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The Skull of *Mammut praetypicum* (*Proboscidea*, *Mammalia*) from the
Collection of the Jagiellonian University in Cracow, Poland

[Pp. 305—324, pls. IX—XV, 2 text-figs.]

Czaszka *Mammut praetypicum* (*Proboscidea*, *Mammalia*) ze zbiorów Uniwersytetu Jagiellońskiego
w Krakowie

Череп *Mammut praetypicum* (*Proboscidea*, *Mammalia*) из коллекции Ягеллонского универси-
тета в Кракове, в Польше

Abstract. The well-preserved mandible and a part of the skull of a Middle Pliocene masto-
don, identified as *Mammut praetypicum* (SCHLESINGER, 1919), are described. Data concerning
the geographical and stratigraphical distribution of this species are given and its origin is dis-
cussed. A reconstruction of the skull is presented.

INTRODUCTION

The mastodon skull described in the present paper was probably found at the end of the nineteenth century or at the beginning of the twentieth century. Unfortunately, the exact locality is unknown. According to the relation of the late Prof. J. FUDAKOWSKI, of Jagiellonian University in Cracow, the skull was probably found by KAMIENIECKI — a landowner and amateur naturalist — in the environs of Balta in Podolia. In 1912 or 1913 the unprepared skull embedded in limestone was transported to the Department of Comparative Anatomy of Vertebrates, Jagiellonian University. It was prepared by Dr. W. KIERNIK, later a professor of Warsaw University, and included in the collection of the above-mentioned Department, in which it is still kept.

The material under description is white, greyish-white or grey in colour and shows a high degree of fossilization. The texture of the bone is preserved and so is the texture of the incisor dentine. Both the molars in the maxilla and those in the mandible are in an excellent state of preservation. The mandible is broken in several places but it shows no deformations or distortions and neither does the fragment of the skull.

When the material was delivered for elaboration, the region of the frontal bone was partly covered with reddish-gold sand and whitish limestone, which have been removed by mechanic preparation. Microsections were performed from the material covering the bones in the Institute of Geology, Polish Academy of Sciences in Cracow, under the direction of Prof. K. BIRKENMAYER in order to examine it for microfauna. However, no traces of the microfauna were found in the preparations. Macroscopic examination of the sand removed from the specimen was carried out by Prof. W. KRACH, of the Institute of Geology, P. A. of Sc. in Cracow, and showed the presence of limestone inclusions.

A detailed description of the relatively well preserved skull is expedient, because it is the first so complete skull fragment of a member of this species so far described. New morphological data obtained on the basis of this material justify the discussion on the origin of this species and its geographical and stratigraphical distribution and they make the attempt at the reconstruction of the skull possible.

Acknowledgments. I dedicate this work to the late Prof. Józef FUDAKOWSKI, who died in 1969 and to whom I am indebted for the only piece of information about the place of finding and the history of the mastodon skull under study.

I wish to express my heartfelt thanks to Prof. Zygmunt GRODZIŃSKI for rendering the fossil remains accessible to me for elaboration. I am indebted to Prof. Krzysztof BIRKENMAYER for carrying out a microscopic analysis of the material stuck to the skull, and to Prof. Wilhelm KRACH for its macroscopic examination. My thanks are also due to Prof. Kazimierz KOWALSKI for his valuable suggestions during the preparation of this paper and to Dr. Jerzy ŚWIECIMSKI for his help with the reconstruction of the skull. I should also like to thank Prof. Heinz TOBIEN (Mainz) for his valuable advice and for criticizing the manuscript.

NOTES ON THE PROBABLE SITUATION OF THE LOCALITY OF THE FIND

The data about the place where the skull was found handed down by Prof. J. FUDAKOWSKI are the only concerning its derivation. The lack of any other data makes me assume that the skull comes from the Balta region in Podolia. Naturally, as this is not quite certain, I assume it with qualification.

As early as the nineteenth century mastodons were known from the environs of Balta (Odessa Province, U. S. S. R.), from the deposits called the Balta sandbeds (Sandschichten von Balta, балтские отложения) (Pavlov, 1894).

It seems probable that the skull under study comes from these very sandbeds, the more so, since *Mastodon americanus* PENNANT forma *praetypica* is known from this locality (SCHLESINGER, 1922). An analysis of the material that covered the bones neither supports nor refutes this possibility (cf. Introduction). A comparison of our bony remains and the material attached to them with the specimens from Balta, especially with the remains identified as *Mastodon borsoni*, might throw some light on the problem of the derivation of the skull.

A survey of the fauna from the sandbeds of Balta was published by WENJUKOW in 1904. According to him, the sand layers of Balta do not form an uniform definite geological horizon; their sedimentation took a very long time, during which the fauna of that region changed very much, its older forms being replaced by the younger ones. WENJUKOV distinguishes two faunal groups, an older, from the Lower Pliocene, which he compares with the faunae from Eppelsheim, Baltavar and other places, and a younger, from the Middle Pliocene, compared with the faunae from Montpellier, Hajnáčka, Fulda, etc., characterized by the prevalence of *Mastodon borsoni*.

The authors of later publications, e.g., BURCHAK-ABRAMOWICZ (1935) and BORYSIAK and BELAYEVA (1948) do not determine the age of the fauna precisely either, but they define it in a general manner as the Pliocene.

Family: *Mammutidae* CABRERA, 1929

Genus: *Mammut* BLUMENBACH, 1799

Mammut praetypicum (SCHLESINGER, 1919)

1877 — *Mastodon Borsoni* VACEK, Abh. geol. Reichsanst. VII, 6—11, Pl. VI, Figs. 1—4

1882 — *Mastodon Zaddachi* JENTZSCH, Schrift. phys.-ökon. Ges. Jahrg. XXIII, 201—205, Pl. V, Fig. 6

1894 — *Mastodon americanus* PAWLOW, Mem. Acad. Imp. sci. VIII, Ser. Vol. 1, No 3, Pl. I, Figs. 1—4, Pl. II, Figs. 2, 6, 7

1901 — *Mastodon Borsoni* PAWLOW, Ann. geol. min. Russie V, 9, Pl. I, Figs. 1, 2

1904 — *Mastodon Borsoni* WENJUKOW, Mater. z. Geol. Russlands XXI, 189, Pl. V, Figs. 2, 4, 7, 8

1907 — *Mastodon Borsoni* ATHANASIU, Anuar. Inst. Geol. Rom. Pl. V, Figs. 12, 13, Pl. VII, Figs. 16, 17, Pl. XI, Figs. 27, 29, Pl. XII, Figs. 30, 31

