANTIQUITATIS

Table 45

Species	Coelodonta	Diceros bicornis	Rhinoceros
Dimensions	uniquitatis		sonuaicus
Maximum length of pelvis	549	491	494
Maximum spacing of the tuber coxae	772	684	700
Minimum spacing of sacral tubers	about 62	78	62
Distance between most ventrally situated points of auricular surfaces	202	160	156
Distance between the middle of acetabula	238	about 228	about 247
Distance between psoas tubercles	about 265	252	about 267
Distance between ischiatic spines	245	210	232
Maximum spacing of the tubera ischii	245	258	296
Distance between the external angle of the wing and the middle of acetabulum *	about 242	about 204	246
Length of the ischium (from the middle of aceta- bulum) *	175	about 193	177
Length of symphysis	about 155	157	165
The smallest anteroposterior dimension of the acetabular branch of the pubis	36	37	33
Minimum distance of the anterior border of ace- tabulum from the auricular surface	233	207	210
Maximum width of the wing of ilium	390	400	430
Minimum width of the shaft of ilium	56 left 59 right	79	65

Dimensions (in mm) of the pelvis in Coelodonta antiquitatis (BLUM.), ZAPUJ No. 683 as compared with those in Diceros bicornis L., MIZ, and Rhinoceris sondaicus DESM., MIZ.

* In projection on the axis of the shaft of ilium or on the axis of the shaft of the ischium.

The pubis is very robust. Its acetabular branch is shaped like a stout beam about 40 mm high and about 35 mm in anteroposterior diameter. Its symphyseal branch has the form of a coarse lamella concave ventrally and convex dorsally. As a result of a strong increase in the thickness of the pubis, it turns anteriorly with its anterior wall which has two borders: dorsal and ventral and not one as is the case in the horse. The ilio-pectineal line terminates, slightly below the level of the dorsal border, in an ilio-pectineal eminence. The pubic tubercle is situated on the ventral side.

The acetabular part of the ischium is shaped like a beam triangular in transverse section. The tuber ischii is triangular, with a nodular ventral surface. The lesser sciatic notch is not very deep and has a blunt border.

A not very high, blunt ischiatic spine is separated from the lesser sciatic notch by a transversally situated groove and strongly ornamented by oblique crests. The surface of bone, situated externally of it and above the acetabulum, is very rough and deeply concave in its posterior part.

The acetabulum is deep, round, about 102 mm in diameter and provided, on the side of the obturator foramen, with a distinct acetabular notch.

The obturator foramen round (105 mm in diameter). A shallow, wide notch for the obturator nerve and accompanying vessels is marked on the posterior border of the pubis which limits it anteriorly. This notch is directed dorsally, anteriorly and laterally.

The ischial arch strongly wedged in the symphysis.

The traces of the following muscle attachments are visible on the surface of pelvis:

A thickened anterior border of the wing, including the tuber sacrale, the crest of ilium and the tuber coxae, except for its external part turned posteriorly, was occupied by the longissimus dorsi and, directly below it, the ilio-lumbar ligament. The external part of the tuber coxae in the form of an isosceles, rough triangle, disposed with its largest height (about 80 mm) along the external border of wing (Text-fig. 11 Ab, Cb; Pl. XX, Fig. 1b), served as an attachment for the tensor fasciae latae. The oblique muscles of abdomen, that is, the obliquus abdominis externus and the obliquus abdominis internus, are on the whole also attached to the shaft of ilium on the tuber coxae and in its region, but their attachment places in *C. antiquitatis* cannot be accurately determined.

The gluteal surface of ilium is smooth and does not allow one to determine precisely the situation of the gluteus medius, which was attached in this region. The attachment of the gluteus medius is only posteriorly limited by semicircular lines with their convexities facing anteriorly (Text-fig. 11 Ac). These lines make up an anterior limitation of the trace of the gluteus profundus extending posteriorly as far as the region between the ischiatic spine and the ace-tabulum inclusively. This region is slightly convex and covered with irregular elevations, while the anterior part of the attachment area, which makes up an almost entire dorsolateral surface of the shaft, is fairly smooth and slightly concave. A crest, which at the same time forms the dorsal border of a triangular preacetabular area ⁸, (Pl. XX, Fig. 1*b*), makes up a lateral limitation of the gluteus profundus.

This poorly developed crest, sometimes almost invisible at all, probably limited dorsally the attachment of the capsularis (Text-fig. 11 C, e), while both tendons of the rectus femoris were attached in the ventral corner of the preacetabular area in which there are two muscle scars adjoining each other or a single, bifid scar (Text-fig. 11 C, f).

A very extensive iliac part of the pelvic surface of ilium was an attachment area of the iliacus, which is limited posteriorly by two vascular grooves running across the shaft approximately on the boundary between the shaft and wing (see above). These grooves represent impressions of iliaco-femoral vessels (the arteria circumflexa and two other accompanying veins). A nutrient foramen for the nutrient artery of ilium occurs in the neighbourhood of the grooves.

The psoas tubercle, in the form of an oval $(25 \times 15 \text{ mm})$, flat and rough area makes up an attachment of the psoas minor.

⁸ An analogous crest is formed in the horse by an attachment of the dorsal tendon of the rectus femoris and of the tendon of the capsularis. These muscles form a distinct depression anteroventrally of this crest.



