Russian J. Theriol. 8(1): 29–36

Unusual tooth pathology in mammoth (*Mammuthus primigenius*) from Yakutia

Irina V. Kirillova

ABSTRACT. Five pathologically modified last generation lower teeth of the wooly mammoth *Mammuthus primigenius* from Alazeya River basin (Yakutia) and Maly Anyui River basin (Chukotka) are studied. The described aberrations represent variants of the same pathology of tooth germ. The studied several tens of last molars of Yakutian mammoths show three main types of deviations appeared during tooth formation, during formation of tooth elements (plates, external cement), and in the process of functioning.

KEY WORDS: Wooly mammoth, tooth pathology, Late Pleistocene, Yakutia, Russia.

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Необычная патология зубов мамонта (*Mammuthus primigenius*) из Якутии

И.В. Кириллова

РЕЗЮМЕ. Описано пять патологически измененных нижних зубов последней смены мамонта (*Mammuthus primigenius*) из долин рек Алазея (Якутия) и Малый Анюй (Чукотка). Показано, что они представляют собой варианты развития одного типа деформации зуба, возникшей на ранней стадии его формирования (до прорезания). Изучение выборки в нескольких десятков М3 мамонта из Якутии с различными отклонениями от нормы позволило объединить последние в три основные группы, возникшие при формировании зуба, при формировании отдельных элементов (пластин, наружного цемента) и при функционировании (стирании) зубов.

КЛЮЧЕВЫЕ СЛОВА: Шерстистый мамонт, зубная патология, поздний плейстоцен, Якутия, Россия.

Introduction

Due to abundant well preserved remains collected from permafrost regions, the wooly mammoth appears to be one of the most studied extinct species. Along with studies of morphology and functioning of dentition, researchers pay attention to deviations and their causes. The described dental pathologies include cases of retarded tooth change, unusual position in a jaw, atypical wear patterns (Vereshchagin, 1960; Garutt, 1977; Niven & Wojtal, 2002; Maschenko & Shpansky, 2005; Maschenko *et al*., 2008). Some new cases of pathological development will be considered below.

Mammoth dentition pathologies are often connected with specific features of individual development. They also provide interest as possibly indicative of organism's reaction to external factors. Several researchers consider that pathologies observed in the mammoth faunal complex representatives are due to the influence of the environment (Musil, 1968; Garutt, 1990; Niven & Wojtal, 2003).

Common occurrence of significant number of aberrant specimens in any organism, modern or extinct, suggests regularity in their emergence. The time of flourishing, decline and total extinction of the mammoth fauna is precisely dated by radiocarbon method. Stages of maximum plant productivity and its decline, as well as the landscapes of this time are also well known (Ukraintseva, 1991; Sulerzhitsky, 1995; Velichko & Zelikson, 2001). The frequent occurrence of aberrant mammoth teeth may be indicative of a change in conditions related to certain developmental changes in the Late Pleistocene environments. This study is dedicated to unusual deviations in the structure of mammoth last generation teeth.

Materials and methods

The materials described in the paper come from the North-East of Russia, mainly from Yakutia, and belong to the Collection of the Ice Age Museum, Moscow, Russia.

While studying an anomalous last generation tooth of a mammoth from Yakutia, about two hundred last generation teeth were examined in search for an analogy. Four of these exhibited well distinguished similar traits; several more had somewhat less expressed features. The set thus composed comprised five teeth, four from the Alazeya basin (Yakutia) and one from the Maly Anyui River (Chukotka). All these belonged to animals with the individual age between 35 and 45 (50) years, as determined by comparison with modern elephants. The particular locations of these specimens are unknown but they came from ice-rich silts of the Edoma Formation widespread in the arctic areas of Eastern Siberia. This provenance indicates the Late Pleistocene age, however, without further details.

A well preserved undamaged last generation tooth F-1940, similar in size, place in dentition and stage of wear and collected in the same area as the pathological teeth was selected as a reference ("normal") specimen. Materials on modern elephants from the collection of the Zoological Museum of Moscow State University were used for comparison. Teeth from the Ice Age Museum collection are marked with the letter "F" preceding the number. The letter "S" marks specimens from the collection of the MSU Zoological Museum.