1911 — *Mastodon Borsoni* TOULA, Abh. geol. Reichsanst. XX, 5, Pl. V, Figs. 1, 2

1917 — *Mastodon (Zygolophodon) cf. borsoni* SCHLESINGER, Denkschr. Naturh. Mus. I, 163—180, Pl. XXII, Fig. 5

1919 — *Mastodon (Mammut) americanus* PENNANT forma *praetypica*, n. sp.; SCHLESINGER, Mitteil. geol. Ges. Wien XI, 142, Pl. VI, Figs. 1—4

1922 — *Mastodon (Mammut) americanus* PENNANT forma *praetypica*, SCHLESINGER, n. f., Geol. Hungaria II, Fasc. 1, 115—116, 227—230, Pl. XIV,

Fig. 5, Pl. XV, Figs. 1—4, Pl. XVI, Figs. 1—2, Pl. XVII, Fig. 1, Pl. XVIII, Fig. 5, Pl. XIX, Fig. 2

1936 — *Pliomastodon americanus praetypica* OSBORN, Proboscidea, pp. 134—135, 139, Pl. I, Figs. 89, 103

Holotype: right upper molars, M^2 - M^3 , and left lower molars, M_2 - M_3

Type locality: Szabadka and Batta-Erd, Hungary

Age: Middle and Lower Pliocene

Material: Complete mandible with dentition in situ: right I_2 , lacking in tip, well-preserved both M_2 and both M_3 (left M_3 partly damaged). Right fragment of skull of same specimen, with teeth in situ: I^2 , lacking in tip, M^2 and half of M^3 ; partly preserved right premaxilla, maxilla, jugal, lacrimal, orbit, postorbital process, and frontal.

Description: The elongated and low mandible, supporting right and left M_2 - M_3 and right I_2 , is well preserved (Pl. IX/2, X/4). The body of the jaw is about twice as long as the height of the ramus. The complete, long and narrow symphysis is a little longer than M_2 and M_3 , and hardly broader in the anterior part. In the frontal view the symphysis has its upper part flattened, whereas its lower part is concavely arched (Pl. XIII/10). The posterior part of the symphysis begins about 5 cm in front of the anterior wall of right M_2 .

Well-developed crests run from the beginning of M_2 about halfway along the symphysis (Fig. 1). The mental foramen occur below the first ridges of M_2 . Neither the temporal processes nor the angles of the jaw are preserved.

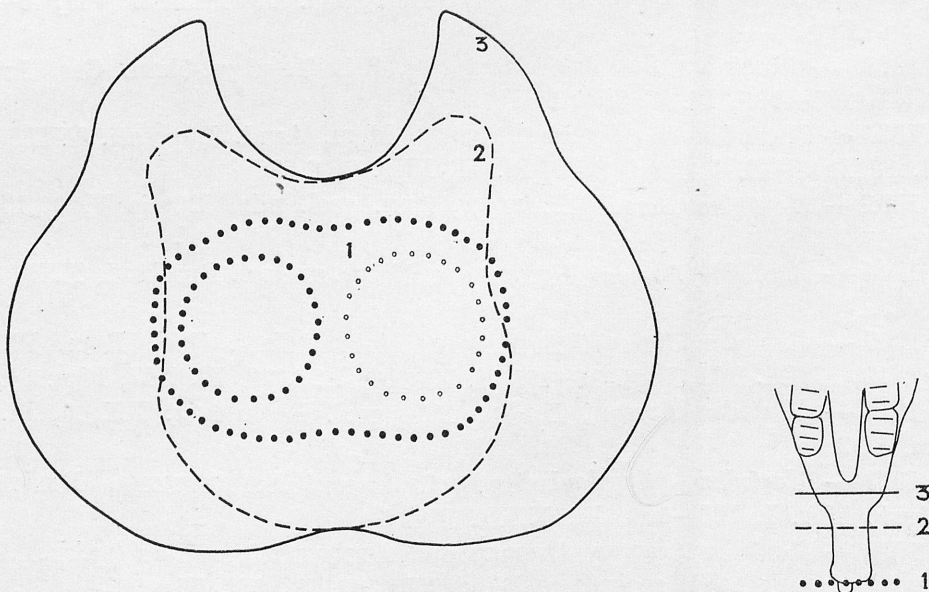


Fig. 1. A diagrammatic drawing showing a cross-section through the mandible of *Mammut praetypicum*. Section 1 elevated. One-half natural size

The two molar series (M_2 - M_3) are subparallel. The distance between the right and left second molars is 10 cm and between the third grinders 8.5 cm. The width between the condyloid processes is considerable and amounts to about 65 cm. The left condyloid process is well preserved; it is 160 mm long and 65 mm broad. The right process is slightly damaged.

Measurements of the mandible, in mm

total length of the body (without I_2)	990
height of the left ramus	450
length of the ramus (anterior-posterior)	300
extreme width of the jaw at the posterior end of the molar series	450
extreme width of the jaw (condyloid processes included)	ca 650
length of the symphysis	305
inner width of the symphysis at its posterior end	55
minimum outer width of the symphysis	95
length of the right molar series (M_2 + M_3)	292

The molar series (M_2 - M_3) lies exactly in the middle of the mandibular half and its length approximates to one-third of the total length of the jaw. The crowns of the molar teeth are low and broad.

The right lower incisor (I_2) is only partly preserved; its tip is lacking. This tusk is small, straight and circular in cross-section (Pl. XIII/10). The length of its part projecting above the jaw is 30 mm and that of the part in the alveolus about 150 mm. The tusk is surrounded by a 1,5-millimetre-thick layer of cement. The diameter at the base of the tooth is 36 mm.

In spite of very careful preparation of the specimen no traces of the left lower incisor have been found, to say nothing of the alveolus. If the two incisors were symmetrical, they certainly ran parallel for their whole length, about 8 mm apart. Thus, they did not touch each other at all.

The second right lower molar (M_2) (Pl. XII/8) is typically trilophodont. The axes of the ridges are subperpendicular to the sagittal axis of the tooth. The breadth of the ridges is not uniform. The third ridge is the broadest, whereas the first and second ridges are narrower. The tooth is worn off to about half its original height and, besides, a little damaged; nevertheless, its description is possible. The pretrite (i.e., situated on the external, labial side in the lower molars and on the internal, lingual side in the upper molars) half-ridges (Halbjoche) are considerably more worn than the post-trite (internal) ones. The two halves of the ridges are almost symmetrical. The cusps of the ridges are not visible. The best-preserved post-trite half of the third ridge forms a more or less uniform crest, which descends obliquely toward the middle of the occlusal surface, where the ridge is split in two by a sagittal furrow (median sulcus). The remains of two nearly completely worn out talons seem to indicate the small measurements of these structures. The synclines between the ridges are V-shaped

in cross-section, but their bottoms become wider toward the labial side. They are not filled with cement.

