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P A L A E O N T O L O G I A  
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REDAKTOR

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No. 29 — 1973

STUDIES ON THE PLEISTOCENE RHINOCEROS  
COELODONTA ANTIQUITATIS (BLUMENBACH)

(BADANIA NAD PLEJSTOCENSKIM NOSOROŻCEM  
*COELODONTA ANTIQUITATIS* (BLUMENBACH))

BY

MAGDALENA BORSUK-BIAŁYNICKA

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



WARSZAWA — KRAKÓW 1973

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PAŃSTWOWE WYDAWNICTWO NAUKOWE

ERRATA

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ACADÉMIE POLONAISE DES SCIENCES  
INSTITUT DE PALÉOZOOLOGIE

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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 *Coelodonta 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 of 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 territory 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

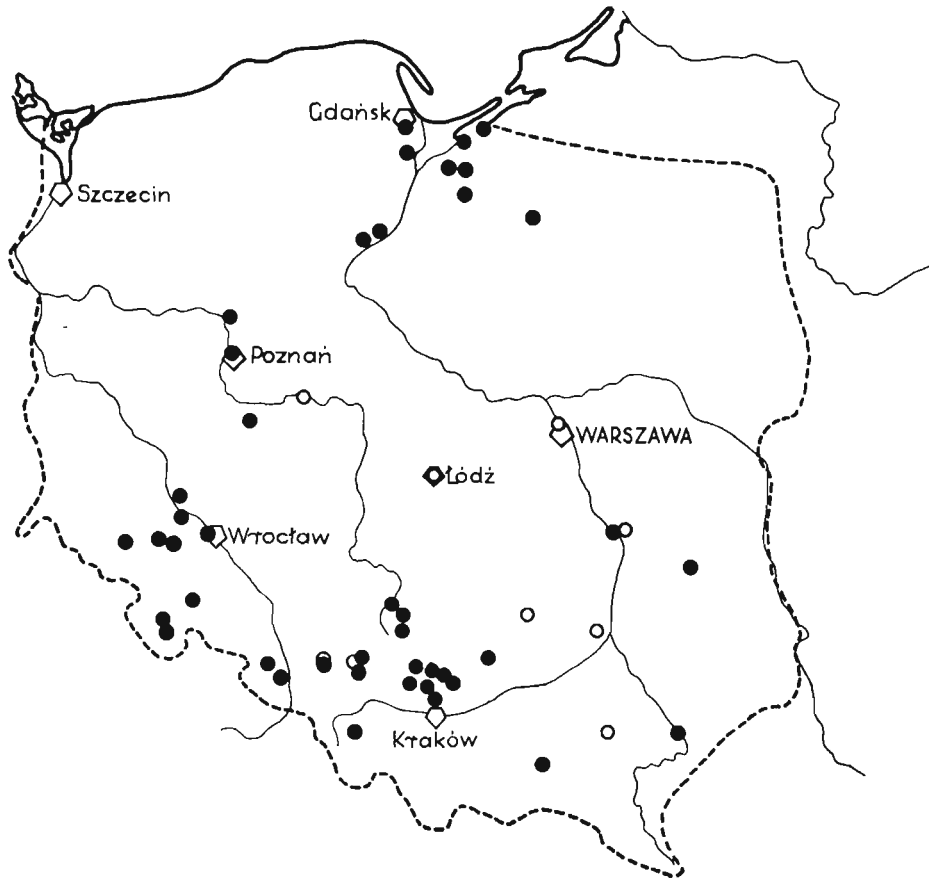


Fig. 1

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 (SICKENBERG, 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 Krowdrza 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 NIEZABITOWSKI (1914). These authors' works also contain the descriptions of the woolly rhino's mandible. GROMOVA (1935) presents a detailed comparison of such mandible with those of



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.

UŁ — 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).