Fig. 11

The right innominate bone; A dorsal view, B ventral view, C lateral view. The left femur; D proximal view, with muscle and ligament attachment areas marked, × ca 1/6; a m. longissimus dorsi, b m. tensor fasciae latae, c m. gluteus medius, d m. gluteus profundus, e m. capsularis, f m. rectus femoris, g m. iliacus, h m. psoas minor, i tendo prepubicus, k m. pectineus, l m. biceps femoris, m m. semimembranaceus and m. semitendineus, o m. obturator externus, p groove for the fascicules of m. obturator internus, r m. gemelli, lsi, ligamentum sacroischiadicum

The ilio-pectineal eminence serves as an attachment for the prepubic tendon belonging to the rectus abdominis and, in addition, for the obliquus abdominis externus and internus, the gracilis and the pectineus. The pectineus is also attached to the pecten ossis pubis between the left and right pubic tubercle. The ventral surface of the pubis is rough. The gracilis and the adductor femoris were attached along the pelvic symphysis and on a concave ventral surface posteriorly of the pecten ossis pubis.

The obturator externus, whose attachment area is relatively smooth and depressed posteriorly, was attached on the ventral side of pelvis around the obturator foramen. Several semicircular lines, whose concavities is facing the obturator foramen, separate this attachment area from the posteromedial part of the ventral surface of the ischium, which is somewhat convex and nodular.

A nodular area projecting with its blunt spine ventrolaterally is formed by the ventral surface of the tuber ischii in its external part. It makes up a trace of the attachment of the short head of the biceps femoris. Shorter heads of the semimembranaceous and the semitendineus are also attached to the ventral surface of the tuber ischii posteriorly of the attachment of the biceps femoris. According to BEDDARD & TREVES, 1889, in *D. sumatrensis* these muscles are grown together to form a single muscle unit, but it is not certain if this phenomenon occurs over their entire length. The quadratus femoris was attached anteriorly of the semimembranaceus.

An attachment of the sacro-sciatic ligament is situated on the pelvic surface of the tuber ischii. This ligament is also attached to the medial surface of the spina ischiadica.

The obturator internus was attached around the obturate foramen on the pelvic surface of the ischium and the ilium. Its traces are visible in particular on the pelvic surface of the os coxae in the region of acetabulum. These are shallow and smooth depressions and more or less distinct bony elevations, situated posteriorly of the ilio-pectineal eminence in continuation of the anterior border of the obturate foramen.

The traces of the obturator internus are also visible on the pelvic surface of the branch of ischium situated posteriorly of symphysis. This muscle was getting out from the inside of pelvis through the lesser sciatic notch (or through the lesser sciatic foramen), whose thick, smooth border is provided in this connection with several shallow, groovelike transverse depressions (Pl. XX, Fig. 1a; Text-fig. 11Ap).

A deep depression (Text-fig. 11 Ar), making up an attachment area of the gemelli is situated ventrally of the posterior part of the spina ischiadica and anteriorly of the lesser sciatic notch.

Femur. (Pl. XX, Figs. 2*a*, *b*; Pl. XXI, Figs. 1*a*, *b*; Pl. XXII, Figs. 1*a*, *b*). — It is the longest of all long bones in the entire skeleton of the woolly rhino. Its physiological length fluctuates within limits of about 450 and 520 mm, the ratio of the minimum width of shaft to its physiological length being 1.75 to 1.92.

The plantar surface of the bone is flat, the dorsal flat proximally and becoming convex distally. A crest dividing the dorsal surface into two areas, runs ventrally along it from the level of the external border to the medial ridge of the trochlea.

The head of femur is round, 90 to 100 mm in diameter, strongly convex and with only slightly separated neck. It is inclined medially at an angle of 60° to the axis of shaft and separated from the muscular part of the proximal end by a wide (about 40 mm) groove. The trochanter major is situated below the level of head and is not divided into the anterior and posterior part. It occurs in the form of a pyramid with a truncate, rounded apex and triangular base. One of its angles faces anteromedially, the other anteroexternally and the third posteriorly. The posterior angle of the trochanter turns distally into the posterior trochanteric ridge running parallel to the shaft towards the third trochanter. This ridge makes up an external limitation of the trochanteric fossa. An about 100 mm long crest runs distal from the anteroexternal angle of the trochanter major.

The third trochanter occurs more or less halfway the length of the external border of femur in the form of a quadrangular plate strongly projecting externally of the shaft and bent anteriorly. Its sharp proximal and distal borders gradually turns into the external border of shaft.

The trochanter minor is developed in the form of a triangular crest with a rounded apex, beginning about 45 mm under the notch of the femoral head and descending to a point about halfway the length of the bone. Its apex, turned anteriorly, is situated at the level about the upper one-third the length of the bone.

The plantar surface of the shaft is very rough in its distal half. In its distal part, a deep supracondyloid fossa (shifted medially as compared with the supracondyloid fossa in the horse) occurs over the intercondyloid fossa and externally of it, there is a shallower, rough depression divided lengthwise by a vertical crest and limited laterally by the lateral supracondyloid crest.

The distal extremity of femur is almost identical with that in the horse, except only for the lateral condyle which is somewhat larger than the medial condyle in the rhino. The articular surface of the lateral condyle overlaps the lateral side farther than the surface of the medial condyle overlaps the medial side. The medial ridge of the trochlea is much stouter and more strongly projecting anteriorly than the lateral ridge. Its articular surface strongly overlaps the medial side.