Left M_2 resembles the right one.

Third right lower molar (M_3) (Pl. XII/8). This tooth has four perfectly well developed ridges and a marked talon composed of three large cusps as a fifth ridge. The largest, main cusp is situated in the middle and shows a small, poorly developed, accessory cusp on its labial side. Only slight remains of the heavily worn small anterior talon (in touch with M_2) are visible. In contradistinction to the second and third ridges, which are approximately the same width, the first and fourth ridges are narrower.

The base of the crown is much broader than the top and therefore the side walls of particular ridges slope relatively gently, especially on the labial side, steeper on the lingual side.

The outline of the crown is an elongated oval. The longitudinal axis of the tooth is slightly bent, so that the ends of the tooth are somewhat turned to the labial side. The tooth is slightly affected by abrasion. Its fourth ridge and the talon were not used at all. Traces of wear can be seen on the first, second and, to a low degree, third pretrite (external) half-ridges.

The axes of the ridges are somewhat oblique in relation to the sagittal axis of the tooth, which seems to be slightly twisted round this last axis. As a result, the crest of the first ridge slants toward the labial side, the crest of the second ridge is approximately horizontal and the crests of the third and fourth ridges incline toward the lingual side. The lingual walls of the ridges are far steeper than the labial ones; they are almost vertical. The walls of the synclines do not meet at a very acute angle, the syncline between the first and the second ridges being the widest (in side view). The farther to the rear, the narrower the synclines become, whereas their bottoms are wider and more rounded on the labial side than on the lingual. The walls of the ridges and the bottoms of the synclines are smooth without any, even very small, cusps. There are, however, wrinkles or rims (Sperrleisten) on the pretrite (external) half-ridges. These separating rims, affected by wear from the very beginning, run from the main cusp of each ridge to the bottom of the syncline, where they approach, but do not join, the opposite rims. The two halves of the ridges are almost symmetrical. There is no cement in the synclines.

Each half-ridge has a well-developed crest, which, as it comes nearer to the sagittal furrow, sometimes divides to form 1—3 hardly distinguishable „secondary“ accessory cusps (Fig. 2 B p. 319), which are best seen on the third ridge of right M_3 .

The inner, lower and smaller, accessory cusps reach the sagittal furrow. The distinct and sharply cut median sulcus divides the ridges of the tooth along its sagittal axis, approximately in the middle of the occlusal surface, into pretrite and post-trite half-ridges.

Such a division of the crest into indistinct accessory cusps is, however, present only on the fourth ridge of the third lower molar. All the ridges of the other

molars form more or less uniform crests, which descend toward the median sulcus.

A part of the side of the skull (Pls. IX/1, X/3) is preserved. It bears a molar series, M^2 - M^3 , and the right tusk. The extant portion of the skull consists of the praemaxilla, maxilla, jugal, lacrimal, orbit, postorbital process and frontal. The sutures are not visible, which makes the exact determination of the limits of particular bones impossible. The incisive sheath is long, narrow and directed slightly downwards. The lower alveolar border reaches the horizontal plane of the occlusal surface of the molars. The tusk is covered with the incisive sheath, i.e., a bony layer of about 20 mm in thickness. Toward the middle of the skull the praemaxilla becomes flattened. The maxillary part is robust. The anterior part of the zygomatic arch is very broad, massive and strong. The orbit is about 120 mm in diameter. The postorbital process forms the posterior end of the preserved part of the skull. The frontal, above the orbit, is heavily cracked and rough. The temporal fossa is very broad and deep.

The right upper incisor, I^2 (Pls. IX/1, X/3) is nearly complete, except for the tip which is broken off. This large and straight tusk, 1000 mm in length, is, however, slightly turned upwards at the end (side view, Pl. X/3). The tooth leaves the skull approximately horizontally, but is directed slightly downwards and markedly outwards. The incisor is circular in cross-section, with a slight external flattening, however. The maximum horizontal diameter, measured at the base of the tusk, close to the alveolus, is 125 mm and the vertical diameter is 117 mm. These diameters at a distance of 50 cm from the alveolus (halfway along the tusk) are, respectively, 123 and 115 mm.

The tusk is covered uniformly with a differentiated layer of dentine or cement, 2—3 mm thick (Pl. XIII/9). The outer layer becomes thicker toward the tip of the tusk.

The annual growth rings are visible (Pl. XI/5, 6). These rings are wider in the terminal part of the tusk and become narrower toward its base. In addition to the transverse constrictions there are regular longitudinal streaks in the outer and inner layers of the dentine.

The second right upper molar, M^2 (Pl. XII/7) has three ridge crests. It is heavily worn. The pretrite (internal) half-ridges are more affected by abrasion than the post-trite (external) ones. The pretrite half-ridge of the first loph is worn off almost to the bottom of the syncline. The second and third ridges are less abraded. The first ridge is the broadest, the second and third lophs are narrower and narrower. The small anterior and posterior talons are completely worn off. At the anterior end of this molar there are traces of wear and contact with the preceding tooth. At the base of the post-trite half-ridge of the first loph there is a row of small conelets, which run from the vestige of the anterior talon to the syncline between the first and second ridges. No other conelets occur in the synclines. The two halves of each ridge are subsymmetrical. The median sulcus is distinct. The posttrite half-ridge of the third loph shows a hardly discernible division into a main and an accessory cusp. The side walls of the crown of this

tooth slope less steeply on the lingual side than on the labial. The heavily worn separating rim is visible on the posterior wall of the third ridge. The synclines are fairly sharply cut into the tooth, but are more rounded on the lingual side.

Only the first and second ridges of the third right upper molar, M^3 , are preserved (Pl. XII/7). The median sulcus is distinct. The ridges form rather uniform crests, which descend towards the median sulcus. Traces of wear can be seen on the first and second ridges. The separating rim is well developed on the anterior wall of the pretrite half-ridge of the first loph. It begins at the lingual top of the crest, runs down to the median sulcus and into the syncline. The anterior talon is heavily worn. The side walls of the ridges are steeper on the labial side than on the lingual. The only extant syncline is fairly wide. The half-ridges are subsymmetrical only that the pretrite half is wider than the post-trite one. No conelets have been found in the syncline.

In both the molars the ridges extend perpendicularly to the sagittal axis of the tooth.

The average thickness of enamel in all the molar teeth ranges from 2 to 4.3 mm.