The study revealed several dozens of last generation teeth with various deviations from the "norm". These were subdivided into three groups. In descriptions, commonly accepted terms were used, namely: *"norm"* means an established measure, a mean value of something; *"anomaly"* means any deviation from the normal structure; *"pathology"* means a deviation usually negative in relation to functioning (of a physiological system, tissue or organ); *"aberration"* means a deviation without an expressed negative impact on functioning.

Determination of generation and position of teeth followed standard methods (Dubrovo, 1960; Gromova, 1965; Garutt & Foronova, 1976).

Description of material

Specimen 1. A mammoth right lower tooth (F-2366) is nearly complete and well preserved. It was collected in the vicinity of Andriushkino village (Yakutia, middle reaches of the Alazeya River). Missing pressure surface, narrowing in the rear part, considerable lateral curvature, overall dimensions and other characteristics (see Tab. 1) suggest that this is the last (sixth) generation tooth. This specimen has a "satellite" tooth composed of four plates. It is fused to the buccal side in the most concave part of the tooth at the level of the 9–11th plates at the crown basis and 8–12th plates at the crown top. Plates are counted from the posterior part of the tooth.

The specimen looks like two fused teeth, or a tooth with a lateral "branch" (Fig. 1A–C). Two lower plates of the "satellite" are parallel to the buccal side of the main tooth, whereas two upper plates occur at the angle of 60° relatively the main tooth. The plates of the "satellite" adjoin closer to each other at the apex due to thinner interplate cement layers in this part in comparison with the basal part where the layers are thicker. The apex of the "satellite" is 1 cm lower the masticatory surface of the main tooth and nearly completely devoid of cement.

In the rear part, plates are more separated farther than in the "normal" tooth; they are slightly displaced relative to the tooth axis and to each other in the outward direction. The base width of the main tooth is considerably larger than that of a "normal" one (Tab. 1), as well seen in the root side (Fig. 1C). Plates of the main tooth are curved at the base, whereas normally they are straight and sit in an upward position (Fig. 1C). The external cement jointly covers both the main and "satellite" teeth.

The masticatory surface of the main tooth is formed normally. The apices of several plates of the "satellite" are slightly damaged.

Specimen 2. A fragment of mammoth right lower tooth (F-1871) is well preserved. Collected in the valley of the Maly Anyui River (right tributary of Kolyma

Table 1. Characters of Yakutian mammoths lower teeth of the sixth generation.

No.	Character	F-2366 complete	F-1871 fragment	F-1950 complete	F-1957 complete	F-1953 complete	F-1940 complete "reference"
1	Number of plates	21 in the main tooth and 4 in the "satellite"	(17)	21 in the main tooth and 2–4 in the "satellites"	19 in the main tooth and 2–4 in the "satellites"	26	26–27
2	Number of worn plates	16	(11)	all	all	17	18–19
3	Number of plates per10 cm	6.5	10	11	11	8	8
4	Tooth length at the crown base, mm	ca. 310	-	253	254	277*	ca. 300
5	Tooth width in the middle part at the base, mm	74	65	61	61	69	58

* The tooth is appears longer if the length of the curved part is added.

