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Abnormal Dental Morphology in the Mammoth *Mammuthus primigenius* Blumenbach, 1799

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Abstract—Several cases of abnormally developed last teeth (M^3/M_3) from the upper and lower jaws of an adult woolly mammoth (*Mammuthus primigenius* Blum.) from the Tomsk Region and several abnormal isolated M^2–M^3 and M_2–M_3 of this species from Eurasia and North America are considered. The dental anomaly in *M. primigenius* from the Tomsk Region consists of the unusual shape and position of plates in the right M^3 and the distal parts of M_3. This anomaly is apparently associated with retardation of the replacement of the previous generation tooth (M^2) and defective formation of M^3 at the stage of mineralization. Cases of dental anomalies in *M. primigenius* are reviewed.

Key words: Woolly mammoth, *Mammuthus primigenius*, dental development, dental anomalies.

INTRODUCTION

A skull fragment and a complete lower jaw of the same adult mammoth (*Mammuthus primigenius* Blum.) have been housed at the Paleontological Museum of Tomsk State University (PM TSU) since the end of the 19th century: PM TSU, nos. 1/36 and 1/57, respectively (Pl. 6, figs. 1, 2). The functioning generation of molars includes M^3 and M_3. Right M^3 and both M_3 display structural anomalies. Anomalies in the dental structure of mammoths and extant elephants and the factors responsible for their occurrence remain insufficiently studied (*Colyer's Variations…*, 1994). The present study considers a number of explanations, which are conventionally classified into biotic and abiotic (including unfavorable environmental impacts).

The specimens examined are assigned to the same individual because of the presence in the skull and the lower jaw of the same functioning tooth generation (M^3/M_3) and the preserved bases of two or three plates and signs of posterior roots of teeth of the previous generation (M^2/M_2). The proportional distinctions of the occlusal surface levels in the upper and lower functioning teeth also indicate that the skull fragment and the lower jaw belong to the same individual. Thus, when superposed, the height of the teeth and the pattern of their occlusal surfaces are complimentary. The coloration of the surface layer and the degree of preservation of bone, enamel, and cement of teeth in the skull and the mandible also do not differ.