Table 46

Dimensions (in mm) of the femur in Coelodonta antiquitatis (BLUM.), Diceros bicornis L., and Rhinoceros sondaicus DESM.

Species Cat. No.		antiqui	tatis		1	D. bicorn	tis		Rh. son- daicus
		PUJ . 683	GI	MIZ	ZIN No. 24729		ZIN No. 615		MIZ
Dimensions	left	right	10.9/1		left	right	left	right	
Distance from the middle of head to the farther- most point of the medial condyle	452	_	520	466	424	430	447	445	459
External length in projection on the longitudinal axis	440	445	494	-	421	420	432	435	_
Length of shaft on the medial side	_	_	about 366		302	306	-	-	_
Maximum width of the proximal end	207	207	225	174	183	186	190	188	197
Width of head	97	94	100	78	88	83	93	90	88
Antero-posterior dimension of head	92	91	100	76	79	79	87	84	89
Minimum width of shaft at the level of the trochanter minor	127	124	146	93	118	110	126	118	119
Width of shaft together with the third trochanter	148	142	-	ш	126	123	135	131	139
Width * of the base of the third trochanter	73	68	72	72	74	70	72	69	79
Width of distal end	148	146	153	121	126	127	127	133	152
Minimum width of shaft below the third tro- chanter	87	85	91	60	62	65	62	62	71
Distance between the lowermost point of the trochanter minor and the distal end	258	266	292	290	268	265	255	252	271
Distance between the lowermost point of the third trochanter and the distal end	176	187	214	178	163	180	193	180	207

* Width here == vertical dimension.

Posteriorly, the epicondyles reach the articular surfaces of condyles and anteriorly approximately the boundary between the condyles and the trochlea. The lateral epicondyle reaches somewhat more anteriorly and distally than the medial one. In its distal part, the extensor fossa in the form of a depressed, triangular surface, is wedged in between the borders of the lateral condyle and the trochlea. On the medial side, a distinct groove for the middle patellar ligament occurs between the epicondyle and the trochlea.

A triangular depression for the round ligament is situated in the posteromedial part of head near its base, that is, in a position corresponding to that of the acetabular notch. The height of this notch amounts to about a half of the radius of the femoral head.

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The attachments of the following muscles are visible on the surface of femur.

The trochanter major is occupied by the gluteal muscles, of which the gluteus profundus is attached on its anterior wall facing anteriorly, proximally and laterally and on its proximal wall ornamented by transverse crests and furrows parallel to each other. The posteroexternal wall serves as an attachment area of the gluteus medius, which also attaches itself to the lateral, strongly ornamented wall of the shaft of the bone between the posterior trochanteric ridge and a crest running distal from the anteroexternal angle of the trochanter.

The plantar, rough surface of the third trochanter and its proximal and distal borders were attachment areas of the gluteus superficialis.

The dorsal surface of the femur was covered with two vastus muscles: the vastus lateralis and vastus medialis, the vastus intermedius being probably absent in the woolly rhino or fused with one of the adjoining vastus muscles, as it is in *D. sumatrensis* (see BEDDARD & TREVES, 1889). A line running through the middle of the dorsal surface of the shaft separates the two parts of the vastus.

In the horse, the vastus lateralis is attached to the entire anteroexternal surface of the femur. According to BRESSOU (1961), in the tapir, this muscle is attached by a tendon under the trochanter major. In the woolly rhino, the proximal quarter of the dorsal surface for the vastus lateralis is covered with a network of crests (Text-fig. 12A, e), while the rest of this surface is smooth, which might indicate that this muscle was attached to the bone in this region.

The vastus medialis was attached to the dorsomedial part of the surface of femur, which is slightly ornamented in its upper part and bordered proximally by the rough line, a dorsal limit and origin of the attachment of this muscle. It is impossible to conclude on how far this attachment reached distally and on what was the relation of this muscle to the vastus intermedius, if it occurred at all.

The trochanter minor serves as an attachment place for the common tendon of the psoas major and the iliacus, which is attached to its dorsal surface covered with conspicous, irregular roughnesses.

A longitudinal, narrow, rough scar of the pectineus begins directly under the trochanter minor and runs along the shaft over a length of about 12 cm.

Many traces of muscle attachments are observed on the plantar surface of femur. Rough depressions, limited by distally convex ridges occur in the trochanteric fossa and below it. On the other hand, a small tubercle is situated in the upper part of the trochanteric fossa. This depression and tubercle make up an attachment area of the obturator internus, the obturator externus and the gemelli muscles. Judging from the mutual positions of these muscles in their initial parts in the pelvis, it should be expected that the attachment of the obturator externus was lowermost of the obturator internus higher and of the gemellus highermost (the last-named is frequently connected with the tendon of the obturator internus).

The facies aspera (Text-fig. 12C) begins at the level of the distal part of the trochanter minor with a medially situated roughness for the quadratus femoris (Text-fig. 12C, k) converging distally with an externally situated attachment area of the tendon of the biceps femoris which is (Text-fig. 12C, l), however, also near the axial part of the femur. These muscle attachment areas fuse together at the level of the medial part of the third trochanter and turn distally into a sharp, externally bent and distally directed crest for the adductor femoris (Text-fig. 12C, m) which terminates near the supracondyloid fossa.