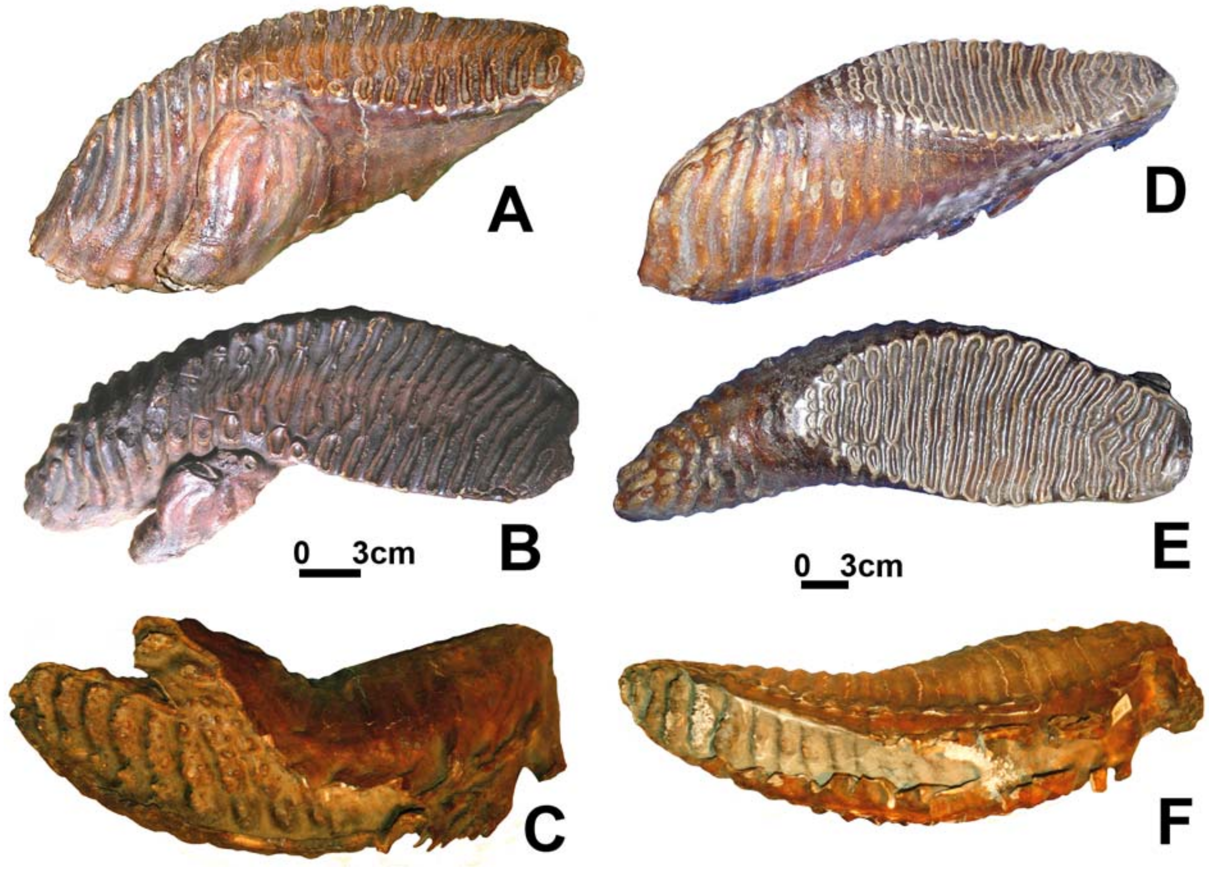

Figure 1. Mammoth teeth (m3) from the Alazeya River Basin.
A–C — pathological F-2366. E–F — normal F-1940. The teeth are in buccal (A, D), occlusal (B, E), and basal (C, F) views.

River in its lower reaches), in the vicinity of the settlement of Anyuisk in 2007. Only the middle part of the tooth is preserved. This specimen is interpreted as the last generation tooth based on its marked crown width (ca. 8 cm), strong curvature, and a significantly narrowed posterior portion.

In the place of maximal convexity, the buccal surface of the tooth has two protrusions formed by flatly fused plates (Fig. 2). The rear protrusion, composed of two plated, is 35 by 57 mm. The other one is situated next to latter and slightly anteriorly. It comprises at least two plates; its dimensions are 60 by 65 mm.

Specimens 3 and 4. Two complete teeth from one individual: left (F-1950) and right (F-1957). Well preserved. The teeth were collected in the vicinity of Andriushkino in 2007. The teeth were identified as the sixth generation according to the following features: lack of the pressure surface, narrowed posterior part, typical curvature and position of roots. Similar dimensions and wear degree of both teeth, and partial symmetry of pathologies suggest the same individual.

Posterior edges of teeth bear a deformation that looks like a curvature. In structure, it represents several plates (2–3) that are displaced and fused to the lateral

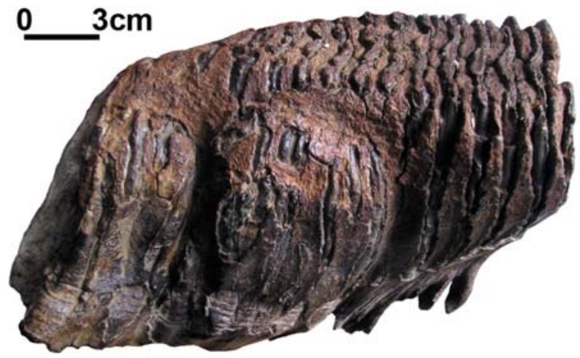

Figure 2. Mammoth m3 from Maly Anyui River (F-1871) in buccal view.

surface of the tooth (Fig. 3). A series of plates in the left tooth (F-1950) are buccally fused forming a separate talon. The posterior edge of the main tooth crown also makes a talon, or a small series of displaced plates. The cement accumulations cover the posterior plates at the tooth base. In the right tooth (F-1957), the major plate is fused buccally and the minor one, lingually.