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*Palaeozoological Laboratory  
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## 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<sup>2</sup> to DP<sup>4</sup> and the process of replacement starts after the use of M<sup>1</sup> has begun. M<sup>2</sup> may erupt still before the loss of DP<sup>2</sup> and DP<sup>3</sup> (which is indicated by the state of skull YM), after the loss of DP<sup>2</sup> and before the loss

of DP<sup>3</sup> (specimen MZ No. VIII/Vm-453 and GIEBEL's observations, 1851), or after the loss of DP<sup>3</sup> 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). DP<sup>1</sup> was probably lost before DP<sup>2</sup> as in skull KGU No. 748. According to NIEZABITOWSKI (*l. c.*), DP<sup>1</sup> falls out after DP<sup>4</sup>. He bases this statement on the state of dentition of skull St I, which, however, indicates that DP<sup>1</sup> (height of crown, 15 mm) fell out rather after DP<sup>2</sup> (height of crown, 8 mm) more or less simultaneously with the loss of DP<sup>3</sup> (height of crown, 15 mm) and decidedly before that of DP<sup>4</sup> (height of crown, 30 mm). As a vestigial tooth, not replaced by a permanent tooth, DP<sup>1</sup> was, however, subject to a considerable variability in regard to the period of its falling out.

The erupting and growth of P<sup>4</sup> and P<sup>3</sup> more or less coincide, as indicated by the dentition of skulls ZAPUJ No. 683, ZG No. II-b-13-1 and others. P<sup>4</sup> wedges in between already grown P<sup>3</sup> and M<sup>1</sup>. The growing of P<sup>4</sup> and M<sup>3</sup> 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<sup>1</sup> to DP<sup>4</sup> and are subsequently followed by M<sup>1</sup>.

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 M<sup>3</sup> 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 M<sup>3</sup>, are as a rule (with few exceptions) fused in aged individuals (M<sup>3</sup> worn-off halfway down or even more). The speno-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<sup>4</sup>. 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<sup>4</sup> and M<sup>3</sup> and prior to M<sup>3</sup> 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-

Table 1

 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	YM	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
Sphenooccipital	-	+	+	+	+	+	+	+	+	+
Parietal	+	+	+	+	+	+	+	+	+	+
Frontal	+	+	+	+	+	+	+	+	+	+
Nasal	-	-	+	+	+	+	+	+	+	+
Parietointerparietal	-	-	+	+	+	+	+	+	+	+
Frontoparietal	-	-	+	+	+	+	+	+	+	+
Synchondrosis interoccipitalis interlateralis	-	-	+	+	+	+	+	+	+	+
Synchondrosis interoccipitalis squamolateralis	-	-	+	+	+	+	+	+	+	+
Parietotemporal	-	-	trace	+	+	+	+	+	+	+
Frontotemporal	-	-	trace	+	+	+	+	+	+	+
Sphenofrontal	-	-	+	+	+	+	?	+	+	+
State of dentition	deciduous M <sup>1</sup> coming into use			P <sup>4</sup> not yet used or coming into use M <sup>2</sup> getting out of alveolus					M <sup>3</sup> fully grown, not yet used	M <sup>3</sup> not fully grown

Table 2

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

Skull, Cat. No. Type of suture	StI	YM	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 between frontals and nasals	—	—	+	+	+?	—	?	+	+	+	+	+	+
Lacrimal — surrounding bones	—	—	—	—	trace	—	trace	trace	+	+	+	+	+
Nasomaxillary	—	—	—	—?	trace?	—	—	—	+	+	+	+	+
Zygomaxillary	—	—	?	?	trace	—	?	—	+	+	+	trace	+
Incisivomaxillary	—	?	?	?	+?	trace	—	?	+	+	+	+	+
State of dentition	deciduous M <sup>1</sup> coming into use			P <sup>4</sup> not yet used or coming into use M <sup>3</sup> getting out of alveolus				M <sup>3</sup> large but not yet used			beginning of the wear of M <sup>3</sup>		

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.  Type of suture	St I	YM	KGU No. 748	ZAPUJ No. 683	ZG No. II-b-13-1	ZIN No. 10707	KGU No. 729	MPL 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	+	posteriorly	+	+	—	+	+	+	+
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 <sup>1</sup> coming into use			M <sup>3</sup> getting out of the alveolus				beginning of the wear of M <sup>3</sup>						M <sup>3</sup> worn-off half down the height of crown or even more			

ervation 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  $M^3$  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  $M^3$ , 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.*  $M^3$  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 tuberos, 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. 3A, 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