Another attachment area of the adductor femoris is situated in the region of the medial epicondyle. Of two muscle scars occurring in the posterior part of this epicondyle, the adductor femoris was probably served by that situated higher-up dorsally of the epicondyle (judging



Fig. 12

The left femur of *Coelodonta antiquitatis* (BLUM.) with muscle and ligament attachment areas marked, \times ca 1/6; A anterior view, B lateral view, C posterior view, D medial view, a m. gluteus profundus, b m. gluteus superficialis, c m. gluteus medius, d m. vastus medialis, e m. vastus lateralis, f m. gastrocnemius, g m. popliteus, h m. obturator externus, i m. obturator internus, j mm. gemelli, k m. quadratus femoris, l m. biceps femoris, m m. adductor femoris, n m. iliopsoas, o m. pectineus, p m. flexor digitalis superficialis, r m. semimembranaceus, t groove for the medial patellar ligament, s m. extensor digitalis longus, l. c. l. and l. c. m., ligamentum collaterale laterale and mediale, l. f. p. l., ligamentum femoropatellare laterale.

from the position of the trace of this attachment in man). The lower situated trace might be connected with the medial head of the gastrocnemius or with the attachment of some fibers of the semimembranaceus, if such an attachment existed at all, since it was not described in D. sumatrensis (BEDDARD & TREVES, 1889).

A roughness, situated on the lateral side of the crest of medial epicondyle (axially of the attachment of the adductor femoris) seems, however, to be a more likely attachment area of the medial head of the gastrocnemius (Text-fig. 12C, f) and, therefore, the muscle scar occurring below the trace of the adductor femoris is here interpreted as a trace of the semimembranaceus.

In *D. sumatrensis*, the adductor magnus, a part of the adductor femoris, contributed to the formation of a tendon arch for the artery, situated at the level of the distal one-third of femur (according to BEDDARD & TREVES, 1889) and, at the same time, at the level of the attachment of the pectineus.

In *C. antiquitatis*, a nutrient foramen, through which the nutrient artery, a branch of the arteria femoralis profunda, penetrates inside the femur, occurs in the proximal part of the surface of the attachment of the pectineus slightly below a point halfway the length of this bone.

A deep supracondyloid fossa (Text-fig. 12) an attachment area of the flexor digitalis superficialis, is situated directly over the intercondyloid fossa (see above). A shallower, very rough ^{6*}

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depression, limited laterally by the crest of the lateral epicondyle and which probably makes up an attachment area of the lateral head of the gastrocnemius, occurs externally of it.

A trace of the attachment area of the popliteus in the form of two smooth depressions situated above each other occurs on the external epicondyle (Text-fig. 12C, g) directly over the condyle. A trace of the attachment of the external femoro-tibial ligament is discernible directly above it and somewhat anteriorly. In the most anterior part, there occurs a round scar of the lateral femoro-patellar ligament.

The presence of a strongly developed extensor fossa on the distal surface of the lateral epicondyle is indicative of the presence of a femoral attachment of the extensor digitalis longus. No such attachment is described by BEDDARD & TREVES (1889) in *D. sumatrensis* (the Extensor communis digitorum they describe probably corresponds to the extensor digitalis longus and lateralis).

A round, depressed scar of the medial femoro-tibial ligament is situated on the medial epicondyle followed posteriorly by an oval scar which is likely to belong to the semimembranaceus (see above).

In the intercondyloid fossa, a depression for the femoral ligament of the lateral meniscus occurs posteromedially, for the anterior cruciate ligament — posteroexternally and for the posterior cruciate ligament (a less distinct trace) — close to the patellar trochlea (Text-fig. 13*F*, *l. c. a.*, *l. c. p.*).

Tibia. — In C. antiquitatis, the tibia is massive, which is manifested in a considerable width and thickness of its extremities. The width of the proximal extremity amounts to about 43 to 46% and its anteroposterior dimension to about 44 to 48% of the external length of this bone, while the width of the distal extremity makes up 35 to 37% of this length. Minimum width of the shaft, occurring approximately halfway the length of shaft represents about 22 to 25% of the external length of tibia.

A strong development of the external part of the tibial tuberosity results in a shift of its apex towards the external side of the proximal extremity. The groove for the middle patellar ligament (Text-fig. 13A, E) is deep and wide (about 30 mm).

The lateral part of the spine is situated at the same level as its medial part. The surface of the medial condyle is slightly concave and that of the lateral condyle concave in the apical region and flat near the external border. The popliteal notch deep (about 20 mm).

The tibial crest very stout and rounded in the proximal one-third of the bone and tapering distally. It runs down to the medial maleolus.

The medial surface of tibia is slightly convex in its proximal part and flattening distally. In its proximal part, the medial border of the bone is bent, with its concavity facing posteriorly. This border is most strongly concave about halfway the length of bone, in the place where the medial border contacts the popliteal line. Farther, it suddenly turns into an almost straight distal part of the border. Moreover, the proximal part of the medial border is very sharp, strongly projecting posteriorly and, consequently, the attachment area of the popliteus is limited to the plantar surface of the bone only.

The medial malleolus projects distally (a dozen or so millimeters below the medial border of the distal articular surface) and medially. Posteriorly, it is limited by a groove running upwards and posteriorly (more or less along the anteromedial curve of the surface of shaft, see below).

The dorsolateral surface of the tibia, slightly convex in its proximal part, turns distally into the dorsal surface.