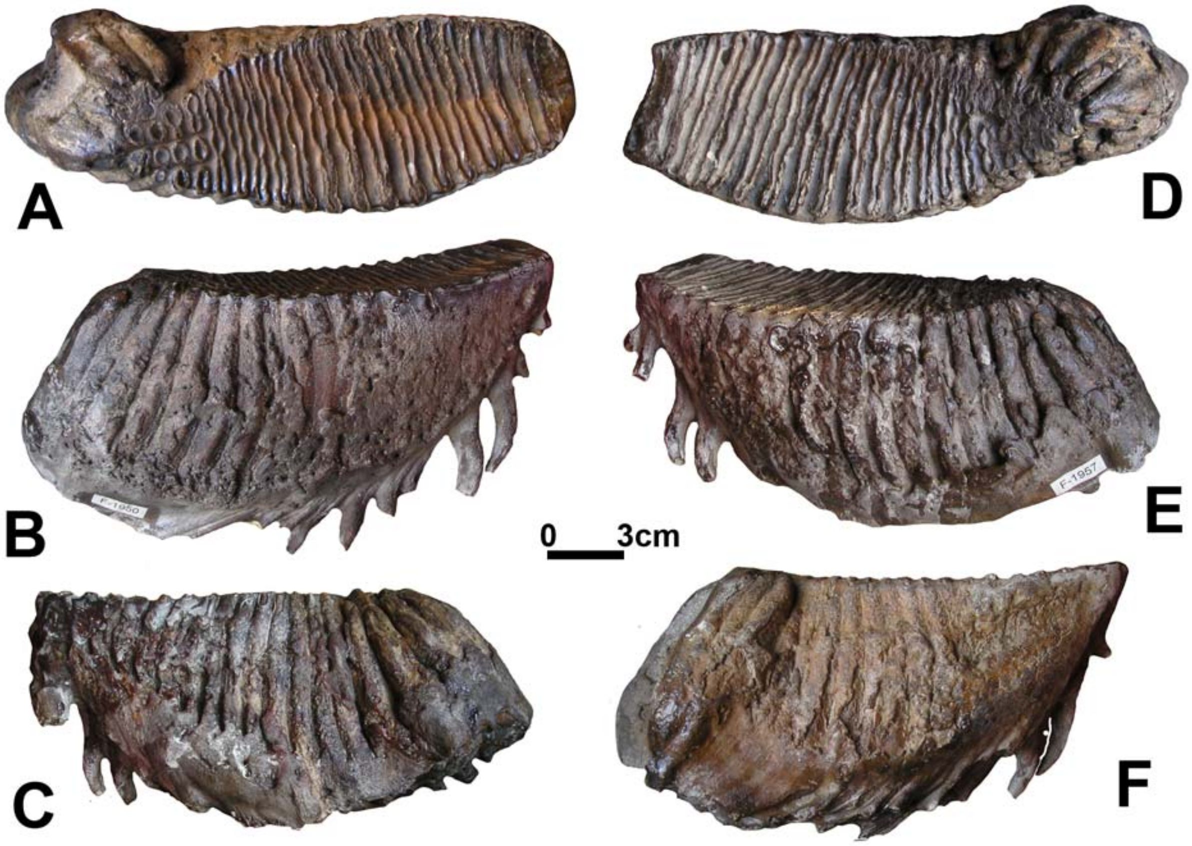

Figure 3. Two mammoth teeth (m3) of the same individual (F-1950 and F-1957) in occlusal (A, D), lingual (B, E), and buccal (C, F) views.

Unlike specimens F-2366 and F-1871, the displaced plates in teeth F-1950 and particularly in F-1957 look incompletely formed. Some of them consist of individualized enamel columns running down to the tooth base and unevenly covered with cement. An additional layer of the external cement, uneven in thickness and distribution, is present on both teeth (Fig. 3).