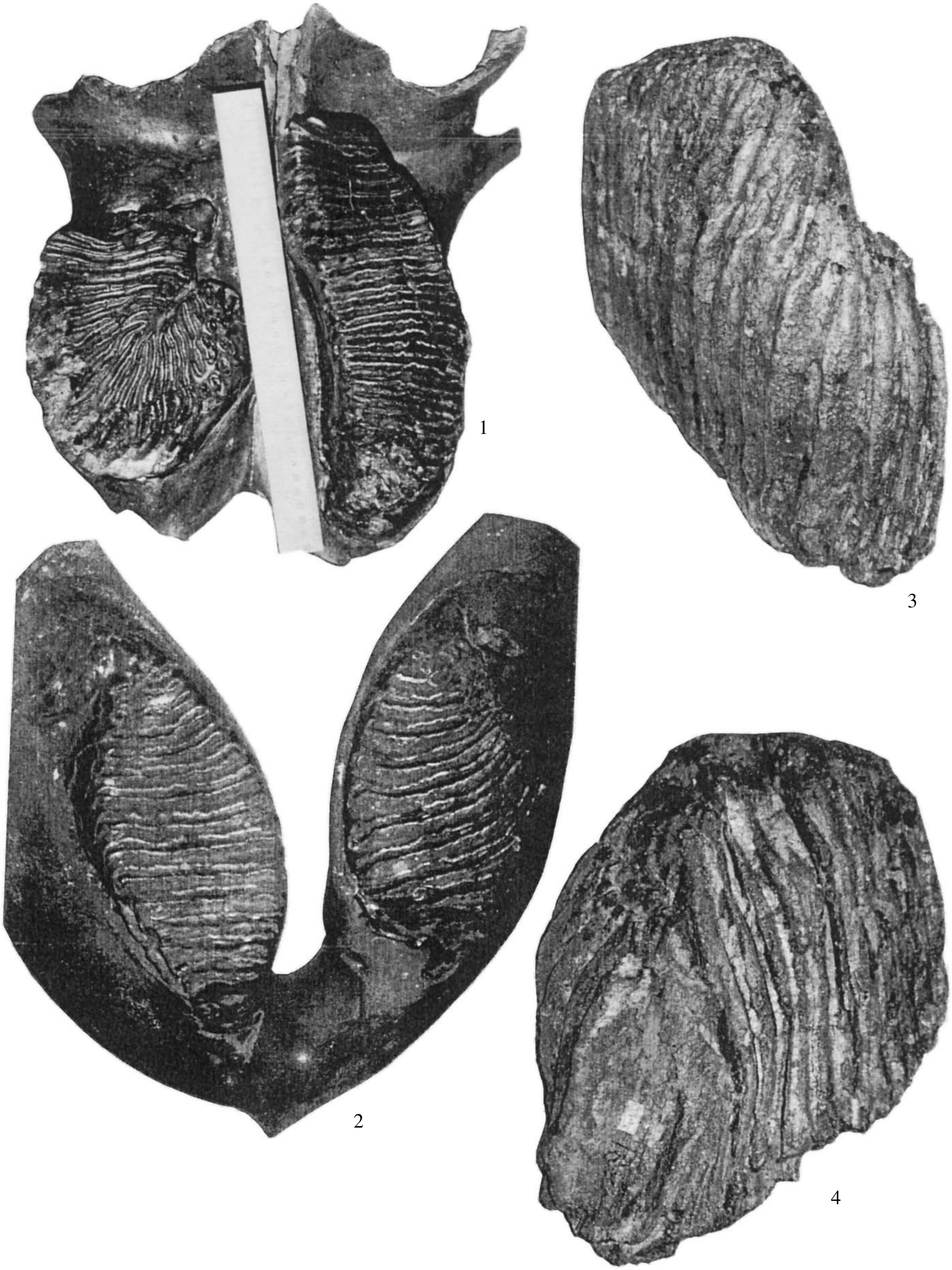
The structural anomaly of M^3 is expressed in the loop-like curvature of the crown, so that the mesial and distal portions are turned medially (Pl. 6, fig. 1). At the same time, the left and right upper teeth strongly differ in the degree of wear (crown height) and the shape of the occlusal surface. In the lower jaw, either M_3 is abnormal in structure, with the distal part of the crown turned laterally (Pl. 6, fig. 2). In addition, right and left M_3 differ in the shape and elevation of the occlusal surface.

A similar anomaly (the lateral turn) is observed in the distal part of the crown of isolated left M^3 of *M. primigenius* (specimen PM TSU, no. 1/116) from unknown locality (Pl. 6, figs. 3, 4).

To date, few structural pathologies of mammoth teeth have been described. All of them are recorded in isolated teeth. The specimen from PM TSU is the most completely preserved mammoth dentition with anomalies in the upper and lower teeth (Kuz'mina and Praslov, 1992; Adam, 1994; Foronova, 1999; Burns *et al.*, 2003).

The specimens described come from the Tomsk Region and were most likely found near the city of Tomsk. The material was probably collected in the 1880s by G.V. Ossovskii during his hydrogeological survey in the territory of Tomsk. Most likely, both the skull and the lower jaw were found in alluvial deposits of the Tom River (Shpansky, 2003). Before the study of the material from the Tomsk Region, no cases of simultaneously occurring and differently expressed developmental anomalies of mammoth teeth were ever reported. In addition, the example studied shows that, in the case of an anomaly in at least a single functioning tooth, the compensatory formation of the normal occlu-

Plate 6



sion is acquired at the expense of normal teeth, by their more intense wear.

The material described allows one to generalize the already available data on anomalies of tooth development in *Mammuthus primigenius* and to classify these cases by the factors causing developmental deviations.

The tooth measurements, the plate number in worn crowns, and the degree of wear were estimated by the techniques proposed by Sher and Garutt (1985) and Garutt and Foronova (1976).

KNOWN ANOMALIES OF TOOTH DEVELOPMENT IN *MAMMUTHUS PRIMIGENIUS*

Representatives of the family Elephantidae normally have the constituent dental plates perpendicular to the long axis of the crown (generations DP_3 to M^3). Tooth replacement proceeds in the horizontal direction. A replacement tooth forms a pressure area at the distal end of the preceding crown. This area is absent only at the distal end of DP_2 and M^3. After the formation of the lower molars of the last generation (M_3), the bone septum completely closes the mandibular canal (*canalis mandibularis*).