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

	Young		Young adult	Old adult	Old
Number of individuals Cat. Nos.	4 MZNo. VIII/Vm-453 (YM), (StI)		5 KGU No. 748	45 —	25 —
Dentition	Deciduous (KGU No. 748 after a loss of the right DP <sup>1</sup> , MZ No. VIII/Vm-453 after a loss of DP <sup>1</sup> and DP <sup>2</sup> , M <sup>1</sup> coming into use)		P <sup>4</sup> and M <sup>3</sup> not yet used in KGU No. 736 and ZAPUJ No. 683, P <sup>4</sup> just coming into use in ZIN No. 10707 KGU No. 729 and ZG No. II-b-13-1	M <sup>3</sup> in the process of abrasion, worn-off not more than down to 2/3 of the height of crown	M <sup>3</sup> 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 individuals. The palatomaxillary suture not fused in 30% of individuals
Nasal bones (Types I, II and III, Text-fig. 4A-C accordingly)	Type I	?	Three individuals — type II; two individuals (ZIN No. 10707 and KGU No. 729) type III	Type III	Type III
The fusion of nasal and intermaxillary bones	Lacking	Present	Present	Present	Present
Osseous nasal septum (Types A-F, Text-fig. 3A-F)	Type A	Type B	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% damaged 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 septum) — 16% of individuals Type E — 4% of individuals

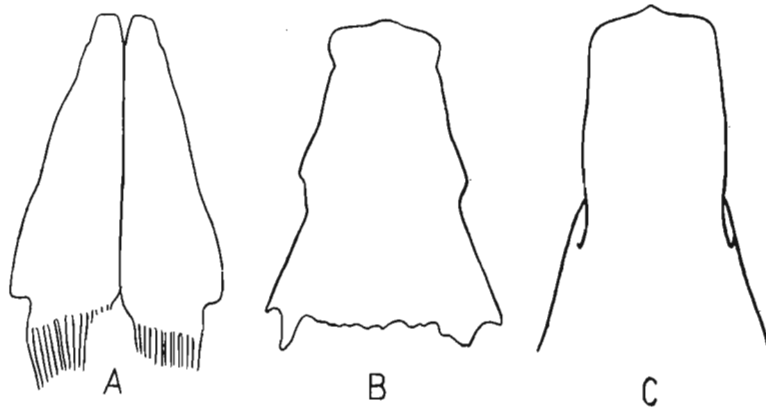


Fig. 2

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. 2*C*). 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 characteristic 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.