Posterior parts of wear surfaces bear small polished areas. They lie in different plane from the main masticatory surface. In these areas, cement and dentine-enamel plates are leveled as a flat even surface. Normally, due to the difference in wear resistance and a correspondent different wear rate, the elephant tooth bears multiple crests formed by protruding harder dentine-enamel plates separated lowered zones of softer cement. In the plates, the harder enamel occurs above the dentine.

V.E. Garutt (1977) gave the following description of mastication in modern elephants: "Clenching the jaws, an elephant compresses the food between its teeth with a tremendous force. After several movements like this resulting in compressing the food, the elephant presses the food accompanied with a horizontal (sliding) movement of lower teeth along the upper ones, after which the food is swallowed. No lateral movement of the lower jaw can be observed". Thus, the food fragmentation in elephants is mainly disintegrating-compressive type, not of the grinding one.

Given this kind of mastication, wear aberration observed in specimens 3 and 4 may indicate the formation of the second wear surface presumably due to pathological position of upper teeth. The posterior part of the main masticatory surface in both teeth bear clearly expressed longitudinal furrows 2–5 cm long and 2 mm deep, better expressed in the left tooth.

Specimen 5. Complete and well preserved left lower tooth (F-1953). Collected in the vicinity of Andriushkino. Lack of pressure surface, narrowing in the rear part, and curvature in the unworn part, considerable lateral curvature and quantitative characters of the specimen (Tab. 1) indicate the last, sixth generation.

The tooth is unusual in having the considerable S-shaped inward curvature of the rear part of the tooth, much exceeding the normal (Fig. 4).

The above described only part of the last generation teeth that show similar anomalous structures on the studied material. In a series of about 50 teeth with deviations (including the described specimens) the curve in the rear part was observed in 12 cases, formation of two and more wear surfaces in 7 cases, fusion of one or more (series) additional plates with the lateral part of the main tooth in 10–11 cases. An additional layer of

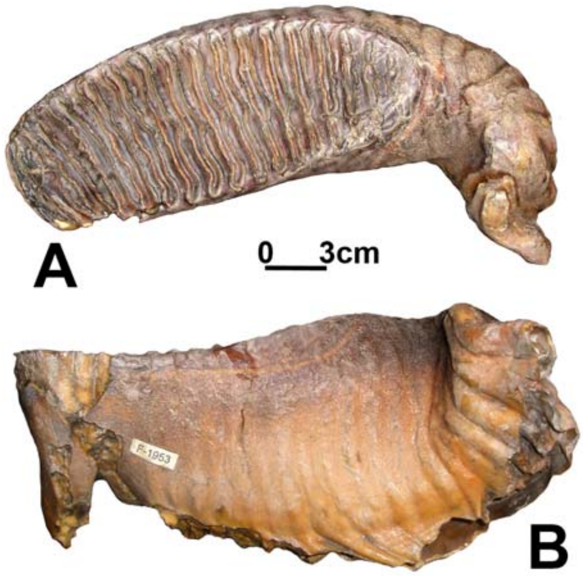

Figure 4. Mammoth m3 with unusually curved posterior part of the tooth (F-1953) in occlusal (A) and labial (B) views.

external cement was observed in 5 times, tuberosity of the external cement (usually in teeth with multiple deviations) in 11 cases. There were further cases with observed dentine outgrowths, the formation of inclined masticatory surfaces, etc.

Some teeth have more than one (up to four) pathologies or other deviations. Only those cases were considered when anomaly might be clearly distinguished from the norm, e.g. the curvature of the posterior part of a sixth generation tooth may be viewed both as a deviation and an individual peculiarity.

The "excessive" curvature in the posterior part of the described specimens appeared to be the most frequently occurring deviation. The most interesting among these is the complete separation of plates or series of plates and their fusion with the lateral (external, as a rule) surface of the tooth. Specimen F-2366 provides the most vivid example of that. It represents not a rare pathology, but an ultimately curved posterior part of the tooth, which is much stronger than one, may derive from the curvature of the lower jawbone. The five teeth with well-expressed characters were described above, but there is at least 5-6 more with less expressed features.

Tuberosity of the external cement of the last generation teeth is also a frequent feature. It commonly accompanies other deviations in the tooth structure.