In the case of normal development, the dental plates are curved because of lateral (in the upper jaw) or medial (in the lower jaw) curvatures of the entire crown, which are associated with the shape of the upper or lower alveoli (Garutt, 1977). In the extremely bent crown, its convex side forms one or, rarely, two or three intercalary plates that compensate on the occlusal surface for the excessive crown curvature (Maglio, 1973). No other additional structures are present in a normal crown of Elephantidae. The occurrence of additional teeth in extant and extinct elephants is confirmed only for the first generation teeth (DP_2) in *Loxodonta africana* Blum. (Morrison-Scott, 1938) and *Archidiskodon gromovi* Garutt et Alexeeva, 1964 (Maschenko, 2002).

The majority of dental anomalies in *M. primigenius* were reported for the teeth of the last generations. The anomalies are usually manifested in a change of the plates' orientation in relation to the longitudinal axis of the crown; in a turn of the crown with reference to the longitudinal axis of the horizontal ramus of the lower jaw, or in additional subdivision of a single tooth crown into incompletely separated parts. There is a record of the fusion of two teeth of sequential generations, which, however, did not affect the plate morphology of both teeth (Burns *et al.*, 2003).

A complete turn of plates relative to the longitudinal axis of the normal tooth crown was described for a lower jaw with a functioning tooth generation (probably, M_2), from the Late Paleolithic site Kostenki 1 (Voronezh Region, radiocarbon age of 22300 ± 200 years) (Kuz'mina and Praslov, 1992). The right tooth is rotated by 90° relative to the longitudinal axis of the mandible. The plates are not bent. The mesial end of the crown is directed perpendicular to the lateral margin of the horizontal ramus. The right ramus of the mandible is thicker than the left one. The occlusal surface of the rotated tooth is 25 mm higher than in the normally oriented tooth.

A fusion of two teeth belonging to successive generations was recorded in a specimen of *M. primigenius* found near Edmonton (Alberta, Canada). These teeth were tentatively determined as M^3–M^4 (Burns *et al.*, 2003; p. 79, text-fig. 1). This specimen was considered to have excessive content of hydroxyapatite [$Ca_5(PO_4)_3(OH)$] on the surface of the roots and the crown. This hypermineralization was probably caused by abnormal development at the early stage of the formation of the distal part of the crown of preceding tooth and the mesial crown part of the replacement tooth. The replacement tooth embraces laterally and from above the tooth of the earlier generation. Plates of the two teeth are not fused with each other, the fusion involves the surface layer only.

In this case, the deformation of the replacement tooth suggests a delayed loss of teeth of one or two previous generations (M^1–M^2), which reduced the space in the alveolus during the growth and development of large teeth of two last generations. The researchers who described the fused teeth proposed that this morphological anomaly was caused by a genetic disorder, the mechanism for the appearance of which in the evolution of elephants was considered by Roth (1989). According to D. Burns and his colleagues, the anterior tooth has 20 plates, and three plates of the anterior talon were lost as a result of wear of the anterior portion of the molar.

A reexamination of this specimen with the use of the technique proposed by Garutt and Sher (1985) led to the conclusion that the anterior talon of the previous tooth was not lost because of wear. This is evident from the presence of the base of the anterior root, which is situated beneath three or four anterior plates of the crown. One of the authors of the present articles (Maschenko) recognized the presence of only 19 plates in this crown. Therefore, the crown of the anterior

Explanation of Plate 6

All specimens belong to *Mammuthus primigenius* Blumenbach, 1799 and come from the Upper Pleistocene of the suburbs of Tomsk, Tomsk Region, Russia.

Fig. 1. Specimen PM TSU, no. 1/36, skull fragment, palatal view, functioning generation of M^3, ×0.32.

Fig. 2. Specimen PM TSU, no. 1/57, lower jaw, occlusal view, functioning generation of M_3, ×0.35.