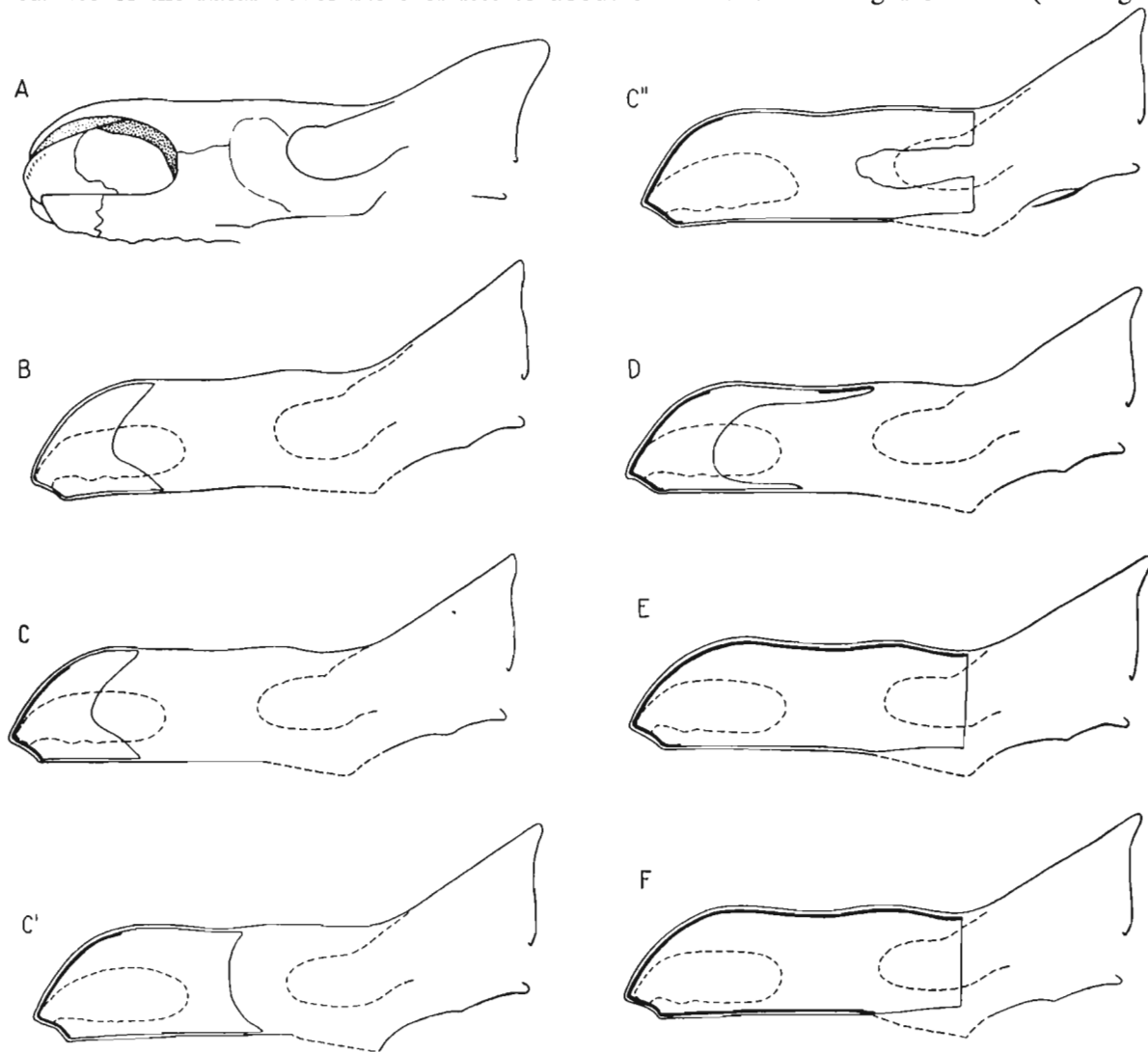


Fig. 3

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.

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-intermaxillary 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. 1D), 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 homogeneous samples (SIMPSON, ROE & LEWONTIN, 1960)<sup>1</sup>.

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<sup>2</sup> 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.

<sup>1</sup> 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.

<sup>2</sup> Cranial angles measured according to ZEUNER, 1934. For definition see Table 7.

Table 5

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

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 $\sigma$	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	216—291	306—366
Theoretical range of variability*	622—860	551—712	327—453	112—194	192—245	213—282	117—192	189—293	276—392

\* 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  $\sigma$  on the basis of the fact that, in the case of normal distributions, 99% of observations are contained within the interval of between  $M - 3\sigma$  and  $M + 3\sigma$  and 95% between  $M - 2\sigma$  and  $M + 2\sigma$ . 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  $\sigma$  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  $M - 3\sigma$  and  $M + 3\sigma$  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 \ Country	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

Character \ Country	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

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

Dimensions	Inv. No.															
	MZ No. VIII/Vm 234	MPL No. IV-3-IA 857	MG No. 3	M No. 369	MG No. 8	MZ No. VIII/Vm 452	RS No. 14	ZAPUJ No. 683	ZG No. II-b-13-3	ZG No. II-b-13-1	ZG No. II-b-13-2	MZ No. VIII/Vm 173	MZ No. VIII/Vm 146	Rz No. 30	MZ No. VIII/Vm 235	ZN No. 32
Maximum length (acrocranium-rhinion measured along the upper surface of skull)	773	807	795	799	744	791	701	746	736	727	672	684	709	733	772	761