A comparative study in modern elephants revealed multiple pathologies in the male Asian elephant (specimen S-152807 exhibited in the MSU Zoological Museum). Only the lower right last generation tooth is situated "normally" in the jaw. Three others protrude far beyond the alveoli (Fig. 5). The masticatory surfaces of the lower teeth have no deviations, whereas the upper teeth bear additional polished surfaces in the anterior part of each tooth. This is probably due to friction against the M2 (while pushing it out), which means a certain flexibility of the fifth generation tooth (or both neighboring teeth) in the tooth row. The left upper M3 formed an enamel outgrowth, and the external cement has an uneven tuberous micro relief (also observed in some mammoth teeth from the Ice Age Museum collection). The latter probably signals a deviation from normal dental functioning.

Discussion

The described teeth deviations (including pathologies) of Yakutian mammoths may be subdivided into three groups. The first one includes the pathologies emerging at early stage of germ formation before the eruption. The second is represented by pathologies of separate elements (plates, crown, etc.). The third one includes deviations caused by atypical functioning (wear pathologies).

Teeth anomalies caused by retarded wear relative to the growth rate were pointed out by V.E. Garutt. The resultant expressed in excessive protrusion of tooth crowns from alveoli sometimes may lead to starvation and premature death. Several cases of this type were recorded in captive animals in zoos and circuses, where animals were unable to get their natural food, as well as from modern elephants in the wild and mammoths.

Tooth pathology is often accounted for as a peculiarity of individual development, i.e. abnormal eruption or retarded development (Maschenko & Shpansky, 2005). However, this is not always the case, and in addition, is not explanatory of the causes. The representative series from Yakutia shows numerous and common deviations in an extensive random collection. It may be regarded as a certain property at the level of mammoth population, and a possible evidence of environmental influences.

Deviation as a norm? Studies of the last generation teeth from the Alazeya River Basin show that 16 of 88 specimens studied exhibit structural deviations, several teeth having two or more (up to 4) at once. This high frequency cannot be accounted for by individual developmental peculiarities only.

A considerable share of deviant teeth was observed in the series of mammoth teeth from the main cultural layer of the Przedmost' Late Paleolithic Site (Czech Republic) as well as in the comparative series from Siberia (Musil, 1968). Series of mammoth teeth with transverse furrow lines over the external cement from the archaeological sites in Poland (Krakow Spadzista Street B) and Germany (Vogelherd) were described by Niven and Wojtal (2002) and Krzemiñska (2008).

The sample from the former site includes 50% of deviant teeth, while the former site shows 74% of anomalous specimens. Niven and Wojtal interpret these peculiarities of external cement as a dysplasia due to a