Two triangular surfaces for the articulation with the fibula are situated on the posterolateral border of the tibia. The proximal one, occupying about a quarter or slightly more of

PLEISTOCENE RHINOCEROS COELODONTA ANTIQUITATIS

Table 47

Species	C. antiquitatis					Rh. sondaicus				
Cat. No. Dimensions	ZAI No.	PUJ 683	ZIN No. 4071	MIZ	ZIN No. 24729		ZI No.	IN 615	MIZ	
Distance between the spine and the middle of the articular surface of the distal extremity	326	324	368		309	309	320	319	_	
Medial length	296	292	335	303	279	280	275	276	280	
Lateral length	276	276	319	299	268	269	270	273	280	
Width of the proximal extremity	125	120	137	108	107 106		116	114	123	
The anteroposterior di- mension of the proximal extremity	127	124	144	about 125	111	110	128	117	135	
Width of shaft	63	60	75	60	52	53	51	53	55	
The anteroposterior di- mension of shaft	58	61	67	43	55	52	65	60	50	
Width of distal extremity	96	95	107	90	97	96	abou	at 110	102	
The anteroposterior di- mension of the distal extremity	75	79	89	66	71	70	73	75	71	
Width of the articular surface of the distal extremity	75	76	89		73	71		_		
The anteroposterior di- mension of the articular surface of the distal extremity	48	53	60		67	59		_		

Dimensions (in mm) of the tibia in Coelodonta antiquitatis (BLUM.), Diceros bicornis L., and Rhinoceros sondaicus DESM.

the length of bone, is, slightly convex, turned posteriorly and with its apex directly downwards. Anteriorly, it fuses with the posterior attachment area of the tibialis anterior (see below). The distal surface, directed with its apex upwards, turned posterolaterally, is shaped like an isosceles triangle extended by a sharp border which halfway the height of shaft passes onto the posterior surface of the bone. A small, flat, semilunar articular surface for the fibula occurs in the distal part of the distal surface for this bone.

The interosseous space is situated approximately in the third (counting from the bottom) quarter of the length of tibia. Its border, formed by the tibia, is blunt, slightly concave and

intersected by oblique grooves for the anterior tibial artery and for the accompanying veins running anteriorly and downwards from the plantar surface of the bone.

The tibia fuses with the fibula relatively lately, which is indicated by the fact that only a relatively low percentage of the bones of shank is preserved connected with each other, (of thirteen tibiae, only three are fused with the fibula).

The plantar surface of tibia is concave in its proximal half and along its entire lateral border and convex in the mediodistal part. The popliteal line runs obliquely upwards from a point halfway the medial border. At a distance equalling one-third the length of the bone from its proximal extremity, the popliteal line meets the above mentioned extension of the external border of the bone and forms, together with it, a distally open angle, inside of which there usually occurs the nutrient foramen.

The lateral articular groove of the distal extremity is wider and shallower than the medial one. Its posterior, lowermost part reaches distally the level of the apex of the medial malleolus. A narrow (a few mm), smooth surface, stretching from the external border of the bone to the apex of the medial articular surface of the distal extremity, runs along its border on the plantar surface of the tibia.

Fibula (Pl. XXIII, Figs. 1a, b, 2). — The fibula is developed over its entire length but strongly reduced in size. The width of its shaft at the level of the interosseous space makes up a bare 38 per cent of the width of the shaft of tibia at the corresponding level. This ratio changes yet more in favor of the tibia towards the extremities (about 32 per cent at the proximal and about 29 at the distal).

In its posteromedial part, the proximal extremity of the fibula is rounded and as compared with the shaft, extended and truncate anteriorly so that its anterior border forms, together with the anterior border of the shaft, a more or less straight line (Pl. XXIII, Fig. 16). Directed posteroexternally, the surface of the head is strongly convex. Its medial part turns distally into the external border of the shaft.

Over its entire length, the shaft is approximately triangular in transverse section, but its distal half is, in relation to the proximal one, slightly twisted clockwise in the right bone and

Cat. No.	PS No. 13	MG No. 12
Dimensions		
Length	285	273
Width of proximal extremity *	40	
The anteroposterior dimension of the		
proximal extremity	40	-
Width of shaft	25	24
The anteroposterior dimension of		
shaft	19	19
Width of distal extremity	32	29
The anteroposterior dimension of		
the distal extremity	50	50

Table 48

Dimensions (in mm) of the fibula in Coelodonta antiquitatis (BLUM.)

· Measured posteriorly.

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anti-clockwise in the left bone, so that the anteromedial and lateral borders turn below the interosseous space into the anterior and posterior borders and the posteromedial into the medial one. In this connection, an external surface extending distally and turning into a macelike distal extremity occurs in the distal part instead of the external border.

A deep groove, running upwards and slightly anteriorly and surrounded posteriorly and anteriorly with tuberosities, occurs on the lateral surface of the distal extremity. The posterior surface of the proximal part of shaft is covered with strong longitudinal tuberosities parallel to the axis of shaft. The posteromedial surface, also, if to a smaller degree, covered with tuberosities, forms, together with a concave external part of the posterior surface of the tibia, a deep fossa.

As a result of the lack of separate specimens of the fibula, its surface facing the tibia has not been studied. Without any doubt it corresponds in its shape to an appropriate surface of the tibia.