Basal length (basion-position, measured parallel to palate)	667	685	638	629	622	654	598	625	626	609	580	621	635	618	666	672
Length of external nares	231	238	224	213	209	226	211	222	220	210	—	223	210	219	212	216
Distance from lacrimal tubercle to nuchal crest	400	420	422	410	417	392	370	381	392	386	380	352	377	379	388	383
Distance from lacrimal tubercle to the posterior margin of external nares	175	165	180	165	141	167	144	157	144	152	116	143	156	151	168	169
Length of palate	317	317	—	282	280	298	290	291	280	274	260	299	298	—	—	300
Length of choanae (to pterygoid process)	120	121	—	—	122	122	120	127	125	128	130	107	108	—	—	138
Distance from basion to posterior alar foramen	175	170	155	—	165	147	140	140	150	155	144	154	159	151	159	158
Width of occiput just above the external acoustic meatus	246	265	268	265	250	267	245	223	222	239	235	235	230	250	245	260
Maximum width of nasal bones	156	173	186	165	140	153	149	143	135	155	145	157	156	153	144	ok. 162
Maximum width of frontal bones	258	245	296	271	235	232	232	216	219	235	226	241	238	237	233	258
Maximum width on zygomatic arches	340	354	386	360	335	345	319	316	300	335	317	332	317	—	ok. 336	ok. 356
Height of occiput	243	239	235	240	235	256	227	218	223	213	212	212	212	235	241	238
Maximum height of skull in the region of the nasal horn	180	190	180	—	170	175	175	155	159	170	157	166	162	160	168	182
Angle $\gamma$ between the axis of the foramen magnum and palate	96	111	103	117	102	98.5	95	104	98	101	94	91	98	—	—	94
Angle $m$ between the axis of the foramen magnum and the parietal part of the skull roof	52	39.5	53.5	43	58	55	52	47	49.5	50.5	53.5	54	49	50	—	52.5
Angle $p$ between the parietal part of the skull roof and occiput	54	57	46	45.5	53	49	55	50	48.5	56.5	54	57.5	57	51.5	—	53
$x = m - o$	-2	-17.5	7.5	-2.5	5	6	-3		1	-6	-0.5	-3.5	-8	-1.5	—	-0.5
Skull proportion coefficient (maximum length to width of occiput above the external acoustic meatus)	3.14	3.04	3	3.02	3	2.96	2.86	3.35	3.31	3.01	2.86	2.91	2.98	2.93	3.15	2.93