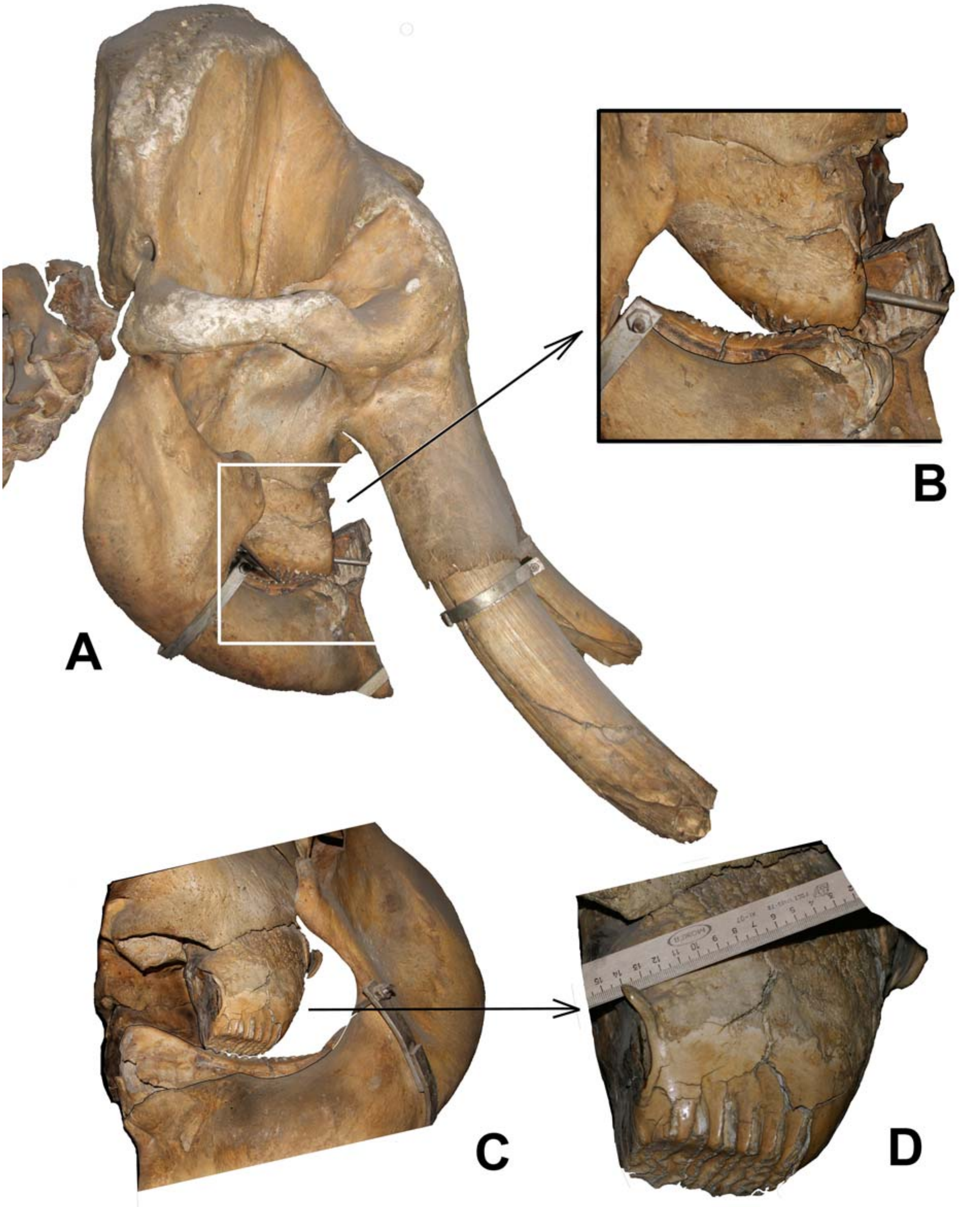

Figure 5. Dental pathology in modern Asian elephant, *Elephas maximus* (S-152807).
A — skull, right side. B — enlarged view of teeth. C — the jaws in left side view. D — upper right tooth with enamel "addendum" and tuberous microrelief of the external cement. Photos by A.B. Kuzmin.

reaction to environmental stress, whereas Maschenko & Shpansky (2005) consider these furrows to be the effect of normal bacterial flora in the mouth. The furrows on teeth from the Ice Age Museum collection vary from 1 to 5–6. This is a frequent trait of teeth of both extant and extinct elephants.

Types of tooth anomalies and their causes. The cases of anomalous structure of mammoth teeth described in literature are connected with distortion of shape or deviation from normal position in the jaw (Maschenko & Shpansky, 2005), with fusion of teeth of neighboring generations (Burns *et al*., 2003), and with formation of extranumeral teeth.

Cases of extranumeral teeth formation are described in mammoths and other proboscids (Essen 2004; Essen *et al*., 2006); in canids and small mustelids (Szuma, 1999), in boars (Konjevic *et al.*, 2006), and woolly rhinoceros (Garutt, 1990).

The causes of extra teeth formation have been unknown yet. These teeth may emerge within the tooth row, or may form a separate row. Due to close locations of dental germs, the duplicates may fuse in crown or root area.

The specimen F-2366 does not represent “fused neighboring teeth” (which is evident from comparison of dimensions of the main tooth and the “satellite”) or “fused duplicates”: the “satellite” is fused with the main tooth along its entire height and represents the plates “missing” in the main tooth (Tab. 1). Initially the specimen represented a normal buccal M3 that separated into two fragments before the eruption that developed further as two almost separate but fused teeth.

Almost in all the above cases fusion of the separated plates occurred on the external, convex side of the tooth. This means that the sixth generation tooth at an early stage had been already convex to match the shape of the lower jaw (the alveolar germ of the tooth is not curved), that is the pathology formed following tooth eruption when anterior wear began, or close to that stage.

The causes of plate separation on the early stage of tooth development may be the following:

(1) Genetically inherited feature. This version cannot be verified. Multiple finds that come from different areas in Yakutia indicate a certain permanent factor that continuously caused emergence of this feature.