An oval, about 30×20 mm, vertically disposed (with its longer axis horizontal) articular surface, limiting externally the lateral articular groove of the extremity of the tibia, is situated on the medial surface of the distal extremity.

Traces of attachments of many ligaments which serve the stifle joint are visible on the surface of the proximal extremity of the tibia (Text-fig. 13E).

The tibial tuberosity makes up an attachment area of the patellar ligaments. A semilunar trace, concave dorsally and situated in the distal part of the groove for the medial patellar ligament on the tibial tuberosity, makes up an attachment area of this ligament (Text-fig. 13 E, l. p.).

A slightly convex oval $(59 \times 22 \text{ mm})$, smooth surface for the lateral patellar ligament and accompanying aponeurosis of the biceps femoris occurs in the proximal part of the tibial tuberosity laterally of the groove. This surface, arranged with its longer diameter nearly horizontal, turns distally into a rough, convex part of tibial tuberosity, covered with vertical ridges and which probably makes up an attachment area of the apeneurosis of the fascia lata (Pl. XXIII, Fig. 2).

A slightly separated, oval $(41 \times 22 \text{ mm})$ area facing anteromedially and slightly proximally, with its longer diameter horizontal, makes a trace of the attachment of the medial patellar ligament, together with which the aponeurosis of the sartorius and the gracilis are attached in this place.

The attachments of the meniscal and cruciate ligaments (Text-fig. 13E) are distributed much the same as in the horse except for the trace of the attachment of the posterior cruciate ligament (Text-fig. 13E, *l. c. p.*) which does not contact the external condyle of the tibia but is separated from it by a deep and wide (about 20 mm) groove probably serving as an attachment area of the posterior ligament of the medial meniscus (Text-fig. 13E, *l. t. m. m*). In the horse, the last-named ligament is attached more laterally along the posterior border of the lateral condyle. The following ligamental scars are distributed posteroanteriorly along the spine: a scar of the posterior ligament of the medial meniscus, a longitudinal scar of the anterior cruciate ligament (between the apexes of the spine) and a round scar of the anterior ligament of the lateral meniscus. The attachment area of the anterior ligament of the medial meniscus is situated anteriorly of the medial condyle in a notch on its anterior border.

The groove separating the tibial tuberosity from the lateral condyle, which in the horse serves for the tendons of the extensor digitalis longus and of the peroneus tertius running from the extensor fossa of the femur and which in *C. antiquitatis* contains only the tendon of the





Bones of Coelodonta antiquitatis (BLUM.) with muscle and ligament attachment areas marked, \times ca 1/6; A the right tibia and fibula, anterior view, B the same bones, lateral view, C the left tibia, medial view, D the left tibia and fibula, posterior view, a m. tibialis anterior, b m. gracilis, c m. semitendineus and m. semimembranaceus, d m. popliteus, e m. flexor digitalis profundus, e_1 m. flexor hallucis longus, e_2 m. tibialis posterior, f mm, peronei, f_1 groove for the tendon of m. peroneus I, g groove for the tendon of m. extensor digitalis longus, h groove for m. flexor digitalis longus, l. c. m., ligamentum collaterale mediale, l. p. l., ligamentum patellare laterale, l. p. m., ligamentum patellare mediale, l. p., ligamentum patellare, l. t. m. m., ligamentum tibiale menisci medialis, l. t. m. I., ligamentum tibiale menisci lateralis, l. c. a., ligamentum cruciatum anterior, l. c. p., ligamentum cruciatum posterior, l. f. m. l., ligamentum femorale menisci lateralis, s, m. extensor digitalis longus.

extensor digitalis longus 9 , is in the latter animal very shallow and its width reaches approximately twenty odd millimeters (Text-fig. 13 B, g).

The tibialis anterior was attached in the proximal part of the anterolateral surface of the tibia. The laterodistal surface of the tibial tuberosity and a triangular, rough area in the posteroproximal, angle of the shaft, adhering anteriorly to the fibula, were probably its attachment area. This rough area extends onto the anterior surface of the proximal extremity of the fibula and, therefore, it is not unlikely that the attachment of the muscle passed onto this bone. The lateral attachment areas of the tibialis anterior are connected with each other by a rough area occupying the proximal part of the lateral surface of the bone (sometimes the proximal one-third of this surface). Sometimes, however, they are separated from this area by distally running crests. On the basis of a bifid structure of this muscle, found by BEDDARD & TREVES (1889) in *D. sumatrensis*, we suppose that it was also bifid in *C. antiquitatis*, but there is no possibility to trace a boundary between its heads.

In its ventral two-thirds, the lateral surface of the tibia is smooth and without any traces of muscle scars. In the life-time, this surface was covered with the heads of the tibialis anterior and the extensor digitalis longus.

A smooth, shifted posteriorly and sometimes depressed attachment area of the medial femoro-tibial ligament occurs on the medial surface of the tibia just below the medial condyle

⁹ The peroneus tertius has not been identified in *D. sumatrensis* (BEDDARD & TREVES, 1889). In the tapir, it tightly grows together with the tibialis anterior (BRESSOU, 1961) and is not attached in the extensor fossa, while this animal's extensor digitalis longus (l. c.) is attached to the condyle of the femur.

(Text-fig. 13C). An extensive, irregular roughness, an attachment area of the gracilis is situated ventrally of it, but in the upper one-third of the bone. In its medial one-third a rough area, shaped like an elongate rectangle (about 75 mm and high 15 mm wide), to which the semitendinosus and the semimembranaceus (Text-fig. $13C_c$) are attached, occurs close behind the tibial crest.