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  $\gamma$  for the skulls of *Coelodonta antiquitatis* (BLUM.) of the European Russia

Values of angle	85°—89°	90°—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 some 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	2.91—3.0	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

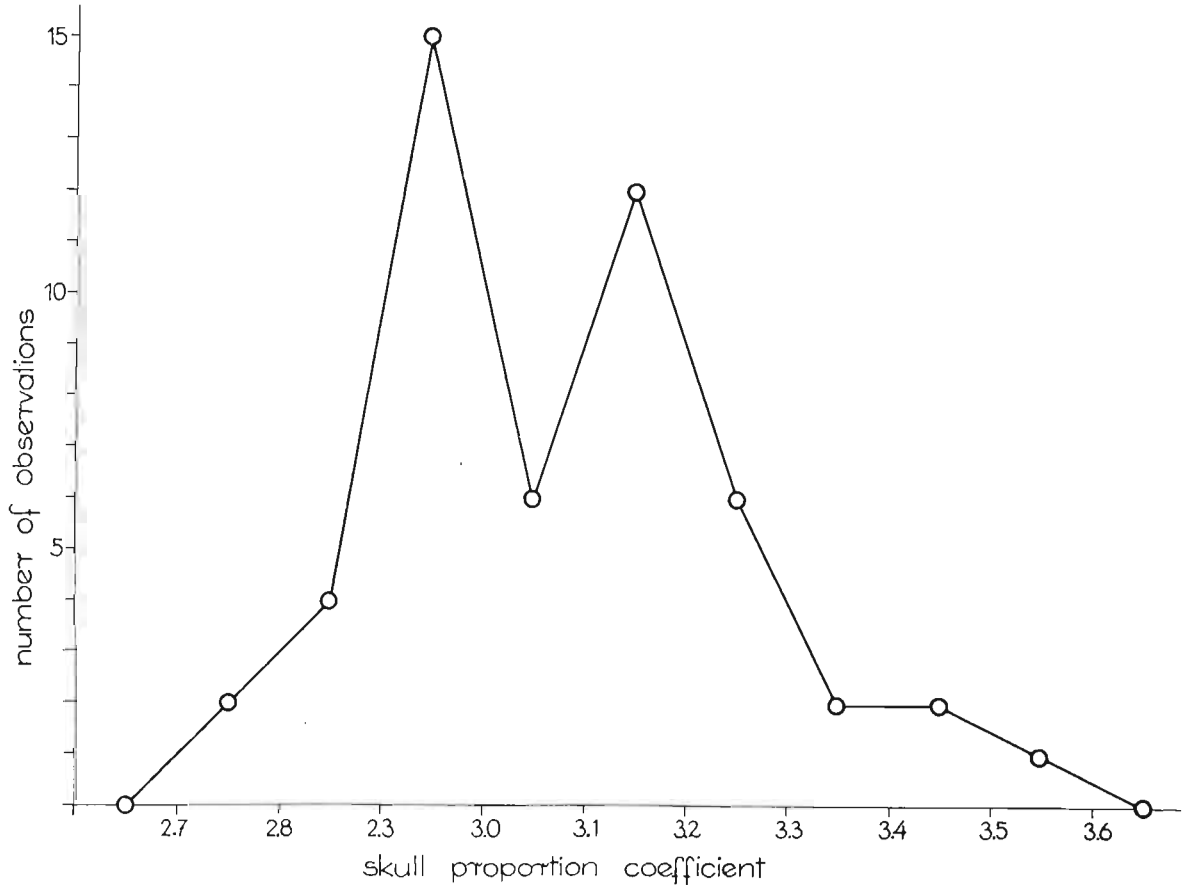


Fig. 4

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

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)

Measurements		Number of observations	Mean M	Standard deviation $\sigma$	Observed range of variability	Theoretical range of variability *
Maximum length (in mm)	P	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)	P	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	629—694	—
Width of occiput above the external acoustic meatus (in mm)	P	15	247.9	11.6	230—268	213—282
	ER	33	257.8	15.82	219—295	—
	USSR	53	247.5	17.8	212—283	—
	S	9	254.4	17.84	228—283	—
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	146—177	—
Skull proportion coefficient	P	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	

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

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 numerous 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	771—790	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	390—409	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)	225—234	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)	670—699	700—729	730—759	760—789	790—819	820—849
Number of observations	0	1 ♀	1 ♀	6 (5 ♀+1 ♂)	1 ♂	4 ♂

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	160—179	180—199	200—219
Number of observations	3 ♀	5 (4 ♀+1 ♂)	2 ♂	4 ♂

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 antiquitatis* (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	670—689	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	850—869	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	335—344
Number of observations	1	2	3	6	3
Width (in mm)	345—354	355—364	365—374	375—384	385—394
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 ( $\gamma$ ). 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  $\gamma$  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  $\gamma$  in both the Polish and Soviet material (Table 29).

Table 29

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

Specimens	Mean values of maximum length of skulls (in mm)
Skulls from Poland with: angle $\gamma$ between 91° and 103°	717
angle $\gamma$ between 104° and 113°	770
Skulls from the USSR. with: angle $\gamma$ below 100°	745
angle $\gamma$ more than 100°	790
skull proportion coefficient below 3.01	752
skull proportion coefficient more than 3.11	782

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  $\gamma$  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  $\gamma$ , 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)	780—799	800—819	820—839	840—859	860—879	—
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  $\gamma$ . 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  $\gamma$  and the development of nasal septum, it follows that 44% of old-adult individuals with angle  $\gamma$  larger than  $101^\circ$  (mean value  $105^\circ$ ) 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  $\gamma$  lesser than  $101^\circ$  (mean value  $96^\circ$ ) 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  $\gamma$  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  $\gamma$ . The smaller angle  $\gamma$  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  $\gamma$ , the ossification might be smaller than in the case of a low value of angle  $\gamma$  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. 1 *a, b*; Pl. IX, Fig. 2 *a, 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 scapular surface bent medially. Its accurate range is not visible. In addition, the 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,

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 Javanese rhinos (Cat. No. MIZ), this area is strongly narrowed ventrally as the result of a poor development of *linea anconea*. They also lack tuberculum 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*) from the rotation axis of the joint which they operate and, on the other, it increases the angle of insertion of some 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 differ 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 ventro-

external 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 woolly 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

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	<i>C. antiquitatis</i>	<i>D. bicornis</i>	<i>Rh. sondaicus</i>
<b>Humerus</b>			
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%
<b>Radius</b>			
the minimum width of shaft	15%—18%	14%	—
the width of distal end	31%—33%	25%—26%	below 29%
<b>Ulna</b>			
the minimum width of shaft	13%—14%	9%—11%	—
the anteroposterior dimension of the shaft (as in Table 42)	12%—14%	11%—12%	—
<b>Femur</b>			
the minimum width of shaft	18%—21%	13%—15%	15%
<b>Tibia</b>			
the width of proximal end	42%—46%	36%—40%	44%
the smallest width of shaft	22%—25%	19%—20%	20%
the width of distal end	35%—37%	30%—36%	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

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)