Figs. 3 and 4. Specimen PM TSU, no. 1/116, isolated left M^3: (3) labial view, ×0.32; (4) distal view, ×0.35.

molar of the two fused molars has a complete number of plates and can be interpreted as a tooth of the fifth generation, i.e., M^2. Consequently, the next molar represents the last (sixth) generation, M^3, rather than an extra molar (M^4). This agrees with the absence of data on the presence in elephants of additional molars in addition to three normal generations of M^1–M^3.

Adam (1994, p. 5, text-figs. 2, 3) described an abnormal mammoth mandible from the Otterstadt locality (Germany). The specimen shows a changed orientation of the occlusal surface of M_2 and deformation of the teeth in the generation M_3 resulting from a delayed molar replacement. The delayed replacement of M_2 by M_3 resulted in a shift of the occlusal surface of M_3 relative to that of M_2. The height of the mesial part of the occlusal surface of M_3 is about 9–10 cm lower than the occlusal surface of M_2. Moreover, this resulted in a deviation from the horizontal pattern of molar replacement, since M_2 was displaced upwards and its mesial side occupied a substantially higher position than the distal side.

Due to the delayed replacement, the tooth of the last generation (M_3) erupted from the alveolus and forms a pressure platform at the lateral surface of M_2 rather than at the distal side. The mesial end of M_3 is located at the fifth or sixth distal plate of M_2. A lack of space inside the alveolus caused the deformation of M_3, so that the crown width became almost equal to its length. The anterior five or six plates of M_3 are shorter and turned in a fan-shaped pattern in relation to the long axis of the crown.

A similar delayed replacement of M_2 by M_3 is rather frequently observed in *Elephas maximus* L. in zoo conditions (specimen PIN, no. 342). In this case, the altered orientation of the occlusal surface and the deformation of the last generation molar are caused by the higher rate of molar formation relative to the wear rate, as a result of the different (less abrasive) diet available to captive animals.

It is hard to infer the same cause for the delayed tooth replacement in the specimen described by Adam (1994) as for the Asiatic elephant. However, the morphological changes in the teeth of the last two generations in the Asiatic elephant and mammoth are almost identical.

The next type of abnormal development of the last generation teeth was only found in the genus *Mammuthus*. Foronova (1999, pl. 10, fig. A) reports it for the left M_3 or M_2 of *Mammuthus trogontherii* Pohlig, 1885 from the Mokhovo locality (Kuznetsk Basin, Russia; specimen held at the Geological Institute of the Siberian Branch of the Russian Academy of Science, no. 6250). The structural anomaly consists of the formation of a longitudinal groove on the occlusal surface, closer to the distal edge of the crown than to the proximal edge. The distal end of the crown (composed of four plates) is positioned at an angle of 55° to its longitudinal axis. The crown consists of 15 plates, the anterior 11 of which are clearly worn. On the occlusal surface, starting from the ninth plate, the lateral segment of the plates becomes isolated and turns distally relative to the longitudinal axis of the crown.

This type of abnormal crown structure essentially differs from all the above mentioned types because of the drastic change in the morphology of the crown plates themselves rather than changes in their position.

An unusual abnormal structure is observed in the left M_2 of *M. primigenius*, specimen PM TSU, no. 1/338 (Pl. 7, fig. 1). The molar was found at a depth of about 12 m in the alluvial deposits of the right bank of the Tom River near the town of Seversk in 1995 (Shpansky, 2003). The anterior root of the tooth is completely formed, its pulp canal is probably open. The posterior roots are not mineralized. Wear affects seven anterior plates. The total number of plates is 20. Eight posterior plates are incompletely covered with cement, which indicates that the tooth is in the state of formation. The occlusal surface is divided into two parts, which are positioned along the longitudinal axis of the crown at an angle of about 150°) to each other. This can be caused by the occlusal surface of the tooth becoming more horizontal in the course of its eruption (Pl. 7, fig. 1). The larger part of its occlusal surface has two distinct longitudinal depressions, which are located between the middle and lateral columns of plates.

The origin of these longitudinal depressions is not clear. The specimen considered does not differ from the cases described above, i.e., the case in question, delayed tooth replacement, and abnormal formation of plates are not caused by an abrasive effect of food on molars during grinding.