SYSTEMATIC POSITION OF THE REMAINS

The species *Mastodon americanus* forma *praetypica* differs fundamentally from *Mastodon borsoni*, in which some investigators are inclined to include it (cf. Discussion). In order to bring into relief also its distinctness from *Mammut americanum* I suggest that the name given it by SCHLESINGER (1919) shall be simplified and that it shall be called *Mammut praetypicum*. Besides, the description of the species presented by SCHLESINGER needs revision and complementing.

The species *Mammut praetypicum* may be characterized as follows:

Diagnosis of the species. The symphysis of the mandible is elongated and equal to about a third of the length of the whole mandibular body or to the length of the tooth row. The skull is relatively high vaulted. The well-developed upper incisors have no enamel. They are circular in cross-section, about 1.5 m (?) long, almost straight except for a slight upwards bend and disposed wide apart, at an angle of 45°. The lower incisors are short, circular in cross-section, arranged horizontally and parallel to each other. The second molars are typically trilophodont, with three ridges. The last molars have four ridges and a half. The well-developed median sulcus divides the tooth along its long axis into pretrite and post-trite half-ridges. There are very distinct separating rims on the pretrite side. No pretrite accessory cusp are present. The ridges are crested, their width in the top part being relatively small. The side walls of the tooth crowns are slanting and there is no cement at the bottom of the synclines.

STRATIGRAPHICAL AND GEOGRAPHICAL RANGES

The data obtained from the remains of *Mammot praetypicum* known so far indicate that this species lived for a long period in the Pliocene, from Lower to Upper Pliocene having a peak of abundance in the Middle Pliocene.

It occurred in the areas of Hungary, Czechoslovakia, Poland, Romania and in the Ukraine in the U. S. S. R.

Finds of *Mammot praetypicum*

Country, Site, Region	Described	
	by *	under the name of
Czechoslovakia Hajnáčka (formerly Ajnácskö)	1) SCHLESINGER 1917 2) SCHLESINGER 1922	<i>Mastodon</i> cf. <i>Borsoni</i> <i>Mastodon americanus</i> forma <i>praetypica</i>
Hungary 1. Szabadka (Bács-Bodrog) 2. Batta-Érd (Fejér) 3. Rákoskeresztút (near Budapest) 4. Szentlőrincz (near Budapest)	VACEK 1877 SCHLESINGER 1922 TOULA 1911 SCHLESINGER 1922	<i>Mastodon Borsoni</i> <i>Mastodon americanus</i> forma <i>praetypica</i> <i>Mastodon Borsoni</i> <i>Mastodon americanus</i> forma <i>praetypica</i>
Poland Toruń District	JENTZSCH 1882	<i>Mastodon Zaddachi</i>
Romania 1. Budești 2. Barbatești 3. Arad 4. Amaradia	ATHANASIU 1907 ATHANASIU 1907 TOULA 1911 ATHANASIU 1907	<i>Mastodon Borsoni</i> <i>Mastodon Borsoni</i> <i>Mastodon Borsoni</i> <i>Mastodon Borsoni</i>
Soviet Union (Ukraine) 1. Pestchany (near Kamenets Podolsky, Odessa District) 2. Krasnoie (Podolia, Winnica District) 3. Pitchougino (Dnepropetrovsk District)	PAWLOW 1894 PAWLOW 1894 PAWLOW 1901	<i>Mastodon americanus</i> <i>Mastodon americanus</i> <i>Mastodon Borsoni</i>

* The materials from the sites mentioned are presented by SCHLESINGER in his work published in 1922 (pp. 101—118, 124—134), in which the author carries out a detailed revision and refers them to *Mastodon americanus* forma *praetypica*.

RECONSTRUCTION OF THE SKULL (PLS. XIV and XV)

In view of the lack of other cranial fragments of this mastodon species in the attempt at reconstruction I could base myself only on the above-described extant part of the skull and the mandible of the same specimen.

Owing to the in situ preservation of the molars it was possible to join the mandible and the skull together. The traces of the suture between the two praemaxillae permitted the determination of the sagittal plane of the specimen. Thus the arrangement of the upper incisors in relation to the whole skull was established. The preserved fragment of the sturdy zygomatic arch allowed the determination of the width of the skull, and the fragment of the frontal suggests its marked vaulting. The lack of the data on the structure of the posterior part of the skull makes the reconstruction of this part disputable.

Basing myself on the analysis carried out by OSBORN (1936, pp. 181—190) on the skulls of American mastodons and concerning the characters in which males differ from females, I assume that the fossil skull under discussion belonged to a male.

DISCUSSION

Earlier investigators generally included the remains that showed characters even only approaching those of *Mastodon borsoni* in this species, and the opinion has lately been held that *Mastodon americanus* forma *praetypica* is nothing but a progressive form of *Mastodon borsoni* (FEJFAR, 1964; RAKOVEC, 1968). However, great morphological differences between *Mastodon borsoni* and *Mammut praetypicum* make me regard them as members of separate species.

Unfortunately, the remains of *Mammut americanum* cannot be distinguished from those of *Mastodon borsoni* and *Mammut praetypicum* only on the basis of the measurements of the molars, because the ranges of these measurements overlap each other (cf. the Tables). On the other hand, the calculated indices would perhaps be significant, if teeth compared were completely developed but still bearing no traces of wearing. The morphological characters play an important role here; the characters, which are distinguishable even on damaged teeth.

In his monograph SCHLESINGER (1922) mentioned the distinct isolated robust pretrite accessory cusps, the poorly developed separating rims, the marked width of the top part of the ridges (Jochgrate) and the steep side walls of the teeth in *Mastodon borsoni*, and the slender pretrite accessory cusps, which rather fuse to form a crest, the distinct well-developed separating rims, the very small width of the ridges at their tops, and the gentle slope of the side walls of the teeth in *Mastodon americanus* forma *praetypica*, as the essential characters in which these forms differ.

In distinguishing these two species OSBORN (1936) paid attention to the fact whether or not the median sulcus was distinctly marked and to the number of cusps in a ridge. The usefulness of these characters was called into question by ANTHONY & FRIANT (1940). SCHLESINGER'S opinion has been supported in more recent literature (LEHMANN, 1950). JÁNOSSY (1955) also analysed his criteria and acknowledged their value.