(2) Physical trauma of the lower jaw during eruption of the last generation tooth. By analogy with modern elephants it is supposed that the eruption occurred near the age of 20 years (Garutt, 1977) when the compact tissue layer of the lower jaw had been completely formed and may protect the tooth from the external impact. This possibility has not been proved, but the occurrence of numerous teeth with similar features contradicts their traumatic origin.

(3) Infectious disease. Modern elephants are subject to infectious diseases, such as herpes and tuberculosis (Elephant Research and Tissue Request Protocol, 2003), which are sometimes fatal. The development of infection is known to be provoked by lowered level of immunity. The plates in elephant tooth germ before the formation of cement are fastened by connective tissue, which, in weak organism, is easily affected by bacteria. Further studies are needed on dental pathological effects of bacterial infections. The causes that continuously reproduced this process were most probably connected with the environment.

The F-2366 tooth pathology may have formed, as in the others, due to the specificity of structure and functioning of mammoth dentition.

Unlike other mammals, mammoths have horizontal replacement of cheek teeth. The dentine-enamel plates constituting the tooth begin wear in the anterior part of the tooth in the course of eruption following the interplate and external cement formation. In the meantime, the posterior, still unerupted plates are not formed completely and begin to fuse by cementation having been connected with the connective tissue before. The M3 germ is not curved. It is only in the course of development the tooth acquires natural curvature to the shape of the lower jaw bone. Splitting into the components, regardless the etiology (infection, trauma), is possible only at early stages of tooth development when the external cement and common base have not been formed yet.

In the cases considered several posterior plates were squeezed out of the juvenile tooth and drifted along the outer surface of the main tooth before they fused with it. In specimen 1 this is a series of four plates, in specimen 2 two separated plates (or two series with two plates in each). The specimen 2 pathology is not reflected in mutual positioning of the plates, as in specimen 1. The specimens described constitute a series with a different degree of expression of the same feature.

The described pathologies could hardly cause death of the animals. However, the “satellite” in the specimen 1 may cause certain uneasiness. The pathology in specimen 2 was evidently indifferent, whereas the pathologies in specimens 3 and 4 most probably hindered the mastication. The symmetrical pathology in two teeth of the same individual could not be explained by trauma, but rather may be considered as a genetic phenomenon. The curve of the posterior edge in specimen 5 was probably “an unsuccessful attempt to separate”. But it could not interfere with the functioning of masticatory system being inside the mandible.

The frequent occurrence of these and other anomalies is not casual and may be a result of decreased immunity caused, in turn, by the environmental change.

Environment stress hypothesis. Was it a stress for mammoth to live in the Ice Age given that it was adapted to extreme conditions? The end of the Ice Age is known for the establishment of continental climate characterized by cold winters with thin snow cover. This changed the type of vegetation, first of all, the decrease of the most nutritive forage, the evergreen plants. Lack of forage in the extreme conditions might be a factor leading to formation of the above pathologies in mammoth.

One may point out two periods with such conditions in the North-East. The first one is in the interval of 44–29 thousand years B.P. (Kargian Interglacial). The macroremains and spore-pollen spectra of plants are indicative of deterioration of the foraging basis of mammoth. In fact, the majority of finds of the mummified remains of mammoths and other animals of the mammoth faunal complex occurred exactly in the sediments of this age (Sulerzhitsky, 1995). Among them there are Berezovka Mammoth (44 ka), Kirgilyakh Mammoth (41 ka), Tirekhtyakh Mammoth (40 ka), and Shandrinka Mammoth (41–32 ka). The second time interval unfavorable for the Late Pleistocene megafauna was the progressing warming of the late glacial (15–10 ka), the very final stage of the Ice Age (more humid and relatively warm climate, degradation of permafrost soils and vegetation) characterized with abruptly changing conditions.

The lacks of necessary nutrients for proper dental functioning and growth/wear balance, as well as changes in feeding mode, are considered to be among the main causes of teeth problems in modern elephants (Fagan *et al*., 2001). It is possible, that multiple teeth deviations observed in Alazeya mammoth reflect the unfavorable changes in their diet.

ACKNOWLEDGMENTS**.** I thank F.K. Shidlovskyi for providing conditions indispensable for this work, G.A. Klevezal and A.S. Tesakov for editing the manuscript and advice, A.N. Kharitonov for translating the text into English.

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