In *D. sumatrensis* (according to BEDDARD & TREVES, 1889), the two muscles are fused with each other and form a single muscle unit, attached with a flat tendon parallel to the tibial crest and posteriorly of it.

A groove, occurring posteriorly of the medial maleolus, probably served as a passage for the tendon of the flexor digitalis longus running (Text-fig. $13C_h$) from the posterior surface of the tibia onto the medial side and distally towards the last digital phalanxes. A posterodistally oblique trace of this groove is not always quite distinct. Its direction is emphasized by a deflection of the medial surface in this region. Proximally this deflection the medial surface turns anteromedially (see above).

A smooth area, to which the short medial ligament is attached, stretches over the distal and posteromedial surface of the medial maleolus. The long medial ligament was attached posteriorly of the short one along the border of the distal articular surface.

The popliteus, running obliquely from the medial border of the tibia, through the posterior surface of its lateral condyle, to the lateral epicondyle of the femur, was attached to the muscular lines which are situated in the dorsal part of the posterior surface of the tibia distally of the popliteal line. In addition, particular parts of the flexor digitalis profundus (= the flexor communis digitorum in BEDDARD & TREVES, 1889) are attached to the posterior surface of the shank. In *D. sumatrensis (l. c.)*, the flexor digitalis profundus is attached to the tibia only in its distal and external part and, besides, to the fibula up to the proximal border of its head and on the fascia of the popliteus. The depression of the external surface of the tibia below the level of the popliteal line and the surface of fibula, which adheres to it and forms together with it a deep fossa, would make up an attachment area of a part of the flexor digitalis profundus, most likely the flexor hallucis longus. Two vertical crests (one of them running along the posteromedial border of the bone) situated in the proximal half of the fibula on its posteromedial surface, as well as a longitudinal tuberosity near the lateral border make up traces of attachments of the tibialis posterior and part of the flexor hallucis longus. The flexor digitalis longus was probably attached mostly or completely to the fascia of the popliteus.

The distribution of the attachments of particular parts of the flexor digitalis profundus is, however, hypothetical to a considerable extent and, therefore, it seems advisable to consider this muscle as a whole (cf. Text-fig. 13).

The fibula provided attachments for the peronei over its entire anterolateral surface. The number and trace of these muscles cannot be, however, determined. They were probably developed similarly as those in D. sumatrensis in which, according to BEDDARD & TREVES (1889), four peronei muscles occur. Two of them are attached in the distal part of the fibula, the third (non-homologous to the peroneus tertius of the horse) somewhat below and the fourth branches off from the first.

In C. antiquitatis, the muscle scars, which occur on the lateral surface of the fibula, are grouped in its proximal and posterior part, the remaining part of the lateral surface of the shaft being smooth. A groove running vertically over the lateral side of the distal extremity of fibula was probably assigned for the tendon of the first fibular muscle. The long lateral ligament was attached to the tuberosities which surround the groove and the short lateral ligament to the anterior and proximal parts of the fibula. In addition, the ligamentum annulare, keeping the tendon of peroneus I inside the groove, was probably attached to these tuberosities.

Calcaneum. — The length of the shaft of calcaneum amounts, on the external side, to about 110 mm, the width below the tuber calcis to about 40 mm and the anteroposterior dimension in this same place to about 55 mm. Surfaces for the articulation with the astragalus are situated on the anteromedial side of the calcaneum. The highest of these surfaces, situated medially, is concave in the distal and convex in the proximal part which is caused by its passing onto the upper surface of the processus cochlearis. The distal and medial surfaces are connected with each other. The distal one is shaped like a narrow strip running anteriorly and outwards, the medial one is subround.

A longitudinal, distinctly bifid surface for the lateral part of the cuboid, whose both parts are arranged at an obtuse angle to each other, occurs on the distal side of the shaft. Its anterior, shorter and narrower part is flat, the posterior concave.

Table 49

Dimensions (in mm) and indexes (in %) of the calcaneum and os tarsale I and IV in Coelodonta antiquitatis (BLUM.) Cat. ZAPUJ No. 683

	Dimensions	
	Total length	120
	Length of shaft up to the apex of processus cora-	
	coideus	48
	Maximum width (in projection)	87
1	Maximum width to total length	72
	Anteroposterior dimension of the tuber calcis	71
	Anteroposterior dimension of the tuber calcis to	
	total length	59
	Width of the tuber calcis	53
	Width of the tuber calcis to total length	44
	Anteroposterior dimension at the level of processus	
	coracoideus	66
	Width to length of the fossette for the cuboid	25/45
	Total height of os tarsale I	59
	Width of os tarsale I	20
	Length of os tarsale I	30
	Height of os tarsale IV	37
	Width of os tarsale IV	42
	Length of os tarsale IV (together with the posterior	
	process)	67
	1	

The sustentaculum tali angularly converges medially. Its dorsal surface slopes towards the astragalus, so that the fossa for the tendon of the hallucis longus is open externally. The tubercles for part of the short medial ligament, which should be situated on the dorsal surface of the sustentaculum tali, are invisible in the specimen from Podbaba (ZAPUJ No. 683). On the other hand, a tubercle for part of the short lateral ligament occurs on the external surface of the shaft of calcaneum in the place where it turns into the processus cochlearis. The tuber calcis strongly project posteriorly, forming a posteriorly facing wall, while the posterior border of the shaft is directed posteriorly and downwards. A strong trace of Achilles' tendon in the form of a distinctly separated, oval protuberance and with its longitudinal, 50 mm long axis arranged transversally, occurs in the posterior part of the tuber calcis. A projection for the flexor digitalis superficialis, adhering to it anteriorly, turns ventrally into swollen borders of the lateral surfaces of the tuber calcis. These surfaces are strongly swollen.