The known examples of anomalies in the structure and development of teeth of *Mammuthus* show that the most frequent and clearly expressed cause of their occurrence are probably the delayed replacement of M^2 by M^3 and M_2 by M_3, because they have the longest period of formation. There are only two cases (Foronova, 1999) that allow an assumption of more profound changes in morphology, involving the formation of plates themselves and irreducible to mechanical deformations of molars during their formation. In elephants, such morphogenetic disorders result in various modifications in the shape of plates and are described for *E. maximus* in cases of teeth affected directly inside the jaw at the stage of their formation (*Colyer's Variations…*, 1994).

DESCRIPTION

S k u l l f r a g m e n t, specimen PM TSU, no. 1/36. This is a skull fragment with completely preserved maxillae, the bases of alveoli of permanent tusks, choanae, and the base of the right zygomatic process of the maxilla (Pl. 6, fig. 1; Pl. 7, fig. 2). The distance from the choanae to the anterior margin of the left molar is 234 mm, the maximal distance between the lateral sides of crowns of M^3 is 289 mm. The minimal distance

Plate 7

Explanation of Plate 7

All specimens belong to *Mammuthus primigenius* Blumenbach, 1799 and come from the Upper Pleistocene of the Tomsk Region, Russia.

Fig. 1. Specimen PM TSU, no. 1/338, isolated left M_2, distal view, ×0.5; Tomsk Region, town of Seversk, right bank of the Tom River.

Fig. 2. Specimen PM TSU, no. 1/36, skull fragment, lateral view, functioning generation of M^3, ×0.2; vicinity of Tomsk.

Fig. 3. Specimen PM TSU, no. 1/57, lower jaw, lateral view, functioning generation of M_3, ×0.086; vicinity of Tomsk.

between the medial sides of crowns of M^3, 33 mm. The diameter of alveoli of permanent tusks is approximately 152 mm. The alveolus of the left M^3 (106 mm) is approximately 1.5 times narrower than the alveolus of abnormal right, M^3 (148 mm). A root of the previous generation molar is preserved anteromedial to the left M^3, and a depression containing a fragment of the distal root is observed on the lateral side. No remains of the previous generation molar are present in front of the left M^3. The occlusal surface of the right tooth is approximately 40 mm higher than that of the left molar (in natural position).

The left M^3 retains 26 plates. Twenty two of them are affected by wear. Three anterior plates are heavily worn, almost to their bases. Three complete plates are located above the anterior root of M^3. The crown is 260 mm long and 106 mm wide; the plate frequency (per 10 cm) is 9. The plates are 10–12 mm long and 95 mm wide. The enamel is 1.5 mm thick. Plates are oriented in the way typical for the family Elephantidae, i.e., perpendicular to the longitudinal axis of the crown. The mesial margin of the crown is elevated above the alveolus, as in the wear pattern of M_2 in the mammoth mandible from the Otterstadt locality, Germany (Adam, 1994, p. 5, text-fig. 3).

The right M^3 preserves 19 plates. All plates are affected by wear. The tooth length is 156 mm. The maximal width of the curved crown is 152 mm. The crown length along the lateral edge from the mesial to distal crown margins is 395 mm. The enamel is 1.7 mm thick. No other standard measurements are applicable to this abnormal tooth.

Plates of the anterior part of M^3 (first to sixth) are arranged normally, i.e., perpendicular to the long axis of the crown. From the seventh to the last, the plates are located in fan-shaped pattern, which results in a uniform curvature of the crown, with its internal distal end closely pressed against its internal mesial end. On the internal side of the crown, the spaces between the plates are very short or absent (plates closely adjoin each other). These spaces gradually increase from the internal side of the crown to the external side, where they achieve the maximum width.

The curvature of the crown of M^3 and its base is followed by the curvature of roots.

L o w e r j a w, specimen PM TSU, no. 1/57, complete mandible (Pl. 6, fig. 2; Pl. 7, fig. 3). The jaw dimensions and alveolar diameter of permanent tusks indicate that the skull fragment described and the lower jaw belong to a large male between 45 and 50 years of age, as judged by the development of teeth and their wear stage.