Measurements (in mm.) of molars
of *Mammut praetypicum*, *Mastodon borsoni* and *Mammut americanum*

M 2 inferior

Species		<i>M. praetypicum</i>			<i>M. borsoni</i>			<i>M. americanum</i>	
Site		Podolia		Batta-Erd (SCHLESIN- GER 1922)	Kuchougan (ALEKSEVA 1965)	Hajnáčka (FEJFAR 1964)	Hidvégh (SCHLESINGER 1922)	Missouri (SCHLESIN- GER 1927)	Michigan (SKEELS 1962)/o
		right molar	left molar						
1	Length	112	113	116	117	121	128	125	120,1
2	Breadth (maximum)	88 ₍₃₎	88 ₍₃₎	87 ₍₃₎	87	96	100	88 ₍₃₎	98,9
3	Breadth (minimum)	74 ₍₁₎	74 ₍₁₎	—	—	985	—	—	—
4	Height (maximum)	47 ₍₃₎	51 ₍₃₎	57 ₍₃₎	55	54	70 ₍₂₎	55	—
5	Breadth of ridge *	65 ₍₃₎	65 ₍₃₎	46 ₍₃₎	—	43 ₍₃₎	—	50 ₍₃₎	—
6	Breadth/length index	0,78	0,77	0,75	0,74	0,79	0,78	0,70	0,82
7	Length/breadth index	1,27	1,28	1,33	1,34	1,39	1,28	1,42	1,22
8	Breadth (max.)/breadth of ridge	1,35	1,35	1,89	—	2,23	—	1,76	—

Notes: * transversal distance of main cusp.

() The numbers in brackets indicate the ridges
on which the breadth was measured.

/o average dimensions of teeth in the American mastodon.

M2 superior

Species		<i>M. praetypicum</i>				<i>M. borsoni</i>				<i>M. americanum</i>			
Site		Podolia (right molar)	Budești (ATHANASIU 1907)	Szabadka	Rákospo- resztűt	Peschana (ALE- KSEEVA 1965)	Hajnáčka (FEJFAR 1964)	Salgata (ATHANASIU 1907)	Velenje (RAKOVEC 1968)	Ohio	Missouri	Michigan (SKEELS 1962)/o	
		(SCHLESIN- GER 1922)				(SCHLESINGER 1922)							
1	Length	117	114	105	116	107	108	120	119	120	125	119	119,9
2	Breadth (max.)	86 ₍₁₎	85	82 ₍₃₎	82 ₍₂₎	83	91,5	90	91 ₍₂₎	94 ₍₃₎	97 ₍₂₎	82	97,3
3	Breadth (min.)	85 ₍₃₎	—	—	—	—	—	—	—	—	—	—	—
4	Height (max.)	47 ₍₂₎	—	—	57 ₍₃₎	—	45	—	52 ₍₃₎	50 ₍₃₎	67 ₍₃₎	58	—
5	Breadth of ridge *	—	—	—	44	—	47	—	—	—	54 ₍₂₎	43	—
6	Breadth/length index	0,73	0,74	0,78	0,71	0,77	0,85	0,75	0,76	0,78	0,78	0,69	0,81
7	Length/breadth index	1,36	1,34	1,28	1,41	1,29	1,13	1,33	1,31	1,27	1,29	1,45	1,23
8	Breadth (max.)/breadth of ridge	—	—	—	1,86	—	1,94	—	—	—	1,79	1,90	—

M3 inferior

Species		<i>M. praetypicum</i>					<i>M. borsoni</i>				<i>M. americanum</i>																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																							
Site		Podolia		Hajnáčka	Szabadka	Batta-Erd	Anastasiewka (ALEKSEVA 1965)	Hajnáčka (FARAR 1964)	Hidvég	Vác	(SCHLESINGER 1922)								Michigan (SKEELS 1962)/o																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																															
		right molar	left molar																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																															

M3 superior

Species	<i>M. praetypicum</i>			<i>M. borsoni</i>			<i>M. americanum</i>					
Site	Podolia (Right molar)	Szabadka	Batta-Erd	Peshana	Reni	Dorus	Velenje (RAKOVEC 1968)	Ohio	Missouri	Michigan (SKEELS 1962)/o		
	(SCHLESINGER 1922)			(ALEKSEVA 1965)			(SCHLESINGER 1922)					
1	Length	154	172	161	—	—	165,5	195	114	174	163	192,1
2	Breadth (max.)	95 ₍₁₎	90 ₍₂₎	88	84	85	99 ₍₂₎	110 ₍₂₎	88	90 ₍₂₎	94 ₍₂₎	105,3
3	Breadth (min.)	—	—	—	—	—	—	—	—	—	—	—
4	Height (max.)	53 ₍₂₎	50 ₍₂₎	—	47	76	53 ₍₁₎	69 ₍₁₎	ca. 45	53 ₍₂₎	—	—
5	Breadth of ridge *	55 ₍₂₎	50 ₍₃₎	—	—	—	—	50 ₍₁₎	—	49 ₍₂₎	—	—
6	Breadth/length index	—	0,58	0,54	0,55	—	0,60	0,56	0,77	0,79	0,58	0,55
7	Length/breadth index	—	1,71	1,85	1,83	—	1,67	1,77	1,29	1,93	1,73	1,83
8	Breadth (max.) /breadth of ridge	1,72	1,80	2,02	—	—	—	2,20	—	1,83	—	—

DUBROVO (1970) did not distinguish these forms into two species. After her all the remains of zygodont mastodons found on the territory of the Soviet Union belong to *Zygodontophodon borsoni*. However, it ought to be mentioned that the molars of the described by her new species *Zygodontophodon gromovae* (from Inner Mongolia) seem to be similar to the molar teeth described in the present paper.

In his study SCHLESINGER (op. cit.) based himself on the materials from different localities of the sometime Austro-Hungarian Monarchy: Szabadka, Batta-Érd, Rákoskeresztút, Szentlőrincz and Ajnácskö (now Hajnáčka, Czechoslovakia). He introduced the name *Mastodon americanus* forma *praetypica* in 1919 (establishing it in 1922) and stated the membership of this form in the evolutionary line of *Mastodon americanus*; in an earlier paper (1917) he, however, described it as *Mastodon* cf. *borsoni*.

OSBORN (1936) quotes SCHLESINGER's materials and refers them all to *Pliomastodon americanus praetypica*.

FEJFAR (1964), in turn, adopts the criteria established by SCHLESINGER (op. cit.) for *Mastodon americanus* forma *praetypica* as the characters typical of the progressive Pleistocene form of *Zygodontophodon borsoni*. With respect to one of the localities mentioned by SCHLESINGER, namely Hajnáčka, he writes (FEJFAR, 1964; p. 64): "All finds of the zygodont form of the mastodon from Hajnáčka belong to the progressive form (of *Mastodon borsoni* — author's note) mentioned by SCHLESINGER under the designation *M. (Mammut) americanus* PENNANT forma *praetypica*. I presume that it is the Pleistocene form *M. borsoni*, which is a direct descendant of the typical Pliocene form."