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

\* The tibio-femoral coefficient = the ratio of the length of tibia to the length of femur × 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 and 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 inadapative 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 P<sup>2</sup>. Old adult, male (?), Würm, Góra Puławska.
- (3) MZ No. VIII/Vm-137. A complete skull except for P<sup>2</sup>-M<sup>2</sup> on both sides. M<sup>3</sup> 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 M<sup>2</sup> and M<sup>3</sup> strongly worn; alveoli of P<sup>2</sup> and P<sup>3</sup> 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 P<sup>2</sup> lacking. Young adult. Sex: indeterminate. Stratigraphic age: unknown. Wola Przemkowska, 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 P<sup>2</sup> and P<sup>3</sup> and the left M<sup>2</sup> lacking. Old adult. Sex: indeterminate. Stratigraphic age: unknown. Transylvania, Hammersdorf near Hermanstadt, Sibiu, Rumania.
- (11) MPL No. IV-3, IA 857. A complete skull. Except for the left and right M<sup>3</sup>, all teeth lacking. Old adult. Male. Stratigraphic age unknown. Łódź.
- (12) MG. Provisional 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 P<sup>2</sup> and left P<sup>2</sup> and P<sup>3</sup> lacking. Individual age on the boundary between young adult and old adult. Sex indeterminate. 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 indeterminate. 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 P<sup>2</sup> and M<sup>3</sup> and left P<sup>2</sup>-P<sup>4</sup> and M<sup>3</sup> lacking. Individual age: a younger representative of old adults. Male (?). Stratigraphic age unknown. Konin, Józwin 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 indeterminate. Stratigraphic age unknown. Siberia.
- (18) MG. Provisional number M-8. Cat. No. lacking. A cast of skull with part of dentition preserved. Old (?). Sex indeterminate. Origin unknown.
- (19) M. S. E. A skull described by STACH (1956). Old. Sex indeterminate. Stratigraphic age unknown. Wadowice.
- (20) MZ No. VIII/Vm-233. A cranium. Young, sex indeterminate. Würm, Góra Puławska.
- (21) MZ No. VIII/Vm-453. The left half of the visceral part of skull with DP<sup>3</sup>, DP<sup>4</sup> and P<sup>2</sup>-P<sup>4</sup> in the maxilla. Young, sex indeterminate. 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 P<sup>2</sup> and M<sup>1</sup> and left P<sup>3</sup>-P<sup>4</sup> and M<sup>1</sup> preserved. Young adult. Sex indeterminate. 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 indeterminate, 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-BIAŁYNICKA, 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 acrocranium 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 synchondrosis interoccipitalis squamolateralis 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 process 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  $150^\circ$  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 (horizontal) 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 lacrimo-maxillary suture and leads to a canal which runs between these bones. This canal is connected 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

long (measuring from the ventral lacrimal foramen), slightly ascends medially, thus tightening the orbit.

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. 5A) suddenly bends dorsally at an angle of about  $150^\circ$  to  $155^\circ$ , 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 zygomatici; 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  $180^\circ$  (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 sphenoccipital suture is sharp, unpaired, having muscle scars on both sides and crestlike posteriorly. 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 P<sup>2</sup>. 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 I<sup>2</sup> and I<sup>3</sup>), 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 woolly 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. 5 B *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. 5 B, *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 capitis) 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. 5 B *g*), by means of a common tendon of the cleidomastoideus, sternomastoideus and longissimum capitis, as is the case in domestic mammals (NICKEL, SCHUMMER & SEIFERLE, 1968). The rectus capitis 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. 5 B, *c*).