The size of this animal, estimated by the probable proportion of the mandible to the long limb bones, exceeded the mean for *M. primigenius* (Garutt and Tikhonov, 2001; Maschenko, 2002).

The mandibular canal is closed by a bone septum. Each lower jaw ramus has two mental foramina. The extra excrescences of the surface (compact) layer in the shape of roughnesses and expansions are present at the base of the external side of the right horizontal ramus near the attachment of the masseteric aponeurosis. The anterior margin of the ascending ramus is vertical, while the mental process is short.

The occlusal surface of the right M_3 is approximately 45 mm higher than that of the left one, and the right M_3 is positioned more medially compared with its left counterpart. The length of the horizontal ramus is 437 mm, the depth of the lower jaw is 435 mm. The maximal width of the lower jaw is 560 mm. The length of the ascending ramus is 295 mm. The distance between the external edges of the articular heads of the mandible is 470 mm. The length/width of the head of the mandible is 78/75 mm. The thickness/height of the horizontal ramus is 178/154 mm. The thickness and height of the right and left horizontal rami differ slightly. The distance between the anterior/posterior ends of alveoli of functioning teeth is 51/210 mm. The length of the interalveolar crest is 174 mm. The thickness/depth of the symphysis is 75/84 mm. The divergence angle of the mandibular rami is 96°.

The distal end of the right crown (starting from the 17th plate) is laterally curved at an angle of 45° relative to the longitudinal axis of the horizontal ramus (Pl. 6, fig. 2). The right molar has a distinct contraction behind the last worn plate, which is followed by the laterally curved part of the crown. There are 23 visible plates (two or three posterior plates are probably inside the alveolus). The preserved anterior root indicates that only one anterior plate is obliterated by wear. In this case, the number of plates in this crown could have been 24.

The length of the occlusal surface of the right M_3 is 228 mm, 15 plates are affected by the wear. The overall crown length is 242 mm. The maximal width of the crown is 110 mm. The plate frequency per 10 cm is 7.5. The plate is 15 mm long and 104 mm wide; the spaced between plates are 4–6 mm wide. The enamel is approximately 1.6 mm thick.

The left crown is more heavily worn than the right one, so that the anterior root is already absent, and only its alveolus is preserved. The occlusal surface is concave in the central part and much wider than that of the right tooth. The crown of the left M_2 is similar to that of the right M^2. Its distal part is curved and the distal end of the crown is directed anteriorly (Pl. 6, fig. 1). Six or seven plates of the distal, curved part of M_2 are separated from the main part of the crown by marked contraction, as in the right tooth. The total number of preserved plates in the left M_2 is 17. Eleven plates are affected by wear. The length of the occlusal surface is 187 mm. The width of plates notably decreases in mesiodistal direction. The maximal length of the crown is approximately 230 mm, the maximal width of the crown is 110 mm. The enamel is approximately 1.4 mm thick.

I s o l a t e d l e f t M^3, specimen PM TSU, no. 1/116. The molar is moderately worn, with 16 plates preserved. Three or four anterior plates are completely worn, while two or three posterior plates are broken off. Seven plates are affected by wear. The last five plates are curved laterally, with the last preserved plate being parallel to the longitudinal axis of the crown (Pl. 7, figs. 2, 3). As a result of the crown curvature, the lateral edges of the last five plates are tightly pressed to each other, whereas the medial edges are arranged in the fan-shaped manner. The length of the preserved part of the crown is 215 mm, the maximal crown width is 90 mm. The number of plates per 10 cm is 8. The plates are 13 mm long, the enamel is approximately 2 mm thick. The structural anomaly of the crown of this specimen strongly resembles that of the teeth of the mandible (PM TSU, no. 1/57). Likewise, it is probably associated with the delayed eruption of the tooth of the previous generation.

The tooth anomalies described are most likely caused by a delay in the replacement of the preceding teeth (M^1/M_1 and M^2/M_2), which results in a lack of space inside alveoli during the teeth formation and, hence, causes deformation of molars of the subsequent generations.

This is the first observation that the delayed eruption and replacement of last generation teeth in mammoth produce synchronous dental anomalies in the lower and upper jaws that cause compensatory changes in molar morphology in order to provide normal food mastication.