A comparison of the plaster casts of the molars belonging to the Hajnáčka mastodons, which I received by courtesy of Dr. O. FEJFAR, with the teeth being described in this paper clearly shows the differences between them; and thus the left M_3 , No 4287, Ústředni ústav geologický, Prague, from Hajnáčka (Fig. 2A)

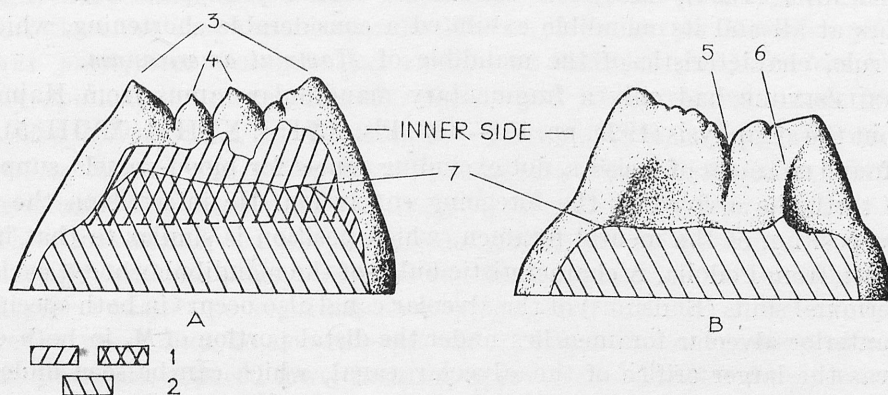


Fig. 2. Posterior view of unworn third ridges of third lower molars. A. *Mastodon borsoni* (left M_3) from Hajnáčka (No 4287, Ústředni ústav geologický, Prague); B. *Mammut praetypicum* (right M_3) from Podolia. 1. cement, 2. cross-section of crown base, 3. main cusps, 4. accessory cusps, 5. median sulcus, 6. separating rim, 7. bottom of syncline. One-half natural size

has much more well-developed accessory cusps, poor separating rims (the characters, according to SCHLESINGER, typical of *Mastodon borsoni*) and cement in the synclines, which features are absent from the teeth used for the present study (Fig. 2B).

In his discussion of the teeth from Velenje in Yugoslavia RAKOVEC (1968, p. 345) writes that their pretrite accessory cusps are only exceptionally small. A layer of cement is also well seen in the synclines of these teeth. The separating rims are well developed and the top part of the ridges is narrow. The median sulcus is distinct and it cuts deep into the tooth. RAKOVEC states further that all the characters mentioned by FEJFAR are typical of the youngest form of *Zygolophodon borsoni*.

Having compared the descriptions and illustrations presented by FEJFAR and RAKOVEC, I am of the opinion that they really coincide and the specimens in question belong to one and the same form. According to me, both FEJFAR and RAKOVEC are right to include it in *Zygolophodon (Mastodon) borsoni*. Nevertheless, I must state that in spite of some resemblances, such as the well-developed separating rim and deep median sulcus, the teeth described in this paper are quite different from those dealt with by the above-mentioned authors, in contradistinction to which they are completely lacking in cement in the synclines and have poorly developed — hardly present — pretrite accessory cusps. Thus, the remains described by me cannot be reckoned even in the youngest form of *Mastodon borsoni*. I think that they belong to a separate form.

The characters of the molars (Fig. 2) of the specimens under description agree in their structural details with the teeth referred to by SCHLESINGER (1922, p. 167) as remains of *Mastodon americanus* forma *praetypica*. The illustrations of materials that SCHLESINGER had at his disposal (1922, Pl. XV Figs. 1—4, Pl. XVI Fig. 2, Pl. XIX Fig. 2) also correspond with the teeth from Podolia.

Some divergencies occur in the structure of the mandible. According to SCHLESINGER (1922), *Mastodon americanus* forma *praetypica* had no lower incisors at all and its mandible exhibited a considerable shortening, which is, as a rule, characteristic of the mandible of *Mammot americanum*.

SCHLESINGER had only a fragmentary mandibular ramus from Hajnáčka, without the symphysis (1922, pp. 101—103, Pls. XVI: 1, XVII: 1, XVIII: 5). Having found no traces of incisors, not excluding canals for blood-vessels supplying these teeth, he arrived at the foregoing conclusion. He inferred on the basis of the position of the mental foramen, which position is similar to that in the specimen from Podolia. A characteristic bulge of the mandibular body, enclosing the terminal sinus (Endsinus) of the alveolar canal also occurs in both specimens. The anterior alveolar foramen lies under the distal portion of M_2 in both cases, whereas the larger orifice of the alveolar canal, which can be seen under the anterior part of M_3 in SCHLESINGER's material, is missing in my specimen. In SCHLESINGER's specimen (op. cit., Pl. XVIII: 5) the posterior part of the symphysis is just near the anterior part of M_2 and in the mandible from Podolia it is ahead of M_2 by its whole length. It may well be that the mandible from Haj-

náčka was by so much shorter than that from Podolia. In spite of these differences it may be admitted that the mandibular fragments being compared show similar anatomical relations and, therefore, I consider them to be remains of the same species. Thus, the assumption that the symphysis of the mandible of *Mammot praetypicum* is elongated and bearing incisors and its comparison with the corresponding part of the mandible of *Mastodon borsoni* show remarkable differences.

The authors who studied the remains of *Mastodon borsoni* (ANTHONY & FRIANT, 1940; BERGOUNIOUX & CROUZEL, 1960; ALEKSEEVA & FIRU, 1962) agree that the mandible of this mastodon was short and had very small, reduced incisors, which in some specimens were lacking at all. According to ALEKSEEVA (1965), *Mastodon borsoni* differs fundamentally from all the other, chronologically older, zygodont mastodons in the structure of the anterior part of the mandible. All the forms of this group of mastodons, contemporary with the hipparion fauna, have an elongate symphysis, whose length is at least equal to the length of the row of molar teeth, but never shorter than it. It may therefore be supposed that *Mammot praetypicum* belonged to this very group of mastodons and thus was even older than *Mastodon borsoni*. Having practically no data concerning the site of finding of the remains under study, I presume, basing myself on the morphological details, that *Mammot praetypicum* is really older than *M. borsoni*, which does not exclude their simultaneous occurrence.

The structure of the anterior part of the mandible best expresses the direction of the evolution of the mastodon, i.e., a gradual shortening of the mandible and, what follows, of the skull. This also leads to a gradual shortening of the lower incisors up to their complete disappearance. This process is quite well traceable in both *Mastodon borsoni* and *M. americanum* (SKEELS, 1962).