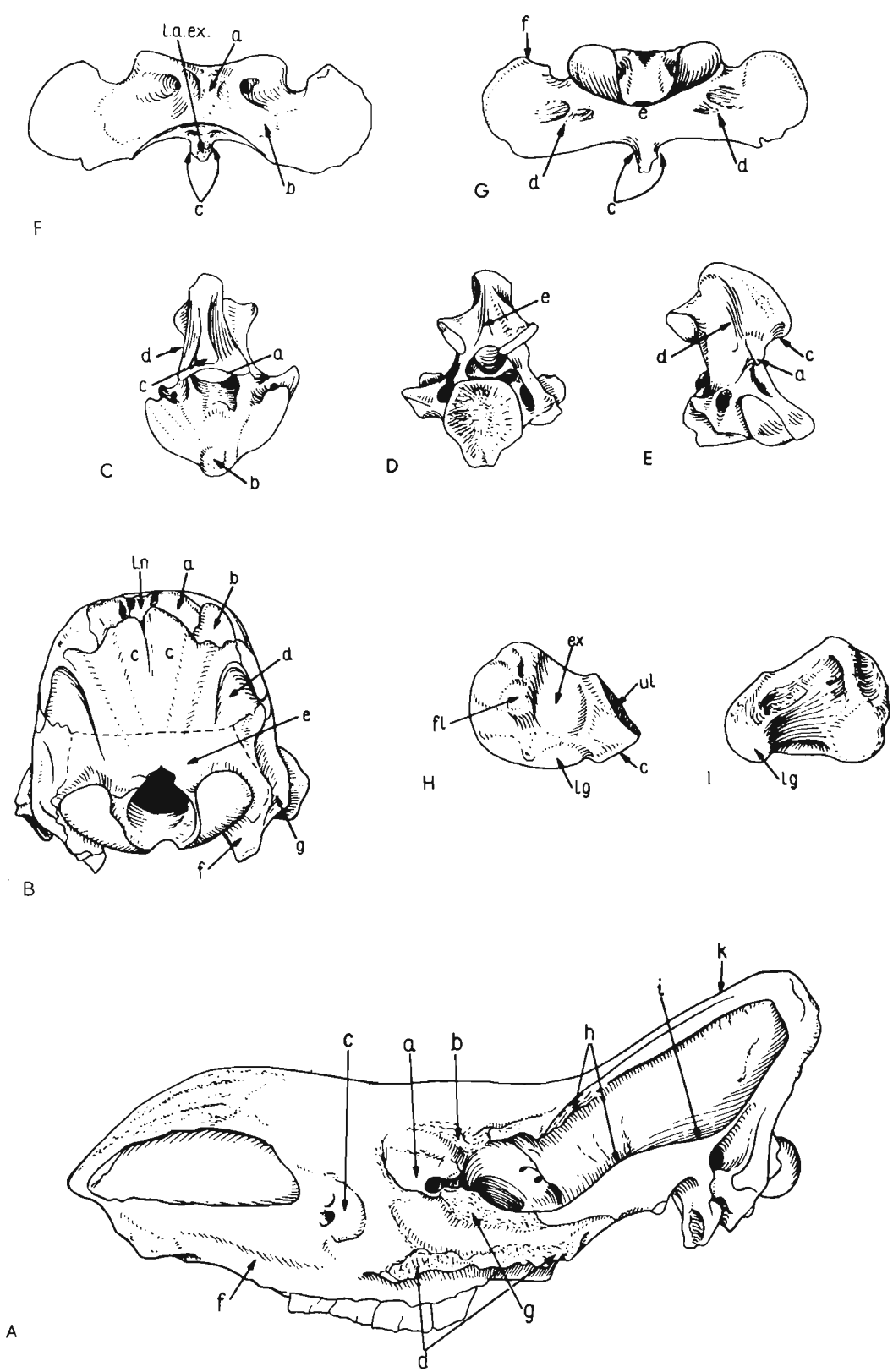


Fig. 5

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, *I. 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. 5 *B, 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 jugulo-hyoideus, 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. 5 *A, 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. 5 *A, 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 nasolabialis, *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 processus 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 *auricularis* 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 labii 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

Table 33

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

Measurement	Cat. No.		ZIN		ZIN	GI No.	ZIN
	ZAPUJ No. 683		No. 10725		No. 16948	$\frac{83}{112}$	No. 10735
Infradentale-gonion caudale length	507	517	527	524	605	500	465
Infradentale-condyilion 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	126		175		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		69	86	—
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	224		249	244	298	240	241

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  $115^\circ$  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 mylchoideus 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 horizontally and in the sagittal plane.

Table 34

Dimensions of atlas in *Coelodonta antiqutatis* (BLUM.) in mm

Dimensions	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

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

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

Dimensions	Cat. No.	ZAPUJ No. 683	IG No. 1791N	IG No. 1657
	Length of body with dens (from below)		about 116	131
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	—	—

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 brachio-cephalicus. 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 vertebrae (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

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

Serial number of vertebra	III	IV	V	VI	VII
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

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 cranio-ventrally 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 vertebrae 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 (*vide* 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 vertebrae<sup>3</sup>.

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.

<sup>3</sup> 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 I, 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 vertebrae 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

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	Dimensions																					
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	XVII	XVIII	I	II	III	IV
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	