DISCUSSION AND CONCLUSIONS

The structural dental anomalies considered using the examples of *M. primigenius* and one representative of *M. trogontherii* show that the delayed tooth eruption, which produced these anomalies, appeared in different populations (geographically remote from each other) and were most likely caused by distinctions of individual physiology. So far there is no evidence of hereditary factors in the development of these anomalies.

It is possible to assume that the anomalies described were not lethal for mammoths. They have a prolonged development from the beginning of the mineralization of the affected teeth till the end of their formation and partial wear. However, judging from compensatory changes in abnormal molars, the pathological changes did complicate food processing.

It is probable that the other causes of dental anomalies, such as infectious disease, traumatic injuries, or a combination of these reasons were very rare or absent from the material described; however, they may possibly encountered when studying new material in future. Traumatic changes of dental structure that occur at early stages of the molar formation (during the mineralization of plates) have been described in the extant Asiatic elephant (*Colyer's Variations…*, 1994). All anomalies addressed in this study do not concern the earliest stage of tooth development, the stage of embryonic odontogeny.

The changes observed in the material described here are mainly associated with the mechanical stress of the crown plates during the mineralization stage and with the growth of teeth under conditions of deficient space inside alveoli. All described dental pathologies occur in the last and penultimate teeth generations (M^2–M^3) and are not observed in teeth of the generations DP_2–DP_4. Thus, it is possible to conclude that the abnormal pattern studied is characteristic of the longest formed and longest functioning teeth of individual mammoths. It is noteworthy that the delayed replacement of teeth also occurs in the generations of DP_2–DP_4 (Maschenko, 2002). However, this seems not to result in significant morphological changes in subsequent generations of teeth.

Previously, there were no data that an anomalous structure of a functioning tooth induces compensatory changes in other functioning teeth of the same generation. The study of the mandible and the skull from Tomsk and the review of other cases of abnormal dental development in mammoths allow the following conclusions to be drawn. First, anomalies of the tooth structure may occur simultaneously in the upper and lower jaws, and, second, the abnormal structure of even a single molar of the four simultaneously functioning teeth can cause the compensatory modification of the shape and position of occlusal surfaces in other teeth.

It is worth noting that dental pathologies are most probably not linked to a deterioration of the environment of the species *M. primigenius* during the Late Pleistocene. There are no regular occurrences of abnormal teeth structure in the latest known populations of this species. Known cases of dental injuries incurred during the mammoths' lifetimes are usually connected to normal physiological processes. This type of modification is exemplified by the dissolution of cement on lateral sides of the tooth crown in *M. primigenius*. This is manifested in narrow longitudinal strips located one above the other (which are not abnormal in terms of crown development), as is observed in mammoths from the Late Paleolithic site of Krakow-Spadista (Poland) and Vogelhert Cave (Germany) (Niven and Wojtal, 2003). This pattern is associated with bacterial activity in the mouth.

The zones of secondary dissolution of cement on lateral sides of teeth are only observed in the teeth at the latest stages of functioning. These are generations DP_4–M^1 when not less than 50% of the crown are already abraded and the roots are resorbed. These structures are caused by the secondary biochemical dissolution of the cement at the contact of soft tissues of the gum with the surface layer of cement. As a tooth gradually comes out of the alveolus, the contact boundary is displaced downwards, thus forming the next stripe of the secondary dissolution that is located lower and distally compared to the previous one. A crown can bear from one up to three such stripes.

These dental defects are caused by physiological processes connected with the termination of the active alimentation of a tooth and the reduction of the pulp canal. During this period, the dissolution of cement is not compensated by its formation, and the active alimentation of the tooth is suppressed or terminated. These changes are caused by processes that accompany normal replacement of teeth rather than by unfavorable environmental conditions at the end of the Pleistocene, as was assumed by Niven and Vojtal (2003).

Dental anomalies of the mammoth are relatively rare, judging by their infrequent occurrence in samples from localities throughout Eurasia. Most likely, these pathologies are not geologically synchronous and appeared in different individuals independently of general evolutionary processes in the mammoth lineage. Therefore, they cannot be used as indicators of environmental hostility for mammoths during the Late Pleistocene of Eurasia.

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