The upper incisors of *Mastodon borsoni* described and illustrated, e.g., by JÁNOSSY (1955) and RAKOVEC (1968), are oval in cross-section, almost quite straight and parallel to each other (JÁNOSSY, 1955, pp. 89—90, Fig. 1, Pl. VI: 1). I think therefore that the remains described by JÁNOSSY as *Mastodon aff. americanus praetypicus* SCHLESINGER should be included in *Mastodon borsoni*. In my opinion, the morphological characters of these remains stand closer to *Mastodon borsoni* than to *Mammot praetypicum*. Thus, the upper incisors of *Mastodon borsoni* also differ from those of *Mammot praetypicum*, these last being circular in cross-section, relatively thicker, and with their tips wide apart.

The above-mentioned morphological data support the opinion that *Mastodon borsoni* and *Mammot praetypicum* are two distinct species, that is, that *Mammot praetypicum* cannot be regarded as a progressive form of *Mastodon borsoni*. However, these data do not rule out the fact that *Mammot americanum* (shortened mandible, reduced lower incisors, upper incisors bent strongly upwards), may have derived from *Mammot praetypicum* but it could not, (even partly) have derived from *Serridentinus*, whose members lived in Eurasia and in America from the Middle Miocene to the Middle Pliocene (ALEKSEEVA, 1959; KUBIAK 1968).

On the other hand, it is often assumed nowadays (TOBIEN, 1964) that the evolutionary lines of the Eurasian and American mastodons were parallel, that these animals evolved independently of each other. Now, it is difficult to establish the origin of *Mastodon borsoni* and *Mammot praetypicum* definitively. They probably arose from *Turicius*. This problem, however, needs further close studies.

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STRESZCZENIE

Szczątki opisanego mastodonta obejmują dobrze zachowaną zuchwę z zębami trzonowymi M_2 i M_3 oraz prawym siekaczem I_2 , jak również fragment prawej połowy czaszki z zębami trzonowymi M^2 i częścią M^3 oraz prawym ciosem I^2 . Materiały te są przechowywane w Zakładzie Anatomii Porównawczej Kęrowców Uniwersytetu Jagiellońskiego w Krakowie.

Miejsce znalezienia szczątków nie jest dokładnie znane. Najprawdopodobniej pochodzą one z Podola, z okolic Bałty (балтские отложения, Одесская область).

Analiza materiału wskazuje na przynależność szczątków do gatunku *Mastodon (Mammut) americanus* PENNANT forma *praetypica* SCHLESINGER (synonim *Pliomastodon americanus praetypica* OSBORN). Ze względu na dyskusję wokół szczątków formy *praetypica* i jej przynależności systematycznej z jednej strony, a istnienie wyraźnych cech na badanym materiale, odbiegających zarówno od cech *Mastodon borsoni*, jak i *Mammut americanum* z drugiej strony, autor proponuje określenie wszystkich dotychczas znanych szczątków tego mastodonta nazwą gatunkową *Mammut praetypicum*.

Gatunek ten występował najprawdopodobniej w dolnym i środkowym pliocenie (pont — lewant) na terenie środkowej i wschodniej Europy.

Mammut praetypicum zajmuje według autora pod pewnymi względami miejsce pośrednie pomiędzy *Mastodon borsoni* a *Mammut americanum*; natomiast niektóre cechy wskazują na to, że *Mammut praetypicum* występował czasowo co najmniej równolegle z *Mastodon borsoni*, względnie był od niego starszy. *Mastodon borsoni* i *Mammut praetypicum* pochodzą prawdopodobnie od *Turicius*.

Ze względu na zachowaną znaczną część czaszki oraz całą żuchwę podjęto próbę rekonstrukcji czaszki.

РЕЗЮМЕ

Остатки описываемого мастодонта представлены хорошо сохранившейся челюстью с коренными зубами M_2 и M_3 и правым бивнем I_2 , фрагментом правой половины черепа с коренными зубами M^2 и частью M^3 , а также правым резцом I^2 . Материалы хранятся в Институте сравнительной анатомии позвоночных Ягеллонского университета в Кракове.

Место находки остатков точно не известно. Вероятнее всего, они происходят из районов Подолии в окрестностях г. Балты (балтские отложения, Одесская область, СССР). Анализ материала свидетельствует о принадлежности остатков к виду *Mastodon (Mammut) americanus* PENNANT forma *praetypica* SCHLESINGER (синоним *Pliomastodon americanus praetypica* OSBORN). Принимая во внимание дискуссию вокруг остатков формы *praetypica* и ее систематического положения с одной стороны, а также наличие в исследуемом материале множества признаков, по которым он существенно отличается от *Mastodon borsoni* и *Mammut americanum* с другой стороны, автор предлагает все известные ныне остатки этого мастодонта обозначать видовым названием *Mammut praetypicum*.

Этот вид, вероятно, существовал в нижнем и среднем плиоцене (понт — левант) на территории средней и восточной Европы.

По мнению автора, *Mammut praetypicum* занимает промежуточное положение между *Mastodon borsoni* и *Mammut americanum*; некоторые признаки указывают на то, что на протяжении некоторого времени *Mammut praetypicum* существовал одновременно с *Mastodon borsoni*, или же был древнее. *Mastodon borsoni* и *Mammut praetypicum* вероятнее всего происходят от *Turicius*.

Хорошая сохранность значительной части черепа и целой нижней челюсти обусловила попытку реконструкции черепа описываемого мастодонта.

PLATES

Plate IX

Mammut praealticum. Superior views of: 1. fragment of skull with right tusk, 2. mandible of same specimen. One-tenth natural size

1

2



H. Kubiak

Plate X

Mammut praetypicum. Lateral views of: 3. fragment of skull with right tusk, 4. mandible of same specimen. One-tenth natural size

3

4



H. Kubiak

Plate XI

Mammut praetypicum. Annual growth rings of the upper tusk. 5. proximal part of the tusk.
6. distal part of the same tusk. One-half natural size