A tuberosity, occuring in the posterior and lower corner of the lateral wall of the calcaneum, continues along the posterior border of the shaft. This tuberosity was related to the plantar ligament running towards the posterior surface of the cuboid and metatarsale IV or maybe to the long lateral ligament.

Astragalus (Pl. XIX, Figs. 3*a-b*). — The trochlea consists of a narrower, more strongly domed medial and a wider, less curved lateral crest. Both crests are separated from each other by a not very deep groove, slightly deflecting anterolaterally (which is not equally distinct on the distal articular surface of the tibia). The articular surface of the trochlea overlaps the lateral and medial sides forming on them a surface for the articulation with the lateral and tibial meleolus respectively.

Two articular surfaces occur on the distal extremity. The medial one, assigned for the navicular is large (about 43×39 mm), quadrangular, slightly convex sagittally and very slightly convex, nearly flat, transversally. The lateral one is oval (about 60×20 mm) and arranged with its longer diameter obliquely anteriorly and outwards.

Three articular surfaces for the calcaneum occur on the posterior side of the astragalus. The proximal and dorsolateral surface is undulate, concave in its upper, wider part and convex in its lower part. It is shaped like a triangle with its apex directed laterally and downwards and

Cat. No.	ZAPUJ	IG Z
Dimensions	No. 683	No. 373
Lateral height (perpendicular to the		
distal articular surface)	73	80
Medial height (as above)	77	80
Maximum width (in projection)	91	105
Maximum width to length on the		
medial side	118	131
Maximum anteroposterior dimension		
on the medial side	56	65
Anteroposterior dimension to length		
on the medial side	73	84
Maximum width of the distal articular		
surface in projection	71	80
Anteroposterior dimension of the		
distal articular surface	44	52
Inclination angle of the crests of		
trochlea to the distal articular		
surface		36

Table 50

Dimensions and indexes (in %) of the astragalus of Coelodonta antiquitatis (BLUM.) (linear dimensions in mm)

its purpose is to articulate with the shaft of the calcaneum, similarly as the underlaying oval surface running over the surface for the cuboid and proximally limited by a wide fossa of the astragalus. The surface for the sustentaculum tali, a rounded square in outline, is slightly convex and connected with the distal surface for the shaft of the calcaneum.

A ligamental fovea for the short medial ligament is situated on the lateral side of the bone posteriorly of the articular surface for the lateral moleolus. A tubercle, strongly projecting in its posterior part outside the medial surface of the bone and distally, occurs in a similar position but slightly more posteriorly on the medial side. A trace of the short lateral ligament in the form of a round surface about 20 mm in diameter is visible on its surface. Anteriorly, this trace turns, without any distinct boundary, into the medial surface of the bone. A projecting tuber (processus medialis tali, POPLEWSKI, 1948), to which are attached a part of the long lateral ligament and the dorsal tarsal ligament, running towards os tarsi centrale, os tarsale III, metatarsale II and III, occurs above the surface for the navicular (also on the medial surface). A destroyed, semilunar surface, which makes up an extension of the surface for the navicular, is situated on the posteromedial side of the bone over the surface for the navicular.

Os tarsale IV and V. — The anterior, approximately square surface turns into the lateral surface of the bone. The boundary between these surfaces is emphasized by the presence of a tuberosity, occurring at a bend between them.

The medial surface is composed of two walls arranged at an angle to each other (the proximal one is almost horizontal) and forming a projecting part of the cuboid which wedges in between the navicular and os tarsale III. Articular surfaces for corresponding bones are visible on these walls.

The purpose of the proximal surface is to articulate the cuboid externally with the calcaneum and medially with the astragalus. The distal surface articulates with os metatarsale IV and maybe also with the lateral process of os metatarsale III.

The cuboideum extends posteriorly in the form of a robust, posteriorly directed process for the plantar ligament.

The surface for the articulation with os metatarsale IV is concave sagittally but convex transversally and overlaps the lateral wall of the bone.

Os tarsale I. — A flat bone turning posteriorly into a tapering process provided with a tuberosity and probably related to the attachment of the tibialis anterior. In a physiological position of the bone, this process is directed laterally (that is, towards the axis of the limb) and somewhat distally so that its tuberosity is situated at the level of os metatarsale III and its flat part on the posterior surface of os tarsale II.

The anterior part of os tarsale I is provided with three surfaces: the upper one, for the navicular, subround and facing proximally, the middle one, for os tarsale II and the lower one, situated on the posterior surface of the bone behind the surface for os tarsale II.

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All photographs \times ca 1/5



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Rhinoceros	sondaicus	Desm.						34,	35
	MIZ								

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Rhinoceros	sondaicus	Desm.							35
	MIZ								

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Diceros	bicornis	L.								35
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All photographs \times ca 1/4

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Diceros bicornis	L.								35
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