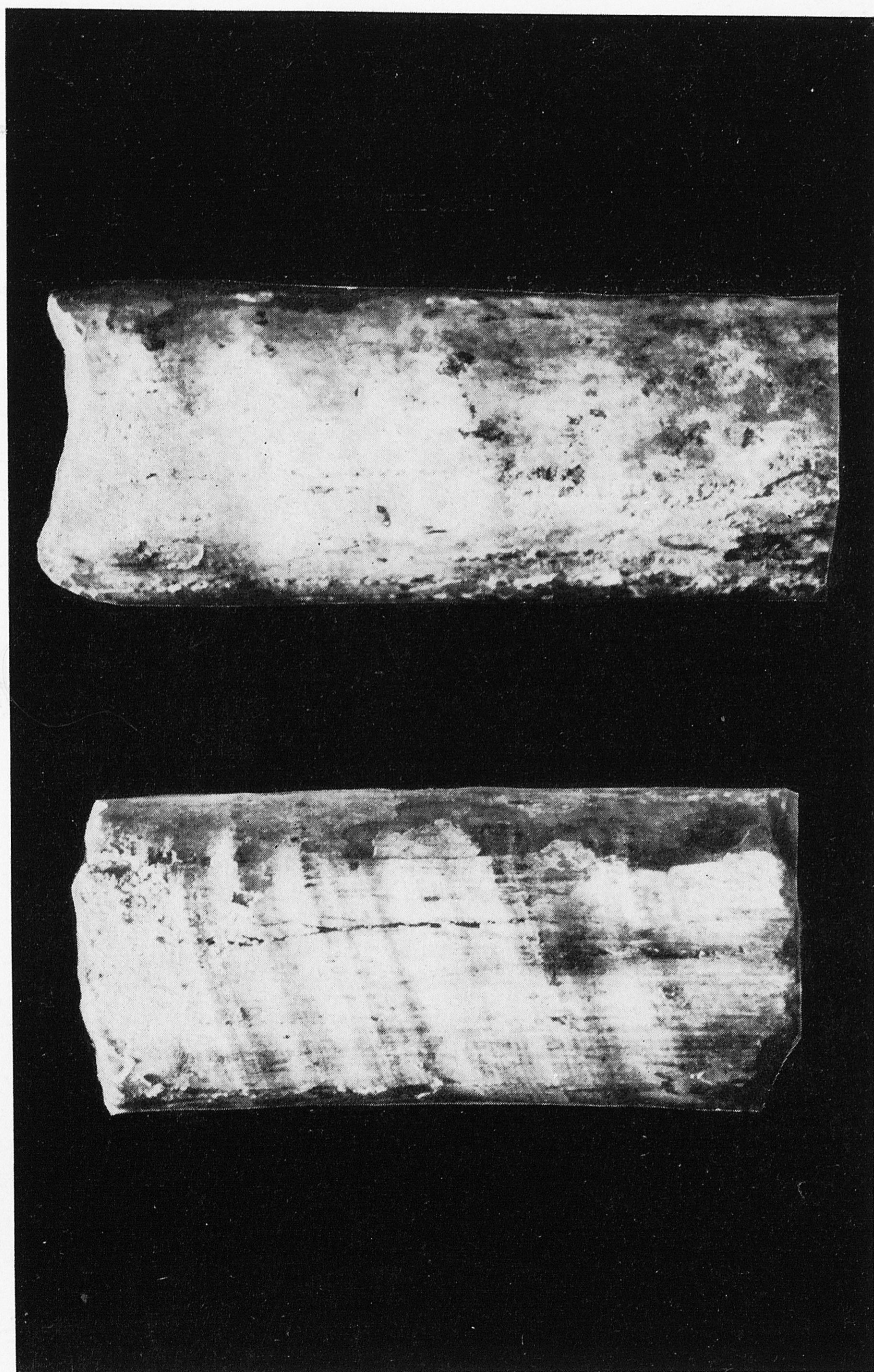


Plate XII

Mammut praetypicum. Crown views of: 7. second and third right upper molars, 8. second and third right lower molars. One-third natural size



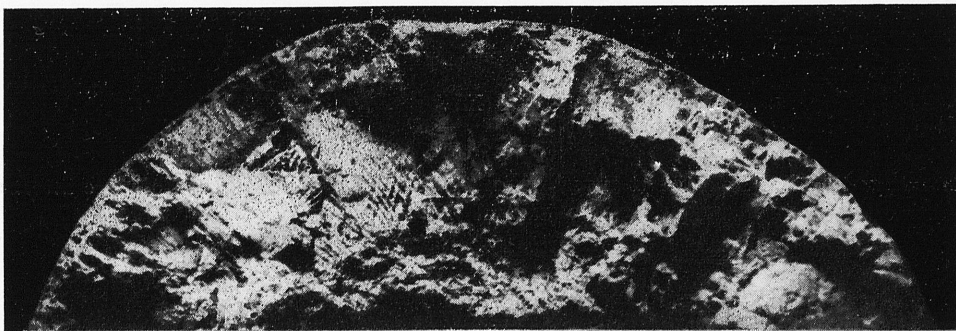
7



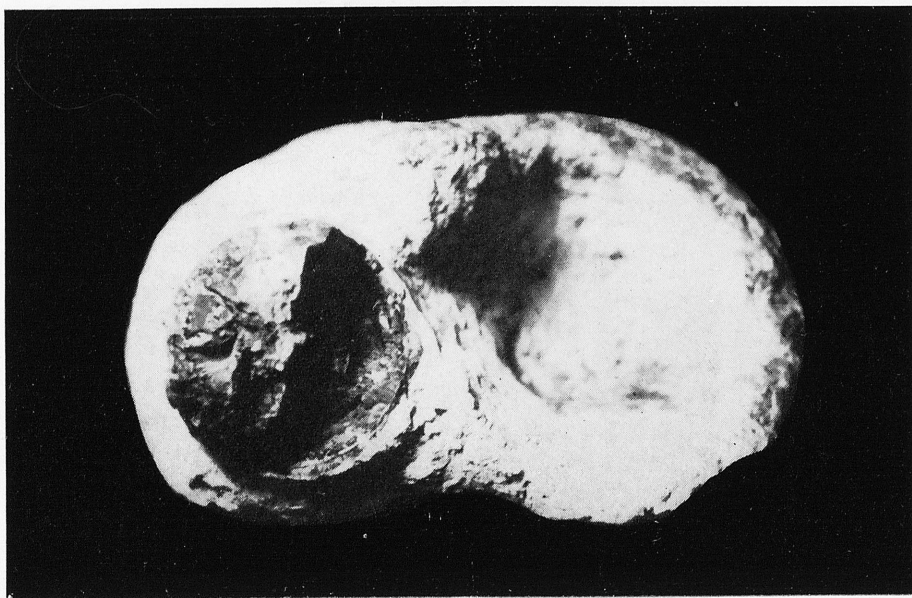
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Plate XIII

Mammut praetypicum. 9. cross-section of an upper tusk showing the inner structure of dentine (tusk-trajectories) in detail. Natural size. 10. Anterior view of mandible with partly preserved right tusk. Natural size



9



10

Plate XIV

Mammot praetypicum. An attempt at restoration of the skull. Lateral view. About one-fifteenth natural size



Plate XV

Mammut praetypicum. An attempt at restoration of the skull. Superior view. About one-fifteenth natural size

